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Extralimital Fossils of the “Gondwanan” Family *Sphaeropsocidae* (Insecta: Psocodea)

DAVID GRIMALDI¹ AND MICHAEL S. ENGEL²

ABSTRACT

Two new species and genera of minute, coleopteriform psocopterans, family *Sphaeropsocidae* (Nanopsocetae), are described from fossils preserved in Cretaceous ambers: *Sphaeropsocoides canadensis* Grimaldi and Engel, n.gen., n.sp., from the Campanian of western Canada; and *Sphaeropsocites lebanensis* Grimaldi and Engel, n.gen., n.sp., from the Neocomian of Lebanon. These are the first described Mesozoic species of the family. *Sphaeropsocus kuenowii* Hagen in mid-Eocene Baltic amber is redescribed in detail. The 14 described Recent species of the family (in the genera *Sphaeropsocopsis* and *Badonnellia*) have natural distributions that are largely restricted to southern portions of the Southern Hemisphere, but Eocene and now Cretaceous fossils reveal a formerly global distribution of the family. Hypothesized relationships of the five genera indicate basal positions of the fossil genera, and probably an entirely Tertiary age of the Recent genera *Sphaeropsocopsis* and *Badonnellia*, which would thus be too young for these two genera to have been affected by gondwanan drift.

INTRODUCTION

Breeding amidst the humus of southern temperate forests are minute, beetlelike insects with elytriform forewings, which are the *Sphaeropsocidae*, coelacanth of the Psocoptera. Like coelacanth, these were first known as fossils, but in this case exquisitely preserved in mid-Eocene Baltic amber (Hagen, 1882:

fig. 1). Living relatives were not discovered until the early 1930s (again like coelacanth), some 50 years later, based on a species from Tasmania (Hickman, 1934). That Tasmanian species, *Sphaeropsocus recens* Hickman, was later transferred to a new but obviously closely related genus, *Sphaeropsocopsis*, along with four Recent species from Chile, Argentina, and Ascension Is-

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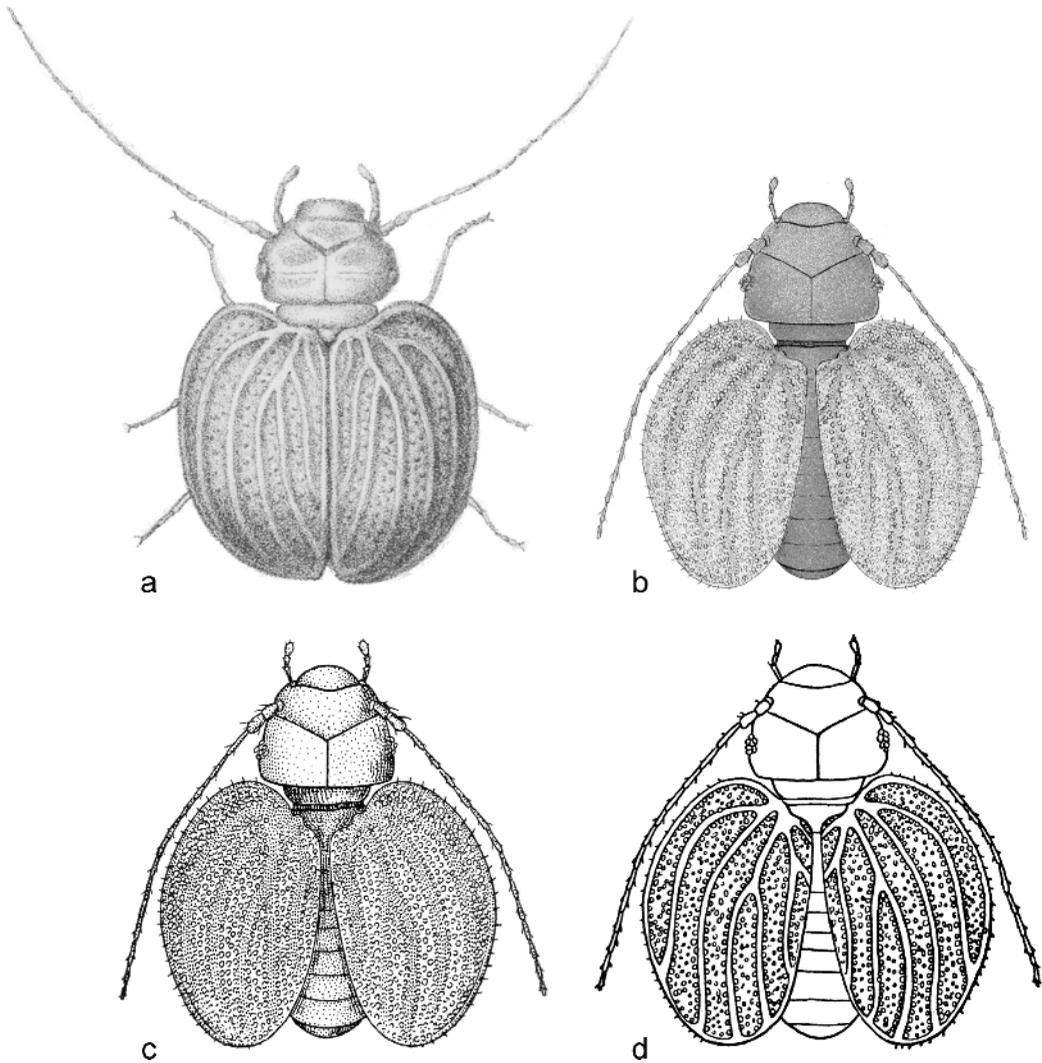


Fig. 1. *Sphaeropsocus kuenowii* Hagen (slightly reconstructed), as originally illustrated by Hagen, 1882 (a), by Enderlein, 1911 (b), by Badonnel, 1951 (c), and by Bekker-Migdisova and Vishniakova, 1962 (d). All authors erroneously depicted this species with a fully developed, Y-shaped frontal “suture” (which is actually an ecdysial cleavage furrow or scar; since true sutures represent segmental lines). In fact, note how later authors had simply redrawn Enderlein’s illustration. Interestingly, Hagen (1882) was far more accurate than his successors in the description and depiction of this species, the latter of whom erroneously depicted a forked cubital, a long stem of vein M, and the anterior margin of the forewing as barely cordate. Despite improvements in optics, the iconography of this interesting species suffered from a steady decline in original and critical observations.

land (Badonnel, 1962, 1963). Since that time four additional Recent *Sphaeropsocopsis* species have been discovered from Chile, Angola, and St. Helena Island in the southern Atlantic (Badonnel, 1967, 1971, 1972; Camousseight and New, 1994; Lienhard and

Ashmole, 2000). The closely related Recent genus *Badonnelia* contains four species from Chile (Badonnel, 1963, 1967, 1972; Camousseight and New, 1994) and one species is widespread throughout Europe, *B. titei* Pearman (reviewed in Lienhard and Smi-

thers, 2002). With the possible exception of a putative but as yet undescribed *Sphaeropsocopsis* from California (Mockford, 1993) and *B. titei*, both of which are plausibly introduced, the Recent Sphaeropsocidae are essentially or even entirely a gondwanan group. Yet the Baltic amber species indicates these insects roamed far into the Northern Hemisphere during at least the Eocene.

