

NEW FOSSIL LABIDOSTOMATIDS (ACARI: LABIDOSTOMATIDAE) FROM EOCENE AMBER AND PRESENCE OF AN APUSTULATE SPECIES IN EUROPE

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ABSTRACT — Modern-looking labidostomatid mites were found in collections of Eocene amber from diverse origins. Six of ten specimens from Baltic amber could be unequivocally assigned to the extant genus *Labidostoma* Kramer, 1879. These specimens showed affinities, notably by cheliceral morphology, with the extant Holarctic subgenus *Cornutella*, comprising large mites that commonly inhabit superficial soil layers. However, because of the unusual position of setae *la* and setation of the palps, the new subgenus *Pseudocornutella* was proposed. The habitus of a second species (two specimens from Baltic amber) resembles that of the previously described fossil *L. (N.) paleoluteum*. However, because of the unequivocal absence of the paired lateral gland-like pustule, it was assigned to the "apustulate" genus *Sellnickiella*, the extant species of which show a "Gondwanan" distribution. This is an indication that the modern distribution of the genus *Sellnickiella* results from extinctions over large parts of its former range. The new species probably belongs to an extinct lineage, having a large fenestration behind the lateral eye. Two additional Baltic specimens remain identified only to the family level. We also report the first finding of Labidostomatidae from Bitterfeld (Germany) amber and Rovno (Ukraine) amber.

KEYWORDS — new species; *Sellnickiella*; *Labidostoma*; taxonomy; new subgenus; Tertiary; Paleogene; paleontology; pseudo-Gondwanan

INTRODUCTION

Information from the study of fossil data can strengthen or contradict previous interpretations based solely on the distribution of contemporary taxa. Previous analysis of the generic distributions of extant species of the mite family Labidostomatidae concluded that the modern distribution resulted from successive fragmentation of earlier distributions, and that continental drift had segregated the taxa: the distribution of the genus *Sellnickiella* Feider and Vasiliu, 1969 in the southern hemisphere illustrates this phenomenon. This genus is charac-

terized by the absence of a post-ocular gland-like pustule and it now has a typical "Gondwanan" distribution (Feider and Vasiliu, 1969, Bertrand, 1990a, b). That the early differentiation of the genus occurred before, or at least during, the Mesozoic is a credible hypothesis (Bertrand *et al.* 2012).

The modern European labidostomatids are poorly diversified with three described genera: *Labidostoma* Kramer, 1879, *Eunicolina* Berlese, 1911 and *Akrostomma* Robaux, 1977. Within *Labidostoma*, three main subgenera, or "lineages", have been identified: the eponymous subgenus *Labidostoma*

(i.e. *L. (L.) integrum* Berlese, 1911), the lineage *Nicoletiella* (i.e. *L. (N.) luteum* Kramer, 1879 and *L. (N.) denticulatum* (Schränk, 1781)) and *Cornutella* (*L. (C.) cornutum* (Canestrini and Fanzago, 1877)). Recently, *L. (N.) paleoluteum* Dunlop and Bertrand, 2011 was described from Baltic Amber.

Recent surveys of amber mite collections allowed opportunity to present a wider overview of the European mite diversity in forest soils during the mid-Tertiary. Three specimens from the Baltic (Eocene) amber collections of the Museum of Helminthological Collections in the Center of Parasitology, Russian Academy of Sciences (MGCP) are conspecific, and their preparation permitted a detailed and precise description. The identification of the remaining specimens was more difficult, due to their orientation in the amber pieces and the condition of conservation; notwithstanding, one among them presented some characters not yet found in the present labidostomatid fauna of the northern Hemisphere. Four additional amber specimens were provided by Christel and Hans Werner Hoffeins (personal collection, Hamburg, Germany = Hoffeins coll.). One is conspecific with a species from MGCP, two are not preserved well enough to observe generic or specific characters, and the last specimen from Bitterfeld (Germany) amber dated by different authors from Eocene (Hoffeins and Hoffeins, 2003, Weitschat, 2008) to Oligocene (Knuth *et al.*, 2002; Fuhrmann, 2005) probably belongs to an unknown species. One additional, poorly preserved specimen was found in the collection of the Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev (SIZK), from the Rovno (Ukraine) Eocene amber deposit.

The study of fossil labidostomatids offers multiple opportunities: (i) because the heavily sclerotized cuticle resists deformation within the matrix and facilitates high quality observations, (ii) because the labidostomatids are a primitive and homogeneous group (phylogenetically placed near the root of the highly diverse trombidiform mites), (iii) because the fossils may help us understand which characters are plesiomorphic or derived, (i.e. common to fossil species and modern taxa), and (iv) of course, to try to answer the question: "Was the

diversity some millions of years ago comparable to the modern diversity?" Specifically, our objectives are to describe two new species of Labidostomidae from Baltic amber and emphasize the importance of these fossils for understanding the historical biogeography of the family.

MATERIALS AND METHODS

Material examined — Seven labidostomatid specimens from Baltic amber collection of the MGCP bear the inventory numbers Ar-41 (*Sellnickiella balticae* **n.sp.**), Ar-267 (poorly preserved, probably also *S. balticae*), Ar-2, Ar-97, Ar-294, Ar-382, and Ar-410 (all females *L. electri* **n.sp.**). Only Ar-41 allows precise observations of small-scale characters, but legs and many setae were lost (probably it was already partly decomposed when covered with resin). Four specimens from the Hoffeins coll., included one female of *L. electri* **n.sp.** (922-6, from Baltic amber), one male with large lateral eyes and pustules, which is not described here (369-9, Bitterfeld amber), and two other specimens (385-1 and 922-11, both Baltic amber) that were not identifiable, one being mostly obscured by a dense network of fissures, the other containing dark shapeless mass inside imprint, not showing any detail. One female in Rovno amber (k-6482a from SIZK) was unidentifiable; most of the cuticle is decomposed and the imprint of the oculoglandular region is destroyed by bubbles.

