FOSSIL PERSPECTIVES ON THE EVOLUTION OF INSECT DIVERSITY

Thesis submitted by

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Abstract

A key contribution of palaeontology has been the elucidation of macroevolutionary patterns and processes through deep time, with fossils providing the only direct temporal evidence of how life has responded to a variety of forces. Thus, palaeontology may provide important information on the extinction crisis facing the biosphere today, and its likely consequences.

Hexapods (insects and close relatives) comprise over 50% of described species. Explaining why this group dominates terrestrial biodiversity is a major challenge. In this thesis, I present a new dataset of hexapod fossil family ranges compiled from published literature up to the end of 2009. Between four and five hundred families have been added to the hexapod fossil record since previous compilations were published in the early 1990s. Despite this, the broad pattern of described richness through time depicted remains similar, with described richness increasing steadily through geological history and a shift in dominant taxa after the Palaeozoic. However, after detrending, described richness is not well correlated with the earlier datasets, indicating significant changes in shorter term patterns. Corrections for rock record and sampling effort change some of the patterns seen. The time series produced identify several features of the fossil record of insects as likely artefacts, such as high Carboniferous richness, a Cretaceous plateau, and a late Eocene jump in richness. Other features seem more robust, such as a Permian rise and peak, high turnover at the end of the Permian, and a late-Jurassic rise.

The growth rate of hexapod family richness appears to have significantly slowed through time, and short term increases in hexapod richness, after adjustment for sampling bias, tend to reduce origination in the following interval, consistent with density-dependent processes. Increases in plant family richness are associated with higher hexapod extinction and lower family richness. Several potential abiotic drivers are identified, though the important drivers are different before and after adjusting for sampling bias in the hexapod record. In unadjusted data, higher richness is associated with periods of low temperature, high atmospheric oxygen concentrations, and seas rich in organic nutrients, whilst after adjusting for sampling bias, high richness is associated with high sea levels, and high marine productivity.

Tests on the origination and extinction rates of subgroups of hexapods suggest that the origin of wings represented a major macroevolutionary event, which led to greater faunal turnover. The Holometabola have achieved their present high family richness not by great changes in the average rates of origination or extinction but by a subtle widening of the difference between origination and extinction relative to some other groups, and by peaks in origination at key moments in evolutionary history.

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The Natural History Museum in London have very kindly tolerated my presence for many years, provided me with a base and a fiancée, which is rather good of them.

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Declaration

The material in this thesis is my own work, except where specific references have been given to the work of others. Where data has been obtained from external sources, this is specified in the text.

Chapter 1

General Introduction

1.1 Abstract

Palaeontology provides unique insights into macroevolution by providing the only direct evidence of the past history of life. Understanding how macroevolutionary forces responded to past changes may help us respond to the current biodiversity crisis. Explaining the extraordinary taxonomic richness of insects is a major challenge in macroevolution. Recent developments in palaeoentomology suggest that new compilations of the insect fossil record are required. In this chapter, I provide for the general reader an introduction to major questions in macroevolution and palaeontological diversity studies. I then introduce the hexapods as a study group, and summarize knowledge of their evolutionary history and what current knowledge of insect fossils says about some of the major macroevolutionary questions. I outline the characteristics of previous insect fossil datasets, and propose a new dataset of the ranges of fossil insect families to help further understanding of the evolutionary history of insects. The chapter ends by introducing the aims of the thesis, and outlining how they will be addressed in the subsequent chapters: to show how our knowledge of the insect fossil record has changed in the last 15 years; to attempt to correct for preservation and sampling biases in the insect record; to test for associations between hexapod macroevolution and environmental factors; and to identify potential key innovations which may contribute to the conspicuously high diversity of insects seen today.

1.2 General Background and Rationale

Macroevolution is variably defined as evolution above the species level, or the study of large scale patterns in evolution (Stanley, 1979), but over recent years has increasingly come to mean the study of the evolutionary properties of clades (Mayhew, 2006); groups of species which share a common ancestor. One major property of clades is their species richness. Understanding this property of clades has been a challenge ever since Darwin (Friedman, 2009), not only because richness is so variable from clade to clade (Willis, 1922), but also because that variability defines the constituents of modern communities (Strong *et al.*, 1984). In this thesis I address the evolution of richness in one of the most speciose groups of organisms: the hexapods (insects and their six-legged relatives).

Explaining contemporary species richness is challenging because of the long time-span over which it has evolved (Magurran and May, 1999). This means that studies on contemporary processes, whilst sometimes enlightening (Schluter, 2000), are unlikely to give us a complete understanding. What is needed are ways to determine what has actually occurred in the past. Palaeontology, the study of fossils, provides vital evidence about past evolutionary history by revealing the different types of organism that have existed at different points in time (Benton and Harper, 2009). With such data, it is possible to estimate how global taxonomic richness has changed through time by some measure of the number of different taxa described at different intervals in the past (Phillips, 1860; Sepkoski, Jr., 1981; Benton, 1995; Alroy *et al.*, 2008). Fluctuations in such data over time indicate changes in the identities of organisms present, which indicate extinctions (last occurrences) in the case of reductions in diversity, and originations (first occurrences) in the case of increases. These three measurements (richness, extinctions and originations) in turn constitute some of the main variables of interest in the field of macroevolution (Stanley, 1979). An understanding of two of these variables, changes in richness and extinction, is also of paramount importance for predicting and mitigating the current biotic crisis. Thus, the study of the deep past has the potential to help us to understand the future (Alroy, 2010*a*; Mayhew, 2011).

Although clade richness is dependent on the rate of origination and extinction in a proximate sense, origination and extinction are both controlled by other, ultimate variables (Mayhew, 2007). What kinds of ultimate variables are involved has proved to be one of the major controversies in Palaeontology (Benton, 2010). The Red Queen (biotic drivers) and the Court Jester (abiotic drivers) represent two competing paradigms about the environmental control of macroevolutionary processes. The Red Queen paradigm (Van Valen, 1973) proposes that biotic forces are the major control on macroevolution, acting through ecological interactions. Although many ecological interactions could contribute to the Red Queen, one of the most often proposed has been competition between taxa. If such competition exists, as the richness of taxa increases there could be a tendency for the rate of increase to slow; so called density-dependent processes (Benton, 1997). If, however, density-dependence is unimportant, taxon richness might tend to expand without apparent limits (Benton, 1995). Indeed, in principle, interactions between organisms could have a positive effect on diversification, if the presence of some taxa promotes opportunities for others (Mitter *et al.*, 1988).

The Court Jester paradigm (Barnosky, 2001) was erected as a contrast to the Red Queen, in which extraneous abiotic forces exert the primary effect on macroevolution. Unsurprisingly, since the fossil record is primarily characterized by faunal turnover across geological stages (Phillips, 1860), episodic extrinsic extinction forces are often implicated. These include bolide impacts (e.g. Arens and West, 2008), volcanism (Wignall, 2001), and sea level changes (Purdy, 2008; Alroy, 2010*b*; Hannisdal and Peters, 2011). However, abiotic variables may also promote origination. Variables suggested to do so include increased nutrient availability (Cárdenas and Harries, 2010), and warm temperatures (Mayhew *et al.*, 2008, 2012).

As well as environmental drivers of macroevolutionary change, drivers may be intrinsic to the organisms involved and caused by evolutionary innovations within them (Hunter, 1998). Some of the most important innovations in the history of life have involved so-called major transitions (Maynard Smith and Szathmary, 1995), which describe the major shifts in the way genetic information is transmitted across generations. These include steps such as the origin of cells, sexual reproduction, and multicellularity, all of which preceded the major eon where most fossils occur, the Phanerozoic, and without which current levels of biodiversity would be unthinkable. However, since that time, less substantial changes to morphology, physiology and behaviour have occurred that may nonetheless have stimulated great changes in taxonomic richness by altering macroevolutionary rates (De Queiroz, 2002).

The macroevolutionary insight afforded by the fossil record comes with its own challenges and pitfalls. It has long been recognised that biases in the fossil record may distort our view of the diversity dynamics of prehistoric life, although this issue and how to best correct for it has provoked much debate (Benton *et al.*, 2011; Dunhill *et al.*, 2012). Several conditions have to be met in order for an organism living in the deep past to be described by a palaeontologist today. The organism needs to die in a suitable location and condition to promote fossilization, and the deposit types need to preserve essential diagnostic features. These required (taphonomic) conditions may vary considerably from organism to organism. The deposits need to survive in sufficient quantity to the present day and then need to be worked by palaeontologists interested in those particular organisms. These latter, sampling, issues have been the subject of much recent interest. In particular it has been noted that there is often a good correlation between the number of taxa, originations and extinctions in the fossil record, taken at face value, and measures of the rock record or collection effort (Peters, 2005; Smith and McGowan, 2005).

Seminal work by Raup (1972) suggested two routes to correct for sampling bias; subsampling the raw data systematically to produce fair samples within successive time periods (essentially a pre-analysis technique), and modelling based on control variables (essentially an analytical correction technique). The *Paleobiology Database* project (PBDB; http://paleodb.org) encapsulates the considerable research effort put into subsampling methods (see **Error! Not a valid bookmark self-reference.**), while the latter has gained prominence recently in studies of taxonomic groups for which the large sample sizes needed for subsampling are not available (e.g. Barrett *et al.*, 2009; Butler *et al.*, 2009, 2012; Benson *et al.*, 2010; Benson and Butler, 2011; Benson and Mannion, 2012; Lloyd, 2012). Associations of fossil diversity with measures of the rock record have been the main evidence used to argue for an attempt at removing the influence of sampling on apparent richness. Several different 'rock amount' proxies have been used to counter this potential bias of unfair sampling. Counts of formations (rock strata with comparable lithology and other properties) have been and continue to be widely used (e.g. Barrett *et al.*, 2009; Butler *et al.*, 2009; Benson *et al.*, 2010). However, the use of formation counts has been criticised as it may not be any more accurate than the diversity signal it is being used to correct (Benton, 2010). Correlations of formation number and diversity may be due to species-area effects, so should be expected to be correlated, although not causally but driven rather by a third factor (sometimes called the 'common cause hypothesis'), such as sea-level variation for marine organisms (Peters and Heim, 2011). Sea level could control both marine palaeodiversity and the amount of sedimentary rock deposited (Benton, 2010; Hannisdal and Peters, 2011).

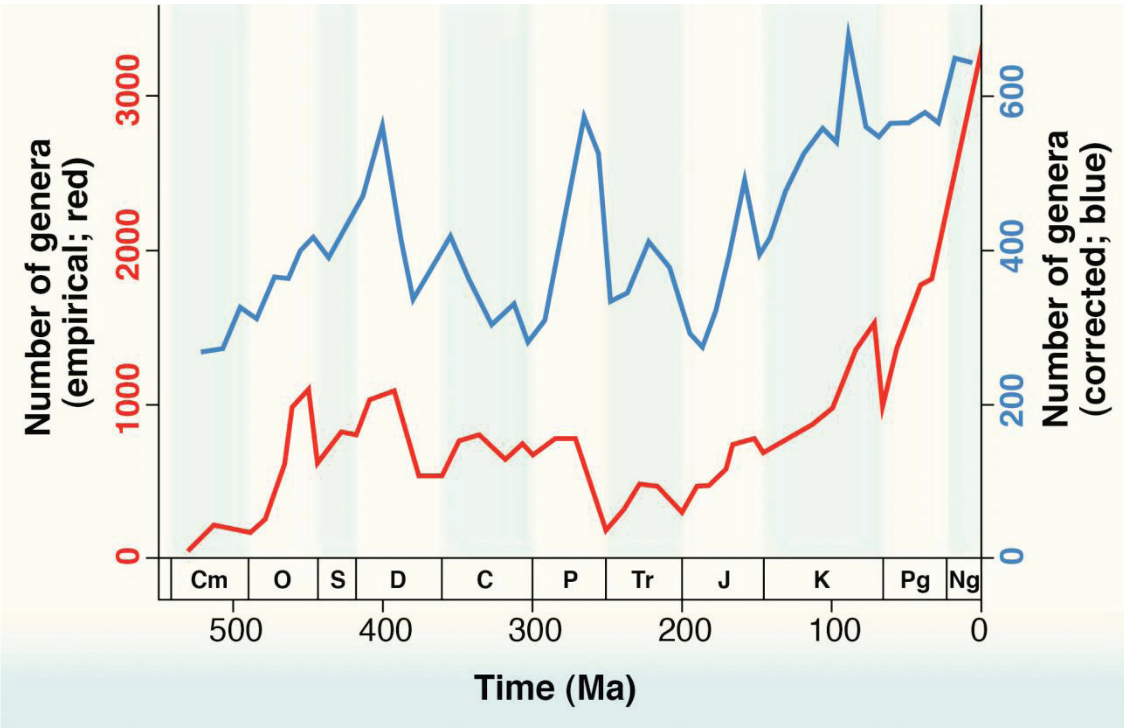

Figure 1-1 Richness of marine genera through the Phanerozoic. The red line represents observed genus richness from Sepkoski's compendium. The blue line represents the richness curve after standardized subsampling by Alroy *et al.* (2008). **Cm** = Cambrian; **O** = Ordovician; **S** = Silurian; **D** = Devonian; **C** = Carboniferous; **P** = Permian; **Tr** = Triassic; **J** = Jurassic; **K** = Cretaceous; **Pg** = Palaeogene; **Ng** = Neogene. Figure from Benton (2009).

Palaeodiversity data are usually compiled in the form of taxonomic databases of fossils giving either temporal ranges or discrete occurrence data. Commonly, criticisms of such databases focus around the integrity of the data and its resilience to the addition of further information (Benton, 1999). Substantial additional knowledge, both taxonomic and stratigraphic, of the fossil records of tetrapods (Maxwell and Benton, 1990) and all marine animal families (Sepkoski, Jr., 1993), has nonetheless yielded very similar variation in originations and extinctions though time. This supports the notion that broad biological signals can be seen through the statistical noise of an imperfect fossil record. However, the effect of additional data on macroevolutionary patterns has not been tested for the majority of terrestrial groups. This is important because many terrestrial taxa, such as hexapods, preserved only in exceptional conditions (*Lagerstätten* taxa), are likely to have substantially incomplete fossil records where the potential for change is much greater.

Hexapods comprise over 50% of extant described species richness (Figure 1-2) and are evolutionarily successful by any measure: temporal persistence, species richness, morphological diversity, biomass and ecological impact (Grimaldi and Engel, 2005). An explanation of how and why this group has come to so dominate terrestrial biodiversity is a major challenge in macroevolutionary biology.

Three main published compilations of the insect fossil record exist, all documenting the stratigraphic ranges of taxa from their first and last occurrences: the genus level dataset of Carpenter (1992), and family level data of Ross and Jarzembowski (1993) and Labanderia (1994). The field of palaeoentomology has expanded rapidly in the last two decades, with large increases in the number of active researchers and consequent

Figure 1-2 Described modern species richness showing the dominance of insects. Figure from Grimaldi and Engel (2005)

publication output (Ross, 2010), as well important changes in taxonomy (e.g. the resurrection of the order Cnemidolestodea by Béthoux, 2005), the dating of fossil deposits (e.g. the recognition of the mid-Cretaceous age of Burmese amber; see Ross *et al.*, 2010) and the exploration of newly known insect-bearing formations globally (e.g. the Eocene amber deposits of India; Rust *et al.*, 2010). Thus, the previous compilations of the hexapod fossil record are now very out of date: previous conclusions on the macroevolutionary history of insects based on these records should be revisited in light of new data and new hypotheses tested. In this thesis I update the described stratigraphic ranges of fossil insect families in order to address a number of the major issues in palaeontology and macroevolution described above. The next sections first introduce the hexapods and their fossil record, before describing what is currently known about the above major questions from the study of their fossils. I then outline the aims and structure of the remainder of the thesis.

1.3 Systematics and Evolution of the Hexapoda

1.3.1 Origin of hexapods

The epiclass Hexapoda comprises a large group of terrestrial arthropods that all possess six legs. It consists of the Insecta *sensu stricto* (or Ectognatha, after the externally protruding mouthparts) and the Entognatha (after the mouthparts which are generally recessed into the gnathal pouch in the head) (Grimaldi and Engel, 2005). Although there have been suggestions that hexapods might be polyphyletic, monophyly of the Hexapoda, Entognatha and Insecta is no longer in doubt (Grimaldi, 2010; Trautwein *et al.*, 2012).

The position of hexapods within the Arthropoda (invertebrates morphologically characterised by a segmented body plan; Giribet and Edgecombe, 2012) has proved a contentious issue. The traditional view held that hexapods are the sister clade to the Myriapoda (centipedes and millipedes), based largely on shared morphological similarities including but not limited to: loss of the second pair of antennae; structure of the mandibles; and possession of tracheae, the branching network of tubules which make up an open and largely passive respiratory system (Grimaldi, 2010). This grouping is variously termed Atelocerata ("without horns", after the absence of the second pair of antennae) or Tracheata (after the tracheal respiratory system) (Grimaldi, 2010). The alternative, and now better supported, position is a grouping with the Crustacea in a clade interchangeably called Pancrustacea (Zrzavý and Štys, 1997) or Tetraconata (Dohle, 2001), the latter being named after the four crystalline cone cells in the ommatidia (individual sections) of their compound eyes (Giribet and Edgecombe, 2012). Myriapoda are considered the sister group to Tetraconata, together forming the Mandibulata (Giribet and Edgecombe, 2012).

There is currently no strong consensus on the exact relationship between hexapods and crustaceans. Competing hypotheses consist of a sister-group relationship between the two, or hexapods derived from several possible positions within a paraphyletic Crustacea. The greatest weight of evidence from molecular and morphological studies now tends to suggest some form of the latter (Budd and Telford, 2009; Giribet and Edgecombe, 2012). While recent molecular studies have reinforced a hexapod-branchiopod sister relationship (Andrew, 2011), the emerging field of neuronal cladistics recovers branchiopods as sister to a hexapod-malacostracan clade (Strausfeld and Andrew, 2011).

Hexapods, then, are probably a terrestrial branch of the Crustacea; however, the timing and route of terrestrialisation are unknown. A marine, putative stem-hexapod was described from the Lower Devonian (Emsian; ~405 Ma; see Figure 1-3) Hunsrück Slate as '*Devonohexapodus bocksbergensis*' by Haas *et al*. (2003). Given that the 'Atelocerata/Tracheata' hypothesis was still well contested at that time, this attribution had two implications: 1) Hexapoda first evolved in a marine setting; and 2) Hexapoda and Myriapoda independently transitioned onto land. However, Kühl and Rust (2009) showed that the holotype was in fact a distorted specimen of *Wingertshellicus backesi*, while considering this species unplaced within the Arthropoda but at least ruling out a

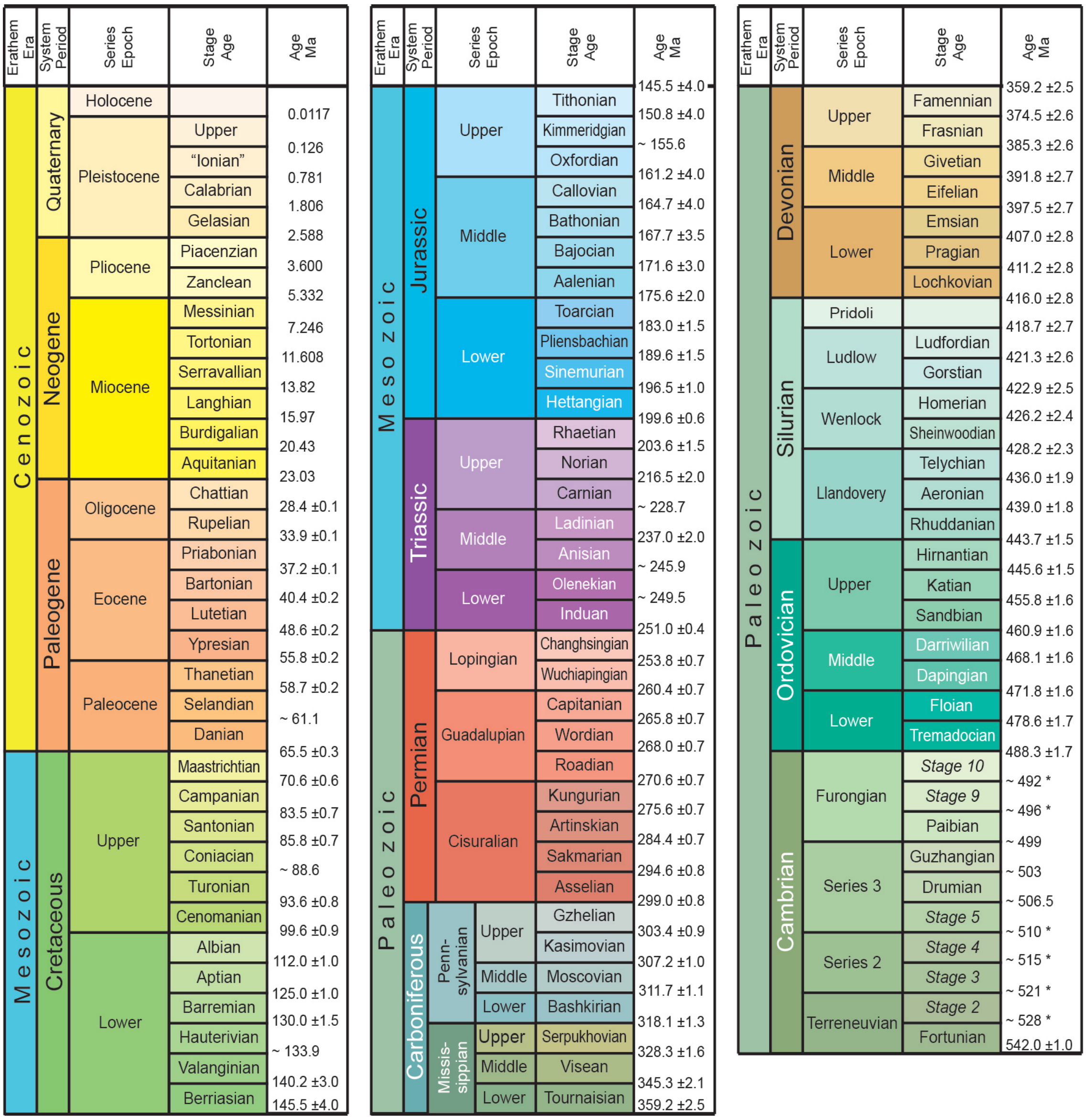

Figure 1-3 The Geological Time Scale, showing the eras, periods, epochs and stages of the Phanerozoic Eon. Time in millions of years before present (Ma). Modified from Ogg *et al.* (2008).

position within Mandibulata. The precise origins of Hexapoda remain unknown, particularly obscured by a very sparse-to-non-existent early fossil record. Molecular clock estimates place the divergence of Hexapoda from Crustacea at around 510 Ma, in the middle Cambrian (Rehm *et al.*, 2011), yet the oldest fossil hexapods are found in rocks 100 Myr younger than this (see section 1.3.1.1). This may easily be explained by the near total absence of terrestrial deposits from before the Permian, at least in Western Europe (Kenrick *et al.*, 2012), although such an ancient estimated origin does have significant implications for hexapod evolution: if they originated around 510 Ma, this was long before any terrestrial plants or animals are known and so would likely have taken place in a marine setting, despite the fact that all known basal hexapod clades are terrestrial (Grimaldi, 2010) and all Devonian hexapod fossils have been found in terrestrial/freshwater deposits.

1.3.1.1 Apterygota

Both phylogenies and fossils suggest that the hexapods were primitively wingless, and then evolved wings at a later stage (Hennig, 1969; Grimaldi and Engel, 2005). These

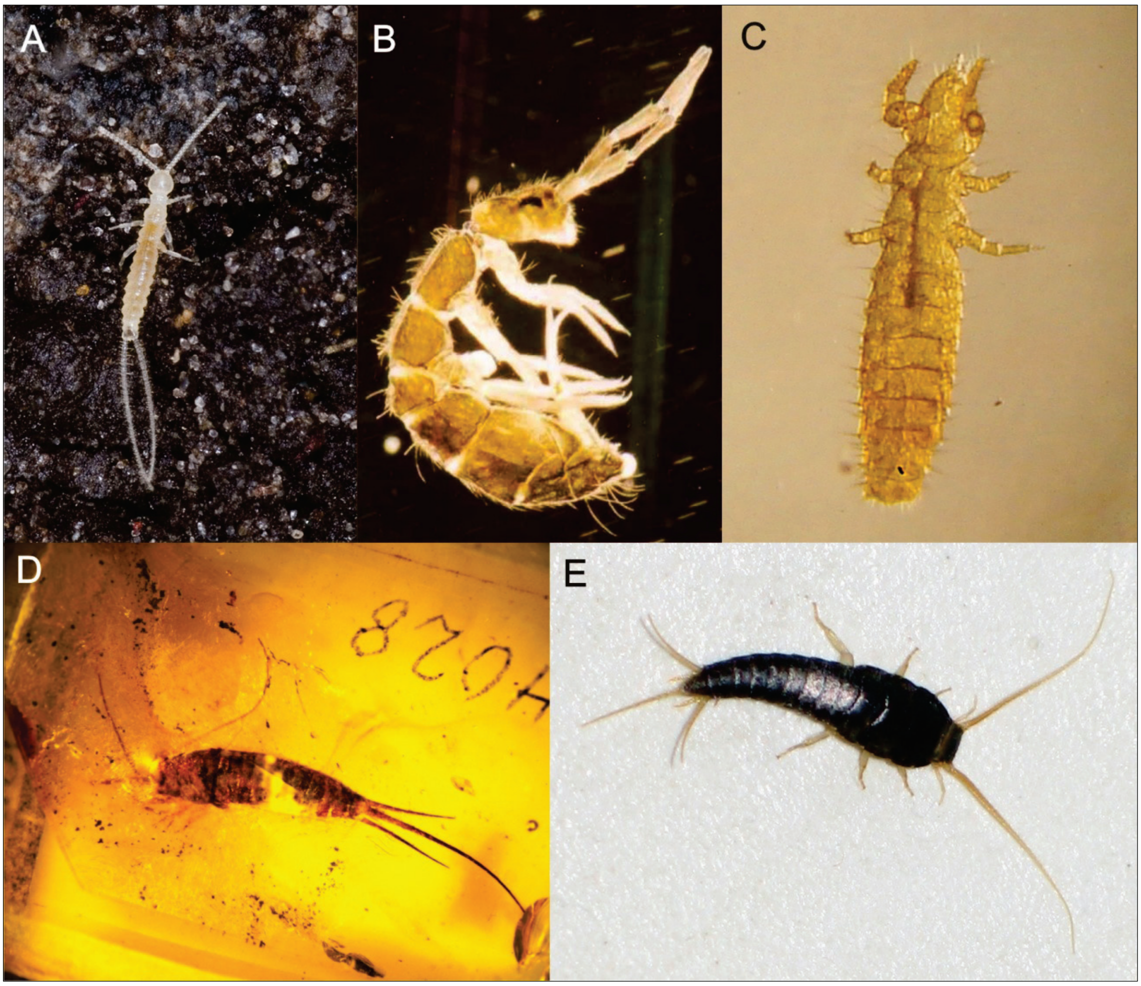

Figure 1-4 Representative members of the 'Apterygota'. Within Entognatha **A:** Diplura: Campodeidae: *Campodea staphylinus*. **B:** Collembola: Isotomidae: *Isotoma anglicana*. **C:** Protura: Acerentomidae: *Acerentomon* sp. Within Ectognatha **D:** Archaeognatha: Machilidae sp. (Eocene Baltic amber; © NHM Picture Library). **E:** Zygentoma: Lepismatidae: *Lepisma saccharina*. All images from Wikimedia Commons unless otherwise stated. Not to scale.

primitively wingless forms are often collectively known as the Apterygota (Carpenter, 1992). The Apterygota comprise the entognath (non-insect hexapod) orders Diplura, Protura (absent from the fossil record) and Collembola (springtails), as well as the ectognath (true insect) orders Archaeognatha (bristletails) and Zygentoma (silverfish) (Figure 1-4). This is a paraphyletic grouping and even the two true insect orders do not form a monophyletic pairing, as the silverfish are more closely related to the winged insects (Pterygota) than they are to the bristletails (Grimaldi and Engel, 2005). Apterygote fossils first appear from the Pragian stage of the earliest Devonian (~410 Ma), where the springtail *Rhyniella praecursor* is described from the Rhynie Chert in Scotland. Also present in those deposits are the mouthparts of another hexapod, *Rhyniognatha hirsti*, which contains autapomorphies of true Insecta, and indeed winged insects (Engel and Grimaldi, 2004). Because only the mouthparts have been found, it is unknown if this animal was genuinely winged, but this does nonetheless date the origin of the apterygote insects to before this date. The other extant apterygote orders (Zygentoma and Archaeognatha) do not definitively appear in the record until the Moscovian (Upper Carboniferous; see Figure 1-3), although a putative archaeognathan was found from the Emsian (Lower Devonian) of the Gaspé Peninsula in Canada (Labandeira *et al.*, 1988; Grimaldi, 2010).

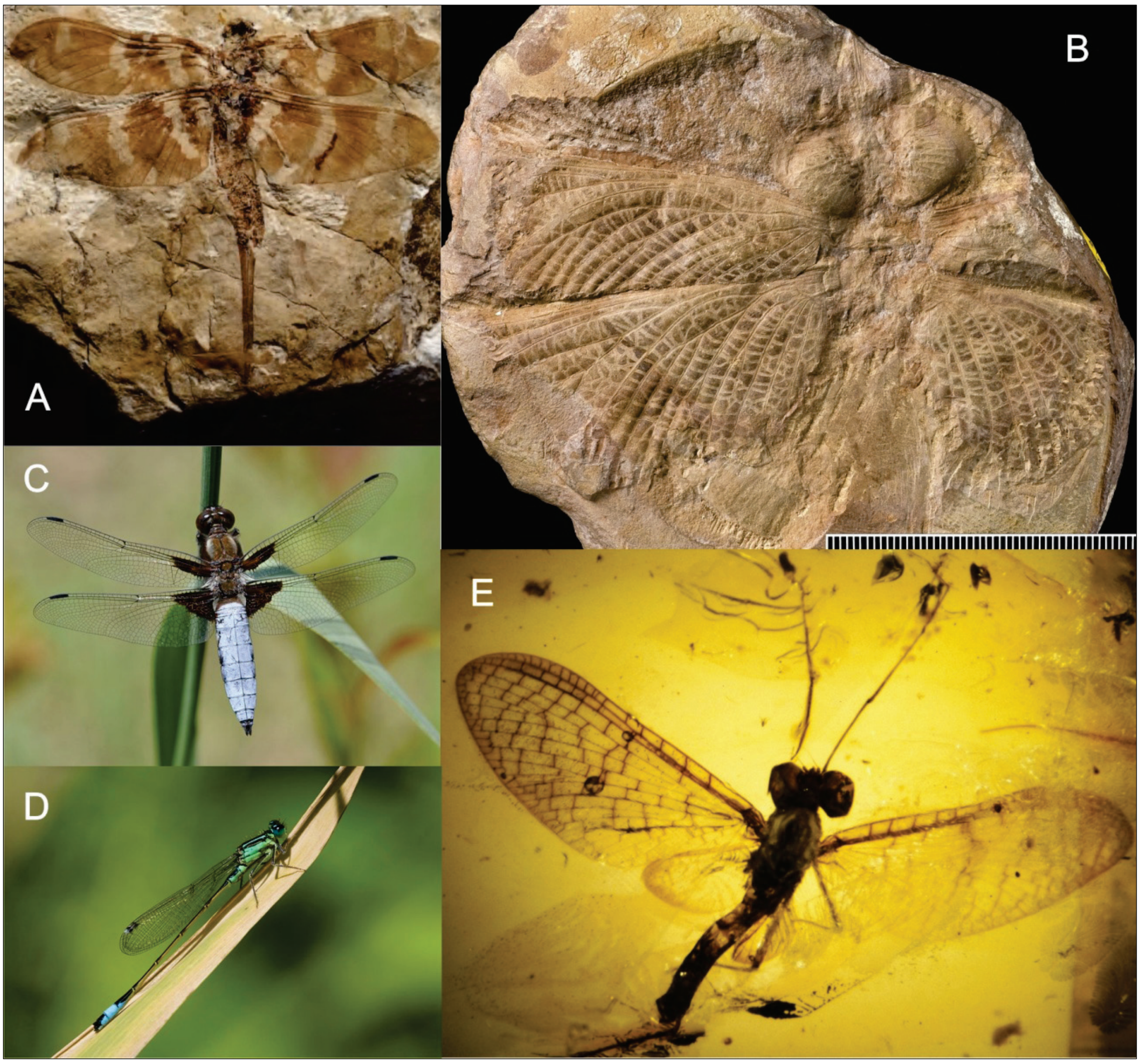

Figure 1-5 Representative members of the Palaeoptera. A: Palaeodictyoptera: Spilapteridae: *Dunbaria fascipennis* (Permian of Elmo, Kansas, USA; taken from Grimaldi and Engel, 2005). **B:** Palaeodictyoptera: Lithomateidae: *Lithomantis carbonarius* (Carboniferous Middle Coal Measures, Scotland; © NHM Picture Library). **C:** Odonata: Anisoptera: Libellulidae: *Libellula depressa*. **D:** Odonata: Zygoptera: Coenagrionidae: *Ischnura elegans*. **E:** Ephemeroptera: Heptageniidae sp. (Eocene Baltic amber; © NHM Picture Library). All images from Wikimedia Commons unless otherwise stated. Not to scale.

1.3.1.2 Palaeoptera

After the first insect records in the Pragian, there is a large gap in the hexapod record, known as Romer's gap (Ward *et al.*, 2006), until the mid-Carboniferous when diverse fully-winged insects appear in the fossil record (Jarzembowski and Ross, 1996; Labandeira, 2005). Included in these forms were the Palaeoptera: those pterygote (winged) insect orders which primitively do not possess the ability to fold their wings over the abdomen at rest. Palaeoptera comprise Ephemeroptera (mayflies), the extinct palaeodictyopterid orders (Palaeodictyoptera, Megasecoptera, Dicliptera and Diaphanopterodea) and the odonatopteran orders (Geroptera, Protodonata and Odonata; dragonflies, damselflies and their extinct relatives) (Figure 1-5). Authoritative reviews of insect systematics have variously viewed Palaeoptera as monophyletic (e.g. Carpenter, 1992), paraphyletic (e.g. Grimaldi and Engel, 2005) or an intractable problem (Trautwein *et al.*, 2012), although recent work on head morphology has given strong support to palaeopteran monophyly (Blanke *et al.*, 2012). Palaeoptera comprised an important fraction of the Palaeozoic insect faunas, although a number of orders went

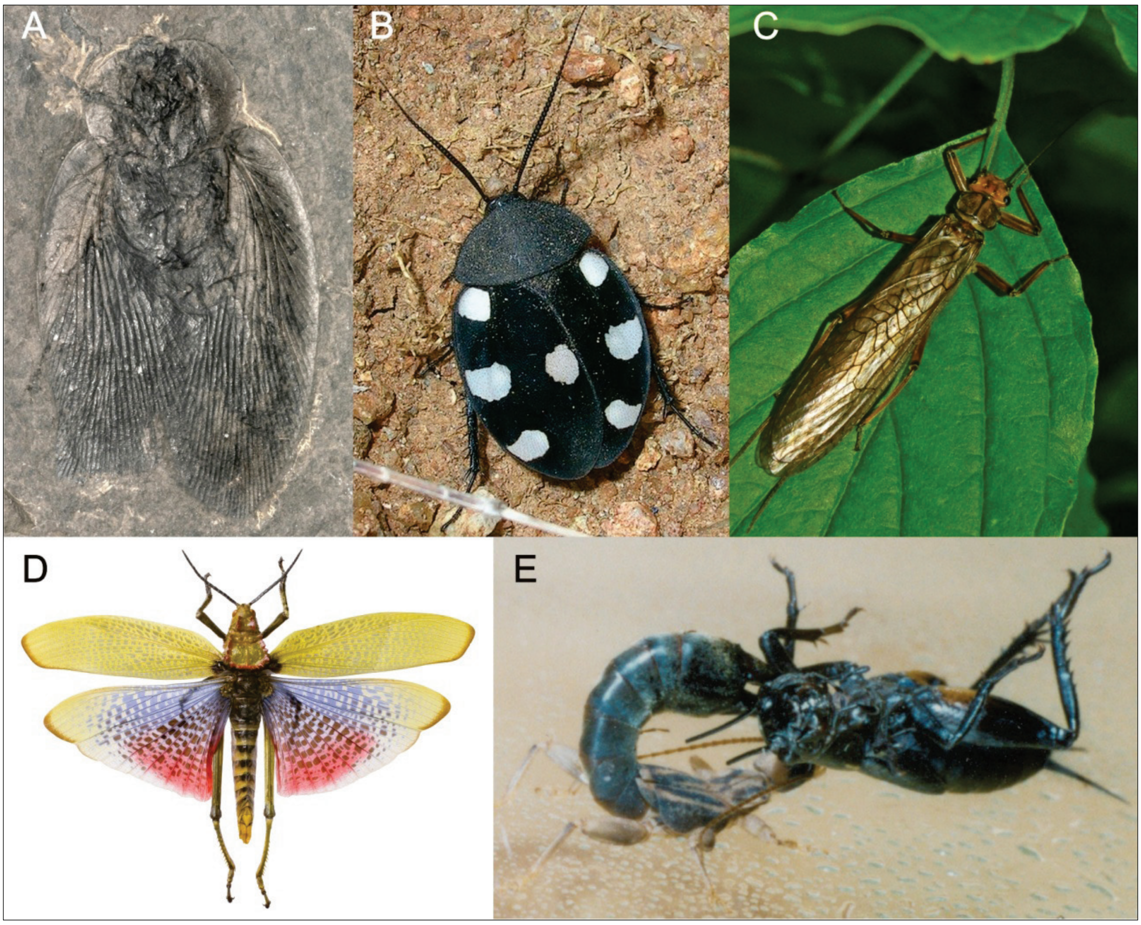

Figure 1-6 Representative members of the Polyneoptera. A: Blattodea: Phyloblattidae: *Phyloblatta brongniarti* (Upper Carboniferous, Commentry, France; © NHM Picture Library) **B:** Blattodea: Polyphagidae: *Therea petiveriana*. **C:** Plecoptera: Perlidae: *Dinoceras ferreri*. **D:** Orthoptera: Pyrgomorphidae: *Phymateus morbillosus* (© NHM Picture Library) **E:** Dermaptera: Pygidicranidae: female *Tagalina papua* having caught a cricket (taken from Matzke and Klass, 2005). All images from Wikimedia Commons unless otherwise stated. Not to scale.

extinct at the end of the Palaeozoic after which only Odonata and Ephemeroptera continued to the Recent (Grimaldi and Engel, 2005).

1.3.1.3 Polyneoptera

Along with the first fossil palaeopteran communities were found other orders of insects which had developed the ability to fold their wings along the body, but lacking the more derived features in other groups described below. Collectively these are grouped in the Polyneoptera. Polyneoptera have proven to be a difficult group to define precisely, with synapomorphies based mainly on an expanded anal region of the hind wing which has been secondarily reduced or lost in some orders (Grimaldi and Engel, 2005), although recent phylogenies provide some support for monophyly based on nuclear DNA sequences (Ishiwata *et al.*, 2011; Trautwein *et al.*, 2012). Polyneoptera are traditionally thought of as the earliest-branching group of Neoptera (winged insects which possess wing folding), comprising the orders “Protorthoptera” (polyphyletic waste-basket taxon), Dermaptera (earwigs), Grylloblattodea (ice crawlers), Mantophasmatodea (rock crawlers/heelwalkers) (in some classifications grouped with Grylloblattodea in the order Notoptera, e.g. Arillo and Engel, 2006), Plecoptera (stoneflies), Embioptera (webspinners), Zoraptera (angel insects), Phasmatodea (stick and leaf insects), Caloneurodea (extinct), Orthoptera (grasshoppers and crickets), Blattodea

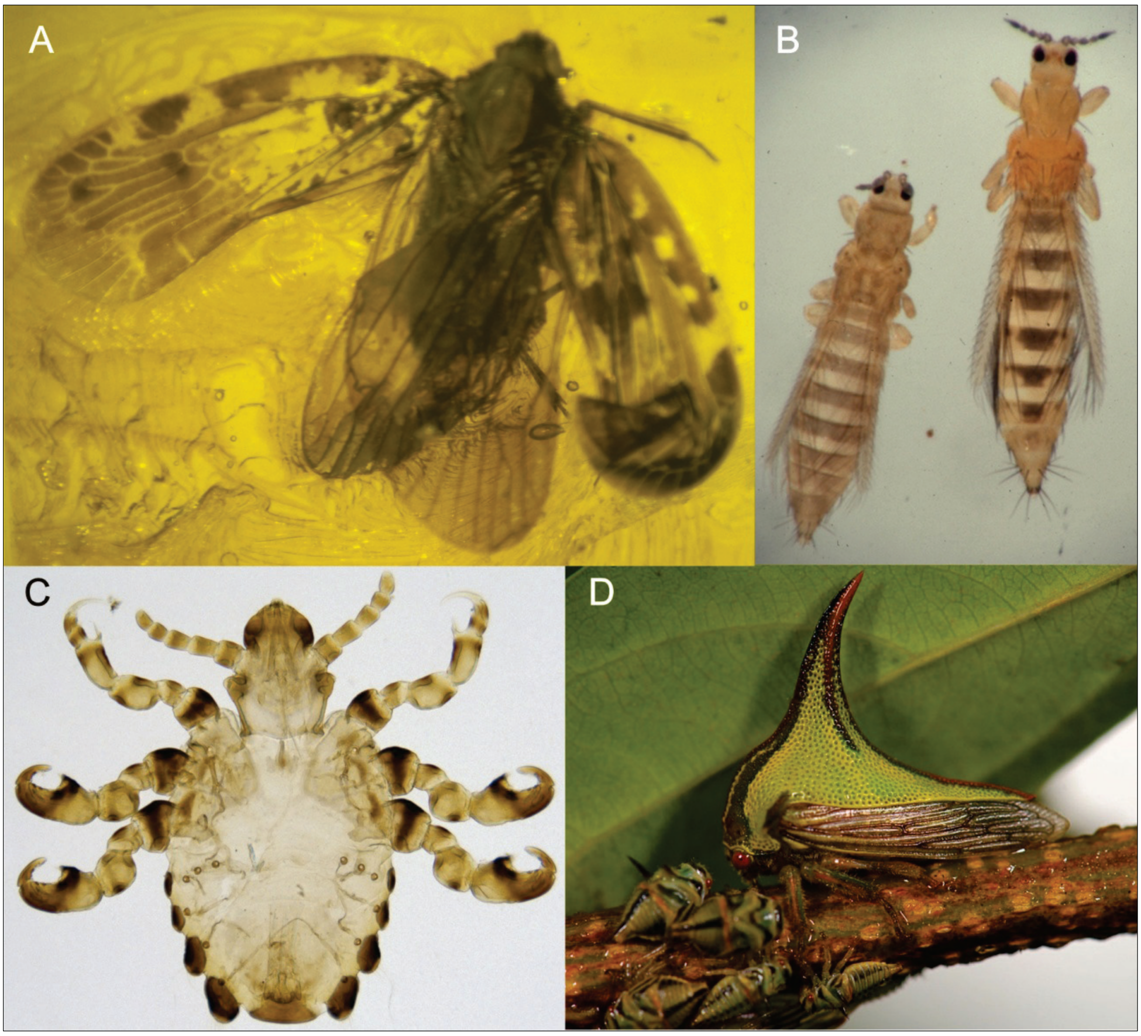

Figure 1-7 Examples of Paraneoptera. A: Hemiptera: Achilidae sp. (Eocene Baltic amber; © NHM Picture Library) **B:** Thysanoptera: Thripidae: *Thrips tabaci* (left) and *Frankliniella occidentalis* (right). **C:** Psocodea: Phthiridae: *Phthirus gorilla* (© NHM Picture Library) **D:** Hemiptera: Membracidae: *Umbonia crassicornis*. All images from Wikimedia Commons unless otherwise stated. Not to scale.

(cockroaches), Isoptera (termites), Mantodea (praying mantises) (Grimaldi and Engel, 2005; Trautwein *et al.*, 2012) and the recently reinstated extinct order Cnemidolestodea (Béthoux, 2005) (Figure 1-6). Along with the Palaeoptera above, Polyneoptera suffered a number of extinctions at order level at the end of the Palaeozoic, and also into the Mesozoic, although several orders are also first known from the Mesozoic. As implied above, the classification of many early Polyneoptera has been particularly problematic, leading to the formation of waste-basket groups and a fluid taxonomy.

1.3.1.4 Paraneoptera

Paraneoptera are a group of insects with mostly sucking mouthparts and includes the Psocoptera (book lice), Phthiraptera (parasitic lice, now usually included with Psocoptera in the order Psocodea), Thysanoptera (thrips) and Hemiptera (true bugs) (Figure 1-7), with evidence for monophyly of the group being generally good if not unequivocal (Trautwein *et al.*, 2012). Many phylogenies (e.g. Wheeler *et al.*, 2001) consider them the sister group to the Holometabola (below). Paraneoptera are first common in the fossil record during the Permian. The parasitic groups only appear relatively late in the record, a likely result of the reduced probability of preservation due to their specialized and wingless lifestyle.

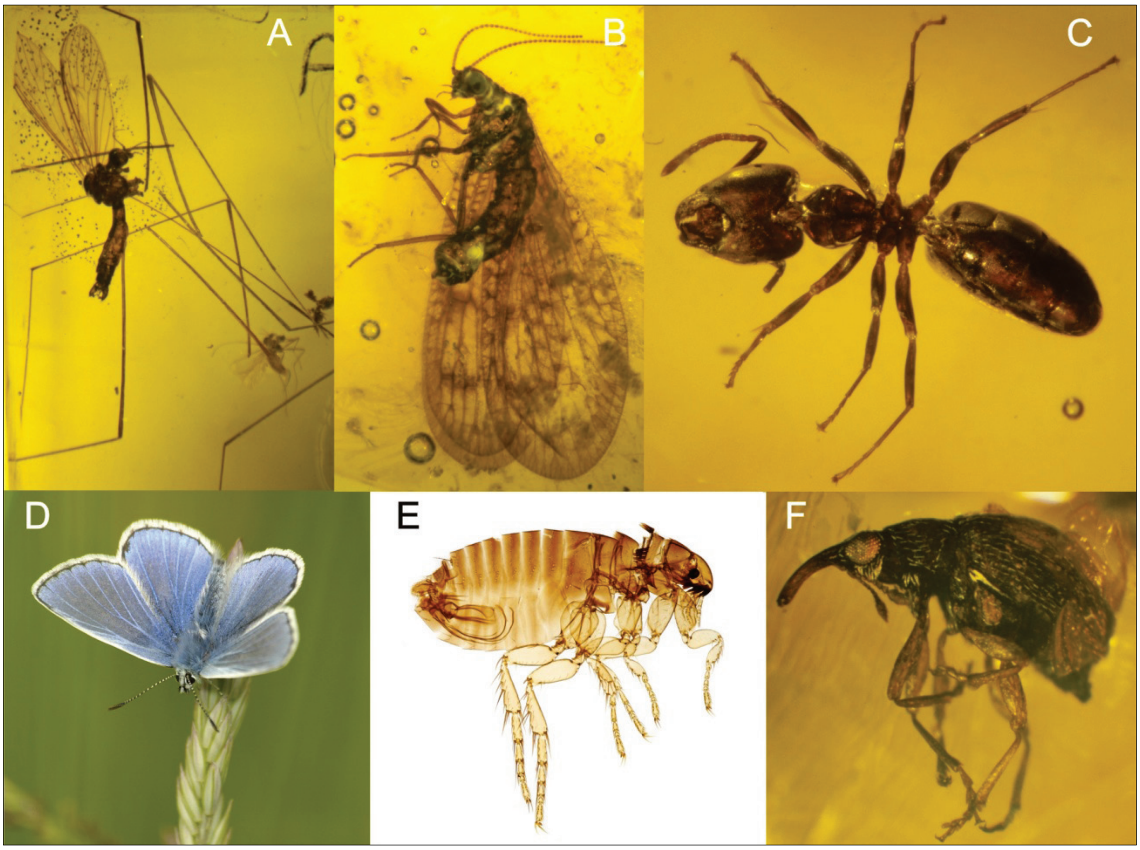

Figure 1-8 Examples of Holometabola. A: Diptera: Tipulidae sp. (Eocene Baltic amber) **B:** Neuroptera sp. (Baltic amber) **C:** Hymenoptera: Formicidae sp. (Baltic amber) **D:** Lepidoptera: Lycaenidae: *Polyommatus icarus* **E:** Siphonaptera: Pulicidae: *Ctenocephalides felis* **F:** Coleoptera: Curculionidae sp. (Miocene Dominican amber). All images © NHM Picture Library. Not to scale.

1.3.1.5 Holometabola

Finally, Holometabola, also known as the Endopterygota, are those insects which undergo complete metamorphosis during ontogeny, with such distinct larval and adult forms that they can be thought of as separate evolutionary modules capable of independent evolution (Yang, 2001). The opposite of holometabolism is incomplete metamorphosis, or hemimetabolism, which represents the more similar nymphal and adult stages of the Palaeoptera, Polyneoptera and Paraneoptera (above), without a distinct pupal stage. Holometabola include many of the most familiar types of insects in modern communities. Orders included are Coleoptera (beetles), Raphidioptera (snakeflies), Megaloptera (dobsonflies), Neuroptera (lacewings and antlions), Hymenoptera (wasps, ants and bees), Mecoptera (scorpionflies), Siphonaptera (those wretched fleas), Strepsiptera (twisted wing parasites), Diptera (true flies), Trichoptera (caddisflies) and Lepidoptera (moths and butterflies) (Figure 1-8). Support for a monophyletic Holometabola is strong (Wiegmann *et al.*, 2009; Trautwein *et al.*, 2012). The oldest holometabolan fossils are contentious; Labandeira (2011) accepts some in the late Carboniferous, although the origin of Holometabola has been dated at ~390 Ma by molecular clocks (Rehm *et al.*, 2011).

1.4 Explanations of hexapod richness using the fossil record

As mentioned in Section 1.2 above, explanations of richness can be phrased in terms of proximate and ultimate variables (Mayhew, 2006, 2007). Proximate variables are the cladogenetic variables and processes which contribute to richness, including the time available for evolution, rates of speciation, rates of extinction and, where appropriate, ecological carrying capacity for insect taxa. Ultimate variables are those ecological/environmental (e.g. temperature) and phenotypic variables (such as wing folding and complete metamorphosis etc.) which may affect the proximate variables. Below I summarize the existing fossil evidence for how these variables have affected hexapod macroevolution.

1.4.1 Proximate variables

Previous studies, based mainly on the datasets of Ross and Jarzembowski (1993, in the large Fossil Record 2 compendium edited by Benton, 1993, hereinafter referred to as "FR2") and Labandeira (1994), have investigated insect diversity and origination/extinction rates through time at the family level. Analyses of these data suggest that extinction rates for insect families are low relative to tetrapods (Labandeira and Sepkoski, Jr., 1993; Jarzembowski and Ross, 1996), because a relatively high proportion of families present in the late Mesozoic survived to the present (Figure 1-9). All things being equal this low extinction rate is likely to contribute to the high richness of the hexapods. The comparison between insects and tetrapods is apt, since both appear in the fossil record at about the same time.

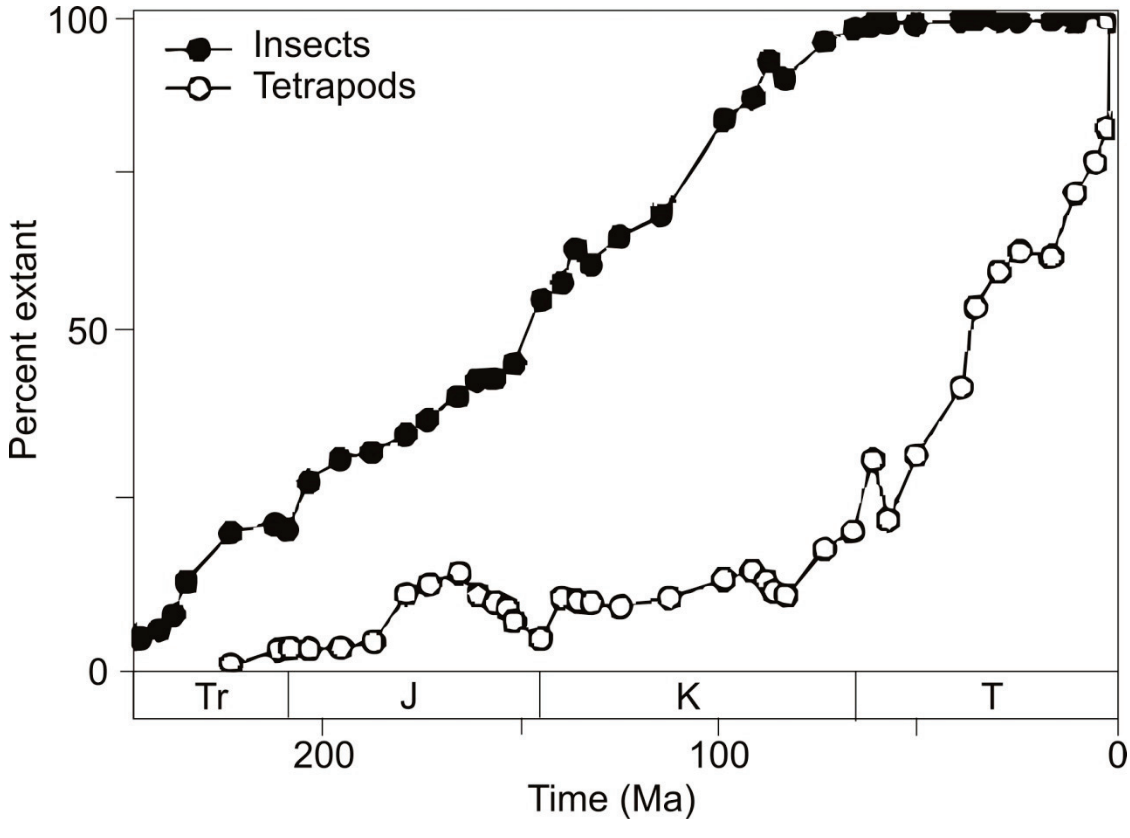

Figure 1-9 Lyellian survivorship plot, showing the proportion of families through time which remain extant for insects and terrestrial tetrapods. **Tr** = Triassic, **J** = Jurassic, **K** = Cretaceous, **T** = Tertiary (Cenozoic). Redrawn and modified from Labandeira and Sepkoski (1993).

Although extinction rates in general have been low, there have been episodes of higher extinction (Figure 1-10). Five distinct "mass extinction" events have been recognized in insects (Labandeira, 2005): late Pennsylvanian, end-Permian, Late Jurassic, late Early Cretaceous and end-Cretaceous. Only the first four of these are pronounced in the family level record (Figure 1-10): the end-Cretaceous extinction not being apparent, although this can be detected using different kinds of data, such as by charting the changes in plant-herbivore interactions across the Cretaceous-Palaeogene boundary (Labandeira *et al.*, 2002). The lack of an end-Cretaceous extinction of insect families is one major reason why the survival of Mesozoic families to the present has been so high, but work on different data suggest that this cannot be extrapolated to infer that extinction at the species level has also been low.

In general, originations at the family level in the hexapods have been episodically variable, as with extinctions, although mostly originations have been rather higher (Labandeira, 2005), explaining the general progressive rise in richness through time. As with the extinctions, five peaks in originations occur, all this time detectable in the family record. These occur in the Pennsylvanian, Permian, Late Jurassic, Early Cretaceous, and Oligocene.

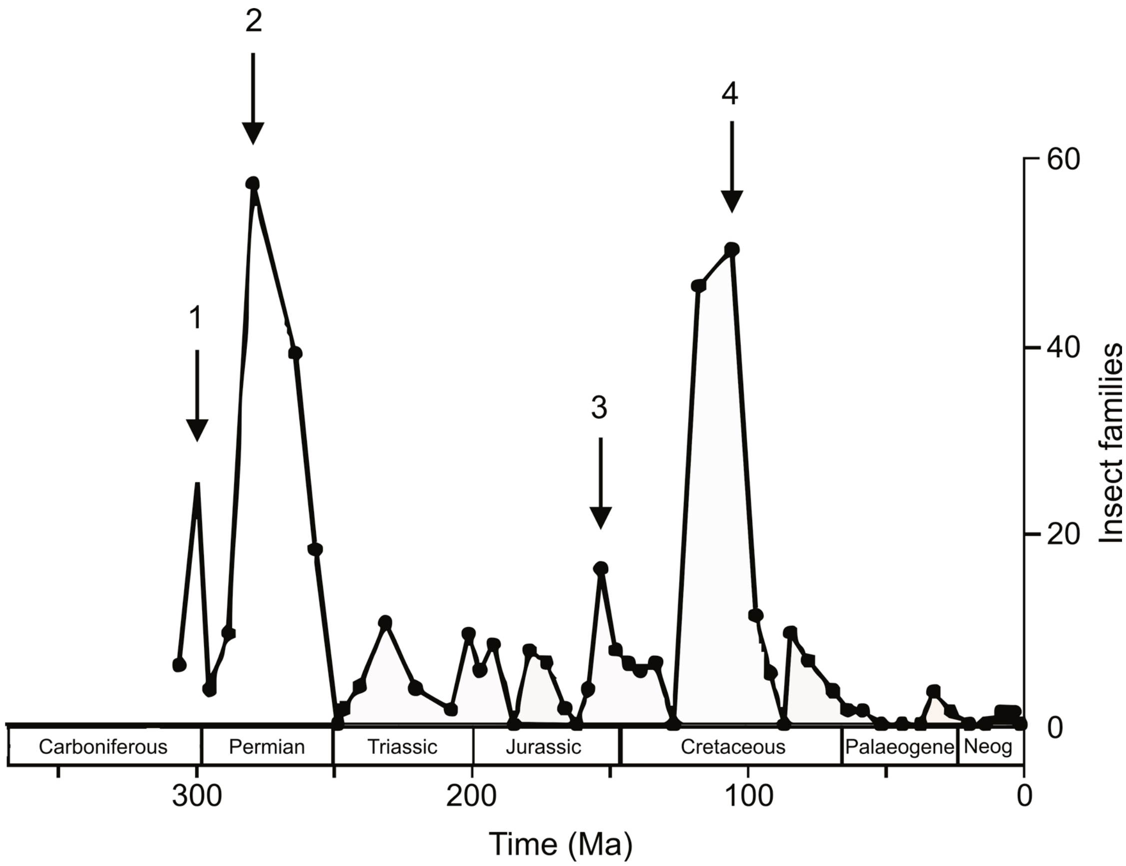

Figure 1-10 Insect family extinctions in the fossil record, based on raw data from Labandeira (1994). Arrows indicate the four mass extinctions generally recognised in insects (see text). Modified from Labandeira (2005; fig. 4b).

Conspicuously high current diversity raises the question of whether there are any limits to diversity and origination in insects. Jarzembowski (2001, 2003) described ordinal richness growth through time as following a logistic model (making allowances for the end-Permian mass extinction) and family/genera data as consistent with an exponential model. This, it was suggested, indicated a global "carrying capacity" of 31 orders. Family diversity was described as having not reached any upper limit. This conclusion was also consistent with work by Eble (1999), who found no evidence for a decline in originations as richness increased in insects. However, Labandeira and Sepkoski (1993) found that the growth of the number of families through time is less than linear on a log scale, suggestive of logistic growth, indicating that richness approached saturation in recent times, with rates of diversification decreasing.

The extent to which the apparent diversity of insect families through time is affected by biases in the fossil record should be considered. Jarzembowksi and Ross (1996) attributed a pronounced dip in diversity and origination of families in the Middle Jurassic to under-recording caused by stratigraphic issues surrounding that epoch in Asia. They identified a need for better stratigraphic resolution to better understand diversity. Labandeira and Sepkoski (1993) conceded that a peak in diversity through the Carboniferous and Permian could be caused by just a few siderite concretion deposits and that the subsequent dip in the Triassic could be an artefact of the lack of appropriate deposits in that time interval. This would cause any extinctions to be recorded in the preceding interval, and originations in the following interval. However, they believed that the apparent end-Permian extinction event was real because the later Triassic faunas have more in common with those of today than those found in the Upper Permian. No systematic attempt was made to quantify the effects of rock outcrop on the perceived diversity of insects through time. Labandeira (2005) and previous workers have also considered the Eocene spike in originations to be largely artefactual, due to exceptional preservation conditions including Baltic amber and other contemporary deposits. Instead they suggest that many of these taxa actually originated earlier.

Finally, Labandeira (2005) also briefly considered the phenomenon of the Pull-of-the-Recent on insect diversity at the family level. The Pull-of-the-Recent is an artefact, especially affecting data on taxic ranges, whereby diversity tends to rise towards the Recent because of its better known record. In particular, taxa found in the Recent have their ranges pulled forward, when they might otherwise have had an earlier last occurrence if the Recent record was ignored; thus Recent richness is accentuated. Some studies of insect richness through time have attempted to compensate for the poorer known more distant record by filling in apparent gaps inferred from sister group relationships on phylogenies (so called ghost ranges) (Davis *et al.*, 2010, 2011). These studies show that richness becomes more flat nearer the Recent as a result of this, to some extent compensating for the Pull-of-the-Recent.

1.4.2 Ultimate variables

As described in Section 1.2 above, environmental factors affecting diversity fall under the 'Red Queen' (biotic) or 'Court Jester' (abiotic) paradigms (Benton, 2009). The role of competition (a Red Queen variable) amongst the hexapods themselves was discussed in the previous section under the heading of limits to taxic richness. Interactions affecting richness can also occur with other (non-hexapod) taxa. Of these, perhaps the most discussed types of interaction occur between insects and plants. Many insects today have close relationships with angiosperms (flowering plants) and so may be expected to have radiated along with angiosperms in the past. Surprisingly, Labandeira and Sepkoski (1993) indicated that the rapid expansion of angiosperms in the Albian-Cenomanian coincides with a decrease of insect diversity, rather than a co-radiation as expected; a conclusion also reached by Jarzembowski and Ross (1996). However, Ross *et al*. (2000) recognised that, while a general decrease in family richness can be observed, the Early Cretaceous is the time of highest origination of insect families in the Mesozoic. Whilst other non-fossil evidence makes it likely that insect-angiosperm interactions are one of the main causes of insect richness at the species level (e.g. Mitter *et al.*, 1988; Farrell, 1998), Labandeira and Sepkoski (1993) and Labandeira (2005) noted that insects had already evolved most of their trophic mechanisms 100 Myr before angiosperms became widespread, so a co-radiation did not drive insect disparity at higher taxonomic levels.

Turning to the Court Jester paradigm, many abiotic variables could be tested against insect family richness, origination and extinction through time, although there has been a singular lack of empirical testing in the literature. One factor explicitly linked to insect macroevolution has been atmospheric oxygen concentrations. This interest arises chiefly because the evolution of flight (see below) may be energetically more favourable in high oxygen concentrations (Dudley, 1999, 2000), allowing conditions favourable for the diversification of winged insects. Indeed, oxygen concentrations have been statistically linked to changes in insect body size through time (Clapham and Karr, 2012), which could promote diversity by opening up new ecological opportunities.

Of other abiotic factors none have explicitly been linked to the insect fossil record. Mayhew *et al*. (2008) compared the richness of both marine and terrestrial families in Benton (1993) against global temperature and atmospheric CO_2 concentrations. They found that standing diversity was generally low during 'greenhouse' phases but with a high taxonomic turnover. A 10 Myr lag was seen in the effect of temperature on origination rate but not with extinction rate, suggesting that extinction is linked with temperature while origination rises to fill the ecological niches left by extinctions. However, after sampling standardization, Mayhew *et al*. (2012) found the opposite relationship for marine invertebrates, with high global temperatures associated with higher richness, although turnover also increased during these times. Temperature and atmospheric CO_2 concentrations therefore deserve explicit testing against the insect record. Other factors falling under the Court Jester paradigm normally apply more specifically to marine invertebrates, such as a range of marine isotopic proxies (e.g. Cárdenas and Harries, 2010) and sea level (e.g. Purdy, 2008). These may still be worth testing against the insect record because the terrestrial and marine environments are not totally isolated from each other, and because many factors and processes in the Earth-Biosphere system interact (Hannisdal and Peters, 2011).

In addition to environmental variables, intrinsic factors affecting insect macroevolution have received some attention from fossil studies. The evolution of complete metamorphosis is widely considered to be a key innovation in insect evolution. Jarzembowski and Ross (1996) identified the radiation in the Permian of the Holometabola as one of two major ordinal radiations in insects. Yang (2001) compared fossil diversification rates of the Holometabola with their non-holometabolous sister group, to see if complete metamorphosis had allowed any increase. Using Labandeira's (1994) data, Yang suggested that complete metamorphosis in insects appears to allow higher rates of diversification in the Holometabola than is present in the 'Hemimetabola'. Other potential key innovations identified using non-fossil studies include the insect bauplan, wings (Apterygota vs. Palaeoptera) and wing folding (Palaeoptera vs. Polyneoptera) (Mayhew, 2007), although none have yet received explicit tests from fossil studies.

1.5 Insect fossil record datasets

1.5.1 Problems with existing data

Three main published compilations of the insect fossil record exist: Carpenter (1992), Ross and Jarzembowski (1993, FR2; supplemented by Jarzembowski and Ross, 1996), and Labandeira (1994). Carpenter's treatise compiled data at the genus level, framed within the traditional class system but only included literature up to 1983 and the data were only dated to period or epoch level. Ross and Jarzembowski (1993) followed the higher taxonomic system of the treatise but only updated family ranges, not genera. Labandeira (1994), compiled a similar dataset also at the family level.

In the context of the analysis of taxic richness, FR2's low dating resolution is problematic. Monotypic families can appear to range through an entire epoch even though the actual record exists for only a single point in time (e.g. Archaeognatha: Triassomachilidae) and the ranges of other families can be uncertain by up to 50 Myr. To compensate for this, some studies (e.g. Mayhew *et al.*, 2008) have analysed FR2 data with both minimum and maximum assumptions of range. In the case of Mayhew *et al*. (2008), a significant negative correlation was found between terrestrial family diversity and mean global temperature when using the maximum range assumption (with a ten million year lag) but not with the minimum assumption. There is no obvious reason (except perhaps for the Signor-Lipps effect, i.e. it is unlikely that the last observed occurrence is actually the true one, so extinction events appear shifted back in time) to prefer the results of one assumption over the other, so a key area for improvement is to increase the resolution of the ranges consistently to the stage level, and to retest hypotheses without the need for maximum and minimum assumptions.

In contrast, Labandeira (1994) claimed 98% of his families resolved to stage and criticized FR2 for not attempting the same. Jarzembowski and Ross (1996) correctly pointed out that many deposits (from the Chinese Mesozoic in particular) were not confidently dated (sometimes even to period) at that time, implying that the accuracy of dating in Labandeira (1994) may be questionable. Indeed, Labandeira not only asserted a more precise date for deposits that FR2 remained more cautious about, he did so with more than one inconsistent date for at least one deposit. The Laiyang Formation in

China, currently dated as Barremian, is stated in Labandeira (1994) as Albian (uppermost Lower Cretaceous) for the only occurrence of the raphidiopteran family Huaxiaraphidiidae, but as Tithonian (uppermost Jurassic) for the earliest occurrence of the hemipteran family Schizopteridae. This kind of inconsistency only becomes apparent when carefully checking each family with the references cited for the range, as the details of the first and last occurrences (such as specimen details and deposit) are not stated in his list. My purpose is not to cast aspersions on the importance of these works (any dataset will contain errors and room for improvement, as undoubtedly that presented in this thesis will), but simply to highlight the need for continued revision of what we consider acceptable data standards. It is worth mentioning here the enormous effort being put by Matthew Clapham (UC Santa Cruz) and a small army of his students into recording fossil insect data in the Paleobiology Database (www.pbdb.org). He estimates that they have 65–70% coverage of insect genera that have a fossil record at the time of writing (M. E. Clapham, pers. comm. 2012). A community-based, occurrence database approach is undoubtedly best practice moving forward with this type of study, as taxic ranges, such as those used here and in the other datasets mentioned, can be extracted from them, whilst the opportunity for novel types of analysis increases. This does not mean that the more traditional datasets are not also valuable though.

1.5.2 Updating the fossil record

Since 1994, great progress has been made in dating non-marine deposits across the globe. One of the most significant events was the re-dating and further study of Burmese amber, extending the first occurrence of many families from the late Eocene Baltic amber (c.34–37 Ma) to the latest Lower Cretaceous (c.112–96 Ma) (Ross and York, 2004). Significant changes in taxonomic concepts have also taken place since the publication of FR2. A revision of some ‘Protorthoptera’ by Béthoux and Wieland (2009) suggested that they are in fact basal mantids, pushing the origin of the Mantodea from the Early Cretaceous back into the Late Carboniferous. This also suggests that other ‘Protorthoptera’ could be basal members of other orders, thus changing the character of the end-Permian extinction at the insect ordinal level. Indeed, study of insect phylogenies suggests that many orders likely originated earlier than is suggested by the fossil record alone and so probably crossed the Permian-Triassic boundary (Davis *et al.*, 2010). Some ordinal revisions have also taken place, such as the inclusion of the Triassic group Titanoptera as part of the Orthoptera (Béthoux, 2007).

In addition to these large scale revisions, about four hundred families of hexapods have been added to the fossil record since 1994 (see Chapter 3). Whether this increase has a large or little effect on the shape of fossil family richness through time will be interesting. Sepkoski (1993) compared two compendia of fossil marine families published ten years apart and found that, despite half of the information changing since the first, the picture of macroevolutionary change had remained essentially the same. By contrast, Alroy (2000*a*) found that ten years additional data combined with new analytical protocols produced major differences in the diversity curves for North American Cenozoic mammals.

Miller (2000) recounted a PaleoNet Listserver correspondence where an unnamed systematist complained that taxonomic databases compiled by non-specialists will be distorted and full of "white noise". Miller noted that, for the purposes of diversity studies, decades of additional data have often made little significant difference to some existing data-sets. Sepkoski and Kendrick's (1993) study showing that the inclusion of paraphyletic taxa did not have a negative impact on studies of diversity at the family and genus level is particularly encouraging when considering insects, as many ancestral (by definition paraphyletic) families occur in the literature. A further rebuttal to the need for specialist taxonomic knowledge cited by Miller is from Adrain and Westrop (2000), who compared their own, state-of-the-art trilobite database with that of an unpublished compendium by Sepkoski, and found that, despite numerous systematic and stratigraphic errors in Sepkoski's data, the diversity trajectories were almost identical.

1.5.3 Use of the family rank

The use of family-level data compilations was defended by Labandeira and Sepkoski (1993) through: having been used in other similar studies on different taxonomic groups; correlating with underlying species diversity; being more robust to sampling biases than species or genera; being more taxonomically stable among researchers; and the fact that families tend to have discrete life habits with morphologies reflecting trophic guild. However, Labandeira (2005) suggested that genus level data will provide finer resolution of fossil diversity. Family data are also more practical: there are approximately 25,000 described species of fossil insect (Labandeira, 2005), which is clearly outside the scope of a single PhD. In addition, while reflecting underlying diversity, families are not as prone to poor representation in the fossil record. Using the range-through method, where a taxon is considered present for the period of time between its first and last occurrence in the fossil record, partially negates the effects of rock record fluctuations when making standard diversity counts through time, although this would still be an issue for rates of origination and extinction, particularly considering the Signor-Lipps effect. Additionally, many finds can be identified to family but not genus or species, so using the family rank can also help diminish the severity of the Lagerstätten effect.

1.6 Aims and outline of the thesis

The overall aim of this thesis is to progress understanding of the evolutionary history of the hexapods. I do this through building on past datasets of the ranges of fossil insect families by incorporating recent developments in the stratigraphic dating of deposits, taxonomic revisions, novel family descriptions, and changes to the known ranges of families already described. These new data (Appendix 3) are compiled in an electronic relational database (Chapter 2) and then used to answer a series of palaeontological and macroevolutionary questions. In Chapter 3, I ask how the new dataset differs from previous equivalent data and investigate how the respective richness, origination and extinction series have changed as a result. In Chapter 4, I investigate for the first time the relationship between the insect fossil record and measures of the record of fossil insect-bearing deposits, as well as measures of sampling effort. I use these relationships in a first-pass attempt to control for sampling biases in the richness, origination, and extinction records. In subsequent chapters I use both the corrected and uncorrected data to address some of the major macroevolutionary questions highlighted above. In Chapter 5, I test the association of richness, origination and extinction rates with a suite of biotic and abiotic variables, thus addressing the relevance of the Red Queen and Court Jester paradigms. I also ask if the data best fit expansionist or logistic models of clade growth. In Chapter 6, I test the evidence for a number of key evolutionary innovations in the hexapods. Finally, Chapter 7 summarizes the findings from these various chapters, outlines their significance, and identifies profitable areas of future research.

Chapter 2

Data Collection and Storage

2.1 Introduction

In order to investigate the macroevolutionary history of hexapods (insects and close relatives), data on the known ranges of hexapod families in the fossil record were mined from 2,500 articles published between 1996 and end-2009, building on the work of Ross and Jarzembowski (1993), supplemented by Jarzembowski and Ross (1996). These data were stored in a relational database of my own design, the key features of which are: 1) a geological timescale based on Ogg *et al*. (2008); a hierarchical taxonomic module based on the higher taxonomy given in Grimaldi and Engel (2005); a hierarchical geographic module storing continent, country, area, locality and deposit; and a table for specimen data which acts as a central hub linking the timescale, taxonomy and geography modules to fossil data. This chapter details the design of the database, using that design as a framework to discuss issues in data collection including uncertainty in dating deposits, issues surrounding conflicting nomenclature and systematics, and the nature of using either range- or occurrence-based data in studies of fossil diversity.

2.2 Data collection

2.2.1 Literature search

In the first instance, the literature search focussed on the reprints-collection provided by Andrew Ross, organised by year from 1994 onwards. Although this proved an excellent starting point and provided many otherwise difficult-to-obtain papers, doing the search by year made it difficult to learn the taxonomy of the different groups and deal efficiently with conflicting opinions in the literature. The most efficient solution I found was to comprehensively search various internet-based databases of literature (including Web of Knowledge, Google Scholar and the International Palaeoentomological Society library page) for all papers dealing with a specific order, download these into the pdf and reference management software Mendeley, and tackle each order in turn. The completed dataset draws on nearly 3,000 published works, 2,500 of which were published between 1996 and end-2009. The EDNA fossil insect database (http://edna.palass-hosting.org/) provided an excellent resource for checking literature and older occurrence data, although much of the taxonomy needs to be updated.

2.2.2 Geological time scale and deposit dates

Knowledge of the absolute ages of the geological record has improved over the years. Both Benton (1993) and Labandeira (1994) used the geological time scale of Harland *et al*. (1990). For this update, the stage names and dates of Ogg *et al*.'s (2008) International Stratigraphic Chart (International Commission on Stratigraphy; www.stratigraphy.org) are used as refinements in dating and correlation of regional stratigraphy make this the international standard to which most earth scientists now adhere, making the dataset more comparable with the work of other researchers.

Ranges of families were often only given to epoch (or even period, in the case of some Carboniferous and Permian families) in Ross and Jarzembowski (1993; herein FR2). This is partly to do with the restricted stratigraphic knowledge of the time but also from using Carpenter's hexapod volumes of the *Treatise on Invertebrate Paleontology* (Carpenter, 1992) as a starting point for the data-set, itself fairly vague on fossil dates. The result of this is that, in some cases, only a single "e.g." specimen from one deposit is mentioned as the start/end of the range, where in fact there are more deposits within that period/epoch (but not in the same stage) containing the family in question. Thus, some families appear as single-interval taxa and would be left out of diversity curves using only "cross-over" taxa (see Chapter 3). More recent stratigraphic work has improved resolution so that family ranges within periods and epochs can be shown to stage level. An example from the insects is for the Mischopteridae (Megasecoptera), listed in FR2 as "e.g. *Mischoptera douglassi*, Mazon Creek C2" but, in fact, specimens have long been known from Commentry (France), giving the family a range of Moskovian–Kasimovian. By lumping the data from different time intervals together, apparent diversity can be greatly exaggerated.

However, occasionally the reverse can be true. For example, the megasecopteran family Brodiopteridae is listed in FR2 as ranging from Namurian B (*Brodioptera stricklani* from the Manning Canyon Shale Formation, Utah, USA) to Westphalian A (*Brodioptera cumberlandensis* from Joggins coalfield, Nova Scotia, Canada [erroneously cited as coming from the United States]). Both of these regional stages fall within the Carboniferous Bashkirian stage (lowermost Pennsylvanian), rendering these families, which previously had ranges, single-interval taxa on this scale. On balance, the consistency afforded by use of the ICS scale along with improved resolution of many other family ranges more than makes up for these very occasional losses in range data.

Despite improvements in recent years, not all deposits have been easy to date. As already mentioned in Chapter 1.5.1, Chinese terrestrial Mesozoic strata remain difficult and the dating of the Yixian Formation has proved to be particularly contentious. Stratigraphers had long argued over whether the deposits were Jurassic or Lower Cretaceous. This proves to be particularly significant as some of the earliest occurrences of angiosperm macrofossils and several other important groups occur in these deposits. Radiometric dates have since confirmed a Lower Cretaceous (Barremian–Aptian) age (see Zhou *et al.*, 2003; Zhang *et al.*, 2010).

Also of particular difficulty are amber deposits, which are most often dated indirectly by the sediments in which they are found. This provides only a minimum age as amber is frequently redeposited. The Burmese amber provides a striking example of this. Previously assumed to be Oligocene in age, it is now accepted as Lower Cretaceous (Albian) (Ross and York, 2004; Ross *et al.*, 2010) and extends the range of some families back from the Cenozoic.

Where uncertainties still exist over the dating of a deposit, a consensus view was adopted or the youngest of the possible stages was used by convention and a note of this made in the database. This only occurred in a minimal number of cases thus far and has mostly involved choosing a later stage when a deposit has been dated to a stage boundary (e.g. Shanwang Formation in China).

2.2.3 Taxonomic system

The families listed needed to be organised into a higher taxonomic framework in order to be more biologically informative and to facilitate access for other researchers who may wish to use the data to answer different questions to those addressed by this project. The traditional Class system, as set out by Carpenter (1992) and adopted in FR2, contains non-cladistic groupings at higher taxonomic levels, in particular the 'Apterygota', used to group the primitively wingless insects of the orders Archaeognatha, Monura (now considered to nest within Archaeognatha) and Zygentoma. In modern classification schemes, the 'Apterygota' is considered to be a paraphyletic grouping.

Even within modern classification schemes there are different schools of thought regarding the extinct orders of fossil insects. These can be (very) crudely characterised as the Russian scheme, outlined in Rasnitsyn and Quicke (2002), and the Eur-American scheme, as shown in Grimaldi and Engel (2005). Both of these texts are authoritative and widely referenced but, in the interests of consistency, the scheme used in Grimaldi and Engel (2005 p. 111, 147) has been followed here, as it seems to have gained dominance in recent years, with minor changes adopted from more recent taxonomic revisions to reflect a modern phylogenetic scheme. This is set out in Appendix 1. The main differences from Grimaldi and Engel (2005, p. 147) are that the polyneopteran Titanoptera are now included in the Orthoptera, following Béthoux (2007), and that no distinction is made between the stem-dictyopteran "Blattodea" (Protoblattoidea in some classifications) and the paraphyletic crown-group "Blattaria" (not inclusive of termites). These together are collectively referred to as "Blattodea", in quote marks to acknowledge the group's paraphyly. Termites (Isoptera) are maintained as a separate order as a convenience despite the recommendations of Inward *et al*. (2007) to demote them to a superfamily of Blattodea.

The focus on families over genera or species is partly to do with greater taxonomic stability between workers (Labandeira and Sepkoski, Jr., 1993). There is not always total agreement and in these cases a consensus view was taken, or that of a particular senior authority, and a note of it made in the database.

2.3 Database design and implementation

2.3.1 Design

It became clear early on that a relational database was the best way to store the data: it reduces the amount of repetition of information, increases ease of data entry and allows the manipulation of data in various ways which are useful for analyses.

The structure of the database, compiled in Microsoft Access, can be broken down into 'modules' (see Figure 2-1) as follows.

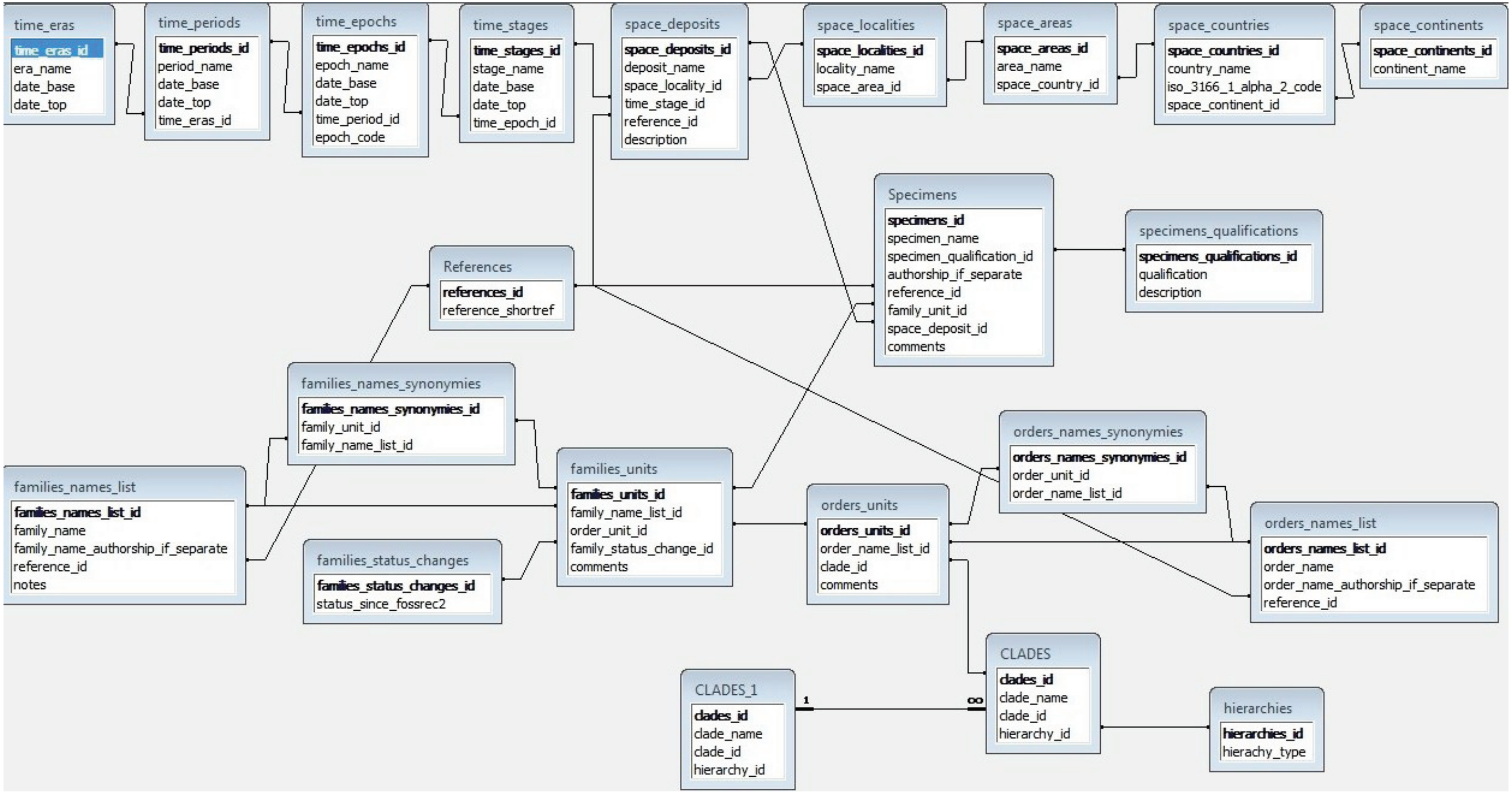

Figure 2-1 Schematic view of database designed to hold fossil hexapod data. Lines between tables indicate where the unique key from records in one table is used as a foreign key for records in another, thus linking up the information held in each. Note that all sections of the database are ultimately connected via the Specimens table. Groups of connected tables sharing the first word of their titles are referred to as 'modules' in the text.

2.3.1.1 References

A record of the source of all data in the database is kept in an external bibliographic database, using the programme JabRef, which is based on the BibTeX reference management software. The BibTeX key (a unique identifier given to each reference) from the external bibliographic database is used as the primary key (unique identifier given to each row/record in a table) in this table, which is then used as a foreign key (a field in a table which allows each record to be linked to records in a different table) in the specimens, deposits, orders_names_list and families_names_list tables. The reference_shortref field is simply a text field where the authors and keywords of the paper can be typed so as to be recognisable to the operator. For example, when used as a foreign key in another table, the references_id value 'Ponomarenko2009' will appear in a drop-down list as 'Ponomarenko et al. 2009 Mesozoic Trichoptera distribution', to make it more user-friendly.

2.3.1.2 Time

Using dates and division names from Ogg *et al*. (2008), the Time module forms a straight hierarchy of Era – Period – Epoch – Stage. The time_stages table is the only connection to the rest of the database and data can be arranged by any of the time tables through their hierarchical linkage.

2.3.1.3 Space

A straight hierarchy is again used, from highest to lowest: Continents – Countries – Area – Locality – Deposit.

The space_countries table was populated with the official ISO3166 list, downloaded from www.iso.org/iso/list-en1-semic-3.txt, which provides a ".txt" format, semicolon delimited list which is easy to import into Access.

The space_areas table is deliberately vague to in order to accommodate regions/provinces/mountain ranges as necessary. Likewise, space_localities is variously used for the names of towns, quarries, rivers etc.

The table space_deposits is used for the formation or other geological unit as necessary. By linking to the Stage table it provides an intersection of the Space and Time modules, allowing data to be queried/arranged geographically, temporally, or a combination of both, simply from the deposit in which a specimen is found. This avoids having to repeatedly input geographic and temporal data for each specimen once a deposit is in the database. The reference_id field is for providing a literature reference for the chronological date assigned to the deposit and "description" is a free text field used mainly to discuss any assumptions which have been made in the assignment of a stage to the deposit.

Some deposits do not fit comfortably into this scheme. Baltic amber in particular has posed a problem as many collections are based on material coming from widespread secondary deposits of the amber (including washed up onto the shores of various countries) with rarely a mention of the collecting locality. Dating of the amber, too, is problematic. It is found *in situ* in deposits known as the Blue Earth, which straddle the

Eocene/Oligocene boundary, and occurs only in the lower part (Weitschat and Wichard, 2002). Some authors (e.g. Engel, 2008) consider it to be middle Eocene based on glauconite dates, while FR2 holds it to be latest Eocene (Priabonian). In this case I have followed FR2 as glauconite dating is notoriously inaccurate and the amber from the Blue Earth does not appear to have been transported or eroded and so was likely not redeposited (A. Ross pers. comm., 2008).

2.3.1.4 Clades

This module, comprising the 'CLADES' and 'hierarchies' tables, deals with taxonomic levels above orders. These follow the system laid out in Grimaldi and Engel (2005, p. 111, 147) with the exclusion of superorders (Appendix 1). The name 'clades' is used to indicate that higher taxa of varying rank are included.

Since some orders are placed directly into higher clades than others, a problem of hierarchy becomes apparent since there are varying numbers of steps between Epiclass Hexapoda and the orders – two minimum (e.g. Archaeognatha) and seven maximum (all orders in Paraneoptera and Holometabola). If a straight hierarchy was used (as in the Time and Space modules), 'dummy' clades would have to be erected to make the number of steps equal for all orders. This would be cumbersome and unhelpful for showing clearly the relationships and could be problematic when querying and presenting the data. To deal with this problem a single table was constructed to hold all the higher clades and the nested structure created by using reflexive relationships, where the primary key of the table is used as a foreign key in another field within the same table, so linking up records within the table rather than between tables. The self-referential nature of this set-up is indicated in the relationships view (Figure 2-1) by the 'CLADES_1' table, which does not actually exist in the database. Using this function, MS Access requires all rows to have a reflexive value so the highest rank must refer to itself. As a precaution (lest a query get caught in an infinite, self-referring loop) a 'dummy' top clade is put in the table.

The hierarchies table simply assigns a numerical rank to indicate the level of nesting. It is not generally used but was included pre-emptively as an extra lookup field to use in queries.

In retrospect, this reflexive structure could be used across all taxonomic units. This would allow families that do not fit neatly into any orders to be placed directly in higher clades without the need for 'dummy' orders in the database (e.g. Pterygota incertae sedis: Vogesonymphidae Sinitshenkova and Papier in Sinitshenkova *et al.*, 2005). However, what gains could be made in convenience would be lost in the clarity of keeping the Families and Orders modules separate.

2.3.1.5 Orders

For both orders and families the problem of synonymy poses a particular problem with the possibility of future taxon name changes. To allow for this, a three-table solution was devised where the orders (or families) are considered primarily as nameless units (i.e. the orders_units table) and the names as separate entities (orders_names_list table) which can be applied to the order units (order_name_list_id field in the orders_units table). The orders_names_list table contains all order names used (valid or not) along with references for the authorship of valid taxon names. The currently valid names are linked to the order units and, in a separate table, the synonyms are linked to the order units. Names can be swapped and changed without fundamentally affecting the nature of the unit or the parent/child relationships it has with higher and lower taxa. The clade_id field in the orders_units table allows the assignation of each order to a higher clade.

2.3.1.6 Families

The Family module is essentially the same as orders in the arrangement of units and names. Instead of a linkage to the clades table, the families_units table uses a foreign key for the orders_units table to indicate which order each family belongs to. An additional feature is the families_status_changes table. This provides three alternatives to classify the family units; 1) no change, 2) range change and 3) new in list. These refer to the status of the family in relation to the data in FR2, so allowing an overview of how much the picture of the fossil record of insects has changed since 1993. "No change" is self-explanatory. "Range change" involves a change in the range of a family, whether an extension or contraction from the finding of new specimens, but also includes improved/revised dating of deposits from which known specimens occur. "New in list" can refer to newly described families, those brought out of synonymy or Recent families which now have a fossil record.

2.3.1.7 Specimens

The 'specimens' table forms the central hub of the database and is the point where space/time is connected through to the taxonomic modules. Each row of data corresponds to either a species, genus or indeterminate specimen of a particular family known from a specific deposit, and so not strictly speaking a specimen in the sense used in collections management. For each 'specimen' there should be a name, authorship (if applicable), a choice of 'mentioned in' or 'described in' followed by the reference for the data, the family it belongs in and the deposit it was found in. There is also a free text field to insert any comments.