Here we further document the former global spread of Sphaeropsocidae by describing the first Cretaceous species, from the Early Cretaceous of Lebanon and Late Cretaceous of western Canada. This is an appropriate opportunity to also redescribe *Sphaeropsocus kuenowii* Hagen, based on detailed examination of the type and of new material, and to consider relationships of the five genera.

MATERIALS AND METHODS

Some amber pieces were prepared according to the protocols described by Nascimbene and Silverstein (2000), particularly the more fractured and brittle Cretaceous pieces. This involved preliminary trimming and grinding, then embedding the pieces in a very durable epoxy, and finally trimming, grinding, and polishing (often within less than one millimeter of the inclusion) so that the inclusion could be studied with compound microscopy at 100–400 \times . The Lebanese amber specimen in this study was collected in the 1970s by Aftim and Fadi Acra from near Jezzine and dates to approximately 120–125 Ma (Azar, 2000). The Canadian amber specimen was collected by J.F. McAlpine and J.E.H. Martin (1969) in the 1960s from near Cedar Lake, Manitoba, in outcrops of the Campanian-aged Foremost Formation (ca. 75–80 Ma). Baltic amber derives from vast deposits of the blaue Erde in northern Europe, which is mid-Eocene in age, ca. 45 Ma (Kosmowska-Ceranowicz, 1987; Ritzkowski, 1997).

Institutions that are repositories for the material examined are the following:

AMNH	American Museum of Natural History, New York, Division of Invertebrate Zoology (Acra Collection of Lebanese amber)
CNC	Canadian National Collection of Insects and Spiders, Agriculture

Canada, Ottawa, Ontario; courtesy of Dr. Jeff Cumming.

MCZ	Museum of Comparative Zoology, Department of Entomology, Harvard University, Cambridge MA; courtesy of Dr. Phil Perkins.
NHM	Natural History Museum, London, Department of Palaeontology; courtesy of Dr. Andrew J. Ross.
KU	Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence.

The following abbreviations are used herein for the various genera in the family so as to avoid confusion when discussing them together in condensed form: *Sphaeropsocus* (*S.*), *Sphaeropsocopsis* (*Sp.*), *Sphaeropsocoides* (*Sd.*), and *Sphaeropsocites* (*Si.*).

SYSTEMATICS

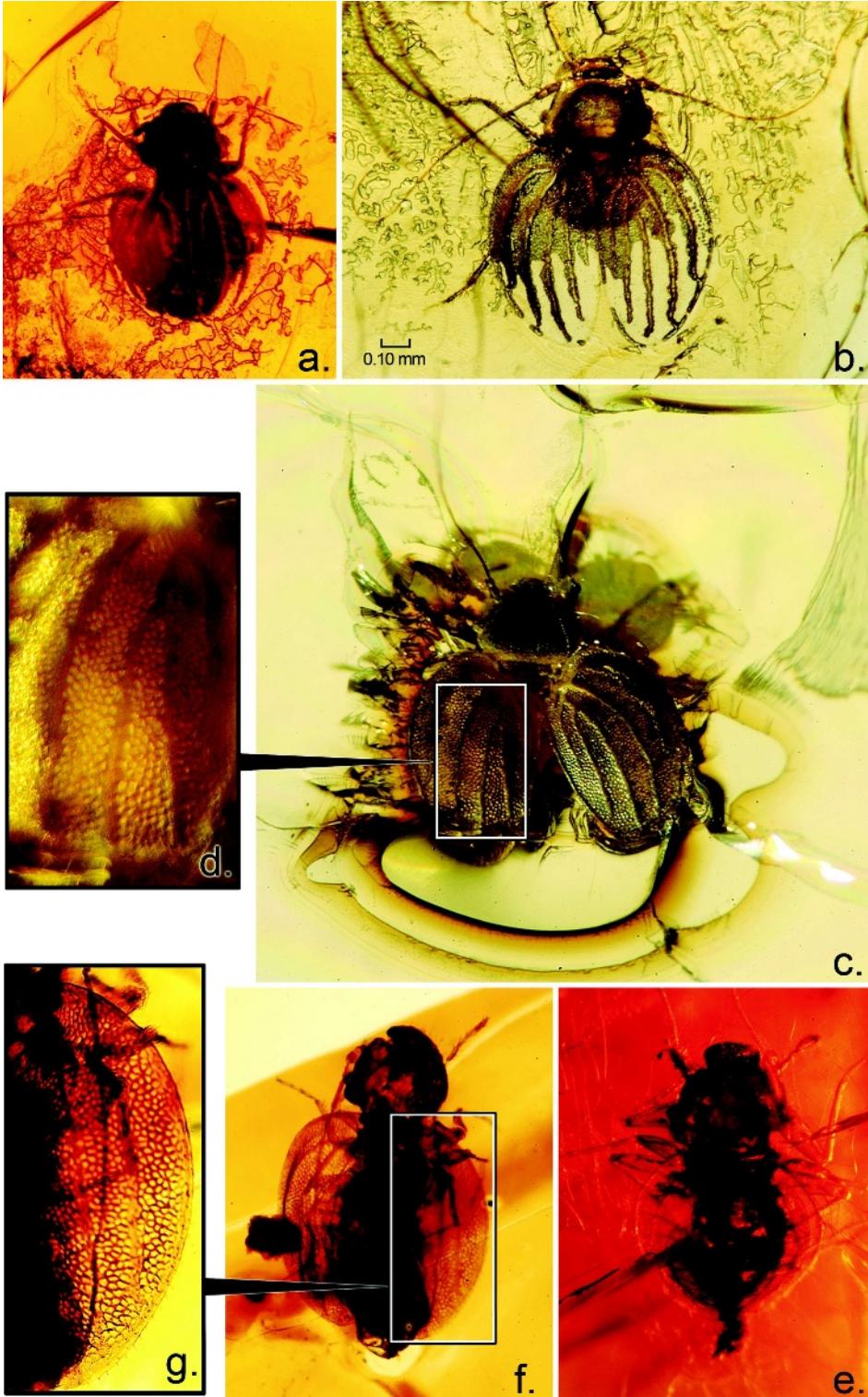
FAMILY SPHAEROPSOCIDAE KOLBE

Sphaeropsocini Kolbe, 1883: 190. Type genus: *Sphaeropsocus* Hagen, 1882. Handlirsch, 1907: 702 [elevated to familial rank]; Menon, 1942: 24; Pearman, 1958: 52; Bekker-Migdisova and Vishniakova, 1962: 230; Mockford, 1993: 63.

DIAGNOSIS: Minute, prognathous psocopteran (ca. 1.0 mm in body length); forewings of female elytriform (male micropterous), with reduced venation and fine to coarse punctation or areolation; hind wings absent; coxae closely situated; compound eyes with 0–10 ommatidia; ocelli absent.

INCLUDED GENERA: *Sphaeropsocopsis* Badonnel (nine Recent species: Chile, Angola, Tasmania, St. Helena Is.), *Badonnelia* Pearman (five Recent species: Chile, Europe), *Sphaeropsocus* Hagen (Baltic amber), *Sphaeropsocites* n.gen. (Lebanese amber), and *Sphaeropsocoides* n.gen. (Canadian amber). Another fossil, perhaps the fourth fossil species, is preserved in amber from the Late Cenomanian-aged Dolganian Formation (ca. 93–94 Ma) of the Taimyr Peninsula, Siberia (Rasnitsyn and Quicke, 2002: fig. 164), currently being studied elsewhere.

