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Fossil Liposcelididae and the lice ages (Insecta: Psocodea)

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Fossilized, winged adults belonging to the psocopteran family Liposcelididae are reported in amber from the mid-Cretaceous (*ca* 100 Myr) of Myanmar (described as *Cretoscelis burmitica*, gen. et sp. n.) and the Miocene (*ca* 20 Myr) of the Dominican Republic (*Belaphopsocus dominicus* sp. n.). *Cretoscelis* is an extinct sister group to all other Liposcelididae and the family is the free-living sister group to the true lice (order Phthiraptera, all of which are ectoparasites of birds and mammals). A phylogenetic hypothesis of relationships among genera of Liposcelididae, including fossils, reveals perfect correspondence between the chronology of fossils and cladistic rank of taxa. Lice and Liposcelididae minimally diverged 100 Myr, perhaps even in the earliest Cretaceous 145 Myr or earlier, in which case the hosts of lice would have been early mammals, early birds and possibly other feathered theropod dinosaurs, as well as haired pterosaurs.

Keywords: Burmese amber; Dominican amber; Liposcelididae; sister group; lice

1. INTRODUCTION

The paraphyletic nature of several orders of insects has become well known in recent years (reviewed in Grimaldi & Engel 2005), one of the most striking being an origin of lice (order Phthiraptera) within the Psocoptera. This interesting scheme of relationships was first proposed in the morphological study by Lyal (1985), who specifically posited that lice are most closely related to the psocopteran family Liposcelididae (also often spelled as Liposcelidae). This family of psocopterans, known as 'book lice', is best known for the minute, pale, wingless species in the genus *Liposcelis* that are commonly found scuttling across damp, mildewed pages. Molecular study later corroborated this relationship (Yoshizawa & Johnson 2003), further illuminating a biological trend from free-living, morphologically generalized, detritivorous psocopterans, to the reduced and inquilinous liposcelidids and finally to the highly specialized ectoparasitic lice. Lice have radiated into nearly 5000 species and are exceptional among blood-feeding and ectoparasitic insects in that the entire life cycle is spent on a bird or mammal host. The intimate association of lice with their hosts is a main reason why lice are typically very host specific, often restricted to a single species or genus of host, and why lice show more cospeciation with hosts than do other groups of insects (reviewed in Grimaldi & Engel 2005).

The origin and early evolution of lice is completely obscure because, unsurprisingly, fossilization of lice requires exceptional circumstances and so their fossils are exceedingly scarce. *Megamenopon*, a well preserved bird louse of the living family Menoponidae from the Eocene oil shales of Eckfeld maar near Manderscheid, Germany (Wappler *et al.* 2004), is the earliest definitive phthirapteran. Nits, or louse eggs, are preserved in Baltic amber of slightly younger Eocene age (Voigt 1952), but these yield little about their identity. Reports of lice from the Triassic of India (Kumar & Kumar 2001; Kumar 2004) are actually of mites (published photographs, e.g. Kumar 2004: figs. 6, 8 clearly show chelicerae and a body divided into a prosoma and opisthosoma, and what were reported as 'antennae' are instead macrosetae). *Saurodectes vrsanskyi* from the Zaza Formation shales of Baissa, Siberia (Barremian or slightly younger Neocomian in the Early Cretaceous, *ca* 130 Ma) is a putative louse or close relative thereof, but also an exceedingly bizarre insect (a revised, original reconstruction of it is in Grimaldi & Engel 2005). At 17 mm body length it is far larger than any living louse (suggesting it had a huge host) and it had huge protuberances on each side of the head, but it also had some features consistent with Phthiraptera, including a small thorax and apparent aptery, short sprawling legs, a largely membranous abdomen (with tergites and sternites lost or vestigial), and large spiracles and lateral tracheal trunks. While *Saurodectes* remains an enigma, it did exist when diverse, large vertebrates were known to possess vestiture, some of which were possibly homeothermic.

Only within the past 5–6 years has the fossil record of louse habitat (i.e. vertebrate vestiture) become much clearer. The earliest direct evidence of feathers remains *Archaeopteryx*, the most primitive bird, known from the Late Jurassic (*ca* 152 Ma) of Solnhofen and Eichstätt, Germany. Phylogenetic relationships of diverse, feathered theropods from the Early Cretaceous of China, however, suggest that feathers evolved in the Jurassic prior to *Archaeopteryx* (Clark *et al.* 2002). None of the non-avian theropods could apparently fly, but some had elaborate pennaceous feathers that presumably were used for displays and/or gliding, including various dromaeosaurs (close relatives of birds), and maniraptorans (slightly more

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distant avian relatives). Even the juveniles of some tyrannosaurids had a thin vestiture of downy feathers, but the oldest fossils of these theropod groups are no older than Late Jurassic. Given that birds are a recently evolved group of theropods, the earliest divergence of feathered theropods was perhaps mid-Jurassic, 180 Ma. It was not until the latest Cretaceous and Early Tertiary that there occurred the radiation of the largest lineage of Recent birds, the passerines (Baker *et al*. 2002). The fossil record of hair is exceedingly sparse compared to that of feathers, but presumably hair is at least as ancient as feathers. Assuming that the earliest monotremes and therian mammals had hair like their modern relatives, it is reasonable to estimate the origin of hair at least since the mid-Cretaceous, but much older multituberculates and triconodonts (Novacek 1999) may also have had hair. Likewise, some pterosaurs had hair-like vestiture (presumably an aid in thermoregulation; Wellnhofer 1991; Buffetaut & Mazin 2003), so these animals would likewise have provided suitable louse habitat. Thus, there was ample ecological opportunity for at least 100 Ma of Mesozoic louse existence.

