

# New and Little-Known Orthopteroid Insects (Polyneoptera) from Fossil Resins: Communication 4

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**Abstract**—New taxa of Ensifera and Caelifera orthopterans (Insecta, Orthoptera), from the families Grylotalpidae [Marchandiinae, subfam. nov. (Lower Cretaceous)], Haglotettigoniidae [*Haglotettigonia aenigmatica*, sp. nov. (Lower Cretaceous)], Tettigoniidae [Meconematinae: *Archixizicus occidentalis*, gen. et sp. nov. (Eocene), *Eogrigioria gracilis*, gen. et sp. nov. (Eocene), *Miophlugis rostratus*, gen. et sp. nov. (Miocene)], Stenopelmatidae [Siinae: *Electrosia baltica*, gen. et sp. nov. (Eocene); Gryllacridinae: *Plesiolarnaca prior*, gen. et sp. nov. (Eocene)] and Tridactylidae [Mongoloxyna: *Birmitoxya intermedia*, gen. et sp. nov. (Upper Cretaceous)]. The Eocene species *Lipotactes martynovi* Zeun. and *L. bispinatus* Weidn. are transferred to the genus *Eomortoniellus* Zeun. (Tettigoniidae: Tympanophorinae); *Prorhaphidophora zeuneri* Chop. and *P. tachycinoides* Chop. are transferred to the genus *Protroglophilus* Gor. (Rhaphidophoridae: Protroglophilinae). The Eocene species *E. handlirschi* Zeun., species of the genus *Protroglophilus*, and a possible member of the genus *Succinotettix* Piton (Tetrigidae: Tetriginae), as well as a Miocene representative of the genus *Archaeoellipes* Heads (Tridactylidae: Tridactylinae) are also discussed.

**Keywords:** Orthoptera, new and little-known taxa, fossil resins.

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## INTRODUCTION

In the fourth paper of this series, the following taxa of the suborder Orthoptera are treated: the mole cricket family (Grylotalpidae) from the superfamily Grylloidea and the superfamilies Tettigonioidea, Stenopelmatoidea, Tridactyloidea, and Tetragoidea. In the earlier papers of the series, members of the infraclass Polyneoptera of uncertain order, members of the order Dictyoptera, and members of the order Orthoptera, superfamily Grylloidea, families Mogoplistidae and Gryllidae were discussed (Gorochoy, 2006, 2007, 2010). The classification of the order Orthoptera used in this paper is based on studies of the morphological evolution of both recent and fossil forms (Gorochoy, 1995a, 1995b, 2001).

## MATERIAL

The material studied is stored in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN); Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN); Natural History Museum, London (BNHM); National Museum of Natural History, Washington (NMNH); and Muséum national d'histoire naturelle (MNHN).

## SYSTEMATIC PALEONTOLOGY

Suborder Ensifera

Infraorder Gryllidea

Superfamily Grylloidea Laicharting, 1781

Family Grylotalpidae Leach, 1815

Subfamily Marchandiinae Gorochoy, subfam. nov.

Type genus *Marchandia* Perrichot, Neraudeau, Azar, Menier et Nel, 2002; French amber; Lower Cretaceous.

**Diagnosis** [compiled from Martins-Neto (1991, 1995) and Perrichot et al. (2002)]. General habitus typical of this family: pronotum very large, compared to other body structures; foreleg fossorial, with thick femur, strongly shortened and strongly dilated tibia, strong fossorial spurs apically on this tibia, characteristic bladelike processes on protarsomeres 1 and 2; mid- and hindleg non-specialized (cursorial), considerably thinner than foreleg, and with longer tarsi without any visible processes (hindleg larger than midleg, but metafemur almost not dilated, not saltatorial); arolium undeveloped. Features especially characteristic of this family: absence of any visible process both on base of profemur and on protrochanter, as well as absence apically on protibia of any non-articulate denticles being part of protibial apex, but not modified spurs (two articulate fossorial spurs apically on foreleg well developed).

**Composition.** Type genus from the Lower Cretaceous of France, as well as *Cratotetraspinus* Martins-Neto, 1997 (= *Tetraspinus* Martins-Neto, 1995, nom. praeocc.), *Palaeoscapteriscops* Martins-Neto, 1991, and possibly *Archaeogryllotalpoides* Martins-Neto, 1991 from Lower Cretaceous deposits of Brazil.

**Comparison.** The family Gryllotalpidae, as it currently appears, comprises three subfamilies: Marchandiinae (extant), Scapteriscinae, and Gryllotalpinae (the latter two subfamilies are recent, and were earlier treated by the author as tribes: Gorochov, 1984, 1995a). The new subfamily is similar to Scapteriscinae in the presence of only two fossorial spurs on the protibia and in the absence of any non-articulate (additional) fossorial teeth, processes of protibial apex, but it is well distinguished from it by the absence on the protrochanter of a process, which additionally strengthens the protibia of Scapteriscinae during burrowing. The new subfamily is distinguished from Gryllotalpinae both by the absence of non-articulate fossorial teeth on the protibia (in Gryllotalpinae the protibia has one or two such teeth in addition to the two articulate fossorial spurs) and by the absence basally on the profemur of a process, which in Gryllotalpinae has the same function as the process of protrochanter in Scapteriscinae.

**Remarks.** Marchandiinae could well be the ancestral group of both recent subfamilies of Gryllotalpidae, but the genus *Marchandia* is somewhat deviating, since its protibia apparently shows a trend of increasing the number of fossorial teeth, similar to the trend found in Gryllotalpinae, but realized not by the emergence of new (additional) teeth, but by the bifurcation of one of the two fossorial spurs (Perrichot et al., 2002, Fig. 4).

#### Infraorder Tettigoniidea

Superfamily Tettigoniidea Stol, 1788

#### Family Haglotettigoniidae Gorochov, 1988

#### Genus *Haglotettigonia* Gorochov, 1988

This is the only genus in this subfamily. It is still known only from a single impression of a male tegmen from the Lower Cretaceous deposits of Transbaikalia, and represents the most primitive version of the venation of the stridulatory apparatus in the recent superfamily, preserving many features of the superfamily Hagloidea, ancestral to Tettigoniidea and Stenopelmatoidea (Gorochov, 1988, 1995a). Thus, it is currently virtually impossible to compare this genus with the inclusions of small nymphs from the Lower Cretaceous of Lebanon, described below, which had not yet formed even rudiments of wings. These nymphs are placed, quite provisionally, in this genus and family, because they definitely belong to the superfamily Tettigoniidea (since they have lateral lobes on tarsi, found in most katydids, as well as plantulae on the metabasitarsus and pronotum with posterior lobe

elongate and tapering towards apex), have no protuberance-like rostrum, typical to most katydids, above and/or between the antennae, and more or less match the genus *Haglotettigonia* in age (no other equally ancient Tettigoniidea are known to date).

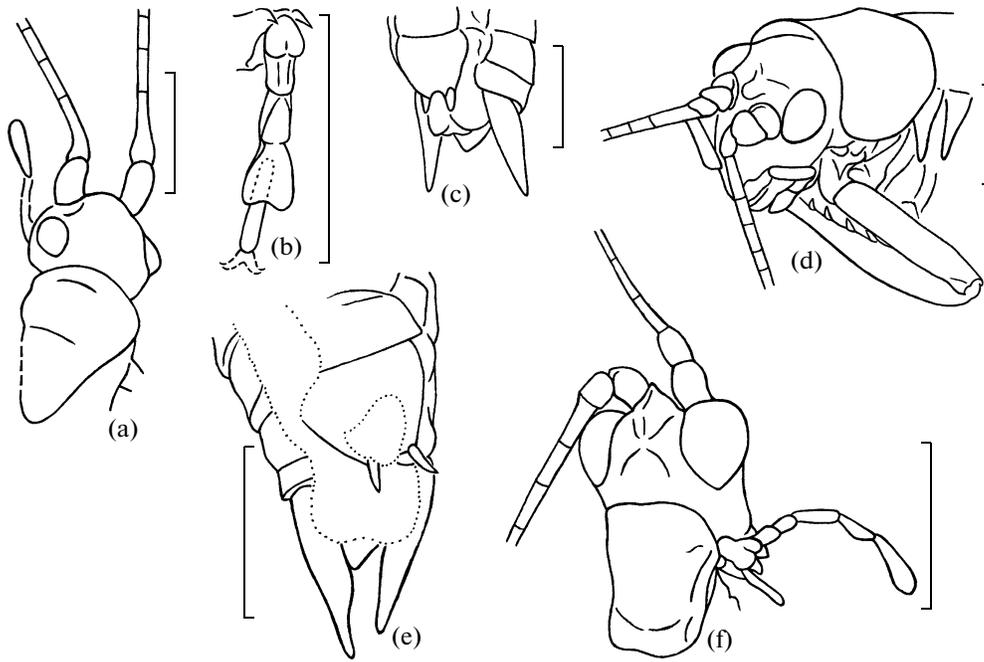
#### ?*Haglotettigonia aenigmatosa* Gorochov, sp. nov.