COMMENTS: Most psocopteran systematists attribute the family name to Menon (1942), but it was actually validated much earlier by Kolbe (1883) as a tribe and sub-



sequently applied by Handlirsch (1907) as a family. The family belongs to the Nanopsocetae,³ which is presently known to consist of a monophyletic lineage that also contains the Pachytroctidae, the Liposcelididae, and the lice (order Phthiraptera⁴). This grouping is based on morphology (Pearman, 1936) and DNA sequences (Johnson et al., 2004). Pachytroctidae is a family of 10 genera and approximately 90 described species, whose natural distribution is circum-tropical and warm temperate. Liposcelididae is a family of one extinct and nine Recent genera with 181 described species, most of which are in the familiar genus of “book lice,” *Liposcelis*. The most interesting aspect of the Liposcelididae is that they are the sister group to the true, ectoparasitic lice (Lyal, 1985; Yoshizawa and Johnson, 2003). The fossil record of lice is virtually nonexistent, but like the Sphaeropsocidae all the fossils of Liposcelididae are preserved in amber. A recent study of fossil Liposcelididae indicates an origin of the family and probable divergence from the lice in the Early Cretaceous or possibly latest Jurassic (Grimaldi and Engel, 2005b), which is an age that corresponds well with the fossil record of Sphaeropsocidae that we report here.

Genus *Sphaeropsocus* Hagen

Sphaeropsocus Hagen, 1882: 226. Type species: *Sphaeropsocus kuenowii* Hagen, 1882, by monotypy.
Palaeotroctes Enderlein, 1911: 350. Type species: *Atropos succinica* Hagen, 1882, by monotypy. Synonymy vide Pearman, 1958: 51.

DIAGNOSIS: (modified from Badonnel, 1963; Smithers, 1972; Mockford, 1993). Disting-

uished from *Badonnelia* on the basis of less reduced venation of the female forewings (vide *Badonnelia*, infra); distinguished from *Sphaeropsocopsis* by not having the apices of Rs, M, or Cu fused; from *Sphaeropsocites* by having P₄ not swollen, eyes distant from posterior margin of head, M and Rs not fused, and no crossveins; from *Sphaeropsocoides* by having very short to virtually no stems for R, M, and Cu, and tibiae without apical spurs.

Sphaeropsocus kuenowii Hagen

Figures 1, 2a–d, 3, 4

Sphaeropsocus künowii Hagen, 1882: 226. In Baltic amber. Name emended to *kuenowii* in accordance with ICZN (1999: Art. 32.5.2.1).
Atropos succinica Hagen, 1882: 231. Synonymy vide Pearman, 1958: 51.
Troctes succinicus (Hagen); Kolbe, 1883: 190.
Palaeotroctes succinicus (Hagen); Enderlein, 1911: 350.
Sphaeropsocus künowi Enderlein, 1911: 352. *Lapsus calami* pro *Sphaeropsocus kuenowii* Hagen, 1882.

DIAGNOSIS: As for genus (vide supra).

DESCRIPTION: (Female) (measurements based on KU B-144): Minute psocopteran, body length *sans* forewings ca. 0.60 mm, with forewings 1.0 mm. **Head:** Prognathous; broad, width 0.8× the length. Anterior tentorial pits short, sulcuslike, convergent just above clypeus; tentorium well-developed, with tentorial bridge and anterior tentorial arms; median “coronal suture” extended from posterior margin of head to level of eyes. Ocelli absent. Compound eyes small, with seven facets not contacting each other. Clypeus of modest

³ The name Nanopsocetae was first established by Pearman (1936) and not by Broadhead (1950) as widely cited by many authorities.

⁴ The difficulty of paraphyly of Psocoptera, Troctomorpha, and Nanopsocetae with respect to the true lice could be easily obviated by the demotion of Phthiraptera to a category within the infraorder Nanopsocetae and the reduction of its constituent suborders to more subordinate categories. The family-group classification of the lice would be entirely unaffected. This would certainly be preferable to the splitting of Psocoptera into innumerable new orders, would minimize the number of taxonomic changes (only five changes), and would permit the reflection of hierarchical relationships in the classification of “higher” Psocodea. Such a classification should be seriously considered by louse systematists.

←

Fig. 2. Photomicrographs of fossil Sphaeropsocidae. a–d. *Sphaeropsocus kuenowii* Hagen in mid-Eocene Baltic amber. a. Holotype, MCZ 235. b. KU B-144. c, d. KU B-148, showing detail of the areolate, elytrous forewings. e. *Sphaeropsocites lebanensis* Grimaldi and Engel, n.gen., n.sp., holotype, AMNH JS-284. f, g. *Sphaeropsocoides canadensis* Grimaldi and Engel, n.gen., n.sp., holotype CNC 642. All photos except “d” to the same scale.

