
The oldest Liposcelididae in the Lowermost Eocene amber of the Paris Basin (Insecta: Psocoptera)

A. NEL, G. DE PLOËG and D. AZAR

Muséum national d'Histoire naturelle, Laboratoire d'Entomologie and UMR 8569
45 rue Buffon, F-75005 Paris, France. Nel E-mail: anel@mnhn.fr Azar E-mail: azar@mnhn.fr

ABSTRACT

The oldest known liposcelidid, *Embidopsocus eocenicus* n. sp., is described from the Lowermost Eocene amber of the Paris Basin. It has close affinities with the Nearctic and Afrotropical species *E. femoralis* (BADONNEL 1931) and the fossil species *E. saxonicus* GÜNTHER 1989 from Saxonian amber. An annotated list of fossil Liposcelididae is given. *Miotroctes rousei* PIERCE 1960 is considered as a Psocoptera *incertae sedis* n. sit.

KEYWORDS | Psocoptera. Liposcelididae. *Embidopsocus eocenicus* n. sp. Eocene French amber. Commented list.

INTRODUCTION

The psocopteran family Liposcelididae is scarce in the fossil record. It is known by less than 6 species, ranging between the Upper Eocene and the Miocene (Spahr, 1992). Thus, the present discovery, a very well preserved specimen in the Lowermost Eocene amber of the Paris basin, is of great systematic interest. It demonstrates the great antiquity of this family.

SYSTEMATIC PALAEONTOLOGY

Order: Psocoptera SHIPLEY, 1904

Family: Liposcelididae ENDERLEIN, 1911

GENUS *Embidopsocus* HAGEN 1866

Type species: *Embidopsocus luteus* HAGEN 1866 (Recent species).

Embidopsocus eocenicus n. sp.

Figures 1 to 3

Material: Holotype specimen PA 4151 1/5 (female), mounted in Canada balsam, in collection De Ploëg and Indivision Langlois-Meurine, deposited in Muséum National d'Histoire Naturelle, Paris. Specimens collected in Le Quesnoy all bear the letter PA for Paris (meaning Paris Basin), followed by a number that is the ordinal number in the collection.

Occurrence: Le Quesnoy, Chevrière, region of Creil, Oise department, France.

Geological age: Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal. The amber is autochthonous and very different from the Baltic amber in age, chemical composition and origin (Feugueur, 1963; Nel et al., 1999).

Etymology: After the Eocene period.

Diagnosis: This species is very closely related to *Embidopsocus femoralis* (BADONNEL 1931) and *Embidopsocus saxonicus* GÜNTHER 1989. It is characterized as follows: fore wing vein R apically curved forward, instead of being straight (unique character); absence of annulations of first two flagellomeres; presence of four sensilla on mx4 instead of two; eyes smaller (antero-posterior diameter 60 µm instead of 90 µm in *E. femoralis*); preclu-

nial abdominal terga with bands of sclerotization well pronounced (Mockford, 1987); thorax and head apparently completely bare.

Description: The characters follow their order of importance in the discussion on the systematic position of the fossil. (1) antenna 15-segmented (13 flagellomeres); (2) flagellomeres from the third onward annulated with cuticular sculpture and a distal constriction bearing 2 setae, but the first and the second not so; (3) labial palp 2-segmented, with minute basal segment and rounded distal segment; (4) all tarsi 3-segmented; (5) fore wing lacking sclerotized pterostigma; (6) second maxillary palp segment without any small sensillum on inner side; (7) body small, 1.94 mm long; (8) wings without scales; (9) vein IIA absent; (10) tarsal claw with one apical tooth and no small denticulations before it; (11) coxae of opposite sides widely separated by sternal plates; (12) fore wing with only 2 long simple veins, R and M, occupying main body of the fore wing but not reaching wing margin; wing chaetotaxy not visible; (13) hind legs not extending beyond apex of body, hind femur 0.48 mm long, hind tibia 0.36 mm long, hind tarsus 0.12 mm long; (14) antennae relatively short, 0.88 mm long; (15) epicranial suture absent; (16) eye small compared to the head size (antero-posterior diameter, 60 µm, head 0.36 mm long and 0.4 mm wide); (17) about 25 to 30 ommatidia in eye; (18) ocelli close together (40 µm apart), but not grouped on a tubercle; (19) pronotum divided into 3 lobes, median lobe with median longitudinal line; (20) meso- and metanota well separated; (21) hind femur swollen; (22) wing rounded apically; (22) hind wing without any visible vein; (23) no pulvilli; (24) hind femur lacking lateral protuberance; (25) no T-shaped sclerite on subgenital plate; (26) maxillary palp four-segmented; (27) mx4 fusiform, not ovoid nor rounded and not wider than mx3; (28) a group of 4 short setae on apico-ventral surface of mx4; (29) no visible sculpture on head; (30) preclunial abdominal terga with a slender transverse band of heavy sclerotization; (31) middle coxae situated almost halfway between anterior and posterior margins of meso-metanotum; (32) coxal attachment lateral and partly visible from above; (33) a sclerotized intersegmental plate between pro- and mesothoracic sterna; (34) a single strong spur on distal end of hind tibia on inner side, but no long setae associated with another heavier seta; (35) outer side of hind tibia with very long setae, longer than first tarsal segment; (36) sclerotized bands of mesosternum absent, structure of mesosternum identical to that of alate of *E. femoralis* (Badonnel, 1955, fig. 181); (37) lateral part of sternellum without any short setae; (38) thorax and abdominal apex without visible setae; (39) no field of conical sensillae on each side of anterior margin of front; (40) fore femur with a small spine near middle of inner face; (41) no sensilla on two basal flagellomeres; (42) no visible setae on head; (43) abdominal tergites

