The first fossil Bothriocerinae from Eocene Baltic amber with notes on recent taxa (Hemiptera, Fulgoromorpha, Cixiidae)

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With 14 figures

Abstract

The first fossil representative of Bothriocerinae (Hemiptera: Fulgoromorpha: Cixiidae) from Eocene Baltic amber is described. This small group is currently distributed only in the New World. The fossil presents the evidence of a wider distribution of this group in the past. *Bothriobaltia pietrzeniukae* gen. and sp. n. is described and illustrated. Fossil record of the family, paleogeography of the Eocene, distribution pattern, phylogeny and ecology of the group in view of fossil record are discussed.

Key words: *Bothriobaltia pietrzeniukae* gen. and sp. n., Bothriocerinae, Eocene Baltic amber, zoogeography, paleogeography, phylogeny, morphology

Introduction

Fossil representatives of the family Cixiidae have rarely been described (Szwedo 2002); the representatives of this family enter the fossil record in the Jurassic (Fennah 1961). Bothriocerinae have not been described from fossil resins yet, with the only exception of an unnamed specimen from Oligocene/Miocene Dominican amber, figured in Schlee (1990). Some other specimens of Bothriocerinae in the same resin are stored in the Natural History Museum, London (A. J. Ross, personal communication).

The specimen described below is one of Gustav Carl Berendt's historic collection, housed in the Paläontologisches Institut der Humboldt-Universität in Berlin. The subfamily Bothriocerinae is regarded as one of the oldest groups of Cixiidae planthoppers, displaying, according to Emeljanov (1989), peculiar and primitive characters.

Taxonomic note

Only two recent genera have been ascribed to the subfamily Bothriocerinae (Emeljanov 1989), but in Wilson et al. (1994) some species representing Cixiinae (species of the genera *Achaemenes* Stål, *Brixia* Stål and *Nymphocixia* Van Duzee) are mistakenly listed as belonging to Bothriocerinae.

The genus *Bothriocera* Burmeister, 1835 comprises over 40 species. The taxonomic status of some of them is doubtful and needs reconsideration. The most obscure species is *Bothriocera westwoodi* (Stål, 1856), described from Mexico. Stål's (1856) original description is brief and not illustrated. The first illustration of this species is to be found in Fowler (1904). Specimens ascribed to this species were discussed by Metcalf (1938), who presented drawings of male genitalia, and Caldwell (1943), who discussed the coloration, and interpreted male genitalia of the forms ascribed to *B. westwoodi* Stål. According to Kramer (1983) the type is no longer extant, which precludes restudy.

The genus *Bothrioceretta* was established by Caldwell (1950) for the species: *nigra* (Fowler, 1904) and *albidipennis* (Fowler, 1904). In 1971 Fennah, described the subgenus *Adanella*, within the genus *Bothriocera* Burmeister, 1835, to which he ascribed the species: *albidipennis* (Fowler, 1904), *excelsa* (Fowler, 1904), *nigra* (Fowler, 1904) and *pellucida* (Fowler, 1904). Emeljanov (1989) has elevated the status of the subgenus *Adanella* to the generic level. Regarding the characters given by Caldwell (1950) and Fennah (1971), the species included by the latter to *Adanella* should be placed in *Bothrioceretta*.

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List of species ascribed to the genus *Bothrioceretta* Caldwell is as follow:

Bothrioceretta Caldwell, 1950: Caldwell 1950: 289

Type-species: *Bothriocera nigra* Fowler, 1904: 84, Table IX, Figs 19, 19a

Adanella Fennah, 1971: Fennah 1971: 312

Type-species: *Bothriocera albidipennis* Fowler, 1904: Fowler 1904: 84, by original designation by Fennah 1971: 313

albidipennis Fowler, 1904: Fowler 1904: 84, Table IX, Figs 17, 17a, 18; "Mexico, Omilteme in Guerrero"
excelsa Fowler, 1904, comb. n.: Fowler 1904: 83, Table IX, Figs 15, 15a; "Mexico, Amula, Xucumanatlan, Sierra de las Aguas Escondidas, and Omilteme in Guerrero, 6000 to 8000 feet"
nigra Fowler, 1904: Fowler 1904: 84, Table IX, Figs 19, 19a; "Mexico, Cuernavaca in Morelos"
pellucida Fowler, 1904, comb. n.: Fowler 1904: 83, Table IX, Figs 16, 16a; – "Mexico, Omilteme in Guerrero 8000 feet"

The following key could be used to recognize genera ascribed to Bothriocerinae

1(2) Transverse carina on vertex present and parallel to posterior margin of head. Subantennal carina not complete **3**
2(1) Transverse carina of vertex absent or strongly shifted to posterior margin, creating small areolets in posterior angles of vertex. Subantennal carina complete. Anterior margin of maxillary plate convex ..... ***Bothriocera* Burmeister, 1835**
3(4) Hind leg tibia with small lateral spines. Anterior margin of maxillary plate concave. Tegmen with single vein RA, wing with vein RP not bifurcated. Eocene, Baltic amber ..... ***Bothriobaltia* gen. n.**
4(3) Hind leg tibia without lateral spines. Anterior margin of maxillary plate straight. Tegmen with vein RA bifurcated. Medioventral process of pygofer distinctly elongated ..... ***Bothrioceretta* Caldwell, 1950**

Systematics

Bothriobaltia gen. n.

Type-species: *Bothriobaltia pietrzeniukae* sp. n., Eocene Baltic amber, here designated. Gender: feminine.

Etymology. Combination of the names "*Bothriocera*" – a genus of cixiid planthopper and "Baltic" name of the sea.