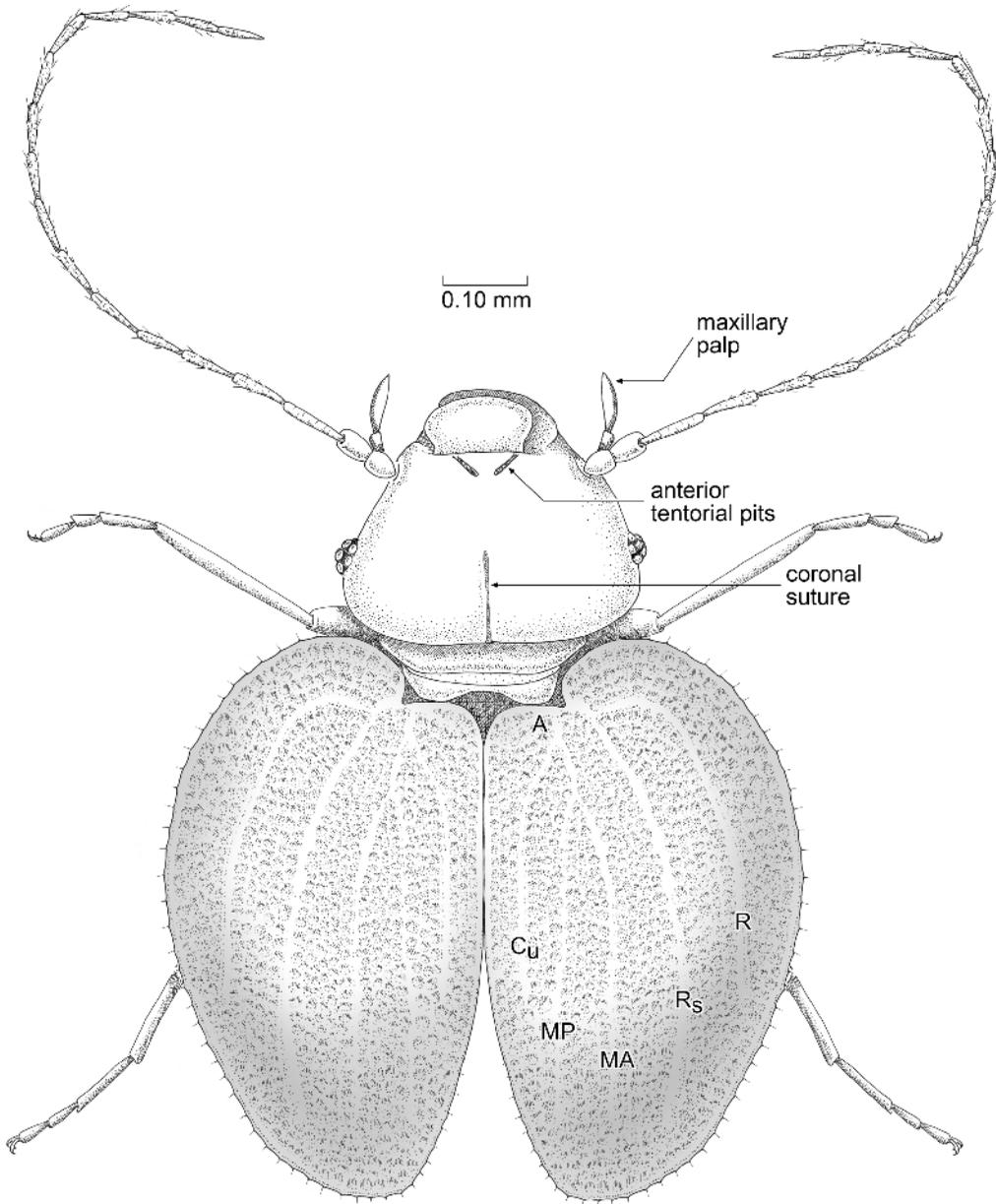


Fig. 3. Dorsal habitus of *Sphaeropsocus kuenowii* Hagen (KU B-144), in mid-Eocene Baltic amber, slightly reconstructed.

size; mandibles large; labial palps highly reduced (pair of small 1-segmented polyps on anterior margin of labium), area between labium and occipital foramen membranous. Maxillary palps 4-segmented, lengths of segments (longest to shortest): P4-2-3-1. Apical palpomere (P₄) spindle-shaped, apical

half with oval sensillar area on ventral surface. Right lacinia protrudent, apex with one small and two large teeth. Antenna length 10.5 mm; scape and pedicel twice width of flagellomeres, approximately half the length of basal flagellomere. Flagellum with 13–14 articles, each flagellomere with

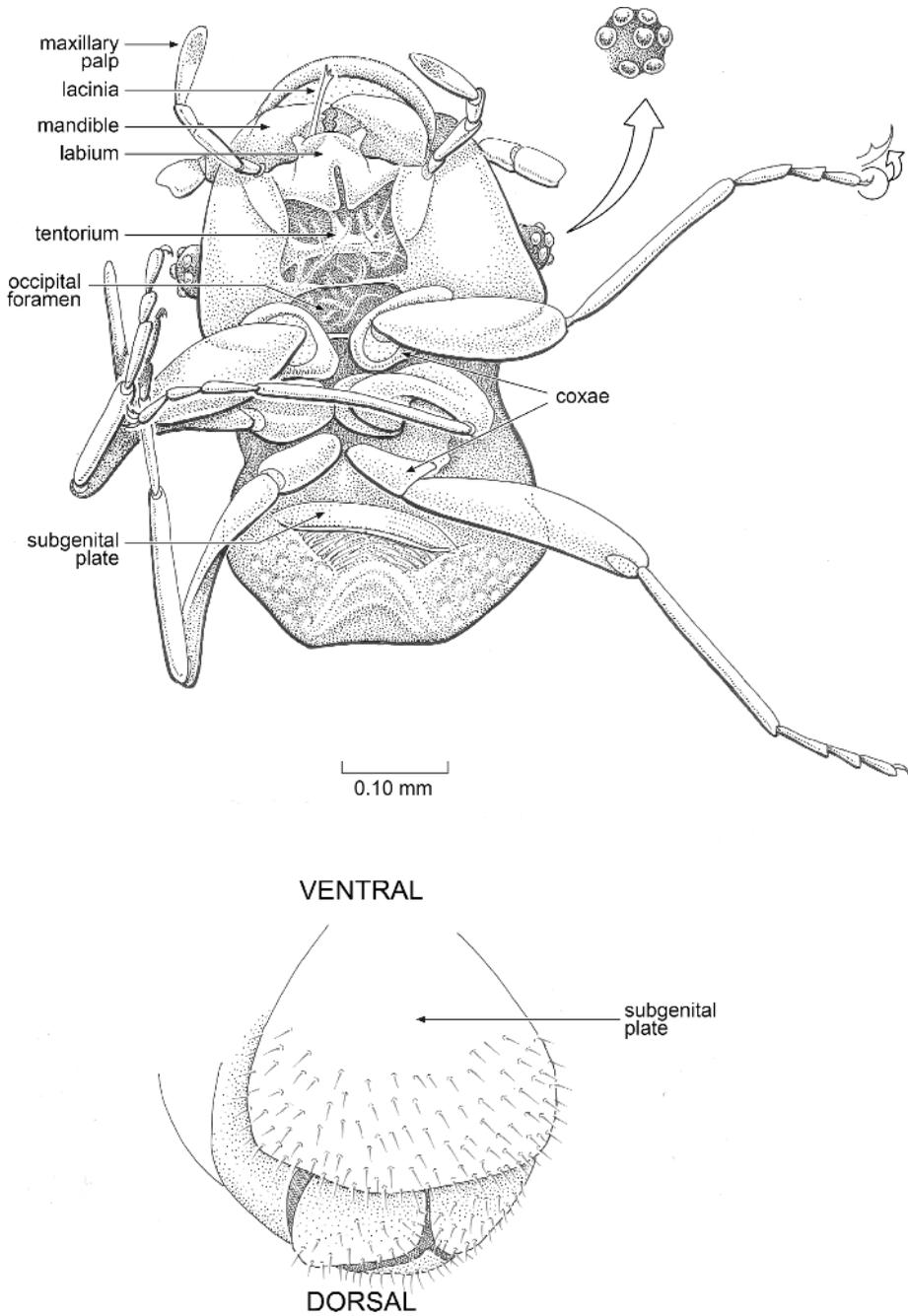


Fig. 4. Ventral habitus of *Sphaeropsocus kuenowii* Hagen (KU B-148), with detail of compound eye and terminal sternites.

fine annuli, and all but basal flagellomere with sparse setulae.

Thorax: Short, dorsally with only pronotum and mesoscutum exposed. Legs of moderate length, ca. 0.60–0.65 mm. Coxae large, opposites of each pair nearly touching medially; procoxae larger than metathoracic pair. Femora thick, width of profemur 3.5× width of protibia, of metafemur 2.7× width of metatibia; profemoral length 0.18 mm; meta-femoral length 0.25 mm. All tibiae approximately equal in length (0.20 mm) and width; no apical spurs present. Tarsi trimerous, total length 0.13 mm; basal tarsomere slightly longer than others; pretarsal claw with pre-apical tooth. **Wings:** Forewings present only (hind wings absent); forewing elytrous, carapacelike, length 0.67 mm, greatest width 0.38 mm; anterior margin cordate. Surface of wing between veins areolate, with dense, irregular depressions. Venation highly reduced, consisting of: circumambient C, R and Rs, MA and MP, Cu, and very short A (for proportions see fig. 3). Stem of R and M very short, but length variable even between wings of same specimen. Surface of veins minutely papillate, devoid of areolae. Apices of veins not reaching margin of wings. Outer margin of wing with row of minute, stiff setulae. Wings meet in straight line for approximately half their mesal length; divergent mesally in apical half.