Preparation and observation — Preparations shaped to allow close (less than 200 µm of amber) observation of one to three sides of the mite were made using a hand-held Proxxon GG 12 rotary tool; surfaces were ground and polished with a polishing machine (OpenScience PollyOne and MiniPolly), using a sequence of abrasives. All processing of the pieces was done under a dissecting microscope, assisted by plastic holders with sticky tape (some holders are described in detail by Sidorchuk, 2011). From sample Ar-97, with an extended bubble around the fossil, cuticle was extracted and mounted in a cavity slide with glycerol for preliminary observations. Fragments were subsequently water-washed, dried and embedded in small drops of epoxy resin (Epo-Thin, Buehler). Ex-

tra resin was removed with paper tissue before curing. After the resin cured, these embedded pieces were washable, safe to manipulate, and observable in glycerol or immersion oil as if they lacked embedding. For storage, cuticle pieces were mounted on a cavity slide with glycerol, and sealed with Red Insulating Varnish. Amber fragments from which cuticle was removed were embedded in Epo-Thin and observed on cavity slides with glycerol, then stored in plastic tubes. Amber samples with intact inclusions were treated as described by Sidorchuk and Norton (2011).

Imaging — Image stacks were obtained using a Scope Tec DCM 500 camera mounted on a Jenaval compound microscope with additional incident illumination, and then combined (layered) with the aid of Helicon Focus Pro (v. 5.0). Color was adjusted with the GIMP graphic suite. Drawings were made with a Wacom Intuos 4M pen tablet using a live capture from the camera transferred through VLC media player (v. 0.9.9) as a background in the Inkscape (v. 0.48.0 r9654) graphic suite (Sidorchuk and Vorontsov 2010; Sidorchuk and Vorontsov in press).

Terminology — We use emendation of the original name (*Labidostomma* Kramer, 1879) by Oudemans, 1904: *Labidostoma*, Labidostomatidae, Labidostomatides, derived from Greek roots "labido" and "stoma". Morphological notations follow F. Grandjean (1942a, b, c).

FAMILY LABIDOSTOMATIDAE

OUDEMANS, 1904

GENUS *Sellnickiella* FEIDER & VASILIU,
1969

Feider and Vasiliu (1969) proposed the genus *Sellnickiella* for *Labidostoma brasiliense* Sellnick, 1922 and some African and Australian species described by Womersley (1935) and Atyeo and Crossley (1961a and b). *Sellnickiella* differs from the other genera by the absence of an anterolateral projection of the dorsal shield, and especially by the absence of lateral pustules (or gland-like organs). Today, this genus is, as far as we know, is present today only in the southern Hemisphere, namely in Australia, South

Africa and South America - *i.e.* it has a typical "Gondwanan" distribution (Bertrand and Theron, 1992; Bertrand, 1997). The genus is discriminated mainly by the combination of lacking a lateral pair of pustules (gland-like organs) and having a famulus that is bifid in the eponymous subgenus *Sellnickiella*, which has eight described species, and simple in *Dicatriella* (Feider and Vasiliu, 1970), the second (monobasic) subgenus. Most species of the genus *Sellnickiella* are characterized by having a slim, elongated body and lengthened leg tibiae, especially those of the first pair.

The specimen found in amber was provisionally assigned to the genus *Sellnickiella* essentially on the basis of the absence of the lateral pustules combined with the presence of eyes. Proportions of visible characters correspond to the definition given by Feider and Vasiliu (1970) for *Sellnickiella*: (i) posterior trichobothria quasi as long as the distance *bop-gm*, (ii) "collier antérieur" of dorsal shield (characteristic of the subgenus *Dicatriella*) is absent, (iii) tibia I long, more than 100 μm . Difficulties in obtaining complete and reliable observations (especially for the famulus) prevent us from assigning the species to either of the subgenera, *i.e.* *Sellnickiella* and *Dicatriella*.

Sellnickiella balticae n. sp.

(Figures 1-2)

Type designation and repository. The holotype and only described specimen (male) is an inclusion in Baltic amber with MGCP collection inventory number Ar-41 (Figure 2E). The holotype is now contained in an Epo-thin enforced triangular amber piece measuring 0.5 x 1.5 x 4 mm, stored in a Parafilm-sealed Eppendorf tube with immersion oil. The tube is labeled (external printed label wrapped with sticky tape, internal label pencil-written) "MGCP Ar 41 HOLOTYPE *Sellnickiella balticae*". The piece is currently on loan to the first author and will be housed in the Museum of Helminthological Collections in the Center of Parasitology of the Severtsov's Institute of Problems of Ecology and Evolution, Russian Academy of Sciences (Moscow).

