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In search of the sister group of the true lice: A systematic review of booklice and their relatives, with an updated checklist of Liposcelididae (Insecta: Psocodea)

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> Abstract

The taxonomy, fossil record, phylogeny, and systematic placement of the booklouse family Liposcelididae (Insecta: Psocodea: 'Psocoptera') were reviewed. An apterous specimen from lower Eocene, erroneously identified as *Embidopsocus eocenicus* Nel et al., 2004 in the literature, is recognized here as an unidentified species of *Liposcelis* Motschulsky, 1852. It represents the oldest fossil of the genus. Phylogenetic relationships within the family presented in the recent literature were re-analyzed, based on a revised data matrix. The resulting tree was generally in agreement with that originally published, but the most basal dichotomy between the fossil taxon *Cretoscelis* Grimaldi & Engel, 2006 and the rest of the Liposcelididae was not supported. Monophyly of *Liposcelis* with respect to *Troglotroctes* Lienhard, 1996 is highly questionable, but the latter genus is retained because of lack of conclusive evidence. Paraphyly of Psocoptera (i.e., closer relationship between Liposcelididae and parasitic lice) is now well established, based on both morphological and molecular data. Monophyly of Phthiraptera is questionable, but support for the 'Polyphyly of Lice Hypothesis' is still not definitive. A checklist of valid names of all presently recognized Liposcelididae taxa (10 genera, 200 species) is also included with information on their geographical distribution. Because monophyly of the subfamily Embidopsocinae is highly questionable, we list the genera alphabetically without adopting the usual subdivision into two subfamilies.

> Key words

Liposcelididae, booklice, Psocoptera, Phthiraptera, parasitic lice, phylogeny.

1. Introduction

Liposcelididae (Fig. 1) are a family of the insect order Psocodea (*sensu* HENNIG 1966; YOSHIZAWA & JOHNSON 2006). Within the "superorder Psocodea" (*sensu* HENNIG 1953), two "orders" have long been recognized, i.e., Psocoptera (non-parasitic members: psocids, barklice, and booklice) and Phthiraptera (parasitic members: chewing and sucking lice). However, paraphyly of Psocoptera with regard to Phthiraptera is now widely accepted (KRISTENSEN 1991; GRIMALDI & ENGEL 2005; BESS et al. 2006). Therefore, some authors have recognized Psocodea as the only valid taxon and have rejected formal use of the order name Psocoptera (HENNIG 1966; LYAL 1985; YOSHIZAWA & JOHNSON 2006).

Since LYAL (1985) proposed a close phylogenetic affinity between Liposcelididae and parasitic lice based on cladistic analysis of morphological data, the Liposcelididae have been considered to be a key taxon in uncovering the origins and evolution of parasitism in lice. Liposcelididae are minute free living insects (Fig. 1) usually classified under Psocoptera, but they share a lot of features with parasitic lice (LYAL 1985; GRIMALDI & ENGEL 2005). However, the character

Fig. 1. Habitus of *Liposcelis* spp. on millimeter squares (females). **A**: *L. bostrychophila* (Section II, Group D). **B**: *L. pearmani* (Section I, Group B) (©Albert de Wilde).

states shared between Liposcelididae and parasitic lice are mostly reductions, and phylogenetic significance of such characters has been questioned (LYAL 1985; YOSHIZAWA & JOHNSON 2006). Recently, several molecular-based phylogenetic analyses were performed to test Lyal's hypothesis. Results from the molecular analyses support strongly the hypothesis but, in turn, provide some novel insights into the origins and evolution of parasitism in lice. These include the possibility of polyphyly of parasitic lice. Because Phthiraptera has long been recognized as one of the best supported monophyletic insect groups (HENNIG 1966; KRISTENSEN 1991; JAMIESON et al. 1999; GRIMALDI & ENGEL 2006), this result was highly surprising and is still debated.

In this paper, we provide a review of the present taxonomic and systematic status of the family Liposcelididae and its relatives. This review was originally presented at the 4th Dresden Meeting on Insect Phylogeny (September 2009). The main topic at the meeting was the phylogenetic importance of Liposcelididae bridging free living barklice and parasitic lice. However, taking this opportunity, we also provide more extensive review of the family including the intra-familial taxonomy and fossil records. A checklist of valid names of all currently recognized Liposcelididae taxa (10 genera, 200 species) is presented in Appendix 2.

2. Taxonomy of Liposcelididae

Liposcelididae is classified under the psocodean suborder Troctomorpha. The suborder is subdivided into two infraorders, Amphientometae and Nanopsocetae. Together with Sphaeropsocidae and Pachytroctidae, Liposcelididae are assigned to the Nanopsocetae (LIENHARD & SMITHERS 2002). The parasitic lice (Phthiraptera) are close relatives of Liposcelididae (LYAL 1985; YOSHIZAWA & JOHNSON 2003; JOHNSON et al. 2004; MURREL & BARKER 2005) making Troctomorpha and Nanopsocetae both paraphyletic, unless the suborder and infraorder are re-defined to include parasitic lice.

Liposcelididae are usually divided into two subfamilies, Embidopsocinae and Liposcelidinae (see below). However, the checklist in Appendix 2 does not employ this traditional system (see chapter 4). Except for the specialized cave-dwelling species *Troglotroctes ashmoleorum* (see LIENHARD 1996) all species of the Liposcelidinae have been assigned to the genus *Liposcelis* (ca 130 spp.). In contrast, Embidopsocinae was further subdivided into seven genera, although this subfamily contains fewer species (ca 70) than Liposcelidinae.

Generally, the Embidopsocinae are considered to represent more plesiomorphic forms within the family. For example, members of Liposcelidinae are all apterous whereas winged forms are relatively frequent in Embidopsocinae. Monophyly of Embidopsocinae is questionable (GRIMALDI & ENGEL 2006; see also below). Genera traditionally assigned to Embidopsocinae are *Belapha*, *Belaphopsocus*, *Belaphotroctes*, *Chaetotroctes*, *Embidopsocus*, *Embidopsocopsis* and *Troctulus* (see LIENHARD & SMITHERS 2002). All embidopsocine genera are small, each containing less than five species, except for *Belaphotroctes* (19 spp.) and *Embidopsocus* (43 spp.). The genera *Chaetotroctes*, *Embidopsocopsis,* and *Troctulus* are

all monotypic. The monotypic fossil genus *Cretoscelis* was originally considered to be the sister group of all other Liposcelididae (Grimaldi & Engel 2006; see also below).

The largest genus, *Liposcelis*, is subdivided into four species groups (A, B, C, D) belonging to two sections, groups A and B to section I and groups C and D to section II. These subdivisions are based on suggestions published by Badonnel (1962, 1963, 1967) and have more recently been defined and included in keys by Lienhard (1990, 1998) and Mockford (1993). These sections and species groups, based on usually well visible characters of tergite fusions and chaetotaxy, are very useful for organizing this large genus in practice, but their monophyly is debatable and has not yet been tested by phylogenetic analyses. Thus members of section II are characterized by a probably symplesiomorphic 'annulate type' of abdominal segmentation (lacking fusion of tergites), while section I is characterized by the apomorphic fusion of tergites 3–5, resulting in an abdomen of the 'compact type' (Fig. 1).

The monotypic genus *Troglotroctes* is suggested by Grimaldi & Engel (2006) to be imbedded phylogenetically within *Liposcelis* because the latter genus is, as compared to the former, characterized only by plesiomorphies. *Troglotroctes* is characterized by highly autapomorphic specializations related to its cave-dwelling behavior (Lienhard 1996). *Troglotroctes* can be assigned to the species group D of *Liposcelis* on the basis of the presence of a pair of setae on the posterior half of the prosternum (see Lienhard 1996), but this character state is probably plesiomorphic even at the level of Liposcelididae because possibly homologous setae are also present in Embidopsocinae. Therefore, monophyly of *Liposcelis* excluding *Troglotroctes* cannot be offhand rejected on the basis of available data.