Diagnosis. Transverse carina of vertex present, shifted anteriad, in comparison to *Bothrioceretta* Cald. Anterior margin of maxillary plate convex (similarly to *Bothriocera* Burm.). Single vein RA on tegmina (bifurcated in recent genera), single vein RP on wings (bifurcated in recent genera). Hind tibia with four small lateral spines (no lateral spines in recent forms). Anal tube concave, with two lateral lobes joined behind by the turned down apical margin of anal tube. Medioventral process of pygofer not strongly elongated (similarly to *Bothriocera* Burm.).

Description. Head in dorsal view narrower than pronotum, with vertex divided by anteriad transverse carina. Lateral margins of vertex elevated, subparallel. Anterolateral margins of frons distinctly protruded, converging ventrad in lower portion. Median carina of frons distinct, bifurcated in the upper portion. Median ocellus prominent. Lateral ocellus prominent, located above antenna in front of eye. Antennae sunk in preocular cavities, placed anteriad of compound eyes. Subantennal carina not complete, reaching posteriorly the ventral margin of compound eye. Anterior margin of maxillary plate concave. Rostrum long, reaching beyond hind leg coxae; apical segment about as long as subapical segment (Figs 1 & 2).

Pronotum narrow, mesonotum rhomboid, with three longitudinal, almost parallel, elevated carinae.

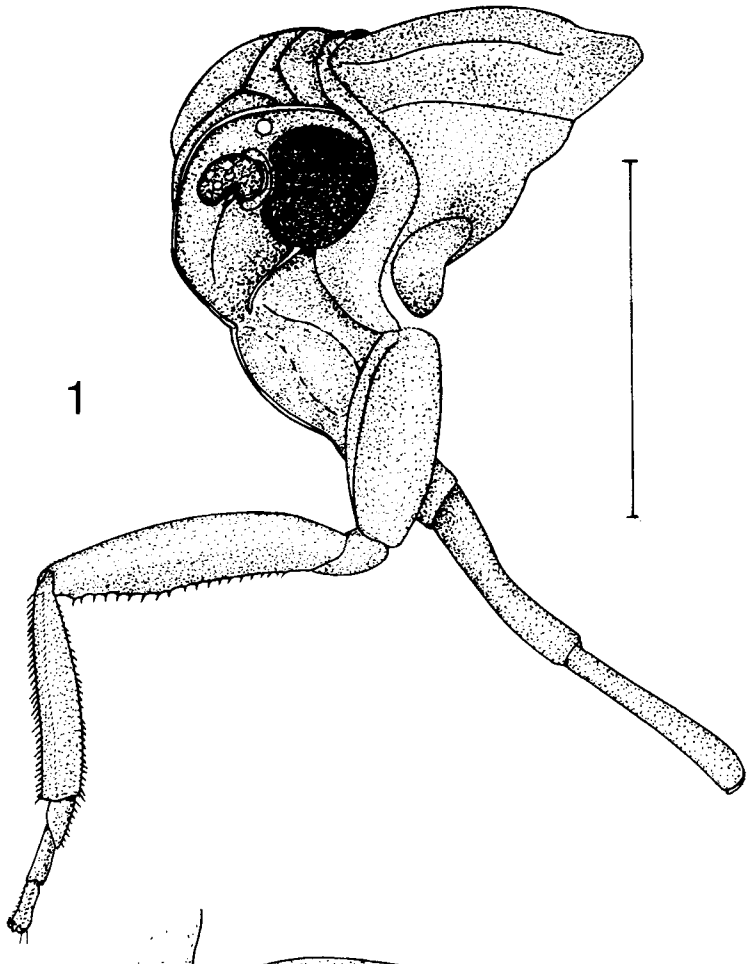
Tegmina semicoriaceous, with clavus reaching the middle of the posterior margin of tegmen; stigma distinct, setiferous tubercles absent. Tegmen venation typical of subfamily members. Veins R and M separate from one point; transverse veinlet uniting them with CuA starts at the same level; vein RA single (Figs 3, 13 & 14).

Wing hyaline, with single vein ScRA (Figs 4, 13 & 14).

Fore femora with carina on the internal surface obsolete and ventral projection of femur not distinct (Fig. 5).

