

Notes on Otiocerini with a second record of Derbidae in Eocene Baltic amber (Hemiptera: Fulgoromorpha: Derbidae)

JACEK SZWEDO

Insect Syst. Evol. Szwedo, J.: Notes on Otiocerini with a second record of Derbidae in Eocene Baltic amber (Hemiptera: Fulgoromorpha: Derbidae). *Insect Syst. Evol.* 36: 161-172. Copenhagen, June, 2005. ISSN 1399-560X.



The tribal classification of Derbidae with respect to Otiocerini is presented and discussed. Key to extant and fossil genera of Otiocerini is provided. New genus and species from Eocene Baltic amber – *Lugeilangor elektrokleistis* gen. n. et sp. n. of Derbidae tribe Otiocerini Muir is described. It seems to be related to the extant Asian-Pacific genera *Paralyricen* Muir, 1913, and *Flaccia* Stål, 1866. It is the second record of the family Derbidae in Eocene Baltic amber inclusions. Palaeobiological and biogeographical significance of the fossil is discussed.

Szwedo, J.: Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, PL 00-679 Warszawa, Poland. (szwedo@miiz.waw.pl)

Introduction

Insects placed in Derbidae constitute a huge and highly differentiated family of planthoppers, housing a large number of species (Hemiptera: Fulgoromorpha: Fulgoroidea). It is one of the larger families of Fulgoroidea. The classification of the family was studied by Muir (1913, 1917, 1918a, b, 1923, 1930), Kirkaldy (1906), and Metcalf (1938). Classification and evolution of Derbidae were elaborated by Fennah (1952) and Emeljanov (1994a), but the distribution of some characters still remains controversial and the available data are not sufficient to substantiate the phylogeny of the group.

Derbidae from Eocene Baltic amber are very poorly known, only several taxa have been mentioned – *Positrona shcherbakovi* Emeljanov, 1994, of Otiocerini (Emeljanov 1994b) and unnamed Cedusini (Szwedo 2002). More fossil taxa are recorded from Oligocene/Miocene resins of the New World: Dominican amber – *Cedusa credula* Emeljanov et Shcherbakov, 2000, and *Dysimia imprudens* Emeljanov et Shcherbakov, 2000 and Mexican amber – *Cedusa baylissae* Szwedo et Ross 2003 and *Copallinges chiapasensis* Szwedo, 2004. A few other unnamed Derbidae are known from Oligocene/Miocene Dominican amber – specimens figured in Poinar & Poinar (1999) and

Eocene Bitterfeld amber (Szwedo 2002). From Miocene strata of Stavropol' (Northern Caucasus Mts.) another species *Mysidioides migdisovae* Emeljanov, 2002, of the tribe Otiocerini has recently been described (Emeljanov 2002). Another record of this family from Upper Triassic strata of Brazil (Pinto 1956) is based on misinterpreted material (Emeljanov 1994b; Szwedo 2002; Szwedo, Bourgoin & Lefebvre 2004). This fossil known as *Sanctipaulus mendesi* Pinto, 1956, has been transferred to Trichoptera, undetermined family, by Martins-Neto et al. (2003).

Taxonomy

Representatives of the family Derbidae may be difficult to identify. They are fragile-winged insects 4–16 mm long with bright coloration (O'Brien 2002). Most of them bear a row of apical spines on the second hind tarsomere, still some of them (e.g. *Sayiana* Ball, 1928, *Otiocerus* Kirby, 1821 – Otiocerini) have a single spine on each side. In most derbids, the apical segment of rostrum is as long as wide, but in some genera (e.g. *Ipsnola* Signoret, 1885, *Goneokarella* Fennah, 1952, or *Neodawnaria* O'Brien, 1982 – representing more basal tribes of Derbidae – Ipsnolini Emeljanov, 1994, Goneokarellini Emeljanov, 1994

and Dawnarioidini Emeljanov, 1994, respectively) it is longer. Body size varies from 4 to 16 mm. Extant Derbidae occur in three common habitus, the first is a group of moth-like insects with their tegmina and wings spread, the second group has tectiform tegmina. The third group holds their tegmina and wings curled in the tubes, with costal and commissural margins of tegmen nearly touching each other, encircling similarly rolled wing, and placed at an angle of 45° to the body axis. The only common features of such different forms are the characters of genitals in both sexes (O'Brien & Wilson 1985). The higher classification of extant Derbidae has recently been presented by Emeljanov (1994a), but there still remain numerous taxonomic problems within the group, and Derbidae, as well as their subunits, are sometimes believed to be paraphyletic (Emeljanov & Fletcher 2004). Representatives of the family occur in temperate and tropical zones (mainly in the New World and Australian regions). Nymphs of Derbidae planthoppers seem to be obligatory fungivorous, they have been collected under bark of live trunks and decaying logs (O'Brien 1991, Yang & Yeh 1994, Emeljanov & Fletcher 2004). Imagines occur above the ground, they are usually associated with monocots (particularly palms) and woody dicots, a few species feed on ferns. Most derbids are monophagous or strictly oligophagous (Wilson et al. 1994).

The first division of Derbidae was proposed by Muir in 1913 (Muir 1913), when he sorted the genera into four "groups". The attempt to classify Derbidae was continued by the same author (Muir 1917), who divided the family into four subfamilies: Derbinae, Otiocerinae, Cenchreinae and Rhotaninae. In 1918, Muir proposed the subfamily Zoraidinae to comprise the tribes Zoraidini and Sikaianini (Muir 1918a) and the subfamily Derbinae with the tribes Derbini, Cenchreini, Rhotanini and Otiocerini (Muir 1918b). Later, (Muir 1923, 1930) this division was reaffirmed and the system was adopted in Metcalf's "General Catalogue of the Hemiptera" (Metcalf 1945). The generic classification of Derbidae was discussed by Fennah (1952), who retained Muir's tribal division but rejected subfamilies. Recently, Emeljanov (1994a) presented a more detailed system based on external morphological characters (Fig. 16). He divided Derbidae into three subfamilies and 18 tribes. The subfamily Cedusinae comprises the tribes Ipsnolini, Goneokarellini, Vinatini, Cedus-

ini, Phrygiini, and recently (Emeljanov & Fletcher 2004) the tribe Breddiniolini Fennah, 1950, formerly placed in Achilidae (Fennah 1950b; Emeljanov 1990, 1992) but lately transferred here. Derbinae comprise the tribes Cedochreini, Dawnarioidini, Derbini, Cenchreini and Nicertini, while Otiocerinae include the tribes: Kamendakini, Rhotanini, Otiocerini, Patarini, Neocyclocarini, Pheniciini, Zoriaidini and Sikaianini. According to Emeljanov (1994a), the taxa placed in the tribe Mysidiini, proposed by Broomfield (1985), are to be placed within Derbini.