An alternative approach to dating the ages of parasites involves phylogenetic patterns of host use, but unfortunately there are as of yet no clear patterns for lice. The basal suborder of lice, Amblycera (Lyal 1985; Yoshizawa & Johnson 2003), feeds on birds and mammals, including marsupials in Australia (Boopiidae lice) and in South America (Trimenoponidae lice). No monotremes are parasitized by lice, so assuming lice invaded early therian mammals this also would place their minimal age as 120 Ma, since this is when stem-group therians first appeared (Novacek 1999). The discovery of definitive Mesozoic Phthiraptera is an exceedingly remote possibility, and even amongst the feathered theropods from China no remains of lice have been found in their exquisitely preserved feathers. Certainly such a discovery remains within the realm of possibility given the identification of putative parasitic mite eggs attached to Cretaceous feathers (Martill & Davis 1998). Here, we use the sister-group dating method (Hennig 1981), applied to the first known Mesozoic liposcelidid and its relationships, to estimate the minimal time of divergence between this family and lice.

The family Liposcelididae contains the following living genera, traditionally classified into two subfamilies (Smithers 1972; Lienhard & Smithers 2002): in the Embiopsocinae are *Belapha* Enderlein (2 species: Africa), *Belaphopsocus* Badonnel (3 species: circumtropical), *Belaphotroctes* Roesler (18 species: southern US, neotropical, Africa), *Chaetotroctes* Badonnel (1 species: Brazil), *Embidopsocus* Hagen (37 species: cosmopolitan), *Troctulus* Badonnel (1 species: Africa), and in the Liposcelidinae are *Troglotroctes* Lienhard (1 troglobitic species: Ascension Island), and *Liposcelis* Motschulsky (117 species: cosmopolitan). The habits of liposcelidids, particularly *Liposcelis*, appear to be intermediate between those of the other detritivorous psocopterans and the ectoparasitic lice (reviewed in Grimaldi & Engel 2005). Several *Liposcelis* species occur in nests of ants, birds, and mammals (Broadhead 1950; Rapp 1961; Wlodarczyk 1963; Mockford 1971; New 1972; Baz 1990; Lienhard 1990), and some have even been found in the fur and plumage of mammals and birds (Pearman 1960; Mockford 1967; Badonnel 1969). Presumably they feed on detritus like faecal material, exfoliated skin, and shed fur and feathers. *Liposcelis bostrychophila* Badonnel is the most ubiquitous inquiline of vertebrates in the Liposcelididae, and it has even been found in fungus-infected human nails (Lin *et al*. 2004). A transition from being an inquiline detritivore to an obligate parasite appears not to have involved major dietary barriers.

2. SYSTEMATICS

(a) *Genus* Cretoscelis *Grimaldi & Engel, gen. nov.*

Diagnosis. Distinguished from all other genera of winged Liposcelididae by the plesiomorphic presence of the following: small patch of sensilla at base of apical palpomere (P_4); presence of Rs in forewing (all other genera lack Rs); presence of Pearman's Organs (PO) on hind and possibly mid-coxae (similar structures on fore coxae); ocelli on slightly raised mound or tubercle. Apomorphically with an oval-shaped depressed area on the ventral surface of fore femur.

Type Species. *Cretoscelis burmitica*, n. sp., by original designation

Etymology. For Cretaceous, and *-scelis*, a root (meaning foot) derived from the type genus of the family. The name is feminine.

(b) Cretoscelis burmitica *Grimaldi & Engel, sp. nov. (figure 1*a–c*)*

Diagnosis. As for the genus (*vide supra*).

Description. Body length 1.21 mm. Body dorsoventrally flattened. *Head*: fully prognathous; width 317 μm; cuticular pattern on vertex finely imbricate. Eyes small, with approximately 50 facets. Ocelli present, close (separated by distances approximately equal to ocellus diameter), on slightly raised mound. Clypeus bulbous, greatest width slightly less than half the distance between outside margins of eyes. Apical margin of clypeus with row of approximately 10 fine, stiff setulae. Labial palp short, apical segment oval; mandible obscured. Maxillary palpus with four segments; apical segment broadest, width 2× that of palpomere 3 (P_3), P_4 with preapical sensory area and what appear to be small group of sensilla at base. Lacinia protrudes well beyond anterior margin of clypeus, lacinial apex with two larger teeth and minute one between them. Antenna with 12–14 antennomeres (10–12 flagellomeres); scape and pedicel broader than flagellomeres; each flagellomere with fine annulations and apical whorl of 4–5 long, stiff setulae (four apical flagellomeres with fewer apical setulae). Length of antenna 649 μm (figure 1*b*).

Thorax. Short, 239 μm long. Pronotum very short, length one-sixth length of head; pronotal width 4.5× the length. Pronotum with hemispherical central lobe; lateral lobes very narrow, having three fine setulae at apex. Structure of meso- and metanotum obscured.

Wings. Transparent, diaphanous, oar-shaped, and folded flat over abdomen. Apex of forewing extended past apex of abdomen by 0.22× length of wing. All veins are very light, slightly thicker than membrane on remainder of wing; veins devoid of fine, irregular crinkling over most of rest of wing membrane. Forewing 1.22 mm long, 0.42 mm wide, with vein *R* reaching to mid-length of wing, incomplete (apex not touching wing margin); *R*s present, branching off *R* at apical 0.10× length of *R*

