Family Affinity of the Genus *Palaeopsychops* Andersen with Description of a New Species from the Early Eocene of British Columbia, Canada (Neuroptera: Polystoechotidae)

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Ann. Entomol. Soc. Am. 96(3): 171–180 (2003)

ABSTRACT *Palaeopsychops dodgeorum* sp. n. from the Early Eocene Okanagan Highlands of Quilchena, British Columbia, Canada is described. The systematic position of the genus *Palaeopsychops* Andersen, 2001 is discussed, interpreting this as most closely associated with Polystoechotidae. *Osmylites protogaea* (Hagen 1862) is considered as *nomen nudum* and an objective synonym of *Osmylites excelsa* (Oppenheim, 1888), *syn. n.*

KEY WORDS Eocene, Polystoechotidae, Neuroptera, Okanagan Highlands, fossil insects

THE FAMILY POLYSTOECHOTIDAE is now a relict group represented by only four species belonging to three genera: *Polystoechotes* Burmeister, 1839, *Platystoechotes* Carpenter, 1940, and *Fontecilla* Navás, 1932, which are restricted to the New World (Oswald 1998). Although fossils of this family are few and controversial, occurrences in the Mesozoic of insects referable to Polystoechotidae indicate that this family may have been more diverse and widespread. The Early Jurassic species *Mesopolystoechus apicalis* Martynov, 1937, described from Tajikistan, Central Asia, has been considered the single member of the family Mesopolystoechotidae Martynova, 1949. Lambkin (1988) implied his opinion of possible synonymy of Mesopolystoechotidae and Polystoechotidae when he referred to *M. apicalis* as a polystoechotid (p. 455) and "probable Polystoechotidae" (p. 457). He also reviewed the other four fossil species from the Late Triassic to Late Jurassic probably belonging to Polystoechotidae: *Lithosmylidia lineata* Riek, 1955 (Late Triassic of Australia); *Kasachstania fasciata* Panfilov, 1980, *Osmyliodea distincta* Panfilov, 1980, and *Pterocalla superba* Panfilov, 1980 (all from the Late Jurassic of Kazakhstan). Another two species were assigned to Mesopolystoechotidae by Whalley (1988) [*Megapolystoechus magnificus* Tillyard, 1933 (Late Triassic of England)] and Hong (1983) [*Mesopolystoechus wangyingziensis* Hong, 1983 (Middle Jurassic of China)]. Apart from these occurrences, there are undescribed species from the Late Jurassic of Kazakhstan and Early Cretaceous of southern Siberia that very likely belong to this family (Makarkin, personal observation).

Late Cretaceous and Tertiary Polystoechotidae have hitherto been unknown, because the single described species (*Polystoechotes piperatus* Cockerell, 1908 from Late Eocene of Florissant) was considered to be a psychopsid (Carpenter 1943, MacLeod 1970). However, examination of the holotype shows that a polystoechotid affinity is most probable, although this species certainly doesn't belong to the genus *Polystoechotes.* Unfortunately, the sole specimen of this species is an incomplete and poorly preserved forewing, and its systematic position is not clear. Another Tertiary genus, *Palaeopsychops* Andersen, 2001, was recently described from the Late Paleocene/Early Eocene of Denmark in the family Psychopsidae, however, we consider this genus as most closely associated with Polystoechotidae (see "Determination of Family Affinity").

A large lacewing was recently figured along with a short description by Archibald and Mathewes (2000, Figs. 6A, 20). The authors briefly discussed its possible family affinity, comparing it with Osmylidae and Polystoechotidae. In this paper we provide a detailed description of this specimen and discussion of its systematic position. We interpret this as a new species of the genus *Palaeopsychops.*

Materials and Methods

The specimen is from the Early Eocene lacustrine shales of the "Coldwater beds" exposed along the banks of Quilchena Creek at Quilchena in south-central British Columbia, Canada. The Quilchena locality is the oldest of the "Okanagan Highlands" series of fossiliferous Eocene shale and amber deposits in British Columbia and Washington State. This locality bears numerous fossil insect, fish, plant, and bird

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0013-8746/03/0171–0180$04.00/0

(feather, coprolite) remains. Although most shale from Quilchena is easily worked, unfortunately the particular nature of the matrix of this fossil (relatively large-grained, consolidated to the fossil, and not flaking away with needles) makes preparation unusually problematic.

Terminology of forewing venation and wing spaces employed here mainly follows Oswald (1993a, 1998), in particular with regards to the median vein: "MA" of authors (e.g., Carpenter 1940; MacLeod 1970) is the most proximal branch of Rs, and "MP"' is simply M.

Taxonomy

Palaeopsychops Andersen 2001

Palaeopsychops Andersen 2001: 422.

Diagnosis. Distinguished from other polystoechtid genera by the following combination of forewing characters: (1) broad-subtriangular in shape [more or less elongate in all other genera, except for *Fontecilla*]; (2) hind margin of wing not falcate [falcate in *Fontecilla*]; (3) M_2 strongly pectinately branched (shared by fossil genus *Pterocalla*) [few pectinate branches in all other genera]; (4) outer gradate series of crossveins in radial space well developed (shared by all extant genera) [absent in fossil genera, except hindwings of *Mesopolystoechus apicalis* and *Osmyliodea distincta* (but see discussion)]; (5) transverse bands (fasciae) distinct [absent in all extant genera and never detected in any fossil genus].