Abdomen: Short, globose, approximately same size as head, dorsally obscured by forewings, ventrally exposing little or very obscure segmentation. Apical half of abdomen ventrally covered with large subgenital plate; plate with posterior margin entire (not bilobed or emarginate). In KU B-144 subgenital plate lifted, exposing what appears to be two opposing brushes of fine setulae and pocked surface of cuticle.

HOLOTYPE: MCZ 235 (fig. 2a), “no. 103” in handwriting [presumably Hagen’s]. Specimen was preserved in a square chip of amber that was heavily crazed and darkened to a very deep red from years of exposure (it was originally mounted between a piece of folded paper that was then pinned, and may have originally been stored in a pinned collection). The piece was embedded in epoxy at the AMNH and ground and polished in order to expose fresh surface for viewing critical details.

ADDITIONAL MATERIAL EXAMINED: KU B-144, -148, -154, all of which are preserved in middle Eocene Baltic amber from Germany, as well as a specimen preserved in Late Eocene amber from the Rovno region of the Ukraine (Engel and Perkovsky, 2006a, 2006b).

COMMENTS: This species has been referred to frequently in literature on insect fossils, and illustrations of it often reproduced and re-figured (e.g., Badonnel, 1951; Carpenter, 1992) (fig. 1). Despite this, and the fact it is not particularly rare in Baltic amber, this intriguing species has never been redescribed in detail. We have found that Hagen’s original illustration (fig. 1a) and description are remarkably accurate, which we can modify only slightly. The short vein A of the forewing is not present in the type specimen, and in other specimens A branches off at the very base of the stem of M + Cu, not off of Cu as depicted by other authors. Also, the longitudinal veins are incomplete and do not reach the wing margin.

Genus *Sphaeropsocopsis* Badonnel

Sphaeropsocopsis Badonnel, 1963: 322. Type species: *Sphaeropsocopsis chilensis* Badonnel, 1963, by original designation.

DIAGNOSIS: Modified from Badonnel (1967, 1971, 1972), Smithers (1972), and Mockford (1993): (Female) Forewings with 4–5 main longitudinal veins (generally missing MP), apices of at least Rs, M, and Cu fused distally (but distant from wing margin); wing membrane finely and densely areolate; maxillary palpomere 4 (P₄) fusiform; female terminalia with V3 deeply lobed.

INCLUDED SPECIES: There are nine described species in the genus, all of them Recent. Five of the species are known only from Chile: *Sp. chilensis* Badonnel, 1963; *Sp. microps* Badonnel, 1963 (specimens “cf. *microps*” are also reported from Ascension Island in the mid-Atlantic); *Sp. spinosa* Badonnel, 1972; *Sp. valdiviensis* Badonnel, 1972; and *Sp. valeriae* Badonnel, 1967. *Sphaeropsocopsis argentina* (Badonnel, 1962) occurs in Argentina (but has also been introduced into the United States; see Relationships and Biogeography, below); *Sp. recens* occurs in Tasmania and southeastern Australia (Hickman, 1934); *Sp. riesi*

Badonnel, 1972 occurs in Angola; and there is a blind cave species on St. Helena Island (*Sp. myrtleae* Lienhard and Ashmole, 1999). *Sphaeropsopsis myrtleae* was placed into this genus only on the basis of undivided mesothoracic sternites and eye reduction; the brachypterous forewings are so reduced as to obscure whether they possessed the characteristic venation and areolae.

Mockford (1993) mentioned a possible *Sphaeropsocus* from California, known only from three ♀ specimens representing possibly two species, but which may be a *Sphaeropsopsis*. According to Mockford (1993: pg. 64) these specimens have six veins “including Cu₂, but Cu₁ is simple and joins M₂ distally” (this last feature diagnostic of *Sphaeropsopsis*). Given that one species from Argentina, *Sp. argentina* (Badonnel, 1962), has been introduced into the United States, it is quite possible that the California specimens were also from an introduced population.

Genus *Badonnelia* Pearman

Badonnelia Pearman, 1953: 262. Type species: *Badonnelia titei* Pearman, 1953, by original designation.

DIAGNOSIS: Distinguished from *Sphaeropsopsis* entirely on the basis of apomorphic features: Forewings also elytrous but bent down at sides of abdomen, with only two main veins and “hexagonal pattern of ridges.” Compound eye with seven ommatidia (vs. “variable”). Cuticle of body with fine granular microsculpture. Fourth maxillary palpal segment (P₄) subcylindrical, elongate (vs. “fusiform”).

INCLUDED SPECIES: There are five described species, the first four of which are from Chile: *B. castrii* Badonnel, 1963; *B. granulosa* Badonnel, 1972; *B. similis* Badonnel, 1963; *B. testacea* Badonnel, 1972; and *B. titei*. *Badonnelia titei* is widespread throughout western Europe, from the UK to Finland and Sweden, and to Switzerland, but probably introduced to that area.

COMMENTS: As diagnosed this genus would appear to render *Sphaeropsopsis* paraphyletic, since it is defined entirely on the basis of characters that are apomorphic with respect to these genera. Before any formal synonymy of genera is proposed it would be important to examine the detailed morphology of as many

Recent species of sphaeropsocids as possible. Such a study should also determine the exact relationship of *B. titei* to the other (austral) species of the genus, although based on published descriptions it appears to be typical of other species in the genus.

It must be seriously considered that *B. titei* is a species as yet unknown from Chile or which is a senior synonym of one of the four species described by Badonnel, but which was introduced to western Europe. Thus far, the species is known from Belgium, Finland, Great Britain, Ireland, Luxembourg, Norway, Sweden, and Switzerland. A Europe-Chile disjunction is an extremely unusual distribution for any group of organisms, particularly for a group that we hypothesize as very young and derived from a naturally austral group (*Sphaeropsopsis*). Most significant is that published anecdotes reveal the “librophilous” nature of *B. titei* and how it is easily spread by humans. O’Connor (1987), for example, documented how *B. titei* was received in a shipment of books to Scotland, and even the type specimen of the species was found in the binding of an old atlas in the museum at Tring, England (Pearman, 1953)! (Full citation of the “type locality” was not specified, but apparently it was not the page with a map of Chile). We believe that *Badonnelia* is probably naturally endemic to Chile.

Sphaeropsocoides Grimaldi and Engel, new genus

TYPE SPECIES: *Sphaeropsocoides canadensis*, new species, in Cretaceous Canadian amber.

DIAGNOSIS: Anterior margin of forewing slightly less cordate than in Recent genera. Venation most similar to that of *Sphaeropsocus*, with five main veins, their apices not meeting wing margin (but closer to margin in *Sphaeropsocoides*) nor apically fused; and with stem of R, stem of M, and Cu slightly longer. Antennal flagellum with 12 segments (vs. 13–14); tibia with two apical spurs; pretarsal claw with small preapical tooth.

ETYMOLOGY: Base of the name is from the type genus of the family, and the suffix *-oides* from the Greek *-eides* or *-eidos*, meaning “like” or “having the form of”.

Sphaeropsocoides canadensis Grimaldi and Engel, new species
Figures 2f–g, 5

DIAGNOSIS: As for genus (see above).