A key to the genera of Liposcelididae (except *Cretoscelis* and *Troglotroctes*) is given by Lienhard (1991). Lienhard (1990, 1998) proposes a key to the Western Palaearctic species of *Liposcelis*, which contains also almost all widely distributed domestic species. Some of them have a cosmopolitan distribution (see Appendix 2) and are important pests in stored food (see Lienhard 2004b).

3. Fossil records of Liposcelididae

Not many fossils are available for Liposcelididae. The oldest fossil of the family is known from the mid Cretaceous (ca 100 Mya) of Myanmar and is assigned to the monotypic genus *Cretoscelis* (only including *C. burmitica*). This genus was originally considered to represent the most basal split from the rest of the family (Grimaldi & Engel 2006), but our revised data do not support this view (see below).

The other known fossil species of Liposcelididae can all be assigned to extant genera (reviewed by Nel et al. 2004): *Embidopsocus saxonicus* (early Miocene, ca 22 Mya, see Günther 1989; upper Eocene or Miocene [?] according to Nel et al. 2004), *E. eocenicus* (lower Eocene, ca 53 Mya, see Nel et al. 2004), *Belaphotroctes similis* (late Oligocene – early Miocene, ca 30 Mya, see Mockford 1969; the synonymy with the extant *B. ghesquierei*, proposed by Mockford 1972, was not accepted by Nel et al. 2004), *Belaphopsocus dominicus* (Miocene, ca 20 Mya, see Grimaldi & Engel 2006), *Liposcelis atavus* (in Baltic amber, see Enderlein 1911; late Eocene, ca 40 Mya, see Schlee & Glöckner 1978) and two unnamed *Liposcelis* species (late Oligocene – early Miocene, ca 30 Mya, see Mockford 1969; Miocene, ca 20 Mya, see Grimaldi & Engel 2006).

The genus *Miotroctes* Pierce, 1960, represented by a single species, *M. rousei* Pierce, 1960, was once classified under Liposcelididae (Lewis 1989). However, the only available specimen lacks many characters of importance for deciding its systematic placement (antennae, labial palpi, and tarsi). Nel et al. (2004) concluded that the assignment of this species to Liposcelididae is only weakly supported by its small body size and thus is inappropriate; therefore it should rather be placed in Psocodea *incertae sedis*.

Nel et al. (2005) reported an apterous booklouse fossil specimen from the lower Eocene (ca 53 Mya) and identified it as *Embidopsocus eocenicus*. However, the photograph of the specimen (Nel et al. 2005: fig. 5A) clearly shows that the specimen has a tubercle on the anterior margin of the hind femur. This character state is regarded as an autapomorphy of Liposcelidinae (Grimaldi & Engel 2006). Other superficial features of the specimen also resemble those of *Liposcelis* (shape of head, shorter legs, shape of thoracic sterna) rather than *Embidopsocus*, so that it should be assigned to *Liposcelis*. The oldest *Liposcelis* fossil previously known was from the late Oligocene (*L. atavus*). Thus, the lower Eocene specimen reported by Nel et al. (2005) represents at present the oldest fossil record of *Liposcelis*.

4. Phylogeny within Liposcelididae

To date, the only formal phylogenetic analysis within the Liposcelididae is that performed by Grimaldi & Engel (2006). They analyzed morphology of both extant and fossil taxa and presented the most parsi-

monious tree. However, the phylogenetic estimation performed by GRIMALDI & ENGEL (2006) involved several problems. It is not the aim of this review paper to provide a completely revised list of characters or even to perform a completely new phylogenetic analysis, but some important issues concerning the original data presented by GRIMALDI & ENGEL (2006) are discussed in the following, before re-analyzing the slightly revised data matrix.

Most importantly, although they noted that "The lice were employed as outgroup ..." and "... no attempt was made to code other nanopsocete families ..." (p. 630), they listed four synapomorphies uniting Phthiraptera and Liposcelididae (GRIMALDI & ENGEL 2006: p. 631, fig. 4). Without using more distant outgroups, synapomorphies for Liposcelididae and Phthiraptera can never be identified. Therefore, this single evidence clearly shows that they actually employed other psocodean taxa as outgroup without specification. This is also evident from their character matrix because the character states coded for the outgroup do not occur in lice (e.g., Character 1-0: body uncompressed).

Even if we accept that the above-mentioned statement on outgroup selection is simple misprint, and GRIMALDI & ENGEL (2006) actually selected outgroup taxa from other, closely related psocodean families (i.e., nanopsocetae families), the character codings for the outgroup contain some problems as follows: **(1)** Character 9: the character state ocelli well separated on raised surface was adopted for the outgroup. However, in Trogiomorpha and Troctomorpha, ocelli are usually closely positioned on a flat surface (YOSHIZAWA 2005) so that this character state (9-2) should be applied to the outgroup. **(2)** Character 19: presence of Pearman's organ was adopted for the outgroup. However, no Pearman's organ can be observed in Pachytroctidae and Sphaeropsocidae (original observation by CL) so that the absence of the organ (19-1) should be the character coding for the outgroup. **(3)** Character 25: separation of female 9th and 10th abdominal tergites was adopted for the outgroup. However, fusion of 9th and 10th abdominal tergites is widely observed in the other psocodeans (YOSHIZAWA 2002, 2005; CL, original observation) so that the fused condition (25-1) should be adopted for the outgroup.

Four evident errors of character coding concern also the following important characters for ingroup taxa: **(1)** Character 10: Presence of ocelli in apterous forms was coded for *Embidopsocus*, *Embidopsocopsis* and *Chaetotroctes*, and the absence of ocelli in apterous forms supported a sistergroup relationship between Liposcelidinae and the clade composed of *Belapha*, *Belaphopsocus*, *Belaphotroctes* and *Troctulus* (= *BBBT* clade). However, ocelli are absent in the apterous forms of *Embidopsocus* and *Embidopsocopsis* (CL, original observation) and the apterous form is unknown for *Chaetotroctes* (BADONNEL 1973). Therefore, state 10-1 should be adopted for *Embidopsocus* and *Embidopsocopsis*, and the state of this character is unknown for *Chaetotroctes*. **(2)** Character 12: At least males are always apterous in all Nanopsocetae (MOCKFORD 1993). Within Liposcelididae winged forms are known in all Embidopsocinae genera, except *Troctulus* (see below). The coding of this character should be modified to "(0) wings present at least in some females" and "(1) both sexes obligately apterous". Character state 12-0 is present in all Nanopsocetae (including *Cretoscelis* and *Belaphopsocus dominicus*) but not in *Liposcelis* and *Troglotroctes*, which show character state 12-1 (original observation by CL). The character has to be coded as unknown (?) for *Troctulus*, because the only specimen known of this genus is an apterous female (BADONNEL 1955). **(3)** Character 16: Absence of Rs vein was adopted for all liposcelidids excluding *Cretoscelis* and thus it supported monophyly of Liposcelididae excluding *Cretoscelis*. However, presence of Rs vein is evident for *Belapha*, *Belaphopsocus*, *Belaphotroctes*, *Chaetotroctes*, *Embidopsocopsis* and *Embidopsocus* (original observation by CL), so that the absence of Rs cannot support the basal split of *Cretoscelis* from the rest of Liposcelididae. **(4)** Character 22: Absence of a metatibial spur (22-1) was adopted for all liposcelidids except *Cretoscelis*, *Embidopsocus*, *Embidopsocopsis* and *Chaetotroctes*. However, a metatibial spur is also present (22-0) in *Belaphotroctes* and *Belapha*, while it is absent (22-1) in *Belaphopsocus*, *Troctulus* and the Liposcelidinae (original observation by CL).