**Etymology.** From the Latin *aenigmatosa* (enigmatic).

**Holotype.** MNHN, no. 623H, inclusion of an early instar nymph without genicular area of left hindleg and some parts of tarsi; Lebanese amber; Lower Cretaceous, Barremian–Lower Aptian.

**Description** (Figs. 1a, 1b; 2a). The coloration is not preserved. The head is relatively high, clearly hypognathous; the eyes are moderately large; the rostrum between the antennae is almost undeveloped (only a short, gentle, and rounded convexity is present, similar to the one found in recent and fossil members of Hagloidea); the distance between the antennae is approximately equal to the width of the scape; the bases of the antennae are positioned at the level of the lower half of the eyes; the maxillary palpus is not very long, with distinctly (but not strongly) dilated distal portion of the apical palpomere (Fig. 1a). The pronotum is moderately elongate; its posterior lobe gradually tapers towards the rounded apex and reaches approximately the level of the bases of midlegs; the lateral field of pronotum in anterior part is rounded ventrally, and in middle and posterior parts evenly slanting in dorsal direction (the humeral sinuses are absent; this feature is probably a nymphal character; Fig. 1a). The legs are moderately long and relatively slender (the metafemur is dilated insignificantly, weakly saltatorial); the pro- and mesofemur have no developed armament, and the metafemur has one pair of very short inarticulate spurs apically; spines and spurs on the pro- and mesotibia are not visible, but something resembling elongate setae (if they are not fissures in the amber) is visible along almost the entire internal surface of the protibia, these setae being slightly longer than the width of the protibia, and the mesotibia is slightly swollen (this swelling is especially visible in the distal half of the tibia); the metatibia is subequal in length to the metafemur, with rather numerous short and slender spines along the entire dorsal surface (these spines alternate with slightly longer setae), as well as at least one pair of larger (but not long) and slightly hooked ventral setae (Fig. 1b); the tarsi are relatively long, with tarsomeres 1 and 2 lacking any lateral lobes, but having one pair of small pillowlike lobes (plantulae) proximally on the sole of the metabasitarsus; tarsomere 3 has large posterolateral lobes (adaptation to attaching to smooth surfaces of leaves) (Fig. 1b); the arolium is absent. The abdominal apex is typical of the small nymphs of the infraorder Tettigoniidea.

**Measurements,** mm. Body length, 4.5; pronotum length, 1.4; profemur length, 1.2 (paratype,



**Fig. 1.** Tettigoniodea: *?Haglotettigonia aenigmata*, sp. nov., holotype (early instar nymphs), Lebanese amber (a, b): (a) head and pronotum in dorsal and slightly lateral view (but head and pronotum turned in opposite directions), (b) metatarsus in ventral and slightly lateral view; *Archixizicus occidentalis*, sp. nov., holotype (male middle instar nymph), Baltic amber (c, d): (c) abdominal apex partly in ventral and partly lateral view, (d) anterior portion of body with foreleg partly in frontal and partly lateral view; (e) *Eogrigioria gracilis*, sp. nov., holotype (male late instar nymph), Baltic amber, abdominal apex in ventral and slightly lateral view; (f) *Miophlugis rostratus*, sp. nov., holotype (early instar nymph), Dominican amber, head and pronotum in dorsal and slightly lateral view. Scale bar, 1 mm.

1.5); protibia length, 1.3; metafemur length, 2.9; metatibia length, 3.

**Comparison.** As mentioned above, the comparison of this species, described from small nymphs, with *H. egregia* Gor., described from an isolated male tegmen from the Lower Cretaceous of Transbaikalia, is currently impossible. The new species differs from the other known Tettigoniodea in the presence of a short, gentle, and rounded rostrum on the head (i.e., in the absence of the protuberance-like shape of the rostrum, typical of most katydids) in combination with the relatively broadly set antennal cavities, the low (slanting) posterior half of the lateral lobes of pronotum, the presence of saltatorial hindlegs (capable of at least weak jumps), and the presence of large lateral lobes on tarsomere 3. The latter character distinguishes the new species also from all the members of the superfamily Hagloidea (the legs of which are known) and from most Stenopelmatoidea; the new species differs from Gryllacridinae and Schizodactylinae in the less high head and in the presence of an elongate posterior lobe of the pronotum tapering towards the apex. In addition, the described nymphs might prove to belong to the superfamily Phasmomimoidea; however, this is unlikely, because members of this superfamily are not known from fossils later than Jurassic (Gorochov, 2000) and had considerably longer basitarsi.

**Material.** Holotype and paratype MNHN, no. 1064ABC, inclusion of only partly preserved early instar nymph (head damaged; body in places strongly flattened, in places fractured; right hindleg and considerable parts of other legs not preserved), from Lebanese amber (Lower Cretaceous, Barremian–Lower Aptian).

#### Family Tettigoniidae Stol, 1788

#### Subfamily Meconematinae Burmeister, 1838

#### Tribe Meconematini Burmeister, 1838

#### Genus *Archixizicus* Gorochov, gen. nov.

**Etymology.** From the generic name *Xizicus*.

**Type species.** *A. occidentalis*, sp. nov.

**Diagnosis** (male middle instar nymph). Head relatively high, short and clearly hypognathous (facial surface almost not slanting), with relatively small eyes and short finger-shaped upper tubercle on rostrum; rostrum not flattened dorsally and with broadly rounded apex (lower tubercle of rostrum completely undeveloped); distance between antennae approximately half as wide as scape (Fig. 1d). Pronotum relatively short, with short rounded-angular posterior lobe of disc; lateral lobes of pronotum without humeral cavity (possibly a nymphal character). Legs moderately elongate, not slender; pro- and mesotibia slightly thickened in middle part, with strong and rather short

spines on ventral surface (Fig. 1d); metafemur distinctly saltatorial, armed only with short inarticulate spur on external genicular lobe; metatibia with rather numerous small spines on dorsal surface and at least one short external dorsal spur. Both pairs of wings in adults probably fully developed (rudiments of these wings represented in middle instar nymphs as rather large lobes protruding laterally). Epiproct elongate and narrowly rounded apically; genital plate with styli and cavity between them (Fig. 1c).

**Species composition.** Type species.

**Comparison.** The new genus is distinguished from the other genera of the tribe by the following combination of characters: the head is not slanting, not flattened, and not elongate; the upper tubercle of the rostrum is finger-shaped (not flattened dorsally) and with a broad, rounded apex; the pronotum is short; the pro- and mesotibia are slightly swollen and with short (strong) spines ventrally; the metafemur is distinctly saltatorial and with one short apical spur externally; both pairs of wings in adults were probably fully developed; the male epiproct is elongate, and the male genital plate has styli and a cavity between them (in the tribe Meconematini such characters of abdominal apex are usually preserved in late instar nymphs and adults).

*Archixizicus occidentalis* Gorochov, sp. nov.

**Etymology.** From the Latin *occidentalis* (western).

**Holotype.** ZIN, Balt. 4, inclusion of male middle instar nymph, lacking some fragments of hindlegs; Baltic amber; Late Eocene.

**Description** (Figs. 1c, 1d; 2b). The coloration is not sufficiently preserved, but the middle of the clypeus, the scape, the lateral lobes of pronotum, the wing rudiments, and the lateral areas of abdominal tergites are more or less darkened. The spines of the protibia are larger than those of the mesotibia; the former has at least four external and two internal spines; the metatibia is probably slightly longer than the metafemur (the tibia of one hindleg is not preserved, and the tibia of the other is pressed to the femur, but the distal portion of the femur and the base of the tibia of this other leg have not been preserved). The wing rudiments of both pairs are equal in size, almost triangular and narrowly rounded apically (Fig. 1d). The abdominal apex is as in Fig. 1c.

**Measurements**, mm. Body length, 7; pronotum length, 1.8; profemur length, 2; protibia length, 2.5; metafemur length, 5.6, estimated metatibia length, 5.7.