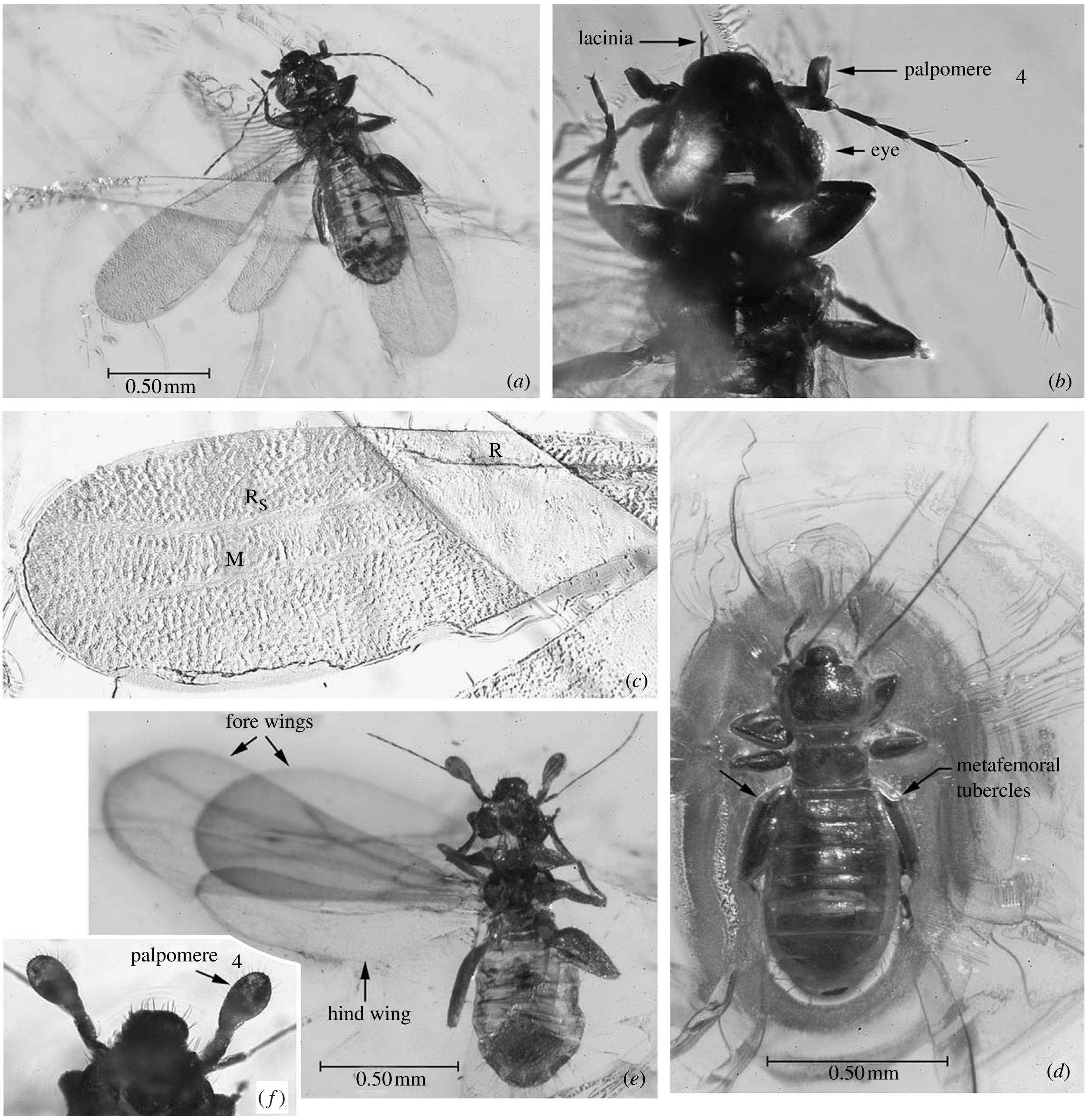

Figure 1. Photomicrographs of fossil Liposcelididae in amber. (*a–c*) *C. burmiticus* gen. n., sp. n. (AMNH Bu912) in 100 Myr Burmese amber. (*a*) Habitus, ventral view. (*b*) Head and thorax, dorsal view. (*c*) Forewing, showing surface texture. (*d*) *Liposcelis atavus* Enderlein, in 45 Myr Baltic amber (Eocene; KU Ba149). (*e–f*) *Belaphopsocus dominica* sp. n., in 20 Myr Dominican amber (Miocene; AMNH DR14-908). (*e*) Habitus, ventral view. (*f*) Detail of front of head.

but base of *R*s absent, such that *R* not directly connected to *R*s; *R*s slightly curved, not reaching wing margin. Vein M present in forewing, incomplete at both ends, apex distant from wing margin. No trace of Cu or A is visible. Hind wing 0.85 mm long, less symmetrical than forewing, with one longitudinal vein (presumably *R*) having no branches, incomplete; *R* off center, slightly closer to costal margin of wing. No wing coupling structures present on hind margin of forewing and costal margin of hind wing.

Legs. Bases distantly spaced, distances approximately 1, 3 and 2× coxal diameters of fore, mid and hind legs, respectively. Bases of mid-legs closer to bases of hind legs than to fore legs. Sternellum without long setae. Each coxa with an oval-shaped, finely granular area on ventral surface, pair on hind coxae and possibly mid-coxae apparently PO; PO on metacoxa a narrow oval structure. Profemur broad, greatest width 0.5× length, with large elliptical depression in center of ventral surface. Mesofemur with greatest width merely 0.3× length of femur. Metafemur broad and very large, greatest width 0.45× the length, length 292 µm, 1.7× that of profemur. Tibiae simple, only metatibia with apical spur (spur length equal to greatest width of tibia); tibiae slightly shorter than femora, length of metatibia 241 µm. Three tarsomeres present, middle tarsomere shortest; pretarsal claw with preapical tooth. Pulvillus structure obscure.

Abdomen. Length 702 µm. Chaetotaxy on apex of abdomen as figured (figure 2). Presence or absence of abdominal spiracles 1 and 2 obscure.