Therefore, we employed here two Nanopsocetae families, Pachytroctidae and Sphaeropsocidae, as new outgroup taxa and re-analyzed the data matrix presented in GRIMALDI & ENGEL (2006), after including the above mentioned changes (Tab. 1 and Appendix 1; also available online as an electronic supplement and at http://kazu.psocodea.org/data). The tree was rooted on Sphaeropsocidae according to the previous molecular systematic placement of this family within Nanopsocetae (JOHNSON et al. 2004). The maximum parsimony analysis with equal character weighting yielded six equally parsimonious trees (tree length = 30, consistency index = 0.80, retention index = 0.78). Application of successive weighting method (FARRIS 1969; CARPENTER 1988) reduced the number of equally parsimonious trees to two, and Fig. 2 shows their strict consensus tree, which corresponds to one of six parsimonious trees obtained from the equally weighted analysis. The tree is basically identical with that presented in GRIMALDI & ENGEL (2006), but none of the six trees supported a basal divergence between *Cretoscelis* and the rest of Liposcelididae. Although closely positioned ocelli on raised surface (character

	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345
Sphaeropsocidae	00000	000–1	00112	11010	00001
Pachytroctidae	11000	00021	00010	00110	00001
Cretoscelis	11010	0001?	?0111	01101	00001
Embidopsocus	11010	00021	00111	01111	00001
Embidopsocopsis	11010	00021	00111	01111	00001
Chaetotroctes	11010	0002?	00111	01111	00001
Troglotroctes	11010	00021	11–––	–––11	11001
Liposcelis	11010	00021	01–––	–––11	11001
***Belaphotroctes*1**	11011	00021	00111	01111	00001
***Belaphotroctes*2**	11011	00021	10111	01111	00011
Belapha	11012	10021	00111	01111	00011
Belaphopsocus	11112	11121	10111	01111	01111
Belaphopsocus dominicus	11111	0112?	?0111	01111	01111
Troctulus	11011	11121	1?111	?1111	01101

Tab. 1. Data matrix for phylogenetic analysis (revised from Grimaldi & Engel 2006); the first two lines read vertically indicate the character number.

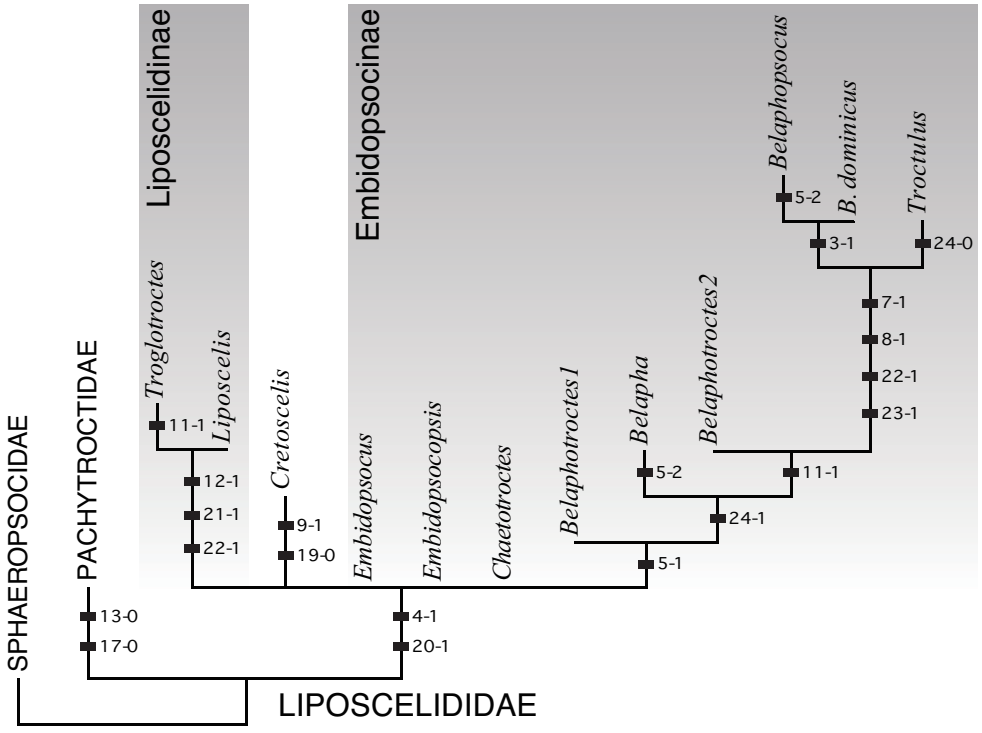

Fig. 2. Strict consensus of two equally parsimonious trees estimated by the successive weighting analysis of the data matrix as presented in Tab. 1. Numbers indicate 'character - character state' as presented in Appendix 1.

9-1) and presence of Pearman's organ (19-0) in *Cretoscelis* were originally regarded as plesiomorphies supporting the basal split of the genus from the rest of liposcelidids (Grimaldi & Engel 2006), these character states resulted here as autapomorphies of *Cretoscelis*. Especially, although Grimaldi & Engel (2006) homologized the structure on the internal surfaces of hind coxae of *Cretoscelis* with Pearman's organ, the condition of the organ in *Cretoscelis* is far different from that in the other psocodeans. Pearman's organ is a paired structure on the internal surfaces of both hind coxae. In all psocodeans having the organ, the left and right hind coxae are in touch so that the Pearman's organs on the two coxae are also always closely contacted with each other (Yoshizawa 2005). In contrast, the hind coxae of *Cretoscelis* are widely separated and there is no contact between the surfaces of left and right Pearman's organs (Grimaldi & Engel 2006). Little is known on the function of Pearman's organ, but the different conditions of the organs between *Cretoscelis* and the other psocodeans seem to provide further evidence for their different origins.

Our Liposcelididae tree (Fig. 2) shows an unresolved basal polytomy among *Cretoscelis*, *Embidopsocus*, *Embidopsocopsis*, *Chaetotroctes*, Liposcelidinae, and the *BBBT* clade. Accordingly, monophyly of Embidopsocinae remained unsupported, and a sister-group relationship between the Liposcelidinae and the *BBBT* clade as presented in GRIMALDI & ENGEL (2006) was not supported either. Monophyly of the *BBBT* clade is supported by the broadened terminal maxillary palpomere (5-1). Phylogenetic relationships among genera in the *BBBT* clade were relatively well resolved. *Belaphotroctes* was separated into two groups by presence/absence of the pretarsal protuberance or vesicle (Character 24). *Belaphopsocus* and *Troctulus* composed a clade well supported by antennal flagellomeres reduced to seven or eight (7-1), annuli of flagellomeres reduced or absent (8-1), absence of the metatibial spur (22-1), and dimerous tarsi (23-1). Character state 22-1 is also observed in Liposcelidinae but considered to be a homoplasy. *Belapha* and *Belaphopsocus* share an apomorphic rounded terminal maxillary palpomere (5-2), but presence of this character state in these genera was also optimised as homoplasious. Monophyly of Liposcelidinae was supported by both sexes obligately apterous (12-1), presence of metafemoral tubercle on anterior margin (21-1), and absence of the metatibial spur (22-1), however, no apomorphy unique to *Liposcelis* was found, whereby paraphyly of the genus relative to *Troglotroctes* cannot be excluded.

