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Fossil Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea) from Baltic Amber

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Abstract

Palaeocharis rex **n. gen.** and sp. (Eucharitidae: Eucharitinae) and *Perilampus pisticus* **n. sp.** (Perilampidae: Perilampinae) are described from Baltic amber. *Perilampus renzii* (Peñalver & Engel) is transferred to Torymidae: *Palaeotorymus renzii* **n. comb.** *Palaeocharis* is related to *Psilocharis* Heraty based on presence of one anellus, linear mandibular depression, dorsal axillular groove, free prepectus and a transverse row of hairs on the hypopygium. This fossil is unique in comparison with extant Chalcidoidea because there are two foretibial spurs instead of a single well-developed calcar. *Perilampus pisticus* is placed into the extant *Perilampus micans* group because the frenum and marginal rim of the scutellum are visible in dorsal view and the prepectus forms a large equilateral triangle. The phylogenetic placement of both genera is discussed based on an analysis of both a combined morphological and molecular (28S and 18S) and morphology-only matrix. Morphological characters were used from an earlier study of Eucharitidae (Heraty 2002), with some characters revised to reflect variation in Perilampinae. Baltic amber is of Eocene age, which puts the age of divergence of these families at more than 40 mya.

Key words: amber, phylogeny, Eocene, ribosomal DNA, morphology, ant, parasitoid

Introduction

Chalcidoidea represent one of the most recent explosive radiations of insects, and is estimated to contain as many as 375,000 to 500,000 species (Heraty & Gates 2003, Noyes 2003). Little is known about the early evolution of the superfamily. Their proposed origin is during the late Jurassic or early Cretaceous (~163–144 mya) (Yoshimoto 1975; Schlee and Glöckner 1978, Zherichin & Sukacheva 1973, Roskam 1992; Rasnitsyn 2002). The first fossils referable to Chalcidoidea (Mymaridae; the proposed sister group of the remaining chalcidoids) are known from Campanian Cedar Lake amber (83–74 mya). Khutelchalcididae was described from late Jurassic or early Cretaceous deposits (Rasnitsyn *et al.* 2004), but its placement in Chalcidoidea was rejected by Gibson *et al.* (2007). The proposed sister group of Chalcidoidea, the Mymarommatoidea, are known from late to middle Cretaceous Albian-Cenomanian deposits (~100 mya) (Schlüter 1978, Fursov *et al.* 2002, Engel & Grimaldi 2007; Gibson *et al.* 2007).

The known diversity of Chalcidoidea during the Cretaceous is surprisingly low, with only two families currently recognized, Mymaridae and Tetracampidae (summarized in Yoshimoto 1975, Darling & Sharkey 1990, Engel & Grimaldi 2007). *Enneagmus* Yoshimoto, the sole trichogrammatid wasp described from Cretaceous amber, recently was transferred to Mymaridae (Huber 2005). Taxa described as Tetracampidae by Yoshimoto likely do not belong to this family, but their true affinities are uncertain (Gumovsky and Perkovsky 2005). Chalcididae illustrated by Whalley (1981) likely belong to this same group (J.S. Noyes, personal communication). Machado *et al.* (2001) originally proposed an origin of 90 mya for the fig-pollinating

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Agaonidae, but this has since been modified to 60 mya (Ronsted *et al.* 2005). If true, then no modern chalcidoid taxa other than Mymaridae and "Tetracampidae" appear until after the Cretaceous boundary. Some potential Chalcidoidea similar to Torymidae or Pteromalidae are known from New Jersey amber (Turonian), but these need critical evaluation (Gary Gibson (CNIC) and David Grimaldi (AMNH), personal communication).

In contrast, numerous specimens of Chalcidoidea have been described from either compression or amber deposits from the Oligocene-Miocene period (34–7 mya), and many represent extant genera (e.g. Huber 1927; Doutt 1973ab; Grissell 1980; Skalski 1988; Darling 1996; Machado *et al.* 2001; Gumovsky 2001; Engel 2002, 2009; Peñlaver & Engel 2006; Peñlaver *et al.* 2006; Gibson 2008, 2009). Because of the lack of any Paleocene records for Hymenoptera, the real diversification of Chalcidoidea appears to begin during the Eocene (55–35 mya). Various Baltic amber deposits record a mix of both extant and extinct genera in the Eupelmidae (Trjapitsyn 1963; Gibson 2008, 2009), Encyrtidae (Sugonyaev 1962; Simutnik 2001, 2002; Simutnik & Perkovsky 2006), Tetracampidae (Gumovsky & Perkovsky 2005), and Torymidae (Brues 1923). Hong (2002) described and illustrated a number of chalcidoid families from Fushun amber in China (Torymidae, Eurytomidae, Pteromalidae, Eulophidae, Perilampidae and two potentially new families), which is dated as early Eocene and comparable in age to Baltic amber. Unfortunately, many of the taxa are suspect in their placement and will require further study, and the proposed taxonomic names therein are also invalid because no depositories were listed for the material being described (J.S. Noyes, personal communication). Genera belonging to Perilampidae and Pteromalidae (Pteromalinae) have been reported from Baltic amber but are highly suspect (Helm 1884, Menge 1855, Larsson 1978). The extant genus *Perilampus* (Perilampidae) was recorded from Baltic amber (Brischke 1886), but no specimens are available for study, and the record by Brischke was considered dubious by Peñalver and Engel (2006). Subsequently, *Perilampus renzii* (Peñalver & Engel 2006) was described from a compression fossil from early Oligocene deposits in eastern Spain (~30 mya). The proposed sister group of Perilampidae, the Eucharitidae, has not been recorded from the fossil record, but the distribution of endemic species groups of Oraseminae are suggestive of a southern hemisphere or Gondwanan pattern of radiation during the late Cretaceous or early Eocene (Heraty 2002).

Eucharitidae and Perilampidae are regarded as a monophyletic group based largely on the presence of an active, well-sclerotized, first-instar larva or planidium (Heraty & Darling 1984; Darling 1992). Both Perilampidae and Eucharitidae deposit their eggs away from the host, and almost always either onto or into plant tissue (Clausen 1940). A potential behavioral synapomorphy for Perilampidae (Chrysolampinae, Perilampinae, Philomidinae) plus Eucharitidae is the habit of initial parasitism and feeding on the host larva by the planidium, followed by development as an ectoparasitoid of the host pupa (Darling & Miller 1991; Darling 1992; Heraty 2000, 2002; Heraty *et al.* 2004). Within Perilampidae, where known, Chrysolampinae are parasitoids of Curculionidae (Darling & Miller 1991), Philomidinae are parasitoids of Halictidae (Darling 1992), and Perilampinae are primary or secondary parasitoids of a number of hosts including Anobiidae, Chrysopidae, Diprionidae, Tachinidae and Ichneumonidae (Darling 1995). Eucharitidae are parasitoids of Formicidae (Heraty 2002; Heraty *et al.* 2004). No adult synapomorphies support the monophyly of the two families and later instar larvae are hypermetamorphic and highly divergent in morphology even between subfamilies. Monophyly of Perilampidae is more difficult to support, with either Perilampinae or Perilampinae + Chrysolampinae considered as the sister group of a consistently monophyletic Eucharitidae (Darling 1992; Heraty 2000, 2002; Heraty *et al.* 2004). With further outgroup sampling and sequence data, Perilampidae are monophyletic, including Philomidinae, Akapalinae (biology unknown) and Eutrichosomatinae (curculionid parasitoids) (Munro and Heraty, unpublished).

Herein we report on the first fossil eucharitid from Baltic amber, confirm *Perilampus* from Baltic amber, and dispute the identity of a "stem-group" perilampid fossil described by Peñalver & Engel (2006). The occurrence of relatively modern species of derived Perilampinae and Eucharitinae in Baltic amber puts the age of divergence of these families at more than 40 mya and provides new insights into the timing of both taxonomic and ecological diversification within Perilampidae and Eucharitidae.

Materials and methods

The two amber specimens were received from the collection of Jens-Wilhelm Janzen (Germany) deposited at the American Museum of Natural History (AMNH). These were imaged using the Syncroscopy® Automontage imaging system with a Leica M16 microscope or a GT-Vision® digital imaging system. Images were optimized in Adobe Photoshop 7.0.

Morphological terms follow Heraty (2002) for the desciption of the new eucharitid, whereas terms and format follow Bouček (1956) for the description of the new perilampid to facilitate comparison. Characters that could be reasonably assessed, although not with certainty, are indicated by [?] in the descriptions.