The tribe Otiocerini is to be recognized by the following combination of characters. Tegmina (Figs. 5 & 10 – 15) not very long and narrow, usually more than 2.5 times as long as broad. Clavus open, apex of clavus extended to submarginal vein of membrane, connected with margin of tegmen only by short veinlet *icu*. Procutital cell with distinctly shifted points of connection of *icu* and CuA_1 , separated by part of submarginal peripheral vein. In this area, submarginal peripheral vein distinctly moved away from margin of tegmen, and procutital cell placed obliquely. Apical cells, at least of vein M, always short. Wing length more than half of tegmina, jugal margin with stridulatory plate, stridulatory plate with concave external margin. Second hind tarsomere always provided with more than 4 apical teeth. Head is usually narrow, antennae show remarkable variation, also between sexes. The tribe Otiocerini comprises about 40 genera (placement of some of them within the unit remains controversial), distributed in North and Central America, South Africa, Oriental and Australian regions, with most genera and species recorded from the Philippines, Indonesia and Pacific Ocean archipelagos. Some genera formerly placed in Otiocerini (Fennah 1952) have been moved by Emeljanov (1994a) to other tribes. The placement of genus *Aculocephala* Metcalf, 1945 from New Caledonia, related by Muir (1913) with *Otiocerus* Kirby and not mentioned by Fennah (1952) remains not certain. The second genus which need to be re-examined is *Muirileguatia* Metcalf, 1945, from the Mascarenes. It was placed by Fennah (1952) in Cenchreini, but complex of characters as: open clavus, closed procutital cell, second hind tarsomere with six apical teeth suggests its placement in Otiocerini. Unfortunately, no data exist on the stridulatory plate of the hind wing in both of genera mentioned above. There are no reliable data on the genus

Labicerus Erichson, 1848, described from British Guiana, and Fennah (1952) omitted it in his key. He also argued the status of the genus *Amalopota* Van Duzee, 1889, from North and Central America, as subgenus of *Anotia* Kirby, 1821, or separate genus; *Amalopota* Van Duzee was not included in the Fennah's key (Fennah 1952). Emeljanov (1998) also believes *Amalopota* Van Duzee as synonym of *Anotia* Kirby.

The following key is to identify Otiocerini genera (based on keys provided by Fennah 1952, 1956 and 1971, supplemented and updated, taxa treated by Fennah as subgenera are treated here as genera).

1. Vein M not arising from radius or arising basad of Sc+R fork 2
 - Vein M arising from R distad of Sc+R+M fork... 31
2. First antennal segment short, as broad as long, or broader..... 3
 - First antennal segment more than twice as long as broad..... 27
3. Sc+R forking at or basad of middle of tegmen, subcostal cell elongate..... 4
 - Sc+R forking distad of middle of tegmen, subcostal cell short..... 26
4. Subantennal process absent or very small; lateral pronotal carinae absent or very small (antennal cephalothoracic complex weakly developed)..... 5
 - Subantennal process well developed (antennal cephalothoracic complex well developed)..... 19
5. Head in profile apically forming a curve, or subconical; frons not wider at base than at apex.... 6
 - Head in profile angulate at apex, or frons wider at base than at middle..... 18
6. Vertex little produced beyond eyes; anterior margin in profile subparallel to anterior margin of eye..... 7
 - Vertex considerably produced beyond eyes 10
7. Frontal carinae contiguous at base
 - *Tempora* Matsumura, 1914
 - Frontal carinae rarely contiguous at base..... 8
8. Fork of posterior branch of vein M_1 much shorter than fork of M_2 , base of which is approximately at equal distance from wing margin and from first crossvein *m-cu*. RA with three postnodal terminals. CuA_1 continues with wing margin..... *Pyrrhonice* Emeljanov, 1994
 - Fork of anterior branch of M_1 is approximately as long as fork of M_2 , base of which is close to wing margin and is far from veinlet *m-cu*. RA with two postnodal terminals..... 9
9. Second veinlet *m-cu* leaving CuA_1 far beyond first cubital cell. Second claval cell is markedly shorter than vein $Pcu+A_1$. Fork of RA close to nodal $ScRA_1$. CuA_1 does not reach tegmen margin, but merges with CuA_2 into single submarginal vein *Pyrrhoneura* Kirkaldy, 1906
 - Second *m-cu* placed near apex of first cubital vein. Second claval cell is not shorter than $Pcu+A_1$. Fork of RA shifted away from nodal $ScRA_1$. CuA_1 continues on tegmen margin *Positrona* Emeljanov, 1994
10. Antennae not reaching as far as apex of head 11
 - Antennae reaching to apex of head; if not then base of costal margin of tegmen triangularly produced 13
11. Vertex not two-thirds as long as mesonotum; tegmen broadest two-thirds from base
 - *Cobacella* Fennah, 1952
 - Vertex at least as long as mesonotum; tegmina broadest three-quarters from base 12
12. Head distinctly produced before eyes; margin of head in profile not subparallel to eye.....
 - *Swezeyia* Kirkaldy, 1906
 - Head produced before eyes for two-thirds length of eye; margin of head in profile subparallel to eye *Eusyphax* Fennah, 1956
13. Vertex and frons in profile subconical or narrowly rounded; most apical cells in tegmen more than twice as long as broad..... 14
 - Vertex and frons in profile deeply and evenly rounded; apical cells in tegmina not twice as long as broad..... 15
14. Antennae cylindrical, long, reaching beyond anterior margin of head..... *Kuranda* Distant, 1907
 - Antennae cylindrical, long, reaching almost to anterior margin of head..... *Deribia* Westwood, 1841
15. Costal appendage not developed..... 16
 - Costal margin of tegmen near base produced in a triangular reflected lobe 17
16. Costal margin of tegmen not produced, costa narrow; veinlets not crowded together, usually inconspicuous..... *Anotia* Kirby, 1821
 - Costa broad; veinlets crowded together to give the appearance of stigma *Amalopota* Van Duzee, 1889
17. Mesonotum bituberculate; antennae with appendage..... *Iquitosa* Fennah, 1945
 - Mesonotum smooth; antennae simple *Sayiana* Ball, 1928
18. Frons at base at least as wide as at apex
 - *Swezeyia* Kirkaldy, 1906
 - Frons narrower at base than at apex; vertex in profile sinuate..... *Kampulokara* Muir, 1913
19. Lateral pronotal carinae not forming a prominent subfoliate ridge 20
 - Lateral pronotal carinae forming a subfoliate ridge 22
20. In profile vertex not ascending distad; forming an even curve with frons... *Nesocore* Kirkaldy, 1907
 - In profile vertex ascending distad..... 21
21. In profile vertex ascending, and curved backward..... *Nesoniphax* Kirkaldy, 1907
 - In profile vertex ascending, but not curved backward..... *Nesoneura* Kirkaldy, 1907
22. Subantennal process spatulate, attached to gena by a slender stalk 23
 - Subantennal process not spatulate, attached to gena along a broad base..... 24
23. Head in profile considerably produced beyond eyes; antennae either small with large sensorial, or with second segment produced, bearing laminae so as to appear pectinate
 - *Kaha* Kirkaldy, 1906
 - Head in profile not much produced beyond