Molecular based phylogenies of Liposcelididae are very limited. Most previous molecular analyses only included species of the genus *Liposcelis* as exemplars of the family (YOSHIZAWA & JOHNSON 2003; JOHNSON et al. 2004; MURRELL & BARKER 2005). JOHNSON & MOCKFORD (2003) included two species of *Liposcelis* and one species of *Embidopsocus* as outgroup taxa for their phylogenetic analyses, and the clade *Liposcelis* + *Embidopsocus* was strongly supported (86–94% bootstrap support [BS]) by combined data of multiple genes (nuclear 18S and mitochondrial 12S, 16S and COI). Recent analyses by YOSHIZAWA & JOHNSON (2010) include four species of *Liposcelis* and one species of *Embidopsocus*, and monophyly of the family was very strongly supported (100% BS and Bayesian posterior probability [PP]) by combined nuclear 18S, Histone 3 and wingless, and mitochondrial 16S and COI gene sequences. Therefore, although taxon sampling was so limited, monophyly of the Liposcelididae is tentatively supported by DNA sequence data. Molecular data of the other liposcelidid genera are unavailable to date, mostly because of difficulties in amplifying and sequencing their genes, so that the phylogenetic relationships among genera of the family have not yet been analyzed with molecular data.

5. Phylogenetic position of Liposcelididae

The family Liposcelididae has long been assigned to the order Psocoptera. SEEGER (1979) provided the first potential evidence for the monophyly of Psocoptera including Liposcelididae (but excluding Phthiraptera) on the basis of morphology of egg membrane and embryology. According to LYAL (1985), this includes three gain (g) and three loss (l) characters: extremely thin egg chorion (g), absence of micropyles (l), absence of aeropyles (l), absence of chorionic sculpturing (l), unusual position in egg by embryo (g), and unusual manner of folding of embryonic appendages (g). Of them, the first four characters are probably mutually dependent, strongly related to the thinness of the egg chorion, and thus should not be counted separately (LYAL 1985). Another character suggested by SEEGER (1979) as an autapomorphy of Psocoptera is the very particular behavior of the egg-larva during hatching; this character was referred to again by LIENHARD (1998) but not by LYAL (1985). It is a gain character perhaps correlated with the particular position of the embryo in the egg (see SEEGER 1979: p. 47). Unfortunately the phylogenetic significance of the characters suggested by SEEGER (1979) as autapomorphies of Psocoptera has never been discussed in detail by subsequent authors. Most of these characters are difficult to observe, and none of them is mentioned in standard descriptions of Psocodea taxa. SEEGER (1979: fig. 5) explicitly mentions the presence of what he considers to be the corresponding plesiomorphic character states in Phthiraptera. In view of the possible validity of these characters as autapomorphies for Psocodea, the possibility of character reversals in Phthiraptera should be discussed.

In contrast, paraphyly of Psocoptera (with regard to Phthiraptera) has also long been assumed (HENNIG 1966). LYAL (1985) performed the first formal cladistic analysis of Psocoptera and Phthiraptera based on extensive morphological observations. As a result, a total of 12 apomorphies shared by Phthiraptera and part of Psocoptera were identified: **(1)** one character supporting Phthiraptera + Troctomorpha + Psocomorpha (absence of paraproct spine [l]); **(2)** seven characters supporting Phthiraptera + Troctomorpha (development of T-shaped sclerite in female subgenital plate [g: absent in some members], absence of Pearman's organ [l], absence of trichobothrial field [l], reduction of labial palpi [l], reduction of wings [l], loss of ocelli [l: not consistent within Liposcelididae], and fusion of mesonotum and metanotum [g]); and **(3)** four characters supporting Phthiraptera + Liposcelididae (dorsoventral compression of head [l], reduction of compound eyes [l], shortening of legs [l], and loss

of abdominal spiracles 1 and 2 [l]). In contrast, there are only 7 autapomorphies characterizing Psocoptera (Seeger 1979; Lyal 1985), and independence of some of them is questionable (see above). The parsimonious interpretation of this character distribution indicates paraphyly of Psocoptera and also a close relationship between Liposcelididae and Phthiraptera. However, as also mentioned by Lyal (1985), 10 of 12 apomorphies suggesting the paraphyly of Psocoptera are reduction characters, and the two gain characters involve some ambiguities in their interpretation of homology and character distribution. Grimaldi & Engel (2005) listed eight synapomorphies of Liposcelididae and Phthiraptera as follow: reduction in wings, flattened body, enlarged hind femora, fusion of meso- and metanotum, loss of abdominal spiracles 1 and 2, reduction or loss of labial palpi, prognathous head, and eyes reduced or lost. Again, all these character states are reductions and/or strongly associated with life in narrow spaces such as under bark, animal nests, and between bird plumage or mammal pelage. On the other hand, the "loss character" concerning abdominal spiracles indeed reflects a highly specific apomorphic heterogeneity within a serially arranged organ system (tracheal spiracles) and thus rather seems to be highly conclusive.

As discussed above, morphological evidence for the Liposcelididae + Phthiraptera is far from decisive. Nevertheless, Lyal's hypothesis is widely accepted (Kristensen 1991; Grimaldi & Engel 2005) because the relationship "seems to make very good sense from an evolutionary-ecological point of view" (Kristensen 1991: p. 136). There are many records of the species of Liposcelididae in the plumage of birds and pelage of mammals, as well as in their nests (Pearman 1960; Rapp 1961; Wlodarczyk 1963; Badonnel 1969; Mockford 1971; New 1972; Lienhard 1986; Baz 1990). This association is thought to be a short-term commensalism which may have given rise to a permanent association in lice (Hopkins 1949).

Recent molecular phylogenetic analyses have provided very strong support for paraphyly of Psocoptera, but, these in turn have generated new controversies concerning the monophyly of Phthiraptera. Yoshizawa & Johnson (2003) showed the first molecular evidence for the close relationship between Liposcelididae and Phthiraptera using mitochondrial 12S and 16S rDNA sequences. In the analyses, Liposcelididae and Phthiraptera always compose a monophyletic group which is supported by high statistical values (86–97% BS). In contrast, monophyly of Phthiraptera was not supported by the analyses, and Liposcelididae tended to compose a clade with the chewing louse genus *Trinoton* (suborder Amblycera). However, resolution of the deep relationships within the Lipocelididae + Phthiraptera lineage is only poorly resolved by mitochondrial data. Placements of Pachytroctidae and the Liposcelididae + Phthiraptera clade were also unstable. Monophyly of Nanopsocetae + Phthiraptera (i.e., sistergroup relationship between Pachytroctidae and Liposcelididae + Phthiraptera) was only supported by the neighbor joining analysis, and monophyly of Troctomorpha + Phthiraptera was never supported from the mitochondrial data set.

Johnson et al. (2004) provided a further molecular-based test for the problem using more slowly evolving nuclear 18S gene sequences. The result from the analyses was surprising: lice were divided into two groups, and the louse suborder Amblycera was placed as the sister taxon of Liposcelididae, suggesting polyphyly of Phthiraptera. This clade received very high statistical support (82% BS and 100% PP), suggesting that the 18S data contain consistent signal supporting the relationship. The paraphyletic Pachytroctidae was sister to Amblycera + Liposcelididae, but support for this relationship was low (52% BS and 62% PP). Monophyly of another louse lineage composed of three suborders, Ischnocera + Rhynchophthirina + Anoplura, was also strongly supported (82% BS and 100% PP). The family Sphaeropsocidae is placed at the most basal split of the Nanopsocetae + Phthiraptera clade, but this placement of the family (61% BS and 70% PP) and also the monophyly of Nanopsocetae + Phthiraptera (58% BS and 76% PP) were not strongly supported. Monophyly of Troctomorpha + Phthiraptera was supported but with very weak statistical support (less than 50% BS and PP). Murrell & Barker (2005) also recovered Liposcelididae + Amblycera (with 76–89% BS and 100% PP) using the same gene marker, but an unidentified exemplar of Sphaeropsocidae was placed to the suborder Trogiomorpha in their analyses. Many morphological pieces of evidence (e.g., presence of T-shaped internal sclerite in the female subgenital plate; hypopharyngeal filaments proximally fused) and molecular data (Johnson et al. 2004) contradict this placement of Sphaeropsocidae. The sample used in Murrell & Barker (2005) was likely to be misidentified (S. Cameron, pers. comm.).