For extant families, a dummy 'specimen' (always named 'Extant') is placed in the deposit 'Extant' with an age of Holocene so that ranges can be calculated.

2.3.2 Future improvements to database design

One obvious area that could be improved is the process of synonymising one family (or order) unit with another already in the database. When this happens, all specimens referred to the junior synonym must have their family assignation changed by hand in the tables. At present this is a trivial matter as usually no more than four or five 'specimens' are assigned to any particular family. But in future, if this database is expanded to attempt a more comprehensive cataloguing of fossil insects and the genus and species levels, some automation of this process would be desirable.

2.3.3 Data output

MS Access querying does not easily allow tailoring of output with text formatting. To do this in Access would require Visual Basic, which is prohibitively expensive. An excellent alternative is to convert the database into MySQL format and query it with the programming language PHP; all open source and web-based. MySQL has the added advantage of lending itself well to designing an online resource that could be used easily by other researchers around the world. This is something to consider in the future.

2.3.3.1 PHP code

PHP allows the connection to a database over an HTTP (internet or web) connection to execute queries, storing the results temporarily and manipulating them in your own programmes or scripts. It allows the scripting of functionality into encapsulated functions which can be called at specific times to run different queries in succession and output tailored results. This is crucial to outputting the nested structure of the data in a list.

Text formatting is applied around the data from the database but the PHP functions will be called dynamically when required, so the formatting need take place only once and is then applied appropriately depending on the context of the data. It is then applied to each set of data repetitively until the results from the data are exhausted.

The scripting process can be caricatured as a 4-step process:

1) List each clade
2) On each clade, list the orders belonging to that clade
3) On each order, list the order synonymies, list the first and last specimens and list the families within the order
4) On each family, list the family synonymies and the first and last specimens within the family

In essence, the query provides output with the most recent data by indentifying first and last specimens for each family and order from the database, then populates a list similar in style to FR2, without the need to manually change the details and reference list. The full PHP script is provided in Appendix 2.

2.4 On counting methods

The dataset used in this thesis is based on the range-through counting method for fossil taxa, where a taxon's range is calculated from its first and last known occurrences in the fossil record, and is assumed (reasonably) to exist throughout that duration. This is biologically reasonable but may fall foul of misidentifications giving artificially large ranges. Range-through data are also particularly prone to the Pull-of-the-Recent (Alroy, 2010*c*; see Chapters 1 and 4), as the Recent is better sampled than any stratigraphic stage and so only a single occurrence of a taxon needs to be known in order to 'pull' its range through to the present. This is a cumulative effect, as time intervals closer to the present are more likely to have taxa which remain extant (Alroy, 2010*c*). Additionally, if one wishes to investigate and correct for sampling biases in the fossil record, range through data make this difficult as the richness of each stage is only related to the rock record of that stage by the amount added or taken away from the richness of the previous stage (itself an accumulation of all the stages before it; see Chapter 4). These problems disappear if one counts only the actual occurrences ("in bin" sampling) of taxa in deposits through time (Alroy, 2010*c*) and this has become the dominant form for fossil diversity studies today. However, with over 25,000 species of fossil insect described (Labandeira, 2005), such a dataset would be entirely impractical for the life of a single PhD project. As mentioned in Chapter 1, Matthew Clapham (University of California, Santa Cruz), along with a small army of graduate students, has made considerable progress in compiling the fossil record of hexapods in the Paleobiology Database. However, his dataset covers perhaps 65–70% of genera in the insect fossil record (M. E. Clapham, pers. comm. 2012), so there is still much work to be done, especially in light of rapid increase in the rate of publication in palaeoentomology (Ross, 2010). A community-based occurrence dataset is undoubtedly the future of diversity studies, so I fully endorse the Clapham lab's efforts and will look to that dataset in future for the questions which remain unanswered in this thesis.

2.5 The dataset and its uses

A taxon-by-taxon hard copy listing of the data is presented in Appendix 3, allowing researchers without experience of relational databases to make short queries of particular taxa of interest, and serving as a standard reference from which the following chapters are derived. In the next chapter, these data are compiled into time series of richness, origination rates and extinction rates and compared to previous datasets to observe how the dataset has changed overall since previous compilations were made, and their main features. In subsequent chapters the time series are used to address the major palaeontological and macroevolutionary questions outlined in Chapter 1.

Chapter 3

Insect Richness in the Fossil Record - Fifteen Years of discovery

3.1 Abstract

Time series on standing richness, originations and extinctions are compiled from a new dataset on the fossil record of hexapod families, using range-through methods. The major features of these time series are compared with those of previous datasets which used the same broad approach. About a third of families are new since 1994, over half have experienced changes in their known stratigraphic range and only about ten percent have unchanged ranges. Despite these large additions to knowledge, the broad pattern of described richness through time remains similar, with described richness increasing steadily through geological history and a shift in dominant taxa after the Palaeozoic. However, after detrending, described richness is not well correlated with the earlier datasets, indicating significant changes in shorter term patterns. There is reduced Palaeozoic richness, peaking at a different time, and a less pronounced Permian decline. A pronounced Triassic peak and decline is shown and a more pronounced Cretaceous rise with little subsequent decline. Origination and extinction rates are broadly similar to before, with a broad decline in both through time but episodic peaks, including end-Permian turnover. Origination more consistently exceeds extinction than before and exceptions are mainly Palaeozoic. These changes suggest that some inferences about causal mechanisms in insect macroevolution are likely to differ as well.

3.2 Introduction

A key contribution of palaeontology to the study of the diversity of life has been the elucidation of macroevolutionary patterns and processes through deep time, with fossils providing the only direct temporal evidence of how life has responded to a variety of biotic and abiotic forces (Mayhew, 2007; Alroy, 2010*a*; Ezard *et al.*, 2011; Benson and Mannion, 2012). If there are general rules underlying macroevolutionary responses to these forces, studying the past may also inform the future. Palaeontology can therefore, potentially, provide important information on the future progression of the extinction crisis facing the biosphere today, and its likely consequences (Mayhew *et al.*, 2008; Alroy, 2010*a*).

In addition to such strategic questions, palaeontological data can help solve many basic questions of perennial interest. Comprising over 50% of described species (Grimaldi and Engel, 2005), hexapods (insects and their close relatives such as springtails) form a major component of almost all terrestrial ecosystems. An explanation of how and why this group has come to so dominate terrestrial biodiversity is a major challenge in macroevolutionary biology.

Palaeodiversity data are usually compiled in the form of taxonomic databases of fossils giving either temporal ranges or discrete occurrence data. Commonly, criticisms of such databases focus around the integrity of the data and its resilience to the addition of further information (Benton, 1999). Substantial additional knowledge, both taxonomic and stratigraphic, of the fossil records of tetrapods (Maxwell and Benton, 1990) and all marine animal families (Sepkoski, Jr., 1993), has nonetheless yielded very similar variation in originations and extinctions though time. This supports the notion that broad biological signals can be seen through the statistical noise of an imperfect fossil record. However, the effect of additional data on macroevolutionary patterns has not been tested for the majority of terrestrial groups. This is important because many terrestrial taxa, such as insects, preserved only in exceptional conditions (*Lagerstätten* taxa) are likely to have substantially incomplete fossil records where the potential for change is much greater.

Using data on the temporal ranges of families, Labandeira (1994), and Labandeira and Sepkoski, Jr. (1993) considered that, apart from the Late–end-Permian extinction, no other mass extinction event known from other groups appears to have had any major impact on insects. Further to this, a steady increase in insect family richness began in the Triassic and was due, not to particularly high levels of origination, but to consistently low extinction – noticeably lower than that in the Palaeozoic. The rise of angiosperms during the Cretaceous apparently did not cause any increase in levels of origination in insects and may even have caused some decline in richness into the Late Cretaceous. However, Labandeira and Sepkoski, Jr. (1993) noted that much of the variation around this long term trend of increasing richness could be linked to specific rich fossil deposits (*Lagerstätten*) or stages where insect-bearing fossil deposits are poorly known and so are cautious with any such interpretations. Jarzembowski and Ross (1996), using data based on but slightly updated from Ross and Jarzembowksi (1993), highlighted four major insect origination events during the Permo-Carboniferous, Early Jurassic, Early Cretaceous and the Eocene. They concurred with Labandeira and Sepkoski, Jr. (1993) that today's exceptionally high insect diversity is the result of low extinction levels and sustained origination but disagreed that insects were essentially immune to mass extinction after the end-Permian event. Highlighting in particular an apparent decline in family richness seen in the Upper Cretaceous record, they suggest a causal link to the radiation of angiosperms. Additionally, Ross *et al*. (2000) noted the increase in counts of origination and extinction in the Cretaceous as evidence of ecological turnover associated with angiosperms.

The field of palaeoentomology has expanded rapidly in the last two decades, with large increases in the number of active researchers and consequent publication output (Ross, 2010), as well important changes in taxonomy (e.g. the resurrection of the order Cnemidolestodea by Béthoux, 2005), the dating of fossil deposits (e.g. the recognition of the mid-Cretaceous age of Burmese amber; see Ross *et al.*, 2010) and the exploration of newly known insect-bearing formations globally (e.g. the Eocene amber deposits of India; Rust *et al.*, 2010).

To take account of these developments, in the first instance, a new dataset of the temporal ranges of hexapod families, compiled from literature published up to the end of 2009, is compared with that of Ross and Jarzembowski (1993; data from literature published up to the end of 1991) and Labandeira (1994) by documenting changes and additions to the data. Then richness time series derived from these datasets are compared to assess any change in the signal provided by the fossil record in light of additional data. A breakdown of the new data show which main groups of hexapods make a dominant contribution to the signal through time. From the first and last occurrence data, rates of origination and extinction can be calculated per stage indicating the timing of major radiation and extinction events as well as long-term trends and the relative importance of these to hexapod family richness.

3.3 Methods

3.3.1 Changes and additions to the hexapod fossil record

To assess the amount of change in the new dataset (NEW; see Chapter 2 and Appendix 3) relative to the fossil insect family datasets presented by Ross and Jarzembowski (1993) and Labandeira (1994) (referred to herein as FR2 and LAB, respectively), each family in NEW is categorised in the following ways with respect to FR2 and LAB: ‘no change’, ‘new in list’ and ‘range change’. The first of these is self-explanatory with respect to LAB, which, like NEW, presents data at stage resolution. However, FR2 presents data at both epoch and stage level, and no change for a family where data in FR2 were given at epoch or period level represents a case where the data in NEW confirm it was indeed present throughout that epoch or period. ‘New in list’ can refer to newly described families, those brought out of synonymy or Recent families which now have a fossil record. ‘Range change’, used only for comparison with FR2, involves a change in the recorded stratigraphic range of a family, whether an extension or contraction from the finding of new specimens but also includes improved resolution or revised dating of deposits from which previously known specimens occur (i.e. the deposit is now dated to a different stage). Since most of the LAB data is resolved to stage level and so is more directly comparable with the new data, range change is subdivided into three categories: contraction, extension and shift. A contraction is any situation where the NEW range has fewer stages than recorded in LAB, while an extension is any family where the new range covers a greater number of stages. This does not distinguish between whether the first and/or last occurrence has changed to create the contraction or extension and can also include instances where the NEW range has no overlap with that in LAB, e.g. the palaeodictyopteran family Hanidae, P1(Artinskian) in LAB but C2(Gzhelian)–P1(Sakmarian) in the new dataset. Shifts represent when the NEW range for a family covers a different set but the same total number of stages.

Difficulty was met when considering FR2. The basis for that dataset was taken from family ranges given in the hexapod volumes of the *Treatise on Invertebrate Paleontology* (Carpenter, 1992), which had a stratigraphic resolution of only epochs or sometimes even periods, and then adding data from additional literature. The result is that FR2 gives stratigraphic ranges variously at stages, epochs or periods, making any sort of consistent comparison between it and other datasets difficult, other than at very coarse resolution.

3.3.2 Derivation of richness time series from origination and extinction data

Before describing how various time series can be derived from first and last occurrence data, it is worth defining the four classes of taxa which can be counted in a time interval (Foote, 2000) (Figure 3-1).

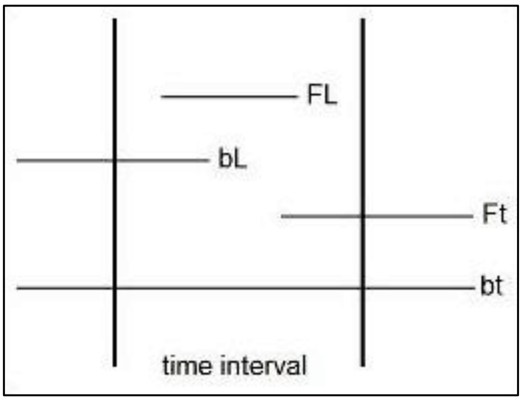

Figure 3-1 The four classes of taxa which can be recorded in an interval using first and last occurrence data. After Foote (2000). The horizontal axis represents time progressing from left to right. The vertical lines represent the start (left) and end (right) of a specified time interval of interest. Horizontal lines represent the temporal ranges of four types of taxa of interest: **FL** originates and goes extinct within the interval, **bL** originates before and becomes extinct within the interval, **Ft** originates within and continues beyond the interval and **bt** originates before and continues after the interval.

Some taxa (bt :bottom, top) originate before the time interval in question and have their last occurrence sometime after it, thus crossing the bottom and top boundaries. Some taxa (bL: bottom, Last) originate before the interval and have their last occurrence in it. Others (Ft: First, top) first appear in the interval and range beyond it. Finally, still others (FL: First, Last – also known as single-interval taxa) appear to originate and go extinct entirely within the interval, never crossing either the bottom or top boundaries. The term ‘single-interval taxon’ is preferable to the commonly used term ‘singleton’ when describing such taxa (as unfortunately done in, e.g. Alroy, 2000*b*; Foote, 2000; Fitzgerald and Carlson, 2006) as the word is already in common usage in ecology for taxa represented by one specimen (Preston, 1948; Alroy, 2010*c*).

Two commonly-used counting methods exist for deriving diversity time series from first and last occurrence data – range through (RT) and boundary crossers (BC), and a third employed here, minimum assumption (MIN) (Peters and Foote, 2001; Alroy, 2010*c*). These are applied to NEW and LAB data, while with the FR2 data only range through is used but under two assumptions – $FR2^{+}$ and $FR2^{-}$, explained below.

RT is the classic method of counting a taxon as present in every stage between and including its first and last occurrences in the fossil record (or up to the present day if still extant), as well as those which originate and go extinct within the same time interval (known as single-interval taxa or FL in the notation given above), used, for example, by Sepkoski, Jr. (1993), Labandeira and Sepkoski, Jr. (1993) and Jarzembowski and Ross (1996). This is the sum total of taxa observed and inferred to exist within a time interval and can be written as RT=bt+Ft+bL+FL. For FR2, inconsistent stratigraphic resolution makes it necessary to use maximum and minimum assumptions of the ranges given when comparing with datasets at stage level. $FR2^{+}$, then, is based on the assumption that the family originates in the first stage of the interval in which lies its first appearance and goes extinct in the last stage of the interval containing its last appearance, while $FR2^{-}$ assumes the origination in the last stage of the interval of first appearance and extinction in the first stage of the interval of last appearance (Mayhew *et al.*, 2008). Consequently, any family which is recorded at epoch or period level but in only one interval is removed from the $FR2^{-}$ series.

The BC series are made up of only those taxa which range between two or more time intervals, i.e. excluding single-interval taxa (FL). However, they are not simply RT minus FL. Rather, BC series represent the number of taxa crossing the bottom boundary into the interval, thereby tying diversity to a single point in time (the boundary) and not adding that diversity to events which occur cumulatively within the interval. It can be written as BC=bt+bL. By restricting the richness count to taxa which cross a single point in time, the data record an actual faunal cohort rather than the accumulation of taxa which exist throughout an interval. The specific advantage of this is that it is immune to changes in interval length, while it might be expected that longer intervals will accumulate more taxa than shorter ones, thereby inflating the richness measurement for that observation point. BC series have found use in some more recent palaeodiversity studies (Bambach, 1999; Alroy, 2000*a*; Alroy *et al.*, 2001) and have been advocated within the palaeoentomological community more recently by Ponomarenko and Dmitriev (2009). As these are values for interval boundaries, in order to make possible the comparison with data within intervals (placed at stage-midpoint) the geometric mean of the bottom and top boundaries of each interval are used for analyses, i.e.

$$\sqrt{BC_1 \times BC_2}$$

where BC_1 and BC_2 are the number of bottom and top boundary crossers of a given interval, respectively. Possible drawbacks of excluding single-interval taxa are that it excludes some true biological variation; may increase taxonomic bias by virtue of eliminating particular types of organism from the data; and the data then cease to represent all described variation, which is one of their chief merits.

The MIN series is derived from only the first, last and single-interval taxa, without filling in ranges. Like RT, this is a summation of events within a stage and can be written as MIN=Ft+FL+bL. This is the most conservative of the three as it makes the minimum assumption of what has actually been recorded in each stage and is more directly related to sampling proxies such as formation or collection counts (Peters and Foote, 2001). It can be viewed as a subset of sampled-in-bin counts (counting only taxa which have actually been recorded in a time bin, rather than merely inferred to have existed at that time). Of course, it is a highly truncated version of true sampled-in-bin counts as the original purpose of the dataset was to record only first and last occurrences (Chapter 2).

To complement descriptive comparisons detailed in section 3.3.1, untransformed RT data from FR2, LAB and NEW are correlated using Spearman's rank correlation to illustrate overall similarity. Spearman's correlation was used because even when logged the data were skewed, breaking parametric assumptions. The normal associated probabilities are not reported because autocorrelations in the data invalidate them. Bootstrap estimates for significance of correlations are instead calculated using the `boot.ci` function from the `boot` library in R to re-sample the original data 9999 times, each time recalculating the correlation coefficient, to generate a bootstrapped distribution of the test statistic which indicates the extent of uncertainty in it. Confidence intervals at the 95% and 99% level are calculated using the `bca` (bias corrected and accelerated or BC_a) method due to Efron (1987), which corrects for the bias (the difference between the mean of the bootstrap replicates and the true correlation) and asymmetry of the bootstrap distribution (Efron, 1987). Where the confidence intervals do not bracket zero, the correlation can be said to be significantly different from zero. Correlations were also explored for two detrended versions of each time series: first differencing explores the changes between successive time steps (stages), whilst generalized differencing (first differencing of the residuals from linear regression) quantifies the successive changes after removing the overall long term trend. Differences were calculated using the statistical programming language R (R Development Core Team, 2011). All correlations are on data from the Serpukhovian (top of Early Carboniferous, stage midpoint 323.2Ma) to Piacenzian (top of the Pliocene, stage midpoint ~3.1Ma), as this is the range for which there is a reasonable fossil record of hexapods (i.e. including the long period of almost no record before the Carboniferous would increase all of the coefficients simply from a lack of data).

3.3.3 Calculating origination and extinction rates

The rates of origination and extinction employed here are Foote's (2000) estimated per-capita rates, $\hat{p}$ and $\hat{q}$ respectively. They are derived as follows:

$$\hat{p} = -\ln (N_{bt} / N_t) / \Delta t$$

$$\hat{q} = -\ln (N_{bt} / N_b) / \Delta t$$

where N_t is the total number of taxa crossing the top boundary out of the interval (i.e. bt+Ft), N_b is the total number crossing the bottom boundary into it (i.e. bt+bL) and N_{bt} is the number of taxa crossing both the bottom and top boundary. The advantage of using these over counts of events within an interval is that they are robust to variation in interval duration, disregard single-interval taxa (which are prone to disproportionately distort the signal) and are independent of each other as they are derived from numbers of taxa passing into and out of intervals rather than the addition of events taking place within them. Due to inconsistent stratigraphic resolution, this is not attempted for the FR2 data.

3.4 Results

3.4.1 Changes in the data

The NEW dataset contains a total of 1454 families of Hexapoda, of which 1436 are Insecta. In comparison to FR2, a substantial amount of change has left only 8% of families with the same ranges as recorded in 1993; 35% are new to the record, and well over half have a change in the recorded range (Figure 3-2A). The picture is broadly similar when compared to LAB (Figure 3-2B), with 10% remaining unchanged and 30% new. The majority of the range changes are made up of roughly equal amounts of extensions and contractions, and only 7% of the total representing a shift in range. Although the NEW dataset has a higher total number of families (1454) than either FR2 (1008 in downloaded data from www.fossilrecord.net, although 1083 are in fact listed in the original publication) or LAB (1272; 1276 if including 'uncertain' families), 230 and 263 families listed in FR2 and LAB, respectively, are not included in NEW due mostly to taxonomic revisions.

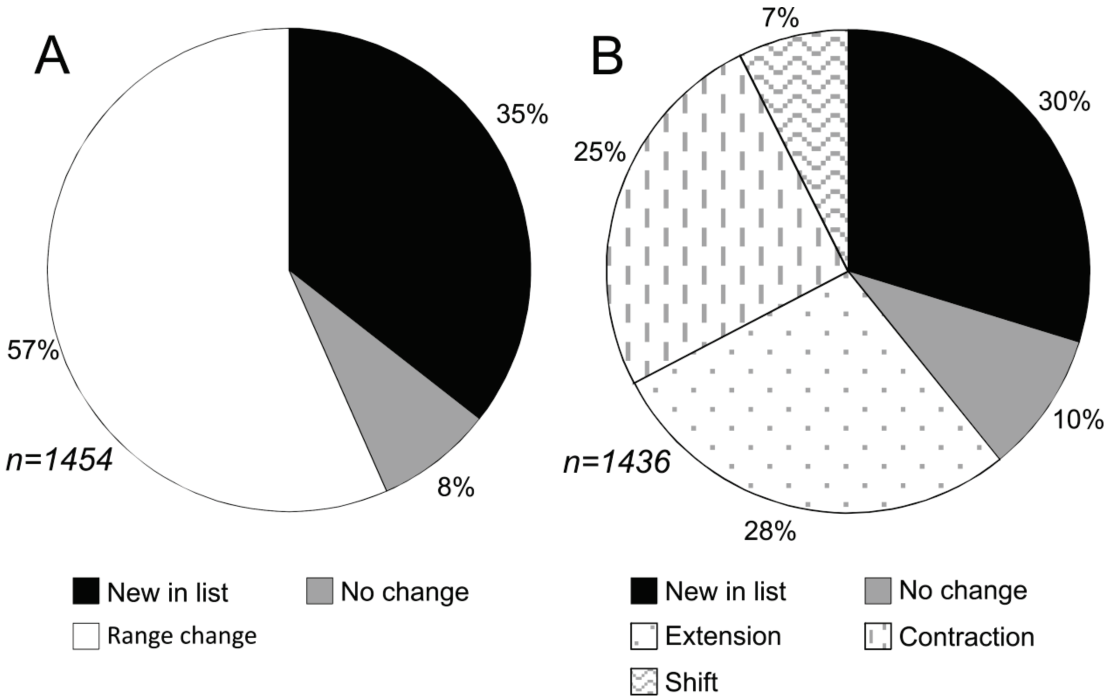

Figure 3-2 Proportions of changes in new data for family stratigraphic range compared with previous datasets **(A)** FR2 (Ross and Jarzembowski, 1993) all hexapods and **(B)** LAB (Labandeira, 1994) all insects.

3.4.2 Richness series from new and previous datasets

The richness time series of all three datasets show broad similarities in long-term trends of increasing richness and the synchronicity (or nearly so) of several pulses (Figure 3-3) but some differences are worth noting.

For the Palaeozoic, the RT series from NEW and LAB are more similar to each other than to $FR2^+$. However, the NEW series shows consistently lower richness than LAB and the two main peaks are offset by one stage, reaching a maximum of 105 families by NEW RT and 153 by LAB RT (Figure 3-3). $FR2^+$ shows a gradual and steady increase in richness through the Palaeozoic with a dramatic drop at the end-Permian (~250 Ma), after reaching a maximum of 168 families (Figure 3-3; although note that $FR2^-$ shows no such increase and decline but rather remains conspicuously flat through until the Late Triassic at around 210 Ma). This is not mirrored by LAB RT and NEW RT, which show slightly less sharp declines from the Early–Middle Permian towards the end-Permian, when a small increase is seen in the final stage (Changhsingian, data point at 252 Ma). The BC series in NEW and LAB mirror the peaks and troughs of the RT curves but with a lower range of variation (Figure 3-3).

In the Triassic (251–200 Ma) all three datasets show a marked increase in richness, with the largest increase in the Carnian (223 Ma) for $FR2^+$ (up to 123 families) and NEW (171 families) and in the Ladinian (233 Ma) for LAB (117 families) (Figure 3-3). The NEW RT curve shows the most pronounced Triassic peak followed by an apparent crash in richness, mirrored in the NEW MIN series but NEW BC shows a smooth increase with only a slight decrease after the Carnian.

The Jurassic (200–146 Ma) continues the long-term increase in described richness (Figure 3-3). The NEW RT series shows a distinct, four-pulsed increase (at 190, 179, 158, and 148 Ma); the first three are followed by drops in richness, although this is not reflected in the BC series which shows an uninterrupted, fairly smooth increase. An almost identical pattern is seen in LAB RT while $FR2^+$ shows two distinct increases followed by plateaus.

During the Early Cretaceous (146–100 Ma) a more rapid rise is seen, most steeply in NEW RT. LAB and FR2 are similar in then showing a pronounced and sustained drop in richness after their synchronous peaks in the Aptian (point at 119 Ma) in both RT and BC series while the NEW RT series continues to increase, albeit at a decelerated rate until it plateaus across a similar range of stages as LAB and FR2. This plateau is accompanied by very low values in the NEW MIN series. No marked drop in richness is apparent at or near the Cretaceous/Palaeogene boundary (65.5 Ma).

The NEW RT series averages 15% and 26% higher across the Cretaceous and Tertiary compared with LAB and FR2, respectively ending with maxima of 695 (NEW), 549 (FR2) and 625 (LAB) families. All three show the most rapid increase in richness in the entire fossil record through the Tertiary with very little deviation between RT (or $^+$) and BC (or $^-$) series.

The morphological groups/clades (see Chapter 1) dominating richness in NEW (RT) varied at different times (Figure 3-5). The earliest known hexapod families are in the 'Apterygota'. These contribute very little to hexapod fossil richness in the long term. The Carboniferous and Permian peaks and subsequent declines are seen only in the Palaeoptera and Polyneoptera. Paraneoptera and Holometabola had originated before the Permian peak but show no sign of any decline towards the end-Permian, rather a slow but steady increase in richness (Figure 3-5). The Late Triassic peak seen in the RT (but not BC) series is apparent in all groups except Apterygota. Except for occasional pulses of increased richness, which are synchronous with the other three major contributing groups, Palaeoptera show very slow and steady growth in richness, only attaining their previous Palaeozoic richness in the Tertiary from ~60 Ma onwards. A broadly similar pattern is seen in Polyneoptera. Paraneoptera, however, continue their steady increase from the Palaeozoic and show a pronounced increase during the Early Cretaceous, between ~150 and 100 Ma (Figure 3-5). This then levels out until they enter a phase of rapid expansion in the Tertiary, from ~65 Ma onwards. The Holometabola enter a more rapid phase of expansion earlier than the Paraneoptera, from ~200 Ma onwards. They show a pronounced jump in richness at 128 Ma (Barremian), being the largest contributing group to the rapid rise in richness during the Early Cretaceous seen in the NEW RT series. This is followed by a long plateau and then the most rapid expansion phase seen in the entire hexapod fossil record from the lower Eocene (52.2 Ma) onwards (Figure 3-5).

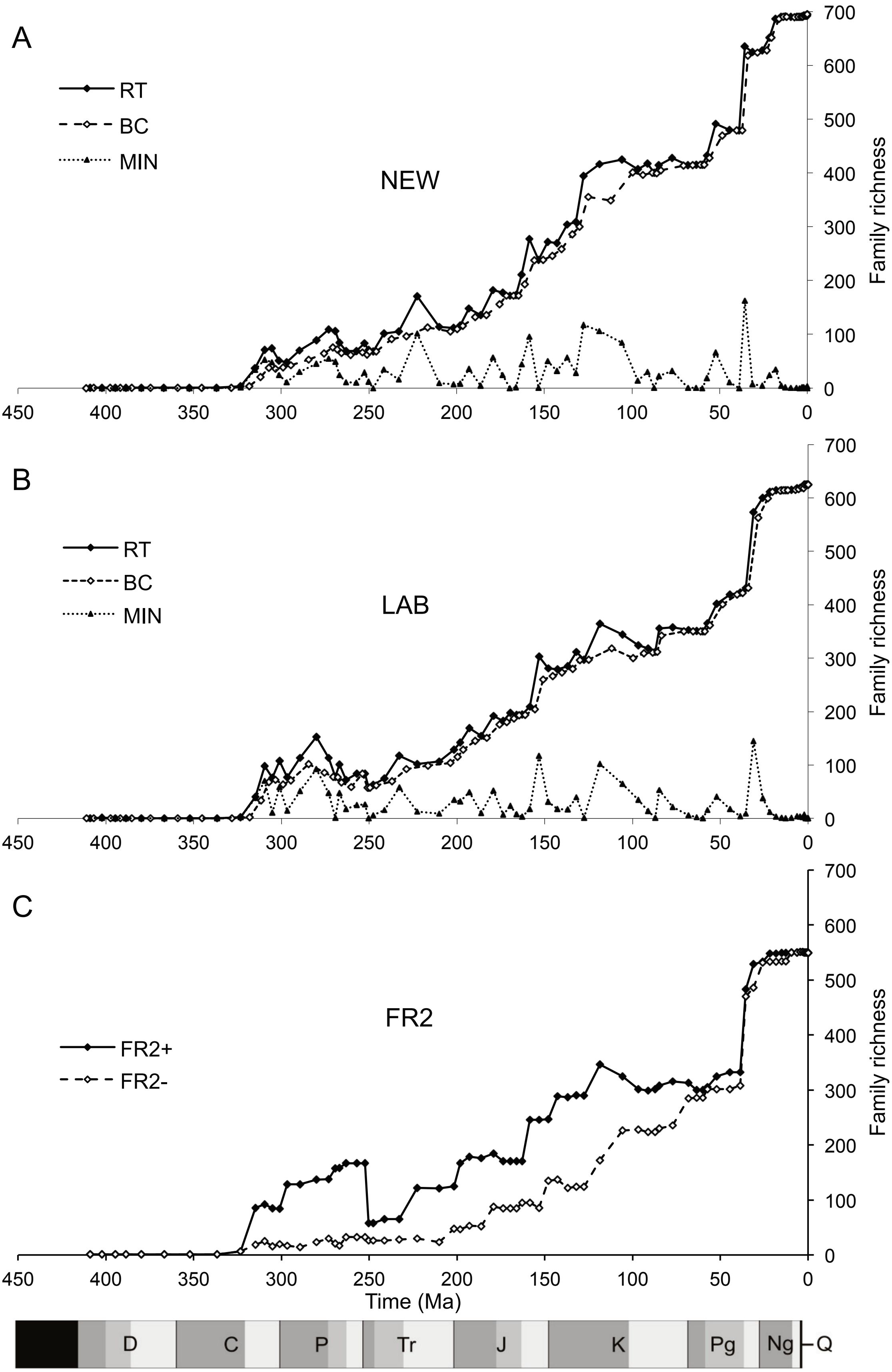

Figure 3-3 Family richness of insects through time. Richness time series derived from **(A)** NEW data, presented here **(B)** LAB data from Labandeira (1994) and **(C)** FR2 data from Ross and Jarzembowski (1993). **RT** = range through, i.e. all taxa ranging anywhere into an interval, with maximum (+) and minimum (–) assumptions for FR2, plotted at stage-midpoints. **BC** = boundary crossers, i.e. taxa crossing interval boundaries, plotted at stage boundaries. **MIN** = minimum richness, representing firm occurrences within stages (i.e. first, last and single-interval taxa records).

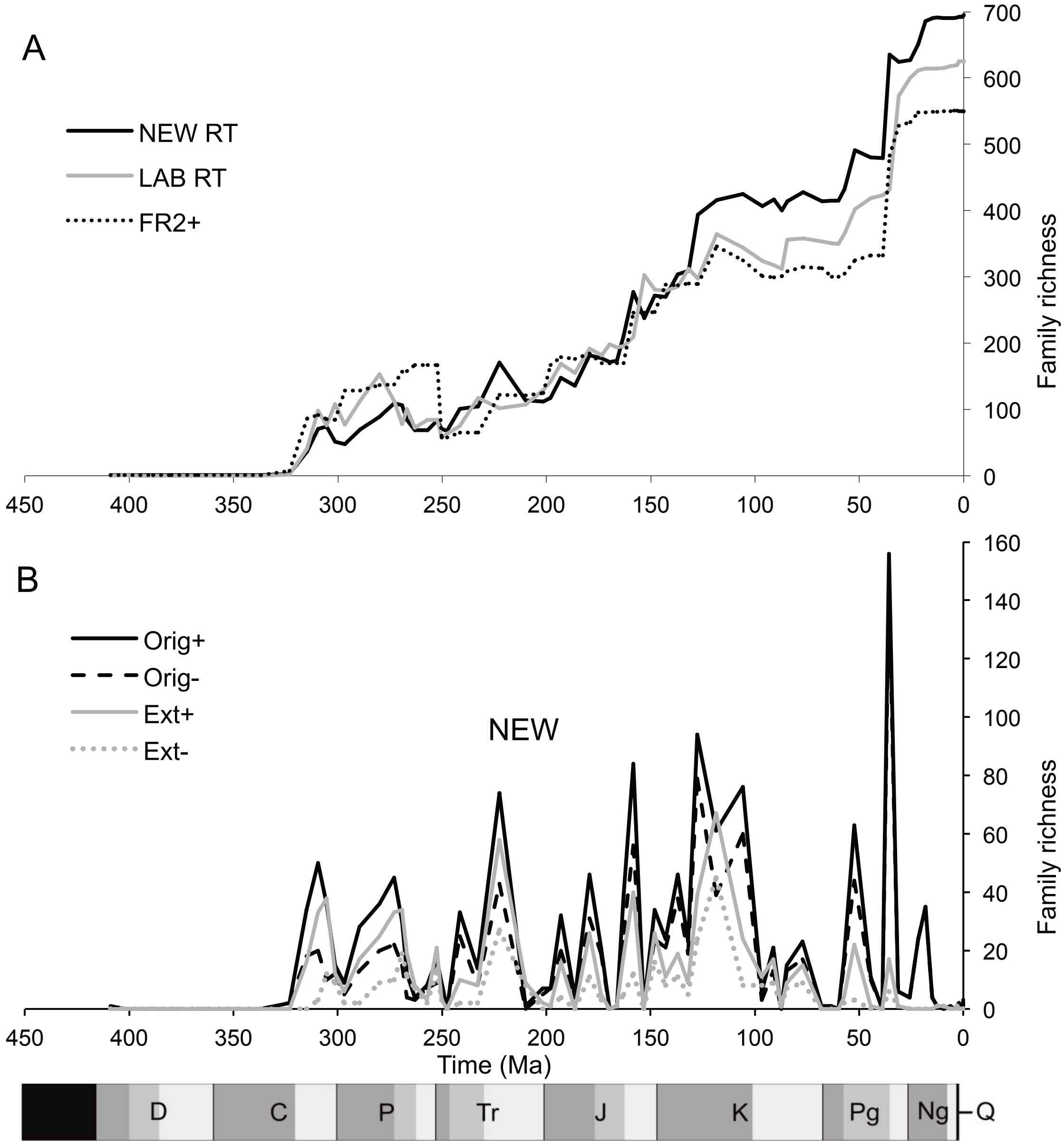

Figure 3-4 (A) Range through time series for NEW, LAB and FR2. **(B)** Origination (Orig) and extinction (Ext) counts, both including (+) and excluding (–) single interval taxa, from NEW.

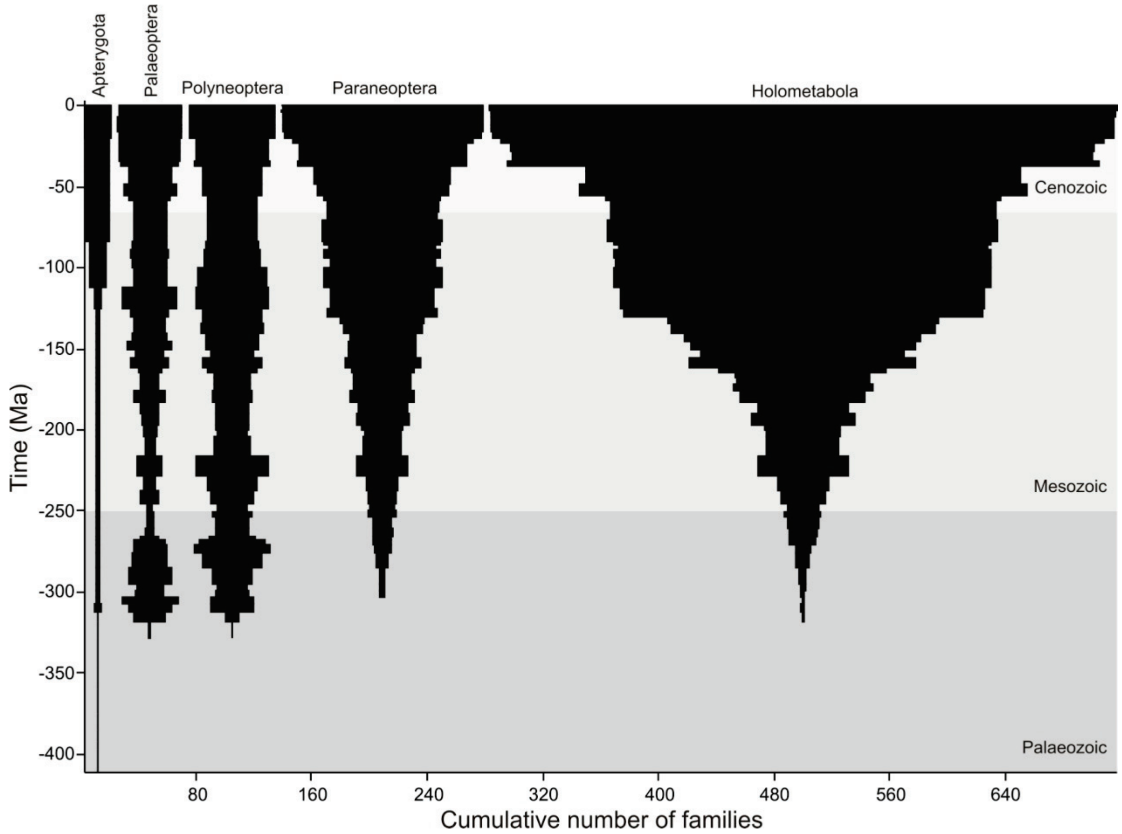

Figure 3-5 Spindle diagram showing range through family richness from the NEW data in major constituent groups of hexapods through time, generated using PAST (Hammer *et al.*, 2001).

Both the FR2$^+$ and LAB RT series are highly correlated (i.e. strongly co-vary) with NEW RT (Table 3-1), with all values of Spearman's rho greater than 0.95 and significant at the 99% confidence limit. This decreases substantially with both first and generalised differencing. (Table 3-1), and correlations between NEW RT and LAB RT lose significance, whilst those between NEW RT and FR2+ retain their significance.

Table 3-1 Spearman rank correlations between richness time series using raw values and after first differencing and generalised differencing. NEW = new fossil hexapod family richness data presented here, **LAB** = insect family richness data from Labandeira (1994), **FR2** = hexapod family richness data from Ross and Jarzembowski (1993), **RT** = range through, **BC** = boundary crossers, **$^+$** = maximum assumption of richness and **$^-$** = minimum assumption of richness for FR2 (see 3.3.2), $\hat{p}$ = *per capita* origination rate and $\hat{q}$ = *per capita* extinction rate (see 3.4.3) Significance assessed using bootstrapping. * = significant at 95% confidence limit, ** = significant at 99% confidence limit.

	LAB RT	LAB BC	FR2$^+$	FR2$^-$	LAB $\hat{p}$	LAB $\hat{q}$
Raw values						
NEW RT	.976**		.956**			
NEW BC		.982**		.979**		
NEW $\hat{p}$					.277	
NEW $\hat{q}$						.559**
First difference						
NEW RT	.183		.367*			
NEW BC		.331*		.135		
NEW $\hat{p}$					-.070	
NEW $\hat{q}$						-.028
Generalized difference						
NEW RT	.241		.442**			
NEW BC		.273		.111		
NEW $\hat{p}$					.191	
NEW $\hat{q}$						.375*

3.4.3 Calculated origination and extinction rates

First and last occurrences occur episodically throughout the fossil record of insects (Figure 3-4B), with an apparent synchrony between origination and extinction through time with origination outstripping extinction. The modal origination occurs in the Palaeogene with large peaks in the Triassic, Late Jurassic and Early Cretaceous. Modal extinction occurs in the Early Cretaceous with large peaks in the late Carboniferous, Permian, Triassic, later Jurassic and Early Cretaceous. Per capita rates of origination and extinction ($\hat{p}$ and $\hat{q}$, respectively; Figure 3-6), however, show distinctly different profiles in the Palaeozoic and post-Palaeozoic (boundary at 251 Ma) in both NEW and LAB data. Greater variance is seen in the Palaeozoic for both rates in both datasets as well as the highest values reached in each. As for raw counts, per capita origination rates stay robustly higher than extinction from the Triassic onwards and both show long term declines towards the present. There are some notable differences between NEW and LAB: the timing and size of Permian origination peaks differs; there is no Late Cretaceous origination peak; the Carboniferous extinction peak is more pronounced, and those in the Permian less pronounced, not exceeding originations by much. As a result, Spearman rank correlations of these rates between NEW and LAB show no significant relationship in origination rates, while the extinction rates are positively correlated in the raw and generalised differenced time series but retain no relationship after first differencing (Table 3-1). In general, origination rates seem to more consistently exceed extinction rates.

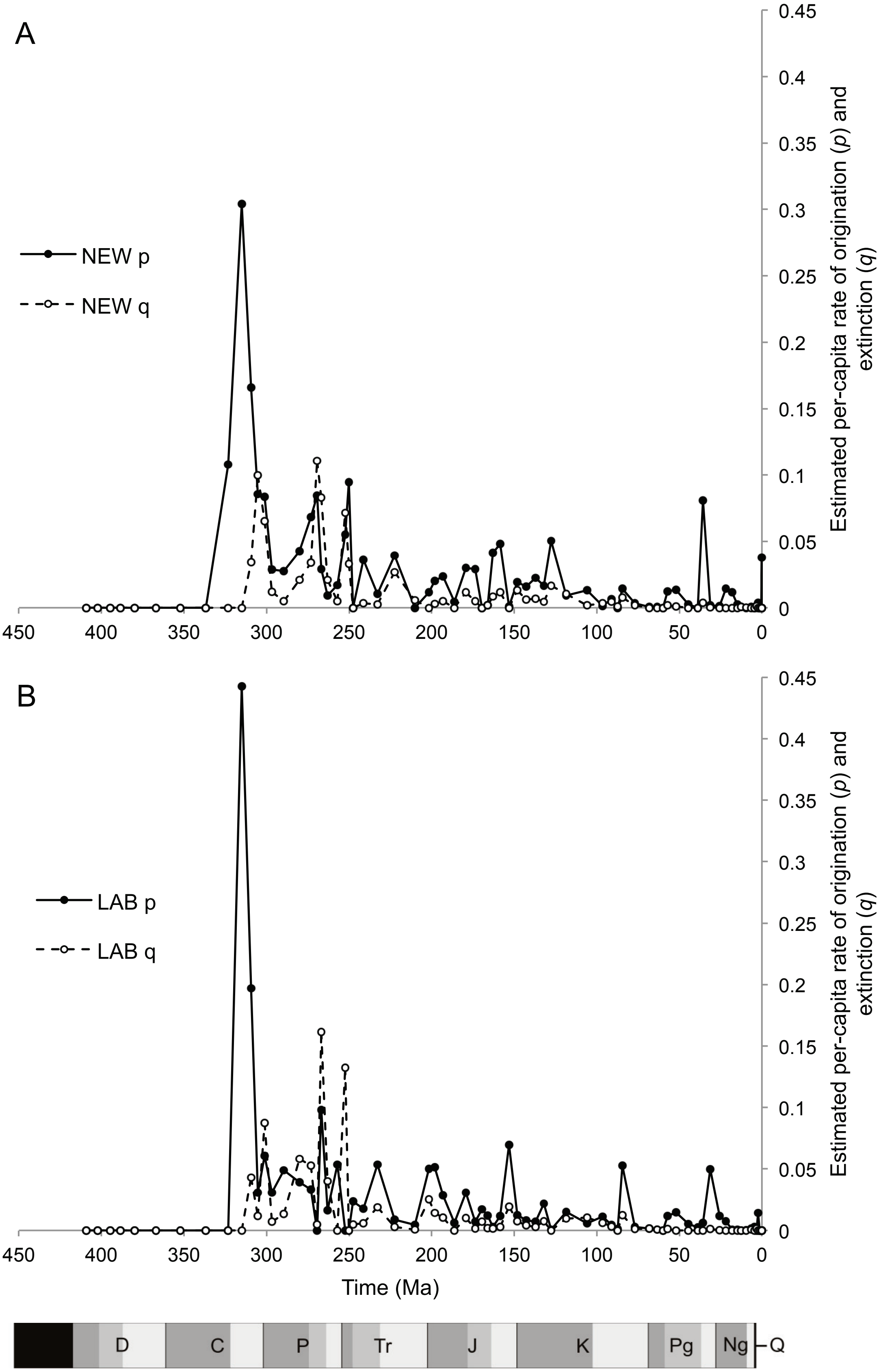

Figure 3-6 Estimated per-capita rates of origination $\hat{p}$ and extinction $\hat{q}$ from **(A)** new insect family data and **(B)** Labandeira (1994).

3.5 Discussion

3.5.1 Changes in the data

The robustness of macroevolutionary patterns through time in the insects, to new discoveries over fifteen years (eighteen years from FR2 data up to end 1991), was tested by compiling a new dataset of fossil hexapod family-richness from literature published up to the end of 2009. Only ten percent of families in the new data remain unchanged over that time, with about 60% of families having different stratigraphic ranges, and 30% of families being completely new to the fossil record. For scientists interested in the details of individual fossil families, for example for dating phylogenies above family level (e.g. Davis *et al.*, 2011), the current dataset represents a substantial improvement over previous datasets available. The implication is that the previous fossil insect datasets now have largely historical interest only and should not be used for future macroevolutionary research. Studies based on them ideally require re-assessment.

While the change in ranges from FR2 in the NEW data (Figure 3-2A) can be attributed largely to improvement in the stratigraphic resolution of family ranges to stages, the differences from LAB (Figure 3-2B) require more subtle explanation. Extensions of known ranges in fossil families are to be expected, with continued exploration of fossil sites and descriptions of new finds likely to turn up new first or last occurrences, such as the incredible rate of discovery in Mesozoic deposits of China (e.g. see Ren *et al.*, 2010). The high proportion of range contractions (25%) seems at first unexpected but can be ascribed to differences in the dates for fossil deposits used (e.g. the Karabastau Formation, Kazakhstan: Kimmeridgian in LAB but Oxfordian in NEW) and extensive changes in taxonomy reducing the number of fossils included in some families, such as in a recent review of termites by Engel *et al*. (2009) wherein several fossil taxa, previously attributed to extant families, were reassigned, thus contracting the known range of some families and removing the Hodotermitidae from the fossil record altogether.

The rate of discovery of new fossil hexapods seems disproportionately concentrated in the Cretaceous, with high numbers of publications on the extensive Yixian Formation in China (Ren *et al.*, 2010), continued interest in the Crato Formation in Brazil (Martill *et al.*, 2007), a new supply of Burmese amber (Grimaldi *et al.*, 2002; Ross *et al.*, 2010) and abundant new amber deposits in France (Perrichot and Néraudeau, 2009) and Spain (Delclòs *et al.*, 2007), although new material continues to be found across almost the entire temporal range of hexapods (Grimaldi and Engel, 2005; Ross, 2010; for a recent example see Garrouste *et al.*, 2012). There are an estimated 1067 extant hexapod families (data compiled from the relevant sections of Resh and Cardé, 2009), implying that ~370 extant families (35%) are not yet known from the fossil record and could in principle be found in future. This sets a broad potential upper limit to the height of the richness curve, indicating substantial, but not excessive, potential for future discovery at the family level. The majority of these (196 families) are from the Holometabola. However, in terms of proportion of extant families represented in the fossil record, Holometabola have the most coverage with ~69%, followed closely by Polyneoptera

(65%), Paraneoptera (64%) and Palaeoptera (58%). Only 33% of extant Apterygota families have a fossil record, perhaps a result of their small size, habitats, and lack of wings (Grimaldi and Engel, 2005).

Other informative ways of assessing the potential for future discovery, beyond the scope of the present study, would be to construct collector curves to observe if the number of taxa described through time has asymptoted (e.g. Smith, 2007; Puchalski *et al.*, 2008; Bernard *et al.*, 2010), or by quantifying the gaps in the record implied by phylogenies (e.g. Wills, 2001; Smith, 2007; Ksepka and Boyd, 2012). Both are beyond the scope of this project. Although some data pertinent to the former (dates of description of extinct families) are present in the current data, one would additionally need to compile the date at which extant families were first described from the fossil record, which is not normally their date of first description.

3.5.2 Changes in the richness series

Despite major changes to the ranges of insect families over fifteen years of discovery, changes to the pattern of described richness through time derived from those data seem less extensive. Correlations between the time series of the new and previous datasets show that the broad pattern of rise in discovered taxa through time is very similar to that previously described. The generally steady rise in richness through time suggests support for the previous conclusion (Labandeira and Sepkoski, Jr., 1993) that no logistic limits to family richness have yet been met. However, some of the Cenozoic rise may be attributable to the Pull-of-the-Recent (Jablonski *et al.*, 2003) whereby the ranges of extant taxa are pulled forward, accentuating the richness rise nearer the present. Sampling may also have been strongly affected by the abundance of suitable deposits, such as Baltic amber which coincides with the Eocene rise (Labandeira, 2005). These issues will be examined more specifically in later chapters.

Other important features preserved in the NEW richness series include evidence for a mass extinction at the end-Permian. The Permian drop in richness is however less abrupt than in FR2. This effect is probably due to the improved temporal resolution from epoch to stage, which pulls the ranges of taxa in FR2 forward to the end of the Permian. At stage level resolution, many of these families are instead seen to have last occurrences before the end Permian. In turn, the asynchronicity in extinction may be genuine, but probably is also an artefact of an incomplete record (the Signor-Lipps effect; Signor and Lipps, 1982) which tends to drag extinctions backwards in time. The major turnover in dominant taxa (Figure 3-5) accompanying the Permian to Triassic interval is strongly reminiscent of the end-Permian extinction in many other taxa (e.g. Brusatte *et al.*, 2008). In the hexapod case there was a replacement of the Palaeozoic fauna of mainly Palaeoptera and Polyneoptera by a fauna dominated by Paraneoptera and Holometabola, which appear to have suffered little reduction in their richness (Jarzembowski and Ross, 1996; Labandeira, 2005). Studies on the coherence of these different faunas would be useful (see Alroy, 2004).

Despite the evidence for an end-Permian extinction, the NEW richness data leave no evidence of an end-Cretaceous extinction, in common with previous data (Ross *et al.*, 2000; Labandeira, 2005). Given the known widespread ecosystem impacts of this event, it is difficult to imagine that insects were completely unaffected but extinction may have occurred below the family level. Some genus-level data provide some support for this (Jarzembowski and Ross, 1996), as do some studies of trophic interactions (Labandeira *et al.*, 2002), but others suggest a weaker extinction in insects than in other taxa (Wappler *et al.*, 2009).

Although all datasets show an increase in richness in the Triassic, a subsequent drop is suggested by the NEW RT series. Many non-insect taxa apparently experienced a mass extinction at the end-Triassic (Raup and Sepkoski, Jr., 1982; Benton, 1995) but there has never been good evidence for this in insects. However, the drop is lost in the NEW BC series (Figure 3-4), indicating that it is due primarily to abundance of single interval taxa and hence may be an artefact of sampling bias. Indeed the total number of extinctions detected at the end-Triassic boundary is close to zero, indicating that it would be premature to suggest an insect extinction then (Figure 3-4).

Surprisingly, the overall level of richness in the NEW data is not always higher than the old data. This is mostly the case in the Palaeozoic, where there was an historical tendency by early workers such as Handlirsch and Tillyard to oversplit taxa, while revisions have decreased the number of valid families. Additionally, and perhaps more importantly, of the 324 families in the new data with ranges in the Palaeozoic, 28% of them represent contractions with respect to LAB. This suggests a specific effect of taxonomy on apparent richness that may be important for other researchers.

The correlations between the differenced time series for the new and old data, although positive, are much less strong than for the raw time series, suggesting moderate differences in the shorter term variation in richness from stage to stage. This is potentially important when assessing the drivers behind diversity change (see Chapter 5), as time series are generally detrended to remove spurious correlations, and it is the short term variation around the long term trends that are analysed (e.g. Mayhew *et al.*, 2008; Hannisdal and Peters, 2011). The Palaeozoic contains much of the discordance between the series (Figure 3-4A), with FR2 and NEW having very different shapes while the richness peaks of LAB and NEW are offset from each other. Declines seen in both LAB and FR2 during the Early–mid-Cretaceous (~120–85 Ma) are not shared by NEW, which shows more of a plateau.

3.5.3 Patterns of origination and extinction

Labandeira (2005) picks out five major periods of originations in the insects and four major extinctions. Of the originations, all are still found in the NEW origination series (Figure 3-4), namely in order, the Late Carboniferous (first appearance of winged insects and colonization of forested ecosystems); Early Permian (colonization of wider environments and the rise of Paraneoptera and Holometabola); Late Jurassic (radiation of communities on advanced seed plants); Early Cretaceous (radiations in decomposer and freshwater systems); and the Eocene–Oligocene (primarily a sampling artefact that may represent earlier radiations that are poorly sampled). The main addition to this description in the NEW data is the higher peak in the Triassic, which Labandeira (2005) attributes to a rebound from the Permian extinction.

In terms of extinctions, the Late Carboniferous peak is attributed by Labandeira (2005) to changes in plant communities and trophic structure. The Permian extinction is high in absolute numbers of extinctions but lower in *per capita* rates (cf. Figure 3-4, Figure 3-6) and is generally attributed to high continentality and hot dry climates on land (Benton, 2003). In addition, there were substantial extinctions in the Late Jurassic (attributed to competitive turnover during the simultaneous radiation; Labandeira, 2005) and the Early Cretaceous (attributed to competitive turnover of taxa adapting to new environments, including angiosperms; see Jarzembowski and Ross, 1996; Ross *et al.*, 2000). The NEW series add to this a large peak in extinctions in the Triassic, as seen for originations. As discussed above, this may represent the detection of the more general end-Triassic mass extinction, although it may also be an artefact of sampling bias.

In general the high agreement between the timing of originations and extinctions in NEW and FR2 is consistent with the findings of similar studies on other taxa (Maxwell and Benton, 1990; Sepkoski, Jr., 1993), suggesting that the great potential for change in the insect fossil record has not translated into major changes in pattern. Some previous authors (Sepkoski, Jr., 1993) have interpreted this as encouragement that incomplete and partially erroneous data can preserve broad generalizations about the history of life. However, recent experiences with alternative ways of compiling the data suggest that other issues with the data can remain important in correctly describing and interpreting them (Alroy, 2000*a*, 2008; Alroy *et al.*, 2008).

In general there is high synchronicity between the origination and extinction series (Figure 3-4), which is the pattern expected if one depends on the other biologically, but is also expected if they are both simply artefacts of sampling, hence determined by the availability of insect-bearing deposits (see Chapter 4). The pattern is not simply due to the abundance of single interval taxa (Figure 3-4), suggesting perhaps some biological signal in the data.

Originations mostly exceed extinctions across intervals, explaining the consistent rise in family level diversity through time, as well as high extant richness (Ross *et al.*, 2000; Mayhew, 2002, 2007). In terms of rates, the decline from the Palaeozoic to Mesozoic and Cenozoic is the most obvious feature, in common with other family and genus level analyses (Benton, 1995; Alroy, 2008). Explanations for this include lineage sorting, density-dependent processes and the fact that higher taxa are disproportionately described for older groups (Alroy, 2008). Some of the peaks are different in height in the NEW data compared to LAB (Figure 3-6); a result of taxonomic changes and shifts in the dating of deposits. The Late Cretaceous (85 Ma) LAB origination peak is not seen in NEW, probably from range extensions pulling more first occurrences back to Lower Cretaceous deposits.

In summary, a new compilation of the fossil ranges of insect families shows changes in the ranges of a high proportion of families, and significant changes in short term richness and some origination and extinction patterns, but little change in broad temporal patterns. Having explored these major features of the data in outline, I turn in the following chapters to explore potential explanatory variables, with more formal hypothesis testing. A major current issue in palaeobiology is to what extent the patterns of richness, origination and extinction in the fossil record through time reflect macroevolutionary processes, or whether they are artefacts of sampling (Benton *et al.*, 2011; Smith and McGowan, 2011). This is explored in Chapter 4.

Chapter 4
Biases in the Hexapod Fossil Record

4.1 Abstract

The fossil record provides the only direct evidence for the past diversity of life. Much attention has been given to correcting biases, which may distort estimates of richness. Whilst much recent effort has focussed on standardized subsampling of the fossil record, another avenue involves post-hoc controls or modelling. This chapter explores the relationship between the face-value insect fossil record and the rock record of insect bearing deposits and collections. Measures of the insect-bearing rock record (counts of deposits) and sampling (counts of collections) correlate strongly with the per-stage counts of first and last family occurrences, but, unsurprisingly, less with the range-through family richness counts. The rock record, and the proportion of extant taxa in each stage, also indicates a substantial Pull-of-the-Recent from the late Eocene onwards. An existing method is then developed to model expected insect originations and extinctions given the rock record and sampling for each stage, and to use this to develop adjusted family-richness curves through time which account for variation in rock record and sampling. The curves produced identify several features of the fossil record of insects as likely artefacts, such as high Carboniferous richness, a Cretaceous plateau, and a late Eocene jump in richness. Other features seem more robust, such as a Permian rise and peak, high turnover at the end of the Permian, and a Late Jurassic rise. Whilst not unequivocal, these new time series may be used to assess the robustness of various hypotheses tests in subsequent chapters.

4.2 Introduction

It has long been recognised that biases in the fossil record may distort our view of the diversity dynamics of prehistoric life. The seminal work in this field by Raup (1972) identified several biases which may affect palaeobiodiversity studies and suggests two routes to correct for these; subsampling, and modelling based on control variables. The *Paleobiology Database* project (PBDB; http://paleodb.org) encapsulates the considerable research effort put into subsampling methods, while the latter has gained prominence recently in studies of taxonomic groups for which the large sample sizes needed for subsampling are not available (e.g. Barrett *et al.*, 2009; Butler *et al.*, 2009, 2012; Benson *et al.*, 2010; Benson and Butler, 2011; Benson and Mannion, 2012; Lloyd, 2012). The fossil record of insects has heretofore never been investigated with a view to identifying and correcting rock-record and sampling biases, despite the prominent position of insects as major components of most terrestrial ecosystems, both in terms of taxic richness and biomass (Grimaldi and Engel, 2005), with the resultant importance in understanding their macroevolutionary history. Using a dataset of fossil hexapod originations and extinctions compiled from literature published up to the end of 2009 (see Chapter 3 and Appendix 3), an attempt is made here to identify, and where possible remove, the effects of rock-record and sampling biases in order to produce an adjusted richness curve through time. This may be further used to elucidate any relationships between insect richness, origination and extinction, a variety of biotic and abiotic forces (see Chapter 5) and test for logistic or exponential growth of the Hexapoda.

Since Raup (1972) demonstrated the correlation between sedimentary rock volume and apparent diversity in the Phanerozoic, several different 'rock amount' proxies have been used to counter this potential bias of unfair sampling. Counts of formations (rock strata with comparable lithology and other properties) have been and continue to be widely used (e.g. Barrett *et al.*, 2009; Butler *et al.*, 2009; Benson *et al.*, 2010). However, the use of formation counts as a proxy has been criticised as it may not be any more accurate than the diversity signal it is being used to correct (Benton, 2010). Correlations of formation number and diversity may be due to species-area effects, so should be expected to be correlated, although not causally but driven rather by a third factor (sometimes called the 'common cause hypothesis'), such as sea-level variation (Peters and Heim, 2011). Sea level could control both palaeodiversity and the amount of sedimentary rock deposited (Benton, 2010). While this is a strong possibility when applied to the record of shallow marine, benthic invertebrates, where the depositional environment and suitable habitat are one and the same, there is evidence that the common cause hypothesis does not apply to pelagic marine tetrapods (Benson and Butler, 2011) and non-avian dinosaurs (Butler *et al.*, 2011) as no relationship was found to exist between diversity of these groups and sea level.

In the case of insects, fossils are found in a wide variety of depositional environments (from deep marine to fresh water lakes and amber) (Grimaldi and Engel, 2005), so the present conception of common cause affecting the record of terrestrial organisms is of less concern. It still remains the case that formations are highly variable units which reflect rock heterogeneity rather than any independent measure, so can vary greatly in their vertical thickness and geographical extent. Rock outcrop area, as measured on geological maps, has been used to demonstrate strong correlations of map area and diversity through time as evidence of rock record bias (e.g. Smith, 2001; Smith and McGowan, 2007) and a further refinement of this to the area of exposure (rather than outcrop, which can be covered by superficial sediments and thus not able to be collected from) recovers this relationship more strongly (Dunhill, 2011, 2012), but these measurements do not capture variation in fossil productivity of deposits or collection/publication efforts. Rock outcrop area can lead to biases depending on the type of rock. For instance clay formations, which provide good preservation potential, can cover a large area but have hardly any exposures, whereas more indurated rock (e.g. limestones, sandstones) can be thinner yet form prominent landforms with lots of exposures. In any case, these data are not readily available for global fossil insect deposits. An alternative is to use a sampling proxy, the number of collections recorded to contain the fossil group of interest, which should capture elements of collection efforts based on the assumption that large numbers of fossils from a formation are more likely to end up in several separate collections, as opposed to deposits which yield only a few fossils (Butler *et al.*, 2012).

Fossil record data can potentially suffer from a number of biases besides that of available sampling opportunity. Variable lengths of time intervals used as observation points might be expected to affect the data as, all else being equal, a longer interval provides more opportunity for sedimentary rock to be deposited while more taxa may originate or become extinct in that time. Range-through data (data where the temporal range of taxa is inferred from first and last occurrences only) are particularly prone to the Pull-of-the-Recent (Alroy, 2010*c*), as the Recent is better sampled than any stratigraphic stage and so only a single occurrence of a taxon needs to be known in order to 'pull' its range through to the present. This is a cumulative effect, as time intervals closer to the present are more likely to have taxa which remain extant (Alroy, 2010*c*). Looking at the proportion of taxa in each stage which remain extant will indicate where a strong Pull-of-the-Recent effect is possible. Despite strong biases affecting fossil data, some biological signal is likely to be retained in range-through data (see Hannisdal and Peters, 2011). In particular, the relative number of observed originations to extinctions within each stage may elucidate where genuine shifts in diversity dynamics have occurred.

A strong relationship between origination, extinction and the rock record would indicate that there may be sufficient bias in the fossil record to warrant an adjustment (Peters and Ausich, 2008; Peters and Heim, 2010; Smith and McGowan, 2011). A modelling approach to remove geological and sampling signal from diversity curves is attempted here using the method pioneered by Smith and McGowan (2007) and further developed by Lloyd (2012). This approach assumes that diversity was constant through time and apparent variations are due entirely to changes in the rock available to be sampled or on the level of sampling, based on the proxy used. The residuals of the observed diversity from the model are then interpreted as times of genuinely higher or lower diversity than expected based on the available rock/sampling. This approach requires that the number of taxa actually sampled within each time interval is used, which is not available for the range-through dataset used here. Instead, recorded first and last appearances of taxa (i.e. originations and extinctions as seen from the fossil record) are used to separately model the expected number of originations and extinctions in the insect fossil record, from which an adjusted richness curve can be constructed. This can then be used to show whether features of insect family richness through time may be genuine or more likely the result of changes in rock record availability or sampling.

4.3 Methods

4.3.1 Fossil and rock record data

The fossil data used are the counts of first (originations) and last (extinctions) occurrences of hexapod families per geological stage (see Appendix 3), along with richness calculated from the range-through assumption. Separate time series for each variable are used, both including (denoted by $^{+}$) and excluding (denoted by $^{-}$) single-interval taxa, because the latter are more prone to sampling biases (Foote, 2000). Two proxies are used: 1) A rock amount proxy, consisting of counts of formations contributing to the fossil dataset ('HBF' – hexapod bearing formations) and 2) a sampling proxy, consisting of counts of collections containing hexapods in the Paleobiology Database ('HBC' – hexapod bearing collections) accessed on 16.05.2012. As the latter was independently compiled, some geological formations were given slightly different ages to those used in the present hexapod dataset, so these were adjusted to match. Additional formations which do not contribute first or last occurrence data are also present. Although not collected specifically for this project, assurances have been given that no major secular biases having been added in compiling the HBC data (M. Clapham, pers. comm., 2012). The major contributors to the HBC dataset are Matthew Clapham and his students (87%), with additional contributions from John Alroy, James Jepson, Conrad Labandeira and Dena Smith. All data is at the level of geological stage, using the timescale of Ogg *et al.* (2008), with stage mid-points used as observation points. Time series run from the Serpukhovian (323.2 Ma; Lower Carboniferous/Mississippian) to the Piacenzian (3.094 Ma; Pliocene).

4.3.2 Associations between the rock and fossil records

The origination, extinction and sampling proxy data are skewed even after square root transformations (log transformation in this case is not appropriate due to zero values in the time series), thus breaking parametric assumptions, so the non-parametric test of Spearman's rank correlation is used on the raw data (see Chapter 3). Standard probability values from statistical tables are not appropriate as time series data usually violate the assumption of independent datapoints. Bootstrap estimates for significance of correlations are instead calculated using the `boot.ci` function from the `boot` library in R to re-sample the original data 9999 times, each time recalculating the correlation coefficient, to generate a bootstrapped distribution of the test statistic which indicates the extent of uncertainty in it. Confidence intervals at the 95% and 99% level are calculated using the `bca` (bias corrected accelerated or BC_a) method due to Efron (1987), which corrects for the bias (the difference between the mean of the bootstrap replicates and the true correlation) and asymmetry of the bootstrap distribution (Efron, 1987). Where the confidence intervals do not bracket zero, the correlation can be said to be significantly different from zero.

Correlations are performed between stage duration and originations, extinctions, HBF, HBC, range-through richness (NEW RT; Chapter 3) and time to see if interval duration has a strong effect on events recorded per stage – all else being equal, more events are expected in longer stages. In order to ascertain whether apparent fossil hexapod diversity may be driven by sampling biases, correlations of originations and extinctions with the rock and sampling proxies, NEW RT, and time, are performed. The latter set of correlations (with the exclusion of time) is repeated with the time series after both first differencing and generalized differencing (see Chapter 3.3.2) in order to remove secular trends in the data which can lead to spurious correlations, and test the association of only the short-term variation in the datasets.

Partial Spearman's correlations are performed using the `pcor.test` function from the `ppcor` library in R between originations and extinctions, and both rock record proxies and stage duration in order to ascertain whether the rock and sampling proxies remain strongly correlated with originations/extinctions when stage duration is taken into account and *vice versa*. This is to assess whether stage duration or the record is more influential on the apparent numbers of originations and extinctions.

4.3.3 Pull of the Recent

The percentage of families within each stage which remain extant today (also known as Lyellian survival) was plotted alongside the raw counts of extant and extinct families in each stage through time. Times when extant families comprise a substantial proportion of the total mark the potential for a strong Pull-of-the-Recent effect. As strength of the Pull-of-the-Recent is also affected by the completeness of the fossil record in stages close to the Recent, this is also examined.

4.3.4 Relative frequency of originations and extinctions

Given that both originations and extinctions are strongly correlated with both rock and sampling proxies (see Results), and hence likely reflect bias, the relative frequency of origination and extinction is more likely to reflect true biological changes. For each stage, originations + extinctions are plotted on the x-axis against originations – extinctions on the y-axis. High values on the x-axis indicate high sampling potential, while the y-axis represents variation in the proportion of originations to extinctions, hence potentially true biological changes. If the relationship of originations to extinctions is relatively invariant, most of the plotted points should cluster closely to a straight line. Any stages which fall outside of this main spread would indicate a time interval in which the diversity dynamics deviate from the usual.

4.3.5 Correcting for rock amount and sampling

The modelling method devised by Smith and McGowan (2007) and then extended by Lloyd (2012) is the starting point for our approach, but it was used to correct the number of originations and extinctions, rather than richness. The reason is that strong correlations exist between the rock record/sampling proxies and the number of originations and extinctions in the hexapod data, but not richness, making its use on the richness data hard to justify. This does not mean that the richness data are unaffected by rock and sampling biases, because they depend heavily on the origination and extinction events.

First, the fossil data and rock record/sampling proxy are independently sorted from lowest to highest values. A statistical model is then fitted to these sorted data to predict expected values of the fossil data given a value of the relevant proxy. Smith and McGowan (2007) fitted only a linear model to the data (after log transformation) but Lloyd (2012) added logarithmic, exponential, sigmoidal and polynomial models to take account of any nonlinearity in the relationship between the variables. The best model is chosen by use of the sample size-corrected Akaike Information Criterion (AIC_c) (see Johnson and Omland, 2004), where the value must be reduced by more than two compared with the next simplest model in order for the improvement in fit to the data to be justified by the added complexity of the model. Use of the R code provided by Lloyd (2012) to automate the process consistently returned a fourth order polynomial model for the data used here. However, no higher polynomials were included in the code so it is possible that an arbitrarily high order polynomial could provide a still better fit justified by the AIC_c value. A complication is that high order polynomials become prone to over-fitting (when a model follows idiosyncratic errors or short term trends in the data which do not reflect the relationship of interest). Furthermore, all of the models allow a free intercept. In the case of the data used here, this resulted in the originations/extinctions predicted by zero rock record/sampling to be a positive value, which is nonsensical. A negative intercept can make sense as it may be necessary to sample a certain amount before finding any of the relevant taxa. However, as the two proxies used here are directly linked to the presence of fossil hexapods, the intercept is forced through zero for linear up to sixth order polynomials.

Once the choice of model is made, the modelled (predicted) values of origination/extinction are subtracted from the observed values and the residuals plotted. The [1.96 × standard deviation] of the mean modelled origination/extinction values is taken as a confidence limit, as any excursions beyond these limits may be seen as significantly different from that expected by the rock record/sampling proxies alone (Lloyd, 2012). To test the efficacy of each model at removing the rock record/sampling signal, the model residuals (i.e. observed minus predicted values) are again correlated against the sampling proxy. Removal of the rock record signal should result in a correlation not significantly different from zero.

Previous studies using this method have used counts of taxa actually sampled within the time intervals studied. The hexapod family range-through richness curve relates to the sampling proxy only in how much change there is from the last sampling interval. This is driven by the recorded number of originations and extinctions, so these are used instead. The novel step introduced here is to model originations and extinctions per stage, rather than standing diversity, and to then use these values to predict what richness should look like in each stage if sampling opportunities were equal across stages. This is achieved using the following estimation procedure:

$$Oadj = Omean\left(\frac{Ostage}{Opred}\right)$$

where *Oadj* is the number of originations (or extinctions) in a stage, adjusted for the rock record in that stage, *Omean* is the mean number of originations (or extinctions) across all stages, *Ostage* is the observed originations or extinctions in that stage, and *Opred* is the predicted number of originations in that stage given the value of the rock record proxy used. The ratio of *Ostage/Opred* is assumed to be one unless *Ostage* falls more than 1.96 standard deviations away from *Opred*. This is to prevent the often large differences in the *Oadj* values that can arise where there is not good evidence that *Ostage* differs from *Opred*. These adjusted counts of originations and extinctions are then summed cumulatively to create a time series of richness estimates by:

$$richness_{(t+1)} = \left(richness_{(t)} - extinctions_{(t)}\right) + originations_{(t+1)}$$

where t is any particular time interval (stage).

Lloyd (2012) notes that his method should not be used with range-through richness data due to the Pull of the Recent separating the relationship of diversity with sampling proxies, nor with datasets which include *Lagerstätten* deposits as these can introduce large imbalances. The first of these is somewhat circumvented by using originations and extinctions, as described above. The second is more difficult to address. What constitutes a *Lagerstätte* is very loosely defined – essentially any deposit where preservation is greater than usual for the time series. Since any deposit with an appreciable number of identifiable insect fossils is usually described as a fossil *Konservat-Lagerstätte*, the whole time series consists of such deposits, thus the objection is effectively removed. Of course, this does not take into account the spectacular preservation often found in amber. However, the use of the PBDB collections sampling proxy should take into account the potential for greater numbers of fossils from more productive deposits, including amber.

4.3.6 Origination and extinction rates

Further to an adjusted richness curve, adjusted rates of origination and extinction can be calculated with the rock record/sampling-corrected time series:

$$Adjusted\ origination\ rate = \frac{adjusted\ originations}{adjusted\ richness}/\Delta t$$

$$Adjusted\ extinction\ rate = \frac{adjusted\ extinctions}{adjusted\ richness}/\Delta t$$

where Δt is the duration of the interval (stage) in question.

All tests were performed in the statistical programming language R (R Development Core Team, 2011).

4.4 Results

4.4.1 The rock record

Although the record of fossil insect collections (HBC) is more variable than that of formations (HBF), peaks and troughs roughly track each other indicating a strong correlation (Figure 4-1). The series of first and last occurrences (i.e. the count of taxa known to have been sampled within each stage) covers a similar range of variation to the HBC and also co-varies with the sampling proxies. Prominent deposits contributing to the peaks in sampling include the Carbondale Formation (Upper Carboniferous, Moscovian, 309.4 Ma), Madygen Formation (Upper Triassic, Carnian, 222.6 Ma), Karatau Formation (Upper Jurassic, Oxfordian, 158.4 Ma), Crato Formation (Lower Cretaceous, Aptian, 118.5 Ma) and the Baltic amber (Eocene, Priabonian, 3.5 Ma), whilst temporal intervals of poor sampling include the Induan (250.2 Ma) and Olenekian (247.7 Ma) in the Early Triassic, the Bajocian (169.6 Ma) and Bathonian (166.2 Ma) in the Middle Jurassic, much of the Late Cretaceous, and the Bartonian (38.8 Ma) in the Eocene.

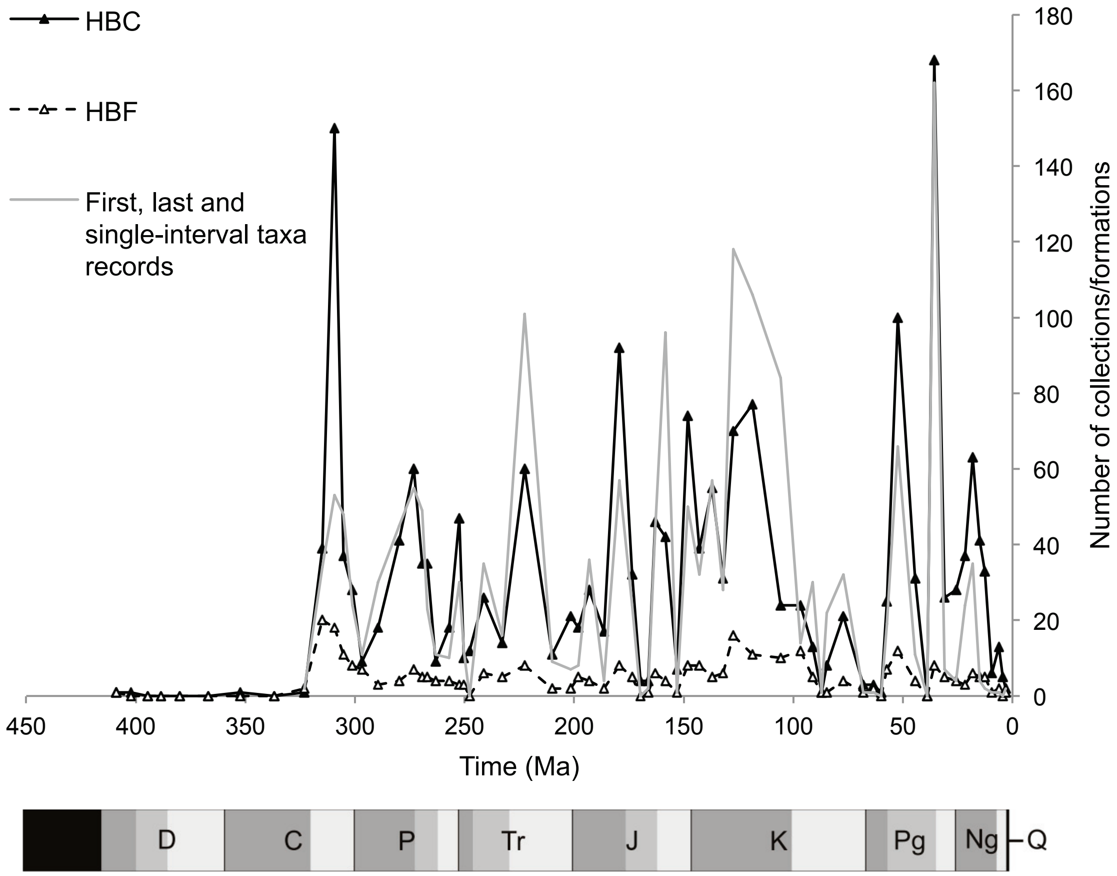

Figure 4-1 Rock record/sampling proxies and sampled taxa through time. HBC = collections containing fossil hexapods recorded in the Paleobiology Database. **HBF** = insect-bearing formations recorded in the present dataset. **First, last and single-interval taxa records** of hexapod families in the fossil record.

The proportion of extinct and extant taxa through time (Figure 4-2) shows that elements of the modern fauna began to appear in the Late Permian just before 250 Ma and increased in the Late Jurassic (~153–148 Ma). The number of presently extinct taxa in each stage declines steadily after the Barremian (127.5 Ma, Early Cretaceous) and forms an insignificant portion of the fauna before the end of the Cretaceous at 65.5 Ma.

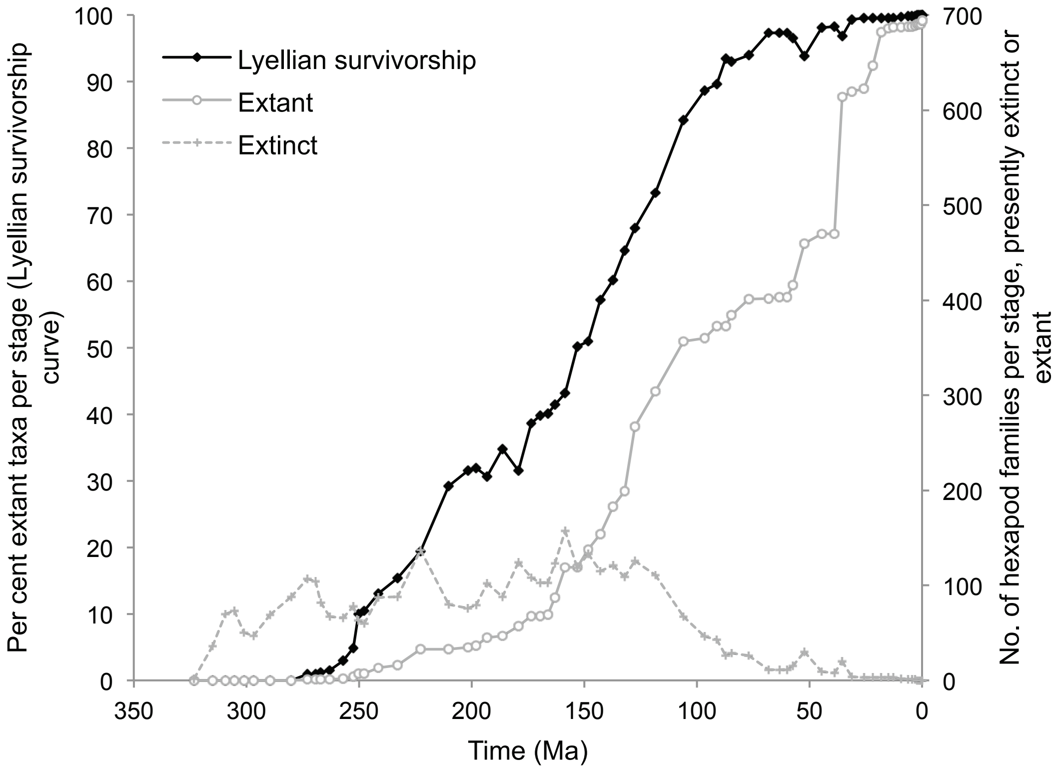

Figure 4-2 Lyellian survivorship curve showing the proportion of taxa in each stage which remain extant today (left y-axis) and numbers of hexapod families in the fossil record per stage which are now extinct or extant (right y-axis).

An examination of the relationship between the amount of data present in a stage and the proportions of first and last occurrences shows a general trend of increased originations relative to extinction with increased data (Figure 4-3). The Priabonian (37.2–33.9 Ma), age of the famous Baltic amber and Florissant Shales, stands noticeably outside the main scatter of points but lies on the trajectory of the overall trend. Stages with fewer originations than extinctions are relatively few and mostly clustered at low levels of data. The Kasimovian, Roadian and Aptian stages provide exceptions, although in the case of the first two removal of single-interval taxa places them back into the main spread of points.

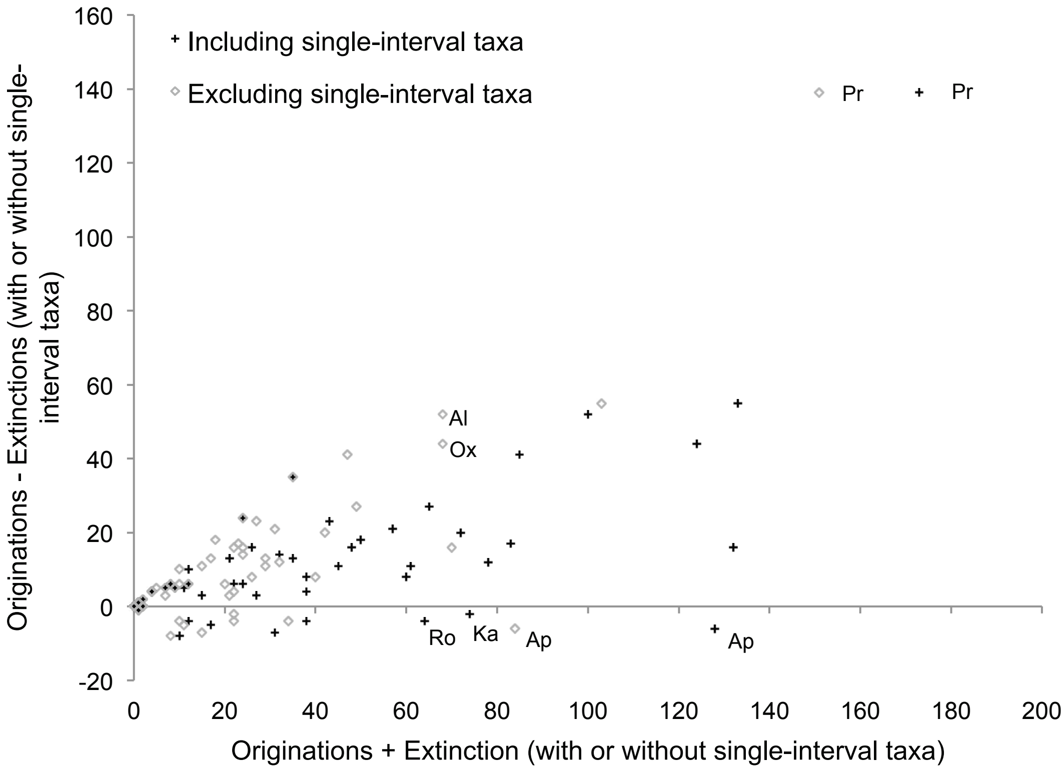

Figure 4-3 Relationship between the amount of data known from a stage (originations + extinctions) and the relative proportions of originations and extinctions, shown by subtracting extinctions from originations. Negative values on the y-axis indicate a greater number of last than first occurrences. **Ka** = Kasimovian (305.3 Ma, Late Carboniferous/Mississippian), **Ro** = Roadian (269.3 Ma, Middle Permian/Guadalupian), **Ox** = Oxfordian (158.4 Ma, Late Jurassic), **Ap** = Aptian (118.5 Ma, Early Cretaceous), **Al** = Albian (105.8 Ma, Early Cretaceous) and **Pr** = Priabonian (35.55 Ma, uppermost Eocene).

4.4.2 Correlations between rock record/sampling and fossil record

The synchronicity of both rock/sampling proxies and the originations and extinctions data (Figure 4-1) is borne out by the formal correlations (Table 4-1) and these remain highly significant both after first differencing and generalized differencing. Stage duration is weakly but still significantly correlated with originations and extinctions, while of the rock and sampling proxies only HBF has a significant relationship with it. Originations and extinctions ($Orig^+$ and Ext^+) per stage are significantly correlated and the relationship holds, although is weakened, when single interval taxa are removed ($Orig^-$ and Ext^-).

Table 4-1 Spearman rank correlations between time series using raw values and after first differencing and generalized differencing. Orig$^+$ = originations including single-interval taxa, **Orig$^-$** = originations excluding single-interval taxa, **Ext$^+$** = extinctions including single-interval taxa, **Ext$^-$** = extinctions excluding single-interval taxa, **HBF** = Hexapod-Bearing Formations recorded in the present dataset, **HBC** = Hexapod-Bearing Collections in the Paleobiology Database, **NEW RT** = hexapod range-through richness curve presented in Chapter 3, **Time** = stage midpoints as Ma (i.e. positive values) going from oldest (highest) towards the present (youngest). Significance assessed using bootstrapping. ***** = significant at 95% confidence limit, ****** = significant at 99% confidence limit.

	Orig$^+$	Orig$^-$	Ext$^+$	Ext$^-$	HBF	HBC	NEW RT	Time
Raw values								
Stage duration	.408**	.390**	.368**	.265*	.334**	.230	-.251	.301*
Orig$^+$			.829**		.778**	.839**	-.139	.269*
Orig$^-$				.597**	.737**	.816**	-.033	.145
Ext$^+$	–				.691**	.681**	-.307*	.440**
Ext$^-$		–			.596**	.555**	-.246	.355*
HBF	–	–	–	–		.772**	-.120	.233
HBC	–	–	–	–	–		-.001	.121
NEW RT	–	–	–	–	–	–		-.979**
First difference								
Orig$^+$			.766**		.586**	.783**	.852**	
Orig$^-$				.543**	.587**	.733**	.792**	
Ext$^+$	–				.422**	.761**	.875**	
Ext$^-$		–			.347*	.629**	.756**	
HBF	–	–	–	–		.661**	.523**	
HBC	–	–	–	–	–		.752**	
Generalized difference								
Orig$^+$			.751**		.694**	.830**	.493**	
Orig$^-$				.438**	.562**	.749**	.333*	
Ext$^+$	–				.625**	.716**	.746**	
Ext$^-$		–			.477**	.519**	.683**	
HBF	–	–	–	–		.711**	.516**	
HBC	–	–	–	–	–		.461**	

Partial Spearman correlations indicate a strong correlation between originations/extinctions and the rock/sampling proxies, even when stage duration is taken into account, while with stage duration the relationship is much weaker when the rock/sampling proxies are taken into account (Table 4-2).

Table 4-2 Partial Spearman correlations between originations, extinctions, rock/sampling proxies and stage duration. Bold text indicates which variable is being controlled for in each set of correlations.

	Orig$^+$	Orig$^-$	Ext$^+$	Ext$^-$
Stage duration				
HBF	.745	.699	.649	.528
HBC	.838	.810	.659	.527
HBF				
Stage duration	.250	.226	.201	.096
HBC				
Stage duration	.406	.360	.297	.169

4.4.3 Modelling originations and extinctions

Cubic (third order polynomial) models were significantly better fits than the linear or quadratic models (according to the AIC$_c$ values) while showing the decrease in accumulation of taxa with further sampling typical of species-area curves, which the higher order polynomials did not, so cubic models are used for all combinations (Figure 4-4, Figure 4-5). Square root transformation of the variables before model fitting allowed a better fit with lower order polynomials except for extinctions inclusive of single interval taxa (Figure 4-5 A, D). Model-predicted values were back-transformed where necessary. In originations (Figure 4-4), the model fits are better at lower values where the majority of data points reside. As extinctions are generally lower than originations, allowing a negative intercept for the models may have provided a better fit (Figure 4-5), although necessitating a lower threshold of zero for the predicted values, but the decision was made to treat both sets of data the same. Use of the HBC sampling proxy returns generally tighter range of variation, notably reducing the Priabonian (35.55 Ma) origination spike in the model residuals.

To test the effectiveness of the models at removing rock record/sampling signal, the model residuals are correlated with originations, extinctions and the relevant rock/sampling proxies (Table 4-3). All the comparisons of model residuals with rock/sampling proxies show weak negative correlations. For HBC, only three of the 12 correlations performed against model residuals were significantly different from zero and only at the 95% confidence limit. For HBF, eight out of 12 correlations are significantly different from zero, two of which at the 99% confidence limit. In general, model residuals from HBF-derived models retain a significant positive relationship with observed originations and extinctions while residuals from the HBC-derived models do so much less.