- eyes; antennae moderately large with small sensorial *Nesokaha* Muir, 1913
24. Procubital cell of tegmen distinctly longer than wide; vertex in mid line shorter than wide at base *Lugeilangor* gen. n.
- Procubital cell of tegmen about as long as wide; vertex in mid line longer than wide at base 25
25. Vertex truncate at apex; lateral carinae of frons not contiguous, except rarely at middle of frons *Flaccia* Stål, 1866
- Vertex acutely angulate, lateral carinae meeting at apex and remaining contiguous along frons nearly to base *Paralyricen* Muir, 1913
26. In profile vertex and frons forming a curve, not meeting angulately *Makula* Distant, 1907
- In profile apex of head angulate; tegmina with costal margin more or less sinuate and interrupted by an angular projection; a distinct pre-costal area in basal third *Banksiella* Muir, 1917
27. Subantennal process present *Neodendrokara* Muir, 1917
- Subantennal process absent 28
28. Head in profile not much produced beyond eyes, apically rounded. *Dendrokara* Melichar, 1914
- Head in profile considerably produced beyond eyes, apically narrowly rounded or angulate 29
29. Head in profile rounded at apex *Shellenius* Ball, 1928
- Head in profile angulate at apex 30
30. Head in profile notched near apex, beyond which apex angulately ascends *Apache* Kirkaldy, 1901
- Vertex in profile not notched, apex of head ascending in a curve *Otiocerus* Kirby, 1821
31. Subantennal process present *Mysidioides* Matsumura, 1905
- Subantennal process absent or very small 32
32. Antennae with first segment much longer than broad *Phra* Distant, 1916
- Antennae with first segment not longer than broad 33
33. Antennae longer than frons 34
- Antennae shorter than frons 38
34. Tegmen with veins RA and RP₁ dilated at apex; vertex elongate, strongly ascending distally; mesonotum with a vertical flange-like lobe on line of each obsolete lateral carina *Anomaladerbe* Muir, 1922
- Tegmen with longitudinal veins not dilated at apex, or dilated only in subapical portion, dilatation not reaching apical margin; vertex relatively short; mesonotum without vertical laminae on disc 35
35. Frons in profile semicircularly rounded; vertex not ascending *Platonax* Metcalf, 1938
- Frons in profile shallowly convex; vertex ascending distally, or very short 36
36. Tegminal vein M with 4 sectors; vertex ascending distad; antennae flattened 37
- Tegminal vein M with 5 sectors; vertex very short, not ascending; antennae cylindrical *Platocerella* Fennah, 1952
37. Antennae not larger than face, flattened and compressed, elongate oval in profile *Niphadodite* Kirkaldy, 1907
- Antennae distinctly longer than face, very large, flat, thin *Platocera* Muir, 1913
38. Antennae with second segment branched near base; appendage curved; frons at least as wide at base as at apex *Harpanor* Fennah, 1950
- Antennae with second segment cylindrical or slightly depressed, devoid of appendage 39
39. Vertex little produced beyond eyes; frons distinctly wider at apex than at base 40
- Vertex markedly produced beyond eyes; frons compressed throughout, apex not wider than base *Archara* Metcalf, 1945
40. Subantennal process present 41
- No subantennal process; ocelli absent; clypeus two-thirds length of frons *Homometria* Fennah, 1952
41. Tegmen with subapical parts of veins RA and RP not dilated; veinlet *r-m* lying before second sector of M; ocelli present or indicated; clypeus as long as frons *Heronax* Kirkaldy, 1906
- Tegmen with subapical parts of veins RA and RP dilated and thickened; veinlet *r-m* lying behind second sector of M; ocelli absent; clypeus shorter than frons *Pepleuca* Emeljanov, 1998

Family DERBIDAE Spinola, 1838

Subfamily Otiocerinae Muir, 1917

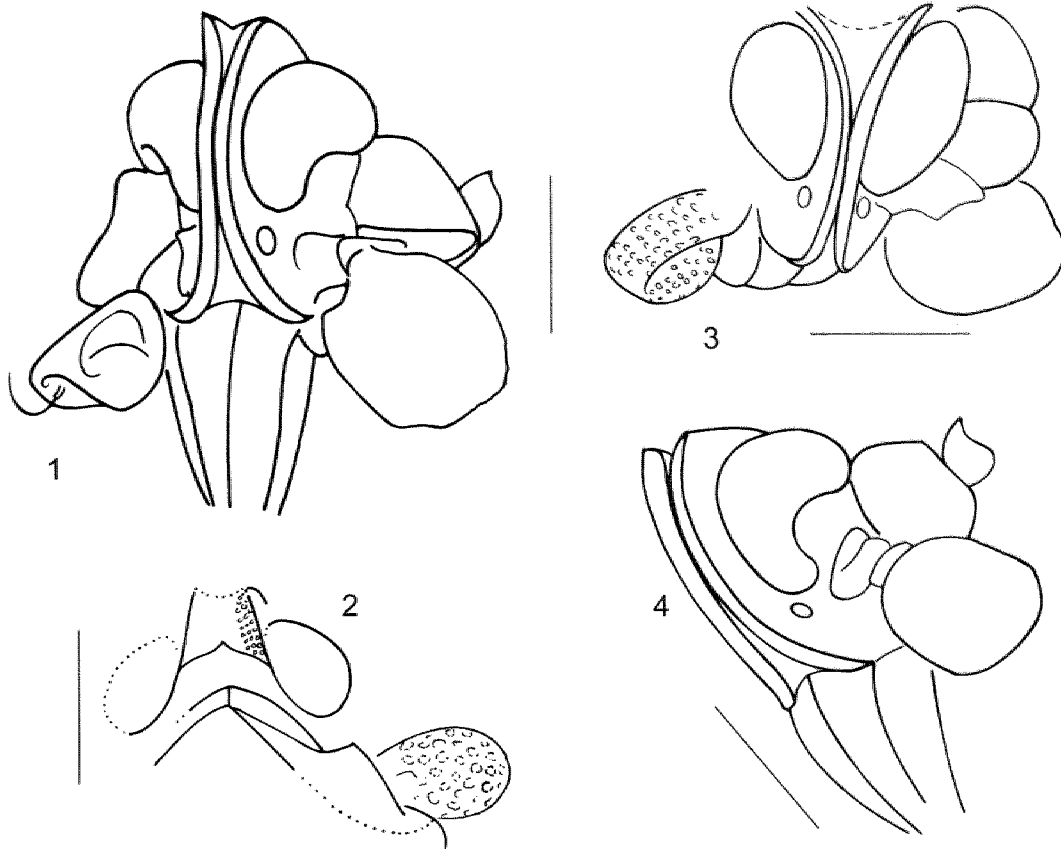
Tribe Otiocerini Muir, 1917

Genus *Lugeilangor* gen. n.

Type species. – *Lugeilangor elektrokleistis* sp. n., here designated.

Etymology. – From the name of the god of one of the tribes inhabiting the Caroline Islands – Lugeilang. Gender: masculine.

Diagnosis. – *Lugeilangor* gen. n. seems to be related to the extant genera *Paralyricen* Muir, 1913 and *Flaccia* Stål, 1866, but differs in the characters of the head and tegmen venation. Anterior margin of vertex slightly narrower than posterior margin (distinctly narrower in *Paralyricen* and *Flaccia*); vertex in mid line shorter than wide at base (longer than wide at base in *Paralyricen* and *Flaccia*); in lateral view frons and vertex slightly angulate at point of junction (joined roundly in *Paralyricen*, distinctly angulate in *Flaccia*). Tegmen with apical portion slightly widened (distinctly widened in *Paralyricen* and *Flaccia*); costal margin almost straight (costal margin similar in *Paralyricen*, costal margin distinctly curved at base in *Flaccia*); veins ScRA₁ and M forked at the same level (vein ScRA₁ forked anteriorly of M first forking in *Flaccia*, posteriorly of first M forking in *Paralyricen*) vein ScR forked anteriorly of 1/2 of tegmen length (as



Figs 1–9. *Lugeilangor elektrokleistis* gen. n. et sp. n. 1. Face in anterior view; scale bar 1 mm. 2. Anterior part of the body; scale bar 1 mm. 3. Head in anterodorsal view; scale bar 1 mm. 4. Head in frontolateral view; scale bar 1 mm.

in *Flaccia*, in *Paralyricen* ScR forked at $\frac{1}{5}$ of tegmen length); vein ScRA₁ forked at half of tegmen length (posteriad of half of tegmen in *Paralyricen*, anteriad of half of tegmen in *Flaccia*); vein M first fork at half of tegmen length (posteriad of half of tegmen in *Paralyricen*, anteriad of half of tegmen in *Flaccia*); M with 8 terminals (9 terminals in *Paralyricen* and *Flaccia*); procubital cell distinctly longer than wide (only merely longer than wide in *Paralyricen* and *Flaccia*).