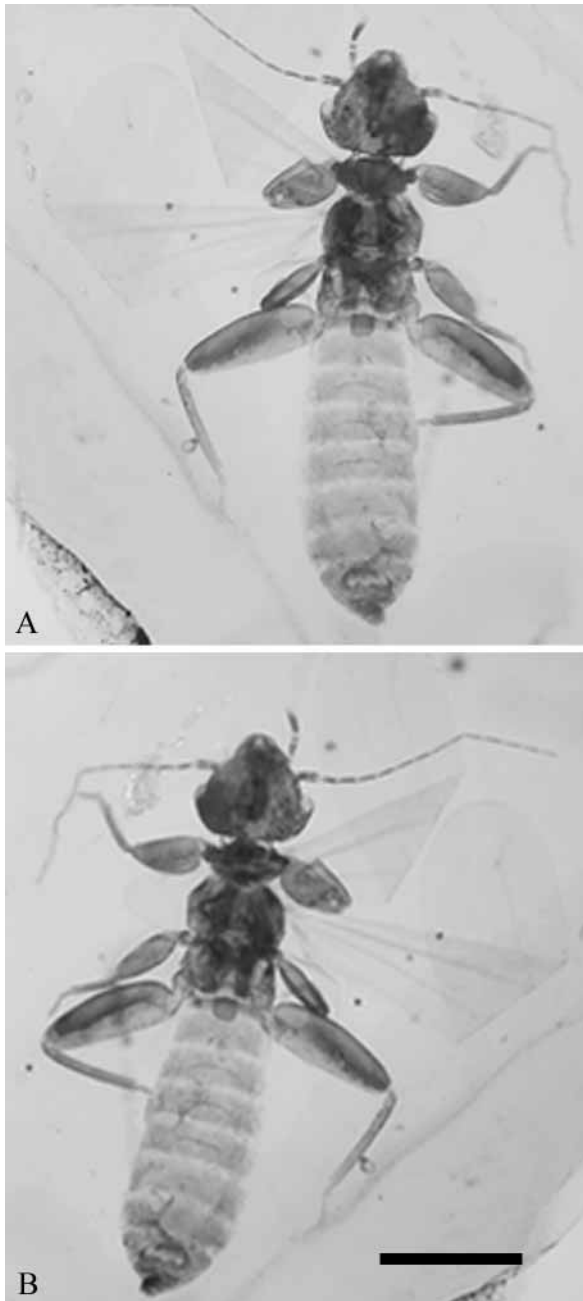


FIGURE 1 | *Embidopsocus eocenicus* n. sp., holotype specimen PA 4151 1/5. A) Photograph of dorsal view. B) Photograph of ventral view. Scale bar: 0,5 mm.