Type. Holotype, female: AMNH Bu912, in mid-Cretaceous (upper Albian–Cenomanian) amber from Kachin Province, Myanmar, excavated from near Tanai

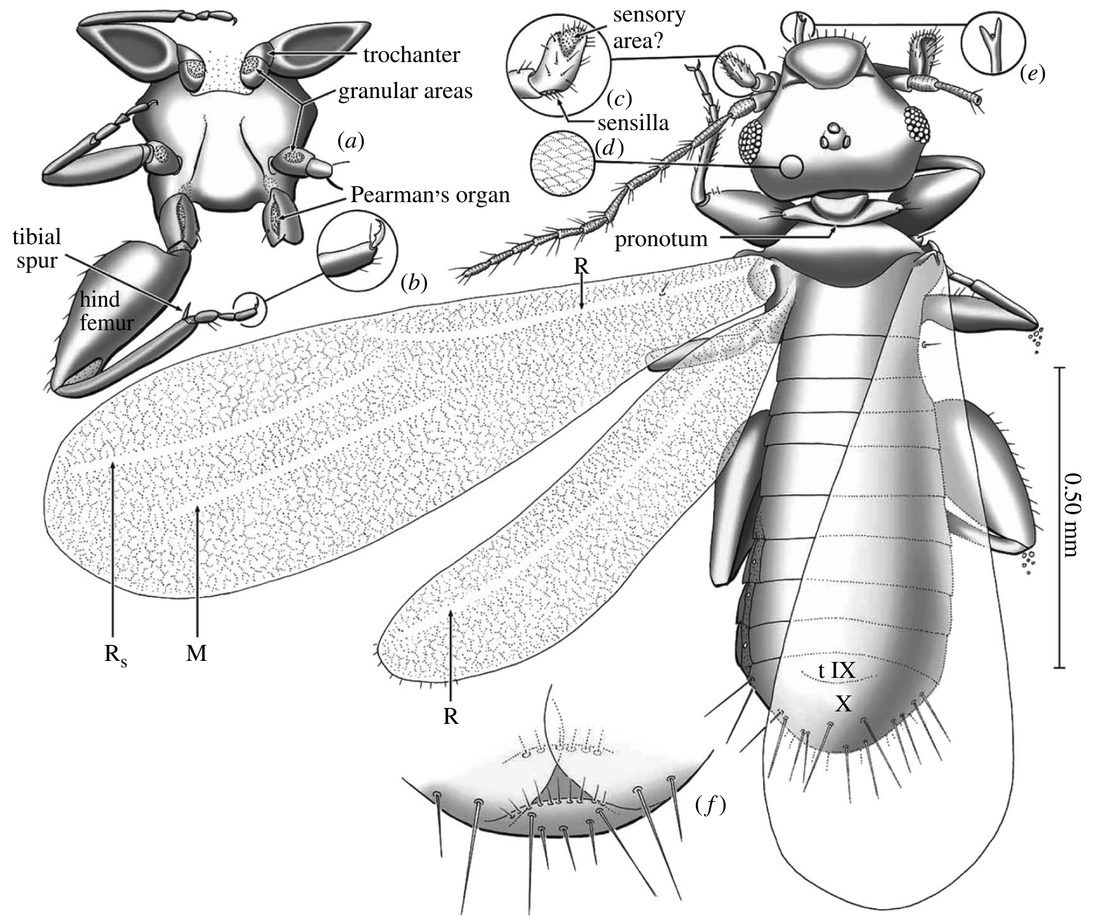

Figure 2. Dorsal habitus and details of holotype of *C. burmitica* n.gen., n.sp. in Cretaceous Burmese amber, the oldest and most primitive Liposcelididae. The family is the sister group to the lice, order Phthiraptera. (*a*) Ventral view of thorax. (*b*) Pretarsus. (*c*) Maxillary palp segment P_4 (ventral view). (*d*) Imbricate cuticular pattern on head. (*e*) Apex of lacinia. (*f*) Chaetotaxy of abdominal apex (ventrally, enlarged).

by Leeward Capital Corporation in 1998 (see Grimaldi *et al.* 2002). The amber was embedded in epoxy and trimmed and polished to a thin chip 1.5 mm thick, with surfaces parallel to the broad surfaces of the insect, so that the inclusion could be observed under a compound microscope. Holotype housed in the collection of amber fossils in the Department of Entomology (Division of Invertebrate Zoology), AMNH.

Etymology. In reference to burmite, a name often applied to amber from Myanmar.

(c) *Genus* Belaphopsocus *Badonnel 1955*

Belaphopsocus dominicus *Grimaldi & Engel sp. nov. figure 1*e,f

Diagnosis. Macropterous female with well developed eyes and ocelli; antenna with 7 flagellomeres; head with approximately 30 short, stiff setae; P_4 broad, length 1.5× the width, fringed with long setulae but apparently devoid of small, stout sensilla; two tarsomeres, metatibial spurs lacking; pretarsus with small vesicle.