▶

Fig. 1. *Bothriobaltia pietrzeniukae* gen. and sp. n. Anterior part of body in left latero-dorsal view. Scale bar: 1 mm.
Fig. 2. *Bothriobaltia pietrzeniukae* gen. and sp. n. Head in right latero-ventral view. Scale bar: 1 mm.
Fig. 5. *Bothriobaltia pietrzeniukae* gen. and sp. n. Left fore leg. Scale bar: 0.5 mm.
Fig. 10. *Bothriocera* sp., specimen from Argentina, left fore leg. Scale bar: 0.5 mm.
Fig. 11. *Bothriocera signoreti*, outer view of left fore leg (redrawn form Myers, 1929).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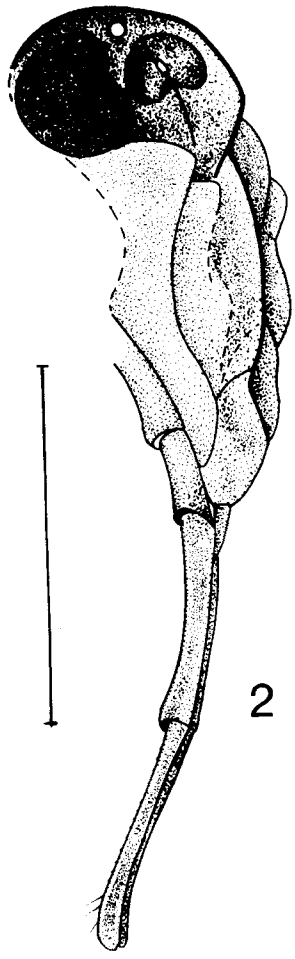
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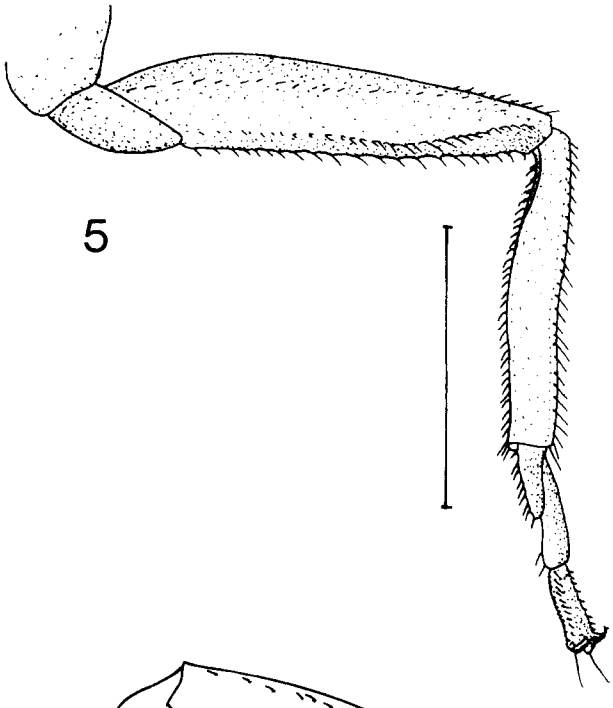
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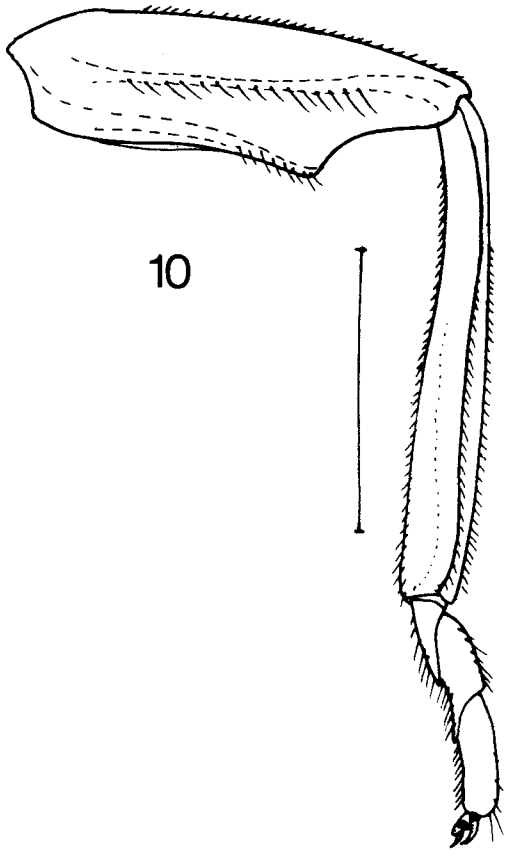
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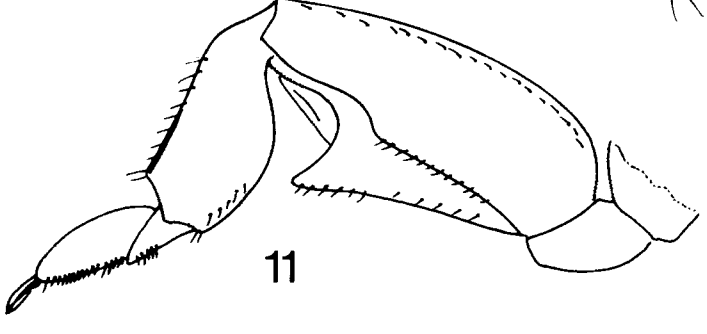
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Hind tibia twice as long as femur, with four small but distinct lateral spines (Fig. 6).

Pygofer with a distinct medioventral process. Anal tube without elongated ventral projections, with posteroventral margins united. Aedeagus with elongated shaft and a small apical process on the right side (Fig. 8).

***Bothriobaltia pietrzeniukae* sp. n.**

Etymology. Named in honour of Dr. Erika Pietrzeniuk, Curator of amber collection, Paläontologisches Institut, Humbold-Universität zu Berlin.

Diagnosis. Tegmina without colour pattern. Shaft of aedeagus, on the right side, with a small apical process projecting ventrad; major flagellar process stout in right lateral view. Styles with a narrow shaft, distinctly upturned dorsally, its apical portion trapezoid, the upper margin convex. Anal tube distinctly convex on the ventral margin, in lateral view narrowest at base.

Description. Total length about 4.8 mm, length of body: 3.2 mm.

Head narrower than pronotum, with transverse carina dividing vertex into two compartments, shifted anteriad, parallel to the hind margin of vertex. Lateral margins of vertex slightly elevated above the level of disc and slightly converging anteriad. Anterolateral margins of frons distinctly elevated above the level of face and converging at the level of half of anteclypeus length. Median carina of frons strongly raised, bifurcated in the upper portion; this bifurcation designates anterior margin of vertex (Figs 1 & 2). Median ocellus prominent. Epistomal suture parabolic as in *Bothriocera* Burm., directed basad, anterior angles of postclypeus lifted. Lateral margins of head elevated, forming deep cavities that shield bases of antennae. Lateral ocellus prominent, located above antenna in front of eye. Anterior portion of subantennal carina not reaching anterolateral margins of head; posterior end reaching the ventral margin of compound eye. Anterior margin of maxillary plate concave, slightly bent in the lower portion. Compound eye slightly higher than wide, with a distinct concavity in the anterior part. Antennae sunk in preocular cavities, scape short, pedicel about as wide as high, with a distinct concavity, flagellum about 0.16 mm long. Rostrum 1 mm long, reaching beyond hind coxae, apical segment 0.44 mm long, slightly shorter than subapical segment (Figs 1 & 2).

Pronotum 0.06 mm long in the midline, collar-like, narrow.

Mesonotum 0.88 mm long in the midline, tricarinate. Posterior angle of mesonotum angulate. Mesonotal disc slightly convex in the anterior portion, almost flat in the middle portion, slightly concave in at scutellum, delicately wrinkled. Lateral portion of mesonotum concave (Figs 1 & 2).

