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TERTIARY GIANT LACEWINGS (NEUROPTERA: POLYSTOECHOTIDAE): REVISION AND DESCRIPTION OF NEW TAXA FROM WESTERN NORTH AMERICA AND DENMARK

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SYNOPSIS A preliminary definition of the Polystoechotidae (Insecta, Neuroptera) based on wing characters is provided. Tertiary Polystoechotidae are revised; the genus *Palaeopsychops* Andersen (10 species) and the new collective genus *Polystoechotites* gen. n. (6 species) are recognised. Ten new species (eight named) are described from the earliest Early Eocene Fur Formation (Denmark) and the Early to early Middle Eocene Okanagan Highlands (Quilchena and Horsefly River, British Columbia, Canada and Republic, Washington, USA): *Palaeopsychops quadratus* sp. nov. (Fur Formation); *Palaeopsychops setosus* sp. nov. (Horsefly River); *Palaeopsychops marringerae* sp. nov., *Palaeopsychops timmi* sp. nov., *Polystoechotites lewisi* gen. *et* sp. nov., *Polystoechotites barksdalae* gen. *et* sp. nov., *Polystoechotites falcatus* gen. *et* sp. nov. (Republic); *Palaeopsychops douglasae* sp. nov., *Polystoechotites* sp. A, *Polystoechotites* sp. B (Quilchena). *Polystoechotes piperatus* Cockerell from Late Eocene of Florissant (Colorado, USA) is assigned to *Polystoechotites*. Neuroptera *incertae sedis* sp. A (Republic) is determined as either an aberrant polystoechotid, or belonging to a family of psychopsid-like Neuroptera. *Palaeopsychops setosus* sp. nov. bears a dense cover of macrotrichia across a portion of the wing membrane, not previously known in the order. Extended floating time of polystoechotids increased negative taphonomic bias, in most depositional settings probably lowering their fossil assemblage representation. In some, taphonomic factors such as the presence of mat-forming organisms may have enhanced their fossil representation to greater than their community representation. This scenario is proposed for the Fur Formation, consistent with lithological evidence and palaeogeographic reconstruction. Dispersal of *Palaeopsychops* between Denmark and the Okanagan Highlands (direction unknown) was probably by the North Atlantic route, not before the late Palaeocene, during periods of continuous land connection between North America and northern Europe. Polystoechotidae in the Eocene, as today, appear to have ranged in forested regions of microthermal to lower mesothermal climate.

KEY WORDS fossil insects, Okanagan Highlands, Florissant, Fur Formation, zoogeography, taphonomy

Contents

INTRODUCTION

The relictual neuropteran insect family Polystoechotidae is now restricted to the Western Hemisphere (North America, Meso-America and south-western South America: Fig. 1) with only four extant species in three genera: *Polystoechotes punctatus* (Fabricius, 1793), *P. gazullai* Navás, 1924, *Fontecilla graphicus* Navás, 1932 and *Platystoechotes lineatus* Carpenter, 1940. This family is thought to be closely related to another relictual family, Ithonidae, together considered to be among the most morphologically primitive extant families of Neuroptera (Henry 1982; Tauber & Adams 1990; Aspöck 2002).

Fossils ascribed to this family have been reported from the Late Triassic to Early Cretaceous of Eurasia and Australia and from the Palaeogene of Europe and North America (see lists in Ren *et al*. 2002 and Makarkin & Archibald 2003). Preliminary revision of Mesozoic taxa, however, confidently includes only Asian occurrences in the family (see below).

The Tertiary fossil record of Polystoechotidae has been tentative until quite recently. *Polystoechotes piperatus* Cockerell, 1908, from the Late Eocene of Florissant, Colorado, was originally placed in the Hemerobiidae (*sensu lato*) (Cockerell 1908) and although later assigned to the Polystoechotidae by some authors (Cockerell 1913; Laurentiaux 1953), it was generally considered to be in the Psychopsidae in the second half of the Twentieth Century (Carpenter 1943; MacLeod 1970; Andersen 2001). Recently, Makarkin & Archibald (2003) suggested that it could still belong to the Polystoechotidae. The Tertiary fossil record of this family has only become well established in the last few years, with four new species of the genus *Palaeopsychops* Andersen,

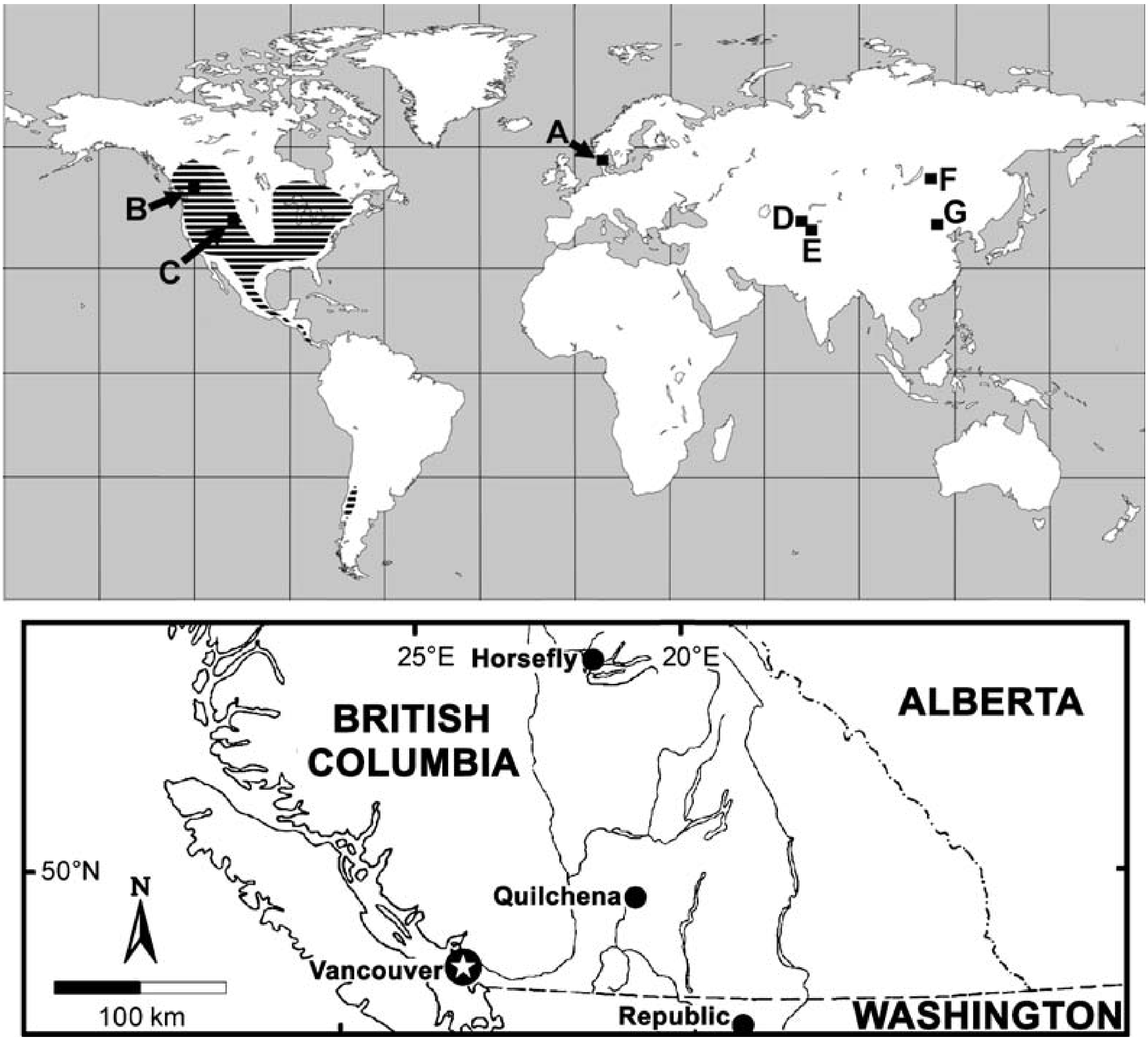

Figure 1 Present distribution and fossil record of the family Polystoechotidae. Modern distributions (approximate) are the crosshatched regions of North, Meso- and South America. Tertiary occurrences: **A**, Fur Formation (Denmark); **B**, Okanagan Highlands (see bottom map for individual localities: Republic (USA), Quilchena and Horsefly (Canada)); **C**, Florissant (USA). Mesozoic occurrences (those considered here to be most probable, see the text): **D**, Karatau (Kazakhstan), Late Jurassic; **E**, Shurab (Tajikistan), Early Jurassic; **F**, Baissa (Transbaikalia, Russia), Early Cretaceous; **G**, Daohugou (Inner Mongolia, China), Middle Jurassic.

2001 being described from the 'Mo-clay' of Denmark and another example of this genus from the Okanagan Highlands locality of Quilchena, British Columbia, Canada (Andersen 2001; Makarkin & Archibald 2003).

In this paper we provide a preliminary definition of the family based on wing characters, revise the Tertiary Polystoechotidae, summarise the available data on their biogeography and ecology and discuss the possible taphonomic biases affecting members of the family as well as the dispersal scenarios of *Palaeopsychops*. Understanding the relationship of the Danish species of *Palaeopsychops* (Andersen 2001) with those of North America has been hindered by significant errors and omissions in their original descriptions (see Makarkin & Archibald 2003). Therefore, we have re-examined their type material, redescribe them here and, consequently, establish one new Danish species. We further describe nine new polystoechotid species from three Okanagan Highlands localities: Quilchena and Horsefly River, British Columbia, Canada and Republic, Washington, USA. We place four of these in *Palaeopsychops*; for five we propose the new collective genus *Polystoechotites* gen. nov., in which we also place *Polystoechotes piperatus*. The remaining specimens examined are too incomplete to determine below family or order level.

MATERIAL AND METHODS

Material examined

This study is based on the examination of 26 impression fossil specimens of Polystoechotidae (and Neuroptera *incertae sedis*) from the following fossil collections: **AMNH** the

American Museum of Natural History, New York, NY, USA; **GMUC** the Geological Museum, University of Copenhagen, Denmark; **GZG**, Geowissenschaftliches Zentrum der Universität Göttingen, Museum, Sammlungen & Geopark, Göttingen, Germany; **SCSU**, St. Cloud State University, St. Cloud, Minnesota, USA; **SFU**, Simon Fraser University, Burnaby, British Columbia, Canada; **SR**, the Stonerose Interpretive Center, Republic, Washington, USA; **UA**, University of Alberta, Edmonton, Alberta, Canada. Danekræ are designated Danish national heritage objects (here borrowed from the GMUC).

Okanagan Highlands specimens were collected using light hand tools and prepared, when necessary, with pins and similar tools. In some Okanagan Highlands specimens, chemical interactions between the matrix and particular wing pigments during diagenesis have resulted in the matrix removing cleanly from wing areas of dark colouration, but adhering to areas known from other specimens to be light fascia or dots (e.g. see Fig. 13A, SR97-08-05). This has been noted in other taxa (e.g. Mecoptera: Archibald 2005). The matrix from each site containing these fossils (Okanagan Highlands, Florissant and Denmark) is briefly described below (see Ecology and Distribution and Taphonomy, sections, below).

Because of differences in preservation quality, crossveins are not equally visible or interpretable in the examined specimens, particularly in the radial area. Line drawings of wing venation interpret crossvenation conservatively, which may result in an underestimation of the actual number of crossveins present in some wings.

Polystoechotidae reported here from the Okanagan Highlands are almost all preserved as isolated wings (11 out of 14), which are mostly at least somewhat damaged, indicating support for increased floating time (see taphonomy, below), or alternatively, damage by transport or other physical disturbance between death and deposition such as consumption of the body by scavengers (fish, birds, amphibians or other insects). These specimens include six isolated fore-wings, two isolated hind-wings, three isolated wings not determinable and three wings with at least parts of other wings. Three complete insects were reported from the Fur Formation by Andersen (2001), although they are somewhat damaged or poorly preserved. The 31 additional specimens he examined were all reported to be fore-wings (Andersen 2001): of these we re-examined 10 specimens and found nine fore-wings and one hind-wing (the holotype of *P. maculatus*). Fore- and hind-wings are easily distinguished by character states listed below in the description of Polystoechotidae. The single Florissant specimen is a fore-wing. The reason for this discrepancy in fore- and hind-wing representation is not known.

Illustrations

Digital photography was carried out using a JVC 3-CCD camera adapted to interface with Auto-Montage version 4.0 (Syncroscopy 2002) (MCZ) and with a Nikon Coolpix 9500 (GMUC: Figs 5C, 6A–B, 10A–C, E). A small amount of distilled water or alcohol was added to some fossils at times during drawing and photography. Drawings were produced directly from the specimens using a camera lucida attachment on a Leica MZ7.5 microscope, except figures 10D and 23D, which were drawn from photographs. Dotted lines in drawings indicate faintly seen morphology, dashed lines indicate folds, creases, or the edge of missing or obscured regions. There is no representation of hypothesised missing morphology.

Taxonomic approach

Genus-level

Difficulties in defining Tertiary genera of Polystoechotidae, represented mainly by isolated wings (see above), include factors particular to this family, beyond the problems in taxonomic determination that are general to palaeontology resulting from incomplete, damaged and poorly preserved specimens. Most individual character states of wing venation and shape are widely spread in various combinations among the polystoechotid genera and are also found outside the family. In *Platystoechotes*, for example, the lack of distal fusion in Sc and R1, by which the wings of this genus may be easily separated from those of other polystoechotid genera, is a plesiomorphic trait found elsewhere within the order Neuroptera; a costal gradate series of crossveins in the fore-wing, a further characteristic of this genus, also occurs in some Eocene *Palaeopsychops* species, as well as in other distantly related families (Hemerobiidae, Permithonidae and many others). Fossil genera of this family (including *Palaeopsychops*) described from wings alone may be defined only by a *combination* of characters; the more characters that are used in such a definition, the less likely all of them are to be preserved on a given fossil.

Given the difficulties presented by these fossils, we recognise here only one orthotaxon of generic rank of Tertiary Polystoechotidae that we find to be well-diagnosable, *Palaeopsychops* (orthotaxa and parataxa as defined by Rasnitsyn 1996). While we are aware of the possibility that the species placed here within it may represent more than one genus; only future, more complete fossils can provide the evidence necessary to more conclusively demonstrate this.

For the other species described and revised here, which lack sufficient preserved characters to conform with or define such a diagnosis, we employ parataxonomy in generic placement (see Taylor 1964; Rasnitsyn 1986, 1996; Dlussky & Rasnitsyn 2002). This system allows the naming and grouping of taxa (of organisms or works produced by them) into parataxa, artificial groups where the phylogenetic positions of included taxa are undeterminable at that level (e.g. larval forms, fossil woods, ichnofossils), thereby avoiding the need to shoehorn fossils into orthotaxa (terminology as in Rasnitsyn 1996). In many cases parataxa act as holding bins until better-preserved and more complete specimens can confirm or refute the sometimes strong supposition as to their orthotaxonomic determination. Rasnitsyn (1986) defined three types of parataxa: the formal taxon, the taxon *incertae sedis* and the collective group, of which we employ the latter two.

Species-level

The primary difficulty in species assignment in these fossils is one often encountered in palaeoentomology: that of determining conspecific isolated fore- and hind-wings. Only in several of the Fur Formation specimens are fore- and hind-wings found articulated (fragments are associated in some Okanagan Highlands specimens) and only in the one articulated specimen examined by us (paratype 1 of *P. abruptus*) are the fore- and hind-wing characters somewhat clearly preserved (see Fig. 8). Andersen (2001) mentions three complete specimens of Danish *Palaeopsychops*, the other two are:

paratype 6 of *P. latifasciatus*, in which the venation and colour patterning are indistinctly preserved and a specimen too poorly preserved to assign to species, in which the wings are folded completely over each other (Andersen 2001: fig. 8). Thus, apart from the evidence provided by the partially known fore- and hind-wings of *P. abruptus*, it is not possible at present to associate 'hind-wing species' with 'fore-wing species' apart from general judgements of size and shape and we recognise the possibility that some of these 'hind-wing species' may be synonyms of 'fore-wing species.' A conservative species-count, therefore, includes only those with known fore-wings.

Upon re-examination of the Danish *Palaeopsychops* species, we find some character states considered diagnostic by Andersen (2001) to be invalid (e.g. the veins MP and CuA do not converge distally and fuse into a short vein in *P. maculatus*). Within the 11 fore-wing specimens that we examined, wing colour patterning, however, falls into discrete and distinctive groups (although the patterning of *P. latifasciatus* and *P. abruptus* is rather similar, these species are separable by venational characters). Therefore, we consider colour patterning a valid and useful diagnostic character as employed by Andersen (2001) and apply it as well to diagnoses here. This character is particularly useful as it is invariably preserved in known specimens both in Denmark and North America.

Terminology and abbreviations

Here we follow Comstock's (1918) venational terminology, with a few exceptions in accordance with current usage in neuropterology (e.g. Comstock's M_{1+2} is our MA, Cu_1 is CuA) and in the naming of Rs branches. For all neuropteran families Comstock (1918) named the most proximal branch of Rs as R5, followed by R4, R3 and then with either one (R2a) or many (R2a, d, c,), accessory branches with R2 being the most distal branch. This method of naming Rs branches is problematic, however, in those neuropteran families (including Polystoechotidae) whose species have variable (unstable) venation; therefore, here we designate the most proximal branch Rs1, next Rs2, etc. Other wing terminology (e.g. spaces) follows Oswald (1998). Venation abbreviations used are as follows: 1A-3A, anal veins; CuA, anterior cubitus; CuP, posterior cubitus; hv, humeral veinlet; MA, MP, anterior and posterior branches of media (M); n, distal nygma; R1, first branch of radius; Rs, radial sector; Rs1, most proximal branch of Rs; Sc, subcosta.

Abbreviations for climatic terms are: MAT, mean annual temperature; CMMT, coldest month mean temperature; PETM, Palaeocene–Eocene Thermal Maximum. As the MAT categories 'temperate', 'subtropical' and 'tropical' are somewhat conflated with modern-world latitudinal identities often not applicable to the Palaeogene (e.g. 'tropical' implies a geographical region as well as a particular range of MAT), we use Wolfe's (1979) terminology: microthermal, MAT <13°C; mesothermal, MAT >13°C, <20°C; megathermal, MAT >20°C. Abbreviations for palaeoclimate determination methodologies: NLR, nearest living relative; LMA, leaf margin analysis; CLAMP, Climate–Leaf Analysis Multivariate Program.

Although the term 'Tertiary' is no longer recognised as a formal unit of time (International Commission on Stratigraphy 2004), we use it here informally, as we do terms such as 'Early Eocene' and 'early Middle Eocene' in order to facilitate the flow of the text, recognising that 'Palaeogene and Neogene (part)', 'Ypresian' and 'Lutetian' will be understood by these terms, respectively.

ECOLOGY AND DISTRIBUTION

Extant

The family Polystoechotidae is currently distributed in parts of both the Nearctic and Neotropical regions, typically associated with forests of microthermal to lower mesothermal climate (Fig. 1). Microhabitat preferences have not been established.

Polystoechotes punctatus is the most widely ranging of the four extant species, known from cool-temperate regions of both southern Canada (British Columbia, Alberta, Ontario and Quebec) and the United States (in mountainous regions in the south, but absent in the prairies) (Banks 1905). This region includes a variety of forest types, from the Eastern Deciduous zone through the coniferous forests of the west. It is currently most common in the Mixed Coniferous forests of the northwestern United States, where it may be locally abundant (Banks 1905; Carpenter 1940; Penny 2002). *Polystoechotes punctatus* appears to be 'less common now that it formerly was in Wisconsin' (Throne 1971: 86) and 'in the past half century it appears to have disappeared from much of its former range in temperate North America, including all of the eastern USA and Canada' (Penny 2002: 290). Its range extends into Mexico, Costa Rica and Panama (Penny 2002) where it inhabits forests of high mountain chains, characteristically at 1500 m at Monteverde, Costa Rica (Penny 2002). Low-latitude montane regions may be inhabited by a mixed 'tropical-temperate' insect assemblage, where cool upland MAT is combined with low temperature seasonality (Archibald & Farrell 2003).

Platystoechotes lineatus is only reported from mid to high elevation (600–2700 m) forests of the Sierra Nevada Mountains in California and is (or was) locally common, e.g. in Sequoia National Park (Carpenter 1940).

The remaining two species, *Polystoechotes gazullai* and *Fontecilla graphicus*, occur in the forests of Central Chile (Navás 1932; Oswald 1998). Similarly, the Cenozoic distribution of the mecopteran family Eomeropidae in the Western Hemisphere includes the Okanagan Highlands and Florissant in the Eocene (but also Pacific Russia) and Central Chile at the present (Archibald *et al.* 2005).

Tertiary

The Tertiary record of the family is exclusively from the Eocene of western North America and northern Europe (Fig. 2); it is not known at present from other Tertiary localities containing rich insect assemblages, e.g. the Green River Formation (western USA), Baltic Amber, Dominican Amber. Like extant members of the family, Eocene Polystoechotidae are known from microthermal to mid-mesothermal forests (but the climatic parameters of the Fur Formation insects' source habitat are unresolved).

Florissant

Insect fossils at the Florissant National Monument and surrounding region are found in Late Eocene lacustrine shale units of the Florissant Formation. Fossils have been known at Florissant since the mid-1800s, with insects receiving a large

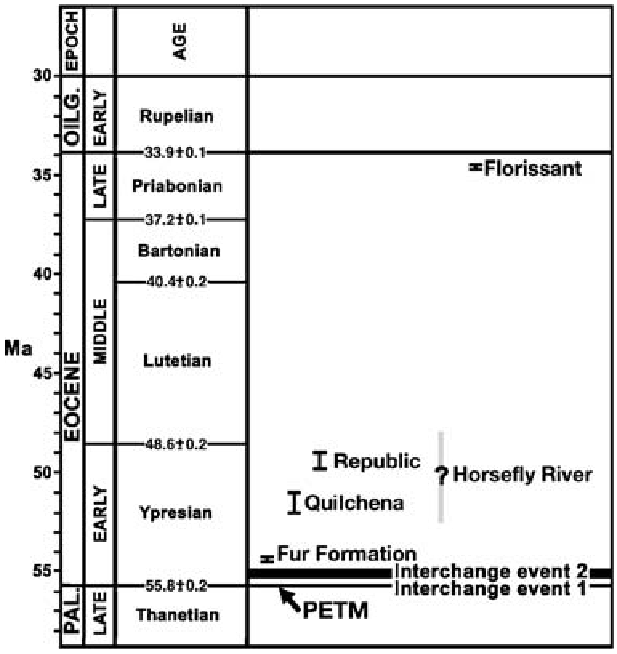

Figure 2 Stratigraphic position of Eocene Polystoechotidae-bearing deposits. Interchange events 1 and 2 are intercontinental mammalian dispersal events between Europe and North America (from Woodburne & Swisher 1995), see the text. **PETM**, Palaeocene/Eocene Thermal Maximum.

amount of attention, particularly at the end of the 19th century by Samuel Scudder and in the first half of the 20th century by Theodore Cockerell. A general review of the geology, biota and history of work at Florissant was recently provided by Meyer (2003). The Florissant Formation is dated Late Eocene at 34.07 ± 0.10 Ma by ^{40}Ar–^{39}Ar decay (Evanoff *et al.* 2001).

