## New and little known taxa of "neotenic" Lycidae (Coleoptera), with discussion of their phylogeny

# Новые и малоизвестные таксоны "неотеничных" Lycidae (Coleoptera), с обсуждением их филогении

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КЛЮЧЕВЫЕ СЛОВА: Coleoptera, Lycidae, новое подсемейство, новые трибы, новые рода, новые виды, таксономия, Афротропическая и Неотропическая области.

ABSTRACT. A new subfamily of "neotenic" netwinged beetles, Mimolibnetinae subfam.n., two new tribes, Dominopterini tr.n. and Electropterini tr.n., four new genera, Tishechkinia gen.n., Dominopteron gen.n., Nanolycus gen.n. and Prioceraton gen.n., and seven new species, Mimolibnetis patruelis, Dominopteron hispaniolum, Electropteron nepos, E. cursarius, Nanolycus gnomus, Ceratoprion sobrinus and Pseudacroleptus gorgonus spp.n., are described from the Afrotropical and Neotropical regions. Extant representatives of the fossil genus Electropteron Kazantsev, 2012 (previously known only from the Dominican amber) are described for the first time, also from the Dominican Republic. The genera Ceratoprion Gorham, 1884, Mimolibnetis Pic, 1936 and Electropteron are redescribed, and Mimolibnetis apicalis Pic, 1936 and M. obscurus Pic, 1936 are illustrated. Tishechkinia carltoni (Kazantsev, 2005), comb.n. is transferred to *Tishechkinia* gen.n. from Neolyrium Kazantsev, 2005, and Prioceraton ignavum (Kazantsev, 2008), comb.n. is transferred to Prioceraton gen.n. from Ceratoprion. A cladistic analysis of the «neotenic» lycid lineages is provided.

РЕЗЮМЕ. Из Афротропической и Неотропической областей описывается новое подсемейство "неотеничных" Lycidae, Mimolibnetinae subfam.n., две новых трибы, Dominopterini tr.n. и Electropterini tr.n., четыре новых рода, Tishechkinia gen.n., Dominopteron gen.n., Nanolycus gen.n. и Prioceraton gen.n., и семь новых видов, Mimolibnetis patruelis, Dominopteron hispaniolum, Electropteron nepos, E. cursarius, Nanolycus gnomus, Ceratoprion sobrinus и Pseudacroleptus gorgonus spp.n. Впервые описываются рецентные представители ископаемого рода Electropteron Каzantsev, 2012 (ранее известного лишь из Доминиканского янтаря), также из Доминиканской Республики. Приводятся переописания родов

Ceratoprion Gorham, 1884, Mimolibnetis Pic, 1936, Electropteron и иллюстрации Mimolibnetis apicalis Pic, 1936 и М. obscurus Pic, 1936. Tishechkinia carltoni (Kazantsev, 2005), comb.n. переносится в Tishechkinia gen.n. из Neolyrium Kazantsev, 2005, а Prioceraton ignavum (Kazantsev, 2008), comb.n. переносится в Prioceraton gen.n. из Ceratoprion. Приводится кладистический анализ "неотеничных" групп Lycidae.

#### Introduction

"Neotenia", or, in case of Lycidae, complete absence in the female metamorphosis of the pupa stage, is presumed to be a widespread phenomenon among Lycidae of the tropical areas. As females are (or presumed to be) so morphologically different, their mode of life is apparently also different and they still remain, with very few exceptions, undiscovered. Apart from the unavailability of females despite sometimes noticeable presence of males in collections, the latter in most cases may be separated from "normal" lycids at first glance, due to a number of their morphological peculiarities, both of hypothetically plesio- and apomorphic nature.

First genera of net-winged beetles with unknown females were described at the end of the XIX century (oriental *Lyropaeus* Waterhouse, 1878, *Atelius* Waterhouse, 1878 and *Scarelus* Waterhouse, 1878), and at the beginning of the XX century a first higher taxon, Leptolycinae, was established for the Caribbean *Leptolycus* Leng et Mutchler, 1922 [Leng & Mutchler, 1922]. Since then several dozen "neotenic" genus- and several family-group taxa were described, from all parts of the Palaeotropical zone, with the exception of Madagascar. An apparently "neotenic" taxon was also found in the Dominican amber [Kazantsev, 2012]. Although, as recent surveys reveal [e.g., Kazantsev, 1999; 2005a; 2005b;

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2009a; 2009b; Kazantsev & Zaitsev, 2009], morphology of these beetles demonstrates an astounding range of conditions, their classification is still rather geographic than phylogenetic, with oriental taxa grouped in Lyropaeinae or Miniduliticolinae, Afrotropical — in Dexorinae, and neotropical taxa — in Leptolycinae or attributed to Calopterini (Lycinae) [e.g., Bocák & Bocáková, 2008]. One of the aspects of the problem is that many, if not most, "neotenic" genera are monotypic, and quite a number of their type species have been known so far just by the holotypes, due to their rarity, effectively precluding their comprehensive morphological and phylogenetic analysis.

A possibility to study recently collected "neotenic" Lycidae, sometimes in decent series, allows, apart from describing new taxa, to contribute to the knowledge of morphology of this group and to attempt addressing the problem of its phylogeny. A new subfamily, two new tribes, four new genera and several new species, including two extant species in the previously exclusively fossil *Electropteron* Kazantsev, 2012, were discovered in the Afro- and Neotropical material. Presented below are descriptions of these new taxa, complemented with redescriptions of several poorly known «neotenic» lycids and followed by a cladistic analysis.

The following abbreviations are used in this paper: FMNH — Field Museum of Natural History, Chicago; ICM — Insect Center, Moscow; INBio — Instituto Nacional de Biodiversidad, Heredia, Costa Rica; LSAM — Louisiana State Arthropod Museum, Baton Rouge; MNHN — Muséum national d'Histoire naturelle, Paris.

#### Material and Methods

The material studied was glued on cardboard plates. For examination specimens were relaxed in water, then, for approximately 24 hours, in 10% KOH at room temperature. The KOH treated parts of the body, including the aedeagi and ultimate abdominal segments, were placed in microvials with glycerin.

MSP-1 zoom stereoscopic dissecting microscope with x8–x80 magnification range and Micromed-2/3–20 zoom stereoscopic light microscope with x100–x400 magnification range were used.

#### **Taxonomy**

#### Mimolibnetis Pic, 1936

Type species: *Mimolibnetis apicalis* Pic, 1936 (designated in Kazantsev, 1999).

REDESCRIPTION. Male. Alate, slender, elongate. Head subquadrate, not narrowed behind eyes. Fastigium acute, ca. 60 degrees. Eyes moderately large, spherical. Labrum minute, transverse, lightly sclerotized, lying inside epistoma. Mandibles vestigial. Maxillary palps slender, four-segmented, with ultimate palpomere pointed distally. Labium miniature, prementum fused to gula, palps minute, one-segmented (Fig. 4). Gula long. Antennal prominence conspicuous, but relatively short, antennal sockets separated by minute lamina. Antenna with ten segments, moderately long, filiform to slightly flat-

tened; margins of antennomeres uneven; antennomere 2 short, much shorter than antennomere 3; pubescence on antennomeres 3–10 represented by long scarce hairs (Figs 1–3).

Pronotum transverse, with inconspicuous narrow median carina and transverse heart-shaped structure in posterior half; posterior angles produced laterally (Figs 1–3). Prosternum short, semi-triangular (Fig. 5). Thoracic spiracles elongate, small, not projecting beyond coxae. Mesoventrite transverse, not divided by median suture, slightly concave anteriorly, semi-fused to mesepisternum, separated by partial, present in posterior half, transverse suture; mesepimeron almost as long and wide as mesepisternum. Mesonotum with scutellum not attaining to anterior margin, scutal halves not divided; scutellum with inconspicuous postnotal projection (Fig. 6). Elytra elongate, narrowing distally, completely covering wings, with four primary costae, costa 1 present in proximal third, costa 2 present proximal two thirds (Figs 1-3); interstices 2-4 with one row of more or less regular subquadrate cells, interstices 1 and 5 with two rows of irregular cells; long erect pubescence uniform. Metanotum transverse, with slightly convex scutoscutellar ridge subequal in length to allocrista; prescutum with median suture; intrascutal suture inconspicuous; scutellum with median suture anteriorly; postnotal plate short, without median suture. Metaventrite subquadrate, with blunt posterior angles; discrimen incomplete, attaining to middle. Metendosternite small, without transverse suture and lateral arms. Metathoracic wing with fringe of short hairs, sparser and more decumbent at anterior, denser and straighter at posterior margins; anal cell closed; wedge cell present, Cu veins vestigial.

Protrochantins slightly more prominent than mesotrochantins. Pro- and mesocoxae elongate; metacoxae narrowly separated. Legs slender; trochanters elongate, but considerably shorter than femurs, cylindrical, connected to femora obliquely, with anterior incision occupying more than half its length (Fig. 7); femurs widened and flattened, tibiae slightly curved proximally and strongly widened distally, tibial spurs prominent; tarsomeres 1–4 narrow, without plantar pads; all claws simple.

Abdomen with 9 ventrites (visible sternites), ventrite 1 almost completely interrupted medially by metaventrite and metacoxae. Abdominal spiracles minute, located on lateral surface of tergites ventrally; tergites undivided. Paraproct not divided by median suture, proctiger not subdivided (Fig. 8); sternite 9 narrow, with short spiculum gastrale. Aedeagus symmetric; short phallobase provided with elongate median process and short, but conspicuous latero-proximal apodemes; parameres developed (Figs 9–10).

Female. Unknown, presumably larviform.

REMARKS. Mimolibnetis is among the rare Lycidae that possess conspicuous latero-proximal apodemes of the phallobase (Figs 9-10); the nearest approach of these are the lateral apodemes of *Electropteron* Kazantsev, 2012 described below and Leptolycus [Kazantsev, 2009b]; the other related groups where similar structures occur being Omalisidae and Euanomini (Thilmaninae) in Drilidae [Kazantsev, 2010]. At the same time the obliquely connected to femurs trochanters (Fig. 7) of Mimolibnetis, of all the net-winged beetles, are shared only by Dexoris Waterhouse, 1878 and Lampyrolycus Burgeon, 1937, also from Africa. As for the tibial spurs, which are manifest in Mimolibnetis, the (presumably) neotenic lycids seem to lack them in Western Hemisphere (with the exception of Lycinella Gorham, 1884 and Dominopteron gen.n.), while the Oriental «neotenic» taxa happen to have them, except for Scarelus Waterhouse, 1878. In the Afrotropical region of the three «neotenic» genera two (Mimolibnetis and Lampyrolycus) have tibial spurs, and one (Dexoris Waterhouse, 1878) does not.

Another peculiarity of *Mimolibnetis*, of all lycids reported only in *Neolyrium* Kazantsev, 2005 from the Neotropics, is the location of abdominal spiracles at the edge of tergites. This condition has also been observed in *Thilmanus* Gemminger, 1869 (Thilmaninae, Drilidae). On the other hand, the prementum fused to the gula (Fig. 4) has no match in the family, while the semi-fused mesoventrite in *Mimolibnetis* matches that only of *Platerodrilus* Pic, 1921 and seems to be a transitional condition between *Dominopteron* gen.n. and the rest of Lycidae.

In *Mimolibnetis obscurus* Pic, 1936 (Fig. 3) the phallobase is almost as long as the median lobe of the aedeagus [Kazantsev, 1999].

### *Mimolibnetis patruelis* Kazantsev **sp.n.** Figs 1, 4–10

MATERIAL: Holotype, ♂, Cameroon, Southwest Prov., W Limbe, Bakingili, 35 m, FIT, 1–15.VII.2004, M. Fischer leg. (ICM); paratype, ♂, same label (ICM).

DESCRIPTION. **Male**. Dark brown; head anteriorly and ventrally, antennomeres 1–2, pronotum, tibiae and tarsi yellowish brown; prosternum, meso- and metaventrite, penultimate tergite and legs, except tibiae and tarsi, yellow.

Eyes relatively large, interocular distance ca. 1.5 times greater than eye radius. Antennae attaining to elytral two thirds, with antennomere 2 transverse, about 8 times shorter

than antennomere 3, antennomere 3 the longest, 1.3 times longer than antennomere 4.

Pronotum transverse, ca. 1.6 times as wide as long, bisinuate basally, straight anteriorly, with conspicuous median suture and small acute posterior angles; margins roughly punctured. Scutellum with small subquadrate postnotal plate, slightly emarginate at apex (Figs 1, 6).

Abdomen with two ultimate segments protruding beyond elytra (Fig. 1).