Tegula about twice as wide as long, delicately carinated.

Tegmina 3.76 mm long, transparent, without colour markings, 2.3 times longer than wide. Clavus reaching the middle of the posterior margin of tegmen. Stigma distinct, semicircular, with corrugated texture, typical of representatives of subfamily. Longitudinal veins R and M, together with transverse veinlet uniting them with CuA, branching at the same level. Vein RA single, RP with three branches, MA with three branches, MP with two branches. CuA bifurcates slightly beyond the bifurcation of claval veins. CuA_2 and CuP united by two transverse veinlets. Claval veins PCu and A_1 united at the level of midpoint of claval suture (Figs 3, 13 & 14).

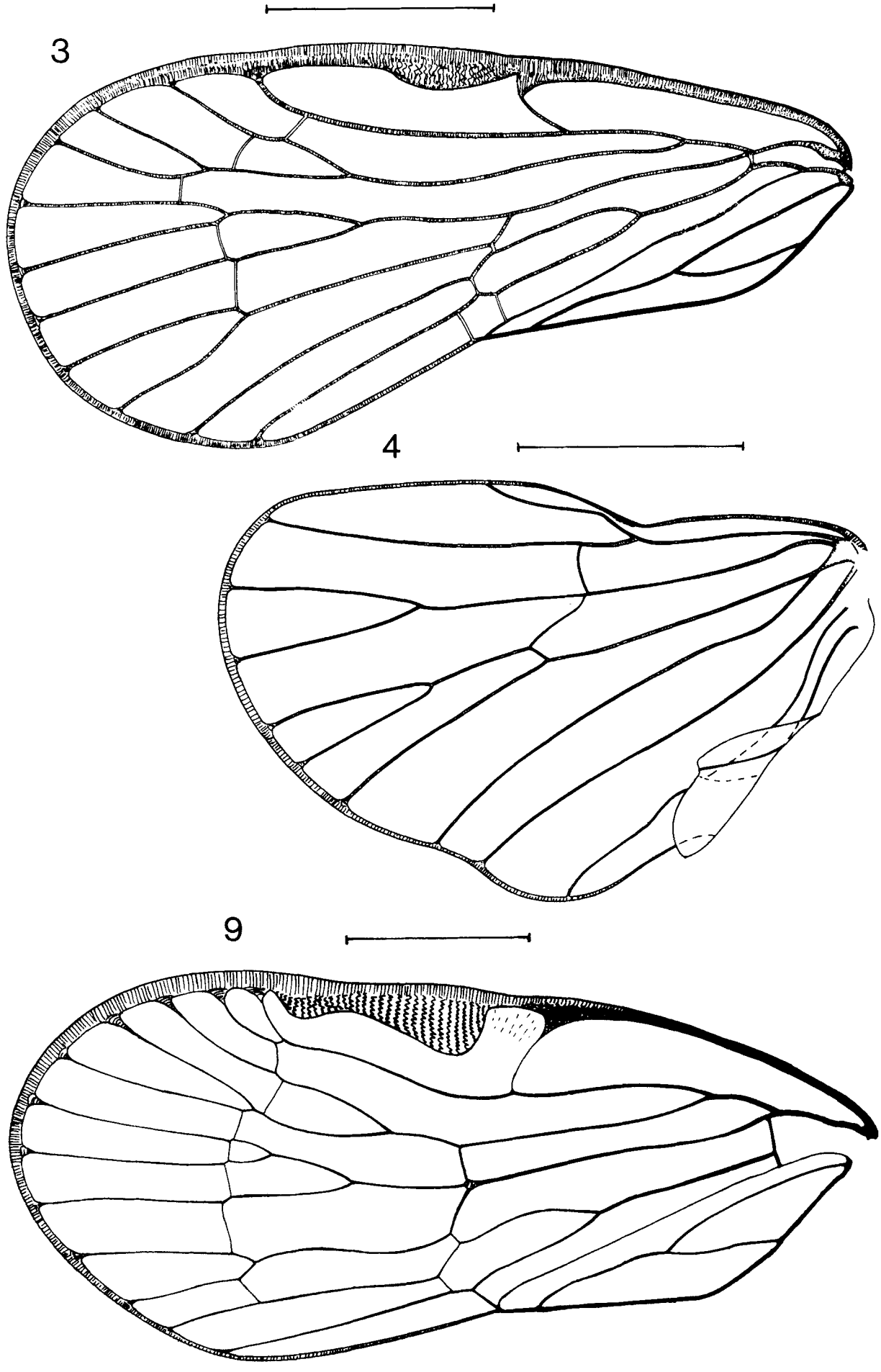
Wing wide, its shape typical of the subfamily, hyaline. Vein ScRA single, reaching the wing margin distinctly before its apex. Vein RP single, vein M bifurcated, vein CuA with three branches. Veins CuP and PCu not bifurcated; anal veins not bifurcated (Figs 4, 13 & 14).

Fore legs with quite long femur (0.72 mm), longer than tibia (0.56 mm long), quadrangular in cross section. Carina on the internal surface of femur obsolete, ventral projection of femur not distinct, ventral margins with rows of short, stout setae. Tibia quadratic in cross section, with margins covered with rows of setae. Basitarsomere shorter (0.12 mm), second and apical tarsomeres of subequal length (0.16 mm), claws and arolium distinct (Figs 1, 5).