DESCRIPTION: (Female) (measurements based on holotype, CNC 642): Minute psocopteran, body length with forewings 0.97 mm. Body somewhat compressed, so proportions are probably slightly distorted. **Head:** Prognathous; broad, width approximately equal to length. Anterior tentorial pits unapparent; pair of long, fine setae on anterior margin of head; median “coronal suture” extended from posterior margin of head to level of anterior margin of eyes. Ocelli absent. Compound eyes small, with approximately six facets not contacting each other [difficult to discern]. Clypeus of modest size; labial palpi visible in CNC 644, a pair of small lobes on anterior margin of labium [paraglossae?]; fine, stiff setae on margins, with 1 thick seta at apex of palp having slightly bifid apex. Maxillary palp 4-segmented, lengths of palpomeres (longest to shortest): P4-2-3-1. Apical palpomere (P₄) narrow ovoid to spindle-shaped, apical half with dark area, presumably sensillar area. Palpomeres P₂ and P₃ each with lateral patch of dense microtrichia (presumably sensilla). Lacinia protrudent, length equal to that of P₄, apex with one small and two large teeth. Antenna length 8.1 mm; scape and pedicel twice width of flagellomeres, slightly longer than half the length of basal flagellomere. Flagellum with 12 articles, each flagellomere with fine annuli.

Thorax: Short, dorsally with only pronotum and mesoscutum exposed. [Leg lengths and other proportions difficult to discern], ca. 0.60–0.65 mm. Tibiae with pair of small apical spurs, length of spurs approximately equal to width of tibia. Tarsi trimerous, total length 0.13 mm; basal tarsomere slightly longer than others; basal and second tarsomere each with small apical spur; pretarsal claw with pre-apical tooth. **Wings:** Forewings present only (hind wings absent); forewing elytrous, carapacelike, length 0.60 mm, greatest width 0.31 mm; anterior margin slightly cordate. Surface of wing between veins areolate, with dense, irregular depressions. Venation highly reduced, consisting of: circumambient C, short

R and Rs, MA and MP, Cu, and very short A (for proportions see fig. 4a). Stem of R short; stem of M approximately twice the length. Surface of veins devoid of areolae. Apices of veins barely touching margin of wings. Outer margin of wing with row of minute, evenly-spaced, stiff setulae. Wings meet in straight line for slightly less than half their mesal length; divergent mesally in apical half.

Abdomen: Obscured by forewings and by distortion from compression in holotype. Subgenital plate large, shape of posterior margin typical of family (entire, not bilobed or emarginate).

TYPE MATERIAL: Holotype CNC 642, which is slightly compressed dorsoventrally (especially the head and abdomen). Paratype CNC 644, which displays some details very well (fig. 4b), but those fragments of the body that are preserved are greatly compressed. Forewings of the holotype specimen are fortuitously cleared, which confirmed that the hind wings are indeed absent.

ETYMOLOGY: The specific epithet is based on Canada, the country of origin.

COMMENTS: This species appears to be an extinct sister group to *Sphaeropsocus* and *Sphaeropsocopsis*, based on the following plesiomorphic features: presence of apical tibial spurs, the palpal segmentation, shape of the anterior margin of the wing, and the long R and M stems.

Sphaeropsocites Grimaldi and Engel,
new genus

TYPE SPECIES: *Sphaeropsocites lebanensis*, new species, in Early Cretaceous Lebanese amber.

DIAGNOSIS: Apomorphically distinguished from all other genera of the family by palpomere P₄ swollen; clypeus very large; eyes situated very posteriad on head; each forewing virtually hemispherical in shape (inner margins touching for entire length, not divergent apically); vein M short and fused to middle of Rs; course of all veins converging towards mesal margin of wing. Plesiomorphically distinguished from all other genera by non-cordate shape (lack of humeral arc) on wing base, by fine punctation (vs. areolate surface) on forewing, and less reduced venation: Rs apically branched, crossveins between R-Rs and M-Cu, incomplete crossvein between R and C, vein A long, slight claval furrow present.

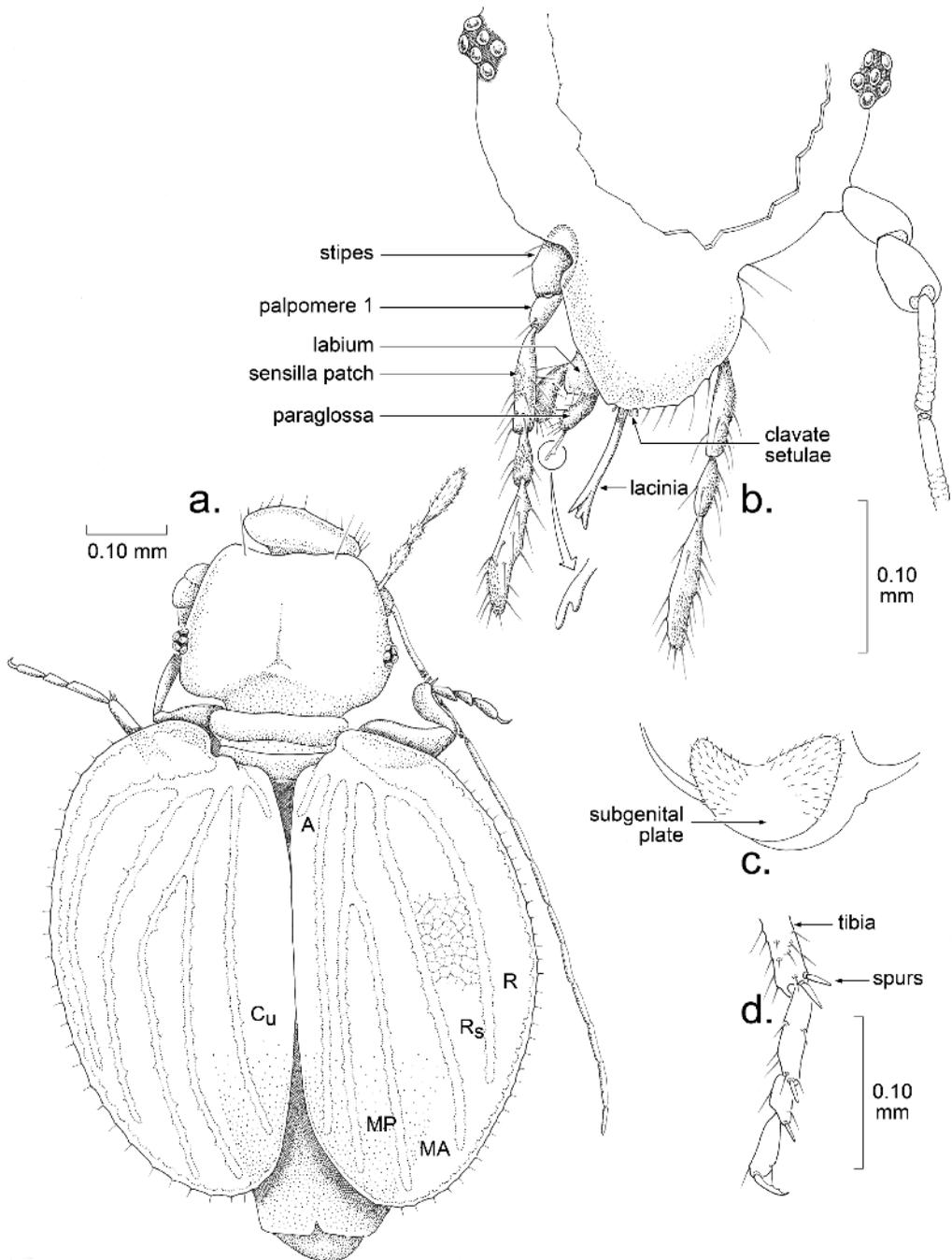


Fig. 5. *Sphaeropsocoides canadensis* Grimaldi and Engel, new genus and species, in Campanian-aged amber from western Canada. **a.** Dorsal habitus of holotype, CNC 642. **b–d.** Details of paratype, CNC 644. **b.** Anterior portion of head. **c.** Apical sternites. **d.** Mesotarsus.