Phylogenetic analyses were based on combined morphological and molecular and morphology-only datasets previously used for an analysis of relationships in Eucharitidae (Heraty *et al*. 2004). Morphological data are based on 88 of 101 morphological characters as used by Heraty (2002), with 5 characters ordered (31, 36, 42, 54, 72). Character summaries are presented in Heraty (2002) and Heraty *et al.* (2004). Generic level (polymorphic) coding for the 55 included extant species of Eucharitidae was maintained from these earlier analyses, whereas the coding was refined and scored by species for the 15 extant Perilampidae and four Pteromalidae (Pteromalinae) outgroups to better resolve relationships within Perilampidae. One additional taxon, *Psilocharis pacifica* Heraty, was added to this dataset, with the same morphological coding as for other *Psilocharis*. The GeneBank accession numbers for *P. pacifica* are GQ453403 (28S) and GQ453404 (18S). The revised coding including fossil taxa and revised character definitions is included in Table 1. Fossil taxa were coded as missing data for the molecular partition. The molecular partition included 28S-D2, 28S-D3 and 18S E23 (1262 aligned bases) as described in Heraty *et al.* (2004).

Both datasets were analyzed using PAUP*4.0ß10 (Swofford 2002) using 500 random addition heuristic searches and tree bisection reconnection (TBR) branch swapping. Pteromalinae were used as the outgroup. Successive approximations character weighting was applied to the resulting trees using the maximum value of the rescaled consistency index and a base weight of 1000, with the resulting trees rescaled to unity character weights and compared in length to the most parsimonious tree (Heraty *et al*. 2004). All results were condensed to collapse branches with a minimum length of zero. Bootstrap support was evaluated with 1000 replicates using the closest starting tree option.

Results

The combined morphology and molecular analysis resulted in a set of 48 equally parsimonious trees (length 2076, r.i. 0.82), which reduced to a single tree after successive approximations weighting (SAW) analysis (length 2080) (Fig. 1). The SAW-combined data tree was four steps longer but resulted in higher resolution within clades; a consensus of the unweighted trees lacked resolution in Perilampinae and resulted in collapse of the Psilocharitini (thin branches, Fig. 1). In the SAW-combined results, 'Psilocharitini' formed a paraphyletic grade to Eucharitini, with *Palaeocharis* and *Psilocharis* monophyletic (Fig. 1). These results are virtually identical to those presented in Heraty *et al.* (2004), but with a switch in the order of clades within Psilocharitini, with *Neolosbanus* as the sister group of *Psilocharis* + Eucharitinae. Similar results are found with analyses of only the molecular data (fossils excluded), with *Neolosbanus* basal in unweighted trees and switching with *Psilocharis* in the SAW tree. Monophyly of Psilocharitini is not supported in analyses that include molecular data. Unambiguous morphological character state changes are plotted onto a reduced version of the combined results in Fig. 2. The proposed Eocene divergence period (Fig. 2) is loosely hypothesized based on absolute criteria of fossil presence and their proposed sister group divergence.

The morphology-only dataset resulted in a set of 24 equally parsimonious trees (length 374, r.i. 0.82), which reduced to a single tree after SAW (length 377; results not shown). The SAW-morphology tree was three steps longer but fully resolved for relationships between higher groups; a consensus of unweighted trees was largely unresolved for subfamilies of both Perilampidae and Eucharitidae. In the SAW results,

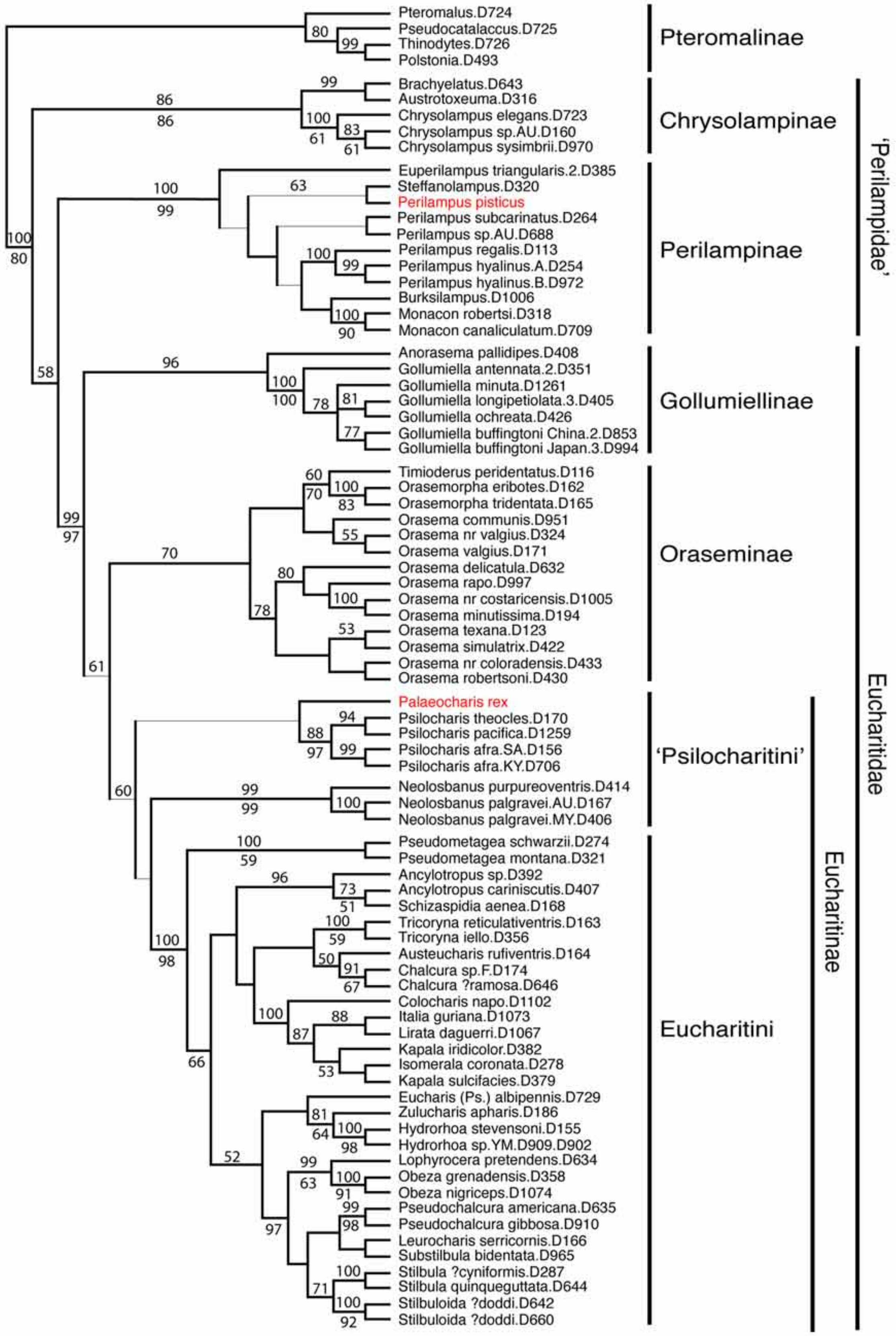


FIGURE 1. Combined morphological and molecular results. Single successive-weighted tree (length 2080) of a set of 48 unweighted parsimony trees (length 2076, r.i. 0.82). Thin branches collapse in the unweighted trees. Bootstrap values (1000 replicates) for combined data above branches and for compatible nodes in morphology-only data below branches. Apostrophes around Perilampidae and Psilocharitini refer to their potential paraphyly (see text).