Description. – Vertex trapezoid, concave, wider at base than long in mid line, slightly produced before compound eyes. Lateral carinae of vertex covered with a row of sensory pits. Frons narrow, slightly widened at base and near the line of junc-

tion with vertex, slightly longer than clypeus. Lateral carinae of frons contiguous, slightly diverging in upper portion, and more distinctly diverging near frontoclypeal suture. Frontoclypeal suture convex. Clypeus tricarinate, distinctly convex. Subantennal process not spatulate, broadly attached to gena. First joint of antenna about as wide as long, second joint subovoid, distally subtruncate and subbifid, covered with sensory pits.

Pronotum short in mid line, with median carina, lateral carinae well developed.

Tegmen only slightly widening in apical portion, clavus open, reaching almost half of tegmen length. Costal margin almost straight, not distinctly curved at base, basal portion thickened. Basal cell about three times as long as wide. Veins Sc+R+M leave basal cell with short common

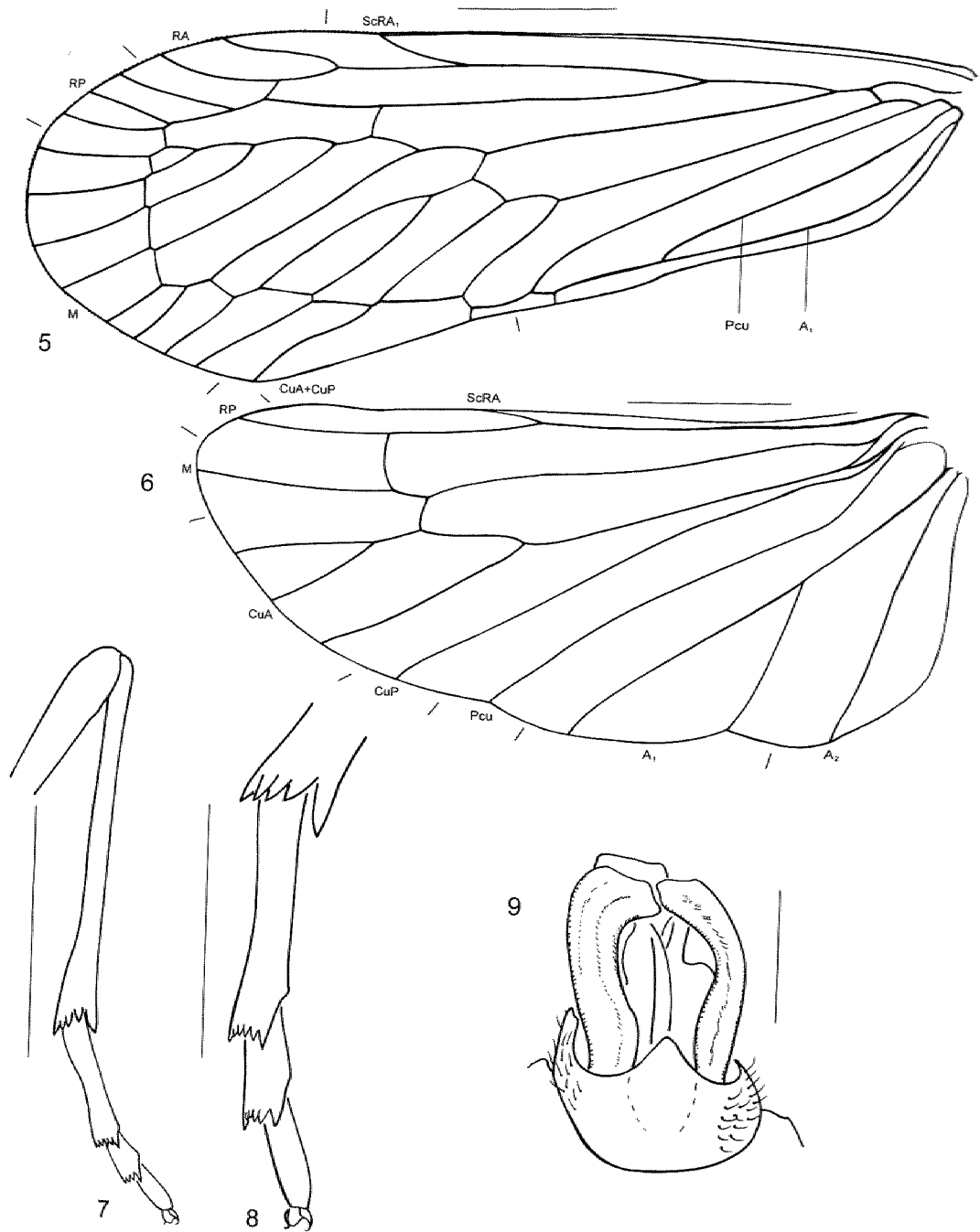


Fig. 5. Left tegmen; scale bar 1 mm. Fig. 6. Left wing; scale bar 1 mm. Fig. 7. Hind leg; scale bar 1 mm. Fig. 8. Hind tarsus; scale bar 1 mm. Fig. 9. Male genital block in ventral view; scale bar 1 mm.

stalk, vein ScR forked before $\frac{1}{3}$ of tegmen length, veins ScRA₁ forked at half of tegmen length, RA₂ with two terminals. Vein RP with three terminals. Vein M with first forking at half of tegmen length, with eight terminals reaching apex of tegmen, anterior branch with six terminals, posterior branch with two terminals. Vein CuA first forking distinctly before half of tegmen length. Procubital cell about 4 times as long as wide. Claval veins Pcu and A₁ united at $\frac{1}{3}$ of tegmen length.

Wing long, membranous. Vein RP reaches margin above the apex, M with single terminal, veinlet *r-m* long, vein CuA with three terminals. Stridulatory apparatus not visible, probably not developed.

Hind leg slender, hind tibia without lateral teeth, with 5 apical teeth, tibio-metatarsal formula 5 : 6 : 6. Hind basitarsomere longer than combined length of mid and hind tarsomeres.

Male genital block distinct, pygofer with angulate triangular median process, lateral lobes of pygofer with elongate processes. Styles slightly asymmetrical, elongate, with lateral carination, apical portion widened, almost straight at apex.

Female not known.

Lugeilangor elektrokleistis sp. n.

(Figs 1–9)

Diagnosis. – Head with compound eyes about 2.4 times as wide as vertex in posterior margin. Vertex at base about 1.7 times as wide as long in mid line. Pronotum about 1.9 times as wide as head with compound eyes, pronotum shorter than vertex in mid line. Tegmen 2.65 times as long as wide, with apical margin not sinuate. Genital styles in ventral view curved mediad at apex, widened in apical portion, with distinct lateral carinations.

Description. – Total length about 6.7 mm, length of body 4.06 mm. Vertex (Figs 2 & 3) trapezoid, about 0.17 mm in mid line, 0.28 mm at base, with lateral carinae distinctly elevated, posterior margin excavate. Frons in mid line 0.77 mm long, with lateral carinae subparallel, contiguous near eyes, narrowly separate at base and near apex (Figs 1 & 4). Clypeus about 0.69 mm long in mid line, distinctly convex, tricarinate, frontoclypeal suture convex.