Hind coxa with distinct meracanthal spine, trochanter quite short, femur 0.94 mm long, slightly thickened. Tibia 1.8 mm long, twice as

►

Fig. 3. *Bothriobaltia pietrzeniukae* gen. and sp. n. Left tegmen. Scale bar: 1 mm.
Fig. 4. *Bothriobaltia pietrzeniukae* gen. and sp. n. Right wing. Scale bar: 1 mm.
Fig. 9. *Bothriocera* sp., specimen from north Argentina, left tegmen. Scale bar: 1 mm.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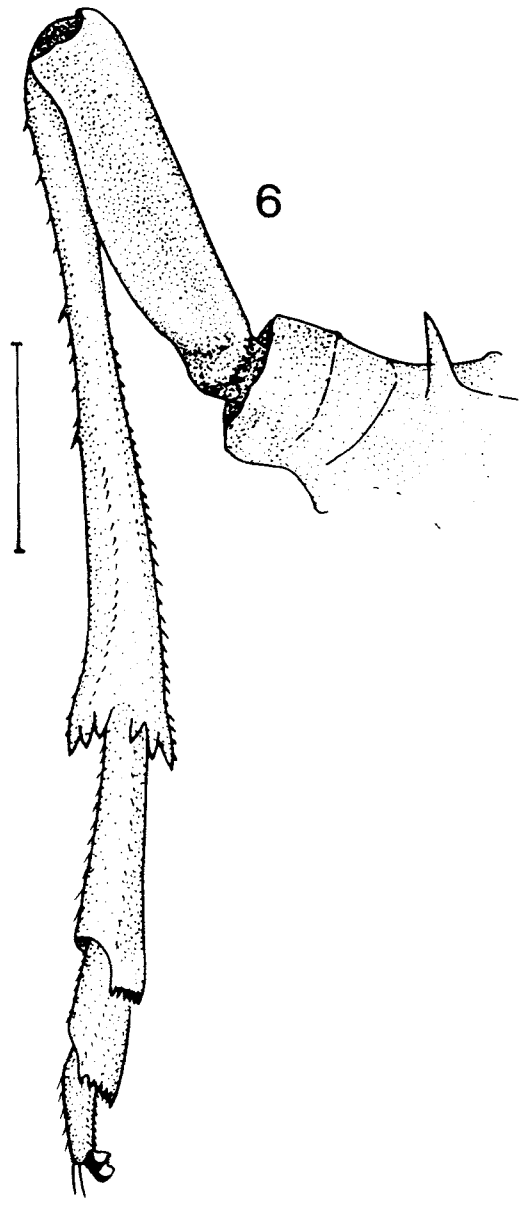

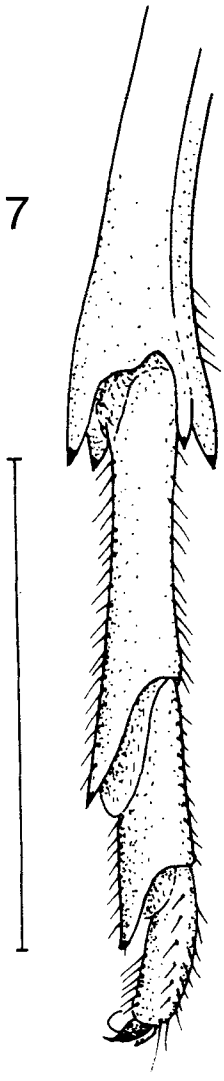

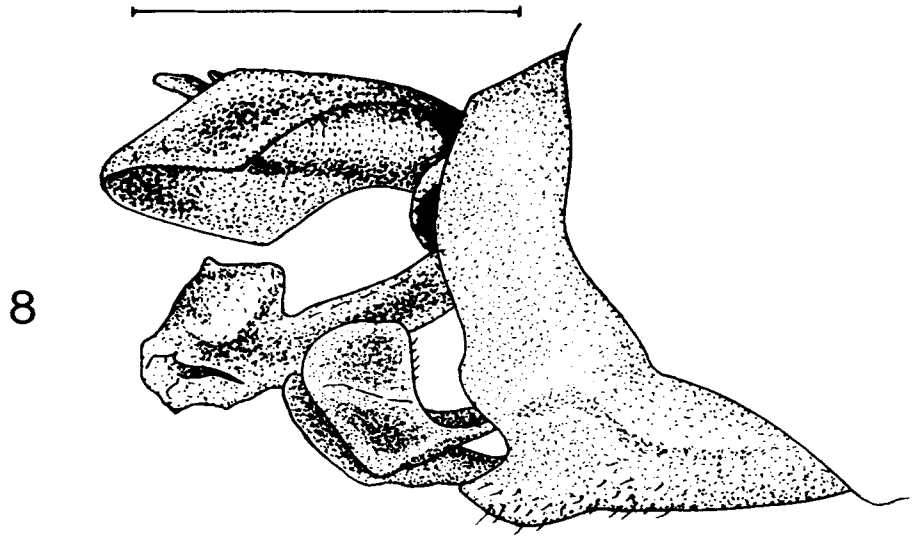

Fig. 6. *Bothriobaltia pietrzeniukae* gen. and sp. n. Right hind leg. Scale bar: 0.5 mm.
Fig. 7. *Bothriobaltia pietrzeniukae* gen. and sp. n. Right hind tarsus. Scale bar: 0.5 mm.
Fig. 8. *Bothriobaltia pietrzeniukae* gen. and sp. n. Male genital block in right lateral view. Scale bar: 0.5 mm.

long as femur, with four small but distinct lateral spines, quadrangular in cross section, with margins covered with rows of short setae, six apical spines with distinct diastema: 3 + 3 (Fig. 6). First tarsomere longest (0.44 mm), with seven apical spines, second tarsomere 0.34 mm long, with 2 lateral spines and four medial spines, medial spines with short setae; apical tarsomere shortest (0.2 mm), with distinct rows of short, stout setae delimiting plantar surface. Claws and arolium distinct, two longer apical chaete present (Figs 6, 7).