The flora of the Florissant montane forest was recently revised by Manchester (2001). It was dominated by a species of the extinct fagaceous genus *Fagopsis*, with *Cedrelospermum*, *Chamaecyparis*, *Typha* and *Populus* also being common. MAT is estimated as a lower mesothermal ∼13–14°C by CLAMP (Gregory & McIntosh 1996), or mid-mesothermal ∼17°C by NLR (Leopold & Clay-Poole 2001). The presence of frost-intolerant taxa such as palms indicates mild winters (Gregory & McIntosh 1996; Leopold & Clay-Poole 2001).

Denmark

The Danish insects discussed here are from the marine Fur Formation, about 50-60 m of diatomite and tephra layers, which, with the Ølst Formation, constitute the Mo-clay in the northern Jutland region (Larsson 1975; Pedersen & Surlyk 1983; Heilmann-Clausen *et al.* 1985). The depositional environment was in the Palaeocene–Eocene precursor of the North Sea, which was an almost or entirely enclosed inland body, open to the Atlantic at least at times (Bonde 1997). Insects have been known from the Mo-clay since 1798 (Rust 1999); Larsson (1975) reported 1802 Mo-clay insect fossils catalogued while a little over two decades later, Rust (1999) reported over 20 000 collected.

The Fur Formation Polystoechotidae are earliest Early Eocene in age. Volcanic ash layers within the Mo-clay have been numbered from −39 (lowest) to +140 (highest) (Larsson 1975). An Early Eocene age of 54.04 ± 0.14 Ma has been determined for layer +19 and 54.52 ± 0.05 Ma for layer −17 by the Ar^{40}–Ar^{39} method (Chambers *et al.* 2003). The Palaeocene–Eocene boundary it is now defined as coincident with the beginning of the carbon isotope (δ^{13}C) excursion (CIE) at 55.8 ± 0.2 Ma (Aubry *et al.* 2003; Schmitz *et al.* 2004). A δ^{13}C spike is found below the Fur Formation in the basal ∼15 m of the Ølst Formation, which Heilmann-Clausen & Schmitz (2000) suggested could represent this event; Schmitz *et al.* (2004) do determine this as the CIE and find, therefore, that the Palaeocene–Eocene boundary lies at (or very close to) the base of the Ølst Formation. Polystoechotidae discussed here were recovered from laminated carbonate concretions above the CIE and the dated tephra layers, between layers +25 and +30 in the 'upper insect level' (Andersen 2001).

The Fur Formation megaflora is reviewed in Larsson (1975), but apparently remains largely understudied. Fur Formation palynology has focussed mostly on marine microplankton for biostratigraphical zonation; a recent study of the terrestrial microflora also concentrated on biostratigraphy (Willumsen 2004).

Henriksen (1922: 36) reported of the insect assemblage that 'all of these forms unmistakably point to a tropical climate. . .' based on the presence of thermophilic taxa, many of whose nearest living relatives are found in the East Indies (see also Rust 1999). Isotope analysis (δ^{18}O/δ^{16}O) of mollusc shells indicated North Sea sea-surface palaeotemperatures at Fur Formation time as having a roughly low-megathermal MAT (Buchardt 1978: fig. 2). This probably reflects coastal temperatures, as sea-surface MAT tracks sea level terrestrial MAT quite closely (Greenwood & Wing 1995). The marine depositional environment of the Fur Formation presents problems, however, for characterisation of the environments of these strongly allochthonous plants (micro- and megaflora) and insects. They were transported from source habitats that we model to have been between an undetermined distance to the north, to regional of their depositional location in Denmark, supported by palaeogeographical reconstructions of North Sea volcanic ash and diatomite deposition (see, Taphonomy, below). Furthermore, the presence of thermophilic insects may indicate raised CMMT, not high MAT there (Archibald & Farrell 2003; Greenwood *et al.* 2005). The climatic parameters of the source habitat of the polystoechotids, therefore, remains unresolved.

Okanagan Highlands

The three North American localities bearing the new species reported here are among the Okanagan Highlands series of Early to early Middle Eocene fossiliferous coal (at times amber bearing) and lacustrine shale deposits that extend about 1000 km from Republic, Washington, USA, through south-central British Columbia, Canada to the northern-most locality at Driftwood Canyon (see Fig. 1). This was an upland region of considerable topographic relief (e.g. Wolfe *et al.* 2003; Tribe 2005), with forests hypothesised to be the antecedent of the modern eastern North American deciduous forest, albeit including elements not found there today (Greenwood *et al.* 2005) (part of the range of *Polystoechotes punctatus* is in the eastern North American deciduous forest). A mesic climate with upper microthermal to lower mesothermal MAT values are estimated for the region as a whole (Greenwood *et al.* 2005), representing a climatic regime in ways analogous with modern low-latitude montane regions

(Archibald & Farrell 2003): cool MAT values supporting micro-mesothermal floral elements such as *Abies* and *Picea*, yet with mild enough winters to allow frost-intolerant biota, e.g. palms (Greenwood *et al.* 2005; Moss *et al.* 2005).

The Republic localities are exposures of the Klondike Mountain Formation in and around the town of Republic, in Ferry County, north-central Washington State. The Early Eocene fossiliferous lacustrine shales are in the lower portion of the Tom Thumb Tuff Member, dated 49.4 ± 0.5 Ma by ^{40}Ar–^{39}Ar decay (Wolfe *et al.* 2003). Republic insects have been determined to family level by Lewis (1992) and Wehr & Barksdale (1996). The Republic flora is reported in many places (e.g. Wolfe & Wehr 1987; DeVore *et al.* 2005). The climate was upper microthermal (MAT ~9 °C, NLR; ~10 °C, LMA), with mild winters similarly indicated by the presence of frost-intolerant floral elements, e.g. the banana relative *Ensete* and a cycad (Greenwood *et al.* 2005).

The Quilchena fossils are from a small outcrop of Coldwater Formation (Princeton Group) shale on Quilchena Creek, about 4 km south of the town of Quilchena, B.C. ^{40}Ar-^{39}Ar analysis gives an Early Eocene age of 51.5 ± 0.4 Ma for this exposure (Greenwood *et al.* 2005). The insect assemblage was determined to family level by Archibald & Mathewes (2000). Mathewes & Brooke (1971) summarised the flora of Quilchena based on early studies, with updates on the megaflora list provided by Greenwood *et al.* (2005). The climate was lower mesothermal (MAT ~15 °C: NLR, LMA) (Greenwood *et al.* 2005). A detailed compilation of the fossil flora, including megafossils as well as pollen and spores is ongoing by R. Mathewes. Further, detailed palaeoclimatic analyses are also continuing by R. Mathewes and D. Greenwood.

The Horsefly River sediments are exposures of shale, sandstone, with intercalated tephra beds of an unnamed formation (unnamed group) outcrop on the Horsefly River, about 8 km north and east of the town of Horsefly in the Cariboo region of south-central British Columbia. These beds are considered coeval with other Okanagan Highland sites (Early, or perhaps early Middle Eocene) by correlation of biota (e.g. Wilson 1977); tephra samples are currently being radiometrically analysed (J. Mortensen & S. B. Archibald, work in progress). Wilson (1977) treated the insect assemblage at family level (with those of other Okanagan Highlands sites). The flora of Horsefly has not been reported in detail since Penhallow (1908) and is currently being examined by S. R. Manchester, R. Stockey & S. B. Archibald. The Horsefly River climate is estimated as upper microthermal (MAT ~13 °C, NLR; ~10 °C, LMA: Greenwood *et al.* 2005).

Mesozoic

Mesozoic Polystoechotidae are only known outside the Western Hemisphere. They are represented with confidence (see below) in four Early Jurassic to Early Cretaceous localities from Asia: Karatau in southern Kazakhstan, Shurab in Tajikistan, Baissa in Transbaikalia, Russia and Daohugou in Inner Mongolia, China.

Dispersal

The disjunct range of *Palaeopsychops* in both Early Eocene western North America and Denmark reflects the well-documented biogeographical pattern seen in plants and mammals in the early Palaeogene (below). The known range of Polystoechotidae as a whole is exclusively outside the Western Hemisphere previous to the Cenozoic, co-occurring in both Western and Eastern Hemispheres only in the Early Eocene and exclusively within the Western Hemisphere since; the implications of this record are less clear.

Figure 3 Early Eocene intercontinental dispersal routes between Europe and North America open to *Palaeopsychops*: across the northern Atlantic route (most likely, dotted line) or across Asia via Beringia (but note Obik Sea barrier). Reconstruction of Early Eocene continental and shoreline position, redrawn from Hooker & Dashzeveg (2003), modified from Smith *et al.* (1994) and Bonde (1997). De Geer and Thulean land bridges may not have been open at the same time. **A**, Fur Formation; **B**, De Geer Land Bridge; **C**, Thulean Land Bridge; **D**, Okanagan Highlands; **E**, Florissant; **F**, Obik Sea; **G**, Bering Land Bridge; **Eur**, Europe; **Gr**, Greenland; **N Am**, North America.

Palaeopsychops

Although Europe, Greenland and North America were not yet fully tectonically separated in the Cretaceous, high sea levels created dispersal barriers for *Palaeopsychops* both between Europe and North America by intervening Atlantic waters and between eastern and western North America by an epicontinental sea, the Midcontinental Seaway. A route between North America and Europe across Central Asia and through Beringia was blocked by another extensive epicontinental sea in the modern Ural Mountains region, the Obik Sea (or West Siberian Sea, also called the Turgai Straights), in the early Palaeogene and much of the Late Cretaceous (Fig. 3; Smith *et al.* 1994). Denk (2004) hypothesises that the Obik Sea provided a sufficient barrier to prevent *Fagus* (beech) from entering Europe from Asia until the Oligocene, consistent with the findings of Enghoff (1995) and Sanmartín *et al.* (2001).

At the close of the Palaeocene, increased land area between northern Europe and Greenland due to a rapid and substantial sea-level drop combined with regional uplift and extensive flood basalt volcanism connected Europe and North America by land bridges via Greenland through at least part of the Early Eocene (Knox 1998; Tiffney 2000; Tiffney & Manchester 2001; Schmitz & Pujalte 2003; Schmitz *et al.* 2004). Dispersal corridors include the southern Thulean route through northern Britain, the Faroe Islands, Greenland to North America and the northern De Geer route from Fennoscandia to northern Greenland and North America. Southern Greenland was then at ~45°N, roughly equivalent to the palaeolatitude of the Fur Formation at ~ 47°N (Scotese *et al.* 1988; Smith *et al.* 1994: Fig. 3). A mild, equable climate was found in (globally cooler) Middle Eocene forests with an upper microthermal MAT, sustaining thermophilic biota at ~78°N (Basinger *et al.* 1994; Kotyk *et al.* 2003).

The insect-bearing beds of the Fur Formation are above the CIE (above). These δ^{13}C-rich beds are hypothesised to represent a sudden sediment failure of continental shelf deposits, which released CH_4 into the ocean and atmosphere (Dickens *et al.* 1995; Katz *et al.* 1999; Thomas *et al.* 2002). Kent *et al.* (2003) suggest a comet impact as a trigger for the CIE, but Schmitz *et al.* (2004) present evidence that the initiating factor was extensive flood-basalt and explosive volcanism in the Faero-Greenland region.

A brief (perhaps <10 ky) spike of increased global temperature, the Palaeocene–Eocene Thermal Maximum (PETM) is associated with the CIE, during which surface ocean water temperature increased by 4–5°C in low latitudes and 8–10°C in high southern latitudes and warming of the deep-sea is associated with large-scale benthic extinctions (Kennett & Stott 1991; Pak & Miller 1992; Dickens *et al.* 1995; Bains *et al.* 1999; Zachos *et al.* 2001, 2003; Aubry *et al.* 2003; Schmitz *et al.* 2004).

The PETM is coeval with notable floral and faunal first appearances, extinctions and changes in distribution. This brief period is thought to have triggered range extensions into higher latitudes and across land bridges in those regions previously closed by climate, coincident with this period of continuous land connection (Hooker 2000). The appearance of a number of mammalian orders simultaneously in Europe and North America (from an undetermined geographic origin) immediately following the PETM is termed 'the mammalian dispersal event' (Beard & Dawson 1999; Hooker 2000; Bowen *et al.* 2002). Woodburne & Swisher (1995) number discrete intercontinental mammal interchange events, the first two of which predate both Fur Formation and Okanagan Highlands time (Fig. 2). They consider the first of these to have been a minor immigration event from Europe to North America, associated with the PETM. At the time of interchange event 2, a major Europe to North America immigration, generic similarity of mammals between Europe and North America was greater than at any other time in the Cenozoic (Woodburne & Swisher 1995). Mammals show rapid evolution resulting in increased endemism immediately following dispersal at the PETM (Rea *et al.* 1990).

Manchester (1999) and Tiffney (2000) discuss Early Palaeogene migrations of plant taxa across the North Atlantic. Manchester (1999: 501) finds 'numerous shared elements' between Europe and North America; these are coincident with Woodburne & Swisher's interchange events 1 and 2 (but see caveats concerning floral interchange at the PETM in Harrington 2003; Wing *et al.* 2003). Based on fossil fruits and seeds, Manchester (1994) found 30 genera (about 20%) in the Eocene nut beds flora of the Clarno Formation (Oregon, USA), to be in common with the London Clay flora and 15 species (10%) to be indistinguishable between them. He suggested that an interchange was most likely before the Middle Eocene and was more likely across the North Atlantic rather than Beringia, a route blocked by the Obik Sea.

Early Eocene insect genera also provide evidence of North American–European dispersal. Another neuropteran besides *Palaeopsychops* has been found in both the Okanagan Highlands and the Fur Formation, the chrysopid genus *Protochrysa* Willmann & Brooks, 1991 (our current research). The mecopteran genus *Cimbrophlebia* Willmann, 1977 (Mecoptera: Cimbrophlebiidae), previously known only from the Fur Formation (Willmann 1977), has recently been found at the Okanagan Highlands site at McAbee, British Columbia (SBA, current research) (see map in Greenwood *et al.* 2005: Fig. 1). An ant genus is also found in common between the Fur Formation and the Okanagan Highlands (SBA, current research). Much of the published work on Okanagan Highlands fossil insects in the latter half of the twentieth century has been to family level (Greenwood *et al.* 2005); as this fauna becomes better known at the generic level, we expect that insects will increasingly reflect the Eocene cross-Atlantic distributions demonstrated in plants and mammals (as well as a cross-Beringial distributions between East Asia and North America). Matthews (1979) discussed Palaeogene insect dispersals across the North Atlantic and Beringial land bridges affecting the modern composition of the Canadian insect fauna.

This pattern is supported by neontological data. Sanmartín *et al.* (2001) examined the distributions of Holarctic biota based on the phylogenies of 770 species of extant, non-marine animals with disjunct ranges (including insects) and their estimated times of divergence by molecular clock analyses. They found that eastern Nearctic–western Palaeoarctic dispersal was most common in the early–middle Tertiary, more commonly across the North Atlantic than by the Beringial route (see also Enghoff 1995).

The Bering land bridge connected North America to East Asia with continuous land at this time (Fig. 3; Hamilton 1983) and is similarly associated with Late Palaeocene–Early Eocene biotic dispersal (Graham 1972; Tiffney 1985; Moran 1989; Beard & Dawson 1999; Manchester 1999; Tiffney & Manchester 2001; Bowen *et al.* 2002; Archibald *et al.* 2005). Migration of *Palaeopsychops* between Europe and North America via Asia is argued against, however, by the barrier of the Obik Sea (above). Furthermore, no species of the genus or of one closely related to it, have been found in the early Palaeogene of far-eastern Asia (e.g. the Tadushi Formation in Primorye, Russia), although these localities have only been briefly examined to date, and this could also be due to taphonomic factors (see below). Migration between Europe and North America directly through the North Atlantic route appears most likely.

Polystoechotidae

As all reported Mesozoic occurrences of Polystoechotidae are outside the Western Hemisphere (and only with confidence in Central and East Asia: see above) and as the oldest known occurrence of the family in the Western Hemisphere (to which they are restricted today) is in the Okanagan Highlands, associated with cross-Atlantic dispersal events of other biota, this might be thought to represent the entrance of the family into this hemisphere.

Their absence in the North and South American Mesozoic record may, however, only reflect the paucity of these localities in this region relative to Asia (the rich Cretaceous Aptian Brazilian Crato Formation and Turonian New Jersey amber deposits are exceptions), rather than the absence of the family in the Western Hemisphere at that time. The absence of Polystoechotidae from the Jurassic and Cretaceous record of Europe (e.g. Dobbertin, Solnhofen, Wealden and Purbeck) seems to be significant, although, once again, possible exclusion by the taphonomic conditions described below must be taken into account. A biogeographical history of the family further requires taxonomic resolution of the problematic possible Mesozoic taxa discussed below.

TAPHONOMY

Diatoms

Florissant

The shale in which insects are found at Florissant consists of thin lamina couplets of diatomite and carbonaceous sapropel (McLeroy & Anderson 1996; Harding & Chant 2000). Harding & Chant (2000) proposed a taphonomic model for Florissant biota in which annual mass aggregation blooms of diatoms are key. Individual diatoms in bloom aggregates adhere to each other by extracellular polymer mucus, which would also trap insects contacting such blooms at or near the water surface and subsequently transport them together to the substrate in anoxic bottom waters each year at bloom termination. This mucus is hypothesised to promote the fine-level preservation of morphology that is characteristic of Florissant fossils, possibly by promoting mineral encasement. The oldest-known preserved chitin, from an Oligocene weevil (Coleoptera: Curculionidae) from the Enspel Fossillagerstätte, Germany, was found in association with abundant diatoms, although the authors implied only that their presence may be correlated with, not causally linked to, the exceptional preservation (Stankiewicz *et al.* 1997). O'Brien *et al.* (2002) do, however, make such a causal connection; they suggest that mucus from diatom mats as well as that produced by associated bacteria are directly responsible for fine-level insect preservation at Florissant.

Denmark

Larsson (1975) presented a taphonomic model for the marine Fur Formation, with insects transported by active flight or passively by wind and set on the sea surface at the depositional site, an estimated 100 km offshore. In years of toxic dinoflagellate bloom (red tide), fish would suffer mass mortality, removing predation as the insects moved through the water column to the seabed. He noted, however, that this had not been demonstrated: although dinoflagellates are well known from the Fur Formation (e.g. Hansen 1979), such mass mortality assemblages of fish have not been found. Kohring & Schlüter (1995) provided discussion of seasonal assemblage sorting. Rust (1998) extended Fur Formation taphonomy, in particular examining differing biases towards members of various insect orders (not including Neuroptera). We suggest that a taphonomic model that emphasises the role of diatoms, similar to that proposed for Florissant, may further explain this fossil assemblage.

The predominance of modern marine diatom blooms and of diatomaceous sediments indicates a wide-spread phenomenon, particularly in coastal temperate to sub-polar regions (Alldredge & Gotschalk 1989). Extensive areas may be covered in these bloom aggregates: bands of gelatinous surface layer aggregates were observed in the Adriatic 100 m in length and 40 m wide, affecting an area of 10 000–14 000 km^2; winds and currents carried portions of this bloom from Cesenatico to Ancona, some 110 km (Stanchowitsch *et al.* 1990). Direct sea floor observations suggest significant transport to the seabed of upper ocean material by entrapment in diatom aggregates following seasonal blooms, reaching the seabed before they can be consumed by grazers, sinking rapidly, at rates of about 100 m/day (Smetakec 1985; Alldredge & Gotschalk 1989; Alldredge *et al.* 1995). Present-day blooms of marine diatoms, their aggregation and subsequent mass sedimentation on the sea floor have been observed at Isefjord, Denmark (Kiørboc *et al.* 1994).

The diatomite of which the Fur Formation is formed is composed of couplets of alternating light-coloured, diatom-rich and dark-coloured carbonaceous laminae, each 1–2 mm thick. Bonde (1974) proposed that these couplets are varves, i.e. annual, each resulting from a yearly cycle of diatom bloom and deposition, then carbonate deposition. Diatoms constitute a large proportion of this sediment, about 65 wt% (Pedersen & Buchard 1996), with chain-forming genera (*Trinacria*, *Hemialus* and *Solium*) predominating (Mitlehner 1996). Spring–summer mass aggregates of diatoms and their mucus could act as large sticky traps on or near the water surface for insects that flew or were carried by winds out onto them. At bloom cessation, they would then be transported intact, rapidly (over the course of a few days) to the substrate as in the Florissant model, but in a marine setting. We agree with Kohring & Schlüter (1995) that this insect assemblage should reflect a strong seasonal bias.

Bonde (1974) hypothesised a prevailing north wind, as ash layers within the Fur Formation are identified by petrology and geochemistry with a volcanic source possibly 1100 km to the (Eocene) north in the Faroe–Greenland region (Knox 1997; Larsen *et al.* 2003). These winds would create a surface current, deflected by the Coriolis effect to produce nutrient-rich upwelling in the depositional area, supporting rich plankton life in surface waters and anoxic conditions at the seabed (Bonde 1974). Diatomite (and possibly diatom-derived siliceous mudstone) deposits along the southwest Scandinavian coast support coastal upwelling in this region (Bonde 1997; Danielsen & Thomsen 1997: fig. 6). However, anoxic seafloor conditions for much of the formation are further supported by fossils undisturbed by scavenging, lack of substrate bioturbation (most horizons) and the rarity of fossil benthic biota (Bonde 1974).

The previously presumed source of Fur Formation insects was the southern Scandinavian coast, which, located about 100 km north of the deposition area, was the nearest land source (Bonde 1974). The same prevailing offshore north winds hypothesised by Larsson (1975) to have carried insects from this area could, however, also have moved diatom–mucus mats from an insect collection area of diatom bloom much nearer to the coastline, to the depositional area of aggregate sink, requiring (perhaps much) less distance between habitat and entrapment. The pattern of tephra distribution from the hypothesised volcanic source to the North Sea depositional zone further supports either prevailing north winds, or alternatively, transport by surface currents: 'the same process could account for the concentration of diatoms within the Mo-clay' (Knox 1997: 9). At bloom termination, the insect assemblage would be transported rapidly to the seabed, the diatom mats providing immediate covering.

Okanagan Highlands

Wilson (1976) showed annual varve couplets in Horsefly shale, with dark sapropel layers interpreted as winter and early spring deposition, while light diatom-rich lamina were interpreted as summer deposition (also see Wilson 1993; Wilson & Barton 1996; Barton & Wilson 2005). He modelled the Horsefly River depositional environment as a deep-water anoxic setting in a stratified lake. Diatom species at Horsefly have recently been described (Wolfe & Edlund 2005). Matrix originally consisting of couplets composed of diatomaceous and carbonaceous laminae (but obscured through differing diagenesis) is also present at the Okanagan Highlands locality at McAbee and some of those in the Princeton region, British Columbia (Mustoe 2002, 2005). Mustoe (2002) reported that shale samples examined from Republic are composed primarily of clastic sediments, however, he suggests (G. Mustoe, pers. comm.) that those results are equivocal as to the presence of diatom blooms there, suggesting further research is needed; samples analysed from Quilchena do not show evidence of diatomaceous origin.

Fossil assemblage and community representation

Polystoechotidae have a higher fossil assemblage species richness in the Okanagan Highlands than in the Fur Formation, indicating higher species richness in that regional Eocene community. The chances of the preservation of Neuroptera in general are higher, however, in the Fur Formation than in the Okanagan Highlands, producing greater specimen richness within that fossil insect assemblage.