Both mitochondrial and nuclear ribosomal genes of Pachytroctidae, Liposcelididae, and Phthiraptera exhibited several unusual evolutionary trends, including increased substitution rate, modifications of secondary structure, and nucleotide composition biases (Page et al. 1998, 2002; Yoshizawa & Johnson 2003; Johnson et al. 2004). All these properties make phylogenetic estimation unstable so that monophyly of Liposcelididae + Phthiraptera and polyphyly of Phthiraptera might be artifacts (i.e., long branch attraction: Felsenstein 1978). Especially, modifications of secondary structure make sequence alignments extremely difficult, resulting in reduction of confidently alignable data and/or increased risk of mis-alignments (Page et al.

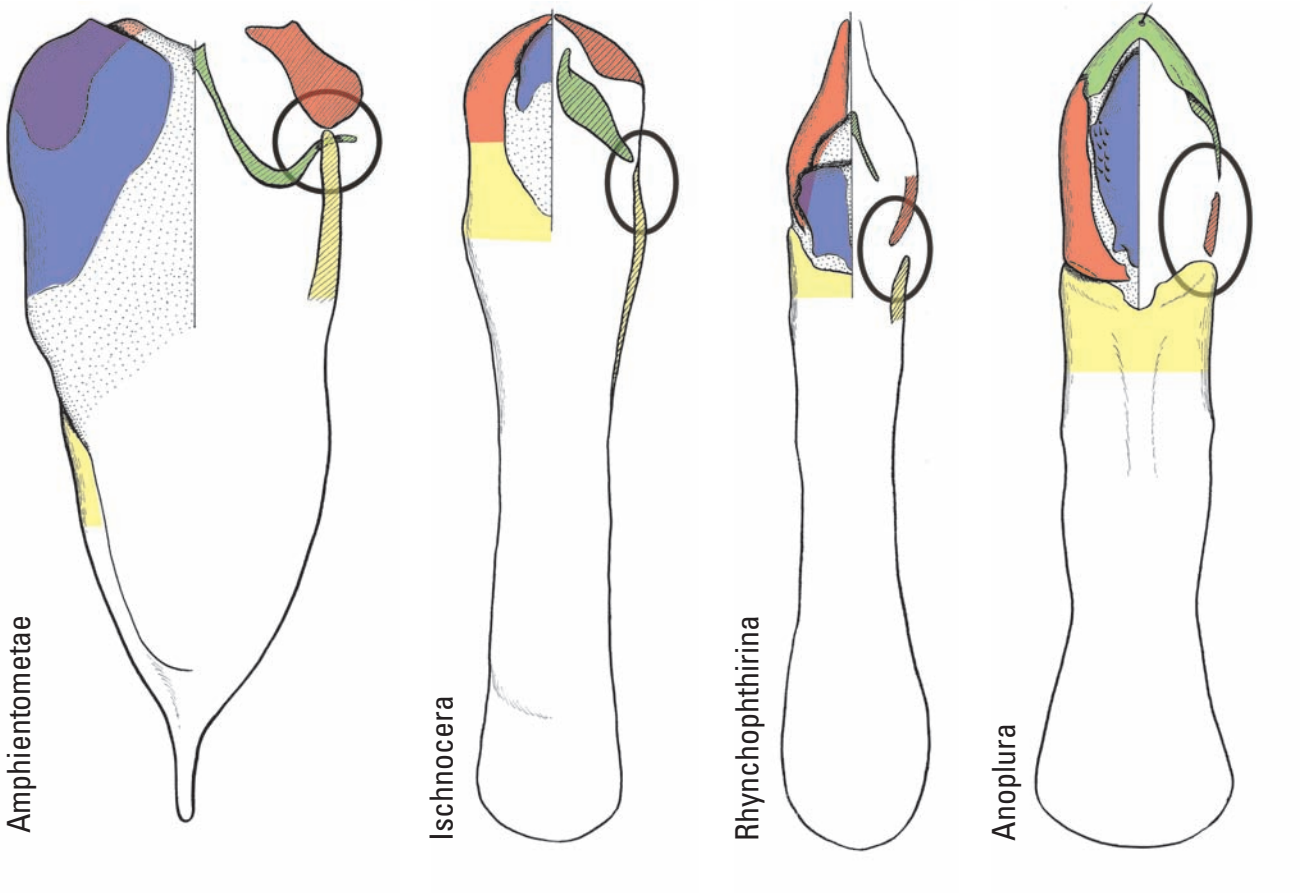

Fig. 3. Phallic organ of lice and relatives in ventral view. Indicated on phallic organ, four sets of sclerites are recognized: phallobase (yellow), parameres (red), ventral plates of mesomere (blue) and dorsal plate of mesomere (green). Ventral structures were omitted from the right half of each figure. In Pachytroctidae, Liposcelididae and Amblycera, blue sclerite articulates with yellow, red, and green sclerites at the point circled. This character state is not observed in other groups (highlighted with circles).

2002; Yoshizawa & Johnson 2003). Grimaldi & Engel (2006) raised some criticism to the polyphyly of Phthiraptera hypothesis as follow: (1) this hypothesis required the loss and the re-development of free-living habits and associated traits (wings, fully developed eyes, ocelli etc.); (2) this hypothesis also requires two origins of features, including ectoparasitism, fusion of the head to the thorax, distinctive egg structure, and loss of the fourth nymphal instar; (3) there is a morphocline in lice in the reduction of mouthparts from Liposcelididae through Amblycera to Anoplura; (4) one gene would not be sufficient for deciphering relationships in this group. Of them, points 1 and 2 are not independent questions but are different aspects of a single question. Johnson et al. (2004) mentioned only the possibility of independent origins of parasitism in lice, which is the most parsimonious interpretation, and did not consider the possibility of re-development of free-living habits and related characters. Apart from this point, the criticism raised by Grimaldi & Engel (2006) must be carefully considered and should be tested in future studies. Especially, inclusion of more molecular data is highly desired to test the polyphyly-of-lice hypothesis. A couple of ongoing projects which include both mitochondrial and nuclear ribosomal and protein-coding genes also supported the polyphyly-of-lice hypothesis (Kjer et al. 2006; Yoshizawa & Johnson 2010). However, support for this hypothesis from the genes other than 18S is still unclear (Yoshizawa & Johnson 2010). Grimaldi & Engel (2006: p. 632) also stated that the critical taxon Sphaeropsocidae was not analyzed by Johnson et al. (2004), but this criticism is simply not justified because a representative of the family (*Badonnelia titei*) was analyzed in Johnson et al. (2004).

Although Phthiraptera have long been considered to be a strongly supported monophyletic group (Hennig 1966; Kristensen 1991; Jamieson et al. 1999; Grimaldi & Engel 2006), support for the louse monophyly comes only from morphological and behavioral characters which are considered to be reductions or specializations associated with parasitic lifestyle. Phylogenetic utility of such character states is highly questionable (Lyal 1985; Smith et al. 2004). Morphology-based suspicion of non-monophyly of Phthiraptera was first raised from a spermatological study. Jamieson (1987) presented the results of his spermatological analysis and mentioned that there is no synapomorphy uniting Mallophaga and Anoplura. However, in the subsequent publication, Jamieson et al. (1999) just assumed the monophyly of Phthiraptera without any spermatological evidence and noted that "there seems no reason to doubt that the Mallophaga and Anoplura comprise a monophyletic group".