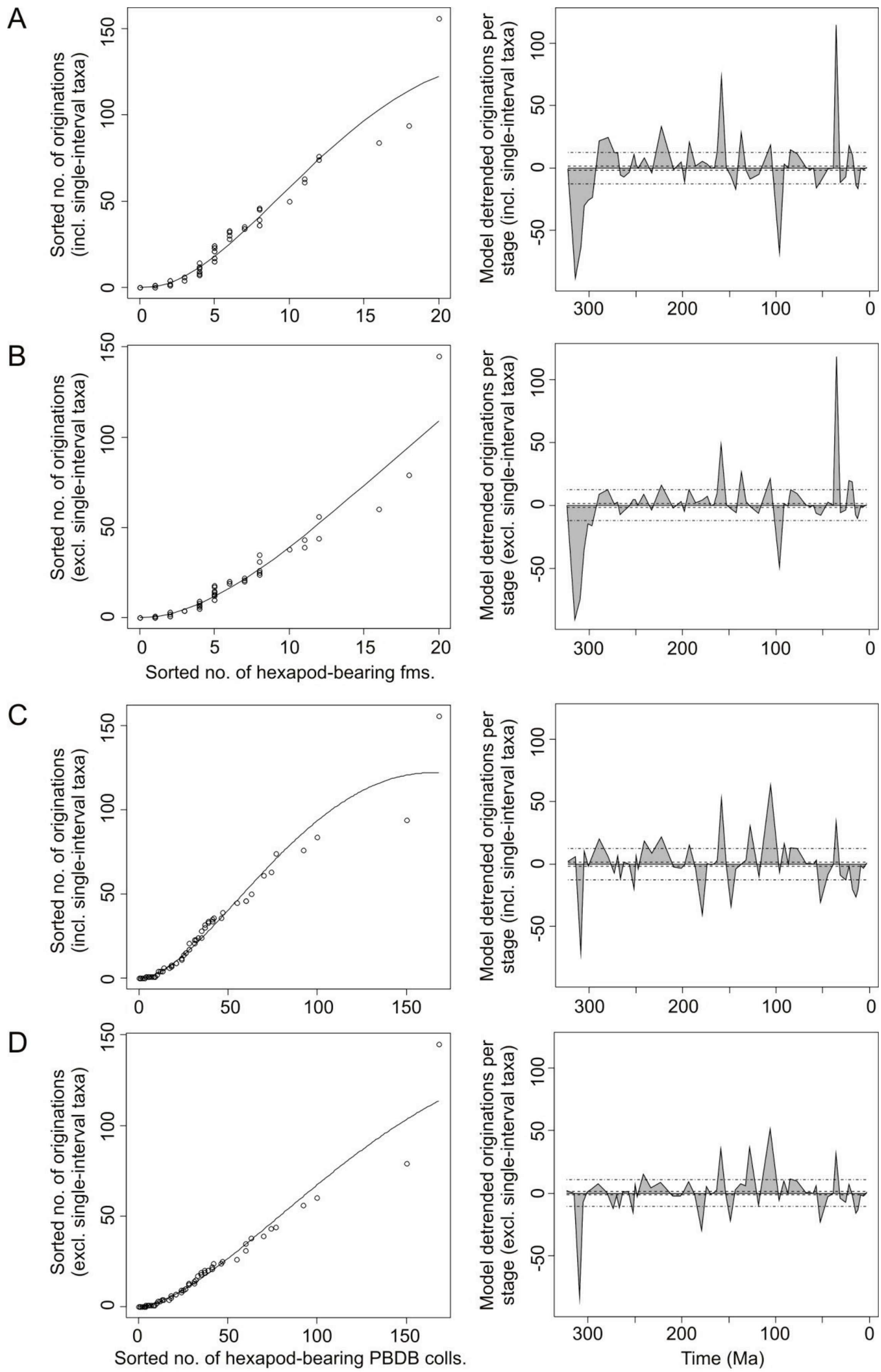

Figure 4-4 A–D Modelled originations. Independently sorted variables and the model fit applied (left), with model residuals (observed – predicted) plotted with 95% confidence limits (right). Inner dashed line = 1.96 standard errors of the modelled mean, outer dot-dashed line = 1.96 standard deviations of the modelled mean. Square-root cubic models, back-transformed.

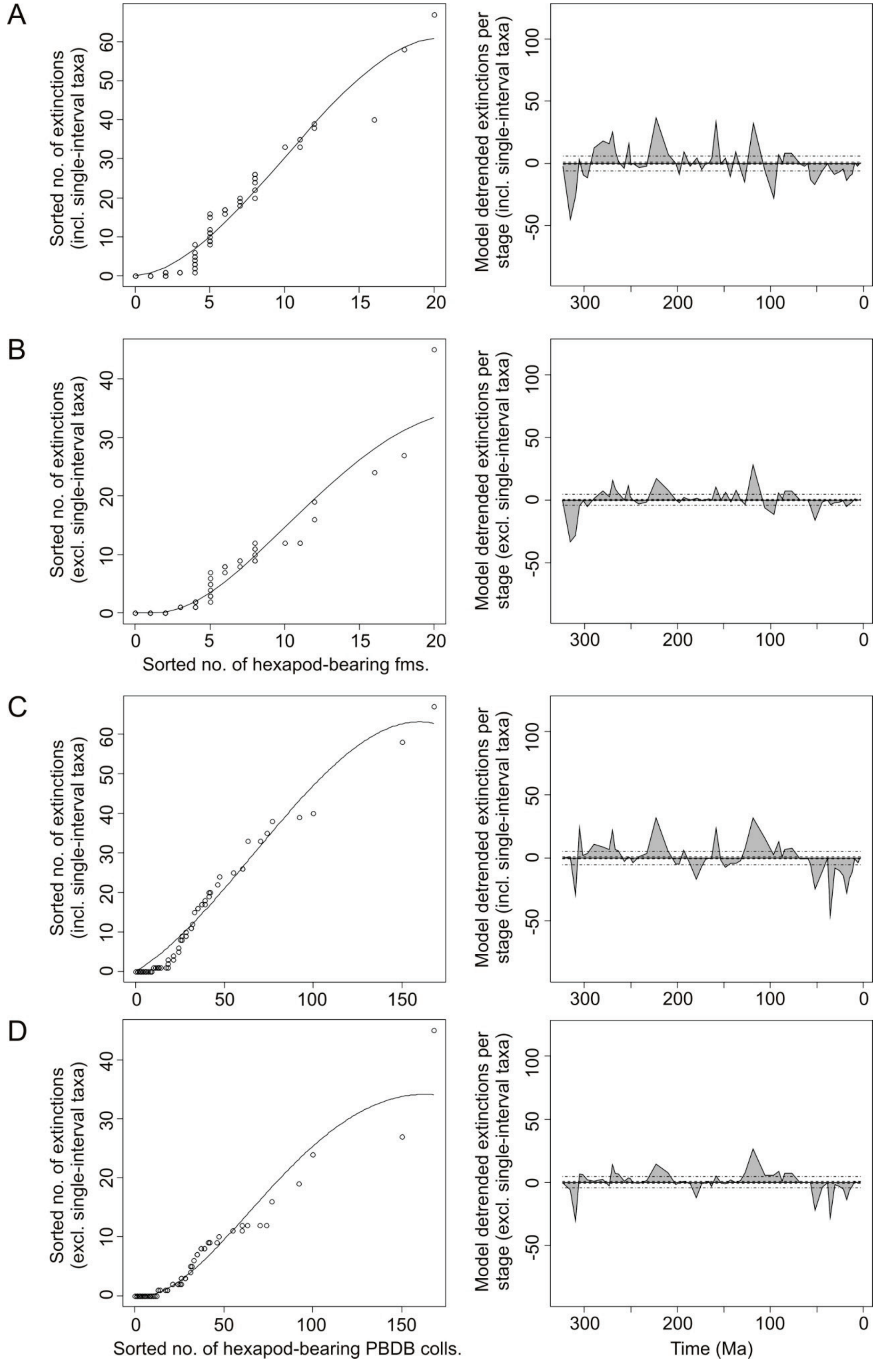

Figure 4-5 A–D Modelled extinctions. As for Figure 4-4, except for **A** and **D**, for which the data were not square root transformed before model fitting.

Table 4-3 Relationship between model residuals and fossil and rock records. Residuals of observed minus rock record-predicted values for originations (with and without single interval taxa; **Orig$^+$**, **Orig$^-$**) and extinctions (with and without single interval taxa; **Ext$^+$**, **Ext$^-$**), modelled with either hexapod-bearing formations (**HBF**) or Paleobiology Database collections (**HBC**). Spearman's rank correlation with bootstrapped significance measures. * = significant at 95% confidence limit, ** = significant at 99% confidence limit.

	Orig$^+$	Orig$^-$	Ext$^+$	Ext$^-$	HBF	HBC
Model residuals						
Raw values						
Orig$^+$ HBF	.272				-.307*	
Orig$^+$ HBC	.244					-.223
Orig$^-$ HBF		.377**			-.258	
Orig$^-$ HBC		.326*				-.181
Ext$^+$ HBF			.356*		-.332*	
Ext$^+$ HBC			.481**			-.163
Ext$^-$ HBF				.408**	-.411**	
Ext$^-$ HBC				.560**		-.244
First difference						
Orig$^+$ HBF	.549**				-.177	
Orig$^+$ HBC	.280					-.244
Orig$^-$ HBF		.554**			-.160	
Orig$^-$ HBC		.356*				-.230
Ext$^+$ HBF			.603**		-.317*	
Ext$^+$ HBC			.262			-.297
Ext$^-$ HBF				.627**	-.366*	
Ext$^-$ HBC				.322*		-.382*
Generalized difference						
Orig$^+$ HBF	.298*				-.294*	
Orig$^+$ HBC	.211					-.267
Orig$^-$ HBF		.463**			-.255	
Orig$^-$ HBC		.379*				-.177
Ext$^+$ HBF			.425**		-.313*	
Ext$^+$ HBC			.306*			-.300*
Ext$^-$ HBF				.444**	-.425**	
Ext$^-$ HBC				.476**		-.290*

4.4.4 Adjusted richness estimates for fossil Hexapoda

Richness estimates derived from both sampling proxies using the Orig$^-$ and Ext$^-$ data produced curves with multiple large excursions into supposedly 'negative' richness and so are not considered further. With the Orig$^+$ and Ext$^+$ data, only a single stage gave problematic results. In the Santonian (observation point at 84.65 Ma, Late Cretaceous), observed origination and extinction values fall only slightly outside 1.96 standard deviations from the mean modelled values, that imply an increase in richness to levels not known even in the extant fauna. This notable excursion cannot be justified from the paucity of data known from that stage, and is likely to be a Type I error (an incorrect positive result). The ratio of observed to expected values for this stage is therefore set to the default of 1.

Compared with the observed range-through richness curve, both rock/sampling proxy adjusted estimates share the same upward trend towards the Recent although ultimately achieving a higher richness than observed from the fossil record alone (Figure 4-6). The HBC$^+$-adjusted curve shares less short-term variation with NEW RT (Spearman's rho = 0.379**) in the first differences compared with the same correlation for HBF$^+$-adjusted curve (rho = 0.565**). Neither correlate significantly with the observed boundary-crosser richness (NEW BC) in the first differences (Table 4-4), although a weak relationship is recovered from generalized differencing (Table 4-4). None of the adjusted richness estimates (with or without single interval taxa) show any correlation with either of the sampling proxies using raw data, first differences or generalized differences (Table 4-4).

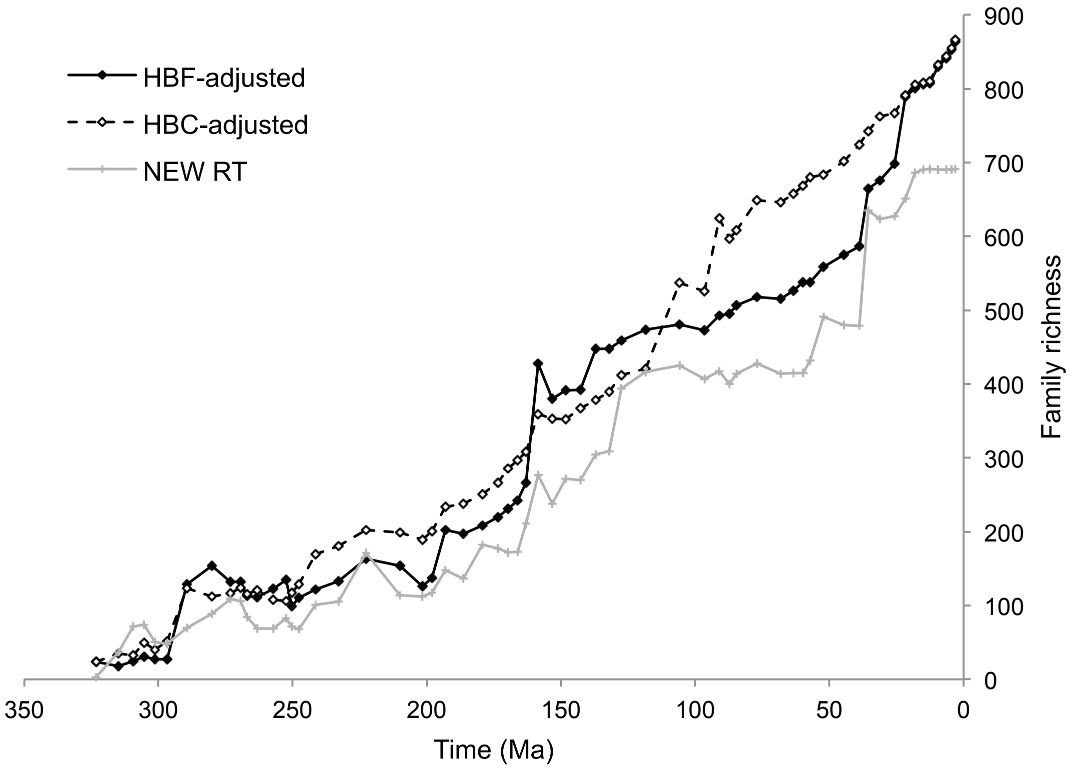

Figure 4-6 Rock record/sampling-adjusted richness estimates for fossil hexapod families. HBC-adjusted = richness estimate adjusted for Hexapod-Bearing Collections in the Paleobiology Database, **HBF-adjusted** = richness estimate adjusted for Hexapod-Bearing Formations contributing to the observed family range data used here, **NEW RT** = the observed hexapod family Range-Through curve. Time series derived from datasets inclusive of single interval taxa.

Both adjusted richness estimates show greatly subdued peaks in the Carboniferous compared with observed (section preceding 300 Ma) while the peaks in the Permian (~300–250 Ma) occur earlier than observed. The shallower decline towards the end-Permian in the HBC-adjusted curve compared with NEW RT is contrasted with an increase followed by a sharp drop in the HBF-adjusted curve. A decline in richness through the Late Triassic (~225–200 Ma) is common to all three curves while a Late Jurassic (Oxfordian, 158.4 Ma) spike is shown in all three curves to varying extents. A mid–Late Cretaceous ‘plateau’ starting from the Barremian (127.5 Ma) seen in NEW RT is not replicated in either corrected curve. Large jumps at the Ypresian (52.2 Ma) and Priabonian (35.55 Ma) seen in NEW RT are likewise not replicated in HBC-adjusted and only the latter by HBF-adjusted, albeit slightly less pronounced. The final plateau at end of NEW RT towards the present is seen instead as a steady increase in the adjusted curves.

Table 4-4 Relationships between hexapod family richness estimates derived from models including ($^+$) or excluding ($^-$) single-interval taxa, for measures adjusted using Hexapod-Bearing Formations (**HBF**) and Hexapod-Bearing Collections (**HBC**) sampling proxies. **NEW RT** = the observed hexapod family range-through richness curve, **NEW BC** = observed hexapod family range-through richness at interval boundaries (geometric mean of upper and lower boundaries for each stage calculated for correlations). Spearman's rank correlation with bootstrapped significance levels. * = significant at 95% confidence interval, ** = significant at 99% confidence interval.

	HBC$^+$	HBC$^-$	HBF	HBC	NEW RT	NEW BC
Adjusted richness estimates						
Raw values						
HBF$^+$	.987**		-.219		.986**	.988**
HBC$^+$				-.177	.983**	.995**
HBF$^-$		.919**	-.148		.683**	.675**
HBC$^-$				-.058	.693**	.668**
First difference						
HBF$^+$	.457**		-.026		.565**	.193
HBC$^+$				-.083	.379**	.257
HBF$^-$		.484**	-.018		.472**	.292*
HBC$^-$				-.101	.269	.391**
Generalized difference						
HBF$^+$	.590**		.099		.645**	.309*
HBC$^+$				-.001	.464**	.362*
HBF$^-$		.639**	.119		.676**	.560**
HBC$^-$				-.047	.476**	.595**

4.4.5 Rates of origination and extinction

Using the sampling proxy-adjusted origination and extinction data, per-million year rates of origination and extinction are calculated from the corresponding adjusted richness estimate curves (Figure 4-7). The three sets of values for originations (A) and extinctions (B) are largely synchronous. All show the highest rates in the Palaeozoic (pre- ~250 Ma) along with the highest range of variation. The peaks of origination and extinction around the Permo-Triassic boundary at 251 Ma bear highlighting. The peaks in origination around that transition for all three occur in the Induan (the first stage in the Triassic), although this is only a slight increase from the Changhsingian (last stage in the Permian) in the observed rate; and the peaks in extinction rate for all three occurs in the Changhsingian.

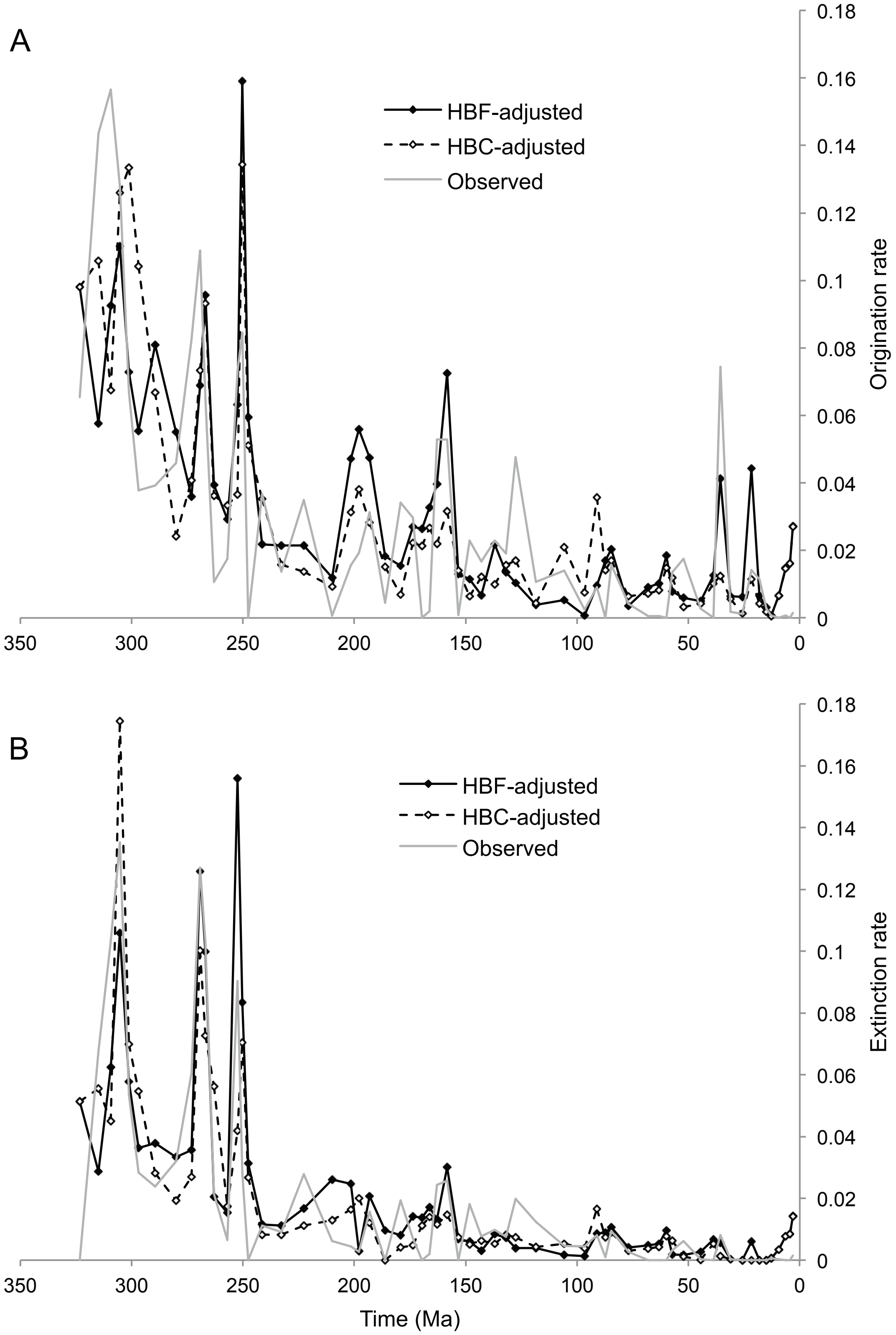

Figure 4-7 Per-million year rates of A) origination and B) extinction of hexapod families in the fossil record. HBF-adjusted rates derived from data adjusted for rock record influence based on a model of Hexapod-Bearing Formations. **HBC-adjusted** rates derived from data adjusted for sampling influence based on a model of Hexapod-Bearing Collections in the Paleobiology Database.

4.5 Discussion

The issue of biases in the fossil record, and how to best correct for them, has provoked much debate (Benton *et al.*, 2011). Until now, no attempt has been made to correct for such biases in the fossil record of hexapods. Here, strong correlations are reported between observed hexapod originations and extinctions and two separate proxies, one for rock amount and another for sampling. Using these proxies, a modelling approach is used to correct for their influence on apparent originations and extinctions, which are then used to derive 'corrected' range-through richness curves. These corrected curves show important differences from previous uncorrected curves.

Strong correlations exist between counts of originations, extinctions and rock record/sampling proxies. There is no such correlation with the raw richness data, although positive correlations exist with the differenced time series. Such associations have in the past been the main evidence used to argue for an attempt at removing the influence of the rock record and sampling on apparent richness in the observed fossil record (Raup, 1972; Smith and McGowan, 2011). The fact that associations are strongest with originations and extinctions but not richness is expected on two counts; first, that the richness data are range-through data, rather than direct counts per stage. Hence, originations and extinctions, which are direct counts, should be more sensitive to rock record changes and sampling than richness is. Second, hexapod fossils, and arthropods in general (Wills, 2001), require exceptional preservation conditions compared to many other taxa (Grimaldi and Engel, 2005), so that both first and last occurrences would be expected to cluster strongly in stages where such conditions are more common. The fact that first and last occurrences correlate so well with each other could mean two things. First, they could be biologically and causally associated, such as through density-dependent controls on diversity (Alroy, 2008). However, the fact that they also both correlate so well with the rock record suggests that this is mainly an artefact of the rock record variation. The fact that there is no obvious lag between origination and extinction, as commonly seen in the marine record (Kirchner and Weil, 2000; Alroy, 2008), suggests further that the rock record is the major control. Although stage duration does correlate significantly with origination and extinction counts, this is much weaker than the association with rock record and sampling, and may simply reflect a coincident trend for stage duration, and originations and extinctions, to decrease through time. A comprehensive analysis of causation in these variables (e.g. Hannisdal and Peters, 2011) is, however, beyond the scope of this thesis.

Using the modelling approach of Smith and McGowan (2007) and Lloyd (2012), expected values of origination and extinction given the observed certain rock record and sampling for a stage were estimated. A novel step taken here is to estimate corrected originations and extinctions, rather than richness directly, and use these adjusted time series to estimate how richness would appear if sampling opportunities were equal across all stages. The resulting adjusted richness estimates both share an approximately linear increase towards the recent, with some short-term variation around this trend. A linear increase is very much the default expectation given that cumulative richness is estimated by adding on the mean originations and extinctions for each stage, adjusting them according to deviations from expectation based on the rock record (see Methods). In principle, long periods with relatively high adjusted originations or extinctions could have been seen, giving rise to substantial deviations from a linear increase. However, there is little evidence for such deviations once the rock record is corrected for.

Previous, uncorrected richness curves (Labandeira and Sepkoski, Jr., 1993; Jarzembowski and Ross, 1996; Ross *et al.*, 2000; Chapter 3) have suggested, variably, peaks in richness in the Carboniferous and Permian, an end-Permian extinction, a Late Triassic peak, a Late Jurassic peak, a plateau in the Cretaceous–Palaeocene and a sharp increase in the Eocene. Our corrected richness curves suggest which of these apparent features are most robust and which are more suspect and likely due to sampling bias. The most obvious suspect features are the Cretaceous plateau and Eocene jump. The latter has long been suspected to be due to the occurrence of Baltic amber and Florissant Shales (Labandeira and Sepkoski, Jr., 1993), whilst the Late Cretaceous and Palaeocene are relatively deposit-poor. Whilst a reduced Eocene jump is still present in the HBF adjusted curve, it disappears almost entirely from the HBC-adjusted curve, which probably better controls for the exceptional sampling by virtue of recording collections rather than just deposits: Baltic Amber appears as just a single deposit but is responsible for a huge number of fossil insects and many collections (Weitschat and Wichard, 2002). The Cretaceous–Palaeocene plateau is also less evident and disappears completely from the HBC adjusted curve, suggesting again that it is largely accountable to changes in the rock record and intensity of sampling. The apparent Carboniferous peak in insect richness, after Romer's gap (Ward *et al.*, 2006), coinciding with the first winged insect fossils, also coincides with abundant fossil bearing deposits, suggesting that a peak in richness may also be more apparent than real. Finally, there is little evidence for a decline in richness at the end-Permian, although origination and extinction rates were probably very high then, suggesting high turnover rather than a substantial or long-term loss in richness.

In contrast, evidence is retained for the presence of a Permian peak in richness, coinciding with the radiation of Palaeoptera and Polyneoptera (Chapter 3), a Triassic peak, coinciding with radiations in all major hexapod groups, and an end-Triassic loss of families, again across all groups. A Late Jurassic radiation is also retained. These features deserve greater focus in the search for biological explanatory causes. Many of these inferences are supported by the examination of the relative extent of originations and extinctions in a stage (Figure 4-3). The Roadian shows a high number of extinctions relative to originations and forms part of the decline after the Permian richness peak (Figure 4-6). Similarly, the Kasimovian has more extinctions than originations and coincides with the richness low before the Permian rise. The Oxfordian represents the Late Jurassic rise in richness and represents a time of high availability of fossils and high number of first occurrences but low number of last occurrences. The Priabonian however, representing a large number of originations compared to extinctions, is probably heavily influenced by the Pull of the Recent (see below).

The Pull of the Recent is the tendency for the ranges of fossil taxa to be pulled forwards towards the present, inflating apparent richness in range-through datasets (Alroy, 2010*c*). In the present data, this tendency probably derives mainly from the influence of extant taxa, which do not have their last fossil occurrence recorded. The Lyellian survival plot (Figure 4-2) illustrates the potential effect of this pull by showing the proportion of taxa in a stage which are extant. In the Paleozoic, only a couple of taxa are extant. By the Early Cretaceous however, over half of the taxa in a stage are extant. If they had had their last fossil appearance recorded in the same way that other taxa had, it is likely that extinction rates would appear higher and taxonomic richness nearer the Recent would appear lower. A critical issue is how well sampled the Recent fauna would be in the various Cenozoic stages (Jablonski *et al.*, 2003). The Pliocene contains relatively few fossil insect bearing deposits but earlier, in the Miocene to late Eocene (Figure 4-1), are some of the most productive deposits which would likely form the last fossil occurrence of many taxa. From this time the raw record suggests that richness rose by about 40%, suggesting a substantial Pull of the Recent which our “corrected” richness curves do not control for.

The corrected origination and extinction rates indicate, like the uncorrected rates (Chapter 3), a decline in rates through time. This may partly reflect the Pull of the Recent which elevates richness near the Recent, as well as depressing last occurrences, but given the great temporal extent of the decline, is unlikely to be the sole cause. This issue is addressed further in later chapters. The adjusted rates suggest much higher turnover in taxa at the end-Permian than suggested by previous measures, suggesting that this is a robust feature of the insect record, in contrast to an overall drop in richness. A Late Permian extinction does feature in the corrected numbers of extinctions (Figure 4-5, right hand column), but not universally or very prominently. One possible reason is that it is only obvious once standing richness and stage duration are taken account of in the rate calculation. The comparison of observed and expected originations and extinctions (Figure 4-4 and Figure 4-5, right hand columns) (Mayhew *et al.*, 2012) also suggest relatively low turnover in the Carboniferous, Triassic, Middle Jurassic and Cretaceous, consistent with the corrected richness curves.

The corrected richness curves presented here are a first attempt to control for sampling bias in the insect fossil record. Whilst interesting, and suggesting new avenues of research, they could probably be improved upon. One approach, beyond the scope of the present thesis, would be to implement standardized subsampling (Alroy, 2010*a*, 2010*b*, see 2010*c*). One problem might be that the sampling intervals might have to be quite large to cover sufficient collections and another might be heterogeneity in the preservation conditions leading to bias in the apparent collection curves. Staying with the modelling approach, the current methodology was unsuccessful with data that omitted singleton interval taxa because the implied rates sometimes forced richness to become negative. Even with the full data, errors in the rate estimates are likely and can lead to implausible richness estimates, such as found in the Santonian here (see Results). The method also assumes that the rock and sampling proxies capture the essential biases, which need to be controlled for, which may not be the case (Benton *et al.*, 2011), and that the relationship of originations and extinctions to rock proxy variation is constant through time (see Smith and McGowan, 2007). Other modellers may also take alternative, defensible, views on the best way to model this relationship, particularly on the necessity of pre-transformation of the data, and on the degree to which higher-order polynomial functions should be tolerated. Finally, although we do not use the modelling approach on richness data, extinctions may still be prone to Pull-of-the Recent and may distort the relationship between the rock proxy and observed extinctions. None of these issues have simple solutions but this work serves to highlight them for future attention. For the present, the adjusted richness, origination and extinction time series provide first-pass attempts to test the robustness of various features of the record and are used in subsequent chapters to test various further hypotheses on insect macroevolution.

Chapter 5

Associations between environmental factors and the hexapod fossil record

5.1 Abstract

The Red Queen (biotic drivers) and the Court Jester (abiotic drivers) represent two competing paradigms about the environmental control of macroevolutionary processes. The relative importance of these paradigms has never been explicitly tested for the hexapods, which constitute more than half of all described extant species. Here, the Red Queen paradigm is tested by looking for changes in the long term rate of accumulation of fossil families, indicating density dependent growth of the clade, as well as testing for associations in the short term variation in richness, origination and extinction. Associations between plant and hexapod richness are also tested. The Court Jester is tested by associations between a number of potential environmental drivers, including temperature, atmospheric and isotopic variables. The growth rate of hexapod family richness appears to have significantly slowed through time, and short term increases in hexapod richness, after adjustment for sampling bias, tend to reduce future origination, consistent with density-dependent processes. Increases in plant family richness are associated with higher hexapod extinction and lower family richness. Several potential abiotic drivers are identified, though the important drivers are different before and after adjusting for sampling bias in the hexapod record. In unadjusted data, higher richness is associated with periods of low temperature, high atmospheric oxygen concentrations, and seas rich in organic nutrients, whilst after adjusting for sampling bias, high richness is associated with high sea levels, and high marine productivity. Overall the new hexapod data are consistent with a joint model in which both biotic and abiotic forces influence hexapod macroevolution.

5.2 Introduction

It has long been recognized that environmental forces play an important role in shaping macroevolution. As well as helping us to understand the past history of life on Earth, comprehending the role of such forces in changing taxonomic richness, and rates of speciation or extinction, is likely to help us to predict the consequences of current environmental change, and the possible future of life on Earth (Alroy, 2008; Mayhew, 2011). In this chapter we use data on the family-level richness, origination and extinction of fossil hexapods through time (Chapters 3 and 4) to attempt to identify environmental variables associated with changes in insect macroevolution.

The Red Queen paradigm in palaeontology (Van Valen, 1973) proposes that biotic forces are the major control on macroevolution, acting through ecological interactions. Originally proposed from observations of a relatively constant risk of extinction through time, and generally attributed to the ever-present forces of predation and parasitism, the paradigm has been extended to incorporate any biotic force acting on any macroevolutionary variable (Benton, 2009). For example, predation intensity has been suggested to control taxonomic richness through time (Huntley and Kowalewski, 2007) as well as just extinction. Observations on the long term slow-down in the rate of accumulation of fossil taxa through time in marine invertebrates have been used to infer density-dependent models of macroevolution (Kitchell and Carr, 1985), implying a role for competition between taxa (Benton, 1997). More recently, evidence has accumulated for shorter term feedbacks between richness, origination and extinction in marine taxa (Alroy, 2008; Ezard *et al.*, 2011), again implying density-dependent competition between taxa. However, range-through data for terrestrial taxa have failed to provide such compelling support for density-dependence (Benton, 1997, 2010).

As well as biotic variables, abiotic variables have a, now well-established, role in explaining the history of life. The Court Jester paradigm (Barnosky, 2001) was erected as a contrast to the ever-present biotic forces, in which extraneous abiotic forces such as bolide impacts had more episodic effects (e.g. Arens and West, 2008). A number of abiotic forces have been proposed to be important in the marine realm, including sea level changes (Purdy, 2008; Alroy, 2010*b*; Hannisdal and Peters, 2011), nutrient availability (Cárdenas and Harries, 2010), plate tectonic events (Valentine and Moores, 1970), volcanism (Wignall, 2001), and global climate (Mayhew *et al.*, 2008, 2012).

Whilst it remains common for palaeontological studies to address the effects of single environmental variables, few have considered multiple variables simultaneously, and it therefore remains difficult to effectively assess their relative influence in a balanced way. Benton (2009) has suggested that the Red Queen may dominate over smaller spatial and temporal scales whilst the Court Jester dominates over larger scales. However, in multivariate analyses, Ezard *et al*. (2011) found that both biotic and abiotic forces influence the long term evolution of marine forams, affecting alternative macroevolutionary variables differently. Mayhew *et al*. (2012) found similar results in a large analysis of marine invertebrates.

Insect macroevolutionary work has been dominated by studies of extant taxa (Mayhew, 2007) and suggests that biotic forces are likely to have played a very important role in speciation. Comparative studies indicate that interactions between insects and plants have generated large fractions of terrestrial biodiversity (e.g. Mitter *et al.*, 1988; Farrell, 1998). No statistical studies have been performed linking plants with fossil insect diversity, although Labandeira and Sepkoski (1993) noted no apparent increase in the accumulation of fossil families during the radiation of the angiosperms. Indeed, Jarzembowski and Ross (1996) noted an increase in extinction of insect families in the Cretaceous, which they suggested was due to the replacement of gymnosperm and pteridophyte communities by angiosperms, with consequent turnover of insect families. Other indications of Red Queen effects on fossil insects come from the general increase in insect mouthpart diversity concurrent with that of richness (Labandeira, 1997), perhaps indicating that the widening of insect trophic interactions played an important role. Also, Labandeira and Sepkoski (1993) suggested that the growth of insect families through time had been close to exponential, although showed some deviation in a logistic direction nearer to the Recent. Consistent with the exponential model, Eble (1999) showed that insect originations were independent of the richness of families, unlike in many marine taxa. Conversely, Davis *et al*. (2011) used phylogenetic trees to infer gaps in the fossil record of Odonatoidea and described a more logistic growth of the clade as a result of this infilling.

There has been much less work on possible abiotic variables that might have contributed to insect diversity. Geographically, many insect groups are richer in the tropics (Mayhew, 2007), and this reflects differences in net diversification rate with latitude (Cardillo, 1999), which are likely ultimately influenced by regional climate. However, no such studies have yet been repeated in the temporal dimension. It has long been noted that the initial radiation of winged insects in the Carboniferous coincided with a rise in atmospheric oxygen concentrations and the rise of both flight and large body size has been attributed to such changes (Clapham and Karr, 2012).

In this Chapter, possible environmental controls on the family level insect fossil record, outlined in Chapters 3 and 4, are investigated. Biotic controls are tested over long time scales by testing for exponential clade growth, as well as by searching for shorter-term associations between richness, origination and extinction. Furthermore, associations between the family level record of plants and insects are tested. The possible effects of a variety of abiotic predictors, including temperature and atmospheric oxygen concentrations, are also assessed. Analyses are also performed that consider all variables simultaneously, allowing as far as possible, a balanced assessment of the Red Queen and Court jester paradigms for the long term history of insects.

5.3 Methods

5.3.1 Data

Fossil data, representing the response variables in our analyses, included the number of hexapod fossil families from the new family-level range-through dataset (NEW RT) (Chapter 3), representing the complete and unaltered data; boundary-crossers from the same dataset (NEW BC) (Chapter 3), representing a more robust but less complete richness measure; Foote's (2000) $\hat{p}$ (origination) and $\hat{q}$ (extinction) rate metrics from the NEW observed data (Chapter 3.3.3); the adjusted richness estimate after accounting for the number of hexapod-bearing collections (HBC RT); and the HBC-adjusted origination and extinction rates (Chapter 4.3.6).

As explanatory variables we used the richness of fossil plant families (range-through) published in Benton (1993) with the data downloaded from http://www.fossilrecord.net/fossilrecord/index.html. Although the plant fossil record has undergone important revisions since the publication of that dataset (Cascales-Miñana and Cleal, 2012), it remains the only comparable stage-level dataset easily available. In addition to this potential biotic driver, the hexapod richness, origination and extinction rate variables above were also sometimes included as drivers, under the hypothesis of density dependence.

Several abiotic, 'Court Jester' environmental variables were also tested as potential drivers of hexapod diversity dynamics. These included several widely-used marine isotopic time series: $^{87}Sr/^{86}Sr$, $\delta^{34}S$, $\delta^{18}O$, $\delta^{13}C$, as well as measures of eustatic sea level, partial pressure of atmospheric oxygen (ppO_2), the ratio of carbon dioxide in the atmosphere relative to today (RCO_2) and seawater temperature. The $^{87}Sr/^{86}Sr$, $\delta^{34}S$, $\delta^{18}O$ and $\delta^{13}C$ data are after Prokoph *et al*. (2008), arranged into per-stage averages and provided by Dr Mark Bell. The $^{87}Sr/^{86}Sr$ ratio is generally considered to reflect continental weathering (Purdy, 2008; Cárdenas and Harries, 2010) and mid-ocean ridge activity (Hannisdal and Peters, 2011). $\delta^{34}S$ is often considered an indicator of organic nutrient content in the oceans and shelf redox conditions (Cárdenas and Harries, 2010; Hannisdal and Peters, 2011), and is included here under the general understanding that the oceanic and terrestrial environments interact, hence changes in the relevant processes in the ocean may reflect changes on land. In addition, it is interesting to ask if similar variables can be correlated with both marine and terrestrial faunas as this may help infer causality. Likewise, $\delta^{18}O$ is an inverse indicator of seawater temperatures, although likely reflects terrestrial surface temperatures as well. $\delta^{13}C$, an indicator of oceanic primary productivity, is included for the same reasons as $\delta^{34}S$. The eustatic sea level curve is a composite of those presented in Haq *et al*. (1987) and Haq and Schutter (2008) to cover the desired time interval. Oxygen partial pressure was taken from Clapham and Karr (2012), itself derived from Berner (2009), with the present-day value added to the end of the series in order to cover the desired time interval. RCO_2 data is taken from the GEOCARB III model (Berner and Kothavala, 2001), provided to Peter Mayhew courtesy of Dana Royer. The temperature variable is an estimate of low latitude shallow-sea temperatures from the red curve in figure 4 of Royer *et al*. (2004), again provided to Peter Mayhew courtesy of Dana Royer, in degrees Celsius relative to today. This is derived from $\delta^{18}O$ measurements but with a correction for the effects of changing seawater pH (Royer *et al.*, 2004).

As additional explanatory variables we included rock-record and collections-record data: the hexapod-bearing formations (HBF) and hexapod-bearing collections (HBC) counts per stage (Chapter 4), since these were shown to be important predictors of the observed hexapod fossil record.

5.3.2 Data transformations

Data intended for use in pairwise correlations (5.3.3) and multiple regression analysis (5.3.4) were treated as follows. It is preferable for time series analyses to be conducted on evenly-spaced sampling intervals (Mayhew *et al.*, 2012). This was achieved by generating interpolated series with Akima splines (Akima, 1970) using the `aspline()` function from the `Akima` library in R, which is then resampled at even sampling intervals. In this case, all series were resampled every 5 Myr (from 320 to 5 Ma) as this allows for almost the same number of data points as in the original hexapod richness dataset (from Serpukhovian to Recent), hence does not artificially alter power, and lies between the modal and mean stage lengths in the series (4.5 and 5.34 Myr, respectively). Many of the series are bounded by zero so it was necessary to impose a lower threshold for $\hat{p}$ and $\hat{q}$ rates as well as counts of hexapod-bearing formations and collections, as some points dropped below this (although due to the mean standardization performed later, this probably would have had a negligible effect). The datasets are then transformed to normalize them if necessary (commonly log or square root, Table 5-1) and detrended using smoother splines to remove longer term (~100 Myr or greater) patterns. The removal of long term patterns is necessary because they can lead to spurious correlations between unrelated variables. The appropriate spline was chosen from examining autocorrelation plots of the residuals of a number of potential detrenders, whose sensitivity to short term patterns in the data is reflected in the degrees of freedom (d.f.) of the spline, with larger numbers of d.f. reflecting greater sensitivity to short term patterns (Table 5-1). The detrended series were then mean-standardized so that they are all on the same scale for plotting and to aid assessment of statistical coefficients.

Table 5-1 Transformations and detrenders applied to each variable before mean-standardizing, and the resulting *p*-value from the Shapiro-Wilk normality test.

Variable	Transformation	Detrender spline (d.f.)	*p*-value
NEW RT	None	5	0.753
NEW BC	None	3	0.543
HBC RT	None	7	0.358
$\hat{p}$ (origination) rate	Fourth root	3	0.334
$\hat{q}$ (extinction) rate	Fourth root	7	0.954
HBC-adjusted origination rate	$\log_{10}$	7	0.992
HBC-adjusted extinction rate	Cube root	5	0.068
$^{87}Sr/^{86}Sr$	None	7	0.678
$\delta^{34}S$	$\log_{10}$	5	0.136
$\delta^{18}O$	Squared	3	0.849
$\delta^{13}C$	$\log_{10}$, residuals squared	5	0.153
Eustatic sea level	Squared	5	0.112
ppO_2	None	5	0.411
RCO_2	Square root	5	0.156
Temperature	None	7	0.279
Plants	None	5	0.463
Hexapod-bearing formations	None	5	0.138
Hexapod-bearing collections	Square root	5	0.516

5.3.3 Pairwise correlations

Associations between variables were initially assessed with Pearson's product-moment correlation coefficient. As the data points in a time series are commonly serially autocorrelated, standard confidence intervals cannot be trusted and instead were estimated by bootstrapping of the test statistic (see 3.3.2). Correlations were performed for unlagged data as well as for lags (i.e. fossil predictor variables lagging behind explanatory variables) of 1 (5 Myr) and 2 (10 Myr) time steps.

5.3.4 Multiple regressions

Multiple regression analysis allows the simultaneous consideration of several explanatory variables against the response variable and can elucidate relationships not apparent in bivariate correlations. Models are constructed by stepwise subtraction from a full model containing only main effects, based on minimising the AIC (Akaike Information Criterion) (see Johnson and Omland, 2004) score, using the `step()` function in R. Once `step()` has removed as many terms as it can without increasing the AIC score, `drop1()` is used to check whether the removal of any further terms increases the AIC score by less than two and has a non-significant effect on the performance of the model (using an F test). This is done iteratively until no more terms can be removed without significantly reducing model performance.

The models produced include a mix of both biotic (Red Queen) and abiotic (Court Jester) variables, allowing the analyses to test the relevance of these competing paradigms. The response variables investigated are those listed in the first column of Table 5-1 from NEW RT to HBC-adjusted extinction rate. For each response variable, two biotic predictors are used (from richness, origination rate or extinction rate, depending on which is the response) as well as a suite of environmental predictors. Separate analyses are performed with unlagged data and with response variables lagged by 1 and 2 time steps. Biotic predictors for NEW/HBC RT at lags 1 and 2 are also lagged with respect to the environmental predictors, so are in step with the response variables. For $\hat{p}$ and $\hat{q}$ rates and HBC-adjusted origination/extinction rates, biotic predictors are not lagged with the response.

A potential problem with models involving many explanatory variables is the confounding influence of correlated explanatory variables, or multicollinearity, which makes it difficult to interpret whether the effects on the response variable represents a true relationship or a spurious correlation (Graham, 2003). Each set of variables were tested for multicolinearity by calculating the variance inflation factor (VIF) using the `vif()` function in the `car` package in R. A threshold VIF of 10 or above is generally seen to indicate unacceptably high covariance between explanatory variables (but see O'Brien, 2007). The simplest way to correct for this is to remove one of the variables or combine them into a single index. Here, temperature is left out of the models *a priori*, because the temperature data were derived from $\delta^{18}O$ data, and hexapod-bearing collections were used as the preferred fossil record proxy to hexapod-bearing formations, based on the results of pairwise correlations (

Table 5-2).

As for the bivariate correlations above, due to the non-independence of data in time series, confidence limits on the regression coefficients are calculated by bootstrapping of the regression coefficients.

5.3.5 Logistic vs. exponential growth

Density dependent clade growth (part of the extended Red Queen paradigm) can be detected by short term patterns in time series (Alroy, 2008) but also by long term patterns (Benton, 1995; Lane and Benton, 2003; Davis *et al.*, 2011). The long term expectation with exponential growth (the expansionist model without density dependence) is for logged richness to show a linear increase over time (Benton, 1997). Significant non-linearity, however, with a deceleration of richness increase through time, implies a more logistic (or equilibrial) growth pattern, reflective of density dependent growth (Davis *et al.*, 2011). To test whether logistic or exponential growth may have occurred in hexapods on the whole, the observed range-through richness (NEW RT) and hexapod-bearing collections adjusted (HBC RT) series are logged, then a comparison made of the fits of simple linear and quadratic regressions. As in the multiple regression models, model choice is informed by comparison of AIC scores and the more complex model (i.e. quadratic in this case) must be accompanied by a reduction of the AIC by more than 2 in order to be justified. Significant autocorrelation was present in the residuals of both datasets, detected using the Durbin-Watson test, so significance values for the model terms are calculated using bootstrapping as above.

Violation of model assumptions was tested graphically and the sensitivity of each model to outliers was assessed using Cook's distance. Highly influential points (those with a Cook's distance value greater than 0.5) were dropped to see if this affected the result. However, caution is advised when doing this with time series as outliers are real data in the series and may influence other data points. Despite this, if the results are the same after removal of outliers, then they may be considered robust.

Conducting many individual analyses increases the total risk of making a Type 1 error somewhere within the test family (Benjamini and Hochberg, 1995). However, it is not a simple process to account for this problem: it is somewhat arbitrary how to define the limits of the test family, and simple Bonferoni correction is notably over-conservative (Benjamini and Hochberg, 1995). It is further not simple to implement corrections for multiple comparisons when significance is estimated using the bootstrapping approach, as it is in our case. We therefore adopt a more descriptive approach to the problem by reporting only experiment-wise significance but also reporting the expected Type 1 error rate as a measure of the probability of false positives.

5.4 Results

5.4.1 Pairwise correlations

One hundred and ninety nine pairwise correlations of fossil data (columns) and environmental variables (rows) were performed (Table 5-2). By chance alone we would expect to find ten significant results at the 5% significance level: 38 are actually found, and many of these are highly significant. Overall, however, few of the bivariate correlations are strong. The strongest correlations are between the rock record and collections measures with richness (NEW RT) and $\hat{p}$ (origination) rate, with no lag (see Chapter 4). Of the other variables, plant family richness shows a negative correlation with HBC-adjusted richness (HBC RT), which diminishes with lagging, and also positively correlates with $\hat{q}$ (extinction) rates. $\delta^{18}O$ shows a weak positive correlation with observed richness (NEW RT and NEW BC) at no lag, and a negative correlation with HBC RT. $\delta^{13}C$ is positively correlated with HBC-adjusted extinction rates at lags of 1 and 2, and also with HBC-adjusted origination rates, and negatively correlated with HBC-adjusted origination rates at a lag of 2. Eustatic sea level is positively correlated with adjusted richness (HBC RT) and, although the strength of this relationship weakens at a lag of 1, it becomes stronger still at a lag of 2. This is in contrast to the relationship of sea level with observed richness (NEW RT and NEW BC) which is significantly negative at lags of 1 and 2.

NEW RT (observed richness) is strongly correlated with both $\hat{p}$ (origination) and $\hat{q}$ (extinction) rates (Table 5-3, upper left quadrant). There is a marginally non-significant positive correlation between $\hat{p}$ and $\hat{q}$. At lags of 1 (5 myr) and 2 (10 myr) these relationships disappear, except for a significant negative correlation between $\hat{p}$ (lagged 10 Myr behind) and $\hat{q}$.

Table 5-2 Relationship of the fossil record of hexapods (columns) with environmental variables (rows). Fossil record measures: **NEW RT** = the observed range-through family richness presented in Chapter 3, **NEW BC** = the observed boundary-crosser richness (Chapter 3), **HBC RT** = richness adjusted for hexapod-bearing collections (Chapter 4), $\hat{p}$ and $\hat{q}$ = Foote's (2000) origination and extinction metrics, respectively, derived from observed first and last appearance data (Chapter 3), **HBC orig** and **HBC ext** = estimates of origination and extinction rates adjusted for hexapod-bearing collections (Chapter 4). Values given are Pearson's *r* with bootstrapped significance measures. * = significant at 95% confidence limit, ** = significant at 99% confidence limit.

	NEW RT	NEW BC	HBC RT	$\hat{p}$ rate	$\hat{q}$ rate	HBC orig	HBC ext
$^{87}Sr/^{86}Sr$	-.063	.028	-.227	-.122	-.099	.098	.132
$\delta^{34}S$	-.047	-.085	.022	.154	-.231	-.041	-.215
$\delta^{18}O$	.187*	.276*	-.246*	.088	.087	.095	.105
$\delta^{13}C$	.203*	.069	-.046	-.165	.269*	-.265*	-.068
Eustatic sea level	-.086	-.082	.325**	-.089	.112*	.012	.050
ppO_2	.217**	.195*	.102	-.299*	.270	-.058	.184
RCO_2	-.125	-.052	-.109	.111	-.136	.197	.242
Temperature	-.086	-.044	.150	.125	-.156	.079	.132
Plant diversity	.049	-.016	-.347**	.225	.289**	-.162	-.143
Hexapod-bearing formations	.387**	.207	-.213	.498**	-.025		
Hexapod-bearing collections	.385**	.145	-.144	.541**	.215		
one step earlier							
$^{87}Sr/^{86}Sr$	-.096	-.059	-.110	-.250*	-.204	.096	.020
$\delta^{34}S$	.088	-.018	.189	.071	-.080	.036	-.015
$\delta^{18}O$	.229*	.315**	-.307*	.103	.002	.011	-.033
$\delta^{13}C$	.010	.004	-.133	-.182	.210	.031	.326**
Eustatic sea level	-.253*	-.189	.277	-.294*	.064	-.006	.134
ppO_2	.022	.110	.045	-.289**	.073	.056	.189
RCO_2	.048	-.017	-.064	.108	-.156	.155	.110
Temperature	-.056	-.070	.037	.157	.007	.077	.191
Plant diversity	.123	.155	-.236*	.141	.273*	-.082	-.083
two steps earlier							
$^{87}Sr/^{86}Sr$	-.038	-.126	.017	-.139	-.143	.066	-.062
$\delta^{34}S$	.170	.042	.234*	-.052	.083	.070	.024
$\delta^{18}O$	.350**	.371**	-.266	.229	.045	-.058	-.166
$\delta^{13}C$	-.263*	-.113	-.197	-.242	-.049	.246*	.304**
Eustatic sea level	-.336*	-.291*	.341**	-.255	-.002	.180	.233*
ppO_2	-.149	.015	.008	-.201	-.233	.165	.142
RCO_2	.123	.072	-.005	.166	-.024	.091	.014
Temperature	-.014	-.060	-.014	.100	.232	.090	.241*
Plant diversity	.218	.322	-.153	.098	.125	.054	-.069

In the equivalent adjusted fossil data (Table 5-3, lower right quadrant), there are fewer and different relationships. Adjusted richness (HBC RT) is not significantly correlated with the adjusted extinction rate, nor with unlagged origination rate either (Figure 5-1A) but a significant negative correlation is seen with lagged origination (Figure 5-1B): high diversity is followed by a period of lower originations, while low diversity is followed by a period of increased diversification. The concurrent origination and extinction rates are strongly positively correlated (Figure 5-1C, D), while originations are negatively correlated with lagged extinctions in the HBC-adjusted data.

Table 5-3 Relationships between richness, origination and extinction in the hexapod fossil record. **NEW RT** = the observed range-through family richness presented in Chapter 3, **NEW BC** = the observed boundary-crosser richness (Chapter 3), **HBC RT** = richness adjusted for hexapod-bearing collections (Chapter 4), $\hat{p}$ and $\hat{q}$ = Foote's (2000) origination and extinction metrics, respectively, derived from observed first and last appearance data (Chapter 3), **HBC orig** and **HBC ext** = estimates of origination and extinction rates adjusted for hexapod-bearing collections

	NEW RT	$\hat{q}$ rate	$\hat{q}$ rate lag 1	$\hat{q}$ rate lag 2	HBC RT	HBC ext	HBC ext lag 1	HBC ext lag 2
$\hat{p}$ rate	.449**	.307	.132	.073				
$\hat{p}$ rate lag 1	-.051	-.182						
$\hat{p}$ rate lag 2	-.165	-.315**						
$\hat{q}$ rate	.413**							
$\hat{q}$ rate lag 1	.220							
$\hat{q}$ rate lag 2	-.045							
HBC orig					.103	.647**	.021	-.393**
HBC orig lag 1					-.305*	.425**		
HBC orig lag 2					-.376**	-.046		
HBC ext					-.019			
HBC ext lag 1					-.151			
HBC ext lag 2					.013			

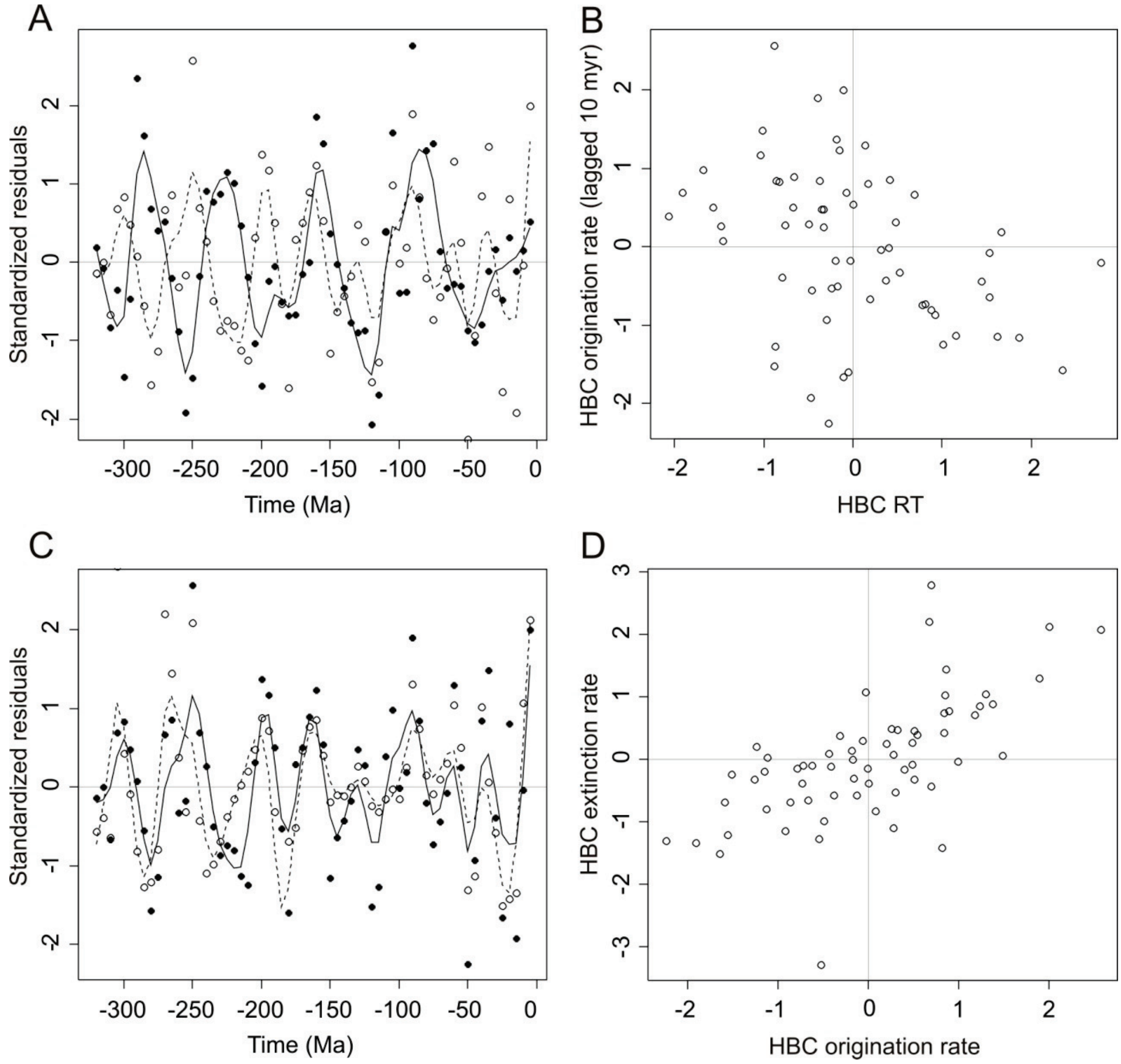

Figure 5-1. Associations between hexapod macroevolutionary series. Family richness, adjusted for hexapod-bearing collections (HBC RT; solid circles, solid 25df smoother line) and HBC-adjusted origination rate (open circles, dashed 25df smoother line) through time (**A**), and plotted against each other (**B**) (origination lagged). **C:** HBC-adjusted origination rate (solid circles, solid 25df smoother line) and HBC-adjusted extinction rate (open circles, dashed 25df smoother line) through time. **D:** HBC-adjusted origination rate crossed HBC-adjusted extinction.

5.4.2 Multiple regressions

Eighteen multivariate models were tested, with six showing appreciable explanatory power with a multiple R-squared value of >0.4 while 12 have values of <0.3 (Table 5-4). Across the 18 multivariate models, a total of 184 associations were tested. Based purely on chance, one would expect just over nine of these to test significant at or above the 5% level: 45 are actually found.

Several features stand out in the different analyses (Table 5-4). First, the biotic variables are some of the strongest predictors, with exceptions being for observed extinctions ($\hat{q}$), and adjusted richness (HBC RT). Different environmental variables predict macroevolution in the adjusted and non-adjusted fossil records (bottom and top half of Table 5-4, respectively). For the non-adjusted data (NEW RT, $\hat{p}$ and $\hat{q}$), $^{87}Sr/^{86}Sr$, $\delta^{34}S$, ppO_2 (Figure 5-2A, B) and $\delta^{18}O$ (Figure 5-2C, D) are the strongest predictors, whilst for the adjusted data the most important predictors are $\delta^{13}C$ and sea level. Atmospheric CO_2 concentrations (RCO_2) are generally not important, being retained in only one model. As in the bivariate analyses, plant richness appears in some models (Figure 5-2E, F).

The direction of association of the variables are generally as expected from the bivariate analyses (Table 5-2), although many of the regression coefficients are larger than their respective correlation coefficients in the bivariate analyses (Table 5-4), indicating that the consideration of multiple explanatory variables is probably beneficial. For the biotic variables, observed richness and originations associate positively, as do originations and extinctions in the adjusted data. Four significant associations appear between hexapod macroevolution and plant richness (Table 5-4): as for the bivariate correlations these are positive associations between plant richness and hexapod extinctions, and negative associations between plant richness and hexapod richness (Figure 5-2E). Atmospheric oxygen concentrations are positively associated with richness, but negatively with origination and extinction rates. Temperature (i.e. inverse $\delta^{18}O$) is negatively associated with richness, but $\delta^{34}S$ is positively associated with richness. $^{87}Sr/^{86}Sr$ is negatively associated with richness and origination. Sea level positively associates with richness and, at a lag, with higher turnover. $\delta^{13}C$ is positively associated with extinction and negatively with origination.

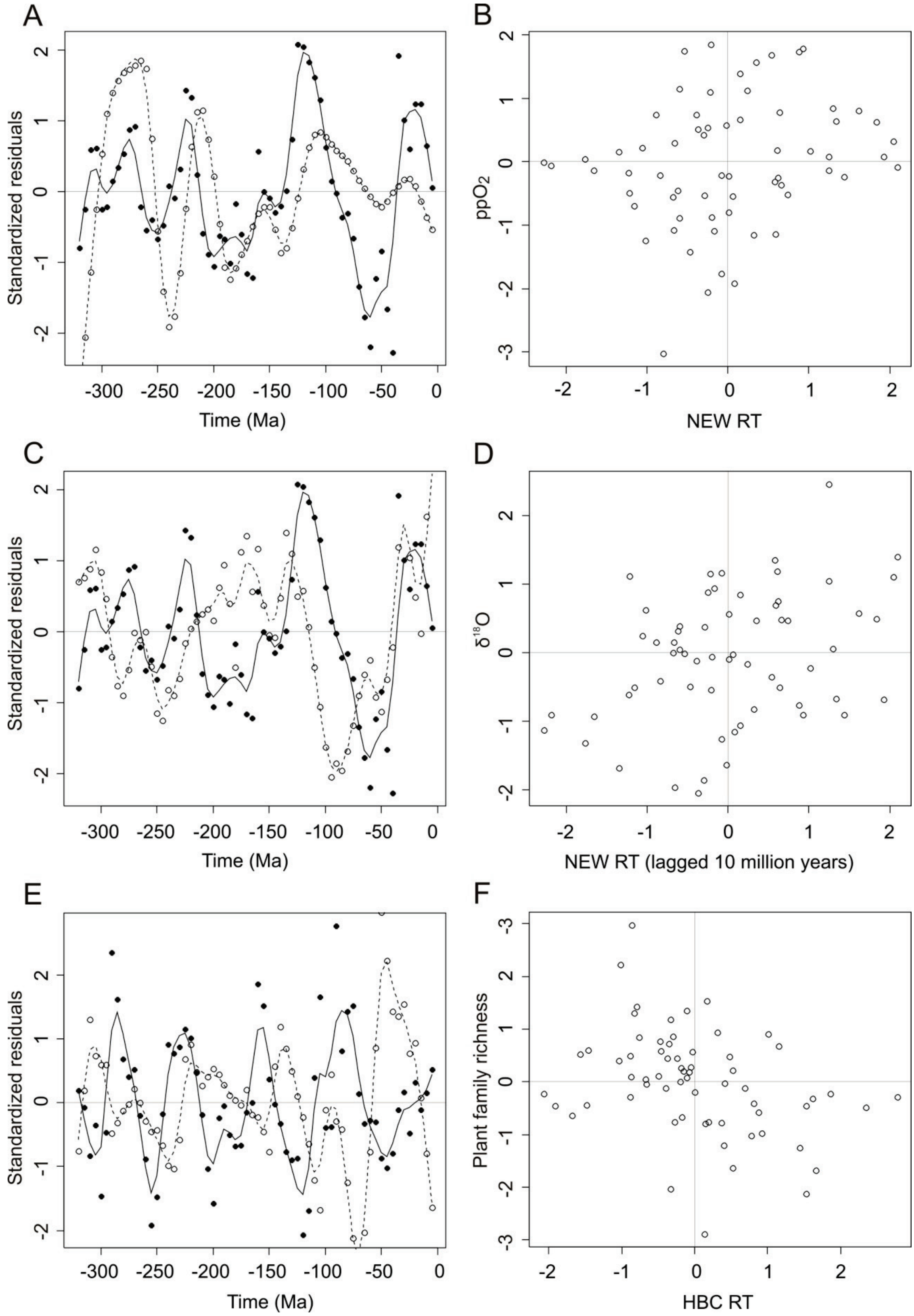

Figure 5-2 Associations between hexapod macroevolutionary series and environmental variables. **A**: Family richness (NEW RT; solid circles, solid 25df smoother line) and partial oxygen pressure (open circles, dashed 25df smoother line) plotted through time and (**B**) against each other. **C**: Family richness (NEW RT; solid circles, solid 25df smoother line) and $\delta^{18}O$ (i.e. inverse temperature; open circles, dashed 25df smoother line) through time and (**D**) against each other, with NEW RT lagged 10 Myr behind. **E**: Family richness, adjusted for hexapod-bearing collections (HBC RT; solid circles, solid 25df smoother line) and plant family richness (open circles, dashed 25df smoother line) through time and (**F**) against each other.

Table 5-4 Linear multiple regression models between the hexapod fossil record and biotic and abiotic predictors, constructed by step-wise subtraction. Two biotic predictors, identified in columns 2 & 3, are assessed in each analysis. Coefficients are shown for variables included in the final models, with significance assessed by bootstrapping of the test statistic. Variables are as for Tables 5-2 and 5-3. Non-inclusion of Hexapod Bearing Collections in an analysis is indicated with a dash (—).

Response variable	Biotic predictor 1	Biotic predictor 2	Biotic variable 1	Biotic variable 2	$^{87}Sr/^{86}Sr$	$\delta^{34}S$	$\delta^{18}O$	$\delta^{13}C$	Eustatic sea level	ppO_2	RCO_2	Plants	Hexapod-bearing collections	Multiple R^2
NEW RT	$\hat{p}$ rate	$\hat{q}$ rate	0.474***			0.324**	0.419***			0.692***		-0.257*	0.282*	0.523
NEW RT one step later	$\hat{p}$ rate one step later	$\hat{q}$ rate one step later	0.466***	0.235*		0.384***	0.352***			0.445***			—	0.434
NEW RT two steps later	$\hat{p}$ rate two steps later	$\hat{q}$ rate two steps later	0.290*	0.361**		0.405***	0.487***	-0.361**		0.542***			—	0.519
$\boldsymbol{\hat{p}}$ rate	NEW RT	$\hat{q}$ rate	0.348**	0.211*	-1.96					-0.459***			0.263*	0.524
$\boldsymbol{\hat{p}}$ rate one step later	NEW RT	$\hat{q}$ rate			-0.387***					-0.414***			—	0.219
$\boldsymbol{\hat{p}}$ rate two steps later	NEW RT	$\hat{q}$ rate		-0.321**			0.260*						—	0.163
$\boldsymbol{\hat{q}}$ rate	NEW RT	$\hat{p}$ rate	0.400***									0.269**		0.243
$\boldsymbol{\hat{q}}$ rate one step later	NEW RT	$\hat{p}$ rate										0.269*	—	0.075
$\boldsymbol{\hat{q}}$ rate two steps later	NEW RT	$\hat{p}$ rate			-0.230					-0.289*			—	0.109
HBC RT	HBC orig	HBC ext			-0.251*				0.257**			-0.343**		0.259
HBC RT one step later	HBC orig one step later	HBC ext one step later							0.279*				—	0.076
HBC RT two steps later	HBC orig two steps later	HBC ext two steps later						-0.246	0.384**				—	0.174
HBC orig	HBC RT	HBC ext		0.668***				-0.310**					—	0.515
HBC orig one step later	HBC RT	HBC ext	-0.289**	0.430***									—	0.264
HBC orig two steps later	HBC RT	HBC ext	-0.501***						0.369**				—	0.252
HBC ext	HBC RT	HBC orig		0.690***				0.316***			0.206*		—	0.518
HBC ext one step later	HBC RT	HBC orig						0.330***					—	0.107
HBC ext two steps later	HBC RT	HBC orig		-0.417***					0.260**				—	0.218

5.4.3 Logistic vs. exponential growth

Over the time period for which there is a reasonable hexapod fossil record (Serpukhovian–Piacenzian), the log of observed richness (NEW RT; Figure 5-3A) through time fits a quadratic model significantly better than a simple linear one (reduction in AIC of 7.055; 99.9% CI: -0.0252, -0.0004), with an increase in the variance explained of 2.09%.

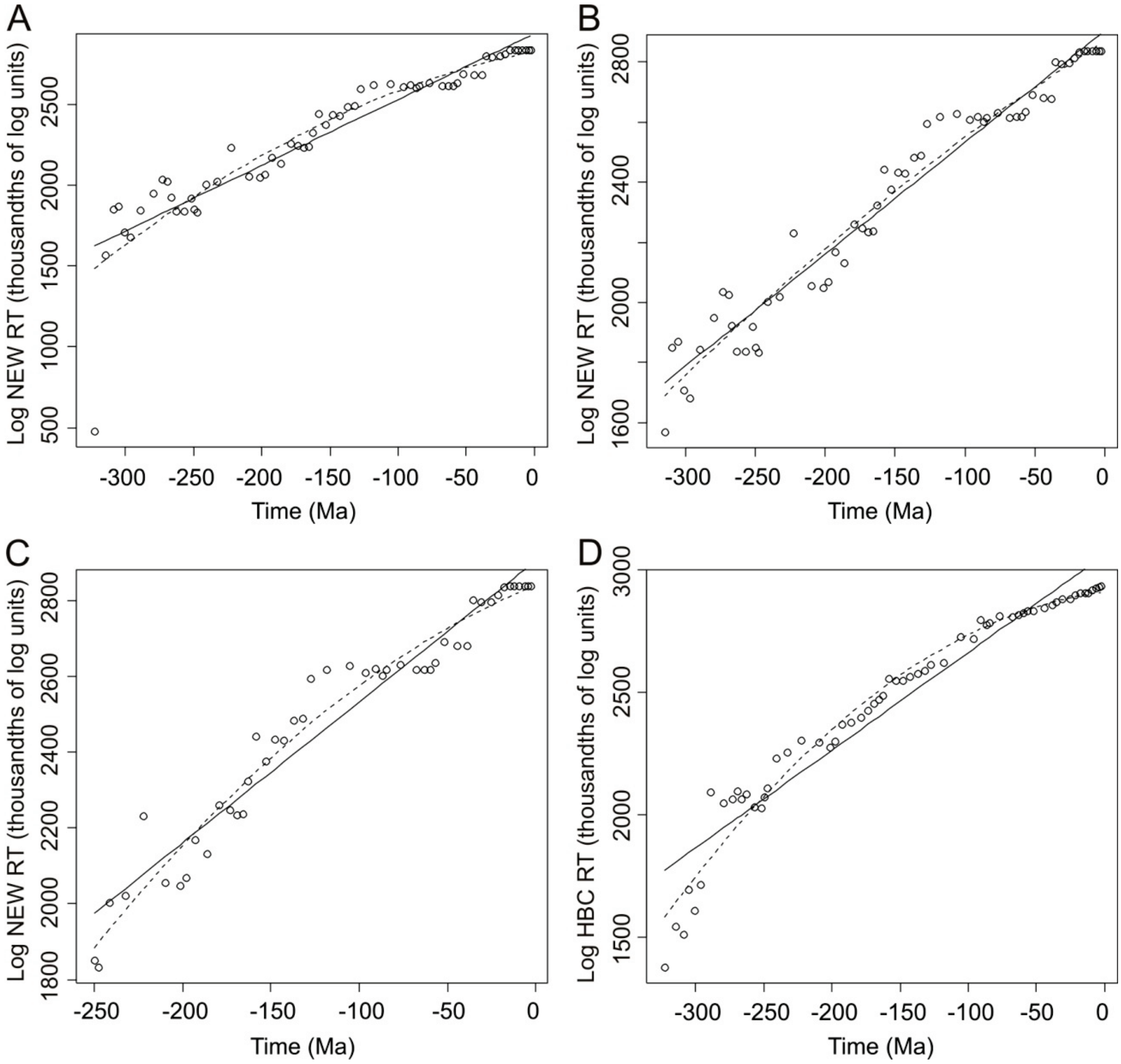

Figure 5-3 The fit of exponential and quadratic regressions on logged hexapod family richness through time. Solid lines are from simple linear regressions (representing an exponential/expansionist growth model) and dashed lines from quadratic regressions (representing a logistic growth model). All diversity data has been logged. **A:** NEW RT from Serpukhovian–Piacenzian. Multiple R^2: linear = 0.8491, quadratic = 0.8699. Squared term in quadratic model significant at 99.9% confidence limit. **B:** NEW RT from Bashkirian–Piacenzian. Multiple R^2: linear = 0.9546, quadratic = 0.9575. Squared term in quadratic model not significant. **C:** NEW RT from Induan–Piacenzian. Multiple R^2: linear = 0.9385, quadratic = 0.9565. Squared term in quadratic model significant at 99% confidence limit. **D:** HBC RT from Serpukhovian–Piacenzian. Multiple R^2: linear = 0.9251, quadratic = 0.9701. Squared term in quadratic model significant at 99.9% confidence limit.

However, the first data point is a significant outlier with high leverage (Cook's distance >1). Removal of this point (Figure 5-3B) changes the outcome so that the quadratic model is marginally not a significantly better fit (reduction in AIC of 2.074: 95% CI: -0.0050, 0.0001) than the simple linear regression, with only a 0.29% increase in variance explained. However, since the Palaeozoic and post-Palaeozoic are widely considered to represent two major evolutionary faunas (Labandeira, 2005), the post-Palaeozoic data were considered separately (Figure 5-3C). In this instance, the quadratic regression does provide a significant improvement in fit (reduction in AIC of 14.25; 99% CI: -0.0124, -0.0020) from the simple linear regression at the 99% confidence limit, with an increase in variance explained of 1.8%.

Using the adjusted richness estimates (HBC RT) (Chapter 4), gives a less ambiguous picture (Figure 5-3D). The quadratic regression provides a significantly better fit than the simple linear regression at the 99.9% confidence limit (reduction in AIC of 54.041; 99.9% CI: -0.0148, -0.0049), with a 4.5% increase in variance explained, although there is a suggestion that the first datum may be having a stronger effect than other points. Looking only at post-Palaeozoic data (not shown), the quadratic regression remains significantly better at the 99.9% confidence level (reduction in AIC of 39.623; 99.9% CI: -0.0104, -0.0027) but the increase in variance explained compared to the simple linear regression is only 1.79%.

5.5 Discussion

The main findings of this chapter are that: range-through data support a weak deceleration in the accumulation of fossil insect families over time; data adjusted for sampling collections also show some support for density-dependent processes because short term increases in richness are followed by reduced origination rates. The face-value richness record is predicted by temperature, atmospheric oxygen concentrations, and plant richness in ways consistent with previous work on insects or other taxa. However, for the fossil data that have been adjusted for sampling effort, other abiotic variables tend to predominate, such as sea level and marine productivity. Each of these is discussed below in the context of previous work on hexapods and the fossil record generally.

Previously, the evidence for density-dependent growth of insect taxa has been mixed. Although Labandeira and Sepkoski (1993) noted that the rate of accumulation of fossil insect taxa had slowed, indicating a slight reduction in the rate of growth of the clade, Davis *et al*. (2011) showed for Odonatoidea that the reduction in rate is probably greater than observed from the fossil record alone once gaps in the record are taken into account, because many families have earlier originations than shown by their first fossils. Against this, Eble (1999) showed no association between family level originations and richness, unlike for marine taxa, suggesting exponential processes.

The long term data here are generally consistent with the conclusions of Labandeira and Sepkoski (1993), in that they suggest a depression in the rate of accumulation of log families (Figure 5-3), although quite a slight one, accounting for only a small amount of the total variation in log richness: for large parts of the face-value record, growth is consistent with an exponential model (Figure 5-3B). However, given that both the unadjusted and adjusted record likely include a large Pull-of-the-Recent (Chapter 4), it is likely that the true rate of growth of insect families has slowed further than shown here, a picture further endorsed by the likely effect of infilling ghost ranges (Davis *et al.*, 2011). Given that the new fossil dataset accumulated in this thesis (Chapter 3) seems to show an increase in the number of taxa accumulated near the Recent compared to earlier datasets, a result of the increased discovery of fossil families from the Cenozoic, it is notable that this has still produced a picture very similar to that of Labandeira and Sepkoski (1993). The meaning of a modest depression in the rate of accumulation of fossil families through time is ambiguous. Whilst consistent with density-dependent processes, richness can in principle rise exponentially at lower taxonomic levels whilst not doing so at higher taxonomic levels (see Lane and Benton, 2003). One likely reason for this is that taxa that originate nearer the Recent are more likely to be assigned to existing, rather than novel, higher taxa, and conversely only taxa that have accumulated distinctive characteristics over time since their split from a common ancestor will be afforded distinctive family status. Additionally, the accumulation of species-rich clades through time can make the family rates appear to decrease while the underlying species rates may continue unchanged (Flessa and Jablonski, 1985).

The short term associations between richness, origination and extinction contain some possible evidence of density-dependent processes in clade growth but likely reflect several other factors. The strongest indication of density-dependence is from the collections-adjusted data, where richness is associated with a future lowering of originations, a finding that runs counter to Eble's (1999) study of the insect record, which used data that did not account for sampling effects. In the adjusted data is also a positive correlation between origination and extinction, an association that could represent density-dependence as well, but the lack of lags in the system makes this uncertain. It is possible that this represents sampling artefacts which have not been effectively removed by the sampling adjustment procedure (Chapter 4), since the insect fossil record has gaps (Chapter 4), leading to concentrations of originations and extinctions in well-sampled stages. Although the same relationship is marginally significant in the non-adjusted data, different statistical tests do suggest an association between originations and extinctions (Chapter 4; Table 4-1), and there are further correlations between richness, origination and extinction without lags, suggesting again an artefactual clustering of first and last fossil finds due to gaps in the fossil record. The association between high origination and future low extinction in the adjusted data (Figure 5-1) probably just reflects periodicity of short term fluctuations in the adjusted rates.

The other way in which the Red Queen paradigm is tested here is through associations between the hexapod and the plant family record (Figure 5-2E, F). One possible prediction is that both should positively correlate with each other, reflecting the fact that plants provide resources for phytophagous insects and thus indirectly other insects feeding at higher trophic levels. Positive associations between phytophagy and species richness and have been found in numerous neontological studies (Mayhew, 2007). Labandeira and Sepkoski (1993) found, however, that the Cretaceous radiation of angiosperms apparently had no noticeable effect on the accumulation of insect families.

Indeed, if changes in plant richness represent turnover of the major constituents of plant communities, this might initially have negative effects on insect communities, as suggested by Jarzembowski and Ross (1996). The results of this study support the latter suggestion because they suggest negative associations between insect family richness and plant richness, and positive associations between plant richness and insect extinction rates. These results are not necessarily at odds with the neontological studies as they report associations through time rather than across clades. However, if doubts exist over the true biological signal in the hexapod family level data, the same must be said of plant richness. Although the relationships are significant, they are never strong.

Turning to abiotic variables, the most striking finding is that different variables seem to predict the insect record dependent on whether attempts to control for sampling bias have previously been imposed (Table 5-4). Analyses of the marine invertebrate fossil record have similarly found that controls for sampling can alter the results of correlations with environmental variables (Alroy, 2010*b*), although this can depend on the type of control used (Mayhew *et al.*, 2012). This study provides further support for that notion, and whilst interesting, does raise the question of whether the unadjusted data or the adjusted data carry the greatest biological signal. Recent work on the marine invertebrate record (Smith *et al.*, 2012) has suggested that rock-record correction tends to have very similar effects to sample-standardization, suggesting convergence on an underlying biological signal, although there is no guarantee that the same will be true for hexapods. Erroneous rock record data may make the situation worse rather than better (Benton *et al.*, 2011).

If the unadjusted record is taken at face value, results are consistent with some previous work. A positive association between richness and atmospheric oxygen concentrations (Figure 5-2A, B) is consistent with the idea that flying organisms benefit energetically from such conditions, and fits the initial radiation of Pterygota in the Carboniferous. This coincides with lower turnover of taxa (lower origination and extinction rates). There is also a positive association between $\delta^{18}O$ and richness or origination, indicating lower richness rises after temperature rises (Figure 5-2C, D). Whilst seemingly inconsistent with the present positive association between richness and temperature across space, the richness association does conform to previous analyses on both marine and terrestrial taxa from range-through datasets (Mayhew *et al.*, 2008). A cautionary observation is that this association is reversed for marine invertebrates when sample standardization is applied (Mayhew *et al.*, 2012), and indeed it disappears here once controlling for the number of collections (Table 5-4). A negative correlation between insect richness and temperature might emerge through interactions with terrestrial productivity if, for example, lush plant growth tends to depress global temperatures (through fixing and burying atmospheric CO_2) but increases insect habitat availability. This hypothesis remains to be tested explicitly. The lack of significant relationships seen between hexapods and CO_2 in these models seems surprising, given the profound effects CO_2 has on insect physiology (Nicolas and Sillans, 1989; Guerenstein and Hildebrand, 2008). It could be that, while CO_2 has significant effects on individual insects, that does not translate into changes in macroevolutionary rates. Alternatively, a stronger association may be recovered by analysing a genus-level dataset.

Perhaps surprisingly, a number of marine environmental proxies appear to significantly predict the hexapod fossil record. For example, both $\delta^{34}S$ and $^{87}Sr/^{86}Sr$, often taken to indicate organic and inorganic nutrient status in the oceans, significantly predict the unadjusted record in multivariate models. The relationships are positive between $\delta^{34}S$ and richness (Table 5-4), indicating that a higher organic nutrient status in the ocean is associated with higher insect richness. The relationships are negative for $^{87}Sr/^{86}Sr$ and predict unadjusted origination, extinction, and adjusted richness. In addition to these relationships, $\delta^{13}C$ significantly predicts macroevolutionary variables, mainly in the adjusted fossil data. Because the past interpretation of these variables mainly related to the marine environment, why they might be associated with the hexapod record is not clear. One general possibility is that changes in the marine system do reflect changes to the terrestrial realm in some way, and it is these changes in the terrestrial realm that affect the hexapod record. Most abiotic environmental proxies so far tested do relate in some way to some part of the fossil record (Mayhew, 2011), and this probably reflects a strongly linked Earth-Biospheric system in which changes to one element of the system have cascading effects on others (Hannisdal and Peters, 2011). It remains likely therefore that many of these correlations are incidental, or spurious, or reflect associations that are not causative. Although statistical advances based on Information Theory do hold some promise to help untangle such causative cascades (Hannisdal and Peters, 2011), it remains unknown how much advance can be made in disentangling such a rich multivariate system by statistical inference alone.

The final important variable emerging from these analyses is sea level change, which is positively associated with richness and turnover in the adjusted fossil data. High sea levels are well known to promote marine invertebrate richness (Purdy, 2008; Hannisdal and Peters, 2011; Mayhew *et al.*, 2012), which likely occurs through the flooding of continental shelves, increasing suitable shallow sea habitats. High sea levels could, in contrast, promote diversity and turnover in terrestrial faunas by promoting isolation and endemism through the flooding of continental interiors.

It should be acknowledged that the possibility remains that the history of insect evolution could have been dominated by idiographic causation or *contingency* (Gould, 2001), whereby insect taxa originate and go extinct due to unique configurations of drivers, rather than by any consistent and predictable causative forces; it may be that terrestrial ecosystems are too complex to be captured by the types of models employed here.

Notable omissions from these analyses are measures of volcanic activity and extra-terrestrial bolide impacts, which are widely implicated in the Late Permian and end-Cretaceous extinctions, respectively. This is due to a lack of appropriate datasets available which lend themselves well to the type of analyses performed here. Although the corrected and uncorrected richness series (Chapters 3, 4) do not show a pronounced decrease in richness near the Cretaceous-Palaeogene boundary, the use of the family level may be hiding a decrease at lower taxonomic levels. The decrease in richness during the Late Permian and high turnover rates around the Permian-Triassic boundary would allow for an interpretation involving the effects of large igneous provinces known from that time. However, these are isolated events, while the focus here has been on how the overall systems of interactions between hexapods and environmental variables has behaved across history.

Overall these analyses provide further evidence for a strongly coupled Earth-Biosphere system, but also one in which both the Red Queen and Court Jester contribute significantly at large temporal and spatial scales, mirroring results for marine invertebrates (Ezard *et al.*, 2011; Mayhew *et al.*, 2012). These analyses are unlikely to be the final word on this subject. In particular, they suggest a need to control for sampling biases using alternative techniques to better understand whether the findings for adjusted or unadjusted fossil data are more reliable. Not all relevant abiotic variables have been included in this analysis, and, for example, information on the distribution of the continental land masses, the area of terrestrial biomes, volcanism and bolide impacts could reveal further interesting associations. The data on plant diversity could probably be considerably improved and associations between insects and particular plant taxa, or with other organisms, remain untested.

Although two major predictors of the face-value hexapod fossil record are sampling measures (Chapter 4) and environmental factors (this chapter), previous work on hexapod macroevolution has suggested that morphological and developmental evolutionary innovations may have played a very important role in generating the extant richness of hexapods (Mayhew, 2007). In the next chapter, the growth profiles of major constituent groups of hexapods are investigated separately, with consideration of the key morphological and life history innovations, which may be responsible for their variable macroevolutionary trajectories.

Chapter 6

Key Innovations and the Hexapod Fossil Record

6.1 Abstract

Key innovations are evolutionary novelties that explain the species richness of diverse clades. In the hexapods, which make up over half of all described extant species, several innovations have been posited to have contributed to that richness, including wings, wing folding, and complete metamorphosis. Although these hypotheses have been extensively tested using phylogenies of extant taxa, fossil tests have been scant. Here, a new dataset on hexapod family fossil ranges is used to test for key innovations by assessing differences in origination and extinction rates, and limits to the growth of richness, within and across major morphological groups. Although Palaeoptera (primitive winged insects) have higher origination and extinction rates than Apterygota (wingless insects), other major groupings do not differ significantly in these rates. Origination rates are generally greater than extinction rates across all groupings, but the average net rate of diversification is generally similar across groups, only being higher in Holometabola compared to Apterygota and Polyneoptera. Paraneoptera and Holometabola show the most marked slowdown in the rate of accumulation of taxa over time. Overall our data suggest that the origin of wings represented a major macroevolutionary event, which led to greater faunal turnover. The Holometabola have achieved their present high family richness not by great changes in the average rates of origination or extinction but by a subtle widening of the difference between origination and extinction relative to some other groups, and by peaks in origination at key moments in evolutionary history.

6.2 Introduction

Understanding why some groups of organism are very speciose, whilst others are species poor, is a problem that has fascinated evolutionary biologists ever since Darwin (Magurran and May, 1999; Schluter, 2000; Friedman, 2009). The macroevolutionary approach to solving this problem uses data on the past history of life to understand differences in richness across clades, and draws on two major sources of information (Hunter, 1998): The neontological approach uses phylogenies of extant taxa to infer changes in past processes (Mooers and Heard, 1997). The alternative approach is palaeontological, using information from the fossil record (Benton and Harper, 2009). Phylogenies of extant taxa allow one to study processes at the species level and in the absence of a fossil record, but inferences about speciation and extinction rates rest on assumptions that are often untested and possibly incorrect (e.g. Rabosky *et al.*, 2012). Fossils, although often studied at taxonomic levels above the species, and though prone to sampling biases (Peters, 2005), provide direct evidence about the timing of changes in rate, as well as extinctions (Alroy, 2010*a*). In this chapter I use a new dataset on the fossil ranges of insect families to explore the causes of variability in richness across different morphological groups, representing possible key innovations.

Key innovations are novel phenotypic characters such as morphologies, behaviours, or developmental pathways that enhance species richness (Hunter, 1998). They are one of several types of factor that may explain species richness in diverse groups. Other types of factors include clade age (McPeek and Brown, 2007) and changes in environmental conditions (Chapter 5). Interactions may also occur between these factors; for example, a particular key innovation might only enhance richness given some other environmental condition (De Queiroz, 2002). Heard and Hauser (1995) suggested three general ecological mechanisms by which key innovations might work: a) by escape from competition into a new adaptive zone; b) by decreasing the probability of extinction; and c) by favouring ecological or reproductive specialization. These in turn are roughly equivalent to changing three macroevolutionary parameters; the carrying capacity of taxa in the environment; the extinction rate; and the speciation rate (Mayhew, 2007). Although functional studies may suggest that one or more of these mechanisms is most likely, for studies of extant phylogenies explicit data supporting these mechanisms may be lacking. In contrast, fossil studies are intrinsically better able to provide data on these different macroevolutionary parameters, thus aiding inference of the mechanism.

The hexapods comprise over half of all described species and explaining this richness is therefore central to understanding the macroevolution of life on Earth (Mayhew, 2007). A variety of key innovations have been proposed to influence insect richness and can be divided into those innovations that have evolved multiple times (convergent traits) in the group and those that have evolved uniquely. Examples of convergent traits include polyandry (Arnqvist *et al.*, 2000), exploiting plants (Mitter *et al.*, 1988; Farrell, 1998), sexual dimorphism (Misof, 2002), and tongue length (for hoverflies, Katzourakis *et al.*, 2001). Functional arguments can be made about the mechanisms operating for each of these studies but, because the data come exclusively from extant species, direct evidence for the macroevolutionary mechanisms is absent.

Four progressive evolutionary steps have traditionally been recognized in the evolutionary history of the hexapods (Chapter 1.3.1), based largely on the sequence in which they appear in the fossil record (Carpenter, 1992; Figure 6-1), as well as their status as primitive or derived states in phylogenetic studies (e.g. Hennig, 1969). These are the evolution of the wingless insects, the evolution of wings, wing folding, and complete metamorphosis. Collections of orders which possess one or more of those characteristics, but sometimes not others, can be usefully defined thus (Jarzembowski and Ross, 1996):

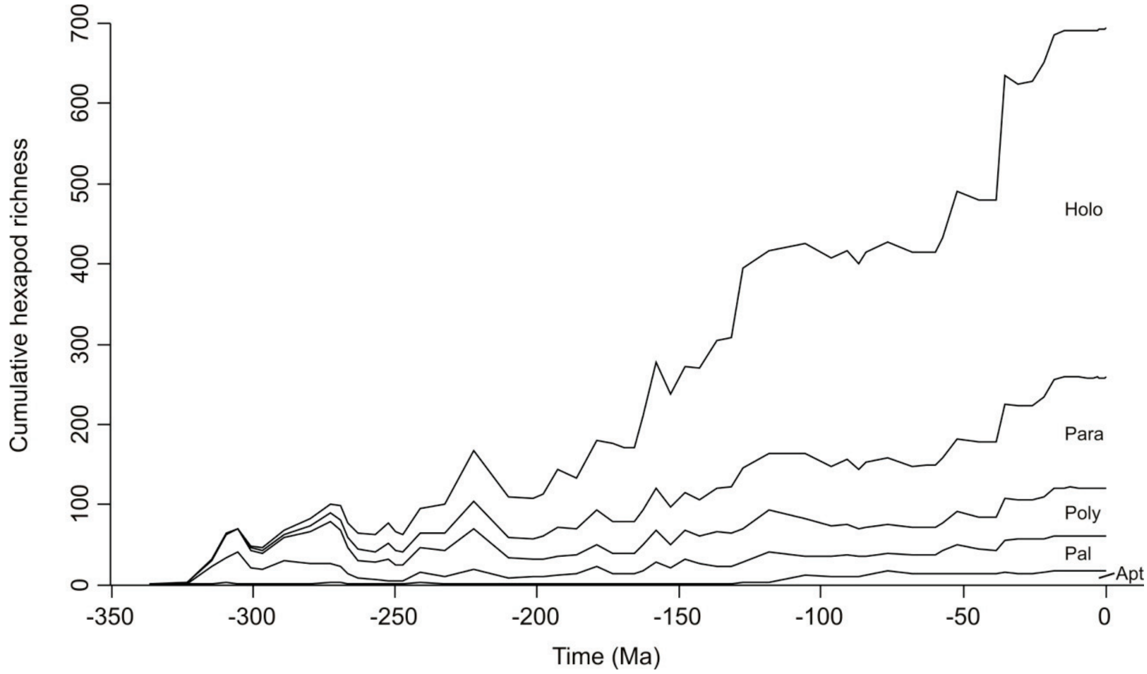

Figure 6-1 Cumulative hexapod richness by 'clade'. Family richness of each group is represented by the area between lines. **Apt** = 'Apterygota', **Pal** = Palaeoptera, **Poly** = Polyneoptera, **Para** = Paraneoptera, **Holo** = Holometabola.