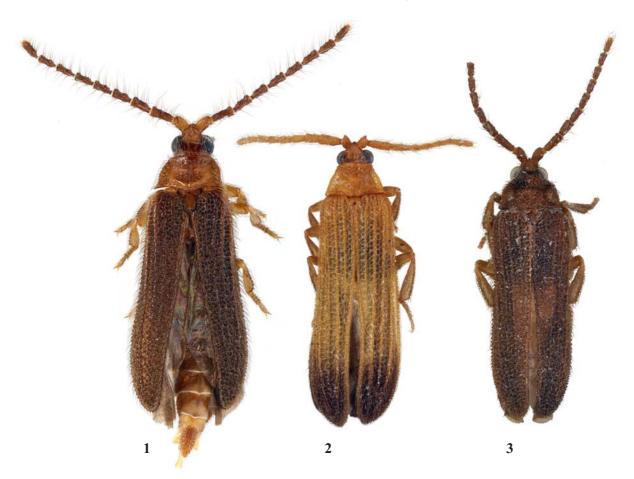
Aedeagus with bottle-shaped, proximally widened median lobe; parameres about half length of median lobe, rounded distally (Figs 9–10); apices of parameres and apex of median lobe conspicuously exposed (Fig. 1).

Female. Unknown.

Length: 2.8–2.9 mm (from anterior part of head to apices of elytra). Width (humerally): 0.7–0.8 mm.

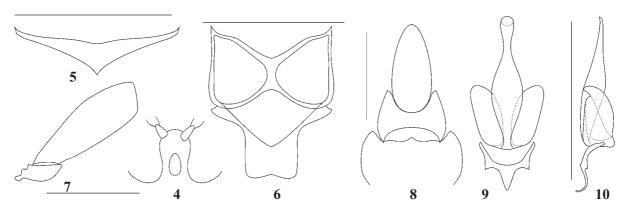
ETYMOLOGY. The name of the new species is derived from the Latin noun «paternal cousin», alluding to its similarity with *M. apicalis* Pic, 1936, the type species of the genus.

DIAGNOSIS. *M. patruelis* **sp.n.**, being similar both to *M. apicalis* (Fig. 2) and *M. obscurus* (Fig. 3) (lectotypes in MNHN), differs by the longer and more erect antennal and elytral pubescence (Fig. 1), bottle-shaped median lobe, short and rounded distally parameres of the aedeagus, with short phallobase, as well as exposed apices of parameres and median lobe (Figs 1, 9–10).



Figs 1–3. General view of Mimolibnetis, males: 1 — Mimolibnetis patruelis sp.n.; 2 — Mimolibnetis apicalis; 3 — Mimolibnetis obscurus; 1 — holotype; 2–3 — lectotypes.

Рис. 1–3. Общий вид Mimolibnetis, самцы: 1 — Mimolibnetis patruelis **sp.n.**; 2 — Mimolibnetis apicalis; 3 — Mimolibnetis obscurus; 1 — голотип: 2–3 — лектотипы.



Figs 4–10. Details of *Mimolibnetis patruelis* **sp.n.**; holotype male: 4 — labium; 5 — prosternum; 6 — mesonotum; 7 — hind trochanter and femur; 8 — ultimate tergites; 9–10 — aedeagus; 4–5, 7, 9 — ventral view; 6, 8 — dorsal view; 10 — lateral view. Scale: 0.5 mm. Рис. 4–10. Детали строения *Mimolibnetis patruelis* **sp.n.**; голотип, самец: 4 — нижняя губа; 5 — переднегрудь; 6 — мезонотум; 7 — задний вертлуг с бедром; 8 — вершинные тергиты; 9–10 — эдеагус; 4–5, 7, 9 — снизу; 6,8 — сверху; 10 — сбоку. Масштабная

#### Tishechkinia Kazantsev gen.n.

Type species: Neolyrium carltoni Kazantsev, 2005

линейка: 0.5 мм.

DESCRIPTION. **Male**. Alate, elongate, flattened, small (3.2–3.4 mm long) (Fig. 11). Head transverse, narrowed behind eyes. Fastigium acute, ca. 30 degrees. Subantennal sutures conspicuous. Tentorium represented by posterior pits and a pair of relatively long slender ventral arms. Eyes relatively large (interocular distance ca. 1.5 times as long as diameter), spherical. Labrum lightly sclerotized, lying inside

epistoma. Mandibles vestigial. Maxillae reduced to paired fused cardo and stipes; palps absent. Labium miniature, reduced to prementum with a pair of narrow elongate sensillae; palps absent. Gula absent (Fig. 13). Antennal prominence conspicuous, antennal sockets separated by minute lamina. Antenna 10–segmented, relatively long, reaching over elytral middle; antennomeres 3–10 conspicuously flattened, 3–9 slightly dentate; antennomere 3 the longest, 6 times longer than antennomere 2 and 1.3 times longer than



Figs 11–12. General view of *Tishechkinia* **gen.n.** and *Dominopteron* **gen.n.**, males: 11 — *Tishechkinia* carltoni; 12 — *Dominopteron* hispaniolum **gen.n.**, sp.n., 11 — paratype; 12 — holotype.

Рис. 11—12. Общий вид *Tishechkinia* gen.n. и *Dominopteron* gen.n., самцы: 11 — *Tishechkinia* carltoni; 12 — *Dominopteron* hispaniolum gen.n., sp.n., 11 — паратип; 12 — голотип.

antennomere 4; antennal hairy pubescence short and decumbent, scaliform pubescence relatively dense.

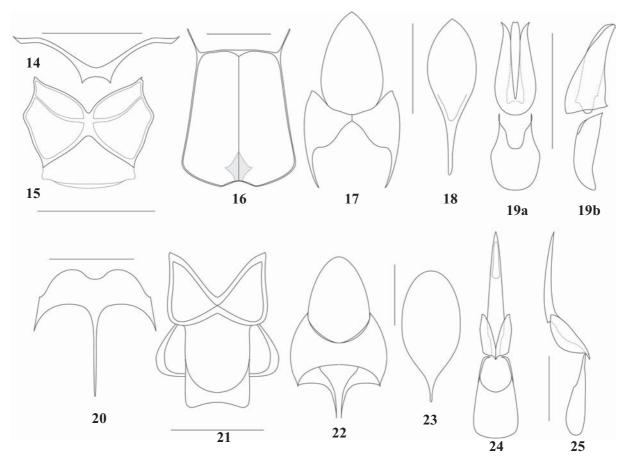
Pronotum transverse, trapezoidal, margined at sides, with narrow median carina transformed into very narrow groove in posterior two thirds; anterior margin almost straight, posterior margin conspicuously bisinuate; anterior angles prominent, posterior angles long and acute (Fig. 11). Prosternum short, V-shaped, posteriorly bifurcate (Fig. 14). Thoracic spiracles elongate, relatively small, slightly protruding beyond prothorax. Mesoventrite transverse, slightly concave anteriorly, separated from mesepisternum by conspicuous suture and semi-triangular sternopleural sclerite; mesepimeron conspicuously narrower and shorter than mesepisternum.

Mesonotum with scutellum not attaining to anterior margin, mesoscutal halves divided; scutellum with very short and almost straight distally postnotal plate (Fig. 15). Elytra long,

almost 9 times longer than pronotum, almost parallel-sided, dehiscent in distal two thirds, slightly narrowing posteriorly, bicostate, with equally developed primary costae (2 and 4) reaching elytral apices; interstices finely irregularly alveolate; short elytral pubescence uniform. Metanotum transverse, with straight scuto-scutellar ridge forming no loop; allocristae inconspicuous, about twice as short as scutoscutellar ridge; intrascutal suture small, emerging at distal third of scutum; scutellum with complete median suture; postnotal plate very short, with two small median semicircular appendices. Metaventrite elongate, with rounded, almost straight posterior angles; discrimen (metasternal suture) complete, attaining to mesosternum (Fig. 16). Metendosternite small, broad, without transverse suture, with small arms (Fig. 16). Metathoracic wing with vein Sc joining RA near apical hinge; anal cell long, almost rectangular distally;



Fig. 13. Head of *Tishechkinia carltoni*, paratype, ventral view. Puc. 13. Голова *Tishechkinia carltoni*, паратип, снизу.



Figs 14–25. Details of *Tishechkinia* **gen.n.** and *Dominopteron* **gen.n.**, holotype males: 14–19 — *Tishechkinia carltoni*; 20–25 — *Dominopteron hispaniolum* **gen.n.**, **sp.n.**; 14, 20 — prosternum; 15, 21 — mesonotum; 16 — metaventrite; 17, 22 — ultimate tergites; 18, 23 — ultimate sternite; 19, 24–25 — aedeagus; 14, 16, 18, 19a, 20, 23–24 — ventral view; 15, 17, 21–22 — dorsal view; 19b, 25 — lateral view. Scale: 0.25 mm.

Рис. 14—25. Детали строения *Tishechkinia* **gen.n.** и *Dominopteron* **gen.n.**, голотипы, самцы: 14—19 — *Tishechkinia* carltoni; 20—25 — *Dominopteron* hispaniolum **gen.n.**, **sp.n.**; 14, 20 — переднегрудь; 15, 21 — мезонотум; 16 — метаветрит; 17, 22 — вершинные тергиты; 18, 23 — вершинный стернит; 19, 24—25 — эдеагус; 14, 16, 18, 19a, 20, 23—24 — снизу; 15, 17, 21—22 — сверху; 19b, 25 — сбоку. Масштабная линейка: 0.25 мм.

wedge cell semi-closed; cu-a brace vestigial, located at proximal third of wedge cell; Cu veins vestigial.

Protrochantins subequal in size to mesotrochantins. Proand mesocoxae elongate; metacoxae rather broadly separated, their meral sutures extending to half length of coxa. Legs relatively short; trochanters elongate, about as long as half of tibia, cylindrical, connected to femora distally; femurs and tibiae flattened, straight and moderately wide, tibial spurs absent; tarsomeres 1–4 narrow, without plantar pads; all claws simple.

Abdominal spiracles located laterally on membrane between sternite and tergite. Paraproct undivided; proctiger medially short, with median suture (Fig. 17); spiculum gastrale relatively short, distinctly shorter than distal portion of sternite 9 (Fig. 18). Aedeagus symmetric, with long, slightly outwardly hooked parameres, elongate straight median lobe and relatively large phallobase; phallobase without median suture (Fig. 19).

Female. Unknown, probably paedomorphic and larvi-

ETYMOLOGY. The genus is named after Dr. A.K. Tishechkin (Santa Barbara, California) who together with Dr. C.E. Carlton collected the type series of the type species. Gender feminine.

DIAGNOSIS. *Tishechkinia* **gen.n.** differs from *Neolyrium*, the only other Neotropic lycid taxon with 10–segment antennae, by the reduced maxillary palps (Fig. 13), relatively longer antennomere 2 (only 6x shorter than antennomere 3 vs. 16x shorter in *Neolyrium*), divided scutal halves and almost straight distal margin of postnotal plate of the mesonotum (Fig. 15) (vs. undivided scutal halves and deeply incised postnotal plate in *Neolyrium*), short spiculum gastrale, which is distinctly shorter than distal portion of sternite 9 (Fig. 18) (vs. spiculum gastrale about as long as distal portion of sternite 9 in *Neolyrium*), short legs (Fig. 11) and by the long parameres and internal position of median lobe of the aedeagus (Fig. 19) vs. short parameres and distal position of median lobe of the aedeagus in *Neolyrium* [Kazantsev, 2005a].

DISTRIBUTION. *Tishechkinia carltoni* (Kazantsev, 2005), **comb.n.**, from Ecuador, is the only known species of the genus.

### Tishechkinia carltoni (Kazantsev, 2005), comb.n. Figs 11, 13–19

Neolyrium carltoni Kazantsev, 2005: 57.

MATERIAL: Holotype  $\circlearrowleft$ , Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, 0°40.5′S 76°24′W, FIT  $\circlearrowleft$ 1, 23–30.VI.1999, A.K. Tishechkin, C.E. Carlton leg. (LSAM); paratypes, 11  $\circlearrowleft$  $\circlearrowleft$ 7, same label; Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, 0°40.5′S

76°24′W, FIT ○ 1, 17–23.VI.1999, A.K. Tishechkin & C.E. Carlton leg.; Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, 0°40.5'S 76°24′W, FIT ♂2, 20–29.VI.1999, C.E. Carlton & V.L. Moselev leg.; Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, 0°40.5'S 76°24′W, FIT O'M1, 28.V-5.VII.1999, C.E. Carlton & A.K. Tishechkin leg.; Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, 0°40.5′S 76°24′W, FIT  $\circlearrowleft$  3, 28.VI-5.VII.1999, A.K. Tishechkin leg.; Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, 0°40.5'S 76°24′W, FIT 0<sup>7</sup>6, 4–17.VII.1999, A.K. Tishechkin, C.E. Carlton leg.; Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, 0°40.5'S 76°24′W, FIT ♂3, 18–23.VII.1999, A.K. Tishechkin leg.; Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, FIT ♂2, 25.VII-3. VIII. 1999, A.K. Tishechkin leg.; Ecuador, Napo, Yasuni National Park, Yasuni Biological Station, 0°40′32′′S 76°23′50′′W, FIT ♂1, 25.VII-4.VIII.1999, A.K. Tishechkin leg.; Ecuador, Napo, Yasuni Res. Stn. on mid Rio Tiputini, 0°40.5′S 76°24′W, FIT 0'6, 26.VII-4.VIII.1999, A.K. Tishechkin leg. (ICM and LSAM); 2 0'0', Ecuador, Orellana, Yasuni Research Station, FIT, 11-26.VII.2008, A.K. Tishechkin leg. (ICM).