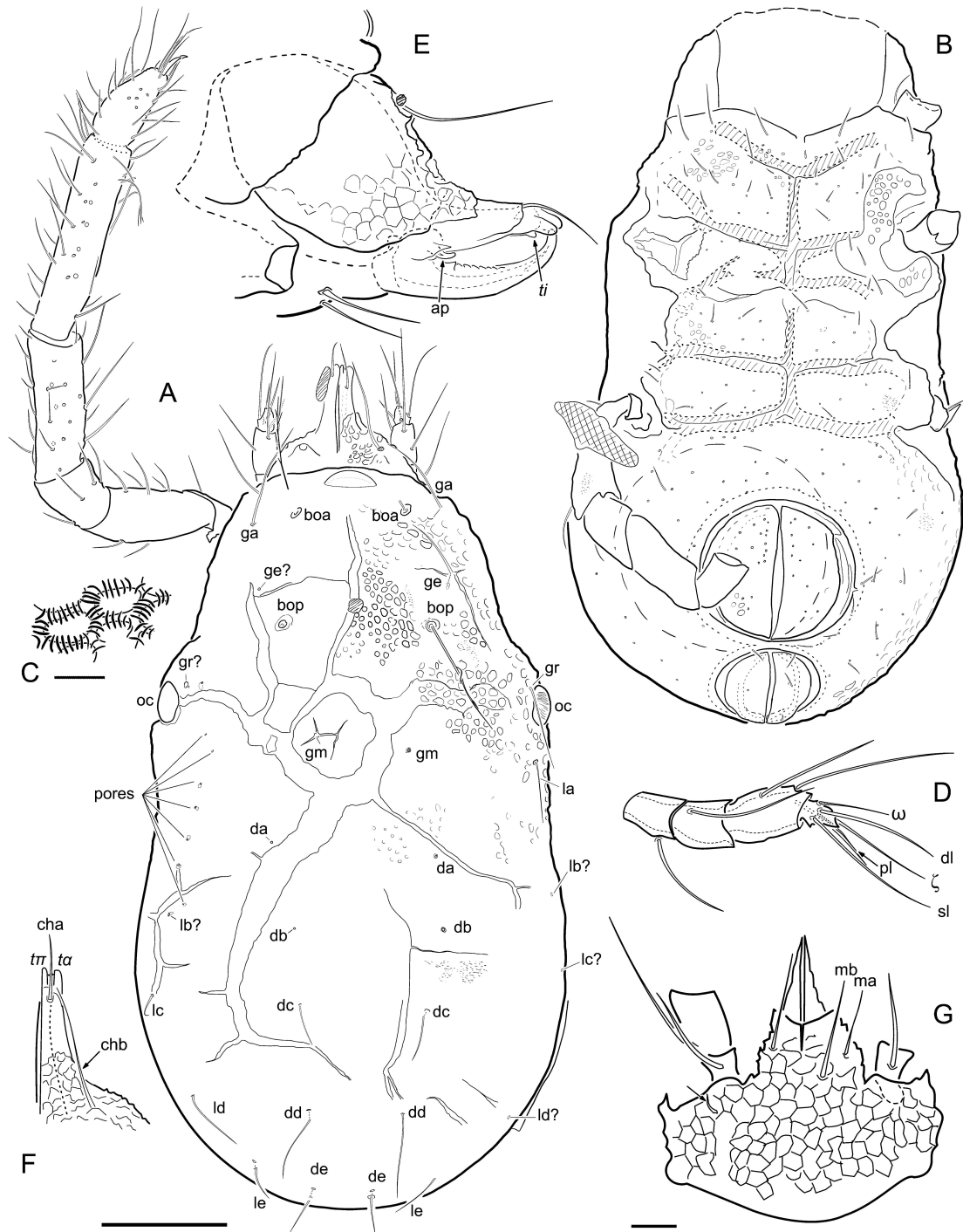


FIGURE 1: *Sellnickiella balticae* n. sp., male, holotype (MGCP Ar-41). Dotted lines indicate vaguely visible structures, dashed lines are structures visible by transparency: A – Dorsal view; B – Ventral view; C – Alveoli of centrodorsal area (between *boa*); D – Palp right, lateral view; E – Infracapitulum and chelicera, lateral view; F – Right chelicera, dorsal; G – Infracapitulum, ventral; Scale bars: A, B – 100 μ m, C – 10 μ m, D-G – 20 μ m.