Fossil assemblage specimen representation

Neuroptera as a whole represent about 3.8–5.0% of the Fur Formation insects, depending on the museum collection (Rust 1999). This seems to be an abnormally high representation of the order. Where unbiased sample data are available, Early Tertiary Lacustrine shales consistently include less. The Okanagan Highlands locality of McAbee contains 1.5% Neuroptera out of 1307 insects in an unbiased collection (current research), the Palaeocene Tadushi Formation, Primorye, Russia, contains about 0.3% out of approximately 3000 insects (Zherikhin 1978) while the latest Eocene Bembridge Marls, England, contains about 0.1 % (Jarzembowski 1980). None are known from the Middle Eocene Eckfeld Maar, Germany (Wappler 2003), the Middle Eocene Messel, Germany (Lutz 1987) or the late Early–Middle Eocene Bournmouth Group, England (Jarzembowski 1996). Modern forest communities show a representation of Neuroptera of less than 1% of insects in differing geographical regions, by differing sampling methods: e.g. less than 1% in tropical forest canopy fogging samples in Borneo (Stork 1988); 0.45 % in composite interception trap (window and Malaise) samples in forests of Queensland, Australia (Basset 1988); and 0.25% in light trap samples in mixed broadleaved–coniferous forests of Primorye, Russia (Storozhenko *et al.* 2003). Mass extant insect sampling is ongoing in western Massachusetts and Costa Rica (SBA, current research).

Where Polystoechotidae were present in a regional community, taphonomic factors may exclude them from a fossil assemblage. The chances of members of the family being present in the fossil assemblage should be indicated by the relative representation of Neuroptera as a whole in that assemblage.

The larger representation of specimens of both the family and the order in the Fur Formation than in both lacustrine and modern community samples indicates either taphonomic bias in favour of their preservation there or, alternatively, a greater presence of individuals in the regional community; the latter possibility can only be addressed through assessment of the former.

To enter the compression fossil record, insects must be transported through two major stages. First, they must be transported some distance from their source habitat and deposited on the surface of a lake or sea and secondly, they must break the surface tension, travel through the water column, then onto and into the substrate. Differential abdominal swelling due to gasses produced during decomposition may also have produced differential sorting. Furthermore, water density, rate of sinking, salinity, the presence of a pycnocline (halocline, thermocline), lake structure (e.g. meromictic, monomictic), annual layer turnover, or oxygen levels in bottom waters (determining the presence of decomposing bacteria) further affect insect taphonomy (Lutz 1997, 1998*a*,*b*; Rust 1998; and others). Most of these factors are applicable after an insect breaks the surface tension and enters the water column; we will primarily consider here factors that we suggest are important in sorting insects by wing surface/body mass (SM) index value (see below) during the habitat-to-water surface transport stage, until breaking the surface tension and sinking. We will discuss these in reverse order.

Increased floating time in the water's surface tension increases the chances of an insect being consumed by scavengers, degraded by decomposition and the elements, or washing ashore before it can enter the water column (Martínez-Delclòs & Martinell 1993; Wagner *et al.* 1996; Lutz 1997, 1998*a*; Rust 1998). Morphological factors affecting the floating time of Neuroptera in general, and of Polystoechotidae in particular, include wing surface structure and wing shape and size in relation to the body.

Actualistic studies have shown that insects with large wing surface/body mass ratio (high 'SM index') have a longer floating time (Wagner *et al.* 1996). Out of 97 insect species in the 14 orders studied by Wagner *et al.* (1996), only some Lepidoptera showed a higher SM value than the Neuroptera examined. Furthermore, they found SM index and wing wettability to be highly correlated. Insects such as Diptera and Hymenoptera, with low SM indices, are able to clean their wings with their legs and their wings are wettable; high SM index insects rely on 'self-cleaning' wings that repel water by surface microsculpturing, the shed drops clearing away contaminants such as dirt particles and fungal spores. All Neuroptera that they examined had such microsculpturing, similar to that found in Odonata and Ephemeroptera.

Both high SM value and water repellence would keep Neuroptera floating longer on the surface tension. We infer taphonomic bias resulting from these factors to be strong in Polystoechotidae in particular. The pilose wings of *Palaeopsychops setosus* sp. nov. (see below), would have resulted in even more difficulty for the insect to break through surface tension, as do those of Lepidoptera, whose scale-covered wings greatly increase surface area and therefore also the adhesion force that holds the insect to the water's surface. Martínez-Delclòs & Martinell (1993) found that lepidopteran specimens placed in an aquarium remained in the surface tension until they disarticulated and decomposed into unrecognisable fragments. They speculate that the occasional entrance of lepidopterans into the fossil record may be associated with surface algal mats that stabilise the insect until sinking, consistent with the diatom aggregate hypothesis discussed above. Only two lepidopteran specimens have been reported from the Okanagan Highlands (Douglas & Stockey 1996); fossil Diptera and Hymenoptera are common there (SBA, current research).

Large numbers of moth fossils – about 1700 – have been recovered from the Fur Formation, interpreted by Rust (2000) as recording a mass migration event. This is in startling contrast to the previously known 600–700 lepidopteran fossils worldwide, about 500 of which have been found in fossil resins (Kristensen & Skalski 1999). This indicates support for their general scarcity elsewhere in the Tertiary fossil record as reflecting taphonomic bias rather than their low representation in communities (Rust 2000). Martínez-Delclòs *et al.* (2004) find that well-preserved compression fossil insects with large wings such as these moths (and very small insects) are usually associated with cyanobacterial mats (they exclude the Fur Formation), which reduce decay and promote rapid fossilisation.

Although the distance from source habitat to placement on the water's surface may have been less (perhaps significantly so) than the possible 100 km from the Scandinavian shoreline (see above), some unknown distance from entrapment to shore then to source habitat was involved. The offshore north winds discussed above may have had a positive effect on habitat-to-sea-surface transport for high SM index insects, as well as on prevention of subsequent drift ashore (if not immediately trapped in diatom mats, also lessening this) and in generating a seaward surface current for transport of mats (see above).

A high SM index would not only produce a general negative bias towards Neuroptera by extending floating time in general, but may have provided a positive bias in the Fur Formation, by enhancing their aerial transport by offshore winds. Although some insect taxa may have actively flown over the sea in mass migrations (Hymenoptera, Ichneumonidae: Ansorge 1993; Hymenoptera, Formicidae, Rust & Andersen 1999; Lepidoptera: Rust 2000), outside such instances, the composition of the general assemblage is suggestive of passive transport as aerial plankton (Larsson 1975; Rust 1999).

The composition of modern insect assemblages deposited on the sea surface varies by location and recent weather conditions (Bowden & Johnson 1976). Collections from the water surface in the middle of the North Sea included no Neuroptera and <1% Lepidoptera (Bowden & Johnson 1976); insects may be found in varying densities across the surface of the Black Sea, probably transported by winds, including indeterminate Neuroptera and Lepidoptera (not quantified) (Zaitsev 1970). A sample from up to 50 km off the Oregon (USA) coast, however, showed 4% Neuroptera (Bowden & Johnson 1976), a similar representation to that of the Fur Formation. Although a source population percentage of Neuroptera from the Oregon coast was not provided, this is above the sampled modern forest representations mentioned above, suggestive that positive sorting for Neuroptera may occur under some coastal water conditions.

Extant Polystoechotidae are weak fliers, which we assume to have been the case with these fossil species; however, their broad, large wings in relation to their relatively light body mass could act to keep them as aerial plankton for longer, as those insects with heavier bodies in relation to wing size would drop out of suspension during transport. Furthermore, stronger fliers would have higher success in resisting wind transport.

This appears contrary to the aerial sorting process proposed by Wilson (1980), where weak fliers may be sorted out of assemblage in near-shore depositional environments, while stronger fliers predominate in offshore ones. In settings such as he considered, e.g. the lacustrine Horsefly River deposits, active transport may well have predominated over passive transport. Largely passive transport of insects offshore by wind in the Fur Formation (apart from import of migratory insects), we hypothesise, would result in sorting in the reverse of Wilson's scenario.

Wilson's (1980) near-shore/offshore model in Okanagan Highlands lakes is based on analysis of both autochthonous aquatic (fish) and allochthonous terrestrial (insects, plants) assemblages. He associated a particular distance from shore depositional environments with individual fossil localities by comparing the intralacustrine distributions of extant fish genera and age classes with those represented in the fossil assemblages. He further analysed the relative disarticulation of insect specimens, insect taxon sorting by aerial transport and the relative occurrences of wood, fern foliage and angiosperm and conifer organs. Diatom mats, however, could confuse these insect and plant data. At the Horsefly River deposits, diatoms have been demonstrated to be richly abundant (see above); lateral transport of these mats by currents could move insect and plant assemblages collected in them either closer to or further from shore, post-aerial sorting. Furthermore, entrapment in mats would probably change ratios of insect specimen articulation. Only further, actualistic studies may resolve the relative effects of these factors in such lakes.

Community species richness

Of the 15 specimens of Okanagan Highlands Polystoechotidae (and comparable indeterminate Neuroptera) considered here, these represent at least 11 species (two indeterminate fragmentary specimens could belong to additional species and see species only known from fore- or hind-wings, see above). This indicates a high species richness in the region. Polystoechotidae in the Fur Formation is represented, however, by 34 specimens in 5 species. Although any pilose-winged species such as *P. setosus* would have decreased chances of preservation (see below), we assume no other general taphonomic bias that would operate on species within the family, skewing the observed fossil species richness to produce these data.

Summary of taphonomy

The increased representation in the marine Fur Formation of polystoechotid specimens in relation to Tertiary lacustrine deposits and also the hyper-abundance of Lepidoptera, upon which similar taphonomic biases operate, provides support for the hypothesis that the factors unfavourable to their preservation were not active, or were intermittently lessened there. We hypothesise that Polystoechotidae species and those of other Neuroptera had a positive taphonomic bias there through:

- Greater distance from source habitat to water surface in aerial transport than in lacustrine settings, resulting in increased sorting.
- High SM index promotes positive bias in passive wind dominated aerial transport.
- Positive bias for weak fliers in passive aerial transport (some high SM index insects are strong fliers, e.g. dragonflies).
- Offshore winds and consequent surface currents prevented drift-to-shore.
- Larger area of water body lessens chance of drift-to-shore.
- Entrapment in diatom aggregates decreased decay and stabilised insects' bodies post mortem on or near the surface.
- Diatom aggregates decreased predation possibilities while floating.
- At bloom termination diatom aggregates rapidly transported insects to sea floor.
- Entrapment in aggregates decreased predation in the water column.
- Diatoms provided immediate covering on substrate.
- Diatoms promoted early diagenesis.

Lacustrine depositional settings may usually have been dominated by negative taphonomic factors for Neuroptera through:

- Greater (to an unknown degree) active aerial transport and hence decreased positive bias for high SM index insects.
- Less distance in aerial transport, which removed or significantly lessened the high SM index sorting advantage to the degree that winds were a factor.
- Increased negative bias for poor fliers such as Polystoechotidae in active transport.
- Extended floating time as a result of high SM index and of water-repellent wing surface sculpture, which increases the chances of predation.
- Extended floating time increases decay on the surface.
- Extended floating time increases chance of drifting ashore.
- Smaller area of the water body increases chances of drifting ashore with longer floating time.

In some lacustrine settings, the presence of mat-forming organisms may ameliorate these negative factors to some degree, increasing the presence of fossil Neuroptera by those diatom aggregate effects listed for the Fur Formation. Diatom species that bloom near, but not at, the water surface may add some, but not as great a positive bias for high SM index insects as those species that aggregate at the surface layer, causing a range in strength of this effect.

In accordance with the above mentioned authors, we assume that the Fur Formation insect assemblage represents specimens placed on the sea's surface by both active import (e.g. mass migration over the sea, consisting of a taxonomically restricted group (although the numbers of individuals may be high)) and passive (wind) import, a more taxonomically generalised group. We propose two general habitat source classes. First, a regional subset, probably megathermal, dominated by passive-transport insects imported from nearer the coastline by diatom aggregates at a particular time each year and also including active-transport insects, which could be flying at any time of the year but were rarely preserved outside the season of diatom aggregation. Secondly, a subset from source habitats unknown distances to the north, with unknown climatic parameters, imported by diatom aggregates and exclusively including those that fly in the season of diatom bloom, but also dominated by passively transported insects while including some active transport insects.

The wind-induced currents that may have transported ash from a volcanic source in the Faero–Greenland region are reconstructed to move southward along the Scandinavian coast to the Fur Formation depositional area (Bonde 1974: unnumbered figure; Knox 1997: fig. 2). This is mirrored in the southern portion of the hypothesised current by the pattern of diatom deposition that stretches from present-day northern Denmark thinning northward along the Norwegian coast (Danielsen & Thomsen 1997: fig 6). This depositional area represents the region of bloom termination, not of its origin, and so is not indicative of the extent of its transport, which is governed by both the length of the blooms and the rate of the current. The transport of ash in these currents, perhaps from as far as the Greenland coast, is suggestive that some portion of the insects in the Fur Formation could have originated in source habitats quite some distance northward. We propose that diatom bloom aggregate mats may have travelled 'conveyor belt-like' southward at a discrete time each year along, and possibly close to, the Norwegian coastline, trapping insects from a variety of source habitats as it proceeded, beginning in its region of origin and finally depositing them at bloom sink in northern Denmark.

The Florissant, Horsefly River and McAbee localities all show evidence of annual diatom bloom events, providing support for positive bias for the preservation of Polystoechotidae. However, the family is currently represented by single specimens from Florissant and Horsefly River and none are currently known from the McAbee, where Neuroptera and large Dinopanorpidae (Mecoptera) (Archibald 2005) with similar morphology and, therefore, presumably similar taphonomic sorting are both well represented. Twelve species of Lepidoptera are known from Florissant, a high number as compression fossils outside the Fur Formation (Meyer 2003). It is possible that negative selection bias by active aerial transport sorting offsets positive bias by extensive diatom advantage at these sites, or that further negative factors not considered by us here were dominant for Polystoechotidae in these localities (but not for other Neuroptera at Florissant or for Neuroptera and Dinopanorpidae at Horsefly River and McAbee), however, these data may also suggest a low community presence at Florissant and Horsefly River, as well as a low presence or absence in the McAbee community.

At the Republic locality, we find Polystoechotidae are relatively numerous (eight specimens), as are other neuropterans and dinopanorpids (museum collections: unbiased sample data not available). Mat-forming organisms such as diatoms have not yet been demonstrated as present there, although we predict that possibility to explain these data, if our model is correct. Quilchena, where diatoms are not indicated, has yielded five specimens (other Neuroptera are well-represented (our current research), but no Dinopanorpidae). Given the current knowledge of Quilchena, we cannot explain these occurrences there. We find it quite possible that the Polystoechotidae was well-represented in those communities. The only two lepidopteran fossils reported from the Okanagan Highlands are from Republic and Quilchena (Douglas & Stockey 1996).

DIVERSITY IN FOSSIL POLYSTOECHOTIDAE

The Eocene record of Polystoechotidae has greater taxonomic diversity of the family than the present (four species in three genera). Including those described here, there are between 12 (fore-wing) and 16 (total) Eocene species (excluding Polystoechotidae *incertae sedis* and Neuroptera *incertae sedis* sp. A) in an indeterminate number of genera (see Material and Methods, Taxonomic Approach, above). Unquestionably, the taxonomic diversity in the Tertiary will be increased by future investigations: the rate of discovery is high. Nine described genera of presumed Polystoechotidae and several other unnamed taxa which are probably members of this family, are known from the Mesozoic (for overviews, see Ren *et al*. 2002; Makarkin & Archibald 2003 and below). Unfortunately, there is a large gap in the record of Polystoechotidae, from the Early Cretaceous Neocomian to the earliest Eocene (i.e. ~80 Ma long), which crosses two major biotic crises, namely at the mid-Cretaceous (Zherikhin 1978) and at the Cretaceous/Palaeogene boundary (e.g. Whalley 1988*a*; Labandeira *et al*. 2002). Known Mesozoic Polystoechotidae are probably not closely related to the Early Eocene taxa. Furthermore, some of these (*Lithosmylidia* Riek, 1955 and *Meilingius* Ren *et al*., 2002) are very doubtfully assigned to this family and a polystoechotid determination of some (*Megapolystoechus* Tillyard, 1933 and *Kirgisellodes* Martynov, 1937) is only suggested (see below).

The Early Eocene species may initially be thought to resemble psychopsid-like neuropterans by their large size, relatively broad fore-wing and rich venation. Indeed, all species described hitherto, except *Palaeopsychops dodgeorum*, were originally (or subsequently) assigned to the family Psychopsidae. Although these species differ from extant Polystoechotidae in these ways, we determined them as being most closely associated with this family by a suite of characters, including the pectinate branching of MP in the fore-wing, the presence of the distal nygma between Rs1 and Rs2 and others previously discussed (Makarkin & Archibald 2003). The material described and revised here provides further evidence of their polystoechotid affinity. This includes (besides the configuration of the longitudinal veins conforming to this family, see below for diagnosis and description) the following character states observed on specimens in this assemblage: (1) the branched and strongly recurrent humeral veinlet in the fore-wing; (2) Sc is fused to R1 in the pterostigmal region of both wings; (3) the costal space of both wings are moderately dilated beyond the point of Sc/R1 fusion; (4) the radial space of both wings with one (outer) or two (inner and outer) regular gradate series; (5) the coupling apparatus in the hind-wing is very similar to that of the extant Polystoechotidae with the humeral lobe somewhat triangular and carrying a frenulum of long and dense bristles (Fig. 4), which is different from that of Psychopsidae (*cf*. Tjeder 1960: figs 326–327; Oswald 1993: fig. 33). Using these character states, the polystoechotid affinity of most of these species (those with more complete wings) is now confident. Other character states found in some of them are not known in extant Polystoechotidae (e.g. numerous crossveins in the subcostal space, which are, however, present in the Late Triassic *Megapolystoechus magnificus* Tillyard, 1933, a species that has been questionably placed in the family Polystoechotidae, as well as in other families, see below). We may, however, expect morphological diversity to increase with greater taxonomic diversity.

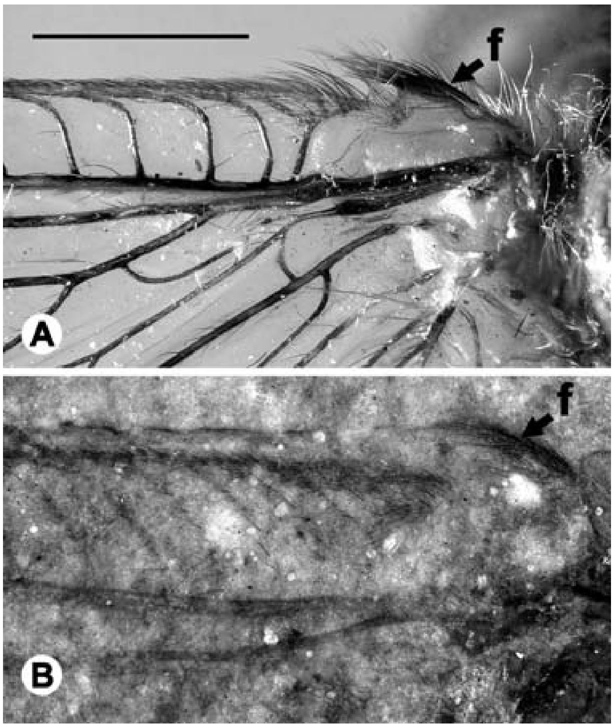

Figure 4 Comparative coupling apparatus in hind-wings of the extant *Polystoechotes punctatus* (Fabricius) and the Early Eocene *Palaeopsychops abruptus* Andersen. **A**, *Polystoechotes punctatus*, MCZ, White Mountains, New Hampshire, USA; **B**, *Palaeopsychops abruptus*, paratype 1 GMUC, Danekræ No. 168. **f**, frenulum. Both to scale; scale bar = 2 mm.

The Late Eocene *P. piperatus*, with its elongate, narrower wing bears even less resemblance to Psychopsidae (and greater resemblance to modern Polystoechotidae, see below), yet it too has previously been treated as a psychopsid (Carpenter 1943; MacLeod 1970).

The wings of Eocene polystoechotids show a greater range of morphological diversity in the North American assemblage than in the European. Although *Palaeopsychops* is represented by five to six species each in both continents, all of the European species are more similar to each other by the characters of wing shape, venation and colour patterning than are those in North America. Moreover, several species (i.e. *Polystoechotites* sp. A., *P. falcatus, P. lewisi, P. barksdalae, P. piperatus*) from North America that are here assigned to the collective genus *Polystoechotites* display wing shapes (falcate or greatly broadened), venation (greater numbers of subcostal crossveins) and/or colour patterns (wholly dark or lacking fasciae) that might be used to justify their recognition as discrete genera.

SYSTEMATIC DESCRIPTIONS

Family **POLYSTOECHOTIDAE** Handlirsch, 1906

1906 Polystoechotidae Handlirsch: 42.
1949 Mesopolystoechotidae Martynova: 160.

Diagnosis. Medium-sized to large neuropterans most similar to Ithonidae, Prohemerobiidae, Osmylopsychopidae, Brongniartiellidae and Psychopsidae, with wings distinguished from those of these and other families in the order by the following unique combination of character states: (1) humeral veinlet recurrent, pectinately branched in both wings (in hind-wing with at least 1 branch); (2) costal space markedly expanded after fusion of Sc, R1 in both wings; (3) MP pectinately branched in fore-wing; (4) CuA pectinately branched in both wings; (5) CuP, (6) 1A normally deeply dichotomous in both wings; (7) outer gradate series of crossveins present in radial space of both wings; (8) distal nygma present between Rs1, Rs2 in both wings; (9) basal crossvein between M, stem of Rs sigmoid in hind-wing.

Description. (Based on wings).

Fore-wing, Elongate oval to broad-subtriangular in shape, 18–50 mm long. Trichosors present. Membrane without microtrichia (except for extreme basal portions). Basal nygma (if present) between stem of Rs, M; distal nygma (if present) between Rs1, Rs2. Costal space expanded basally, narrowed towards apex, after fusion of Sc, R1 (or subcostal space distal to termination of Sc in *Platystoechotes*) expanded again. No pterostigma present. Humeral veinlet strongly recurrent, pectinately branched. Subcostal veinlets usually forked. Veinlets of Sc+R1 long, oblique, forked, many dichotomously. One–two basal crossveins in subcostal space, no distal crossveins. Sc apically fused with R1 (not fused in *Platystoechotes* or *Fontecilla*). Sc+R1, or R1 (*Platystoechotes*), entering margin anterior to wing apex. R1 space narrower, or at most, equal width as subcostal space (except for *Pterocalla* and *Kasachstania*), with <10 longer prestigmal, stigmal crossveins, <5 shorter distal crossveins. Origin of Rs close to base of wing. Rs with 9–34 pectinate branches, normally not forked, dichotomously branched after outer gradate series. Radial space with crossveins arranged in two regular gradate series, or with numerous irregularly spaced crossveins anterior to outer gradate series. Outer gradate series continuing through cubital space to anal space. MA few-branched after outer gradate series. MP pectinately branched in distal portion with oblique branches. Fork of Cu close to wing base. CuA pectinately branched with oblique branches parallel to that of MP. CuP, 1A normally deeply dichotomous. 2A normally deeply pectinate. 3A with few anteriorly directed pectinate branches. Jugal lobe present.