#### Dominopteron Kazantsev gen.n.

Type species: Dominopteron hispaniolum Kazantsev, sp.n. DESCRIPTION. Male. Alate, slender, elongate, flattened (Fig. 12). Head elongate, parallel-sided behind eyes, finely granulose. Fastigium acute, ca. 30 degrees. Tentorial ventral arms vestigial; dorsal tentorial maculae present. Eyes relatively small, flattened. Labrum transverse, small, sclerotized, located anteriad of epistoma. Mandibles vestigial. Maxillary palps four-segmented, slender, very narrow, with ultimate palpomere pointed distally. Labium consisting of non-paired prementum and a pair of three-segment minute palps; ultimate palpomere pointed distally. Gula long, gular sutures prominent, gular area bulging. Antennal prominence prominent, elongate, triangularly produced forward, antennal sockets separated by minute lamina. Antenna 11-segmented, relatively long, reaching over elytral apices, filiform; antennomere 3 considerably longer than antennomere 2; antennomeres 3–11 roughly granulose; scaliform pubescence absent, hairy pubescence short and decumbent (Fig. 12).

Pronotum elongate, trapezoidal, ca. 9 times shorter than elytra, with fine median carina in anterior and inconspicuous narrow median furrow in posterior half, finely granulose; median suture absent; posterior margin medially slightly produced posteriorly, anterior margin slightly concave; anterior angles prominent and acute, posterior angles long and acute (Fig. 12). Prosternum relatively long, deeply medially emarginate anteriorly, with long narrow posterior process (Fig. 20). Thoracic spiracles elongate, rather prominent, protruding beyond prothorax, with additional basal sclerite. Mesoventrite transverse, fused to mesepisternum; mesepimeron conspicuously narrower and 2 times shorter than mesepisternum. Mesonotum with scutellum not attaining to anterior margin, mesoscutal halves not divided; scutellum with relatively large, elongate, emarginate distally, dorsally alveolate postnotal plate (Fig. 21). Elytra long, not dehiscent, tapering posteriorly, with three primary costae (2-4) (costa 1 noticeable proximally): costa 2 reaching elytral four fifths, costa 3 reaching two fifths, costa 4 reaching elytral apices; costa 4 conspicuously more developed in elytral two thirds; interstices with one row of regular elongate cells; short decumbent pubescence on longitudinal and transverse costae (Fig. 12). Metanotum elongate, with somewhat concave scuto-scutellar ridge forming no loop; allocrista considerably shorter than scuto-scutellar ridge; intrascutal suture small, emerging at middle of allocrista; scutellum with complete, but inconspicuous median suture. Metaventrite elongate, almost triangular, with concave sides and straight posterior angles; discrimen (metasternal suture) complete, attaining to mesosternum. Metendosternite small, very narrow, without arms and transverse suture. Metathoracic wing with vein Sc joining RA near apical hinge; anal cell elongate, pointed distally; wedge cell absent; cu-a brace vestigial, located just below apex of anal cell; Cu veins vestigial.

Mesotrochantins conspicuously slenderer than protrochantins. Pro- and mesocoxae elongate; metacoxae distinctly separated. Legs slender; trochanters elongate, but considerably shorter than tibia, cylindrical, connected to femora distally; femurs not flattened, narrow; tibiae slightly flattened, straight and narrow, tibial spurs conspicuous; tarsomeres 1–4 narrow, without plantar pads; all claws simple.

Abdominal spiracles located laterally between sternite and tergite. Paraproct undivided, proctiger without median suture (Fig. 22); sternite 9 without spiculum gastrale (Fig. 23). Aedeagus symmetric, with shortened parameres; median lobe elongate, slightly curved and pointed distally; elongate phallobase without median suture (Figs 24–25).

Female. Unknown, probably paedomorphic and larvi-

ETYMOLOGY. The name of the genus is derived from «Dominican Republic», according to the country where it occurs, and «pteron», the Greek for «wing». Gender neuter.

DIAGNOSIS. *Dominopteron* **gen.n.** differs from *Nanolycus* **gen.n.**, also from the Dominican Republic, by the longer head and pronotum (Fig. 12), conspicuous gular sutures and bulging gular area, regular and conspicuous elytral reticulation (Fig. 12). The new genus differs from *Ceratopriomorphus* Pic, 1922, described from Brazil, by the long head, barely compressed antennomeres and bicostate elytra. It differs from *Cessator* Kazantsev, 2009, also with long head and relatively long antennomere 3, by the parallel-sided behind eyes head, long pronotum, regularly and conspicuously reticulated elytra, undivided mesoventrite and differently structured aedeagus (Figs 24–25).

Dominopteron gen.n. appears to be quite unique in Lycidae in having relatively long and medially emarginate prosternum, provided with a long narrow posterior process (Fig. 20). It is similar to *Scarelus* Waterhouse, 1878, another «neotenic» lycid, in the shape of the anterior prosternal margin [Kazantsev, 2005b], and, at the same time, to Omalisidae, in the shape of the posterior process [Kazantsev, 2007; 2010]. It also differs from all studied net-winged beetles by the fused condition of the mesoventrite. Such condition is typical of Lampyridae, the sister group of Lycidae, or *Cantharis* Linnaeus, 1758, in Cantharidae.

DISTRIBUTION. *Dominopteron hispaniolum* **sp.n.**, the only species of the genus, was discovered on the Greater Antillean island of Hispaniola.

### Dominopteron hispaniolum Kazantsev **sp.n.** Figs 12, 20–25

MATERIAL: Holotype, o'', Dominican Republic, Hato Mayor, env. Los Haitíses, 8 km W Sabana de la Mar, 20 m, mesic lowland forest, sweeping, 14.II.2006, S. Kazantsev leg. (ICM); paratype, o'', same label (ICM).

DESCRIPTION. Male. Dark brown to black; frons distally, antennomere 11, transverse band at elytral fourth fifths and legs, except tibiae distally and tarsi, yellowish testaceous (Fig. 12).

Eyes relatively small, interocular distance ca. 1.3 times greater than their diameter. Antennae long, antennomere 10 attaining to elytral apices, with antennomere 2 wider than long and about 7 times shorter than antennomere 3 (Fig. 12).

Pronotum elongate, ca. 1.2 times longer than wide, somewhat constricted anteriorly, posterior angles ca. 45°. Scutellum trapezoidal, with slightly emarginate at apex (Fig. 12).

Elytra long, 4.5 times as long as wide at humeri, with elongate roundish cells in interstices; bottom of cells glabrous (Fig. 12).

Aedeagus with shortened, almost three times shorter than median lobe, parameres; phallobase widened distally (Figs 24–25).

#### Female. Unknown.

Length: 3.5–3.6 mm. Width (humerally): 0.55–0.6 mm. ETYMOLOGY. The name of the new species is derived from the country where it was collected.

DIAGNOSIS. *Dominopteron hispaniolum* **sp.n.** may be easily distinguished from other lycid taxa by the generic characters. Unlike other Hispaniolan «neotenic» lycids *D. hispaniolum* **sp.n.** has a yellow postdiscal band on elytra (Fig. 12), which is more typical of net-winged beetles from the mainland Neotropics.

#### Electropteron Kazantsev, 2012

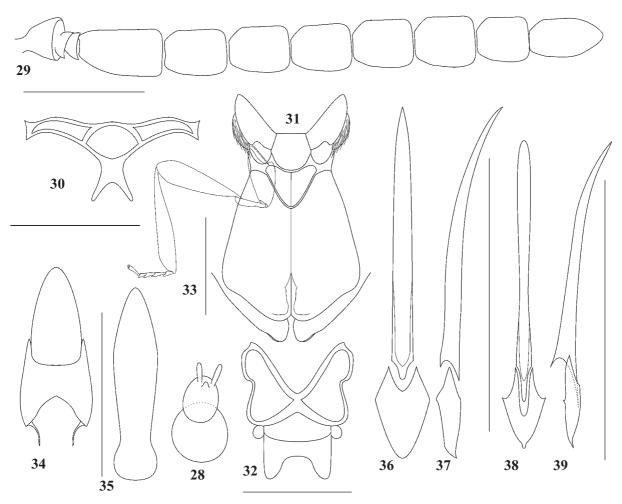
Type species: *Electropteron avus* Kazantsev, 2012 (by monotypy). REDESCRIPTION. **Male**. Alate, slender, elongate (Figs 26–27). Head elongate, narrowed behind eyes, alveolate, with conspicuous round excavation behind antennal prominence, in relatively long dense pubescence. Fastigium acute. Posterior tentorial pits minute; ventral arms seemingly absent; dorsal

tentorial maculae small and approximate. Eyes moderately large, spherical. Labrum minute, transverse, lying inside epistoma. Mandibles vestigial. Maxillary palps slender, four-segmented, with ultimate palpomere miniature, pointed distally. Labium greatly reduced, consisting of free non-paired prementum with a pair of one-segment sensillae and noticeable short ligula (Fig. 28). Gula short, lying anteriad of posterior tentorial pits, gular sutures somewhat approximate anteriorly, but well separated posteriorly. Antennal prominence inconspicuous, antennal sockets separated by minute lamina. Antenna 11segmented, relatively long, with antennomeres 4-11 conspicuously flattened, with rounded angles; antennomeres 2 and 3 wider than long, subequal in length and considerably shorter than antennomere 4; antennal pubescence long and erect (Figs 26, 29), complemented with scarce minute roundish scales on antennomeres 4-11.

Pronotum short and transverse, trapezoidal, with obscure median furrow; median suture absent; posterior angles acute, conspicuously produced laterally (Fig. 26). Prosternum relatively short, semi-triangular, with median part separated by conspicuous sutures (Fig. 30). Thoracic spiracles elongate, relatively small, not protruding beyond prothorax, provided with additional basal sclerite. Mesoventrite transverse, straight anteriorly, separated from mesepisternum by transverse su-



Figs 26—27. General view of *Electropteron*, holotype males: 26 — *E. nepos* **sp.n.**; 27 — *E. cursarius* **sp.n.** Рис. 26—27. Общий вид *Electropteron*, голотипы, самцы: 26 — *E. nepos* **sp.n.**; 27 — *E. cursarius* **sp.n.** 



Figs 28–39. Details of *Electropteron*, holotype males: 28–37 — *E. nepos* **sp.n.**; 38–39 — *E. cursarius* **sp.n.**; 28 — labium; 29 — antenna; 30 — prosternum; 31 — ventrum; 32 — mesonotum; 33 — middle leg; 34 — ultimate tergites; 35 — ultimate sternite; 36–39 — aedeagus; 28–31, 33, 35–36, 38 — ventral view; 32, 34 — dorsal view; 37, 39 — lateral view. Scale: 0.5 mm.

Рис. 28–39. Детали строения *Electropteron*, голотипы, самцы: 28–37 — *E. nepos* **sp.n.**; 38–39 — *E. cursarius* **sp.n.**; 28 — нижняяя губа; 29 — антенна; 30 — переднегрудь; 31 — вентрум; 32 — мезонотум; 33 — средняя нога; 34 — вершинные тергиты; 35 — вершинный стернит; 36–39 — эдеагус; 28–31, 33, 35–36, 38 — снизу; 32, 34 — сверху; 37, 39 — сбоку. Масштабная линейка: 0.5 мм.

tures; mesepimeron conspicuously narrower and slightly shorter than mesepisternum (Fig. 31). Mesonotum with scutellum not attaining to anterior margin, mesoscutal halves not divided; scutellum with short, parallel-sided, distally emarginate postnotal plate (Fig. 32). Elytra long, almost parallel-sided, slightly dehiscent distally, with four primary costae: costae 2 and 4 noticeably stronger, attaining to elytral apices and costae 1 and 3 noticeable proximally, interstices alveolate; suberect dense elytral pubescence uniform. Metanotum subquadrate, with convex scuto-scutellar ridge forming wide loop posteriorly; allocrista subequal in length to scuto-scutellar ridge; intrascutal suture small, emerging at middle of allocrista; scutellum without median suture. Metaventrite with blunt posterior angles; anterior part separated by complete mesosternal sutures; discrimen (metasternal suture) complete, attaining to mesosternum (Fig. 31). Metendosternite small, simple, slightly widening distally, with no lateral arms and no transverse suture (Fig. 31). Metathoracic wing with vein Sc joining RA near apical hinge; anal cell long, triangular distally; wedge cell absent; cu-a brace absent; Cu veins connected to M.