**Material.** Holotype.

**Genus *Eogrigoriora* Gorochov, gen. nov.**

**Etymology.** From the generic name *Grigoriora*.

**Type species.** *E. gracilis*, sp. nov.

**Diagnosis** (male late instar nymph). Head slightly flattened dorsoventrally, short and almost opisthognathous (facial surface slanting), with relatively small eyes and cone-shaped upper tubercle on rostrum; rostrum not flattened dorsally and with narrowly rounded apex (lower tubercle of rostrum reduced to small convexity); distance between antennae approximately one third of scape width. Pronotum elongate, with moderately elongate oval posterior lobe of disc (shape of lateral lobes of pronotum unclear, but humeral cavities probably absent). Legs long and slender; protibia slightly dilated near tympana, with rudiments of open and elongate tympana on both sides, as well as with relatively long and slender spines on ventral surface; mesofemur weakly thickened in middle part, with more or less identical spines; metafemur saltatorial, armed with short inarticulate spur, at least on external geniculate lobe; metatibia with numerous small spines on dorsal surface and four spurs, of which two dorsal being short and two ventral moderately elongate. Both pairs of wings in adults probably fully developed (rudiments of these wings represented in late instar nymphs as large overturned lobes overlaying one another). Epiproct with angular lobe apically; genital plate with styli, but probably without cavity between them (Fig. 1e).

**Species composition.** Type species.

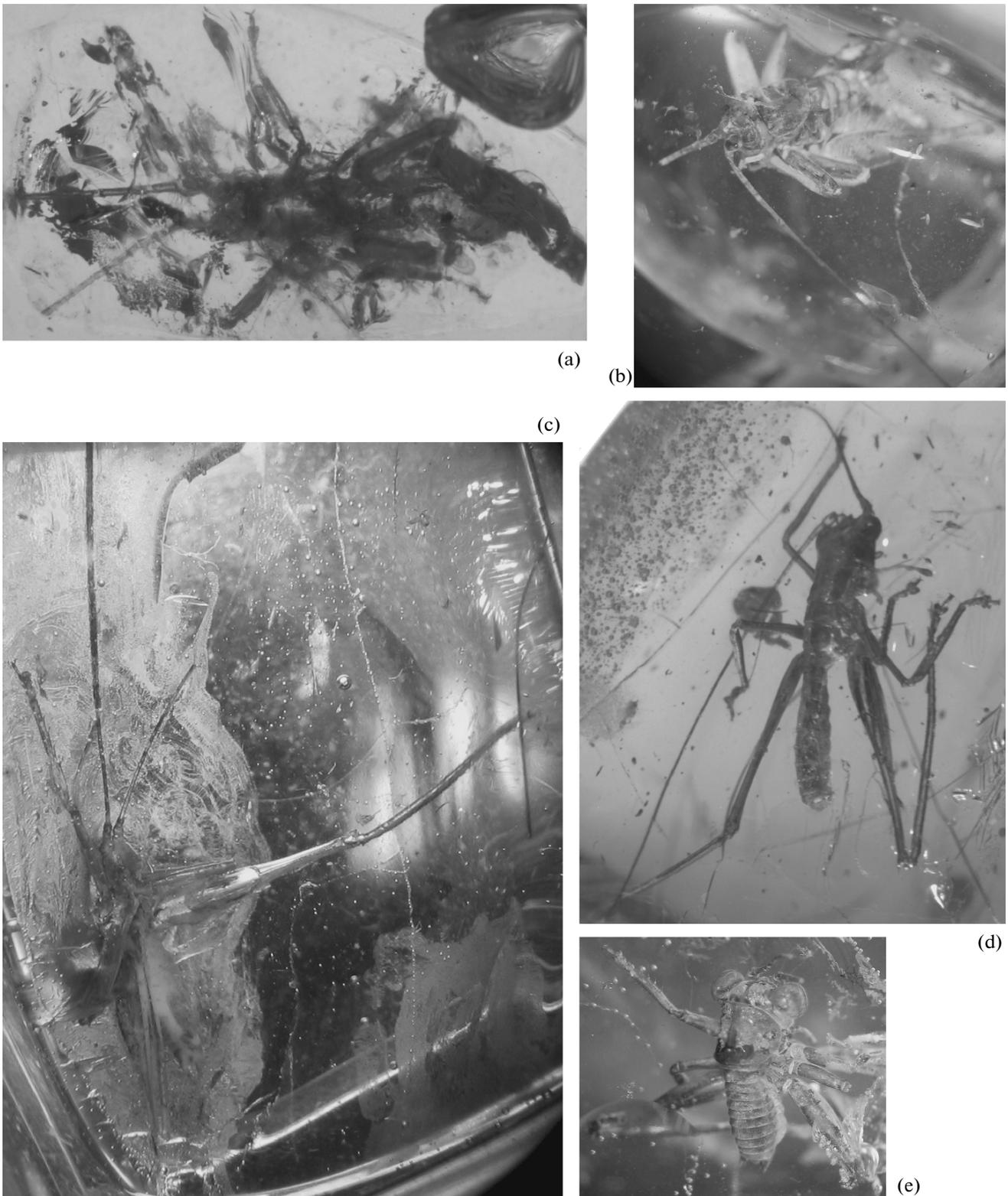
**Comparison.** The new genus is especially similar to the recent genus *Grigoriora* Gor., which comprises several rather diverse species from Southeast Asia (Gorochov, 1998, 2008), but differs from it in the presence of short apical spurs on the metafemur. The new genus is distinguished from the other genera of the tribe by the almost opisthognathous head, the long and slender legs, as well as by the rather long and slender spines on the ventral surface of the pro- and mesotibia.

*Eogrigoriora gracilis* Gorochov, sp. nov.

**Etymology.** From the Latin *gracilis* (slender).

**Holotype.** ZIN, Balt. 5, inclusion of male late instar nymph with damaged upper portion of pronotum and small fragments of hindlegs; Baltic amber; Late Eocene.

**Description** (Figs. 1e; 2c). The coloration is uniformly light (or not preserved). The spines on the protibia are subequal in length to those on the mesotibia; the former has five pairs of spines, getting shorter towards the apex of the tibia, and one pair even shorter ventral spurs (the external of which is extremely small), and the latter has external spines and a spur similar to the internal spines and spur of the former (the internal armament of the mesotibia is not visible); the metatibia is insignificantly longer than the metafemur. The rudiments of the tegmina are probably reaching the apex of metanotum, and the hindwing rudiments are probably reaching the second abdominal tergite (the latter rudiments are partly overlaying



**Fig. 2.** Photographs of Tettigonioida inclusions: (a) *?Haglotettigonia aenigmata*, sp. nov., holotype, Lebanese amber, body in dorsal view; (b) *Archixizicus occidentalis*, sp. nov., holotype, Baltic amber, body in lateral and slightly dorsal view; (c) *Eogrigniora gracilis*, sp. nov., holotype, Baltic amber, body in ventral and slightly lateral view; (d) *Miophlugis rostratus*, sp. nov., holotype, Dominican amber, body in dorsal and slightly lateral view; (e) *Eomortoniellus handlirschi* Zeun., specimen Balt. 6, Baltic amber, body in dorsal and slightly lateral view.

the former laterally and dorsally). The abdominal apex is as in Fig. 1e.

**Measurements**, mm. Body length, 7.2; estimated pronotum length, 2.5; profemur length, 2.8; protibia length, 3.5; metafemur length, 6.4; metatibia length, 7.

**Material**. Holotype.

### Tribe Phlugidini Eichler, 1938

#### Genus *Miophlugis* Gorochov, gen. nov.

**Etymology**. From the Miocene and the generic name *Phlugis*.

**Type species**. *M. rostratus*, sp. nov.

**Diagnosis** (early instar nymph). Head slightly flattened dorsoventrally, weakly elongate and almost opisthognathous (facial surface slanting and, as in other Phlugidini, slightly concave), with moderately large eyes (only slightly longer than half of head visible in dorsal view) and cone-shaped upper tubercle on rostrum; rostrum slightly flattened dorsally, with rather broad base and almost pointed apex (Fig. 1f); this apex slightly protruding anteriorly beyond anterior margins of eyes (lower tubercle of rostrum absent); antennal cavities virtually touching each other under upper tubercle of rostrum. Pronotum short, but considerably longer than wide; posterior margin of disc transversely truncated; lateral lobes without humeral cavity (possibly nymphal character) (Fig. 1f). Legs long and slender; pro- and mesofemur without visible spines; protibia without dilation, with relatively short and slender spines on ventral surface (these spines not longer than width of protibia); mesotibia slightly dilated in proximal half, without spines (with only one pair of small ventral spurs visible); metafemur rather narrow, almost not saltatorial, without visible spurs; metatibia with numerous very small dorsal spines in distal half and poorly visible small spurs.