The Apterygota as defined in Carpenter (1992), comprise the entognath (non-insect hexapod) orders Diplura, Protura (absent from the fossil record) and Collembola (springtails), as well as the ectognath (true insect) orders Archaeognatha (bristletails) and Zygentoma (silverfish). This is a paraphyletic grouping based mainly on the primitive absence of wings, and even the two true insect orders do not together form a monophyletic group, as the silverfish are more closely related to the winged insects (Pterygota) than they are to the bristletails (Grimaldi and Engel, 2005).

The Palaeoptera are those pterygote (winged) insect orders which primitively do not possess the ability to fold their wings over the abdomen at rest, a feature of the Neoptera and itself considered a key innovation in the great success of the insects (Carpenter, 1992; Mayhew, 2002; Grimaldi and Engel, 2005). Palaeoptera comprise Ephemeroptera (mayflies), the extinct palaeodictyopterid orders (Palaeodictyoptera, Megasecoptera, Dicliptera and Diaphanopterodea) and the odonatopteran orders (dragonflies, damselflies and their extinct relatives). Authoritative reviews of insect systematics have variously viewed Palaeoptera as monophyletic (e.g. Carpenter, 1992), paraphyletic (e.g. Grimaldi and Engel, 2005) or an intractable problem (Trautwein *et al.*, 2012), although recent work on head morphology has given strong support to palaeopteran monophyly (Blanke *et al.*, 2012).

Polyneoptera have proven to be a difficult group to define precisely, based mainly on an expanded anal region of the hind wing which has been secondarily reduced or lost in some orders (Grimaldi and Engel, 2005), although recent phylogenies provide some support for monophyly based on nuclear DNA sequences (Ishiwata *et al.*, 2011; Trautwein *et al.*, 2012). Polyneoptera are traditionally thought of as the earliest-branching group of Neoptera (winged insects which possess wing folding), comprising the orders "Protorthoptera" (polyphyletic waste-basket taxon), Dermaptera (earwigs), Grylloblattodea (ice crawlers), Mantophasmatodea (rock crawlers/heelwalkers) (in some classifications grouped with Grylloblattodea in the order Notoptera, e.g. Arillo and Engel, 2006), Plecoptera (stoneflies), Embioptera (webspinners), Zoraptera (angel insects), Phasmatodea (stick and leaf insects), Caloneurodea (extinct), Orthoptera (grasshoppers and crickets), Blattodea (cockroaches), Isoptera (termites), Mantodea (praying mantises) (Grimaldi and Engel, 2005; Trautwein *et al.*, 2012) and the recently reinstated extinct Cnemidolestodea (Béthoux, 2005).

Paraneoptera are a group of insects with mostly sucking mouthparts and includes the Psocoptera (book/bark lice), Phthiraptera (parasitic lice, now usually included with Psocoptera in the order Psocodea), Thysanoptera (thrips) and Hemiptera (true bugs), with evidence for monophyly of the group being generally good if not unequivocal (Trautwein *et al.*, 2012). Many phylogenies (e.g. Wheeler *et al.*, 2001) consider them the sister group to the Holometabola (below), together forming the clade Eumetabola.

Finally, Holometabola are those insects which undergo complete metamorphosis during ontogeny, with such distinct larval and adult forms that they can be thought of as separate evolutionary modules capable of independent evolution (Yang, 2001). Orders included are Coleoptera (beetles), Raphidioptera (snakeflies), Megaloptera (dobsonflies), Neuroptera (lacewings and antlions), Hymenoptera (wasps, ants and bees), Mecoptera (scorpionflies), Siphonaptera (those wretched fleas), Strepsiptera (twisted wing parasites), Diptera (true flies), Trichoptera (caddisflies) and Lepidoptera (moths and butterflies). Support for a monophyletic Holometabola is strong (Wiegmann *et al.*, 2009; Trautwein *et al.*, 2012).

Evidence for the above putative key innovation steps has largely come from sister-group comparisons (Mayhew, 2002; Davis *et al.*, 2010), which suggests that a large shift in net diversification rate occurred at or after the origin of wings, but not before, consistent with several key innovation hypotheses. However, these studies gave no indication of which macroevolutionary parameters may have changed. Fossil studies have been much rarer, but Yang (2001) used Labandeira's family level data (1994) to suggest that extinction rates had not differed between Holometabola and Paraneoptera, and hence that differences in origination rates probably account for the larger increase in families in Holometabola.

In this chapter, I use a new dataset on the ranges of fossil hexapod families to test for the effects of potential key innovations, by looking for significant differences in the rates of origination and extinction across the major morphological groupings of hexapods outlined above. Specifically, I test for the effect of the insect *bauplan* (Entognatha vs. apterygote Ectognatha: i.e. 'Apterygota' split into its insect and non-insect orders), wings ('Apterygota' vs. Palaeoptera), wing folding (Palaeoptera vs. Polyneoptera), complete metamorphosis (Paraneoptera vs. Holometabola). To control for ecological characteristics, I also compare the orders Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies), as these all have terrestrial adults but aquatic nymphs/larvae with similar lifestyles, and possess different combinations of the putative key innovations (mayflies have wings but not wing folding; stoneflies have wing folding but not complete metamorphosis, and caddisflies have both plus complete metamorphosis). Although it is self-evident that origination rates within any temporally long-lasting group must, on the whole, be higher than extinction rates (or else the lineage would have gone extinct), the consistency and magnitude of the difference may vary between groups, and is investigated here. Finally, hexapods as a whole exhibit a tendency towards logistic growth (i.e. a deceleration in richness increase towards the present), indicating density-dependent processes (Chapter 5): but this may vary between constituent clades of hexapods suggesting varying importance of competition and adaptive zones. Hence I test for logistic growth in each of the major groups.

6.3 Materials and Methods

Foote's (2000) origination rate $\hat{p}$ and extinction rate $\hat{q}$ (Chapters 3 and 4), along with the difference between them, are calculated for each stage from first and last appearance data for each of 'Apterygota', Palaeoptera, Polyneoptera, Paraneoptera and Holometabola. The same is also done for Entognatha, ectognath 'Apterygota', Ephemeroptera, Plecoptera and Trichoptera.

The Friedman test is used to test whether the difference in distribution of rates between selected groups is significant. The Friedman is a non-parametric test which deals explicitly with the non-independence of repeated measures and so is more appropriate for time series data than a parametric ANOVA (Conover and Iman, 1981). The median value for each time series is reported to indicate which group has a higher distribution. Stages where the two series being compared both have a value of zero are removed. As the data are rank-transformed for the Friedman test, this has no effect on the test statistic (and so no effect on the conclusions) but moves the median values away from zero, thus making them easier to interpret. However, because the different combinations of series will lead to different stages being removed depending on which groups are compared (e.g. Palaeoptera against 'Apterygota' or Polyneoptera), the median values reported are not comparable across tests. Deletion of double-zeros is not performed for the comparison of $\hat{q}$ between Entognatha and apterygote Ectognatha, as the time series would be reduced to a single data point. A second exception is in the comparison between Ephemeroptera, Plecoptera and Trichoptera: stages are only removed if there is a zero value across all three orders, so the median values may be compared between these analyses. The number of stages included in each test is reported.

The groups considered have different first appearances in the fossil record, so comparisons are only made from the first point at which both are present. The first stage in the series for each test is reported, although it is not necessarily kept in the series for the analysis after removal of zero-value stages.

The tests for logistic or exponential growth in each clade follow the procedure detailed in Chapter 5.3.5: the log of range-through richness ($\times 1000$) is modelled through time using a linear or quadratic model, testing the goodness of fit by AIC scores, and significance via bootstrapping of the test statistic.

6.4 Results

6.4.1 Rates of origination and extinction

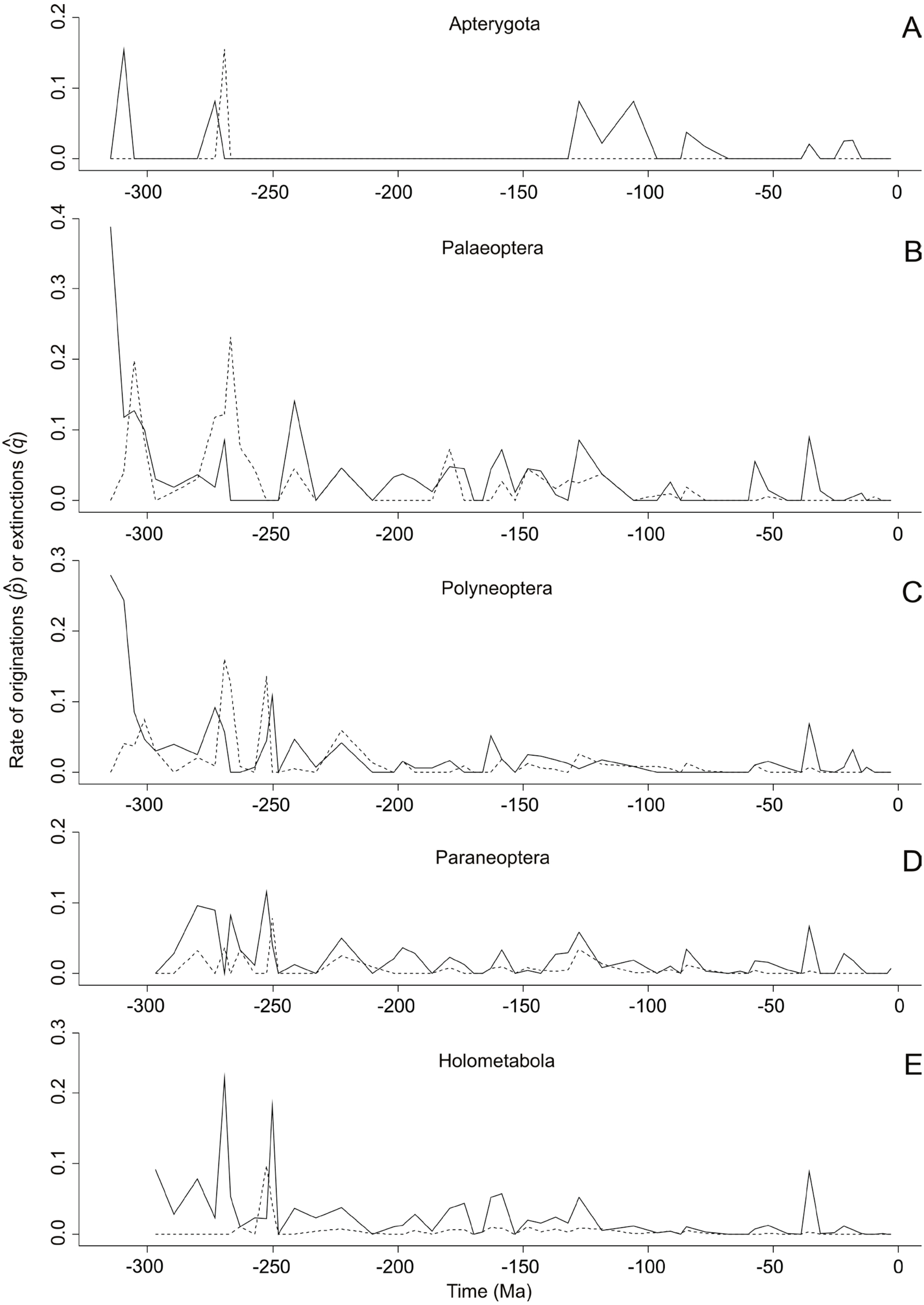

Figure 6-2 Origination ($\hat{p}$; solid lines) and extinction ($\hat{q}$; dashed lines) rates in **A:** 'Apterygota'; **B:** Palaeoptera; **C:** Polyneoptera; **D:** Paraneoptera; and **E:** Holometabola, through time.

As for the whole of the hexapods (Chapter 3), origination and extinction rates are highest at the start of the time series and appear to decline towards the recent (Figure 6-2). This appears to be particularly strong in Palaeoptera and Polyneoptera, which dominated richness in the Palaeozoic, and less so in the other groups, though it is still a feature of the Paraneoptera and Holometabola records. Origination rates appear to be generally higher than extinction rates, although there are stages where extinctions outweigh originations for certain groups (Figure 6-2).

6.4.2 Tests of key innovations

Aptyergota and Palaeoptera show significant differences in their origination and extinction rates after accounting for variability across sampling intervals (Table 6-1). Palaeoptera have the highest medians in both cases. None of the other pairwise tests of key-innovation hypotheses give a significant result, indicating that origination and extinction rates remained similar on average across these pairwise categories.

Table 6-1 Tests for the effects of key innovations: rates of origination and extinction between groups. Significant *p*-value from Friedman test indicates strong separation in the distribution of rates, while the reported median indicates which distribution is greater.

Group 1	Group 2	Key Innovation	Starting stage	Stage no. included	Group 1 median	Group 2 median	*p*-value
$\hat{p}$ (origination)							
Entognatha	Apterygote Ectognatha	Insect *bauplan*	Moscovian	8	0.026	0.016	0.479
‘Apterygota’	Palaeoptera	Wings	Bashkirian	36	0.000	0.037	<0.001
Palaeoptera	Polyneoptera	Wing folding	Bashkirian	41	0.030	0.017	0.206
Paraneoptera	Holometabola	Complete metamorphosis	Asselian	46	0.015	0.013	0.881
‘Apterygota’	Holometabola	NA	Asselian	44	0.000	0.016	<0.001
Palaeoptera	Holometabola	NA	Asselian	46	0.013	0.014	0.456
Polyneoptera	Holometabola	NA	Asselian	45	0.009	0.016	0.053
Ephemeroptera	Plecoptera	Combination	Roadian	22	0.000	0.000	0.439
Ephemeroptera	Trichoptera	Combination	Roadian	22	0.000	0.015	0.818
Plecoptera	Trichoptera	Combination	Roadian	22	0.000	0.015	0.108
$\hat{q}$ (extinction)							
Entognatha	Apterygote Ectognatha	Insect *bauplan*	Moscovian	59	0.000	0.000	0.317
‘Apterygota’	Palaeoptera	Wings	Bashkirian	26	0.000	0.032	<0.001
Palaeoptera	Polyneoptera	Wing folding	Bashkirian	36	0.022	0.009	0.303
Paraneoptera	Holometabola	Complete metamorphosis	Artinskian	32	0.005	0.003	0.209
‘Apterygota’	Holometabola	NA	Asselian	28	0.000	0.005	<0.001
Palaeoptera	Holometabola	NA	Asselian	35	0.013	0.004	0.128
Polyneoptera	Holometabola	NA	Asselian	36	0.008	0.003	0.045
Ephemeroptera	Plecoptera	Combination	Roadian	11	0.041	0.000	0.366
Ephemeroptera	Trichoptera	Combination	Roadian	11	0.041	0.000	0.206
Plecoptera	Trichoptera	Combination	Roadian	11	0.000	0.000	1.000
$\hat{p} - \hat{q}$							
‘Apterygota’	Palaeoptera	Wings	Bashkirian	41	0.000	0.008	0.527
Palaeoptera	Polyneoptera	Wing folding	Bashkirian	46	0.006	0.005	0.768
Paraneoptera	Holometabola	Complete metamorphosis	Asselian	45	0.012	0.012	0.366
‘Apterygota’	Holometabola	NA	Gzhelian	45	0.000	0.012	0.002
Palaeoptera	Holometabola	NA	Gzhelian	48	0.000	0.012	0.083
Polyneoptera	Holometabola	NA	Moscovian	48	0.002	0.012	0.021
Ephemeroptera	Plecoptera	Combination	Roadian	19	0.013	0.000	0.491
Ephemeroptera	Trichoptera	Combination	Kungurian	23	0.000	0.005	1.000
Plecoptera	Trichoptera	Combination	Roadian	19	0.000	0.015	0.108

Further comparisons show that Holometabola have significantly higher origination and extinction rates than ‘Apterygota’ but not significantly different in either to Palaeoptera. Origination rates are marginally non-significantly higher, and lower extinction rates significantly lower in Holometabola than in Polyneoptera.

Significant differences between origination and extinction rates are detected in all groups except for Polyneoptera (marginally non-significant), Ephemeroptera and Plecoptera. The most highly significant differences between $\hat{p}$ and $\hat{q}$ are seen in Paraneoptera ($p < 0.001$) and Holometabola ($p < 0.001$) (Table 6-2). The net rate of diversification ($\hat{p} - \hat{q}$) is very low on average for all groups (Table 6-1), and differs significantly between Holometabola and both Apterygota and Polyneoptera. However, it does not differ significantly between Apterygota and Palaeoptera, Palaeoptera and Polyneoptera, or between Paraneoptera and Holometabola.

Table 6-2 Tests for the effects of key innovations: rates of origination and extinction within groups. Significant *p*-value from Friedman test indicates strong separation in the distribution of rates, while the reported median indicates which distribution is greater.

Group	Starting stage	Stage no. included	Median $\hat{p}$	Median $\hat{q}$	*p*-value
‘Apterygota’	Serpukhovian	11	0.026	0.000	0.011
Palaeoptera	Bashkirian	40	0.032	0.015	0.045
Polyneoptera	Bashkirian	44	0.016	0.008	0.052
Paraneoptera	Asselian	39	0.019	0.004	<0.001
Holometabola	Gzhelian	47	0.016	0.001	<0.001
Ephemeroptera	Asselian	18	0.051	0.000	0.157
Plecoptera	Roadian	11	0.028	0.000	0.096
Trichoptera	Artinskian	16	0.033	0.000	0.008

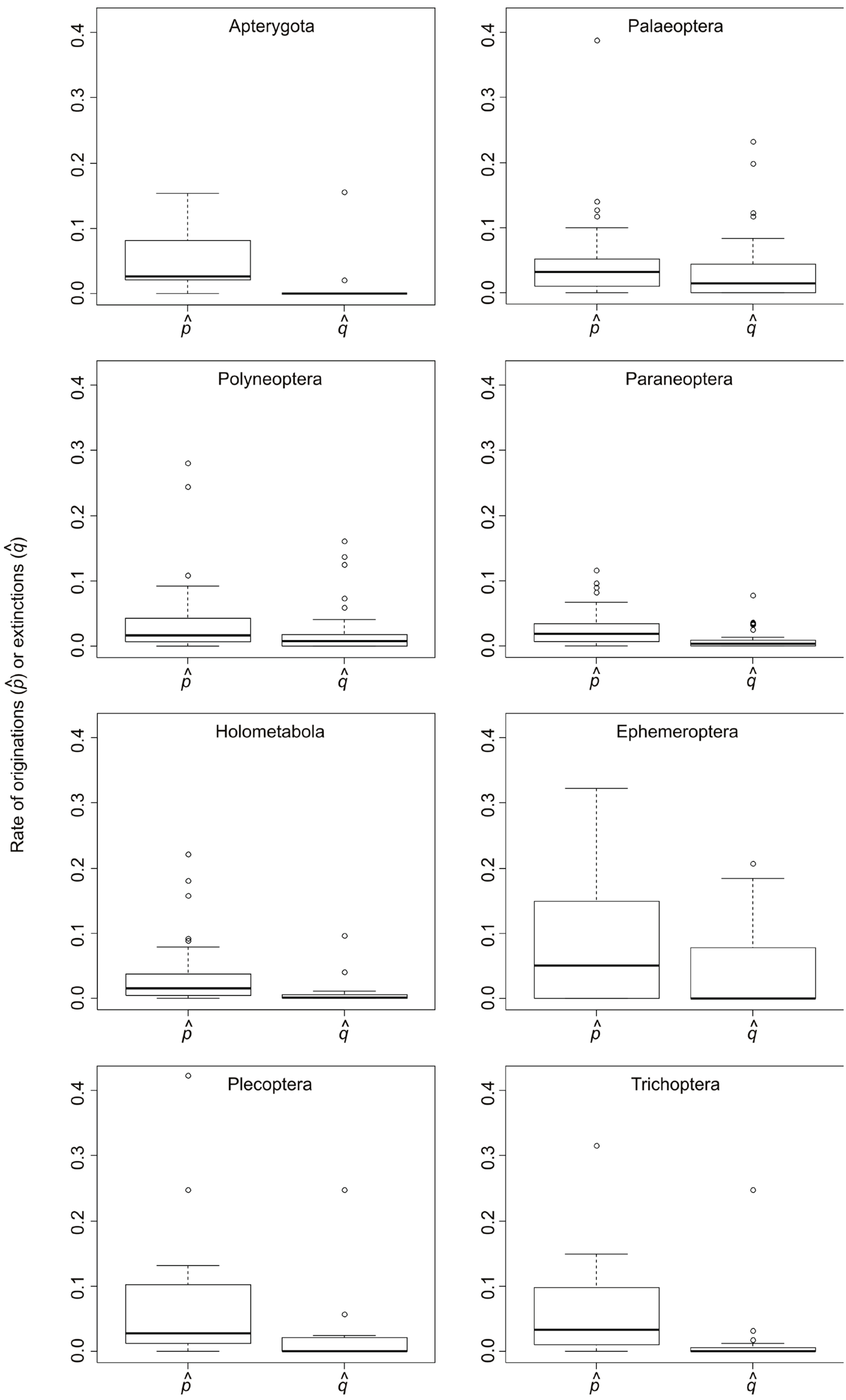

Figure 6-3 Distribution of Foote's (2000) $\hat{p}$ and $\hat{q}$ rates within selected 'clades' and orders. Stages in which both $\hat{p}$ and $\hat{q}$ within each group are zero have been removed. See Table 6-2 for Friedman test statistics. Boxplots: base of box = lower quartile (Q1); top of box = upper quartile (Q3); bold line = median (Q2); lower tail is the lowest point within 1.5× the interquartile range (Q1 to Q3) below Q1; upper tail is the highest point within 1.5× the interquartile range above Q3; and open circles are outliers.

6.4.3 Logistic vs. exponential growth in hexapod 'clades'

In Apterygota (Figure 6-4A), the quadratic function describing log richness over time provided a significant improvement in fit compared to a linear model (reduction in AIC of 34.832; 99.9% CI of b for x^2: 0.0086, 0.0284), with an increase of variance explained of 12.01%. The quadratic term is positive, indicating a greater-than-exponential increase through time.

Raw palaeopteran richness is suggestive of two distinct phases in the Palaeozoic and post-Palaeozoic (Figure 6-4B), and a single curve would prove a poor representation, so regressions were performed only on post-Permian data. In the full run of post-Palaeozoic data (Figure 6-4C), even though the squared term did improve the fit of the model according to AIC (reduction of 6.19) and increase the variance explained by 3.79%, this was non-significant (95% CI of b for x^2: -0.0205, 0.0006). However, the first two points in the time series are influential (Cook's distance ~0.5) and were thus removed (Figure 6-4D). After removal, the extra variance explained by the quadratic term (0.0019%) is no longer justified (AIC increase of 1.6), indicating that the simple linear (exponential) model is the better explanation of post-Palaeozoic palaeopteran richness growth.

Polyneoptera were less clear, with the quadratic term offering insufficient improvement in fit to be justified (AIC decrease of just 0.0141) and neither model explaining much variance (Figure 6-4E). Removal of the first point (Cook's distance = 0.5) results in the quadratic model being a significantly better fit (AIC decrease of 7.478; 99.9% CI: 0.0004, 0.0105) than the simple linear, with an increase in variance explained of 7.85% (Figure 6-4F). However, the overall fit of the model is low and clearly does not capture the important variation in richness change.

The preceding three groups contrast with Paraneoptera and Holometabola, in both of which a quadratic growth term is strongly justified (Figure 6-5). A quadratic model is a better fit for Paraneoptera (AIC reduction of 40.409; 99.9% CI: -0.0232, -0.0057), accounting for 5.43% more variance than the simple linear model (Figure 6-5A). The first three points in the series were identified as potentially having a disproportionate effect on the outcome (Cook's distance above or near to 0.5) and so were removed, but the conclusion remains the same (AIC reduction of 27.964; 99.9% CI: -0.0129, -0.0037) although with only a 2.01% increase in variance explained (Figure 6-5B).

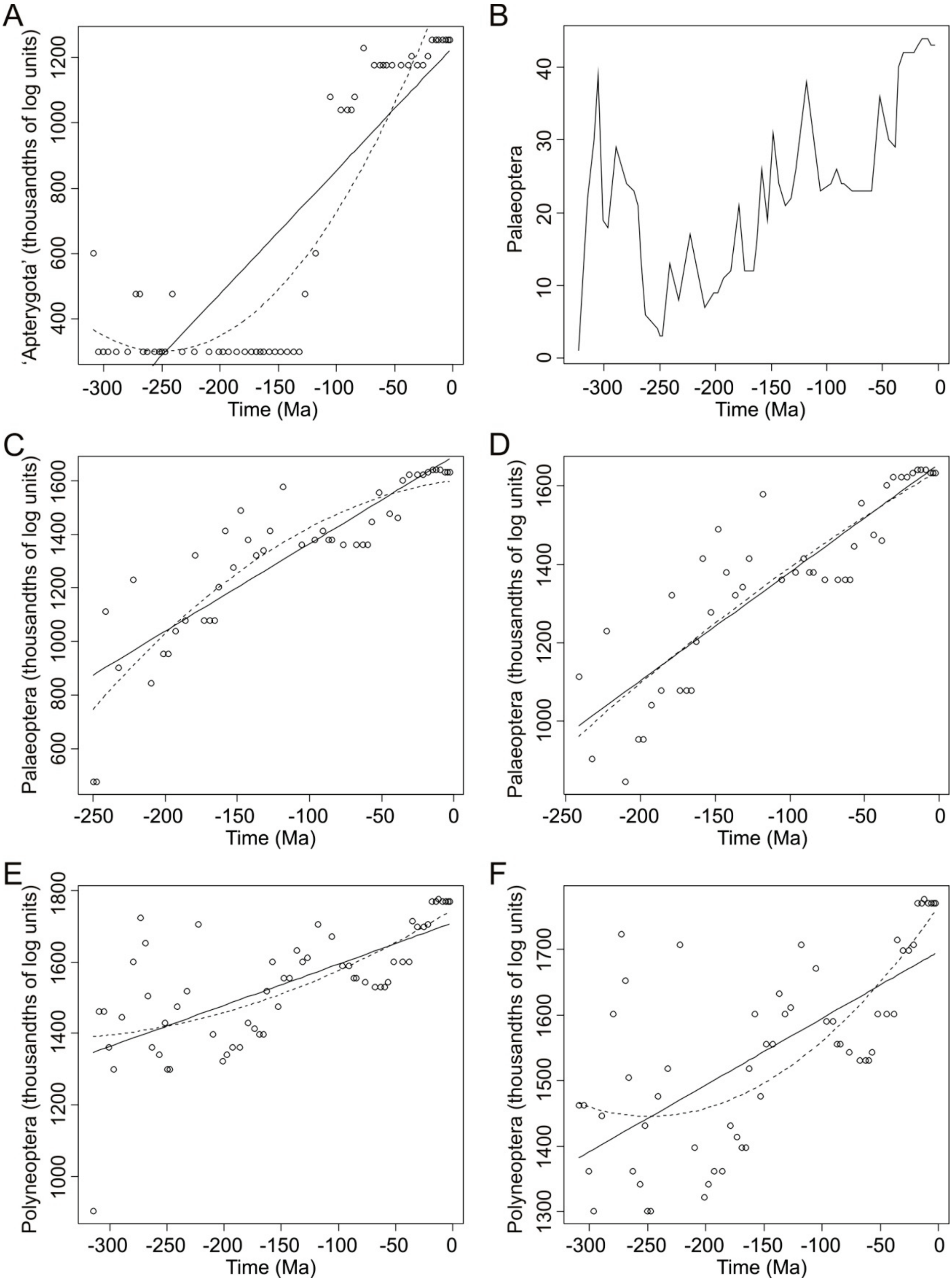

Figure 6-4 Tests for logistic (quadratic regression; dashed lines) vs. exponential (simple linear regression; solid lines) on logged richness in selected hexapod 'clades'. **A:** 'Apterygota' from Moscovian–Piacenzian. Multiple R^2: linear = 0.7414, quadratic = 0.8615. Squared term in quadratic model significant at 99.9% confidence limit. **B:** Raw family richness of Palaeoptera from Serpukhovian–Piacenzian. **C:** Post-Palaeozoic Palaeoptera from Induan–Piacenzian. Multiple R^2: linear = 0.7631, quadratic = 0.801. Squared term in quadratic model not significant. **D:** Post-Palaeozoic Palaeoptera from Anisian–Piacenzian. Multiple R^2: linear = 0.7791, quadratic = 0.781. Squred term in quadratic model not significant. **E:** Polyneoptera from Bashkirian–Piacenzian. Multiple R^2: linear = 0.4755, quadratic = 0.4928. Squared term in quadratic model not significant. **F:** Polyneoptera from Moscovian–Piacenzian. Multiple R^2: linear = 0.4713, quadratic = 0.5498. Squared term in quadratic model significant at 99.9% confidence limit.

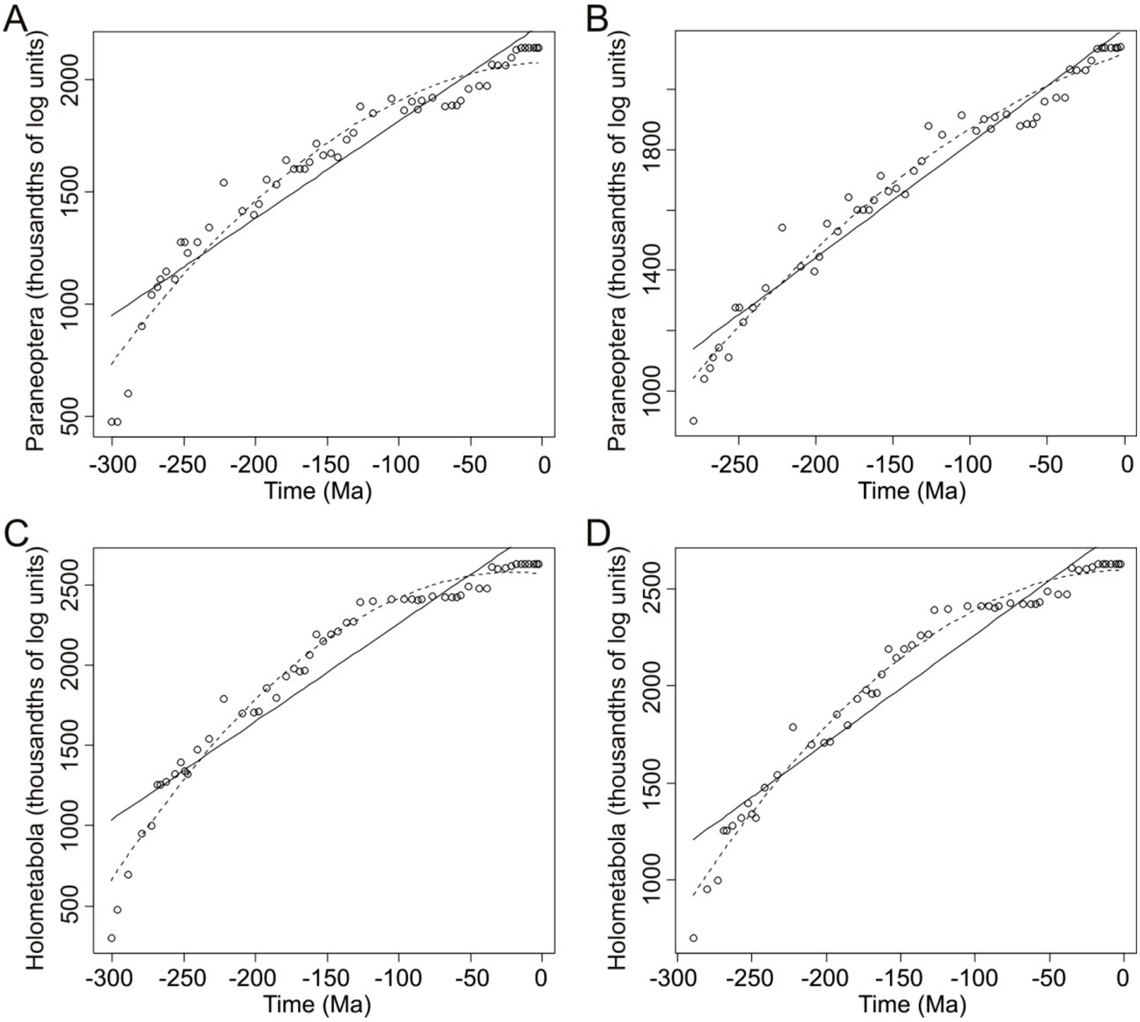

Figure 6-5 Tests for logistic (quadratic regression) vs. exponential (simple linear regression) on logged richness in Eumetabola clades. **A:** Paraneoptera from Gzhelian–Piacenzian. Multiple R^2: linear = 0.8965, quadratic = 0.9508. Squared term in quadratic model significant at 99.9% confidence limit. **B:** Paraneoptera from Artinskian–Piacenzian. Multiple R^2: linear = 0.9527, quadratic = 0.9728. Squared term in quadratic model significant at 99.9% confidence limit. **C:** Holometabola from Gzhelian–Piacenzian. Multiple R^2: linear = 0.8899, quadratic = 0.974. Squared term in quadratic model significant at 99.9% confidence limit. **D:** Holometabola from Sakmarian–Piacenzian. Multiple R^2: linear = 0.9172, quadratic = 0.9813. Squared term in quadratic model significant at 99.9% confidence limit.

Finally, the growth in Holometabola family richness is also best described by a quadratic model (reduction in AIC of 80.191; 99.9% CI: -0.0324, -0.0169), explaining 8.41% more variance than the simple linear model (Figure 6-5C). Removal of the first two points in that series (Cook's distance nearly 1 and nearly 0.5, respectively) has little effect on the overall outcome (reduction in AIC of 79.743; 99.9% CI: -0.0266, -0.0151), still accounting for 6.41% more variance than the simple linear model.

6.5 Discussion

The main findings of this Chapter are: that origination and extinction rates are higher in Palaeoptera than Apterygota; and that there is no evidence for significant changes in origination and extinction rates from Palaeoptera to Polyneoptera and Paraneoptera to Holometabola. However, origination rates are consistently higher than extinction rates within the above groups, and the average difference is significantly higher in

Holometabola than in Apterygota and Polyneoptera. Paraneoptera and Holometabola show the best evidence for a slow-down in the rate of accumulation of fossil families.

The observation that Palaeoptera have higher rates of origination than Apterygota (Table 6-1) is consistent with the notion of wings being a key innovation in the evolution of insects. Davis *et al*. (2010) found, using sister-taxon comparisons, that under some phylogenetic assumptions, a shift in the net-rate of diversification coincident with the origin of wings can be inferred. In broader sister-taxon comparisons, De Queiroz (1998) showed that the origin of wings in insects is part of a wider pattern predicting high richness amongst winged compared to non-winged taxa. These studies say nothing about the macroevolutionary mechanisms involved, and in principle a higher rate of origination and a lower rate of extinction could both be involved (Mayhew, 2007). Our study provides the first direct evidence from fossils that origination rates are involved as part of this process. Several possible short term ecological mechanisms may be at work: for example, wings may open new adaptive zones leading to reduced carrying capacity limits on species richness (see below), or they may increase the frequency of colonization events that eventually lead to speciation (Mayhew, 2007).

As well as origination rate increases, the data suggest a consistent increase in the rate of extinction between apteryogote and palaeopteran insects (Table 6-1, Figure 6-2), indicating greater turnover in the latter group (Chapter 3). The higher turnover is reflected in the relative dominance of palaeopteran families in Palaeozoic communities followed by a decrease that was only slowly reversed in the Mesozoic and Cenozoic, during which other groups accumulated richness more rapidly (Figure 6-1). It can be questioned if the greater turnover reflects a real biological signal or whether this might instead reflect preservation potential. Apterygote insects tend to be small, saprotrophic and live in cryptic environments such as in soil, whilst Palaeoptera and other insects are often larger, possess wings which are often better preserved, and are able to enter, by flight, environments, such as lagoons, which encourage preservation. Higher preservation potential might lead to greater numbers of first and last appearances, falsely implying higher turnover. However, Labandeira and Sepkoski (1993) tested variation in preservation potential by observing the correlation between the number of extant families per order with the number fossilized in the latest Tertiary. They found a very high correlation in which the only outlying order was Lepidoptera. Although a crude test, this suggests as a first approximation that apterygotes and palaeopterans conform to roughly the same pattern as most other insects, and that preservation potential is roughly equivalent to most other orders. If so, one can ask why extinction rates might be so high in Palaeoptera. Studies of extinction risk amongst extant taxa, for example, tend to show that higher dispersal, which is likely conferred by wings, decreases extinction risk (e.g. Kotiaho *et al.*, 2005). On the other hand, the pattern of high extinction being associated with high origination within Palaeoptera conforms to the pattern found by Stanley (1979) across taxa. One possible explanation, which requires testing, is that the novel environments exploited by pterygote insects turn over more rapidly than the arguably constant and homogeneous soil environments exploited by apterygotes, such that wings have encouraged origination into those environments but as a consequence also extinction. It is notable for example that even Holometabola still have higher extinction rates than Apterygota (Table 6-1). A better understanding of the circumstances under which the evolution of wings took place may help to better understand these issues but such questions remain largely unanswered (Kingsolver and Koehl, 1994).

Despite these differences in the origination and extinction rates, the net rate of diversification (origination minus extinction) does not differ significantly from Apterygota to Palaeoptera. If the averages truly do not differ, this would imply that re-running history might not necessarily give a richer Palaeoptera than Apterygota. The time series plots (Figure 6-2B) suggest some asynchrony between origination and extinction, but originations generally outweigh extinctions, suggesting that there would be a good chance of Palaeoptera surviving to the present again. It is questionable whether wings on their own should be regarded as a key innovation based on this evidence: macroevolutionary rates have apparently been altered, including origination rates, but it is unclear whether the greater resulting turnover must inevitably have led to a higher richness.

In contrast to these differences found between apterygote and paleopteran insects, no other differences in origination or extinction were found for other putative key innovation steps. Some phylogenetic studies (e.g. Mayhew, 2002) have suggested that the origin of Neoptera with their wing flexion was the origin of the major insect radiation, but this is not reflected by a significant difference in origination or extinction rates between Palaeoptera and Polyneoptera. The phylogenetic inference above relies on particular topological assumptions that may not be correct (see Davis *et al.*, 2010), extant species richness data that are incomplete, and also on diversification models that may be questionable (see Rabosky *et al.*, 2012). Yang (2001) tested the difference between the extinction rates of hemimetabolous and holometabolous insects by plots of Lyellian survival (Chapter 4) and found no difference, consistent with extinction data here. The data in this chapter are arguably more robust in that they better reflect extinction throughout the temporal ranges of the different groups, whilst Lyellian survival is very sensitive to events closer to the Recent by virtue of always comparing past faunas with extant faunas.

Yang (2001) also inferred a higher origination rate in Holometabola than Hemimetabola from differences in the net accumulation of taxa across stages (an additive model of change as opposed to the multiplicative models used here). Our analyses do not support this contention (Table 6-1) and indeed the median origination rates in Paraneoptera and Holometabola actually indicate a non-significant decrease in origination rate. The lack of an increase in average origination or decrease in extinction rates from Paraneoptera to Holometabola does beg the question of how Holometabola achieved their current high richness. Their net rate of diversification does not differ from Paraneoptera either (Table 6-1). However, this net rate is significantly higher than Polyneoptera and Apterygota, and extinction rates are also lower than in Polyneoptera. This does suggest that were history to be re-run, Holometabola would predictably be richer in these re-runs than the above two groups, but not richer than Paraneoptera. In all, this does not provide strong evidence for complete metamorphosis being a key innovation.

However, there are two noticeable stages where origination rates in Holometabola are higher than those of other taxa, about 270 (Kungurian; Lower Permian) and 250 (Induan; Lower Triassic) Ma (Figure 6-2). At these points in time, Holometabola changed from being a minor component of the fauna to being a major component of the fauna (Figure 6-1), a feature that was sustained thereafter (Figure 6-2), when macroevolutionary rates were very similar in all winged insects. The relatively short time during which this shift occurred can nonetheless strongly influence subsequent richness, because *per capita* rates of origination and extinction affect richness multiplicatively rather than additively. Groups which start out with different richness and which share the same average *per capita* rate thereafter will accumulate taxa differently simply because of different starting values. This implies that one important reason for the domination of the more derived Holometabola and Paraneoptera is how they responded to these key moments in Earth history when the groups which dominated the Palaeozoic declined. Similar scenarios have been constructed to explain changes in richness in marine invertebrates (Alroy, 2010*a*). The replacement of Palaeoptera and Polyneoptera by Holometabola may be linked with metamorphosis. Possibly Holometabola are better suited to speciating rapidly into newly vacant niches than other insects. Fast larval development, allowed by dedicated feeding morphologies in the larvae, may increase rates of population growth, and the exploitation of ephemeral habitats, contributing to recovery from population bottlenecks, and more rapid adaptation to new environments. These assertions, whilst plausible, largely lack supporting evidence.

It is of course possible that very small differences in the average rates are truly present between some of these groups but not detected. Differences are unlikely to be detected when the average rates are low, whilst because they affect richness multiplicatively, small differences in average rates can lead to noticeable differences in richness. It is also possible that differences are not present at the family level but present at other taxonomic levels. However, even if either of these possibilities were true, our data still rule out more extreme key innovation scenarios.

As well as the above major groups, this chapter considered comparisons between three orders (mayflies, stoneflies, and caddisflies) which differ in putative key innovations but which share a common basic ecology. These comparisons generally conform to the results for the more inclusive groups above. There are no detectable changes in the origination or extinction rates from mayflies to stoneflies to caddisflies. Differences between origination and extinction rates were smallest for mayflies and stoneflies, but were highly significant for caddisflies, reflecting their higher richness.

Future studies may wish to consider other traits which are more dispersed through phylogeny where multiple comparisons of rate differences between sister clades can be compared, such as wing-shape symmetry (see Wootton, 2002) or ecological factors such as feeding mechanisms. However, the latter suggestion runs into the difficulty of being difficult to define for many extinct families.

One of the mechanisms by which key innovations may operate is through opening up new adaptive zones that lift density-dependent limits to richness (Heard and Hauser, 1995). Taxa that are limited in this regard may thus be expected to show a slowdown in the rate of accumulation of new taxa with time. In fact the taxa that show the strongest evidence of such limits are the Holometabola and Paraneoptera (Figure 6-5), which also have the highest richness. This suggests that the effect of putative key innovations has not been to release organisms from competitive limits but instead allows organisms to approach limits that would otherwise not be met.

The interpretations above assume that the rates and richnesses are primarily due to changes in underlying macroevolutionary processes. However, other interpretations may be possible. It is widely acknowledged that sampling biases strongly affect the number of taxa discovered in different stages of the fossil record (Peters and Foote, 2002; Peters, 2005; Smith and McGowan, 2005; Lloyd, 2012; Chapter 4). Although this chapter has taken no explicit steps to correct for sampling bias within the data that are analysed, comparisons are entirely made across the same sets of stages and thus control for the underlying sampling biases that vary across stages. Also, in the tests for logistic growth, the important findings relate to differences across groups over similar time intervals, and thus although the true trajectories of the growth curves may be different to those outlined here (in particular, probably flatter due to the Pull-of-the-Recent; Chapter 4), the comparisons between groups are probably qualitatively robust.

There may still be taphonomic or other biases that affect different groups differently within stages, although as suggested above current data give no indication that this is a serious issue at the order level or above. Standard methods to control for sampling effort (Lloyd, 2012) would do nothing to control for these taphonomic issues, and instead subsets of the data would need to be used that consider only some kinds of deposit, a task to which the current data are ill-suited. There may be more subtle biases affecting different groups that are harder to detect and tease apart. For example, groups that dominate close to the Recent may be disproportionately affected by the Pull-of-the-Recent (Chapter 4), which inflates origination rates and reduces extinction rates. However, the low extinction rates of Holometabola were present even from the beginning of the Triassic (Figure 6-1), before the Pull-of-the-Recent became significant (Chapter 4).

In conclusion, the analyses considered in this chapter suggest that the origin of flight raised macroevolutionary rates in insects. However, it remains uncertain whether this would inevitably have led to Palaeoptera being richer than Apterygota. There is however evidence that Holometabola would inevitably have become richer than Apterygota and Polyneoptera, but no evidence that metamorphosis itself is a key innovation. Holometabola have achieved their Recent dominance by temporarily high origination rates at the Palaeozoic/Mesozoic boundary that allowed them to replace the Palaeozoic faunas, and by a subtle difference in the net rate of diversification compared to some other groups primarily driven by a lower extinction rate. This consideration of new fossil data suggests specific and novel mechanisms by which evolutionary novelties have operated which can be further tested by future functional and ecological studies. It also suggests that organism-specific factors strongly affect insect macroevolution alongside environmental parameters (Chapter 5).

Chapter 7

General Discussion

7.1 Introduction

The overall aim of this thesis has been to progress understanding of the evolutionary history of the insects. The first step was to build on past datasets of the ranges of fossil insect families by incorporating recent developments in the stratigraphic dating of deposits, taxonomic revisions, novel family descriptions, and changes to the known ranges of families already described, using data gleaned from the extensive palaeoentomological literature published up to the end of 2009. These new data (Appendix 3) were compiled in an electronic relational database of my own design (Chapter 2) which could then be used to answer a series of palaeontological and macroevolutionary questions.

In Chapter 3, I asked how the new dataset differs from previous equivalent data and investigated how the respective richness, origination and extinction series have changed as a result, finding that there have been substantial changes in the fossil record since the early 1990s and, although broad patterns remain similar, short-term variations in richness have changed. These differences suggest that inferences made about causal mechanisms in insect macroevolution may have changed also. However, this is based on the face-value record of range-through richness counts. In Chapter 4, I investigated for the first time the relationship between the insect fossil record and measures of the record of fossil insect-bearing deposits, as well as measures of sampling effort. I used these relationships in a first-pass attempt to control for sampling biases in the richness, origination, and extinction records. These adjusted estimates indicate that the Carboniferous peak, Cretaceous plateau and Eocene jump in the observed richness are likely artefacts of rock record and sampling biases. Other features, such as the Permian rise and peak, high turnover at the end of the Permian and a Late Jurassic rise, seem more robust. Both face-value and adjusted richness series were then taken forward for further analyses.

In Chapter 5, I tested the association of richness, origination and extinction rates with a suite of biotic and abiotic variables, thus addressing the relevance of the Red Queen and Court Jester paradigms, finding that the potential drivers of insect diversity are different before and after correcting for sampling bias. I also asked if the data best fit expansionist or logistic models of clade growth, finding that for hexapods on the whole, there is significant nonlinearity in log richness increase, suggesting a logistic slow-down in growth towards the Recent. This is found for both face-value and adjusted richness estimates. In Chapter 6, I tested the evidence for a number of key evolutionary innovations in the hexapods, finding that wings appear to be a key innovation in the evolution of insects with rates of origination and extinction significantly higher in Palaeoptera than Apterygota; other groups' rates were not significantly different from each other. The net diversification rate of Holometabola (insects with complete metamorphosis) is significantly higher than Apterygota and Polyneoptera, but not significantly different from those of other groups. Holometabola appears to have achieved its present high family richness not by great changes in the average rates of origination or extinction but by a subtle widening of the difference between origination and extinction relative to some other groups, and by temporary peaks in origination at key moments in evolutionary history. The groups with the highest modern day family richness, Paraneoptera and Holometabola, show the strongest slow-down in accumulation of families through time, suggesting that there may be an upper limit to richness which these groups are approaching.

In the remainder of this chapter I outline the significance of these findings and achievements, chapter by chapter, in the context of previous work. I then briefly consider the significance of the thesis as a whole and suggest profitable areas for future researchers to pursue.

7.2 The updated hexapod fossil record

Since the datasets of Ross and Jarzembowski (1993) and Labandeira (1994) were compiled, there have been substantial changes and additions to the hexapod fossil record. The new dataset presented in Chapter 3 and Appendix 3 has over 500 new families compared to Ross and Jarzembowski (1993) and 430 new families compared to Labandeira (1994), while range changes are seen in over 50% of the families in the new dataset and only 8–10% have shown no change (Figure 3-2). The richness curves derived from these three datasets are very highly correlated; however, detrending reduces this substantially, indicating that there have been changes in the pattern of short-term variation seen in the fossil record of hexapods since the early '90s (Table 3-1).

Although the broad pattern of described richness through time depicted remains similar, with described richness increasing steadily through geological history and a shift in dominant taxa after the Palaeozoic, some noticeable differences exist (Figure 3-4A). There is reduced Palaeozoic richness, peaking at a different time, and a less pronounced Permian decline. A pronounced Triassic peak and decline is shown and a more pronounced Cretaceous rise with little subsequent decline. Origination and extinction rates are broadly similar to before, with a broad decline in both through time but with episodic peaks, including end-Permian turnover. Origination more consistently exceeds extinction than before and exceptions are mainly Palaeozoic.

These short-term variations are novel in that the simplest expectation from additional data is for an even increase in richness across the whole time series, so the reduced Palaeozoic richness is particularly surprising while the largest increases relative to the older datasets are concentrated in the Upper Triassic and Lower Cretaceous (Figure 3-4A). The robustness of this dataset is difficult to gauge: while the broad pattern of increasing richness preserved from the previous datasets suggests that a further 15 years of additional data may not affect this much, the concentration of changes into just a few stages conversely suggests that the curve is sensitive to new discoveries of spectacular fossil deposits which garner a disproportionate amount of intense collecting and publishing effort by palaeoentomologists, relative to the rest of the temporal record. Despite the difficulties in dealing with taxonomic levels lower than the family for fossil insects, the focus of attention may shift towards genus richness through time. Conrad Labandeira (pers. comm., 2012) is compiling a dataset of insect genus range data, which will be of intense interest for comparing with that of the family level. Further to this, databases compiled by individual researchers and kept on private computers are fast becoming a thing of the past, with advances in biodiversity informatics, typified by such resources as the Encyclopedia of Life (EOL), the Global Biodiversity Information Facility (GBIF) and, of particular relevance here, the Paleobiology Database (PBDB), becoming major global repositories for information on the natural world. However, datasets such as that provided here in Appendix 3, as well as those of Labandeira (1994) and Ross and Jarzembowski (1993), continue to find utility as benchmarks of the fossil record at the time, as well as representing more complete datasets for dating phylogenies of evolutionary lineages than genus level datasets.

7.3 Bias correction

In Chapter 4, I found that measures of the insect-bearing rock record (counts of deposits) and sampling (counts of collections) correlate strongly with the per-stage counts of first and last family occurrences, justifying an attempt to correct for these potential biases (Smith and McGowan, 2011). Based on the modelling approach of Smith and McGowan (2007) and Lloyd (2012), the novel step taken was to estimate corrected originations and extinctions, rather than richness directly, and to use those adjusted time series to estimate how richness would appear if sampling opportunities were equal across all stages. The corrected curves show important differences from the face-value richness curve presented in Chapter 3.

Previous, uncorrected, richness curves (Labandeira and Sepkoski, Jr., 1993; Jarzembowski and Ross, 1996; Ross *et al.*, 2000; Chapter 3) have suggested, variably, peaks in richness in the Carboniferous and Permian, an end-Permian extinction, a Late Triassic peak, a Late Jurassic peak, a plateau in the Cretaceous–Palaeocene and a sharp increase in the Eocene. The latter two features are not replicated by the sampling-adjusted curve (HBC RT; Figure 4-6), suggesting that they are attributable to changes in the rock record and sampling intensity. The apparent Carboniferous peak in insect richness, after Romer's gap (Ward *et al.*, 2006), coinciding with the first winged insect fossils, also coincides with abundant fossil bearing deposits and is not replicated in either the sampling- or rock-adjusted curves. An apparent hexapod family decline in the Cretaceous seen in previous datasets has become more of a plateau, while sampling-adjusted series suggest this is merely an artefact of low preservation and sampling intensity. This throws into doubt the interpretation that the rapid spread of angiosperms during this interval had an initial detrimental effect on insect communities (Jarzembowski and Ross, 1996; Labandeira, 2005). Finally, the decline in richness during the Late Permian seen in the observed data is greatly reduced in the sampling-adjusted curve, while the rock-adjusted curve shows an increase with a sharp drop at the end-Permian. Origination and extinction rates around the Permian-Triassic boundary are seen to be high in all three series (Figure 4-7).

The similarities, between the adjusted and non-adjusted time series, are as important as the differences, as these indicate which features of the face-value richness record are more robust. Evidence is retained for the presence of a Permian peak in richness, coinciding with a radiation of Palaeoptera and Polyneoptera, a Triassic peak, coinciding with radiations in all major hexapod groups, and an end-Triassic loss of families, again across all groups. A mid-Jurassic radiation is also retained.

The overall trajectory of these curves likely suffers from a strong Pull-of-the-Recent effect, where there is tendency for the ranges of fossil taxa to be pulled forwards towards the present, inflating apparent richness in range-through datasets (Alroy, 2010*c*). In these data, this tendency probably derives mainly from the influence of extant taxa, which do not have their last fossil occurrence recorded. By looking at the proportion of taxa within each stage which remain extant today (Figure 4-2), we can see that, by the Early Cretaceous, over half of the families present are extant. If they had had their last fossil appearance recorded rather than having their ranges simply pulled through to the Recent, it is likely that extinction rates would appear higher and taxonomic richness nearer the Recent would appear lower.

The algorithm used to adjust the face-value richness data represents a novel application of a pre-existing method originally intended for use on occurrence data. This allows the identification of potentially artefactual features of the face-value fossil record in a numerical way, which otherwise would remain a matter of conjecture. The method, as outlined in Chapter 4, is a first-pass attempt at such corrections and may be developed further. For instance, pre-transformation of the data may be desirable, which may then reduce the need for the use of higher polynomial models. The various proxies for the rock record might be developed further, for example using rock outcrop or exposure area instead of formations counts, or publications instead of collections (Benton *et al.*, 2011). Modelling methods for the correction of rock record or sampling biases are gaining in use, particularly with taxa for which the large numbers of samples required for sampling standardization are not available (e.g. Barrett *et al.*, 2009; Butler *et al.*, 2009, 2012; Benson *et al.*, 2010; Benson and Butler, 2011; Benson and Mannion, 2012; Lloyd, 2012). Ideally, the results of both modelling methods and sampling standardization will converge on similar curves, giving confidence to the results of both methodologies (Smith *et al.*, 2012). In principle, the new method employed here could be used for range-through data for any taxonomic group providing there is enough data to characterise the expected relationship between originations, extinctions and the rock/sampling proxy used.

7.4 Environmental and biotic correlates of hexapod richness

Multivariate models including a broad range of environmental proxies and fossil data identify the following possible drivers of hexapod richness: the face-value richness record is predicted by temperature, atmospheric oxygen concentrations, and plant richness; for fossil data that have been adjusted for sampling effort, other abiotic variables tend to predominate, such as sea level and marine productivity.

The Red Queen paradigm was tested here by looking for associations between richness, originations and extinctions within hexapods, as well as between these measures and plant richness through time. The short term associations between richness, origination and extinction contain some possible evidence of density-dependent processes in clade growth but likely reflect several other factors. The strongest indication of density-dependence is from the collections-adjusted data, where richness is associated with a future lowering of originations. In the adjusted data is also a positive correlation between origination and extinction, an association that could represent density-dependence as well, but the lack of lags in the system makes this uncertain. It is possible that this represents sampling artefacts which have not been effectively removed by the sampling adjustment procedure used in Chapter 4, leading to concentrations of originations and extinctions in well-sampled stages. A negative association between hexapod family richness and plant richness, and positive associations between plant richness and hexapod extinction rates was found, but only in the face-value record. However, no bias-adjustment was attempted on the plant data, so this may explain why the association exists only in the unadjusted hexapod data if both groups are subject to similar geological preservation biases.

A further test of the Red Queen paradigm involves the detection of logistic slow-down in the accumulation of families through time, indicating a possible limit or ‘carrying capacity’ for richness. This was tested for hexapods on both face-value and sampling-adjusted range-through data by comparing the fits of linear and quadratic curves to log richness. A quadratic curve shows a significantly better fit to both corrected and uncorrected time series than the linear model, with the extra complexity of the quadratic term justified by the reduction in AIC value (Figure 5-2). This is in keeping with Labandeira and Sepkoski (1993), who noted that the rate of accumulation of fossil insect taxa had slowed towards the present.

For the abiotic, Court Jester variables, the results vary depending on whether the fossil data has been adjusted for measures of sampling intensity, as has been found for marine taxa (Alroy, 2010*b*; Mayhew *et al.*, 2012). Unadjusted, face-value data richness is positively associated with atmospheric oxygen concentrations, consistent with the idea that flying organisms benefit energetically from such conditions. This coincides with lower turnover of taxa (lower origination and extinction rates). There is also a positive association between $\delta^{18}O$ and richness or origination, indicating relatively higher richness after falls in temperature (inverse $\delta^{18}O$). Additionally, a number of marine environmental proxies appear to significantly predict the hexapod fossil record. For example, both $\delta^{34}S$ and $^{87}Sr/^{86}Sr$, often taken to indicate organic and inorganic nutrient status in the oceans, significantly predict the unadjusted record in multivariate models.

The relationships are positive between $\delta^{34}S$ and richness, indicating that a higher organic nutrient status in the ocean is associated with higher insect richness. The relationships are negative for $^{87}Sr/^{86}Sr$ and predict unadjusted origination, extinction, and adjusted richness. In addition to these relationships, $\delta^{13}C$ significantly predicts macroevolutionary variables, mainly in the adjusted fossil data.

Finally, sea level change is positively associated with richness and turnover in the adjusted fossil data. High sea levels are well known to promote marine invertebrate richness (Purdy, 2008; Hannisdal and Peters, 2011; Mayhew *et al.*, 2012), which likely occurs through the flooding of continental shelves, increasing suitable shallow sea habitats. High sea levels could, in contrast, promote diversity and turnover in terrestrial faunas by promoting isolation and endemism through the flooding of continental interiors. Alternatively, many of these relationships could be spurious due to the highly integrated nature of the Earth-Biosphere system (Hannisdal and Peters, 2011).

This work represents the first statistical comparisons between the full hexapod fossil record with environmental variables. Regardless of the interpretations made of the specific results here, it is apparent that correcting for rock and sampling biases does matter and changes the relationships seen with other variables. The robustness of the findings may be questioned on the grounds that improvements to the proxy datasets used may change the relationships recovered. Furthermore, since the sampling-adjusted richness series recovers different associations with environmental proxies to the face-value series, it would increase confidence in these results to have independent verification from a sampling standardized series based on occurrence data. Many variables which could have influenced diversification were not tested here, including but not limited to continental dispositions, volcanism, extra-terrestrial impacts, biome areas and distributions, and other palaeoclimatic variables. In the case of volcanism and impacts, widely considered to have played an important if not exclusive role in the late-Permian and end-Cretaceous extinctions, no appropriate datasets which lend themselves to the type of analyses performed here were available. Given the highly interconnected nature of the Earth-Biosphere system, new statistical methods such as information transfer (Hannisdal and Peters, 2011) may help in future to untangle webs of causation.

7.5 Density dependence and key innovations

Evidence for potential key innovations was investigated by testing for significant differences in origination and extinction rates, in the first instance, between the following groups: Endognatha vs. apterygote Ectognatha (insect *bauplan*); ‘Apterygota’ vs. Palaeoptera (wings); Palaeoptera vs. Polyneoptera (wing folding); and Paraneoptera vs. Holometabola (complete metamorphosis/holometabolism). I found that origination and extinction rates are higher in Palaeoptera than Apterygota, consistent with the notion of wings being a key innovation in the evolution of insects, but that there is no evidence for significant changes in origination and extinction rates from Palaeoptera to Polyneoptera and Paraneoptera to Holometabola. However, origination rates are consistently higher than extinction rates within all of the above groups, and the average difference is significantly higher in Holometabola than in Apterygota and Polyneoptera, but not compared to Paraneoptera. This suggests that, were history to be re-run, Holometabola would have inevitably ended up with higher richness than Apterygota or Polyneoptera but not necessarily higher than Paraneoptera. The eventual dominance of Holometabola appears to come down to two noticeable stages where its origination rates are higher than those of other taxa; about 270 (Kungurian; Lower Permian) and 250 (Induan; Lower Triassic) Ma (Figure 6-2). At these points in time, Holometabola changed from being a minor component of the fauna to being a major component of the fauna (Figure 6-1), a feature that was sustained thereafter (Figure 6-2), when macroevolutionary rates were very similar in all winged insects.

Tests for significant non-linearity in the accumulation of log richness through time were performed for these same subgroupings of hexapods. Although this was found for insects on the whole (Chapter 5), indicating a logistic slow-down in the rate of accumulation of new families in the fossil record, this signal is in fact dominated by the Paraneoptera and Holometabola (Chapter 6), which show much stronger non-linearity. Evidence for logistic growth in Apterygota, Palaeoptera and Polyneoptera is equivocal.

Findings consistent with wings as a key innovation in the evolution of insects give support to previous studies. Davis *et al*. (2010) found that a shift in the net-rate of diversification coincident with the origin of wings can be inferred, and De Queiroz (1998) showed that the origin of wings in insects is part of a wider pattern predicting high richness amongst winged compared to non-winged taxa. Fossil data can help elucidate the macroevolutionary mechanism at work, and the novel contribution here is evidence that origination rates have been part of this process.

It is perhaps surprising that complete metamorphosis was not seen necessarily to be a key innovation in these tests. Yang (2001) tested the difference between the extinction rates of hemimetabolous and holometabolous insects but found no difference, consistent with the extinction data here. However, he inferred a higher origination rate in Holometabola based on the net accumulation of taxa across stages (which is an additive model rather than a multiplicative model like that used here), an interpretation not supported by the analysis here. The differences compared are based on *per-capita* rates, rather than just the raw counts of first and last appearances. I believe this to be a strength of the analyses, as diversification is a multiplicative process and so early or occasional differences may quickly become very large differences, while the underlying rates in fact remain largely similar. However, these rates are derived in part from the range-through richness value and so a future comparison based on rates derived from occurrence data would help to support or undermine these findings. The choice of geological stage as the observation points may be problematic as they are of variable length, some of which are very short and may contain little data. One solution is to combine some stages to reduce heterogeneity in bin length (e.g. Alroy *et al.*, 2008) or to discard stages and instead use regular, 10 million year bins (e.g. Clapham and Karr, 2012; Mayhew *et al.*, 2012). Additionally, no correction was applied to the data for the relationships of originations and extinction with rock and sampling proxies, and these may differ between groups. Further interesting avenues of research may be to test whether there is any systematic effect of ecological niche, rather than taxonomic group, and also whether genus-level data show different patterns to that of the family data. However, these questions will have to await the maturation of appropriate datasets.

7.6 Significance and further work

The new dataset of hexapod family fossil ranges (Chapter 3; Appendix 3) represents an additional 15 years of data from a rapidly expanding field compared with the previous available compendia of Ross and Jarzembowski (1993) and Labandeira (1994). These previous datasets now have largely historical interest only and should not be used for future macroevolutionary research. Studies based on them ideally require re-assessment. A specific use of this dataset, not utilised in this thesis, is for scientists interested in the details of individual fossil families, for example for dating phylogenies above family level (e.g. Davis *et al.*, 2011). That the richness curve derived from the new data shares practically no short-term variation with the previous datasets suggests that the changes in pattern over time remain volatile and a further 15 years of additional data may change the richness curve again.

The major turnover in dominant taxa (Figure 3-5) accompanying the Permian to Triassic interval is strongly reminiscent of the end-Permian extinction in many other taxa (e.g. Brusatte *et al.*, 2008). In the hexapod case there was a replacement of the Palaeozoic fauna of mainly Palaeoptera and Polyneoptera to a fauna dominated by Paraneoptera and Holometabola, which appear to have suffered little reduction in their richness (Jarzembowski and Ross, 1996; Labandeira, 2005). Studies on the coherence of these different faunas would be useful (see Alroy, 2004). Despite the evidence for a Permian extinction, the new richness data leave no evidence of an end-Cretaceous extinction, in common with previous data (Ross *et al.*, 2000; Labandeira, 2005). Given the known widespread ecosystem impacts of this event, it is difficult to imagine that insects were completely unaffected but extinction may have occurred below the family level. Some genus-level data provide some support for this (Jarzembowski and Ross, 1996), as do some studies of trophic interactions (Labandeira *et al.*, 2002), but others suggest a weaker extinction in insects than in other taxa (Wappler *et al.*, 2009). The completion of Conrad Labandeira's genus-level dataset will help to shed light on this but he feels there is still a significant time until this will happen (C. C. Labandeira pers. comm., 2012).

Analyses of the marine invertebrate fossil record have found that controls for sampling can alter the results of correlations with environmental variables (Alroy, 2010*b*), although this can depend on the type of control used (Mayhew *et al.*, 2012). This study provides further support for that notion, and whilst interesting, it does raise the question of whether the unadjusted data or the adjusted data carry the greatest biological signal. Recent work on the marine invertebrate record (Smith *et al.*, 2012) has suggested that rock-record correction tends to have very similar effects to sample-standardization, suggesting convergence on an underlying biological signal, although there is no guarantee that the same will be true for hexapods. Erroneous rock record data may make the situation worse rather than better (Benton *et al.*, 2011).

The tests of key innovation hypotheses presented in Chapter 6 are to my knowledge the first explicit comparisons of both origination and extinction rates through time between constituent groups of fossil hexapods. While confirming the findings of several other studies that wings are a key innovation, they undermine the perception that the advent of complete metamorphosis in the Holometabola must have coincided with an increase in origination rates. This is based on family-level data and so a repeat of these tests with genus data would be desirable.

A full understanding of macroevolution for any taxonomic group requires consideration of the fossil record as the only direct evidence for past changes. To this end, many palaeontologists over the years have engaged in the compilation and analysis of large databases holding records of either fossil taxon ranges or occurrences, with notable past efforts including Sepkoski's marine family compendium (Sepkoski, Jr., 1982, 1992) and the multi-authored Fossil Record 2 (Benton, 1993). Recent work has focussed on the Paleobiology Database, a multi-contributor, dynamic, online database which is increasingly being seen as the standard for fossil diversity studies. There are a number of advantages to this approach. Future work on the hexapod fossil record should undoubtedly focus on compiling an occurrence-based dataset rather than one based on the range-through method (Alroy, 2010*c*). Ideally, greater involvement from the palaeoentomological community in entering new data from their own publications would make this process much quicker and less labour intensive for any one person. The work presented here represents a benchmark for the state of our knowledge of the hexapod fossil record at the end of 2009, and may be used in future as a point of reference for changes in our knowledge through time.

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Appendix 1

Taxonomic scheme adopted in the database. Numbers refer to level of nesting in the hierarchy. Orders nested directly within each clade and not further down the hierarchy are listed immediately beneath the numbered clade name. Relevant synonyms are placed in parenthesis.

1. Hexapoda

    2. Entognatha
        Diplura
        Protura
        Collembola

    2. Ectognatha/Insecta
        Archaeognatha (Machilida, Monura)

        3. Dicondylia
            Zygentoma (Lepismatida)

            4. Pterygota
                Ephemeroptera (Ephemerida, Ephemeridea, Plectoptera)

                5. Metapterygota

                    6. Palaeodictyopterida
                        Palaeodictyoptera (Dictyoneurida)
                        Megasecoptera (Mischopterida, Eubleptidodea)
                        Dicliptera (Archodonata, Permothemistida)
                        Diaphanopterodea (Paramegasecoptera)

                    6. Odonatoptera
                        Geroptera
                        Protodonata (Meganisoptera)
                        Odonata

                    6. Neoptera
                        Paoliida (Protoptera)

                        7. Polyneoptera
                            "Protorthoptera"
                            Dermaptera
                            Grylloblattodea
                            Mantophasmatodea
                            Plecoptera
                            Embiodea
                            Zoraptera
                            Phasmatodea
                            Caloneurodea
                            Orthoptera (Titanoptera)

continued on next page…

7. Polyneoptera *continued…*
    Mantodea
    "Blattodea" (Blattaria, Protoblattoidea)
    Isoptera

7. Eumetabola

    8. Paraneoptera
        "Psocoptera"
        Phthiraptera (Mallophaga, Anoplura)
        Thysanoptera (Thripida)
        Hemiptera

    8. Holometabola
        Coleoptera (Scarabaeida)
        Raphidioptera
        Megaloptera
        Neuroptera (Planipennia)
        Hymenoptera (Vespida)
        "Mecoptera" (Panorpida)
        Siphonaptera (Pulicida)
        Strepsiptera
        Diptera
        Trichoptera
        Lepidoptera
        Miomoptera
        Glosselytrodea (Jurinida)

Appendix 2

What follows is a detailed description of the php code used to create the output list from the database (see Appendix 3).

The programme written has 9 custom functions which are called upon to extract the right data out of the database and output it to the results page.

```
function do_query()
function list_clades()
function list_orders()
function list_families()
function list_specimens()
function extreme_specimen()
function list_family_synonymies()
function list_order_synonymies()
function qualification()
```

The brackets () (also known as the 'bubble') after the function names indicate that this is a function. The brackets can be populated with comma-delimited arguments which may vary and change the way the function behaves and change the output of the function. Custom functions are set up to accept as many or as few arguments required and they are only necessary if the function needs special information with which to execute. For example, the list_orders() function will accept an argument of 'clade_id', which will vary on each pass as the programme is cycling through the clades as it will be passed to the function on each iteration of the list_clades function. This will be used in the database query and hence change the result.

Listed above are the 9 functions built for this purpose. However, PHP has native functions that can be called upon which are used in the programme.

What follows is a brief overview of some of the native PHP functions and constructs used:

```
if([condition]):
 // Do something
else:
// Do something else
endif;
```

This is an 'if' statement. If the condition in the bubble is matched, the function will execute the code immediately after condition, otherwise it will execute the code in the 'else' portion of the function. The 'else' portion is optional, so 'if' statements can be used purely to do something if the condition is matched.

```
while([condition]){
// Do something
}
```

Similar to the 'if', the ‘while’ function will continue to do something while the condition is matched (where an 'if' will only do something once). The 'while' function has mostly been used when interpreting the result returned from the database, e.g.:

```
while($row=mysql_fetch_object($result)){
 // Do something
}
```

This example uses another native PHP function (`mysql_fetch_object($result)`) which runs a query and returns the results from the database. The ‘while’ in this case will continue to execute for each row the query returns. This is a key feature in the programme because it allows the cycling through of each clade and, within that cycle, calling a separate function to list the orders and so on.

The third important native function used in the programme is the '`echo()`' function. 'echo' simply means 'write to the window', so text wanted in the final output is passed through this function. This consists of a mixture of static text (the formatting remains consistent regardless of the data values from the database) and dynamic text (text that will vary for each row in the database).

These functions are 'nested', so although they have been independently defined, they do not do anything until they are requested and it is the point at which they are requested that determines what impact they have on the output. As such, they are called in the order that their output is needed to appear in the window. This is listed in the 4-step script objective above.

The first step to call is the `list_clades()` function. While cycling through the clades, the `list_orders()` function is called thereby sending in the current clade as an argument to vary the output of the `list_orders()` function. While cycling through the orders the `list_families()` function is called, again making it specific to the current order. This means that the entire programme is sequenced and the output can be started by simply calling the first function:

```
list_clades()
```

Once this is called, the other functions are sequenced and the various procedures follow like a chain of dominos.

Explanation of PHP custom functions

What follows is a break down each function in the order they are called in the programme.

‘**`list clades`**’

```
function list_clades($clades_id = 2,$pref="")
{

      $result = do_query("SELECT * FROM `clades` WHERE clades_id !=
```

```
".$clades_id." AND clade_id = ".$clades_id);
      while ($row = mysql_fetch_object($result)) {
      echo "<br />\begin{center}\\textbf{".$row-
>clade_name."}\end{center}<br />";
            list_orders($row->clades_id);
            list_clades($row->clades_id,$pref."-->");
      }

}
```

function `list_clades()` explained:

Objective of function: Output name of clades belonging to argument 'clades_id'.

Arguments: `$clades_id` is the first argument and has a default value unless a different one is provided. The default is '2', which is the highest level of clades in the database. `$pref` allows a prefix to be sent to the function which will be appended to the prefix sent in before and hence illustrate the level of nesting within the clades. This is optional.

Description of `list_clades()`:

1) Run the query on the database to return all entries from the clades table whose `clade_id` (parent) matches the one sent to the function as argument #1 – or, if none was supplied, where the parent `clade_id` is 2.
2) While there is a result (i.e. for every row) output some formatted text, then the value of the field '`clade_name`' from this current row, then add some more pre-formatted text. Echo (or output) this text to the window.
3) Run the `list_orders` function, sending in this row's `clades_id` value to the function as an argument.
4) List the clades that belong to this current clade, again sending in this current clade as an argument.

‘**`do query`**’

```
function do_query($sql)
{
      mysql_connect("localhost", "fullfatm_insect", "insect");
      mysql_select_db("fullfatm_insectrec");
      return mysql_query($sql);
}
```

function `do_query()` explained:

Objective of function: Connect to the database, run a query and return the results.
Arguments: This function has one argument, the SQL query to be run on the database.

Description of `do_query()`:

1) Connect to the database
2) return the results of the query

'**list orders**'

```
function list_orders($clade_id = NULL,$pref="")
{
      if($clade_id != NULL):
            $result = do_query("SELECT * FROM `orders_units`,
`orders_names_list` WHERE `orders_units`.`clade_id` = ".$clade_id."
AND `orders_names_list`.`orders_names_list_id` =
`orders_units`.`order_name_list_id` ORDER BY REPLACE(order_name, '\"',
'')");
            while ($row = mysql_fetch_object($result)) {
                        echo "<br />\begin{flushleft}O. ".$row-
>order_name." \citealt*{".$row->reference_id."}\n\r";
                        //echo "(";
                        list_order_synonymies($row->orders_units_id);
                        //echo ") ";
                        $first = extreme_specimen($row-
>orders_units_id,"DESC");
                        $last = extreme_specimen($row-
>orders_units_id,"ASC");
                        echo $first->period_name."(".$first-
>stage_name.")-".$last->period_name."(".$last-
>stage_name.")\end{flushleft}<br />";
                        list_families($row->orders_units_id);

            }
      endif;
}
```

function `list_orders()` explained:

Objective of function: Output the order name, synonymies in brackets, first and last specimens and then list the families belonging to the order. Do this for each order returned in the database results.

Arguments: `$clade_id` will determine which orders to get as they will need to belong to the supplied argument. $pref is an optional prefix value which will be appended to on each level of nesting within the orders.

Description of `list_orders()`:
1) Run the query on the database to get all orders belonging to the supplied clade.
2) For each row (while...) output formatted text and the order name of this current row.
3) Output a bracket character.
4) Run the `list_order_synonymies()` function, sending this order as the

argument.
5) Output a closing bracket.
6) Establish '`$first`' as being the first specimen by running the `extreme_specimen()` function and sending in '`DESC`' as the second argument.
7) Establish '`$last`' as being the last specimen by running the `extreme_specimen()` function and sending '`ASC`' in as the second argument.
8) Output formatted text and the period name and stage name of the first and last specimens.
9) Run the `list_families()` function to list families belonging to this order.

'**list order synonymies**'

```
function list_order_synonymies($order_id)
{
      if($order_id != NULL):
            //echo "<ul>";
            $result = do_query("
SELECT * FROM orders_names_list as `on`
JOIN `orders_names_synonymies` as `os` ON `os`.`order_name_list_id` =
`on`.`orders_names_list_id` WHERE `os`.`order_unit_id` = ".$order_id."
ORDER BY `on`.`order_name` ASC");



            $synarr = array();


            while($syn = mysql_fetch_object($result))
            {
                  //echo "RESULTS!";
                  array_push($synarr,$syn->order_name);
                  //echo $syn->family_name.", ";
            }


            if(!empty($synarr)):
                  $size = sizeof($synarr);
                  $count = 1;
                  echo "(";
                  foreach($synarr as $order):
                  echo $order;
                  if($count < $size):
                  echo ", ";
                  endif;
                  $count++;
                  endforeach;
```

```
                echo ") ";
            endif;

            //echo "</ul>";
      endif;
}
```

function `list_order_synonymies()` explained:

Objective of function: Output a list of synonyms for a given order.

Arguments: `$order_id` – the order in which to list the synonyms.

Description:

1) Run the query to return the names.
2) For each row, add it to a list (an 'array') of synonyms.
3) If the list is not empty, output a bracket.
4) For each name in the list output its value.
5) If the iteration is not at the end of the list, output a comma.
6) At the end of the loop, close the bracket.

‘**extreme specimen**’

```
function extreme_specimen($order_id,$order)
{
      if($order_id != NULL):
            //echo "<ul>";
            $result = do_query("
SELECT
`sp`.*,`sd`.`deposit_name`,`sl`.*,`sa`.*,`co`.*,`ts`.*,`tep`.*,`tp`.*,
`fu`.*,`or`.* FROM `specimens` as `sp`
 join `space_deposits` as `sd`
 ON `sp`.`space_deposit_id` = `sd`.`space_deposits_id`
 join `families_units` as `fu`
ON `sp`.`family_unit_id` = `fu`.`families_units_id`
 join `orders_units` as `or`
ON `fu`.`order_unit_id` = `or`.`orders_units_id`
join `space_localities` as `sl`
 ON `sd`.`space_locality_id` = `sl`.`space_localities_id`
join `space_areas` as `sa`
 ON `sl`.`space_area_id` = `sa`.`space_areas_id`
join `space_countries` as `co`
 ON `sa`.`space_country_id` = `co`.`space_countries_id`
 join `time_stages` as `ts`
 ON `sd`.`time_stage_id` = `ts`.`time_stages_id`
```

```
join `time_epochs` as `tep`
 ON `ts`.`time_epoch_id` = `tep`.`time_epochs_id`
join `time_periods` as `tp`
 ON `tep`.`time_period_id` = `tp`.`time_periods_id`  WHERE
`fu`.`order_unit_id` = ".$order_id." ORDER BY `ts`.`date_base`
".$order." LIMIT 1");
            return mysql_fetch_object($result);


            //echo "</ul>";
      endif;
}
```

`function extreme_specimen()` explained:

Objective: To return the row of the specimen belonging to a given order which is either the first or last occurrence, depending on the value of the second argument.

Arguments: `$order_id` – the order which the specimen must belong to. `$order` – the chronlological order to sort the results by.

Description of `extreme_specimen()`:

1) The function is essentially one complicated query which joins up all the tables relating the specimen to the time periods and sorts the results by the date_base field in the time_stages table, either `ASC` (ascending) or `DESC` (descending), which will either give you the last or the first specimen, respectively.

'**`list families`**'

```
function list_families($order_id = NULL)
{
      if($order_id != NULL):
            echo "";
            $result = do_query("SELECT * FROM `families_units`,
`families_names_list` WHERE `families_units`.`order_unit_id` =
".$order_id." AND `families_names_list`.`families_names_list_id` =
`families_units`.`family_name_list_id` ORDER BY REPLACE(family_name,
\"'\", '')");
            while ($row = mysql_fetch_object($result)) {
                        echo "<br />\begin{indentfamily}<br /><br />F.
".$row->family_name." ";
                        if(!empty($row-
>family_name_authorship_if_separate)): echo $row-
>family_name_authorship_if_separate. " \emph{in} ";endif;
                        if(!empty($row->reference_id)): echo
"\citealt*{".$row->reference_id."}";endif;


                        //echo "(";
```

```
                        list_family_synonymies($row-
>families_units_id);
                        //echo ") ";



                        echo " \n\r";
                        $first = list_specimens($row-
>families_units_id, "DESC");
                        $last = list_specimens($row-
>families_units_id, "ASC");
                        if(($first != false) && ($last != false))
                        {

                              if($first->specimens_id == $last-
>specimens_id)
                              {
                                    // BOTH SAME
                                    $spec = $first;
                                    echo $spec->epoch_code;
                                    if(!empty($spec->epoch_code)) echo
"(";
                                    echo $spec->stage_name;
                                    if(!empty($spec->epoch_code)) echo
")";
                                    if(!empty($row->comments)) echo
"<br />\\\\".$row->comments."<br />";
                                    //echo "\\\\";
                                    if(strpos($spec->specimen_name,
"e.g.") !== false)
                                    {
                                          echo"<br
/>\begin{indentspecimen}<br />".$spec->specimen_name."
".qualification($spec->specimen_qualification_id,$spec-
>authorship_if_separate)."{".$spec->reference_id."}, ".$spec-
>deposit_name.", ".$spec->locality_name.", ".$spec->area_name.",
".$spec->country_name.".  ";
                                          if(!empty($spec->comments))
echo "(".$spec->comments.") ";
                                          echo "<br
/>\end{indentspecimen}<br />\n\r";
                                    }else{
                                          echo"<br
/>\begin{indentspecimen}<br />First and Last: ".$spec->specimen_name."
".qualification($spec->specimen_qualification_id,$spec-
>authorship_if_separate)."{".$spec->reference_id."}, ".$spec-
>deposit_name.", ".$spec->locality_name.", ".$spec->area_name.",
".$spec->country_name.".  ";
                                          if(!empty($spec->comments))
echo "(".$spec->comments.") ";
```

```
                                        echo "<br
/>\end{indentspecimen}<br />\n\r";
                                        }
                                        echo "";
                                }else{
                                        echo "";
                                        //echo $first-
>epoch_code."(".$first->stage_name.")&ndash;".$last-
>epoch_code."(".$last->stage_name.")";
                                        echo $first->epoch_code;
                                        if(!empty($first->epoch_code))
echo "(";
                                        echo $first->stage_name;
                                        if(!empty($first->epoch_code))
echo ")";
                                        echo "-";
                                        echo $last->epoch_code;
                                        if(!empty($last->epoch_code)) echo
"(";
                                        echo $last->stage_name;
                                        if(!empty($last->epoch_code)) echo
")";
                                        if(!empty($row->comments)) echo
"<br />\\\\".$row->comments."<br />";
                                        //echo "\\\\";
                                        echo"<br
/>\begin{indentspecimen}<br />First: ".$first->specimen_name."
".qualification($first->specimen_qualification_id, $first-
>authorship_if_separate)."{".$first->reference_id."}, ".$first-
>deposit_name.", ".$first->locality_name.", ".$first->area_name.",
".$first->country_name.".  ";
                                        if(!empty($first->comments)) echo
"(".$first->comments.") ";
                                        echo "<br
/>\end{indentspecimen}<br />\n\r";
                                        if($last->space_deposits_id !=
4)// Extant
                                        {
                                echo"<br />\begin{indentspecimen}<br
/>Last: ".$last->specimen_name." ".qualification($last-
>specimen_qualification_id,$last->authorship_if_separate)."{".$last-
>reference_id."}, ".$last->deposit_name.", ".$last->locality_name.",
".$last->area_name.", ".$last->country_name.".  ";
                                if(!empty($last->comments)) echo
"(".$last->comments.") ";
                                        echo "<br
/>\end{indentspecimen}<br />\n\r";
                                        }
```

```
                              }



                        }else{
                              if(!empty($row->comments)) echo "<br
/>\\\\".$row->comments."<br />";
                        }


                        echo "<br />\end{indentfamily}<br/>";


                        //echo "</li>";


            }
            //echo "</ul>";
      endif;
}
```

`function list_families()` explained:

Objective: To output the family name, reference ID, list the family synonymies and list the first and last specimens within the family (or just one specimen if both entries are the same).

Arguments: `$order_id` – the order that the families must belong to.

Description:

1) Query the database to get all families belonging to the supplied order.
2) For each family row...
3) Output the family name within formatted text.
4) If the row has an `authorship_if_separate` value, output it.
5) If the row has a `reference_id` value, output it
6) Run the `list_family_synonymies()` function to output the family synonyms.
7) Establish the first specimen by running the `list_specimens()` function.
8) Establish the last specimen for the family.
9) If there are two specimens (i.e if both first and last have a value)...
10) If both specimens are the same, output formatted text and the data for the specimen.
11) If the two specimens are different, output formatted text and specimen data for both.
12) If there are not two specimens, simply output any comments if they exist.

'**list family synonymies**'

```
function list_family_synonymies($family_id)
{
```

```
	if($family_id != NULL):
		//echo "<ul>";
		$result = do_query("
SELECT * FROM families_names_list as `fn`
JOIN `families_names_synonymies` as `fs` ON `fs`.`family_name_list_id`
= `fn`.`families_names_list_id` WHERE `fs`.`family_unit_id` =
".$family_id." ORDER BY `fn`.`family_name` ASC");

		$synarr = array();

		while($syn = mysql_fetch_object($result))
		{
			//echo "RESULTS!";
			array_push($synarr,$syn->family_name);
			//echo $syn->family_name.", ";
		}

		if(!empty($synarr)):
			$size = sizeof($synarr);
			$count = 1;
			echo "(";
			foreach($synarr as $family):
			echo $family;
			if($count < $size):
			echo ", ";
			endif;
			$count++;
			endforeach;
			echo ") ";
		endif;



		//echo "</ul>";
	endif;
}
```

function `list_family_synonymies()` explained:

Objective: To output a list of synonyms for a given family.

Arguments: `$family_id` – the family for which to look for synonyms

Description:

1) Like the `list_order_synonymies` function, query the database for results.
2) Add the results to an array.
3) Output a comma delimited list.

‘**list specimens**’

```
function list_specimens($family_id = NULL ,$order = "DESC")
{
      if($family_id != NULL):
            //echo "<ul>";
            $result = do_query("SELECT
`sp`.*,`sd`.`deposit_name`,`sd`.`space_deposits_id`,`sl`.*,`sa`.*,`co`
.*,`ts`.*,`tep`.*,`tp`.* FROM `specimens` as `sp`
 join `space_deposits` as `sd`
 ON `sp`.`space_deposit_id` = `sd`.`space_deposits_id`
join `space_localities` as `sl`
 ON `sd`.`space_locality_id` = `sl`.`space_localities_id`
join `space_areas` as `sa`
 ON `sl`.`space_area_id` = `sa`.`space_areas_id`
join `space_countries` as `co`
 ON `sa`.`space_country_id` = `co`.`space_countries_id`
 join `time_stages` as `ts`
 ON `sd`.`time_stage_id` = `ts`.`time_stages_id`
join `time_epochs` as `tep`
 ON `ts`.`time_epoch_id` = `tep`.`time_epochs_id`
join `time_periods` as `tp`
 ON `tep`.`time_period_id` = `tp`.`time_periods_id`  WHERE
`sp`.`family_unit_id` = ".$family_id." ORDER BY `ts`.`date_base`
".$order." LIMIT 1");
            return mysql_fetch_object($result);


            //echo "</ul>";
      endif;
}
```

`function list_specimens()` explained

Objective: To return to the function that called it a row from the database for either the first or last specimen in a given family.

Arguments: `$family_id` – the family the specimen must belong to. `$order` – whether to get the first or last.

Description:

1) Like the `extreme_specimen()` function, this is just one complex query joining the time tables and space tables together as one row and returning the row whose family matches the one supplied in the argument. The result is limited to 1 and is ordered by the `date_base` filed on the `time_stages` table, either `ASC` (ascending) or `DESC` (descending) for the last or first specimens, respectively.

Appendix 3

What follows is the output from the database. In the electronic version of this thesis, citations in the text are hyperlinked to the relevent place in the reference list for ease of use.

Epiclass Hexapoda

Class Entognatha

O. Collembola Lubbock, 1871 Devonian(Pragian)-Quaternary(Holocene)

F. Arrhopalitidae K1(Albian)-Holocene

First: *Arrhopalites* sp. in Delclòs et al. (2007), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Bourletiellidae K1(Albian)-Holocene

First: *Fasciosminthurus* sp. in Delclòs et al. (2007), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Brachystomellidae K2(Campanian)-Holocene

First: *Bellingeria cornua* Christiansen and Pike, 2002, Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Entomobryidae P1(Kungurian)-Holocene

First: *Permobrya mirabilis* Riek, 1976, carbonaceous shales, middle Ecca Group, Haakdoornfontein, near Pretoria, South Africa. (This species could belong to the Praentombryidae (Christiansen and Nascimbene, 2006).)

F. Hypogastruridae K2(Campanian)-Holocene

First: Mentioned in Christiansen and Pike (2002), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Isotomidae D1(Pragian)-Holocene

First: *Rhyniella praecursor* in Greenslade and Whalley (1986), Rhynie chert, Aberdeenshire, Scotland, United Kingdom.

F. Neanuridae K1(Albian)-Holocene

First: e.g. *Protodontella minicornis* Christiansen and Nascimbene, 2006, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Oncobryidae Christiansen and Pike, 2002 K2(Campanian)

First and Last: *Oncobrya decepta* Christiansen and Pike, 2002, Canadian amber (Medicine Hat), Medicine Hat, Alberta, Canada.

F. Onychiuridae K1(Albian)-Holocene

First: *Onychiurus* sp. in Delclòs et al. (2007), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Poduridae K2(Campanian)-Holocene

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Praentomobryidae Christiansen and Nascimbene, 2006(Praentombryidae) K1(Albian)

e.g. *Praentomobrya avita* Christiansen and Nascimbene, 2006, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Protentomobryidae K2(Campanian)

e.g. *Protentomobrya walkeri* in McKellar et al. (2008), Canadian amber (Cedar Lake), Cedar Lake, Manitoba, Canada.

F. Sminthuridae K1(Albian)-Holocene

First: e.g. *Grinnellia ventis* Christiansen and Nascimbene, 2006, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Tomoceridae K1(Albian)-Holocene

First: Mentioned in Christiansen and Nascimbene (2006), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

O. Diplura Börner, 1904 Carboniferous(Moscovian)-Quaternary(Holocene)

F. Campodeidae Eoc.(Priabonian)-Holocene

First: *Campodea darwinii* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Japygidae Mio.(Aquitanian)-Holocene

First: Figured in Poinar (1992), Mexican amber, Simojovel, Chiapas, Mexico. (Wilson and Martill (2001) believe this specimen is a beetle larva.)

F. Procampodeidae Mio.(Burdigalian)-Holocene

First: Figured in Poinar (1992), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Testajapygidae Kukalová-Peck, 1987 C2(Moscovian)

First and Last: *Testajapyx thomasi* in Wilson and Martill (2001), Carbondale Formation, Mazon Creek, Illinois, United States.

Class Insecta (= Ectognatha)

O. Archaeognatha Börner, 1904 (Machilida, Microcoryphia, Monura)
Carboniferous(Moscovian)-Quaternary(Holocene)

F. Dasyleptidae C2(Moscovian)-P2(Roadian)

First: "*Dasyleptus*" sp. in Engel (2009a), Carbondale Formation, Mazon Creek, Illinois, United States. (Assignment to Dasyleptidae is questionable (Rasnitsyn, 2000a).)