Pronotum (Fig. 2) 0.14 mm long in mid line, 1.25 mm wide in mid line, with distinct median carina. Tegmen (Fig. 5) 5.87 mm long, 2.22 mm

wide, with clavus reaching almost to the half of tegmen length. Wing (Fig. 6) 4.67 mm long, about twice as long as wide. Hind femur (Fig. 7) about 0.91 mm long, slender, hind tibia about 1.5 mm long, slender, without later teeth, with five apical teeth, hind basitarsomere (Fig. 8) 0.49 mm long, with 6 apical teeth, mid and apical tarsomeres subequal in length, about 0.27 mm long, tarsal claws and arolium distinct.

Male genital (Fig. 9) block slightly shorter than the rest of abdomen measured along the lateral margin. Pygofer with distinct median angulate triangular process and elongate lateral process, covered with short setae, length of pygofer in mid line 0.46 mm, width of pygofer in ventral view 0.69 mm. Genital styles about 0.8 mm long.

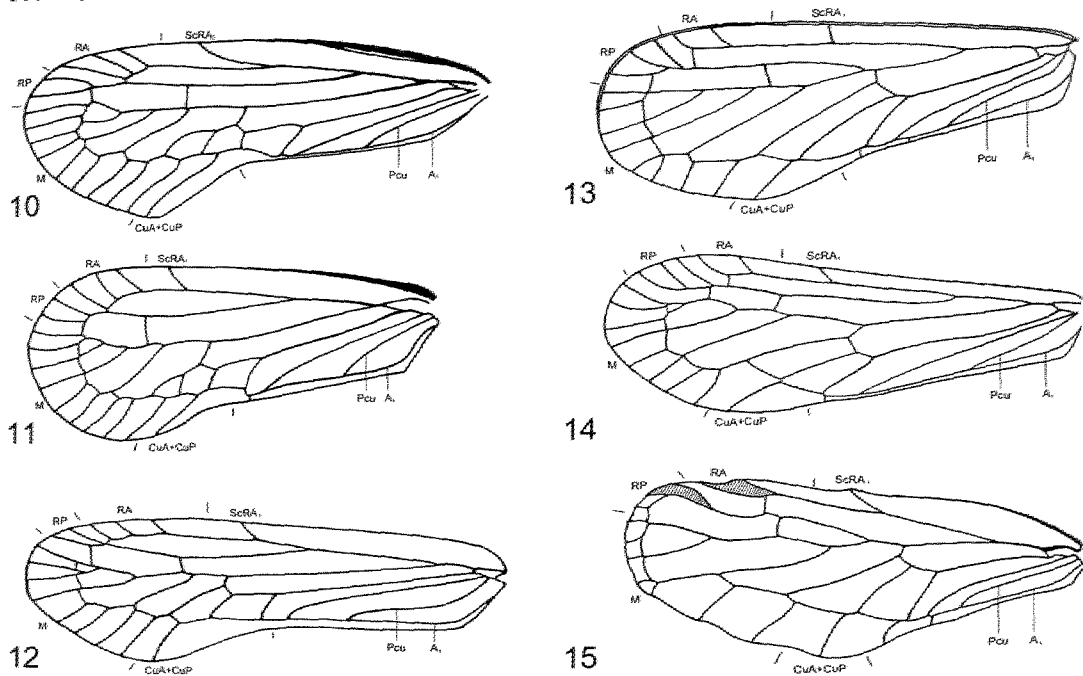
Etymology. – Species name *elektrokleistis* is derived from Ancient Greek words *electron* – amber and *ikleistis* – sunk.

Distribution and geological horizon. – Baltic region. Baltic amber, Eocene, 50–40 Ma.

Material examined. – Holotype, male; Eocene, Baltic amber inclusion, Zoological Museum of the University of Copenhagen, labelled: [Auchenorrhyncha / 28 – 3; A.K. Andersen / 1968]; red label [HOLOTYPE]; [*Lugeilangor* / *elektrokleistis* Szwedo, 2005 / det. Szwedo 2004 / Baltic amber, Eocene]. Subquadrangular piece of amber (11 × 7 × 3 mm), reddish, polished, with cracks and fissures; inclusion partly destroyed, dorsal portion of the thorax missing, right tegmen and wing destroyed, fore and mid legs missing, face, left antenna and ventral portion of the body covered with milky veil.

Discussion

Fossil Derbidae are poorly known, and only several Baltic amber inclusions of the family have been described or mentioned. Only representatives of the tribes Otiocerini (*Positrona shcherbakovi* Emeljanov, 1994) and unnamed Cedusini (Szwedo 2002) are mentioned from this source of fossils. Evolution of Derbidae has been discussed by Fennah (1952) and Emeljanov (1994a), but the distribution of some characters remains controversial and the available data are not sufficient to substantiate the phylogeny of the group. The tribe Otiocerini Muir, 1917, is regarded as one of the more advanced in the Emeljanov's scheme (1994a). He proposes them as a sister group of Kamendakini Emeljanov, 1994 (Fig. 16), but with reservations – he admits that it is also possible for Nicertini Emeljanov, 1992 and Otiocerini to be sister groups. Fennah (1952) relates Otiocerini



Figs 10–15. Tegmina of Otiocerini. Fig. 10. *Flaccia pindarus* Fennah, 1970 (redrawn after Fennah 1970). Fig. 11. *Paralyricen jepsoni* Muir, 1913 (redrawn after Muir 1913). Fig. 12. *Otiocerus regalis* Fennah, 1952 (redrawn after Fennah 1952). Fig. 13. *Mysidioides sapporoensis* Matsumura, 1900 (redrawn after Yang & Wu 1993). Fig. 14. *Positrona shcherbakovi* Emeljanov, 1994 (redrawn after Emeljanov 1994b). Fig. 15. *Anomaladerbe pembertonii* Muir, 1922 (redrawn after Muir 1922).

with Rhotanini Muir, 1917, placed by Emeljanov (1994a) as a sister group to the clade uniting Otiocerini and Kamendakini. The only fossils described from Baltic amber belong to Otiocerini and representatives of the other tribes are not described from this period, even from older strata. The other species known from Baltic amber inclusions – *Positrona shcherbakovi* (Fig. 14) – is related to the genera *Pyrrhonice* Emeljanov, 1994, and *Pyrrhoneura* Kirkaldy, 1907. The relationships of some of the recently recognized tribes remain unclear, also their volume and placement of particular genera within higher units are obscure. This makes implementation of scarce fossil data to the phylogenetic analysis very difficult at this moment.

The fossil Otiocerini are very interesting in terms of biogeographical pattern. The extant genera related to *Positrona*. – *Pyrrhonice* and *Pyrrhoneura* are recently distributed in tropical Africa, and Java, Luzon, the Philippines, Fiji Islands, Samoa Islands, Tonga Islands, and Tuvalu Islands

respectively (Metcalf 1945; Fennah 1950a, 1956, 1971; Emeljanov 1994b). *Lugeilangor* is related to *Paralyricen* and *Flaccia* (Figs. 10 & 11), distributed in Ceylon, the Philippines, Caroline Islands, Fiji Islands, Cook Islands and Society Islands, and India, Java, Fiji Islands and Rennell and Bellona Islands, respectively (Metcalf 1945; Fennah 1950a, 1956, 1958, 1970, 1971). This may suggest a much wider distribution of the tribe in the past, during the Eocene. This could be related with climatic and habitat conditions in the Scandinavian Peninsula during the Eocene, which was warmer and more humid (Larsson 1978, Wolfe 1985, Wing & Sues 1992, Krassilov 2003). If Otiocerini were distributed far to the north on the Northern Hemisphere during the Eocene, the question arises about the routes of migration from/to South Eastern Asia and Pacific archipelagos. One possibility is through Eocene European archipelagos and then through subsequently appearing Tethys Ocean archipelagos (Audley-Charles, Ballantyne & Hall 1988; Prothero 1994; Hall 1996). This possible