Discussion. The genus *Palaeopsychops* was described from the Late Paleocene/Early Eocene of Denmark ("Mo-clay"), with four species: *P. latifasciatus* Andersen (type species), *P. abruptus* Andersen, *P. angustifasciatus* Andersen, and *P. maculatus* Andersen. The latter species is possibly a synonym of one of the other three, as the holotype is a hindwing, not forewing as in Andersen (2001) (the costal space not expanded basally as in forewings). With the present description of *Palaeopsychops dodgeorum*, the genus expands its distribution to North America.

Palaeopsychops represents the single described Tertiary genus in the family. A number of genera were erected from the Late Jurassic to Late Triassic (see introduction) and none from the Cretaceous. *Palaeopsychops* is easily distinguished from all extant genera (see "Diagnosis"). Of the Jurassic-Triassic genera only the genus *Mesopolystoechus* Martynov, 1937 is similar to *Palaeopsychops*, as seen from the venation of a hindwing of *Palaeopsychops maculatus* (Andersen 2001: Fig. 12). The type species (*M. apicalis*) is represented by a well preserved, but incomplete hindwing (Martynova 1962: Fig. 860). The single known specimen of *Osmyliodea distincta* is also a hindwing. However, the venation of hindwings in many Neuroptera greatly differs from that of forewing, and so does not allow comparison between genera described from only forewings and those described solely from hindwings. Therefore, there is insufficient reason to consider congeneric another species assigned to *Mesopolystoechus* by Hong (1983), that is represented only by an incomplete forewing.

In the drawing of the holotype of *Palaeopsychops latifasciatus* (Fig. 10: Andersen 2001), the subcosta, anterior radial trace ("R_1"), and anterior sectoral trace ("Rs") all terminate together, however, the photograph (his Fig. 3) shows that whereas Sc and R_1 do probably fuse, Rs runs separately to the wing margin, as in our specimen. We find it most probable that in other species of *Palaeopsychops* the configuration of these veins is the same, and therefore, we assume that there is no "*vena triplica* " in this genus (see Oswald 1993b: 41 for discussion of this character). Because the distal nygma (not mentioned in the text of Andersen (2001), but clearly seen in the photograph, Fig. 3) is situated in the neuropteran forewing between the most proximal two branches of Rs, it follows then that Andersen's M_1 is actually the most proximal branch of Rs, his M_2 is M_1, his Cu_1 is M_2 (Andersen 2001: Fig. 10), his Cu_2 is CuA, and his A_1 is CuP (Andersen 2001: Fig. 9).

Palaeopsychops dodgeorum New Species

Neuroptera *incertae sedis:* Archibald and Mathewes 2000: 1445, 1448, Figs. 6A, 20.

Diagnosis. Distinguished from other species of genus by numerous, irregularly arranged crossveins in radial space (in all other species of *Palaeopsychops* these crossveins form inner gradate series), somewhat more elongate shape of forewing.

Description. Forewing broad-subtriangular in shape, length 45 mm. Trichosors indistinct, visible only at hind wing margin where margin well-preserved (see Fig. 5, not shown in Fig. 1). Distal nygma distinct, appearing as small bulge in dilation between most proximal two branches of Rs (see Fig. 4). Costal space basally expanded, narrowed toward apex, with complete gradate series of crossveins parallel to anterior wing margin. Subcostal veinlets always forked, sometimes several times. Subcostal space rather wide along entire length, crossveins not preserved. Apical portion of Sc not preserved (possibly obscured by matrix). R_1 (or $Sc+R_1$) entering margin apparently at wing apex, with branches long and forked. R_1 space somewhat narrower than subcostal space, with ≈10 crossveins. Origin of Rs not preserved (possibly obscured by matrix), but clearly close to base of wing. Rs with numerous (33–34 in number) pectinate branches, sometimes fusing with one another; many irregularly spaced crossveins between them in central part of wing. Outer gradate series in radial space distinct, nearly parallel to posterior margin, continuing radiomedially to anal space. Fork of M not detected (obscured by matrix); anterior branch of M (M_1) concave, unbranched before outer gradate series; posterior branch of M (M_2) convex, pectinately branched in distal portion (with ≈8–10 long, parallel and rather oblique branches). Cu divided into CuA and CuP close to base of wing. CuA strongly convex basally, distally slightly concave and pectinately branched (with 11–12 long and rather oblique