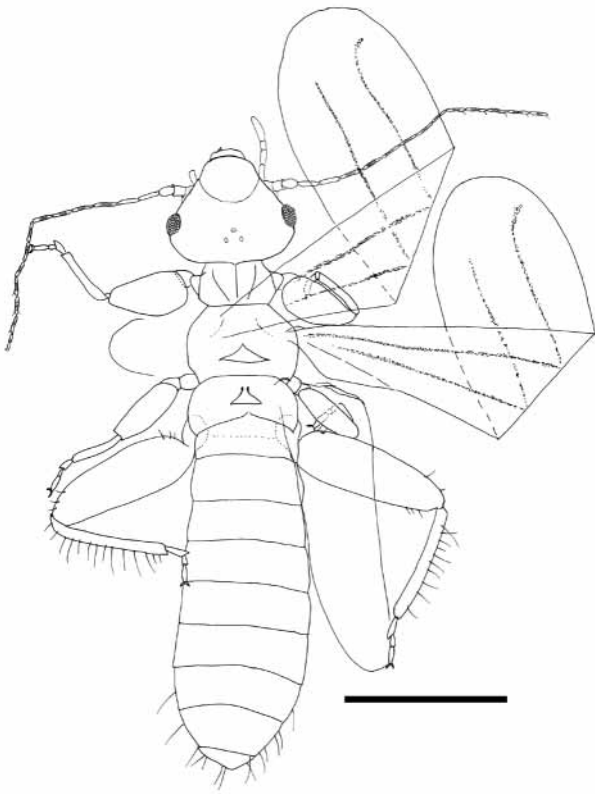


FIGURE 2 | *Embidopsocus eocenicus* n. sp., holotype specimen PA 4151 1/5, drawing of dorsal view. Scale bar: 0.5 mm.

apparently bare, except few setae on the margin of segment 8; (43) fore wing R well separated from costal margin and parallel with M in its apical half; (44) median lobe of pronotum narrow, similar to that of *E. femoralis* (Badonnel, 1955, fig. 167); (45) anterior lobe of mesotergum, meso- and meta-scutellum well developed; (46) no apical spur on median tibia; (47) wing 1.54 mm long; (48) a row of small spines on the inner apical margin of fore tibia; (49) hind femur 0.16 mm wide; (50) interocular distance 0.32 mm; (51) lacinia tip identical to that of *E. femoralis* (Mockford, 1987, fig. 27), i.e. with lateral and median cusps nearly equal in length, both relatively short, lateral shallowly bilobed, and a sizeable tooth between the 2 cusps. Body coloration useless because of 'false' colours due to fossilisation into amber

Discussion: This fossil falls into the Troctomorpha because of the characters (1) to (5), into the Nanopsocetae because of characters (6) to (10), and into the Liposcelididae Enderlein because of characters (11) to (23) (Badonnel, 1955, 1967, 1969, 1972; Smithers, 1972; Mockford, 1993). The genus *Liposcelis* MOTSCHULSKY 1852 (subfamily Liposcelinae) can be excluded because of characters (24) and (25). Among the Embidopsocinae, the genera *Belapha* ENDERLEIN 1917 and *Belaphopsocus* BADONNEL 1955 can be excluded because their mx4 is circular. Their

females are apterous. *Belaphopsocus* has tarsi 2-segmented. *Troctulus* BADONNEL 1955 has tarsi 2-segmented and antenna 10-segmented, posterior tibia without spine and mx4 ovoid (Badonnel, 1955; Smithers, 1972). The genus *Belaphotroctes* ROESLER 1943 can be excluded because of characters (2), (27), (29), (30). Also *E. eocenicus* n. sp. has stronger fore wing veins R and M (Smithers, 1972,