To provide further morphology-based test for the polyphyly-of-lice hypothesis, Yoshizawa & Johnson (2006) examined the characters of male genitalia. Male genitalia are usually situated within the external body wall and they are not exposed to the outside. Therefore, these structures should be less affected by the selective pressure related to the parasitic lifestyle. As a result of the phylogenetic analysis based on the male genitalic characters, a close relationship among Pachytroctidae, Liposcelididae and Amblycera was supported by a single synapomorphy: direct articulation between basal plate (yellow) and ventral plate (blue) and between ventral plate and mesomere (green) (Fig. 3: highlighted with circles). In Ischnocera, Rhynchophthirina and Anoplura, the basal plate is directly articulated with the mesomere (green) and paramere (red), and the ventral plate is not directly related to the basal plate nor mesomere (Fig. 3: highlighted with circles), showing the plesiomorphic condition as observed in Sphaeropsocidae and Amphientometae, another infraorder of Troctomorpha (Fig. 3). However, the apomorphic condition as observed in Pachytroctidae, Liposcelididae, and Amblycera was also observed in a few of the sampled Ischnocera. In addition, no character supporting the sister relationship between Liposcelididae and Amblycera was identified in male genitalia (Yoshizawa & Johnson 2006). Therefore, this character system also failed to provide unambiguous support for the polyphyly-of-lice hypothesis, although this hypothesis was considered to be the best from the male genitalic structure. It should also be noted that no apomorphy supporting the monophyly of Phthiraptera was identified in this character system.

In summary, a close relationship between Liposcelididae and Phthiraptera is now well established based on both morphological and molecular data sets and is now generally accepted (Grimaldi & Engel 2005). Alternatively, although monophyly of Phthiraptera is strongly suggested from characters which are strongly related to the parasitic lifestyle, character systems which are considered to be less affected from the parasitic lifestyle (male genitalia, spermatological characters, and DNA) never support their monophyly. Although 18S sequence data strongly suggest a sister-group relationship between Liposcelididae + Amblycera, support for this relationship from other molecular and morphological data is not convincing. Therefore, phylogenetic relationships between booklice and louse suborders should be regarded as unresolved to date. In addition, systematic positions of two other Nanopsocetae families, Sphaeropsocidae and Pachytroctidae, are very unstable even by 18S alone or combined multiple gene data.

6. Perspective

Establishment of a reliable higher level classification of Nanopsocetae + Phthiraptera, especially the exact placement of Liposcelididae, is the key issue in uncovering the origins and evolution of parasitism in lice. However, as discussed in this review and YOSHIZAWA & JOHNSON (2010), the problem seems not settled yet.

Recent systematic studies depend more and more on DNA sequence data. However, difficulties in using molecular data for the higher systematics of Nanopsocetae + Phthiraptera have also been revealed. For example, amplifying and sequencing DNA of pachytroctids, liposcelidids and true lice are generally difficult, possibly due to the accelerated substitution rate and unusual evolutionary trends observed in their genome. Such unusual molecular evolutionary trends also provide higher risk for artifact-based errors in alignments and phylogenetic estimations. Therefore, discovery of gene markers that do not exhibit unusual evolutionary trends will be a key in establishing a stable higher systematics of Nanopsocetae + Phthiraptera.

JOHNSON et al. (2003) showed that a nuclear protein-coding gene, Elongation Factor 1α, does not exhibit dramatically accelerated substitution pattern as observed in the mitochondrial COI. Difficulties in alignment as detected for the ribosomal genes are not relevant for the protein-coding genes. Therefore, the nuclear protein-coding regions are expected to be good gene markers in establishing a reliable higher level phylogeny of Nanopsocetae + Phthiraptera. Now the entire genome of the human louse has been sequenced (PITTENDRIGH et al. 2006) and also new techniques such as EST (Expressed Sequence Tags) are available to find useful gene markers effectively. Use of retroposon markers for phylogenetic estimation becomes more easy-to-use according to the accumulations of genome information from many insects (KRAUSS et al. 2008), and the markers are known to be less homoplasious and very reliable in estimating deep phylogenetic pattern (RAY et al. 2006). Dramatical gene rearrangements in the mitochondrial genome as identified in some phthirapterans (SHAO et al. 2001; COVACIN et al. 2006; CAMERON et al. 2007) may also provide additional insights for the phylogenetic affinity of lice and their relatives, if such rearrangements are also detected in Liposcelididae and other groups of Nanopsocetae. Therefore, importance of molecular-based approaches for the higher systematics of Nanopsocetae + Phthiraptera will continue to increase. Although extreme simplification and convergence of morphological characters seem frequent in Phthiraptera and Nanopsocetae, additional morphological analyses such as internal morphology and embryology are also potentially promising approaches towards establishing a reliable phylogeny.

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9. Appendix 1

Characters used for phylogenetic analysis (modified from GRIMALDI & ENGEL 2006)

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 absent.
5. Maxillary palpomere P4: (0) slender, like preceding palpomeres; (1) broad, width ≥ 1.5x that of P3; (2) extremely broad, width almost equal to its length.
6. Short, stout sensilla on maxillary palpomere P4: (0) absent; (1) present.
7. Antenna: (0) nine or more flagellomeres; (1) seven or eight flagellomeres.
8. Flagellomeres: (0) fine annuli present; (1) annuli indistinct or absent.
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 in apterous forms: (0) present; (1) absent.
11. Compound eyes in apterous forms: (0) with numerous ommatidia; (1) with two ommatidia.
12. Wings: (0) present at least in some females; (1) 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 in forewing and hindwing; (1) forewing with R, M only, hindwing with R only; (2) forewing with several longitudinal veins, hindwing absent.
16. Forewing Rs: (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.

10. Appendix 2

Checklist of valid names of the presently recognized Liposcelididae taxa, with information on geographical distribution of the species (country of type locality mentioned first), based on LIENHARD & SMITHERS (2002) and LIENHARD (2003a,b, 2004a, 2005, 2006, 2007, 2008, 2009, 2010).

LIPOSCELIDIDAE

Belapha Enderlein, 1917.

Belapha globifer (Laing, 1925). Guyana.
Belapha schoutedeni Enderlein, 1917. Congo, Angola.

Belaphopsocus Badonnel, 1955.

Belaphopsocus badonneli New, 1971. Brazil, Colombia, Paraguay, Mexico.
Belaphopsocus dominicus Grimaldi & Engel, 2006. Dominican Republic (Miocene amber).
Belaphopsocus murphyi Lienhard, 1991. Singapore.
Belaphopsocus vilhenai Badonnel, 1955. Angola, Congo.

Belaphotroctes Roesler, 1943.

Belaphotroctes alleni Mockford, 1978. USA, Mexico.
Belaphotroctes angolensis Badonnel, 1955. Angola.
Belaphotroctes antennalis Badonnel, 1973. Angola.
Belaphotroctes atlanticus Lienhard, 1996. Madeira Island.
Belaphotroctes badonneli Mockford, 1963. USA, Mexico.
Belaphotroctes brunneus Badonnel, 1970. Brazil.
Belaphotroctes fallax Badonnel, 1973. Angola.
Belaphotroctes ghesquierei Badonnel, 1949. Congo, Angola, Ivory Coast, Madagascar, USA, Mexico, Cuba, Brazil, Colombia, Canary Islands, UAE.
Belaphotroctes hermosus Mockford, 1963. USA, Mexico.
Belaphotroctes major Badonnel, 1973. Brazil.
Belaphotroctes mimulus Badonnel, 1973. Brazil.
Belaphotroctes ocularis Badonnel, 1970. Brazil.
Belaphotroctes remyi Badonnel, 1967. Madagascar.
Belaphotroctes simberloffi Mockford, 1972. USA.
Belaphotroctes similis Mockford, 1969. Mexico (Late Oligocene – Early Miocene amber).
Belaphotroctes simulans Badonnel, 1974. Congo.
Belaphotroctes striatus Badonnel, 1970. Brazil.
Belaphotroctes traegardhi (Ribaga, 1911). South Africa.
Belaphotroctes vaginatus Badonnel, 1973. Brazil.

Chaetotroctes Badonnel, 1973.