Protrochantins subequal in size to mesotrochantins. Proand mesocoxae elongate; metacoxae narrowly separated from each other. Legs slender; trochanters elongate, but considerably shorter than femora, cylindrical, connected to femora somewhat obliquely (anterior incision occupying ca. one half in *E. nepos* **sp.n.**), but considerably less so in *E. cursarius* **sp.n.**); femora and tibiae flattened, straight and narrow, tibial spurs absent; tarsomeres 1–4 narrow, without plantar pads; all claws simple (Fig. 33).

Abdominal spiracles minute, located laterally in membrane between sternite and tergite. Paraproct undivided, proctiger relatively long, without median suture (Fig. 34); spiculum gastrale absent, ultimate sternite dilated proximally (Fig. 35). Aedeagus symmetric, with elongate straight median lobe; parameres absent; phallobase with noticeable lateral apodemes, median phallobasal suture absent (Figs 36–39).

#### Female. Unknown.

DIAGNOSIS. A possibility to study extant representatives of this previously strictly fossil genus allows complementing its diagnosis. *Electropteron* is somewhat similar to *Ceratoprion* Gorham, 1884, distributed in the highlands of Central America and the Ands south to Ecuador, differing by the nonserrate antennomeres 4–11, their erect pubescence, absence of the median longitudinal pronotal carina, divided prosternum

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and metaventrite (Figs 26–31), absent parameres of the aedeagus (Figs 36–39), etc. *Electropteron* also has affinities with *Tainopteron* Kazantsev, 2009, from Puerto Rico, but is distinguishable by the flattened antennomeres 4–11, less transverse pronotum, longer elytra completely covering folded wings, divided metaventrite (Fig. 31) and differently structured ultimate abdominal segments (Figs 34–35), as well as by the absent parameres of the aedeagus (Figs 36–39). The divided prosternum appears to be a symplesiomorphy of *Electropteron* and *Tainopteron*. *Electropteron* differs from *Leptolycus* by the characteristic flattened antennomeres 4–11 (Fig. 29), relatively narrow divided prosternum (Fig. 30), divided metaventrite (Fig. 31) and longer elytra, completely covering the body.

Electropteron is unique in the family in possessing complete mesosternal sutures in the anterior part of metaventrite (Fig. 31), which seem to represent a plesiomorphy of the taxon. The nearest groups where similar structures occur are the Omalisidae and Euanomini (Thilmaninae) in Drilidae [Kazantsev, 2010].

### Electropteron nepos Kazantsev **sp.n.** Figs 26, 28–37

MATERIAL: Holotype, ♂, Dominican Republic, Hato Mayor, env. Los Haitíses, 8 km W Sabana de la Mar, 20 m, mesic lowland forest, sweeping, 14.II.2006, S. Kazantsev leg. (ICM); paratypes, 3 ♂♂, same label (ICM).

DESCRIPTION. Male. Dark brown; pedicel, pro- and mesothorax, elytra proximally, ultimate tergite and sternite, pro- and mesocoxae, pro- and mesotrochantins yellowish testaceous; antennomere 11 white (Fig. 26). Head with deep round excavation behind antennal prominence, in long dense pubescence. Fastigium acute, ca. 75 degrees. Eyes moderately large, interocular distance ca. 1.2 times greater than eye diameter. Antenna attaining to elytral two thirds, with antennomere 3 wider than long, subequal in length to antennomere 2 and ca. 8 times shorter than antennomere 4 (Fig. 29).

Pronotum short, ca. 7 times shorter than elytra, transverse and about twice as wide as long, trapezoidal, with almost straight sides, rounded anterior and prominent acute (ca. 50°) posterior angles. Scutellum short, parallel-sided, conspicuously emarginate distally (Figs 26, 32). Elytra long, 3.1 times as long as wide at humeri, slightly dehiscent in distal two thirds, with four primary costae: costae 2 and 4 noticeably stronger, attaining to elytral apices; costa 1 present in proximal fourth, costa 3 present in proximal two thirds, interstices alveolate; suberect dense elytral pubescence uniform.

Legs slender and narrow; tarsomere 2 the longest, subequal in length to tarsomere 5.

Aedeagus with elongate straight pointed apically median lobe; phallobase with relatively small median incision and inconspicuous lateral apodemes (Figs 36–37).

Female. Unknown.

Length: 4.0–4.1 mm. Width (humerally): 0.75–0.8 mm. ETYMOLOGY. The name of the new species is derived from the Latin noun «grandson», alluding to its hypothetic relationship with the fossil *E. avus* Kazantsev, 2012, described from the Dominican amber.

DIAGNOSIS. *E. nepos* **sp.n.** may be easily distinguished from the amber *E. avus* by the less widened distally antennae (Figs 26, 29) and from *E. cursarius* **sp.n.** — by the coloration, deeper head excavation, conspicuously shorter head pubescence, as well as by the structure of the aedeagus (Figs 36–37).

### Electropteron cursarius Kazantsev **sp.n.** Figs 27, 38–39

MATERIAL: Holotype, ♂, Dominican Republic, Barahona, E Sierra Bahoruco, NE Paraiso, 1200 m, 14.VII.2007, S. Sevak leg. (ICM).

DESCRIPTION. **Male**. Uniformly dark brown; antennomere 11 white.

Eyes relatively small, interocular distance ca. 1.8 times greater than eye diameter. Antennae nearly attaining to elytral two thirds; antennomere 3 ca. 10 times shorter than antennomere 4 (Fig. 27).

Pronotum transverse, trapezoidal, about 1.8 times wider than long, with slightly concave sides, conspicuous blunt anterior and prominent acute (ca. 45°) posterior angles. Scutellum short, parallel-sided, triangularly emarginate distally (Fig. 27).

Elytra long, about 10 times longer than pronotum and 5 times longer than wide at humeri, slightly dehiscent in distal half, with four primary costae: costae 2 and 4 slightly more prominent, attaining to elytral apices; costa 1 present in proximal third, costa 3 present in proximal half, interstices alveolate; uniform short pubescence dense and suberect (Fig. 27).

Aedeagus with slender, slightly widened distally median lobe; phallobase with deep incision and conspicuous lateral apodemes (Figs 38–39).

Female. Unknown.

Length: 4.9 mm. Width (humerally): 0.75 mm.

ETYMOLOGY. The name of the new species is derived from the Latin noun «pirate», alluding to its almost uniformly dark brown to black coloration and to the geographic area (the Caribbean) where it occurs.

DIAGNOSIS. *Electropteron cursarius* **sp.n.** may be easily distinguished from *E. nepos* **sp.n.** by the uniformly dark brown body, except for the ultimate antennomere, which is white (Fig. 27), shallower head excavation and somewhat shorter head pubescence, smaller pronotum, slenderer ultimate abdominal segments, as well as by the structure of the aedeagus, with slenderer, but less pointed distally median lobe and deeper incision and more conspicuous lateral apodemes of the phallobase (Figs 38–39).

#### Nanolycus Kazantsev gen.n.

Type species: Nanolycus gnomus Kazantsev, sp.n.

DESCRIPTION. Male. Alate, slender, elongate (Fig. 40). Head elongate, widened behind eyes, finely alveolate. Fastigium acute, ca. 45 degrees. Eyes small, spherical, somewhat flattened. Labrum transverse, lightly sclerotized, lying anteriad of epistoma. Mandibles vestigial. Maxillary palps slender, four-segmented, with ultimate palpomere pointed distally. Labium greatly reduced. Gula short. Antennal prominence conspicuous, triangular; antennal sockets separated by minute lamina. Antenna 11–segmented, moderately long, not attaining to elytral apices, filiform; antennomere 2 transverse, much shorter than antennomere 3 and consequent antennomeres; hairy pubescence moderately long, dense and decumbent, scaliform pubescence absent (Fig. 40).

Pronotum conspicuously transverse, trapezoidal, finely alveolate, with inconspicuous median carina in anterior and narrow median furrow in posterior half; anterior margin concave, posterior margin conspicuously bisinuate; anterior angles conspicuous, posterior angles small and acute (Fig. 40). Prosternum short, semi-triangular, slightly emarginate anteriorly (Fig. 42). Thoracic spiracles elongate, small, provided with basal sclerite. Mesoventrite transverse, concave anteriorly, separated from mesepisternum by perpendicular bar; mesepimeron conspicuously narrower and 2 times shorter than mesepisternum. Mesonotum with scutellum nearly attaining to anterior margin, mesoscutal halves not divided; scutellum with transverse and emarginate distally postnotal plate (Fig. 43). Elytra long, ca. 9 times longer than pronotum, not dehiscent, slightly narrowing posteriorly, with two developed primary costae, costa 2 attaining elytral middle and costa 4 reaching elytral apices, and costa 1 noticeable proximally (Fig. 40); interstices finely alveolate; moderately long decumbent pubescence uniform. Metanotum elongate, with convex scuto-scutellar ridge; allocristae longer than scuto-scutellar ridge; intrascutal suture small, inconspicuous, emerging at distal fourth of scutum; scutellum without median suture. Metaventrite elongate, trapezoidal, with almost straight posterior angles; discrimen (metasternal suture) complete, attaining to mesosternum. Metathoracic wing with hairy fringe on posterior margin; vein Sc joining RA near apical hinge; anal cell long, semi-open; wedge cell long; cu-a brace absent; Cu veins connected neither to M, nor to A veins (Fig. 40).

Protrochantins subequal in size to mesotrochantins. Proand mesocoxae elongate; metacoxae short, narrowly separated. Legs relatively short; trochanters elongate, but considerably shorter than half of tibia, cylindrical, connected to femora distally; femurs robust, slightly flattened, tibiae straight and narrow, tibial spurs absent; tarsomeres 1–4 narrow, without plantar pads; all claws simple.

Abdominal spiracles located laterally between sternite and tergite. Paraproct undivided, elliptical; proctiger without median suture, with long proximal apodemes (Fig. 44); spiculum gastrale very long, considerably longer than distal portion of sternite 9 (Fig. 45). Aedeagus symmetric, with elongate narrow median lobe and very long phallobase; phallobase without median suture; parameres absent (Figs 46–47).

Female. Unknown, probably paedomorphic and larviform.

ETYMOLOGY. The name of the genus is derived from «nanus», the Latin for «very small», and the genus name «Lycus». Gender masculine.

DIAGNOSIS. *Nanolycus* **gen.n.** differs from *Dominopteron* **gen.n.**, also from Hispaniola, by the shorter head and pronotum, absent gular sutures, irregular elytral reticulation, more approximate metacoxae and the male genital structure (Figs 46–47). The new genus differs from *Ceratopriomorphus* Pic, 1922 by the filiform antennae and bicostate elytra (Fig. 40). It differs from *Cessator* Kazantsev, 2009, described from Puerto Rico, also with long head, relatively long antennomere 3 and very long spiculum gastrale, by the medially undivided mesoventrite and differently structured mesonotum, metanotum and aedeagus.

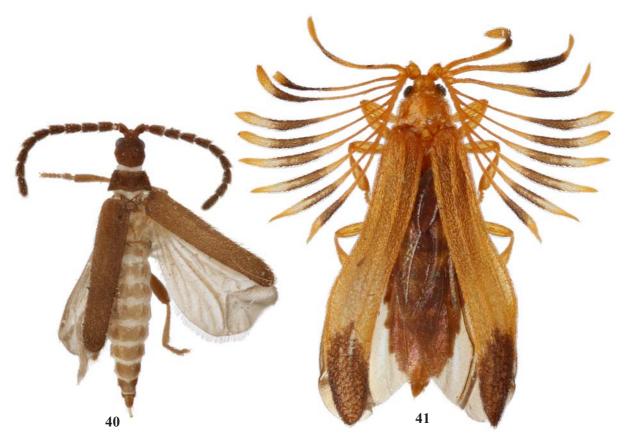
DISTRIBUTION. *Nanolycus gnomus* **sp.n.**, the only species of the genus, was discovered on Hispaniola.

### Nanolycus gnomus Kazantsev **sp.n.** Figs 40, 42–47

MATERIAL: Holotype,  $\circlearrowleft$ , Dominican Republic, Hato Mayor, env. Los Haitíses, 8 km W Sabana de la Mar, 20 m, mesic lowland forest, sweeping, 14.II.2006, S. Kazantsev leg. (ICM); paratype,  $\circlearrowleft$ , same label (ICM).

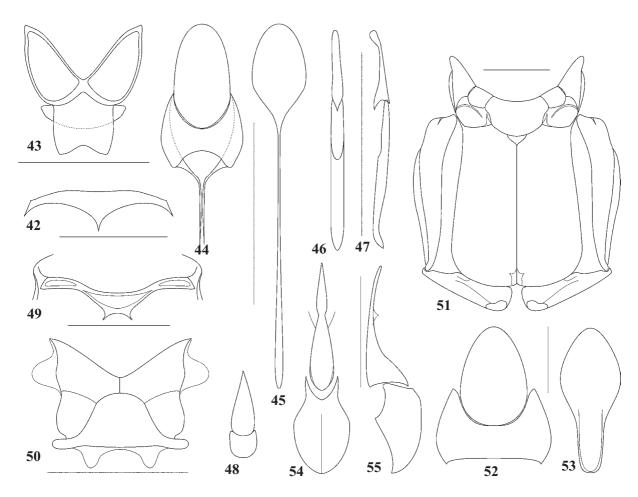
DESCRIPTION. Male. Uniformly dark brown.