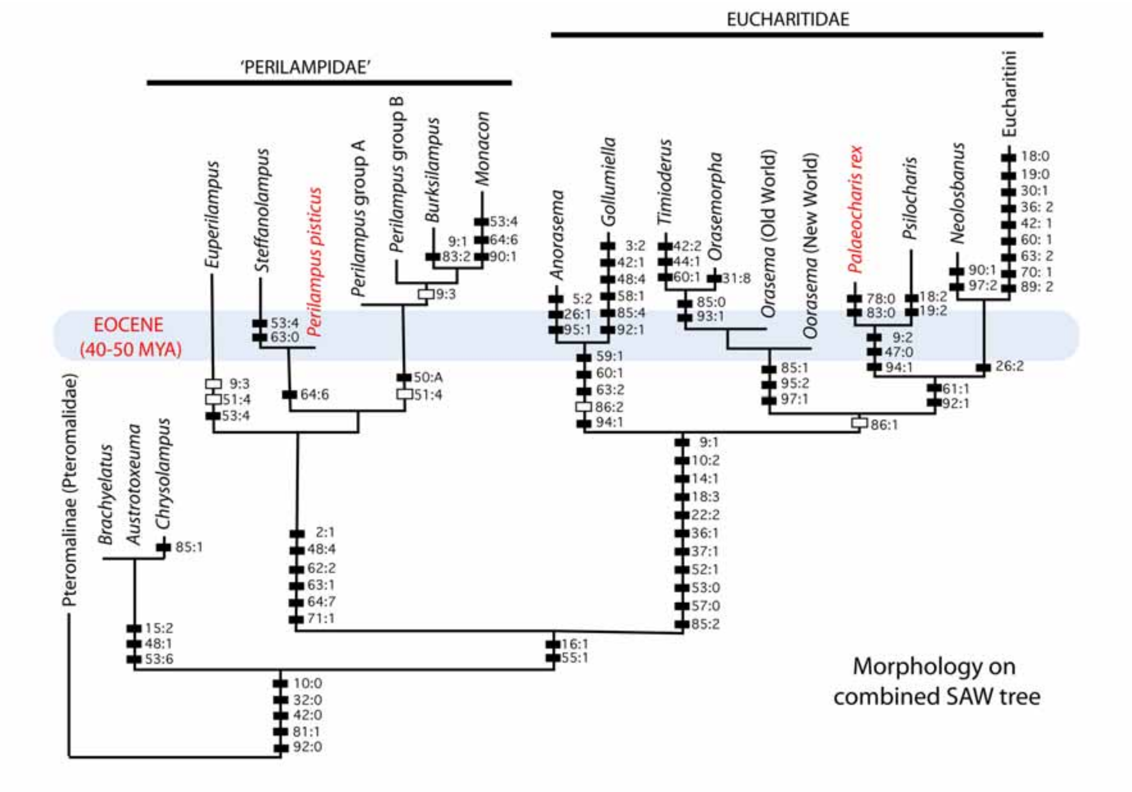


FIGURE 2. Unambiguous and selected ambiguous (open boxes) morphological state changes plotted onto condensed version of combined SAW morphology and molecular tree in Fig. 1. Fossil taxa in red. Branch lengths arbitrarily scaled to show hypothesized pre- and post-Eocene divergences.

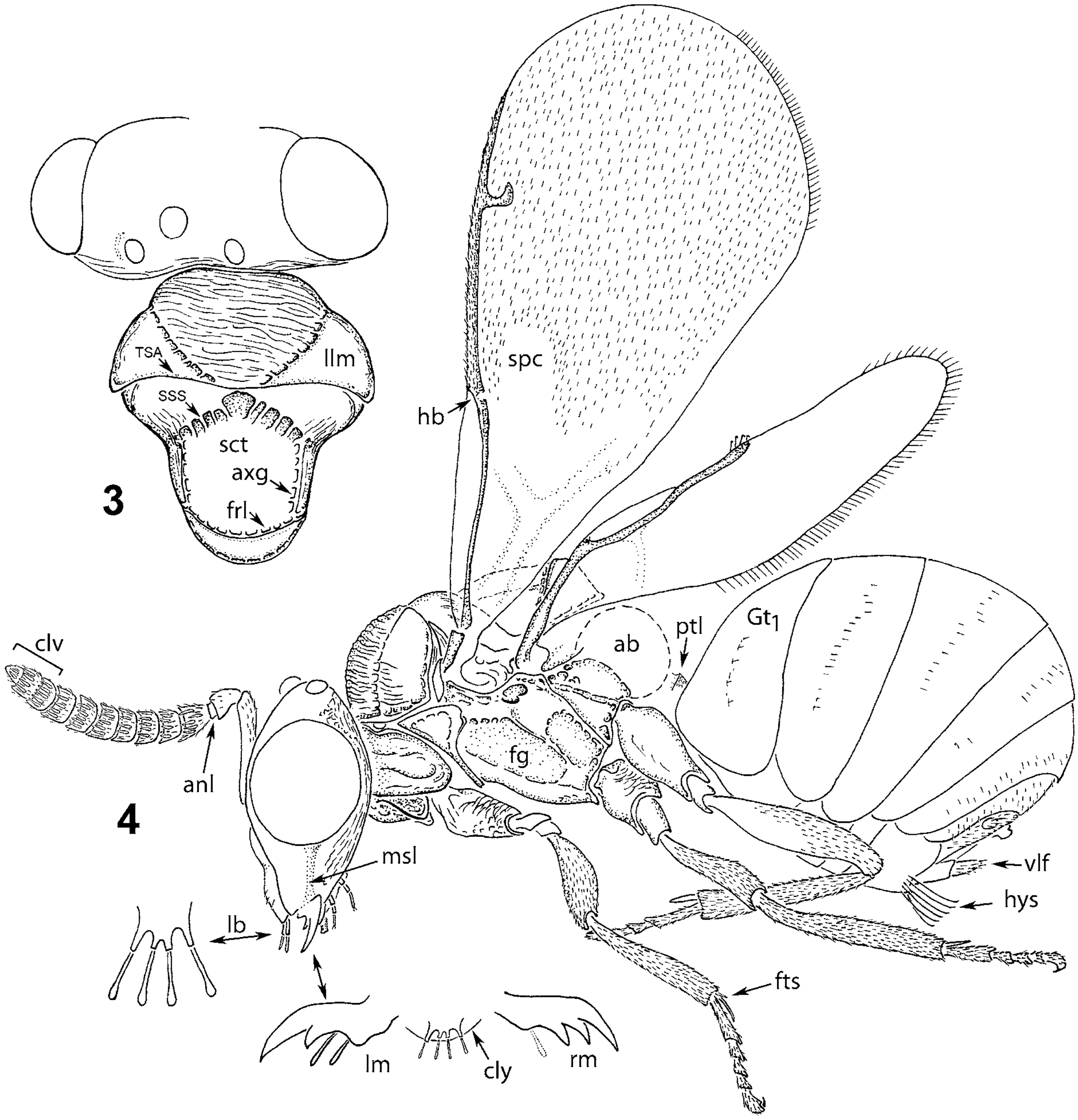
Psilocharitini, including *Palaeocharis*, was monophyletic and sister group to Gollumiellinae + Eucharitinae, which is the same as the results from earlier morphology-only analyses that were rejected on the strength of the molecular data (Heraty 2002, Heraty *et al.* 2004). The relationships between *Palaeocharis*, *Psilocharis* and *Neolosbanus* were unresolved. For Perilampinae, the major difference was in placement of *Euperilampus* as a derived rather than basal group, with *Steffanolampus* as sister group to *P. pisticus* + remaining Perilampinae.

'Perilampidae' (Chrysolampinae, Perilampinae) were paraphyletic in all analyses. We regard this as an artifact of limited outgroup sampling, and monophyly of Perilampidae is generally supported in more extensive molecular analyses (Munro and Heraty unpublished).

Palaeocharis rex n. gen. and sp.

(Figs 3–11)

Diagnosis. This genus is most similar to the extant genus *Psilocharis*, with which it shares a sharp triangular second tooth on the left mandible (lm, Fig. 4; truncate in *Neolosbanus*, cf. fig. 204 in Heraty 1994), broadly impressed femoral groove (fg, Fig. 4; cf. *Psilocharis* figs 223–225 in Heraty 1994), bare speculum (spc, Fig. 4), cylindrical separated valvifer, and transverse band of long hypopygial setae. It differs from *Psilocharis* by having three clearly delineated claval segments, apparent absence of marginal clypeal setae (difficult to see), rounded clypeal margin (cly, Figs 4, 8), a minute extra foretibial spur (fts, Fig. 4), posteriorly directed stigmal vein (Figs 4, 9; linear in *Psilocharis* and *Neolosbanus*), and a short transverse petiole with a dorsal carina (longer than broad without a carina in *Psilocharis* and *Neolosbanus*).



FIGURES 3–4. *Palaeocharis rex*, female: **3,** head and mesosoma in dorsal view; **4,** habitus with details of labrum, and mouthparts. Abbreviations: ab = air bubble; anl = anellus; axg = axillular groove; clv = clava; cly = clypeus; fg = femoral groove; frl = frenal line; fts = fore tibial spur; Gt_1 = Gastral tergite 1; hb = hyaline break; hys = hypopygial setae; lb = labrum; llm, lateral lobe of mesoscutum; lm = left mandible; msl = malar sulcus; ptl = petiole; rm = right mandible; sct = scutellum; spc = speculum; SSS = scutoscutellar sulcus; TSA = transcutal articulation; vlf = 3^{rd} valvifer.

Description of Female. Length 2.39 mm. Body color, including legs and antennae, dark brown to black. Wings hyaline, forewing venation brown.