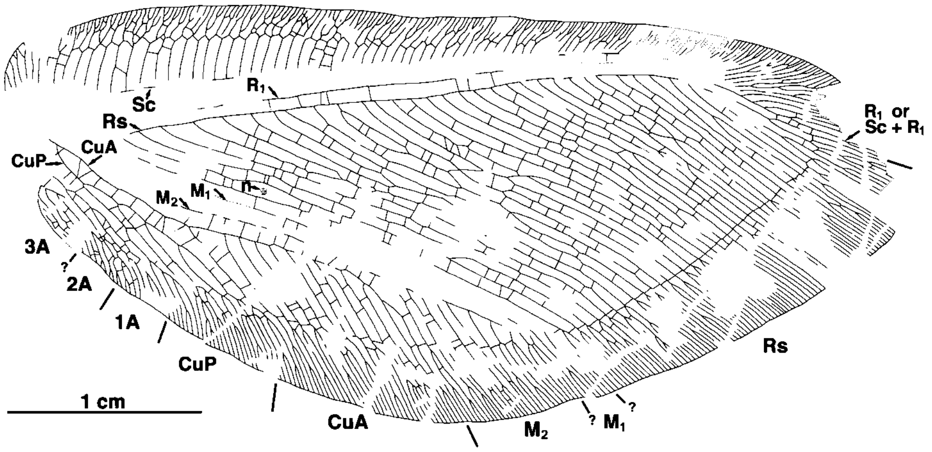

Fig. 1. *Palaeopsychops dodgeorum*, forewing venation of the holotype Q-0422a, b (composite drawing from part and counterpart). 1A–3A, anal veins; CuA, anterior cubitus; CuP, posterior cubitus; M_1, M_2, anterior and posterior branches of media; n, distal nygma; R_1, first branch of radius; Rs, radial sector; Sc, subcosta. Demarcation lines show a question mark where precise limits are not certain.

branches parallel to that of M_2). CuP pectinately branched, branches (four in number) strongly oblique; 1A comparatively short, dichotomously branched; 2A pectinately branched, with branches rather long; 3A poorly preserved, few-branched. Jugal lobe, if present, not preserved (possibly obscured by matrix). Wing pattering represented by maculations throughout, evident on the part (Q-0042a) (see Fig. 3). Near costal margin fasciae more conspicuous, oblique and wide. Outer gradate series clearly shaded.

Type Material. HOLOTYPE: a rather well preserved, almost complete left forewing, Quilchena, British Columbia, Canada, Early Eocene. Depository: fossil collection of Simon Fraser University (Burnaby, British Columbia, Canada) (Q-0422 a, part; Q-0422 b, counterpart).

Etymology. The specific epithet is in honor of Kenneth Dodge and his father Ken Dodge, who collected and generously donated this specimen to the Simon Fraser University collection; the Latin suffix *-orum* shows genitive case of plural nouns.

Discussion. We assign this new species to the genus *Palaeopsychops* by agreement with all principal characters of the diagnosis: forewing venation, similar size, and color pattering. We treat the numerous crossveins scattered in the radial space of our specimen as a specific character, and the fusing of some of the branches of Rs with one another as possibly an individual abnormality of this specimen. Such anomalous specimens occur at times in extant species of various families (Makarkin, personal observation). *P. dodgeorum* is known only from the holotype forewing. Andersen stated that this particular specimen is "presumably a hindwing 4.5 cm long, as it is without pigmentation pattern" (Andersen 2001: 433). No coloration of this specimen was reported in Archibald and Mathewes (2000), nor evident in the accompanying photograph of the counterpart (Q-0042b), however, subsequent examination of the part, particularly with oblique lighting, clearly shows pigmentation pattern (see Fig. 3). Furthermore, absence of coloration in a fossil wing does not necessarily indicate absence in life; the type specimen of *P. maculatus*, a hindwing (above), has clearly preserved color patterns; and the basally broadened costal region in our specimen make this readily identifiable as a forewing.

The distal portion of M_2 on our specimen may appear to be a continuation of CuA obscured by matrix in middle of M_2-CuA. Concavity and convexity relationships of veins indicate, however, that M_2 is entirely (except most basally) strongly convex, and the distal part of CuA is slightly concave (Fig. 2), which allows this to be considered as the distal portion of M_2, not CuA. Because of incomplete preservation of venation in this portion of the wing, this interpretation is tentative.

Determination of Family Affinity

The genus *Palaeopsychops* is of considerable interest because of its large size and dense venation, particularly *P. dodgeorum.* At first glance, this and another similar specimen from Quilchena (Archibald and Mathewes, 2000, Figs. 6B and 21), as well as possibly others in the Okanagan Highlands (unpublished), should be placed with psychopsid-like neuropterans. Nevertheless, we consider this genus as most closely associated with Polystoechotidae. Such large neuropterans as *Palaeopsychops dodgeorum* often have dense venation and numerous crossveins presumably resulting from the structural demands of large wing size, but not always, as in *Mesopsychopsis hospes* (Germar 1839), and may appear then superficially similar to psychopsid-like neuropterans. The systematics of fossil neuropterans is in need of revision, including phylogenetic analysis along with extant Neuroptera. Descriptions of taxa that are often obsolete or incomplete and in need of redescription are scattered throughout

Fig. 2. *Palaeopsychops dodgeorum,* Q-0422b.

the literature. Examples include classifications of the order and diagnoses of its families done by Martynova (1962) and Carpenter (1992). Therefore, in our analysis of family affinity we will consider all neuropteran families.