Chaetotroctes lenkoi Badonnel, 1973. Brazil.

Cretoscelis Grimaldi & Engel, 2006.

Cretoscelis burmitica Grimaldi & Engel, 2006. Myanmar (Cretaceous amber).

Embidopsocopsis Badonnel, 1973.

Embidopsocopsis newi Badonnel, 1973. Brazil.

Embidopsocus Hagen, 1866.

Embidopsocus angolensis Badonnel, 1955. Angola, Ivory Coast.
Embidopsocus antennalis Badonnel, 1949. Congo.
Embidopsocus bousemani Mockford, 1987. USA.
Embidopsocus brasiliensis Badonnel, 1973. Brazil.
Embidopsocus citrensis Mockford, 1963. USA, Mexico.
Embidopsocus congolensis Badonnel, 1948. Congo, Angola, Ivory Coast.
Embidopsocus cubanus Mockford, 1987. Cuba, Mexico.
Embidopsocus distinctus Badonnel, 1955. Angola.
Embidopsocus echinus Badonnel, 1955. Angola.
Embidopsocus enderleini (Ribaga, 1905). Italy, Belgium, France, Netherlands, Great Britain, Madeira Island, Argentina, South Africa.
Embidopsocus eocenicus Nel, De Ploëg & Azar, 2004. France (Lowermost Eocene amber).
Embidopsocus femoralis (Badonnel, 1931). Mozambique, Angola, Mexico, USA.
Embidopsocus flexuosus Badonnel, 1962. Argentina, Brazil.
Embidopsocus frater Badonnel, 1973. Brazil.
Embidopsocus granulosus Badonnel, 1949. Congo.
Embidopsocus hainanicus Li Fasheng, 2002. China.
Embidopsocus intermedius Badonnel, 1969. Angola.
Embidopsocus jikuni Li Fasheng, 2002. China.
Embidopsocus kumaonensis Badonnel, 1981. India.
Embidopsocus laticeps Mockford, 1963. USA, Jamaica, Mexico.
Embidopsocus lenah Schmidt & New, 2008. Tasmania.
Embidopsocus leucomelas (Enderlein, 1910). Paraguay, Brazil.
Embidopsocus luteus Hagen, 1866. Cuba, Mexico, Brazil.
Embidopsocus machadoi Badonnel, 1955. Angola.
Embidopsocus mendax Badonnel, 1973. Argentina, Brazil.
Embidopsocus mexicanus Mockford, 1987. Mexico, USA.
Embidopsocus minor (Pearman, 1931). Great Britain (imported from Ghana), Congo, Ivory Coast.
Embidopsocus needhami (Enderlein, 1903). USA, Canada.
Embidopsocus oleaginus (Hagen, 1865). Sri Lanka, Congo.
Embidopsocus pallidus Badonnel, 1955. Angola.
Embidopsocus paradoxus (Enderlein, 1905). Cameroon.
Embidopsocus pauliani Badonnel, 1955. Angola, Ivory Coast, Galapagos Islands.
Embidopsocus pilosus Badonnel, 1973. Brazil.
Embidopsocus porphyreus Li Fasheng, 2002. China.
Embidopsocus sacchari Mockford, 1996. Venezuela.
Embidopsocus saxonicus Günther, 1989. Germany (Upper Eocene or Miocene amber).
Embidopsocus similis Badonnel, 1973. Brazil.
Embidopsocus thorntoni Badonnel, 1971. Galapagos Islands, USA (imported from Ecuador).
Embidopsocus trichurensis Menon, 1942. India, Philippines.
Embidopsocus trifasciatus Badonnel, 1973. Angola.
Embidopsocus vilhenai Badonnel, 1955. Angola.

Embidopsocus virgatus (Enderlein, 1905). Paraguay, Argentina, Brazil.
Embidopsocus zhouyaoi Li Fasheng, 2002. China.

Liposcelis Motschulsky, 1852.

Liposcelis spec. Apterous specimen described by NEL et al. (2005) and erroneously assigned to *Embidopsocus eocenicus* Nel et al., 2004. France (Lower Eocene amber).
Liposcelis abdominalis Badonnel, 1962. Argentina.
Liposcelis aconae Badonnel, 1974. Spain.
Liposcelis albothoracica Broadhead, 1955. Great Britain, Cape Verde Islands, Senegal, Mexico. Often in stored grains.
Liposcelis alticolis Badonnel, 1986. Colombia.
Liposcelis ambigua Badonnel, 1972. Chile.
Liposcelis angolensis Badonnel, 1955. Angola, Kenya.
Liposcelis annulata Badonnel, 1955. Angola, Kenya.
Liposcelis anomala Badonnel, 1955. Angola.
Liposcelis antennatoides Li Zhihong & Li Fasheng, 1995. China.
Liposcelis arenicola Günther, 1974. Germany, former Czechoslovakia, Greece, former USSR.
Liposcelis atavus Enderlein, 1911. Baltic amber (Late Eocene).
Liposcelis australis Smithers, 1996. Australia.
Liposcelis ayosae Lienhard, 1996. Canary Islands.
Liposcelis badia Wang Zi-Ying, Wang Jin-Jun & Lienhard, 2006. China.
Liposcelis barrai Badonnel, 1969. Gabon.
Liposcelis bengalensis Badonnel, 1981. India.
Liposcelis bicolor (Banks, 1900). USA, Austria, France, Germany, Great Britain, Spain, Switzerland.
Liposcelis bicoloripes Badonnel, 1955. Angola.
Liposcelis bogotana Badonnel, 1986. Colombia.
Liposcelis borbonensis Badonnel, 1977. Reunion.
Liposcelis bostrychophila Badonnel, 1931. Mozambique etc. – Cosmopolitan, very common in stored products.
Liposcelis bouilloni Badonnel, 1974. Congo, China.
Liposcelis broadheadi Badonnel, 1969. Mozambique.
Liposcelis brunnea Motschulsky, 1852. Former USSR etc. – Nearly cosmopolitan, often domestic.
Liposcelis canariensis Lienhard, 1996. Canary Islands.
Liposcelis capitisecta Wang Zi-Ying, Wang Jin-Jun & Lienhard, 2006. China.
Liposcelis castrii Badonnel, 1963. Chile.
Liposcelis chilensis Badonnel, 1963. Chile.
Liposcelis cibaritica Li Zhihong & Li Fasheng, 2002. China.
Liposcelis compacta Lienhard, 1990. Greece, France, Malta, Spain, Algeria.
Liposcelis corrodens (Heymons, 1909). Germany etc. – Nearly cosmopolitan, often domestic.
Liposcelis decolor (Pearman, 1925). Great Britain etc. – Nearly cosmopolitan, often domestic.
Liposcelis delamarei Badonnel, 1962. Argentina.
Liposcelis deltachi Sommerman, 1957. USA, Hawaii Islands, Mexico.
Liposcelis dentata Badonnel, 1986. Colombia.
Liposcelis desertica Badonnel, 1955. Angola.
Liposcelis dichromis Badonnel, 1967. Chile.
Liposcelis discalis Badonnel, 1962. Argentina.
Liposcelis distincta Badonnel, 1955. Angola, Ivory Coast.
Liposcelis divinatoria (Müller, 1776). Nomen dubium (see comment in LIENHARD & SMITHERS 2002: p. 84).
Liposcelis edaphica Lienhard, 1990. Greece, China.
Liposcelis elegantis Li Fasheng & Li Zhihong, 1995. China.
Liposcelis entomophila (Enderlein, 1907). Colombia etc. – Cosmopolitan, very often domestic.
Liposcelis exigua Badonnel, 1931. Mozambique, Angola, Congo.
Liposcelis fallax Badonnel, 1986. Colombia.
Liposcelis fasciata (Enderlein, 1908). Taiwan, China.
Liposcelis flavida Badonnel, 1969. Gabon.
Liposcelis formicaria (Hagen, 1865). Former USSR, Germany, Poland, Romania, Mongolia, USA.
Liposcelis fusciceps Badonnel, 1968. Brazil, Mexico, USA.
Liposcelis globiceps Badonnel, 1967. Chile.
Liposcelis guentheri Badonnel, 1982. Mongolia.
Liposcelis hirsuta Badonnel, 1948. Congo, Burkina Faso, Togo.
Liposcelis hirsutoides Mockford, 1978. USA, Mexico, Venezuela.
Liposcelis jilinica Li Zhihong & Li Fasheng, 2002. China.
Liposcelis keleri Günther, 1974. Germany, Austria, Cyprus, France, Greece, Hungary, Italy, Morocco, Spain, Sweden, Switzerland, former Yugoslavia, Iran.
Liposcelis kidderi (Hagen, 1883). Kerguelen Islands.
Liposcelis kipukae Mockford & Krushelnycky, 2008. Hawaii Islands.
Liposcelis kyrosensis Badonnel, 1971. Cyprus, Greece, Italy.
Liposcelis lacinia Sommerman, 1957. USA.
Liposcelis laoshanensis Li Zhihong & Li Fasheng, 2002. China.
Liposcelis laparvensis Badonnel, 1967. Chile.
Liposcelis lenkoi Badonnel, 1968. Brazil.
Liposcelis liparoides Badonnel, 1962. Argentina, Chile.
Liposcelis lunai Badonnel, 1969. Angola.
Liposcleis machadoi Badonnel, 1969. Angola.
Liposcelis maculata Lienhard, 1996. Morocco.
Liposcelis maracayensis Mockford, 1996. Venezuela.
Liposcelis marginepunctata Badonnel, 1969. Angola, Equatorial Guinea.
Liposcelis maunakea Mockford & Krushelnycky, 2008. Hawaii Islands.
Liposcelis mendax Pearman, 1946. Great Britain etc. – Nearly cosmopolitan, usually domestic.
Liposcelis meridionalis (Rosen, 1911). France, Italy, Greece, Romania, Great Britain, Scilly Islands, Madeira Island, Spain, former USSR, Armenia, Morocco.
Liposcelis mimula Badonnel, 1986. Colombia.
Liposcelis minuta Badonnel, 1974. Congo, Cape Verde Islands.
Liposcelis mira Badonnel, 1986. Mexico.
Liposcelis montamargensis Badonnel, 1967. Chile.
Liposcelis myrmecophila Broadhead, 1950. Great Britain, Belgium, France, Portugal, Spain.
Liposcelis nasus Sommerman, 1957. USA, Mexico.
Liposcelis naturalis Li Zhihong & Li Fasheng, 2002. China.
Liposcelis nigra (Banks, 1900). USA, Canada.
Liposcelis nigritibia Li Fasheng & Li Zhihong, 1995. China.
Liposcelis nigrocincta Badonnel, 1962. Argentina.
Liposcelis nigrofasciata Badonnel, 1963. Chile.