Head. Subtriangular in frontal view; eyes rounded, protruding and bare; median ocellus anterior to lateral ocelli. Frons and lower face smooth and shining; ocellar-ocular depression absent; scrobal depression shallow with rounded lateral margins; occiput circularly colliculate (Fig. 8), dorsal occipital margin rounded. Clypeus smooth, anteclypeus absent [?], clypeal margin slightly rounded (Fig. 8); supraclypeal area present, swollen medially and with distinct lateral sulci. Genal depression longitudinally impressed (msl, Fig. 4); hypostomal lobes broadly separated. Mandibles falcate, 3/2 dentate with inner tooth of left mandible sharp (Figs 4, 8);

labrum with 4 digits (lb, Figs 4, 8); maxillary and labial palpi 3-segmented. Antenna 13-segmented with a cylindrical flagellum; scape narrow and elongate; anellus transverse (anl, Figs 4, 6); funicle 7-segmented, basal funicular segment about as long as broad; clava with three distinct, partially fused segments; multiporous plate sensilla large and numerous on all flagellomeres beyond anellus (mps, Figs 4, 6).

Mesosoma. Pronotum not visible in dorsal view. Mesoscutum with anterior margin evenly rounded, lateral margin rounded with weak lateral flange extending over spiracle, posterolaterally not extended over tegula; dorsum bare; notauli deeply impressed and converging but not meeting at midline (Fig. 3); transscutal articulation (TSA) present. Scutoscutellar sulcus (SSS) diagonal, meeting anteriorly at TSA; axilla rounded and smooth; scutellar disc (sct) smooth and bare; axillular sulcus (axg) present. Frenal line (frl) present and complete dorsally; posterior margin of scutellum slightly convex dorsally anterior to frenal line (Fig. 4); frenum broadly rounded. Metanotum with broad rounded flange laterally, overlapping propodeum and partially overlapping propodeal spiracle which is close to the dorsal margin [?]; [propodeal disc obscured by air bubble (ab)]; callus smooth, rounded and without hairs [?]; metepimeral groove present and foveate. Femoral groove broadly and shallowly impressed (fg, Figs 4, 7); mesepimeron mostly smooth, transepimeral sulcus present as crenulate dorsal margin of lower mesepimeron; anteroventral margin of acropleuron grooved for reception of posterior margin of prepectus; mesepisternum with anteromedial margin slightly overlapping posterior margin of prepectus; ventral margin of mesepisternum slightly rounded between the fore and midcoxae (Fig. 4). Prepectus associated with mesepimeron, not fused with pronotum, and in a different plane from pronotum; dorsal half of prepectus triangular, reaching tegula, and broadly foveate medially with a small notch in the posterior margin (Fig. 4), ventral half strongly narrowed; pronotal spine absent; spiracle not enclosed. Mesocoxa without lateral groove or carina; hind coxa semiglobose and smooth; foretibia with one large, curved and acuminate spur and another lateral minute spur (Fig. 4, fts); mid and hind tibia each with 1 spur. Forewing venation distinct (Figs 4, 8); parastigma possibly with hyaline break (hb, Figs 4, 9 [may be artifact]); stigmal vein narrowed basally and with strong posterior projection (=uncus? [?]), perpendicular to forewing margin; postmarginal vein more than 3 times as long as stigmal vein; basal area bare [?], speculum bare; disc with dense fine setae and distinct marginal fringe (Figs 4, 9). Hind wing venation complete; fringe present.

Metasoma. Petiole (ptl, Fig. 4) not clearly visible, appears to be short, possibly transverse and truncate basally [?], with a weak dorsal carina [?], and smooth [?]. Gastral terga smooth and bare except for medial band of short setae; posterior margin of tergites even [?]. First gastral sternite appears smooth [?]. Hypopygium with transverse band of 10 long hairs (hys, Figs 4, 10). Valvifer cylindrical, setose and clearly separated basally from third valvula (vlf, Figs 4, 11). Sclerotized epiproct present. Ovipositor acicular [?; based on shape of sheath].

Holotype. Female. Baltic Amber: Lutetian; purchased 2007 from Jens-Wilhelm Janzen AMNH Ba-JWJ686). Deposited in AMNH.

Etymology. Genus name from the combination of Greek (*palaeo,* ‘ancient’ and *charis* ‘loveliness’); gender feminine. Species epithet from the Latin (*Regis*, ‘king’).

Phylogenetic Placement. *Palaeocharis* is clearly placed within Eucharitidae based on several unambiguous synapomorphies (Fig. 2). Its placement as a sister group of *Psilocharis* is weakly supported based on presence of linear and smooth mandibular depression (msl, Fig. 4; 9:2) and presence of a distinct axillular groove (47:0). A similar malar sulcus is found in some *Orasema*, and the presence of an axillular groove is variable across Eucharitidae and likely plesiomorphic. The transverse line of long hairs on the hypopygium in *Palaeocharis* and most *Psilocharis* is clearly derived (hys, Figs 4, 10; 94:1). However, the state is not shared by all *Psilocharis*, with *Psilocharis aenigma* Heraty having only two long hypopygial hairs. In Heraty (2002), the line of hairs was coded as polymorphic and optimized as independently derived within the genus. Its occurrence in *Palaeocharis* makes it synapomorphic for the two genera, with the two long hairs within *Psilocharis* a derived feature. However, a similar line of hypopygial hairs also occurs in *Anorasema* Bouček and *Gollumiella* Hedqvist (both Gollumiellinae), and it can be optimized on Figure 2 as either plesiomorphic for Eucharitidae (derived in the common ancestor) or independently derived in both groups.

Placement of *Palaeocharis* + *Psilocharis* within the paraphyletic tribe 'Psilocharitini' + Eucharitinae is supported by the mesepimeron overlapping the prepectus and grooved to articulate with the acropleuron (61:1) and loss of the antecostal sulcus (92:1; difficult to see on fossil). This group is excluded from *Neolosbanus* + Eucharitini by not having an elongate second flagellar segment (26:2). However, the position of *Neolosbanus* and *Psilocharis* was unstable in the various parsimony and SAW analyses, with Psilocharitini monophyletic in morphology-only analyses. Features shared by *Palaeocharis*, *Psilocharis* and *Neolosbanus* include a transverse anellus (anl, Fig. 4; 24:0 [plesiomorphic and not shown on cladogram), four digitate labrum (lb, Figs 4, 8; 17:1 [plesiomorphic]), free prepectus (Figs 4, 5, 7; 63:0 [plesiomorphic]), and a relatively long first gastral tergite, which is about as long as the second tergite (Figs 4, 5: 86:1). In the morphology-only analysis, with Gollumiellinae shifted to Eucharitini, monophyly of Psilocharitini is supported by the grooved prepectus (61:1) and the shape of the prepectus (64:1). The anellus is absent in some *Neolosbanus* and all Eucharitini, and the prepectus is fused to the pronotum (63:2) in all Eucharitini. Based on the appearance of the cylindrical valvifer (vlf, Figs 4, 11; similar to *Psilocharis theocles* (Walker), cf. fig. 264, Heraty 1994), the ovipositor is probably acicular, which within Eucharitidae may be a derived feature (reversal from an apically enlarged ovipositor; 95:2). A dorsal occipital carina, which is characteristic of extant Psilocharitini, appears to be absent (occiput rounded but difficult to see). The petiole is difficult to see, but appears to be short (83:0), cylindrical and smooth, which is unlike any species of either Gollumiellinae or Psilocharitini, which all have an elongate petiole (Heraty 1994, Heraty *et al.* 2004). *Palaeocharis* is excluded from Gollumiellinae, which have a very short first gastral tergite (less than half as long as second laterally), and the prepectus fused with the pronotum (Heraty *et al.* 2004). Molecular data clearly drive the higher level relationships proposed for Eucharitidae (Figs 1, 2; Heraty *et al*. 2004), but morphological data generally support a grouping of *Palaeocharis* and *Psilocharis* in combined and morphology-only analyses.

***Perilampus pisticus* Darling n. sp.**

(Figs 12–15)

Description of Male. Length approximately 2 mm. Body color, including antennae and legs black, with weak iridescent reflections [?]. Wings hyaline [?], forewing venation brown.

Head. Quadrate and about twice [?] as broad as long in frontal view, in dorsal view transverse, distinctly wider than pronotum; vertex, inner and outer orbits smooth, without distinct sculpture (Fig. 12); ocelli forming a broad isosceles triangle, OOL longer than POL; frontal carina absent, scrobal cavity not deep and bounded by weak rounded keels (Fig. 13); malar sulcus distinct, about 0.2 times eye height; supraclypeal area glabrous, quadrate. Mandibles large and robust, right with 3 distinct teeth. Antenna: scape narrowly linear, weakly expanded apically [?], length about 5 times maximum width [?]; pedicel and funicular segments subequal in length, anellus about 0.2 times length of first funicular segment.