There are 35–47 families currently recognized in the order Neuroptera [= Planipennia] depending on synonymy. We have here divided them into three groups with regard to the genus *Palaeopsychops:*

(1) Those families that we exclude because of fundamental venational difference. The following families have no species reasonably resembling *Palaeopsychops:* Chrysopidae, Conioptegyridae, Hemerobiidae (*Promegalomidae*), Mantispidae (*Promantispidae*), Berothidae, Rhachiberothidae, Dilaridae, Sisyridae, Nevrorthidae, Kalligrammatidae, Mesoberothidae, Mesithonidae. Of these, the following are too small in size to include these large insects, and are strongly different in the configuration of their principal veins: Conioptegyridae, Berothidae, Rhachiberothidae, Dilaridae, Sisyridae, Mesoberothidae, Mesithonidae, Nevrorthidae. The others have characters that automatically exclude them from consideration: Hemerobiidae have at least two "radial sectors" (=oblique radial branches of Oswald 1993a), and are too small (here and below, only forewing venation is considered, if otherwise not indicated); in Kalligrammatidae, the entire wing is filled with closely spaced crossveins (including the subcostal space); the venation of Chrysopidae is strongly distinct (M_1, M_2, CuA, and CuP

Fig. 3. *Palaeopsychops dodgeorum,* Q-0422a.

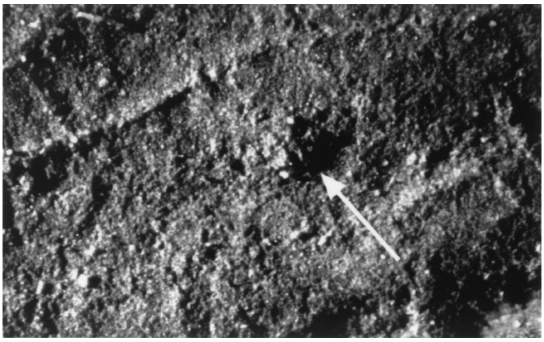

Fig. 4. *Palaeopsychops dodgeorum*, Q-0422b. The distal nygma, between the most proximal two branches of Rs (arrow).

never have strong pectinate branching); and Mantispidae have an easily visible pterostigma, if not, the subcostal space is distally broad.

All of the Permian families (Permithonidae, Palaemerobiidae, Parasisyridae, Permegalomidae, Permopsychopsidae, Permosisyridae, Sialidopsidae, and Archeosmylidae) are now considered to be synonyms of the Permithonidae (Whalley 1988, Novokshonov 1996). Within Permithonidae, *Permorapisma* Tillyard, 1926 (Late Permian of Australia) superficially most resembles *Palaeopsychops* in having comparatively large size (≈20 mm), dense venation, and numerous crossveins (see Carpenter 1992: Fig. 192.2), however, that genus as well as all other genera of Permithonidae may be easily distinguished from *Palaeopsychops* by the following characters: costal space tapering toward wing base, origin of Rs shifted distally, M dichotomously branched and occupying a comparative large area, CuA with few distal pectinate branches, CuP simple or rarely with only marginal "end-twigging." These traits exclude this family from consideration.

The families Myrmeleontidae, Palaeoleontidae, Ascalaphidae, Nymphidae, Nemopteridae, Crocidae, Babinskaiidae (comprising the superfamily Myrmeleontoidea), Mesochrysopidae, and Allopteridae all have wings narrow to elongate-oval (except for Nemopteridae), with sizes comparable to our specimen (sometimes almost identical in shape and size, e.g., in myrmeleontid Palparinae), but upon close examination, their venation has basic features very different from that of *Palaeopsychops.* In all of these families (except Nymphidae) trichosors are absent, subcostal veinlets (at least in basal half) are entirely simple, the costal space is narrow and not expanded basally, and most have branches of Rs, M and CuA more or less zig-zagged because of numerous crossveins (except Crocidae, Mesochrysopidae, Allopteridae, and Babinskaiidae for the latter character), and many other features characteristic of each family show conclusively that *Palaeopsychops* does not belong to this family group. Only Nymphidae bears some external similarity with *Palaeopsychops,* in that there is dilation of the costal space (e.g., in *Osmylops* Banks, 1913 and *Myiodactylus* Brauer, 1866) but this extends along the entire length, except near the wing base where this is narrowed, and the subcostal veinlets are sometimes forked. However, in all species of this family, humeral vein is not branched, and the branches of Rs are somewhat zig-zagged because of the presence of numerous crossveins (including in R_1 space) as in other members of Myrmeleontoidea.

The family Osmylidae comprises many genera both in the recent and fossil fauna, with occurrences recorded from the Early Jurassic to the Miocene. Osmylids have rather conservative venation, which includes such features as the costal space tapering toward the wing base; the basal subcostal veinlets are always simple; Rs and its branches somewhat zigzagged (in most Kempyninae Rs is straight, only its branches are slightly zig-zagged); crossveins occur throughout almost the entire body of the wing; CuA and CuP are almost always straight (except for *Porismus* McLachlan, 1868 and *Gumilla* Navás, 1912), parallel to hind margin of the wing, and pectinately branched. For these reasons, Osmylidae may be clearly ruled out.

