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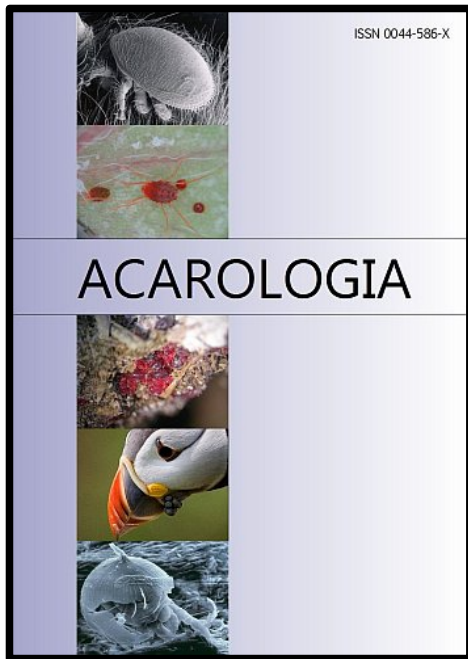
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Before the summer turns to winter: the third labidostommatid genus from Baltic amber has subtropical kin

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ABSTRACT — Following the discovery of the genera *Labidostomma* and *Sellnickiella* in Paleogene amber, a fossil of the genus *Eunicolina* was found for the first time in a piece of Baltic amber from the Hoffeins collection. The genus is known by four extant species: three European and one American. *Eunicolina* is distinguished notably by the multiplication of the pustules around the posterior part of the dorsal shield. The presence of this genus in Baltic amber confirmed that the family was represented in the early Cenozoic by genera whose members are presently confined to rather warm or cool, or Mediterranean climatic conditions, either in the South or in the North hemisphere, or cosmopolitan. The past and present distributions of the labidostommatid genera known from Baltic amber are discussed with respect to environmental changes. A key for orienting the identification of the genera and subgenera of Labidostommatidae is provided, including the fossil species.

KEYWORDS — Baltic amber; Labidostommatidae; *Eunicolina*; Eocene; biogeography

INTRODUCTION

Fossil record of edaphic predatory mites is rather impressive, with about 20 valid species of Parasitiformes and more than 250 species of Acariformes (Dunlop *et al.* 2015). Of the latter, the fossil representatives of the family Labidostommatidae may help to understand the historical biogeography of this group. The extant Labidostommatoida (Prostigmata) are represented by a single and primitive family of Prostigmata, exhibiting plesiomorphic characters (*i.e.* plesiomorphic dorsal chaetotaxy, shape of the famulus, *etc.*), characterized by a heavily armored dorsal shield and a complete ventral armature (Walter *et al.* 2009). As most of the ma-

ior groups of Acari, Labidostommatidae have probably existed well before the major adaptive breakthrough that had happened between the late Mesozoic and Cenozoic, from 60 to 100 Ma (Krantz 2009). To date, less than twenty fossil labidostommatid specimens are identified from European Eocene amber. Two genera, *Sellnickiella* Feider & Vasiliu, 1969 (with one species) and *Labidostomma* Kramer, 1879 are known from Baltic amber, and one unidentified member of the family—from Ukrainian amber (Sellnick 1931a; Dunlop and Bertrand 2011; Sidorchuk and Bertrand 2013, Dunlop *et al.* 2015).

Eocene amber of Europe is a serendipitous window to the European environment just before the Eocene-Oligocene transition, marked by the loss of

many tropical and subtropical elements. During this period, the global change from a warm climate (= late Eocene with dominant evergreen subtropical flora) to a cooler temperate seasonal climate (= early Oligocene with mixed evergreen and deciduous flora) eradicated from north latitudes many species, whereas vast stretches of seas breaking up the land continuity disturbed the genetic communication between the terrestrial ecosystems (Collinson 1992).