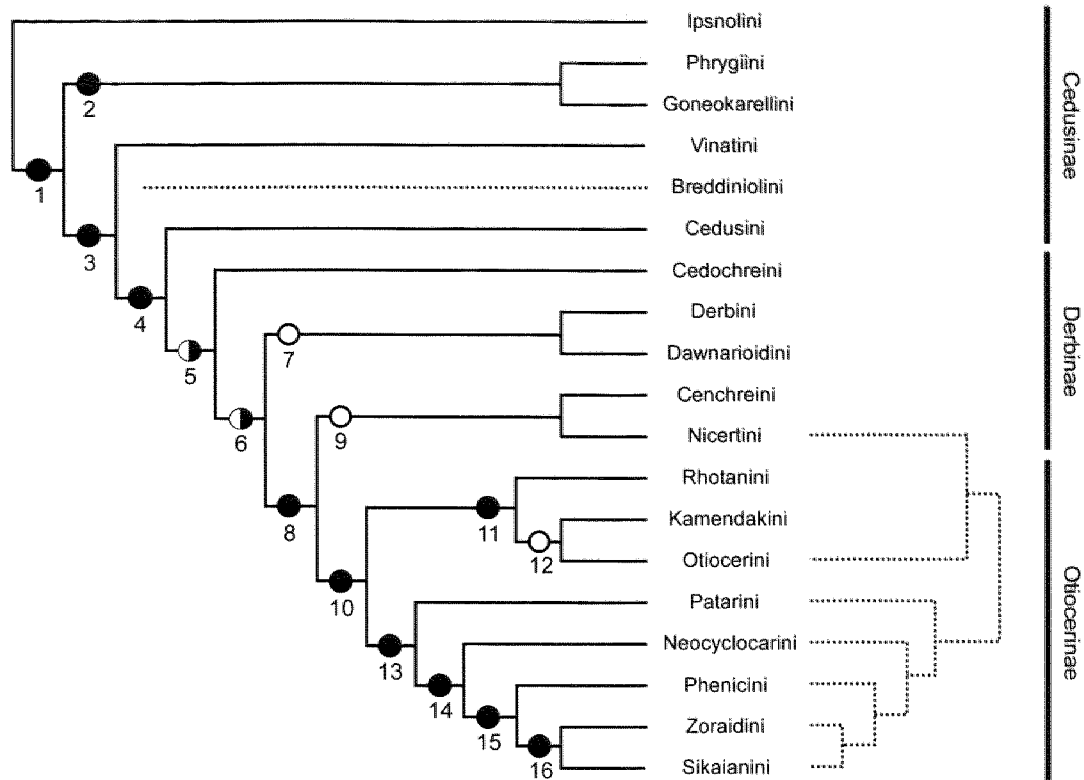


Fig. 16. Phylogenetic scheme of Derbidae; Filled circles show nodes at which relatively reliable synapomorphies are known; half-filled circles mark only conditional synapomorphies not known in all tribes above the node, because of supposed reversions or losses; white circles show hypothetical nodes not having necessary substantiation. 1 – subapical setae on the first and second hind tarsal segments absent; 2 – branches of CuA_1 in hind wings X-wise converged; 3 – branching of CuA_1 in the hind wing reduced; 4 – hind wings with nodal vein $ScRA_1$ converged with the hook; 5 – tegmen with costa with sensory pits; 6 – sensory pits on the head (on frons only) and tegminal veins; 7 – hypothetical node; 8 – closed procubital cell; 9 – hypothetical node; 10 – hind wing with stridulatory plate with concave outer margin; 11 – hind wing with apex of vein RP shifted to anterior margin of the wing; 12 – hypothetical node; 13 – hind wing with stridulatory plate with convex outer margin; 14 – tegmen with veinlet $m-cu$ shifted distally of the first branching of M; 15 – base of clavus with scutellar groove; 16 – appearance of veinlet icu , bases of hind wing anal veins fused, appearance of lateral teeth on hind tibia, clavus open. Breddiniolini are placed in Cedusinae based on the lack of sensory pits on the head and forewings together with the branches of CuA in tegmina not anastomosing and lack of stridulatory plate on the jugal margin of hind wing. Dotted line presents alternative (but likely variant) proposal of relationships among some tribes. After Emeljanov (1994b), modified, with data provided by Emeljanov & Fletcher (2004) included.

migration is to be related with climatic changes, cooling and drying of the climate after terminal Eocene event (Colinson 1992; Prothero 1994). There exists also another possibility, namely that representatives of Otiocerini were widespread far to the north of Europe and Asia, which could be associated with palaeogeographical, palaeoclimatological and palaeovegetational conditions of the Northern Hemisphere in the Palaeogene (Vakhra-

meev et al. 1970; Flerov et al. 1974; Ushakov & Yasamanov 1984; Sloan & Thomas 1998; Graham 1999; Collinson 2000; Krassilov 2003). It seems possible that, like other animals, Otiocerini derbids migrated from South Eastern Asia to North America through Beringian bridge, from Europe to North America through North America – Greenland – Europe continuity (Flerov et al. 1974; Stucky 1992; Milner, Milner & Evans 2000; Hoo-

ker 2000), and to the African continent through corridor connections, mainly Gibraltar corridor, before the Strait of Gibraltar was formed in the late Miocene (Hooker 1998; Milner, Milner & Evans 2000). Even though the data are very scarce, it could be suggested that the recent distribution of Otiocerini resulted from numerous events of dispersal and differentiation of at least the last 50 million years, and that the recent pattern of distribution is a result of reduction of a wider distribution in the past. In this, Otiocerini are similar to many other groups found in Baltic amber inclusions which have Palaeotropical affinities (Zherikhin 1970, 1971; Szadziewski 1998; Weitschat & Wichard 1998; Andersen 2000). The place of origin of Otiocerini and Derbidae as a whole, still remains enigmatic, as no derbids or derbid-like planthoppers are known yet from older deposits, e.g. Lower Cretaceous Burmese amber, Lebanese amber, Cretaceous deposits of Russian Far East or Brazil (Szwedo 2002; Szwedo, Bourgoin & Lefebvre 2004). The fossil record of Otiocerini is indeed sparse, other explanations for the origins and history of distribution of the tribe may be just as valid.

Acknowledgments

I wish to thank COBICE program, Zoological Museum in Copenhagen, which made this study possible. I wish to thank the late Prof. Dr. Nils Möller Andersen and Dr. Stig Andersen for their help and assistance during the visit. I am greatly indebted to the reviewers of the manuscript for their comments and suggestions. I also wish to thank Mrs. Krystyna Warchał for the language improvement of the manuscript.