(2) Those whose statuses are doubtful or unclear. The family Nymphitidae was established by Handlirsch (1906–1908) for three Late Jurassic genera: *Nymphites* Haase, 1890, *Gigantotermes* Haase, 1890, and *Sialium*Westwood, 1854. Martynova (1949) added three other Mesozoic genera (*Epigambria* Handlirsch, 1939, *Chrysoleonites* Martynov, 1925, and *Mesonymphes* Carpenter, 1929) and excluded *Gigantotermes* from the family. Later she added the Early Jurassic *Sogjuta* Martynova, 1958 and synonymized this family with the extant Nymphidae (Martynova 1962). Subsequently, two other genera were referred to Nymphitidae: *Minonymphites* Hong, 1980 (Middle Triassic of China) and *Baissoleon* Makarkin, 1990a (Early Cretaceous of Siberia).

At present, the composition and status of this family remains one of most unresolved within Neuroptera. Of the recent authors who have considered it as a separate family (Whalley 1988, Makarkin 1990a, Carpenter 1992), only the latter gives a diagnosis, although this is very short. Carpenter considered this family as containing four genera: *Nymphites, Sialium, Chrysoleo-*

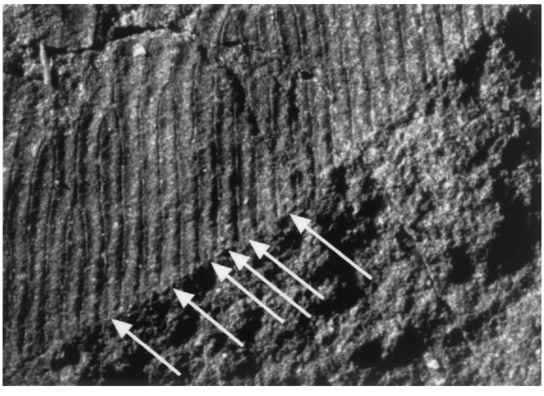

Fig. 5. *Palaeopsychops dodgeorum*, Q-0422b. Detail of the wing hind margin showing trichosors (arrows).

nites, and *Sogjuta.* Of these, *Sogjuta* appears to be an osmylid (Lambkin 1988), and *Chrysoleonites* is believed to be a member of Mesochrysopidae (Panfilov 1980). The type genus includes three species: *Nymphites priscus*(Weyenbergh, 1869) (type species), *N. braueri* Haase, 1890, and *N. lithographicus* Handlirsch, 1906. Unfortunately, the type species is represented by an incomplete and rather poorly preserved specimen, which is in need of redescription, and appears to be in too poor condition to allow determination of family affinity with certainty. This family is in strong need of revision, and its true status will become clear only after its type species is redescribed.

Palaeopsychops, however, is very far from the type genus of Nymphitidae, which possesses the features characteristic of the families of Myrmeleontoidea and Osmylidae, i.e., the groups that we have ruled out (forewings elongate, the costal space narrow, the subcostal veinlets in basal half of wing simple, CuA is strongly parallel to the hind margin).

The Epiosmylidae Panfilov, 1980 contain only one species, *Epiosmylus longicornis* Panfilov, 1980 (Late Jurassic of Karatau, Kazakhstan). This family has hitherto been considered a synonym of Osmylidae (Lambkin 1988, Makarkin 1990b). Examination of the holotype, however, shows that this synonymy is possibly unwarranted, as it lacks two characters found within almost all Osmylidae: trichosors and a sigmoid vein connecting R and M basally in the hind wing. It may be interpreted, however, that this species represents either an isolated branch within Osmylidae or else a separate family; it remains difficult at present to determine between these possibilities. In any case, *Palaeopsychops* is very far from *Epiosmylus* (e.g., in the latter, the forewings are elongate, the costal space narrow, the subcostal veinlets in basal half of the wing are simple and widely spaced, and CuA and CuP are strongly parallel to the hind margin).

Handlirsch (1939) erected Epigambriidae for *Epigambria longipennis* (a small species, 8 mm long, from the Early Jurassic of Germany), and was of the opinion that another two species from Late Jurassic of Germany and England possibly belong to this family: *Osmylites protogaeus* (Hagen, 1862) (see below under Osmylitidae) and *Osmylopsis buplicata*(Giebel, 1856) (now *familia incertae sedis:* Carpenter 1992). Subsequent authors (Martynova 1949, 1962; Ross and Jarzembowski 1993) placed the *Epigambria* within Nymphitidae, synonymizing Nymphitidae and Epigambriidae, however, as the only known specimen is an incomplete hindwing with characters undefined and insufficient to determine even placement in any superfamily, synonymy is not justified. It would be better to consider *Epigambria "Neuroptera incertae sedis"* as treated by Carpenter (1992).