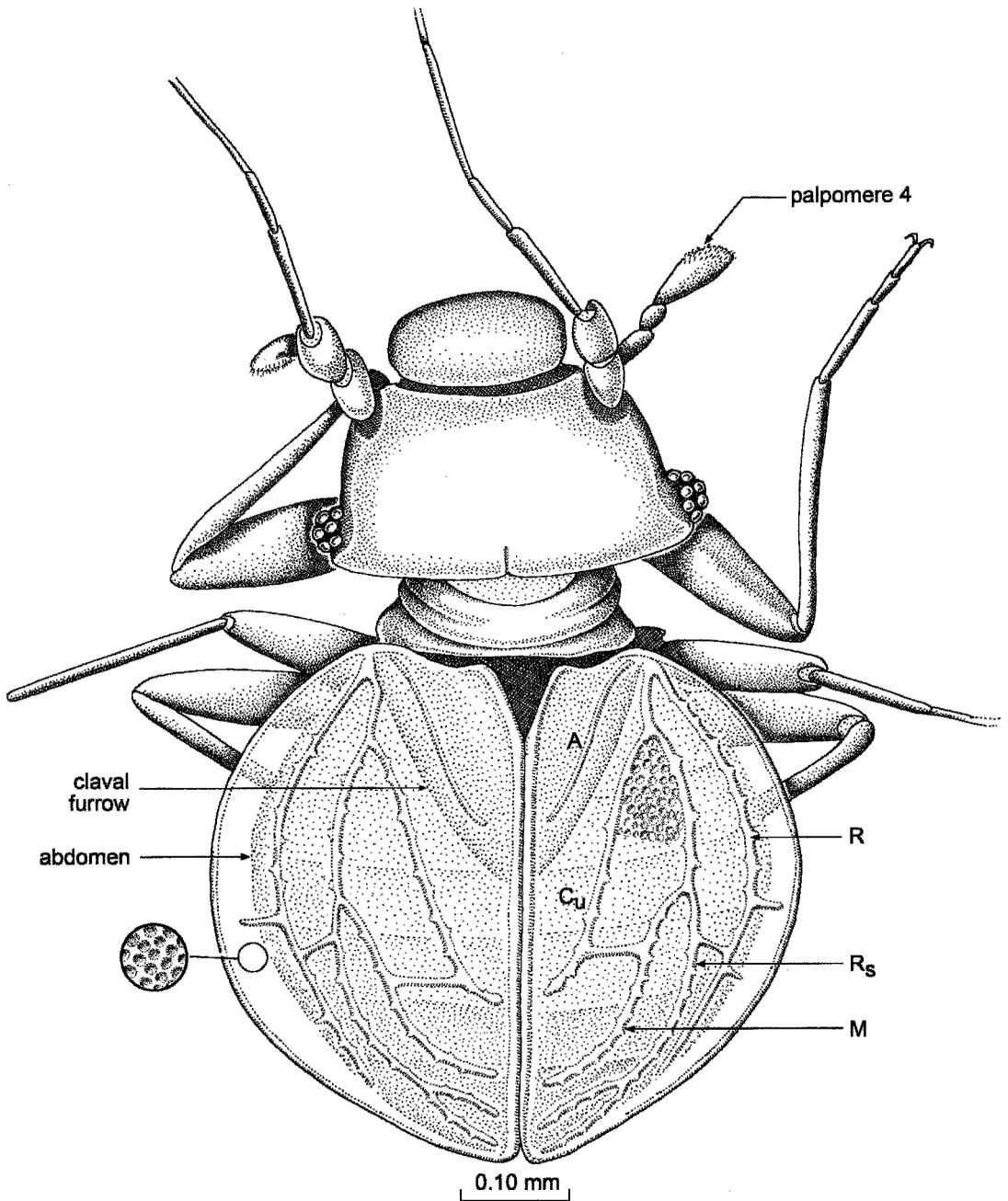


Fig. 6. *Sphaeropsocites lebanensis* Grimaldi and Engel, new genus and species, in Neocomian-aged amber from Lebanon. Dorsal habitus of holotype AMNH JS-284.