Hind-wing. Elongate oval to subtriangular. Distinguished from fore-wing by the following combination of character states: costal space basally not expanded, with simple subcostal veinlets; R1 space wider or at most equal width as subcostal space (except for *Pterocalla* and *Kasachstania*); basal nygma absent; humeral veinlet only slightly recurrent; without crossveins in subcostal space (weakly developed basal in *Polystoechotes gazullai*); R1 space with oblique prestigmal crossveins (except *P. lewisi*, where crossveins perpendicular); radial space with two regular gradate series of crossveins; basal sigmoid crossvein between M, stem of Rs present; fork of M closer to base than in fore-wing (except for *Platystoechotes*); MP with fewer, shorter pectinate branches or dichotomous; CuA much closer to hind margin, with ~6–11 shorter branches; 3A with fewer anteriorly directed pectinate branches, or deeply forked.

Occurrence. Early Jurassic to Recent of Eurasia and the Western Hemisphere.

Genera included. Three extant genera (see Introduction above); six fossil genera: *Mesopolystoechus* Martynov, 1937 (Early Jurassic of Shurab, Tajikistan; Middle Jurassic of Wangyingzi, Hebei, China: 2 species), *Jurapolystoechotes* Ren *et al*., 2002 (Middle Jurassic of Daohugou, Inner Mongolia, China: 1 species), *Kasachstania* Panfilov *in* Dolin *et al*., 1980, *Osmyloides* Panfilov *in* Dolin *et al*., 1980 and *Pterocalla* Panfilov *in* Dolin *et al*., 1980 (all from the Late Jurassic of Karatau, Kazakhstan, all monotypic), two or three undescribed species of undetermined genera from the Early Cretaceous of Baissa, Siberia (pers. obs.), *Palaeopsychops* Andersen, 2001 (Early Eocene of Denmark and western North America: 10 species) and the collective genus *Polystoechotites* gen. nov. (6 species from the Early and Late Eocene of western North America).

Genera of indeterminate affinity. The two monotypic genera, *Megapolystoechus* (Early Jurassic of Worcestershire, England) and *Kirgisellodes* (Late Jurassic of Karatau, Kazakhstan), considered to be within, or closely associated with the family (Whalley 1988*b*; Makarkin & Archibald 2003), require re-examination and/or more complete specimens to clarify their position. Pending this, we do not include them here in the Polystoechotidae.

The holotype and one paratype of *Megapolystoechus magnificus* were examined by SBA at the Natural History Museum, London. Both are incomplete, lacking basal regions. These specimens are most probably hind-wings, by the preserved portions of the costal space, which is not tending to expand basally, and by the position of CuA relative to the wing margin (obviously closer to the hind margin than is characteristic in the fore-wing of other polystoechotid species). Alternatively, if this species does not belong to the Polystoechotidae, both possibilities (fore-wing and hind-wing) are equivalent. While some major venational characters are in agreement with Polystoechotidae (including the distal fusion of Sc and R1 (separate in fig. 1 of Tillyard (1933)) and the outer gradate series of crossveins are distinct (not present in fig. 1 of Tillyard (1933))), this species possesses numerous and densely spaced subcostal crossveins (as in Kalligrammatidae) not characteristic of the family as treated here.

Kirgisellodes ornata (Martynov, 1925) is represented by a single, complete, but rather poorly preserved fore-wing. We interpret the MP of Martynova (1962: fig. 859) to be MP and CuA; if so, this species is known to possess five out of the eight combined fore-wing character states diagnostic of

Polystoechotidae (the remaining three, characters 1, 7 and 8 are not detected in this fossil). Confirmation, however, requires re-examination of the holotype and until this is done, assignment of *K. ornata* to Polystoechotidae would be premature.

GENERA EXCLUDED. The two genera *Lithosmylidia* Riek, 1955 (Late Triassic of Queensland, Australia) and *Meilingius* Ren *et al.*, 2002 (Middle Jurassic of China) apparently do not belong to this family. Of the three to four species of *Lithosmylidia*, Lambkin (1988) considered only the type species, *L. lineata* Riek, 1955, as probable Polystoechotidae; the others were considered 'similar to Osmylidae or Polystoechotidae, but not able to be placed in either' (p. 457). The type specimen is an incomplete fore-wing possessing two character states (4, 5) in part diagnostic of Polystoechotidae, namely the structures of CuA and CuP. These are, however, shared with species of other families (e.g. Prohemerobiidae, Hemerobiidae). Furthermore, Cu is forked very closely to the wing base, a condition not known in the family (Lambkin 1988: fig. 1).

Meilingius, with one, huge (fore-wing 64 mm long) species, *M. giganteus* Ren *et al.*, 2002, was described in Polystoechotidae. However, it possesses only two diagnostic character states (1, 2) of the family as treated here. The structures of MP, CuA and CuP are contrary to those found in the family and are most similar to those of the Permian neuropteran family Permithonidae (it is far from that family by other features, however).

PROBLEMS OF DEFINITION OF THE FAMILY. No definition has previously been provided for any family of Neuroptera taken as a whole, including both the extant and fossil taxa. As the great majority of fossil Neuroptera are known only from disarticulated wings, such a definition can be based solely on characters of this organ. Difficulties in providing such a definition include general problems discussed in part above (e.g. the need for revision of many of the fossil taxa and identification of sufficient character states from damaged, poorly preserved or incomplete specimens) as well as problems particular to the family. Lambkin (1988) provided the most complete characterisation of the wings of Polystoechotidae based on extant representatives. We define the family based on both the extant genera and those fossil genera most similar to them. As a working hypothesis, we treat the extant Polystoechotidae here as monophyletic, with the possibility in mind that revision may indicate otherwise.

Only those character states of the wing that occur in all members of the family, are included in the diagnosis and description, except as noted. Venational character states occurring only in individual species are, for the most part, considered separately below. Ideally, only those taxa possessing the complete set of character states provided in the diagnosis may be assigned to the Polystoechotidae with confidence. This complete set, however, is not always preserved in fossils, resulting in some uncertainty of relationship to the family of some problematic taxa (e.g. *Jurapolystoechotes*). Given these problems, we recognise that the diagnosis and description of the family provided here are preliminary.

The venation of the Polystoechotidae is comparatively primitive within the order; we have determined no venational autapomorphy of the family. Its monophyly, therefore, cannot be established with confidence based only on single characters of the wing. Although a number of character states included in the diagnosis are apomorphic with regards to those of Permian Neuroptera, most occur widely elsewhere in the order (1–3, 7). Other character states are plesiomorphic (8, 9) or their polarity is not clear (4–6). Its generalised venation suggests that the family Polystoechotidae is among the basal Neuroptera, although its phylogenetic position is not clear, as is the case with most 'primitive' families that lack clear venational autapomorphies, e.g. Sisyridae, Nevrorthidae, Ithonidae and Dilaridae. Cladistic analysis of extant neuropteran families based on non-venational characters, however, give a basal position for Nevrorthidae as sister group to all other Neuroptera [Hemerobiiformia + Myrmeleontiformia]; Polystoechotidae + Ithonidae as sister group of other Hemerobiiformia; and Sisyridae and Dilaridae in Hemerobiiformia, far from basal (Aspöck 2002).

PARTICULAR WING CHARACTERS OF EXTANT AND TERTIARY TAXA. The following character states are notably unique in single Early Eocene or extant polystoechotid species, or are distinctive between extant and Early Eocene species. The sole other Tertiary species, the Late Eocene *P. piperatus*, is poorly known; only its wing size, shape and colour patterning are clearly comparable.

Wing size and shape. The majority of Early Eocene polystoechotids have larger wings (longer and wider) than do Recent species (Early Eocene species: fore-wing = 29–50/52 mm long, length/width ratio 1.7–2.4; Recent species: fore-wing 18–34 mm long, length/width ratio 2.5–3.3). The Late Eocene *P. piperatus* is closer to the Recent species (estimated length ~31 mm, length/width ratio 2.48). It is interesting to note that a diverse assemblage of the large, extinct family Dinopanorpidae (Mecoptera) in the Okanagan Highlands (Republic, Princeton region, Falkland, McAbee, Horsefly) bore similar wing size and shape (Archibald 2005).

Colour patterning. Early Eocene polystoechotids (except *Polystoechotites falcatus*) differ greatly from Late Eocene and extant taxa in wing colour patterning: dark/light contrasting colour patterning consists of fasciae, patches, stripes, or there are entirely (portions preserved) dark areas. Colour patterning of the wings of extant and Late Eocene polystoechotids is less distinct; they are mottled or irrorated, with much less contrast in light to dark regions, without broad dark fasciae and large areas of maculation, and never entirely dark-pigmented.

Dense cover of membrane macrotrichia. *Palaeopsychops setosus* is the only member of the order to bear this distinctive trait (discussed further, below).

Sc apically not fused with R1. These veins do not join in *Platystoechotes* (widely spaced) and *Fontecilla* (closely approaching), whereas in all other species of the Polystoechotidae they are apically fused. The polarity of this character is not clear (both states occur in the Permian Neuroptera), but the former state is most probably plesiomorphic in Polystoechotidae and the state of Sc fused with R1 is apparently derived in this family.

Distal fusion of Rs1 and MA in the fore-wing. This character state, found in the sole specimen of *P. quadratus* and some specimens of *P. angustifasciatus*, appears unique within the Neuroptera and is distinctly derived.

Structure of M in the fore-wing. Media forked, divided into MA and MP, both of which are nearly parallel and not branched before their distal portions, is characteristic of extant families of Neuroptera with generalised venation. The structure of M found in the three Early Eocene species *P. abruptus, P. angustifasciatus* and *P. quadratus* (the basal region of M is too poorly preserved to determine in all specimens of other species) i.e. the fork of M is lost and MA originates from Rs1, appears to be unique in Neuroptera and is distinctly apomorphic within the order.

Configuration of MP in the fore-wing. In all Early Eocene species (in specimens where this vein is preserved) MP is strongly pectinately branched, with long branches in both wings. In extant species, there are fewer pectinate branches with moderately long branches.

Costal gradate series of crossveins. This character state is present in the fore-wings of single species of the either extant (*Platystoechotes*) or fossil (*Palaeopsychops*, *Polystoechotites*) genera. It is obviously derived with regard to the state of the absence of crossveins and probably homoplasious among these occurrences.

Subcostal crossveins. In extant Polystoechotidae, there is only one basal subcostal crossvein in the fore-wing and none in the hind-wing, except one weak basal crossvein in *Polystoechotes gazullai* (one distal in *P. lineatus*). In neuropterans of almost all extant families that are characterised by few (or one) subcostal crossveins, the condition of many subcostal crossveins may occur in individual species. Therefore, the presence of several crossveins in the subcostal space of Polystoechotidae, found in two Early Eocene species (in the fore-wing of *Palaeopsychops quadratus* and in the hind-wing of *Polystoechotites lewisi*), while not previously known within the family, is not completely surprising. In Hemerobiidae this character state, when it occurs, is considered 'either a species level apomorphy, or an occasional adventitious condition' (Makarkin *et al.* 2003: 642). The same may be true for Polystoechotidae.

Radial crossveins in the fore-wing. In some of the Tertiary species the arrangement of radial crossveins is as is found in extant species, i.e. forming two regular gradate series, inner and outer (P. *latifasciatus*, *P. quadratus*), sometimes with a few scattered additional crossveins. Many North American Eocene species, however, have only one distinct gradate series (the outer), with numerous scattered crossveins in the radial space anterior to it not forming an inner gradate series. Such a configuration of crossveins occurs in species with varying wing shape and colour patterning (e.g. *Palaeopsychops dodgeorum*, *P. marringerae, P. timmi* and *Polystoechotites* sp. A), some of which could well belong to different genera. Given present knowledge, determining which state is primitive in the family is problematic, as both existed in the sparsely known Mesozoic taxa.

Short crossveins in the area of end-twigging. In many (where clearly preserved, but possibly in all) Early Eocene species, there are short crossveins between the branches of Sc+R1, Rs, M and Cu in the area of end-twigging, a character state that is certainly derived in the family. These range from numerous (*Palaeopsychops timmi*) to scarce (*Polystoechotites lewisi*). In extant and Mesozoic taxa, this occurs only occasionally, perhaps as an anomaly.

Genus ***PALAEOPSYCHOPS*** Andersen, 2001

2001 *Palaeopsychops* Andersen: 422 [Psychopsidae].
2003 *Palaeopsychops* Andersen; Makarkin & Archibald: 172 [Polystoechotidae]

TYPE SPECIES. *Palaeopsychops latifasciatus* Andersen, 2001 (by original designation).

DIAGNOSIS. Distinguished from other polystoechotid genera by the following combination of characters [alternative character states are given in brackets hereafter]. In the fore-wing: (1) broad–subtriangular in shape (length/width ratio <2.4) [more elongate in other genera, length/width ratio >2.5]; (2) hind-wing margin not falcate [falcate in *Fontecilla*]; (3) MA (when preserved) basally fused with Rs1, so that fork of M absent [fork of M present in other genera]; (4) MP strongly pectinately branched with long branches (shared by the Jurassic genus *Pterocalla*) [few pectinate, moderately long branches in other genera]. In the hind-wing: (5) MP strongly pectinately branched with long branches [few pectinate, moderately long branches in other genera].

OCCURRENCE. Ten species from earliest Early Eocene of the Fur Formation of Denmark and the Okanagan Highlands of far-western North America: Early or early Middle Eocene of the Horsefly River locality in British Columbia, Canada; Early Eocene of Quilchena, British Columbia, Canada and Republic, Washington, USA.

DESCRIPTION. *Fore-wing*. Broad–subtriangular, 29–45 mm long, 13.5–21 mm wide (length/width ratio 2.14–2.40). Trichosors present, but often indistinct, not always well preserved. Basal nygma not detected (this area poorly preserved in all examined specimens); distal nygma distinct between Rs1, Rs2. Costal space expanded basally, narrowed towards apex, after fusion of Sc, R1 expanded again. Costal gradate series of crossveins present or absent. Humeral veinlet recurrent, branched. Subcostal veinlets forked (rarely simple). Veinlets of Sc+R1 long, oblique, mainly dichotomously forked. One to two basal crossveins in subcostal space, no distal crossveins, except for *Palaeopsychops quadratus*, which has three indistinct distal ones. Sc apically fused with R1. Sc+R1 entering margin before wing apex. R1 space approximately equal width as subcostal space, with two to seven longer prestigmal and stigmal crossveins preserved and one to four shorter distal crossveins. Rs with numerous (22–34) pectinate branches, not forked before outer gradate series, dichotomously branched after. Crossveins in radial space arranged in two regular gradate series or radial space with numerous irregularly spaced crossveins anterior to outer gradate series. Outer gradate series always present, continuing through cubital space to anal space. Several to many (*P. dodgeorum*) crossveins scattered occasionally in radial to anal spaces. Short crossveins between veins of Sc+R1, Rs, M, Cu in area of end-twigging present, sometimes numerous. Fork of M (when preserved) absent, MA originated from Rs1, not branched before outer gradate series, dichotomously branched after. Sometimes, MA fused with Rs1 distally (at outer gradate series) for short distance (*P. quadratus*, *P. angustifasciatus*). MP pectinately branched in distal portion with 7–10 long, oblique branches. Fork of Cu close to wing base. CuA pectinately branched with 5–12 long, oblique branches parallel to that of MP. CuP, 1A dichotomously branched. 2A pectinately branched, with few long branches. 3A with few anteriorly directed branches. Colour patterning of wing represented mainly by dark fasciae (at least in basal anterior portion).

Hind-wing. Subtriangular, 40–42 mm long, 17–19 mm wide (length/width ratio 2.21–2.35). Trichosors present, nygmata not preserved. Coupling apparatus as in extant polystoechotid genera; frenulum consisting of several long setae (*P. abruptus*: see Fig. 4B). Costa basally covered densely with rather short hairs (*P. abruptus*). Costal space narrow before fusion of Sc, R1, expanded after. Subcostal veinlets not forked basally, forked distally; veinlets of Sc+R1 forked. Humeral veinlet slightly recurrent, branched, covered with dense short hairs (*P. abruptus*). Sc, R1 fused apically; Sc+R1 entering margin before wing apex. Crossveins in subcostal space not detected. Origin of Rs close to wing base. One to four preserved crossveins in R1 space. Rs with 26–28 parallel branches, not forked before outer gradate series. Inner, outer gradate series of crossveins regular, parallel, with additional occasional crossveins proximal, distal to inner series (except *P. douglasae*, in which inner gradate series irregular posteriorly). Scarce short crossveins between veins of Sc+R1, Rs in area of end-twigging sometimes present. Fork of M not preserved. MA dichotomously branched distally. MP with five to seven long pectinate branches distally. CuA nearly parallel to hind margin, pectinatelly branched, with > 10 branches. CuP, anal veins poorly preserved. Colour patterning: central area of wing mainly dark, light near margins, at base, apex.

Remarks. The Early Eocene members of the genus may be divided into two species groups by the arrangement of crossveins in the radial space of the fore-wing. We do not consider here 'hind-wing species' as hind-wing venation may be considerably different from that of fore-wings. One group ('European') comprising four Danish species is characterised by the presence of two more or less regular gradate series (1). The second group ('North American'), containing three of the Okanagan Highlands species, is characterised by numerous crossveins scattered in the radial space anterior to the outer gradate series, which are always distinct (2). It is difficult to determine if these groupings are monophyletic. The presence of state (2) in some species of the collective genus *Polystoechotites* suggests that it may have been widely distributed among North American polystoechotids in the Early Eocene; either this character has little taxonomic value for characterising species groups in the family, or some species of *Polystoechotites* that possess state (2), e.g. *Polystoechotites* sp. A, may belong to *Palaeopsychops*. The first possibility appears more likely.

We assign to the genus *Palaeopsychops* those hind-wings that are similar in venation and colour patterning to *P. maculosus* (the hind-wing of *P. abruptus*, paratype 1, articulated with a fore-wing, although lacking definite colour patterning, has venation similar to that of *P. maculosus*). The Polystoechotidae are represented in the Fur Formation by this single genus, represented by numerous fore-wing specimens; that *P. maculosus* belongs to this genus is most probable.

Palaeopsychops latifasciatus Andersen, 2001 (Fig. 5)

2001 *Palaeopsychops latifasciatus* Andersen: 327, Figs 3, 10.

2003 *Palaeopsychops latifasciatus* Andersen; Makarkin & Archibald: 172.

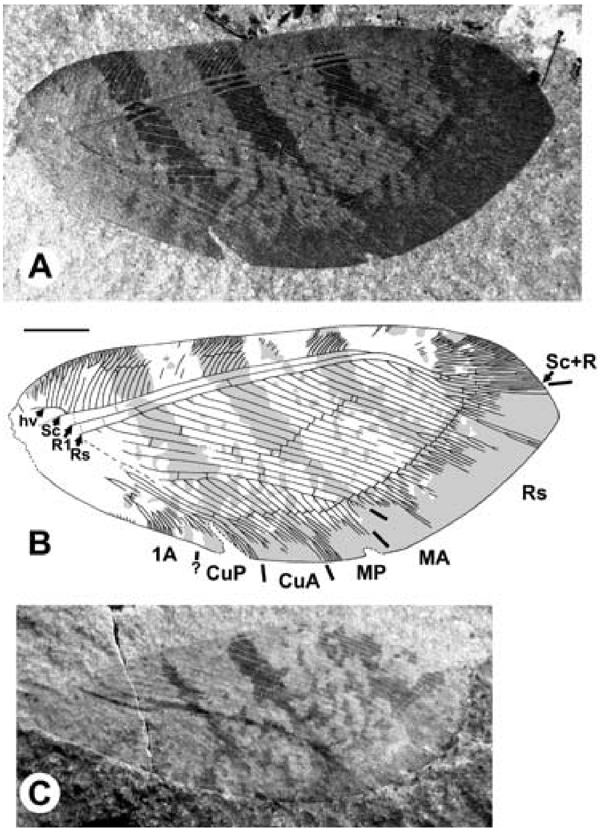

Figure 5 *Palaeopsychops latifasciatus* Andersen, holotype, GMUC, Danekræ No. 308; fore-wing. **A**, photograph of part; **B**, drawing of part. **C**, photograph of paratype 8, GMUC, MGUH27519. For abbreviations see Material and Methods. All to scale; scale bar = 5 mm.

Type material. Holotype: Danekræ number 308 (part and counterpart, both labelled 'Gu 12/3 95'), deposited in GMUC. A rather well preserved, complete fore-wing; Gullerup Strand, Mors (Erwin Rettig, collector). Paratype 8: MGUH27519 (part and counterpart), deposited in GMUC. A rather well preserved, incomplete fore-wing.

Diagnosis. Most similar to *P. abruptus* in general colour patterning, but distinguished from it (and all other Danish *Palaeopsychops*) by the presence of costal gradate series [absent in *P. abruptus*], by broad fasciae through subcostal, R1 spaces [absent or at most narrow in *P. abruptus*].

Occurrence. Earliest Early Eocene, Fur Formation; Denmark.

Description. Holotype: fore-wing 42 mm long, 18 mm wide (length/width ratio 2.3). Trichosors indistinctly preserved. Distal nygma not detected (distinct in 1 specimen: Andersen 2001: fig. 3). Costal gradate series of crossveins parallel to anterior wing margin, apparently not complete. Two basal crossveins (both poorly preserved) detected in subcostal space. R1 space approximately equal width to subcostal space, with two to four crossveins detected (except 3 in apical portion). Origin of Rs poorly preserved. Rs with 23 pectinate branches, not forked before outer gradate series; veinlets in area of end-twigging poorly preserved, short crossveins between them not detected. Crossveins in radial space arranged in two regular, parallel gradate series. Outer gradate series continuing to cubital space. Several crossveins scattered occasionally in radial space. Fork of M not detected; MP with nine branches. Fork of Cu not detected. CuA with only five long branches. CuP poorly preserved, probably dichotomously branched. Anal veins not clearly visible. Wing patterning represented by three conspicuous dark fasciae, small dark spots scattered across wing; areas near hind margin, apical portion of wing in cubital, radial, distal costal spaces entirely dark coloured (Fig. 5A).

Remarks. According to Andersen (2001), the species is represented by nine fore-wing specimens, of which we have examined the holotype (not the specimen that the author incorrectly referred to as the holotype in his fig. 3, but rather the specimen (labelled 'Gu 12/3 95' as in his description of labels (p. 427)) with a label 'Holotype', see Fig. 5), as well as paratype 8. The basal posterior portion of the holotype wing is poorly preserved and may be somewhat displaced (or there is a fold, indicated in Fig. 5B by a dashed line). Two significant areas, the basal portion of MA (which is possibly connected to Rs) and the distal nygma, are both also poorly preserved. However, the holotype and the specimen figured by Andersen (2001: fig. 3) undoubtedly belong to the same species, judging by the similarity of the venation and colour patterning.

The assignment of paratype 8 to this species is disputable: the costal space is not preserved and the (in part) diagnostic presence of a costal gradate series is therefore impossible to detect. The colour patterning of this specimen is quite different from that of the holotype and the paratype shown in Andersen's (2001) fig. 3. It is more similar to that of *P. abruptus* in general appearance in the overall narrowness of the basalmost fasicia and in the narrowing of all fasciae in the R1 space (in other *P. latifasciatus*, these are much broader: Fig. 5C). Preserved venation is similar to that of both the holotype of *P. latifasciatus* and *P. abruptus*. Therefore, we refer paratype 8 tentatively to *P. abruptus*.