Eyes small, interocular distance ca. 1.5 times greater than eye diameter. Antennae attaining to elytral two thirds, with antennomere 2 transverse, about 2.2 times shorter than antennomere 3 (Fig. 40).



Figs 40—41. General view of *Nanolycus* **gen.n.** and *Pseudacroleptus*, holotype males: 40 — *Nanolycus gnomus* **gen.n.**, **sp.n**; 41 — *Pseudacroleptus gorgonus* **sp.n**.

Рис. 40—41. Общий вид Nanolycus gen.n. и Pseudacroleptus, голотипы, самцы: 40 — Nanolycus gnomus gen.n., sp.n; 41 — Pseudacroleptus gorgonus sp.n.



Figs 42–55. Details of *Nanolycus* **gen.n.** and *Pseudacroleptus*, holotype males: 42–47 — *Nanolycus gnomus* **gen.n.**, **sp.n.**; 48–55 — *Pseudacroleptus gorgonus* **sp.n.**; 48 — labium; 42, 49 — prosternum; 43, 50 — mesonotum; 51 — meso- and metavetrite; 44, 52 — ultimate tergites; 45, 53 — ultimate sternite; 46–47, 54–55 — aedeagus; 42, 45–46, 48–49, 51, 53–54 — ventral view; 43–44, 50, 52 — dorsal view; 47, 55 — lateral view. Scale: 42–47: 0.25 mm; 48–55: 0.5 mm.

Рис. 42—55. Детали строения Nanolycus gen.n. и Pseudacroleptus, голотипы, самцы: 42—47 — Nanolycus gnomus gen.n., sp.n.; 48—55 — Pseudacroleptus gorgonus sp.n.; 48 — нижняя губа; 42, 49 — переднегрудь; 43, 50 — мезонотум; 51 — мезо- и метавентрит; 44, 52 — вершинные тергиты; 45, 53 — вершинный стернит; 46—47, 54—55 — эдеагус; 42, 45—46, 48—49, 51, 53—54 — снизу; 43—44, 50, 52 — сверху; 47, 55 — сбоку. Масштабная линейка: 42—47: 0.25 мм; 48—55: 0.5 мм.

Pronotum transverse, about twice as wide as long, narrowed anteriorly, with conspicuous blunt anterior and small acute (ca. 60°) posterior angles. Scutellum parallel-sided, conspicuously emarginate distally (Figs 40, 43).

Elytra long, 2.5 times as long as wide at humeri, slightly narrowing and separately rounded at apex (Fig. 40).

Aedeagus with elongate, slightly narrowed distally median lobe and very long, almost parallel-sided phallobase; phallobase ca. 3 times longer than median lobe (Figs 46–47).

Female. Unknown.

Length: 1.7-1.8 mm. Width (humerally): 0.3 mm.

ETYMOLOGY. The name of the new species is derived from the Latin for «dwarf», alluding to its size, the species being the smallest lycid discovered so far.

DIAGNOSIS. *Nanolycus gnomus* **sp.n.** may be easily distinguished from other lycid taxa by the generic characters.

#### Pseudacroleptus gorgonus Kazantsev **sp.n.** Figs 41, 48–55

MATERIAL: Holotype,  $\circlearrowleft$ , Peru, Loreto, R. Amazon, 68 km SW Iquitos (to Nauta), R. Itaya, 4°11′S 73°26′W, 120 m, 1–9.II.2007, A. Petrov leg. (ICM).

 $DESCRIPTION.\,\textbf{Male}.\,Orange\,testaceous; preapical\,band$ on rami of antennomeres 3-11, apical elytral fourth and abdomen dark brown. Head square, almost not narrowed behind eyes. Fastigium acute, ca. 45 degrees. Dorsal tentorial maculae relatively distant. Eyes relatively small, interocular distance ca. 2 times greater than eye diameter, spherical. Labrum small, transverse, sclerotized, lying anteriad of epistoma. Mandibles vestigial. Maxillary palps slender, foursegmented, with ultimate palpomere miniature, pointed distally. Labium reduced, prementum free, non-paired, palps reduced (Fig. 48). Gula short. Antennal prominence conspicuous, antennal sockets separated by minute lamina. Antenna 11-segmented, attaining to elytral middle; antennomeres 3-10 provided with long rami; pedicel (antennomere 2) strongly transverse, antennomere 3 proper subequal in length to antennomere 2, transverse; antennal pubescence short and decumbent (Fig. 41).

Pronotum small, ca. 8,6 times shorter than elytra, about 1.6 times wider than long, trapezoidal, without median carina or furrow, but with incomplete median suture in the middle; anterior margin rounded; anterior angles rounded, acute posterior angles strongly produced laterally; margins in dense

erect short pubescence (Fig. 41). Prosternum short, V-shaped. noticeably tripartite, relatively broad and bifurcate posteriorly (Fig. 49). Thoracic spiracles elongate, provided with small basal sclerite, slightly protruding beyond propleuron. Mesoventrite transverse, concave anteriorly, separated from mesepisternum by convex transverse suture; mesepimeron conspicuously narrower than, but almost as long as mesepisternum. Mesonotum with scutellum not attaining to anterior margin; scutellum with short bilobed postnotal plate (Fig. 50). Elytra long, 4 times as long as wide at humeri, strongly dehiscent in distal half, each elytron of almost uniform width, with two fully developed primary costae (costae 2 and 4); costa 1 noticeable in proximal fifth; interstices alveolate. Metaventrite with blunt posterior angles; discrimen (metasternal suture) complete, attaining to small mesosternum (Fig. 51). Metathoracic wing with vein Sc joining RA at apical hinge; anal cell long, triangular distally; wedge cell and cu-a brace absent; Cu veins not connected to M.

Protrochantins subequal in size to mesotrochantins. Proand mesocoxae elongate; metacoxae broadly separated. Legs slender; trochanters elongate, considerably shorter than half of pertinent tibia, cylindrical, connected to femora distally; femurs and tibiae conspicuously flattened, straight and slightly widened, tibial spurs absent; tarsomeres 1–4 narrow, without plantar pads; all claws simple.

Abdominal spiracles located dorsally at the edge of sternite, at its distal angle. Paraproct undivided; proctiger without median suture and with short proximal apodemes (Fig. 52); spiculum gastrale relatively short and broad (Fig. 53). Aedeagus symmetric, with elongate, straight, inflated proximally median lobe, constricted at distal third and provided with a pair of lateral bristle-like processes; parameres absent; phal-

lobase only slightly shorter than median lobe, with partial median suture (Figs 54–55).

Female. Unknown.

Length: 6.5 mm. Width (humerally): 1.2 mm.

ETYMOLOGY. The name of the new species is a Latinized form of «gorgon», a Greek mythical female serpenthaired monster, alluding to the long rami of its antennae.

DIAGNOSIS. *P. gorgonus* **sp.n.** may be distinguished from *P. lamellifer* Kazantsev, 2008 and other members of the genus by the coloration, uniform width of each elytron throughout its length (Fig. 41) and the structure of the aedeagus (Figs 54–55).

#### Ceratoprion Gorham, 1884

Type species: Ceratoprion serraticorne Gorham, 1884 (by monotypy).

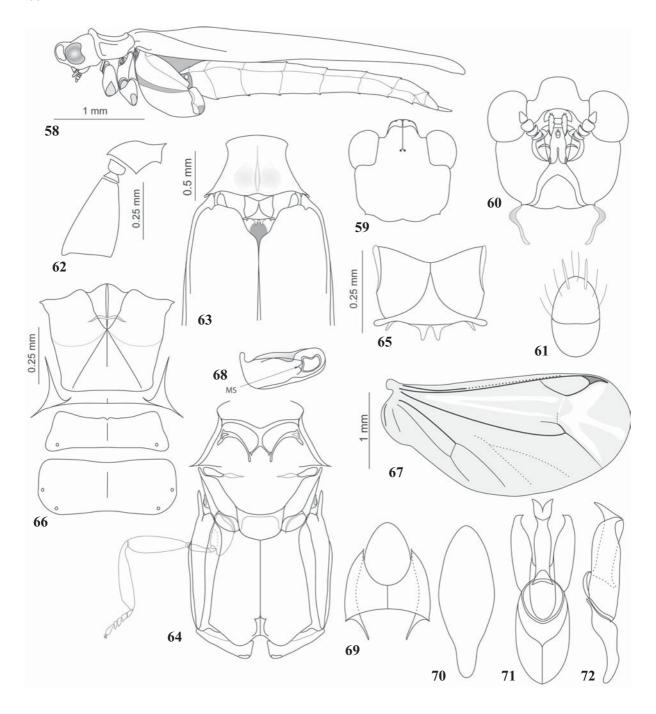
REDESCRIPTION. **Male**. Alate. slender, elongate (Figs 56, 58). Head subquadrate, not narrowed behind eyes (Figs 59–60). Fastigium acute. Tentorium represented by posterior pits (Fig. 59) and a pair of short slender ventral arms; dorsal tentorial maculae approximate. Eyes moderately large, spherical. Labrum small. transverse, lying inside epistoma. Mandibles vestigial. Maxillary palps relatively robust, four-segmented, with ultimate palpomere pointed distally. Labium miniature, reduced to prementum with a pair of sensillae, palps absent (Figs 60, 61). Gula absent. Antennal prominence conspicuous, antennal sockets separated by minute lamina. Antenna 11–segmented, attaining to elytral middle, with antennomeres 4–11 conspicuously flattened and dentate; antennomeres 2 and 3 small, transverse; antennal pubescence short and decumbent (Figs 56, 62).

Pronotum small, over 10 times shorter than elytra, transverse, constricted anteriorly, with fine median carina anteri-



Figs 56–57. General view of *Ceratoprion* and *Prioceraton* **gen.n.**, males: 56 — *Ceratoprion sobrinus* **sp.n.**; 57 — *Prioceraton ignavum*; 56 — holotype; 57 — paratype.

Рис. 56—57. Общий вид Ceratoprion и Prioceraton gen.n., самцы: 56 — Ceratoprion sobrinus sp.n.; 57 — Prioceraton ignavum; 56 — голотип; 57 — паратип.



Figs 58–72. Details of *Ceratoprion sobrinus* **sp.n.**, holotype male: 58 — body outline; 59–60 — head; 61 — labium; 62 — antennomeres 1–4; 63 — pronotum and basal part of elytra; 64 — ventrum; 65 — mesonotum; 66 — metanotum; 67 — hind wing; 68 — metacoxa; 69 — ultimate tergites; 70 — ultimate sternite; 71–72 — aedeagus; 60–62, 64, 67, 70–72 — ventral view; 59, 63, 65–66, 69 — dorsal view; 58, 72 — lateral view. MS — meral suture.

Рис. 58—72. Детали строения *Ceratoprion sobrinus* **sp.n.**, голотип, самец: 58 — очертания тела; 59—60 — голова; 61 — нижняя губа; 62 — антенномеры 1—4; 63 — переднеспинка и базальная часть надкрылий; 64 — вентрум; 65 — мезонотум; 66 — метанотум; 67 — заднее крыло; 68 — задний тазик; 69 — вершинные тергиты; 70 — вершинный стернит; 71—72 — эдеагус; 60—62, 64, 67, 70—72 — снизу; 59, 63, 65—66, 69 — сверху; 58, 72 — сбоку. MS — меральный шов.

orly and inconspicuous narrow median furrow posteriorly; posterior angles strongly produced laterally (Figs 56, 63). Prosternum short, Y-shaped, bifurcate proximally (Fig. 64). Thoracic spiracle elongate, relatively small, provided with additional basal sclerite. Mesoventrite transverse, separated

from mesepisternum just by suture; mesepimeron conspicuously narrower than mesepisternum, but longer than half its length (Fig. 64). Mesonotum with scutellum not attaining to anterior margin, mesoscutal halves not divided; scutellum with very short, emarginate distally postnotal plate (Fig. 65).

Elytra long, dehiscent distally, with four fully developed primary costae, costae 1 and 3 somewhat shorter; interstices with one row of irregular cells; short elytral pubescence uniform (Fig. 56). Metanotum subquadrate, with straight scuto-scutellar ridge forming no loop; allocristae inconspicuous, noticeably shorter than scuto-scutellar ridge; intrascutal suture small, emerging at proximal third of allocrista; scutellum with median suture in distal half (Fig. 66). Metaventrite with blunt posterior angles; discrimen (metasternal suture) complete, attaining to mesosternum (Fig. 64).

Metendosternite small, simple, relatively broad, with minute arms and no transverse suture (Fig. 64). Metathoracic wing with vein Sc joining RA near apical hinge; anal cell long; wedge cell absent; cu-a brace absent; Cu veins weak, connected neither to M, nor to A veins (Fig. 67).