Three genera have been assigned to Panfiloviidae: *Panfilovia* Makarkin, 1990c, *Makarkinia* Martins-Neto, 1997, and *Osmylogramma* Ponomarenko, 1992. However, the status of this family is uncertain. Wings of the type species of *Panfilovia* [*P. acuminata* (Panfilov 1980), from the Late Jurassic of Karatau, Kazakhstan] are elongate-oval with venation resembling that of Kalligrammatidae, e.g., very closely spaced crossveins throughout the wing including subcostal space, moderately expanded costal space for entire length with oblique subcostal veinlets connected by numerous crossveins, Sc and R_1 merged very close to the wing apex; it is possible that it is a kalligrammatid. *Makarkinia,* with *M. adamsi* (Martins-Neto, 1992), described from the Early Cretaceous of Brazil, also shows strong affinity with Kalligrammatidae. *Osmylogramma,* with *O. martinsoni* Ponomarenko, 1992 from Early Cretaceous of Mongolia, resembles *Palaeopsychops* at first glance, but when examined in detail, these genera are different both in venation (in *Osmylogramma,* immediately after $Sc+R_1$ merge they are rather sharply curved anteriad, the cubital space occupies a broader area, closely spaced crossveins fill the entire body of the wing), and in coloration (in *Osmylogramma* the membrane is entirely very dark pigmented).

The family Glottididae was established for the single species *Glottidia multivenosa* Bode, described from the Early Jurassic of Germany (Bode 1953) and recently redescribed by Ponomarenko (1995), who referred it to the Osmylopsychopidae. Although the apical two-thirds of the wing is well preserved, it is hard to assign this species to a family with certainty, as its venation resembles that of Osmylopsychopidae, Brongniartiellidae, and Prohemerobiidae. At any rate, *Palaeopsychops* is unlike *Glottidia* in that *Glottidia* lacks crossveins, M_2 is not pectinately branched, and CuP is rather strongly pectinately branched.

Seven genera from the Late Triassic to Early Cretaceous have been referred to the family Osmylitidae (*Osmylites* Haase, 1890, *Kirgisellodes* Martynov, 1937, *Petrushevskia* Martynova, 1958, *Tetanoptilon* Bode, 1953, *Mesosmylina* Bode, 1953, *Sinosmylites* Hong, 1983 and *Sinosmylites* Hong, 1996 [non Hong, 1983]) (Martynova 1962; Hong 1983, 1996), but all of these vary too greatly from each other in their venation to comprise the same family. The only known species of the type genus is *Osmylites excelsa* (Oppenheim, 1888) [= *Osmylites protogaea* (Hagen, 1862), syn. n.] from Late Jurassic of Germany. It is represented by a single specimen named (but neither described nor illustrated) by Hagen (1862) as *Chrysopa protogaea.* Later this specimen was reexamined by Oppenheim (1888), who illustrated and briefly described it as *Chrysopa excelsa.* When he established the genus *Osmylites,* Haase (1890) included this species as "*Osm*[*ylites*] (*Chrysopa*) *protogaea* Hag. (=*excelsa* Opp. nec Hag."). Thus the gender of this genus is feminine (not masculine) (Article 30.1.4.4 of the International Code of Zoological Nomenclature, 4th ed.), and *Chrysopa protogaea* Hagen, 1862 must be considered as *nomen nudum,* and an objective synonym of *Chrysopa excelsa* Oppenheim, 1888, although the name *O. protogaea* is incorrectly used in the literature to the present (e.g., Lambkin 1988, Ross and Jarzembowski 1993), and the name *O. excelsa* was hitherto considered a junior synonym of *O. protogaea.* The holotype of *Osmylites excelsa,* an overlapping fore and hindwing, has not yet been redescribed. The figures in Oppenheim (1888: Pl. 30, Fig. 2), Haase (1890: Fig. 10) and Handlirsch

(1906–1908: Pl. 48, Fig. 4) show the venation to be poorly preserved. The characters visible in the forewing are: all basal subcostal veinlets simple, widely spaced and nearly at a right angle to Sc; the costal space is rather narrow with a somewhat expanded basal region; CuA has few pectinate branches; and the anal veins are short. No other characters are certain. This species may belong to a number of families: Nymphidae, Mesochrysopidae, even Chrysopidae or Polystoechotidae. Osmylitidae is therefore a grab bag taxon, whose members should be reevaluated, and likely assigned to other families. Placing *Palaeopsychops* in this group therefore would only compound a problem awaiting resolution. Furthermore, of the genera assigned to the Osmylitidae, only *Kirgisellodes* [with *K. ornatus* (Martynov 1925), the single species in the genus described from the Late Jurassic Karatau and possibly belonging to Polystoechotidae], resembles *Palaeopsychops* in having a somewhat similar venational pattern (see Carpenter 1992: Fig. 192.3). *Palaeopsychops* may however be easily distinguished from *K. ornatus,* in which the subcostal veinlets are usually simple, there is an absence of gradate series, and the branches of M_2 and CuA are much shorter.