Description. Body dorsoventrally flattened, length 1.14 mm. HEAD: width 315 μm; with approximately 30 short, stout, stiff setulae that have sharp (not blunt) apices; ~17 such setulae on clypeus, rest on frons, including two inside ocellar triangle; longest setulae approximately 30 μm. Eye with approximately 25 facets; greatest diameter of eye 52 μm. Antenna 531 μm long, with seven flagellomeres, lengths: $f_1=83$ μm, $f_2=68$, $f_3=65$, $f_4=62, f_5=60, f_6=55, f_7=35$. Flagellomeres without fine annulations, $f_{3\text{–}6}$ each with slight constriction (secondary segmentation) in middle; the true segments demarcated by complete articulation, dark apex and longer apical setae. Maxillary palps with four segments, P_2 and P_3 of approximately equal length; P_4 broad, length 1.50× the width, with fringe of fine setulae on margin, some setulae on minute tubercles. No stout, short, conical sensilla apparent on P_4. Three ocelli present, separated from each other by distance approximately 3× ocellar diameter. Lacinia (observable only in terminal view) with one small, two large teeth. Thorax with chaetotaxy not observable, structure as figured (figure 2). Pronotum with humeral lobe elongate, one humeral seta, length 60 μm. Wings long, extended well beyond apex of abdomen, veins darker than membrane. Forewing 1.42 mm long, 0.52 mm wide, with *R* short, ending on costal edge ~0.6× length of wing, *R*s diverging from R~0.8× length of *R*; *R*s slightly arched, reaching wing margin; vein M simple (no branches), apex faint but reaching wing margin. Hind wing 1.04 mm long. Legs: coxae without PO; tarsi dimerous; $t_1=65$ μm, $t_2=85$ μm; all tibiae (including metatibiae) without apical spurs. Protibia with row of ~6 spinules on inner surface. Pretarsus apparently with small, transparent vesicle ventral to claws (any fringe possibly present too obscure for observation). Lengths of metafemur (including metatrochanter) 418 μm, metatibia 235 μm Abdomen: tergites and sternites well developed;

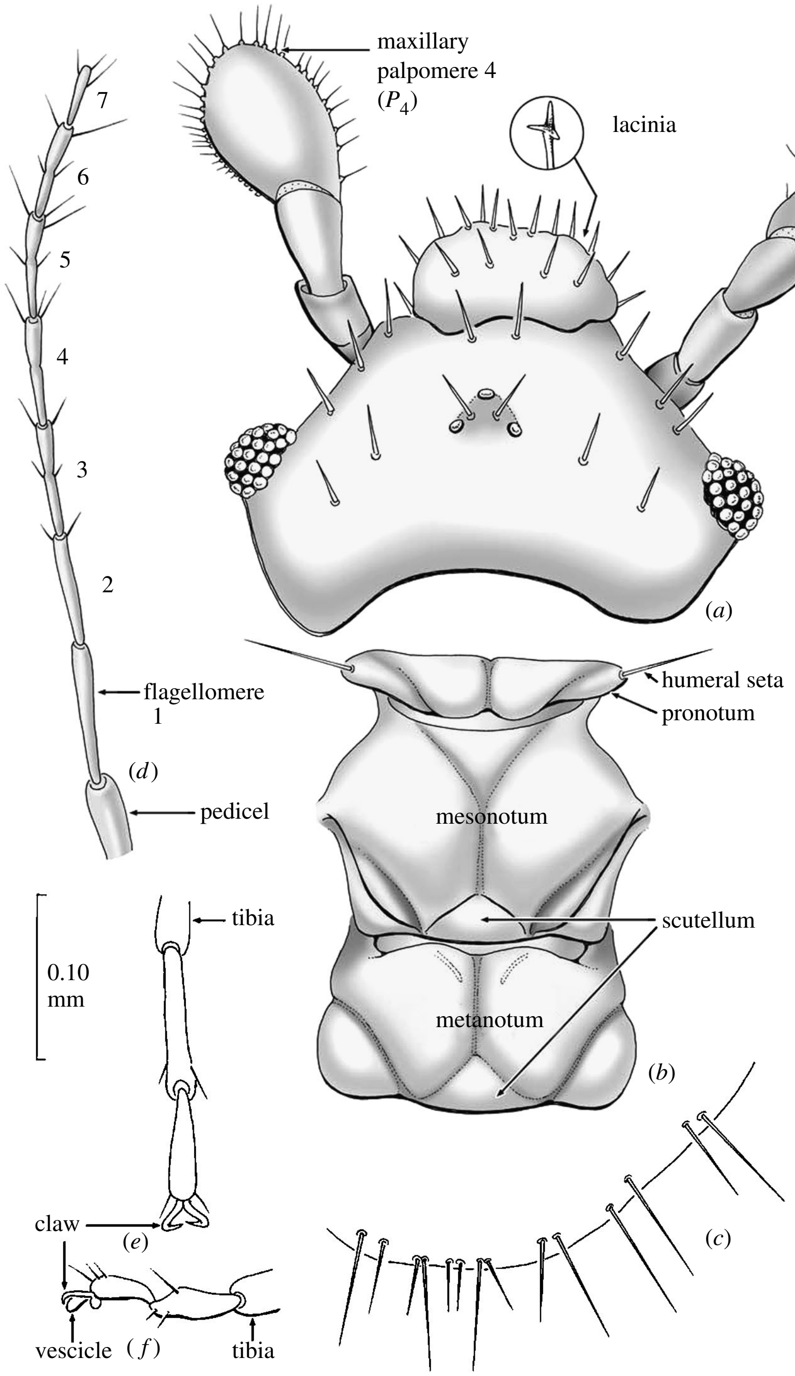

Figure 3. Details of holotype of *Belaphopsocus dominicus*, n.sp. in Miocene Dominican amber. (*a*) Head, dorsal view. (*b*) Thorax, dorsal view. (*c*) Apex of abdomen, dorsal. (*d*) Antennal flagellum and pedicel. (*e*) Hind tarsus, dorsal view. (*f*) Hind tarsus, ventral view. All to the same scale.

apical chaetotaxy as figured (figure 3), length of longest apical setae 70 µm.

Types. Holotype, AMNH DR14-908, a well preserved female in a 9×8×1 mm chip of transparent amber, from the Miocene of the Dominican Republic. Exact provenance within the DR unknown, but all the amber derives from the Miocene (Iturralde-Vinent & MacPhee 1996). *Paratypes*: two further females in Dominican amber: AMNH DR10-1319 and AMNH DR10-1320.