Protrochantins conspicuously more prominent than mesotrochantins. Pro- and mesocoxae elongate; metacoxae distinctly separated; metacoxa with conspicuous meral suture (Fig. 68). Legs relatively long; trochanters elongate, but considerably shorter than half of tibia, cylindrical, connected to femora distally; femurs and tibiae flattened, straight and somewhat widened, tibial spurs absent; tarsomeres 1–4 narrow, without plantar pads; all claws simple (Fig. 64).

Abdominal tergites with partial median suture (Fig. 66). Abdominal spiracles located dorsally at the edge of sternite. Paraproct undivided, egg-shaped; proctiger with median suture (Fig. 69); spiculum gastrale absent (Fig. 70). Aedeagus symmetric, with elongate parameres and elongate straight median lobe; median lobe with modified apex; parameral apices toothed inwardly; phallobase elliptic, with median suture (Figs 71–72).

Female. Unknown.

DIAGNOSIS. *Ceratoprion* differs from *Prioceraton* **gen.n.** by the more robust maxillary palps, different mesoventral structure (Fig. 64), distally emarginate postnotal plate of the mesonotum (Fig. 65), more robust legs, with shorter trochanters (Fig. 64), developed median suture in proctiger (tergite 9) (Fig. 69), absence of spiculum gastrale (Fig. 70) and by the differently structured aedeagus, with conspicuous median suture in phallobase (Fig. 71–72).

REMARKS. Ceratoprion sobrinus sp.n., collected in a decent series, was used for the redescription of the genus. There are reasons to believe that characters of C. serraticorne, the type species of the genus, which was not available for study, described also from Mesoamerica (Panama) and possessing the same type of the male copulatory organs as C. sobrinus sp.n. [Miller, 1991], would not differ considerably from those presented in the above description.

### Ceratoprion sobrinus Kazantsev **sp.n.** Figs 56, 58–72

MATERIAL: Holotype, ♂, Costa Rica, Guanacaste Pr., 9 km S Santa Cecilia, Estac. Pitilla, 700 m, Malaise trap, 1988, GNP Biodiversity Survey (INBio); paratypes, 20 o'o', same label as Holotype; Costa Rica, Guanacaste Pr., Est. Maritza, lado O vol. Orosi, 600 m, Malaise tr., 1988; Costa Rica, Guanacaste Pr., SW side Volcan Cacao, 1000-1100 m, Malaise trap, 1988-1989, GNP Biodiversity Survey; Costa Rica, Alaju Pr., Playuelas, Cano Negro, 20 m, 5-26.I.1993, K. Flores leg.; Costa Rica, Puntarenas Pr., Guacimal, San Luis, 1140 m, Malaise trap, 1.II.1993, Z. Fuentes leg.; Costa Rica, Guanacaste Pr., Tilaran, Tierras Morenas, 800 m, Malaise trap, 30.IX-1.XI.1993, G. Rodrigues leg.; Costa Rica, Alaju Pr., Playuelas, Cano Negro, 20 m, 3-25.I.1994, K. Flores leg.; Costa Rica, Limon Pr., Rio Sardinas, R.N.F.S. Barra del Colorado, 10 m, 2-12.I.1994, F.V. Araya leg.; Costa Rica, Guanacaste Pr., Rio Sn Lorenzo, Tierras Morenas, Tenorio A.C.A, 1050 m, IV.1994, G. Rodrigues leg.; Costa Rica, Limon Pr., Valle La Estrella, R.B. Hitoy Cerere, A.C. Amistad, 100 m, VII.1994, M. Sigura leg.; Nicaragua, Depto Rio San Juan, El Castillo, env. Ref. Bartola, secondary rain forest, FIT, 22–25.II.2000, E. Berbero & F. Penati leg.; Costa Rica, Heredia, nr. Puerto Viejo, 4–5.IV.2003, S.Kazantsev leg. (ICM and INBio).

DESCRIPTION. **Male**. Dark brown; pedicel, antennomere 10 distally, antennomere 11, lateral margins of pronotum and humeral stripes on elytra testaceous (Fig. 56).

Eyes moderately large, interocular distance ca. 1.3 times greater than eye diameter. Antennae attaining to elytral middle, with antennomere 3 small, transverse, subequal in size to antennomere 2 and 6 times shorter than antennomere 4 (Figs 56, 62).

Pronotum small, ca. 10.6 times shorter than elytra, transverse, about 1.5 times wider than long, constricted in anterior third, with fine median carina in anterior and inconspicuous narrow median furrow in posterior half; posterior angles acute, strongly produced laterally. Scutellum short, parallel-sided, emarginate distally (Figs 56, 63).

Elytra long, 3.8 times as long as wide at humeri, slightly narrowing distally, slightly dehiscent in distal fifth (Fig. 56).

Aedeagus robust; median lobe bifurcate distally, slightly longer than parameres; phallobase about twice as long as wide and nearly as long as parameres (Figs 71–72).

Female. Unknown.

Length: 3.7–5.5 mm. Width (humerally): 0.7–1.1 mm.

ETYMOLOGY. The name of the new species is derived from the Latin noun «maternal male cousin», alluding to its apparent relationship with *Ceratoprion serraticorne* Gorham, 1884, the type species of the genus.

DIAGNOSIS. *Ceratoprion sobrinus* **sp.n.** may be easily distinguished from other *Ceratoprion* species by the coloration (Fig. 56) and by the structure of the aedeagus (Figs 71–72).

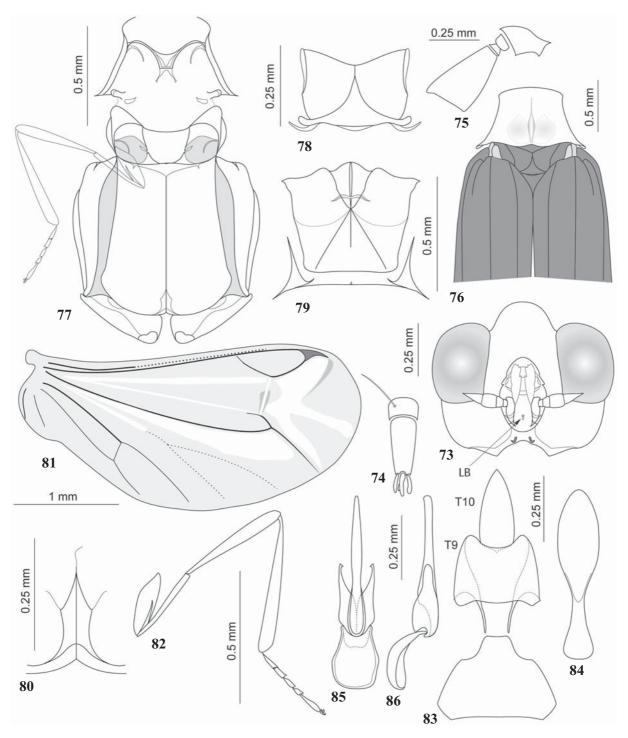
#### Prioceraton Kazantsev gen.n.

Type species: Ceratoprion ignavum Kazantsev, 2008.

DESCRIPTION. Male. Alate, slender, elongate, moderately flattened (Fig. 57). Head transverse, not narrowed behind eyes (Figs 57, 73). Fastigium acute, ca. 45 degrees. Tentorium represented by posterior pits and a pair of short slender ventral arms; dorsal tentorial maculae approximate. Eyes moderately large, spherical. Labrum transverse, lightly sclerotized, lying inside epistoma. Mandibles vestigial, lightly sclerotized. Maxillary palps slender, four-segmented, with ultimate palpomere pointed distally (Fig. 73). Labium consisting of non-paired mentum and prementum; labial palps absent; prementum distally bearing four sensilla (Figs 73-74). Gula absent. Antennal prominence conspicuous, antennal sockets separated by minute lamina. Antenna 11-segmented, relatively long, with antennomeres 3-11 conspicuously flattened, 3–10 slightly dentate; antennomere 3 small, shorter than antennomere 2 (Figs 57, 75); antennal pubescence short and decumbent, complemented with minute roundish scales on antennomeres 3–11.

Pronotum small, ca. 9 times shorter than elytra, with fine median carina in anterior and inconspicuous narrow median furrow in posterior half; posterior angles strongly produced laterally (Figs 57, 76). Prosternum short, V-shaped (Fig. 77). Thoracic spiracles elongate, relatively small, provided with additional basal sclerite. Mesoventrite transverse, separated from mesepisternum by oblique suture and rather broad sternopleural sclerite; mesepimeron conspicuously narrower than mesepisternum, but longer than half its length (Fig. 77). Mesonotum with scutellum not attaining to anterior margin, mesoscutal halves not divided; scutellum

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Figs 73—86. Details of *Prioceraton ignavum*, holotype male: 73 — head; 74 — labium; 75 — antennomeres 1—4; 76 — pronotum and basal part of elytra; 77 — ventrum; 78 — mesonotum; 79 — metanotum; 80 — metendosternite; 81 — hind wing; 82 — middle leg; 83 — ultimate tergites; 84 — ultimate sternite; 85–86 — aedeagus; 73–75, 77, 80–82, 84 — ventral view; 76, 78–79, 83, 85 — dorsal view; 86 — lateral view. LB — labium; T — tergite.

Рис. 73—86. Детали строения *Prioceraton ignavum*, голотип, самец: 73 — голова; 74 — нижняя губа; 75 — антенномеры 1—4; 76 — переднеспинка и базальная часть надкрылий; 77 — вентрум; 78 — мезонотум; 79 — метанотум; 80 — метэндостернит; 81 — заднее крыло; 82 — средняя нога; 83 — вершинные тергиты; 84 — вершинный стернит; 85–86 — эдеагус; 73–75, 77, 80–82, 84 — снизу; 76, 78–79, 83, 85 — сверху; 86 — сбоку. LB — нижняя губа; Т — тергит.

with minute postnotal plate (Fig. 78). Elytra long, almost parallel-sided, dehiscent in distal two thirds, with two fully developed primary costae (costae 2 and 4), costa 1 present

in proximal third and costa 3 noticeable in humeral area (Fig. 57); interstices reticulate; short elytral pubescence uniform. Metanotum subquadrate, with straight scuto-scutel-

lar ridge forming no loop; allocrista inconspicuous, noticeably shorther than scuto-scutellar ridge; intrascutal suture small, emerging at proximal third of allocrista; scutellum with median suture in proximal half (Fig. 79). Metaventrite with blunt posterior angles; discrimen (metasternal suture) complete, attaining to mesosternum (Fig. 77). Metendosternite small, simple, with minute arms and no transverse suture (Figs 77–80). Metathoracic wing with vein Sc joining RA near apical hinge; anal cell long, almost rectangular distally; wedge cell absent; cu-a brace absent; Cu veins weak, connected neither to M, nor to A veins (Fig. 81).

Protrochantins slightly more prominent than mesotrochantins (Fig. 77). Pro- and mesocoxae elongate; metacoxae distinctly separated from each other; meral suture in metacoxae complete (Fig. 77). Legs long and narrow; trochanters elongate, considerably longer than half of tibia, cylindrical, connected to femora distally; femurs and tibiae flattened, straight and narrow, tibial spurs absent; tarsomeres 1–4 narrow, without plantar pads; all claws simple (Figs 77, 82).

Abdominal tergites with partial median suture, except in ultimate tergites. Abdominal spiracles located laterally on membrane between sternite and tergite. Paraproct undivided; proctiger relatively long, without medan suture (Fig. 83); spiculum gastrale relatively long and dilated proximally (Fig. 84). Aedeagus symmetric, with elongate parameres and elongate straight median lobe; parameral apices toothed inwardly; phallobase without median suture (Figs 85–86).

Female. Unknown, probably paedomorphic and larviform.

BIOLOGY. The type series of the only species of the genus, *Prioceraton ignavum*, was collected at 1100 m above sea level in a cloud forest.

ETYMOLOGY. The name of the new genus is derived from the genus name *Ceratoprion*, alluding to the external similarity of the two taxa. Gender neuter.

DIAGNOSIS. Externally Prioceraton gen.n. is fairly similar to Ceratoprion, but differs by the transverse head, slenderer maxillary palps, elongate prementum (Figs 73-74), mesoventrite separated from mesepisternum by an additional transverse sclerite (Fig. 77), distally convex postnotal plate of the mesonotum, elytra without distinct rows of cells, slenderer legs, with longer trochanters (Fig. 78), differently located abdominal spiracles, differently structured ultimate abdominal segments, with elongate proctiger lacking median suture and widened proximally spiculum gastrale (Figs 83-84) and by the male genital structures, with more robust and complex median lobe and absent median suture in the phallobase (Figs 85-86). Some of these characters seem to be autapomorphic for the genus, and testify to its independent status. Prioceraton gen.n. differs from Electropteron gen.n., also with short antennomeres 2 and 3 and reduced labium, by the non-erect antennal pubescence (Fig. 57), medially divided pronotum and undivided prosternum (Figs 76-77), absent mesosternal sutures in anterior part of the metaventrite (Fig. 77) and developed parameres of the aedeagus (Figs. 85–86).