**Species composition**. Type species.

**Comparison**. The new species is readily distinguished from nymphs and adults of the other genera of the tribe by the presence of the upper tubercle on the rostrum, the smaller eyes (in the other Phlugidini they are at least as long as two thirds of the head in dorsal view), by the absence of spines on the profemur, and by the markedly shorter spines on the protibia (in the other Phlugidini these spines are distinctly or considerably longer than the width of the protibia, in nymphs as well as in adults).

**Remarks**. The new genus represents the most primitive version of head structure in this tribe, since in this genus the upper rostral tubercle is retained, and the eyes are not yet as large as in the recent Phlugidini. The prehensile spines of the forelegs in the new genus are less developed, possibly also indicating its greater primitiveness (or a somewhat different type of feeding in early nymphs).

#### *Miophlugis rostratus* Gorochov, sp. nov.

**Etymology**. From the Latin *rostratus* (rostrate).

**Holotype**. NMNH 504426, Acc. 371428, Woodruff (collection reg.) 8872, Brodzinsky / Lopez-Peña [Penha] Collection, inclusion of early instar nymph without distal portion of left hindleg; Dominican amber; possibly Miocene.

**Description** (Figs. 1f; 2d). The coloration is uniformly light (possibly not preserved). The spines on the protibia are poorly distinguishable from setae (and thus cannot be counted); the spurs of the protibia are slightly larger than the above-mentioned spines; the metafemur and metatibia are subequal in length; the metatibia is weakly curved (the structure of the abdominal apex is unclear.)

**Measurements**, mm. Body length, 4.5; pronotum length, 0.7–0.8; profemur length, 1.2; protibia length, 1.4; metafemur length, 3.4; metatibia length, 3.5.

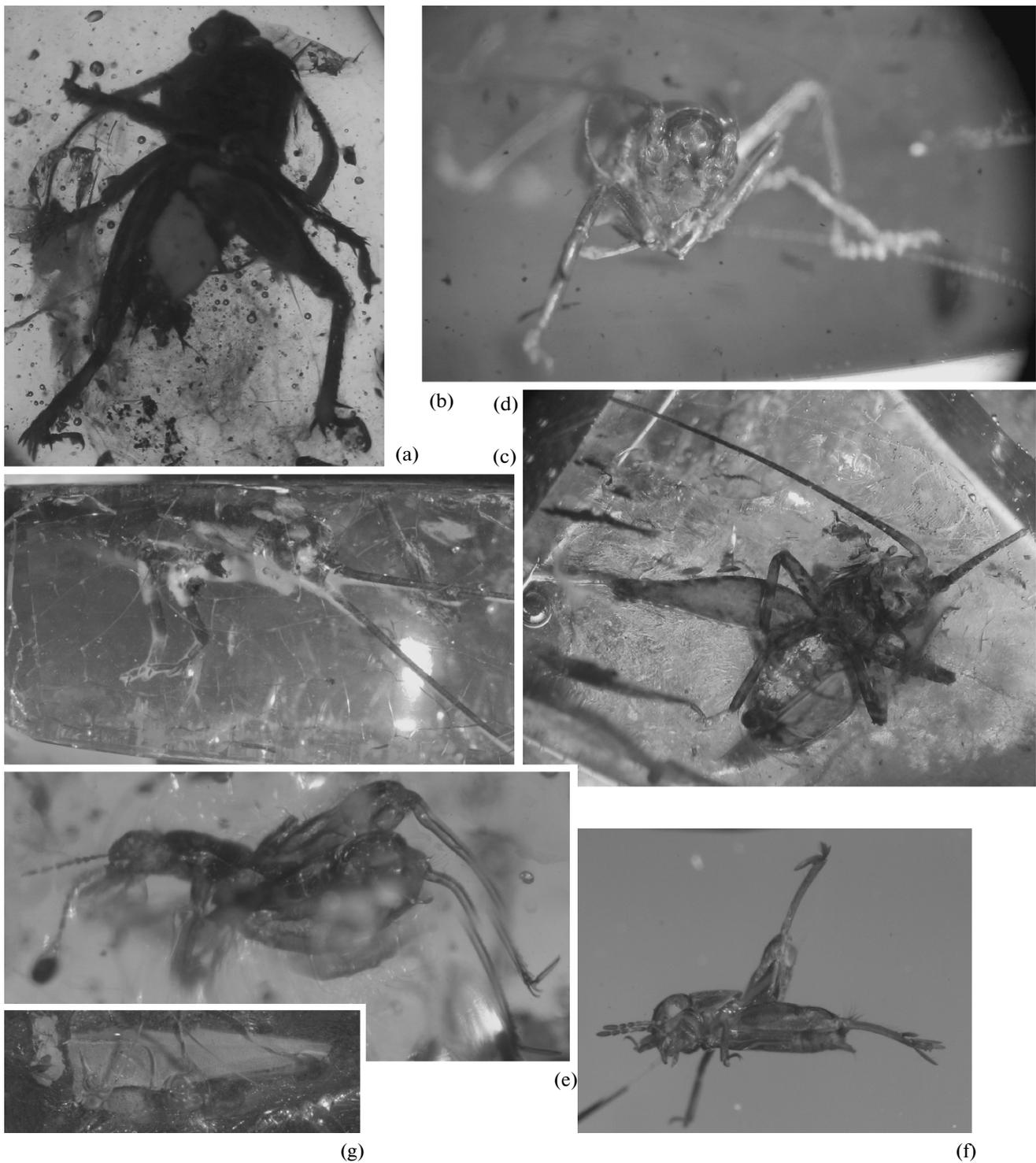
**Material**. Holotype.

### Subfamily Tympanophorinae Brunner-Wattenwyl, 1893

#### Tribe Lipotactini Ingrisch, 1995

#### Genus *Eomortoniellus* Zeuner, 1936

This genus was described and redescribed by the same author to include a single species from the Baltic amber (*E. handlirschi*) without clearly specifying the differences of the new genus and the related recent genera (Zeuner, 1936, 1939). Judging by the characters cited in the same publications in the description of the species, it may be assumed that the author probably distinguished *Eomortoniellus* from the recent Indomalayan genera *Lipotactes* Br.-W. and *Mortoniellus* Griff. by the following characters: the pro- and mesotibia each have six pairs of ventral spines (including spurs); the mesotibia has no spine on the dorsal surface. Based on the latter character, all the specimens of Lipotactini from the Baltic amber examined by Zeuner were attributed to two species, *E. handlirschi* and *Lipotactes martynovi* Zeun. (Zeuner, 1936, 1939). The latter species was included in a recent genus, because one spine was found in it in the proximal portion of the dorsal surface of mesotibia (as in most species of both recent genera). However, this species (as well as some specimens of *E. handlirschi*) have six pairs of spines on the pro- and mesotibia; the latter character separates it from all recent genera of the tribe, which have four to five pairs of such spines (Ingrisch, 1995). In addition, recent members of the genus *Lipotactes* (e.g., *L. amicus* Gor.) are also sometimes lacking the dorsal spine on the mesotibia (reduction of spines is a relatively common phenomenon, sometimes developing extremely quickly and only in some of several closely related forms). Thus, currently it is appropriate to transfer *L. martynovi* into the genus *Eomortoniellus*, which in this case will be distinguished from the recent genera by the greater number of spines on the pro- and



**Fig. 3.** Photographs of Stenopelmatoidea (a, b, c, d), Tridactyloidea (e, f), and Tetrigoidea (g) inclusions: (a) *Electrosia baltica*, sp. nov., holotype, Baltic amber, body in ventral and slightly lateral view; (b) *Plesiolarnaca prior*, sp. nov., holotype, Baltic amber, body in frontal view; (c) *Protroglophilus sukhatshvae* Gor., holotype, Baltic amber, body in lateral and slightly frontal view; (d) *P. zeuneri* (Chop.), specimen Balt. 12, Baltic amber, body in ventral view; (e) *Birmitoxya intermedia*, sp. nov., holotype, Burmese amber, body in lateral view; (f) *Archaeoellipes ?engeli* Heads, specimen NMNH 503419, Dominican amber, body in lateral view; (g) *?Succinotettix* sp., specimen PIN no. 363/87, Baltic amber, body in dorsal and slightly lateral view.