References

- Andersen, N.M. (2000). Fossil water striders in the Eocene Baltic amber (Hemiptera, Gerromorpha). *Insect Systematics and Evolution* 31: 257–284.
- Audley-Charles, M.G., Ballantyne, P.D. & Hall, R. (1988). Mesozoic – Cenozoic rift–drift sequence of Asian fragments from Gondwanaland. pp. 317–330. *In*: Scotese, C.R. & Sager, W.W. (Eds.) *Mesozoic and Cenozoic Plate Reconstructions. Tectonophysics* 155(1/4): 400 pp.
- Broomfield, A.F. (1985). Taxonomy of Neotropical Derbidae in the new tribe Mysidiini (Homoptera). *Bulletin of the British Museum (Natural History)*, Entomology 50(1): 1–152.
- Emeljanov, A.F. (1991). K voprosu ob ob"eme i podrazdeleniakh sem. Achilidae (Homoptera, Cicadina). *Entomologicheskoe Obozrenie* 70(2): 373–392. [In Russian] Translated into English as: Yemel'yanov, A. F. 1992. Toward the problem of the limits and subdivisions of Achilidae (Homoptera, Cicadina). *Entomological Review* 71(1): 53–73.
- Emeljanov, A.F. [(1993 (1992))] Opisanie trib podsem. Achilinae (Homoptera, Achilidae) i utocnenie ikh sostava. *Entomologicheskoe Obozrenie* 71(3): 574–594. [In Russian] Translated into English as: Yemel'yanov, A. F. 1993. Description of tribes of the subfamily Achilinae (Homoptera, Achilidae) and revision of their composition. *Entomological Review* 72(6): 7–27.
- Emeljanov, A.F. (1994a). K voprosu o sisteme i filogenii sem. Derbidae (Homoptera, Cicadina). *Entomologicheskoe Obozrenie* 73(4): 783–811. [In Russian]; Translated into English as: Yemel'yanov, A.F. (1996) On the System and Phylogeny of the Family Derbidae (Homoptera, Cicadina). *Entomological Review* 75(2): 70–100.
- Emeljanov, A.F. (1994b). Pervaya iskopayemaya nakhodka semeistva Derbidae i pereopisanie paleogenovovo roda *Hooleya* Cockerell (Achilidae) (Insecta: Homoptera, Fulgoroidea). *Paleontologicheskii Zhurnal* 3: 76–82. [In Russian]; Translated into English as: Emeljanov, A.F. (1995) The First Find of Fossil Derbidae, And A Redescription of Paleogene Achilid Genus *Hooleya* Cockerell (Achilidae) (Insecta: Homoptera, Fulgoroidea). *Paleontological Journal* 28(3): 92–101.
- Emeljanov, A.F. (1998). A new genus for *Heronax candidus* Anufriev and some taxonomic remarks concerning the Far East Derbidae (Homoptera, Cicadina). *Zoosystematica Rossica* 8(1): 120.
- Emeljanov, A.F. (2002). Nakhodka predstavatelya semeistva Derbidae (Insecta, Homoptera, Fulgoroidea) v miotsene Severnogo Kavkaza. *Paleontologicheskii Zhurnal* 3: 49–50. [In Russian]; Translated into English as: Emeljanov, A.F. (2002) A record of Derbidae (Insecta, Homoptera, Fulgoroidea) in the Miocene of the Northern Caucasus. *Palaeontological Journal* 36(3): 277–278.
- Emeljanov, A.F. & Fletcher, M.J. (2004). *Hemielissum evansi*, a new genus and species of Breddiniolini (Hemiptera: Fulgoromorpha), being the first Australian record of the tribe, with a discussion of the taxonomic position of the Breddiniolini. *Australian Journal of Entomology* 43: 38–42.
- Emeljanov, A.F. & Shcherbakov, D.E. (2000). Kinnaridae and Derbidae (Homoptera, Fulgoroidea) from the Dominican amber. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 2000 (7): 438–448.
- Fennah, R.G. (1950a). Fulgoroidea of Fiji. *Berenice P. Bishop Museum Bulletin* 202: 122 pp.
- Fennah, R.G. (1950b). A generic revision of the Achilidae (Homoptera: Fulgoroidea). *Bulletin of the British Museum (Natural History)* 1: 170 pp.
- Fennah, R.G. (1952). On the generic classification of Derbidae (Fulgoroidea), with descriptions of new Neotropical species. *Transactions of the Royal Entomological Society of London* 103, 4: 109–170.
- Fennah, R.G. (1956). Homoptera: Fulgoroidea. *Insects of Micronesia* 6(3): 39–212.
- Fennah, R.G. (1958). Fulgoroidea od South-Eastern Polynesia. *Transactions of the Royal Entomological Society of London* 110, 6: 117–220.
- Fennah, R.G. (1970). Fulgoroidea (Homoptera) from Rennell and Bellona Islands. *Natural History of Rennell Island, British Solomon Islands* 6: 43–85.