## Prioceraton ignavum (Kazantsev, 2008), comb.n. Figs 57, 73–86

Ceratoprion ignavum Kazantsev, 2008: 289.

MATERIAL: Holotype,  $\circlearrowleft$ , Venezuela, Aragua, Parque nac. Henri Pittier, Est. Biol. Rancho Grande, 10°20'N, 67°41'W, 1100 m, cloud forest, 21–24.VI.1999, Ratcliffe, Jameson, Smith, Villatoko (FMNH); Paratype,  $\circlearrowleft$ , Venezuela, Aragua, Rancho Grande, 10°21'N, 67°41'W, 1100 m, 19.XI.1986 (ICM).

#### Cladistic analysis and phylogeny

Being aware of the drawbacks of a numerical cladistic analysis [e.g., Kluge, 2000], I had to apply a cladistic method to help define position of the regarded "neotenic" taxa, as they seem to possess a number of hypothetically synapomorphous, from the standpoint of insect evolution, characters, i.e., the reduced mandibles, manifest in all «neotenic» lycids, except Ateliini and Miniduliticolini, reduced labium (in many «neotenic» taxa), reduced number of antennomeres (in Lyropaeini, *Neolyrium*, *Tishechkinia*), etc., at the same time sharing both synapomorphous and plesiomorphous characters with a wide range of different lycid lineages.

For examination of characters male specimens of each taxon were KOH cleared and preserved in glycerin or alcohol. All characters were double-checked on non-KOH-cleared material. The following taxa were selected for the analysis:

A. «Neotenic» lycid taxa:

Ceratoprion sobrinus sp.n.

Cessator luquillonis Kazantsev, 2009

Dexoris tessmani Bocák et Bocáková, 1988

Dominopteron hispaniolum sp.n.

Electropteron nepos sp.n.

Leptolycus heterocornis Leng et Mutchler, 1922

Lycinella parvula Gorham, 1884

Lyroneces optabilis (Kleine, 1926)

Mimolibnetis patruelis sp.n.

Nanolycus gnomus sp.n.

Neolyrium duidaense Kazantsev, 2005

Platerodrilus svetae Kazantsev, 2009

Prioceraton ignavum Kazantsev, 2008 Pseudacroleptus gorgonus sp.n. (sp. A)

Pseudacroleptus lamellifer Kazantsev, 2008 (sp. B)

Scarelus umbrosus Kleine, 1932

Tainopteron milleri Kazantsev, 2009

Tishechkinia carltoni (Kazantsev, 2007)

B. Non-neotenic lycid taxa:

Aferos dewittei Kazantsev, 2000, Slipinskiini Aplatopterus rubens (Gyllenhal, 1817), Lopherotini Caenia kirschi Bourgeois, 1880, Calopterini Calochromus glaucopterus (Guerin-Meneville, 1833), Calochromini

Calopteron reticulatum (Fabricius, 1775), Calopterini Cerceros flabellatus (Motschulsky, 1860), Macrolycini Conderis signicollis (Kirsch, 1875), Conderini Dictyoptera aurora (Herbst, 1784), Dictyopterini Dilophotes depressicornis Pic, 1921, Dilophotini Pseudaplatopterus trilineatus (Melsheimer, 1846), Pseudaplatopterina, Erotini

Eros humeralis (Fabricius, 1801), Erotina, Erotini
Eulopheros harmandi (Bourgeois, 1902), Lopherotini
Helcophorus miniatus Fairmaire, 1891, Dictyopterini
Libnetus corporaali Pic, 1921, Libnetini
Lopheros fraternus (Randall, 1838), Lopherotini
Lycostomus praeustus (Fabricius, 1792), Lycini
Lygistopterus sanguineus (Linnaeus, 1758), Calochromini
Macrolycinella dichroma Kazantsev, 2010, Macrolycinellini
Melaneros acuticollis Fairmaire, 1879, Melanerotini
Mesolycus shelfordi (Bourgeois, 1906), Macrolycini
Metriorrhynchus thoracicus (Fabricius, 1801), Metriorrhynchini

Plateros flavoscutellatus Blatchley, 1914, Platerotini Platycis minuta (Fabricius, 1787), Erotina, Erotini Taphes brevicollis Waterhouse, 1878, Taphini Xylobanellus erythropterus (Baudi di Selve, 1871), Conderini

- C. Non-lycid taxon:
- Thilmanus obscurus (Baudi, 1871), Thilmaninae, Drilidae The following set of characters was used (all related to males, except 61–65):
- Gula: 0, absent (ventral closure represented by just occipital sulcus); 1, short, located anteriad of posterior tentorial pits; 2, short, transverse, located posteriad of posterior tentorial pits; 3, elongate, located posteriad of posterior tentorial pits.
- 2. Fastigium: 0, acute; 1, more or less right-angled; 2, blunt.
- 3. Antenna, number of antennomeres: 0, 11; 1, 10.
- 4. Antennomeres: 0, filiform; 1, flattened, but more or less parallel-sided; 2, flattened and dentate; 3, flabellate.
- 5. Pedicel (antennomere 2): 0, elongate, subequal in length to antennomere 3; 1, elongate, but conspicuously shorter than antennomere 3; 2, transverse.
- 6. Antennomere 3: 0, elongate, subequal in length to antennomere 4; 1, elongate, but conspicuously shorter than antennomere 4; 2, transverse or subquadrate.
- 7. Labrum: 0, free, at least proximally located inside oral cavity, 1, free, but entirely located anteriad of epistoma; 2, fused to epistoma/clypeus.
- 8. Mandibles: 0, developed; 1, rudimentary.
- 9. Maxillae, number of palpomeres: 0, 3; 1, palps absent.
- 10. Maxillae, ultimate palpomere: 0, distally pointed, 1, distally flattened and more or less dilated; 2, palps absent.
- 11. Labium, mentum: 0, free; 1, rigidly connected to gular area.
- 12. Labium, prementum: 0, free; 1, rigidly connected to (mentum and) gular area.
- 13. Labium, prementum: 0, divided into a pair of sclerites; 1, divided by median suture; 2, undivided.
- 14. Labium, number of palpomeres: 0, 3; 1, 2; 2, 1 or palps reduced to sensillae.
- Labium, ultimate palpomere: 0, distally pointed; 1, distally flattened and more or less dilated; 2, palps absent.
- 16. Pronotum, median suture (sometimes bifurcate posteriorly or taking shape of a diamond): 0, complete; 1, incomplete, present only anteriorly or posteriorly; 2, absent.
- 17. Prosternum: 0, tripartite, divided into prosternum proper and a pair of sternopleural sclerites; 1, representing a single sclerite.
- 18. Prosternum: 0, triangular or Y-shaped, narrow and medially concave; 1, subrectangular, relatively broad and anteriorly straight or convex.
- 19. Prosternal posterior process: 0, short; 1, long and narrow.
- 20. Mesoscutum, scutellum: 0, small, with respect to scuta; 1, subequal in size to each of the scuta; 2, large, surpassing each of the scuta in size.
- 21. Mesoscutum, scutellum: 0, not reaching anterior margin; 1, touching anterior margin; 2, making conspicuous part of anterior margin..
- 22. Mesoscutum, scutellum: 0, with median suture; 1, without median suture.
- 23. Mesoscutum, scuta: 0, each not divided; 1, each divided by a transverse or oblique suture.
- 24. Mesoscutum, posterior process of scutellum: 0, vestigial, with considerable elytro-scutellar dehiscence; 1, developed and functional, locking folded elytra.
- 25. Mesoventrite: 0, separated from mesepisternum (by suture or suture and additional sclerite); 1, semi-fused with mesepisternum; 2, fused with mesepisternum.
- 26. Mesoventrite, sternopleural sclerite: 0, present; 1, absent.
- 27. Mesoventrite: 0, divided by median suture; 1, without median suture.

- 28. Mesepimeron: 0, subequal in length to mesepisternum; 1, considerably shorter than mesepisternum.
- 29. Mesepimeron: 0, subequal in width to mesepisternum; 1, considerably narrower than mesepisternum.
- 30. Elytron: 0, not coadapted with thoracic and abdominal structures; 1, coadapted with thoracic, but not with abdominal structures; 2, coadapted with thoracic and abdominal structures.
- 31. Elytron: 0, with longitudinal costae and reticulation; 1, with longitudinal costae but without reticulation; 2, without longitudinal costae and reticulation.
- 32. Elytron, epipleuron: 0, absent; 1, present at the base of elytron; 2, present, reaching elytral apex.
- 33. Metaventrite, mesosternal sutures: 0, apparent; 1, absent.
- 34. Metaventrite, discrimen (metasternal suture): 0, reaching anterior margin; 1, not reaching anterior margin.
- 35. Metendosternite, lateral arms: 0, absent; 1, present.
- 36. Metendosternite, transverse suture: 0, absent; 1, present.
- 37. Mesothoracic spiracles, orifice: 0, simple; 1, hooded dorsally.
- 38. Wing: anal lobe: 0, present; 1, absent.
- 39. Wing venation: wedge cell: 0, present; 1, absent.
- 40. Wing venation: cu-a brace: 0, absent; 1, located at or proximad of Cu fork; 2, located distad of Cu fork.
- 41. Trochanters; connection to femurs: 0, direct; 1, oblique (more than a half of their anterior surface incised). Condition 0 attributed to hypothetic ancestor.
- 42. Femurs and tibiae: 0, both flattened; 1, femurs not or little flattened, tibiae flattened; 2, both not or little flattened.
- 43. Tibial spurs: 0, absent; 1, present.
- 44. Tarsomeres 3-4: 0, narrow; 1, widened.
- 45. Tarsomere 1, plantar pad: 0, absent; 1, present.
- 46. Tarsomere 3, plantar pad: 0, absent; 1, present.
- 47. Abdomen, number of ventrites, including invaginated ultimate ventrites: 0, 8; 1, 7.
- 48. Abdomen, median suture on tergites: 0, present; 1, absent.
- 49. Paraproct (male tergite 9): 0, divided by median suture; 1, not divided by median suture, but not fused with proctiger; 2, not divided and fused with proctiger.
- 50. Proctiger (male tergite 10): 0, free; 1, absent.
- 51. Male ultimate ventrite (sternite 9): 0, with short (not surpassing distal part of sternite in length) proximal process; 1, with long (surpassing distal part of sternite in length), but relatively broad proximal process; 2, with long and narrow proximal process (spiculum gastrale).
- 52. Abdominal spiracles, location: 0, on membrane between sternite and tergite; 1, at the edge of sternite; 2, on sternite, rather distant from the edge; 3, at the edge of tergite.
- 53. Aedeagus, phallobase: 0, noticeably composite; 1, uniform
- 54. Aedeagus, phallobase: 0, symmetric; 1, slightly asymmetric (in both halves same structures present); 2, strongly asymmetric.
- 55. Aedeagus, phallobase: 0, without deep ventral incision; 1, with deep ventral incision (making it appear somewhat annuliform).
- 56. Aedeagus, phallobase: 0, located at the axis of median lobe; 1, located at ca. 180 degrees to the median lobe axis.
- 57. Aedeagus, phallobase, latero-proximal apodemes: 0, present; 1, absent.
- 58. Aedeagus, phallobase, median suture (or a pair of lateral sutures): 0, present or phallobase represented by a paired sclerite; 1, absent.
- 59. Aedeagus, median lobe: 0, symmetric; 1, asymmetric.

- 60. Aedeagus, parameres: 0, absent; 1, free, ca. half length of median lobe; 2, free, ca. as long as median lobe; 3, fused with median lobe.
- 61. Female: 0, normal winged beetle, with complete metamorphosis; 1, larviform, without pupal stage, or unknown
- 62. Larva, mandibles: 0, non-opposable; 1, opposable. Condition 0 attributed to all lycid taxa, even when their larvae are unknown, as this condition is one of the diagnostic features of the family. As *Dexoris* and *Mimolibnetis* occupy a somewhat intermediate position between Lycidae and Lampyridae due to «lampyroid» states of certain characters, their condition in 62–64 considered unknown.
- 63. Larva, each mandible: 0, tripartite; 1, one-piece. Condition 0 attributed to all lycid taxa, even when their larvae are unknown, as it is one of the diagnostic features of the family.
- 64. Larva, posterior articulation of mandible: 0, to stipes; 1, to hypostoma. Condition 0 attributed to all lycid taxa, even when their larvae are unknown, as it is one of the diagnostic features of the family.
- 65. Larva, head ventrally: 0, open; 1, closed. Condition 0 attributed to all lycid taxa, even when their larvae are unknown, as it is one of the diagnostic features of the family.

The character states were found to be distributed among the taxa in the following way (see Appendix).