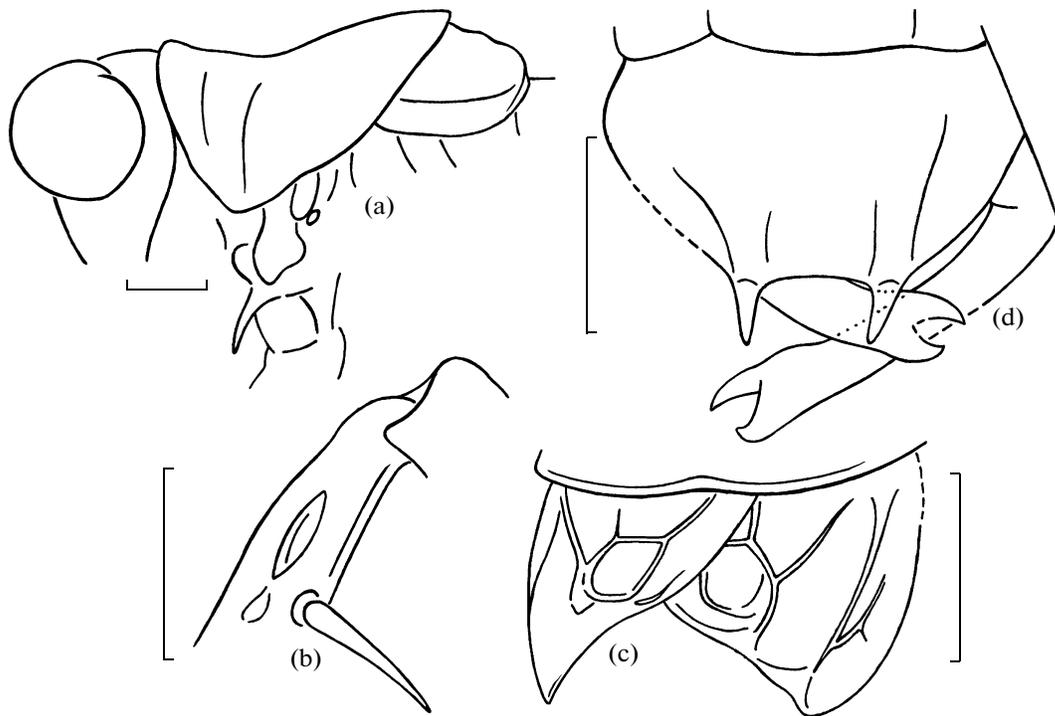


Fig. 4. *Eomortoniellus handlirschi* Zeun. (Tettigoniodea), holotype (male), Baltic amber: (a) anterior half of body without antennae and some ventral structures in lateral view; (b) base of protibia in internal view; (c) tegmina in dorsal and slightly posterior view; (d) abdominal apex in ventral view. Scale bar, 1 mm.

mesotibia and/or by the characteristic cercus of the male: long, relatively thin, arcuate, and apically bifurcated (Figs. 4b, 4d). Another species from the Baltic amber that has two dorsal spines on the mesotibia was described as a possible member of the genus *Lipotactes* (Weidner, 1956: ?*L. bispinatus*). However, this structure of the mesotibia is not found in any recent member of the tribe. It cannot be ruled out that in the Eocene *Lipotactini* the number of spines on the tibiae was simply less stable; the latter species is, therefore, provisionally placed here into the genus *Eomortoniellus*.

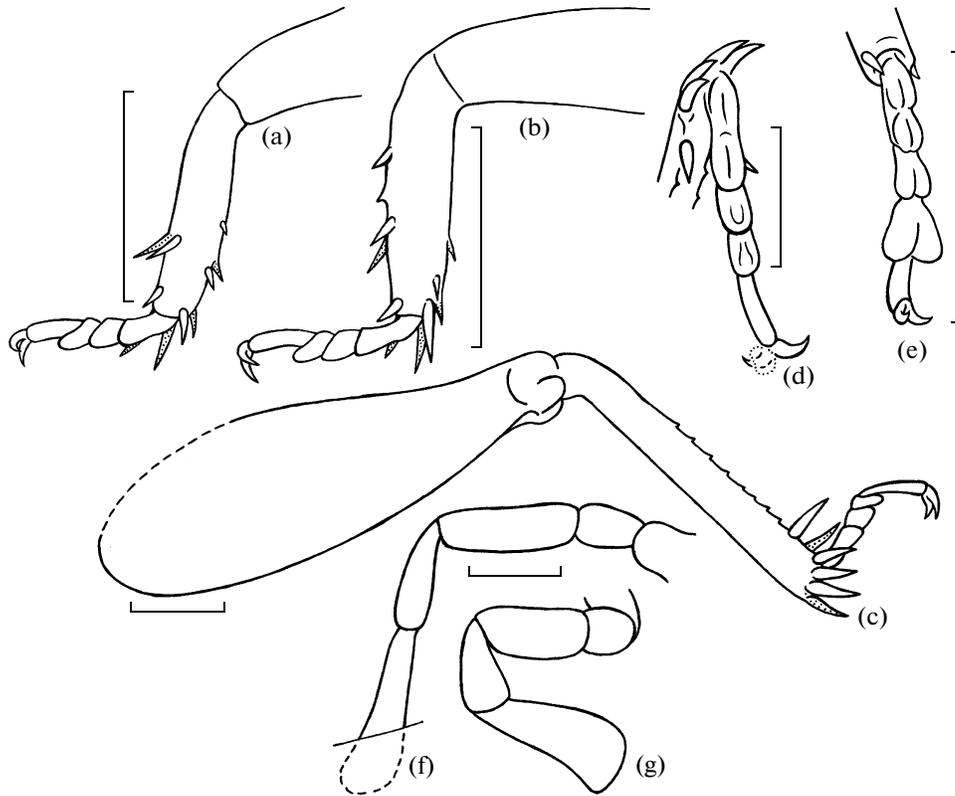
*Eomortoniellus handlirschi* Zeuner, 1936

**Holotype.** BNHM, In. 29119, inclusion of almost complete male; Baltic amber; Late Eocene.

**Redescription** (Figs. 2e; 4a–4d). The earlier descriptions of this species are rather detailed (Zeuner, 1936, 1939), and therefore only the following information is supplemented here: the head is typical of the tribe, but with the rostrum insignificantly larger than in the recent species; the pro- and mesotibia of the holotype have six pairs of ventral spines (including the apical spurs) and no dorsal spine (it should be noted that the number of ventral spines in the examined nymphs, which also have no dorsal spine, is unequal: in the specimen Balt. 6 the pro- and mesotibia have five pairs of spines, but in the specimen Balt. 7 the mesotibia has six pairs of spines, while the protibia has five external and six internal spines on the left leg and

four internal spines on the right leg (the number of external spines on the right leg could not be counted); the internal tympanum is semi-slit-like (at least in the holotype), but near the distal margin has a distinct cavity (Fig. 4b), characteristic of slitlike and even partly open tympana in the group of related subfamilies (*Litroscelidinae*, *Tympanophorinae*, *Saginae*, *Hexacentrinae*, *Conocephalinae*, *Hetrodinae*, *Glyphonotinae*, *Nedubinae*, *Tettigoniinae*, and *Bradyporinae*); the tegmina of the male are short, half covered by the posterior lobe of pronotum (Fig. 4a), and with a developed stridulatory apparatus, the venation of which is as in Fig. 4c; the male genital plate is wide, with rather narrow and not very long styli and almost straight margin between them; the male cercus differs from that of the other species of the tribe in characters listed above in the description of the genus (Fig. 4d).