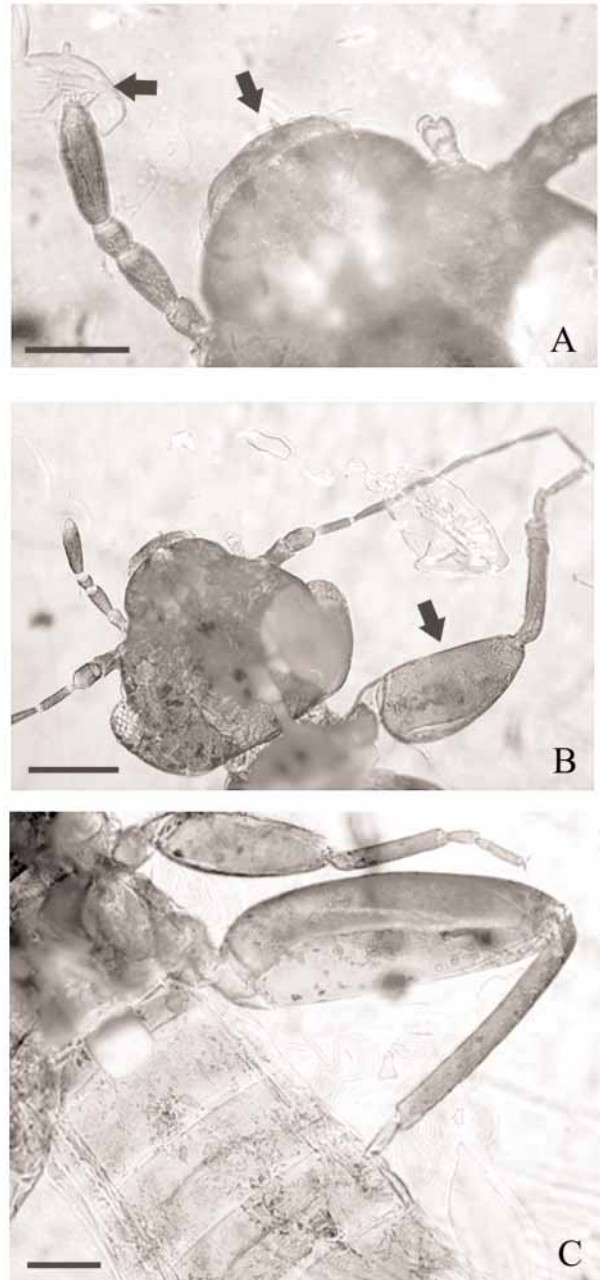


FIGURE 3 | *Embidopsocus eocenicus* n. sp., holotype specimen PA 4151 1/5. A) Photograph of ventral view of apex of head. Arrows showing the four sensilla on mx4 and the lacinia. Scale bar: 0.05 mm. B) Photograph of ventral view of head and fore leg. Arrow showing the small spine near middle of inner face of the fore femur. Scale bar: 0.1 mm. C) Photograph of ventral view of abdomen and hind leg, showing the bands of sclerotization of abdominal terga. Scale bar: 0.1 mm.

figs. 4.249-4.250). The genus *Embidopsocopsis* BADONNEL 1972 can be excluded because of character (37). The genus *Chaetotroctes* BADONNEL 1972 can be excluded on the basis of characters (34), (38) and (39). All the visible characters of this fossil are characteristic of the genus *Embidopsocus* HAGEN 1866 (Smithers, 1972; Badonnel, 1972; Mockford, 1993). Badonnel (1955, 1969, 1972), followed by Mockford (1993), divided this genus into 3 groups. The characters (10) and (36) exclude the groups I and II and make it fall into group III. After Badonnel (1955) and Mockford (1993), this group only includes *E. femoralis* (BADONNEL 1931). After Badonnel (1955), the very particular characters of *E. femoralis* would justify a generic separation from the two other groups of *Embidopsocus*. *E. eocenicus* n. sp. shares with *E. femoralis* the very reduced chaetotaxy on head, thorax and abdomen, characters (22), (41), (43), (44), (45), (46), and the presence of a row of spines on inner face of fore tibia (character 48) and of a spine on inner face of fore femur (but distinctly smaller) (Mockford, 1993, fig. 510). The differences with *E. femoralis* are as follows: wing vein R apically curved forward, instead of being straight (unique character); eyes smaller (antero-posterior diameter 60 µm instead of 90 µm in *E. femoralis*); preclunial abdominal tergite with bands of sclerotization well pronounced.

***Embidopsocus saxonicus* GÜNTHER 1989**

Material: Holotype specimen MB. I.704, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Occurrence: Saxonian amber, Bitterfeld, Halle, Germany.

Geological age: Upper Eocene or Miocene?

Remarks: Günther (1989) considered that this species is also closely related to *E. femoralis*. It differs from *E. eocenicus* n. sp. in its first two flagellomeres distinctly annulated, its fore wing vein R straight and its dimensions: body length 1.6 mm against 1.94 mm in *E. eocenicus* n. sp.; hind femur 0.57 mm long against 0.48 mm in *E. eocenicus* n. sp., hind tibia 0.42 mm long against 0.36 mm in *E. eocenicus* n. sp.

GENUS *Belaphotroctes* ROESLER 1943

Type species: *Belaphotroctes traegardhi* (Recent species).

***Belaphotroctes similis* MOCKFORD 1969**

Material: Holotype specimen UCMP 12670, paratype UCMP 10174, University of California Museum of Paleontology.

Occurrence: Chiapas amber, Mexico.

Geological age: Late Oligocene – Early Miocene.