Etymology. Referring to the source country of the fossil species.

Comments. Two tarsomeres, loss of antennal annulations and the hind tibial spur, a broad maxillary palpomere P_4, seven flagellomeres, and a pretarsal vesicle clearly allies this fossil with *Belaphopsocus* and *Troctulus*. It further shares with *Belaphopsocus* the short, stout setae on the head, but in *Belaphopsocus* these have blunt tips. Also, P_4 in *Belaphopsocus* is virtually round, not oval as in the fossil, and the group comprising the genera *Belapha* + *Belaphopsocus* + *Troctulus* has short, stout sensilla on P_4 that the fossil lacks. The fossil is also noteworthy for the possession of *R*s in the forewing. Thus, the fossil is only provisionally assigned to *Belaphopsocus*.

3. PHYLOGENY

Twenty five morphological characters are listed below that were phylogenetically analysed via a branch-and-bound,

Table 1. Data matrix of morphological characters in Liposcelididae. Dash indicates inapplicable character state; question mark indicates absence of information. Characters 26–30 are autapomorphies and were not included in the analysis but are on the phylogeny (figure 4).

	characters																													
										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3
taxa	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cretoscelis	1	1	0	1	0	0	0	0	1	?	?	?	1	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0
Embidopsocus	1	1	0	1	0	0	0	0	2	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0
Embidopsocopsis	1	1	0	1	0	0	0	0	2	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0
Chaetotroctes	1	1	0	1	0	0	0	0	2	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0
Troglotroctes	1	1	0	1	0	0	0	0	2	1	1	3	———			1	1	1	1	0	0	1	0	0	0	0	1			
Liposcelis	1	1	0	1	0	0	0	0	2	1	0	3	———			1	1	1	1	0	0	1	0	0	0	0	0			
Belaphotroctes 1	1	1	0	1	1	0	0	0	2	1	0	2	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0
Belaphotroctes 2	1	1	0	1	1	0	0	0	2	1	1	2	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0
Belapha	1	1	0	1	2	1	0	0	2	1	0	2	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	0	0	0
Belaphopsocus	1	1	1	1	2	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0
Troctulus	1	1	0	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	0	0	0
B. dominicus	1	1	1	1	1	0	1	1	2	?	?	?	1	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0	0

randomized search using the program Nona (Goloboff *et al*. 1999). The lice were employed as outgroup based on the phylogenetic work of Lyal (1985) and more recent molecular studies. Since most characters were inapplicable outside of this clade no attempt was made to code other nanopsocete families such as Sphaeropsocidae or Pachytroctidae. All characters were coded as non-additive and of equal weight; the matrix is provided in table 1. In lieu of a species-level analysis of Liposcelididae, the genus *Belaphotroctes* was arbitrarily divided into taxa '1' and '2' in order to accomodate polymorphisms. There were a further five characters that are autapomorphic for individual genera; these were not included in the analysis but are included in the final cladogram for diagnostic purposes.

1. Body: (0) uncompressed; (1) dorsoventrally compressed
2. Head: (0) hypognathous; (1) prognathous.
3. Setae on head: (0) mixed-length (typically elongate), slender; (1) short, stout.
4. Epicranial cleavage line: (0) present; (1) highly reduced or completely lost.
5. Maxillary palpomere P_4: (0) slender, like preceeding palpomeres; (1) broad, 1.5× width of P_3 or greater; (2) virtually round.
6. Maxillary palpomere P_4 with short, stout sensilla: (0) sensilla absent; (1) sensilla present.
7. Antenna: (0) more than eight flagellomeres; (1) reduced to seven to eight flagellomeres (always seven in *Belaphopsocus*).
8. Flagellomeres: (0) fine annuli present; (1) annuli reduced or lost.
9. Ocelli (in macropterous forms): (0) well separated on raised surface; (1) closely positioned on raised surface; (2) closely positioned on flat surface.
10. Ocelli: (0) present; (1) absent in apterous forms.
11. Compound eyes in apterous forms: (0) with numerous ommatidia; (1) reduced to two facets.
12. Wings: (0) present; (1) at least male apterous; (2) both sexes with facultative aptery; (3) both sexes obligately apterous.
13. Wing coupling mechanism: (0) present; (1) absent.
14. Wing apex: (0) acutely rounded; (1) broadly rounded (paddle-shaped).
15. Longitudinal venation: (0) typical paraneopteran complement of longitudinal veins; (1) forewing with R, M only, hind wing with *R* only.
16. Forewing *R*s: (0) present; (1) absent.
17. Wing membrane: (0) hyaline, with smooth, often microtrichiated surface; (1) surface with finely crinkled texture.
18. Wing position at rest: (0) held at sides in roof-like position; (1) held flat over abdomen.
19. Pearman's organ (hind, sometimes mid-coxae): (0) present; (1) absent.
20. Metafemur: (0) slender; (1) thickened.
21. Metafemoral tubercle on anterior margin: (0) absent; (1) present.
22. Metatibial spur: (0) present; (1) absent.
23. Tarsi: (0) trimerous; (1) dimerous.
24. Pretarsal protuberance or vesicle: (0) absent; (1) present.
25. Female abdominal tergites 9 and 10: (0) separate; (1) largely fused.

Autapomorphies (not in analysis, diagnostic only):

26. Setae on head and body: (0) with sharp, pointed apices; (1) with blunt apices.
27. Pretarsus: (0) unmodified or with vesicle; (1) with long fringe on membranous vesicle.
28. Sternellum: (0) bare; (1) with 3–4 setulae on each side.
29. Lateral surfaces of head: (0) with just setae; (1) field of small, conical sensilla dorsally on each side.
30. Legs: (0) generally short, unmodified; (1) very long.