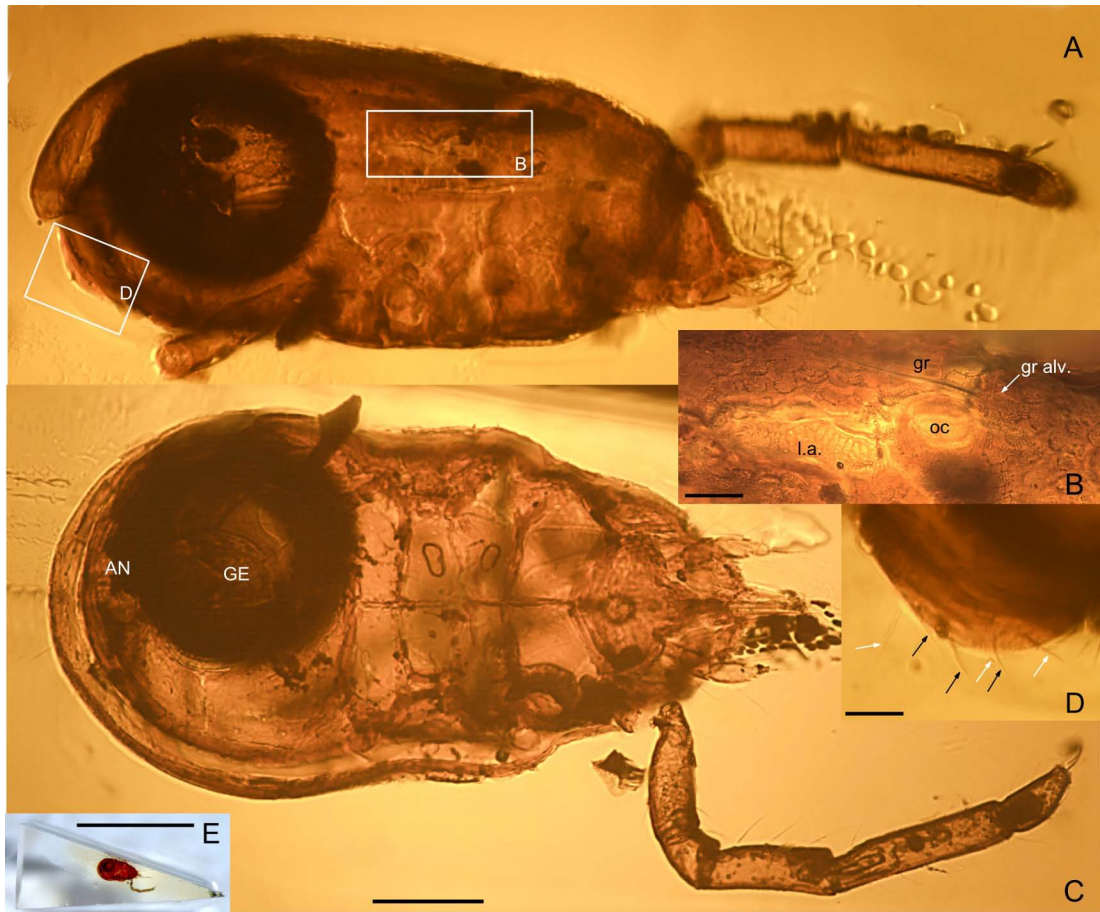


FIGURE 2: *Sellnickiella balticae* n. sp., male, holotype (MGCP Ar-41): A – Lateral aspect, rectangles indicate positions of figures B and D; B – Oculo-glandular area, enlarged: oc-lateral eye, gr.alv.-alveolus of seta gr, l.a.-area of light cuticle (see text for explanation); C – Ventral view, AN-anal opening, GE-genital opening; D – Anal opening, lateral view. Black arrows point to setae of right side, white - left side (two setae poorly visible); E – Holotype piece (MGCP Ar-41); Scale bars: A, C – 100 μm , B, D – 20 μm , E – 2 mm. Each image is combined from 10-20 (B, D) to 50-70 layers.

The type specimen was probably entombed after partial decomposition. Some setae are lacking, and the surface (especially the cerotegument) is not readily visible. Figures mainly show the cuticle (not the amber imprint, which is obscured by epoxy embedding). Most of the setae are conserved but are detached from cuticle and reside on the surface of the imprint (for an explanation of this property of amber fossils, see Sidorchuk and Norton, 2011). Most of the observable detached setae could be identified and drawn (on the figures, dotted lines connect them to the respective original base). Vaguely visible setae and alveoli are shown with dotted lines, those situated on the opposite

surface of a segment with dashed lines. Body ornamentation was observed with a compound microscope under transmitted light via a change in cuticle color from deeper brown to almost yellow in the alveoli, thus, only lighter spots are indicated by ovals on the total drawings, not a network of ridges between them.

Description — The habitus *S. balticae* is that of a long-legged animal with robust (not flattened) elongated body.

Dimensions and proportions — Body length (ca 700 μm) is about 1.7 times its maximum width (ca 410 μm) and 2.5 times its height (ca 280 μm) (Figs. 1A, 2).

Cuticle ornamentation and cerotegument — A cuticular pattern of alveoli is present in the anteriodorsal and lateral parts; alveoli are vague in the area surrounded by setae *gm* and *da* and replaced by almost smooth cuticle with a cerotegument of short striae posteriorly, approximately at the level of setae *db*. The cuticle of the lateral and anterior coxisternal region and lateral ventral plate has lighter oval pits, much like the dorsal cuticle (Figs. 1B, 2C). In the smooth central area and on whole epimeres IV, ornamentation is reduced to short striae. The cheliceral body is ornamented with penta- or hexagonal alveoli.

Dorsal shield — A large median, lens-shaped eye is present (Fig. 1A). One projecting structure about 35 µm long is present on each side; its thin, vague striation and uniformly thick internal wall suggest that it is an eye. Not all setae are observable: left *boa* is about 90 µm long, with five branches visible; right *bop* about 115 µm long, with only two oppressed (probably by resin flow) branches observable. Seta *gr* (preserved on the right side) is about 80 µm long, closely adjacent to the lateral eye. Medial to the *gr* insertion, on the left side, a row of 7-8 pore-like structures starts, coming posteriorad to the level of setal pair *lb*. The anterior unpaired eye is 50 µm wide and 18 µm long. Approximate lengths of preserved setae in dorsal view are: *ga* – 100, *la* – 60, *lc* – 25, *le* – 50, *dc* – 40, *dd* – 80, *de* – 35 µm. In lateral view, the eye is clearly visible as a single, projecting, lens-shaped organ (Fig. 2A, B). No lateral pustules were observed around the eye, and on both sides of the specimen, the remnants of the cerotegument form a common pattern of striae arranged on cuticular thickenings, apart from an irregularly oval light (with thinner cuticle?) area posteroventrad to the eye: here, it consists of more or less oval alveoli tightly adjacent to each other (Fig. 2B). This structure appears on both sides of the specimen so it is unlikely to be an artefact.

Ventral view — A prominent bubble entrapped between the imprint surface and cuticle on the right side of the mite obscures setal alveoli but highlights those of the cuticle.

The ano-genital region (Figs. 1B, 2C-D) — This is partly masked by an internal bubble. Its shape

is normal for male Labidostomatidae, with the anal valves in the anal ring. Adanal setae are thin, smooth, ca 30 µm long (Fig. 2D, arrows). Aggenital setae were not visible. However, each genital valve bears at least 9-10 traces of setal insertions plus a row of 7 and 4 on the left and right valve respectively (visible as light spots under the microscope) along the medial border of each valve that are interpreted as the roots of aggenital setae: the total number was probably between 14 to 17 aggenital setae.

The coxisternal area (Figs. 1B, 2C) — Normally shaped, with strong apodemes I-IV, the central apodeme and some simple setae are visible: coxal setae circa 10 – 15 µm long, those of anterior row on coxae I longer, about 30 µm. No pores were observed with certainty. In a posterior position to the fourth epimere, the lighter spots (seen on the right side) could represent the file of pores. The sum of the remaining setae and basal cuticular alveoli, (setal roots) gives estimated numbers of epimeral setae of 14-5-9-9 from I to IV (lowest hypothesis).

Gnathosoma — In lateral view, (Figs. 1D, E, 2A) the palpi, chelicerae and most of the infracapitulum are observable, infracapitular setae (*ma*, *mb*) are visible (ca 30 – 40 µm long). The palpal chaetotaxy, visible laterally, ventrally and dorsally on the specimen, is typical for the family (1-1-3-4+ω) (Fig. 1D). The tibial setae of the palp are the longest (80 – 100 µm), the terminal seta of the tarsus (eupathidium, ca 70 µm long) is shorter than the other three tarsal setae, and the tarsal solenidion is the shortest phanere (ca 30 µm long).