**Remarks.** *E. handlirschi* differs from *E. martynovi* (Zeun.) and ?*E. bispinatus* (Weidn.) only in the absence of armament on the dorsal surface of the mesotibia. However, judging by the instability of the number of other spines in the former species, it cannot be ruled out that this character could be only intraspecific and, thus, all these species names may prove synonymous. In addition, there is also another possibility: more than three similar species of the tribe *Lipotactini* could have lived together in the Late Eocene succiniferous forests of the Baltic, and the variation in the armament of legs in these species could be identical to that of the recent species (inter-



**Fig. 5.** Stenopelmatoidea, Baltic amber: *Electrosia baltica*, sp. nov., early instar nymphs (a, b, c, d); paratype (a, b) and holotype (c, d): (a) foreleg in external view; (b) midleg in internal view; (c) hindleg in external view; (d) metatarsus in ventral view; (e) *Plesiolarnaca prior*, sp. nov., holotype (early instar nymphs), metatarsus in ventral view and slightly in lateral view; (f) *Protroglyphilus zeuneri* (Chop.), specimen Balt. 11 (middle instar nymph), maxillary palpus in lateral view; (g) *P. sukatshevae* Gor., holotype (middle instar nymph), maxillary palpus in lateral view. Scale bars: 1 mm (a, b, c, d, e) and 0.5 mm (f, g).

estingly, the genital plate in both nymphs treated here has a cavity between the styli, in contrast to the holotype).

**Material.** ZIN, Balt. 6, inclusion of complete male middle instar; ZIN, Balt. 7, inclusion of almost complete middle instar male nymph; all from Late Eocene Baltic amber.

Superfamily Stenopelmatoidea Burmeister, 1838

Family Stenopelmatidae Burmeister, 1838

Subfamily Siinae Gorochov, 1988

Genus *Electrosia* Gorochov, gen. nov.

**Etymology.** From the Greek *electron* (amber) and the generic name *Sia*.

**Type species.** *E. baltica*, sp. nov.

**Diagnosis (early instar nymph).** Head distinctly hypognathous, relatively wide and high (somewhat higher than wide); eyes large for this subfamily, considerably larger than antennal cavities; rostrum between antennae virtually undeveloped (with only short, gentle, and rounded convexity present); distance between antennae approximately twice as great as scape width; bases of antennae positioned at level of

ventral halves of eyes; maxillary palpus not long, with apical palpomere weakly dilated distally. Pronotum relatively large (possibly a nymphal character), but short (somewhat wider than long), with weakly convex anterior margin and almost truncated posterior margin (posterior lobe of pronotum absent), also with straight ventral margin of lateral lobes and slanting-rounded anteroventral and posteroventral angles of these lobes. Legs rather short and strong, adapted to "swimming" in soft soil: femora somewhat longer than their respective tibiae; forelegs insignificantly shorter than midlegs; pro- and mesotibia thick, with four strong fossorial spurs and one pair of no less strong spines in distal half of dorsal surface, as well as with several smaller spines on ventral surface of both pro- and mesotibia and in proximal half of dorsal surface of mesotibia (Figs. 5a, 5b); metatibia slightly thickened towards apex, with four strong fossorial spurs, one pair of large dorsal spines near them, and two series of small spines more proximally (Fig. 5c); all tarsomeres narrow, and basitarsus with weak longitudinal median groove on sole and with very slight narrowing in middle part (Fig. 5d). Metasternum distinctly separated from abdominal sternite 1, with slightly bifurcated posterior portion, this portion somewhat overlaying

unspecialized abdominal sternite 1 ventrally; other parts of abdomen also typical of early instar nymphs of this subfamily.

**Species composition.** Type species.

**Comparison.** The new genus is distinguished from the recent genera *Sia* Gieb. and *Maxentius* Stål by the more strongly developed adaptations to burrowing: the shortened tibiae (especially protibia and mesotibia) and protarsus (the latter is somewhat shorter than meso- and metatarsus). The new genus differs from members of the subfamily Stenopelmatinae (closely related to Siinae) in the absence of fusion between the metasternum and abdominal sternite 1 and in the presence of spines on the ventral surface of the mesotibia; it differs from Oryctopinae in the considerably larger eyes and the less specialized protibia.

*Electrosia baltica* Gorochov, sp. nov.

**Etymology.** From the Latin *baltica* for Baltic (amber).

**Holotype.** ZIN, Balt. 8, inclusion of complete early instar nymph, in some parts covered with white foamy mass; Baltic amber; Late Eocene.

**Description** (Figs. 3a; 5a–5d). The coloration is darkened (details of the coloration could not be examined). The protibia has four rather small spines on the ventral surface (in addition to the large apical spurs and the large spines on the dorsal surface, described in the diagnosis of the genus); the mesotibia has three rather small spines on the ventral surface and two in the proximal half of the dorsal surface (in addition to the large apical spurs and the large spines in the distal half of the dorsal surface, described in the diagnosis of the genus); the metafemur is distinctly dilated, saltatorial (this character is probably typical only of the small larvae, as in mole crickets); the tarsi have normally developed claws (Figs. 5a–5d).

**Measurements**, mm. Body length, 7.5 (paratype, 3.6); pronotum length, 2 (1.7); profemur length, 1.7 (1.3); protibia length, 1.5 (1.1); metafemur length, 5.2 (3.2); metatibia length, 3.5.

**Material.** Holotype and paratype ZIN, Balt. 9, inclusion of early instar nymph without some fragments of hindlegs, almost completely covered with thin layer of white foam; Baltic amber; Late Eocene.

**Subfamily Gryllacridinae Blanchard, 1845**

**Genus *Plesiolarnaca* Gorochov, gen. nov.**

**Etymology.** From the generic name *Larnaca*.

**Type species.** *P. prior*, sp. nov.

**Diagnosis** (early instar nymph). Head distinctly hypognathous, but with weakly slanting facial surface (slightly opisthognathous), distinctly higher than wide; eyes moderately large, not much larger than antennal cavities; rostrum between antennae virtually undeveloped (with only short, gentle, and

rounded convexity present); distance between antennae approximately twice as great as scape width; bases of antennae positioned at level of ventral halves of eyes; maxillary palpus not long, with apical palpomere weakly dilated distally. Pronotum relatively small, approximately as long as wide, with almost straight anterior and posterior margins (posterior lobe of pronotum absent); lateral lobes of pronotum appearing more or less rounded. Legs not long, but slender, without dilations on tibiae and with distinctly dilated (saltatorial) metafemur; tibiae not shorter than their respective femora (legs scansorial); pro- and mesotibia on ventral surface with very slender (bristlelike) spines and spurs, these spines and spurs considerably shorter than width of their respective tibia; metatibia with two series of rather numerous small spines on dorsal surface and at least one pair of short spurs apically; tarsi with one pair of conspicuous posterolateral lobes on tarsomere 3, one pair of inconspicuous (very short) lateral lobes on tarsomere 2, and four rather small swellings on sole of basitarsus (Fig. 5e). Abdomen typical of early instar nymphs of this subfamily.

**Species composition.** Type species.

**Comparison.** The new genus differs from the other genera of the subfamily only in insufficiently reliable characters of the armament of some tibiae and the structure of the tarsi. The very short and slender spines on the pro- and mesotibia of the new genus might be purely larval features, and the weakly developed lateral lobes of tarsomeres 1 and 2 in this genus are found also in some recent genera, the members of which spend rather much time on the ground, and not only on plants (however, this way of life is typical only of the inhabitants of arid regions that have no forests, whereas the Baltic areas were humid and covered with forests in the Late Eocene).

*Plesiolarnaca prior* Gorochov, sp. nov.

**Etymology.** From the Latin *prior* (former, previous).

**Holotype.** ZIN, Balt. 10, inclusion of complete early instar nymph; Baltic amber; Late Eocene.

**Description** (Figs. 3b; 5e). The coloration is light with slightly darkened vertex above frontal sutures, overturned V-shaped spot between antennal cavities, and tergites of the thorax and abdomen (a light median line runs from the point of the fusion of frontal sutures and probably to the posterior abdominal tergites). The mesotibia has five pairs of spines (including spurs); the length of these spines is no greater than half the width of the mesotibia (the number of spines on the protibia could not be counted, but the length of these spines is approximately the same).

**Measurements**, mm. Body length, 3; pronotum length, 0.7; profemur length, 1; protibia length, 1.2; metafemur length, 1.9; metatibia length, 1.9.