Palaeopsychops abruptus Andersen, 2001 (Figs 4B, 6–9)

2001 *Palaeopsychops abruptus* Andersen: 328, figs 4, 7, 9.
2003 *Palaeopsychops abruptus* Andersen; Makarkin & Archibald: 172.

Type material. Holotype: Danekræ number 309 (part and counterpart: both labelled 'K1 4/8 94'), deposited in GMUC. A rather poorly preserved, complete fore-wing; Klitgården, Mors (Erwin Rettig, collector). Paratype 1: Danekræ number 168 (part and counterpart: both labelled '168-1998/21'), deposited in GMUC. An unusually well preserved basal part of whole specimen; Mors (Ole Burholt, collector). Paratype 2: MGUH27520 (part only, labelled 'Limfjorden'), deposited in GMUC. A rather poorly preserved fore-wing lacking basal portion; Limfjorden. Paratype 3: MGUH27521 (part and counterpart: both labelled 'Psy.IV.1995'), deposited in GMUC. A rather well preserved fore-wing lacking apex; Bygholm Vejlerne (boulder), Thy (Stig Andersen, collector).

Diagnosis. Most similar to *P. latifasciatus* (see diagnosis of this species).

Occurrence. Earliest Early Eocene, Fur Formation; Denmark.

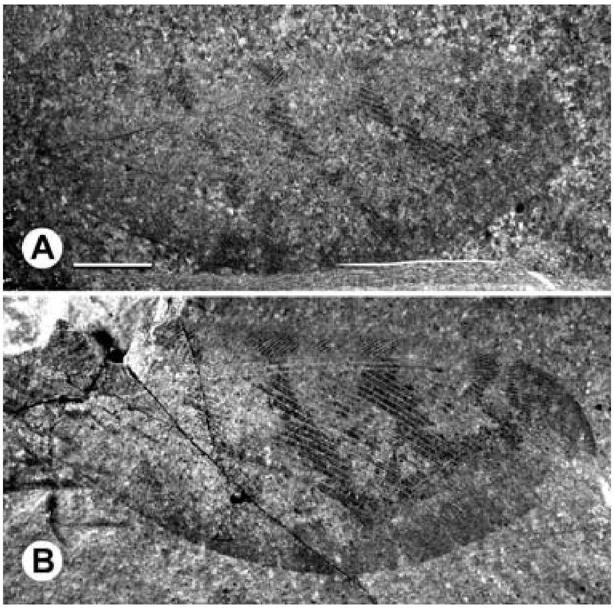

Figure 6 *Palaeopsychops abruptus* Andersen. **A**, photograph of holotype, GMUC, Danekræ No. 309; fore-wing. **B**, photograph of paratype 2 (part), GMUC, MGUH27520; incomplete fore-wing. Both to scale; scale bar = 5 mm.

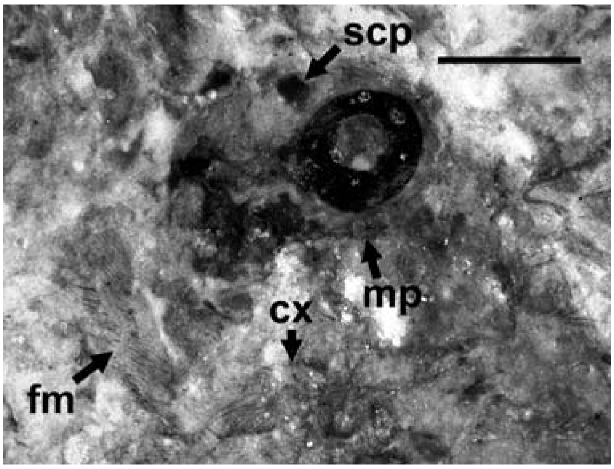

Figure 7 Anterior portion of body of *Palaeopsychops abruptus*, paratype 1, GMUC, Danekræ No. 168. cx, coxa; fm, femur; mp, maxillary palp; scp, scape. Scale bar = 2 mm.

Description. *Holotype*. Length of fore-wing 40 mm, width 16.5 mm (length/width ratio 2.4). Venation poorly preserved, although similar in general to *P. latifasciatus*. No venational characters seen with certainty, except outer gradate series in radial space, absence of costal gradate series at fasciae. Colour patterning rather distinct (Fig. 6A), with three prominent, quite narrow dark fasciae breaking in subcostal space.

Paratype 1 (Fig. 4B, 7–9). Head: scape rather small, short. Maxillary palpi five-segmented, terminal segment pointed. Thorax crushed; notum with short erect hairs; pronotum apparently transverse. Fore coxa, fore femur covered with dense short recumbent hairs, scarce longer erect hairs (Fig. 7). Fore-wing: maximal length of incomplete fore-wing 22 mm, width ~18 mm; length of complete fore-wing 40–44 mm (estimated), width 18–19 mm (estimated) (estimated length/width

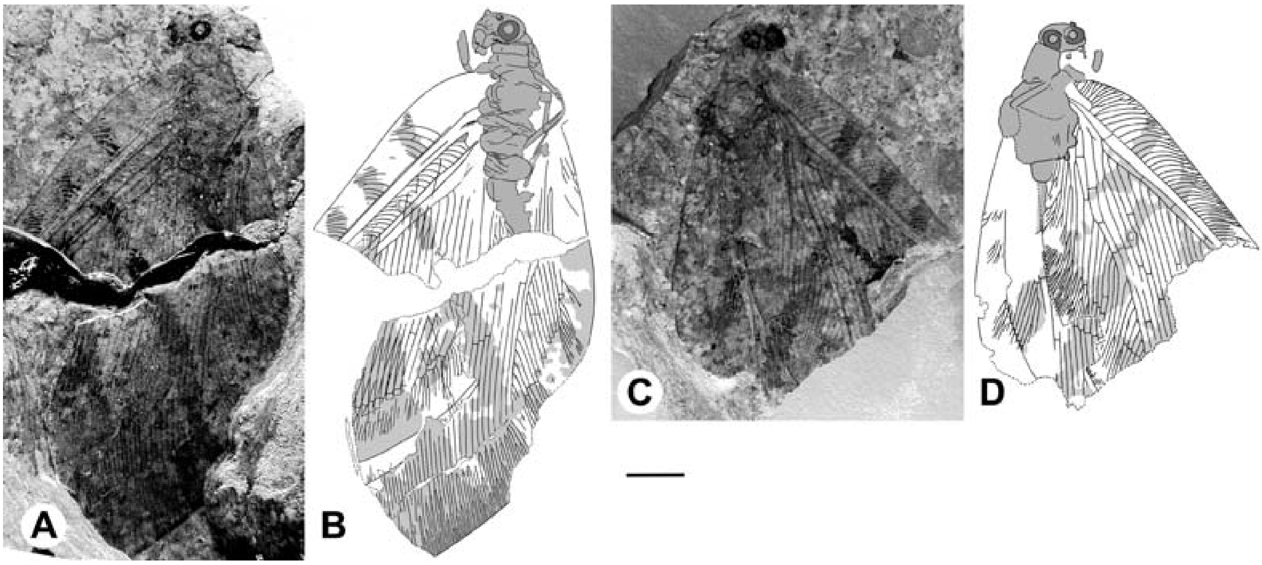

Figure 8 *Palaeopsychops abruptus* Andersen, paratype 1, GMUC, Danekræ No. 168; mostly complete articulated specimen. **A**, photograph of part; **B**, drawing of part; **C**, photograph of counterpart; **D**, drawing of counterpart. Colouration of the body (**B** & **D**) reflects only the apparent limits of preservation. Lines on the body are represented without interpretation; some may represent sclerite borders, others damage or other preservational artefacts. Hairs omitted for clarity. All to scale; scale bar = 5 mm.

ratio 2.1–2.4). Trichosors not visible (margins not well preserved). Distal nygma distinct. Costal gradate series of crossveins not developed (one occasional crossvein detected on counterpart). Subcostal space wide; one basal crossvein detected opposite to origin of Rs. R1 space narrower than subcostal space, with three crossveins preserved in basal half. Rs with more than 13 parallel branches. Radial crossveins poorly preserved, apparently arranged in two regular gradate series, with few additional crossveins. M basally not fused with R possessing small 'stub'. Fork of M not present, but M bent slightly just before basal-most crossvein mp-cua indicating probably its former fork; MA originating from Rs1; MP with seven branches. Cu forked close to wing base. CuA with 6–7 branches. CuP dichotomously branched in distal portion. 1A dichotomously branched, occupying more area than CuP. 2A pectinately branched. Crossveins between branches of Cu forming regular series, which is continuation of outer gradate series. Many hairs present on all veins, many quite long. Hairs appear preserved on membrane as well, in portions of R1 space, immediately posteriad that in Rs area, in area of basal stub of M (but see below). Colour patterning consisting of rather narrow transverse fasciae, breaking in subcostal space. Colour patterning as preserved more precise in anterior half; in posterior half, less distinct, fading from distinct to possibly not present in places (Fig. 8A). Hind-wing: incomplete. Humeral veinlet recurrent and branched. Hairs unusually dense on Costa (particularly basally), humeral veinlet, much longer on frenulum, rare on subcostal veinlets (Fig. 4B); between second to fifth subcostal veinlets pale, rather scarce and longish hairs appear preserved on membrane (but see below). Basal crossvein in subcostal space not detected. R1 space wider than subcostal space in basal half. Branches of Rs (preserved) not forked before outer gradate series, branched after. Radial crossveins not numerous, outer gradate series well preserved. Inner series not preserved. MA with two branches. MP with five to six branches. Cubital, anal veins poorly preserved. True colour patterning not determinable, apparent patterning on hind-wing possibly overprinted from associated fore-wing.

Paratype 2. Length of fore-wing 38–39 mm (estimated), width 16 mm (length/width ratio 2.4). Venation well preserved in apical half of wing, poorly preserved in other areas, particularly no characters detectable with certainty in basal portion, in medial, cubital, anal spaces. Costal gradate series not detected. Rs with 26 branches. Radial crossveins arranged in two regular series. Colour patterning well preserved in distal 2/3 of wing (Fig. 7B), consisting of three quite wide fasciae, without interruption in subcostal space.

Paratype 3. Length of fore-wing 41 mm (estimated), width 17.5 mm (length/width ratio 2.3). Venation rather poorly preserved, particularly in basal portion. Costal gradate series not detected. Radial crossveins apparently arranged in two regular series. Colour patterning well preserved (Andersen 2001: fig. 4), consisting of broad fasciae (in distal portion of wing) breaking in subcostal, R1 spaces.

Remarks. According to Andersen (2001), the species is represented by six fore-wing specimens, of which we have examined the holotype and paratypes 1–3; paratype 1 is exceptionally well preserved, including details of pilosity.

Although paratype 1 is incomplete, its association with the holotype is determined by its diagnostic colour patterning and absence of a costal gradate series. It is difficult to interpret the apparent membrane hairs in the fore-wing of paratype 1: either they belong to the fore-wing membrane or to the underlying hind-wing and are located on its veins, as the majority of these 'membrane hairs' are arranged in regular rows conforming in arrangement and to the presumed positions of wings preserved on the part, and are scarce. The same is true for putative hind-wing membrane hairs: these possibly belong to another wing, overprinted onto it. It is the only specimen examined of the Fur Formation *Palaeopsychops* that is preserved in a rather fine-grained matrix;

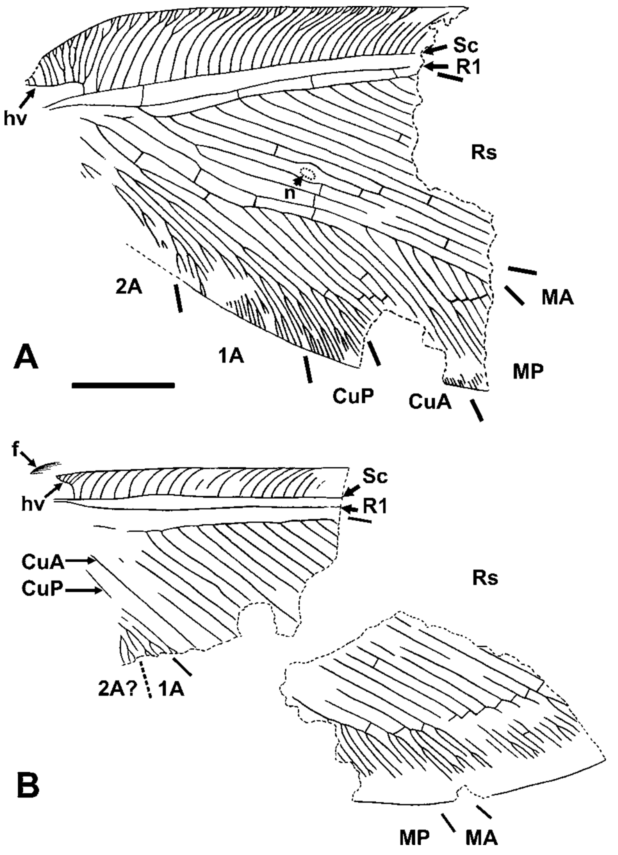

Figure 9 *Palaeopsychops abruptus* Andersen, paratype 1, GMUC, Danekræ No. 168. **A**, drawing of fore-wing; **B**, drawing of hind-wing. **f**, frenulum. For other abbreviations see Material and Methods. Both to scale; scale bar = 5 mm.

lack of setae preserved on the other specimens, preserved in cement-stone matrix, does not indicate their absence in life. The (only known) specimen of *P. setosus* is also preserved in an unusually fine-grained matrix (of specimens examined), more so than the other Okanagan Highlands specimens discussed here. Matrix type undoubtedly plays a large role in hair preservation.

The assignment of paratype 2 to this species is questionable. The colour patterning appears closer to that of the holotype of *P. latifasciatus* than to that of *P. abruptus*, in particular by the absence of the break of fasciae in subcostal space (although fasciae in the subcostal space are not as broad as in *P. latifasciatus*). However, a costal gradate series is not detected and the preserved venation of other portions of the wing does not allow separation of these two species. We consider paratype 2 to tentatively belong to *P. abruptus*, based on the absence of a costal gradate series.

Paratype 3 has character states (the absence of costal gradates series and the break of the fasciae in the subcostal space) that agree well with those of the holotype.

Palaeopsychops angustifasciatus Andersen, 2001 (Fig. 10)

2001 *Palaeopsychops angustifasciatus* Andersen: 429, figs 5, 11.

2003 *Palaeopsychops angustifasciatus* Andersen; Makarkin & Archibald: 172.

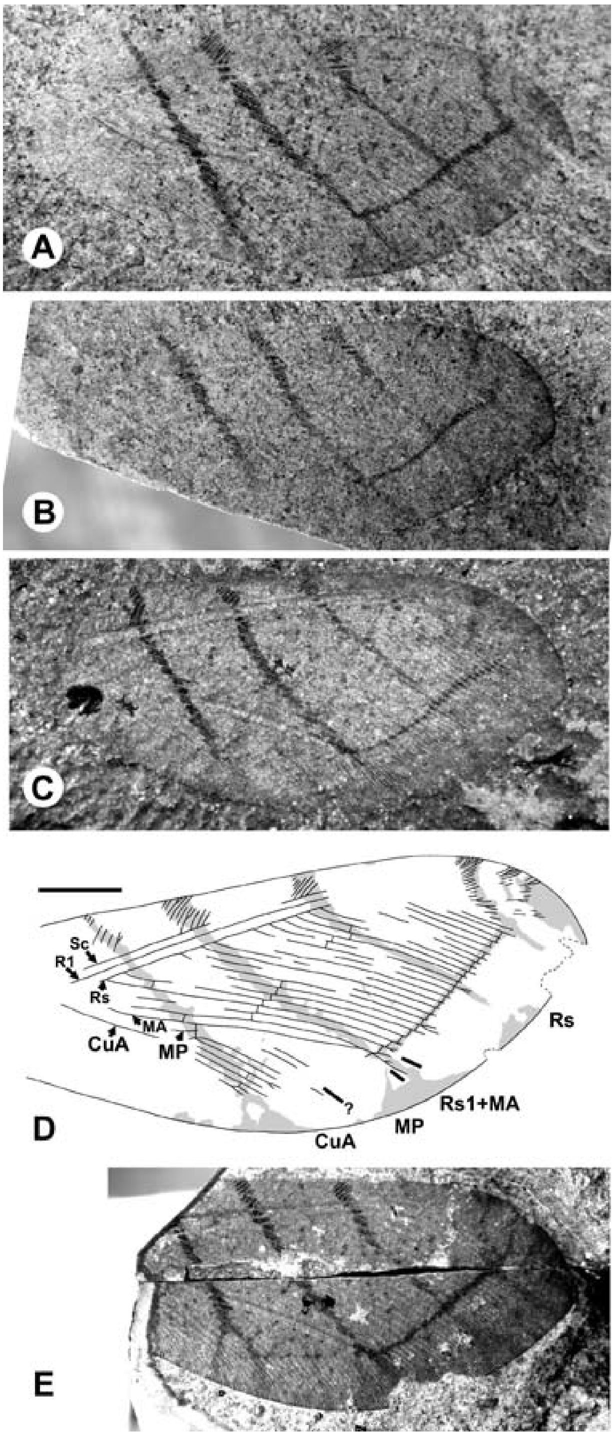

Figure 10 *Palaeopsychops angustifasciatus* Andersen, fore-wings. **A**, photograph of holotype, GMUC, Danekræ No. 89; **B**, photograph of paratype 2, GMUC, MGUH27522; **C**, photograph of GMUC specimen MGUH27524; **D**, drawing of holotype; **E**, photograph of paratype 9, GMUC, MGUH27523. For abbreviations see Materials and Methods. All approximately to scale; scale bar = 5 mm.

Type material. Holotype: Danekræ number 89 (part and counterpart: both labelled '14M-4058'), deposited in GMUC. A rather well preserved, almost complete fore-wing; Ejerslev Molergrav, Mors (Henrik Madsen, collector). Paratype 2: MGUH27522 (part and counterpart: both labelled 'Psy.V.1994'), deposited in GMUC. A rather poorly preserved, incomplete fore-wing; Bygholm Vejlerne (Søren Andersen, collector). Paratype 9: MGUH27523 (part only, labelled 'MOA 742'); deposited in GMUC. A well-preserved, incomplete fore-wing; Mors (Jörg Ansorge, collector).

ADDITIONAL MATERIAL EXAMINED. Specimen MGUH-27524 (part and counterpart, both labelled 'Sv2001'), deposited in GMUC. A rather poorly preserved, almost complete fore-wing; Svalklit (Erwin Rettig (?), collector).

DIAGNOSIS. May be easily distinguished from other species of the genus by distinctive colour patterning (Fig. 10A–C).

OCCURRENCE. Earliest Early Eocene, Fur Formation; Denmark.

DESCRIPTION. *Holotype*. Length of complete fore-wing ~ 36 mm (estimated), width 15.5 mm (length/width ratio ~2.3). Venation poorly preserved (Fig. 10D). Costal space without crossveins in portions where space well-preserved (in fasciae). Rs1, MA clearly fused for short distance at outer gradate series of crossveins. Colour patterning as in Fig. 10A.

Paratype 2. Length of the fore-wing ~ 33 mm, width ~15 mm (estimated) (length/width ratio ~2.2). Venation indistinctly preserved. Costal space without crossveins in portions where costal space well preserved (in fasciae). Distal portions of Rs1, MA not preserved. Colour patterning as in Fig. 10B).

Paratype 9. Length of the fore-wing ~ 29–30 mm (estimated), width 13.5 mm (length/width ratio ~2.2). Venation in general as in holotype. Costal space without crossveins in portions where costal space well-preserved (in fasciae). Rs with ~ 22 branches Rs1, M1 not fused distally. MP with eight to nine branches. CuA with six to seven branches. Colour patterning as in Fig. 10E.

Specimen MGUH27524. Length of the fore-wing 31 mm, width 14 mm (length/width ratio 2.2). Venation in general as in holotype. Costal space without crossveins in portions where well-preserved (in fasciae). Rs with ~ 24 branches. Rs1, M1 nearly fused at outer gradate series (connecting crossvein very short). Fork of M not present; probably MA originating from Rs1 (not clearly visible); Colour patterning as in Fig. 10C.

REMARKS. According to Andersen (2001), the species is represented by 11 fore-wing specimens, of which we have examined the holotype, three paratypes (1, 2 and 9) and specimen MGUH27524. The association of the holotype, paratype 2 and specimen MGUH27524 are undoubted based on their almost identical and distinctive colour patterning (some variation is observed in these specimens in the relative distance between the three transverse stripes, *cf.* Fig. 10A–C), whereas that of paratype 1 is sufficiently distinctive to place it in its own species (see below).

The assignment of paratype 9 to this species is questionable. Some details of colour patterning (deeper forking of the basalmost fascia posteriorly) and venation (Rs1 and MA not fused distally) differ from those of other specimens, including the holotype. We consider, however, these character states as an example of intraspecific variation since this specimen does not differ otherwise from typical specimens.

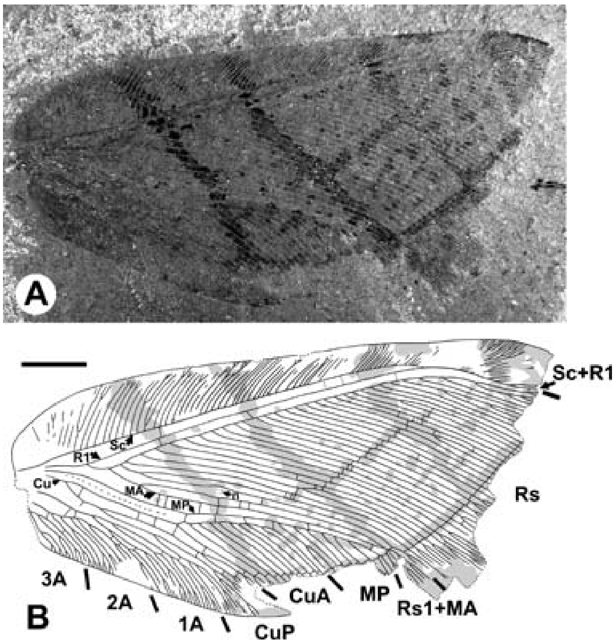

Figure 11 *Palaeopsychops quadratus* sp. nov., holotype, GZG, GZG 001261/1a/1b; fore-wing. **A**, photograph of part; **B**, drawing from part and counterpart. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

Palaeopsychops quadratus sp. nov. (Fig. 11)

2001 *Palaeopsychops angustifasciatus*: Andersen: 429 (*partim*).

TYPE MATERIAL. Holotype: GZG 001261/1a and GZG 001261/1b (part and counterpart), deposited in GZG. A well preserved, almost complete fore-wing, but missing portions of the hind margin from mid-wing to apex; Ejerslev Molergrav, Mors (Mike Reich, collector).

ETYMOLOGY. The specific epithet *quadratus* is from the Latin adjective *quadratus,* 'square,' referring to the shape formed by the crossing of stripes in the forewing.

DIAGNOSIS. Similar to *P. angustifasciatus* by colour patterning of fore-wing, but may be distinguished from it by presence of longitudinal dark stripe along inner gradate series in radial space between second, third transverse fasciae [not present in other species].

OCCURRENCE. Earliest Early Eocene, Fur Formation; Denmark.