An inclusion in a piece of Baltic amber from the Hoffeins collection revealed a new putative labidostomatid specimen. This fossil was more deeply examined: it was the fourth species of Labidostomatidae found in Eocene amber, and the first representative of the genus *Eunicolina* Berlese, 1911. Its extant congeners are large and robust mites, predatory on soft-bodied arthropods of the upper layers in soils. They are infrequently collected but easily identified, notably by neotaxy of the laterodorsal pustules and by ankylosis of the femora of the first pair of legs. All extant species are found under warm temperate to subtropical climatic conditions: three in Mediterranean Europe and one in Virginia (USA). The discovery of this first fossil *Eunicolina* brings new data for a more comprehensive historical biogeography of the family. Our objectives by this contribution are to describe the specimen, analyse available data on the past and present distributions of Labidostomatidae, and provide an identification key to their genera, subgenera and fossil species.

MATERIALS AND METHODS

A piece of Baltic amber (Collection Hoffeins, private collection CHHC piece 588-13), in all likelihood produced by *Pinus succinifera*, dated according to the sediments from Lower to Mid Eocene *i.e.* 37 to 54.5 Ma (Poinar 1992; Weitschat, Wichard 2010). Amber with the mite inclusion was trimmed and polished to obtain a small (approximately 1 mm) lozengic piece (for description of method see Sidorchuk (2013)). The sample was stored in aqueous thymol solution (one or two drops of saturated solution per 1 ml of water). The piece of am-

ber was prepared by E.S., who identified the family, then was examined (M.B.) by light microscopy mounted in a slide with glycerol with large concavity and conserved in a solution of thymol. Image stacks were obtained using the Optikam B3 camera mounted on the compound microscope Optika B600ti and Olympus CH2 with additional incident illumination. Measurements were made on images with camera calibration, and drawings with the help of the software Inkscape™ (v. 0.48.0). Measurements are given with a rather large estimated interval of confidence because inclusion within the piece of amber induced deformation and because orientation is not as easy as that of a free specimen in a slide.

Terminology — In our previous article, we used an emendation of the original name (*Labidostomma* Kramer, 1879) by Oudemans (1904): *Labidostoma*, and its derivations. Oudemans emended the incorrect latinization of the Greek root "στομα", but, according to the International Code of Zoological Nomenclature (ICZN, art. 32.5.1.), this is unjustified emendation: it was not a *lapsus calami*, as the original spelling was twice repeated in Kramer's work (Kramer 1879, p. 13), and as Kramer himself did not refer to the origin of the name from the word "στομα". Unjustified emendation is an available name and has its own author and date — *Labidostoma* Oudemans, 1904 —, which is a junior objective synonym of the name in its original spelling (ICZN, art. 32.5.2.). It can be retained only in one case: if its usage is prevailing (ICZN, art. 33.2.3.1.). It is not so: original spelling, *Labidostomma*, is widely, albeit not universally, used (see References). The name in its original spelling, *Labidostomma* Kramer, 1879, thus should be used, and we use it in the present article.

The family-group name that we used, Labidostomatidae Oudemans, 1904, also needs to be corrected, (ICZN art. 35.4.1.) because this name was originally derived from the unjustified emendation (see above) – thus, double-m spelling is correct. The spelling is also different from the original (Labidostomidae) in that the stem of the name was corrected by Krantz (1978) to comply with ICZN art. 29.3.: as genitive singular of "στομα" is "στοματος", the stem is "στοματ-": fam-