Last: *Dasyleptus brongniarti* in Engel (2009a), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Machilidae K1(Albian)-Holocene

First: Mentioned in Rasnitsyn and Ross (2000), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Meinertellidae (Meunertellidae) K1(Barremian)-Holocene

First: *Cretaceomachilis libanensis* Sturm and Poinar, 1998, Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Triassomachilidae T2(Anisian)

First and Last: *Triassomachilis uralensis* in Bitsch and Nel (1999), Bukobay Formation, Bashkortostan, Ural Mountains, Russian Federation. (Sinitshenkova (2000b) considered *Triassomachilis* to be a mayfly nymph and synonymised it with *Mesoneta* (Mesonetidae), however Grimaldi and Engel (2005) retain this family in Archaeognatha though suggest it requires re-study)

O. Insecta *incertae sedis* ()-()

Dicondylia

O. Zygentoma Börner, 1904 (Lepismatida, Thysanura *sensu stricto*)
Carboniferous(Moscovian)-Quaternary(Holocene)

F. Carbotripluridae Kluge, 1996 C2(Moscovian)

First and Last: *Carbotriplura kukalovae* Kluge, 1996, Whetstone horizon, Radnice Member, Radnice Basin, Bohemia, Czech Republic. (This nymph was originally designated as the paratype of *Bojophlebia prokopi* (Ephemeroptera: Bojophlebiidae) (Kluge, 1996).)

F. Lepidotrichidae (Lepidothrichidae, Lepidothricidae) K2(Santonian)-Eoc.(Priabonian)
Extant relic *Tricholepidion gertschi* assigned to Tricholepidiidae (Engel, 2006).

First: Mentioned in Rasnitsyn (2002l), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

Last: *Lepidothrix pilifera* in Engel (2006), Baltic amber, Baltic, Baltic region, Baltic.

F. Lepismatidae K1(Aptian)-Holocene

First: Figured in Staniczek and Bechly (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Nicoletiidae (Ateluridae, Nicolettidae) Mio.(Burdigalian)-Holocene

First: e.g. *Hemitrinemura exstincta* Mendes and Poinar, 2004, Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Protrinemuridae Mendes, 1988
Previously considered as subfamily Protrinemurinae within Nicoletiidae (Mendes, 2002).

Subclass Pterygota

O. Ephemeroptera Hyatt and Arms, 1890 (Ephemerida, Ephemeridea, Syntonopterida, Syntonopterodea) Carboniferous(Moscovian)-Quaternary(Holocene)

F. Acanthametropodidae (Analetrididae) Eoc.(Priabonian)-Holocene

First: *Analetris secundus* Godunko and Kłonowska-Olejnik, 2006, Baltic amber, Baltic, Baltic region, Baltic.

F. Aenigmephemeridae (Aenigmephemerdae) J3(Oxfordian)

First and Last: *Aenigmephemera demoulini* in Hubbard (1987), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Ameletidae McCafferty, 1991 Eoc.(Priabonian)-Holocene
Previously in Siphlonuridae.

First: e.g. *Baltameletus oligocaenicus* in Godunko et al. (2008), Baltic amber, Baltic, Baltic region, Baltic. (Previously included in Siphlonuridae.)

F. Ameletopsidae Eoc.(Priabonian)-Holocene

First: *Balticophlebia hennigi* in Wichard et al. (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Ametropodidae K2(Turonian)-Holocene

First: *Palaeometropus cassus* Sinitshenkova, 2000a, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Arthropleidae Eoc.(Priabonian)-Holocene

First: *Electrogenia dewalschei* in Wichard et al. (2009), Baltic amber, Baltic, Baltic region, Baltic. (Kluge, 2004 considers this species as family *incertae sedis*.)

F. Australiphemeridae McCafferty, 1991(Palaeoanthidae, Paleoanthidae) K1(Aptian)-K2(Santonian)

First: e.g. *Australiphemera revelata* in McCafferty and Santiago-Blay (2009), Crato Formation, Araripe Basin, Ceará, Brazil.

Last: e.g. *Palaeoanthus orthostylus* Kluge, 1994, Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation. (Originally described in Palaeoanthidae, McCafferty (1997) placed the genus in Australiphemeridae. While this attribution is not certain (Kluge et al., 2006), it is followed in McCafferty and Santiago-Blay (2009) and here.)

F. Babidae Kluge et al., 2006 Eoc.(Priabonian)

First and Last: *Baba lapidea* Kluge et al., 2006, Baltic amber, Baltic, Baltic region, Baltic.

F. Baetidae K1(Barremian)-Holocene

First: Mentioned in McCafferty (1997), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Baetiscidae K1(Aptian)-Holocene
Caririephemera marquesi Zamboni, 2001 shows no characters which identify it as an ephemeropteran (Staniczek, 2007). An unnamed specimen from the Lower Cretaceous of Australia shows affinities to Baetiscidae but has not been formally placed as such (Pescador et al., 2009).

First: *Protobaetisca bechlyi* Staniczek, 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Bojophlebiidae Kukalová-Peck, 1985 C2(Moscovian)

First and Last: *Bojophlebia prokopi* in Wootton and Kukalová-Peck (2000), Whetstone horizon, Radnice Member, Radnice Basin, Bohemia, Czech Republic.

F. Cretomitarcyidae Sinitshenkova, 2000a K2(Turonian)
Family status given in McCafferty (2004), however Staniczek (2007) considers it should belong in stemline of Baetiscidae and sees no reason for a separate family. McCafferty and Santiago-Blay, 2009 retain it as a separate family.

First and Last: *Cretomitarcys luzzi* Sinitshenkova, 2000a, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Epeoromimidae (Epeoromididae) J1(Pliensbachian)-K1(Berriasian)

First: *Epeoromimus kazlauskasi* in Sinitshenkova (2003), Osinovskiy Formation, Chernyi Etap, Kemerovo Region, Russian Federation. (May also occur in the Abashevo Formation.)

Last: e.g. *Epeoromimus* sp. in Sinitshenkova (2002d), Tsagan-Tsab, Khutel-Kara, Dornogovi (East Gobi) Aimag, Mongolia.

F. Ephemerellidae Eoc.(Priabonian)-Holocene
Clephemera clava and *Turfanerella tingi* should be considered Ephemeroptera *incertae sedis* (see Zhang and Kluge, 2007; Jacobus and McCafferty, 2008).

First: *Timpanoga viscata* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Ephemeridae K1(Aptian)-Holocene
Staniczek (2007) erroneously lists the australiphemerid genera *Australiphemera* and *Microphemera* in this family, without comment, while Huang et al. (2007b) list them in both Ephemeridae *and* Australiphemeridae, as well as listing *Ephemera* from the Jurassic Solnhofen Limestone where they probably meant *Mesephemera* of Mesephemeridae, a common mayfly in that deposit (Kluge and Sinitshenkova, 2002).

First: *Cratonympha microcelata* in Staniczek (2007), Crato Formation, Araripe Basin, Ceará, Brazil. (Staniczek (2007) considers the validity and status of this species doubtful.)

F. Euthyplociidae (Eutyplocidae, Pristiplociidae) K1(Barremian)-Holocene

First: Mentioned in Peñalver et al. (1999), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain.

F. Fuyoidae Zhang and Kluge, 2007(Fujoidae) J2(Callovian)

First and Last: *Fuyous gregarius* Zhang and Kluge, 2007, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China. (This species was misidentified as *Mesoneta antiqua* in Ren et al., 2002.)

F. Heptageniidae (Ecdyonuridae, Ecdyuridae) K2(Turonian)-Holocene

First: *Amerogenia macrops* Sinitshenkova, 2000a, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Hexagenitidae (Paedephemeridae, Stenodicranidae) J2(Callovian)-K1(Aptian)
Placement of *Siberiogenites* spp. in this family is ungrounded (see Zhang and Kluge, 2007).

First: *Shantous lacustris* Zhang and Kluge, 2007, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China. (This species was misidentified as *Mesobaetis sibirica* in Ren et al., 2002.)

Last: e.g. *Cratohexagenites longicercus* Staniczek, 2007, Crato Formation, Araripe Basin, Ceará, Brazil. (Huang et al., 2007b erroneously list *Protoligoneuria* (Crato Formation) as from the Baltic amber and date it as Upper Cretaceous.)

F. Isonychiidae Eoc.(Priabonian)-Holocene

Previously placed within Siphlonuridae (e.g. Carpenter, 1992b; Hubbard, 1987) or Oligoneuriidae (Ross and Jarzembowski, 1993), Isonychiidae is now considered a family (Ogden et al., 2009).

First: *Isonychia alderensis* Lewis, 1977, Passamari Formation, Ruby River Basin, Montana, United States.

F. Jarmilidae P1(Sakmarian)

Kluge (2004) appears to consider this a junior synonym of Protereismatidae but Grimaldi and Engel (2005) and Huang et al. (2007b) retain it as a separate family.

First and Last: *Jarmila elongata* in Hubbard (1987), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Leptophlebiidae (Leptophlebidae) K1(Barremian)-Holocene

First: e.g. *Conovirilus poinari* in Godunko and Krzemiński (2009), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Litophlebiidae (Lithophlebiidae, Xenophlebiidae) T3(Carnian)

First and Last: *Litophlebia optata* in Huang et al. (2007b), Molteno Formation, KwaZulu-Natal, Karoo Basin, South Africa.

F. Mesephemeridae (Palingeniopsidae) P2(Roadian)-J3(Tithonian)

First: *Palingeniopsis praecox* in Hubbard (1987), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

Last: e.g. *Mesephemera lithophila* in Hubbard (1987), Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Mesonetidae T2(Anisian)-J3(Tithonian)

First: e.g. *Mesoneta minuta* Sinitshenkova, 2000b, Varengayakha Formation, Urengoi District, Tyumen' Region, Russian Federation.

Last: e.g. *Furvoneta lucida* Sinitshenkova, 2002d, Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Mesoplectopteridae T2(Anisian)

An undescribed specimen from the Permian of Germany assigned to this family is more likely a protereismatid (Kluge and Sinitshenkova, 2002).

First and Last: *Mesoplectopteron longipes* in Sinitshenkova et al. (2005), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Metretopodidae (Metretopdidae) Eoc.(Priabonian)-Holocene

First: e.g. *Siphloplecton jaegeri* in Godunko and Neumann (2006), Baltic amber, Baltic, Baltic region, Baltic.

F. Miracopteridae Novokshonov, 1994b P1(Sakmarian)-P1(Kungurian)

First: Figured in Novokshonov and Aristov (2002), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: *Miracopteron mirabile* in Rasnitsyn (2002b), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Misthodotidae (Eudoteridae, Mistodothidae) P1(Asselian)-T2(Anisian)

First: *Misthodotes stapfi* Kinzelbach and Lutz, 1984, Jeckenbach layers, Niedermoschel, Donnersbergkreis district, Rhineland-Palatinate, Germany.

Last: *Triassodotes vogesiacus* Sinitshenkova & Papier *in* Sinitshenkova et al., 2005, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Neoephemeridae Eoc.(Ypresian)-Holocene

First: *Neoephemera antiqua* Sinitshenkova, 1999, Klondike Mountain Formation, Okanagan Highlands, Washington, United States.

F. Oboriphlebiidae P1(Sakmarian)
Kluge (2004) appears to consider this a junior synonym of Protereismatidae but Grimaldi and Engel (2005) and Huang et al. (2007b) retain it as a separate family.

e.g. *Oboriphlebia moravica* in Hubbard (1987), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Oligoneuriidae (Oligoneuridae) K1(Aptian)-Holocene

First: e.g. *Colocrus*? *magnum* Staniczek, 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Philolimniidae Jacobus and McCafferty, 2006 Eoc.(Ypresian)
Previously in Ephemerellidae.

First and Last: *Philolimnias sinica* in Jacobus and McCafferty (2006), Fushun amber, Guchengzi, Liaoning Province, China.

F. Polymitarcidae (Polymitarcyidae) K1(Barremian)-Holocene

First: *Mesopalingea leridae* in Peñalver et al. (1999), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain. (Originally described by Whalley and Jarzembowski 1985 in Palingeniidae, this species is listed in Potamanthidae by Peñalver et al., 1999 but is provisionally placed in Polymitarcidae by McCafferty, 2004.)

F. Potamanthidae (Pothamanthidae, Pothamantidae) K1(Aptian)-Holocene
McCafferty (2004) lists no fossil specimens in this family.

First: *Olindinella gracilis* in Staniczek (2007), Crato Formation, Araripe Basin, Ceará, Brazil. (Staniczek (2007) considers the status and validity of this species doubtful.)

F. Protereismatidae (Proteismatidae) C2(Gzhelian)-P2(Wordian)

First: Mentioned in Rowland (1997), Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: e.g. *Phthartus rossicus* in Hubbard (1987), Amanak Formation, Kargala, Belozersky District, Orenburg Region, Russian Federation.

F. Sharephemeridae Sinitshenkova, 2002d J3(Tithonian)

First and Last: *Sharephemera cubitalis* Sinitshenkova, 2002d, Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Siphlonuridae (Aphelophlebodidae) T2(Anisian)-Holocene

First: e.g. *Triassonurus doliiformis* Sinitshenkova & Papier *in* Sinitshenkova et al., 2005, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Siphluriscidae Zhou and Peters, 2003 J2(Aalenian)-Holocene

First: *Stackelbergisca shaburensis* in Zhang (2006b), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation. (Zhang and Kluge, 2007 place *Stackelbergisca* in Anteritorna *incertae sedis* but Lin and Huang, 2008 retain it in Siphluriscidae.)

F. Syntonopteridae (Synonopteridae) C2(Moscovian)-P2(Capitanian)

First: e.g. *Lithoneura lameerei* in Garrouste et al. (2009), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: *Gallolithoneura butchlii* Garrouste et al., 2009, Pradineaux Formation, Petit Coulet Redon Hill, Bas-Argens Basin, Provence, France.

F. Tintorinidae Krzemiński and Lombardo, 2001 T2(Ladinian)

First and Last: *Tintorina meridensis* Krzemiński and Lombardo, 2001, Upper Meride Limestone, Val Mara, Canton Ticino, Switzerland.

F. Torephemeridae Sinitshenkova, 1989 T2(Anisian)-K1(Berriasian)

First: *Archaeobehningia mogutshevae* Sinitshenkova, 2000b, Varengayakha Formation, Urengoi District, Tyumen' Region, Russian Federation. (Kluge, 2004 considers *Archaeobehningia* a junior synonym of *Mesogenesia* but Huang et al., 2007b retain it as a separate genus in Torephemeridae.)

Last: *Torephemera longipes* Sinitshenkova, 1989, Tsagan-Tsab, Khutel-Kara, Dornogovi (East Gobi) Aimag, Mongolia.

F. Toxodotidae Sinitshenkova & Papier *in* Sinitshenkova et al., 2005 T2(Anisian)

First and Last: *Taxodotes coloratus* Sinitshenkova & Papier *in* Sinitshenkova et al., 2005, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Triassoephemeridae Sinitshenkova & Papier *in* Sinitshenkova et al., 2005 T2(Anisian)

First and Last: *Triassoephemera punctata* Sinitshenkova & Papier *in* Sinitshenkova et al., 2005, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Triassomanthidae Sinitshenkova & Papier *in* Sinitshenkova et al., 2005 T2(Anisian)

First and Last: *Triassomanthus parvulus* Sinitshenkova & Papier *in* Sinitshenkova et al., 2005, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Voltziaephemeridae Sinitshenkova & Papier *in* Sinitshenkova et al., 2005 T2(Anisian)

First and Last: *Voltziaephemera fossoria* Sinitshenkova & Papier *in* Sinitshenkova et al., 2005, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

O. Pterygota *incertae sedis* Carboniferous(Bashkirian)-Cretaceous(Valanginian)

F. Apheloneuridae P1(Artinskian)-P1(Kungurian)

First: e.g. *Apheloneura minutissima* in Novokshonov (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

Last: *Apheloneura uralensis* Novokshonov, 2000, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Hadentomidae C2(Moscovian)-C2(Kasimovian)
Palaeocixius and *Protoblattina* were removed from Hadentomidae by Béthoux et al. (2005). *Hadentomum* is considered Pterygota *incertae sedis* by Rasnitsyn (2002a).

First: *Hadentomum americanum* in Carpenter (1992b), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: e.g. *Fayoliella elongata* in Carpenter (1992b), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Hebeigrammidae Hong, 2003(Mesogrammatidae j. hom.) K1(Valanginian)
Originally described in the Caloneurodea, this family was considered by Ross and Jarzembowski (1993) and Labandeira (1994) as Orthoptera and by Rasnitsyn (2002d) as Pterygota *incertae sedis*, which is followed here.

First and Last: *Hebeigramma divaricata* in Hong (2003), greyish-black shale, Qingquang village, Weichang County, Hebei Province, China.

F. Herbstialidae C2(Bashkirian)
Rasnitsyn (2002a) considers *Herbstiala* to be Pterygota *incertae sedis*.

First and Last: *Herbstiala herbsti* in Brauckmann and Hahn (1980), seam 16 West, Sophia Jacoba coliery, Heinsberg, North Rhine-Westphalia, Germany.

F. Homoeodictyidae (Homeodictyidae) P2(Wordian)
Rasnitsyn (2002a) considers this family to be Pterygota *incertae sedis*.

First and Last: *Homoeodictyon elongatum* in Rasnitsyn (2002a), Amanak Formation, Kargala, Belozersky District, Orenburg Region, Russian Federation.

F. Montanuraliidae Novokshonov, 1998a P1(Kungurian)

First and Last: *Montanuralia aeria* Novokshonov, 1998a, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Permetatoridae Novokshonov, 1999 P1(Kungurian)

First and Last: *Permetator semitritus* Novokshonov, 1999, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Permoneuridae P1(Artinskian)
Beckemeyer (2000) and Sinitshenkova (2002a) both place this family in Pterygota *incertae sedis*.

First and Last: *Permoneura lameerei* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Rectineuridae C2(Moscovian)
Sinitshenkova (2002a) places this family in Pterygota *incertae sedis*.

First and Last: *Rectineura lineata* in Carpenter (1992b), Yorkian Series, Chislet Colliery, Sturry, Kent, United Kingdom.

F. Stygnidae (Stygneidae) C2(Bashkirian)
Rasnitsyn (2002a) considers this family to be Pterygota *incertae sedis*. This family name is a junior homonym pre-occupied by the extant Opiliones family Stygnidae Simon, 1879.

First and Last: *Stygne roemeri* in Rasnitsyn (2002a), Alfred Mine, Alfred Mine, Upper Silesian Basin, Poland.

F. Sypharopteridae C2(Moscovian)
Rasnitsyn (2002d) included this family in Caloneurodea but this placement was rejected by Béthoux et al. (2004c).

First and Last: *Sypharoptera pneuma* in White (1995), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Vogesonymphidae Sinitshenkova & Papier *in* Sinitshenkova et al., 2005 T2(Anisian)

First and Last: *Vogesonympha ludovici* Sinitshenkova & Papier *in* Sinitshenkova et al., 2005, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Metapterygota

Palaeodictyopterida

O. Diaphanopterodea Handlirsch, 1919 (Diaphanopterida, Diaphanopteroidea, Palaeohymenoptera) Carboniferous(Moscovian)-Permian(Wuchiapingian)

F. Asthenohymenidae (Astenohymenidae, Doteridae) C2(Gzhelian)-P3(Wuchiapingian)

First: e.g. *Asthenohymen zonatus* Sinitshenkova *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: e.g. *Asthenohymen minutus* van Dijk and Geertsema, 1999, Normandien (Estcourt) Formation, Beaufort Group, KwaZulu-Natal, Karoo Basin, South Africa. (Although they acknowledge that Carpenter, 1992b synonymised *Karoohymen* under *Asthenohymen*, thus removing it from Scytohymenidae and Megasecoptera, van Dijk and Geertsema, 1999 describe this species under *Karoohymen* without any explanation for disagreeing with Carpenter, 1992b. Later authors e.g. Shcherbakov et al., 2009 follow Carpenter's arrangement, so this is followed here.)

F. Biarmohymenidae P1(Artinskian)-P1(Kungurian)

First: *Anomalohymen dochmus* Beckemeyer and Engel, 2009, Wellington Formation (OK), Midco, Oklahoma, United States.

Last: *Biarmohymen bardense* in Beckemeyer and Engel (2009), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Diaphanopteridae (Diaphanopteritidae) C2(Kasimovian)
Philiasptilon and *Diaphterum* are excluded from this family by Béthoux and Nel, 2003b.

e.g. *Diaphanoptera munieri* in Béthoux and Nel (2003b), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Elmoidae P1(Sakmarian)-P1(Artinskian)

First: e.g. *Elmodiapha ovata* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic. (Béthoux and Nel (2003b) call for revision of these taxa with recognition of tectonic deformation.)

Last: *Elmoa trisecta* in Beckemeyer and Engel (2009), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Kaltanelmoidae P2(Roadian)
Carpenter (1963b) doubted this family's affinities with Diaphanopterodea.

First and Last: *Kaltanelmoa sibirica* in Rohdendorf (1991), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Martynoviidae C2(Gzhelian)-P2(Wordian)

First: *Phaneroneura rineharti* Sinitshenkova *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: e.g. *Salagouneura chimaira* Béthoux et al., 2003c, Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France.

F. Parabrodiidae C2(Moscovian)-C2(Kasimovian)

First: *Piesbergala leipnerae* Brauckmann and Herd, 2003, Osnabrück Formation, Piesberg quarry, Lower Saxony, Germany.

Last: *Parabrodia carbonaria* in Brauckmann and Herd (2003), Stanton Limestone, Garnett, Anderson County, Kansas, United States.

F. Parelmoidae P1(Artinskian)-P1(Kungurian)

First: e.g. *Parelmoa obtusa* in Beckemeyer and Engel (2009), Wellington Formation (OK), Midco, Oklahoma, United States. (Listed in Beckemeyer and Engel, 2009 under Elmoidae in error (R.J. Beckemeyer pers. comm. 2009).)

Last: e.g. *Permuralia maculata* in Sinitshenkova (2002a), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation. (Formerly *Uralia maculata*, nomen nudum.)

F. Paruraliidae Kukalová-Peck and Sinitshenkova, 1992 P1(Kungurian) e.g. *Paruralia rohdendorfi* in Sinitshenkova (2002a), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Prochoropteridae C2(Moscovian)-C2(Kasimovian)

First: *Prochoroptera calopteryx* in Kukalová-Peck and Brauckmann (1990), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: *Euchoroptera longipennis* in Carpenter (1997), Stanton Limestone, Garnett, Anderson County, Kansas, United States.

F. Rhaphidiopsidae (Raphidiopseidae) C2(Kasimovian)
Sinitshenkova (2002a) considers this family to belong in the Megasecoptera.

First and Last: *Rhaphidiopsis diversipenna* in Brauckmann and Herd (2003), Rhode Island Formation, Narragansett basin, Rhode Island, United States.

F. Triplosobidae C2(Kasimovian)

First and Last: *Triplosoba pulchella* in Prokop and Nel (2009), Upper Coal Measures (Commentry), Commentry, Allier, France. (Prokop and Nel (2009) show that this fossil is closely related to the Diaphanopterodea but do not make a formal attribution to the order, preferring instead leave it unplaced within the Palaeodictyopterida.)

O. Dicliptera Grimaldi and Engel, 2005 (Archodonata, Permothemistida) Permian(Artinskian)-Permian(Roadian)

F. Diathemidae P1(Kungurian)

e.g. *Diathema tenerum* in Sinitshenkova (2002a), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Kansasiidae P1(Artinskian)
Sinitshenkova (2002a) places this family in Permothemistida (=Dicliptera) although Grimaldi and Engel (2005) are more tentative about this attribution.

First and Last: *Kansasia pulchra* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Permothemistidae P1(Kungurian)-P2(Roadian)

First: e.g. *Pauciramus demoulini* in Carpenter (1992b), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: e.g. *Permothemis libelluloides* in Wootton and Kukalová-Peck (2000), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

O. Megasecoptera Brongniart, 1885 (Eubleptidodea, Megasecopterida, Mischopterida, Protohymenoptera) Carboniferous(Bashkirian)-Permian(Roadian)

F. Alectoneuridae Kukalová-Peck, 1975(Allectoneuridae) P1(Sakmarian)

First and Last: *Alectoneura europaea* in Carpenter (1992b), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Anchineuridae Carpenter, 1963a C2(Kasimovian)

First and Last: *Anchineura hispanica* in Brauckmann (1993), Magdalena shales, La Magdalena, León Province, Spain.

F. Aspidohymenidae P2(Roadian)

First and Last: *Aspidohymen extensus* in Carpenter (1992b), Baitugan Formation, Tikhie Gory, Kama River, Tatarstan, Russian Federation.

F. Aspidothoracidae C2(Moscovian)-C2(Kasimovian)

First: e.g. *Aspidothorax tristrata* Brauckmann and Herd, 2003, Osnabrück Formation, Piesberg quarry, Lower Saxony, Germany.

Last: *Aspidothorax triangularis* in Brauckmann and Herd (2003), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Aykhalidae Sinitshenkova, 1994 P1(Asselian)

First and Last: *Aykhal helenae* in Sinitshenkova (2002a), Aykhal Formation, Markha River, Aykhal, Sakha (Yakutia) Republic, Russian Federation.

F. Bardohymenidae C2(Bashkirian)-P1(Kungurian)

First: e.g. *Sylvohymen pintoi* Brauckmann et al., 2003, Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: e.g. *Sylvohymen robustus* in Brauckmann et al. (2003), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Brodiidae C2(Bashkirian)-C2(Moscovian)

First: *Brodia priscotincta* in Brauckmann and Herd (2003), Dudley coal measures, South Staffordshire Coalfield, Staffordshire, United Kingdom.

Last: *Pyobrodia janseni* Zessin, 2006, Osnabrück Formation, Piesberg quarry, Lower Saxony, Germany.

F. Brodiopteridae C2(Bashkirian)

e.g. *Brodioptera stricklani* Nelson and Tidwell, 1987, Manning Canyon Shale Formation, Lehi, Utah, United States.

F. Carbonopteridae C2(Moscovian)

First and Last: *Carbonoptera furcaradii* in Brauckmann (1991), Borehole 38 (Hangard), Neunkirchen, Saarland, Germany.

F. Corydaloididae C2(Kasimovian)

First and Last: *Corydaloides scudderi* in Wootton and Kukalová-Peck (2000), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Engisopteridae Kukalová-Peck, 1975 P1(Sakmarian)

First and Last: *Engisoptera simplices* in Carpenter (1992b), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Eubleptidae C2(Moscovian)

e.g. *Eubleptus danielsi* in Sinitshenkova (2002a), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Foririidae C2(Kasimovian)

First and Last: *Foriria maculata* in Béthoux et al. (2004a), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Ischnoptilidae Carpenter, 1951(Ichnoptilidae) C2(Kasimovian)

First and Last: *Ischnoptilus elegans* in Béthoux et al. (2004b), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Mischopteridae C2(Moscovian)-C2(Kasimovian)

First: *Mischoptera douglassi* in Labandeira (2001), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: e.g. *Mischoptera nigra* in Wootton and Kukalová-Peck (2000), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Moravohymenidae P1(Sakmarian)

First and Last: *Moravohymen vitreus* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Namurodiaphidae Kukalová-Peck and Brauckmann, 1990 C2(Bashkirian)
This family was originally placed in the Diaphanopterodea. Although its systematic position remains uncertain, most authors now place it in Megasecoptera (Sinitshenkova, 2002a; Prokop and Ren, 2007).

First and Last: *Namurodiapha sippelorum* in Brauckmann et al. (2003), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

F. Protagrionidae (Protagriidae) C2(Kasimovian)

First and Last: *Protagrion audouini* in Béthoux and Nel (2003a), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Protohymenidae (Permohymenidae) P1(Asselian)-P2(Roadian)
Beckemeyer, 2000 lists *Permohymen schucherti* in Protohymenidae and neither he nor Sinitshenkova, 2002a mention Permohymenidae at all.

First: *Sunohymen xishanensis* Hong, 1985, Shanxi Formation (Taiyuan Entomassemblage), Xishan Mountain, Shanxi Province, China.

Last: *Ivahymen constrictus* in Rohdendorf (1991), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Scytohymenidae P1(Kungurian)

e.g. *Oceanoptera elenae* Shcherbakov *in* Shcherbakov et al., 2009, Pospelovo Formation, Russky Island, Primorye, Russian Federation.

F. Sphecopteridae Carpenter, 1951 C2(Kasimovian)-P1(Kungurian)

First: e.g. *Sphecoptera gracilis* in Carpenter (1992b), Upper Coal Measures (Commentry), Commentry, Allier, France.

Last: *Cyclocelis* sp. in Rasnitsyn et al. (2005), Lek-Vorkuta Formation, Vorkuta Group, Pechora Cola Basin, Komi Republic, Russian Federation.

F. Sphecorydaloididae Pinto, 1994(Sphecocorydaloididae) P1(Asselian)

First and Last: *Sphecorydaloides lucchesei* in Pinto and Adami-Rodrigues (1999), Bajo de Véliz Formation (Pallero Member), Paganzo Basin, Sierra Grande de San Luis, San Luis Province, Argentina.

F. Vorkutiidae C2(Kasimovian)-P1(Kungurian)

First: *Siberiohymen asiaticus* in Rohdendorf (1991), Alykaeva Formation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

Last: e.g. *Vorkutia dimina* Novokshonov, 1998b, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. 'Xenopteridae' Pinto, 1986 C2(Bashkirian)
This family name is a junior homonym of Xenopteridae Riek (Orthoptera).

First and Last: *Xenoptera riojaensis* Pinto, 1986, Malanzán Formation, Malanzán, La Rioja Province, Argentina.

O. Palaeodictyoptera Goldenberg, 1877 (Anisaxia, Archaehymenoptera, Breyerida, Dictyoneurida, Eopalaeodictyoptera, Hemiodonata, Protocicadida, Protohemiptera, Synarmogoidea) Carboniferous(Serpukhovian)-Permian(Capitanian)

F. Aenigmatidiidae P2(Roadian)

First and Last: *Aenigmatidia kaltanica* in Prokop and Nel (2004), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Ancopteridae Kukalová-Peck, 1975 P1(Sakmarian)
Family transferred from Megasecoptera by Sinitshenkova (2002a).

First and Last: *Ancoptera permiana* in Sinitshenkova (2002a), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Archaemegaptilidae C2(Bashkirian)-C2(Kasimovian)

First: *Archaemegaptilus schloesseri* Brauckmann et al., 2003, Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: *Arachaemegaptilus kiefferi* in Brauckmann et al. (2003), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Archaeoptilidae C2(Kasimovian)
Considered by Carpenter (1992b) to be Palaeoptera *incertae sedis*, Sinitshenkova (2002a) considers Archaeoptilidae to be a distinct family in Palaeodictyoptera.

First and Last: *Archaeoptilus ingens* in Carpenter (1992b), Middle Upper Coal Measures, near Chesterfield, Derbyshire, United Kingdom.

F. Arcioneuridae Kukalová-Peck, 1975 P1(Sakmarian)
Family transferred from Megasecoptera by Sinitshenkova (2002a).

e.g. *Arcioneura juveniles* in Carpenter (1992b), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Breyeriidae C2(Bashkirian)-C2(Kasimovian)

First: *Jugobreyeria sippelorum* in Brauckmann et al. (2003), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: e.g. *Breyeria boulei* in Brauckmann et al. (1985), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Calvertiellidae (Mongolianidae, Mongolodictyidae) C2(Gzhelian)-P2(Capitanian)
Mongolodictyidae is considered a separate family by Sinitshenkova (2002a) but a junior synonym by Béthoux et al. (2007).

First: *Carrizopteryx arroyo* in Béthoux et al. (2007), Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: *Mongolodictya callida* in Béthoux et al. (2007), Tsankhi (Tsankhin) Formation, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia. (Listed by Béthoux et al., 2007 under the original name of *Mongolodictya callida*, however this genus name is a junior homonym of *Mongolodictya* Gorjunova 1988, so was renamed by Ozdikmen2008a.)

F. Caulopteridae Kukalová-Peck, 1975 P1(Sakmarian)
Family transferred from Megasecoptera by Sinitshenkova (2002a).

First and Last: *Cauloptera colorata* in Carpenter (1992b), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Cryptoveniidae C2(Moscovian)
Placed in Palaeoptera *incertae sedis* by Carpenter (1992b), Sinitshenkova (2002a) places this family in the Palaeodictyoptera.

First and Last: *Cryptovenia moyseyi* in Carpenter (1992b), below the Top Hard Coal, Middle Coal Measures, Shipley Manor Claypit, Ilkeston, Derbyshire, United Kingdom.

F. Dictyoneurellidae C2(Kasimovian)
Placed in Palaeoptera *incertae sedis* by Carpenter (1992b), Sinitshenkova (2002a) places this family in the Palaeodictyoptera.

First and Last: *Dictyoneurella perfecta* in Carpenter (1992b), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Dictyoneuridae C2(Bashkirian)-P1(Artinskian)

First: e.g. *Dictyoneura kemperi* in Brauckmann et al. (2003), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: e.g. *Goldenbergia formosa* Sharov and Sinitshenkova, 1977, Nizhnyaya Burguklya Formation, Fatyanikha River, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Elmoboriidae (Elmoboridae) P1(Sakmarian)-P1(Artinskian)

First: *Oboria longa* in Carpenter (1992b), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: *Elmoboria piperi* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Eubrodiidae Sinitshenkova, 2002a C2(Moscovian)
Type genus taken out of the megasecopteran family Brodiidae by Sinitshenkova (2002a).

First and Last: *Eubrodia dabasinskasi* in Carpenter (1997), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Eugereonidae (Cockerelliellidae) C2(Kasimovian)-P1(Sakmarian)

First: e.g. *Dictyoptilus sepultus* in Wootton and Kukalová-Peck (2000), Upper Coal Measures (Commentry), Commentry, Allier, France.

Last: *Eugereon boeckingi* in Sinitshenkova (2002a), Lebachian Shales (Lower Rotliegend), Birkenfeld, Rhineland-Palatinate, Germany.

F. Eukulojidae (Eokulojidae, Eukulojudae, Kulojidae) P2(Roadian)

e.g. *Eukuloja cubitalis* in Sinitshenkova (2002a), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Fouqueidae C2(Moscovian)-C2(Kasimovian)

First: *Neofouquea suzannae* in Carpenter (1997), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: e.g. *Fouquea lacroixi* in Carpenter (1992b), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Frankenholziidae C2(Moscovian)
Family transferred from Megasecoptera by Sinitshenkova (2002a).

First and Last: *Frankenholzia culmanni* in Brauckmann (1991), Frankenholz Mine, Neunkirchen, Saarland, Germany.

F. Graphiptilidae C2(Bashkirian)-C2(Kasimovian)

First: e.g. *Petteiskya volmensis* in Brauckmann et al. (2003), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: e.g. *Graphiptilus heeri* in Brauckmann et al. (1985), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Hanidae Kukalová-Peck, 1975 C2(Gzhelian)-P1(Sakmarian)
Family transferred from Megasecoptera by Sinitshenkova (2002a).

First: *Forcynthia cynthiae* Sinitshenkova *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: e.g. *Hana filia* in Sinitshenkova (2002a), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Heolidae C2(Kasimovian)

First and Last: *Heolus providentiae* in Prokop and Nel (2004), Ten-mile Series, East Providence, Rhode Island, United States.

F. Homoiopteridae (Homiopterigidae, Rochlingiidae, Thesoneuridae) C2(Bashkirian)-C2(Gzhelian)

First: e.g. *Homoioptera vorhallensis* in Prokop et al. (2006), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: e.g. *Parathesoneura carpenteri* in Sinitshenkova (2002a), Kata Formation, Chunya, Siberian Federal District, Russian Federation.

F. Homothetidae C2(Bashkirian)
This family is not included in Carpenter (1992b) but is referred to by Labandeira (1994) and Sinitshenkova (2002a).

First and Last: *Homothetus fossilis* in Handlirsch (1906), Lancaster Formation, Saint John, New Brunswick, Canada.

F. Jongmansiidae C2(Bashkirian)
Considered by Carpenter (1992b) to be Palaeodictyoptera *incertae sedis*, Sinitshenkova (2002a) retains family rank for Jongmansiidae.

e.g. *Jongmansia tuberculata* in Carpenter (1992b), Faisceau de Hendrik, Emma Mine, Limbourg, Netherlands.

F. Lamproptilidae (Lamproptiliidae) C2(Kasimovian)
Synonymised with Spilapteridae by Kukalová (1969a), Lamproptilidae is considered a separate family by Sinitshenkova (2002a).

First and Last: *Lamproptilia grandeuryi* in Wootton and Kukalová-Peck (2000), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Lithomanteidae (Lithomantidae, Lusiellidae, Macropteridae) C2(Bashkirian)-C2(Kasimovian)

First: e.g. *Lithomantis varius* in Brauckmann et al. (2003), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: *Macroptera fariai* in Brauckmann et al. (1985), Alto do Pejao, Douro, Norte Region, Portugal.

F. Lithoptilidae C2(Kasimovian)-C2(Gzhelian)
Previously considered as a junior synonym of Megaptilidae (e.g. Carpenter, 1992b), Sinitshenkova (2002a) considers Lithoptilidae to be a separate family.

First: *Lithoptilus boulei* in Carpenter (1992b), Upper Coal Measures (Commentry), Commentry, Allier, France.

Last: "near *Lithoptilus*" in Rowland (1997), Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States. (Listed by Rowland, 1997 in Megaptilidae but here considered Lithoptilidae.)

F. Lycocercidae (Lycocericidae) C2(Bashkirian)-C2(Gzhelian)

First: *Lycocercus bouckaerti* in Kukalová (1969b), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: e.g. *Madera mamayi* in Carpenter (1992b), Madera Formation, Manzano Mountains, New Mexico, United States.

F. Mecynopteridae C2(Moscovian)
The type species of this monotypic family was listed by Carpenter (1992b) as Palaeodictyoptera, Family Uncertain. Labandeira (1994) lists the family in Megasecoptera after Kukalová-Peck (1975).

First and Last: *Mecynoptera splenida* in Béthoux et al. (2007), Flénu, Wallonia, Hainaut Province, Belgium.

F. Mecynostomatidae C2(Kasimovian)

First and Last: *Mecynostomata dohrni* in Wootton and Kukalová-Peck (2000), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Megaptilidae C2(Kasimovian)

First and Last: *Megaptilus blanchardi* in Wootton and Kukalová-Peck (2000), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Namuroningxiidae Prokop and Ren, 2007 C2(Bashkirian)

First and Last: *Namuroningxia elegans* Prokop and Ren, 2007, Tupo Formation, Qilianshan Mountains, Ningxia/Gansu/Inner Mongolia, China.

F. Peromapteridae C2(Kasimovian)
Formerly considered in Eugereonidae (e.g. Carpenter, 1992b), Sinitshenkova (2002a) considers Peromapteridae to be a seaparate family.

First and Last: *Peromaptera filholi* in Wootton and Kukalová-Peck (2000), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Polycreagridae C2(Kasimovian)
Synonymised with Lycoceridae by Kukalová (1969b), Polycreagridae is considered a separate family by Sinitshenkova (2002a) and Prokop and Ren (2007).

First and Last: *Polycreagra elegans* in Carpenter (1992b), Rhode Island Formation, Narragansett basin, Rhode Island, United States.

F. Psychroptilidae C2(Gzhelian)

First and Last: *Psychroptilus burrettae* in Jell (2004), Wynyard Tillite, Hellyer Gorge, Tasmania, Australia.

F. Saarlandiidae C2(Moscovian)
Considered by Carpenter (1992b) to be Palaeodictyoptera *incertae sedis*, Sinitshenkova (2002a) considers Saarlandiidae to be a distinct family.

First and Last: *Saarlandia flexisubcostata* in Carpenter (1992b), Geisheck Formation, Saarbrücken, Saarland, Germany.

F. Spilapteridae (Neuburgiidae) C1(Serpukhovian)-P1(Kungurian)

First: *Delitzschala bitterfeldensis* Brauckmann and Schneider, 1996, Bitterfeld/Delizsch area, Bitterfeld/Delitzsch area, Saxony-Anhalt, Germany.

Last: e.g. *Dunbaria borealis* in Rasnitsyn et al. (2005), Lek-Vorkuta Formation, Vorkuta Group, Pechora Cola Basin, Komi Republic, Russian Federation.

F. Stobbsiidae C2(Moscovian)
The type genus was listed in Breyeriidae by Carpenter (1992b), Stobbsiidae is considered a separate family by Sinitshenkova (2002a).

First and Last: *Stobbsia woodwardiana* in Carpenter (1992b), Peacock marls, Foley, near Longton, Staffordshire, United Kingdom.

F. Straeleniellidae Laurentiaux-Vieira and Laurentiaux, 1986 C2(Bashkirian)
Family not mentioned at all by Sinitshenkova (2002a).

e.g. *Straeleniella namurensis* Laurentiaux-Vieira and Laurentiaux, 1986, grey-black schists, Amercoeur Colliery, Wallonia, Hainaut Province, Belgium.

F. Synarmogidae C2(Bashkirian)
Synonymised with Lithomantidae by Kukalová (1969b), Synarmogidae is considered a separate family by Sinitshenkova (2002a) and Prokop and Ren (2007).

First and Last: *Synarmoge ferrarii* in Carpenter (1992b), Wendeischen Mines, Ruhr, North Rhine-Westphalia, Germany.

F. Tchirkovaeidae C2(Kasimovian)-C2(Gzhelian)

First: e.g. *Paimbia fenestrata* in Carpenter (1992b), Lower Kata Formation, Paymbu, Siberian Federal District, Russian Federation.

Last: e.g. *Paimbia ultima* Sinitshenkova, 1981, Kata Formation, Chunya, Siberian Federal District, Russian Federation.

Odonatoptera

O. Geroptera Brodsky, 1994 Carboniferous(Bashkirian)-Carboniferous(Bashkirian)

F. Eugeropteridae C2(Bashkirian)

e.g. *Eugeropteron lunatum* in Gutiérrez et al. (2000), Malanzán Formation, Malanzán, La Rioja Province, Argentina.

O. Odonata Fabricius, 1793 (Libellulida, Permodonata)
Carboniferous(Moscovian)-Quaternary(Holocene)

F. Aeschnidiidae J3(Kimmeridgian)-K2(Cenomanian)
Fleck and Nel (2003) figure one specimen and mention another that belong to this family which could be from the Lias but could also be Lower Cretaceous.

First: e.g. *Brunetaeschnidium nusplingensis* in Fleck and Nel (2003), Nusplingen Lithographic Limestone, Westerberg/Grosser Heuberg, Baden-Württenburg, Germany.

Last: *Tauropteryx krassilovi* in Fleck and Nel (2003), Sel'bukhra near Prokhadnoye, Bakhchisarayskiy district, Crimea, Ukraine.

F. Aeshnidae (Aeschnidae) J3(Tithonian)-Holocene

First: *Morbaeschna muensteri* in Nel et al. (1994), Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Aktassiidae J3(Oxfordian)-K1(Barremian)

First: *Aktassia magna* in Nel et al. (1998), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Pseudocymatophlebia hennigi* Nel et al., 1998, Upper Weald Clay Formation (Smokejacks), Smokejacks Brickworks, Surrey, United Kingdom.

F. Allopetaliidae K1(Valanginian)-Holocene

First: e.g. *Baissaeshna zherikhini* Bechly et al., 2001, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Araripechlorogomphidae Bechly and Ueda, 2002 K1(Aptian)

First and Last: *Araripechlorogomphus muratai* in Bechly (2007b), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Araripegomphidae Bechly, 1996 K1(Aptian)

e.g. *Araripegomphus hanseggeri* in Bechly (2007b), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Araripelibellulidae Bechly, 1996 K1(Berriasian)-K1(Aptian)

First: e.g. *Araripelibellula britannica* Fleck et al., 2008, Lulworth Formation, Durlston Bay, Dorset, United Kingdom.

Last: e.g. *Araripelibellula martinsnetoi* in Bechly (2007b), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Araripephlebiidae Bechly, 1998c K1(Aptian)

First and Last: *Araripephlebia mirabilis* in Bechly (2007b), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Archithemistidae (Architemistidae) T3(Rhaetian)-J1(Toarcian)

First: *Archithemis liassina* in Jarzembowski (1999), Cotham Member, Lilstock Formation, Penarth Group2, near Axmouth, Dorset, United Kingdom. (Originally described as *Diastatommites liassina*.)

Last: *Sogdothemis modesta* in Sukatsheva and Rasnitsyn (2004), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan.

F. Asiopteridae (Oreopteridae) J1(Toarcian)-J3(Oxfordian)

First: e.g. *Amblyopteron breve* in Sukatsheva and Rasnitsyn (2004), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan.

Last: e.g. *Asiopteron antiquum* in Nel et al. (1993), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Austroperilestidae Petrulevičius and Nel, 2005 Eoc.(Ypresian)

First and Last: *Austroperilestes hunco* Petrulevičius and Nel, 2005, La Huitrera Formation, Laguna del Hunco, Chubut Province, Argentina.

F. Batkeniidae T2(Anisian)-T3(Carnian)

First: *Voltzialestes triasicus* Nel et al., 1996, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: e.g. *Batkenia pusilla* in Nel et al. (1999c), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Bechlyidae Jarzembowski and Nel, 2002 C2(Moscovian)

First and Last: *Bechlya ericrobinsoni* in Zessin (2008), Farrington Formation, Writhlington, Somerset, United Kingdom.

F. Bolcacorduliidae Gentilini, 2002 Eoc.(Ypresian)

First and Last: *Bolcacordulia paradoxa* Gentilini, 2002, Pesciara site, Monte Bolca limestone, Province of Verona, Veneto, Italy.

F. Bolcathoridae Gentilini, 2002 Eoc.(Ypresian)

First and Last: *Bolcathore colorata* Gentilini, 2002, Pesciara site, Monte Bolca limestone, Province of Verona, Veneto, Italy.

F. Callimokaltaniidae P2(Roadian)

First and Last: *Callimokaltania martynovi* in Zessin (2008), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Calopterygidae (Agriidae) Eoc.(Priabonian)-Holocene

First: Figured in Fleck et al. (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Campterophlebiidae (Karatawiidae) J1(Sinemurian)-K1(Berriasian)

First: *Dorsettia laeta* in Nel et al. (1993), Black Ven Marls, Charmouth, Dorset, United Kingdom.

Last: *Pritykinia rasnitsyni* Nel et al., 2009a, Markha, deposit unknown, Markha River, Aykhal, Sakha (Yakutia) Republic, Russian Federation.

F. Camptotaxineuridae P1(Artinskian)
Huguet et al. (2002) suggest this family could belong in Palaeodictyoptera.

First and Last: *Camptotaxineura ephialtes* in Huguet et al. (2002), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Coenagrionidae (Agrionidae, Coenagriidae, Protoneuridae *partim*) K1(Aptian)-Holocene

First: Figured in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia. (All other pre-Tertiary specimens attributed to this family have since been removed, so the attribution of this specimen to the Coenagrionidae remains tentative.)

F. Cordulegastridae Olig.(Rupelian)-Holocene

First: '*Petalura*' *acutipennis* in Nel and Paicheler (1992), Braunkhole, Sieblos, Hesse, Germany.

F. Cordulephyidae Pal.(Thanetian)-Holocene

First: *Palaeophya argentina* Petrulevičius and Nel, 2009, Maíz Gordo Formation, Salta Group, Salta/Jujuy provinces, Argentina.

F. Corduliidae (Synthemistidae, Sythemistidae) Eoc.(Ypresian)-Holocene

First: *Molercordulia karinae* Bechly, 2005a, Fur Formation (Mo Clay), Limfjord/Mors Peninsula/Fur Island, Jutland, Denmark.

F. Cretacoenagrionidae Bechly, 1996 K1(Hauterivian)

First and Last: *Cretacoenagrion alleni* in Jarzembowski et al. (1998), Lower Weald Clay Formation (Clockhouse), Clockhouse Brickworks, Surrey, United Kingdom.

F. Cretapetaluridae Nel et al., 1998 K1(Berriasian)-K1(Aptian)

First: *Anglopetalura magnifica* Coram and Nel, 2009, Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom.

Last: e.g. *Cratopetalura petruleviciusi* Nel and Bechly, 2009, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Cyclothemistidae Bechly, 1997 T3(Carnian)-J1(Toarcian)

First: *Pseudotriassothemis nipponensis* in Bechly (1997), Momonoki Formation, Ominé Coal Field, Yamaguchi, Japan.

Last: e.g. *Cyclothemis sagulica* in Bechly (1997), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan. (This species, along with *Shurabiola nana*, were erroneously listed under Archithemistidae by Sukatsheva and Rasnitsyn, 2004, in which they had been originally described.)

F. Cymatophlebiidae J2(Callovian)-K1(Barremian)

First: *Sinacymatophlebia mongolica* Nel and Huang, 2009, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

Last: e.g. *Cymatophlebia standingae* in Bechly et al. (2001), Upper Weald Clay Formation (Rudgwick), Rudgwick Brickworks, near Horsham, West Sussex, United Kingdom.

F. Ditaxineuridae P1(Artinskian)-P1(Kungurian)

First: e.g. *Ditaxineura anomalostigma* in Zessin (2008), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

Last: *Proditaxineura pritykinae* in Huguet et al. (2002), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Dysagrionidae (Congqingiidae, Euarchistigmatidae, Thaumatoneuridae) K1(Barremian)-Holocene
For a discussion on the name of this family see Rust et al. (2008).

First: *Congqingia rhora* in Nel and Arillo (2006), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Enigmaeshnidae Nel et al., 2008 K2(Cenomanian)

First and Last: *Enigmaeshna deprei* Nel et al., 2008, Puy-Puy quarry, Tonnay-Charente, Charente-Maritime, France.

F. Eocorduliidae Bechly, 1996 K1(Berriasian)

First and Last: *Eocordulia cretacea* Pritykina, 1986, Mogotuin Formation, Sum of Manlai, Mogotuin-Del-Ula mountain, Ömnögovi (South Gobi) Aimag, Mongolia.

F. Eosagrionidae J1(Toarcian)

First and Last: *Eosagrion risi* in Nel and Paicheler (1993), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Epallagidae (Euphaeidae) Eoc.(Ypresian)-Holocene

First: *Labandeiraia europae* Petrulevičius et al., 2007, Fur Formation (Mo Clay), Limfjord/Mors Peninsula/Fur Island, Jutland, Denmark.

F. Erichschmidtiidae Bechly, 1996 J3(Oxfordian)
Fleck et al. (2003) remove *Prostenophlebia* to Prostenophlebiidae, leaving Erichschmidtiidae with only one genus.

First and Last: *Erichschmidtia nigrimontana* in Bridges (1994), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Eumorbaeschnidae Bechly et al., 2001 J3(Tithonian)

First and Last: *Eumorbaeschna jurassica* in Bechly et al. (2001), Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Euthemistidae J3(Oxfordian)
Bechly (1997) removed *Sphenophlebia*, *Mesoepiophlebia*, *Ensphingophlebia* and *Proeuthemis* to the Sphenophlebiidae, leaving Euthemistidae with only one genus.

e.g. *Euthemis multinervosa* in Jarzembowski (1990), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Frenguelliidae Petrulevičius and Nel, 2003a(Frengueliidae) Eoc.(Ypresian)

First and Last: *Frenguellia patagonica* in Petrulevičius and Nel (2007), La Huitrera Formation, Laguna del Hunco, Chubut Province, Argentina.

F. Gomphaeschnidae (Gomphoaeschnidae) K1(Berriasian)-Holocene

First: e.g. *Cretalloaeschna cliffordae* in Bechly et al. (2001), Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom.

F. Gomphidae (Gomphinidae) Olig.(Rupelian)-Holocene

First: *Ictinogomphus*? sp. in Prokop and Fikaček (2007), Seifhennersdorf diatomite, Upper Lusatia, Free State of Saxony, Germany.

F. Gondvanogomphidae Bechly, 1996(Gondwanogomphidae) K1(Aptian)

First and Last: *Gondvanogomphus bartheli* in Schlüter (2003), Abu Ballas Formation, Abu Ballas, Gilf Kebir, Egypt.

F. Hemeroscopidae K1(Barremian)-K1(Aptian)

First: *Hemeroscopus baissicus* in Vršanský (2008c), Khurilt Formation, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia.

Last: *Abrohemeroscopus mengi* Ren et al., 2003, Jiufotang Formation, Beishan, Yixian County, Liaoning Province, China.

F. Hemiphlebiidae J3(Tithonian)-Holocene

First: *Mersituria ludmilae* Vasilenko, 2005, Doronino Formation, Chernovskie Kopi, Chita, Transbaikalia, Russian Federation.

F. Hemizygopteridae (Hemizypopteridae) P1(Kungurian)

e.g.? *Hemizygopteron* cf. *uralense* in Huguet et al. (2002), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation. (The original description of *Hemizygopteron uralense* (Zalessky, 1955) mentions only that it is from the "Upper Permian" of the Urals. Huguet et al. (2002) state that the specimen is missing but give the same vague locality and age data as the original description. Rohdendorf (1991) synonymises *Hemizygopteron* with *Ditaxineurella* and seems to say it occurs in the Kungurian of Tshekarda. Thus, it is assumed here that both *H. uralense* and *H.* cf. *uralense* come from the same deposit.)

F. Henrotayiidae Fleck et al., 2003(Henrotayidae) J1(Toarcian)

First and Last: *Henrotayia marci* Fleck et al., 2003, Upper Lias (Luxembourg), Bascharage and Sanem, Luxembourg district, Luxembourg.

F. Heterophlebiidae J1(Sinemurian)-J1(Toarcian)

First: *Heterophlebia* sp. in Nel et al. (1993), Black Ven Marls, Charmouth, Dorset, United Kingdom.

Last: *Heterophlebia buckmani* in Ansorge (1999), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Hypolestidae Eoc.(Priabonian)-Holocene

First: e.g.? Figured in Bechly and Wichard (2008), Baltic amber, Baltic, Baltic region, Baltic.

F. Idionychidae Mio.(Langhian)-Holocene

First: *Mioidionyx stavropolensis* Nel et al., 2005d, Vishnevaya Balka, near Senghileevskoye Lake, Stavropol Krai, Russian Federation.

F. Isophlebiidae J2(Aalenian)-K1(Valanginian)

First: Mentioned in Pritykina (2006), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation. (Based on the odontofauna, Pritykina, 2006 considers the Ichetuy Formation to be of Upper Jurassic age, in which case the oldest isophlebiid would be *Hemerobioides giganteus* from the Bathonian (J2) Stonesfield Slate in England, listed by Nel et al., 1993.)

Last: *Nacholonda crassicosta* in Nel et al. (1993), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Isostictidae K1(Aptian)-Holocene

First: *Eoprotoneura hyperstigma* in Bechly (2007b), Crato Formation, Araripe Basin, Ceará, Brazil. (Bechly, 2007b lists this species in Protoneuridae: Isostictinae but this subfamily has subsequently been restored to family level and Protoneuridae shown to be polyphyletic e.g. Bybee et al., 2008.)

F. Juracorduliidae Bechly and Ueda, 2002 J3(Tithonian)

First and Last: *Juracordulia schiemenzi* Bechly, 1998a, Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Juragomphidae Nel et al., 2001b J3(Oxfordian)

First and Last: *Juragomphus karatauensis* Nel et al., 2001b, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Juraheterophlebiidae Fleck et al., 2003 J3(Oxfordian)

First and Last: *Juraheterophlebia kazakhstanensis* Fleck et al., 2003, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Juralibellulidae Huang and Nel, 2007b J2(Callovian)

First and Last: *Juralibellula ningchengensis* Huang and Nel, 2007b, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Kaltanoneuridae P2(Roadian)

First and Last: *Kaltanoneura bartenevi* in Zessin (2008), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Kargalotypidae P2(Wordian)
Bechly (1996) places this family in the Meganisoptera but Nel et al. (2001c) consider it Triadophlebiomorpha, here listed in the Odonata.

First and Last: *Kargalotypus kargalensis* in Nel et al. (2001c), Amanak Formation, Kargala, Belozersky District, Orenburg Region, Russian Federation.

F. Kennedyidae P1(Artinskian)-T3(Carnian)

First: e.g. *Opter brongniarti* in Zessin (2008), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

Last: e.g. *Kennedya carpenteri* in Nel et al. (1999c), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Latibasaliidae Petrulevičius and Nel, 2004 Pal.(Thanetian)

e.g. *Latibasalia elongata* in Petrulevičius and Nel (2007), Maíz Gordo Formation, Salta Group, Salta/Jujuy provinces, Argentina.

F. Lestidae Pal.(Thanetian)-Holocene

First: '*Lestes*' *zalesskyi* in Nel and Paicheler (1994a), spongo-diatomaceous maar, Menat, Puy-de-Dôme, Auvergne, France.

F. Liadotypidae J1(Toarcian)

First and Last: *Liadotypus relictus* in Nel et al. (2001c), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan.

F. Liassogomphidae (Gomphitidae) J1(Toarcian)
The genus *Chrysogomphus* does not belong in this family (see Huang et al., 2003).

e.g. *Liassogomphus brodiei* in Etter and Kuhn (2000), Posidonia Shale (Switzerland), Hemmiken, Basel-Country, Switzerland.

F. Liassophlebiidae J1(Hettangian)-J1(Toarcian)

First: *Bavarophlebia schmeissneri* Nel and Petrulevičius, 2005, Early Lias (alpha 1 & 2), Sandpit Küfner, south of Pechgraben, Kulmbach, Bavaria, Germany.

Last: e.g. *Ferganophlebia insignis* in Sukatsheva and Rasnitsyn (2004), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan.

F. Liassostenophlebiidae Fleck et al., 2003 J1(Toarcian)

First and Last: *Liassostenophlebia germanica* Fleck et al., 2003, "Epsilon" Liassic, Geodenlage 2, Rhine-Danube canal, Bavaria, Germany.

F. Libellulidae K2(Turonian)-Holocene
Condalia woottoni is not a libellulid (see Nel and Paicheler, 1994b).

First: *Palaeolibellula zherikhini* Fleck et al., 1999, Kzyl-Zhar, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Lindeniidae K1(Aptian)-Holocene

First: *Cratolindenia knuepfae* Bechly, 2000, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Liupanshaniidae Bechly et al., 2001 K1(Barremian)-K2(Turonian)

First: *Paraliupanshania britannica* Bechly et al., 2001, Upper Weald Clay Formation (Rudgwick), Rudgwick Brickworks, near Horsham, West Sussex, United Kingdom.

Last: *Paraliupanshania torvaldsi* Bechly et al., 2001, Kzyl-Zhar, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Macromiidae Mio.(Burdigalian)-Holocene

First: *Epophthalmia biordinata* in Nel and Paicheler (1994b), Latah Formation (Washington), Spokane?, Washington, United States.

F. Megapodagrionidae (Megapodogrionidae) Pal.(Thanetian)-Holocene

First: e.g. *Thanetophilosina menatensis* in Azar and Nel (2008), spongodiatomaceous maar, Menat, Puy-de-Dôme, Auvergne, France.

F. Mesochlorogomphidae Fleck et al., 2008 K1(Barremian)

e.g. *Mesochlorogomphus crabbi* Fleck et al., 2008, Upper Weald Clay Formation (Smokejacks), Smokejacks Brickworks, Surrey, United Kingdom.

F. Mesomantidiidae T3(Carnian)

First and Last: *Mesomantidion queenslandicum* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Mesuropetalidae Bechly, 1996 J3(Oxfordian)-K1(Valanginian)

First: e.g. *Mesuropetala auliensis* in Bechly et al. (2001), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Mesurapetala magna* Bechly et al., 2001, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Mitophlebiidae T3(Carnian)

e.g. *Promitophlebia modica* in Bechly (1996), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Myopophlebiidae J1(Toarcian)

e.g. *Paraheterophlebia marcusi* in Fleck et al. (2003), Upper Lias (Luxembourg), Bascharage and Sanem, Luxembourg district, Luxembourg.

F. Nannogomphidae Bechly, 1996 J3(Tithonian)

e.g. *Nannogomphus buergeri* Bechly, 2003, Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Nodalulaidae Lin et al., 2007 K1(Aptian)

First and Last: *Nodalula dalinghensis* Lin et al., 2007, Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Nothomacromiidae Carle, 1995(Pseudomacromiidae) K1(Aptian) *Pseudomacromia* is re-named *Nothomacromia* in Carle (1995).

First and Last: *Nothomacromia sensibilis* in Bechly (2007b), Crato Formation, Araripe Basin, Ceará, Brazil. (*Conan barbarica* is a junior synonym.)

F. Oboraneuridae Zessin, 2008 P1(Sakmarian)

First and Last: *Oboraneura kukalovae* Zessin, 2008, Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Palaeomacromiidae Petrulevičius et al., 1999(Bolcathemidae) Pal.(Thanetian)-Eoc.(Ypresian)

First: e.g. *Curviarculia delicata* Petrulevičius and Nel, 2002, Maíz Gordo Formation, Salta Group, Salta/Jujuy provinces, Argentina.

Last: *Bolcathemis nervosa* in Petrulevičius and Nel (2007), Pesciara site, Monte Bolca limestone, Province of Verona, Veneto, Italy.

F. Paracymatophlebiidae Bechly et al., 2001 J3(Oxfordian)

First and Last: *Paracymatophlebia splendida* Bechly et al., 2001, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Paragonophlebiidae Nel, 2009 J3(Oxfordian)-J3(Tithonian)

First: *Paragonophlebia inexpectata* Nel, 2009, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Paragonophlebia patriciae* Nel, 2009, Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Parastenophlebiidae Bechly, 2005b J3(Tithonian)

First and Last: *Parastenophlebia casta* in Bechly (2005b), Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Paurophlebiidae Bechly, 1996 T3(Carnian)

e.g. *Paurophlebia lepida* in Vasilenko and Rasnitsyn (2007), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Permaeschnidae P1(Artinskian)-P2(Roadian)

First: *Gondvanoptilon brasiliense* in Huguet et al. (2002), Irati Formation, Paraná Basin, São Paulo, Brazil.

Last: *Permaeschna dolloi* in Huguet et al. (2002), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation. (*P. proxima* considered a junior synonym in Huguet et al. (2002).)

F. Permagrionidae (Permagriidae) P1(Sakmarian)

First and Last: *Permagrion falklandicus* in Nel et al. (1999c), Lafonia Formation, Bodie Creek Head, East Falkland, Falkland Islands (Malvinas).

F. Permepallagidae P2(Roadian)
Zessin (2008) removed *Lodevia* from this family.

First and Last: *Permepallage angustissima* in Zessin (2008), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Permolestidae (Solikamptilonidae) P2(Roadian)-P2(Wordian)

First: e.g. *Permolestes gracilis* in Nel et al. (1999c), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

Last: *Epilestes gallica* Nel et al., 1999c, Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France.

F. Permophlebiidae Nel et al., 2001c P3(Wuchiapingian)

First and Last: *Permophlebia uralica* Nel et al., 2001c, Vostochno-Novikbozhskay borehole, Vorkuta Basin, Ural Mountains, Russian Federation. (Age of deposit described as "Early Upper Permian", which could mean Roading (P2).)

F. Petaluridae K1(Aptian)-Holocene

First: *Argentinopetala archangelskyi* Petrulevičius and Nel, 2003b, Anfiteatro de Ticó Formation, Bajo Grande, Santa Cruz Province, Argentina.

F. Pholidoptilidae P2(Roadian)

First and Last: *Pholidoptilon camense* in Huguet et al. (2002), Baitugan Formation, Tikhie Gory, Kama River, Tatarstan, Russian Federation.

F. Piroutetiidae Nel, 1989 T3(Rhaetian)

First and Last: *Piroutetia liasina* in Nel et al. (2001c), "Lower Lias", Fort-Mouchard, Arçures, Jura, France.

F. Platycnemididae (Platycnemidae, Protoneuridae *partim*) Eoc.(Priabonian)-Holocene

First: e.g. *Platycnemis antiqua* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Polytaxineuridae P3(Changhsingian)

First and Last: *Polytaxineura stanleyi* in Huguet et al. (2002), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia. (This species is erroneously listed in Permaeschnidae by Jell (2004).)

F. Priscalestidae Petrulevičius & Wappler *in* Wappler and Petrulevičius, 2007 Eoc.(Lutetian)

First and Last: *Priscalestes germanica* Petrulevičius & Wappler *in* Wappler and Petrulevičius, 2007, Eckfeld maar, Manderscheid, Rhineland-Palatinate, Germany.

F. Progobiaeshnidae Bechly et al., 2001(Progobiaeschnidae) K1(Barremian)-K1(Aptian)

First: *Gobiaeshna occulta* in Bechly et al. (2001), Anda-Khuduk Formation, Anda-Khuduk, Övörkhangai (Ubur-Khangaisk) Aimag, Mongolia.

Last: *Progobiaeshna liaoningensis* Bechly et al., 2001, Yixian unspecified, Yixian Formation, Liaoning Province, China. (The precise locality and deposit of this specimen is unknown (Bechly et al., 2001).)

F. Prohemeroscopidae Bechly and Ueda, 2002 J3(Tithonian)

e.g. *Prohemeroscopus jurassicus* Bechly et al., 1998, Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany. (Originally described in the Hemeroscopidae.)

F. Prostenophlebiidae Fleck et al., 2003 J3(Tithonian)

First and Last: *Prostenophlebia jurassica* in Fleck et al. (2003), Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Proterogomphidae Bechly et al., 1998 J3(Tithonian)-K1(Aptian)

First: *Proterogomphus renateae* Bechly et al., 1998, Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

Last: e.g. *Cordulagomphus winkelhoferi* Bechly, 2007b, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Protolindeniidae J3(Tithonian)

e.g. *Protolindenia viohli* Nel et al., 2001a, Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Protomyrmeleontidae (Protomyrmeleonidae, Triassagrionidae) T3(Carnian)-K1(Hauterivian)

First: e.g. *Ferganagrion kirghiziensis* Nel et al., 2005e, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: *Protomyrmeleon cretacicus* Nel and Jarzembowski, 1998, Lower Weald Clay Formation (Clockhouse), Clockhouse Brickworks, Surrey, United Kingdom.

F. Rudiaeschnidae Bechly et al., 2001 K1(Berriasian)-K1(Aptian)

First: *Fuxiaeschna hsiufunia* Lin et al., 2004, Luohandong Formation, Datai Valley, Huating County, Gansu Province, China.

Last: *Rudiaeshna limnobia* in Bechly et al. (2001), Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Saxonagrionidae Nel et al., 1999a P2(Wordian)

First and Last: *Saxonagrion minutus* in Zessin (2008), Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France.

F. Selenothemistidae (Turanothemistidae) J1(Toarcian)-J3(Oxfordian)

First: *Selenothemis liadis* in Nel (2009), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

Last: *Turanothemis nodalis* in Zessin (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Sieblosiidae (Sublosiidae) Olig.(Rupelian)-Mio.(Tortonian)

First: e.g. *Stenolestes jucunda* in Nel et al. (2005c), Braunkhole, Sieblos, Hesse, Germany.

Last: *Stenolestes hispanicus* in Peñalver et al. (1999), diatomites (Cerdanya), Bellver de Cerdanya, Lleida Province, Spain.

F. Sonidae Pritykina, 1986 K1(Hauterivian)

First and Last: *Sona nectes* Pritykina, 1986, Gurvan-Eren Formation (Myangad), Myangad, Khovd Aimag, Mongolia. (This species contains only the larval specimens as the supposed adults were described as a new family Proterogomphidae Bechly et al. 1998.)

F. Sphenophlebiidae Bechly, 1997 J1(Toarcian)-K1(Hauterivian)

First: e.g. *Mesoepiophlebia veronicae* in Nel et al. (2002), Upper Lias (Luxembourg), Bascharage and Sanem, Luxembourg district, Luxembourg.

Last: e.g. *Proeuthemis pritykinae* in Fleck et al. (2004), Lower Weald Clay Formation (Clockhouse), Clockhouse Brickworks, Surrey, United Kingdom.

F. Steleopteridae J3(Oxfordian)-J3(Tithonian)

First: *Auliella crucigera* in Fleck et al. (2001), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: e.g. *Parasteleopteron guischardi* Fleck et al., 2001, Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Stenophlebiidae (Stenophlebidae) J3(Oxfordian)-K1(Aptian)

First: *Stenophlebia karatavica* in Fleck et al. (2003), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Cratostenophlebia schwickerti* Bechly, 2007b, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Synlestidae (Chlorolestidae, Chorismagrionidae) J3(Tithonian)-Holocene

First: *Gaurimacia sophiae* Vasilenko, 2005, Doronino Formation, Chernovskie Kopi, Chita, Transbaikalia, Russian Federation.

F. Tarsophlebiidae J3(Oxfordian)-K1(Aptian)
Previous Lower Jurassic records do not belong to this family (Fleck et al., 2004).

First: e.g. *Turanophlebia martynovi* in Fleck et al. (2004), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Turanophlebia sinica* Huang and Nel, 2009a, Yixian unspecified, Yixian Formation, Liaoning Province, China.

F. Triadophlebiidae T3(Carnian)

e.g. *Triassophlebia madygenica* in Nel et al. (1999c), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Triadotypidae (Reisiidae) T2(Anisian)-T3(Carnian)

First: e.g. *Triadotypus guillaumei* in Nel et al. (2001c), Bust outcrop, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: *Reisia sodgianus* in Nel et al. (2001c), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Triassolestidae (Italophlebiidae, Mesophlebiidae, Progonophlebiidae, Triassoneuridae, Triassothemidae) T3(Carnian)-J1(Toarcian)

First: e.g. *Triassothemis mendozensis* in Martins-Neto et al. (2007b), Potrerillos Formation (Cerro Bayo), Cerro Bayo, Mendoza Province, Argentina.

Last: *Sogdopterites legibile* in Nel et al. (2002), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan.

F. Valdicorduliidae Bechly, 1996 K1(Hauterivian)

First and Last: *Valdicordulia wellsorum* Jarzembowski and Nel, 1996, Lower Weald Clay Formation (Clockhouse), Clockhouse Brickworks, Surrey, United Kingdom.

F. Xamenophlebiidae T3(Carnian)

First and Last: *Xamenophlebia ornata* in Nel et al. (2001c), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Zacallitidae Eoc.(Ypresian)

First and Last: *Zacallites balli* in Bechly (1998b), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Zygophlebiidae T3(Carnian)

e.g. *Zygophlebiella curta* in Nel et al. (2001c), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

O. Protodonata Brongniart, 1893 (Meganisoptera)
Carboniferous(Bashkirian)-Permian(Wordian)

F. Campylopteridae C2(Kasimovian)
Placement is problematic - formerly in Megasecoptera, could now be Protodonata or Odonata.

First and Last: *Campyloptera eatoni* in Nel and Huguet (2002), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Erasipteridae C2(Bashkirian)-C2(Moscovian)

First: e.g. *Erasipteroides valentini* in Zessin (2006), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: *Erasipterella piesbergensis* in Zessin (2006), Osnabrück Formation, Piesberg quarry, Lower Saxony, Germany.

F. Kohlwaldiidae C2(Moscovian)
Nel et al., 2009b include *Solutotherates analis* (Moscovian, Allegheny Formation, Pennsylvania, United States) in this family.

e.g. *Kohlwaldia kuehni* in Zessin (2008), Grube Kohlwald, Neunkirchen, Saarland, Germany.

F. Lapeyriidae Nel et al., 1999b(Lapeyridae) P2(Wordian)

First and Last: *Lapeyria magnifica* in Béthoux (2008a), Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France.

F. Meganeuridae C2(Bashkirian)-P2(Wordian)

First: e.g. *Sinomeganeura huangheensis* Ren et al., 2008, Tupo Formation, Qilianshan Mountains, Ningxia/Gansu/Inner Mongolia, China.

Last: e.g. *Permotupus minor* Nel et al., 2009b, Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France.

F. Namurotypidae Bechly, 1996 C2(Bashkirian)

First and Last: *Namurotypus sippeli* in Zessin (2006), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

F. Paralogidae C2(Moscovian)-P1(Artinskian)
The specimen listed in Sukatsheva and Rasnitsyn (2004) from the Sai Sagul locality (Sagul Formation) under Paralogidae as *Oligotypus relictus* is probably *Liadotypus relictus*, type of Liadotypidae. '*Oligotypus britannicus*' (nomen nudum) was transfered to Meganeuridae by Nel et al., 2009b.

First: *Oligotypus makowskii* in Nel et al. (2009b), Carbondale Formation, Mazon Creek, Illinois, United States. (Nel et al., 2009b state that the attribution of this species to Paralogidae is questionable and needs revision.)

Last: e.g. *Oligotypus tillyardi* in Rehn (2003), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

Neoptera

O. Neoptera *incertae sedis* Carboniferous(Moscovian)-Jurassic(Sinemurian)

F. Metropatoridae C2(Moscovian)
Placement of this family is difficult as it does not belong in Caloneurodea or Miomoptera, as has been suggested in the past (Béthoux et al., 2004c; Rasnitsyn, 2002g).

First and Last: *Metropator pusillus* in Rasnitsyn (2003), Allegheny Formation, Pennsylvania/Maryland/West Virginia, Ridge-and-Valley Appalachians, United States.

F. Uninervidae P3(Wuchiapingian)-J1(Sinemurian)

First: e.g. *Redactineura acuminata* in van Dijk and Geertsema (1999), Normandien (Estcourt) Formation, Beaufort Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: *Mononeura angustipennis* in Rohdendorf (1991), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

O. Paoliida Handlirsch, 1906 (Protoptera)
Carboniferous(Bashkirian)-Carboniferous(Bashkirian)

F. Katerinkidae Prokop and Nel, 2007 C2(Bashkirian)

First and Last: *Katerinka hilaris* Prokop and Nel, 2007, Suchá Beds, Karviná Formation, Upper Silesian Basin, Moravia, Czech Republic.

F. Paoliidae C2(Bashkirian)

e.g. *Mertovia sustai* in Prokop and Nel (2007), Suchá Beds, Karviná Formation, Upper Silesian Basin, Moravia, Czech Republic.

Polyneoptera

O. Archaeorthoptera *incertae sedis*
Carboniferous(Serpukhovian)-Cretaceous(Cenomanian)

F. Ampelipteridae (Fatjanopteridae, Protoprosbolidae) C1(Serpukhovian)-P2(Roadian)
Supraordinal placement after Béthoux and Nel (2002b).

First: *Ampeliptera limburgica* in Kukalová-Peck and Brauckmann (1992), Gulpen, Gulpen, Limbourg, Netherlands.

Last: e.g. *Tshekardobia magnifica* Novokshonov *in* Novokshonov and Aristov, 2004, Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Cacurgidae C2(Bashkirian)-C2(Moscovian)
Considered here to include those taxa assigned in Carpenter (1992b) until further revision is performed.

First: e.g. *Heterologopsis ruhrensis* in Brauckmann (2005), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany.

Last: e.g. *Cacurgus spilopterus* in Béthoux (2006), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Carpenteropteridae Pinto and Pinto de Ornellas, 1991(Cacurgonarkemidae) C2(Kasimovian)
The species comprising this family were assigned by Béthoux (2007a) as unplaced within Archaeorthoptera. *Carpenteroptera rochacamposi* (previously in *Narkemina*) is added to this family in Martins-Neto et al. (2007a).

e.g. *Carpenteroptera onzii* in Martins-Neto (2005), Anitápolis Formation, Itararé Subgroup, Parana Basin, Fazenda do Juca, Santa Catarina, Brazil.

F. Chresmodidae (Saurophthiridae, Saurophthiriidae, Sternarthronidae) J2(Callovian)-K2(Cenomanian)

First: e.g. *Jurachresmoda sanyica* Zhang, Ren & Pang *in* Zhang et al., 2009b, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

Last: *Chresmoda libanica* in Delclòs et al. (2008), Nammoura "fish beds", El Ghabour valley, Caza Kesrouâne, Mouhafazet Jabal Loubnan, Lebanon.

F. Eoblattidae C2(Kasimovian)

e.g. *Eoblatta robusta* in Béthoux and Nel (2005), Upper Coal Measures (Commentry), Commentry, Allier, France. (Béthoux and Nel, 2005 remove this genus from the Stenoneuridae.)

F. Geraridae C2(Moscovian)-C2(Gzhelian)

First: e.g. *Gerarus vetus* in Béthoux and Briggs (2008), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: *Ploetzgerarus krempieni* Zessin, 2009, Plötz coal seams, near Halle, Saxony-Anhalt, Germany.

F. Omaliidae (Coseliidae) C2(Bashkirian)-C2(Kasimovian)
This family name is a junior homonym of the extant Coleoptera subfamily Omaliinae MacLeay (1825) (ICZN code, Article 53). Family status and position after Béthoux and Nel (2002b).

First: e.g. *Omalia macroptera* in Béthoux and Nel (2005), Sars-Lonchamps, Mons Basin, La Louvière, Wallonia, Hainaut Province, Belgium.

Last: *Omalia anae* Brauckmann et al., 2001, Magdalena shales, La Magdalena, León Province, Spain. (Béthoux and Nel, 2005 dispute whether this species belongs in *Omalia*.)

F. Pachytylopsidae C2(Bashkirian)
Béthoux and Nel (2002b) remove all but the type genus from this family and assign it to the Archaeorthoptera *nec* Panorthoptera. However, Brauckmann and Herd (2006) appear to retain *Protopachytylopsis* in Pachytylopsidae.

e.g. *Protopachytylopsis leckwycki* in Brauckmann and Herd (2006), Tergnee colliery, Wallonia, Hainaut Province, Belgium.

F. Protophasmatidae C2(Moscovian)-C2(Kasimovian)

First: e.g. *Protophasma galtieri* Béthoux and Schneider, 2009, Carbondale Formation, Mazon Creek, Illinois, United States.

Last: *Protophasma dumasii* in Béthoux (2003), Upper Coal Measures (Commentry), Commentry, Allier, France.

O. Blattodea *sensu lato* Brunner von Wattenwyl, 1882 (Blattaria, Blattariae, Blattida, Blattidae, Blattoidea) Carboniferous(Bashkirian)-Quaternary(Holocene)

F. Archimylacridae (Archimylacrididae) C2(Bashkirian)-T3(Carnian)
Kisylblatta unifasciata from the Jurassic of Kyzyl-Kiya is Phyloblattidae and not Archimylacridae, according to Vršanský (2003a).

First: e.g. *Miroblattites costalis* in Özdikmen (2008b), passage beds, Rieu du Coeur, Wallonia, Hainaut Province, Belgium.

Last: Mentioned in Shcherbakov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan. (The identification of Archimylacridae from the Madygen Formation is tentative.)

F. Argentinoblattidae Martins-Neto & Gallego *in* Martins-Neto et al., 2005 T2(Ladinian)
Martins-Neto et al. (2005) list several genera from the Middle Triassic of France and Lower Jurassic of England and Russia which may belong to this family but do not formally attribute them to it.

e.g. *Argentinoblatta herbsti* Martins-Neto & Gallego *in* Martins-Neto et al., 2005, Los Rastros Formation, Bermejo Basin, La Rioja Province, Argentina.

F. Blaberidae (Perisphaeriidae) Eoc.(Ypresian)-Holocene

First: e.g. *Hongoblatta orientalis* in Özdikmen (2008b), Fushun amber, Guchengzi, Liaoning Province, China.

F. Blattidae (Blattoidae) K1(Aptian)-Holocene
Liang et al. (2006) list *Zhujiblatta* Lin, 1980 as Triassic in age. This is likely a mistake as *Zhujiblatta* is from the Chaochuan Formation (Lin, 1994), which is Albian in age (Li et al., 2009).

First: e.g. *Mesoblattinopsis schneideri* in Bechly (2007c), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Blattinopsidae (Blattinopseidae) C2(Kasimovian)-P1(Kungurian)
Béthoux et al. (2009) consider this family to be stem-Dictyoptera and, *contra* Hörnschemeyer and Stapf (2001), do not include *Protoblattinopsis stubblefieldi*. Rasnitsyn (2002c) does not consider *Glaphyrokoris mirandus* from the Moscovian Carbondale Formation (Mazon Creek) to be in this family.

First: e.g. *Blattinopsis* spp. in Béthoux and Nel (2002b), Upper Coal Measures (Commentry), Commentry, Allier, France.

Last: *Glaphyrophlebia subcostalis* in Rasnitsyn et al. (2005), Inta Formation, Vorkuta Group, Pechora Cola Basin, Komi Republic, Russian Federation.

F. Blattulidae (Blattullidae) T2(Ladinian)-K2(Campanian)

First: *Argentinoblattula revelata* Martins-Neto et al., 2005, Los Rastros Formation, Bermejo Basin, La Rioja Province, Argentina.

Last: *Xonpepetla rinconensis* Cifuentes-Ruiz & Vršanský *in* Cifuentes-Ruiz et al., 2006, Cerro del Pueblo Formation, Rincón Colorado, Coahuila, Mexico.

F. Cainoblattinidae Eoc.(Ypresian)

First and Last: *Cainoblattinopsis fushunensis* in Liang et al. (2006), Fushun amber, Guchengzi, Liaoning Province, China.

F. Caloblattinidae Vršanský & Ansorge *in* Vršanský, 2000 T2(Anisian)-K2(Cenomanian)
Vršanský and Ansorge (2007, p.109) mention that the "latest known representatives are from the Late Cretaceous of Siberia (unpublished material)" and give no further details.

First: Mentioned in Vršanský et al. (2002), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: e.g. Mentioned in Vršanský et al. (2002), Obluchye tuffaceous mudstones, Jewish Autonomous Oblast, Far Eastern Federal District, Russian Federation.

F. Corydiidae (Euthyrrhaphidae, Holocompsidae, Homoeogamiidae, Poliphagidae, Polyphagidae, Vitismidae) K1(Berriasian)-Holocene

First: Figured in Vršanský and Ansorge (2001), Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom.

F. Cratovitismidae Bechly, 2007c K1(Aptian)

First and Last: *Cratovitisma oldreadi* Bechly, 2007c, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Delpuenteblattidae Martins-Neto et al., 2007b T2(Ladinian)-T3(Carnian)

First: *Lariojablatta chanarensis* in Martins-Neto et al. (2007b), Los Rastros Formation, Bermejo Basin, La Rioja Province, Argentina.

Last: e.g. *Delpuenteblatta dangeloi* Martins-Neto et al., 2007b, Potrerillos Formation (Cerro Bayo), Cerro Bayo, Mendoza Province, Argentina.

F. Diechoblattinidae (Diechnoblattinidae) P1(Asselian)-K1(Berriasian)
Vršanský et al. (2002) synonymised Diechoblattinidae under Poroblattinidae without discussion. They also state that "Poroblattinidae probably failed to cross the Perm-Triassic boundary" (p. 266), yet show the family extending into the Upper Triassic in their range chart for the order, yet the type species of Diechoblattinidae is from the Cretaceous. To avoid further confusion, Diechoblattinidae is kept separate here.

First: e.g. *Nepioblatta intermedia* in Handlirsch (1937), Pony Springs Member, Maroon Formation, Fairplay, Colorado, United States.

Last: e.g. *Deichoblattina wallaci* in Clifford et al. (1994), Lower Purbeck Beds, Durlston Bay, Dorset, United Kingdom.

F. Eadiidae Vršanský, 2009 K1(Albian)
Vršanský (2009) tentatively placed *Raphidiomimula* from the Burmese amber in this family, however it was placed in Caloblattinidae by Liang et al. (2009).

First and Last: *Eadia aidae* Vršanský, 2009, Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

F. Ectobiidae (Anaplectidae, Blatellidae, Blattellidae, Nyctiboridae, Phyllodromiidae) K1(Berriasian)-Holocene

First: e.g. *Rithma westwoodi* in Ross (2001), Lulworth Formation, Durlston Bay, Dorset, United Kingdom.

F. Fuziidae Vršanský et al., 2009 T3(Carnian)-J3(Oxfordian)

First: Mentioned in Vršanský et al. (2009), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: Mentioned in Vršanský et al. (2009), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Latiblattidae J3(Oxfordian)

First and Last: *Latiblatta lativalvata* in Özdikmen (2008b), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Liberiblattinidae Vršanský, 2002b J3(Oxfordian)-K1(Albian)

First: e.g. *Liberiblattina ihringovae* Vršanský, 2002b, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Leptolythica vincenti* Vršanský, 2009, Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

F. Mancusoblattidae Martins-Neto & Gallego *in* Martins-Neto et al., 2005 T2(Ladinian)
Martins-Neto et al. (2005) list several genera from the Triassic of France and Japan and Lower Jurassic of Russia (Irkutsk Oblast) which may belong to this family but do not formally attribute them to it.

e.g. *Mancusoblatta pulchella* Martins-Neto & Gallego *in* Martins-Neto et al., 2005, Los Rastros Formation, Bermejo Basin, La Rioja Province, Argentina.

F. Mesoblattinidae J1(Toarcian)-K2(Santonian)
Most previously included taxa were rejected from this family by Vršanský and Ansorge (2007).

First: e.g. *Mesoblattina protypa* in Vršanský and Ansorge (2007), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

Last: Mentioned in Vršanský (2008b), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Mylacridae (Archoblattinidae, Mylacrididae, Neorthroblattinidae, Opsiomylacridae) C2(Moscovian)-T3(Carnian)
Vršanský et al. (2002) synonymised Archoblattinidae under Mylacridae without discussion.

First: e.g. *Sooblatta* cf. *deanensis* in Jarzembowski and Schneider (2007), Farrington Formation, Writhlington, Somerset, United Kingdom.

Last: *Austromylacrites latus* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia. (This appears to be a plant fossil, which would make the last occurrence of this family *Cathayiblatta longata* Li et al., 2007 from the Ladinian Tongchuan Formation.)

F. Necymylacridae C2(Bashkirian)-C2(Gzhelian)
Vršanský et al. (2002) state that this family extended into the Lower Permian but provide no data on specimens.

First: e.g. *Necymylacris fascigera* in Schneider (1983), Pottsville Formation, Campbell Ledge, Pittston, Pennsylvania, United States.

Last: e.g.? *Necymylacris scudderi* in Schneider (1983), Lawrence Formation, Douglas County, Kansas, United States.

F. Paucineuridae Hong, 1980 P1(Asselian)
While Liang et al. (2006) list this monotypic family as having an Upper Carboniferous age (as per the original description in Hong, 1980), Zhang et al. (1997) showed the Shanxi Formation to be of lowermost Permian age - a view repeated by Hong (1998a).

First and Last: *Paucineura hsui* in Liang et al. (2006), Shanxi Formation (Xiangning Entomassemblage), Xiangning Region, Shanxi Province, China.

F. Phyloblattidae (Anthracoblattinidae) C2(Moscovian)-K1(Barremian)

First: e.g. *Phyloblatta*? sp. in Jarzembowski and Schneider (2007), Farrington Formation, Writhlington, Somerset, United Kingdom.

Last: Figured in Vršanský (2008c), Bon-Tsagaan Nuur, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia.

F. Poroblattinidae C2(Moscovian)-T3(Carnian)
Schneider et al. (2004) do not consider previous Mesozoic records to belong to this family. Vršanský et al. (2002) also express reservations about the affinities of Mesozoic records, stating that "Poroblattinidae probably failed to cross the Perm-Triassic boundary" (p. 266), yet show the family extending into the Upper Triassic in their range chart for the order.

First: *Poroblatta duffieuxi* in Schneider (1984), Assise de Bruay, Lens, Pas-de-Calais, France.

Last: Mentioned in Shcherbakov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Raphidiomimidae J1(Toarcian)-K1(Aptian)

First: e.g. *Liadoblattina blakei* in Vršanský and Ansorge (2007), Upper Lias (Alderton), Alderton, Gloucestershire, United Kingdom.

Last: Mentioned in Bechly (2007c), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Skokidae Vršanský, 2007 J3(Oxfordian)

First and Last: *Skok svaba* Vršanský, 2007, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Spiloblattinidae (Compsoblattidae, Compsoblattinidae, Spiloblattidae) C2(Moscovian)-T3(Carnian)
Vršanský et al. (2002) synonymised Compsoblattinidae under Spiloblattinidae without discussion.

First: "*Kinklidoblatta*" *morini* in Schneider and Werneburg (2006), Assise de Bruay, Lens, Pas-de-Calais, France. (Schneider and Werneburg, 2006 are uncertain as to the spiloblattinid identity of this species and state that the earliest undoubted spiloblattinids are of Stephanian A (Kasimovian) age.)

Last: Mentioned in Shcherbakov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Subioblattidae T2(Anisian)-T3(Norian)
Papier and Nel, 2001 state that this family is known only from the Triassic. [Andy: The History of Insects chapter says they originate in the Upper Carboniferous but doesn't give any details and I've seen nothing else about it. Have you come across any records?] The species from the Sakmarian Letovice Formation at Obora often listed as *Subioblatta* sp. (e.g. in Zajíc and Štamberg, 2004) is listed as "*Syscioblatta* n. sp. Obora" (Spiloblattinidae) by Schneider and Werneburg, 2006, although they also suggest that Subioblattidae might be most closely related to *Syscioblatta* and therefore fall within the Spiloblattinidae.

First: *Subioblatta undulata* in Papier and Nel (2001), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: e.g. *Samaroblattella kenderlykensis* Papier and Nel, 2001, Tologoy Formation, Ak-Kolka River, Kenderlyk, Zaisan District, Kazakhstan.

F. Umenocoleidae K1(Valanginian)-K1(Albian)
Gorokhov (2006) restricted the composition of this family to the genera *Umenocoleus*, *Petropterix*, *Elytropterix* and *Ponopterix*. Vršanský (2008b) lists this family as present in the Turonian New Jersey amber but this is likely to be *Jantaropterix*, which was removed from this family by Gorokhov (2006). In the description of the type species of this family, *Umenocoleus sinuatus* Chen and Tan, 1973, the deposit it was found in was not reported. It may be from the Chijinbao Formation (Wang Bo pers. comm., 2011) but the stage-age of this specimen is not known for certain other than that it is Lower Cretaceous.

First: *Petropterix sibirix* Vršanský, 2003b, Zaza Formation, Baissa, Buryatia, Russian Federation.

Last: Mentioned in Perrichot et al. (2007), Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

O. Caloneurodea Handlirsch, 1937 (Caloneurida, Caloneuroidea)
Carboniferous(Bashkirian)-Permian(Wordian)

F. Caloneuridae (Amboneuridae, Anomalogrammatidae, Apsidoneuridae, Eohymenidae, Euthygrammatidae, Paleuthygrammatidae, Permobiellidae, Pleisiogrammatidae, Sthenaroceridae) C2(Moscovian)-P2(Wordian)

First: e.g. *Amboneura closei* in Rasnitsyn et al. (2004a), Allegheny Formation, Pennsylvania/Maryland/West Virginia, Ridge-and-Valley Appalachians, United States.

Last: *Eohymen maculipennis* in Rasnitsyn et al. (2004a), Amanak Formation, Kargala, Belozersky District, Orenburg Region, Russian Federation.

F. Hapalopteridae (Aenigmatodidae, Emphylopteridae, Protokollariidae) C2(Bashkirian)-C2(Gzhelian)
Ordinal placement and synonymies after Rasnitsyn et al. (2004a). *Tshecalculus inaspectus* is here considered in its own family in Grylloblattodea after Aristov (2009a).