4. DISCUSSION

A phylogeny of liposcelidid genera, including fossils, is given in figure 4 and overlaid on a geological time scale. The cladogram is based on the strict consensus (length 35 steps, CI = 0.73, RI = 0.81) of three equally parsimonious trees. Topology of the most parsimonious trees differed only in the relative positions of *Belapha* or *Belaphotroctes* 2

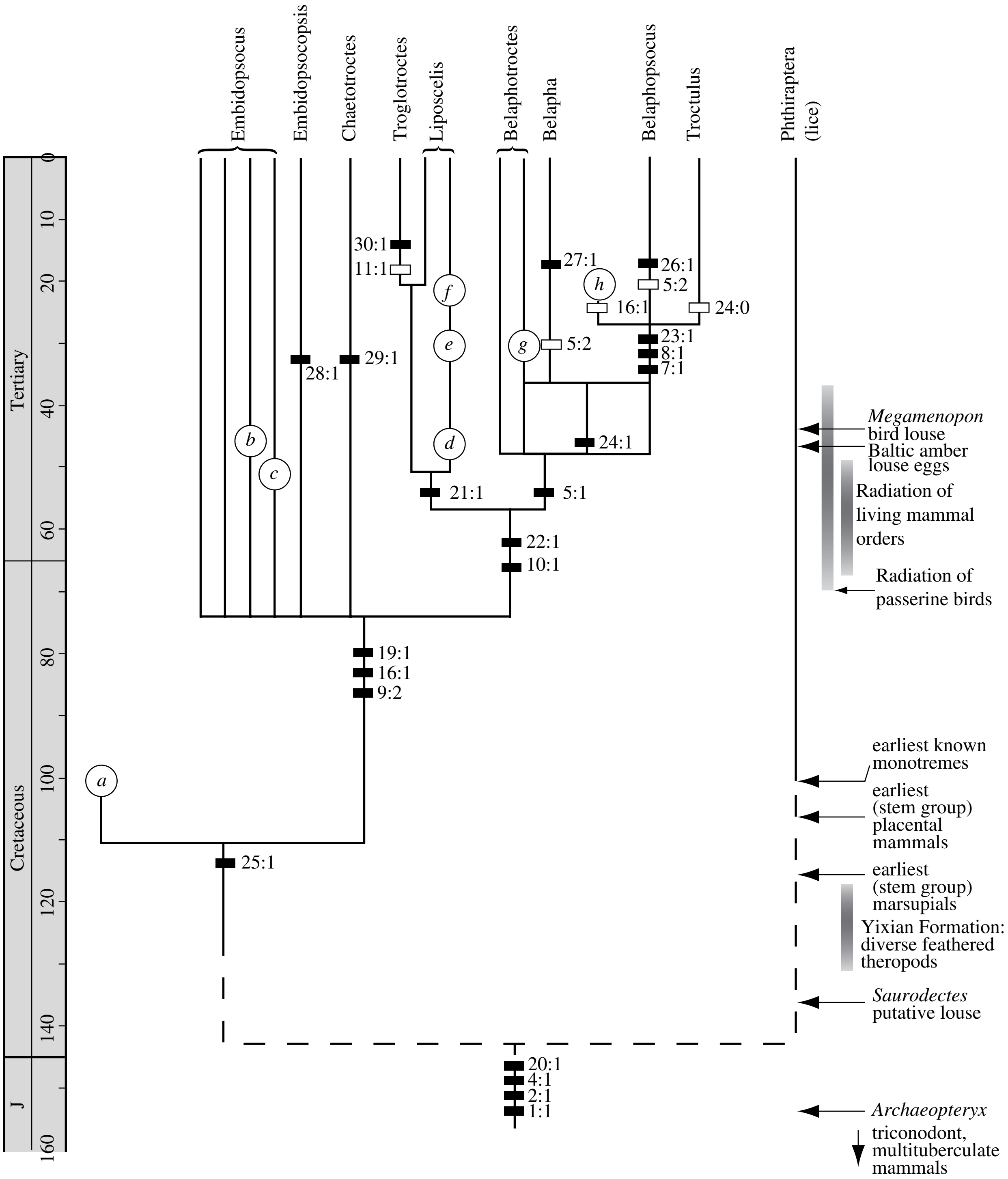

Figure 4. Phylogeny of the Liposcelididae, including fossils (circled letters) and unambiguous characters (numbers), based on a strict consensus tree (length 35 steps, RI 0.81, CI 0.73). Autapomorphies of five genera (characters 26–30) were not included in the analysis but are included here for diagnostic purposes (see text for descriptions). Significant records of definitive and putative louse fossils are included, as are major events germane to louse evolution (i.e. earliest or significant records of feathered and haired tetrapods). There is an excellent correlation between cladistic sequence and chronology of the fossils, indicating an Early Cretaceous origin of Liposcelididae. Lice (order Phthiraptera) probably diverged from the Liposcelididae in the Early Cretaceous to latest Jurassic. Fossils: (*a*) *C. burmitica* Grimaldi & Engel, n. gen., n.sp. (Burmese amber: this report). (*b*) *Embidopsocus saxonicus* Günther (Saxonian amber: Günther 1989). (*c*) *Embidopsocus eocenicus* Nel, Plöeg & Azar (Paris Basin amber: Nel *et al.* 2004). (*d*) *Liposcelis atavus* Enderlein (Baltic amber: Enderlein 1911). (*e*) *Liposcelis* sp. (Mexican amber: Mockford 1969). (*f*) *Liposcelis* sp. (unident nymphs in Dominican amber: AMNH coll.). (*g*) *Belaphotroctes similis* Mockford (Mexican amber: Mockford 1969). (*h*) *Belaphopsocus dominicus* Grimaldi & Engel, n.sp. (Dominican amber: this report).