Chelicerae robust, with a stout and short cheliceral body, heavily sclerotized (Figs. 1E, 2A), with a large and thick fixed digit. The fixed digit ends distally with the usual three teeth: smooth *tα* and *tπ* and small inferior tooth *ti* (Figs. 1E, F). The cheliceral setae are relatively short (>50 µm long and about 25 µm), the proximal cheliceral seta emerges from a short, flattened tubercle. A mandibular appendix is present. The mobile digit has a strong basal tooth followed by at least 7-8 teeth (Fig. 1E).

The infracapitulum (Figs. 1G, 2C) is heavily sclerotized, with a uniformly alveolate cuticle. Lateral lips about half length of labrum, narrow. Both pairs of fundamental infracapitular setae were observed:

(*ma* and *mb*), pair *mb* being the longest. A supplementary seta was observed near the right palp (Fig. 1G, arrow).

Differential diagnosis — The diverse species described in the genus, even if they differ greatly from each other, present some general tendencies, notably the enlarged lateral eyes, similar to those of *S. balticae* **n.sp.**. The new species differs from other *Sellnickiella* by (i) the cuticular fenestration near the lateral eye above the lateral lyrifissure, (ii) quasi symmetric terminal teeth of the chelicera, and (iii) reduced mandibular organ.

Remarks on the new fossil species — By its general shape, this species could be confused with *L. (N.) paleoluteum* if the lateral lenses and cerotegument were not visible. As another distinctive character, the relative lengths of the articles on the first pair of legs can be used, albeit with caution as this trait is prone to optical distortions due to different observation angles in amber: tarsus I in *S. balticae* **n.sp.** is longer than half of the tibia I, while in *L. (N.) paleoluteum* it seems to be shorter than that.

GENUS *Labidostoma* KRAMER, 1879 THE FOSSIL SUBGENUS *Pseudocornutella* SUBGEN. NOV.

As noted above, three subgenera are recognized within the large genus *Labidostoma* Kramer, notably defined on the basis or absence of cornuae, spine like famulus, and an individualized lateral line of pores (subgenus *Labidostoma*), cornuae and primitive famulus, (subgenera *Nicoletiella* and *Cornutella*), the infracapitulum and the chelicerae of these latter subgenera being of two distinct types, notably differing from each other by the insertion of the proximal cheliceral seta. The habitus of the fossil specimens described below resembles that of the type species of *Cornutella*, *L. (C.) cornutum*, upon superficial examination (body shape, dorsal alveoli, chelicerae, large pustules), but they differ by the absence of frontal projections and have laterodorsal *la* setae in a position that is unique in the whole family. Another characteristic trait of these fossils is a presence of additional setae on the palptibia. This trait occurs in one other species of the genus, *Labidostoma*

corsicum Bertrand, 1982, and is considered to be a primitive character state, but was never found in *Cornutella*. For these reasons, the species is placed in a new subgenus of *Labidostoma*, *Pseudocornutella*.

Type species: *Labidostoma* (*Pseudocornutella* subgen. nov.) *electri* **n.sp.**

Differential diagnosis — The cheliceral morphology of *Pseudocornutella* subgen. nov. is similar to that of the subgenus *Cornutella* (identical insertion of proximal cheliceral seta). Frontal and lateral eyes present, pustule present. The diagnostic differences of the new subgenus are (i) seta *la* is situated in between lateral eye and pustule (behind the pustule in *Cornutella*); (ii) palptibia with more than five setae (four in *Cornutella*); (iii) dorsal shield without cornuae (present in *Cornutella*).

Labidostoma (*Pseudocornutella* subgen. nov.) *electri* **n.sp.** (Figures 3, 4)

Type designation, paratypes, and repository. The holotype female of *Labidostoma electri* **n. sp.** is a Baltic amber inclusion with the inventory number MGCP Ar-294. The piece is rectangular, circa 8 x 2 x 2 mm, labeled (etched and in ink) "MGCP Ar 294 HOLOTYPE *Labidostom. electri*". It is Epo-Thin varnished, stored in a Parafilm-sealed Eppendorf tube and is currently on loan to the first author. The holotype will be housed in the Museum of Helminthological Collections in the Center of Parasitology of the Severtsov's Institute of Problems of Ecology and Evolution, Russian Academy of Sciences. Inclusions in Baltic amber piece Ar-97 (female, two complementary pieces of amber and a slide with preserved cuticle fragments), Ar-2 (male?), Ar-382 and Ar-410 (females), (pieces of amber embedded in Epo-Thin) are designated as paratypes and will be deposited at the same institution.

Paratype 922-6 (female) from the Hoffeins collection, will eventually be housed along with the other Arachnida inclusions in one of the German museums having significant amber collections (Christel Hoffeins, pers. comm. 2012).

Etymology — "Electrum" is the Latin transcription of the Greek "ēlektron" (ἤλεκτρον = amber), an-



FIGURE 3: *L. L. (P.) electri* subgen. nov., n. sp., female. (A, D–MGCP Ar-410. B, C, F–H–MGCP Ar-97. E, I–MGCP Ar-294 (holotype)):
A – Dorsal, legs not shown; B – Ventral, legs not shown. Long arrows point to pores, short arrow-to possible podocephalic canal;
C – Anterior trichobothrium; D – Posterior trichobothrium; E – Gnathosoma, ventro-lateral view; F – Tip of the right chelicere, ventral view; G – Right palp, ventral view; H – Tarsus IV right, antiaxial terminal view; I – Leg I left, paraxial view (not all setae visible);
Scale bars: A, B – 100 μ m, C–D, E–G – 20 μ m, H, I – 50 μ m.