First: *Geroneura wilsoni* in Rasnitsyn et al. (2004a), Lancaster Formation, Saint John, New Brunswick, Canada.

Last: e.g. *Carrizarroyo calopterus* Rasnitsyn *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

F. Permostridulidae Béthoux et al., 2003b P2(Wordian)

First and Last: *Permostridulus brongniarti* in Béthoux (2008a), Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France. (Rasnitsyn et al. (2004a) did not consider this taxon in their revision so separate family status is maintained here.)

O. Cnemidolestodea Handlirsch, 1937 Carboniferous(Moscovian)-Permian(Wordian)

F. Cnemidolestidae C2(Kasimovian)

e.g. *Cnemidolestes woodwardi* in Béthoux and Nel (2005), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Ischnoneuridae (Aetophlebiidae) C2(Kasimovian)
The composition and definition of this family is in a state of flux and in need of revision (Béthoux et al., 2003a). It is taken here *sensu* Rasnitsyn (2002j), with the removal of those taxa which have since been assigned to different, natural groups.

e.g. *Ischnoneura oustaleti* in Béthoux and Nel (2005), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Proedischiidae (Narkeminidae, Narkemocagurgidae, Proedischidae) C2(Moscovian)-P1(Asselian)

First: e.g. *Narkema taeniatum* in Béthoux (2005), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: e.g. *Paganzophlebia polyclada* Martins-Neto, Gallego & Brauckmann *in* Martins-Neto et al., 2007a, Bajo de Véliz Formation (Pallero Member), Paganzo Basin, Sierra Grande de San Luis, San Luis Province, Argentina.

F. Spanioderidae (Anthraconeuridae) C2(Moscovian)
The monospecific Anthraconeuridae was restored by Béthoux and Nel (2002b) but the type genus was apparently synonymised with *Miamia* by Béthoux (2008b).

e.g. *Miamia bronsoni* in Béthoux (2008b), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Taiophlebiidae Martins-Neto *in* Martins-Neto et al., 2007a C2(Moscovian)

e.g.? *Cacurgulopsis sanguinettiae* in Martins-Neto (2005), Boituva Formation (Ahrensisporites cristatus zone), Praça da Bandeira, Boituva City, São Paulo, Brazil. (This genus was moved to Taiophlebiidae by Martins-Neto et al., 2007a. The precise stratigraphic age of the other members attributed to this family are not currently known, although all are Upper Carboniferous.)

F. Tococladidae P1(Artinskian)-P2(Wordian)
This family was assigned to the Cnemidolestodea by Béthoux, 2007c. Rasnitsyn (2002e) synonymized Heteroptilidae and Nugonioneuridae with this family without argument, which was rejected by Béthoux et al. (2003a).

First: e.g. *Tococladus rallus* in Béthoux et al. (2003a), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

Last: *Tococladus garrici* Béthoux et al., 2003a, Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France.

O. Dermaptera de Geer, 1773 Triassic(Carnian)-Quaternary(Holocene)

F. Anisolabididae K1(Aptian)-Holocene
Engel and Haas (2007) erect the anisolabidid subfamily Cretolabiinae for the genera *Cretolabia* and *Kotejalabis*, both from the Crato Formation, leaving Spongiphoridae without a fossil record.

First: e.g. *Cratoborellia gorbi* Haas, 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Dermapteridae (Sinopalaeodermatidae, Turanoviidae) J2(Callovian)-J3(Oxfordian)

First: e.g. *Sinopalaeodermata neimonggolensis* in Wappler et al. (2005), Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China. (Originally described with *Jurassimedeola orientalis* Zhang, 2002a. Wappler et al., 2005 list these species in Sinopalaeodermatidae but Engel and Haas, 2007 place it as a junior synonym of Dermapterinae.)

Last: e.g. *Turanovia incompleta* in Wappler et al. (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Diplatyidae Mio.(Burdigalian)-Holocene

First: *Diplatys* (*Syndiplatys*) *protoflavicollis* in Wappler et al. (2005), Masaragawa Formation, Seki, Sado Island, Japan.

F. Forficulidae Eoc.(Ypresian)-Holocene

First: *Forficula paleocaenica* in Wappler et al. (2005), Fur Formation (Mo Clay), Limfjord/Mors Peninsula/Fur Island, Jutland, Denmark.

F. Labiduridae K1(Aptian)-Holocene

First: e.g. *Caririlabia berghoffi* Haas, 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Ocelliidae Spahr, 1990 Eoc.(Priabonian)
Originally thought to belong in Diplura, this family is considered *nomen dubium* by Engel and Haas (2007) as it is probably a junior synonym of another, as yet unidentified, common Baltic amber earwig family.

First and Last: *Ocellia articulicornis* in Wappler et al. (2005), Baltic amber, Baltic, Baltic region, Baltic.

F. Protodiplatyidae (Longicerciatidae, Protodiplateidae, Protodiplatidae) T3(Carnian)-K1(Barremian)

First: Mentioned in Shcherbakov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: e.g. *Longicerciata mesozoica* in Wappler et al. (2005), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Pygidicranidae (Pygidiocranidae) K1(Albian)-Holocene

First: *Burmapygia resinata* Engel and Grimaldi, 2004b, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar. (Engel and Grimaldi (2004b) consider this to be the oldest definitive Pygidicranidae.)

F. Semenoviolidae J3(Oxfordian)

e.g. *Semenovioloides capitatus* in Wappler et al. (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Turanodermatidae Engel, 2003b(Turanodermidae) J3(Oxfordian)
This family may extend into the Cretaceous if *Archaeosoma* (Barremian, Laiyang Fm, China) turns out to be allied (Engel, 2003b).

First and Last: *Turanoderma sepultum* in Wappler et al. (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

O. Embiodea Kusnezov, 1903 (Embiida, Embiidina, Embioptera)
Jurassic(Callovian)-Quaternary(Holocene)

F. Anisembiidae Mio.(Burdigalian)-Holocene

First: e.g. *Glyphembia amberica* Ross, 2003, Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Embiidae Eoc.(Priabonian)-Holocene

First: e.g. *Electroembia antiqua* in Engel and Grimaldi (2006a), Baltic amber, Baltic, Baltic region, Baltic.

F. Notoligotomidae (Burmitembiidae) K1(Albian)-Holocene

First: *Burmitembia venosa* in Engel and Grimaldi (2006a), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Oligotomidae Pleist.(Upper Pleistocene)-Holocene

First: *Oligotoma westwoodi* in Spahr (1992), Tanzanian copal, Tanzanian copal, Tanzanian copal, Tanzania. (Handlirsch (1908) lists this specimen as from 'Zanzibar?'.)

F. Sinembiidae Huang and Nel, 2009b J2(Callovian)

e.g. *Sinembia rossi* Huang and Nel, 2009b, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Sorellembiidae Engel and Grimaldi, 2006a K1(Albian)

First and Last: *Sorellembia estherae* Engel and Grimaldi, 2006a, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Teratembiidae Mio.(Burdigalian)-Holocene

First: *Oligembia vetusta* in Engel and Grimaldi (2006a), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

O. Grylloblattodea Brues and Melander, 1915 (Grylloblattida, Grylloblattoidea) Carboniferous(Bashkirian)-Quaternary(Holocene)

F. Aliculidae Storozhenko, 1997 P1(Sakmarian)-P2(Wordian)

First: *Alicula aera* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic. (Listed as *Permula aera* by Zajíc and Štamberg, 2004 but this was made a junior synonym by Storozhenko, 1997.)

Last: *Tshepanichoptera lacera* Aristov *in* Aristov and Bashkuev, 2008, Chepanikha locality, Rossokha River valley, Zavjalovskii District, Udmurt Republic, Russian Federation.

F. Archiprobnidae (Archiprobnisidae) P2(Roadian)

First and Last: *Archiprobnis repens* in Storozhenko (1997), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Atactophlebiidae (Bardapteridae) P1(Kungurian)-P2(Roadian)
Triaseuryptilon accostai from the Triassic of Argentina does not belong to this family and may not be a grylloblattid (Aristov, 2004a).

First: e.g. *Kirkorella mira* in Aristov (2004b), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: e.g. *Atactophlebia termitoides* in Béthoux et al. (2005), Baitugan Formation, Tikhie Gory, Kama River, Tatarstan, Russian Federation.

F. Bajanzhargalanidae Storozhenko 1992 *in* J3(Tithonian)

First and Last: *Bajanzhargalana magna* Storozhenko, 1988, Ulan-Ereg, Khoutiyn-Khotgor, Dund-Gobi Aimag, Mongolia.

F. Blattogryllidae P3(Changhsingian)-K1(Valanginian)
Blattogryllus karatavicus from the Oxfordian Karabastau Formation at Karatau (Kazakhstan) is a cockroach (Aristov et al., 2006).

First: e.g. *Protoblattogryllus zajsanicus* Storozhenko, 1990, Maichat/Ak-Kolka Formation, Karaungir River, Saur Mountains, Vostochno-Kazakhstanskaya oblast, Kazakhstan.

Last: *Parablattogryllus obscurus* Storozhenko, 1988, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Camptoneuritidae (Camptoneuridae) P2(Roadian)

First and Last: *Camptoneurites reticulata* in Storozhenko (1997), Baitugan Formation, Tikhie Gory, Kama River, Tatarstan, Russian Federation.

F. Chaulioditidae (Tomiidae) P2(Roadian)-T2(Anisian)

First: e.g. *Protomia proteus* in Aristov (2008a), Belebey Formation, Kityak, Kirov Region, Russian Federation. (*Protomia* and *Miralioma* were transferred to Chaulioditidae in Aristov et al. (2009a).)

Last: Mentioned in Aristov (2004c), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Chelopteridae P1(Artinskian)

First and Last: *Chelopterum peregrinum* in Beckemeyer (2004b), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Daldubidae Storozhenko, 1996b C2(Gzhelian)

e.g. *Dalduba faticana* in Storozhenko (2002), Kata Formation, Chunya, Siberian Federal District, Russian Federation.

F. Demopteridae P1(Artinskian)

First and Last: *Demopterum gracile* Carpenter, 1950, Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Epideigmatidae (Paraphenopteridae, Phenopteridae, Sylvaphlebiidae) C2(Moscovian)-P3(Changhsingian)

First: *Epideigma elegans* in Béthoux (2007b), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: *Belmophenopterum pectinatum* Rasnitsyn and Aristov, 2004, Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Euremiscidae P1(Kungurian)-P2(Roadian)

First: e.g. *Euremisca elegans* Aristov, 2004b, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: *Euremisca kazanica* Aristov, 2009d, Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Euryptilonidae (Stereopteridae) P1(Sakmarian)-P2(Roadian)
Karaungirella from Karaungir (Changhsingian) belongs in the miomopteran family Permosialidae (Aristov, 2004a).

First: e.g. *Blania falsa* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic. (This genus, along with *Karaungirella*, *Maculopterum*, *Oborella*, *Quercopterum*, *Sharovipterum*, *Torrentopterum* and *Villopterum*, were transferred from Lemmatophoridae to Euryptilonidae by Storozhenko, 1997.)

Last: Mentioned in Aristov (2004b), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Geinitziidae (Prosepididontidae, Stegopteridae) P1(Kungurian)-J3(Tithonian)

First: *Stegopterum anteanatalis* Aristov, 2004a, Lek-Vorkuta Formation, Vorkuta Group, Pechora Cola Basin, Komi Republic, Russian Federation.

Last: *Shurabia shartegica* Aristov et al., 2009b, Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Gorochoviidae Storozhenko, 1994 T3(Carnian)

e.g. *Gorochovia individua* Storozhenko, 1994, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Grylloblattidae Holocene

First and Last: Extant , Extant, Extant Locality, Extant Area, Extant Country.

F. Havlatiidae P1(Sakmarian)

e.g. *Havlatia annae* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Ideliidae P1(Kungurian)-T3(Norian)
The Carboniferous genus *Protoperla* was moved to Grylloblattodea *incertae sedis* in Béthoux et al. (2005).

First: e.g. *Micaidelia minutissima* Aristov, 2004b, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: *Ideliopsina kenderlykensis* in Aristov (2005), Tologoy Formation, Ak-Kolka River, Kenderlyk, Zaisan District, Kazakhstan.

F. Idelinellidae Storozhenko, 1997 P1(Kungurian)-P2(Roadian)

First: e.g. *Sylvastriga miranda* Aristov, 2004b, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: *Idelinella macroptera* Storozhenko, 1992c, Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation. (Originally described in Ideliidae.)

F. Ivapteridae Aristov, 2009a P1(Kungurian)-P2(Roadian)

First: *Tshekardembia sharovi* in Aristov and Rasnitsyn (2009), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: *Ivaptera sharovi* Aristov, 2009a, Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Jabloniidae P1(Sakmarian)

First and Last: *Jablonia aestiva* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Juraperlidae Huang and Nel, 2007a J2(Callovian)

First and Last: *Juraperla daohugouensis* Huang and Nel, 2007a, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Kargalopteridae Aristov, 2009b P2(Wordian)

e.g. *Kargaloptera connexa* Aristov, 2009b, Amanak Formation, Kargala, Belozersky District, Orenburg Region, Russian Federation.

F. Kortshakoliidae Storozhenko, 1997 P1(Kungurian)-P2(Roadian)

First: *Kortshakolia ideliformis* in Storozhenko (1997), Usyatsk Formation, Balakhonsk Series, Korchakol, Kemerovo Region, Russian Federation.

Last: *Paridelia pusilla* in Storozhenko (1997), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Liomopteridae (Khosaridae) C2(Gzhelian)-T3(Carnian)

First: e.g. *Tapopterum populus* Aristov *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: Figured in Cairncross et al. (1995), Molteno Formation, KwaZulu-Natal, Karoo Basin, South Africa.

F. Madygenophlebiidae Storozhenko, 1992a T3(Carnian)

e.g. *Madygenophlebia bella* Storozhenko, 1992a, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Megakhosaridae P1(Artinskian)-T3(Carnian)

First: Mentioned in Aristov (2009d), Petrolia (Belle-Plains) Formation, Wichita Group, Texas, United States.

Last: Mentioned in Aristov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Mesojabloniidae Storozhenko, 1992b T3(Carnian)

First and Last: *Mesojablonia kukalovae* Storozhenko, 1992b, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Mesorthopteridae T2(Anisian)-T3(Norian)

First: *Austroidelia perplexa* in Jell (2004), Hawkesbury Sandstone, Brookvale Quarry, Beacon Hill, New South Wales, Australia. (Jell (2004) listed this species in Ideliidae but it was transferred to Mesorthopteridae by Storozhenko (1996a).)

Last: Mentioned in Aristov (2005), Tologoy Formation, Ak-Kolka River, Kenderlyk, Zaisan District, Kazakhstan.

F. Neleidae Ansorge, 1996a J1(Toarcian)

First and Last: *Nele jurassica* Ansorge, 1996a, Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

F. Oecanthoperlidae Storozhenko, 1988 K1(Valanginian)

First and Last: *Oecanthoperla sibirica* Storozhenko, 1988, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Permopectinidae Aristov *in* Rasnitsyn et al., 2005 P1(Kungurian)

e.g. *Permopectina tshekardensis* Aristov *in* Rasnitsyn et al., 2005, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Permotermopsidae P1(Kungurian)-P3(Changhsingian)

First: e.g. *Khosaridelia rigida* Aristov *in* Rasnitsyn et al., 2005, Lek-Vorkuta Formation, Vorkuta Group, Pechora Cola Basin, Komi Republic, Russian Federation.

Last: *Khosaridelia vyatica* Aristov, 2009d, Maichat/Ak-Kolka Formation, Karaungir River, Saur Mountains, Vostochno-Kazakhstanskaya oblast, Kazakhstan.

F. Pinideliidae Storozhenko, 1997 P1(Kungurian)

e.g. *Kishertia tricubitalis* in Aristov (2004b), Koshelevka Formation (Iren' Horizon), Kishert' locality, Ural Mountains, Russian Federation.

F. Plesioblattogryllidae Huang et al., 2008b J2(Callovian)

First and Last: *Plesioblattogryllus magnificus* Huang et al., 2008b, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Probnidae (Probnisidae) C2(Gzhelian)-T3(Norian)

First: *Probnis fossor* Aristov *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: *Triassoprobnis humilis* in Aristov (2005), Protopivka Formation, Garazhovka, Izyum District, Ukraine.

F. Protembiidae P1(Artinskian)

First and Last: *Protembia permiana* in Storozhenko (1997), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Protoblattinidae (Protoblattidae) C2(Kasimovian)
Protoblattina brought out of synonymy from *Protoperla* in Béthoux et al. (2005).

First and Last: *Protoblattina bouvieri* in Béthoux et al. (2005), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Protoperlidae C2(Kasimovian)

First and Last: *Protoperla westwoodi* in Béthoux et al. (2005), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Raaschiidae Beckemeyer, 2004b P1(Artinskian)

First and Last: *Raaschia oklahomensis* Beckemeyer, 2004b, Wellington Formation (OK), Midco, Oklahoma, United States.

F. Sinonamuropteridae Peng et al., 2005 C2(Bashkirian)
Originally described in Diaphanopterodea, this family was referred to the Grylloblattodea by Prokop and Ren (2007).

e.g. *Separatonerva qilianshanensis* Peng et al., 2005, Tupo Formation, Qilianshan Mountains, Ningxia/Gansu/Inner Mongolia, China.

F. Skaliciidae (Scalicidae, Skalicidae) P1(Sakmarian)-P2(Wordian)

First: e.g. *Skalicia rara* in Aristov (2009d), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: *Urzhumskalicia kargalensis* Aristov, 2009b, Amanak Formation, Kargala, Belozersky District, Orenburg Region, Russian Federation.

F. Sojanoraphidiidae P1(Artinskian)-P2(Roadian)

First: *Aibolitus minutus* Béthoux and Beckemeyer, 2007, Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States. (Béthoux and Beckemeyer (2007) consider the family placement of this species as uncertain but Aristov (2009d) lists it in this family.)

Last: *Sojanoraphidia rossica* in Storozhenko and Novokshonov (1994), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Stenoneuritidae C2(Kasimovian)

First and Last: *Stenoneurites maximi* in Béthoux et al. (2005), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Sylvabestiidae Aristov, 2000a P1(Kungurian)

First and Last: *Sylvabestia tenuis* Aristov, 2000a, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Sylvardembiidae Novokshonov, 2000 P1(Kungurian)-P2(Roadian)

First: e.g. *Sylvardembia matura* Aristov, 2000b, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: *Barmaleus* sp. in Aristov and Rasnitsyn (2009), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Tillyardembiidae P1(Kungurian)

e.g. *Kungurembia brevicervix* in Aristov and Rasnitsyn (2009), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Tshecalculidae Novokshonov, 2000 P1(Kungurian)
Originally unplaced in Pterygota, Aristov (2009a) lists this family in the Grylloblattodea.

First and Last: *Tshecalculus inaspectus* Novokshonov, 2000, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation. (Rasnitsyn et al. (2004a) list this species in the Caloneurodea: Hapalopteridae but this reference is superceeded by Aristov (2009a).)

F. Tshekardominidae Novokshonov and Aristov, 2002 P1(Artinskian)-P2(Capitanian)

First: *Sigmophlebia engeli* in Aristov (2009d), Wellington Formation (OK), Midco, Oklahoma, United States.

Last: *Tshekardomina mongolica* Aristov, 2009d, Tsankhi (Tsankhin) Formation, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia.

F. Tunguskapteridae Storozhenko and Vršanský, 1995 T1(Induan)-T3(Carnian)

First: *Tunguskaptera eximia* Storozhenko and Vršanský, 1995, Bugarikhta Formation, Nizhnyaya Tunguska river, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

Last: *Ferganamadygenia plicata* Storozhenko and Vršanský, 1995, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

O. Isoptera Brullé, 1832 (Termitida, Termitoidae)
Cretaceous(Valanginian)-Quaternary(Holocene)

F. Archeorhinotermitidae Krishna and Grimaldi, 2003 K1(Albian)
Originally described as a subfamily of Rhinotermitidae but elevated to family in Engel et al. (2009a).

First and Last: *Archeorhinotermes rossi* in Engel et al. (2009a), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Archotermopsidae Engel et al., 2009a Eoc.(Priabonian)-Holocene

First: e.g. *Archotermopsis tornquisti* in Engel et al. (2009a), Baltic amber, Baltic, Baltic region, Baltic.

F. Cratomastotermitidae Engel et al., 2009a K1(Aptian)

First and Last: *Cratomastotermes wolfschwenningeri* in Engel et al. (2009a), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Isoptera *insertae sedis* K1(Valanginian)
NOTE: This is only in here to extend the order range and will be removed and put as a note under the order for publication.

First and Last: *Baissatermes lapideus* Engel et al., 2007a, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Kalotermitidae (Calotermitidae) K1(Albian)-Holocene

First: e.g. *Kalotermes burmensis* Poinar, 2009a, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Mastotermitidae K1(Hauterivian)-Holocene

First: *Valditermes brenanae* in Engel et al. (2009a), Lower Weald Clay Formation (Capel), Capel, Surrey, United Kingdom.

F. Rhinotermitidae Eoc.(Priabonian)-Holocene

First: e.g. *Heterotermes eocenicus* in Engel et al. (2009a), Baltic amber, Baltic, Baltic region, Baltic.

F. Stylotermitidae Eoc.(Priabonian)-Holocene

First: *Parastylotermes robustus* in Engel et al. (2009a), Baltic amber, Baltic, Baltic region, Baltic.

F. Termitidae Olig.(Rupelian)-Holocene

First: *Aiuruocatatermes piovezanae* Martins-Neto and Pesenti, 2006, Entre-C??rregos Formation, Aiuruoca Basin, Minas Gerais, Brazil.

F. Termopsidae Eoc.(Priabonian)-Mio.(Serravallian)
Engel et al. (2009a) restrict the composition of this family to the type genus *Termopsis*.

First: e.g. *Termopsis ukapirmasi* in Engel et al. (2009a), Baltic amber, Baltic, Baltic region, Baltic.

Last: e.g. *Termopsis mallaszi* in Engel et al. (2007b), "volcanic floras" deposit, Tállya, Eperges-Tokajer Mountains, Hungary.

O. Mantodea Burmeister, 1839 (Manteodea, Mantida)
Carboniferous(Kasimovian)-Quaternary(Holocene)

F. Ambermantidae Grimaldi, 2003b K2(Turonian)

First and Last: *Ambermantis wozniaki* Grimaldi, 2003b, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States. (Vršanský, 2008a mistakenly states that this species is a junior synonym of *Jantarimantis zherikhini*.)

F. Baissomantidae Gratshev and Zherikhin, 1994 K1(Valanginian)

e.g. *Baissomantis picta* in Grimaldi (2003b), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Chaeteessidae (Archephemeridae, Chaeteessiidae) K1(Valanginian)-Holocene

First: *Cretophotina selenginensis* in Vršanský (2008c), Sharin-Gol Formation, Sharin-Gol, Selenge Aimag, Mongolia.

F. Cretomantidae Gratshev and Zherikhin, 1994 K1(Valanginian)
Grimaldi (2003b) removes *Electromantis* (Santonian amber from the Kheta Formation, Russia) to Mantodea *incertae sedis*, although he does not explicitly mention the position of *Cretomantis* in his revised system.

First and Last: *Cretomantis larvalis* in Grimaldi (2003b), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Hymenopodidae Eoc.(Ypresian)-Holocene

First: Figured in Zherikhin (2002b), Green River Formation (Colorado), Unitas area, Colorado, United States. (Zherikhin's assignment of this specimen to Hymenopodidae was tentative.)

F. Jantarimantidae Vršanský, 2002a(Archimantidae) K2(Turonian)
Originally described as Archimantidae in Vršanský (2002b) but a replacement name was later given as this was a junior homonym.

First and Last: *Jantarimantis zherichini* in Gorokhov (2006), New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Juramantidae Vršanský, 2002b J3(Tithonian)

First and Last: *Juramantis initialis* in Vršanský (2005), Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Liturgusidae Eoc.(Priabonian)-Holocene

First: Mentioned in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Mantidae (Manteidae, Vatidae) Pal.(Thanetian)-Holocene

First: *Prochaeradodis enigmaticus* in Nel and Roy (1996), spongo-diatomaceous maar, Menat, Puy-de-Dôme, Auvergne, France.

F. Mantoididae Eoc.(Priabonian)-Holocene

First: *Mantoida matthiasglinki* Zompro, 2005, Baltic amber, Baltic, Baltic region, Baltic.

F. Santanmantidae Grimaldi, 2003b K1(Aptian)

First and Last: *Santanmantis axelrodi* in Grimaldi (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Strephocladidae (Strephoneuridae) C2(Kasimovian)-P2(Roadian)
Rasnitsyn and Aristov (2004) synonymise Strephocladidae and Strephoneuridae under Anthracoptilidae but the attribution to the total-group Mantodea of the 'strephocladidaeans' *sensu* Béthoux and Wieland (2009) (including *Mesoptilus* and *Strephoneura*) apart from the other anthracoptilid genera warrants listing the family group here.

First: e.g. *Mesoptilus dolloi* in Béthoux and Wieland (2009), Upper Coal Measures (Commentry), Commentry, Allier, France.

Last: e.g. *Graticladus severus* in Béthoux and Wieland (2009), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Tarachodidae Mio.(Burdigalian)-Holocene

First: Mentioned in Zherikhin (2002b), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

O. Mantophasmatodea Klass et al., 2002 Jurassic(Callovian)-Quaternary(Holocene)

F. Mantophasmatidae Zompro, Klass, Kristensen & Adis *in* Klass et al., 2002(Austrophasmatidae, Ensiferophasmatidae, Raptophasmatidae, Tanzaniophasmatidae) J2(Callovian)-Holocene

First: *Juramantophasma sinica* Huang et al., 2008c, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

O. Orthoptera Olivier, 1789 (Gryllida, Titanoptera)
Carboniferous(Kasimovian)-Quaternary(Holocene)

F. Acrididae (Oedipodidae, Truxalidae) Eoc.(Ypresian)-Holocene
Handlirsch, 1908 mentions *Tyrbula multispinosa* from the Green River Formation in Wyoming but this species has recieved no attention in subsequent literature and is not listed on the Orthoptera Species File.

First: e.g.? Mentioned in Selden and Penney (2009), Horsefly shales, Horsefly river, Cariboo, British Columbia, Canada.

F. Adumbratomorphidae Gorokhov, 1987a P1(Kungurian)

First and Last: *Adumbratomorpha tettigonioides* in Gorokhov (1995b), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Anelcanidae (Parelcanidae) P1(Artinskian)

e.g. *Anelcana dilatata* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Anostostomatidae (Henicidae, Mimnermidae) K1(Aptian)-Holocene

First: *Euclydes ramosfernandesi* Martins-Neto, 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Araripelocustidae Martins-Neto, 1995a(Araripelocustopsidae) K1(Aptian)

e.g. *Araripelocusta brevis* in Heads and Martins-Neto (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Baissogryllidae Gorokhov, 1985(Cearagryllidae) J3(Tithonian)-K1(Aptian)

First: e.g. *Sharategia rasnitsyni* in Gorokhov et al. (2006), Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

Last: e.g. *Notocearagryllus arturandradai* Martins-Neto *in* Martins-Neto and Tassi, 2009, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Bintoniellidae T3(Carnian)-J1(Hettangian)

First: e.g. *Oshiellana primaria* in Gorokhov (2005a), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: *Bintoniella brodiei* in Shcherbakov (2008a), Planorbis zone (Binton), Binton, Warwickshire, United Kingdom.

F. Bouretidae Martins-Neto, 2001 K1(Aptian)

First and Last: *Bouretia elegans* in Heads and Martins-Neto (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Brauckmanniidae Martins-Neto, 2007 K1(Aptian)

First and Last: *Brauckmannia groeningae* Martins-Neto, 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Chorotypidae (Eruciidae) Eoc.(Priabonian)-Holocene

First: *Erucius*? *lewisi* in Martins-Neto (2003), Passamari Formation, Ruby River Basin, Montana, United States. (This species was not mentioned by Carpenter, 1992b. This extant genus is listed under the Chorotypidae in the Orthoptera Species File.)

F. Dzhajloutshellidae Gorokhov, 1994 T3(Carnian)

e.g. *Dzhajloutshella flexuosa* Gorokhov, 2005b, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Elcanidae T2(Anisian)-K1(Albian)

First: *Elcanopsis sydneiensis* in Jell (2004), Hawkesbury Sandstone, Brookvale Quarry, Beacon Hill, New South Wales, Australia. (This species is not mentioned in the Orthoptera Species File (Version 2.0/4.0).)

Last: e.g. *Longioculus burmensis* Poinar et al., 2007, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Episactidae Mio.(Burdigalian)-Holocene

First: *Paleomastacris ambarinus* in Pérez-Gelabert and Rowell (2006), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Eumastacidae J3(Oxfordian)-Holocene

First: *Archaeomastax jurassicus* in Pérez et al. (1997), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan. (Heads, 2008a mistakenly lists this specimen as Lower Jurassic.)

F. Gryllacrididae (Gryllacridae) T3(Carnian)-Holocene

First: *Xenogryllacris reductus* in Jell (2004), Mount Crosby Formation, Ipswich Basin, Queensland, Australia.

F. Gryllavidae Gorokhov, 1986 T2(Anisian)-T3(Carnian)

First: *Galliagryllavus vogesiacus* Marchal-Papier et al., 2000, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: e.g. *Zagryllavus elongatus* in Gorokhov (2005a), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Gryllidae (Eneopteridae, Oecanthidae, Trigonidiidae) K1(Hauterivian)-Holocene

First: *Araripegryllus*? *orientalis* Gorokhov et al., 2006, Lower Weald Clay Formation (Clockhouse), Clockhouse Brickworks, Surrey, United Kingdom.

F. Gryllotalpidae K1(Aptian)-Holocene

First: e.g. *Archaeogryllotalpoides ornatus* in Heads and Martins-Neto (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Haglidae (Isfaropteridae) T2(Anisian)-K1(Barremian)
The extant genus *Cyphoderris* is considered here to be in the Prophalangopsidae, following the Orthoptera Species File.

First: *Prohagla superba* in Jell (2004), Hawkesbury Sandstone, Brookvale Quarry, Beacon Hill, New South Wales, Australia.

Last: Mentioned in Peñalver et al. (1999), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain.

F. Hagloedischiidae Gorokhov, 1986 T2(Anisian)-T3(Carnian)

First: *Voltziahagla pseudoveinosa* Marchal-Papier et al., 2000, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France. (Originally described in Haglidae but transferred to Hagloedischiidae by Gorokhov (2005a).)

Last: *Hagloedischia primitiva* in Gorokhov (2005a), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Haglotettigoniidae Gorokhov, 1988a K1(Valanginian)

First and Last: *Haglotettigonia egregia* in Gorokhov (2005b), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Locustavidae T1(Induan)-T3(Carnian)

First: *Praelocustopsis mirabilis* in Gorokhov (2005b), Bugarikhta Formation, Nizhnyaya Tunguska river, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

Last: e.g. *Brevilocustavus microscopicus* Gorokhov, 2005b, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Locustopseidae (Locustopsidae) T3(Carnian)-Eoc.(Priabonian)
Gorokhov (2005b) transferred the genera *Praelocustopsis* (Induan, Bugarikhta Formation, Siberia) and *Triassolocusta* (Carnian, Blackstone Formation, Australia) to the Locustavidae.

First: Mentioned in Martins-Neto (2003), Cow Branch Formation, Solite quarry, Virginia, United States.

Last: *Zeunerella*? *lewis* Kevan and Wighton, 1981, Passamari Formation, Ruby River Basin, Montana, United States. (Although Gorokhov et al., 2006 state that the Locustopseidae "is known from the Early Triassic-Late Cretaceous" (p.657), nobody to my knowledge has questioned the family attribution of this species.)

F. Mesoedischiidae Gorokhov, 1987b T1(Induan)-T3(Carnian)

First: *Sonoedischia shmakovi* Gorokhov, 2005a, Babiy Kamen', Maltseva/Sosnovaya Fomation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

Last: e.g. *Mesoedischia obliqua* in Gorokhov (2005a), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Mesotitanidae (Clatrotitanidae, Gigatitanidae) P1(Kungurian)-T3(Carnian)

First: *Jubilaeus beybienkoi* in Béthoux and Nel (2002a), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation. (Listed by Béthoux and Nel (2002a) in Tcholmanvissiidae, Béthoux (2007a) moves this genus to Mesotitanidae.)

Last: e.g. *Gigatitan vulgaris* in Gorokhov (2007), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Mogoplistidae Mio.(Burdigalian)-Holocene

First: *Ornebius ambericus* in Heads (2009a), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Myrmecophilidae K1(Aptian)-Holocene

First: *Araripemyrmecophilops gracilis* in Martins-Neto (1995b), Crato Formation, Araripe Basin, Ceará, Brazil. (Heads and Martins-Neto, 2007 did not mention this species as the section on it was omitted from the final print for unknown reasons [S. W. Heads pers. comm. 2011].)

F. Oedischiidae C2(Kasimovian)-P2(Wordian)

First: e.g. *Oedischia williamsoni* in Prokop et al. (2005), Upper Coal Measures (Commentry), Commentry, Allier, France.

Last: e.g. *Iasvia secunda* Béthoux et al., 2002a, Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France.

F. Paratitanidae T3(Carnian)

e.g. *Minititan zherichini* in Gorokhov (2007), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Permelcanidae P1(Artinskian)-T3(Carnian)

First: *Promartynovia venicosta* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

Last: e.g. *Meselcana madygenica* in Gorokhov (2005a), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Permoraphidiidae (Permoraphididae) P1(Artinskian)
Béthoux and Nel (2002b) described *Permoraphidia magnifica* from the Permian of Madagascar but as no further information on the origin or age is known, it has not been included in the range of this family here.

e.g. *Permoraphidia grandis* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Phasmomimidae J3(Oxfordian)
Gorokhov (2000) restricts Phasmomimidae to the genera *Phasmomima* and *Jurophasmomima*.

e.g. *Phasmomima maculomarginata* in Gorokhov (2000), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Prezottophlebiidae Martins-Neto, 2007 K1(Aptian)

First and Last: *Prezotophlebia helbae* Martins-Neto, 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Promastacidae Eoc.(Ypresian)
Gorokhov (1988c) transferred the Palaeocene genus Promastacoides to the Phasmomimidae but later (Gorokhov, 2000) to Susumaniidae.

First and Last: *Promastax archaicus* in Kevan and Wighton (1981), Horsefly shales, Horsefly river, Cariboo, British Columbia, Canada.

F. Proparagryllacrididae T3(Carnian)

e.g. *Kashgarlimahmutia reducta* in Koçak and Kemal (2008), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan. (Both Koçak and Kemal, 2008 and Özdikmen, 2008a both supplied replacement names for the junior homonym Fergania Sharov, however Koçak and Kemal, 2008 has priority as it was published a month earlier.)

F. Prophalangopsidae (Prophalangopseidae) J1(Hettangian)-Holocene

First: *Aboilus tuzigouensis* Lin and Huang, 2006, Badaowan Formation, Kelamayi, Xinjiang Uyghur Autonomous Region, China.

F. Proscopiidae K1(Aptian)-Holocene

First: *Eoproscopia martilli* Heads, 2008a, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Protogryllidae T3(Carnian)-J3(Oxfordian)
Protogryllus minor from the Berriasian Purbeck Beds (United Kingdom) is "Grylloidea incertae sedis" according to Gorokhov et al. (2006).

First: Mentioned in Gorokhov and Rasnitsyn (2002), Molteno Formation, KwaZulu-Natal, Karoo Basin, South Africa.

Last: e.g. *Karataogryllus gryllotalpiformis* in Perrichot et al. (2002), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Pruvostitidae (Kamiidae, Tettavidae) P1(Artinskian)-P2(Wordian)

First: *Paroedischia recta* in Béthoux and Nel (2002b), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States. (Family placement of this species is after Gorokhov, 1995b and the Orthoptera Species File.)

Last: e.g. *Kargalaria maculata* in Gorokhov (1995b), Amanak Formation, Kargala, Belozersky District, Orenburg Region, Russian Federation.

F. Pseudelcanidae Gorokhov, 1987b P1(Kungurian)

e.g. *Pseudelcana permiana* Gorokhov, 1987b, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Pyrgomorphidae Mio.(Serravallian)-Holocene

First: *Miopyrgomorpha fischeri* in Zherikhin (2002c), Oeningen freshwater limestones, Schrotzburg, Baden-Württenburg, Germany.

F. Raphoglidae Béthoux et al., 2002b P2(Wordian)

First and Last: *Raphogla rubra* Béthoux et al., 2002b, Salagou Formation (Mérifons Member), Lodève Basin, Hérault, France.

F. Regiatidae Gorokhov, 1995a J1(Sinemurian)

e.g. *Regiata scutra* in Gorokhov (2005b), Black Ven Marls, Charmouth, Dorset, United Kingdom. (Originally described in the family Haglidae.)

F. Rhaphidophoridae (Raphidiophoridae, Raphidophoridae, Raphydophoridae) Eoc.(Priabonian)-Holocene

First: e.g. *Rhaphidophora antiqua* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Ripipterygidae (Rhipipterygidae) Mio.(Burdigalian)-Holocene

First: *Ripipteryx* sp. in Heads (2009b), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Tcholmanvissiidae P1(Kungurian)-P2(Roadian)

First: *Tcholmanvissia longipipes* in Béthoux and Nel (2002a), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: e.g. *Tcholmanvissia noinskii* in Béthoux and Nel (2002a), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation. (This species also occurs in the Baitugan Formation (Tikhie Gory) (Béthoux and Nel, 2002a).)

F. Tetrigidae K1(Valanginian)-Holocene

First: e.g. *Prototetrix reductus* in Gorokhov and Rasnitsyn (2002), Zaza Formation, Baissa, Buryatia, Russian Federation. (Gorokhov and Rasnitsyn, 2002 mistakenly figure this species under the name *P. reducta*.)

F. Tettigoniidae (Conocephalidae, Locustidae, Phaneropteridae, Tettigonidae) T2(Anisian)-Holocene

First: *Triassophyllum leopardii* Papier et al., 1997, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France. (Gorokhov, 2005b states that this species belongs in the homopteran family Ipsviciidae, however Gall and Grauvogel-Stamm, 2005 maintain its position in Orthoptera and this is followed here.)

F. Tettoedischiidae P1(Kungurian)

e.g. *Tettoedischia minuta* in Béthoux (2007a), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Thueringoedischiidae Zessin, 1997 C2(Gzhelian)-P1(Asselian)

First: e.g.? *Hymenelcana initialis* Gorochov *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: e.g. *Permoedischia moravica* in Zajíc and Štamberg (2004), Říčany Horizon, Padochov Formation, Moravia, Czech Republic.

F. Triassomanteidae (Triassomantidae) T3(Carnian)
Triassomanteodes madygenicus (Madygen Formation) is now considered to be in the Xenopteridae (Gorokhov, 2005a) and *Orichalcum ornatum* (Black Ven Marls) in Locustopseidae (Gorokhov et al., 2006).

First and Last: *Triassomantis pygmaeus* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Tridactylidae K1(Berriasian)-Holocene
The exact position of Mongoloxyinae within Tridactyloidea is uncertain (Heads, 2009b) but is considered here to be in Tridactylidae until further study.

First: *Cretoxya rasnitsyni* Gorokhov et al., 2006, Lulworth Formation, Durlston Bay, Dorset, United Kingdom.

F. Tuphellidae Gorokhov, 1988b T2(Anisian)-J3(Tithonian)

First: *Triassoparacyrtophyllites bifurcatus* Marchal-Papier et al., 2000, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: *Paracyrtophyllites popovi* in Gorokhov (2005a), Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Vitimiidae (Vitimidae) K1(Valanginian)-K1(Barremian)

First: e.g. *Deinovitimia insolita* in Gorokhov et al. (2006), Zaza Formation, Baissa, Buryatia, Russian Federation.

Last: *Deinovitimia occidentalis* Gorokhov et al., 2006, Upper Weald Clay Formation (Capel), Capel, Surrey, United Kingdom.

F. Xenopteridae T3(Carnian)

e.g. *Axenopterum venosum* Gorokhov, 2005a, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

O. Phasmatodea Brunner von Wattenwyl, 1893 (Aeroplanoptera, Phasmatida, Phasmida, Timematodea) Permian(Capitanian)-Quaternary(Holocene)

F. Aerophasmatidae (Cretophasmatidae) J1(Sinemurian)-K2(Turonian)

First: *Durnovaria parallela* in Ansorge (1996b), Black Ven Marls, Charmouth, Dorset, United Kingdom.

Last: *Cretophasma raggei* in Heads and Martins-Neto (2007), Kzyl-Zhar, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Aeroplanidae T3(Carnian)

e.g. *Aeroplana mirabilis* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Agathemeridae Eoc.(Priabonian)-Holocene

First: *Agathemera reclusa* in Tilgner (2001), Florissant Formation, Florissant, Colorado, United States.

F. Archipseudophasmatidae Zompro, 2001 Eoc.(Priabonian)

e.g. *Dvergrphasma fafnir* Zompro, 2005, Baltic amber, Baltic, Baltic region, Baltic.

F. Diapheromeridae Mio.(Burdigalian)-Holocene

First: *Paraphanocles keralasquelelon* in Zompro (2001), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic. (Note: fossil egg figured in Poinar & Poinar 1999 amber book.)

F. Necrophasmatidae J3(Oxfordian)

First and Last: *Necrophasma shabarovi* in Nel et al. (2004a), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Permophasmatidae P2(Capitanian)
Placement of this family in Phasmatodea *sensu lato* remains doubtful (Nel et al., 2004a).

First and Last: *Permophasma kovalevi* in Nel et al. (2004a), Tavan-Tolgoy, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia.

F. Phasmatidae Mio.(Aquitanian)-Holocene

First: Mentioned in Solórzano Kraemer (2007), Mexican amber, Simojovel, Chiapas, Mexico.

F. Phylliidae (Phyllidae) Eoc.(Lutetian)-Holocene

First: *Eophyllium messelensis* Wedmann et al., 2007, Messel Formation, Grube Messel, Hesse, Germany.

F. Prochresmodidae T2(Anisian)-T3(Carnian)

First: *Palaeochresmoda grauvogeli* Nel et al., 2004a, Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: e.g. *Triassophasma* sp. in Gorokhov and Rasnitsyn (2002), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Pseudophasmatidae Eoc.(Lutetian)-Holocene

First: e.g. *Eophasmina manchesteri* in Tilgner (2001), Clarno Formation (Nut Beds), John Day Fossil Beds National Monument, Oregon, United States. (Tilgner, 2001 expresses some doubt about the family placement of these fossil eggs as they resemble some Phasmatidae and the Pseudophasmatidae may not be monophyletic.)

F. Susumaniidae (Hagiphasmatidae) J3(Oxfordian)-Pal.(Thanetian)

First: e.g. *Phasmomimoides minutus* Gorokhov, 2000, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: e.g. *Promastacoides albertae* in Nel et al. (2004a), Paskapoo Formation, eastern foothills, Rocky Mountains, Alberta, Canada. (Originally placed in Phasmomimidae, Gorokhov, 2000 moved this genus to Susumaniidae.)

F. Xiphopteridae T3(Carnian)

e.g. *Xiphopterum curvatum* in Gorokhov and Rasnitsyn (2002), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

O. Plecoptera Burmeister, 1839 (Perlaria, Perlida)
Permian(Kungurian)-Quaternary(Holocene)

F. Baleyopterygidae Sinitshenkova, 1987 J1(Pliensbachian)-K1(Valanginian) Aristov and Rasnitsyn (2009) mistakenly state that *Plutopteryx beata* is of Middle Permian age, when in fact the Bayan-Teg locality is thought to be Middle Jurassic (Rasnitsyn and Zherikhin, 2002).

First: e.g. *Baleyopteryx orthoclada* in Sinitshenkova (2002b), Osinovskiy Formation, Chernyi Etap, Kemerovo Region, Russian Federation.

Last: e.g. *Baissoleuctra irinae* in Ansorge (1993), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Capniidae J1(Toarcian)-Holocene

First: *Dobbertiniopteryx capniomimus* in Liu et al. (2009), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany. (Liu et al., 2009 mistakenly state that this specimen is late Jurassic.)

F. Chloroperlidae J3(Tithonian)-Holocene

First: e.g. *Dipsoperla kunikanensis* Sinitshenkova, 1990, Glushkovo Formation (Unda), Unda, Transbaikalia, Russian Federation.

F. Eustheniidae P3(Changhsingian)-Holocene

First: e.g. *Stenoperlidium permianum* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Euxenoperlidae P2(Roadian)-T3(Carnian)

First: *Euxenoperla oliveri* in van Dijk and Geertsema (2004), Volksrust Formation, Ecca Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: e.g. *Gondwanoperlidium mendozensis* in Martins-Neto et al. (2007b), Potrerillos Formation (Cerro Bayo), Cerro Bayo, Mendoza Province, Argentina.

F. Gripopterygidae J3(Tithonian)-Holocene

First: *Cardioperlisca tshitensis* Sinitshenkova, 1998, Doronino Formation, Chernovskie Kopi, Chita, Transbaikalia, Russian Federation.

F. Leuctridae (Leuctriidae) J3(Tithonian)-Holocene

First: *Lycoleuctra lupina* Sinitshenkova, 1987, Glushkovo Formation (Daya), Daya, Transbaikalia, Russian Federation.

F. Mesoleuctridae T3(Carnian)-K1(Aptian)
Mesoleuctridae do not occur in the Carnian Madygen Formation (Shcherbakov, 2008b).

First: *Capitiperla tonicopoda* Lin, 1992, Huangshanjie Formation, Kerjie, Toksun county, Xinjiang Uyghur Autonomous Region, China. (Originally described as Plecoptera *incertae familiae*, Liu and Ren, 2006 list *Capitiperla* under Mesoleuctridae as does the Plecoptera Species File.)

Last: Mentioned in Liu et al. (2008b), Yixian unspecified, Yixian Formation, Liaoning Province, China.

F. Nemouridae J2(Callovian)-Holocene

First: Mentioned in Liu et al. (2006), Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Palaeonemouridae Sinitshenkova, 1987 P1(Kungurian)-P3(Changhsingian)

First: e.g. *Uralonympha vorkutica* in Sinitshenkova (2004), Lek-Vorkuta Formation, Vorkuta Group, Pechora Cola Basin, Komi Republic, Russian Federation.

Last: e.g. *Palaeonemoura zwicki* in Sinitshenkova (2004), Maichat/Ak-Kolka Formation, Karaungir River, Saur Mountains, Vostochno-Kazakhstanskaya oblast, Kazakhstan.

F. Palaeoperlidae P2(Roadian)-P3(Changhsingian)

First: e.g. *Palaeoperla exacta* in Liu and Ren (2006), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

Last: Mentioned in Sinitshenkova (2002b), Pelyatka Formation, Pelyatka River, Siberian Federal District, Russian Federation.

F. Perlariopseidae T3(Carnian)-K1(Barremian)

First: e.g. *Ramonemoura constricta* in Liu and Ren (2008), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan. (Liu and Ren, 2008 call for the family placement of this species to be reassessed. Shcherbakov, 2008b mentions there are five genera and thirteen species in this family from that deposit but does not name any of them.)

Last: e.g. *Accretonemoura radiata* Sinitshenkova, 1987, Khurilt Formation, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia.

F. Perlidae K1(Aptian)-Holocene

First: *Archaeoperla rarrisimus* Liu, Ren & Sinitshenkova *in* Liu et al., 2008b, Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Perlodidae K1(Berriasian)-Holocene
The Mongolian locality of Khodont is considered here as lowermost Cretaceous, although those who consider it Upper Jurassic would therefore list *Derancheperla collaris* Sinitshenkova, 1990 as the oldest specimen in this family.

First: e.g. *Isoperlodes perstrictus* Sinitshenkova, 1992, Kempendyai locality, Suntar District, Sakha (Yakutia) Republic, Russian Federation.

F. Perlopseidae P1(Kungurian)

e.g. *Perlopsis filicornis* in Aristov and Rasnitsyn (2009), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Platyperlidae T3(Carnian)-K1(Aptian)

First: *Platyperla* sp. in Martins-Neto et al. (2008), Potrerillos Formation (Cerro Bayo), Cerro Bayo, Mendoza Province, Argentina.

Last: Mentioned in Liu et al. (2007a), Yixian unspecified, Yixian Formation, Liaoning Province, China.

F. Siberioperlidae T3(Carnian)-K1(Aptian)

First: *Siberioperla ovalis* in Shcherbakov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: *Sinosharaperla zhaoi* Liu et al., 2007a, Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Taeniopterygidae J2(Callovian)-Holocene

First: e.g. *Mengitaenioptera multiramis* Liu and Ren, 2008, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Tshekardoperlidae Sinitshenkova, 1987(Tschekardoperlidae) P1(Kungurian)

e.g. *Sylvoperlodes zhiltzovae* in Sinitshenkova (2003), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

O. Polyneoptera *incertae sedis* Permian(Asselian)-Cretaceous(Albian)

F. Brachyphyllophagidae Rasnitsyn *in* Rasnitsyn and Krassilov, 2000 J3(Oxfordian)

e.g. *Brachyphyllophagus phasma* Rasnitsyn *in* Rasnitsyn and Krassilov, 2000, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Gelasopteridae P1(Artinskian)

First and Last: *Gelasopteron gracile* in Béthoux et al. (2004c), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Gryllomantidae Gorokhov, 2006 K1(Barremian)-K1(Albian)
Gorokhov (2006) notes that this family may include an undescribed nymph in Dominican amber.

First: e.g. *Gryllomantis lebanensis* in Gorokhov (2006), Bcharreh amber, Caza Bcharreh, Mouhafazet Loubnan Eshemali, Lebanon.

Last: e.g. *Burmantis burmitica* in Gorokhov (2006), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Lemmatophoridae (Germanopriscidae) P1(Asselian)-P2(Wordian)
Beckemeyer (2009) follows Grimaldi and Engel (2005) and Arillo and Engel (2006) in placing this family as Polyneoptera *incertae sedis* while Aristov (2009c) considers places it in Grylloblattodea. *Karaungirella minuta*, listed as last in Ross and Jarzembowski (1993) belongs in the miomopteran family Permosialidae (Aristov, 2004a)

First: e.g. *Artinska* sp. in Hörnschemeyer (1999), Jeckenbach layers, Niedermoschel, Donnersbergkreis district, Rhineland-Palatinate, Germany.

Last: *Kostovatoprisca acuminata* Aristov, 2008a, Galevo (Kostovaty) locality, Kama river, Udmurt Republic, Russian Federation.

F. Mantoblattidae Gorokhov, 2006 K1(Albian)

First and Last: *Mantoblatta mira* Gorokhov, 2006, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Tshekarcephalidae Novokshonov and Rasnitsyn, 2000 P1(Kungurian)-P2(Roadian)

First: *Tshekarcephalus bigladipotens* Novokshonov and Rasnitsyn, 2000, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: *Tshekarcephalus sojanensis* in Aristov and Rasnitsyn (2008), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

O. Protelytroptera (Protelytrida) Permian(Sakmarian)-Permian(Changhsingian)

F. Archelytridae (Apachelytridae, Megelytridae) P1(Sakmarian)-P1(Artinskian)
Shcherbakov (2002) synonymised Apachelytridae and Megelytridae under this family without discussion.

First: e.g. *Ortelytron europeaum* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: e.g. *Archelytron superbum* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Bardacoleidae P1(Kungurian)
This family was transfered to Protelytroptera and the type genus synonymised with *Uralelytron* by Shcherbakov (2002) without discussion.

e.g. *Uralelytron insignis* in Shcherbakov (2002), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Blattelytridae P1(Sakmarian)-P1(Artinskian)
Considered as a separate family by Shcherbakov (2002).

First: Mentioned in Shcherbakov (2002), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: e.g. *Parablattelytron latum* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Dermelytridae P3(Changhsingian)

e.g. *Dermelytron conservativum* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Elytroneuridae P1(Sakmarian)-P1(Artinskian)

First: Mentioned in Shcherbakov (2002), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: *Elytroneura permiana* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Labidelytridae (Stenelytridae) P3(Changhsingian)

e.g. *Labidelytron enervatum* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Permelytridae P1(Artinskian)

First and Last: *Permelytron schucherti* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States. (Beckemeyer, 2000 also lists two genera here considered to be in the separate family Blattelytridae under Permelytridae.)

F. Permofulgoridae P2(Roadian)-P3(Changhsingian)
Carpenter (1992b) does not mention this family nor the two genera assigned to it here. Shcherbakov (2002) places the families Labidelytridae, Permophilidae and Protocoleidae in Permofulgoridae without giving any argument. These families are kept separate here, following Jell (2004).

First: *Arctocoleus ivensis* in Shcherbakov (2002), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

Last: e.g. *Permofulgor belmontensis* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Permophilidae P3(Changhsingian)

e.g. *Permophilus pincombei* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Planelytridae P1(Sakmarian)

First and Last: *Planelytron planum* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Protelytridae P1(Sakmarian)-P1(Artinskian)

First: Mentioned in Shcherbakov (2002), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: e.g. *Protelytron permianum* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Protocoleidae P3(Wuchiapingian)-P3(Changhsingian)

First: *Phyllelytron acuminatum* in van Dijk and Geertsema (1999), Normandien (Estcourt) Formation, Beaufort Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: e.g. *Austrelytron tillyardi* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

O. Protorthoptera Handlirsch, 1906 (Blattinopseida, Eoblattida, Hypoperlida) Carboniferous(Moscovian)-Permian(Changhsingian)

F. Adeloneuridae C2(Moscovian)

First and Last: *Adeloneura thompsoni* in Carpenter (1992b), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Anthracoptilidae (Permarrhaphidae) C2(Kasimovian)-P3(Changhsingian)

First: e.g. *Anthracoptilus* sp. in Rasnitsyn and Aristov (2004), Upper Coal Measures (Commentry), Commentry, Allier, France.

Last: *Jarmilacladus variabilis* Rasnitsyn and Aristov, 2004, Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Anthracothremmidae C2(Moscovian)

e.g. *Melinophlebia analis* in Brauckmann and Herd (2006), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Apithanidae C2(Moscovian)

First and Last: *Apithanus jocularis* in Rasnitsyn (2002k), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Asiopompidae C2(Kasimovian)

First and Last: *Asiopompus tomicus* in Rohdendorf (1991), Alykaeva Formation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

F. Asiuropidae Novokshonov, 1997a P1(Kungurian)

First and Last: *Asiuropa uralensis* Novokshonov, 1997a, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Asyncritidae C2(Moscovian)

First and Last: *Asyncritus reticulatus* Handlirsch, 1911, Carbondale Formation, Mazon Creek, Illinois, United States.

F. Cymbopsidae P1(Sakmarian)
Rasnitsyn (2002c) thinks that this monotypic family could be an abberant member of Blattinopsidae.

First and Last: *Cymbopsis excelsa* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Eucaenidae (Teneopteridae) C2(Moscovian)

e.g. *Eucaenus ovalis* in Labandeira (2001), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Evenkidae C2(Gzhelian)
Not to be confused with Actinopterygii: Evenkiidae.

First and Last: *Evenka archaica* in Rasnitsyn (2002a), Kata Formation, Chunya, Siberian Federal District, Russian Federation.

F. Gerapompidae (Cheliphlebidae, Cheliphlebiidae) C2(Moscovian)
Rasnitsyn (2002k) tentatively included *Aenigmatella* in this family but Brauckmann and Herd (2006) consider it unplaced. Rasnitsyn (2002k) also includes *Cheliphblebia* in this family.

e.g. *Palaeocarria ornata* in Rasnitsyn (2002k), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Herdinidae C2(Moscovian)

e.g. *Herdina mirificus* in Béthoux and Nel (2002b), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Heteroptilidae P1(Artinskian)
Rasnitsyn (2002e) synonymized Heteroptilidae under Tococladidae without argument, which was rejected by Béthoux et al. (2003a).

First and Last: *Heteroptilon costale* in Rasnitsyn (2002e), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Homalophlebiidae C2(Kasimovian)

e.g. *Parahomalophlebia courtini* in Rasnitsyn (2002k), Upper Coal Measures (Commentry), Commentry, Allier, France.

F. Hypermegethidae C2(Moscovian)-C2(Gzhelian)
Previously placed in the Palaeodictyoptera, Sinitshenkova (2002a) places this family in the Hypoperlida.

First: *Hypermegethes schucherti* in Carpenter (1992a), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: *Hypermegethes pilchi* Carpenter, 1992a, Lawrence Formation, Douglas County, Kansas, United States.

F. Hypoperlidae (Martynopsocidae) P1(Kungurian)-P2(Roadian)

First: e.g. *Idelopsocus incommendatus* Novokshonov et al., 2002, Solikamsk Formation, Vishera River, Mogil'nikovo, Ural Mountains, Russian Federation.

Last: e.g. *Hypoperla elegans* in Novokshonov (2001), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Kliveriidae (Kliveridae) C2(Moscovian)

First and Last: *Kliveria incerta* in Brauckmann and Herd (2006), Richard shaft, Dudweiler mine, Saarbrücken, Saarland, Germany.

F. Nugonioneuridae (Nungonioneuridae) P1(Artinskian)
Rasnitsyn (2002e) synonymized Nugonioneuridae under Tococladidae without argument, which was rejected by Béthoux et al. (2003a).

First and Last: *Nugonioneura problematica* in Rasnitsyn (2002e), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Perielytridae P1(Kungurian)

First and Last: *Perielytron mirabile* in Rasnitsyn (2002e), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Prototettigidae (Protettigae, Prototettigae) C2(Moscovian)
Rasnitsyn (2002k) places this family in his 'Eoblattida'.

First and Last: *Prototettix lithanthraca* in Handlirsch (1908), Frankenholz Mine, Neunkirchen, Saarland, Germany.

F. Psoropteridae P1(Artinskian)

First and Last: *Psoroptera cubitalia* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Rigattopteridae Pinto, 1996 P1(Asselian)
Béthoux and Nel (2002b) retain this family in the Protorthoptera.

First and Last: *Rigattoptera ornellasae* Pinto, 1996, Bajo de Véliz Formation (Pallero Member), Paganzo Basin, Sierra Grande de San Luis, San Luis Province, Argentina.

F. Sojanoperidae Novokshonov, 2002b P2(Roadian)

First and Last: *Sojanopus festivum* Novokshonov, 2002b, Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Stenoneuridae C2(Kasimovian)-C2(Gzhelian)

First: e.g. *Stenoneura fayoli* in Rasnitsyn et al. (2004a), Upper Coal Measures (Commentry), Commentry, Allier, France.

Last: Mentioned in Rasnitsyn et al. (2004a), Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

F. Synomaloptilidae P1(Kungurian)
Béthoux et al. (2004c) concurred with Rasnitsyn (2002e) in excluding this monobasic family from the Caloneurodea.

First and Last: *Synomaloptila longipes* in Rasnitsyn (2002e), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Thoronysididae (Thoronysidae) C2(Moscovian)

First and Last: *Thoronysis ingbertensis* in Rasnitsyn (2002k), St. Ingbert Formation, Saarbrücken, Saarland, Germany.

F. 'Orthocostidae' C2(Moscovian)
This family name is not valid as the type genus was renamed, due to homonomy, by Carpenter (1986). Labandeira (1994) lists this family in Palaeodictyoptera but Rasnitsyn (2002e) placed *Boltonocosta* in Hypolerida.

First and Last: *Boltonocosta splendens* in Carpenter (1992b), below the Top Hard Coal, Middle Coal Measures, Shipley Manor Claypit, Ilkeston, Derbyshire, United Kingdom.

O. Zoraptera Silvestri, 1913 Cretaceous(Albian)-Quaternary(Holocene)

F. Zorotypidae K1(Albian)-Holocene

First: e.g. *Zorotypus cretatus* Engel and Grimaldi, 2002, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

Eumetabola

O. Glosselytrodea Martynov, 1938 (Jurinida) Permian(Artinskian)-Jurassic(Callovian)

F. Archoglossopteridae P2(Roadian)

First and Last: *Archoglossopterum shoricum* in Béthoux et al. (2001), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

F. Glosselytridae P2(Roadian)-P2(Capitanian)

First: *Glosselytron multivenosum* in Béthoux et al. (2001), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

Last: e.g. *Glosselytron linguale* Ponomarenko, 2000a, Tsankhi (Tsankhin) Formation, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia.

F. Glossopteridae P1(Kungurian)

e.g. *Glossopterum sharovi* in Béthoux et al. (2001), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Jurinidae P2(Roadian)-P3(Changhsingian)
Rasnitsyn (2002h) proposed to synonymise Archoglossopteridae, Glosselytridae, Glossopteridae and Uskatelytridae under this family, however Grimaldi and Engel (2005), Hong (2007a) and Huang et al. (2007a) discuss them separately.

First: e.g. *Eoglosselytrum kaltanicum* in B'ethoux et al. (2007), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

Last: e.g. *Eoglosselytrum perplexa* in B'ethoux et al. (2007), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Permoberothidae P1(Artinskian)
According to B'ethoux et al. (2007), Permoberothidae does belong to Glosselytrodea, *contra* Béthoux et al. (2001) and Grimaldi and Engel (2005).

e.g. *Permoberotha villosa* in Beckemeyer and Hall (2007), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Polycytellidae P3(Changhsingian)-J2(Callovian)

First: *Karajurina unica* in Béthoux et al. (2001), Maichat/Ak-Kolka Formation, Karaungir River, Saur Mountains, Vostochno-Kazakhstanskaya oblast, Kazakhstan.

Last: *Mongolojurina altaica* in Béthoux et al. (2001), Togo-Khuduk Member, Bakhar Series, Bayankhongor Aimag, Mongolia.

F. Uskatelytridae P3(Wuchiapingian)-J1(Sinemurian)

First: *Uskatelytrum sibiricum* in Béthoux et al. (2001), Erunakovo Formation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

Last: *Mesojurina sogjutensis* in Béthoux et al. (2001), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

O. Miomoptera Martynov, 1927 (Palaeomanteida)
Carboniferous(Bashkirian)-Jurassic(Toarcian)

F. Archaemiopteridae (Archaemionopteridae) C2(Bashkirian)-T2(Ladinian)

First: *Eodelopterum priscum* in Grimaldi and Engel (2005), Vorhalle Beds, Hagen-Vorhalle, Schmiedestraße, Wuppertal, North Rhine-Westphalia, Germany. (NOTE: This is not the correct locality. It's somewhere nearby and the same age but waiting to find out exact details.)

Last: *Triasomiomopteris oblongata* Hong, 2009a, Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China.

F. Palaeomanteidae (Delopteridae, Epimastacidae, Palaeomantidae) C2(Moscovian)-P3(Wuchiapingian)

First: Mentioned in Novokshonov and Zhuzhgova (2004), Carbondale Formation, Mazon Creek, Illinois, United States.

Last: *Palaeomantis* sp. in van Dijk and Geertsema (1999), Normandien (Estcourt) Formation, Beaufort Group, KwaZulu-Natal, Karoo Basin, South Africa.

F. Palaeomantiscidae P1(Kungurian)

e.g. *Sellardsiopsis conspicua* in Novokshonov and Zhuzhgova (2004), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Permembiidae (Letopalopteridae, Sheimiidae, Visheriferidae) P1(Artinskian)-P2(Roadian)

First: *Permembia delicatula* in Aristov and Rasnitsyn (2008), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

Last: e.g. *Soyanembia sharovi* Aristov and Rasnitsyn, 2008, Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Permosialidae (Perloblattidae, Permonkidae, Permosialididae, Tologopteridae) P1(Kungurian)-J1(Toarcian)

First: *Permosialis punctimaculosa* in Novokshonov and Zhuzhgova (2004), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: *Permonka jurassica* in Novokshonov and Zhuzhgova (2004), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan.

Paraneoptera

O. Hemiptera Linnaeus, 1758 (Cimicida, Hemipsocoptera, Palaeohemiptera) Carboniferous(Gzhelian)-Quaternary(Holocene)

F. Acanthosomatidae Eoc.(Lutetian)-Holocene

First: Figured in Wappler (2003), Eckfeld maar, Manderscheid, Rhineland-Palatinate, Germany.

F. Achilidae K1(Barremian)-Holocene

First: e.g. Mentioned in Szwedo (2008a), Bon-Tsagaan Nuur, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia.

F. Adelgidae K1(Albian)-Holocene

First: Mentioned in Koteja and Poinar (2001), Alaskan amber, Kuk deposits, Brooks Range, Alaska, United States.

F. Aetalionidae (Biturritidae, Biturritiidae) J1(Sinemurian)-Holocene

First: e.g. *Absoluta distincta* in Carpenter (1992b), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Albicoccidae Koteja, 2004 K1(Albian)

First and Last: *Albicoccus dimai* Koteja, 2004, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Aleyrodidae (Aleurodicidae, Bernaeidae) J3(Oxfordian)-Holocene

First: *Juleyrodes visnyai* Shcherbakov, 2000a, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Alydidae J3(Oxfordian)-Holocene

First: *Monstrocoreus quadrimaculatus* in Yao et al. (2008), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Anthocoridae K1(Hauterivian)-Holocene

First: e.g. *Eoanthocoris cretaceus* in Shcherbakov and Popov (2002), Turga Formation, Turga River, near Borzai, Transbaikalia, Russian Federation.

F. Aphalaridae (Paleoaphalaridae, Paleoaphalaridae) Eoc.(Priabonian)-Holocene

First: e.g. *Eogyropsylla magna* Klimaszewski, 1997, Baltic amber, Baltic, Baltic region, Baltic.

F. Aphelocheiridae (Atopositidae) Plio.(Piacenzian)-Holocene

First: *Aphelocheirus affinis* in Popov (2007), Willershausen, Harz mountains, Lower Saxony, Germany.

F. Aphididae (Anoeciidae, Aphidae, Callaphididae, Drepanosiphidae, Eriosomatidae, Greenideidae, Hormaphididae, Mindaridae, Pemphigidae, Phloemyzidae, Phloeomyzidae, Sinaphididae) K1(Barremian)-Holocene
Jurocallis longipes from the Upper Jurassic Karabastau Formation is considered Aphidoidea *incertae sedis* in the Aphid Species File (Version 1.0/4.0).

First: e.g. *Sunaphis laiyanensis* in Wang et al. (2006b), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Aphrophoridae K1(Albian)-Holocene

First: Mentioned in Rasnitsyn and Ross (2000), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Aradidae J3(Oxfordian)-Holocene

First: e.g.? *Aradus* sp(p). in Popov and Bechly (2007), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Archegocimicidae (Archaegocimicidae, Diatillidae, Eonabidae) J1(Sinemurian)-K1(Aptian)

First: e.g. *Britannicola senilis* Popov et al., 1994, Apperley locality, Apperley, Gloucestershire, United Kingdom.

Last: Mentioned in Popov and Bechly (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Archescytinidae (Lithoscytinidae, Permothripidae) C2(Gzhelian)-T1(Induan)

First: *Arroyoscyta novaemexicana* Rasnitsyn *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States. (Specimen only tentatively assigned to Archescytinidae and to Hemiptera in general (Rasnitsyn et al., 2004a).)

Last: Mentioned in Shcherbakov (2008a), Bugarikhta Formation, Nizhnyaya Tunguska river, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Archiconiopterygidae Ansorge, 1996a J1(Toarcian)

First and Last: *Archiconiopteryx liasina* in Engel (2004c), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

F. Archijassidae J1(Toarcian)-K1(Barremian)

First: e.g. *Ardela grimmenensis* in Ansorge (2003a), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

Last: *Archijassus plurinervis* in Wang et al. (2006b), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Belostomatidae (Paranoikidae) T3(Carnian)-Holocene

First: Figured in Grimaldi and Engel (2005), Cow Branch Formation, Solite quarry, Virginia, United States.

F. Berytidae (Berythidae) Eoc.(Priabonian)-Holocene

First: Mentioned in Shcherbakov and Popov (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Boreoscytidae P1(Kungurian)-P2(Roadian)
The genus *Megaleurodes* (Aptian, Crato Formation) does not belong to this family (Szwedo, 2007a).

First: *Dinoscyta microcephala* Shcherbakov, 2007a, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: e.g. *Boreoscyta nefasta* in Shcherbakov (2007a), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Burmacoccidae Koteja, 2004 K1(Albian)

First and Last: *Burmacoccus danyi* Koteja, 2004, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Burmitaphidae Poinar and Brown, 2005 K1(Albian)

e.g. *Burmitaphis prolatum* Poinar and Brown, 2005, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Caliscelidae K2(Campanian)-Holocene

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Canadaphididae (Canadaphidae) K1(Barremian)-K2(Campanian)

First: *Nuuraphis gemma* Wegierek, 1991, Bon-Tsagaan Nuur, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia.

Last: e.g. *Alloambria infelicis* in McKellar et al. (2008), Canadian amber (Cedar Lake), Cedar Lake, Manitoba, Canada.

F. Carsidaridae Eoc.(Priabonian)-Holocene

First: e.g. *Carsidarina hooleyi* in Ross and Jarzembowski (1993), Bembridge Marls Insect Limestone, Gurnard/Thorness Bay, Isle of Wight, United Kingdom.

F. Ceratocombidae Eoc.(Priabonian)-Holocene

First: Mentioned in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Cercopidae P3(Changhsingian)-Holocene

First: *Tychticoloides belmontensis* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Cercopionidae Hamilton, 1990 K1(Aptian)

First and Last: *Cercopion reticulata* in Menon et al. (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Ceresopseidae J1(Sinemurian)

e.g. *Ceresopsis costalis* in Shcherbakov (2008c), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Chiliocyclidae T3(Carnian)

e.g. *Chiliocycla scolopoides* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Cicadellidae (Aphrodidae, Ceolidiidae, Eurymelidae, Euscelidae, Iassidae, Jascopidae, Jassidae, Macropsidae, Spinidae, Tettigellidae) T3(Carnian)-Holocene
NOTE: History of Insects says this family known since Lower Cretaceous.

First: e.g. *Eurymelidium australe* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Cicadidae (Tibicinidae) Pal.(Thanetian)-Holocene

First: *Davispia bearcreekensis* in Carpenter (1992b), shales near Eagle coal mine, Foster Gulch, Fort Union Group, Montana, United States. (Shcherbakov, 2009 confirms this record as the oldest currently known Cicadidae.)

F. Cimicidae K1(Albian)-Holocene

First: *Quasicimex eilapinastes* Engel, 2008a, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Ciriacremidae Mio.(Burdigalian)-Holocene

First: *Sulciana macroconi* in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Cixiidae (Cicixiidae) K1(Valanginian)-Holocene
Jell (2004) lists the Triassic genera *Mesocixiodes*, *Mesocixius* and *Triassocixius* in this family but these genera are placed as Fulgoromorpha *incertae sedis* by Szwedo et al. (2004).

First: Figured in Shcherbakov and Popov (2002), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Clastopteridae Eoc.(Priabonian)-Holocene

First: *Clastoptera comstocki* in Carpenter (1992b), Florissant Formation, Florissant, Colorado, United States.

F. Coccidae Eoc.(Priabonian)-Holocene

First: Mentioned in Koteja (2000a), Baltic amber, Baltic, Baltic region, Baltic.

F. Coleoscytidae P2(Roadian)

e.g. *Coleoscyta rotundata* in Szwedo et al. (2004), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Coreidae (Corizidae) T3(Carnian)-Holocene

First: *Kerjiecoris oopsis* in Yao et al. (2008), Huangshanjie Formation, Kerjie, Toksun county, Xinjiang Uyghur Autonomous Region, China.

F. Corixidae T3(Carnian)-Holocene

First: e.g. *Crypsacorixa tachis* Lin, 1992, Huangshanjie Formation, Kerjie, Toksun county, Xinjiang Uyghur Autonomous Region, China.

F. Creaphididae Shcherbakov and Wegierek, 1991(Creaphidae) T3(Carnian)

First and Last: *Creaphis theodora* in Hong et al. (2009), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Cretamyzidae Heie *in* Heie and Pike, 1992 K2(Campanian)

First and Last: *Cretamyzus pikei* in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Cuneocoridae J1(Toarcian)

First and Last: *Cuneocoris geinitzi* in Carvalho (1985), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Curvicubitidae Hong, 1984(Curvicicubitidae) T2(Anisian)-T3(Carnian)

First: e.g. *Beaconiella fennahi* in Jell (2004), Hawkesbury Sandstone, Brookvale Quarry, Beacon Hill, New South Wales, Australia. (Jell, 2004 lists the two species of *Beaconiella* in the family Fulgoridae, however this genus is included in the family Curvicubitidae by Szwedo et al., 2004 following the work of Shcherbakov. Shcherbakov, 2008a mentions this family as occurring in the Anisian of Australia, but does not mention the taxa.)

Last: Mentioned in Shcherbakov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Cydnidae (Latiscutellidae, Pricecoridae) J1(Toarcian)-Holocene

First: Mentioned in Grimaldi and Engel (2005), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Dactylopiidae Mio.(Aquitanian)-Holocene

First: Mentioned in Engel (2004a), Mexican amber, Simojovel, Chiapas, Mexico.

F. Delphacidae (Araeopidae) Eoc.(Ypresian)-Holocene

First: *Delphax senilis* in Szwedo et al. (2004), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Derbidae Eoc.(Priabonian)-Holocene

First: e.g. *Emeljanovedusa gentarna* Szwedo, 2006, Baltic amber, Baltic, Baltic region, Baltic. (Specimen from Poland.)

F. Diaspididae T3(Carnian)-Holocene

First: Mentioned in Wappler and Ben-Dov (2008), Molteno Formation, KwaZulu-Natal, Karoo Basin, South Africa. (This family record is doubtful.)

F. Dictyopharidae K2(Santonian)-Holocene

First: *Netutela annunciator* in Szwedo (2008c), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Dinidoridae Eoc.(Ypresian)-Holocene

First: *Megymenum* sp. in Greenwood et al. (2005), coldwater beds of the Kamloops Group, Quilchena, British Columbia, Canada.

F. Dipsocoridae K1(Barremian)-Holocene

First: Mentioned in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Dracaphididae Hong et al., 2009 T2(Ladinian)

First and Last: *Dracaphis angustata* Hong et al., 2009, Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China.

F. Drepanochaitophoridae Zhang and Hong, 1999 Eoc.(Ypresian)

First and Last: *Drepanochaitophorus fushunensis* Zhang and Hong, 1999, Fushun amber, Guchengzi, Liaoning Province, China.

F. Dunstaniidae P2(Capitanian)-J3(Tithonian)

First: Mentioned in Shcherbakov (2008d), Tsankhi (Tsankhin) Formation, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia.

Last: Mentioned in Dmitriev and Zherikhin (1988), Ulan-Ereg, Khoutiyn-Khotgor, Dund-Gobi Aimag, Mongolia. (For locality information, see `http://palaeoentomolog.ru/Collections/hutiinhotgor.html`.)

F. Dysmorphoptilidae (Dismorphoptilidae, Eoscartarellidae, Eoscartellidae, Eoscarterellidae, Fulgoringruidae) P1(Artinskian)-J2(Callovian)

First: *Fulgoringruo kukalovae* in Martins-Neto and Gallego (2006), Irati Formation, Paraná Basin, São Paulo, Brazil.

Last: *Dysmorphoptila notodon* in Martins-Neto and Gallego (2006), Togo-Khuduk Member, Bakhar Series, Bayankhongor Aimag, Mongolia.

F. Ebboidae Perrichot et al., 2006 K1(Albian)-K2(Cenomanian)

First: *Ebboa areolata* Perrichot et al., 2006, Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

Last: *Ebboa areolata* Perrichot et al., 2006, Salignac/Sisteron amber, near Sisteron, Alpes-de-Haute-Provence, France.

F. Electrococcidae Koteja, 2000b K1(Barremian)-K2(Campanian)

First: *Apticoccus minutus* Koteja and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon. (Koteja and Azar, 2008 note that placement of this species in Electrococcidae is tentative.)

Last: *Electrococcus canadensis* in Koteja and Azar (2008), Canadian amber (Cedar Lake), Cedar Lake, Manitoba, Canada. (Originally placed in Pityococcidae, this specimen was transferred to Electrococcidae by Koteja (2000b).)

F. Elektraphididae (Electraphididae) K2(Santonian)-Plio.(Piacenzian)

First: *Tajmyrella cretacea* in Heie and Wegierek (1998), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

Last: *Schizoneurites* sp. in Heie (1985), Willershausen, Harz mountains, Lower Saxony, Germany.

F. Enicocephalidae K1(Hauterivian)-Holocene

First: *Enicocephalinus acragrimaldii* in Azar (2007), Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

F. Eriococcidae K2(Turonian)-Holocene

First: e.g.? *Keithia luzzii* Koteja, 2000b, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Eurybrachyidae Eoc.(Lutetian)-Holocene

First: *Amalaberga ostrogothiorum* Szwedo and Wappler, 2006, Messel Formation, Grube Messel, Hesse, Germany.

F. Flatidae (Flattidae) Mio.(Aquitanian)-Holocene
Shcherbakov (2006) rejects '*Lechaea*' *primigenia* (Fur Formation) from Flatidae.

First: Mentioned in Shcherbakov (2006), Mexican amber, Simojovel, Chiapas, Mexico.

F. Fulgoridae K1(Aptian)-Holocene

First: Figured in Szwedo (2007a), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Fulgoridiidae J1(Sinemurian)-J3(Oxfordian)
This is a paraphyletic unit (Bourgoin and Szwedo, 2008).

First: *Fulgoridiella raetica* in Szwedo et al. (2004), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

Last: *Aulieezidium karatauense* Szwedo and Żyła, 2009, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Gelastocoridae K1(Aptian)-Holocene

First: e.g. *Cratonerthra corinthiana* in Popov and Bechly (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Genaphididae (Genaphidae) J3(Oxfordian)-K1(Berriasian)

First: *Juraphis crassipes* in Heie and Wegierek (1998), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Genaphis valdensis* in Heie and Wegierek (1998), Lulworth Formation, Dinton, Vale of Wardour, Wiltshire, United Kingdom.

F. Gerridae K1(Albian)-Holocene

First: *Cretogerris albianus* in Damgaard (2008a), Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

F. Granulidae T2(Ladinian)

First and Last: *Granulus* sp. in Wang et al. (2006b), Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China. (NOTE: Monotypic family - would be nice to have the species name but I can't find it.)

F. Grimaldiellidae Koteja, 2000b(Grimaldiidae) K2(Turonian)

e.g. *Grimaldiella resinophila* Koteja, 2000b, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Hadrocoridae J1(Toarcian)
Although listed under *incertae sedis* by Carpenter (1992b), the family has not been synonymised.

First and Last: *Hadrocoris scutellaris* Handlirsch, 1939, Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Hammanococcidae Koteja and Azar, 2008 K1(Barremian)

e.g. *Hammanococcus setosus* Koteja and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Hebridae Mio.(Aquitanian)-Holocene

First: *Stenohebrus glaesarius* in Damgaard (2008a), Mexican amber, Simojovel, Chiapas, Mexico.

F. Hoploridiidae Popov and Shcherbakov, 1991 K1(Valanginian)
Sometimes treated as a subfamily of Karabasiidae. For discussion, see Heads (2008b) and Wang et al. (2009b).

First and Last: *Hoploridium dollingi* in Wang et al. (2009b), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Hydrometridae K1(Aptian)-Holocene

First: e.g. *Cretaceometra brasiliensis* in Damgaard (2008a), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Hylicellidae T1(Induan)-K1(Barremian)
Although Jell (2004) lists *Eochiliocycla angusta* from the Upper Permian Belmont insect beds of Australia in Hylicellidae, Evans (1956) removed this species. Several sources (e.g. Shcherbakov and Popov, 2002 and Shcherbakov, 2008a) explicitly state that Hylicellidae first appear in the Triassic.

First: Mentioned in Shcherbakov (2008a), Babiy Kamen', Maltseva/Sosnovaya Fomation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

Last: Mentioned in , Bon-Tsagaan Nuur, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia. (NOTE: Don't have a good reference for this but it's shown on the PIN collections page at `http://palaeoentomolog.ru/Collections/bontsagan.html`. I would be glad to hear of any references or later occurrences. FR2 says K2...)

F. Hypsipterygidae Eoc.(Priabonian)-Holocene

First: *Hypsipteryx hoffeinsorum* Bechly and Wittmann, 2000, Baltic amber, Baltic, Baltic region, Baltic.

F. Ignotalidae (Ignatolidae) P3(Wuchiapingian)-T1(Induan)

First: e.g. *Megoniella multinerva* in van Dijk and Geertsema (1999), Normandien (Estcourt) Formation, Beaufort Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: Mentioned in Shcherbakov (2008a), Bugarikhta Formation, Nizhnyaya Tunguska river, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Ignotingidae Zhang et al., 2005 K1(Barremian)

First and Last: *Ignotingis mirifica* Zhang et al., 2005, Laiyang Formation, Laiyang County, Shandong Province, China.

F. Ingruidae P1(Kungurian)-P2(Capitanian)

First: e.g. *Scytoneurella major* in Ross and Jarzembowski (1993), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: e.g. Mentioned in Shcherbakov (2000b), Tsankhi (Tsankhin) Formation, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia.

F. Inkaidae Koteja, 1989 K2(Santonian)

First and Last: *Inka minuta* in Koteja (2000a), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Ipsviciidae T2(Anisian)-K1(Aptian)

First: e.g. Mentioned in Gall and Grauvogel-Stamm (2005), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: Mentioned in Shcherbakov and Popov (2002), Shar-Tolgoy Formation, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia. (Locality information for this specimen was kindly provided by Dr Dmitry Shcherbakov [pers. comm., 2011].)

F. Isometopidae Mio.(Aquitanian)-Holocene

First: Mentioned in Solórzano Kraemer (2007), Mexican amber, Simojovel, Chiapas, Mexico.

F. Issidae K2(Campanian)-Holocene
Szwedo et al. (2004) place the Jurassic *Tetragonidium* in Fulgoridiidae and *Elasmocelidium* as Fulgoroidea *incertae sedis*.

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Jersicoccidae Koteja, 2000b K2(Turonian)

First and Last: *Jersicoccus kurthi* Koteja, 2000b, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Karabasiidae J1(Sinemurian)-J3(Tithonian)

First: *Minuta heteropterata* in Wang et al. (2009b), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

Last: *Karabasia evansi* in Wang et al. (2009b), Glushkovo Formation (Daya), Daya, Transbaikalia, Russian Federation.

F. Karajassidae Shcherbakov, 1992 J1(Toarcian)-K1(Hauterivian)

First: Mentioned in Shcherbakov and Popov (2002), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany. (NOTE: I don't know that this specimen is from Grimmen. All the reference said was Lower Jurassic Germany but I'm putting this in for now to get the range.)

Last: e.g. *Gurvania inepta* in Ross and Jarzembowski (1993), Gurvan-Eren Formation (Gurvan-Eren), Gurvan-Eren, Khovd Aimag, Mongolia.

F. Kermesidae Eoc.(Priabonian)-Holocene

First: *Sucinikermes kulickae* in Koteja (2000a), Baltic amber, Baltic, Baltic region, Baltic.

F. Kinnaridae Mio.(Burdigalian)-Holocene

First: e.g. *Oeclidius browni* Bourgoin and Lefèbvre, 2002, Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Kobdocoridae Popov, 1986 K1(Hauterivian)

First and Last: *Kobdocoris aradinus* Popov, 1986, Gurvan-Eren Formation (Myangad), Myangad, Khovd Aimag, Mongolia.

F. Kukaspididae Koteja and Poinar, 2001 K1(Albian)

First and Last: *Kukaspis usingeri* Koteja and Poinar, 2001, Alaskan amber, Kuk deposits, Brooks Range, Alaska, United States.

F. Labiococcidae Koteja, 2000b K2(Turonian)

e.g. *Labiococcus joosti* Koteja, 2000b, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Lachnidae Mio.(Langhian)-Holocene

First: e.g. *Stomaphis eupetes* in Wegierek and Peñalver (2002), Vishnevaya Balka, near Senghileevskoye Lake, Stavropol Krai, Russian Federation.

F. Lalacidae Hamilton, 1990 K1(Barremian)-K1(Aptian)

First: *Cretocixius stigmatosus* in Szwedo (2007a), Lushangfen Formation, Jingxi Basin, Beijing Municipality, China.

Last: e.g. *Lalax mutabilis* in Szwedo (2007a), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Largidae K2(Santonian)-Holocene

First: Mentioned in Poinar (1992), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Lebanococcidae Koteja and Azar, 2008 K1(Barremian)

First and Last: *Lebanococcus longiventris* Koteja and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Leptaphelocheiridae Polhemus, 2000 J2(Callovian)

First and Last: *Leptaphelocheirus lenticulus* Polhemus, 2000, Todilto Formation (Luciano Mesa Member), Warm Springs site, New Mexico, United States.

F. Leptopodidae Mio.(Aquitanian)-Holocene
NOTE: Occurs in Eocene Indian amber (Rust et al. 2010)

First: *Leptosalda chiapensis* in Solórzano Kraemer (2007), Mexican amber, Simojovel, Chiapas, Mexico.

F. Liadopsyllidae (Asientomidae, Lithentomidae) J1(Toarcian)-K1(Barremian)

First: e.g. *Liadopsylla obtusa* in Ouvrard et al. (2010), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

Last: *Liadopsylla mongolica* in Ouvrard et al. (2010), Bon-Tsagaan Nuur, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia. (NOTE: I've only entered data known prior to 2010 - the paper I've referenced extends the range up to Turonian. This will need to be added later.)

F. Ligavenidae Hamilton, 1992 T3(Carnian)-K1(Aptian)

First: e.g. *Ligavena prosboloides* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

Last: *Ligavena gracilipes* in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Lophopidae (Lophophidae) Eoc.(Lutetian)-Holocene
Szwedo et al. (2004) place the Lower Jurassic *Eofulgoridium* in the Fulgoridiidae. *Scoparidea nebulosa*, from the Ypresian Green River Formation, belongs in or close to Issidae (Shcherbakov, 2006).

First: *Baninus thuringiorum* Szwedo and Wappler, 2006, Messel Formation, Grube Messel, Hesse, Germany.

F. Lygaeidae Eoc.(Ypresian)-Holocene
NOTE: No reliable records for Mesozoic occurrences. *Lygaenocoris* is Pachymerididae. Wappler (2003) says Mesozoic all need revision and questions if they're attributable.

First: e.g. Mentioned in Wappler (2003), Ølst Formation, Limfjord/Mors Peninsula/Fur Island, Jutland, Denmark.

F. Magnacicadiidae T2(Ladinian)

First and Last: *Magnacicadia shenciensis* in Wang et al. (2006b), Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China.

F. Malmopsyllidae (Neopsylloididae) J3(Oxfordian)
Szwedo and Żyła (2009) list Malmopsyllidae and Neopsylloididae separately, citing only the original descriptions, but Shcherbakov and Popov (2002) treat them as synonyms. [NOTE: Synonymy upheld by a 2010 paper.]

e.g. *Malmopsylla karatavica* in Ross and Jarzembowski (1993), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Margarodidae Eoc.(Priabonian)-Holocene

First: Figured in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Matsucoccidae K1(Valanginian)-Holocene

First: e.g. *Eomatsucoccus sukachevae* in Koteja (2000a), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Membracidae K1(Albian)-Holocene

First: Mentioned in Perrichot (2004), Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

F. Mesogereonidae T3(Carnian)

e.g. *Mesogereon superbum* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Mesopentacoridae J1(Toarcian)-K1(Aptian)

First: aff. *Mesopentacoris* sp. in Popov (1990), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

Last: *Pauropentacoris macrurata* in Yao et al. (2004), Jiufotang Formation, Beishan, Yixian County, Liaoning Province, China.

F. Mesotrephidae K2(Turonian)

First and Last: *Mesotrephes striata* in Sinitshenkova (2002c), Kzyl-Zhar, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Mesoveliidae (Karanabidae, Karanabiidae) J3(Oxfordian)-Holocene
Damgaard (2008a) preferred not to assign any fossils to this family pending a review of external morphological characters however Szwedo and Żyła (2009) list this family as present in the Karabastau Formation.

First: *Karanabis kiritschenkoi* in Damgaard (2008a), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Mesozoicaphididae Heie *in* Heie and Pike, 1992 K2(Campanian)

e.g. *Mesozoicaphis canadensis* in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Microphysidae K2(Santonian)-Holocene

First: Mentioned in Poinar (1992), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Mimarachnidae Shcherbakov, 2007c K1(Valanginian)-K2(Turonian)

First: e.g. *Mimarachne mikhailovi* Shcherbakov, 2007c, Zaza Formation, Baissa, Buryatia, Russian Federation.

Last: Mentioned in Szwedo (2008b), Kzyl-Zhar, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Miridae J3(Oxfordian)-Holocene
Shcherbakov (2008c) removed *Mirivena robusta* (Jiulongshan Formation, Daohugou, China) from this family.

First: e.g. *Scutellifer karatavicus* in Herczek and Popov (2001), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Monophlebidae (Monophlebiidae) Eoc.(Priabonian)-Holocene
Although Grimaldi and Engel (2005, p.299) record this family in Lebanese amber, it is not recorded by Koteja and Azar (2008).

First: *Monophlebus irregularis* in Koteja (2000a), Baltic amber, Baltic, Baltic region, Baltic.

F. Myerslopiidae K1(Aptian)-Holocene

First: e.g. *Ovojassus concavifer* in Menon et al. (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Nabidae (Velocipedidae, Vetanthocoridae) J1(Sinemurian)-Holocene

First: e.g. *Saldonabis proteus* Shcherbakov, 2008c, Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Naibiidae Shcherbakov, 2007a T3(Carnian)-Pal.(Thanetian)

First: *Coccavus supercubitus* Shcherbakov, 2007a, Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: e.g. *Naibia zherichini* Shcherbakov, 2007a, Sakhalin amber, Lower Due Formation, Starodubskoe, Sakhalin Region, Russian Federation.

F. Naucoridae (Aphlebocoridae, Apopnidae, Saucrolidae) T3(Carnian)-Holocene

First: Mentioned in Shcherbakov (2008a), Cow Branch Formation, Solite quarry, Virginia, United States.

F. Neazoniidae Szwedo, 2007b K1(Hauterivian)-K1(Albian)

First: *Neazonia imprinta* Szwedo, 2007b, Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

Last: *Akmazeina santonorum* Szwedo, 2009, Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

F. Nepidae J3(Tithonian)-Holocene

First: Mentioned in Ponomarenko (1985), Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

F. Nogodinidae Pal.(Danian)-Holocene

First: Mentioned in Shcherbakov (2006), Tsagayan Formation, Arkhara locality, Amur Oblast, Russian Federation.

F. Notonectidae T3(Carnian)-Holocene

First: Mentioned in Shcherbakov (2008a), Cow Branch Formation, Solite quarry, Virginia, United States.

F. Ochteridae (Propreocoridae) J1(Sinemurian)-Holocene

First: *Propreocoris maculatus* in Yao et al. (2007), Black Ven Marls, Charmouth, Dorset, United Kingdom.