- Fennah, R.G. (1971) Homoptera: Fulgoroidea. Supplement. *Insects of Micronesia* 6(8): 563–609.
- Flerov, K.K., E.I. Belyaeva, N.M. Yanovskaya, A.A. Gubeev, I.M. Novodvorskaya, V.C. Kornilova, N.S. Shevyreva, E.N. Kurochkin, V.V. Zherikhin, V.M. Chikvadze, G.G. Martinson, N.V. Tolstikova, A.L. Chepalyga & Fot'yanova, L.I. (1974) *Zoogeografia paleogena Azii*. [Zoogeography of Paleogene of Asia.] Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR. 302 pp. Nauka, Moskva. [In Russian]
- Hall, R. (1996) Reconstructing Cenozoic SE Asia. pp. 153–184. In: Hall, R. & Blundell, D. (Eds.) Tectonic Evolution of Southeast Asia. *Geological Society Special Publication* 106: xiii + 566 pp.
- Hooker, J.J. (1998) Mammalian Faunal Change Across the Paleocene–Eocene Transition in Europe. pp. 428–450. In: Aubry, M.-P., Lucas, S. & Berggren, W.A. (Eds.) *Late Palaeocene–Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records*. xv + 513 pp. Columbia University Press, New York.
- Hooker, J.J. (2000) Paleogene mammals: crises and ecological change. pp. 333–349. In: Culver, S.J. & Rawson, P.F. (Eds.) *Biotic Response to Global Change. The Last 145 Million Years*. xiii + 501 pp. Cambridge University Press, Cambridge. The Natural History Museum, London.
- Krassilov, V.A. (2003) *Terrestrial Palaeoecology and Global Change*. Russian Academic Monographs 1. xvi + 464 pp. Pensoft, Sofia–Moscow.
- Larsson, S.G. (1978) Baltic Amber—A Paleontological Study. *Entomograph*, I. 192 pp. Scandinavian Scientific Press, Klampenborg.
- Martins-Neto, R.G., Gallego, O.F. & Melchor, R.N. (2003). The Triassic insect fauna from South America (Argentina, Brazil and Chile): a checklist (except Blattellera and Coleoptera) and descriptions of new taxa. pp. 229–256. In: Proceedings of the 2nd Congress on Palaeoentomology “Fossil Insects”, Kraków, Poland, 5 – 9 September, 2001. *Acta zoologica cracoviensia* 46 (Supplement – Fossil Insects). 440 pp.
- Metcalf, Z.P. (1938) The Fulgorina of Barro Colorado and Other Parts of Panama. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 82(5): 277–423, Pls. 1–23.
- Metcalf, Z.P. (1945) Part 4. Derbidae. General Catalogue of the Hemiptera. pp. 1–212, 251–252. Smith College, Northampton, Massachusetts, U.S.A.
- Milner, A.C., Milner, A.R. & Evans, S.E. (2000) Amphibians, reptiles and birds: a biogeographical review. pp. 361–332. In: Culver, S.J. & Rawson, P.F. (Eds.) *Biotic Response to Global Change. The Last 145 Million Years*. xiii + 501 pp. Cambridge University Press, Cambridge. The Natural History Museum, London.
- Muir, F. (1913) Part II. Derbidae. On Some New Species of Leaf-Hoppers. *Report of Work of the Experiment Station of the Hawaiian Sugar Planters' Association*, Entomological Series, Bulletin 12: 28–92.
- Muir, F. (1917) The Derbidae of the Philippine Islands. *The Philippine Journal of Sciences*, D. General Biology, Ethnology and Anthropology 12(2): 49–105.
- Muir, F. (1918a) Notes on the Derbidae in the British Museum Collection. – I. Zoraidinae. *Entomologist's Monthly Magazine* 54: 173–177, 202–207.
- Muir, F. (1918b) Notes on the Derbidae in the British Museum Collection. – II. Derbinae. *Entomologist's Monthly Magazine* 54: 228–243.
- Muir, F. (1922) An interesting new Derbid genus (Homoptera). *Proceedings of the Hawaiian Entomological Society* 5: 89–90.
- Muir, F. (1923) On the Classification of the Fulgoroidea. *Proceedings of the Hawaiian Entomological Society* 5(2): 205–268.
- Muir, F. (1930) On the Classification of the Fulgoroidea. *Annals and Magazine of Natural History* (10) 6: 461–478.
- O'Brien L.B. (2002) The Wild Wonderful World of Fulgoromorpha. pp. 83–102. In: Holzinger, W. (Ed.) *Zikaden – Leafhoppers, Planthoppers and Cicadas* (Insecta: Hemiptera: Auchenorrhyncha), *Denisia* 4: 556 pp.
- O'Brien, L.B. & Wilson, S.W. (1985) Planthopper Systematics and External morphology pp. 61–102. In: Nault, L.R. & Rodriguez, J.G. (Eds.) *The Leafhoppers and Planthoppers*. 500 pp. John Wiley & Sons, New York.
- O'Brien, L.B. (1991) Suborder Auchenorrhyncha. pp. 77–85. In: Stehr, F.W. (Ed.) *Immature Insects*. Vol. 2. xiv + 754 pp. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Pinto, I.D. (1956) Arthropodes da Formação Santa Maria (Triássico Superior) do Rio Grande do Sul, com notícias sobre alguns restos vegetais. *Boletim Societad Brasileira de Geologia* 5(1): 79–95.
- Poinar Jr., G.O. & Poinar, R. (1999) *The Amber Forest: A Reconstruction of a Vanished World*. 216 pp. Princeton University Press.
- Prothero, D.R. (1994) *The Eocene–Oligocene Transition. Paradise Lost*. xvii + 291 pp. Columbia University Press, New York.
- Sloan, L.C. & Thomas, E. (1998) Global Climate of the late Palaeocene Epoch: Modeling the Circumstances Associated with the Climatic “Event”. pp. 138–157. In: Aubry, M.-P., Lucas, S. & Berggren, W.A. (Eds.) *Late Palaeocene–Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records*. xv + 513 pp. Columbia University Press, New York.
- Stucky, R.K. (1992) Mammalian Faunas in North America of Bridgerian to Early Arikarean “Ages” (Eocene to Oligocene). pp. 464–493. In: Prothero, D.R. & Berggren, W.A. (Eds.) *Eocene – Oligocene Climatic and Biotic Evolution*. xiv + 568 pp. Princeton University Press, Princeton.
- Szadziewski, R. (1988) Biting midges (Diptera, Ceratopogonidae) from Baltic amber. *Polskie Pismo entomologiczne* 58: 3–283.
- Szwedo, J. (2002) Amber and amber inclusions of planthoppers, leafhoppers and their relatives (Hemiptera, Archaeorrhyncha et Clypeorrhyncha). pp. 37–56. In: Holzinger W. (Ed.) *Zikaden – Leafhoppers, Planthoppers and Cicadas* (Insecta: Hemiptera: Auchenorrhyncha), *Denisia*, 4: 556 pp.
- Szwedo, J. (2004) A new Derbidae planthopper *Copalinges chiapasensis* gen. et sp. nov. from Oligocene/Miocene Mexican amber (Hemiptera: Fulgoromorpha). *Polskie Pismo entomologiczne* 73: 291–298.
- Szwedo, J., Bourgoin, T. & Lefebvre, F. (2004) *Fossil Planthoppers (Hemiptera: Fulgoromorpha) of the*

- World. An annotated catalogue with notes on Hemiptera classification.* 208 pp. Studio S1, Warszawa.
- Szwedo, J. & Ross, A.J. (2003) *Cedusa baylissae* sp. nov. from Oligocene/Miocene Mexican amber (Hemiptera: Fulgoromorpha: Derbidae). *Annals of the Upper Silesia Museum, Entomology* 12: 37–46.
- Ushakov, S.A. & Yasamanov, N.A. (1984) *Dreif materikov i klimaty Zemli. [Drift of continents and climates of the Earth.]* 206 pp. Mysl', Moskva.
- Vakhrameev, V.A., Dobruskina, I.A., Zaklinskaya, E.D. & Meyen, S.V. (1970) *Paleozoiskie i mezozoiskie flory Evrazii i fitogeografia etogo vremeni. [Palaeozoic and Mesozoic floras of Eurasia and phytogeography of this time.]* Trudy Geologicheskogo Instituta 208: 426 pp. [In Russian]
- Weitschat, W. & Wichard, W. (1998) *Atlas der Pflanzen und Tiere im Baltischen Bernstein.* 256 pp. Pfeil-Verlag, München.
- Wilson, S.W., Mitter, Ch., Denno, R.F. & Wilson, M.R. (1994) Evolutionary Patterns of Host Plant Use by Delphacid Planthoppers and Their Relatives. pp. 7–113. In: Denno, R.F. & Perfect, T.J. (Eds.). *Planthoppers. Their Ecology and Management.* x + 799 pp. Chapman & Hall, New York – London.
- Wing, S.L. & Sues, H.D. (1992) Mesozoic and Early Cenozoic Terrestrial Ecosystems. pp. 327–416. In: Behrensmeier, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D. & Wing, S.L. (Eds.) *Terrestrial Ecosystems Through Time. Evolutionary Palaeoecology of Terrestrial Plants and Animals.* The Evolution of Terrestrial Ecosystems Consortium. xix + 568 pp. The University of Chicago Press, Chicago & London.
- Wolfe, J.A. (1985) Distribution of major vegetational types during the Tertiary. *Geophysical Monographs* 32: 357–375.
- Yang, C.-T. & Wu, R.-H. (1993) *Derbidae of Taiwan (Homoptera: Fulgoroidea).* vi + 230 pp. Department of Entomology, National Chung Hsing University, Taichung, Taiwan, ROC.
- Yang, C.-T., Yeh, W.-B. (1994) Nymphs of Fulgoroidea (Homoptera: Auchenorrhyncha) With Descriptions Of Two New Species And Notes On Adults Of Dictyopharidae. *Chinese Journal of Entomology, Special Publication No. 8.* iv + 189 pp. The Entomological Society of Republic of China, Taipei, Taiwan, ROC.
- Zherikhin, V.V. (1970) Zoogeograficheskie svyazi paleogenovykh nasekomykh. [The zoogeographical relationships of Palaeogene insects.] *Doklady na XXII ezhгодnom chtenii pamyati N.A. Kholodkovskogo, 4 aprelya 1969 g.:* 29–88. Nauka, Leningrad. [In Russian]
- Zherikhin, V.V. (1971) The zoogeographical relationships of Baltic amber Rhynchophora (excluding Scolytidae). *Trudy XIII Mezhdunarodnogo Entomologicheskogo Kongressa, Moskva, 1–9 avgusta 1968 g.,* 1: 322–323. Nauka, Leningrad.

Accepted for publication July 2004