Remark: Mockford (1972) synonymized this species with the recent Nearctic *Belaphotroctes ghesquierei* BADONNEL 1949 (see also Spahr, 1992).

GENUS *Liposcelis* MOTSCHULSKY 1852

Type species: *Liposcelis brunnea* MOTSCHULSKY 1852

***Liposcelis atavus* ENDERLEIN 1911**

Material: Holotype specimen in collection Künow, 'Berliner Paläontologische Museum' (Enderlein, 1911). Its present location is unknown.

Occurrence: Baltic amber.

Geological age: Late Eocene.

Remark: This fossil has the particular dorsal obtuse protuberance of hind femora characteristic of the genus *Liposcelis*.

***Liposcelis resinatus* (HAGEN 1882)**

Material: The present location of the holotype is unknown.

Occurrence: In copal of unknown origin.

Geological age: Pleistocene? ('Diluvium', after Enderlein, 1911).

Remark: Hagen (1882) described it in the genus *Atropos*. Enderlein (1911) attributed this fossil to the genus *Liposcelis*. It has the characteristic protuberance of hind femora.

***Liposcelis* sp. (in Mockford, 1969)**

Material: Specimen UCMP 12736, University of California Museum of Paleontology.

Occurrence: Chiapas amber, Mexico.

Geological age: Late Oligocene – Early Miocene.

Remark: This specimen has never been described nor figured.

GENUS *Miotroctes* PIERCE 1960 (in Psocoptera incertae sedis n. sit.)

Type species: *Miotroctes rousei* PIERCE 1960.

***Miotroctes rousei* PIERCE 1960 (in Psocoptera incertae sedis n. sit.)**

Material: Holotype specimen 2.526 (missing), collection of the Los Angeles County Museum (Sphon, 1973).

Occurrence: Southern Calico Mountains, San Bernardino County, California, U.S.A.

Geological age: Barstow Formation, Miocene.

Remarks: This fossil species is based on a single specimen in a silicified nodule. As the antennae, labial palps and tarsi are missing, none of the characters currently used to separate the three recent suborders Trogiomorpha, Troctomorpha and Psocomorpha are available (Smithers, 1972; Mockford, 1993). Only the small dimension of the fossil (body 0.903 mm long) would weakly support some affinities with the Nanopsocetae. Also, the coxae seem to be rather widely separated as in Liposcelididae. Nevertheless, these characters are not sufficient for a definite attribution of this fossil to this family. It can only be considered as a Psocoptera of uncertain position. It is listed in Plecoptera (sic) by Sphon (1973) and in Psocoptera: Liposcelididae by Lewis (1989).

Biogeographic remarks: The recent *E. femoralis* is known from North and Central America and Mozambique and Angola in Africa. A similar repartition (Madagascar, West Africa, Brazil, Mexico and Florida) although known for *Belaphotroctes ghesquierei* (Mockford, 1972), is considered problematic (Mockford, 1993, p. 312). If 'natural', such repartitions would imply that these species are unchanged since the separation of South America and Africa, during the Cretaceous. Cases of very old species are known but they are not so old (Martínez-Delclòs, 1996). The presence in the European Lower and Upper Eocene of 2 species very closely related to *E. femoralis* supports a great antiquity for the 'group III' of *Embidopsocus*. Nevertheless, the specific identity of the American and African populations of *E. femoralis*, if exact, is difficult to explain on the sole basis of historical biogeography and could be related to human activities between Africa and Central America during recent past centuries (slave transportation?). Genetic population studies would help to solve this problem.

ACKNOWLEDGMENTS

This research was partly granted by the French Ministry of Education and Research (DISTB). We thank the factory Lafarge-Granulat for their financial and technical help and authorisation. We also thank the 'Indivision Langlois-Meurinne' for the authorisation of field researches. M. Gilbert Hodebert talent was particularly appreciated for the illustrations.