DESCRIPTION. *Fore-wing*. Preserved length (incomplete) 37 mm (estimated complete length ~ 42 mm), width ~19 mm (length/width ratio 2.2). Trichosors indistinct. Distal nygma present between Rs1, Rs2. No costal crossveins detected. Humeral veinlet not preserved. Subcostal veinlets mainly forked. Subcostal space rather wide along entire length with one crossvein in basal part clearly preserved, three crossveins poorly-preserved in distal part. R1 space narrower than subcostal space, with three to four crossveins. Rs with 31 branches, rarely forked before outer gradate series. Crossveins in radial space arranged in two gradate series: inner series distinct but rather irregular, with several crossveins scattered proximad, distad; outer series regular, parallel to inner series in radial space, continuing as regular series in cubital space, as irregular series in anal space. Short crossveins between branches in area of end-twigging in radial to cubital space not detected, but two crossveins distal to outer series just at boundary of end-twigging preserved. Fork of M not present, MA originated from Rs1, distally fused with it again just before outer gradate series. MP with seven rather irregular branches. Cu forked close to wing base. CuA with nine branches. CuP, 1A dichotomously branched. 2A pectinately branched, with five long branches. 3A short, nearly straight with two anteriorly directed branches, of which more proximal branch deeply forked, parallel to branches of 2A. Irregularly spaced crossveins between MA, MP; MP, CuA; CuA, CuP; anal veins not belonging to gradate series. Colour patterning: light membrane with dark, narrow fasciae, three across width of wing, two along gradate series; small scattered stripes, spots mostly posteriad inner gradate series of crossveins (Fig. 11B).

REMARKS. *Palaeopsychops quadratus* was designated paratype 1 of *P. angustifasciatus* (Andersen, 2001). This new species may be further distinguished from *P. angustifasciatus* (as well as by colour patterning, as in diagnosis) by possession of a longer fore-wing (~42 mm) in comparison with the three specimens of *P. angustifasciatus* (~30–36 mm). Colour patterning shows little variation among the specimens of *P. angustifasciatus* (Fig. 10A–C). The possibility remains that these differences are due to sexual dimorphism within the same species, and this might also be said of any of the other morphologically similar species (e.g. *P. latifasciatus* and *P. abruptus*, or *P. dodgeorum* and *P. marringerae*), however, sexual dimorphism in colour patterning is not reported in extant Polystoechotidae.

Palaeopsychops dodgeorum Makarkin & Archibald, 2003 (Fig. 12)

2003 *Palaeopsychops dodgeorum* Makarkin & Archibald: 172, figs 1–5.

TYPE MATERIAL. Holotype: Q-0422 a, b (part and counterpart), deposited in SFU. A rather well preserved, almost complete left fore-wing; the Quilchena locality (Kenneth Dodge and Ken Dodge, collectors).

OCCURRENCE. Early Eocene, Coldwater Formation; Quilchena, British Columbia, Canada (Okanagan Highlands).

REMARKS. This species was previously described and discussed (Makarkin & Archibald 2003). No additional material has been found. *Palaepsychops dodgeorum* is most close to *P. marringerae* (see below).

Palaeopsychops marringerae sp. nov. (Fig. 13)

TYPE MATERIAL. Holotype: SR97-08-05 (part only), deposited in SR. A well-preserved apical 2/3 of fore-wing; Burke Museum locality UWBM B4131 (Regina Marringer, collector).

ETYMOLOGY. The specific epithet is from the surname of Regina Marringer, the collector of the holotype, in recognition of her contribution to palaeontology by the donation of this specimen to the Stonerose Interpretive Center.

DIAGNOSIS. Close to *P. dodgeorum* in fore-wing shape and venation, but may be easily distinguished from it (as well as from other species) by distinctive colour patterning (transverse bands run at almost right angles to anterior margin in *P. marringerae* and more obliquely in *P. dodgeorum*) and by the distal branching of the Rs branches (many-branched, with numerous short crossveins in area of end-twigging in *P. marringerae*; few branches, with much fewer crossveins in *P. dodgeorum*.

OCCURRENCE. Early Eocene, Klondike Mountain Formation; Republic, Washington, USA (Okanagan Highlands).

DESCRIPTION. Fore-wing. Length of incomplete wing 33 mm, width 20 mm; estimated length of complete fore-wing ~45 mm, width ~20.5–21 mm (length/width ratio 2.14–2.20). Trichosors indistinct (not shown in Fig. 13B). Nygmata not detected. Several costal crossveins in proximal portion of fragment forming irregular series. Subcostal space slightly narrower than R1 space; no crossveins detected in preserved 2/3 of former. Preserved ~3/4 of R1 space with four crossveins. Rs with >23 pectinate branches. Numerous irregularly spaced crossveins in radial space. Inner gradate series not formed. Outer gradate series apparently distinct, but preserved only in dark areas of wing. Terminal M region crumpled, torn to some degree; MA apparently dichotomously branched; MP with >4 rather irregular branches. Cu, anal veins not preserved. Short crossveins between branches of Sc+R1, Rs, M in area of end-twigging rather numerous. Wing patterning distinct, represented by dark membrane with light transverse bands (Fig. 13A).

REMARKS. This species has equal size, similar fore-wing shape and venation to those of *P. dodgeorum*: length/width ratio 2.14–2.18 in the latter and 2.14–2.20 in the new species; both species possess a costal gradate series and numerous irregularly spaced crossveins in the radial space anterior to outer gradate series. They are probably closely related, distinguished from each other, however, by the characters mentioned above.

Palaeopsychops timmi sp. nov. (Fig. 14)

TYPE MATERIAL. Holotype: SR02-25-01 (part only), deposited in SR. A well-preserved basal 2/3 of left fore-wing with colour patterning preserved; Burke Museum locality UWBM locality B4131 (Thomas Timm, collector).

ETYMOLOGY. The specific epithet is from the surname of Thomas Timm, the collector of the holotype, in recognition of his contribution to palaeontology by the donation of this specimen to the Stonerose Interpretive Center.

DIAGNOSIS. May be easily distinguished by distinctive colour patterning (Fig. 14A).

OCCURRENCE. Early Eocene, Klondike Mountain Formation; Republic, Washington, USA (Okanagan Highlands).

DESCRIPTION. Fore-wing. Length of the fragment 37 mm, width 20 mm; estimated length of complete fore-wing ~43–44 mm, width 20 mm (length/width ratio 2.15–2.20). Trichosors indistinct although hind margin well-preserved. Nygmata not detected. Costal space with incomplete, irregular gradate series of crossveins. Subcostal veinlets rather poorly preserved with forkings not visible. Subcostal space

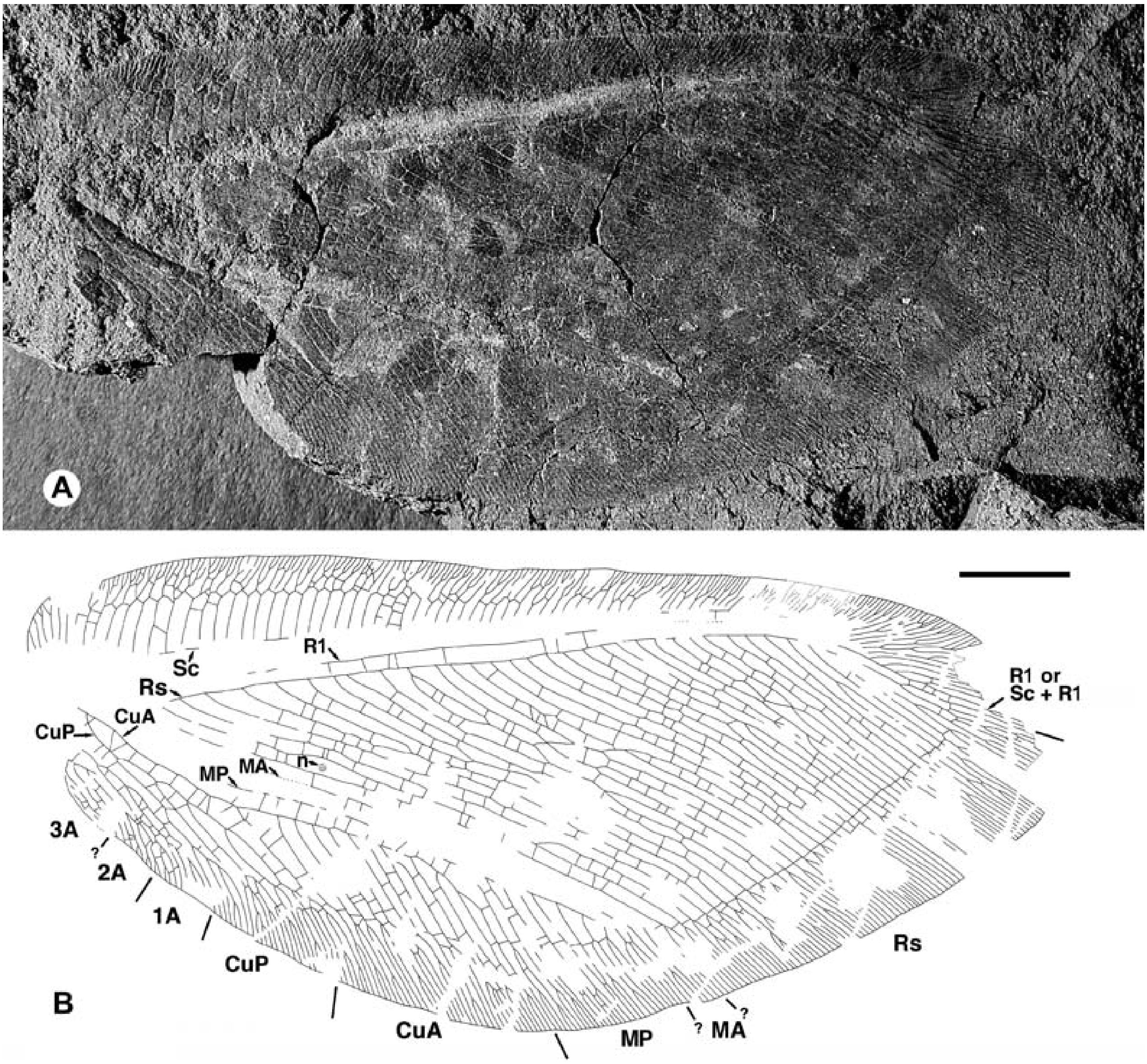

Figure 12 *Palaeopsychops dodgeorum* Makarkin & Archibald, holotype, SFU, Q-0422 fore-wing. **A**, photograph of part, Q-0422a. Note colour patterning, particularly preserved in basal portion. **B**, combined drawing from part and counterpart after Makarkin & Archibald (2003: fig. 1; venational terminology differs in part). Colour patterning preserved faintly, not added here. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

rather narrow along entire length; one to two crossveins in basal part preserved. R1 space approximately as wide as subcostal space, four crossveins preserved basally. Rs with more than 17 parallel branches not forked before outer gradate series, dichotomously forked after. Radial crossveins numerous, irregular (except for outer gradate series), posteriorly closely spaced, anteriorly more scarce. Inner gradate series indistinct and irregular. Outer gradate series distinct, regular, running distantly from hind margin, not continuing as regular series in cubital space. M not fused basally with R; fork of M not detected; MA conspicuously concave; MP with seven to eight rather irregular branches. Fork of Cu not detected. CuA with nine branches. CuP, anal veins poorly preserved, only few details visible (mostly near hind margin of wing). Crossveins between cubital veins numerous, not forming regular series. Short scattered crossveins occurring between branches of end-twigging in radial to cubital space. Colour patterning consisting of light membrane with dark maculations in proximal portion, almost uniformly dark membrane in distal portion (Fig. 14A).

REMARKS. The assignment of this species (as well as that of *P. dodgeorum* and *P. marringerae*) to *Palaeopsychops* is based on the combination of venational characters (1), (2) and (4) of the generic diagnosis, as well as similarity of the general arrangement of venation with that of the type species, *P. latifasciatus*. One of the diagnostic characters of the genus (fork of M absent), however, is not detected here (as well as in specimens of the other two North American 'fore-wing species'); the basal portion of the wing is poorly preserved.

Palaeopsychops timmi differs from other species of *Palaeopsychops* by colour patterning, i.e. by the absence of

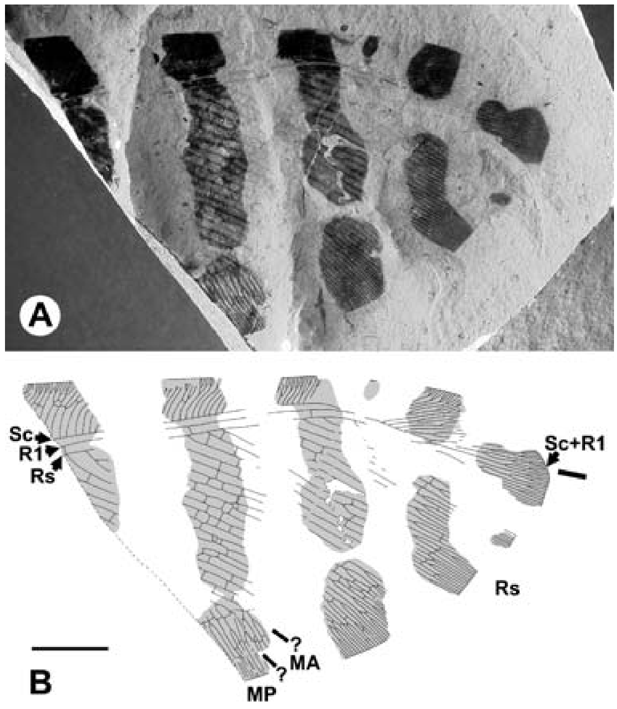

Figure 13 *Palaeopsychops marringerae* sp. nov., holotype, SR, SR97-08-05; fore-wing. **A**, photograph; **B**, drawing. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

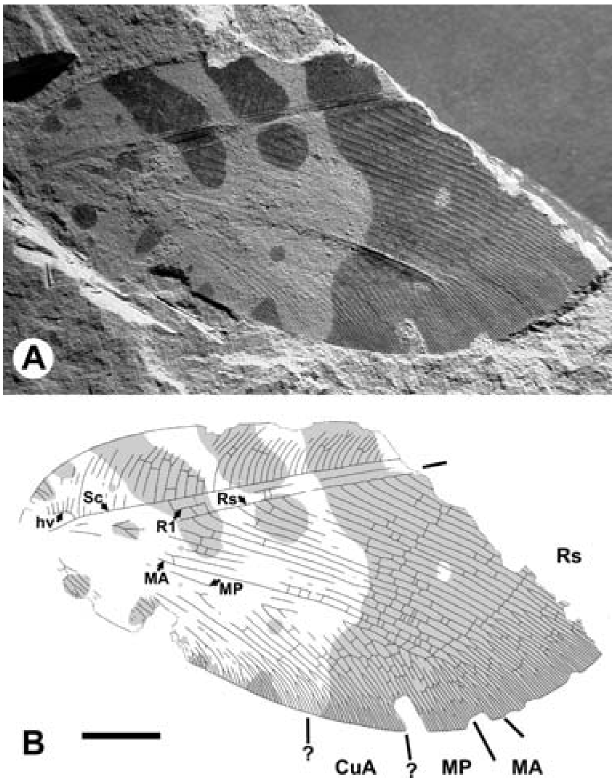

Figure 14 *Palaeopsychops timmi* sp. nov., holotype, SR, SR02-25-01; fore-wing. **A**, photograph; **B**, drawing. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

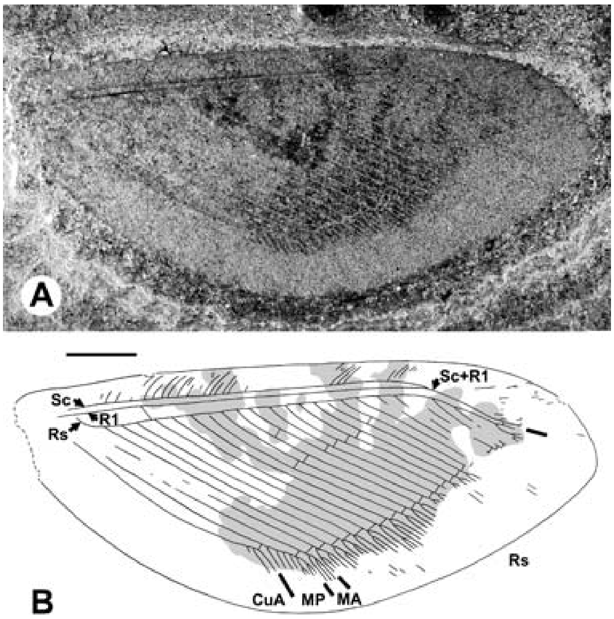

Figure 15 *Palaeopsychops maculatus* Andersen, holotype, GMUC, Danekræ No. 298; hind-wing. **A**, photograph; **B**, drawing. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

distinct transverse bands considered diagnostic for the genus, although the apical portion of this wing is not known (Makarkin & Archibald 2003: 172). For this reason, we exclude this character from the diagnosis of the genus.

Palaeopsychops maculatus Andersen, 2001 (Fig. 15)

2001 *Palaeopsychops maculatus* Andersen: 250, figs 6, 12.
2003 *Palaeopsychops maculatus* Andersen; Makarkin & Archibald: 172, 173.

Type material. Holotype. Danekræ number 298 (part and counterpart: both labelled '14M-B4885'), deposited in GMUC. A rather poorly preserved complete hind-wing; Ejerslev Molergrav, Mors (Henrik Madsen, collector).

Diagnosis. Close to *P. setosus* by similar colour patterning, wing shape and venation (*cf.* Fig. 15B and Fig. 16B), but may be distinguished from it by clearly shorter distance between inner and outer gradate series and somewhat wider basal half of wing.

Occurrence. Earliest Early Eocene, Fur Formation; Denmark.

Description. Hind-wing 40 mm long, 17.5 mm wide (length/width ratio 2.3). Trichosors, nygmata not preserved. Crossveins in subcostal space not detected; two crossveins in R1 space. Rs with ~ 26 parallel branches, not forked before outer gradate series. Inner, outer gradate series of crossveins regular, parallel, with occasional crossveins proximal to inner series (one detected with certainly). MP with five branches. CuA parallel to hind margin, branching not preserved. CuP, anal veins not preserved. Veinlets of end-twigging poorly preserved, short crossveins not detected between them. Colour patterning: central area of wing mainly dark, light near margins, at base, apex (Fig. 15A).

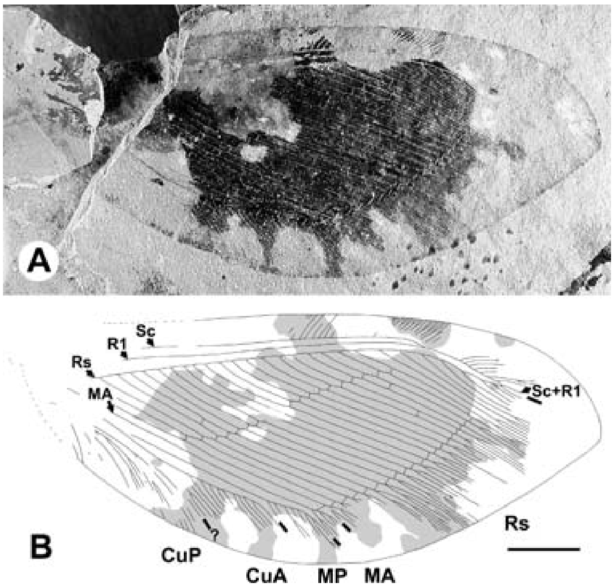

Figure 16 *Palaeopsychops setosus* sp. nov., holotype, UA, UAFIC8354 (part) and UAFIC8335 (counterpart); hind-wing. **A**, photograph of part; **B,** combined drawing from part and counterpart. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

Remarks. The holotype hind-wing represents the only known specimen of the species. It is remarkably similar to that of *P. setosus* in wing shape, size, maculation and most aspects of venation (discounting membrane hairs, as preservation precludes determination of their presence on *P. maculatus*) and differs considerably from other 'hind-wing species' of the Tertiary Polystoechotidae (*Palaeopsychops douglasae, Polystoechotites lewisi*) by these characters. Unfortunately, the hind-wings of *Palaeopsychops abruptus*, the single species with articulated fore- and hind-wings, are insufficiently complete for detailed comparison.

The 'hind-wing species' *P. maculatus* may be a synonym of the 'fore-wing species' *P. latifasciatus*, by the rather broad fasciae in the subcostal space shared between them, but until articulated fore- and hind-wings are found, this is speculative.

Palaeopsychops setosus sp. nov. (Figs 16, 17)

Type material. Holotype. UAFIC 8354 (part) and UAFIC 8335 (counterpart), deposited in UA. Part: a hind-wing with colour patterning and hairs clearly preserved, missing a portion of the basal region; counterpart: a complete hind-wing, faintly preserved (but with mostly distinct venation) without colour patterning or hairs; the Horsefly River locality (H3 of Wilson 1977) (Mark Wilson, collector).

Etymology. From the Latin *setosus*, hairy, bristly.

Diagnosis. Very similar to *P. maculatus*, separated from it by those characters in its diagnosis (above).

Occurrence. Early (or early Middle) Eocene, unnamed formation; Horsefly, British Columbia, Canada (Okanagan Highlands).

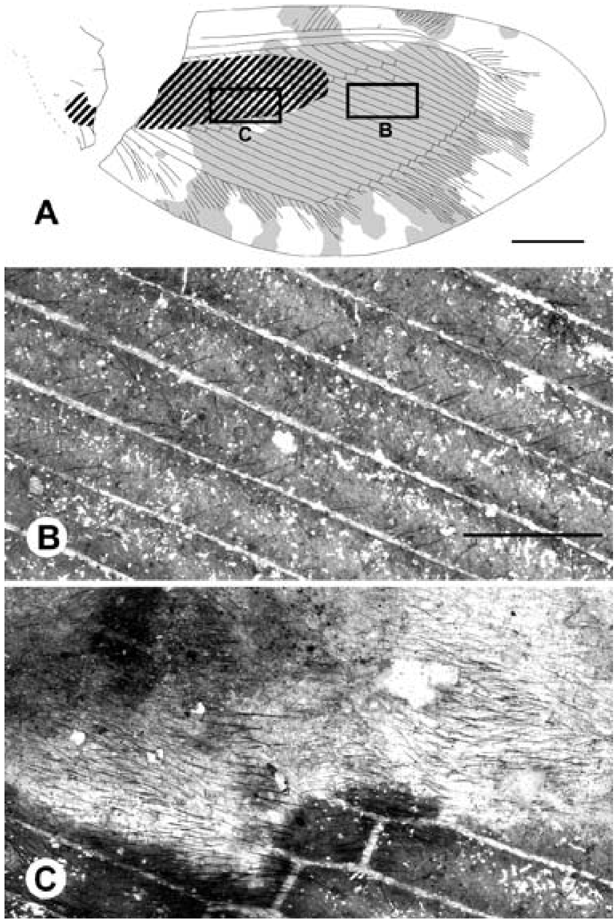

Figure 17 Dense macrotrichia across both membrane and veins in a region of the hind-wing of *Palaeopsychops setosus* (holotype, part). **A**, crosshatching marks region of pilosity; 'B', location of enlarged area shown in Fig. **17B**; 'C', location of enlarged area shown in Fig. **17C**. Scale bar = 5 mm; **B**, close-up in region of normal long macrotrichia on veins, not membrane; **C**, close-up of densely pilose region showing macrotrichia across both light and dark coloured wing areas. **B** and **C** both to scale; scale bar = 1 mm.