**Material.** Holotype.

**Family Rhaphidophoridae Thomas, 1872****Subfamily Protriglophilinae Gorochov, 1989****Genus *Protriglophilus* Gorochov, 1989**

Two genera have been described from the Baltic amber: *Protriglophilus* and *Prorhaphidophora* Chopard, 1936. To date, the former genus included only one species (Gorochov, 1989), and the latter included three species (Chopard, 1936a, 1936b). The type species of the genus *Protriglophilus* is readily distinguished from the type species of the genus *Prorhaphidophora* by the short pro- and mesotarsomere 3, which is almost half as long as the respective tarsomere 2 (in the latter species all tarsi have long tarsomere 3, at least as long as the respective tarsomere 2), as well as by the long plantar pad of both these tarsomeres, at least as long as the body of the respective tarsomere (in the latter species this pad is clearly shorter than the body of the respective tarsomere in all tarsi). In descriptions of the other two species the structure of their pro- and mesotarsus was not specified, but, judging by the presence of small ventral spines on the metafemur and by the shortened metatarsomere 3, these species should probably be transferred into the genus *Protriglophilus*. The new material supports the appropriateness of this transfer, but also demonstrates the strong variation in the armament of the metafemur: the same specimen has two small ventral spines on one leg and no such spines on the other leg. Thus, the genus *Protriglophilus* probably could be distinguished from the genus *Prorhaphidophora* also in the unequal size of the small dorsal spines in the middle part on the metatibia and in the small number of small dorsal spines on the metabasitarsus (about four, including the apical spur, in the former genus, and about seven in the latter genus), as well as, possibly, by the presence of small ventral spines on the metafemur (the latter character is unsuitable for distinguishing some specimens of *Protriglophilus* from *Prorhaphidophora*).

***Protriglophilus sukatshevae* Gorochov, 1989**

**H o l o t y p e.** PIN, no. 363/86, inclusion of middle instar nymph without upper portion of body and distal halves of hindlegs (sex unclear, because abdominal apex ventrally covered with foam); Baltic amber; Late Eocene.

**D e s c r i p t i o n** (Figs. 3c; 5g). This species was sufficiently described earlier (Gorochov, 1989), therefore only some of its characters are listed below: the coloration is on the whole dark (maculation, at least on the legs, is almost undeveloped); the maxillary palpus is short (palpomere 3 is approximately 12 times shorter than the metafemur: Fig. 5g); the pro- and mesofemur have one short internal spur apically; the metafemur has small spines on both ventral carinae; the pro- and mesotibia have one pair of conspicuous ventral spurs and one pair of inconspicuous (small) dorsal spurs apically, as well as small (but clearly visible) ventral spines.

**M a t e r i a l.** Holotype.

***Protriglophilus zeuneri* (Chopard, 1936)**

This species (Fig. 3d) is similar to *P. sukatshevae*, but distinguished from it by the lighter and distinctly maculate coloration, the longer maxillary palpus (palpomere 3 is approximately 10 times shorter than metafemur: Fig. 5f), the metafemur without small spines (Balt. 12) or with small spines exclusively on the internal ventral carina (Balt. 11, but no such spines are present on the other leg of this specimen), and by the pro- and mesotibia having inconspicuous (small) ventral spines, which are not visible at all on the midleg of the specimen Balt. 12.

**M a t e r i a l.** ZIN, Balt. 11, inclusion of middle instar nymph with damaged anterior portion of body and without apices of hindlegs (sex unclear, because abdomen ventrally impossible to examine); ZIN, Balt. 12, inclusion of female middle instar nymph with damaged dorsal portion of body and without distal portion of right hindleg and most of left hindleg; Baltic amber; Late Eocene.

***Protriglophilus ?tachycinoides* (Chopard, 1936)**

This species differs from *P. sukatshevae* and *P. zeuneri* in the absence of spurs apically on the pro- and mesofemur (Chopard, 1936b). If the nymph discussed here, which has no such spurs at least on the foreleg, belongs to this species, then *P. tachycinoides* can be also distinguished by the somewhat shorter legs (the metafemur is less than three times as long as the pronotum, whereas in the two other species it is at least three times as long as the pronotum) and by the absence of small spines on the metafemur. It should be noted that the coloration, the size of the maxillary palpus, the armament of the metafemur and of the pro- and mesotibia of the holotype were not described, and could not be examined in this nymph, and thus it cannot be attributed with certainty to this species, the more so because the small dorsal spines on its metatibia are clearly less numerous than in the holotype, and it has two small dorsal spines (including the apical spur) on the metabasitarsus, whereas the holotype has four.

**M a t e r i a l.** ZIN, Balt. 13, inclusion of complete male middle instar nymph, almost completely covered with foam; Baltic amber; Late Eocene.

## Suborder Caelifera

## Infraorder Tridactylidea

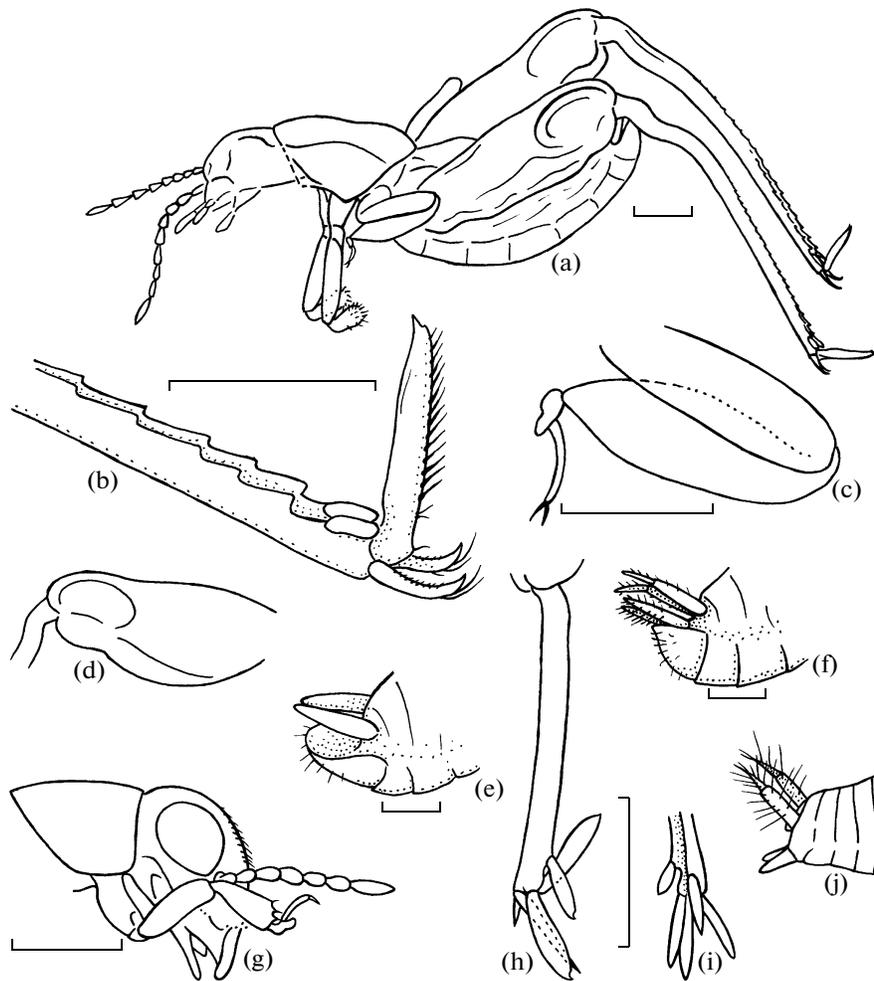
## S u p e r f a m i l y Tridactyloidea Brullé, 1835

**Family Tridactylidae Brullé, 1835****Subfamily Mongoloxyna Gorochov, 1992****Genus *Birmitoxya* Gorochov, gen. nov.**

**E t y m o l o g y.** From the Latin for Burmese (amber) and the generic name *Xya*.

**T y p e s p e c i e s.** *B. intermedia*, sp. nov.

**D i a g n o s i s** (male middle or late instar nymph). Pronotum elongate (distinctly longer than wide and



**Fig. 6.** Tridactyloidea: *Birmitoxya intermedia*, sp. nov., holotype (male middle or late instar nymph), Burmese amber (a, b, c, d, e): (a) body in lateral view; (b) distal portion of hindleg in internal view; (c) midleg in external view; (d) metafemur in external view; (e) abdominal apex in lateral and slightly dorsal view; (f) recent *Dentridactylus* sp., male, abdominal apex in lateral view; *Archaeoelipes ?engeli* Heads, specimen NMNH 503419 (early instar nymph), Dominican amber (g, h, i, j): (g) head, pronotum and foreleg in lateral view; (h) right metatibia and metatarsus in internal view; (i) apex of left hindleg partly in dorsal and partly in internal view; (j) abdominal apex in lateral view. Scale bar, 0.5 mm.

distinctly longer than high). Foreleg somewhat shortened, with femur relatively thin and tibia shorter, moderately dilated apically, with small fossorial denticles (Fig. 6a); midleg with strongly dilated tibia and 2-segmented tarsus (Fig. 6c); metafemur strongly dilated (Fig. 6d); metatibia thin and very long, with two pairs of spurs (longer apical and shorter subapical) and two series of small inarticulate spines dorsally; metatarsus consisting only of basitarsus, considerably longer than apical spurs and slightly bifurcated apically (Fig. 6b). Cercus 1-segmented, rather short; paraproct without articulate processes, or these processes very small and completely hidden under genital plate (Fig. 6e).