The family Solenoptilidae, erected for *Solenoptilon kochi* (Geinitz, 1887), is represented only by the apical portion of a wing from the Early Jurassic of Germany (Handlirsch 1906–1908). Subsequently, three other species were included in the family (Martynova 1949, Bode 1953), although Makarkin (1998) objected to this placement. This latter author described the monotypic genus *Oligogetes* Makarkin from the Late Eocene/Early Oligocene of the Russian Far East, based again on apical portions of wings and placed it tentatively in this family. Data on the Solenoptilidae is very fragmentary. The only precise knowledge on this group is the structure of the apical portion of wing (i.e., the costal space strongly narrow [narrowest in the order among middle and large-sized neuropterans], Sc and R_1 apically not fused, and the crossveins of radial space widely spaced). All these characters are obviously do not present in *Palaeopsychops.*

(3) Those families that are possibilities, at least theoretically, for *Palaeopsychops*. There are two superfamilies to which *Palaeopsychops* may be possibly assigned: Psychopsidoidea or psychopsid-like neuropterans (Prohemerobiidae, Brongniartiellidae, Psychopsidae, Osmylopsychopidae, and Kalligrammatidae: Martynova, 1949) and Ithonoidea (Polystoechotidae, Ithonidae, and Rapismatidae: Tauber & Adams, 1990). The family Kalligrammatidae is excluded, as it has markedly different venation.

Prohemerobiidae is the furthest theoretical possibility for *Palaeopsychops* in this group. The Prohemerobiidae are poorly defined. A variety of genera from the Late Triassic to Late Cretaceous have been referred to this family, making it to a considerable extent a grab bag taxon. Until a comprehensive revision is done (which is strongly necessary), we propose restricting this family to only the type genus, as in Carpenter (1992). Approximately 30 species from Early Jurassic of Germany and England have been referred to the genus *Prohemerobius,* but the majority of them were synomynized by Ponomarenko (1995). We have included Prohemerobiidae in this group only because of basal dilation of costal space, forking of subcostal veinlets, and similar shape of forewing in *Prohemerobius.* However, all genera of this family (even considered in the broadest sense) are unlike *Palaeopsychops* in other respects.

Extant species of Psychopsidae, a small family with an Afro-Oriento-Australian distribution, have rather conservative forewing shape (always very broad) and venation, with the costal space wide along the entire length, the humeral vein branched and proximal humeral trace recurrent, crossveins in the radial space are arranged mostly in 2–3 gradate series, branches of Rs are nearly parallel to the hind margin of the wing, and prominent trichosors are present. All of these characters occur in some fossil genera, e.g., *Propsychopsis* Krüger, 1923 (Eocene Baltic amber), *Baisopsychops* Makarkin, 1997 (Early Cretaceous of Siberia). However, most other genera from the Late Triassic to Late Oligocene (see partial list in Oswald 1993b) referred to this family do not possess most of these traits, in particular they have the costal space expanded basally, narrowing toward the wing apex, the body of the wing is filled with numerous crossveins, and the branches of the Rs are dichotomously branched (e.g., *Embaneura* G. Zalessky, 1953, and *Grammapsychops* Martynova, 1954: Carpenter 1992: Figs. 195.1, 195.2). Recently Andersen (2001) treated Osmylopsychopidae, Brongniartiellidae, and even Kalligrammatidae only as groups within "the Psychopsidae lineage." If the family is broadened to such an undefined status, then this allows assignment to Psychopsidae of genera very unlike modern psychopsids. This family is strongly in need of reevaluation and revision of both extinct and extant taxa. *Palaeopsychops* differs from these insects even when this family is considered in the broadest sense (*sensu lato*) in that M_2 is not pectinately branched and 1A is multibranched and occupies more area, and so it cannot reasonably be considered a psychopsid.

The family Brongniartiellidae is comprised of several Mesozoic genera (Martynova 1949, 1962; Whalley 1988) and is only a theoretical possibility for *Palaeopsychops.* The genus *Brongniartiella* Meunier, 1897 is poorly known because its type species (*Ricania gigas* Weyenbergh, 1869 [= *Brongniartiella problematica* Meunier, 1897] from the Late Jurassic of Germany) needs to be redescribed. The works in which it was illustrated were published >100 yr ago (Weyenbergh 1869, Meunier 1897). The photograph in Meunier (1897) shows that the specimen is apparently a pair of large, broadly subtriangular overlapping wings, with venation similar to that of such genera as *Mesopsychopsis* Handlirsch, 1906, *Embaneura, Grammapsychops, Kagapsychops* Fujiyama, 1978, i.e., the genera very distant venationally from *Palaeopsychops* (see Carpenter 1992: Figs. 195.1, 195.2, 196.5). The genera *Epactinophlebia* Martynov, 1927 and *Actinophlebia* Handlirsch, 1906 have been referred to Brongniartiellidae by some authors (e.g., Carpenter 1992). They resemble *Palaeopsychops* in having a rather similarly shaped forewing, a basal dilation of the costal space, forking of the subcostal veinlets, M is forked into M_1 and M_2 parallel to each other, and CuA has long pectinate branches; they are otherwise unlike *Palaeopsychops,* e.g., M_2 is not pectinately branched, CuP is parallel to the hind margin of the wing and pectinately branched, and crossveins are almost entirely absent.