Description. Hind-wing 40 mm long, 17 mm wide (length/width ratio 2.35). Trichosors, nygmata not preserved. Sc+R1 probably entering margin before wing apex, preserved branches long, forked. Crossveins in subcostal space, R1 spaces not detected (except 1 in latter). Rs with 28 parallel branches, not forked before outer gradate series. Inner, outer gradate series regular, parallel; only few occasional crossveins between series. MP, CuA convergent basally, MP with six to seven branches. CuA parallel to hind margin, with 11 branches. CuA, CuP somewhat divergent basally. Configuration of CuP, anal veins not visible with certainty. Crossveins in medial to anal spaces, short crossveins between branches of end-twigging not detected, apparently because of poor preservation of these areas. Colour patterning: wing membrane mainly dark, light near margins, at base (basalmost portion of wing not available), apex (Fig. 16A). Setose band extends along roughly median portion of wing in basal half; in this, dense macrotrichia ~0.15–0.30 mm long (Fig. 17C) extends across membrane, veins without differentiation (Fig. 17A). Along posterior boundary of band hairs largest, densest, ending abruptly, distinctly; anterior boundary ill defined, grading to finer, sparser hairs to possibly beyond detection or preservation. In other well-preserved regions, macrotrichia present, well-preserved on veins, not membrane as in other Polystoechotidae (Fig. 17B), indicating preserved region of dense trichiation conforms to life condition.

Remarks. In this species (as well as in *P. maculatus* and *P. douglasae*) colour patterning differs markedly from that of fore-wing, perhaps typical for the genus. The presence of a setose region, however, has been hitherto unknown in the genus (and order).

Both microtrichia and macrotrichia occur on neuropteran wings. Microtrichia are present in several families as minute hairs that densely cover the entire wing surface, but they are absent from the wings of extant Polystoechotidae, excluding some extreme basal areas (Riek 1967). They are usually not detectable in impression fossils, although Ren & Yin (2003) noted their presence in beautifully preserved neuropterans from a Middle Jurassic locality in China. Further examination of those fossils, however, indicates that this observation was erroneous (Oswald, pers. comm.). A number of insects from Okanagan Highlands localities (e.g. some Bibionidae (Diptera)) are preserved in such fine-grained matrix that microtrichia are clearly discernable (Rice 1959; pers. obs.). Longer macrotrichia may often be detectable in impression fossils, particularly along the margins of even some of the more poorly preserved wings examined here. In Neuroptera, they are generally restricted to the veins, mostly longitudinal (Tillyard 1918; Killington 1936). In *Palaeopsychops setosus*, however, macrotrichia occur distinctly on and across the wing membrane. This case is very unusual. Although membrane macrotrichia are found in some other insect orders (e.g. Megaloptera, Trichoptera, Lepidoptera, some Mecoptera and Diptera), they are apparently never arranged into such a discrete, dense, setose region, the function of which is unknown.

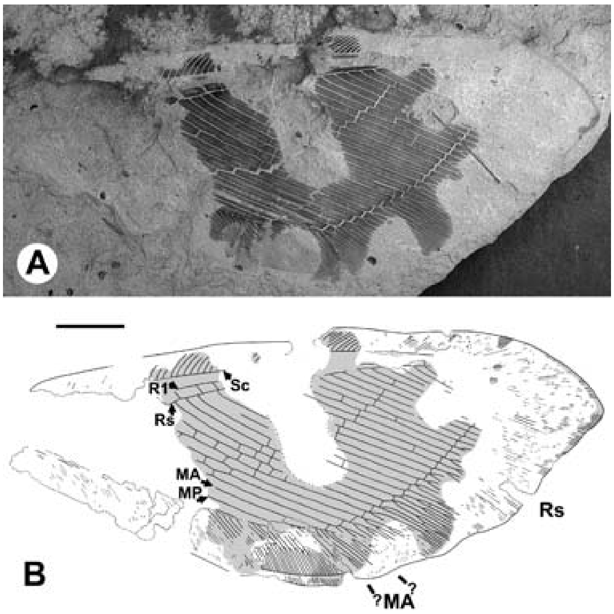

Figure 18 *Palaeopsychops douglasae* sp. nov., holotype, UA, UAFIC7794; hind-wing. **A**, photograph of counterpart; **B,** combined drawing from part and counterpart. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

Palaeopsychops douglasae sp. nov. (Fig. 18)

Type material. Holotype. UAFIC7794a, b (part and counterpart), deposited in UA. Part: a pale, but rather well preserved hind-wing in two parts (not glued) with portions of the mid-wing and basal regions not preserved, without colour patterning; counterpart: more complete, with distinctly preserved colour patterning and crossvenation (in coloured regions); the Quilchena locality (Mark Wilson, collector).

Etymology. The specific epithet is a patronymic in honour of Sheila Douglas, recognising her contribution to palaeoentomology in British Columbia (see Douglas & Stockey 1996).

Diagnosis. May be easily distinguished from other species by undulant hind margin of hind-wing.

Occurrence. Early Eocene, Coldwater Formation; Quilchena, British Columbia, Canada (Okanagan Highlands).

Description. Hind-wing. Length 42 mm, maximal width 19 mm (length/width ratio 2.21). Trichosors indistinct. Hind margin somewhat undulant, therefore apical portion slightly falcate. Costal space poorly preserved, rather narrow basally, boundary not detectable distally. Subcostal veinlets, Sc, R1 mostly indistinct. Subcostal, R1 spaces mainly poorly preserved, four to five crossveins detected in latter. Rs with >26 parallel branches, not forked before outer gradate series, distal to which each branch dichotomously branched forming end-twigging, veinlets of which very closely spaced. MA distally with four long oblique pectinate branches. Distal branching of MP only partially visible (otherwise overlain by preserved, small portion of fore-wing). CuA runs parallel to hind margin of wing, preserved distal portion with nine long, oblique pectinate branches. CuP, anal veins poorly preserved, no details visible. Inner series of gradate crossveins more or less distinct in anterior portion of radial space (but with additional irregularly spaced crossveins proximal, distal to it), disappearing posteriorly where many crossveins occur irregularly scattered between branches of Rs. Outer series of gradate crossveins rather regular, with several additional crossveins. Scarce, irregularly scattered short crossveins in area of end-twigging in radial, cubital spaces; other crossveins in cubital space not detected. Wing colour patterning: uniformly dark in most of central portion; light by hind margin (patches), entire apical portion except for narrow shading along apical margin.

Remarks. The undulant hind margin of the hind-wing in this species is unique within the family and is considered here a species-level apomorphy. This character state occurs rarely in Neuroptera, for example, in some extant Hawaiian species of the hemerobiid genus *Micromus* (Zimmerman 1957). Some fossil species possess it as well, e.g. the Late Cretaceous *Palaeogetes ponomarenkoi* Makarkin, 1990 from Gulkili (Kazakhstan) referred to the Prohemerobiidae (Makarkin 1990) and the Middle Jurassic 'osmylid-like' species *Laccosmylus calophlebius* Ren & Yin from Inner Mongolia (China) (Ren & Yin 2003).

Palaeopsychops douglasae is assigned to *Palaeopsychops* based on general agreement of venation and similarity of colour patterning with those of other species in this genus.

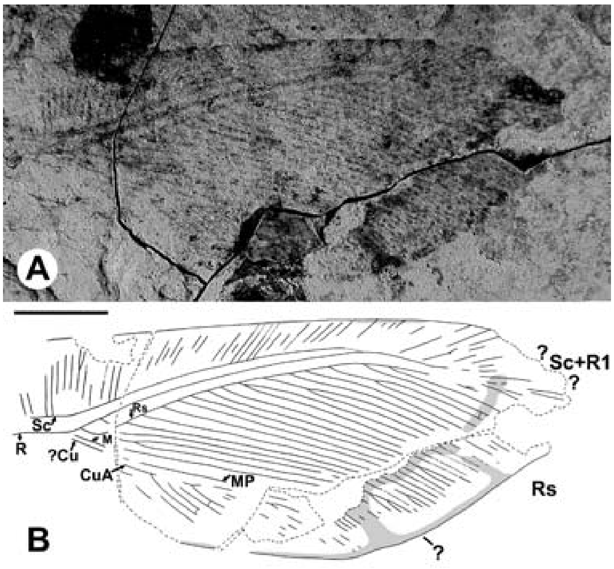

Figure 19 *Polystoechotites piperatus* (Cockerell, 1908), holotype, AMNH, AMNH34871; fore-wing. **A**, photograph; **B**, drawing. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

The branching of MP is only questionably visible, however, we may infer its pectinate branching based on the distal configuration of the preserved portions of MA, MP and CuA.

Genus ***POLYSTOECHOTITES*** gen. nov.

Type species. Collective groups do not have type species (ICZN, 1999: Art. 13.3.2, 42.3.1, 66).

Etymology. *Polystoechot-* (from *Polystoechot*[*idae*], a neuropteran family-group name) + *-ites* (a traditional ending of fossil genus names). Gender masculine.

Description. As a parataxon, *Polystochotites* is an artificial association of polystoechotid species. Although its description is then the same as that of the family, as proposed, this genus is delimited within the Polystoechotidae as the collective group comprised of all fossil species of the family whose generic attributes are unclear and so cannot be placed with sufficient certainly in any known genus.

Remarks. The names of collective groups are regulated by the International Code of Zoological Nomenclature (e.g. ICZN, 1999: Art. 10.3, 23.7, 42.2.1 and 67.14). The species described below are well distinguishable (in particular, by wing maculation) and will undoubtedly be referred to different genera (either existing or new) when more complete specimens are found. The concept of the collective group has not been applied before to fossil Neuroptera. Parataxonomy in general is discussed above (see Materials and Methods, Taxonomic Approach).

Polystoechotites piperatus (Cockerell 1908) (Fig. 19)

1908 *Polystoechotes piperatus* Cockerell: 59; pl. 5, fig. 2.
1943 *Propsychopsis piperatus* (Cockerell); Carpenter: 760.
1970 *Polystoechotes piperatus* Cockerell; MacLeod: 165.
2003 *Polystoechotes piperatus* Cockerell; Makarkin & Archibald: 171.

Type material. Holotype. AMNH34871, deposited in AMNH. A poorly-preserved incomplete fore-wing; Florissant, Station 14 (George Rohwer, collector).

Diagnosis. May be distinguished from other polystoechotid species by Sc, R1 strongly bent basally, clearly shaded hind, outer margin of wing.

Occurrence. Latest Late Eocene, Florissant Formation; Florissant, Colorado, USA.

Description. Fore-wing rather narrow, venation poorly preserved. Length of preserved portion ~27 mm, estimated complete length ~31 mm, width ~12.5 mm (length/width ratio 2.48). Trichosors indistinct. Nygmata not detected. Costal space maximally expanded basally, narrowed towards apex, after possible fusion Sc, R1 expanded again; costal crossveins not detected. Sc, R1 basally bent quite greatly. Subcostal veinlets poorly preserved, their forkings mostly not detectable. Subcostal, R1 spaces wide for entire preserved length. Crossveins in subcostal space not detected. R1 space with only one basal crossvein preserved. Rs with 16 pectinate branches, four forked basally. Crossveins in radial series not detected, except for one in outer gradate series. Branching of MP poorly preserved. CuA pectinately branched (with 5–7 long branches); at least two crossveins between branches clearly visible. CuP, anal veins not preserved. Wing membrane rather pale, mottled with darkish colouration, except outer gradate series, which appears shaded; clearly shaded hind, outer margin of wing (Fig. 19A).

Remarks. The psychopsid affinity of this species was based on 'the very broad costal margin [= costal space] and nearly triangular wing' (Carpenter 1943: 760). Later, MacLeod (1970) re-examined the sole specimen and substantiated this assessment. The costal space is not, however, broader than in Eocene Polystoechotidae and is narrower than in extant and Tertiary Psychopsidae (particularly in the distal portion).

Further more, although the wing shape is difficult to establish due to damage, it is elongate and, at most, subtriangular, not deeply triangular as in psychopsids (although deeply triangular wings may occur in Polystoechotidae, see below: Q-0421, *Polystoechotites* sp. A). Moreover, no characters present in this specimen contradict a polystoechotid affinity. Unfortunately, the venation (e.g. configuration of MA, MP, CuP, anal veins, crossvenation) is too poorly preserved and incomplete to assign this species to an (orthotaxonomic) genus. In spite of this, *P. piperatus* is clearly closer to extant polystoechotid species than to Early Eocene species by its similar colour patterning and elongate fore-wing.

Polystoechotites barksdalae sp. nov. (Fig. 20)

Type material Holotype. SR97-3-9a, b (part and counterpart), deposited in SR. A poorly-preserved (crumpled and torn) fragmentary fore-wing. Part: much of basal half and torn portions of apical portion; counterpart: portion of basal half only; Burke Museum locality UWBM B4131 (Lisa Barksdale, collector).

Additional material examined. SR01-01-14a, b (part and counterpart), deposited in SR. Part and counterpart similar. A rather well-preserved costal space of a fore-wing; Burke Museum locality UWBM B4131, (Barbara and Bob Carl, collectors).

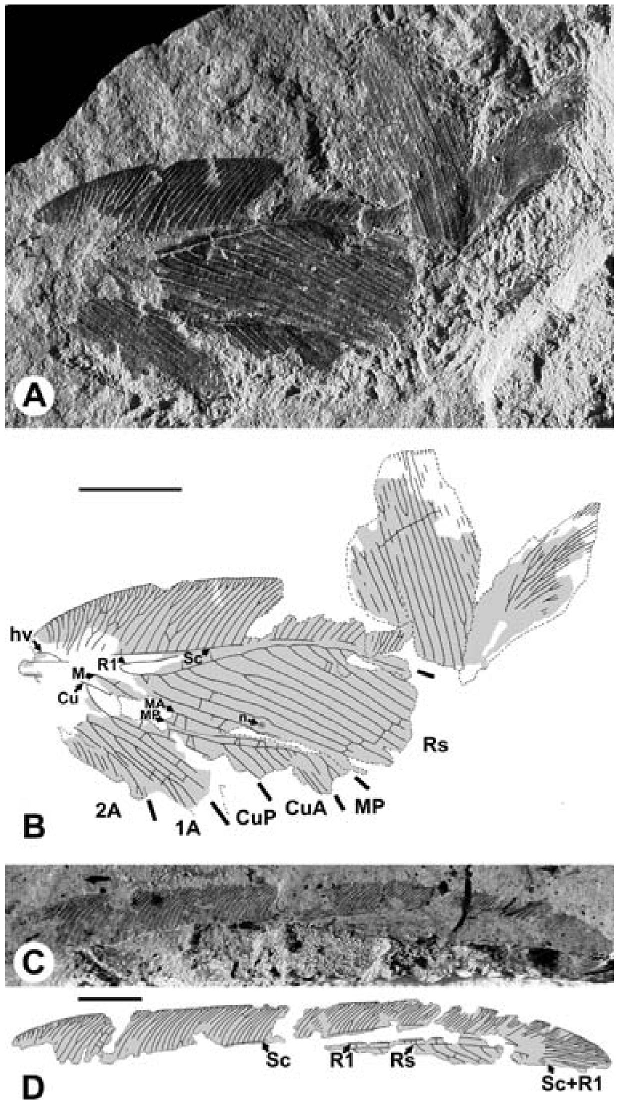

Figure 20 *Polystoechotites barksdalae* sp. nov. **A**, holotype, SR, SR97-3-9, fore-wing photograph of part; **B**, combined drawing of the holotype from part and counterpart. **C**, Specimen SR, SR01-01-14, fragmentary fore-wing, photograph of part; **D**, combined drawing of SR01-01-14 from part and counterpart. For abbreviations see Materials and Methods. A and B to same scale; C and D to same scale; scale bars = 5 mm.

Etymology. The specific epithet is a patronymic formed from the surname of Lisa Barksdale, the collector of the holotype, in recognition of her extensive service to palaeontology at Republic, Washington as curator and collections manager at the Stonerose Interpretive Center (see Acknowledgements, below).

Diagnosis. Easily distinguished from other polystoechotid species by the combination of the following fore-wing characters: colour uniformly dark, costal gradate series absent, two regular gradate series in radial space.

Occurrence. Early Eocene, Klondike Mountain Formation; Republic, Washington, USA (Okanagan Highlands).

Description. Holotype SR97-3-9. Fore-wing. Length of preserved portion ~30 mm (somewhat torn, crumpled), width of basal fragment 12 mm; estimated complete length ~35–40 mm, width ~13–15 mm. Trichosors indistinct along costal margin, otherwise wing margin not preserved. Distal nygma distinct, located between Rs1, Rs2. Costal space maximally expanded at proximal 1/4–1/5 of length, narrowed towards base, apex; four costal crossveins detected, of these three located in proximal portion of space. Humeral veinlet recurrent, branched. All preserved subcostal veinlets forked. Subcostal, R1 spaces overlap each other for almost entire preserved length. R1 space with two crossveins preserved. Rs with >17 preserved pectinate branches, of these four forked before outer gradate series. Two regular series of gradate crossveins (inner, outer) present, additional few crossveins irregularly scattered proximal to inner series. Only small middle portions of MA, MP preserved, distally overlapped by torn portion of wing bearing CuA. CuA pectinately branched (with 7 long, regular branches). CuP pectinately branched with >2 (apparently 3–4) strongly oblique long branches. 1A dichotomously branched. 2A pectinately branched. Crossveins between MA, MP; MP, CuA; CuA, CuP, branches of CuP, 1A quite numerous, irregularly spaced. Wing membrane uniformly dark; veins mostly appear pale (Fig. 20A).

Specimen SR01-01-14 (tentatively assigned to this species). Fore-wing. Length of fragment available 48 mm, width 6 mm, length of fore-wing (estimated) ~50–54 mm. Costal space moderately expanded basally, narrowed toward region of fusing Sc, R1, then again somewhat expanded. About 10 costal crossveins detected, of these five in proximal portion of space. Almost all subcostal veinlets forked. Subcostal space, R1, radial spaces almost not preserved; six crossveins detected in distal portion of R1 space, two in preserved portion of radial space. Colour patterning of preserved fragment uniformly darkish (Fig. 20C).

Remarks. Judging by colouration and preserved venation, SR01-01-14 belongs almost surely to *P. barksdalae*. However, its fragmentary nature leaves room for some doubt and, therefore, this determination is tentative. Both specimens have uniformly dark wings and similar venation in the costal space (i.e. the absence of a complete costal gradate series, but with several crossveins in the proximal portion and very short marginal forkings of subcostal veinlets in the mid-length of the space). The differences in size between these two specimens (fore-wing length (estimated) ~35–40 mm in SR96-3-9 and ~50–54 mm in SR01-01-14 (the smaller is 65–80% the larger) is not as great as that within some extant species, e.g. in *Polystoechotes punctatus*, fore-wing length ranges from 18–34 mm (maximum difference 53%: Carpenter 1940).

This species may belong to the genus *Palaeopsychops*. Unfortunately, it is represented by incomplete and crumpled specimens, whose visible characters are insufficient for precise determination. Moreover, the uniformly dark forewing is not characteristic of *Palaeopsychops*.

Polystoechotites falcatus sp. nov. (Fig. 21)

Type material. Holotype. SR94-5-21 (part only), deposited in SR. A well-preserved apical portion of a wing; Burke Museum locality UWBM A0307B (Rod Bartlett, collector).

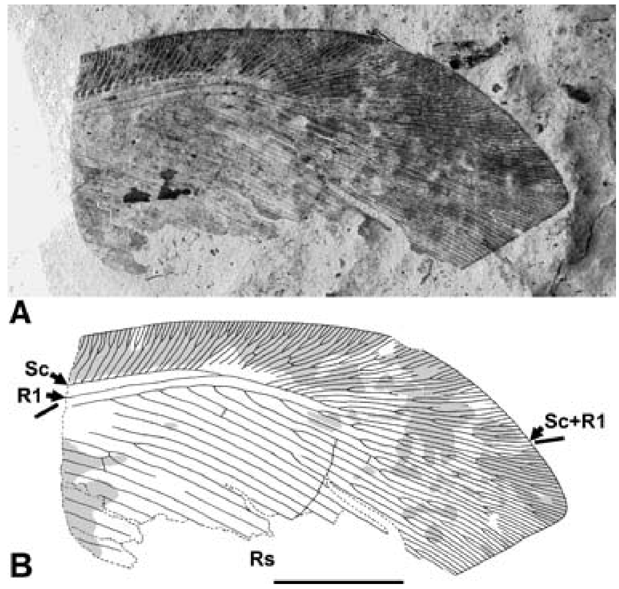

Figure 21 *Polystoechotites falcatus* sp. nov., holotype SR, SR94-5-21; apical portion of fore-wing. **A**, photograph; **B**, drawing. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

Etymology. From the Latin *falcatus*, falcate.

Diagnosis. May be distinguished from other species with falcate wings by its dark costal space [mainly light in *Fontecilla graphicus*] and light radial space [mainly dark in hind-wing of *Polystoechotites douglasae*].

Occurrence. Early Eocene, Klondike Mountain Formation; Republic, Washington, USA (Okanagan Highlands).

Description. Fore-wing slightly falcate. Length of fragment available ~20 mm, width ~10 mm; estimated complete length ~40–45 mm, width ~15 mm. Trichosors distinct along entire preserved wing margin except at costal margin where indistinct (not shown in Fig. 21B). Costal space rather wide before fusion of Sc, R1, expanded after. Sc+R1 enter margin rather well before wing apex. All preserved subcostal veinlets forked; veinlets of Sc+R1 long, oblique, usually dichotomously forked. Subcostal space distally somewhat wider than R1 space. R1 space expanded distal to fusion of Sc, R1. No crossveins detected in preserved portions of subcostal, R1 spaces. Rs (or Rs, M) with 18 preserved branches, of which three forked before outer gradate series; apical-most branches dichotomously branched. Crossveins in radial space poorly preserved, few irregularly scattered present, except for fragment of regular outer gradate series. Small crossveins between branches of Sc+R1, Rs in area of end-twigging, five detected, others possible (difficult to detect with certainty). Wing colour patterning lacking dark fasciae and stripes. Costal space distally, apical portion of wing variegated with dark, light patches. Preserved basal portion of costal space wholly dark; subcostal, R1 and radial spaces almost entirely light (Fig. 21A).

Remarks. We treat this fragmentary wing as a fore-wing, as its subcostal space is wider than the R1 space, characteristic of Tertiary and extant polystoechotid fore-wings (see family description, above). This species is most similar to the single extant species of the genus *Fontecilla, F. graphicus,* by wing shape, venation and some aspects of colour patterning (i.e. in lacking dark fasciae and stripes), but differs from the latter in details of venation (e.g. Sc+R1 entering margin just before [*F. graphicus*] or well before [*P. falcatus*] wing apex) and in other aspects of colour patterning (in *F. graphicus*, wings light, only slightly variegated with dark areas). Unfortunately, it is, at present, impossible to determine if *Polystoechotites falcatus* belongs to this genus or not, by the fragmentary nature of this specimen. It is possible that this similarity of wing shape may be homoplasious.