Liposcelis nuptialis Badonnel, 1972. Chile.
Liposcelis obscura Broadhead, 1954. Great Britain, Egypt, UAE, Yemen.
Liposcelis orghidani Badonnel, 1973. Romania, Greece, Italy, former Yugoslavia.
Liposcelis ornata Mockford, 1978. USA, Mexico, Colombia.
Liposcelis pacifica Badonnel, 1986. Mexico.
Liposcelis paeta Pearman, 1942. India and Great Britain etc. – Nearly cosmopolitan, usually domestic.
Liposcelis paetula Broadhead, 1950. Great Britain, Italy, Canary Islands, Madeira Island, Cape Verde Islands. – Sometimes domestic.
Liposcelis palatina Roesler, 1954. Germany, France, Hungary, Luxembourg, Switzerland, former Yugoslavia.
Liposcelis pallens Badonnel, 1968. USA, China.
Liposcelis pallida Mockford, 1978. USA, Mexico.
Liposcelis parvula Badonnel, 1963. Chile.
Liposcelis pauliani Badonnel, 1967. Madagascar.
Liposcelis pearmani Lienhard, 1990. Great Britain, Austria, former Czechoslovakia, Finland, France, Germany, Hungary, Israel, Italy, Luxembourg, Netherlands, Switzerland, former Yugoslavia, Japan, China, USA. – Widespread, often domestic.
Liposcelis perforata Badonnel, 1955. Angola.
Liposcelis picta Ball, 1940. Cyprus, Lebanon, Israel, Greece, Morocco.
Liposcelis plesiopuber Broadhead & Richards, 1982. Kenya.
Liposcelis prenolepidis (Enderlein, 1909). USA, South Africa.
Liposcelis priesneri Enderlein, 1925. Albania, Cyprus, Greece, Italy, former Yugoslavia.
Liposcelis puber Badonnel, 1955. Angola, Kenya, Senegal.
Liposcelis pubescens Broadhead, 1947. Great Britain etc. – Nearly cosmopolitan, often domestic.
Liposcelis pulchra Lienhard, 1980. Spain.
Liposcelis purpurea (Aaron, 1883). North America.
Liposcelis resinata (Hagen, 1865). Tanzania: Zanzibar (in Copal).
Liposcelis reticulata Badonnel, 1962. Argentina.
Liposcelis romeralensis Badonnel, 1967. Chile.
Liposcelis rufa Broadhead, 1950. Great Britain, Cyprus, France, Greece, Israel, Italy, Morocco, Poland, Portugal, Spain, Switzerland, former Yugoslavia, Canary Islands, USA, Hawaii Islands, Chile, Angola, China, Australia. – Widespread, sometimes domestic.
Liposcelis rufiornata Li Zhihong & Li Fasheng, 1995. China.
Liposcelis rugosa Badonnel, 1945. Morocco, Cyprus, Greece, Portugal, Canary Islands.
Liposcelis sculptilimacula Li Zhihong & Li Fasheng, 1995. China.
Liposcelis semicaeca Lienhard, 1990. Greece, Spain, Portugal.
Liposcelis setosa Badonnel, 1963. Chile.
Liposcelis silvarum (Kolbe, 1888). Germany, Austria, Belgium, Bulgaria, former Czechoslovakia, Finland, France, Hungary, Italy, Luxembourg, Norway, Poland, Portugal, Romania, Spain, Sweden, Switzerland, former USSR, former Yugoslavia, Armenia, Mongolia, Morocco, Canary Islands, USA.
Liposcelis similis Badonnel, 1972. Chile.
Liposcelis sinica Li Zhihong & Li Fasheng, 1995. China.
Liposcelis tamminensis Smithers, 1996. Australia.
Liposcelis tetrops Badonnel, 1986. Senegal.
Liposcelis transvaalensis (Enderlein, 1909). South Africa, Congo (?), India (?).
Liposcelis tricolor Badonnel, 1973. Greece, France, Lebanon, Portugal, Turkey, former Yugoslavia, China. – Sometimes domestic.
Liposcelis triocellata Mockford, 1971. USA.
Liposcelis uxoris Lienhard, 1980. Spain.
Liposcelis villosa Mockford, 1971. USA, Colombia.
Liposcelis volcanorum Mockford & Krushelnycky, 2008. Hawaii Islands.
Liposcelis yangi Li Zhihong & Li Fasheng, 1998. China.
Liposcelis yunnaniensis Li Fasheng & Li Zhihong, 1995. China.

Troctulus Badonnel, 1955.

Troctulus machadoi Badonnel, 1955. Angola.

Troglotroctes Lienhard, 1996.

Troglotroctes ashmoleorum Lienhard, 1996. Ascension Island.

Electronic Supplement Files

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File 1: Yoshizawa&Lienhard-Liposcelididae-ASP2010-ElSuppl-File1.nex.