F. Ortheziidae K1(Hauterivian)-Holocene

First: *Cretorthezia*? sp. in Koteja and Azar (2008), Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

F. Oviparosiphidae J1(Toarcian)-K1(Aptian)

First: *Grimmenaphis magnifica* in Grimaldi and Engel (2005), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

Last: *Sinoviparosiphum lini* in Ren (2002b), Yixian unspecified, Yixian Formation, Liaoning Province, China.

F. Pachymerididae (Hypocimicidae, Psychrocoridae, Sisyrocoridae) T3(Rhaetian)-K1(Aptian)

First: "*Pachymerus*" *zucholdi* in Yao et al. (2008), Cotham Member, Lilstock Formation, Penarth Group1, Strensham, Worcestershire, United Kingdom.

Last: e.g. *Cratocoris schechenkoae* in Popov and Bechly (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Palaeoaphididae (Palaeoaphidae) K1(Valanginian)-K2(Campanian)

First: Mentioned in , Zaza Formation, Baissa, Buryatia, Russian Federation. (NOTE: Should be species listed in Kania and Wegierek, 2008 but not seen it yet.)

Last: e.g. *Longiradius foottitti* in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Palaeoleptidae Poinar and Buckley, 2009 K1(Albian)

First and Last: *Palaeoleptus burmanicus* Poinar and Buckley, 2009, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Palaeontinidae (Paleontinidae) T3(Carnian)-K1(Aptian)
Fletcheriana triassica is included in Dunstaniidae (Wang et al., 2009c). The Permian species *Palaeocicadopsis chinensis* is based on a cockroach clavus (Wang et al., 2006a).

First: '*Fletcheriana*' *magna* in Wang et al. (2009c), Molteno Formation, KwaZulu-Natal, Karoo Basin, South Africa.

Last: e.g. *Colossocossus giganticus* Menon & Heads *in* Menon et al., 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Paraknightiidae P3(Changhsingian)-T3(Carnian)

First: *Paraknightia magnifica* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

Last: Mentioned in Shcherbakov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Parvaverrucosidae Poinar and Brown, 2006(Verrucosidae) K1(Albian)

First and Last: *Parvaverrucosa annulata* in Poinar and Brown (2006), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Pennygullaniidae Koteja and Azar, 2008 K1(Barremian)

e.g. *Pennygullania electrina* Koteja and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Pentatomidae Pal.(Thanetian)-Holocene

First: Mentioned in Wappler (2003), spongo-diatomaceous maar, Menat, Puy-de-Dôme, Auvergne, France. (NOTE: Wappler mentions the earliest of this family is Paleocene of France - I'm assuming Menat until I can find a good reference.)

F. Pereboriidae (Pereboridae) P1(Artinskian)-K1(Barremian)

First: *Gondwanoptera capsii* in Martins-Neto (2005), Irati Formation, Paraná Basin, São Paulo, Brazil.

Last: e.g. *Jiphara wangi* in Wang et al. (2006b), Lushangfen Formation, Jingxi Basin, Beijing Municipality, China.

F. Perforissidae Shcherbakov, 2007b K1(Barremian)-K2(Santonian)

First: *Tsaganema oshanini* Shcherbakov, 2007b, Khurilt Formation, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia.

Last: e.g. *Cixitettix yangi* Shcherbakov, 2007b, Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Phylloxeridae Mio.(Aquitanian)-Holocene

First: Mentioned in Engel (2004a), Mexican amber, Simojovel, Chiapas, Mexico.

F. Piesmatidae (Piesmidae) K1(Albian)-Holocene

First: *Cretopiesma suukyiae* Grimaldi and Engel, 2008b, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Pincombeidae (Pincombaeidae) P3(Changhsingian)-T3(Carnian)

First: e.g. *Pincombea mirabilis* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

Last: *Madygenopsyllidium djailautshoense* in Shcherbakov (2007a), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Pityococcidae Eoc.(Priabonian)-Holocene
Electrococcus canadensis was transferred to the Electrococcidae by Koteja (2000b).

First: *Cancerococcus apterus* in Koteja and Azar (2008), Baltic amber, Baltic, Baltic region, Baltic. (Foldi, 2005 lists this species as the only fossil record of Coelostomidiidae.)

F. Plokiophilidae K2(Campanian)-Holocene

First: Mentioned in Popov (2008), Canadian amber (unspecified), Unspecified, Alberta, Canada.

F. Probascaniidae (Probascanionidae) J1(Toarcian)

e.g. *Probascanion megacephalum* in Popov (1992), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Procercopidae (Procercopoidae) J1(Hettangian)-K1(Aptian)
Often cited as originating in the Triassic but the supposed Triassic records are from the Lower Jurassic Dzhil Formation. See `http://palaeoentomolog.ru/Collections/jur_i.html` NOTE: I can't find any records for Upper Cretaceous specimens. Wang et al. (2006b) list *Cretocercopis* as K2 but this must be a mistake as it's from the Lushangfen Formation, which is Lower Cretaceous.

First: e.g. *Procercopis shawanensis* Zhang et al., 2004, Badaowan Formation, Kelamayi, Xinjiang Uyghur Autonomous Region, China.

Last: e.g. *Anomoscytina anomola* Ren et al., 1998, Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Progonocimicidae (Actinescytinidae, Actinoscytinidae, Cicadocoridae, Eocimicidae, Progonomicidae) P3(Changhsingian)-K1(Aptian)

First: *Actinoscytina belmontensis* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

Last: e.g. Mentioned in Bechly and Szwedo (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Prosbolidae (Cicadopsyllidae, Permocicadopsidae, Permoglyphidae, Prosbolecicadidae, Sojanoneuridae) P1(Artinskian)-K1(Valanginian)

First: e.g. *Prosbole iratiensis* in Martins-Neto (2005), Irati Formation, Paraná Basin, São Paulo, Brazil. (Martins-Neto, 2005 lists *Prosbolecicada gondwanica* in Dysmorphoptilidae, probably by mistake; indeed, Martins-Neto and Gallego, 2006 do not mention it in their review of the family. Shcherbakov, 2000b synonymised Prosbolecicadidae under Prosbolidae and this is followed here.)

Last: *Longimaxilla sinica* in Wang et al. (2006b), Chijinqiao (=Chijinpu) Formation, Xiagou, Jiuquan Basin, Gansu Province, China.

F. Prosbolopseidae (Ivaiidae, Mundidae, Prosbolopsidae) P1(Kungurian)-P2(Capitanian)

First: e.g. *Cicadopsis*? sp. in Shcherbakov et al. (2009), Pospelovo Formation, Russky Island, Primorye, Russian Federation.

Last: Mentioned in Shcherbakov (2000b), Tsankhi (Tsankhin) Formation, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia.

F. Protocoridae J1(Hettangian)-J1(Toarcian)
Pallicoris from the Shiti Formation in Guangxi, China, belongs to the Pachymerididae (Popov et al., 1994).

First: e.g. *Protocoris indistinctus* Popov et al., 1994, Planorbis zone (Binton), Binton, Warwickshire, United Kingdom.

Last: Mentioned in Popov et al. (1994), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Protopsyllidiidae (Eopsyllidiidae, Permaleurodidae, Permaleyrodidae, Permaphidopseidae, Permopsyllidae) P1(Kungurian)-K2(Turonian)
The genera comprising Permaleurodidae belong to this family or related group of Psyllinea according to Shcherbakov (2000a).

First: Mentioned in Geertsema et al. (2002), carbonaceous shales, middle Ecca Group, Haakdoornfontein, near Pretoria, South Africa.

Last: *Postopsyllidium emilyae* Grimaldi, 2003a, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Pseudococcidae Eoc.(Priabonian)-Holocene

First: Mentioned in Koteja (2000a), Baltic amber, Baltic, Baltic region, Baltic.

F. Pseudonerthridae Martins-Neto & Pérez Goodwyn Martins-Neto & Perez Good *in* López Ruf et al., 2005 K1(Aptian)

First and Last: *Pseudonerthra gigantea* in Popov and Bechly (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Psyllidae K1(Aptian)-Holocene

First: Figured in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Pterocimicidae J1(Sinemurian)

First and Last: *Pterocimex jacksoni* in Popov et al. (1994), Black Ven Marls, Charmouth, Dorset, United Kingdom.

F. Putoidae K1(Barremian)-Holocene

First: *Palaeotupo danieleae* Koteja and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon. (Koteja and Azar, 2008 note that placement of this species in Putoidae is tentative.)

F. Pyrrhocoridae Eoc.(Priabonian)-Holocene
Mesopyrrhocoris fasciata from the Lower Cretaceous Laiyang Formation is Cimicomorpha *incertae sedis*, according to Shcherbakov (2008c).

First: e.g. *Dysdercus cinctus* in Meyer (2003), Florissant Formation, Florissant, Colorado, United States.

F. Reduviidae (Phymatidae, Reduvidae) K1(Albian)-Holocene
Liaoxia longa from the Lower Cretaceous Jiufotang Formation is now placed in Nabidae: Vetanthocorini (Yao et al., 2006a; Shcherbakov, 2008c).

First: Mentioned in Poinar and Poinar (2008), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Rhinocolidae Eoc.(Priabonian)-Holocene
Sometimes treated as a subfamily of Psyllidae but kept separate in Pérez-Gelabert (2008).

First: *Protoscena baltica* in Klimaszewski (1997), Baltic amber, Baltic, Baltic region, Baltic. (This species was mistakenly listed by Weitschat and Wichard, 2002 under 'Paleoaphalaridae' [=Aphalaridae: Palaeoaphalarinae].)

F. Rhinopsyllidae (Rhynopsyllidae) Mio.(Burdigalian)-Holocene

First: e.g. *Rhinopsyllida acutealla* in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Rhopalidae J2(Callovian)-Holocene

First: e.g. *Originicorizus pyriformis* Yao, Cai & Ren *in* Yao et al., 2006b, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Ricaniidae Pal.(Thanetian)-Holocene
Szwedo et al. (2004) do not consider that the Mesozoic genera *Qiyangiricania* and *Ricaniites* belong to this family.

First: *Scolypopites bryani* in Jell (2004), Redbank Plains Formation, Ipswich Basin, Queensland, Australia.

F. Saldidae (Enicocoridae, Mesolygaeidae, Xishanidae) K1(Barremian)-Holocene

First: *Mesolygaeus laiyangensis* in Zhang et al. (2005), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Scaphocoridae J3(Oxfordian)

First and Last: *Scaphocoris notatus* in Carpenter (1992b), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan. (NOTE: Genus and species not named in that paper but monotypic family so it goes without saying... Evolution of the Insects at least names the genus, if preferred.)

F. Schizopteridae K1(Barremian)-Holocene

First: Mentioned in Grimaldi and Engel (2005), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Scutelleridae Eoc.(Ypresian)-Holocene

First: Mentioned in Rust (1998), Fur Formation (Mo Clay), Limfjord/Mors Peninsula/Fur Island, Jutland, Denmark.

F. Scytinopteridae (Seytinopteridae) C2(Gzhelian)-K1(Barremian)

First: Mentioned in Shcherbakov (2000b), Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States. (A. P. Rasnitsyn (pers. comm. in Shcherbakov, 2000b, p.S254) considers the attribution of this specimen, referred to by Rowland, 1997, to Scytinopteridae doubtful but adds that it yet requires confirmation, implying that he had not seen it. This may be the putative archescytinid described in Rasnitsyn et al., 2004a but nowhere in the text is this made clear.)

Last: *Sunoscytinopteris lushangfenensis* in Wang et al. (2006b), Lushangfen Formation, Jingxi Basin, Beijing Municipality, China.

F. Serpentivenidae (Serpenivenidae, Serpentiveniidae) P2(Wordian)-T3(Carnian)

First: Mentioned in Aristov and Bashkuev (2008), Chepanikha locality, Rossokha River valley, Zavjalovskii District, Udmurt Republic, Russian Federation.

Last: e.g. *Serpentivena tigrina* in Ross and Jarzembowski (1993), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Shaposhnikoviidae J2(Aalenian)-K2(Santonian)

First: *Tinaphis sibirica* Wegierek, 1989, Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

Last: *Shaposhnikovia electri* in Heie (1987), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Shurabellidae (Shuraveliidae) J1(Hettangian)-J3(Oxfordian)

First: *Shurabella lepyroniopsis*? in Shcherbakov (2008b), unnamed deposit overlying Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: *Shurabella* sp. in Grimaldi and Engel (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Simulaphididae Shcherbakov, 2007a P3(Changhsingian)-T3(Norian)

First: *Simulaphis shaposhnikovi* Shcherbakov, 2007a, Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

Last: Mentioned in Shcherbakov (2007a), Protopivka Formation, Garazhovka, Izyum District, Ukraine. (This record is doubtful.)

F. Sinojuraphididae Huang and Nel, 2008 J2(Callovian)

First and Last: *Sinojuraphis ningchengensis* Huang and Nel, 2008, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Steingeliidae K1(Barremian)-Holocene

First: e.g. *Palaeosteingelia acrai* Koteja and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Stenoviciidae P2(Capitanian)-K1(Barremian)

First: Mentioned in Shcherbakov (2000b), Tsankhi (Tsankhin) Formation, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia.

Last: Mentioned in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Surijokocixiidae Shcherbakov, 2000b(Surijokocixidae) P2(Wordian)-T3(Carnian)

First: e.g. *Surijokocixius tomiensis* in Szwedo et al. (2004), Ilinskoe Formation, Suriyokova (Suriekova), Kemerovo Region, Russian Federation.

Last: e.g. *Tricrosbia minuta* in Szwedo et al. (2004), Mount Crosby Formation, Ipswich Basin, Queensland, Australia.

F. Tajmyraphididae (Taimyraphididae, Taymiraphididae) K1(Barremian)-K2(Campanian)

First: e.g. *Megarostrum azari* Heie *in* Heie and Azar, 2000, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

Last: *Grassyaphis pikei* in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Termitaphididae (Termitiaphididae) Mio.(Aquitanian)-Holocene
Grimaldi and Engel (2008a) suggest that this family may belong within Aradidae.

First: *Termitaradus protera* in Engel (2009b), Mexican amber, Simojovel, Chiapas, Mexico.

F. Tettigarctidae (Cicadoprosbolidae, Protabanidae, Tettigarcitidae) T3(Rhaetian)-Holocene

First: '*Liassocicada*' *ignotata* in Shcherbakov (2009), Cotham Member, Lilstock Formation, Penarth Group1, Strensham, Worcestershire, United Kingdom.

F. Thaumastellidae (Thaumestellidae) K1(Barremian)-Holocene
Considered by Shcherbakov and Popov (2002) to be a subfamily of Cydnidae, family status is maintained here after Grazia et al. (2008).

First: Mentioned in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Thaumastocoridae K2(Turonian)-Holocene

First: Mentioned in Golub and Popov (2000), New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Thelaxidae Eoc.(Priabonian)-Holocene
NOTE: Wegierek & Grimaldi (2010) describe a species from Lebanese amber.

First: *Palaeothelaxes setosa* in Carpenter (1992b), Baltic amber, Baltic, Baltic region, Baltic.

F. Tingidae (Cantacaderidae) K1(Valanginian)-Holocene

First: *Sinaldocader ponomarenkoi* Golub and Popov, 2008, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Triassoaphididae Heie, 1999(Triassoaphidae) T3(Carnian)

First and Last: *Triassoaphis cubitus* in Hong et al. (2009), Mount Crosby Formation, Ipswich Basin, Queensland, Australia. (Jell, 2004 mistakenly lists this species in Aphididae.)

F. Triassocoridae T3(Carnian)-T3(Norian)

First: e.g. *Triassocoris myersi* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

Last: Mentioned in Shcherbakov and Popov (2002), Tologoy Formation, Ak-Kolka River, Kenderlyk, Zaisan District, Kazakhstan.

F. Triozidae Mio.(Burdigalian)-Holocene

First: e.g. *Trioacantha indocilia* in Arillo and Ortuño (2005), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Tropiduchidae K2(Turonian)-Holocene

First: Mentioned in Szwedo (2009), Orapa diamond mines, Orapa, Orapa, Botswana. (Locality data provided by J. Szwedo pers. comm., 2011.)

F. Urostylididae Mio.(Langhian)-Holocene
Name changed by Berger et al. (2001) to correct the spelling and remove homonymy with Ciliophora: Urostylidae Bütschli, 1889.

First: e.g. *Urochela pardalina* in Yao et al. (2004), Shanwang Formation, Linqu County, Shandong Province, China.

F. Veliidae K1(Aptian)-Holocene
This family is paraphyletic with respect to Gerridae (Damgaard, 2008b).

First: Figured in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia. (Familial assignment of this fossil form remains provisional until further specimens are found (Andersen, 1998).)

F. Vianaididae K2(Turonian)-Holocene

First: e.g. *Vianathauma pericarti* Golub and Popov, 2003, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Xylococcidae (Xyloccidae) K1(Valanginian)-Holocene

First: *Baisococcus victoriae* in Koteja (2000a), Zaza Formation, Baissa, Buryatia, Russian Federation.

O. Paraneoptera *incertae sedis* Carboniferous(Gzhelian)-Cretaceous(Campanian)

F. Lophioneuridae (Edgariekiidae) P1(Artinskian)-K2(Campanian)
Generally considered to be a paraphyletic stem-group of Thysanoptera (e.g. Grimaldi and Engel, 2005) however this relationship is questioned by Mound and Morris (2007).

First: e.g. *Cyphoneurodes patriciae* Beckemeyer, 2004a, Wellington Formation (OK), Midco, Oklahoma, United States.

Last: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Permopsocidae P1(Sakmarian)-P1(Artinskian)

First: Mentioned in Rasnitsyn (2002f), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: e.g. *Permopsocus ovatus* in Beckemeyer (2000), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Psocidiidae (Dichentomidae) C2(Gzhelian)-J1(Toarcian)

First: e.g. *Dichentomum*? *arroyo* Rasnitsyn *in* Rasnitsyn et al., 2004a, Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States.

Last: *Liassopsocus lanceolatus* in Ansorge (2003a), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

F. Saurodectidae Rasnitsyn and Zherikhin, 2000 K1(Valanginian)
Originally interpreted as a phthirapteran, Wappler et al. (2004) and Dalgleish et al. (2006) remove it from that order. Grimaldi and Engel (2005) consider affinities with Phthiraptera to be plausible so it is retained here within Paraneoptera.

First and Last: *Saurodectes vrsanskyi* in Dalgleish et al. (2006), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Surijokopsocidae P2(Wordian)

First and Last: *Surijokopsocus radtshenkoi* in Rohdendorf (1991), Ilinskoe Formation, Suriyokova (Suriekova), Kemerovo Region, Russian Federation.

F. Zygopsocidae P3(Changhsingian)

First and Last: *Zygopsocus permianus* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

O. Phthiraptera Haeckel, 1896 Palaeogene(Lutetian)-Quaternary(Holocene)

F. Menoponidae Eoc.(Lutetian)-Holocene

First: *Megamenopon rasnitsyni* Wappler et al., 2004, Eckfeld maar, Manderscheid, Rhineland-Palatinate, Germany.

F. Polyplacidae Pleist.(Upper Pleistocene)-Holocene

First: e.g. *Neohaematopinus relictus* in Mey (2005), permafrost, Indigirka, Sakha (Yakutia) Republic, Russian Federation. (Labandeira, 1994 listed this occurrence under the family Hoplopleuridae.)

O. Psocoptera (Anoplura, Corrodentia, Mallophaga, Psocida)
Jurassic(Toarcian)-Quaternary(Holocene)

F. Amphientomidae K2(Santonian)-Holocene
The specimens mentioned by Rasnitsyn (2002f) as "Amphientomidae: Electrentominae" from the Upper Jurassic Karabastau Formation (considered here as the separate family Electrentomidae [=Manicapsocidae]) belong to the Paramesopsocidae Azar et al., 2008.

First: *Proamphientomum cretaceum* in Nel et al. (2005f), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Amphipsocidae (Polypsocidae) Eoc.(Priabonian)-Holocene

First: *Kolbia ava* in Lienhard and Smithers (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Arcantipsocidae Azar et al., 2009 K1(Albian)

First and Last: *Arcantipsocus courvillei* Azar et al., 2009, Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

F. Archaeatropidae Baz and Ortuño, 2000(Archaetropidae) K1(Albian)
This family may also occur in Lower Cretaceous French and Lebanese amber (see Perrichot et al., 2003; Azar and Nel, 2004).

First and Last: *Archaeatropos alavensis* Baz and Ortuño, 2000, Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Archipsocidae Eoc.(Ypresian)-Holocene

First: *Archipsocus* cf. *puber* in Brasero et al. (2009), Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Archipsyllidae J1(Toarcian)-K1(Barremian)
Considered by Grimaldi and Engel (2005) to be stem Paraneoptera, Huang et al. (2008a) demonstrated that Archipsyllidae are Psocoptera. Permian records of this family are erroneous (Rasnitsyn, 2002f).

First: *Archipsylla primitiva* in Nel et al. (2005f), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

Last: Mentioned in Rasnitsyn (2002f), Bon-Tsagaan Nuur, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia.

F. Caeciliusidae (Caeciliidae) Eoc.(Ypresian)-Holocene

First: e.g. *Eopsocites fushunensis* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Cladiopsocidae Mio.(Burdigalian)-Holocene

First: *Cladiopsocus* sp. in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Compsocidae K1(Albian)-Holocene

First: *Burmacompsocus perreaui* Nel and Waller, 2007, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Dolabellopsocidae (Dolabellapsocidae) Mio.(Burdigalian)-Holocene

First: *Isthmopsocus* sp. in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Ectopsocidae Mio.(Aquitanian)-Holocene

First: *Ectopsocus* sp. in Engel (2004a), Mexican amber, Simojovel, Chiapas, Mexico.

F. Electrentomidae (Manicapsocidae) K1(Albian)-Holocene
Preference of family name after the Psocoptera Species File (Version 1.1/4.0).

First: *Manicapsocidus enigmaticus* in Delclòs et al. (2007), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Elipsocidae J3(Oxfordian)-Holocene

First: Mentioned in Grimaldi and Engel (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan. (Grimaldi and Engel, 2005 list this occurrence as Psocidae however Rasnitsyn, 2002f lists it as in the tribe Elipsocini, which would place it in the family Elipsocidae in the present classification.)

F. Empheriidae K1(Albian)-Eoc.(Priabonian)
Formerly considered a subfamily of Trogiidae (Baz and Ortuño, 2001).

First: e.g. *Empheropsocus arilloi* Baz and Ortuño, 2001, Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

Last: e.g. *Trichempheria villosa* in Engel and Perkovsky (2006), Rovno amber, Klesov/Dubrovitsa, Rivne Oblast, Ukraine.

F. Epipsocidae Pal.(Thanetian)-Holocene

First: Mentioned in Rasnitsyn (2002f), Sakhalin amber, Lower Due Formation, Starodubskoe, Sakhalin Region, Russian Federation.

F. Hemipsocidae Mio.(Burdigalian)-Holocene

First: *Hemipsocus* sp. in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Lachesillidae K2(Santonian)-Holocene

First: *Archaelachesis granulosa* in Nel et al. (2005f), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation. (Nel et al., 2005f suggest that this species may not belong in this family, in which case *Eolachesilla eocenica* from the Oise amber would be the first occurrence.)

F. Lepidopsocidae Eoc.(Ypresian)-Holocene

First: *Thylacella eocenica* Nel et al., 2005f, Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Liposcelididae (Liposcelidae) K1(Albian)-Holocene

First: *Cretoscelis burmitica* Grimaldi and Engel, 2006b, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Mesopsocidae Mio.(Burdigalian)-Holocene
Rasnitsyn (2002f, fig.163) assigns an undescribed specimen from the Upper Jurassic of Karatau to this family, however Azar et al. (2008) identify it as *Paramesopsocus adibi* (Paramesopsocidae).

First: *Mesopsocus* sp. in Peñalver et al. (1996), Ribesalbes, La Rinconada site, Ribesalbes-Alcora, Castellón Province, Spain.

F. Myopsocidae Mio.(Aquitanian)-Holocene

First: *Myopsocus* sp. in Solórzano Kraemer (2007), Mexican amber, Simojovel, Chiapas, Mexico.

F. Pachytroctidae K1(Albian)-Holocene
Although Nel et al. (2005f) removed *Psylloneura*? *perantiqua* (Burmese amber) from this family, a second unnamed specimen identified as belonging to this family remains.

First: Mentioned in Rasnitsyn and Ross (2000), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Paramesopsocidae Azar et al., 2008 J3(Oxfordian)-K1(Barremian)

First: *Paramesopsocus adibi* Azar et al., 2008, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Paramesopsocus lu* Azar et al., 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Peripsocidae Olig.(Chattian)-Holocene

First: Mentioned in Krumbiegel (1997), Bitterfeld amber, Bitterfeld, Saxony-Anhalt, Germany.

F. Philotarsidae Eoc.(Priabonian)-Holocene

First: e.g. *Philotarsopsis antiquus* in Mockford (2007), Baltic amber, Baltic, Baltic region, Baltic.

F. Prionoglariidae K1(Barremian)-Holocene

First: Figured in Grimaldi and Engel (2005), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Pseudocaeciliidae (Pseudocaecilliidae) Eoc.(Priabonian)-Holocene

First: *Electropsocus unguidens* in Lienhard and Smithers (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Psocidae Eoc.(Priabonian)-Holocene

First: e.g. *Psocidus multiplex* in Engel and Perkovsky (2006), Rovno amber, Klesov/Dubrovitsa, Rivne Oblast, Ukraine.

F. Psoquillidae Eoc.(Ypresian)-Holocene

First: *Eorhyopsocus magnificus* Nel et al., 2005f, Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Psyllipsocidae K1(Albian)-Holocene

First: *Psyllipsocus*? *banksi* in Ross and York (2000), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar. (Nel et al., 2005f question the position of this species but do not remove it from from this family. *Parapsyllipsocus vergereaui* Perrichot et al., 2003 may also belong to this family.)

F. Ptiloneuridae Mio.(Burdigalian)-Holocene

First: Mentioned in Rasnitsyn (2002f), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Sphaeropsocidae K1(Hauterivian)-Holocene

First: *Sphaeropsocites lebanensis* Grimaldi and Engel, 2006a, Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

F. Spurostigmatidae Mio.(Burdigalian)-Holocene
Family reinstated by Casasola González (2006).

First: *Spurostigma* sp. in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic. (This genus is listed by Pérez-Gelabert, 2008 under Cladiopsocidae, however it is maintained in a separate family in the Psocodea Species File.)

F. Trichopsocidae Eoc.(Priabonian)-Holocene

First: *Palaeopsocus tener* in Lienhard and Smithers (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Troctopsocidae Mio.(Burdigalian)-Holocene

First: e.g. *Troctopsocopsis* sp. in Solórzano Kraemer (2007), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Trogiidae K1(Albian)-Holocene

First: Mentioned in Poinar and Poinar (2008), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

O. Thysanoptera Haliday, 1836 (Thripida) Triassic(Carnian)-Quaternary(Holocene)

F. Adiheterothripidae (Neocomothripidae, Opadothripidae, Rhetinothripidae, Scaphothripidae, Scudderothripidae, Stenurothripidae) K1(Barremian)-Holocene
NOTE: Adiheterothripidae will have to be swapped with Stenurothripidae when including 2010 papers because of Penalver & Nel.

First: e.g. *Exitelothrips mesozoicus* in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Aeolothripidae (Aeolopthripidae, Aeothripidae, Palaeothripidae) K1(Valanginian)-Holocene

First: *Fusithrips crassipes* Shmakov, 2009, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Heterothripidae Eoc.(Priabonian)-Holocene

First: e.g. *Heterothrips nani* Schliephake, 2001, Baltic amber, Baltic, Baltic region, Baltic.

F. Karataothripidae J3(Oxfordian)

First and Last: *Karataothrips jurassicus* in Shmakov (2008), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Liassothripidae J3(Oxfordian)

First and Last: *Liassothrips crassipes* in Shmakov (2008), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Melanthripidae Eoc.(Ypresian)-Holocene
Formerly a subfamily in Aeolothripidae.

First: Mentioned in Brasero et al. (2009), Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Merothripidae (Jezzinothripidae) K1(Barremian)-Holocene

First: *Jezzinothrips cretacicus* in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Moundthripidae Nel et al., 2007b K1(Hauterivian)-K1(Barremian)
Shmakov (2009) thinks this might belong in Lophioneuridae.

First: *Moundthrips beatificus* Nel et al., 2007b, Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

Last: *Moundthrips beatificus* Nel et al., 2007b, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Phlaeothripidae (Phloeothripidae) Eoc.(Ypresian)-Holocene
Both Zherikhin (2002a) and Grimaldi and Engel (2005) state that the oldest Phlaeothripidae are from the Eocene Baltic amber, suggesting that the record of this family in Spahr (1992) was erroneous. Dr Alexey Shmakov (pers. comm., 2011) has confirmed this.

First: Mentioned in Brasero et al. (2009), Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Thripidae K1(Valanginian)-Holocene

First: *Convexithrips robustus* Shmakov, 2009, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Triassothripidae Grimaldi & Shmakov *in* Grimaldi et al., 2004 T3(Carnian)-T3(Norian)

First: *Triassothrips virginicus* Grimaldi & Fraser *in* Grimaldi et al., 2004, Cow Branch Formation, Solite quarry, Virginia, United States.

Last: *Kazachothrips triassicus* Shmakov *in* Grimaldi et al., 2004, Tologoy Formation, Ak-Kolka River, Kenderlyk, Zaisan District, Kazakhstan.

Holometabola (= Endopterygota)

O. Coleoptera Linnaeus, 1758 (Scarabaeida)
Carboniferous(Moscovian)-Quaternary(Holocene)

F. Acanthocnemidae K2(Cenomanian)-Holocene

First: *Acanthocnemoides sukatshevae* , Begichev Formation retinite, Khatanga River basin, Taimyr, Russian Federation.

F. Ademosynidae T1(Induan)-K1(Barremian)

First: Mentioned in Shcherbakov (2008a), Babiy Kamen', Maltseva/Sosnovaya Fomation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

Last: e.g. *Atalosyne sinuolata* in Tan et al. (2007), Lushangfen Formation, Jingxi Basin, Beijing Municipality, China.

F. Aderidae (Circaeidae, Euglenidae) K1(Barremian)-Holocene

First: Figured in Grimaldi and Engel (2005), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Adiphlebidae C2(Moscovian)

First and Last: *Adiphlebia lacoana* in Béthoux (2009), Carbondale Formation, Mazon Creek, Illinois, United States.

F. Agyrtidae Thomson, 1859 K1(Hauterivian)-Holocene
Formerly treated as a subfamily within Silphidae.

First: *Ponomarenkia parva* in Perkovsky (2001), Turga Formation, Turga River, near Borzai, Transbaikalia, Russian Federation.

F. Anthicidae K1(Barremian)-Holocene

First: *Camelomorpha longicervix* Kirejtshuk, Azar & Telnov *in* Kirejtshuk and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Anthribidae (Urodontidae) K1(Barremian)-Holocene

First: *Cretochoragus pygmaeus* Soriano et al., 2006a, Montsec lithographic limestones, Montsec Range, Lleida Province, Spain.

F. Artematopodidae (Artematopidae) Eoc.(Priabonian)-Holocene

First: e.g. *Electribius balticus* in Kubisz (2000), Baltic amber, Baltic, Baltic region, Baltic.

F. Asiocoleidae P2(Roadian)-P3(Changhsingian)

First: *Asiocoleus novojilovi* , Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

Last: Mentioned in Beattie (2007), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Attelabidae (Rhynchitidae) K1(Valanginian)-Holocene

First: Mentioned in Zherikhin and Gratshev (2004), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Belidae (Oxycorynidae) K1(Barremian)-Holocene

First: e.g. *Distenorrhinoides simulator* in Legalov (2009b), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain.

F. Berendtimiridae Winkler, 1987 Eoc.(Priabonian)

First and Last: *Berendtimirus progenitor* Winkler, 1987, Baltic amber, Baltic, Baltic region, Baltic.

F. Biphyllidae (Biphyliidae) K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk and Azar (2008), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon. (This identification is doubtful.)

F. Boganiidae K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk and Azar (2008), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon. (Identification of these specimens is tentative.)

F. Bostrichidae (Bostrychidae, Lyctidae) K1(Albian)-Holocene

First: Mentioned in Delclòs et al. (2007), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Bothrideridae Eoc.(Priabonian)-Holocene

First: e.g. *Ascetoderes* sp. in Kupryjanowicz (2001), Baltic amber, Baltic, Baltic region, Baltic.

F. Brachyceridae (Erirhinidae) Eoc.(Priabonian)-Holocene

First: e.g. *Oryctorhinus tenuirostris* in Zherikhin (2000), Florissant Formation, Florissant, Colorado, United States.

F. Brachypsectridae Mio.(Burdigalian)-Holocene

First: *Brachypsectra moronei* Costa et al., 2006, Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Brentidae (Apionidae, Brenthidae, Ithyceridae, Nanophyidae) K1(Valanginian)-Holocene
NOTE: Legalov (2009c) treats Ithyceridae as a spearate family and puts together subfamilies which are treated differently by Bouchard et al. (2011).

First: Mentioned in Zherikhin and Gratshev (2004), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Buprestidae T3(Carnian)-Holocene

First: e.g. *Mesostigmodera typica* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Byrrhidae T1(Induan)-Holocene

First: Mentioned in Shcherbakov (2008a), Babiy Kamen', Maltseva/Sosnovaya Fomation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

F. Byturidae K1(Berriasian)-Holocene

First: Figured in Jarzembowski (1992), Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom. (This record is tentative.)

F. Callirhipidae (Callirhypidae) K2(Santonian)-Holocene

First: Mentioned in Ponomarenko (2002a), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation. (Ponomarenko, 2002a does not actually state which Upper Cretaceous amber this family is known from. It could be from Cenomanian Agapa amber.)

F. Cantharidae K1(Aptian)-Holocene

First: Figured in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Carabidae (Carabaeidae, Cicindelidae, Nebriidae, Paussidae) T3(Carnian)-Holocene

First: Figured in Grimaldi and Engel (2005), Cow Branch Formation, Solite quarry, Virginia, United States.

F. Caridae K1(Valanginian)-Holocene
NOTE: Including Baissorhynchinae after Bouchard et al. (2011).

First: e.g. *Baissorhynchus tarsalis* , Zaza Formation, Baissa, Buryatia, Russian Federation. (NOTE: Ponomarenko's website lists specimens from Semen/Semyon [Argun' Formation] as Upper Jurassic but they're actually of uncertain Lower Cretaceous age.)

F. Catiniidae (Catinidae) T3(Carnian)-K1(Albian)

First: e.g. *Catinoides rotundatus* in Tan and Ren (2007), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: e.g. *Catinus ovatus* in Tan and Ren (2007), Dalazi Formation, Zhixin Basin, Liaoning Province, China.

F. Cerambycidae (Cerambicidae, Pseudonepidae) K1(Albian)-Holocene
NOTE: Grimaldi and Engel (2005) (p.393) say *Cerambyomima longicornis* (which they misspell) from Karabastau Fm. is oldest of this family, although it's usually listed in Chrysomelidae. Ponomarenko's website lists it in the latter family as does Zhang (2005). *Willcoxia* from the Upper Triassic of Australia (in Jell, 2004) probably belongs to the Tricoleidae (see Ponomarenko, 2008).

First: Mentioned in Rasnitsyn and Ross (2000), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Cerophytidae J2(Callovian)-Holocene

First: Mentioned in Chang et al. (2009), Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Cerylonidae Eoc.(Priabonian)-Holocene
NOTE: Presumably there's one in Siberian amber but Ponomarenko's website doesn't list it.

First: e.g. *Philothermopsis*? sp. in Kupryjanowicz (2001), Baltic amber, Baltic, Baltic region, Baltic.

F. Chelonariidae K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Chrysomelidae (Bruchidae) J2(Callovian)-Holocene
NOTE: Ponomarenko's website lists Bruchidae separately - listed as subfamily of Chrysomelidae in Bouchard et al. (2011).

First: *Tarsomegamerus mesozoicus* Zhang, 2005, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China. (NOTE: This species moved to Elateridae in 2010 although still listed in Chrysomelidae on Ponomarenko's website. Next oldest is Karabastau Fm.)

F. Ciidae (Cisidae, Cisiidae, Cissidae) K1(Albian)-Holocene

First: Figured in Grimaldi et al. (2002), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Cistelidae Mio.(Aquitanian)-Holocene

First: Mentioned in Engel (2004a), Mexican amber, Simojovel, Chiapas, Mexico.

F. Clambidae K1(Barremian)-Holocene

First: *Eoclambus rugidorsum* Kirejtshuk and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Cleridae K1(Albian)-Holocene

First: Mentioned in Poinar and Poinar (2008), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Coccinellidae Eoc.(Ypresian)-Holocene
NOTE: Ponomarenko's website lists a species figured by Grimaldi and Engel (2005) (p.388) as being from New Jersey amber but it's actually from Dominican amber. There is a brief mention of the family in Upper Cretaceous amber in History of Insects (p.173) but nothing more than that.

First: e.g. Mentioned in Kirejtshuk and Nel (2008), Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Colonidae Pleist.(Gelasian)-Holocene

First: *Colon* sp. in Böcher (1995), Kap København Formation, Peary Land, Northeast Greenland National Park, Greenland.

F. Colymbotethidae Ponomarenko, 1994(Colymbothetidae) T3(Norian)

First and Last: *Colymbotethis antecessor* in Sinitshenkova (2002c), Tologoy Formation, Ak-Kolka River, Kenderlyk, Zaisan District, Kazakhstan.

F. Coptoclavidae T3(Rhaetian)-K1(Aptian)
NOTE: I don't know what became of the Chinese Triassic species in *Agrascapha* or *Chengdecupes* (the latter or which would be the oldest) - Ponomarenko's website doesn't list them and nobody has referred to them recently that I know of.

First: *Holcoelytrum* sp. in Wang et al. (2009a), Cotham Member, Lilstock Formation, Penarth Group1, Strensham, Worcestershire, United Kingdom. (NOTE: I don't know which locality this specimen actually comes from. There might be an issue surrounding whether the genus is j. syn. *Holcoptera* and whether *Holcoptera* belongs to Coptoclavidae or Dytiscidae.)

Last: Mentioned in Wang et al. (2009a), Yixian unspecified, Yixian Formation, Liaoning Province, China. (According to Wolf-Schwenninger and Schawaller, 2007, *Conan barbarica* Martins-Neto is a dragonfly nymph and is, sadly, a junior synonym of *Nothomacromia sensibilis* according to Bechly, 2007b.)

F. Corylophidae (Orthoperidae) K2(Campanian)-Holocene

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Cossonidae Mio.(Aquitanian)-Holocene

First: Mentioned in Engel (2004a), Mexican amber, Simojovel, Chiapas, Mexico.

F. Cryptophagidae K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk and Azar (2008), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon. (This identification is doubtful.)

F. Cucujidae K1(Barremian)-Holocene

First: Mentioned in Poinar and Poinar (2008), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Cupedidae (Cupesidae) T2(Anisian)-Holocene

First: Mentioned in Shcherbakov (2008a), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Curculionidae (Platypodidae, Scolytidae) T2(Anisian)-Holocene
NOTE: Gratshev and Zherikhin (2003) place *Paleoscolytus sussexensis* from the Wadhurst Clay as Coleoptera *incertae sedis*.

First: e.g. *Mesorhynchophora dunstani* in Jell (2004), Ashfield Formation, St. Peters, Sydney, New South Wales, Australia.

F. Dascillidae T3(Carnian)-Holocene

First: e.g. *Leioodes plana* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Dermestidae J3(Tithonian)-Holocene
The oldest known body-fossils of Dermestidae are found in Lebanese amber (Kirejtshuk et al., 2009b). The Triassic taxa in Jell (2004) are considered to be family uncertain (Hava et al., 2006).

First: ichnofossils in Britt et al. (2008), Morrison Formation (upper), Carbon County, Wyoming, United States.

F. Derodontidae Pleist.(Gelasian)-Holocene

First: *Laricobius* cf. *caucasicus* in Böcher (1995), Kap København Formation, Peary Land, Northeast Greenland National Park, Greenland.

F. Discolomatidae (Discolomidae) Mio.(Aquitanian)-Holocene
Engel (2004a) notes that this family was listed in Mexican amber by Poinar (1992) as a hemipteran. Solórzano Kraemer (2007) also lists this family under Hemiptera.

First: Mentioned in Solórzano Kraemer (2007), Mexican amber, Simojovel, Chiapas, Mexico.

F. Dryophthoridae Eoc.(Priabonian)-Holocene

First: e.g. *Stenommatomorphus hexarthrus* Nazarenko *in* Nazarenko and Perkovsky, 2009, Rovno amber, Klesov/Dubrovitsa, Rivne Oblast, Ukraine.

F. Dryopidae K1(Aptian)-Holocene

First: Mentioned in Wolf-Schwenninger and Schawaller (2007), Crato Formation, Araripe Basin, Ceará, Brazil. (NOTE: Ponomarenko's website doesn't mention this specimen under Dryopidae.)

F. Dytiscidae (Dytisicdae) J3(Oxfordian)-Holocene
NOTE: Ponomarenko's website lists the Lower Jurassic *Angaragabus* (Ust-Baley, Toarcian) in Liadytidae. Grimaldi and Engel (2005) say it's a putative dytiscid.

First: *Palaeodytes gutta* , Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Elateridae T2(Ladinian)-Holocene

First: e.g.? *Gemelina triangularis* Martins-Neto & Gallego *in* Martins-Neto et al., 2006, Los Rastros Formation, Bermejo Basin, La Rioja Province, Argentina. (NOTE: This species isn't mentioned anywhere on Ponomarenko's website.)

F. Elmidae Eoc.(Lutetian)-Holocene

First: *Potamophilites angustifrons* , Geiseltal, near Halle, Saxony-Anhalt, Germany.

F. Elodophthalmidae Kirejtshuk and Azar, 2008 K1(Barremian)

e.g. *Elodophthalmus harmonicus* Kirejtshuk and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Endomychidae K1(Barremian)-Holocene
Palaeoendomychus gymnus (Barremian, Laiyang Formation, China) is now placed in Trogossitidae (Schmied et al., 2009).

First: Mentioned in Poinar and Poinar (2008), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Erotylidae (Languriidae) K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk and Azar (2008), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Eucinetidae J3(Oxfordian)-Holocene

First: *Mesocinetus* sp. , Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan. (NOTE: This genus put in own family Mesocinetidae in 2010. Next oldest from Burmese amber.)

F. Eucnemidae K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Geotrupidae (Bolboceratidae) J3(Tithonian)-Holocene

First: *Geotrupoides lithographicus* in Krell (2007), Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany. (This record is doubtful.)

F. Glaphyridae K1(Valanginian)-Holocene

First: e.g. *Cretoglaphyrus rohdendorfi* in Krell (2007), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Glaresidae J1(Hettangian)-Holocene

First: *Aphodiites protogaeus* in Krell (2007), Schambelen Member, Staffelegg Formation, Brugg, Aargau, Switzerland. (The family identity is doubtful.)

F. Gyrinidae J1(Pliensbachian)-Holocene

First: e.g. *Mesogyrus sibiricus* in Prokop et al. (2004), Osinovskiy Formation, Chernyi Etap, Kemerovo Region, Russian Federation.

F. Haliplidae K1(Aptian)-Holocene

First: e.g. *Cretihaliplus chifengensis* in Prokop et al. (2004), Jiufotang Formation, Beishan, Yixian County, Liaoning Province, China. (NOTE: These species aren't listed anywhere on Ponomarenko's website. Next oldest from Cenomanian Redmond Fm. of Labrador.)

F. Haplochelidae Kirejtshuk and Poinar, 2006 K1(Albian)
NOTE: Family synonymised under extant Lepiceridae in a 2010 paper.

First and Last: *Haplochelus georissoides* Kirejtshuk and Poinar, 2006, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Helotidae Mio.(Langhian)-Holocene
NOTE: Not same as Helodidae (j. syn. Scirtidae).

First: e.g. *Helota zhangi* Wegrzynowicz, 2007, Shanwang Formation, Linqu County, Shandong Province, China.

F. Heteroceridae K1(Hauterivian)-Holocene

First: *Heterocerites kobdoensis* , Gurvan-Eren Formation (Myangad), Myangad, Khovd Aimag, Mongolia.

F. Histeridae K1(Albian)-Holocene

First: *Pantostictus burmanicus* Poinar and Brown, 2009, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Hybosoridae J2(Callovian)-Holocene

First: *Jurahybosorus mongolicus* in Krell (2007), Bayan-Teg, Bayan-Teg Coal Quarry, Övörkhangai (Ubur-Khangaisk) Aimag, Mongolia.

F. Hydraenidae J2(Aalenian)-Holocene

First: *Ochtebiites altus* in Ponomarenko (2003a), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation.

F. Hydrophilidae (Epimetopidae, Georissidae, Georyssidae, Helophoridae, Hydrochidae, Hydrophyllidae, Spercheidae) T1(Induan)-Holocene

First: Mentioned in Shcherbakov (2008a), Babiy Kamen', Maltseva/Sosnovaya Fomation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

F. Hygrobiidae Olig.(Chattian)-Holocene

First: *Hygrobia cretzschmari* , Rott paper shales, Bonn, North Rhine-Westphalia, Germany.

F. Jurodidae (Sikhotealiniidae) J2(Aalenian)-Holocene

First: *Jurodes ignoramus* , Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation.

F. Kateretidae (Brachypteridae) K1(Barremian)-Holocene

First: *Lebanoretes andelmani* Kirejtshuk and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Labradorocoleidae K2(Cenomanian)
Ponomarenko (2000b) notes that without investigating the body of the specimen for cryptosterny, it is not possible to say for certain if this family belongs to Coleoptera or Blattodea.

First and Last: *Labradorocoleus carpenteri* , Redmond Formation, Knob Lake District, Labrador, Canada.

F. Laemophloeidae K1(Albian)-Holocene

First: Mentioned , Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Lampyridae Eoc.(Priabonian)-Holocene

First: e.g. "*Lucidota*" *prima* in Meyer (2003), Florissant Formation, Florissant, Colorado, United States.

F. Latridiidae (Lathridiidae) K1(Barremian)-Holocene

First: e.g. *Tetrameropsis mesozoica* Kirejtshuk and Azar, 2008, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Leiodidae (Catopidae, Cholevidae, Leiodesidae, Liodidae) J2(Aalenian)-Holocene

First: e.g. *Mesecanus communis* in Perkovsky (2001), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation.

F. Liadytidae (Lyadytidae) T3(Carnian)-J3(Tithonian)

First: Mentioned in Shcherbakov (2008a), Cow Branch Formation, Solite quarry, Virginia, United States. (Shcherbakov, 2008a lists this as a possible occurrence.)

Last: e.g. *Liadytes longus* in Ponomarenko (2002a), Glushkovo Formation (Unda), Unda, Transbaikalia, Russian Federation.

F. Limnichidae Eoc.(Priabonian)-Holocene

First: e.g. *Palaeoersachus bicarinatus* Pütz et al., 2004, Baltic amber, Baltic, Baltic region, Baltic.

F. Limulodidae Mio.(Aquitanian)-Holocene

First: Mentioned in Engel (2004a), Mexican amber, Simojovel, Chiapas, Mexico.

F. Lucanidae (Paralucanidae) J3(Tithonian)-Holocene
NOTE: Will need to add mention from Jiulongshan Fm. (Daohugou) when including 2010 papers.

First: *Paralucanus mesozoicus* in Krell (2007), Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Lycidae Eoc.(Priabonian)-Holocene

First: e.g. *Miocaenia pectinicornis* in Meyer (2003), Florissant Formation, Florissant, Colorado, United States.

F. Lymexylidae (Lymexilidae, Lymexylonidae) K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Magnocoleidae Hong, 1998b K1(Barremian)

First and Last: *Magnocoleus huangjiapuensis* Hong, 1998b, Qingshila Formation, Huangjiapu, Hebei Province, China.

F. Melandryidae (Serropalpidae) K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Meloidae Pal.(Thanetian)-Holocene

First: e.g. *Zonabris immaculatus* in Engel (2005a), spongo-diatomaceous maar, Menat, Puy-de-Dôme, Auvergne, France.

F. Melyridae (Dasytidae, Malachiidae) K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Micromalthidae J3(Oxfordian)-Holocene

First: Mentioned in Kirejtshuk and Azar (2008), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Monotomidae (Rhizophagidae) K1(Barremian)-Holocene

First: *Rhizophtoma elateroides* Kirejtshuk & Azar *in* Kirejtshuk et al., 2009a, Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Mordellidae (Liaoximordellidae, Praemordellidae) J3(Oxfordian)-Holocene

First: *Praemordella martynovi* in Liu et al. (2008a), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Mycetophagidae K1(Barremian)-Holocene

First: Figured in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Mycteridae Eoc.(Ypresian)-Holocene

First: *Bertinotus gallicus* Kirejtshuk and Nel, 2009, Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Nemonychidae (Eccoptarthridae, Eobelidae) J3(Oxfordian)-Holocene
NOTE: Soriano (2009) considers Eobelinae in Belidae but Ponomarenko's website, Legalov (2009a) and Bouchard et al. (2011) do not.

First: e.g. *Megabrenthorrhinus grandis* in Legalov (2009a), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Nitidulidae (Cybocephalidae) K1(Valanginian)-Holocene

First: e.g. *Crepuraea archaica* , Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Nosodendridae Eoc.(Ypresian)-Holocene

First: *Nosodendron tritavum* , Green River Formation (Wyoming), Unitas area, Wyoming, United States.

F. Noteridae (Phreatodytidae) Pal.(Thanetian)-Holocene

First: Mentioned in Sinitshenkova (2002c), Paskapoo Formation, eastern foothills, Rocky Mountains, Alberta, Canada.

F. Oborocoleidae P1(Sakmarian)

e.g. *Oborocoleus rohdendorfi* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

F. Obrieniidae Zherikhin and Gratshev, 1994 T3(Carnian)-J3(Oxfordian)

First: e.g. *Obrienia kuscheli* in Ponomarenko (2002a), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: *Kararhynchus occiduus* Zherikhin and Gratshev, 1994, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Ochodaeidae K1(Barremian)-Holocene

First: e.g. *Cretochodaeus mongolicus* in Krell (2007), Khurilt Formation, Bon-Tsagaan Group, Bayankhongor Aimag, Mongolia.

F. Oedemeridae K1(Albian)-Holocene

First: Mentioned in Grimaldi and Engel (2005), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Ommatidae (Brochocoleidae, Tetraphaleridae) T2(Ladinian)-Holocene

First: *Notocupes* sp. in Krzemiński and Lombardo (2001), Upper Meride Limestone, Val Mara, Canton Ticino, Switzerland.

F. Parahygrobiidae J3(Oxfordian)

First and Last: *Parahygrobia natans* in Grimaldi and Engel (2005), Uda Formation, Uda River, Buryatia, Russian Federation.

F. Parandrexidae Kirejtshuk, 1994 J2(Callovian)-K1(Barremian)

First: *Parandrexis beipiaoensis* in Zhang (2005), Haifanggou Formation, Beipiao, Liaoning Province, China.

Last: *Martynopsis laticollis* Soriano et al., 2006b, Calizas de la Huérguina Formation (Las Hoyas), Las Hoyas, Cuénca Province, Spain.

F. Passalidae Olig.(Chattian)-Holocene

First: *Passalus indormitus* in Krell (2007), Post, John Day series, Oregon, United States.

F. Passandridae Eoc.(Priabonian)-Holocene

First: e.g.? *Passandra* sp. , Baltic amber, Baltic, Baltic region, Baltic.

F. Peltosynidae
NOTE: Monospecific endemic from Madygen Formation - doesn't seem to be considered a valid family anymore.

F. Permocupedidae (Kaltanocoleidae) P1(Artinskian)-P3(Changhsingian)

First: e.g. *Kaltanicupes ponomarenkoi* in Geertsema et al. (2002), Irati Formation, Paraná Basin, São Paulo, Brazil.

Last: Mentioned in Beattie (2007), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Permosynidae P2(Roadian)-T3(Carnian)

First: e.g. *Permosyne elongata* Ponomarenko *in* Ponomarenko and Mostovski, 2005, Volksrust Formation, Ecca Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: e.g. *Pseudorhynchophora olliffi* in Ponomarenko (2008), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Phalacridae Eoc.(Ypresian)-Holocene

First: Mentioned in Kirejtshuk and Nel (2008), Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Phengodidae (Phenogodidae)
No fossil record?

F. Phloeostichidae K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk and Azar (2008), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon. (Identification of these specimens is tentative.)

F. Pleocomidae K1(Valanginian)-Holocene

First: e.g. *Proteroscarabaeus magnus* in Krell (2007), Zaza Formation, Baissa, Buryatia, Russian Federation. (This record is doubtful.)

F. Praelateriidae (Praelateridae) J1(Hettangian)-J1(Sinemurian)

First: *Megacentrus tristis* , Schambelen Member, Staffelegg Formation, Brugg, Aargau, Switzerland.

Last: e.g. *Praelaterium problematicum* , Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Prionoceridae Eoc.(Ypresian)-Holocene

First: *Prionocerites tattriei* Lawrence et al., 2008, Hat Creek amber, Kamloops Group, British Columbia, Canada.

F. Propalticidae Eoc.(Priabonian)-Holocene

First: *Propalticus* sp. , Baltic amber, Baltic, Baltic region, Baltic. (NOTE: Seems to be an unpublished record on Ponomarenko's site. Next oldest is Kenyan amber.)

F. Prostomidae K1(Albian)-Holocene

First: *Vetuprostomis consimilis* Engel and Grimaldi, 2008b, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Protocucujidae
NOTE: Ponomarenko's website has this listed as Recent only. FR2 and Labandeira have J3 origin.

F. Psephenidae K1(Barremian)-Holocene

First: Mentioned in Soriano et al. (2007), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain.

F. Ptiliidae (Ptilidae) K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Ptilodactylidae K1(Barremian)-Holocene

First: e.g. Figured in Soriano et al. (2007), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain.

F. Ptinidae (Anobiidae) K1(Albian)-Holocene
NOTE: Zherikhin (2002c) mentions that undescribed specimens of this family (as Anobiidae) are known from the "Early Cretaceous of Transbaikalia" (p.354), which could be a number of different deposits. If it's Turga Fm, then it would be oldest.

First: Mentioned in Alonso et al. (2000), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain. (NOTE: Not mentioned in Delclòs et al., 2007 which makes me wonder if it was a misidentification but no way to say for sure.)

F. Pyrochroidae (Pedilidae, Pirochoidae, Pyreochroidae) K1(Aptian)-Holocene

First: *Cretaceimelittomoides cearensis* (nomen nudum) in Wolf-Schwenninger and Schawaller (2007), Crato Formation, Araripe Basin, Ceará, Brazil. (This record is doubtful.)

F. Pythidae Eoc.(Priabonian)-Holocene

First: e.g. *Pythoceropsis singularis* , Florissant Formation, Florissant, Colorado, United States. (NOTE: Also occurs in Baltic amber.)

F. Rhipiceridae (Sandalidae)
No fossil record?

F. Rhombocoleidae P2(Roadian)-K1(Aptian)

First: e.g. *Rhombocoleites danutae* Ponomarenko and Mostovski, 2005, Volksrust Formation, Ecca Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: *Sinorhombocoleus papposus* in Tan and Ren (2009), Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Rhysodidae Eoc.(Priabonian)-Holocene

First: Mentioned , Baltic amber, Baltic, Baltic region, Baltic.

F. Ripiphoridae (Rhipiphoridae) K1(Albian)-Holocene

First: e.g. *Paleoripiphorus deploegi* Perrichot et al., 2004, Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France. (NOTE: Burmese amber specimen renamed in a 2010 paper by Falin & Engel in Alavesia.)

F. Salpingidae (Inopeplidae) K1(Barremian)-Holocene

First: Mentioned in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Scarabaeidae (Aphodiidae, Cetoniidae, Lithoscarabaeidae, Melolonthidae, Melonthidae, Rutelidae) J3(Oxfordian)-Holocene
NOTE: Mention in Daohugou will need to be added for 2010.

First: e.g. *Juraclopus rohdendorfi* in Krell (2007), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Schizocoleidae P2(Roadian)-J2(Bathonian)
NOTE: Ponomarenko's website suggests there is a Lower Cretaceous specimen of *Schizocoleus* somewhere but doesn't list it.

First: e.g. *Palademosyne natalensis* Ponomarenko *in* Ponomarenko and Mostovski, 2005, Volksrust Formation, Ecca Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: *Mimema punctatum* , Stonesfield Slate, Taynton Limestone Formation, Oxfordshire, United Kingdom.

F. Schizophoridae P2(Capitanian)-K1(Barremian)
NOTE: *Sinorhombocoleus papposus* (Yixian Formation: Aptian, probably) moved to this family in Kirejtshuk et al., 2010.

First: *Dikerocoleus divisus* in Tan et al. (2007), Yinping Formation, Houdong, SW Chaohu City, Anhui Province, China.

Last: Figured in Soriano et al. (2007), Calizas de la Huérguina Formation (Las Hoyas), Las Hoyas, Cuénca Province, Spain.

F. Schizopodidae (Electrapatidae) Eoc.(Priabonian)-Holocene

First: *Electrapate martynovi* , Baltic amber, Baltic, Baltic region, Baltic.

F. Scirtidae (Helodidae, Sinodryopitidae) J3(Oxfordian)-Holocene

First: Mentioned in Kirejtshuk and Azar (2008), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Scraptiidae (Scaraptiidae, Scraptidae) J3(Oxfordian)-Holocene

First: Mentioned in Ponomarenko (2002a), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Scydmaenidae K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Silphidae Eoc.(Lutetian)-Holocene
NOTE: Ponomarenko's website places *Mercata festira* (oldest in FR2) in Elateridae, although he spells it *Mercuta feghira*.

First: e.g. *Eosilphites decoratus* , Geiseltal, near Halle, Saxony-Anhalt, Germany.

F. Silvanidae K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Sinisilvanidae Hong, 2002a(Sinislavanidae) Eoc.(Ypresian)

First and Last: *Sinisilvana fushunensis* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Smicripidae Eoc.(Ypresian)-Holocene

First: *Smicrips europeus* Kirejtshuk and Nel, 2008, Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Sojanocoleidae P2(Roadian)

First and Last: *Sojanocoleus reticulatus* in Rohdendorf (1991), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation.

F. Sphaeriusidae (Microsporidae, Spaeriidae, Sphaeriidae) K1(Albian)-Holocene

First: *Burmasporum rossi* Kirejtshuk, 2009, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Sphindidae (Aspidiphoridae) Eoc.(Priabonian)-Holocene

First: Mentioned in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Staphylinidae (Micropeplidae, Pselaphidae, Scaphidiidae, Staphyllinidae) T3(Carnian)-Holocene

First: Figured in Grimaldi and Engel (2005), Cow Branch Formation, Solite quarry, Virginia, United States.

F. Synchroidae Eoc.(Priabonian)-Holocene

First: "*Synchroa*" *quiescent* in Meyer (2003), Florissant Formation, Florissant, Colorado, United States.

F. Taldycupedidae (Taldycupidae) P2(Roadian)-K1(Barremian)

First: e.g. *Taldycupes africanus* Ponomarenko *in* Ponomarenko and Mostovski, 2005, Volksrust Formation, Ecca Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: *Yiyangicupes huobashanense* in Tan and Ren (2009), Lengshuiwu Formation, Yiyang County, Jianxi Province, China.

F. Tenebrionidae (Alleculidae, Lagriidae) T2(Anisian)-Holocene

First: *Adelidium cordatum* in Jell (2004), Ashfield Formation, St. Peters, Sydney, New South Wales, Australia.

F. Throscidae (Trixagidae) K1(Barremian)-Holocene

First: Mentioned in Kirejtshuk et al. (2009a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Trachypachidae (Leptopodocoleidae, Trachypacheidae, Trachypachyidae) T1(Induan)-Holocene

First: Mentioned in Shcherbakov (2008a), Babiy Kamen', Maltseva/Sosnovaya Fomation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

F. Triadocupedidae T3(Carnian)
Ponomarenko's website lists this as a subfamily of Cupedidae but Kirejtshuk and Azar (2008) and Bouchard et al. (2011) maintain it as a separate family.

e.g. *Moltenocupes townrowi* in Ponomarenko (2008), Molteno Formation, KwaZulu-Natal, Karoo Basin, South Africa. (NOTE: Ponomarenko's website lists this species under Cupedidae: Triadocupedinae but keeping elevated as separate family here. Might be better to have a Madygen specimen if you can find a good reference for one.)

F. Triaplidae T1(Induan)-J2(Callovian)

First: Mentioned in Shcherbakov (2008a), Babiy Kamen', Maltseva/Sosnovaya Fomation, Kuznetsk Basin, Siberian Federal District, Russian Federation.

Last: *Mesapus beipiaoensis* in Tan et al. (2007), Haifanggou Formation, Beipiao, Liaoning Province, China. (NOTE: Ponomarenko's website lists this species under Hydrophilidae [and spells the species incorrectly]. Next youngest would be Madygen.)

F. Tricoleidae P3(Changhsingian)-J2(Callovian)
NOTE: I can't find any mentions of Cretaceous specimens. Ponomarenko (2008) gives range only up to Jurassic.

First: e.g. Mentioned in Ponomarenko (2008), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

Last: e.g. *Loculitricoleus flatus* Tan and Ren, 2009, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Tritarsidae Hong, 2002a(Tritarsusidae) Eoc.(Ypresian)

First and Last: *Tritarsus latus* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Trogidae K1(Valanginian)-Holocene

First: e.g. *Trox sibericus* in Krell (2007), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Trogossitidae (Lophocateridae, Ostomatidae, Ostomidae, Peltidae, Trogositidae) J1(Toarcian)-Holocene

First: *Thoracotes dubius* in Schmied et al. (2009), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Tshekardocoleidae (Uralocoleidae) P1(Asselian)-J2(Aalenian)

First: e.g. Mentioned , Jeckenbach layers, Niedermoschel, Donnersbergkreis district, Rhineland-Palatinate, Germany.

Last: *Dictyocoleus jurassicus* in Tan and Ren (2009), Dashankou Group, Subei County, Jiuquan, Gansu Province, China.

F. Ulyanidae Zherikhin, 1993 K1(Valanginian)-K1(Albian)
NOTE: Legalov (2009c) puts this as a subfamily in his conception of Ithyceridae but Bouchard et al. (2011) keep it separate.

First: Mentioned in Zherikhin and Gratshev (2004), Zaza Formation, Baissa, Buryatia, Russian Federation.

Last: *Ulyana nobilis* in Oberprieler et al. (2007), Emanra Formation, Khetana River, Khabarovsk Province, Russian Federation.

F. Zopheridae (Colydiidae) K1(Barremian)-Holocene

First: Figured in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

O. Diptera Linnaeus, 1758 (Muscida) Triassic(Anisian)-Quaternary(Holocene)

F. Acartophthalmidae Eoc.(Priabonian)-Holocene

First: e.g. *Acartophthalmites tertiaria* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Acroceridae (Archocyrtidae) J3(Oxfordian)-Holocene

First: e.g. *Juracyrtus kovalevi* in Hauser and Winterton (2007), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Agromyzidae Eoc.(Ypresian)-Holocene

First: *Foliofossor cranei* in Evenhuis (1994), Reading Formation, Cold Ash, Berkshire, United Kingdom. (This trace fossil record is tentative. Flies figured by Zlobin, 2007 from Bembridge Marls, Isle of Wight.)

F. Anisopodidae (Anisopidae, Anisopodiae, Eopleciidae, Mycetobiidae, Olbiogastridae, Protolbiogastridae, Rhyphidae) J1(Sinemurian)-Holocene
NOTE: Some authors separate Mycetobiidae.

First: *Mesorhyphus rhaeticus* in Evenhuis (1994), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Ansorgiidae Krzemiński and Lukashevitch, 1993 J3(Oxfordian)

First and Last: *Ansorgius predictus* in Krzemiński and Evenhuis (2000), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Antefungivoridae (Antiquamediidae, Pleciomimidae, Sinemediidae) J1(Sinemurian)-K2(Santonian)

First: Mentioned in Ansorge (1996a), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

Last: Mentioned in Evenhuis (1994), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Anthomyiidae Eoc.(Priabonian)-Holocene

First: e.g. *Protanthomyia minuta* Michelsen, 2000, Baltic amber, Baltic, Baltic region, Baltic.

F. Anthomyzidae Eoc.(Priabonian)-Holocene

First: e.g. *Protanthomyza collarti* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Apioceridae K1(Valanginian)-Holocene

First: Mentioned in Grimaldi and Engel (2005), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Apsilocephalidae Nagatomi et al., 1991 K1(Albian)-Holocene
Gaimari and Mostovski (2000) do not consider this family to be a synonym of Rhagionempididae.

First: e.g. *Burmapsilocephala cockerelli* Gaimari and Mostovski, 2000, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Apystomyiidae Nagatomi and Liu, 1994 J3(Oxfordian)-Holocene

First: Mentioned in Mostovski (2009), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Archisargidae (Mesophantasmatidae) J2(Callovian)-J3(Tithonian)

First: e.g. *Archirhagio zhangi* Zhang et al., 2009a, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

Last: *Mesosolva longivena* in Nagatomi and Yang (1998), Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia. (NOTE: Mentioned in this family on Evenhuis website but unplaced in 1994 book.)

F. Asilidae J3(Oxfordian)-Holocene
Dikow (2009) notes that putative specimens of this family from the Karabastau Formation may prove to be stem-Asiloidea and that the oldest definitive Asilidae is *Araripogon axelrodi* from the Crato Formation.

First: Mentioned in Mostovski (2009), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Asiochaoboridae Hong and Wang, 1990 K1(Barremian)

e.g. *Asiochaoborus tenuous* in Evenhuis (1994), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Asteiidae Eoc.(Priabonian)-Holocene

First: e.g. *Succinasteia carpenteri* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Atelestidae K1(Berriasian)-Holocene

First: *Dianafranksia fisheri* in Grimaldi and Engel (2005), Lulworth Formation, Durlston Bay, Dorset, United Kingdom.

F. Athericidae K1(Berriasian)-Holocene

First: *Athericites sellwoodi* Mostovski et al., 2003a, Lulworth Formation, Durlston Bay, Dorset, United Kingdom.

F. Aulacigastridae Eoc.(Priabonian)-Holocene

First: e.g. *Protaulacigaster electrica* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Axymyiidae J2(Callovian)-Holocene

First: e.g. *Psocites fossilis* Zhang, 2004, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Bibionidae (Hesperinidae, Penthetriidae, Pleciidae) J1(Toarcian)-Holocene

First: *Penthetria dubia* in Evenhuis (1994), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Blephariceridae (Blepharoceridae) J2(Callovian)-Holocene

First: e.g. *Brianina longitibialis* Zhang and Lukashevitch, 2007, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Boholdoyidae (Boholdoyiidae) J2(Aalenian)-K1(Hauterivian)

First: *Boholdoya alata* in Krzemiński and Evenhuis (2000), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation.

Last: *Boholdoya thoracica* in Evenhuis (1994), Turga Formation, Turga River, near Borzai, Transbaikalia, Russian Federation.

F. Bolitophilidae (Mangasidae) K1(Hauterivian)-Holocene

First: e.g. *Mangas exilis* in Blagoderov and Grimaldi (2004), Gurvan-Eren (Boro-Nuru), Boro-Nuru, Khovd Aimag, Mongolia.

F. Bombyliidae (Phthiriidae, Systropodidae, Usiidae) K1(Hauterivian)-Holocene
Palaeoplatypygus zaitzevi is included in the Mythicomyiidae following Evenhuis (2002).

First: e.g.? Mentioned in Mostovski (2009), Gurvan-Eren (Boro-Nuru), Boro-Nuru, Khovd Aimag, Mongolia.

F. Calliphoridae Eoc.(Lutetian)-Holocene
Rognes (1997) considers this family as not monophyletic, however, use of the name remains common in recent literature. Grimaldi and Cumming (1999), Zherikhin (2002c) and Grimaldi and Engel (2005) consider *Cretaphormia fowleri* from the Upper Cretaceous Edmonton Formation to be unplaced within Cyclorrhapha.

First: Mentioned in Evenhuis (1994), Geiseltal, near Halle, Saxony-Anhalt, Germany.

F. Camillidae Eoc.(Priabonian)-Holocene

First: e.g. *Protocamilla groehni* Grimaldi, 2008, Baltic amber, Baltic, Baltic region, Baltic.

F. Campichoetidae Eoc.(Priabonian)-Holocene

First: e.g. *Pareuthychaeta electrica* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Canthyloscelidae (Canthyloscelididae, Hyperoscelidae, Hyperoscelididae, Synneuridae) J2(Aalenian)-Holocene

First: *Prohyperoscelis jurassicus* in Evenhuis (1994), Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Carnidae Eoc.(Priabonian)-Holocene

First: e.g. *Meoneurites enigmatica* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Cecidomyiidae (Cecidomiidae, Lestremiidae) J3(Tithonian)-Holocene

First: *Catotricha mesozoica* in Jaschhof (2007), Glushkovo Formation (Daya), Daya, Transbaikalia, Russian Federation.

F. Ceratopogonidae (Leptoconopidae) K1(Hauterivian)-Holocene
Simulidium priscum from the Lulworth Formation belongs in Rhagionidae (Mostovski et al., 2003b).

First: *Minyohelea casca* Borkent, 1997, Austrian amber, Golling, Salzburg, Austria.

F. Chamaemyiidae Eoc.(Priabonian)-Holocene

First: *Procremifania electrica* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Chaoboridae (Chironomapteridae, Dixamimidae, Mesotendipedidae, Rhaetomyidae, Rhaetomyiidae) J1(Sinemurian)-Holocene

First: *Rhaetomyia necopinata* in Borkent (2008), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Chimeromyiidae Grimaldi & Cumming *in* Grimaldi et al., 2009 K1(Hauterivian)-K1(Albian)

First: *Chimeromyia reducta* in Grimaldi et al. (2009), Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

Last: e.g. *Chimeromyia burmitica* Grimaldi & Cumming *in* Grimaldi et al., 2009, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Chironomidae (Tendipedidae) T3(Rhaetian)-Holocene

First: *Aenne triassica* in Blagoderov et al. (2007), Cotham Member, Lilstock Formation, Penarth Group1, Strensham, Worcestershire, United Kingdom.

F. Chloropidae K1(Barremian)-Holocene

First: Mentioned in Solórzano Kraemer (2007), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Chyromyidae (Chyromyiidae) Eoc.(Priabonian)-Holocene

First: e.g. *Gephyromyiella electrica* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Clusiidae Eoc.(Priabonian)-Holocene

First: e.g. *Electroclusiodes meunieri* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Conopidae Eoc.(Ypresian)-Holocene

First: *Poliomyia recta* in Stuke (2003), Green River Formation (Wyoming), Unitas area, Wyoming, United States.

F. Corethrellidae K1(Barremian)-Holocene

First: *Corethrella cretacea* in Borkent (2008), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Cratomyiidae Mazzarolo and Amorim, 2000 K1(Aptian)
This could be a junior synonym of Zhangsolvidae (Willkommen and Grimaldi, 2007).

e.g. *Cratomyoides cretacicus* Wilkommen *in* Willkommen and Grimaldi, 2007, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Crosaphididae (Crosaphidae) T3(Carnian)-J3(Oxfordian)

First: e.g. *Crosaphis anomala* in Martin (2008), Mount Crosby Formation, Ipswich Basin, Queensland, Australia. (Jell, 2004 mistakenly lists this species under Aphididae.)

Last: Mentioned in Evenhuis (1994), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Cryptochetidae (Cryptochaetidae) Eoc.(Priabonian)-Holocene

First: *Phanerochaetum tuxeni* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Culicidae K1(Albian)-Holocene
Evenhuis (1994) lists seven doubtfully placed taxa from the Mesozoic of Germany and China, which are considered not to belong to this family by Poinar et al. (2000).

First: *Burmaculex antiquus* in Harbach (2007), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Curtonotidae Eoc.(Priabonian)-Holocene
Kirk-Spriggs (2007) removed "*Curtonotum*" *gigas* (Gypse d'Aix, France) from this family.

First: Mentioned in Haenni (2003), Baltic amber, Baltic, Baltic region, Baltic. (NOTE: Tentative identification.)

F. Cylindrotomidae Eoc.(Ypresian)-Holocene

First: e.g. *Cylindrotoma borealis* in Evenhuis (1994), Fur Formation (Mo Clay), Limfjord/Mors Peninsula/Fur Island, Jutland, Denmark.

F. Cypselosomatidae Eoc.(Priabonian)-Holocene

First: *Cypselosomatites succini* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Diadocidiidae K1(Albian)-Holocene

First: *Docidiadia burmitica* Blagoderov and Grimaldi, 2004, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Diopsidae Eoc.(Priabonian)-Holocene

First: e.g. *Prosphyracephala kerneggeri* Kotrba, 2009, Baltic amber, Baltic, Baltic region, Baltic.

F. Diplopolyneuridae J1(Sinemurian)
Krzemiński (1992) considered this to belong in Limoniidae but Evenhuis (1994) prefered to keep it separate, pending further study of the type species.

First and Last: *Diplopoyneura mirabilis* in Evenhuis (1994), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Ditomyiidae (Ditomyidae) Pal.(Thanetian)-Holocene

First: *Australosymmerus imperfecta* in Jell (2004), Redbank Plains Formation, Ipswich Basin, Queensland, Australia.

F. Dixidae J1(Sinemurian)-Holocene

First: *Syndixa? liasina* Lukashevitch, 1996, Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Dolichopodidae (Microphoridae) K1(Hauterivian)-Holocene

First: e.g. *Microphorites similis* Grimaldi and Cumming, 1999, Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

F. Drosophilidae Eoc.(Priabonian)-Holocene

First: e.g. *Electrophortica succini* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Dryomyzidae Eoc.(Priabonian)-Holocene

First: e.g. *Prodryomyza electrica* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Elliidae Krzemińska et al., 1993(Eliidae) J3(Oxfordian)-K1(Valanginian)

First: *Polyanka minuta* in Krzemiński and Evenhuis (2000), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Ellia colorissima* in Blagoderov et al. (2002), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Empididae (Protempididae) J3(Oxfordian)-Holocene
Some disagreement exists on whether or not to put Protempididae as a subfamily of Empididae but Mostovski (2009) keeps it here, although he does not mention the species.

First: e.g. *Protempis antennata* in Grimaldi and Engel (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Eoditomyidae (Eoditomyiidae) J1(Toarcian)
NOTE: Blagoderov and Grimaldi (2004) (p.3) mention this family as having a range from early Jurassic to early Cretaceous and cite Ansorge 1996. I don't have the original description to hand so can't check.

First and Last: *Eoditomyia primitiva* Ansorge, 1996a, Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

F. Eomyiidae J3(Oxfordian)-K2(Santonian)

First: *Eomyia veterrima* in Nagatomi and Yang (1998), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: Mentioned in Evenhuis (1994), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Eophlebomyiidae Eoc.(Ypresian)

First and Last: *Eophlebomyia claripennis* in Evenhuis (1994), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Eopolyneuridae J1(Sinemurian)

e.g. *Eopolyneura tenuinervis* in Evenhuis (1994), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Eostratiomyiidae J3(Oxfordian)

First and Last: *Eostratiomyia avia* in Mostovski et al. (2003a), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Ephydridae Eoc.(Priabonian)-Holocene

First: e.g. *Protoscinus perparvus* in Zlobin (2007), Bembridge Marls Insect Limestone, Gurnard/Thorness Bay, Isle of Wight, United Kingdom.

F. Eremochaetidae (Bremochaetidae) J3(Oxfordian)-K1(Aptian)

First: e.g. *Parеremochaetus minor* in Nagatomi and Yang (1998), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: e.g. *Alleremonomus liaoningensis* Ren and Guo, 1995, Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Gasterophilidae Eoc.(Ypresian)-Holocene
NOTE: Subfamily of Oestridae?

First: Mentioned in Rognes (1997), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Glossinidae Eoc.(Priabonian)-Holocene

First: e.g. *Glossina oligocena* in Grimaldi and Engel (2005), Florissant Formation, Florissant, Colorado, United States.

F. Gracilitipulidae Hong and Wang, 1990 K1(Barremian)
Blagoderov et al. (2002) note that a re-examination of the type material may result in synonymisation with Limoniidae, whereas Zhang (2006a) considers it could belong to the Chaoboridae.

First and Last: *Gracilitipula asiatica* in Evenhuis (1994), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Grauvogeliidae Krzemiński et al., 1994(Grauvogelidae) T2(Anisian)

e.g. *Louisa nova* in Blagoderov et al. (2007), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Heleomyzidae (Helomyzidae, Trixoscelidae, Trixoscelididae) Eoc.(Ypresian)-Holocene

First: *Heteromyza detecta* in Evenhuis (1994), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Hennigmatidae Shcherbakov *in* Shcherbakov et al., 1995(Hennigmoatidae, Kuperwoodiidae) T3(Carnian)-K1(Berriasian)
Although the Kuperwoodiinae Lukashevitch, 1995 was elevated to family status by Krzemiński and Krzemińska (2003), this was not accepted by Lukashevitch et al. (2006).

First: e.g. *Kuperwoodia benefica* in Blagoderov et al. (2007), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: *Hennigma cladistorum* in Lukashevitch et al. (2006), Tsagan-Tsab, Khutel-Kara, Dornogovi (East Gobi) Aimag, Mongolia.

F. Heterorhyphidae Ansorge and Krzemiński, 1995 J1(Toarcian)

e.g. *Heterorhyphus triangularis* in Krzemiński and Evenhuis (2000), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

F. Hilarimorphidae J3(Oxfordian)-Holocene

First: *Apystomima zaitzevi* in Grimaldi and Engel (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Hippoboscidae Olig.(Rupelian)-Holocene

First: Figured in Prokop and Fikaček (2007), Seifhennersdorf diatomite, Upper Lusatia, Free State of Saxony, Germany. (The family placement of this species is tentative.)

F. Hoffeinsmyiidae Michelsen, 2009 Eoc.(Priabonian)

First and Last: *Hoffeinsmyia enigmatica* Michelsen, 2009, Baltic amber, Baltic, Baltic region, Baltic.

F. Hongocaloneuridae Hong, 2002a Eoc.(Ypresian)

First and Last: *Hongocaloneura plectilis* in Zhang (2007b), Fushun amber, Guchengzi, Liaoning Province, China.

F. Huaxiasciaritidae Hong, 2002a Eoc.(Ypresian)

e.g. *Huaxiasciarites longus* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Hybotidae (Hybothidae) K1(Albian)-Holocene

First: e.g. *Alavesia prietoi* Peñalver and Arillo, 2007, El Caleyu amber, Ullaga Formation, central Asturian Depression, Asturias Province, Spain. (NOTE: *Alavesia* moved to Atelestidae in 2010 so ?*Meghyperus* sp. in Grimaldi et al. (2002), Burmese amber, will be the oldest.)

F. Hyperpolyneuridae J1(Sinemurian)

First and Last: *Hyperpolyneura phryganeoides* in Krzemiński (1992), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan. (NOTE: I haven't seen this paper but according to Sabrosky et al., 1999 the poor state of preservation prevented family placement of this species. Should it still be included?)

F. Ironomyiidae K1(Valanginian)-Holocene

First: e.g. *Hermaeomyia baisica* Mostovski, 1995, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Keroplatidae (Arachnocampidae, Macroceridae) K1(Berriasian)-Holocene

First: Mentioned in Jarzembowski and Coram (1996), Purbeck Limestone Group, Dorset, England, United Kingdom.

F. Kovalevisargidae Mostovski, 1997 J3(Oxfordian)

e.g. *Kovalevisargus clarigenus* Mostovski, 1997, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Lauxaniidae (Lausaniidae) Eoc.(Priabonian)-Holocene
Trypaneoides ellipticus from Fushun amber probably belongs in Dolichopodidae (Blagoderov et al., 2002).

First: e.g. *Chamaelauxania succini* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Limnorhyphidae J2(Callovian)

First and Last: *Limnorhyphus haifanggouensis* in Zhang (2007b), Haifanggou Formation, Beipiao, Liaoning Province, China.

F. Limoniidae (Archilimoniidae, Architipulidae, Eoasilidae, Gnomuscidae) T2(Anisian)-Holocene

First: *Archilimonia vegesiana* in Blagoderov et al. (2007), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

F. Lonchaeidae Mio.(Messinian)-Holocene

First: e.g. cf. *Dasiops* sp. in Grimaldi and Triplehorn (2008), Grubstake Formation, Suntrana Creek, Alaska, United States.

F. Lonchopteridae K1(Barremian)-Holocene

First: e.g. *Lonchopterites prisca* Grimaldi and Cumming, 1999, Bcharreh amber, Caza Bcharreh, Mouhafazet Loubnan Eshemali, Lebanon.

F. Luanpingitidae Zhang, 1986 J2(Callovian)

First and Last: *Luanpingites flavus* in Zhang (2002b), Xiahuayuan Formation, Luanping County, Hebei Province, China.

F. Lygistorrhinidae K1(Hauterivian)-Holocene

First: *Lebanognoriste prima* Blagoderov and Grimaldi, 2004, Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

F. Megamerinidae Eoc.(Priabonian)-Holocene

First: e.g. *Palaeotanypeza spinosa* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Mesosciophilidae J2(Aalenian)-K1(Aptian)

First: e.g. *Mesosciophilina irinae* in Li and Ren (2009), Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

Last: “*Pseudalysiinia*” *fragmenta* in Li and Ren (2009), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Micropezidae (Calobatidae) Eoc.(Priabonian)-Holocene

First: e.g. *Electrobata tertiaria* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Milichiidae (Milichidae, Phyllomyzidae) K2(Maastrichtian)-Holocene

First: Mentioned in Engel (2000), Kinkora amber, formation unknown, New Jersey, United States.

F. Muscidae Eoc.(Ypresian)-Holocene

First: *Acanthomyites aldrichi* in Evenhuis (1994), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Musidoromimidae J1(Sinemurian)

First and Last: *Musidoromima crassinervis* in Evenhuis (1994), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Mycetophilidae (Sciophilidae) K1(Valanginian)-Holocene
'*Prodocidia spectra*' Whalley, 1985 from the Lower Lias of Charmouth was moved to Ptychopteridae: Eoptychopterinae (Lukashevitch, 2000, 2008).

First: e.g. *Ipsaneusidalys communis* Blagoderov, 1998, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Mydidae (Mydaidae, Mydasidae) K1(Valanginian)-Holocene

First: Mentioned in Mostovski (2009), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Mythicomyiidae J2(Aalenian)-Holocene

First: *Palaeoplatypygus zaitzevi* in Evenhuis (2002), Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Nadipteridae Lukashevitch *in* Shcherbakov et al., 1995 T2(Anisian)-J1(Sinemurian)

First: *Tanus triassicus* in Blagoderov et al. (2007), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: *Nadiptera anachrona* in Krzemiński and Krzemińska (2003), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Natalimyzidae Barraclough and McAlpine, 2006 Eoc.(Priabonian)-Holocene

First: *Natalimyza* sp. in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Nemestrinidae J1(Toarcian)-Holocene

First: Mentioned in Grimaldi and Engel (2005), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

F. Neriidae Mio.(Aquitanian)-Holocene

First: Mentioned in Engel (2004a), Mexican amber, Simojovel, Chiapas, Mexico.

F. Neurochaetidae Eoc.(Priabonian)-Holocene

First: e.g. *Anthoclusia gephyrea* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Nymphomyiidae Eoc.(Priabonian)-Holocene

First: *Nymphomyia succina* Wagner et al., 2000, Baltic amber, Baltic, Baltic region, Baltic.

F. Odiniidae Eoc.(Priabonian)-Holocene

First: e.g. *Protodinia electrica* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Oestridae Eoc.(Ypresian)-Holocene

First: e.g. *Cuterebra ascarides* in Rognes (1997), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Oligophrynidae (Oligophryneidae) J1(Sinemurian)

e.g. *Oligophryne britannica* in Krzemiński and Ansorge (2005), Black Ven Marls, Charmouth, Dorset, United Kingdom.

F. Opetiidae K1(Berriasian)-Holocene

First: *Opetiala shatalkini* Coram et al., 2000, Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom. (Although Grimaldi and Engel, 2005 (p.533) suggest this species may be too primitive to be placed here, Mostovski, 2009 maintains it in Opetiidae.)

F. Opomyzidae Olig.(Chattian)-Holocene

First: e.g. *Opomyza pelidua* in Evenhuis (1994), Rott paper shales, Bonn, North Rhine-Westphalia, Germany.

F. Pachyneuridae (Cramptonomyiidae) J3(Oxfordian)-Holocene

First: e.g. *Tega karatavica* in Krzemiński and Evenhuis (2000), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Palaeophoridae (Paleophoridae) J3(Oxfordian)

First and Last: *Palaeophora ancestrix* in Mostovski (1999), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Pallopteridae Eoc.(Priabonian)-Holocene

First: e.g. *Glaesolonchea electrica* in Grimaldi and Triplehorn (2008), Baltic amber, Baltic, Baltic region, Baltic.

F. Parapleciidae J2(Callovian)

First and Last: *Paraplecia ovata* in Zhang (2002b), Haifanggou Formation, Beipiao, Liaoning Province, China.

F. Paraxymyiidae (Eomycetophilidae) T3(Carnian)-J3(Tithonian)
NOTE: Mentions of Cretaceous specimens are referring to the Glushkovo Fm., as some authors consider it J3/K1.

First: e.g. *Veriplecia rugosa* Blagoderov & Grimaldi *in* Blagoderov et al., 2007, Cow Branch Formation, Solite quarry, Virginia, United States.

Last: *Eomycetophila asymmetrica* in Blagoderov (1999), Glushkovo Formation (Daya), Daya, Transbaikalia, Russian Federation.

F. Pediciidae J2(Aalenian)-Holocene

First: *Praearchitipula notabilis* in Krzemiński and Evenhuis (2000), Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Periscelididae (Periscelidae, Stenomicridae) Eoc.(Priabonian)-Holocene

First: e.g. *Procyamops succini* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Perissommatidae J2(Aalenian)-Holocene

First: *Palaeoperissomma collessi* in Lukashevitch et al. (2006), Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Phoridae (Sciadoceridae) K1(Albian)-Holocene

First: e.g. *Euliphora grimaldii* in Delclòs et al. (2007), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Piophilidae Eoc.(Priabonian)-Holocene

First: *Mycetaulus incretus* in Meyer (2003), Florissant Formation, Florissant, Colorado, United States.

F. Pipunculidae K2(Campanian)-Holocene

First: Mentioned in Poinar and Poinar (2008), Canadian amber (Cedar Lake), Cedar Lake, Manitoba, Canada. (However this is not mentioned in McKellar et al., 2008.)

F. Platypezidae K1(Valanginian)-Holocene

First: e.g. *Proplatypeza parva* in Grimaldi and Cumming (1999), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Platystomatidae Pleist.(Upper Pleistocene)-Holocene

First: e.g. *Scholastes foordi* in Gentilini et al. (2006), Tanzanian copal, Tanzanian copal, Tanzanian copal, Tanzania.

F. Pleciodictyidae J1(Sinemurian)

First and Last: *Pleciodictya modesta* in Evenhuis (1994), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Pleciofungivoridae (Fungivoritidae) J1(Sinemurian)-J3(Tithonian)
NOTE: Allactoneuridae is not a junior synonym of this family according to Sabrosky et al. (1999) who state that "The family name was proposed in a work on fossils, to include four new genera of fossil Diptera, but the type genus was based on an extant species from Java. Later Rohdendorf referred the fossil genera to other families and thus confined Allactoneuridae to Recent Diptera."

First: e.g. *Archihesperinus phryneoides* in Evenhuis (1994), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

Last: e.g. *Bryanka lepida* in Evenhuis (1994), Glushkovo Formation (Daya), Daya, Transbaikalia, Russian Federation.

F. Procramptonomyiidae (Alinkidae) T3(Carnian)-K1(Berriasian)

First: e.g. *Yalea rectimedia* Blagoderov & Grimaldi *in* Blagoderov et al., 2007, Cow Branch Formation, Solite quarry, Virginia, United States.

Last: e.g. *Procramptonomyia zigzagensis* Coram and Jarzembowski, 1999, Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom.

F. Proneottiophilidae Eoc.(Priabonian)

e.g. *Proneottiophilum extinctum* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Prosechamyiidae Blagoderov et al., 2007 T3(Carnian)

e.g. *Prosechamyia trimedia* Blagoderov & Grimaldi *in* Blagoderov et al., 2007, Cow Branch Formation, Solite quarry, Virginia, United States.

F. Protapioceridae Ren, 1998 K1(Aptian)

e.g. *Protapiocera convergens* Zhang et al., 2007, Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Protendipedidae J3(Oxfordian)-K1(Hauterivian)

First: *Protendipes dasypterus* in Evenhuis (1994), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan. (Evenhuis, 1994 mistakenly states that this species was found in the Lower Jurassic of Issyk-Kul, Kyrgyzstan. Rohdendorf, 1991 lists it in Karatau as do Blagoderov et al., 2002.)

Last: *Priscotendipes mirus* in Zhang et al. (2010), Dabeigou Formation, Luanping County, Hebei Province, China.

F. Protobibionidae J3(Oxfordian)-K1(Barremian)
Usually considered to belong within Chironomidae, Evenhuis (1994) treats Protobibionidae as a separate family.

First: *Protobibio jurassicus* in Evenhuis (1994), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Protobibio orientalis* in Evenhuis (1994), Laiyang Formation, Laiyang County, Shandong Province, China. (Evenhuis, 1994 notes that this species requires additional study to confirm its generic placement.)

F. Protobrachyceridae (Protobrachycerontidae) J1(Toarcian)-J2(Callovian)

First: e.g. *Protobrachyceron zessini* in Zhang et al. (2008), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

Last: *Protobrachyceron sinensis* Zhang et al., 2008, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Protomphralidae J3(Oxfordian)
Nagatomi and Yang (1998) rejected *Mesomphrale asiaticum* from this family.

First and Last: *Protomphrale martynovi* in Nagatomi and Yang (1998), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Protopleciidae (Dyspolyneuridae, Palaeopleciidae, Phragmneuridae, Phragmoligoneuridae, Protoligoneuridae) J1(Sinemurian)-J3(Tithonian)
NOTE: Zhang (2007a) mentions that *Lichnoplecia kovalevi* is likely Protopleciidae but then leaves it in Bibionidae.

First: e.g. *Palaeoplecia rhaetica* in Zhang (2007a), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

Last: *Mesoplecia oleynikovi* in Zhang (2007a), Glushkovo Formation (Savina), Savina, Transbaikalia, Russian Federation.

F. Protorhyphidae (Vimrhyphidae) T2(Anisian)-J3(Tithonian)
NOTE: Grimaldi and Engel (2005) say range to Upper Cretaceous but I can't find any support for that.

First: *Vymrhyphus blagoderovi* in Martin (2008), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: *Protorhyphus major* in Zhang (2007b), Glushkovo Formation (Daya), Daya, Transbaikalia, Russian Federation.