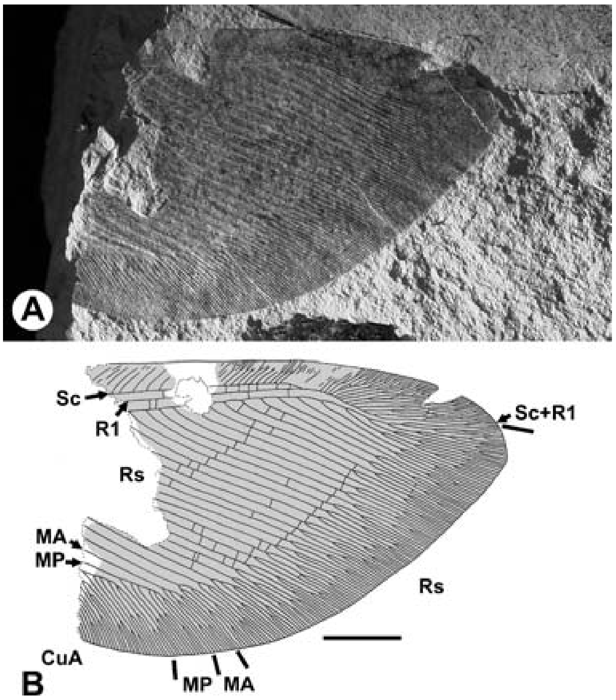

Figure 22 *Polystoechotites lewisi* sp. nov., holotype, SCSU, SCSU-SR-0316 (part) and SR01-01-06 (counterpart); hind-wing. **A**, photograph of part; **B**, combined drawing from part and counterpart. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

Polystoechotites lewisi sp. nov. (Fig. 22)

Type material. Holotype. SCSU-SR-0316 (part), deposited in SCSU; SR01-01-06 (counterpart), deposited in SR. Part: a well-preserved apical half of a hind-wing with distinct colour patterning and crossvenation; counterpart: as complete as part, but with colour patterning, crossvenation indistinctly preserved; Burke Museum locality UWBM A0307 (Standley Lewis, collector).

Etymology. The specific epithet is a patronymic in honour of Standley Lewis, recognising his contribution to palaeoentomology, in particular his pioneering work at Republic (e.g. Lewis 1992).

Diagnosis. May be easily distinguished from hind-wings of other species of the family by the presence of many distal subcostal crossveins and uniformly dark apical half of wing.

OCCURRENCE. Early Eocene, Klondike Mountain Formation; Republic, Washington, USA (Okanagan Highlands).

DESCRIPTION. Hind-wing. Length of preserved portion 26 mm, width 18 mm, estimated complete length 42–44 mm, maximal width 18 mm (length/width ratio 2.3–2.4). Subcostal, R1 spaces nearly equal width, seven crossveins detected in distal part of former, four in latter. Rs with 31 branches, unforked before outer gradate series, distal to which each branch of Rs, MA dichotomously branched, forming end-twigging, these veins so closely spaced that any trichosors present not visible. Three distal-most branches of Rs dichotomously branched. MP with six branches. Preserved portion of CuA with 9–10 branches. Most of the branches of MP, CuA deeply forked. Two more- or -less regular gradate series present in radial space; several additional irregularly spaced crossveins between series. Crossveins in median and cubital spaces not detected. Macrotrichia on longitudinal veins well preserved; in anterior portion of wing longer, denser than in rest of wing, where hairs quite sparse, short. No macrotrichia on membrane detected. Distal portion of wing uniformly darkish with one distinct light spot at anterior margin; light colour seems to dominate in basal portion (Fig. 22A).

REMARKS. Although the wing characters of this species are in general agreement with those of the genus *Palaeopsychops*, two character states are not found in the hind-wings of any other species of Polystoechotidae: the numerous distal subcostal crossveins (none in other Polystoechotidae) and the crossveins in R1 space perpendicular to R1 (oblique in other Polystoechotidae). Furthermore, the shape of the hind-wing is somewhat different from that of other species of *Palaeopsychops*, in that the anterior wing margin before the apex is less curved (the curvature of the pre-apical anterior portion of the wing is more prominent in all other species). We do not, however, consider these traits as a sufficient basis to erect a new genus, therefore we include it in this collective genus.

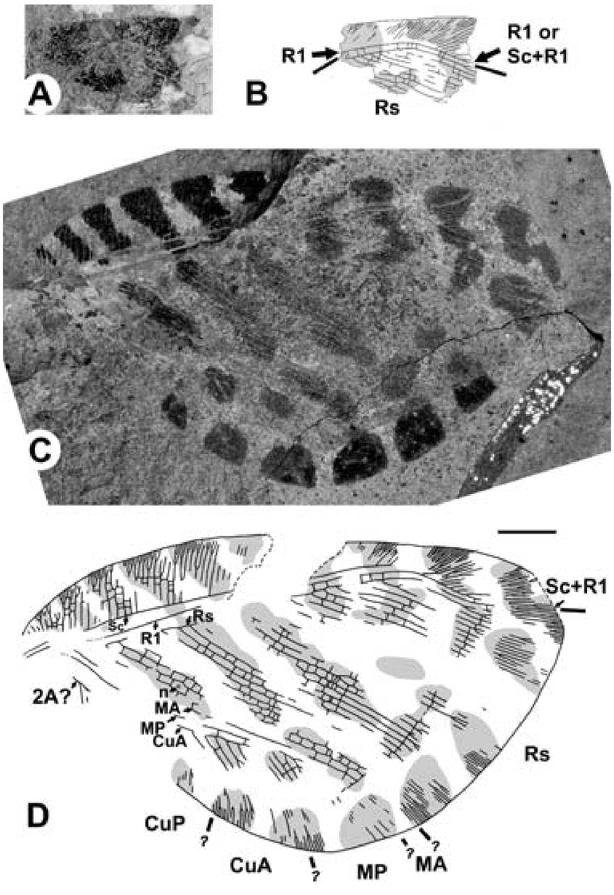

Figure 23 *Polystoechotites* sp. A, specimen SFU, Q-0379; fragmentary wing. **A**, photograph; **B**, drawing. Specimen SFU, Q-0421; fore-wing. **C**, photograph; **D**, drawing. For abbreviations see Materials and Methods. All to same scale; scale bar = 5 mm.

Polystoechotites sp. A (Fig. 23)

MATERIAL EXAMINED. Q-0379 (part only), deposited in SFU. A poorly-preserved apical fragment of a fore-wing; the Quilchena locality (Rolf Mathewes, collector). Photographs of Q-0421 were examined (see below).

DIAGNOSIS. May be easily distinguished from any species of the family by unusually broad fore-wing and distinctive colour patterning (Fig. 23A).

OCCURRENCE. Early Eocene, Coldwater Formation; Quilchena, British Columbia, Canada (Okanagan Highlands).

DESCRIPTION. Fore-wing. Length of fragment available 13 mm. Sc not detected. Costal space apically abruptly expanded. R1 (or Sc+R1), Rs almost equally spaced along entire preserved length. Quite numerous crossveins in R1 space, between branches of Rs spaced more or less regularly. Colour pattern of preserved fragment consists of dark, light maculations (Fig. 23A).

REMARKS. Q-0379 carries little information, due to the fragmentary nature of the specimen. However, the venation and colour patterning are closely similar to those of Q-0421 (Figs 23C & 23D). The specimen Q-0421 (part only) was collected by Glen Guthrie in 1992, also at Quilchena, and deposited in the SFU collection. Unfortunately, this specimen is now missing and, therefore, although it is distinctive, we do not name this species here. A description and revised drawing based on the available photographs of the specimen (Fig. 23D) are provided here.

Q-0421 is a rather well preserved, almost complete fore-wing, unusually broad (length/width ratio 1.7) and triangular in shape, 47 mm long and 28 mm wide. Trichosors are distinct in the apical portion, although indistinct along other preserved margins (not shown in Fig. 23D). The distal nygma appears to be preserved, located in the dilation between Rs1 and Rs2. The costal space is expanded for the proximal ~1/4 of its length, narrowed towards the base and apex and again quite strongly expanded distal to the possible fusion of Sc and R1 (the apical portion of Sc is poorly preserved). The humeral veinlet is apparently recurrent and branched (it is not preserved, but its branches are well preserved). Numerous costal crossveins are present in the proximal portion of the space. All preserved subcostal veinlets are forked. The subcostal and R1 spaces are nearly equally wide. No crossveins are detected in the subcostal space. Five crossveins are preserved in the distal part of the R1 space. Rs has ~ 23 branches. There are numerous, irregularly scattered crossveins present in the radial space, proximal to the outer gradate series. The outer

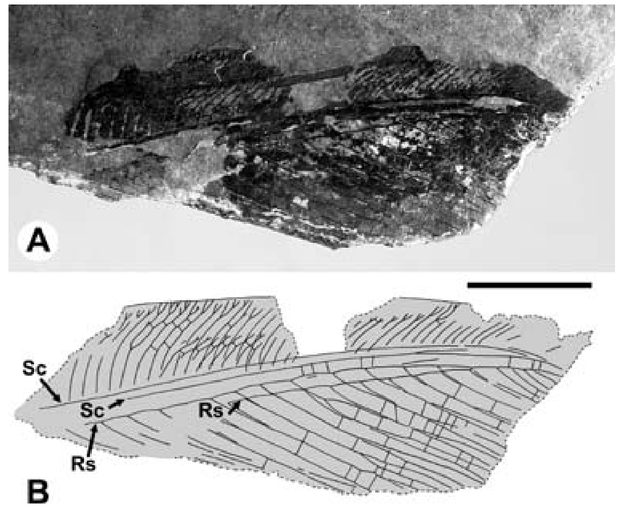

Figure 24 *Polystoechotites* sp. B, specimen SFU, Q-0094; apical portions of overlapping fore-wings. **A**, photograph of part; **B**, combined drawing of part and counterpart. For abbreviations see Materials and Methods. Both to scale; scale bar =5 mm.

gradate series are distinct. MA is poorly preserved; MP has more than four long, pectinate branches. CuA is pectinately branched (with >4 long branches). CuP and the anal veins are poorly preserved. The colour patterning is distinct, and consists of alternating light and dark bands and patches (Fig. 23C).

At first glance, this species seems to belong to some family of psychopsid-like neuropterans by its broad wing with dense venation and numerous crossveins. But detailed analysis of its fore-wing venation shows its polystoechotid affinity: it possesses most (discernible, but possibly all) of the character states enumerated in the diagnosis and its colour patterning conforms wholly to this family (particularly comparable with *Palaeopsychops dodgeorum* and *P. marringerae*). This species differs primarily by its distinctive fore-wing shape.

Polystoechotites sp. B (Fig. 24)

MATERIAL EXAMINED. Q-0094a, b (part and counterpart), deposited in SFU. Part and counterpart: a rather poorly-preserved fragment of two overlapping apical wing portions; the Quilchena locality (Rolf Mathewes, collector).

DIAGNOSIS. May be distinguished from fore-wings of other species with dark colouration by almost complete costal gradate series in distal portion of wing [only few crossveins in *P. barksdalae*] and wider costal space [narrower in *P. barksdalae*].

OCCURRENCE. Early Eocene, Coldwater Formation; Quilchena, British Columbia, Canada (Okanagan Highlands).

DESCRIPTION. Fore-wing. Length of fragment available 22 mm, 8 mm, length of fore-wing (estimated) ~40 mm. Costal space rather strongly expanded; at least 11 costal crossveins detected in one wing and seven in the other indicating possible costal gradate series in proximal portion of space. Subcostal veinlets (where preserved) forked. Sc, R1 fused distally. No crossveins detected in subcostal space, eight in R1 space (one wing). Preserved portions of branches of Rs not forked (except one); between them scattered crossveins not forming gradate series. Colour patterning of preserved apical fragment uniformly dark.

REMARKS. Both overlapping wings are interpreted as fore-wings, based on their broad costal spaces and numerous costal crossveins. Clear indication of the presence of hind-wings is not apparent. Surface patterning in parts of the radial space indicates the possibility of dense trichiation as in *P. setosus*, although this is not well enough preserved to discount the possibility that this is a preservational artefact, not hairs.

Polystoechotidae *incertae sedis* (Fig. 25)

MATERIAL EXAMINED SR97-14-8a (part only), deposited in SR. Rather well-preserved but fragmentary portions of wings; Burke Museum locality UWBM B4131(Cathy Chamberlain, collector). SR01-1-2 (part only), deposited in SR. A rather well preserved, but fragmentary wing; Burke Museum locality UWBM A0307B (Wesley Wehr, collector).

OCCURRENCE Early Eocene, Klondike Mountain Formation; Republic, Washington, USA (Okanagan Highlands).

DESCRIPTION *Specimen SR97-14-8*. Fore-wing. Only small region of pectinate branching of either MP or CuA preserved. Hind-wing. Length of preserved portion 19 mm, width 16 mm, hind-wing length presumably similar to previous specimen. Branches of Rs (preserved portions) parallel, not forked before well-developed end-twigging. One Rs branch with loop-like anomaly. Crossveins poorly preserved (few, weakly visible). Only two crossveins detected in outer gradate series. No other crossveins between branches of Rs preserved except for few short crossveins in end-twigging area. MA dichotomously branched. MP apparently pectinately branched (only distal portion preserved). Preserved portion uniformly somewhat darkish in colour, any patterning not preserved (Fig. 25A).

Specimen SR01-1-2. Wing. Length of fragment available 24 (34 if proximal isolated fragment belongs to this wing) mm, width 8 mm, length of fore-wing (estimated) >40 mm. Costal space apically broadened. Subcostal veinlets forked. Sc+R1 or R1 enter wing margin at about apex. Apical branches of Rs parallel, unforked. Between them, rare irregularly spaced crossveins. Colour patterning preserved darkish throughout preserved portion, with some dark, minute spots in costal, to lesser extent radial spaces interpreted as postmortem artefact (see Remarks, below) (Fig. 25C).

REMARKS. Both specimens may belong to *Polystoechotites lewisi*, *P. barksdalae* or *P.* sp. B. (or to their own taxon or taxa) based on their uniformly darkish colour. However, SR97-14-8 and SR01-1-2 are too fragmentary for determination with certainty below the family level. Groups of minute spots in portions of SR01-1-2 (above) appear consistent with degradation, presumably sustained during (extended?) period of floating before burial (see Taphonomy, above).

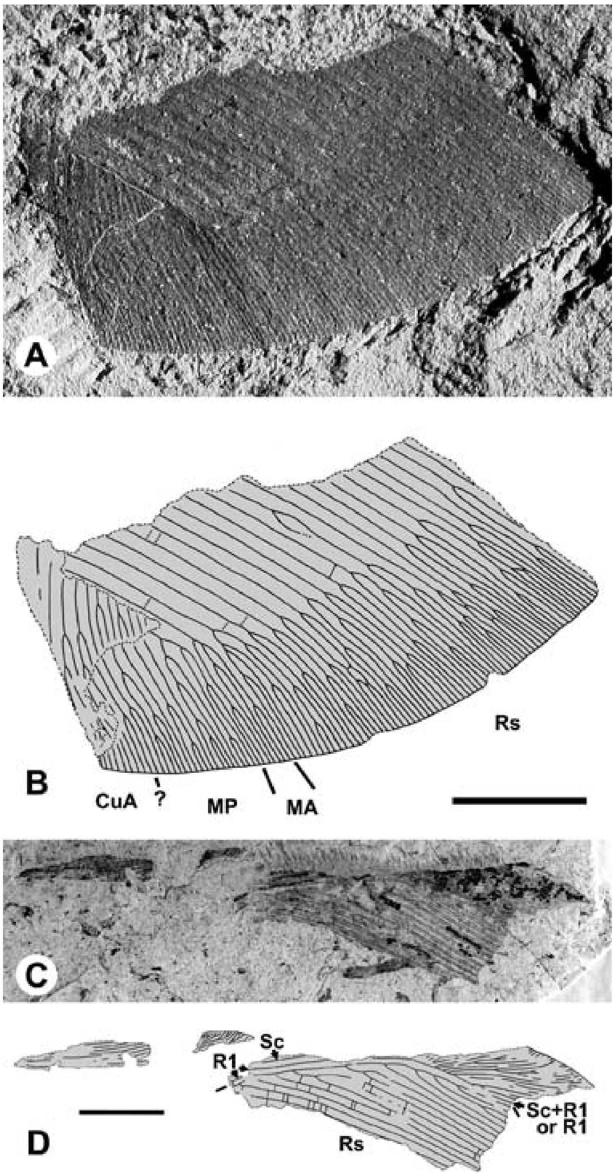

Figure 25 Polystoechotidae *incertae sedis*, fragmentary wings. Specimen SR, SR97-14-8; **A**, photograph; **B**, drawing. Specimen SR, SR01-1-2; **C**, photograph; **D**, drawing. For abbreviations see Materials and Methods. A and B to same scale; C and D to same scale; scale bars = 5 mm.

Neuroptera *incertae sedis* sp. A (Fig. 26)

Material examined. SR95-25-31a, b (part and counterpart), deposited in SR. An apical portion of a fore-wing, poorly preserved, but with distinct colour patterning; Burke Museum locality B4131, Republic (Muriel White, collector).

Diagnosis. May be distinguished from other Tertiary species of Neuroptera by the following combination of characters: fore-wing large with dense crossveins in subcostal and R1 spaces and distinctive colour patterning (Fig. 26A).

Occurrence. Early Eocene, Klondike Mountain Formation; Republic, Washington, USA (Okanagan Highlands).

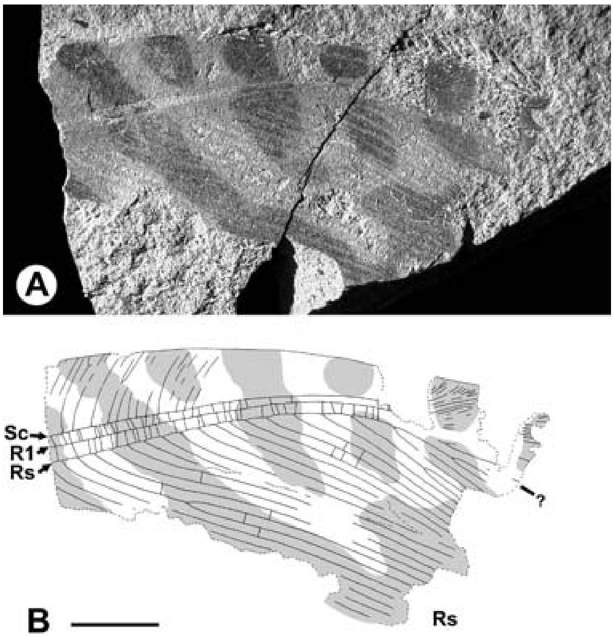

Figure 26 Neuroptera *incertae sedis* sp. A, specimen SR, SR95-25-31; incomplete fore-wing. **A**, photograph of counterpart; **B**, combined drawing from part and counterpart. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.

Description. Fore-wing. Length of fragment available 28 mm, width 15 mm, length of fore-wing (estimated) > 40 mm, maximal width ~20 mm. Costal space wide proximally, narrowed significantly towards apex. Costal crossveins not detected. Subcostal branches, if preserved, forked. Sc, R1 not preserved apically, preserved portions not convergent apically. Subcostal space slightly narrowed toward apex, somewhat narrower than R1 space; both spaces filled with numerous crossveins spaced closely, irregularly. Branches of Rs not forked (except one); crossveins between these difficult to see (about 10 detected, these not forming gradate series). Colour patterning distinct consisting of broad dark bands (alternatively, membrane dark with broad light bands: Fig. 26A).

Remarks. This specimen is poorly preserved in general (especially the crossveins) and fragmentary, but it does possess some clearly visible important characters, i.e. colour patterning and the numerous, closely spaced crossveins in the subcostal and R1 spaces. Wing colour patterning is quite similar to that of other species (particularly *Polystoechotites* sp. A and *Palaeopsychops marringerae*). But in the latter, light bands run almost straight across the width of the wing and in this species they curved toward the apex. Such dense crossveins in the subcostal and R1 spaces that are found in this species are entirely not characteristic of Polystoechotidae (although rare crossveins in these spaces occur in undoubted Polystoechotidae e.g. *Palaeopsychops lewisi*). Moreover, the apical parts of Sc and R1 are not preserved and fusion of these veins cannot be confirmed. The anterior (costal) margin of the wing is smoothly curved in the prestigmal region, in a manner not characteristic of Polystoechotidae (in the latter this margin is nearly straight in this region). The costal space seems wider than usual even for a fore-wing. So, although the colour patterning and general impression of the venation are similar to other species that are here treated as belonging to Polystoechotidae, details of the venation of the preserved fragment do not justify confidence in a Polystoechotid affinity. However, this species is not similar to species of the extant Psychopsidae or to the type species of the Mesozoic psychopsid-like families Brongniartiellidae or Osmylopsychopidae. Therefore this species remains not determined even to family level; most probably, this is either an abnormal species of Polystoechotidae, or it belongs to some family of psychopsid-like Neuroptera.

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ERRATUM

Volume 4(2) : 119 – 155
Tertiary giant lacewings (Neuroptera: Polystoechotidae): revision and description of new taxa from western North America and Denmark
S. B. Archibald and V. N. Makarkin

During the preparation of the final, published and online versions of the above article, errors were introduced into figures 3 and 18 where pre-revision versions were used in place of the final versions.

We apologise to the authors and readers for these errors and reproduce the correct version of the figures below.

Figure 3 Early Eocene intercontinental dispersal routes between Europe and North America open to *Palaeopsychops*: across the northern Atlantic route (most likely, dotted line) or across Asia via Beringia (but note Obik Sea barrier). Reconstruction of Early Eocene continental and shoreline position, redrawn from Hooker & Dashzeveg (2003), modified from Smith *et al.* (1994) and Bonde (1997). De Greer and Thulean land bridges may not have been open at the same time. **A,** Fur Formation; **B,** De Greer Land Bridge; **C,** Thulean Land Bridge; **D,** Okanagan Highlands; **E,** Florissant; **F,** Obik Sea; **G,** Bering Land Bridge; **Eur,** Europe; **Gr,** Greenland; **N Am,** North America.

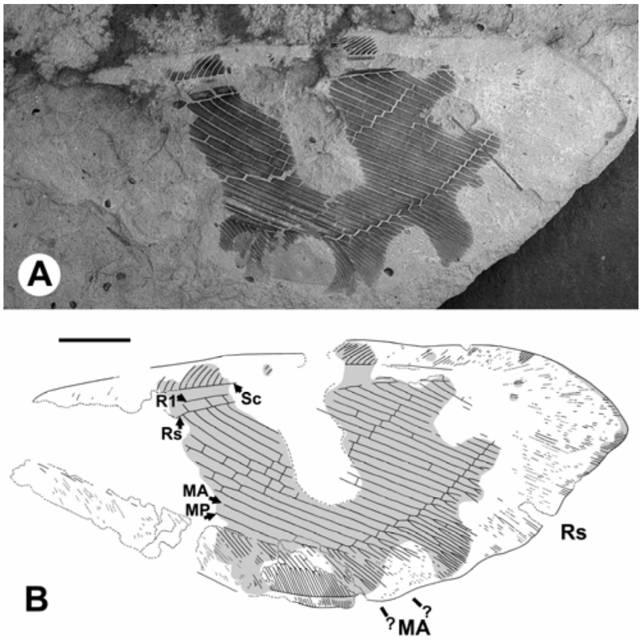

Figure 18 *Palaeopsychops douglasae* sp. nov., holotype, UA, UAFIC7794; hind-wing. **A,** photograph of counterpart; **B,** combined drawing from part and counterpart. For abbreviations see Materials and Methods. Both to scale; scale bar = 5 mm.