Mesosoma. Sculpture foveate-reticulate (Figs 13, 14) unless otherwise noted. Pronotum narrow, only about 0.2 times [?] length of mesoscutum (Fig. 13), without a distinct anterior carina, rounded laterad; mesoscutum and scutellum subequal in length; sidelobes of mesoscutum smooth along notauli; axillula large and triangular, with smooth median area delimited by large foveae (Fig. 14); scutellum only weakly vaulted, frenal line anteapical, the marginal rim forming the apex of scutellum, apex rounded (Fig. 14); metanotum large, straplike, length equal to frenum and marginal rim of scutellum combined, dorsellum indicated by ventral band of smaller foveae; propodeum with distinct median carina and smooth submedian areas delimited laterad by deep foveae (Fig. 14); prepectus large, a broad equilateral triangle, distinctly differentiated from and wider than the adjacent pronotum, with all three sides bordered with coarse punctures (Fig. 13). Forewing venation (Fig. 15): submarginal vein about twice marginal vein, postmarginal vein subequal in length to marginal vein (11:10); stigmal vein 0.4 times marginal vein and making an approximately 60 degree angle with marginal vein, stigma expanded with a distinct uncus.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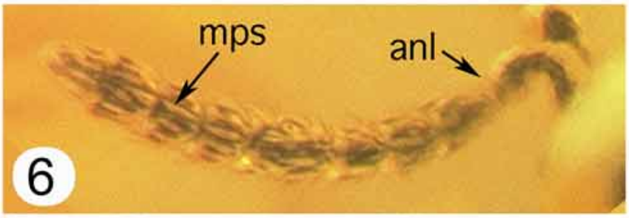
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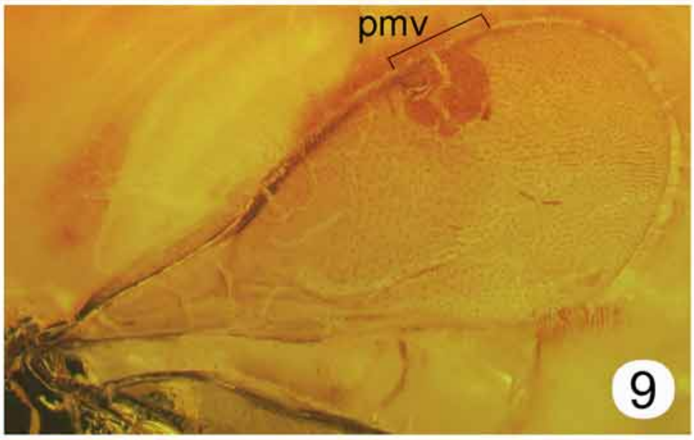
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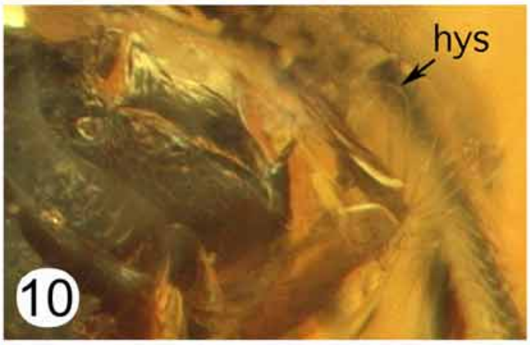
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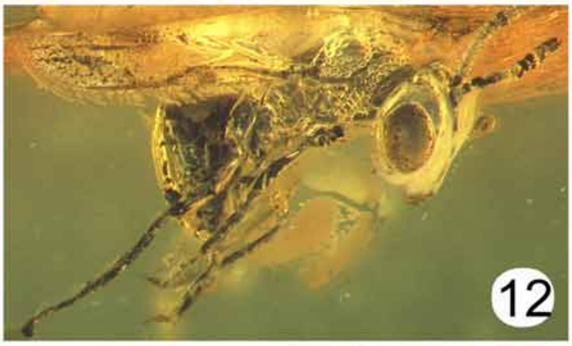
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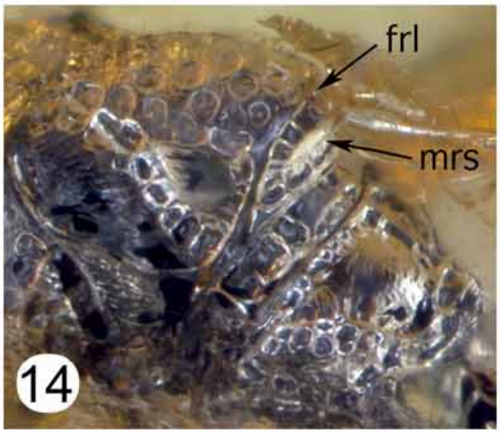
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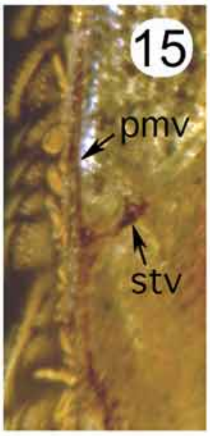
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Metasoma. Petiole inconspicuous, gaster closely associated with mesosoma, short and high in profile (Fig. 12), T2 with laterotergites and about as long as T3 and T4 combined. Sculpture glabrous.

Holotype. Male. Baltic Amber: Lutetian; purchased 2007 from Jens-Wilhelm Janzen AMNH Ba-JWJ687). Deposited in AMNH.

Etymology. From the Latin (*pisticus*, ‘true, genuine’), a reference to this species as the first actual fossil species of *Perilampus*.

Additional Amber Specimens Examined. DCD has also seen specimens or photographs of four additional specimens of Perilampinae in Baltic amber, two in the collection of the American Museum of Natural History (examined, both Eocene [Lutetian], purchased from Jens-Wilhelm Janzen, AMNH B-JWJ-121 and AMNH B-JWJ-191) and two in the Staatliches Museum für Naturkunde Stuttgart (photographs courtesy of Lars Krogmann). These are not regarded as conspecific with *P. pisticus* and a thorough study of this material is currently underway. Interestingly, all 5 specimens have a very large and triangular prepectus, but only the holotype of *P. pisticus* has the short and triangular metasoma characteristic of extant species of *Perilampus*.

Baltic Amber *Perilampus* species were first reported in the literature over 120 years ago (Brischke 1886; repeated in Larsson 1978) but were never formally described. This led to the premature dismissal of Brischke’s report by Peñalver & Engel (2006) because of the age of the work and lack of any subsequent specimens found in Baltic amber.

Phylogenetic Placement. This species is readily referable to the genus *Perilampus* (*sensu* Darling 1996) on the basis of the close association of the triangular prepectus with the pronotum (Fig. 13), short, triangular metasoma (Fig. 12), right mandible with 3 distinct teeth (cf. 2 in Chrysolampinae), marginal vein only about twice as long as stigmal vein (Fig. 15, cf. at least 3.5 times in Chrysolampinae), and absence of the synapomorphies of the other genera of Perilampinae (see Bouček 1978).

Not only is the amber species clearly referable to the genus *Perilampus*, but *P. pisticus* also shares a suite of characters with an informal group of extant Palaearctic species (Bouček 1956, 1971), which we will refer to here as the *Perilampus micans* species group (*P. micans* Dalman, *P. aeneus* (Rosseus), *P. ruschkai* Hellen, *P. maceki* Bouček, *P. cephalotes* Bouček and *P. polypori* Bouček). These species all have a relatively large and broad prepectus (64:6) with all three sides bordered by rows of coarse punctures and a distinct rudiment of the stigmal vein uncus (see Bouček 1956:94, couplet 1). Both of these characters are also present in *P. pisticus* (Figs 13, 15) and in *Steffanolampus salicetum* (Steffan), with the latter considered as the most basal genus of Perilampinae because the prepectus, although large and triangular, is not fused with the pronotum (Darling 1988). In addition, the frenum shape and orientation of the scutellar disc associate the amber species with both *S. salicetum* and *P. micans*. In all three species, the scutellar disc is not vaulted and the frenal line is complete dorsally and forms a carina that parallels the marginal rim of the scutellum (Fig. 14). In all other species of *Perilampus* and in the other genera of Perilampinae, the scutellar disc is vaulted over the frenum with the frenal line forming the apex of the scutellum (51:4). Based on outgroup comparison with Chrysolampinae, the configuration of the scutellum is plesiomorphic in the amber fossil, *S. salicetum* and *P. micans*, suggesting that these species are components of a basal grade of species that ultimately gave rise to the extant species of Perilampinae.

◄

FIGURES 5–15. 5–11, *Palaeocharis rex*, female: **5,** habitus; **6,** antenna; **7,** head and mesosoma, lateral view; **8,** head, posterior view; **9,** forewing and partial hindwing, ventral view; **10,** gaster, apex in posterolateral view; **11,** gaster, apex in posterior view. **12–15,** *Perilampus pisticus*, male: **12,** habitus; **13,** head and anterior mesosoma, enlargement of 10; **14,** scutellar complex and propodeum, dorsolateral view; **15,** forewing venation, postmarginal vein to top. Abbreviations: anl = anellus; frl = frenal line; hys = hypopygial setae; lb = labrum; mps = multiporous plate sensilla; mrs = marginal rim of scutellum; pmv = postmarginal vein; stv = stigmal vein; vlf = 3rd valvifer.