being closer to the clade of *Troctulus*, *Belaphopsocus* and *B. dominicus*, and in whether *Troctulus* or *B. dominicus* is basal in the terminal clade with *Belaphopsocus*. Monophyly of the family is essentially defined by the fusion of abdominal terga 9 and 10; all other defining features are either shared with Phthiraptera or they are wing characters that obviously do not exist for lice. There are only eight known fossil Liposcelididae (two as of yet unnamed), all of them exquisitely preserved in amber (fossil taxa are in circled numbers on the phylogeny in figure 4, see legend for listing). The ambers are from the Miocene of the Dominican Republic; Oligocene of southern Mexico; Eocene of Oise, France and the Baltic Region; and Cretaceous of Myanmar (fossil insect deposits are reviewed in Rasnitsyn & Quicke, 2002; Grimaldi & Engel 2005). The traditional classification of two subfamilies, Embidopsocinae and Liposcelidinae, is not supported, but this should eventually be tested with an exhaustive set of characters and taxa. *Embidopsocus* may be a paraphyletic stem group at the base of the Liposcelididae, since we are unaware of any defining feature of the genus that is synapomorphic with respect to other liposcelidids. In fact, paraphyly apparently abounds in the taxonomy of Liposcelididae, since *Embidopsocopsis* and *Chaetotroctes* appear to be modified *Embidopsocus*, *Troglotroctes* a modified *Liposcelis* and *Belapha* a modified *Belaphotroctes*. A revised classification should be based on a more comprehensive phylogenetic analysis of morphological and molecular characters of as many species as possible. Our analysis serves primarily to estimate the relationships of the fossils.

The most striking result is that there is a perfect correlation between the age of earliest appearance and the cladistic rank of genera. *Cretoscelis*, the most primitive genus, is the only Cretaceous liposcelidid known, extending the geological age of the family twice that of the previously oldest known member (*Embidopsocus eocenicus*). All other fossils of the family are Tertiary and belong to modern genera; they seem to possess all of the derived generic features that living relatives of their respective genera do. *Embidopsocus* is Early to mid-Eocene and branches off next in the phylogeny (apparently paraphyletically); *Liposcelis* is mid-Eocene and later, and it is sister to the *Belapha* group. The *Belapha* group (*Belapha*, *Belaphotroctes*, *Belaphopsocus*, *Troctulus*) has distinctive synapomorphies and the group is entirely Oligocene and younger. In fact, *Belaphotroctes similis* in Mexican amber is morphologically very similar to living specimens of the genus (Mockford 1969). This correlation confirms that *Cretoscelis* represents a basal divergence of the family and thus an origin for the family in probably the Early Cretaceous. As the sister group to the Liposcelididae, lice should have diverged from them at a corresponding time.

Interestingly, the monophyly of Phthiraptera—one of the best defined orders in Insecta—has been seriously questioned. Yoshizawa & Johnson (2003) sequenced the 12S and 16S rDNA genes for five *Liposcelis* species (but no other liposcelidids), and they found the phylogenetic position of *Liposcelis* was either unresolved among basal branches of lice or the genus was embedded within lice. Another recent hypothesis (Johnson *et al.* 2004), based on sequences from the 18S rDNA gene, proposed that the lice are actually polyphyletic, specifically that Amblycera are closely related to Liposcelididae and the related psocopteran family Pachytrochidae, and that all other lice are a sister group to these (the related nanopsocete family Sphaeropsocidae was not included in their analysis). We agree with Johnson *et al.* (2004) that the many unique characters defining louse monophyly (Kristensen 1975, 1991; Hennig 1981; Grimaldi & Engel 2005) are characters of great reduction or loss and are thus problematic to homologize, but we find louse polyphyly implausible for several reasons. (i) It requires the loss and then re-development of free-living habits and traits associated with ectoparasitism, such as wings, fully developed eyes, ocelli, etc; (ii) this hypothesis also requires two origins of a suite of features distinctive to lice, including ectoparasitism on homeothermic vertebrates, partial to complete fusion of the head to the thorax, distinctive egg structure (with a hydropile and operculum), the cementing of eggs to host pelage using glue-like spumaline that is secreted from the female accessory gland, and loss of the fourth nymphal instar; (iii) also, there is a morphocline or transformation series in lice in the reduction of mouthparts, from the generalized, mandibulate condition in Liposcelididae with a tentorium, to reduced mandibles and tentorium in Amblycera (traditionally considered the most basal louse suborder), to further loss and reduction (such as of laciniae) in Anoplura along with internalization of the labium; (iv) lastly, it is unclear why one gene (18S) would be sufficient for deciphering relationships in this group, when studies employing even eight genes (including 18S) have given some obviously erroneous relationships (i.e. barnacles and flies: Giribet *et al.* 2001). Indeed, the bootstrap values in Johnson *et al.* (2004) that support the clade Amblycera + Liposcelididae + Pachytrochidae as well as this group plus all other lice are quite low, revealing significant conflict within that data.

Given the morphological evidence, and until compelling molecular evidence indicates otherwise, it seems very reasonable to assume monophyly of Phthiraptera and thus a single origin of specialized ectoparasitism in Psocodea. This specialized lifestyle apparently originated in the Early Cretaceous, fed by diverse early mammals, haired pterosaurs, and feathered theropods at that time. Phthiraptera probably did not significantly diversify, though, until the large radiations of placental mammals and passerine birds that took place in the Tertiary, which can justifiably be considered an ‘age of lice’.

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