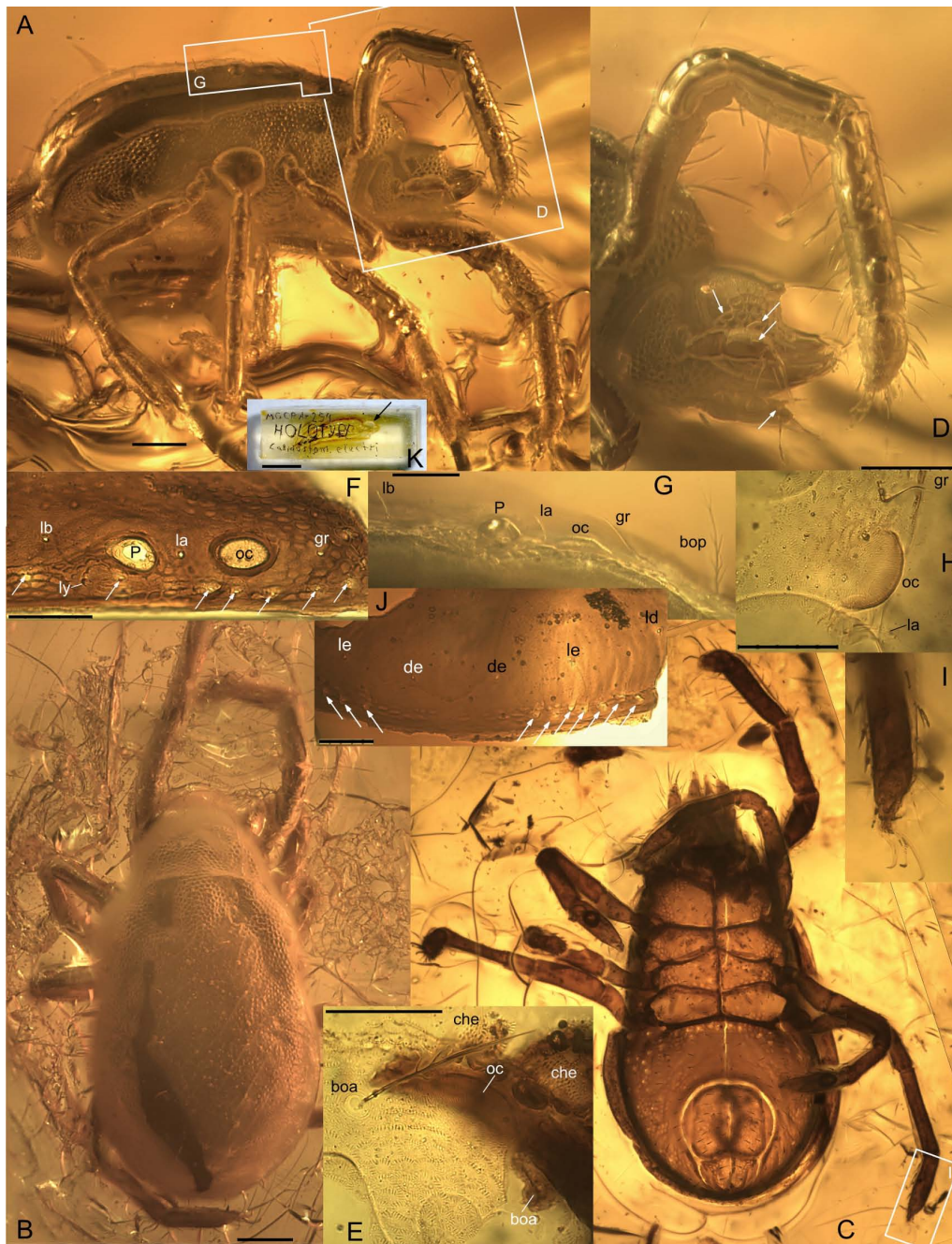


FIGURE 4: *L. (P.) electri* subgen. nov., n. sp., female (A, D, G, K–MGCP Ar-294 (holotype), combined illumination (reflected and transmitted light). B–MGCP Ar-410, combined illumination. C, E, F, H–J–MGCP Ar-97, transmitted light): A – Oblique lateral view, dry specimen. White-bordered areas show positions of detailed images, orientations of which slightly differ from A due to additional preparation of specimen; B – Dorsal view, dry specimen; C – Ventral view, specimen split along upper border of ventral shield and filled with epoxy resin. Rectangle shows position of figure I; D – Enlargement of oblique lateral view showing gnathosoma and leg I. Arrows point to palpsetae additional to normal setation of Labidostomatidae; E – Anterodorsal area, mostly cerotegument and setae. Amber piece is split, part of cuticle removed and piece filled with epoxy resin; F – Oculo-glandular region, lateral view of separated cuticle fragment. Arrows point to pores; G – Oculo-glandular region of dry specimen, oblique ventro-lateral view; H – Lateral eye and setae *gr* and *la* preserved in a separated piece of amber (same piece as E); I – Tarsus IV; J – Posterior view of dorsal shield, separated cuticle fragment. Arrows point to pores; K – Holotype piece, arrow indicates position of specimen. A, C, D are combined from 30–40 layers each, B, E, H from 60–80, F, G, I, J from 10–20. Scale bars: A–D – 100 μ m, E–J – 50 μ m, K – 2 mm. Abbreviations: P–pustule, che–chelicera, oc–ocellus.

cient Greeks having noted the electrostatic properties of this substance.

Description — The habitus of *L. (P.) electri* **n. sp.** is that of a long-legged animal, resembling *L. cornutum* in the coloration and the general habitus with an elongated body. It differs by the absence of anterolateral projections on the dorsal shield.

Dimensions and proportions — Holotype length *ca.* 710 μm , width more than 400 μm , height not less than 280 μm . Proportion of length to width is 1.8, to height 2.4. Other specimens (length x width): 680 x 415 μm (Ar-97), 670 x 415 μm (Ar-410), 610 x 400 μm (Ar-382), Ar-2 not less than 525 x 385 μm .