Pygofer with a distinct medioventral process, covered with short setae, the posterior margin of pygofer slightly curved posteriad in lateral view. Anal tube 0.46 mm long, without elongated ventral projections, ventral margins united posteriad, ventral margin concave, anal tube narrowest at base in lateral view. Styles distinct, club-like, with a narrow shaft, distinctly upturned dorsally, its apical portion trapezoid, mildly bent, with the upper margin convex, the posterior margin with a few setae. Aedeagus with a somewhat longer shaft, with a small apical process projecting ventrad on the right side, major flagellar process stout in right lateral view (Fig. 8).

Material. Holotype: male, Baltic amber, coll. G. C. Berendt, MB.I. 1983, Paläontologisches Museum des Humboldt-Universität, Berlin. Specimen quite well preserved, right fore and mid legs, and left mid leg lacking. Left hind tarsus partly destroyed. The piece of amber is dark coloured, polished, with some cracks and bubbles of air.

Discussion

Cixiidae belongs to the most ancient families among Fulgoromorpha, and Bothriocerinae seems to be the most basal and derivative subfamily. It was suggested that Bothriocerinae are related with Cixiinae: Oecleini (Emeljanov 1989, 1997). On the other hand, Cixiidae might be a paraphyletic taxon and the place of Bothriocerinae within Cixiidae is currently in discussion and not certain (Holzinger et al. 2001).

Bothriobaltia gen. n. differs from the recent genera regarding tegmen venation, wing venation and some characters of the head capsule. Presence of transverse carina on vertex is a common character of *Bothriobaltia* gen. n. and *Bothrioceretta* Caldwell. It should be plesiomorphic feature, but in *Bothriobaltia* gen. n. the transverse carina is placed more anteriad than in *Bothrioceretta*. Median carina of the facial part is bifurcated in the upper portion, bifurcation is distinct, the branches reach lateral carinae of head, similar to some representatives of genera *Bothriocera* Burmeister and *Bothrioceretta*. Subantennal carina in *Bothriobaltia* gen. n. is not united with anterolateral carina of head, it is distinctly removed from anterolateral carina of head (probably plesiomorphic condition), in *Bothriocera* it seems to be continuation of the latter, in *Bothrioceretta* the anterior margin of subantennal carina blurs before it joins anterolateral carina. In *Bothriobaltia* gen. n. the posterior margin of subantennal carina reaches the ventral margin of compound eye; in *Bothriocera* it reaches the lower portion of the anterior margin of compound eye, and in *Bothrioceretta* the posterior end does not touch compound eye, but runs near its margin and turns ventrad, approaching the hind margin of head. An important feature of *Bothriobaltia* is the concave shape of the anterior margin of maxillary plate. This line is convex in *Bothriocera* and straight *Bothrioceretta*. These features, in recent representatives of the group, have been reported formerly by Fennah (1971).

Tegmina of *Bothriobaltia* gen. n. are similar to these of *Bothrioceretta* in respect of length/width ratio, but the clavus reaches the midpoint of the posterior margin of tegmen, similar to *Bothriocera*. Regarding tegmen venation, *Bothriobaltia* gen. n. differs from other Bothriocerinae (Fig. 11) in single vein RA, the basal portion of longitudinal veins R and M is similar to that of *Bothrioceretta* – these veins, together with transverse veinlet uniting them with Cu, begin at one point. The exceptional characters of *Bothriobaltia* gen. n. are the quite small stigma, but with corrugated texture, typical of Bothriocerinae, and two transverse veinlets uniting CuA_2 and CuP (Figs 3, 10). *Bothriobaltia* gen. n. differs from recent genera in single vein RP on wing.

Fore femur features of *Bothriobaltia* gen. n. – ventral projection not distinct and obsolete internal carina – seem interesting, because in recent *Bothriocera* the fore legs are distinctly fossorial (Fig. 11); femoral ventral projection is distinct in nymphs and adults (Figs 11 & 12). Representatives of both recent genera have no the lateral spines on the hind tibiae, small spines are present in *Bothriobaltia* gen. n.

Genital characters of *Bothriobaltia* gen. n. are typical of the subfamily. Regarding the features of aedeagus, the small apical process of aedeagal