F. Protoscatopsidae J2(Aalenian)-J3(Oxfordian)

First: *Mesoscatopse rohdendorfi* in Amorim (2008), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation.

Last: *Protoscatopse jurassica* in Amorim (2008), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Pseudopomyzidae Eoc.(Priabonian)-Holocene

First: e.g. *Eopseudopomyza kuehnei* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Psilidae Eoc.(Priabonian)-Holocene

First: e.g. *Electrochyliza succini* in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Psychodidae (Phlebotomidae) T3(Carnian)-Holocene

First: *Triassopsychoda olseni* Blagoderov & Grimaldi *in* Blagoderov et al., 2007, Cow Branch Formation, Solite quarry, Virginia, United States.

F. Psychotipidae Shcherbakov *in* Shcherbakov et al., 1995 T3(Carnian)
Elevated to family status by Krzemiński and Krzemińska (2003). Although *Psychotipa* was listed under Limoniidae by Blagoderov et al. (2007), this family has not been formally synonymised.

e.g. *Psychotipa predicta* in Krzemiński and Krzemińska (2003), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Ptychopteridae (Architendipedidae, Eolimnobiidae, Eoptychopteridae) J1(Sinemurian)-Holocene
The Family Eoptychopteridae was synonymised by Lukashevitch (2008). Lukashevitch (2008) doubts the assignment to this family of a specimen from the Triassic (Carnian) Cow Branch Formation, Virginia, USA.

First: e.g. *Eoptychoptera*? *spectra* in Lukashevitch (2000), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Pyrgotidae Eoc.(Priabonian)-Holocene

First: e.g. Mentioned in von Tschirnhaus and Hoffeins (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Rangomaramidae Jaschhof and Didham, 2002 Eoc.(Priabonian)-Holocene
Heterotricha was included in this family by Rindal (2007).

First: e.g. *Heterotricha hirta* in Chandler (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Rhaetaniidae Krzemiński and Krzemińska, 2002 T3(Rhaetian)

First and Last: *Rhaetania dianae* in Blagoderov et al. (2007), Cotham Member, Lilstock Formation, Penarth Group1, Strensham, Worcestershire, United Kingdom.

F. Rhagionemestriidae J3(Oxfordian)-K1(Barremian)

First: e.g. *Nagatommukha karabas* Mostovski and Martínez-Delclòs, 2000, Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Iberomosca kakoeima* Mostovski and Martínez-Delclòs, 2000, Montsec lithographic limestones, Montsec Range, Lleida Province, Spain.

F. Rhagionempididae J3(Oxfordian)-J3(Tithonian)
NOTE: There seems to be some confusion over whether this family is extant or not. Evenhuis makes it clear this is because of homonomy of an extant genus of Apsilocephalidae with the type genus of Rhagionempididae but later papers don't seem to have picked up on that. Specimens in Evenhuis listed as Middle Jurassic are from Uda Formation (Oxfordian).

First: e.g. *Probolbomyia modesta* in Mostovski (2009), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Shevioptera sinitsae* in Evenhuis (1994), Ukurey Formation (=Glushkovo?), Olov Depression, Transbaikalia, Russian Federation.

F. Rhagionidae (Palaeostratiomyidae, Palaeostratiomyiidae) J1(Pliensbachian)-Holocene
Blagoderov et al. (2007) do not consider the Middle Triassic species *Gallia alsatica* Krzemiński and Krzemińska, 2003 to belong to this family.

First: *Palaeobrachyceron nagatomii* in Nagatomi and Yang (1998), Abashevo Formation, Chernyi Etap, Kemerovo Region, Russian Federation.

F. Richardiidae Eoc.(Priabonian)-Holocene

First: e.g. *Pachysomites inermis* in Meyer (2003), Florissant Formation, Florissant, Colorado, United States.

F. Sarcophagidae Eoc.(Priabonian)-Holocene
NOTE: Zherikhin (2002c) mentions the "complete absense of fossil" Sarcophagidae.

First: Mentioned in Wichard and Weitschat (1996), Baltic amber, Baltic, Baltic region, Baltic.

F. Scathophagidae (Scatophagidae) Eoc.(Priabonian)-Holocene
Zherikhin (2002c) doubts the records of this family from the Baltic amber and Florrisant.

First: e.g. *Cordylura exhumata* in Meyer (2003), Baltic amber, Baltic, Baltic region, Baltic.

F. Scatopsidae K1(Barremian)-Holocene

First: Figured in Azar (2007), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Scenopinidae J3(Oxfordian)-Holocene

First: Mentioned in Mostovski (2009), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Sciaridae (Archizelmiridae, Sciaroidae) J3(Oxfordian)-Holocene

First: *Archizelmira kazachstanica* in Grimaldi et al. (2003), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Sciomyzidae K1(Barremian)-Holocene

First: e.g. Mentioned in Blagoderov and Martínez-Delclòs (2001), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain. (NOTE: Zherikhin, 2002c considers the family placement of these species as doubtful.)

F. Sepsidae Eoc.(Priabonian)-Holocene

First: e.g. *Themira saxifica* in Meyer (2003), Florissant Formation, Florissant, Colorado, United States.

F. Serendipidae Evenhuis, 1994(Paratendipedidae) K1(Barremian)

e.g. *Serendipa laiyangensis* in Brooks and Evenhuis (1995), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Siberhyphidae Kovalev *in* Kalugina and Kovalev, 1985(Syberhyphidae) J2(Aalenian)

First and Last: *Siberhyphus lebedevi* in Krzemiński and Evenhuis (2000), Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Simuliidae (Simulidae) J2(Aalenian)-Holocene

First: *Simulimima grandis* in Lukashevitch (2008), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation.

F. Sinoditomyiidae Hong, 2002a Eoc.(Ypresian)

e.g. *Sinoditomyia maculosa* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Sinonemestriidae Nagatomi and Yang, 1998 K1(Barremian)

First and Last: *Sinonemestrius tuanwangensis* in Nagatomi and Yang (1998), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Sinotendipedidae Hong and Wang, 1990(Sinotendipidae) K1(Barremian)

First and Last: *Sinotendipes tuanwangensis* in Evenhuis (1994), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Spaniidae K1(Albian)-Holocene

First: *Litoleptis fossilis* Arillo et al., 2009, San Just amber, Escucha Formation, Maestrat Basin, Teruel Province, Spain.

F. Sphaeroceridae (Borboridae) Eoc.(Priabonian)-Holocene

First: e.g. *Sphaerocera sepultula* in Evenhuis (1994), Bembridge Marls Insect Limestone, Gurnard/Thorness Bay, Isle of Wight, United Kingdom.

F. Stratiomyidae (Stratiomyiidae, Stratiomyriidae) J3(Oxfordian)-Holocene

First: Mentioned in Mostovski (2009), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Syringogastridae Mio.(Burdigalian)-Holocene

First: e.g. *Syringogaster miocenecus* Grimaldi *in* Marshall et al., 2009, Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Syrphidae K2(Santonian)-Holocene

First: Mentioned in Grimaldi and Engel (2005), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Tabanidae K1(Berriasian)-Holocene

First: *Eotabanoid lordi* Mostovski et al., 2003a, Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom.

F. Tachinidae Eoc.(Ypresian)-Holocene
NOTE: Zherikhin (2002c) considers Palaeogene finds "highly questionable" (p.384).

First: *Vinculomusca vinculata* in Rognes (1997), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Tanyderidae J1(Toarcian)-Holocene

First: e.g. *Nannotanyderus grimmenensis* Ansorge and Krzemiński, 2002, Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

F. Tanyderophrynidae (Tanyderophryneidae) J3(Oxfordian)

First and Last: *Tanyderophryne multinervis* in Evenhuis (1994), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Tephritidae Mio.(Burdigalian)-Holocene

First: e.g. *Ceratodaucus priscus* in Arillo and Ortuño (2005), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Tethepomyiidae Grimaldi and Arillo, 2008 K1(Albian)-K2(Turonian)

First: e.g. *Tethepomima holomma* Grimaldi and Arillo, 2008, Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

Last: *Tethepomyia thauma* in Grimaldi and Arillo (2008), New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Tethinidae Mio.(Aquitanian)-Holocene

First: Mentioned in Solórzano Kraemer (2007), Mexican amber, Simojovel, Chiapas, Mexico.

F. Thaumaleidae (Thaumalaeidae) J3(Tithonian)-Holocene

First: *Mesothaumalea fossilis* in Wagner et al. (2008), Glushkovo Formation (Daya), Daya, Transbaikalia, Russian Federation.

F. Therevidae J3(Oxfordian)-Holocene

First: *Rhagiophryne bianalis* in Mostovski (2009), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Tillyardipteridae Lukashevitch and Shcherbakov, 1999 T3(Carnian)

First and Last: *Tillyardiptera prima* in Blagoderov et al. (2007), Mount Crosby Formation, Ipswich Basin, Queensland, Australia.

F. Tipulidae K1(Albian)-Holocene
Considered here in the strict sense, not including Limoniidae or Cylindrotomidae.

First: e.g. Mentioned in Perrichot (2004), Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France. (It is not certain from the text if these specimens are Tipulidae *sensu stricto*.)

F. Tipulodictyidae J1(Sinemurian)

First and Last: *Tipulodictya minima* in Evenhuis (1994), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Tipulopleciidae J3(Oxfordian)

First and Last: *Tipuloplecia breviventris* in Evenhuis (1994), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Trichoceridae J1(Toarcian)-Holocene

First: e.g. *Mailotrichocera mikereichi* Krzemińska, Krzemiński & Ansorge *in* Krzemińska et al., 2009, Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Ulidiidae (Otitidae, Pterocallidae) Eoc.(Priabonian)-Holocene

First: e.g. *Melieria atavina* in Meyer (2003), Florissant Formation, Florissant, Colorado, United States.

F. Valeseguyidae Amorim and Grimaldi, 2006 K1(Albian)-Holocene

First: *Cretoseguya burmitica* Amorim and Grimaldi, 2006, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Vermileonidae J2(Aalenian)-Holocene
Protobrachyceron spp. (Toarcian, Grimmen) are in the Protobrachyceridae. See Krzemiński and Ansorge (2000) for details.

First: Mentioned in Evenhuis (1994), Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Vladipteridae Shcherbakov *in* Shcherbakov et al., 1995 T2(Ladinian)-T3(Norian)
Considered to be mecopteran by Krzemiński and Krzemińska (2003).

First: *Triassochoristites jinsuoguanensis* in Blagoderov et al. (2007), Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China. (This genus and species was originally described by Hong and Guo, 2003 in Mecoptera: Mesopanorpodidae.)

Last: *Vladiptera kovalevi* in Blagoderov et al. (2007), Tologoy Formation, Ak-Kolka River, Kenderlyk, Zaisan District, Kazakhstan.

F. Xylomyidae (Solvidae) J3(Oxfordian)-Holocene

First: *Xylomya? shcherbakovi* in Grimaldi and Engel (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Xylophagidae (Coenomyiidae, Rachiceridae) J3(Oxfordian)-Holocene

First: *Ganeopteromyia calypso* in Grimaldi and Engel (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Zhangobiidae Evenhuis, 1994(Palaeolimnobiidae) K1(Barremian)
Blagoderov et al. (2002) note that a re-examination of the type material may result in synonymisation with Limoniidae.

e.g. *Zhangobia laiyangensis* in Sabrosky et al. (1999), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Zhangsolvidae Nagatomi and Yang, 1998 K1(Barremian)

First and Last: *Zhangsolva cupressa* in Nagatomi and Yang (1998), Laiyang Formation, Laiyang County, Shandong Province, China.

O. Holometabola *incertae sedis* Jurassic(Sinemurian)-Jurassic(Oxfordian)

F. Dictyopdipteridae J1(Sinemurian)

e.g. *Dictyodiptera multinervis* in Carpenter (1992b), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Strashilidae Rasnitsyn, 1993a J3(Oxfordian)

First and Last: *Strashila incredibilis* in Grimaldi and Engel (2005), Bada (Zun-Nemetey) Formation, Mogzon, Transbaikalia, Russian Federation.

O. Hymenoptera Linnaeus, 1758 (Vespida) Triassic(Carnian)-Quaternary(Holocene)

F. Agaonidae (Agaontidae) Mio.(Burdigalian)-Holocene
"*Tetrapus*" *mayri* from the Florissant Formation does not belong in this family (Lopez-Vaamonde et al., 2009).

First: e.g. *Tetrapus delclosi* in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Ampulicidae K1(Barremian)-Holocene

First: Mentioned in Ohl (2004), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Anaxyelidae J2(Callovian)-Holocene

First: Mentioned in Ortega-Blanco et al. (2008), Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Andreneliidae Rasnitsyn and Martínez-Delclòs, 2000 K1(Barremian)

First and Last: *Andrenelia pinnata* in Zhang and Rasnitsyn (2008), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain.

F. Andrenidae Eoc.(Priabonian)-Holocene
Engel (2001) considered species attributed to this family from Florissant and the Baltic amber to be dubiously assigned and requiring further work.

First: e.g. *Libellulapis antiquorum* in Engel (2001), Florissant Formation, Florissant, Colorado, United States.

F. Angarosphecidae Rasnitsyn, 1975(Baissodidae) K1(Berriasian)-Eoc.(Ypresian)
Previously treated as a subfamily of Sphecidae *sensu lato* and represents a paraphyletic grade leading to other apoid families (Bennett and Engel, 2006).

First: e.g. *Pompilopterus wimbledoni* Rasnitsyn & Jarzembowski *in* Rasnitsyn et al., 1998, Lulworth Formation, Durlston Bay, Dorset, United Kingdom.

Last: *Eosphecium naumanni* Pulawski et al., 2000, coldwater beds of the Kamloops Group, Quilchena, British Columbia, Canada. (Bennett and Engel, 2006 consider that this species could be a plesiomorphic species of Sphecidae or Crabronidae.)

F. Aphelinidae Eoc.(Priabonian)-Holocene

First: Mentioned in Perkovsky et al. (2007), Rovno amber, Klesov/Dubrovitsa, Rivne Oblast, Ukraine.

F. Apidae (Anthophoridae, Bombidae, Ctenoplectridae, Xylocopidae) K1(Aptian)-Holocene
Ctenoplectra, the type genus of Ctenoplectrini, was previously placed in Mellitidae with *Ctenoplectrella*. However, *Ctenoplectrella* belongs in Apidae (Engel, 2001).

First: Figured in Osten (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Archaeocynipidae Rasnitsyn and Kovalev, 1988 K1(Valanginian)

e.g. *Archaeocynips villosa* Rasnitsyn and Kovalev, 1988, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Argidae Eoc.(Priabonian)-Holocene
An older fossil potentially of this family is *Manevalia pachyliformis* from the Thanetian of Menat, France, belonging either to Argidae or Pterygophoridae (Nel, 2004).

First: *Sterictiphora konowi* in Nel (2004), Florissant Formation, Florissant, Colorado, United States.

F. Armaniidae K1(Albian)-K2(Turonian)
The status of this taxon remains controversial. Some authors (e.g Archibald et al., 2006) consider it to be a subfamily of Formicidae.

First: e.g. *Khetania mandibulata* in Engel and Grimaldi (2005), Emanra Formation, Khetana River, Khabarovsk Province, Russian Federation.

Last: e.g. *Orapia minor* in Engel and Grimaldi (2005), Orapa diamond mines, Orapa, Orapa, Botswana.

F. Austroniidae (Trupochalcididae, Trupochalcidiidae) K1(Valanginian)-Holocene

First: Figured in Rasnitsyn (2002i), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Bethylidae K1(Valanginian)-Holocene

First: *Cretobethylellus lucidus* in Perrichot and Nel (2008a), Gidari (Ghidari) Formation, Pavlovka, Transbaikalia, Russian Federation.

F. Bethylonymidae J3(Oxfordian)-K2(Turonian)

First: e.g. *Bethylonymellus cervicalis* in Rasnitsyn (2002i), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: Mentioned in Brothers and Rasnitsyn (2003), Orapa diamond mines, Orapa, Orapa, Botswana.

F. Blasticotomidae Eoc.(Priabonian)-Holocene

First: *Paremphytus ostentus* in Shinohara (1983), Florissant Formation, Florissant, Colorado, United States.

F. Brachyceritidae Hong, 2002a Eoc.(Ypresian)

First and Last: *Brachycerites furvus* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Braconidae (Aphidiidae, Brachonidae, Branconidae, Eoichneumonidae) K1(Berriasian)-Holocene

First: e.g. *Purichneumon britannicus* in Perrichot et al. (2009), Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom.

F. Cephidae K1(Valanginian)-Holocene

First: *Mesocephus sibiricus* in Zherikhin (2002c), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Ceraphronidae K1(Barremian)-Holocene

First: Figured in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Chalcididae (Chalcidae) Eoc.(Priabonian)-Holocene
Heraty and Darling (2009) state that there are no Chalcididae known from the Cretaceous and that a specimen previously assigned to this family from the Lebanese amber belongs in Tetracampidae.

First: e.g. *Chalcis perdita* , Florissant Formation, Florissant, Colorado, United States.

F. Chrysididae K1(Hauterivian)-Holocene

First: *Dahurochrysis veta* in Ross and Jarzembowski (1993), Turga Formation, Turga River, near Borzai, Transbaikalia, Russian Federation.

F. Cimbicidae Pal.(Thanetian)-Holocene

First: *Cenocimbex menatensis* Nel, 2004, spongo-diatomaceous maar, Menat, Puy-de-Dôme, Auvergne, France.

F. Cleistogastridae (Brachycleistogastridae, Sinoryssidae) J2(Aalenian)-K2(Turonian)
The position of this family remains uncertain but is not placed in Megalyridae (Perrichot, 2009). "*Mesaulacinus*" *rasnitsyni* (Yixian Formation, Chengde) is considered Apocrita *incertae sedis* until re-study of the type specimen Rasnitsyn (2008).

First: *Cleistogaster buriatica* in Rasnitsyn et al. (2003), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation.

Last: Mentioned in Brothers and Rasnitsyn (2003), Orapa diamond mines, Orapa, Orapa, Botswana.

F. Colletidae (Stenotritidae) Mio.(Burdigalian)-Holocene

First: e.g. *Chilicola electrodominicana* in Arillo and Ortuño (2005), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Crabronidae (Astatidae, Larridae, Pemphredonidae, Philanthidae, Trypoxylidae) K1(Berriasian)-Holocene

First: *Iwestia provecta* Rasnitsyn & Jarzembowski *in* Rasnitsyn et al., 1998, Lulworth Formation, Durlston Bay, Dorset, United Kingdom. (Rasnitsyn et al., 1998 note that this specimen may lie close to Pemphredonina which here is considered in Crabronidae. The Catalog of Sphecidae [http://research.calacademy.org/ent/catalog_sphecidae] lists this specimen in Crabronidae.)

F. Cynipidae K2(Campanian)-Holocene

First: *Tanaoknemus ecarinatus* Liu & Engel *in* Liu et al., 2007b, Canadian amber (Medicine Hat), Medicine Hat, Alberta, Canada.

F. Daohugoidae Rasnitsyn and Zhang, 2004b J2(Callovian)

First and Last: *Daohugoa tobiasi* Rasnitsyn and Zhang, 2004b, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Diapriidae K1(Aptian)-Holocene
Cretacoformica explicata (Koonwarra fossil beds) and *Coramia minuta* (Durlstone Formation) do not belong to this family (Perrichot and Nel, 2008b).

First: *Cretapria tsukadai* in Perrichot and Nel (2008b), Choshi amber, Toriakeura Formation, Chiba, Japan.

F. Diprionidae Eoc.(Ypresian)-Holocene

First: Mentioned in Nel (2004), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Dryinidae K1(Barremian)-Holocene

First: *Aphelopus palaeophoenicius* in Engel (2003a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Electrotomidae Eoc.(Priabonian)

First and Last: *Electrotoma succini* in Zherikhin (2002c), Baltic amber, Baltic, Baltic region, Baltic.

F. Embolemidae K1(Valanginian)-Holocene

First: e.g. *Baissobius minimus* Rasnitsyn, 1996, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Encyrtidae Eoc.(Priabonian)-Holocene

First: e.g. *Eocencnemus vichrenkoi* Simutnik *in* Simutnik and Perkovsky, 2006, Rovno amber, Klesov/Dubrovitsa, Rivne Oblast, Ukraine.

F. Eostephanitidae Hong, 2002a Eoc.(Ypresian)

First and Last: *Eostephanites tenuis* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Ephialtitidae (Karataidae) J1(Toarcian)-K1(Aptian)

First: e.g. *Thilopterus lampei* Rasnitsyn et al., 2003, Upper Lias (Schandelah), Schandelah, Lower Saxony, Germany.

Last: *Cratephialtites kourios* in Osten (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Eucharitidae Eoc.(Priabonian)-Holocene

First: *Palaeocharis rex* Heraty and Darling, 2009, Baltic amber, Baltic, Baltic region, Baltic.

F. Eulophidae (Aphelidae) K1(Albian)-Holocene

First: Mentioned in Koteja and Poinar (2001), Alaskan amber, Kuk deposits, Brooks Range, Alaska, United States.

F. Eupelmidae K2(Campanian)-Holocene

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Eurytomidae Eoc.(Ypresian)-Holocene

First: e.g. *Eoeurytomites badius* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Evaniidae (Cretevaniidae) K1(Hauterivian)-Holocene

First: e.g. *Lebanevia azari* Basibuyuk et al., 2002, Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

F. Expansicornidae Hong, 2002a(Expansicornrdae) Eoc.(Ypresian)

First and Last: *Expansicornia conulata* Hong, 2002a, Fushun amber, Guchengzi, Liaoning Province, China.

F. Falsiformicidae (Falciformicidae) K1(Barremian)-K2(Cenomanian)

First: Mentioned in Rasnitsyn (2002i), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

Last: e.g. *Falsiformica cretacea* in Ross and Jarzembowski (1993), Agapa amber, Dolganian Formation, Nizhnyaya Agapa River, West Taimyr Peninsula, Siberian Federal District, Russian Federation.

F. Figitidae (Charipidae, Eucoilidae, Palaeocynipidae, Rasnicynipidae, 'Rasnitsyniidae') K2(Turonian)-Holocene

First: e.g. *Syneucoila magnifica* Liu & Engel *in* Liu et al., 2007b, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Formicidae (Dolichoderidae, Megapteritidae, Paleosminthuridae, Sphecomyrmidae) K1(Aptian)-Holocene

First: *Cariridris bipetiolata* in Osten (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Fushunochrysidae Hong, 2002b Eoc.(Ypresian)

First and Last: *Fushunochrysites eocenicus* Hong, 2002b, Fushun amber, Guchengzi, Liaoning Province, China.

F. Gallorommatidae Gibson et al., 2007 K1(Albian)-Eoc.(Priabonian)

First: e.g.? *Galloromma kachinensis* Engel and Grimaldi, 2007c, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

Last: *Galloromma agapa* in Gibson et al. (2007), Baltic amber, Baltic, Baltic region, Baltic. (Formerly *Palaeomymar apaga*, placed in Mymarommatidae.)

F. Gasteruptiidae (Aulacidae, Baissidae, Kotujellidae, Manlayidae) K1(Berriasian)-Holocene

First: e.g. *Manlaya anglica* in Zhang and Rasnitsyn (2004), Lulworth Formation, Durlston Bay, Dorset, United Kingdom. (Zhang and Rasnitsyn, 2008 do not mention this species.)

F. Gerocynipidae Liu & Engel *in* Liu et al., 2007b K2(Cenomanian)

e.g. *Gerocynips sibirica* in Liu et al. (2007b), Ola Formation, Obeshchayushchii Creek, Madagan Region, Russian Federation.

F. Halictidae (Rhophitidae) Eoc.(Ypresian)-Holocene
Cretaceous trace fossils previously attributed to Halictidae can not be placed so precisely to family, according to Engel and Archibald (2003).

First: *Halictus*? *savenyei* Engel and Archibald, 2003, coldwater beds of the Kamloops Group, Quilchena, British Columbia, Canada.

F. Heloridae J2(Callovian)-Holocene

First: Mentioned in Rasnitsyn and Zhang (2004a), Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Ibaliidae Eoc.(Priabonian)-Holocene

First: *Protoibalia connexiva* in Liu et al. (2007b), Florissant Formation, Florissant, Colorado, United States.

F. Ichneumonidae K1(Valanginian)-Holocene

First: e.g. *Palaeoichneumon freja* Kopylov, 2009, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Jurapriidae J3(Oxfordian)-K2(Turonian)

First: *Jurapria sibirica* in Rasnitsyn and Brothers (2007), Uda Formation, Uda River, Buryatia, Russian Federation.

Last: *Chalscelio orapa* Rasnitsyn and Brothers, 2007, Orapa diamond mines, Orapa, Orapa, Botswana.

F. Karatavitidae J1(Toarcian)-J3(Oxfordian)

First: *Grimmaratavites mirabilis* Rasnitsyn et al., 2006a, Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

Last: e.g. *Karatavites angustus* in Rasnitsyn and Zhang (2010), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Khutelchalcididae Rasnitsyn et al., 2004b K1(Berriasian)

First and Last: *Khutelchalcis gobiensis* Rasnitsyn et al., 2004b, Tsagan-Tsab, Khutel-Kara, Dornogovi (East Gobi) Aimag, Mongolia.

F. Leucospidae Mio.(Burdigalian)-Holocene

First: *Leucospis glaesaria* in Arillo and Ortuño (2005), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Limnetidae Hong, 1983 J2(Callovian)

First and Last: *Limnetus wangyingziensis* Hong, 1983, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Liopteridae K2(Campanian)-Holocene

First: e.g. *Proliopteron redactus* Liu & Engel *in* Liu et al., 2007b, Canadian amber (Medicine Hat), Medicine Hat, Alberta, Canada.

F. Maimetshidae (Maimetsheidae) K1(Barremian)-K2(Santonian)

First: *Andyrossia joyceae* in Rasnitsyn and Brothers (2009), Upper Weald Clay Formation (Capel), Capel, Surrey, United Kingdom.

Last: *Maimetsha artica* in Rasnitsyn and Brothers (2009), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Megachilidae Pal.(Thanetian)-Holocene

First: *Probombus hirsutus* in Michez et al. (2009), spongo-diatomaceous maar, Menat, Puy-de-Dôme, Auvergne, France.

F. Megalodontesidae (Megalodontidae) K1(Aptian)-Holocene

First: *Jibaissodes giganteus* in Blank et al. (2009), Yixian Formation (Chengde), Chengde, Hebei Province, China.

F. Megalyridae (Megaliridae) K1(Albian)-Holocene

First: e.g. *Valaa delclosi* Perrichot, 2009, Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Megaspilidae K1(Albian)-Holocene

First: Mentioned in Grimaldi et al. (2002), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Melittidae Eoc.(Ypresian)-Holocene

First: *Palaeomacropis eocenicus* Michez & Nel *in* Michez et al., 2007, Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Melittosphecidae Poinar and Danforth, 2006 K1(Albian)

First and Last: *Melittosphex burmensis* in Poinar (2009b), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Mesoserphidae J2(Callovian)-K1(Aptian)
NOTE: Rasnitsyn always gives this family a range into the Lower Jurassic in his hymenopteran range charts but I can't find any information on specimens from that age.

First: e.g. *Karatauserphus* sp. in Rasnitsyn and Zhang (2004a), Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

Last: Figured in Osten (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Monomachidae K1(Aptian)-Holocene

First: Mentioned in Rasnitsyn and Martínez-Delclòs (2000), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Mutillidae (Cretavidae) K2(Campanian)-Holocene
Brothers (2003) prefers not to include *Cretavus sibiricus* and several other fossils from this family, which would leave the earliest records as from the Priabonian Baltic amber.

First: *Cretavus sibiricus* in Manley and Poinar (2003), Kass suite, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Mymaridae K1(Barremian)-Holocene

First: Mentioned in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Mymarommatidae K1(Albian)-Holocene

First: e.g. Mentioned in Delclòs et al. (2007), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Ormyridae K2(Campanian)-Holocene

First: Mentioned in Gumovsky (2001), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada. (McKellar et al., 2008 do not list this family in Canadian amber.)

F. Orussidae K1(Albian)-Holocene

First: Mentioned in Delclòs et al. (2007), Álava amber, Escucha Formation, Basco-Cantabrian Basin, Álava Province, Spain.

F. Paleomelittidae Engel, 2001 Eoc.(Priabonian)

First and Last: *Paleomelitta nigripennis* Engel, 2001, Baltic amber, Baltic, Baltic region, Baltic.

F. Pamphiliidae (Pamphilidae) J2(Callovian)-Holocene
Mesolyda (*Pesarinia*) *rara* from the Middle Jurassic Jiulongshan Formation (Liaoning), China, more likely belongs in either Siricidae or Sepulcidae according to Blank et al. (2009).

First: Mentioned in Rasnitsyn and Zhang (2004a), Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China. (These specimens are not named as *Mesolyda rara*, so are unaffected by the comment above.)

F. Paroryssidae (Parorysidae) J3(Oxfordian)
The specimen figured by Rasnitsyn and Zhang (2004a) as Paroryssidae gen. et sp. nov. from the Callovian Daohugou beds was later described as *Praeparyssites orientalis* in Karatavitidae by Rasnitsyn et al. (2006a).

e.g. *Microryssus antennatus* in Vilhelmsen (2004), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Paxylommatidae K2(Campanian)-Holocene

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Pelecinidae (Iscopinidae, Pelecinopteridae) J2(Callovian)-Holocene

First: e.g. *Archaeopelecinus tebbei* Shih et al., 2009, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Peradeniidae Naumann and Masner, 1985 Eoc.(Priabonian)-Holocene

First: *Peradenia galerita* Johnson et al., 2001, Baltic amber, Baltic, Baltic region, Baltic.

F. Perilampidae Eoc.(Priabonian)-Holocene
Putative Perliampidae described by Hong (2002a) in Fushun amber are suspect in their placement and require further study, according to Heraty and Darling, 2009.

First: e.g. *Perilampus pisticus* Heraty and Darling, 2009, Baltic amber, Baltic, Baltic region, Baltic.

F. Platygastridae K2(Turonian)-Holocene

First: Mentioned in Rasnitsyn (2000b), New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Pompilidae K1(Albian)-Holocene
Pompilopterus ciliatus from the Lower Cretaceous Zaza Formation is an angarosphecid (Rasnitsyn et al., 1998; Engel and Grimaldi, 2006c).

First: *Bryopompilus interfector* Engel and Grimaldi, 2006c, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Praeaulacidae (Anomopterellidae) J2(Callovian)-K1(Aptian)

First: e.g. *Praeaulacus daohugouensis* Zhang and Rasnitsyn, 2008, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

Last: e.g. *Wesratia nana* in Zhang and Rasnitsyn (2008), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Praeichneumonidae K1(Berriasian)-K1(Aptian)

First: *Praeichneumon townesi* , Tsagan-Tsab, Khutel-Kara, Dornogovi (East Gobi) Aimag, Mongolia.

Last: *Scolichneumon rectivenius* in Ren (2002b), Yixian Formation (Chengde), Chengde, Hebei Province, China.

F. Praesiricidae J3(Oxfordian)-K1(Aptian)
NOTE: Using 2010 paper because it's easier. Doesn't change the range from pre-2010 literature as *Sinosepulca gigathoracalis* (Yixian Fm.) was placed in this family by Blank et al. (2009).

First: *Aulidontes mandibulatus* in Gao et al. (2010), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: e.g. *Rudisiricius belli* Gao et al., 2010, Dawangzhangzi beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Proctotrupidae (Proctitrupidae, Serphidae) K1(Berriasian)-Holocene

First: e.g. *Pallenites calcarius* Rasnitsyn & Jarzembowski *in* Rasnitsyn et al., 1998, Lulworth Formation, Durlston Bay, Dorset, United Kingdom.

F. Protimaspidae Liu & Engel *in* Liu et al., 2007b K2(Campanian)

First and Last: *Protimaspis costalis* in Liu et al. (2007b), Canadian amber (Cedar Lake), Cedar Lake, Manitoba, Canada.

F. Protosiricidae Rasnitsyn and Zhang, 2004a J1(Toarcian)-J3(Oxfordian)

First: *Liasirex sogdianus* in Sukatsheva and Rasnitsyn (2004), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan. (Family placement after Rasnitsyn and Zhang, 2004a.)

Last: e.g. *Protosirex xyelopterus* in Rasnitsyn (2006), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Pteromalidae (Cleonymidae) Eoc.(Priabonian)-Holocene
The fossils described as *Eopteromalites fushunensis*, *Leptogasterites brunneus* and *L. furvus* by Hong (2002a) belong in Scelionidae according to Johnson et al. (2008). NOTE: I can't find a Cretaceous record although Labandeira references Poinar 1992 (amber book) for Santonian. Looking at it on Google Books, I can only see it listed in Dominican and Mexican amber.

First: Figured in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Rhopalosomatidae K1(Albian)-Holocene
Engel (2008b) considers *Mesorhopalosoma cearae* from the Aptian Crato Formation (Brazil) not to show characters sufficient for a placement in Rhopalosomatidae but may represent a stem-group to this family. Osten (2007) considers it to belong to Angarosphecidae.

First: *Eorhopalosoma gorgyra* Engel, 2008b, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Roproniidae (Beipiaosiricidae) J2(Callovian)-Holocene

First: e.g. *Beipiaosirex parva* in Blank et al. (2009), Haifanggou Formation, Beipiao, Liaoning Province, China.

F. Sapygidae K1(Barremian)-Holocene

First: Mentioned in Peñalver et al. (1999), Montsec lithographic limestones, Montsec Range, Lleida Province, Spain. (Neither Bennett and Engel, 2005 or Osten, 2007 mention this occurrence.)

F. Scelionidae K1(Valanginian)-Holocene

First: Figured in Rasnitsyn (2002i), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Sclerogibbidae K1(Barremian)-Holocene

First: *Sclerogibbodes embioleia* Engel and Grimaldi, 2006b, Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Scolebythidae K1(Barremian)-Holocene

First: e.g. *Uliobythus terpsichore* Engel and Grimaldi, 2007a, Hammana/Mdeyrij amber, Caza Baabda, Mouhafazet Jabal Loubnan, Lebanon.

F. Scoliidae (Scolidae) K1(Barremian)-Holocene

First: e.g. *Cretoscolia conquensis* Rasnitsyn and Martínez-Delclòs, 2000, Calizas de la Huérguina Formation (Las Hoyas), Las Hoyas, Cuénca Province, Spain.

F. Sepulcidae (Parapamphiliidae) J1(Sinemurian)-K2(Cenomanian)

First: *Sogutia liassica* in Rasnitsyn et al. (2003), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

Last: *Prosyntexis okhotensis* Rasnitsyn, 1993b, Ola Formation, Obeshchayushchii Creek, Madagan Region, Russian Federation. (Originally described as *Trematothorax okhotensis*.)

F. Serphitidae K1(Albian)-K2(Campanian)

First: e.g. *Serphites* sp. in Rasnitsyn (2002i), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

Last: e.g. *Serphites doxus* in McKellar et al. (2008), Canadian amber (Cedar Lake), Cedar Lake, Manitoba, Canada.

F. Sierolomorphidae K1(Albian)-Holocene

First: Mentioned in Poinar and Poinar (2008), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Signiphoridae Eoc.(Priabonian)-Holocene

First: Mentioned in Perkovsky et al. (2003), Rovno amber, Klesov/Dubrovitsa, Rivne Oblast, Ukraine.

F. Siricidae (Gigasiricidae, Myrmiciidae, Pararchexyelidae, Pseudosiricidae, Sinosiricidae) J2(Callovian)-Holocene
Previous reports of this family in the Lower Jurassic of Kyrgyzstan were erroneous (Rasnitsyn and Zhang, 2004a).

First: e.g. *Gigasirex* spp. in Rasnitsyn and Zhang (2004a), Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Sphecidae Eoc.(Priabonian)-Holocene
According to the Catalog of Sphecidae (`http://research.calacademy.org/ent/catalog_sphecidae`), no fossils of Sphecidae *sensu stricto* older than that from the Florissant Formation have been found.

First: *Hoplisidea kohliana* in Menke and Rasnitsyn (1987), Florissant Formation, Florissant, Colorado, United States.

F. Stephanidae K2(Turonian)-Holocene
Chosia yamadai Fujiyama, 1994 is not a stephanid (see Engel and Grimaldi, 2004a).

First: *Archaeostephanus corae* Engel and Grimaldi, 2004a, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Stigmaphronidae K1(Valanginian)-K2(Campanian)

First: *Aphrostigmon vitimense* in Engel and Grimaldi (2009), Zaza Formation, Baissa, Buryatia, Russian Federation.

Last: *Tagsmiphron canadense* Engel and Grimaldi, 2009, Canadian amber (Cedar Lake), Cedar Lake, Manitoba, Canada.

F. Stolamissidae Liu & Engel *in* Liu et al., 2007b K2(Turonian)

First and Last: *Stolamissus mirabilis* Liu & Engel *in* Liu et al., 2007b, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Tanaostigmatidae Eoc.(Priabonian)-Holocene

First: *Leptoomus janzeni* Gibson, 2008, Baltic amber, Baltic, Baltic region, Baltic.

F. Tenthredinidae K1(Barremian)-Holocene

First: *Palaeathalia laiyangensis* in Nyman et al. (2006), Laiyang Formation, Laiyang County, Shandong Province, China.

F. Tetracampidae K1(Barremian)-Holocene

First: Mentioned in Heraty and Darling (2009), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon. (This specimen was previously referred to Chalcididae.)

F. Thysanidae Mio.(Aquitanian)-Holocene

First: Mentioned in Solórzano Kraemer (2007), Mexican amber, Simojovel, Chiapas, Mexico.

F. Tiphiidae (Methocidae, Tiphidae) K1(Aptian)-Holocene

First: *Architiphia rasnitsyni* in Engel et al. (2009b), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Torymidae K2(Campanian)-Holocene

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Trichogrammatidae Eoc.(Priabonian)-Holocene
Huber (2005) transferred the Canadian amber *Enneagmus pristinus* to Mymaridae. McKellar et al. (2008) appear not to have seen this and list it in Trichogrammatidae, citing only the original description by Yoshimoto (1975).

First: Mentioned in Perkovsky et al. (2007), Rovno amber, Klesov/Dubrovitsa, Rivne Oblast, Ukraine.

F. Trigonalidae K1(Albian)-Holocene
Nel et al. (2003b) remove all previously described Lower Cretaceous species from this family.

First: *Albiogonalys elongatus* Nel et al., 2003b, Archingeay amber, Archingeay-Les Nouillers, Charente-Maritime, France.

F. Vespidae (Eumenidae, Masaridae, Vespoidae) K1(Valanginian)-Holocene

First: e.g. *Curiosivespa antiqua* in Brothers and Rasnitsyn (2008), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Xyelidae T3(Carnian)-Holocene

First: e.g. *Archexyela ipswichensis* Engel, 2005b, Mount Crosby Formation, Ipswich Basin, Queensland, Australia.

F. Xyelotomidae J1(Toarcian)-K1(Aptian)
Nel et al. (2004b) consider this family to likely be paraphyletic.

First: *Pseudoxyelocerus bascharagensis* Nel et al., 2004b, Upper Lias (Luxembourg), Bascharage and Sanem, Luxembourg district, Luxembourg.

Last: e.g. *Synaptotoma limi* Gao et al., 2009, Dawangzhangzi beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Xyelydidae (Xyelididae) J1(Toarcian)-K1(Aptian)

First: e.g. *Sagulyda arcuata* in Rasnitsyn et al. (2006b), Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan.

Last: *Sinoprolyda meileyingensis* in Ross and Jarzembowski (1993), Jiufotang Formation, Beishan, Yixian County, Liaoning Province, China. (Rasnitsyn et al., 2006b do not mention this species.)

O. Lepidoptera Linnaeus, 1758 (Papilionida)
Jurassic(Sinemurian)-Quaternary(Holocene)

F. Acrolophidae Mio.(Burdigalian)-Holocene

First: *Acrolophus* sp. in Peñalver and Grimaldi (2006), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Adelidae Eoc.(Priabonian)-Holocene

First: *Adela kuznetzovi* in Fernández-Rubio (1999), Baltic amber, Baltic, Baltic region, Baltic.

F. Archaeolepidae J1(Sinemurian)

First and Last: *Archaeolepis mane* in de Jong (2007), Black Ven Marls, Charmouth, Dorset, United Kingdom.

F. Blastobasidae Mio.(Burdigalian)-Holocene

First: Mentioned in Peñalver and Grimaldi (2006), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Bucculatricidae K2(Turonian)-Holocene

First: *Bucculatrix platani* in Lopez-Vaamonde et al. (2006), Kzyl-Zhar, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Castniidae Eoc.(Priabonian)-Holocene

First: *Dominickus castnioides* in de Jong (2007), Florissant Formation, Florissant, Colorado, United States. (de Jong, 2007 expresses some doubt about the placement of this fossil.)

F. Coleophoridae (Coelophoridae) Eoc.(Ypresian)-Holocene

First: Figured (ichnofossil) in Labandeira (2002), Klondike Mountain Formation, Okanagan Highlands, Washington, United States.

F. Copromorphidae Eoc.(Priabonian)-Holocene

First: *Copromorpha fossilis* in Fernández-Rubio (1999), Bembridge Marls Insect Limestone, Gurnard/Thorness Bay, Isle of Wight, United Kingdom.

F. Cosmopterigidae (Cosmopterygidae, Walshiidae) Mio.(Aquitanian)-Holocene
NOTE: Might be one in Messel. See refs in Labandeira.

First: Mentioned in Grimaldi and Engel (2005), Mexican amber, Simojovel, Chiapas, Mexico.

F. Cossidae Eoc.(Priabonian)-Holocene

First: e.g. *Gurnetia durranti* in Fernández-Rubio (1999), Bembridge Marls Insect Limestone, Gurnard/Thorness Bay, Isle of Wight, United Kingdom.

F. Elachistidae (Ethmiidae) Eoc.(Priabonian)-Holocene

First: e.g. *Elachistites inclusus* in Fernández-Rubio (1999), Baltic amber, Baltic, Baltic region, Baltic.

F. Eolepidopterigidae J3(Oxfordian)-K1(Aptian)

First: e.g. *Eolepidopteryx jurassica* in Kozlov et al. (2002), Uda Formation, Uda River, Buryatia, Russian Federation.

Last: *Xena nana* in Bechly (2007a), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Eriocraniidae Eoc.(Priabonian)-Holocene
There is no body-fossil record of this family as '*Dyseriocrania*' *perveta* (Burmese amber) belongs in *Sabatinca* (Ross and York, 2000) and '*Electrocrania*' *immensipalpa* (Baltic amber) belongs in *Micropterix* (Kozlov, 1988) (both Micropterigidae).

First: Mentioned (mines) in Grimaldi and Engel (2005), Bembridge Marls Insect Limestone, Gurnard/Thorness Bay, Isle of Wight, United Kingdom.

F. Gelechiidae Eoc.(Ypresian)-Holocene

First: Mentioned in Brasero et al. (2009), Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Geometridae K2(Turonian)-Holocene

First: Figured in Harris and Raine (2002), Monro Conglomerate, Rakaia Gorge, Canterbury, New Zealand.

F. Gracillariidae (Phyllocnistidae) K2(Cenomanian)-Holocene

First: Mentioned (ichnofossil) in Kristensen et al. (2007), Dakota Formation, Rose Creek, Kansas, United States.

F. Heliodinidae Eoc.(Priabonian)-Holocene

First: *Baltonides roeselliformis* in Fernández-Rubio (1999), Baltic amber, Baltic, Baltic region, Baltic.

F. Heliozelidae Eoc.(Ypresian)-Holocene

First: Mentioned (mines) in Grimaldi and Engel (2005), Klondike Mountain Formation, Okanagan Highlands, Washington, United States.

F. Hepialidae Pal.(Thanetian)-Holocene

First: *Prohepialus incertus* in Fernández-Rubio (1999), spongo-diatomaceous maar, Menat, Puy-de-Dôme, Auvergne, France.

F. Hesperiidae Mio.(Aquitanian)-Holocene

First: *Pamphilites abdita* in Braby et al. (2005), Gypse d'Aix, Aix-Basin, Provence, France.

F. Incurvariidae K1(Barremian)-Holocene

First: *Incurvarites* sp. in Poinar and Milki (2001), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Lophocoronidae (Lophiocoronidae) K2(Santonian)-Holocene

First: Mentioned in Grimaldi (1999), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation. (Doubt exists as to the placement of this fossil according to Grimaldi, 1999.)

F. Lycaenidae Mio.(Aquitanian)-Holocene
Riodinella nympha (Green River Formation) and *Lithopsyche antiqua* (Bembridge Marls Insect Limestone) do not belong in this family but are unplaced within Rhopalocera (Hall et al., 2004).

First: *Aquisextana irenaei* in Braby et al. (2005), Gypse d'Aix, Aix-Basin, Provence, France.

F. Lyonetiidae (Prolyonetiidae) Eoc.(Priabonian)-Holocene

First: *Prolyonetia cockerelli* in Fernández-Rubio (1999), Baltic amber, Baltic, Baltic region, Baltic.

F. Micropterigidae (Micropterygidae) J3(Oxfordian)-Holocene

First: e.g.? *Aulipterix mirabilis* in Kozlov et al. (2002), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Mnesarchaeidae K2(Santonian)-Holocene

First: Mentioned in Kristensen and Skalski (1999), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Nepticulidae K2(Cenomanian)-Holocene
Grimaldi and Engel (2005) appear not to accept the placement of Jurassic trace fossils previously assigned to this family.

First: Mentioned (mines) in Grimaldi and Engel (2005), Dakota Formation, Rose Creek, Kansas, United States.

F. Noctuidae (Arctiidae, Ctenuchidae, Lymantriidae, Syntomidae) Olig.(Chattian)-Holocene
Placement of the fossil egg from the Campanian Magothy Formation, Massachusetts (Gáll and Tiffney, 1983) in Noctuoidea is highly doubtful (Kristensen and Skalski, 1999; Kozlov et al., 2002).

First: *Philodarchia cigana* in Grimaldi and Engel (2005), Tremembé Formation, Taubaté Basin, São Paulo, Brazil.

F. Notodontidae Mio.(Aquitanian)-Holocene

First: Mentioned in Kvaček et al. (2004), Most Formation, Bílina, Bohemia, Czech Republic.

F. Nymphalidae (Danaidae, Libytheidae, Satyridae) Eoc.(Ypresian)-Holocene

First: Mentioned in Peñalver and Grimaldi (2006), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Oecophoridae Eoc.(Ypresian)-Holocene

First: e.g. Mentioned in Brasero et al. (2009), Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Papilionidae Eoc.(Ypresian)-Holocene

First: e.g. *Praepapilio colorado* in de Jong (2007), Green River Formation (Colorado), Unitas area, Colorado, United States.

F. Pieridae Eoc.(Priabonian)-Holocene

First: *Stolopsyche libytheoides* in de Jong (2007), Florissant Formation, Florissant, Colorado, United States.

F. Plutellidae (Plutelidae) Eoc.(Priabonian)-Holocene

First: *Epinomeuta truncatipennella* in Fernández-Rubio (1999), Baltic amber, Baltic, Baltic region, Baltic.

F. Psychidae Eoc.(Priabonian)-Holocene

First: e.g. *Palaeopsyche secundum* Sobczyk and Kobbert, 2009, Baltic amber, Baltic, Baltic region, Baltic.

F. Pterophoridae Mio.(Aquitanian)-Holocene

First: *Pterophorus oligocenicus* in Fernández-Rubio (1999), Gypse d'Aix, Aix-Basin, Provence, France.

F. Pyralidae (Pyralididae) Eoc.(Priabonian)-Holocene
Possible earlier records of this family come from feeding traces from the Klondike Mountain Formation (Labandeira, 2002).

First: e.g. *Glendotricha olgae* in Fernández-Rubio (1999), Baltic amber, Baltic, Baltic region, Baltic.

F. Riodinidae Mio.(Burdigalian)-Holocene

First: *Voltina dramba* in Peñalver and Grimaldi (2006), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Sesiidae (Aegeriidae) Eoc.(Priabonian)-Holocene

First: Mentioned in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Sphingidae Eoc.(Priabonian)-Holocene

First: Mentioned in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Symmocidae Eoc.(Priabonian)-Holocene

First: *Oegoconiites borisjaki* in Poinar (1992), Baltic amber, Baltic, Baltic region, Baltic.

F. Thyrididae Eoc.(Priabonian)-Holocene
Hexerites primalis from the Green River Formation of Colorado does not belong in this family (Kristensen and Skalski, 1999).

First: Mentioned in Kristensen and Skalski (1999), Baltic amber, Baltic, Baltic region, Baltic.

F. Tineidae Eoc.(Ypresian)-Holocene

First: Mentioned in Brasero et al. (2009), Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Tortricidae Eoc.(Priabonian)-Holocene

First: e.g. *Tortricites skalskii* in Zherikhin (2002c), Baltic amber, Baltic, Baltic region, Baltic.

F. Undopterigidae (Undopterygidae) J3(Tithonian)-K1(Aptian)

First: *Undopterix sukatshevae* in Grimaldi and Engel (2005), Glushkovo Formation (Unda), Unda, Transbaikalia, Russian Federation.

Last: *Undopterix caririensis* in Bechly (2007a), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Xyloryctidae (Scythrididae) Eoc.(Priabonian)-Holocene
NOTE: *Oegoconiites* from the Baltic amber belongs to Symmocidae. There seems to be disagreement over whether *Scythropites balticella* belongs here or in Yponomeutidae, or if the species actually belongs in *Architinea* (Tineidae).

First: Mentioned in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Yponomeutidae (Argyresthiidae) Eoc.(Priabonian)-Holocene

First: Mentioned in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Zygaenidae Olig.(Rupelian)-Holocene

First: *Neurosymploca? oligocenica* Fernández-Rubio and Nel, 2000, Céreste, Lubéron, Alpes-de-Haute-Provence, France.

O. Mecoptera Packard, 1886 (Mecaptera, Nannomecoptera, Panorpida, Paramecoptera, Paratrichoptera) Carboniferous(Bashkirian)-Quaternary(Holocene)

F. Aneuretopsychidae Rasnitsyn and Kozlov, 1990(Aneuropsychidae) J3(Oxfordian)-K1(Barremian)

First: e.g. *Aneuretopsyche rostrata* in Labandeira et al. (2007), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

Last: *Jeholopsyche liaoningensis* Ren, Shih & Labandeira *in* Ren et al., 2009, Yixian Formation, Huangbanjiguo Village, Beipiao, Liaoning Province, China.

F. Anormochoristidae P1(Artinskian)

First and Last: *Anormochorista oligoclada* in Novokshonov (2004), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

F. Archipanorpidae T3(Carnian)

First and Last: *Archipanorpa magnifica* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Austropanorpidae (Austropanorpodidae) Pal.(Thanetian)
Novokshonov (2002a) tentatively places this family within Orthophlebiidae but Archibald (2005) mentions it as a separate family.

First and Last: *Austropanorpa australis* in Jell (2004), Redbank Plains Formation, Ipswich Basin, Queensland, Australia. (Jell, 2004 lists this species in Panorpidae.)

F. Belmontiidae (Parabelmontiidae) P3(Changhsingian) e.g. *Belmontia mitchelli* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Bittacidae J2(Callovian)-Holocene
Without the inclusion of Neorthophlebiidae, Bittacidae does not range down into the Upper Triassic as is often reported (e.g. Novokshonov, 2002a; Krzemiński, 2007).

First: e.g. *Formosibittacus macularis* Li et al., 2008, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Boreidae J3(Tithonian)-Holocene

First: *Palaeoboreus zherichini* in Grimaldi and Engel (2005), Ulan-Ereg, Khoutiyn-Khotgor, Dund-Gobi Aimag, Mongolia.

F. Choristidae K1(Aptian)-Holocene

First: *Cretacochorista parva* in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Cimbrophlebiidae J1(Toarcian)-Eoc.(Ypresian)
Novokshonov (2002a) considered this to be a junior synonym of Bittacidae, however Archibald (2009) maintains it as a sister group.

First: Mentioned in Archibald (2009), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

Last: e.g. *Cimbrophlebia brooksi* Archibald, 2009, Klondike Mountain Formation, Okanagan Highlands, Washington, United States.

F. Dinopanorpidae Pal.(Thanetian)-Olig.(Rupelian)

First: *Dinopanorpa* sp. in Archibald (2005), Tadushi Formation, Sikhote Alin Range, Primorye, Russian Federation.

Last: *Dinopanorpa megarche* in Archibald (2005), Khutsin Formation, Amgu (Amagu), Terney District, Primorye, Russian Federation.

F. Eomeropidae (Eomeropeidae, Notiothaumidae) J2(Callovian)-Holocene
The Triassic families formerly placed here are now considered to form the separate family Thaumatomeropidae (Novokshonov, 2002a; Archibald et al., 2005).

First: *Tsuchingothauma shihi* Ren and Shih, 2005, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Holcorpidae Eoc.(Priabonian)
NOTE: History of Insects tentatively places this in Orthophlebiidae but a 2010 paper keeps it separate and extends the range.

First and Last: *Holcorpa maculosa* in Grimaldi and Engel (2005), Florissant Formation, Florissant, Colorado, United States.

F. Kaltanidae (Cyclopteridae, Cyclopterinidae, Cycloristidae, Cycochoristidae) C2(Gzhelian)-K1(Valanginian)

First: e.g. Figured in Rasnitsyn et al. (2004a), Bursum Formation (Red Tanks Member), Carrizo Arroyo, New Mexico, United States. (These specimens may belong to a new family rather than Kaltanidae according to Rasnitsyn et al., 2004a, however Ren et al., 2009 [supporting online material] accept their placement here.)

Last: *Cretacechorista qilianshanensis* in Sun et al. (2007a), Chijinqiao (=Chijinpu) Formation, Xiagou, Jiuquan Basin, Gansu Province, China. (NOTE: I find this alarming. The next youngest is uppermost Permian. Grimaldi and Engel, 2005 show this family going extinct at the end Permian.)

F. Liassophilidae (Laurentipteridae, Pseudodipteridae) T2(Anisian)-J2(Aalenian)

First: *Laurentiptera gallica* in Krzemiński and Krzemińska (2003), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: e.g. *Ijapsyche sibirica* in Novokshonov (2002a), Cheremkhora Formation, Iya River, Irkutsk Region, Siberian Federal District, Russian Federation.

F. Meropeidae T2(Ladinian)-Holocene

First: *Sinothauma ladinica* Hong and Li, 2007, Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China.

F. Mesopanorpodidae P3(Wuchiapingian)-K1(Aptian)
Novokshonov (2002a) considered this a junior synonym of Permochoristidae but Hong (2007b) and Sun et al. (2007b) maintain it as a separate family.

First: e.g. *Prochoristella balgowanensis* van Dijk and Geertsema, 1999, Normandien (Estcourt) Formation, Beaufort Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: *Prochoristella leongatha* in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Mesopsychidae T3(Carnian)-K1(Barremian)

First: e.g. *Mesopsyche triareolata* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia.

Last: *Vitimopsyche kozlovi* Ren, Labandeira & Shih *in* Ren et al., 2009, Yixian Formation (Shimen), Shimen Village, Yangshulin Township, Hebei Province, China.

F. Muchoriidae Willmann, 1989(Munchoriidae) J2(Aalenian)

First and Last: *Muchoria reducta* in Willmann (1989), Ichetuy Formation, Novospasskoye, Mukhorshibirsky District, Buryatia, Russian Federation.

F. Nannochoristidae P3(Wuchiapingian)-Holocene
This family is treated as the separate order Nannomecoptera by Beutel and Baum, 2008.

First: *Neochoristella goodalli* van Dijk and Geertsema, 1999, Normandien (Estcourt) Formation, Beaufort Group, KwaZulu-Natal, Karoo Basin, South Africa.

F. Neorthophlebiidae T2(Ladinian)-J3(Tithonian)
Novokshonov (2002a) considered this a junior synonym of Bittacidae but Hong (2009b) maintains it as a separate family. *Yanorthophlebia hebeiensis* from the Lower Cretaceous Yixian formation was tranferred to *Liassochorista* (Permochoristidae) by Novokshonov (1997b).

First: e.g. *Ctenophlebia tongchuanensis* Hong, 2009b, Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China.

Last: *Neorthophlebia yunnanensis* Zhang & Hong *in* Zhang et al., 2003, Tuodian Formation, Lufeng, Yunnan Province, China.

F. Orthophlebiidae T2(Ladinian)-K1(Aptian)
Choristopanorpa drinnani from the Aptian Koonwarra Fossil Beds of Australia do not belong in this family according to Willmann and Novokshonov (1998) and was not included in the reclassification of fossil Orthophlebiidae by Hong and Zhang (2007).

First: e.g. *Protorthophlebia* (*Psomophlebia*) *curta* Hong, 2009b, Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China.

Last: *Neoparachorista clarkae* in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Panorpidae K1(Albian)-Holocene

First: *Solusipanorpa gibbdorsa* in Sun et al. (2007a), Chaochuan Formation, Zhuji, Zhejiang Province, China.

F. Panorpodidae Eoc.(Priabonian)-Holocene

First: e.g. *Panorpodes brevicauda* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Parachoristidae (Choristopanorpidae, Neoparachoristidae, Triassochoristidae) P2(Roadian)-K1(Aptian)
Parachorista uralensis from the Kungurian Koshelvka Formation was transferred to *Kamopanorpa* (Trichoptera: Microptysmatidae) by Novokshonov (1992).

First: *Parachorista opposita* , Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation. (NOTE: Can't find a reference for this yet.)

Last: e.g. *Choristopanorpa drinnani* in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia. (Jell, 2004 lists *Choristopanorpa* and *Neoparachorista* in Orthophlebiidae, where they were originally placed but have since been removed from and placed in Parachoristidae, according to the system in Novokshonov, 2002a..)

F. Permocentropidae P2(Roadian)

First and Last: *Permocentropus philopotamoides* in Novokshonov (2002a), Iva-Gora limestones, Soyana River, Arkhangelsk Region, Ural Mountains, Russian Federation. (NOTE: HoI doesn't mention the species name but does give the locality.)

F. Permochoristidae (Agetopanorpidae, Caenoptilonidae, Choristopsychidae, Eosetidae, Idelopanorpidae, Mesochoristidae, Petrochoristidae, Petromantidae, Protochoristidae, Protopanorpidae, Tychtodelopteridae, Tychtopsychidae, Xenochoristidae) P1(Artinskian)-K1(Aptian)
This concept of the family is probably paraphyletic, according to the findings of Ren et al. (2009).

First: e.g. *Protopanorpa permiana* in Beckemeyer and Hall (2007), Wellington Formation (KS), Elmo site, Dickinson County, Kansas, United States.

Last: *Prochoristella leongatha* in Jell (2004), Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria, Australia.

F. Permopanorpidae (Lithopanorpidae, Martynopanorpidae, Trachopterygidae) P1(Artinskian)-T3(Carnian)

First: e.g. *Permopanorpa inaequalis* in Beckemeyer and Hall (2007), Wellington Formation (OK), Midco, Oklahoma, United States.

Last: e.g. *Neopermopanorpa mesembria* in Jell (2004), Mount Crosby Formation, Ipswich Basin, Queensland, Australia.

F. Permotanyderidae P3(Changhsingian)
Jell (2004) lists *Mesotanyderus jonesi* from the Upper Triassic Mount Crosby Formation in this family but Carpenter (1992b) placed it in Mecoptera *incertae sedis* and Ren et al. (2009) show the family occurring only in the Upper Permian.

e.g. *Permotanyderus ableptus* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Permotipulidae P2(Wordian)-P3(Changhsingian)

First: *Permila borealis* in Krzemiński and Krzemińska (2003), Ilinskoe Formation, Suriyokova (Suriekova), Kemerovo Region, Russian Federation.

Last: *Permotipula patricia* in Jell (2004), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Protomeropidae (Marimerobiidae, Permomeropidae, Platychoristidae, Protomeropeidae) C2(Bashkirian)-P3(Changhsingian)
The ordinal placement of this family remains contentious (e.g. Nel et al., 2007a; Sukatsheva et al., 2007).

First: *Westphalomerope maryvonneae* Nel et al., 2007a, Veine Maroc, Faisceau de Modeste, Bruay-la-Bussière, Pas-de-Calais, France.

Last: e.g. *Permomerope australis* in Sukatsheva et al. (2007), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Pseudopolycentropodidae (Pseudopolycentropidae, Pseudopolycentropididae) T2(Anisian)-K1(Albian)

First: *Pseudopolycentropus triasicus* in Grimaldi et al. (2005a), Grès à Voltzia, Bas-Rhin/Moselle, Northern Vosges Mountains, France.

Last: e.g. *Parapolycentropus burmiticus* Grimaldi & Rasnitsyn *in* Grimaldi et al., 2005a, Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

F. Robinjohniidae P3(Changhsingian)
Novokshonov (2002a) mentions that a species of this family has been found in Krasnoyarsk Province of Siberia but does not give any further information.

First and Last: *Robinjohnia tillyardi* in Grimaldi and Engel (2005), Belmont insect beds, Newcastle Coal Measures, Belmont/Warner's Bay, New South Wales, Australia.

F. Sibiriothaumatidae Sukatsheva and Novokshonov, 1998 K1(Berriasian)

First and Last: *Sibiriothauma jakutensis* Sukatsheva and Novokshonov, 1998, Kempendyai locality, Suntar District, Sakha (Yakutia) Republic, Russian Federation.

F. Thaumatomeropidae (Thaumatomeropeidae) T3(Carnian)
Comprising the six species from the Madygen Formation formerly placed in Eomeropidae (Archibald et al., 2005).

e.g. *Thaumatomerope sogdiana* in Shcherbakov (2008b), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Tomiochoristidae P2(Roadian)-T2(Ladinian)
Novokshonov (2002a) considered this a junior synonym of Kaltanidae but Hong (2006) maintains it as a separate family.

First: e.g. *Tomiochorista minuta* in Hong (2006), Kuznetsk Formation (Mitino Horizon), Kaltan, Kemerovo Region, Russian Federation.

Last: e.g. *Glyptochorista martynovae* Hong, 2006, Tongchuan Formation, Hejiafang, Tongchuan District, Shaanxi Province, China.

F. Volitorididae (Voltidorididae) K1(Aptian)
NOTE: Should these synonyms be the other way around?

First and Last: *Volitoridia fulvis* in Sun et al. (2007a), Xiguayuan Formation, Fengning, Hebei Province, China.

O. Megaloptera Latreille, 1802 (Cordydalida)
Permian(Kungurian)-Quaternary(Holocene)

F. Corydalidae J3(Tithonian)-Holocene
NOTE: 2010 paper has in Daohugou.

First: Mentioned in Ponomarenko (2002b), Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Corydasialidae Wichard et al., 2005 Eoc.(Priabonian)

First and Last: *Corydasialis inexspectatus* Wichard et al., 2005, Baltic amber, Baltic, Baltic region, Baltic.

F. Euchauliodidae T3(Carnian)

First and Last: *Euchauliodes distinctus* in Wichard et al. (2005), Molteno Formation, KwaZulu-Natal, Karoo Basin, South Africa. (Ansorge (2001) suggested that this family may belong in Polyneoptera near to Grylloblattodea while Engel (2004b) suggested it could represent stem-group Corydalidae.)

F. Parasialidae P1(Kungurian)-P2(Capitanian)

First: *Parasialis rozhkovi* Novokshonov, 1994b, Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

Last: *Parasialis ovata* Ponomarenko, 2000a, Tsankhi (Tsankhin) Formation, Bor-Tolgoy, Ömnögovi (South Gobi) Aimag, Mongolia.

F. Sialidae (Dobbertiniidae) J1(Toarcian)-Holocene

First: *Dobbertinia reticulata* in Engel and Grimaldi (2008a), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

O. Neuroptera Linnaeus, 1758 (Myrmeleontida, Planipennia, Schwickertoptera) Permian(Artinskian)-Quaternary(Holocene)

F. Aetheogrammatidae Ren and Engel, 2008 K1(Aptian)

First and Last: *Aetheogramma speciosa* Ren and Engel, 2008, Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Araripeneuridae Martins-Neto, 2002 K1(Aptian)
Engel and Grimaldi (2008a) consider this to be a primitive subfamily of Myrmeleontidae. (NOTE: A 2010 paper keeps it separate.)

e.g. *Caririneura regia* in Martins-Neto et al. (2007c), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Archeosmylidae (Archaeosmylidae) P3(Wuchiapingian)-J1(Toarcian)
Engel and Grimaldi (2008a) place this family in Permithonidae but it is considered separate by Ponomarenko and Shcherbakov (2004) and Shcherbakov et al. (2009).

First: cf. *Archeosmylus* sp. in van Dijk and Geertsema (1999), Normandien (Estcourt) Formation, Beaufort Group, KwaZulu-Natal, Karoo Basin, South Africa.

Last: e.g. *Archeosmylus complexus* in Jarzembowski (1999), Upper Lias (Alderton), Alderton, Gloucestershire, United Kingdom.

F. Ascalaphidae K1(Aptian)-Holocene
Mesascalaphus from the Yixian Formation belongs in Mesochrysopidae (Makarkin and Menon, 2005; Ren and Makarkin, 2009).

First: *Cratoscalapha electroneura* in Martill et al. (2007), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Ascalochrysidae Ren and Makarkin, 2009 K1(Aptian)

First and Last: *Ascalochrysa megaptera* Ren and Makarkin, 2009, Jianshangou beds (Yixian), Yixian Formation, Liaoning Province, China.

F. Babinskaiidae Martins-Neto and Vulcano, 1989 K1(Valanginian)-K1(Aptian)

First: e.g. *Baisonelia vitimica* Ponomarenko, 1992, Zaza Formation, Baissa, Buryatia, Russian Federation.

Last: e.g. *Babinskaia pulchra* in Martins-Neto et al. (2007c), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Berothidae K1(Barremian)-Holocene

First: *Banoberotha enigmatica* in Engel and Grimaldi (2008a), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Brongniartiellidae J3(Tithonian)-K1(Valanginian)
Makarkin (2010) restricts the composition of this family to the type genus and *Pseudopsychopsis*. NOTE: It was just too big a pain not to use this paper and its system. The taxa were all over the place.

First: e.g. *Brongniartiella gigas* in Makarkin (2010), Solenhofen Lithographic Limestone, Solenhofen/Eichstadt, Bavaria, Germany.

Last: e.g. *Pseudopsychopsis gradata* Makarkin, 2010, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Chrysopidae (Limaiidae) J3(Oxfordian)-Holocene
Placement of Limaiidae within Chrysopidae after Ren and Makarkin (2009).

First: e.g. *Mesypochrysa latipennis* in Nel et al. (2005a), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Coniopterygidae J3(Oxfordian)-Holocene
Archiconiopteryx liasina from the Upper Lias of Mecklenburg is a hemipteran (see Ansorge, 1996a).

First: *Juraconiopteryx zherichini* in Engel and Grimaldi (2007b), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Dilaridae Eoc.(Priabonian)-Holocene

First: *Cascadilar eocenicus* in Engel and Grimaldi (2008a), Baltic amber, Baltic, Baltic region, Baltic.

F. Epigambriidae J1(Toarcian)
This family is considered valid by Engel and Grimaldi (2008a). Makarkin and Archibald (2003) consider the type genus to be Neuroptera *incertae sedis*.

First and Last: *Epigambria longipennis* in Makarkin and Archibald (2003), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Grammolingiidae Ren, 2002a J2(Callovian)

e.g. *Grammolingia boi* Ren, 2002a, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Hemerobiidae (Promegalomidae) J3(Oxfordian)-Holocene

First: *Promegalomus anomalus* in Engel and Grimaldi (2007b), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Ithonidae (Rapismatidae) K1(Barremian)-Holocene

First: *Principiala rudgwickensis* Jepson et al., 2009, Upper Weald Clay Formation (Rudgwick), Rudgwick Brickworks, near Horsham, West Sussex, United Kingdom.

F. Kalligrammatidae (Makarkiniidae) J1(Toarcian)-K1(Aptian)
Andersen2001b moved *Paractinophlebia* (Upper Lias, Alderton, Gloucestershire, England) to Prohemerobiidae.

First: Mentioned in Makarkin et al. (2009), Upper Lias (Kerkhofen), Kerkhofen, Bavaria, Germany.

Last: e.g. *Makarkinia adamsi* in Makarkin et al. (2009), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Mantispidae (Liassochrysidae, Liassochrysopidae) J1(Toarcian)-Holocene
Wedmann and Makarkin (2007) consider *Mantispidiptera* and *Whalfera* not to belong to this family.

First: *Liassochrysa stigmatica* in Wedmann and Makarkin (2007), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Mesithonidae J1(Toarcian)-K1(Valanginian)

First: *Sibithone prodroma* in Ansorge (1996a), Upper Lias (Grimmen), Grimmen, Mecklenburg-Vorpommern, Germany.

Last: e.g. *Mesithone angusta* Makarkin, 1999, Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Mesoberothidae (Proberothidae) T3(Carnian)
Jell (2004) was apparently unaware that *Proberotha* Riek, 1955 was a junior homonym of *Proberotha* Krüger,1923 and was replaced with *Mesoberotha* by Carpenter (1991).

e.g. *Mesoberotha superba* in Jell (2004), Mount Crosby Formation, Ipswich Basin, Queensland, Australia. (As *Proberotha*.)

F. Mesochrysopidae (Mesochrysopsidae) J1(Toarcian)-K1(Aptian)
Allopteridae and Tachinymphidae placed here after Makarkin and Menon (2005), Menon and Makarkin (2008) and Ren and Makarkin (2009).

First: *Protoaristenymphes bascharagensis* in Nel et al. (2005a), Upper Lias (Luxembourg), Bascharage and Sanem, Luxembourg district, Luxembourg.

Last: e.g. *Dryellina placida* Martins-Neto and Rodrigues, 2009, Crato Formation, Araripe Basin, Ceará, Brazil.

F. Myrmeleontidae (Myrmeleonidae, Myrmeliontidae) K1(Barremian)-Holocene

First: Mentioned in Engel and Grimaldi (2007b), Lebanese amber (unknown), unknown horizon, unknown locality, Lebanon.

F. Nemopteridae (Roeslerianidae) K1(Aptian)-Holocene

First: e.g. *Roesleria exotica* in Martins-Neto et al. (2007c), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Nevrorthidae (Neurorthidae) Eoc.(Priabonian)-Holocene
The placement in this family of a specimen in Burmese amber by Grimaldi et al. (2002) is not clear, according to Makarkin and Perkovsky (2009).

First: e.g. *Rophalis relicta* in Makarkin and Perkovsky (2009), Baltic amber, Baltic, Baltic region, Baltic.

F. Nymphidae (Nymphitidae) J2(Callovian)-Holocene
Epigambria, from the Lower Jurassic of Germany, is best considered as Neuroptera *incertae sedis* according to Makarkin and Archibald (2003). Engel and Grimaldi (2008a) list it in its own family in Neuropterida.

First: *Liminympha makarkini* Ren and Engel, 2007, Jiulongshan Formation, near Daohugou, Ningcheng county, Inner Mongolia, China.

F. Osmylidae (Epiosmylidae) J1(Sinemurian)-Holocene

First: e.g. *Sogjuta speciosa* in Makarkin and Archibald (2003), Dzhil Formation, Sogyuty, Issyk-Kul, Kyrgyzstan.

F. Osmylitidae J3(Oxfordian)-K1(Valanginian)
Makarkin and Archibald (2003) effectively disbanded the former concept of this family and suggested that the type species (*Osmylites excelsa*) could belong to a number of different families. Makarkin and Menon (2005) redefined the family as comprising *Chrysoleonites*, *Baissoleon* and *Osmylites* and considered it a monophyletic grouping separate from Mesochrysopidae, *contra* Ponomarenko (2003b). Similarly, Nel et al. (2005a) rejected the placement of *Osmylites* in Mesochrysopidae.

First: e.g. *Chrysoleonites intactus* in Makarkin and Menon (2005), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan. (NOTE: Species names not given.)

Last: *Baissoleon cretaceus* in Makarkin and Menon (2005), Zaza Formation, Baissa, Buryatia, Russian Federation. (NOTE: Species name not given.)

F. Osmylopsychopidae (Osmylopsychopsidae) T3(Carnian)-J1(Toarcian)
It is difficult to place *Glottopteryx multivenosa* between Osmylopsychopidae and Prohemerobiidae, so it remains *incertae sedis* (Makarkin and Archibald, 2005).

First: e.g. *Petropsychops superba* in Grimaldi and Engel (2005), Blackstone Formation, Ipswich Basin, Queensland, Australia.

Last: e.g. *Actinophlebia aenea* in Makarkin and Archibald (2005), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany. (NOTE: Species name not given, just genus placement.)

F. Palaeoleontidae Martins-Neto, 1992 K1(Aptian)-K2(Coniacian)
Engel and Grimaldi (2008a) consider this as the basalmost subfamily of Myrmeleontidae.

First: e.g. *Parapalaeoleon magnus* Menon and Makarkin, 2008, Crato Formation, Araripe Basin, Ceará, Brazil.

Last: *Metahemerobius kalligrammus* in Menon and Makarkin (2008), Antibes Formation, Antibes, Kemerovo Region, Russian Federation. (The age of this species is often cited as Maastrichtian-Danian, however the deposit it is from is Coniacian [V. A. Makarkin pers. comm. 2011].)

F. Panfiloviidae (Grammosmylidae, Panfilovidae) J3(Oxfordian)
Apart from the type genus, two other genera have been previously attributed to this family. *Makarkinia* is close to Kalligrammatidae and *Osmylogramma* belongs in some psychopsoid family (V. N. Makarkin pers. comm., 2011).

First and Last: *Panfilovia acuminata* in Makarkin and Archibald (2003), Karabastau Formation, Karatau Range, Tien Shan mountains, Kazakhstan.

F. Permithonidae (Palaemerobiidae, Parasisyridae, Permegalomidae, Permopsychopsidae, Permosisyridae, Sialidopseidae, Sialidopsidae) P1(Artinskian)-T1(Induan)
NOTE: Jepson and Penney (2007) give a range up to Tithonian (Solenhofen) based on a 1991 textbook by Kukalova-Peck. I can't check it now but Grimaldi and Engel (2005) only shows this family in the Permian. Depends partly on if you include Archeosmylidae.

First: e.g. *Permipsythone panfilovi* in Martins-Neto (2005), Irati Formation, Paraná Basin, São Paulo, Brazil.

Last: *Permantispa emelyanovi* Ponomarenko and Shcherbakov, 2004, Limptekon Formation, Tunguska Basin, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Polystoechotidae (Mesopolystoechotidae) T3(Carnian)-Holocene

First: e.g.? *Lithosmylidia lineata* in Engel and Grimaldi (2008a), Mount Crosby Formation, Ipswich Basin, Queensland, Australia.

F. Prohemerobiidae J1(Toarcian)
Prohemerobiidae is in need of revision (Makarkin and Menon, 2007) and is best to only include the type genus, pending revision (V. N. Makarkin, pers. comm. 2011).

e.g. *Prohemerobius dilaroides* in Makarkin and Menon (2007), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

F. Psychopsidae T3(Carnian)-Holocene

First: *Triassopsychops superba* in Engel and Grimaldi (2008a), Blackstone Formation, Ipswich Basin, Queensland, Australia.

F. Rafaeliidae (Rafaelidae) K1(Aptian)
Engel and Grimaldi (2008a) do not consider the order Schwickertoptera Bechly, 2008 to be valid and maintain the position of this family in Neuroptera.

e.g. *Rafaeliana maxima* in Nel et al. (2006), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Rhachiberothidae (Rachiberothidae) K1(Hauterivian)-Holocene

First: e.g. *Chimerhachiberotha acrasarii* Nel et al., 2005b, Jezzine amber, Jouar Ess-Souss, Mouhafazet Loubnan El-Janoubi, Lebanon.

F. Sisyridae Eoc.(Ypresian)-Holocene
Cratosisyrops gonzagi from the Aptian Crato Formation (Brazil) does not belong to this family (Nel et al., 2003a; Grimaldi and Engel, 2005).

First: *Paleosisyra eocenica* Nel et al., 2003a, Oise amber, Le Quesnoy, Houdancourt, Oise, Picardie, France.

F. Solenoptilidae J1(Toarcian)-Eoc.(Priabonian)
Makarkin (1998) restricted the composition of this family to the type species and tentatively *Oligogetes*.

First: *Solenoptilon kochi* in Makarkin and Archibald (2003), Upper Lias (Dobbertin), Dobbertin, Mecklenburg-Vorpommern, Germany.

Last: *Oligogetes relictum* Makarkin, 1998, Bol'shaya Svetlovodnaya (Biamo), Barachek Creek, Pozharsky District, Primorye, Russian Federation.

O. Raphidioptera Navás, 1916 (Raphidiida, Raphidiodea, Raphidioidea) Jurassic(Sinemurian)-Quaternary(Holocene)

F. Alloraphidiidae K1(Valanginian)-K2(Cenomanian)

First: e.g. *Alloraphidia asiatica* in Jepson and Jarzembowski (2008), Zaza Formation, Baissa, Buryatia, Russian Federation.

Last: *Alloraphidia dorfi* in Jepson and Jarzembowski (2008), Redmond Formation, Knob Lake District, Labrador, Canada.

F. Baissopteridae (Baissoraphidiidae) K1(Valanginian)-K1(Aptian)

First: e.g. *Baissoptera elongata* in Jepson and Jarzembowski (2008), Zaza Formation, Baissa, Buryatia, Russian Federation.

Last: e.g. *Baissoptera brasiliensis* in Jepson and Jarzembowski (2008), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Inocelliidae (Inocellidae) J2(Callovian)-Holocene

First: *Sinoinocellia liaoxiensis* in Jepson and Jarzembowski (2008), Haifanggou Formation, Beipiao, Liaoning Province, China. (Jepson and Jarzembowski (2008) list this species as Lower Cretaceous in age but the original description clearly attributes it to the Haifanggou Formation which is taken here to be Callovian.)

F. Mesoraphidiidae (Huaxiaraphidiidae, Jilinoraphidiidae, Mesoraphidae, Sinoraphidiidae) J1(Sinemurian)-K2(Campanian)

First: *Metaraphidia confusa* in Jepson and Jarzembowski (2008), Black Ven Marls, Charmouth, Dorset, United Kingdom.

Last: Figured in Engel and Grimaldi (2008a), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Priscaenigmatidae Engel, 2002(Eomantispidae) J1(Sinemurian)-J1(Toarcian)
Aspöck and Aspöck (2004) consider this family not to belong to this order, however Perrichot and Engel (2007) defend the placement.

First: *Priscaenigma obtusa* Whalley, 1985, Black Ven Marls, Charmouth, Dorset, United Kingdom.

Last: *Hondelagia reticulata* in Engel (2002), Upper Lias, Hondelage, Braunschweig, Lower Saxony, Germany.

F. Raphidiidae (Raphididae) K2(Campanian)-Holocene
Austroraphidia brasiliensis from the Crato Formation is now placed in Baissopteridae.

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

O. Siphonaptera Latreille, 1825 (Pulicida)
Palaeogene(Priabonian)-Quaternary(Holocene)

F. Ctenophthalmidae Eoc.(Priabonian)-Holocene

First: e.g. *Palaeopsylla baltica* in Whiting et al. (2008), Baltic amber, Baltic, Baltic region, Baltic.

F. Pulicidae Mio.(Burdigalian)-Holocene
The specimen figured as "Pulicid indet." by Jell (2004) is too fragmentary to identify, according to Grimaldi and Engel (2005).

First: *Pulex larimerius* Lewis and Grimaldi, 1997, Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Rhopalopsyllidae (Rhopallopsyllidae) Mio.(Burdigalian)-Holocene

First: *Rhopalopsyllus* sp. in Whiting et al. (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

O. Strepsiptera Kirby, 1815b (Stylopida) Cretaceous(Albian)-Quaternary(Holocene)

F. Bohartillidae Mio.(Burdigalian)-Holocene

First: e.g. *Bohartilla kinzelbachi* in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Elenchidae Mio.(Burdigalian)-Holocene

First: *Protelencholax schleei* in Pérez-Gelabert (2008), Dominican amber, Cordillera Septentrional, near Santiago, Dominican Republic.

F. Mengeidae K1(Albian)-Eoc.(Priabonian)
This family is likely paraphyletic (Grimaldi et al., 2005b).

First: Mentioned in Poinar and Poinar (2008), Burmese amber (Burmite), Hukawng Valley, Kachin State, Myanmar.

Last: e.g. *Mengea tertiaria* in Pohl et al. (2005), Baltic amber, Baltic, Baltic region, Baltic.

F. Myrmecolacidae Eoc.(Lutetian)-Holocene
Pseudococcites eocaenicus from the Eocene brown coal of the Geisel valley near Halle (Saale, Germany) is Strepsiptera *incertae sedis* (Pohl, 2009).

First: *Stichotrema* sp. in Grimaldi et al. (2005b), Messel Formation, Grube Messel, Hesse, Germany.

F. Protoxenidae Pohl et al., 2005 Eoc.(Priabonian)

First and Last: *Protoxenos janzeni* Pohl et al., 2005, Baltic amber, Baltic, Baltic region, Baltic.

F. Stylopidae Eoc.(Priabonian)-Holocene

First: *Jantarostylops kinzelbachi* in Grimaldi et al. (2005b), Baltic amber, Baltic, Baltic region, Baltic.

O. Trichoptera Kirby, 1815a (Phryganaeida, Phryganeida)
Permian(Sakmarian)-Quaternary(Holocene)

F. Baissoferidae J3(Oxfordian)-K1(Valanginian)

First: Mentioned in Ponomarenko et al. (2009), Uda Formation, Uda River, Buryatia, Russian Federation. (NOTE: This would be *Baissoferus udaensis* but they don't mention the genus or species.)

Last: e.g. *Baissoferus latus* in Ivanov and Sukatsheva (2002), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Beraeidae Eoc.(Priabonian)-Holocene

First: e.g. *Bereodes pectinatus* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic. (NOTE: Species name not given in ref. Two other species from Bembridge Marls exist but couldn't find good reference.)

F. Brachycentridae K1(Valanginian)-Holocene

First: *Baissoplectrum separatum* Ivanov, 2006, Zaza Formation, Baissa, Buryatia, Russian Federation. (Ponomarenko et al., 2009 express some doubt about the placement of this species in this family.)

F. Calamoceratidae J3(Tithonian)-Holocene

First: e.g. Mentioned in Ponomarenko et al. (2009), Doronino Formation, Chernovskie Kopi, Chita, Transbaikalia, Russian Federation.

F. Cladochoristidae P2(Wordian)-T3(Carnian)

First: *Cladochorista* sp. in Aristov and Bashkuev (2008), Chepanikha locality, Rossokha River valley, Zavjalovskii District, Udmurt Republic, Russian Federation.

Last: e.g. *Cladochorista multivenosa* in Ivanov and Sukatsheva (2002), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Dipseudopsidae K2(Turonian)-Holocene

First: e.g. *Phylocentropus swolenskyi* Wichard and Lüer, 2003, New Jersey amber, South Amboy Fire Clay (Raritan Formation), New Jersey, United States.

F. Dysoneuridae (Disoneuridae) J2(Aalenian)-K1(Berriasian)
NOTE: There might be younger in the Utan Formation but I can't find any age data other than Lower Cretaceous.

First: *Oncovena borealis* in Sukatsheva (2000), Itat Formation, Kubekovo, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

Last: e.g. *Palaeoludus popovi* Sukatsheva and Jarzembowski, 2001, Durlston Formation (Stair Hole Member), Durlston Bay, Dorset, United Kingdom.

F. Ecnomidae Eoc.(Priabonian)-Holocene

First: e.g. *Archaeotinodes igneusaper* Melnitsky, 2009, Baltic amber, Baltic, Baltic region, Baltic.

F. Electralbertidae K2(Campanian)

First and Last: *Electralberta cretacica* in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Glossosomatidae J3(Tithonian)-Holocene

First: *Dajella tenera* in Ivanov and Melnitsky (2006), Glushkovo Formation (Daya), Daya, Transbaikalia, Russian Federation.

F. Goeridae Eoc.(Priabonian)-Holocene

First: e.g. *Lithax herrlingi* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Helicophidae K1(Barremian)-Holocene

First: Figured in Sukatsheva and Jarzembowski (2001), Upper Weald Clay Formation (Capel), Capel, Surrey, United Kingdom. (This specimen was only tentatively placed in Helicophidae by Sukatsheva and Jarzembowski, 2001.)

F. Helicopsychidae Eoc.(Priabonian)-Holocene

First: e.g. *Electrohelicopsyche taeniata* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic.

F. Hydrobiosidae (Atopsychidae) J3(Tithonian)-Holocene

First: *Bullivena grandis* in Sukatsheva (2000), Shar-Teg Formation, Shar-Teg Ula, Gobi-Altai Aimag, Mongolia.

F. Hydropsychidae Eoc.(Priabonian)-Holocene

First: e.g. *Hydropsyche viduata* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic. (NOTE: Species name not given in ref.)

F. Hydroptilidae K1(Aptian)-Holocene

First: e.g. *Cratorella media* in Bechly (2007a), Crato Formation, Araripe Basin, Ceará, Brazil.

F. Lepidostomatidae K1(Barremian)-Holocene

First: *Eucrunoecia ridicula* Sukatsheva and Jarzembowski, 2001, Upper Weald Clay Formation (Capel), Capel, Surrey, United Kingdom.

F. Leptoceridae K1(Valanginian)-Holocene

First: *Creterotesis coprolithica* Ivanov, 2006, Zaza Formation, Baissa, Buryatia, Russian Federation. (Ponomarenko et al., 2009 express some doubt about the placement of this species in this family.)

F. Limnephilidae Eoc.(Priabonian)-Holocene

First: Mentioned in Ivanov and Sukatsheva (2002), Passamari Formation, Ruby River Basin, Montana, United States.

F. Microptysmatidae P1(Sakmarian)-P3(Changhsingian)

First: *Microptysmella moravica* in Zajíc and Štamberg (2004), Obora locality, Bačov Beds, Letovice Formation, Moravia, Czech Republic.

Last: e.g. *Kamopanorpa latipennata* Novokshonov, 1994a, Maichat/Ak-Kolka Formation, Karaungir River, Saur Mountains, Vostochno-Kazakhstanskaya oblast, Kazakhstan.

F. Molannidae Eoc.(Priabonian)-Holocene

First: e.g. *Molanna crassicornis* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic. (NOTE: Species name not given in ref.)

F. Necrotauliidae (Necrotaulidae) T3(Carnian)-K1(Valanginian)
This paraphyletic family is sometimes considered to be stem-Amphiesmenoptera (Ansorge, 2003b) or stem-Trichoptera (Grimaldi and Engel, 2005). NOTE: *Necrotaulius kritus* Lin 1986 is from the Cretaceous of south China somewhere and might be the last record. Can't find deposit info.

First: e.g. *Necrotaulius proximus* in Kozlov et al. (2002), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

Last: Mentioned in Ponomarenko et al. (2009), Zaza Formation, Baissa, Buryatia, Russian Federation.

F. Ningxiapsychidae Hong and Li, 2004 K1(Albian)

First and Last: *Ningxiapsyche fangi* Hong and Li, 2004, Naijiahe Formation, Liupanshan, Ningxia Province, China.

F. Odontoceridae (Odontoceratidae) K2(Santonian)-Holocene

First: Mentioned in Ivanov and Sukatsheva (2002), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Philopotamidae J1(Toarcian)-Holocene
The attribution to this family of *Prophilopotamus asiaticus* from the Madygen Formation is not well supported (Ivanov and Sukatsheva, 2002; Shcherbakov, 2008b), although it remains listed in this family by Wang et al. (2009d).

First: *Dolophilodes* (*Sortosella*) *shurabica* Sukatsheva *in* Sukatsheva and Rasnitsyn, 2004, Sagul Formation, Sai-Sagul, Batkenskii District, Kyrgyzstan.

F. Phryganeidae (Phryganaeidae) J3(Tithonian)-Holocene

First: e.g. Mentioned in Ponomarenko et al. (2009), Glushkovo Formation (Unda), Unda, Transbaikalia, Russian Federation.

F. Plectrotarsidae (Plectotarsidae) J3(Tithonian)-Holocene

First: e.g. Mentioned in Ponomarenko et al. (2009), Doronino Formation, Chernovskie Kopi, Chita, Transbaikalia, Russian Federation.

F. Polycentropodidae K1(Berriasian)-Holocene

First: e.g. Mentioned in Ponomarenko et al. (2009), Kempendyai locality, Suntar District, Sakha (Yakutia) Republic, Russian Federation.

F. Prorhyacophilidae T3(Carnian)

e.g. *Prorhyacophila furcata* in Ivanov and Sukatsheva (2002), Madygen Formation, Madygen/Dzhailoucho, south Fergana Valley, Kyrgyzstan.

F. Psychomyiidae (Psychomyidae) K2(Campanian)-Holocene

First: Mentioned in McKellar et al. (2008), Canadian amber (Grassy Lake), Grassy Lake, Alberta, Canada.

F. Rhyacophilidae J3(Oxfordian)-Holocene

First: Mentioned in Ponomarenko et al. (2009), Bada (Zun-Nemetey) Formation, Mogzon, Transbaikalia, Russian Federation.

F. Sericostomatidae K2(Santonian)-Holocene
Ivanov and Sukatsheva (2002) suggest that specimens from Bon-Tsagan could belong to this family, which would extend the record back to the Barremian.

First: Mentioned in Sinitshenkova (2002c), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Stenopsychidae Eoc.(Priabonian)-Holocene

First: *Stenopsyche initata* in Weitschat and Wichard (2002), Baltic amber, Baltic, Baltic region, Baltic. (NOTE: Species name not given in ref.)

F. Stereochoristidae T3(Carnian)

First and Last: *Stereochorista frustrata* in Jell (2004), Blackstone Formation, Ipswich Basin, Queensland, Australia. (Note that Carpenter, 1992b considered this genus unplaced within Neoptera.)

F. Taymyrelectronidae (Taimyrelectronidae) K2(Santonian)

First and Last: *Taymyrelectron sukatshevae* in Ross and Jarzembowski (1993), Yantardakh amber, Kheta Formation, Taimyr, Krasnoyarsk Krai, Siberian Federal District, Russian Federation.

F. Uraloptysmatidae Ivanov, 1992 P1(Kungurian)

First and Last: *Uraloptysma maculata* in Ivanov and Sukatsheva (2002), Koshelevka Formation, Tshekarda, Ural Mountains, Russian Federation.

F. Vitimotauliidae J3(Tithonian)-K2(Cenomanian)

First: e.g. *Multimodus* sp. in Ponomarenko et al. (2009), Ulan-Ereg, Khoutiyn-Khotgor, Dund-Gobi Aimag, Mongolia.

Last: *Multimodus bureensis* in Sinitshenkova (2002c), Kyndal Formation, Urgal River Basin, Far Eastern Federal District, Russian Federation.

F. Xiphocentronidae Mio.(Aquitanian)-Holocene

First: *Xiphocentron chiapasi* Wichard et al., 2006, Mexican amber, Simojovel, Chiapas, Mexico.

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