**Species composition.** Type species.

**Comparison.** The new genus is distinguished from the other Mongoloxysiinae (all Early Cretaceous),

or rather from those genera of this subfamily for which impressions of the body are known (*Monodactyloides* Shar., *Cratodactylus* Martins-Neto, and *Baisoxya* Gor. et Maehr), by the considerably longer pronotum and metatibia.

**Remarks.** This genus is placed in Mongoloxysiinae based on the following reasoning. Its 1-segmented cercus and the absence (or underdevelopment) of paraproctal processes do not allow placing it in Tridactylinae (in which subfamily even in nymphs the cercus is distinctly 2-segmented and not so short, and the paraproctal processes are long and protruding far beyond the margins of the genital plate: Fig. 6f). The subfamily Rhipipteriginae is more primitive than Tridactylinae in some characters (the 1-segmented cercus and the presence of the ovipositor), but more modified in other characters (Rhipipteriginae display

weakened adaptation to burrowing, expressed in the narrowed pro- and, especially, mesotibia). However, Rhipipteriginae are, in contrast to the new genus, synapomorphic with Tridactylinae in the development of long and articulate paraproctal processes. More primitive structure of the male abdomen is found in *Cylindrachetidae*, which, like *Birmitoxya*, have 1-segmented cercus and paraproct without long processes, but have developed a specialized underground way of life, become incapable of jumping, and lost the ovipositor. The only group the known characters of which allow including the new genus is the subfamily Mongoloxiinae. On the other hand, the structure of the abdomen of this subfamily is unknown. But the habitus of Mongoloxiinae is close to that of *Birmitoxya* and the recent Tridactylidae, and the age and structure of the tegmen of Mongoloxiinae, in comparison with Tridactylidae, suggest that Mongoloxiinae are more primitive in the structure of the terminalia: the structure of the male abdominal apex as in *Birmitoxya* (and in *Cylindrachetidae*) and the presence of the ovipositor as in Rhipipteriginae. This suggestion implies that the ovipositor could also be present in the unknown female of the new genus.

*Birmitoxya intermedia* Gorochoy, sp. nov.

**E t y m o l o g y.** From the Latin *intermedia* (intermediate).

**H o l o t y p e.** BNHM, In. 20188-2, inclusion of complete middle or late instar nymph; Burmese amber; possibly Upper Cretaceous.

**D e s c r i p t i o n** (Figs. 3e; 6a–6e). The coloration is more or less uniform, rather dark. The antenna is clearly longer than the head. The pro- and mesofemur are subequal in length; the mesotibia is insignificantly longer than the mesofemur; the metatibia is considerably longer than the metafemur; the apical (ventral) spurs of the metatibia are almost twice as long as the subapical (dorsal) spurs and approximately 2.5 times shorter than the metabasitarsus.

**M e a s u r e m e n t s,** mm. Body length, 3.8; pronotum length, 1; metafemur length, 2; metatibia length, 2.3; metabasitarsus length, 0.5.

**M a t e r i a l.** Holotype.

**Subfamily Tridactylinae Brullé, 1835**

**Tribe Tridactylini Brullé, 1835**

**Genus *Archaeoellipes* Heads, 2010**

This genus was described very recently (Heads, 2010) for a single adult male from Dominican amber. The young nymph from the same locality studied here belongs evidently to the same genus, as it is characterized by the below-listed features. Head relatively large, with very large eyes. Pronotum relatively small and rather short (insignificantly wider than long and distinctly wider than high), weakly dilating towards posterior third, with almost straight anterior margin and

roundedly convex posterior margin; ventral margin of lateral lobes of pronotum more or less rounded in anterior half and slanting in posterior half (Fig. 6g). Foreleg visibly shorter than midleg, without processes on femur and trochanter; profemur thick; protibia slightly shorter than profemur, distally dilated and non-bifurcated, with three fossorial denticles apically (Fig. 6g); midleg simple, rather slender; meso- and metafemur approximately equal in length to their respective tibiae; metafemur typical of this subfamily (considerably dilated, saltatorial); metatibia moderately slender, with four large almost leaf-shaped spurs apically and without any spines and/or denticles proximal of these spurs (Figs. 6h, 6i); pro- and mesotarsus similar in structure and size, 2-segmented, with short basitarsus (provided apically with characteristic plantar lobe), tarsomere 2 longer than tarsomere 1, and claws normally developed (Fig. 6g); metatarsus represented only by more or less leaf-shaped basitarsus, insignificantly longer than largest spurs of metatibia and lacking additional preapical hook (Figs. 6h, 6i). Abdomen typical of early instar nymphs of this subfamily (Fig. 6j).

**M a t e r i a l.** It should be noted that the tribe Tridactylini is understood here as identical to the subfamily Tridactylinae sensu Günther (1980), and Günther's subfamily Dentractylinae is treated here as the second tribe of the subfamily Tridactylinae. This allows viewing the family Tridactylidae in a broader sense, i.e., including three subfamilies: the recent Tridactylinae and Rhipipteriginae, as well as the Cretaceous Mongoloxiinae.

*Archaeoellipes ?engeli*, Heads, 2010

**M a t e r i a l.** NMNH 503419, Acc. 371428, Woodruff (collection reg.) 7859, Brodzinsky / Lopez-Pena (Penha) Collection, inclusion of complete early instar nymph, near dorsal portion of thorax with a bubble blocking this part of body from view; Dominican amber; possibly Miocene.

This nymph (Figs. 3f; 6g–6j) is not identical to the holotype of this species, but the differences between them may be connected with the differences in their ages. The coloration is moderately darkened, with somewhat darker anterior and dorsal portions of the head; pronotum; and dorsal half of metafemur. The head (Fig. 6g) on the facial surface has numerous short setae, directed more or less ventrally, and 7-segmented antennae. Apical (ventral) spurs of the metatibia are less than twice as long as the subapical (dorsal) spurs of this tibia (Figs. 6h, 6i). The abdominal apex is as in Fig. 6j.

**M e a s u r e m e n t s,** mm. Body length, 2; pronotum length, 0.6; profemur length, 0.35; protibia length, 0.3; metafemur length, 1.1; metatibia length, 1.

## Infraorder Acridoidea

Superfamily Tetrigoidea Rambur, 1838

Family Tetrigidae Rambur, 1838

Subfamily Tetriginae Rambur, 1838

Genus *Succinotettix* Piton, 1938

The genus was described for a single species from the Baltic amber and placed in the subfamily "Tetricinae" (Piton, 1938). The characters given in the original description do not allow clearly distinguishing this genus from the recent genera of Tetriginae, except for the enigmatic presence of a large tympanum on both sides of the first abdominal tergite. Such tympana are lacking in recent Tetrigoidea; thus, it cannot be ruled out that the author of the genus could have taken by mistake some irregularities of the integument for tympana (the shape of pronotum and tegmina exclude the possibility that *Succinotettix* belongs to the subfamily Acridoidea, many members of which actually have tympana on the abdomen). It is unclear to which genus belongs the other species from the Baltic amber (*Acrydium bachofeni* Zeun.). The author of this species, on the one hand, placed it in Tetriginae, by including it in the recent genus *Acrydium* Geoffr. (= *Tetrix* Latr.), and on the other hand, specified that the reduced tegmina of this species are still longer than in any other recent species (Zeuner, 1937). The only thing known about the tegmina of *S. chopardi* Piton (the type species of the genus *Succinotettix*) is that they are small and oval, but it is unclear how small they are. Thus, it cannot be ruled out that *A. bachofeni* could be the second species of the genus *Succinotettix*, or even a synonym of *S. chopardi*.

Only the dorsal portion of the body can be examined in the specimen PIN, no. 363/87, ?*Succinotettix* sp., from the Late Eocene Baltic amber, but even this portion is partly covered by fissures in the amber (Fig. 3g). The characters that could be seen do not mismatch the description of the genus (Piton, 1938), but also do not allow distinguishing this specimen from *A. bachofeni* (e.g., the entire tegmina are not visible). The inclusion probably represents the adult stage.

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