Discussion

Perilampus pisticus is the only *bona fide* species of Perilampidae recorded from the fossil record, thus putting the origin of the genus before the middle Eocene, 40–50 mya. This species is also referable to an extant species group and in no way challenges our generic concepts based on extant species. *Jambiya vanharteni* Heraty & Darling (2007), a recently discovered extant species of Perilampidae (unplaced to subfamily) from Yemen, presents a much more serious challenge to current classification than does this 45 mya amber species. For example, if included in the current analysis (results not presented), *Jambiya* is either the sister group of Perilampinae + Eucharitidae (morphology/parsimony) or the sister group of Eucharitidae alone (combined morphological and molecular or morphology-only SAW analyses).

The only other validly described fossil species placed in Perilampidae is *Perilampus renzii* Peñalver & Engel (2006). This species was recently described and illustrated from an early Miocene compression fossil from the Rubielos de Mora Basin, Spain. However, the morphological justification for referring this unique specimen to Perilampidae is extremely weak. The degree of preservation was considered by the authors as “exceptional” and allowed the preparation of detailed camera lucid drawings of the holotype female, which will be the basis for the discussion which follows.

None of the characters used by Peñalver & Engel (2006) to assign the fossil to the Perilampidae are diagnostic. The only three possibly suggestive features mentioned are the distinct and enlarged pronotal collar, rather high metasoma, and the large, non-bulging prepectus which is apparently fused to the pronotum. The first two characters are widespread in Chalcidoidea and the prepectus illustrated in their fig. 3a bears no resemblance to the prepectus of any species of Perilampinae or Chrysolampinae. They correctly note that the “exserted ovispositor [sic]” is similar to *Steffanolampus*, the basal genus of Perilampinae (Darling, 1988) and unlike any species of *Perilampus,* but they assign the fossil species to the latter genus noting that that ovipositor is almost certainly plesiomorphic. The implication is that the fossil is a “stem group” Perilampidae.

There is another more parsimonious interpretation of the Rubielos de Mora fossil; it is not in any way related to the Perilampidae. Based on their fig. 3, it is much more likely that the species belongs to the chalcidoid family Torymidae (Monodontomerinae *sensu* Grissell 1995). Long, upturned and exserted ovipositors are widespread in the Torymidae (see females in Grissell 1995, figs 62–71). In addition, the forewing venation (fig. 3b) is very torymid-like, particularly the short stigmal vein with a long uncus projecting toward the postmarginal vein (Gibson 1993). Also illustrated (fig. 3a) are two short circular lobes above the base of the ovipositor sheath. These are very similar to the exserted cerci that are characteristic of the Torymidae (cf. Grissell 1995, figs 26–30; Gibson 2003, fig. 26). Noticeably absent in fig. 3a is the enlarged hind coxa characteristic of many Torymidae (Grissell 2003), but only three legs are preserved (foreleg and two midlegs?) and we regard the absence of this distinctive character of Torymidae as the result of incomplete preservation. The family Torymidae was recorded by Brues (1910) from the Florissant of Colorado where he described and illustrated one species of *Torymus* with an exserted ovipositor and described four species of *Palaeotorymus*, one of which also was illustrated with an exserted ovipositor. Grissell (1995, Appendix VI) reviewed the fossil Torymidae and examined the Brues type material. He noted that Brues’ defining wing venation feature of *Palaeotorymus* was absent in the holotype of the type species (e.g., extremely elongate postmarginal vein) and that the wing venation was similar to extant Monodontomerini. The wing venation of the Rubielos de Mora fossil is consistent with the Grissell’s concept of Monodontomerini. *Perilampus renzii* is herein formally transferred to the Torymidae: *Palaeotorymus renzii* (Peñalver and Engel) [**new combination**].

Conclusions

Fossils provide the only direct evidence of extinct species and lineages and therefore provide unique information on phylogeny, biogeography, and the actual and estimated ages of lineages (Grimaldi & Engel

2005). But only if their morphology is correctly interpreted in the context of extant species and the temptation to "squeeze very basal taxa into taxonomic categories that have much more restrictive definitions" (Grimaldi & Engel 2005) is avoided. We suggest that this is exactly what happened in the case of the case of the Rubielos de Mora fossil. There is no convincing morphological evidence that this specimen has anything to do with modern Perilampidae. Furthermore, there is no rationale for a "stem group" perilampid approximately 20 million years later in the fossil record than an unequivocal species of the derived genus *Perilampus*.

The discovery of the two Baltic amber fossils described here firmly establishes the minimum age of derived Perilampinae and Eucharitinae at 40 mya. The actual time of divergence of Perilampidae and Eucharitidae must be considerably earlier, particularly when Chrysolampinae, a group for which there are no known fossils, is considered. Minimally, lineages for each of Chrysolampinae, Gollumiellinae and Oraseminae must have been established at a similar or earlier time period (Fig. 2). For Eucharitidae, this earlier divergence correlates well with the distribution of endemic species groups of *Orasema*, which based on distribution and relationships of extant taxa was proposed to have evolved in the late Cretaceous to early Eocene (Heraty 2002).

These two amber fossils and the proposed cladograms suggest that the mode and tempo of diversification was rather different in Perilampidae and Eucharitidae. Perilampidae seems to have undergone a much earlier morphological diversification than Eucharitidae. By the Eocene, there has already been generic diversification of the Chrysolampinae and Perilampinae, with the fossil species clearly referable to a modern genus. There then appears to be a subsequent period of stasis within Perilampinae, with most extant species of *Perilampus* differing little morphologically from this Eocene fossil. The eucharitid fossil, however, belongs to the relatively derived Eucharitinae ('Psilocharitini'). It is not referable to a modern genus, although it differs little in general habitus from Gollumiellinae or Oraseminae. In contrast to Perilampinae, the generic diversification of the more derived and morphologically diverse Eucharitini, based on both geographic distribution and molecular divergence data, appears to have taken place much later, during the Miocene or Oligocene (Carmichael 2006). This scenario of diversification in the two families is consistent with their host associations. Eucharitidae are all ant parasitoids, whereas Perilampidae attack a wide range of hosts. Chrysolampinae and the basal lineages of Perilampinae all attack Coleoptera, the order parasitized by many of the most basal clades of Chalcidoidea (Bouček 1988) and more generally, parasitoid Hymenoptera (Whitfield 1998). It is tempting to speculate that Eucharitidae owe their origin to parasitism of ants, an uncommon host for Chalcidoidea, and radiated in response to these new opportunities. Recent studies have placed the origin of ants and modern lineages during the mid to late Cretaceous, 75–135 mya, although there is general agreement that the diversification and ecological dominance of the ants did not occur until the Eocene coincident with the radiation of angiosperms (Brady 2003, Ward & Brady 2003, Moreau *et al*. 2006, Brady *et al.* 2006). Thus the timing is right for a congruent radiation of both ants and their parasitoids.

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Literature cited

Bouček, Z. (1956) Notes on the Czechoslovak Perilampidae (Hymenoptera - Chalcidoidea). *Acta Faunistica Entomologica Musei Nationalis Pragae,* 1, 83–98.

Bouček, Z. (1971) A new black *Perilampus* from Europe (Hym., Perilampidae). *Entomologist*, 104, 52–55.

Bouček, Z. (1978) A generic key to Perilampinae (Hymenoptera, Chalcidoidea) with a revision of *Krombeinius* n.gen. and *Euperilampus* Walker. *Entomologica Scandinavica,* 9, 299–307.

Bouček, Z. (1988) Chalcidoidea "down under". *In*: Gupta, V. (Ed.), *Advances in parasitic Hymenoptera research: proceedings of the II Conference on the Taxonomy and Biology of Parasitic Hymenoptera, held at the University of Florida, Gainesville, Florida*. E.J. Brill, New York, NY, pp. 273–282.

Brady, S.G. (2003) Evolution of the army ant syndrome: The origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. *Proceedings of the National Academy of Science,* 100, 6575–6579.

Brady, S.G., Schultz, T.R., Fisher, B.L. & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Science*, 103, 18172–18177.

Brischke, D. (1886) Die Hymenopteren des Bernsteins. *Schriften der Naturforschenden Gesellschaft in Danzig*, 6, 278–279.

Brues, C.T. (1910) The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. *Bulletin of the Museum of Comparative Zoology,* 54, 1–125.