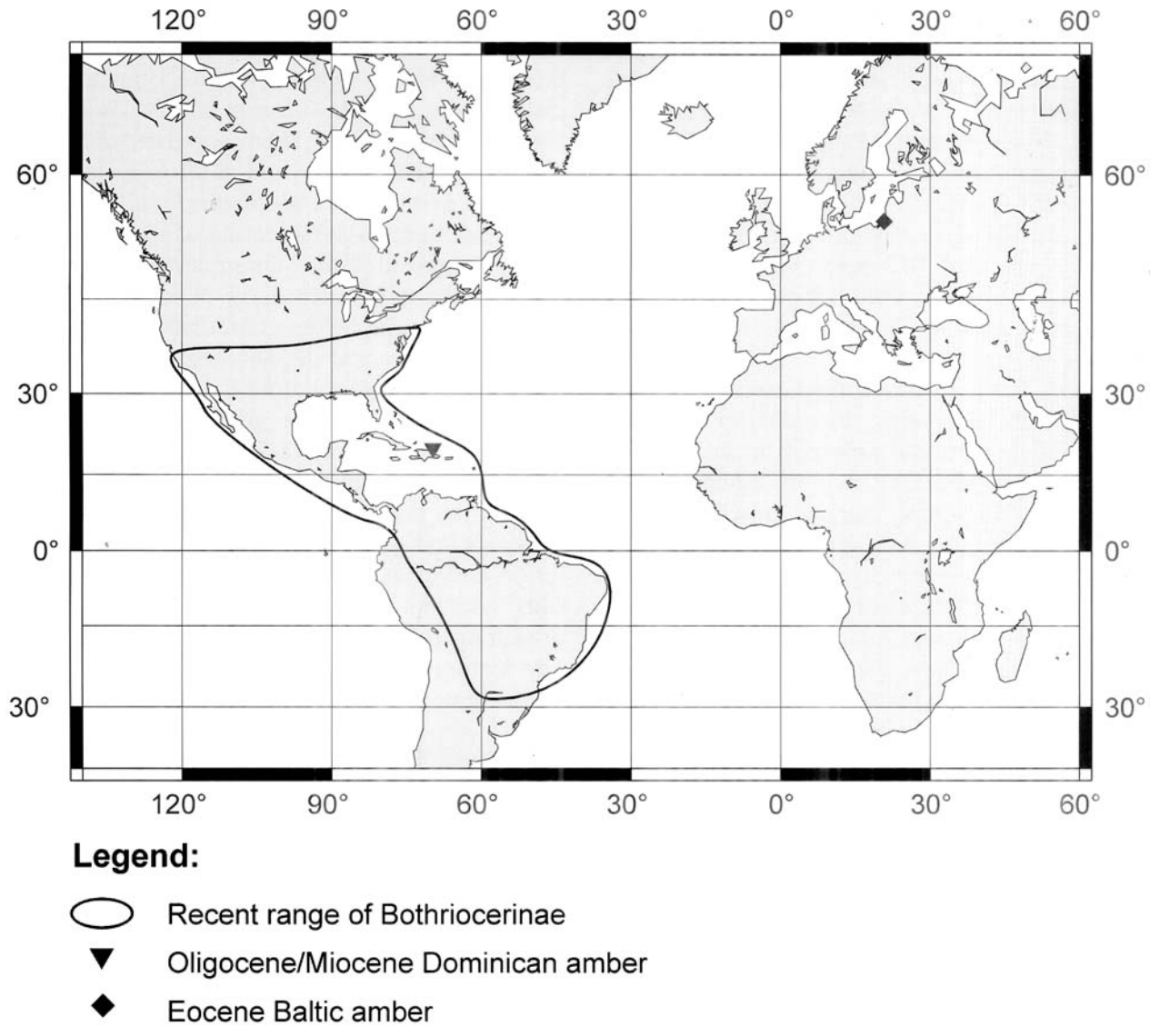

Fig. 12. Recent distribution of Bothriocerinae and localities of fossil records.

shaft, together with the lack of additional processes and appendages of aedeagal flagellum, place *Bothriobaltia* gen. n. close to *Bothrioceretta*.

Transverse carina of vertex is undoubtedly a plesiomorphic character, the lack of additional structures of aedeagus also seems a primitive state. These features relate *Bothriobaltia* gen. n. to *Bothrioceretta*.

Recently Bothriocerinae are distributed in southern parts of North America, Central America including the islands of Carribean region, and northern parts of South America (Metcalf 1936, Caldwell 1943, 1950a, 1950b, Caldwell & Martorell 1951, Fennah 1943, 1949, 1971, Kramer 1983), reaching to northern Argentina on the south (Fig. 13). The discovery of a representative of this subfamily in Baltic Amber is unexpected and very interesting. Representatives of Cixiidae were widespread in the Cretaceous period, but the known fossils do not show any features at marked variance from the corresponding features in modern species. Forms resembling Bothriocerinae has not been reported.

The global climate during the Cretaceous and the Early Cenozoic is thought to have been warmer than on present climatic conditions, and for at least first 10 My of the Eocene a large part of Earth, including continental interiors, had climates with winter temperatures much higher than modern today (Greenwood & Wing 1995). It is worth noting, that during the Eocene, the northern parts of North America, southern parts of Greenland, and the Scandinavian Peninsula were covered with vegetation of warm temperate zone. During warm periods it was the paratropical forest on the south and the microphyllous broadleaved evergreen forest to the north, in cool intervals it was the mixed coniferous forest on north and the microphyllous broadleaved evergreen forest to the south (Wolfe 1985). The

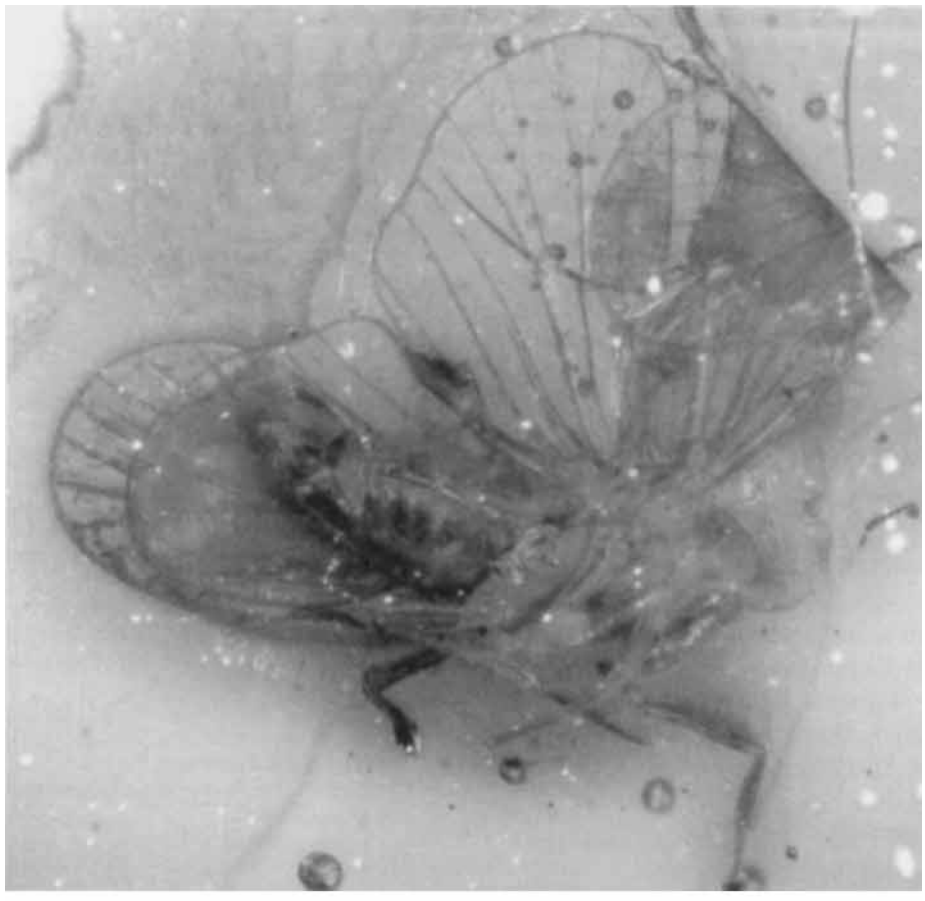

Fig. 13. *Bothriobaltia pietrzeniukae* gen. and sp. n. Right general view.