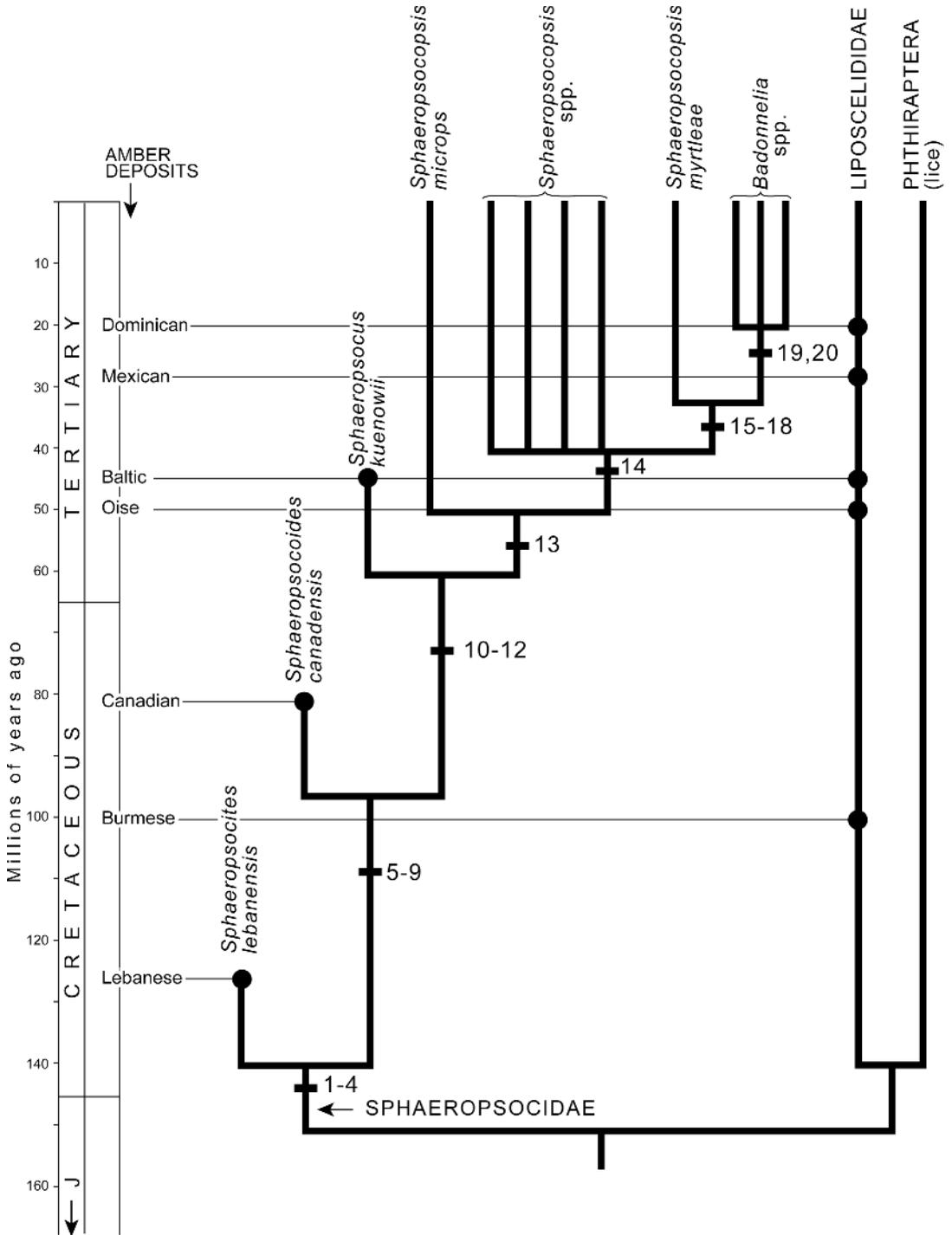


Fig. 7. Cladogram of living and extinct genera. Refer to table 1 for a list of the numbered characters supporting the clades.

- Humeral angle of forewing present but not enlarged; stem of M well developed.....
 *Sphaeropsocoides* n.gen.
4. Forewings with distinct venation, although in brachypterous forms veins are reduced and greatly desclerotized (e.g., *Sp. myrtleae*); humeral angle chordate, sometimes weakly so..... *Sphaeropsocopsis* Badonnel
- Forewing without venation, strongly arched dorsally and extending ventrally on sides to form tear-dropped carapace; humeral angle entirely reduced and tapering gently along wing length..... *Badonnelia* Pearman

RELATIONSHIPS AND BIOGEOGRAPHY

A preliminary cladogram of sphaeropsocid relationships is provided in figure 7, based on all fossil and living genera and 16 morphological characters (excluding ones defining the family) (table 1). All characters are entirely consistent with each other (there is apparently no homoplasy), so there was no need for a data matrix and digital analysis. As recently found with the closely related family Liposcelididae (Grimaldi and Engel, 2005b), there is a perfect correlation between the chronology of fossils and the branching sequence of the cladogram.

The oldest fossil of the family, *Si. lebanensis* in Early Cretaceous amber, branches off first. Despite unusual, autapomorphic features of this species, it possesses an array of features that are plesiomorphic to all other species of the family. These features include a forewing humeral area that is not expanded, wings that meet medially for their entire length, an enlarged vertex, and venation: vein A is present and is least reduced among all known species, a claval suture is present, and crossveins (three in number) are present. Tibial apices of *Si. lebanensis* are obscure, but spurs are possibly present. The species that branches off next is *Sd. canadensis* in Late Cretaceous Canadian amber. It lacks the large (i.e., cordate-shaped) humeral angle of the more derived species, and it has a pair of small tibial spurs on the apices of at least the fore and mid tibiae. The undescribed sphaeropsocid in mid-Cretaceous amber from Taimyr, Siberia (Rasnitsyn and Quicke, 2002: fig. 164) is still being studied elsewhere, so our comments are based entirely on the published photograph. Like *Sphaeropsocus* and *Sphaeropsocoides* in Baltic and Canadian amber (respectively), the

TABLE 1
**Characters Used in the Phylogeny of
 Sphaeropsocidae** (see fig. 7)

-
1. Ommatidia reduced to 0–10; ocelli lost.
 2. Forewings elytrous, sclerotized, carapacelike.
 3. Forewing venation reduced, with dense punctation or areolae.
 4. Hind wings lost.
 5. Vertex of head enlarged.
 6. Vein A reduced in size, to usually just a spur.
 7. Claval suture lost.
 8. All crossveins lost.
 9. Humeral area of wing expanded, arched.
 10. Tibial spurs lost.
 11. Stem of vein M shortened.
 12. Humeral area of wing greatly expanded, cordate in shape.
 13. Vein A completely lost.
 14. Apices of veins connected and looped near margin of wing.
 15. Elytra short, not reaching posterior margin of abdomen.
 16. Humeral area of wing greatly reduced.
 17. Veins very lightly sclerotized.
 18. Venation high reduced, to one or no veins.
 19. Venation entirely lost.
 20. Lateral surfaces of wings folded against lateral surfaces of abdomen.
-

Siberian amber specimen appears to lack crossveins, it has incomplete apices of the wing veins, and a fairly short stem to vein M. If this is the case, then it would be phylogenetically intermediate between the Baltic and Canadian amber species. *Sphaeropsocus kuenowii* in Baltic amber is the sister group to living species since it retains an anal vein (albeit a vestigial one). *Sphaeropsocopsis microps* is perhaps the most primitive Recent species since the apices of the forewing veins are not connected and so do not loop together near the wing margin. In lieu of detailed comparisons among the eight remaining species of the Recent *Sphaeropsocopsis*, relationships are as yet unresolved but this scheme does include a lineage that consists of the blind, troglobitic species from St. Helena Island, *Sp. myrtleae*, and *Badonnelia*. This putative sister-group relationship is based on reduced venation, lightly sclerotized wing veins, and reduction in the wing humeral area. As such, *Sphaeropsocopsis* appears to be paraphyletic with respect to *Badonnelia*. *Badonnelia* is clearly a very specialized and

monophyletic group since the veins are entirely lost and the lateral parts of the forewings have grown down along the sides of the abdomen.

An understanding of relationships allows better interpretation of the interesting distribution of Sphaeropsocidae. It appears very likely that Recent species of the family are naturally gondwanan, since *Sp. argentina* has been introduced to the southern United States from Argentina, and it is quite possible that *B. titei* in Europe and a *Sphaeropsocopsis* from California were also introduced from Chile or Argentina (Mockford [1993] considered the California specimens to be *Sphaeropsocus*, but based on the revised definitions by the present authors this species belongs to *Sphaeropsocopsis*). If this is the case, then most Recent sphaeropsocids are actually austral. The Austral Region includes the temperate regions of southeastern Australia (including Tasmania), New Zealand, New Caledonia and the Fijian Islands, Chile and Argentina, and sometimes southernmost Africa. Taxa with distributions that have an austral disjunction are classically interpreted as relicts of gondwanan drift (Hennig, 1960; Brundin, 1966; summarized in Grimaldi and Engel, 2005a).

Laurasian fossil Sphaeropsocidae would appear to refute an hypothesis that Recent species of the family were affected by gondwanan drift (though Lebanon probably has a gondwanan origin). In fact, the Cretaceous and Eocene fossil sphaeropsocids comprise just stem groups to the Recent species. Extralimital fossils critically depend on the concept of Sphaeropsocidae, which in this case was expanded to include more primitive, extinct species. Grimaldi (1992) established criteria for when fossils can be used to interpret formerly more widespread distributions of Recent lineages, specifically that the fossils must belong to the crown group. Fossil Sphaeropsocidae do clearly establish, though, the possibility that Recent Sphaeropsocidae could have expanded their distribution outside of Recent ones at some time. More importantly, the phylogeny of the family indicates that the Recent genera *Sphaeropsocopsis* and *Badonnelia* (fig. 7) are probably entirely Tertiary in age and thus too young to have been affected by Cretaceous tectonics.

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