REFERENCES

- Badonnel, A., 1931. Contribution à l'étude de la faune du Mozambique, voyage de M. P. Lesne (1928-1929). 4^{ème} note. – Copéognathes. Annales de Sciences Naturelles, Série Botanique, Zoologie, 14, 229-260.
- Badonnel, A., 1955. Psocoptères de l'Angola. Subsidio para o Estudo da Biologia na Lunda, Companhia de Diamantes de Angola (Diamang), Serviços Culturais, Museo do Dundo, Lunda, Angola, Lisboa, Publicações Culturais, 26, 1-266.
- Badonnel, A., 1967. Insectes Psocoptères. Faune de Madagascar, 23, 1-235.
- Badonnel, A., 1969. Psocoptères de l'Angola et des pays voisins, avec révision de types africains d'Enderlein (1902) et de Ribaga (1911). Subsidio para o Estudo da Biologia na Lunda, Companhia de Diamantes de Angola (Diamang), Serviços Culturais, Museo do Dundo, Lunda, Angola, Lisboa, Publicações Culturais, 79, 1-152.
- Badonnel, A., 1972. Espèces brésiliennes de la sous-famille des Embidopsocinae (Psocoptera: Liposcelidae). Bulletin du Muséum National d'Histoire Naturelle (Zoologie), 87, 1097-1139.
- Enderlein, G., 1911. Die Fossilien Copeognathen und ihre Phylogenie. Palaeontographica, 58, 279-360.
- Feugueur, L., 1963. L'Yprésien du Bassin de Paris. Essai de Monographie stratigraphique. Mémoires pour servir à l'explication de la Carte Géologique Détaillée de la France, Publication du Ministère de l'Industrie, Paris, 568 pp.
- Günther, K.K., 1989. *Embidopsocus saxonicus* n. sp., eine neue fossile Psocoptera-Art aus Sächsischen Bernstein des Beterfelder Raumes (Insecta, Psocoptera: Liposcelidae). Berlin, Mitteilungen der Zoologische Museum, 65, 321-325.
- Hagen, H.A., 1882. Beiträge zur Monographie der Psociden. Stettiner Entomologische Zeitung, 43(7-9), 265-300.
- Lewis, S.E., 1989. Miocene insects localities in the United States. Occasional Papers in Paleobiology of the St. Cloud State University, 3(4), 1-13.
- Martínez-Delclòs, X., 1996. El registro fósil de los insectos. Boletín de la Asociación Española de Entomología, 20(1-2), 9-30.
- Mockford, E.L., 1969. Fossil insects of the order Psocoptera from Tertiary amber of Chiapas, Mexico. Journal of Paleontology, 43, 1267-1273.
- Mockford, E.L., 1972. New species, records, and synonymy of Florida *Belaphotroctes* (Psocoptera: Liposcelidae). The Florida Entomologist, 55, 153-163.
- Mockford, E.L., 1987. Systematics of North American and Greater Antillean species of *Embidopsocus* (Psocoptera: Liposcelidae). Annals of the Entomological Society of America, 80, 849-864.
- Mockford, E.L., 1993. North American Psocoptera (Insecta). Flora & Fauna Handbook, 10. Gainesville, Florida, ed. Sandhill Crane Press, 455 pp.
- Nel, A., de Plöeg, G., Dejoux, J., Dutheil, D., de Franceschi, D., Gheerbrant, E., Godinot, M., Hervet, S., Menier, J.-J., Augé, M., Bignot, G., Cavagnetto, C., Duffaud, S., Gaudant, J., Hua S., Jossang, A., de Lapparent de Broin, F., Pozzi, J.-P., Paicheler, J.-C., Bouchet, F., Rage, J.-C., 1999. Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basal, MP7): Le Ques-

- noy (Oise, France). Paris, Comptes-Rendus de l'Académie des Sciences, Sciences de la Terre et des Planètes, 329, 65-72.
- Pierce, W.D., 1960. Fossil arthropods of California. 23 Silicified insects in Miocene nodules from the Calico Mountains. Bulletin of the Southern California Academy of Sciences, 59, 40-49.
- Roesler, R., 1943. Über einige Copeognathengenera. Stettiner Entomologische Zeitung, 104, 1-14.
- Smithers, C.N., 1972. The classification and phylogeny of Psocoptera. Sydney, Australian Museum Memoir, 14, 1-351.
- Spahr, U. von, 1992. Ergänzungen und Berichtigungen zu R. Keilbachs Bibliographie und liste der Bernsteinfossilien, Klasse Insecta (Ausgenommen: "Apterygota", Hemipteroidea, Coleoptera, Hymenoptera, Mecopteroidea). Stuttgarter Beiträge zur Naturkunde, (B), 182, 1-102.
- Sphon, G.G., 1973. Additional type specimens of fossil Invertebrata in the collections of the Natural History Museum of Los Angeles County. Los Angeles County Museum, Contribution in Science, 250, 1-68.

**Manuscript received March 2002;
revision accepted July 2002.**