Cuticle ornamentation and cerotegument — The body cuticle is distinctly sclerotized, ornamented with almost pentagonal alveoli, vanishing in the central and posterior part of the dorsal shield, where fine granulations and scarce silhouettes of thin alveoli replace the well marked alveolar pattern (Fig. 4B). Alveoli are clearly visible in lateral view on both the ventral and dorsal shields, and dorsally on the anterior part from the posterior trichobothria to the front (Figs. 4A, B, E, F, H), on the cheliceral body and infracapitulum (Fig. 4D). On the central part of the coxal areas, the central and posterior part of the dorsal shield, legs and palps the cuticle is almost smooth, with short striae of cerotegument forming a ring-like pattern around some setae, especially on legs (Figs. 3B, E, I, 4B, D). The alveolar ornamentation is visible on the exterior margins of each coxa.

Dorsal shield — The body is truncated anterad, convex; a large median, lens-shaped eye (*ca.* 40 μm) is clearly visible (Figs. 3A, 4B, E). A lateral eye of about same size and shape as the median eye is well separated from a bulging, obliquely oval pustule about 35 μm long and 20 μm high. Both eye and pustule are situated at the level of the second epimere. The dorsal setae themselves are visible on the amber imprints (Figs. 3A, 4A, B, G, H), with the insertion points of missing setae present on cuticle fragments (Figs. 4 F, J). Two pairs of trichobothria (*boa* and *bop*), rather long (more than 125 μm), each with at least three or four branches (Figs. 3C, D, 4G). Aspidosomal setae: *ga* (*ca.* 75 μm long), *ge*, *gm*, *gr* (25 to 50 μm long). The dorsal shield bears the usual

rows of simple dorsal and laterodorsal setae (*la* to *le*, *da* to *de*), *la* being the longest, *ca* 50 μm . Position of *la* (Figs. 3A, 4A, B, F, G, H) is highly unusual: it is situated between the lateral eye and pustule, not behind the pustule as usually occurs in this family. On the margins of the dorsal shield (observed on separated cuticle fragments) a line of pores is visible forming a row underlining the relief of the shield: this line of pores is continued from anterior to seta *gr* (Fig. 4F, arrows) to a level between setae *de* and *le*, where it is interrupted (Fig. 4J).

Ventral view, female (Figs. 3B, 4C) — A line of pores is visible behind the fourth epimeral plates (four on each side).

Ano-genital region — Genital and anal flaps articulated, surrounded by a sclerotized ring and 17-20 setae outlining a circle (Fig. 3B). At least 17-18 setae are present on each genital flap, with the usual setation of three setae on each anal flap.

Coxisternal area (Figs. 3B, 4C) — Epimeral plates show characteristic shapes of the coxae in the genus with visible apodemes, similar to the modern species. Approximate epimeral chaetotaxy: 18(?)–10-7-11 setae. The pair of epimeral pores of the first coxae (coxal pores) was not visible, certainly due to the state of preservation of the specimens.

Gnathosoma. Palps (Figs. 3E, G, 4C, D) — The palps are more or less easily observable on three specimens (Ar 97, 294 and 410). One small lateral tarsal seta could represent the tarsal solenidion. The visible tarsal setation is compatible with the familial formula 4+ ω . Despite the constraints of the orientation of the mite in the amber, some additional setae were observed in our specimens compared to the "normal" palpal chaetotaxy in the family, which is constant (1-1-3-4+ ω). The most probable hypothesis is that (i) the genu-tibial article conserves the usual tibial and genual setae (labeled Ti1, Ti2 and Ti3 on figures 3E, G; on Fig. 3A unlabeled but present), and that (ii) two primitive setae remain. The latter are located more proximally, one being dorsal and the other lateral, on the antiaxial side of the article (labeled Ge2 and Ge1, respectively, and indicated with arrows on figure 4D). Right palp of Ar-97, left palp of Ar-294 and both palps of Ar-410 show one seta situated on the paraxial side of the

palp (labeled Ti4 on Figs. 3 E, G; arrow points to short visible fragment on Fig. 4D). The left palpfemur of the holotype bears an additional seta in a dorsal position (Fig. 3E, arrow on Fig. 4D), which is the only one visible on specimen Ar-97 (Fig. 3G). The femora could not be observed in Ar-410. The palptrochanter bears a single seta. Thus, the most probable formula of palp setation in *electri* is 1-2-6-4+ ω . Chelicerae robust, well sclerotized (Figs. 3E, F, 4D, E). Fixed digit: distal seta *chb* rather short, teeth $t\alpha$ and $t\pi$ of almost same length, $t\pi$ slightly shorter and narrower in ventral view (figure 3F); tooth *ti* about half-length of $t\pi$, rather thick in lateral view (figure 3E). Movable digit armed with a row of sharp teeth, the tip of this digit accommodated between teeth of the other digit. A cheliceral appendage is present, almost triangular in oblique lateral view (Figs. 3E, 4D). Proximal seta *cha* is inserted on a moderately long tube-like tubercle, resembling that of *L. (C.) cornutum* but shorter.

Infracapitulum — Observation of the holotype was limited by orientation in the amber. Specimens Ar-97 (figures 3B, 4C) and Ar-294 (Figs. 3E, 4D) showed that the lateral lips have a large base and are slightly shorter than the labrum (Fig. 3B). The short adoral setae are visible, the two pairs of the infracapitular setae *ma* and *mb* are present and the cuticle of ventral surface is foveolate (Figs. 3B, E, 4D).