Certain hypothetically important characters offering clear discrete conditions, such as the presence or absence of tibial spurs (character 43), number of ventrites (character 47), location of abdominal spiracles (character 52), symmetry of the phallobase (character 56), symmetry of the median lobe of the aedeagus (character 59) were weighted 2, 2, 2, 3 and 3 out of 9, respectively; all the rest were weighted 1.

The analysis of the data matrix by Phylip Pars, version 3.63, with *Thilmanus obscurus* as the outgroup resulted in six most parsimonious cladograms, one of which, demonstrating clades Thilmanus: 16.00, Mimolibnetis: 9.00, ((Taphes: 3.00, (Libnetus: 6.87, ((Platycis: 2.00, (Xylobanellus: 2.00, Conderis: 3.00): 3.00, (Dictyoptera: 3.00, (Helcophorus: 2.00, ((Lopheros: 1.67, Eulopheros: 1.67): 2.67, Eros: 1.00): 2.00, (Pseudaplatopterus: 4.00, Aplatopterus: 3.00): 2.00): 2.00): 1.00): 2.53, ((Calopteron: 6.07, Caenia: 5.80): 2.73, (Macrolycinella: 2.40, ((Metriorrhynchus: 7.38, Lycostomus: 6.75): 3.75, ((Lygistopterus: 3.00, Calochromus: 9.00): 3.00, (Mesolycus: 9.00, (((Plateros: 5.00, Melaneros: 7.00): 3.13, (Dilophotes: 11.21, Cerceros: 9.46): 3.33): 4.63, Aferos: 2.50): 1.75): 2.50): 3.50): 4.72): 2.33): 2.53): 4.00): 4.13): 3.67, (Scarelus: 6.33, Lycinella: 7.67): 4.00, (Platerodrilus: 9.33, (Dominopteron: 5.33, ((Tishechkinia: 2.83, ((Prioceraton: 3.00, Neolyrium: 2.00): 3.50, Lyroneces: 6.50): 1.67): 3.50, (Electropteron: 5.17, (Nanolycus: 3.50, Cessator: 4.50): 2.33): 2.50, (Leptolycus: 6.33, (Tainopteron: 2.00, (PseudacroleptusB: 0.00, PseudacroleptusA: 0.00): 6.00, (Dexoris: 13.00, Ceratoprion: 3.00): 3.00): 1.67): 3.00): 6.00): 3.33):3.00): 5.33, is illustrated (Fig. 87). The cladogram required a total of 337.000 steps.

The family appears to be divided into six subfamilies, Mimolibnetinae **subfam.n.**, Erotinae, Lycinae, Ateliinae, Miniduliticolinae (represented by *Platerodrilus*) and Leptolycinae (Fig. 88). The family tree is complemented with Alyculinae, a seventh family, no representative of which was included in the cladistic analysis, but whose status raises no questions.

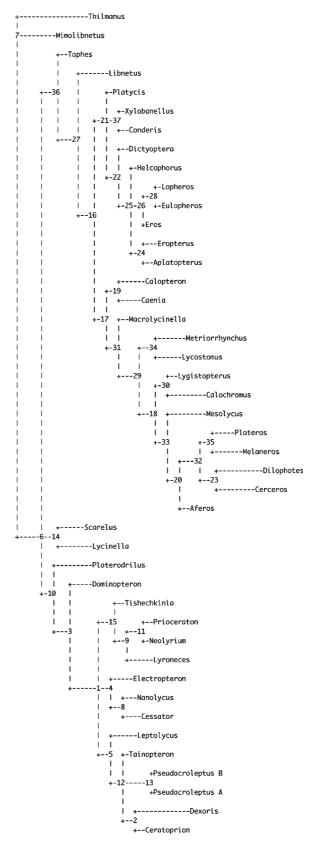


Fig. 87. Most parsimonious cladogram with *Thilmanus obscurus* as outgroup.

Рис. 87. Наиболее экономная кладограмма с *Thilmanus obscurus* в качестве внешней группы.

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The tribes are preliminarily distributed among the subfamilies in the following way:

#### 1. Subfamily Mimolibnetinae Kazantsev, subfam.n.

Type genus: Mimolibnetis Pic, 1936.

DIAGNOSIS. The subfamily is characterized by the fused to gula prementum (Fig. 4), semi-fused mesoventrite, obliquely connected to femurs trochanters (Fig. 7), location of abdominal spiracles at the edge of tergites and lateroproximal apodemes of the phallobase (Figs 9–10). While the latero-proximal apodemes of phallobase seem to be symplesiomophous with *Thilmanus* (Thilmaninae, Drilidae), as well as with *Electropteron* and *Leptolycus*, the tergal location of abdominal spiracles, fused to gula prementum, semi-fused mesoventrite, and obliquely connected to femurs trochanters hypothetically are autapomorphous for the lineage, with the tergal location of abdominal spiracles homoplastic with *Neolyrium* and the obliquely connected to femurs trochanters homoplastic with *Dexoris* and *Lampyrolycus*.

The subfamily includes only one genus, *Mimolibnetis* Pic, 1936.

#### 2. Subfamily Erotinae Leconte, 1881

Type genus: Eros Newman, 1838.

The subfamily includes tribes Conderini Bocák et Bocáková, 1990, Dictyopterini Houlbert, 1922, Erotini Leconte, 1881, Lopherotini Kazantsev, 2012 and Proterotaphini Kazantsev, 2012. The position and status of Libnetini Bocák et Bocáková, 1990, Taphini Bocák et Bocáková, 1990 (placed at the root of the «non-neotenic» clade) and Lycoprogentini Bocák et Bocáková, 2008 (not included in the analysis), as well as the more exact relationships between the taxa in the subfamily have to be defined with reference to the available female characters, which are not included in the analysis for the purpose of the present paper.

#### 3. Subfamily Lycinae Laporte, 1836

Type genus: Lycus Newman, 1838.

The subfamily includes tribes Calochromini Lacordaire, 1857, Calopterini Kleine, 1933, Lycini Laporte, 1836, Macrolycini Kleine, 1929, Macrolycinellini Kazantsev, 2012, Melanerotini Kazantsev, 2010, Metriorrhynchini Kleine, 1926, Platerotini Kleine, 1929, Slipinskiini Bocák et Bocáková, 1992 (represented by *Aferos*) and Thonalmini Kleine, 1933 (not represented). The position and status of Dilophotini Kleine, 1929 and Eurrhacini Bocáková, 2005, as well as the more exact relationships between the taxa in the subfamily have to be defined with reference to the available female characters, which are not included in the analysis for the purpose of the present paper.

REMARKS. The tribe Macrolycinellini is hereby transferred from Erotinae to Lycinae in accordance with its placement by the cladogram (Fig. 87).

#### 4. Subfamily Ateliinae Kleine, 1929

Type genus: Atelius Waterhouse, 1878.

The subfamily includes one tribe, Ateliini. The systematic position of *Lycinella*, which is placed in one clade with Ateliinae in the analysis (Fig. 87), has to be defined after an additional study.

#### 5. Subfamily Miniduliticolinae Kazantsev, 2003

Type genus: Miniduliticola Kazantsev, 2003.

The subfamily includes tribes Miniduliticolini Kazantsev, 2003 and Platerodrilini Kazantsev, 2004.

#### 6. Subfamily Alyculinae Bocák et Bocáková, 2008

Type genus: Alyculus Kazantsev, 2003.

The subfamily includes only one genus, *Alyculus* Kazantsev, 2003.

#### 7. Subfamily Leptolycinae Leng et Mutchler, 1922

Type genus: Leptolycus Leng et Mutchler, 1922.

The subfamily includes tribes Antennolycini Bocák et Bocáková, 2008, Dexorini Kleine, 1933, Dominopterini Kazantsev **tr.n.**, Electropterini Kazantsev **tr.n.**, Leptolycinae Leng et Mutchler, 1922 and Lyropaeini Bocák et Bocáková, 1989.

REMARKS. The name Dexorini was proposed for a single monotypic genus, *Dexoris*, after 1930, without a formal description or a bibliographic reference to such a description [Kleine, 1933], however available, also because it was used as valid before 2000, as in Bocák et Bocáková [1989; 1990] and was not rejected therein (Article 13.2.1 of the ICZN).

#### Tribe Dominopterini Kazantsev, tr.n.

Type genus: Dominopteron Kazantsev, gen.n.

DIAGNOSIS. The new tribe is characterized by the relatively long and medially emarginate prosternum, provided with a long narrow posterior process (Fig. 20) and by the fused condition of the mesoventrite. Both characters seem to be autapomorphous, unique for the net-winged beetles, but probably homoplastic with Omalisidae (the long narrow posterior process of the prosternum) and Lampyridae (fused mesoventrite).

The tribe includes only one genus, *Dominopteron* Kazantsev, **gen.n.** 

#### Tribe Electropterini Kazantsev, tr.n.

Type genus: Electropteron Kazantsev, gen.n.

DIAGNOSIS. The new tribe is characterized by a peculiar combination of plesiomorphous and apomorphous characters, which may be considered its autapomorphy. The apomorphic characters include the greatly reduced mandibles and labium. On the other hand, the complete mesosternal sutures in anterior part of the metaventrite (Fig. 31), manifest in the type genus of the tribe, seem to represent a plesiomorphy of the taxon, unique for the family. Another unique plesiomorphy, manifest in another member of the tribe, *Cessator*, is the mesoventrite divided by median suture. Both characters appear to be homoplasies with Omalisidae and Drilidae (Thilmaninae).

The tribe includes the genera *Cessator* Kazantsev, 2009, *Electropteron* Kazantsev, **gen.n.** and *Nanolycus* Kazantsev, **gen.n.** and is confined to the Greater Antilles.

#### Discussion

Several years ago I suggested that due to a number of hypothetically plesiomorphic characters not reported elsewhere in the Coleoptera the Lycidae may prove to represent one of the basal elements in the Polyphaga and the Coleoptera may turn out be non-monophyletic [Kazantsev, 2006]. This was disputed by Beutel et al. [2007] who presented several objections. Of all objections, however, only one, which asserts that the mentioned morphologic peculiarities of lycids are the result of their soft-bodiness and/or tendency to the neotenic development, seems to be relevant. This assertion is easy to prove. One should just take other soft-bodied beetles (e.g., Cantharidae, Malachiidae or Meloidae) and demonstrate that their mor-

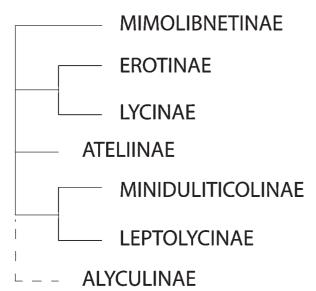


Fig. 88. A phylogenetic tree of subfamilies of Lycidae. Puc. 88. Филогенетическое древо подсемейств Lycidae.

phology has undergone similar changes; also, one should take other neotenic coleopterans (e.g., Micromalthidae) and demonstrate that their morphology has been similarly transformed. Secondly, one should take non-neotenic lycids (e.g., Lycini or Dictyopterini) and demonstrate that they do not possess the bizarre features come across in their neotenic relatives. Although this seemed easy to prove, Beutel and his co-authors preferred not to do soand for a good reason: the evidence is quite the opposite. Indeed, the available data suggest that in no other softbodied and/or neotenic lineage of coleopterans morphological changes are similar to those of lycids; at the same time all net-winged beetles, neotenic and non-neotenic alike, share the same complex of morphologies, with the hypothetically archaic conditions found in the non-neotenic groups as often as in neotenic ones. For instance, the ventrally open head with the head capsule divided into five sclerites, tripartite mandibular structure with the mandible proper hinged to a free stipes, functional metathoracic spiracles and presence of trochanter 1 and trochanter 2 are widespread in the larvae of both «neotenic» and non-neotenic Lycidae; similarly, the adult mesoventrite often separated from the mesepisternum not only by a suture, but also by an additional sternopleural sclerite or the absence of epipleuron, an element of coadaptation of elytron and abdomen, are reported not only in all or many many "neotenic", but in all or a number of lycids that show no disposition to neoteny at all [Kazantsev, 2005b]. Therefore, the assertion that all often unique and (hypothetically) plesiomorphous morphologies of lycids result from their soft-bodiness and/or neotenia is an established fact, is simply not true. Until it is proven, all morphological data ought to be contemplated and ignoring them, though convenient to help keep the accepted concepts intact, seems to be hardly consistent with scientific principles.

The presented cladistic analysis, with a member of the Drilidae family used as an outgroup, which placed all

"neotenic" lineages in a separate Lycidae lineage (Fig. 87), seems to indicate possible autapomorphous nature of their "neoteny". However, such conclusion can be made only tentatively, pending a study of the larvae and females in at least some of the taxa of this branch of netwinged beetles, also keeping in mind that in *Thilmanus*, used as the outgroup for the analysis, larval and female forms have not been discovered either.

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Appendix. The character states. Приложение. Состояния признаков.

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Appendix. Приложение.

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