Brues, C.T. (1923) Some new fossil parasitic Hymenoptera from Baltic amber. *Proceedings of the American Academy of Arts and Sciences,* 58, 327–346.

Carmichael, A. (2006) *The phylogenetics and biogeography of the parasitoids of large poneromorph ants (Eucharitini: Eucharitidae).* MSc thesis, University of California, Riverside, California.

Clausen C.P. (1940) The oviposition habits of the Eucharidae (Hymenoptera*). Journal of the Washington Academy of Sciences*, 30, 504–516.

Darling, D.C. (1988) Comparative morphology of the labrum in Hymenoptera: the digitate labrum of Perilampidae and Eucharitidae (Chalcidoidea). *Canadian Journal of Zoology*, 66, 2811–2835.

Darling, D.C. (1992) The life history and larval morphology of *Aperilampus* (Hymenoptera: Chalcidoidea) with a discussion of the phylogenetic affinities of the Philomidinae. *Systematic Entomology,* 17, 331–339.

Darling, D.C. (1995) Perilampidae, Chapter 11.13. *In*: Hanson, P.E. & Gauld, I.D. (Eds.), *Hymenoptera of Costa Rica*. Oxford University Press, Oxford, pp. 351–354.

Darling, D.C. (1996) A new species of *Spalangiopelta* (Hymenoptera; Pteromalidae; Ceinae) from Dominican amber: Phylogenetic and biogeographic implications. *Journal of the Kansas Entomological Society,* 69, 248–259.

Darling, D.C. & Miller, T.D. (1991) Life history and larval morphology of *Chrysolampus* (Hymenoptera: Chalcidoidea: Chrysolampinae) in western North America. *Canadian Journal of Zoology,* 69, 2168–2177.

Darling, D.C. & Sharkey, M.J. (1990) Chapter 7. Order Hymenoptera. *In*: Grimaldi, D. (Ed.), Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History,* 195, 123–153.

Doutt, R.L. (1973a) The genus *Polynemoidea* Girault (Hymenoptera: Mymaridae). *Pan-Pacific Entomologist*, 49, 215–220.

Doutt, R.L. (1973b) The fossil Mymaridae (Hymenoptera: Chalcidoidea). *Pan-Pacific Entomologist,* 49, 221–228.

Engel, M.S. (2002) The first leucospid wasp from the fossil record (Hymenoptera: Leucospidae). *Journal of Natural History,* 36, 435–441.

Engel, M.S. (2009) The first fossil leptofoenine wasp (Hymenoptera, Pteromalidae): A new species of *Leptofoenus* in Miocene amber from the Dominican Republic. *ZooKeys,* 13, 57–66.

Engel, M.S. & Grimaldi, D.A. (2007) New false fairy wasps in Cretaceous amber from New Jersey and Myanmar (Hymenoptera: Mymarommatoidea). *Transactions of the Kansas Academy of Science*, 110, 159–168.

Fursov V.N., Shirota Y., Nomiya, T. & Yamagishi, K. (2002) New fossil mymarommatid species, *Palaeomymar japonicum* sp. nov. (Hymenoptera: Mymarommatidae), discovered in Cretaceous amber from Japan. *Entomological Science*, 5, 51–54.

Gibson, G.A.P. (1993) Superfamilies Mymarommatoidea and Chalcidoidea. *In*: Goulet, H. and Huber, J.T. (Eds.). Hymenoptera of the World: An Identification Guide to Families. Agriculture Canada, Ottawa, pp. 570–655.

Gibson, G.A.P. (2003) Phylogenetics and classification of Cleonyminae (Hymenoptera: Chalcidoidea: Pteromalidae). *Memoirs on Entomology, International*, 16, 1–339.

Gibson, G.A.P. (2008) Description of *Leptoomus janzeni*, n. gen. and n. sp. (Hymenoptera: Chalcidoidea) from Baltic amber, and discussion of its relationships and classification relative to Eupelmidae, Tanaostigmatidae and Encyrtidae. *Zootaxa,* 1730, 1–26.

Gibson, G.A.P. (2009) Description of three new genera and four new species of Neanastatinae (Hymenoptera, Eupelmidae) from Baltic amber, with discussion of their relationships to extant taxa. *ZooKeys*, 20, 175–214.

Gibson, G.A.P., Read, J. & Huber, J. (2007) Diversity, classification and higher relationships of Mymarommatoidea

(Hymenoptera). *Journal of Hymenoptera Research*, 16, 51–146.

Grimaldi, D. & Engel, M.S. (2005) *Evolution of Insects*. Cambridge University Press, New York, NY, 772 pp.

Grissell, E.E. (1980) New Torymidae from tertiary amber of the Dominican Republic and a World list of fossil torymids. *Proceedings of the Entomological Society of Washington*, 82, 252–259.

Grissell, E.E. (1995) Toryminae (Hymenoptera: Chalcidoidea: Torymidae): a redefinition, generic classification and annotated world catalogue of species. *Memoirs on Entomology, International*, 2, 1–474.

Grissell, E.E. (2003) Discovery of *Monodontomerus osmiae* Kamijo (Hymenoptera: Torymidae) in the New World. *Proceedings of the Entomological Society of Washington*, 105, 243–245.

Gumovsky, A.V. (2001) The status of some genera allied to *Chrysonotomyia* and *Closterocerus* (Hymenoptera: Eulophidae, Entedoninae), with description of a new species from Dominican amber. *Phegea*, 29, 125–141.

Gumovsky, A.V. & Perkovsky, E.E. (2005) Taxonomic notes on Tetracampidae (Hymenoptera: Chalcidoidea) with description of a new fossil species of *Dipriocampe* from Rovno amber. *Entomological Problems*, 35, 123–130.

Helm, O. (1884) Beiträge zur Kenntnis der Insekten des Bernsteins (Bericht über die 18 Wanderversammlung des westpreußischen botanisch-zoologischen Vereins zu Christburg). *Schriften der naturforschenden Gesellschaft in Danzig*, N.F. 9, 220–231. As cited in Larsson (1978).

Heraty, J.M. (1994) Classification and evolution of the Oraseminae in the Old World, with revisions of two closely related genera of Eucharitinae (Hymenoptera: Eucharitidae). *Life Sciences Contributions, Royal Ontario Museum*, 157, 174 pp.

Heraty, J.M. (2000) Phylogenetic relationships of Oraseminae (Hymenoptera: Eucharitidae). *Annals of the Entomological Society of America*, 93, 374–390.

Heraty, J.M. (2002) A revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the World. *Memoirs of the American Entomological Institute*, 68, 1–359.

Heraty, J.M. & Darling, D.C. (1984) Comparative morphology of the planidial larvae of Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea). *Systematic Entomology*, 9, 309–328.

Heraty, J.M. & Darling, D.C. (2007) A new genus and species of Perilampidae (Hymenoptera: Chalcidoidea) with uncertain placement within the family. *Proceedings of the Entomological Society of Ontario*, 138, 33–47.

Heraty, J.M. & Gates M.E. (2003) Biodiversity of Chalcidoidea (Hymenoptera) at El Edén Ecological Reserve, Mexico. *In*: Gómez-Pompa, A., Allen, M.F., Fedick, S. L. & Jiménez-Osornio, J. J. (Eds.), Proceedings of the 21st Symposium in Plant Biology, "*Lowland Maya Area: Three Millenia at the Human-Wildland Interface*". Haworth Press, pp. 277–292.

Heraty, J., Hawks, D., Kostecki, J.S. & Carmichael, A. (2004) Phylogeny and behaviour of the Gollumiellinae, a new subfamily of the ant-parasitic Eucharitidae (Hymenoptera: Chalcidoidea). *Systematic Entomology*, 29, 544–559.

Hong, Y.C. (2002) *Amber insects of China*. Beijing Science and Technology Press, Beijing, 653 pp.

Huber, J. (2005) The gender and derivation of genus-group names in Mymaridae and Mymarommatidae (Hymenoptera). *Acta Societatis Zoologicae Bohemicae*, 69, 167–183.

Huber, L.L. (1927) A taxonomic and ecological review of the North American chalcid-flies of the genus *Callimome*. *Proceedings of the U.S. National Museum*, 70, 1–114.

Larsson, S.G. (1978) Baltic Amber – a palaeobiological study. *Entomonograph*, 1, 1–192.

Machado, C.A., Jousselin, E., Kjellberg, F., Compton, S.G. & Herre, E.A. (2001) Phylogenetic relationships, historical biogeography and character evolution of fig-pollinating wasps. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 685–694.

Menge, A. (1855) Lebenszeichen vorweltlicher, im Bernstein eingeschlossener Thiere. *Programm der öffentlichen Prüfung der Schüler der Petrischule, Petrischule*, pp. 1–32. As cited in Larsson (1978).

Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: Diversification in the age of angiosperms. *Science*, 312, 101–104.

Noyes, J.S. (2003) Universal Chalcidoidea Database. Available from: http://www.nhm.ac.uk/research-curation/research/projects/chalcidoids/index.html (accessed 8 July 2009).

Peñalver, E. & Engel, M.S. (2006) Two wasp families rare in the fossil record (Hymenoptera): Perilampidae and Megaspilidae from the Miocene of Spain. *American Museum Novitates*, 3540, 1–12.

Peñalver, E., Engel, M.S. & Grimaldi, D. (2006) Fig wasps in Dominican amber (Hymenoptera: Agaonidae). *American Museum Novitates*, 3541, 1–16.

Rasnitsyn, A.P. (2002) Order Hymenoptera Linné, 1758. *In*: Rasnitsyn, A.P. & Quicke, D.L.J. (Eds.), *History of Insects*. Kluwer Academic Publishers, 544 pp.

Rasnitsyn, A.P., Basibuyuk, H.H. & Quicke, D.L.J. (2004) A basal chalcidoid (Insecta: Hymenoptera) from the earliest Cretaceous or latest Jurassic of Mongolia. *Insect Systematics & Evolution*, 35, 123–135.

Ronsted, N., Weiblen, G.D., Savolainen, V. & Cook, J.M. (2005) 60 million years of co-divergence in the fig-wasp symbiosis. *Proceedings of the Royal Society B-Biological Sciences*, 272, 2593–2599.

Roskam, J.C. (1992) Evolution of the gall-inducing guild. *In*: Shorthouse, J.D. & Rohfritsch, O. (Eds.), *Biology of insect-induced galls*. Oxford University Press, New York, NY, pp. 34–49.

Schlee, D. & Glöckner, W. (1978) Bernstein. *Stuttgarter Beiträge zur Naturkunde (Serie C)*, 8, 1–72.

Schlüter, T. (1978) Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. *Berliner geowissenschaftliche Abhandlungen. Reihe A*, 9, 1–150.

Simutnik, S.A. (2001) A find of encyrtid wasp (Hymenoptera, Chalcidoidea, Encyrtidae) in Late Eocene Rovno amber (Ukraine). *Vestnik Zoologii*, 35, 81–84, 102.

Simutnik, S.A. (2002) A new genus of encyrtid wasps (Hymenoptera, Chalcidoidea, Encyrtidae) from late Eocene Rovno amber (Ukraine). *Vestnik Zoologii*, 36, 99–102.

Simutnik, S.A. & Perkovsky, E.E. (2006) A description of the encyrtid male (Hymenoptera, Chalcidoidea, Encyrtidae) with archaic structure of metasoma from Rovno amber. *Vestnik Zoologii*, 40, 283–286.

Skalski, A.W. (1988) A new fossil trichogrammatid from the Sicilian amber (Hymenoptera: Chalcidoidea: Trichogrammatidae). *Fragmenta Entomologica*, 21, 111–116.

Swofford, D.L. (2002) PAUP*. Version 4.0 ß10. Sinauer, Sunderland, Mass.

Sugonyaev, E.S. (1962) On the fauna and ecology of Chalcidoidea (Hymenoptera), parasites of Diaspididae and other Coccoidea from Leningrad oblast Referat. *Zoologicheskiy Zhurnal*, *Biol*., 1963, No. 7E43. (Translation). *Trudy Zoologicheskogo Instituta. Akademiya Nauk SSSR. Leningrad*, 31, 172–196.

Trjapitsyn, V.A. (1963) A new hymenopteran genus from Baltic amber. *Paleontologicheskiy Zhurnal, Moscow*, 3, 89–95.

Ward, P.S. & Brady, S.G. (2003) Phylogeny and biogeography of the ant subfamily Myrmeciinae (Hymenoptera : Formicidae). *Invertebrate Systematics*, 17, 361–386.

Whalley, P. (1981) *Insects from Lebanese amber.* Unpublished report, British Museum Natural History (Geology), 11 pp.

Whitfield, J.B. (1998) Phylogeny and evolution of host-parasitoid interactions in Hymenoptera. *Annual Review of Entomology*, 43, 129–51.

Yoshimoto, C.M. (1975) Cretaceous chalcidoid fossils from Canadian amber. *Canadian Entomologist*, 107, 499–529.

Zherichin, V.V. & Sukacheva, I.D. (1973) On Cretaceous insect bearing ambers (retinites) of northern Siberia. *Reports of the 24th Annual Readings in Memory of N.A. Kholodkovsky (Leningrad)*, pp. 3–48.

Table 1. Morphological state coding for outgroups, Perilampidae and fossil taxa (Eucharitidae not listed, see Heraty 2002). D numbers after name are UCR molecular voucher codes. Characters as defined in Heraty (2002) or as discussed in text*. Not all characters are used for the analyses as discussed in Heraty (2002).

	Morphological Characters (1-101)
	11
	11111111112222222222333333333344444444445555555555666666666677777777778888888888999999999900
	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901
Pteromalidae	
Polstonia sp.D493	00010011010000300??00??0700000?????0000001000000000050111001010000000000100001000020230?0001?00000000
Pseudocatalaccus sp.D725	00010011010000300430000070000072000000000100000000005001100001000000000020000000000000100000100000000000
Pteromalus sp.D724	00010011010000300430000070000072000000000100000000005000000000000000000000100000000000000000001000000000
Thinodytes sp.D726	00010011020000?00430000070000072000000000200001300006010000000000000000000100000000000000000001000000000
Chrysolampinae	
Austrotoxeuma sp.D316	00010001000000200430000070000070000000000000001100006000100000000000000000200000001020000000000000000000
Brachyelatus sp.D643	00010001000000200430000070000070000000000000001100006000100000000000000000200000001000000000000000000000
Chrysolampus elegans.D723	00010001000000200430000070000070000000000000001100006000100000000000000000200003001020100000000000000000
Chrysolampus sp.AU.D160	00010001000000200430000070000070000000000000001100006000100000000000000000200000001020100000000000000000
Chrysolampus sysimbrii.D970	00010001000000200430000070000070000000000000001100006000100000000000000000200003001020100000000000000000
Perilampinae	
Burksilampus sp.D1006	0101000110000031243000007000007000000000000000040A40501010000217000000102000010010200000000000000000000
Euperilampus triangularis.D385	01110001300000312430000070000070000000000000000400404010100002170000001020000000100000000000000000000
Monacon canaliculatum.D709	0111000130000031243000007000007000000000000000040A40401010000216000000102000030010000000010000000000
Monacon robertsi.D318	0111000130000031243000007000007000000000000000040A40401010000216000000102000030010000000010000000000
Perilampus pisticus (fossil)	010?0001000000312430?00700000?????00000000000000040000501010000216000000?020000000?000000000??0??????0
Perilampus hyalinus.D254	0111000130000031243000007000007000000000000000040A40501010000217000000102000000010000000000000000000
Perilampus hyalinus.D972	0111000130000031243000007000007000000000000000040A40501010000217000000102000000010000000000000000000
Perilampus regalis.D113	0111000130000031243000007000007000000000000000040A40501010000217000000102000000010000000000000000000
Perilampus subcarinatus.D264	0111000100000031243000007000007000000000000000040A40501010000217000000102000000010000000000000000000
Perilampus sp.D688	0101000100000031243000007000007000000000000000040A40501010000217000000102000000010000000000000000000
Steffanolampus salicetum.D320	01010001000000312430000070000070000000000000000400004010100002060000001020000000100000000000000000000
Eucharitidae	
Palaeocharis rex (fossil)	00010010220001311330 0??0700000??????10000000000000001???0000010010000000100000001100??1000001?100?0???

*New character states added to Heraty (2002) to resolve Perilampidae: **9**, Malar sulcus: state 3, sulcus obliterated by oblique carinae. **48**, Frenal line: state 4, distinct raised transverse carina across anterior margin of scutellum (distinguished from groove or change in sculpture; changed to state 4 in all *Gollumiella*). **50**, Frenum shape: state 10 (A), frenum foveate, with strong parallel carinae. **51,** Frenum orientation: state 4, scutellar disc vaulted, frenum and marginal rim of scutellum not visible in dorsal view. **53**, Propodeal disc: state 4, foveate along midline, lateral panels strongly and evenly rugose; state 5, single median carina, lateral panels smooth; state 6, single median carina, lateral panels with irregular sculpture. **64**, Shape of prepectus: state 6, large equilateral triangle; state 7, straplike ventrally, triangular adjacent to prepectus (strongly narrowed in *Euperilampus* and some *Perilampus*). **78**, Length of postmarginal vein of forewing: state 3, 1–2.5X as long as broad.