The family Osmylopsychopidae was originally established for the genus *Osmylopsychops* Tillyard, 1923. The type species (*O. spillerae* Tillyard, 1923 from the Late Triassic of Australia) was at first known from two wing fragments. Further, fragmentary occurrences of *O. spillerae* were published by Riek (1955) and Lambkin (1992). Lambkin reexamined them in greater detail, and published a precise new reconstruction of the forewing venation, significantly revising that of Tillyard (1923). Later, Riek (1956) and Ponomarenko (1986, 1995) assigned several genera from the Late Triassic of Australia and the Jurassic of Germany and England to this family, including some that had been previously placed in Brongniartiellidae (e.g., *Pterinoblattina* Scudder, 1885, *Actinophlebia* Handlirsch, 1906). *Osmylopsychops spillerae* superficially resembles *Palaeopsychops dodgeorum* in that it has similar wing shape, heavy basal dilation of the costal space, CuA and CuP are arranged similarly, but in the former the origin of Sc is shifted distad, M is well-developed with several dichotomous branches occupying a larger area, 1A and 2A are well-developed and multibranched, and no gradate series is present. Osmylopsychopidae is the most likely family designation for *Palaeopsychops* within the Psychopsoidea, but the characters mentioned above make such possibilities significantly problematic.

Since 1923, when Rapismatidae was named, Ithonidae and Rapismatidae have been considered separate families, but recently Penny (1996) synonymized them, describing the genus *Adamsiana,* which has a mixture of character states found in both families. In the recent fauna there are ≈40 known species, which are distributed in Australia, mountainous areas of the Oriental Region (*Rapisma* McLachlan 1866), and in the western hemisphere from Central America to southern North America (Carpenter 1951, Riek 1974, Barnard 1981, Penny 1996). Fossil occurrences are unknown, but Riek (1974) believed that *Rapisma* is the only living representative of the family Brongniartiellidae. Ithonidae (*Rapismatidae*) share all basic characters of the forewing venation with Polystoechotidae. However, in this family M_2 is not pectinately branched (except for *Oliarces* Banks, 1908, in which this vein has a few pectinate branches), a gradate series of crossveins is never present, and R_1 and Rs are usually widely spaced apically. Thus, although there is a theoretical possibility that *Palaeopsychops* belongs to Ithonidae, this seems less likely than that it belongs to Polystoechotidae.

Polystoechotidae (*Mesopolystoechotidae*). See Introduction for the family composition and its geographical and possible geological distributions. We agree with Lambkin (1988) on the possible synonymy of Mesopolystoechotidae and Polystoechotidae, and consider them together here. The venation of extant species is described by Carpenter (1940), Lambkin (1988), and Oswald (1998). This completely conforms with the venation of *Palaeopsychops,* as is evident in these fossils. Also, when the forewing venation of *Polystoechotes punctatus* Fabricius is examined with special reference to concavity and convexity relationships, it is evident that M_2 is entirely (except most basally) strongly convex and CuA is strongly convex in the proximal half, i.e., very similar to *Palaeopsychops dodgeorum.*

However, there is difficulty in the determination of family for the fossil genera assigned to this family, as there are no autapomorphic characters of the venation, and so assignment to this family cannot be clearly determined by wings alone without some doubt. The basal dilation of the costal space, the presence of a recurrent proximal humeral trace and a branched humeral vein, and a strongly pectinately branched CuA are possibly found throughout Polystoechotidae (distinguishing them from Permian neuropterans), however, the family shares these with many other families (e.g., the second character is present also in Hemerobiidae, Mesithonidae, some Mesozoic Berothidae, primitive Mantispidae, Psychopsidae, Prohemerobiidae, Brongniartiellidae, and Ithonidae), and thus these characters are not diagnostic. Most other features characteristic of the family are plesiomorphic, e.g., the presence of nygmata, the presence of prominent trichosors, and Sc and R_1 are apically fused (in *Platystoechotes* these are free). Therefore assignment of *Palaeopsychops* to this family is formally preliminary, however, taken together as a whole, those features shown to be present suggest Polystoechotidae as the most likely family designation.

Thus, although there is a theoretical possibility of assigning the genus to Psychopsidoidea, the possibility is greater for Ithonoidea, and greater still that it belongs to Polystoechotidae.

Acknowledgments

We thank Kenneth and Ken Dodge, who have provided such pleasurable companionship in fossil collecting through the years; Rolf Mathewes, who granted access to the Simon Fraser University collection and for his support over many years; Guy Rose, owner of the site, for continued support of scientific research at Quilchena; Stig Andersen, Geological Museum, Copenhagen, for providing us with an advance copy of his paper in press; Bushra Hussaini and David Grimaldi, American Museum of Natural History, for loan of the type of *Polystoechotes piperatus*; and Stephen Gaimari and an anonymous reviewer for helpful comments that improved this paper. Funding (S.B.A.) was provided in part by a Natural Science and Engineering Research Council scholarship and a Putnam Expeditionary Grant.

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Received for publication 21 March 2002; accepted 16 January 2003.