Legs and leg chaetotaxy (figures 3H, I, 4A, B, C, D, I) — The legs are similar to those observed in modern species of the genus: PI elongated, genua I and tibiae I are the longest articles. Legs divided into articles in normal fashion: PI meso-telofemur articulation is clearly functional (figure 4D). Tibia I longer than genu I (ca. $\times 1.3$). Femur I long, with at least 4 rows of dorsal setae and 3 ventral on the mesofemur. On PII, PIII, PIV, the longest article is either the tibia (PIV) or the femur (PII & PIII). Claws: on PI two unguis, three asymmetrical on PII, PIII and PIV (figure 4I). Tarsus I: famulus hardly visible, but it seems to have several branches; two large dorsal solenidia; proximal tarsal setae erect and long, terminal setae short and simple. Tibia I (Figs. 3I, 4D): apparently with two distal solenidia, erect and in a dorsal position, but not clearly visi-

ble. At least 6 verticils of setae on tibia I, five on the genu. Numerous setae on each article, at least ventral rows of eight setae on tibia I, setae seem longer on distal articles. Tarsi II, III and IV: barbed setae (scobales in Feider & Vasiliu's (1972) nomenclature) are visible (Figs. 3H, 4I), ventral setae near the distal extremity shorter.

Remarks on *L. (P.) electri* n. sp. — Considering other amber species, *L. (P.) electri* n. sp. is distinguishable from *Sellnickiella balticae* by having the paired pustule (gland-like organ). *L. (P.) electri* n. sp. clearly differs from *L. (N.) paleoluteum*: the new species is larger, and the cuticular alveoli are characteristic, with thin walls, as in the cuticular pattern of the modern *L. (C.) cornutum* (in *L. paleoluteum* the walls are relatively thick and there are fewer striations crossing them). The posterior pair of trichobothria differs in having more ramifications than in *L. paleoluteum*. The main characters for identification are: (i) the presence of large gland-like organs and large frontal and lateral eyes, between which seta *la* is located in *L. (P.) electri*; (ii) palpal tibia bears more than five tibial setae; (iii) the chelicera of *L. (P.) electri* n. sp. has the distal tooth of the fixed digit asymmetrical.

DISCUSSION

The new species demonstrate the presence in Eocene Baltic Amber (more than 40 Ma) of the genus *Sellnickiella* and a second species of *Labidostoma*, following that described by Dunlop and Bertrand (2011). All these fossil species are large, long legged, with large eyes, long setae on the body and palps, and robust chelicerae. Such morphology in modern species corresponds to life in the upper layers of soil and litter, and on exposed surfaces, as opposed to the smaller and short-legged species with reduced lenses that colonize the deeper soil layers, like *Akrostomma* Robaux 1977 and the blind *L. jacquemarti* Coineau 1964.

Notwithstanding the scarcity of fossil mite descriptions, the presence of these carnivores in amber suggests that Paleogene biodiversity was comparable to current diversity. These fossils show a strong degree of stasis, *i.e.* little major morphologi-

cal change over long periods of geological time, further supporting a general opinion on the evolution of mites being a very slow process (Bernini, 1991).

The origin of labidostomatid mites can only be inferred. Among the Actinotrichida, the most ancient unequivocal fossils are Devonian (Hirst 1923, Kethley *et al.*, 1989), *i.e.* the primitive endostigmatic mites that share plesiomorphies with both Oribatida and Trombidiformes. Some fossil Trombidiformes belonging to families that are supposedly more specialized than labidostomatids (Bdellidae, Anystidae, Acarophenacidae, Resinacaridae, Tanaupodidae) have been found in Cretaceous resins (Ewing, 1937; Zacharda and Krivolutsky, 1985; Magowski, 1994; Khaustov and Poinar, 2010; Judson and Małol, 2009, respectively). The highly specialized plant-parasitic lineage Eriophyidae existed as early as the Triassic (Schmidt *et al.*, 2012). In the case of one of the most specialized groups of Trombidiformes, the Hydracarina, it is obvious that the ancient and Pangean origin of the group reduces their value in biogeography at the superfamilial level (Cook, 1974, Proctor and Harvey 1998). By analogy, we should consider the modern distribution of Labidostomatid genera and subgenera, and certainly too of the primitive Trombidiformes, reflecting overall the successive extinctions (difficult to be evaluated by the scarcity of fossils), rather than the dispersal from the breakups caused by continental drift or the other tectonic events.

The same tendencies are shown by Oribatida s.s.: the oldest unequivocal oribatid fossils are from the Devonian (Norton *et al.*, 1988), and some of them can be assigned to modern families (Subías and Arillo, 2002). All known Carboniferous, Jurassic and Cretaceous oribatid mites are assigned to the modern families with one exception (see Subías and Arillo, 2002 and Arillo *et al.*, 2012 for further references). Many genera and even some of their species have survived since the Eocene (Sellnick, 1918, 1931; Norton, 2006; Sidorchuk and Norton, 2010), and some genera since the Lower Cretaceous (Arillo *et al.*, 2012). This contrasts with the Astigmatina, which are represented in the fossil record by a single Eocene family, notably different from all the modern lineages (Klimov and Sidorchuk, 2011;

Sidorchuk and Klimov, 2011), and hypopi that were described as new genus within Tyroglyphidae, from Oligocene amber from Mexico (Türk, 1963).

The examples given by the three fossil labidostomatids illustrate two general considerations: (i) the contemporary subgenera, or their close relatives, were already present in the European biota in the Eocene and (ii) the family has remained homogeneous across several tens of millions of years.

In particular, the presence of a *Sellnickiella* species in Baltic amber proves that a Laurasian lineage used to exist. These "apustulate" labidostomatids (lacking the gland-like organ) are now restricted in distribution to the southern Hemisphere, a pattern that is usually interpreted as a primary Gondwanan distribution. In this instance, the current distribution clearly resulted from the reduction of a wider, perhaps formerly cosmopolitan, range. This case is not unique: paleontological evidence of wider past distributions is known for plants (e.g. Araucariaceae), mammals (e.g. Tubulidentata), and numerous arthropods, including chelicerates (e.g. the spider family Archaeidae). Discoveries of families that are now restricted to the southern landmasses in fossil strata of the North Hemisphere can be regarded as common (see Eskov, 1987 for a review of such cases and further references). These findings confirm the important role played by the southern continents in the conservation of biodiversity that succumbed to changes in the Holarctic Region, such as continentalisation of climates and changing floras. To our knowledge, this is the first case where such evidence has been found for Acari.

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