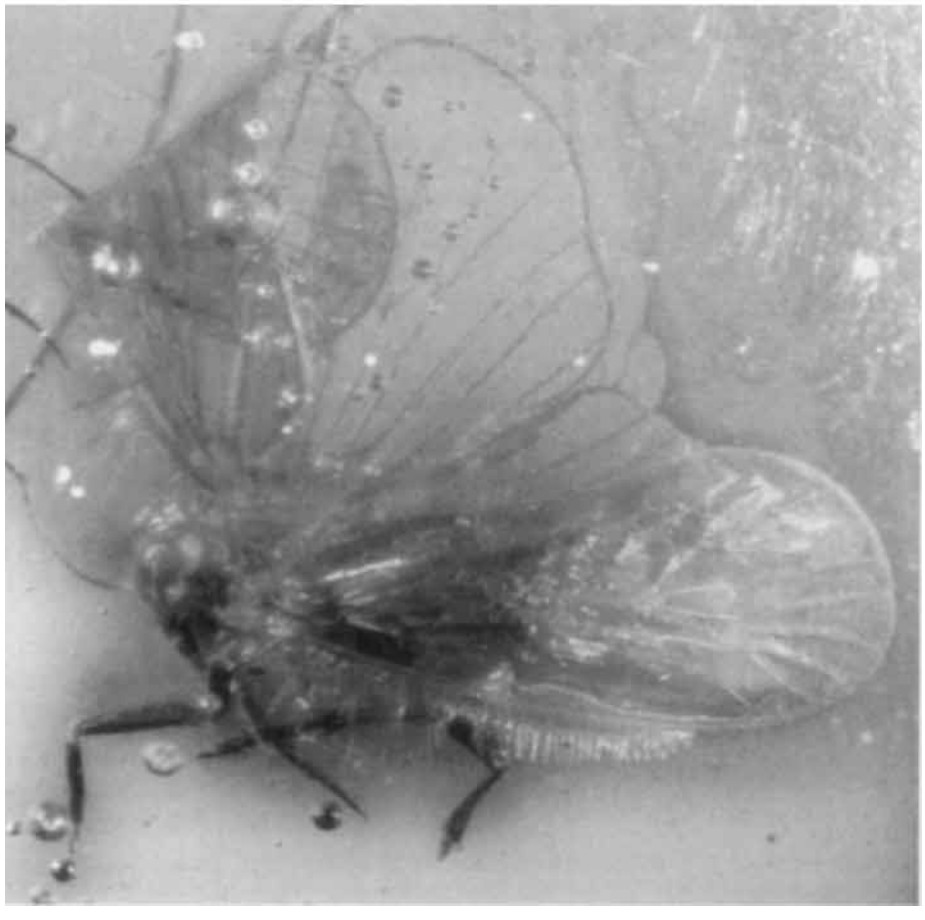

Fig. 14. *Bothriobaltia pietrzeniukae* gen. and sp. n. Left general view.

mixed coniferous forest of the Scandinavian Peninsula was the area where the amber-forest grew. The most important component of this forest was the still mysterious "*Pinus succinifera*" – probably a collective name for resin (amber) producing tree (or trees). Over 200 species of different plants of the amber-forest have been identified (Czeczott 1961, Dahlstrom & Brost 1996, Pielińska 1998), among them also some representatives of the groups regarded as host plants of Bothriocerinae (Wilson et al. 1994). The Eocene amber-forest is regarded as a mixed pine-oak forest, but cypresses (*Chamaecyparis*), thujas (*Thuites*) or *Glyptostrombus* trees, and – on forest margins – date palms (*Phoenix*), magnolias (*Magnolilepis*) and *Cinnamonum* trees were also present. Representatives of the families Poaceae, Commelinaceae, Polygonaceae, Ericaceae and others, ususally herbaceous have also been identified among fossil plants of the amber-forest (Czeczott 1961, Larsson 1978, Krzemińska et al. 1992, Dahlstrom & Brost 1996).

Faunas of North America and Europe were similar and closely related during the Eocene, as it theriological data indicate. For the Lower Eocene the European-North American zoogeographical region was erected, in the Middle and Upper Eocene there were isolated European and North American regions, and their resemblance was gradually decreasing (Flerov et al. 1974). Also insect faunas seem to have been similar, e.g. from Tertiary deposits of Europe and North America common genera are known, like *Hammapteryx* Scudder (Hemiptera: Ricaniidae) or *Pactopus* LeConte (Coleoptera: Throscidae) and many others (Zherikhin 1971, Flerov et al. 1974, Ross, Jarzembowski & Brooks 2000).

During the Eocene, Bothriocerinae could have inhabited the whole region of Europe and North America. Later, in the Oligocene/Miocene, representatives of Bothriocerinae occurred in Caribean region (Schlee 1990, A. J. Ross, personal communication). The question of the place of origin of Bothriocerinae remains unresolved. The recent distribution suggests American origins of the group. It is noteworthy that *Bothrioceretta* is recently distributed in Mexico, and *Bothriocera* is widely distributed in North, Central and northern parts of South America. It seems, that the recent richness of Bothriocerinae species dates back to ancient times, although some species inhabiting recently arisen islands of the Antilles group, could have originated as a result of post-glacial migrations and island radiation.

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