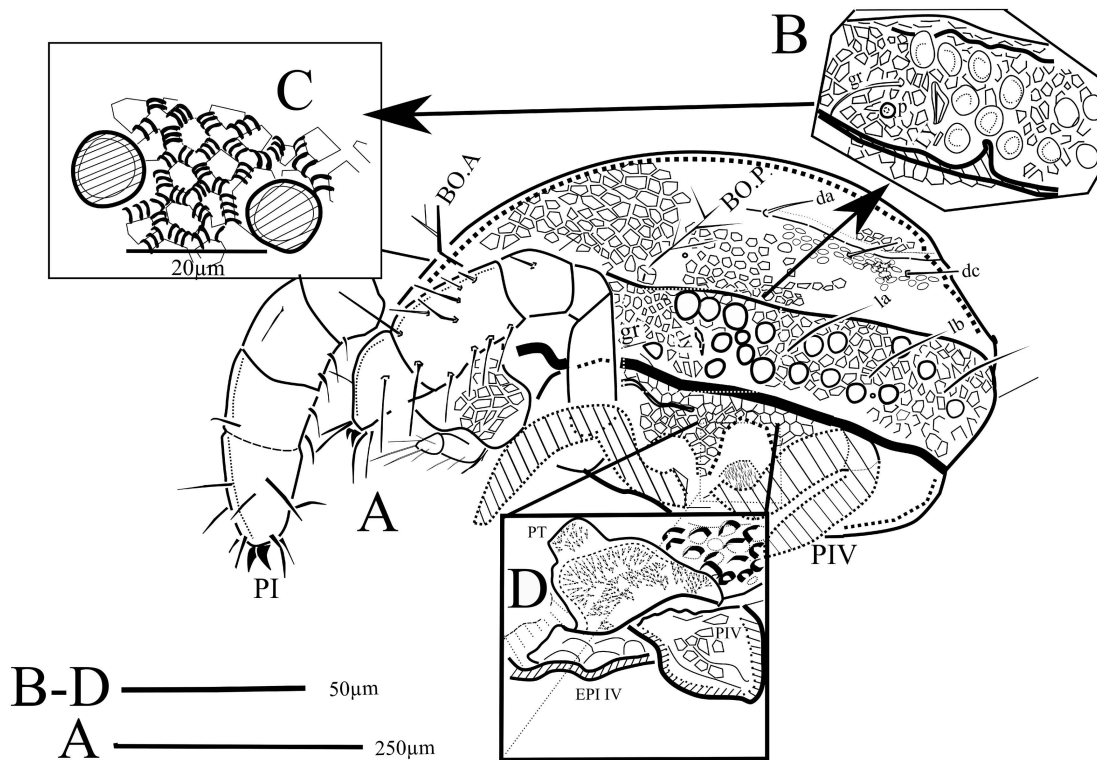


FIGURE 1: *Eunicolina glaesi* n. sp. — A. Lateral view, right side. B. Oculo-pustular zone, details. C. Detail of the cuticle, pattern in the lateral zone. D. Enlarged view of the acetabula IV, showing the villosity in pit *PT* ("puits tégumentaire" in Coineau 1964). Abbreviations: *BO.A*, *BO.P*: anterior and posterior trichobothria; *la*, *lb*: lateral setae of the dorsal shield; *da*, *db*, *dc*: dorsal setae of the dorsal shield; *EPI IV*: fourth epimeral plate; *PI*, *PIV*: first and fourth legs. Star: possible lateral eye.

ily Labidostomatidae Oudemans, 1904, superfamily Labidostomatoidea Oudemans, 1904, cohort/infraorder Labidostomatina Krantz, 1978. This is the spelling to be used, and we use it below.

Notation follows the works on this family by Grandjean (1942 a, b, c), and on the genus by Coineau (1964).

RESULTS

Genus *Eunicolina* Berlese, 1911

Diagnosis — Heavily armoured labidostomatid mites with pronounced neotaxy of pustules on each side of the dorsal shield, the deep hollow at the level of the fourth pair of legs, where the reticulated cuticle is replaced by a dense carpet of villosity, the trichobothria with few long branches, the anterolateral margins of the dorsal shield projected as cornua, the regressive famulus, the proximal tooth on

the fixed digit of the chelicera which fits in a corresponding hollow of the mobile digit. Type species — *Eunicolina tuberculata* Berlese, 1911 (redescription in Vistorin, 1980: 376).

Eunicolina glaesi n. sp. (Figs 1-5, 6B, 6C)

Type designation and repository — The holotype and only described specimen is an inclusion in Baltic amber from the private C. & H.W. Hofeins Collection (specimen CHHC 588-13, which will be eventually transferred to the Museum für Naturkunde, Berlin). This specimen is an adult, having the entire dorsal shield (nymphal stages of labidostomatids are less chitinized, with the dorsal shield divided into paired lateral and dorso-lateral sclerotized zones), and, having the rounded genital ring (Fig. 6), it is a male (labidostomatid females have an oval ano-genital ring).

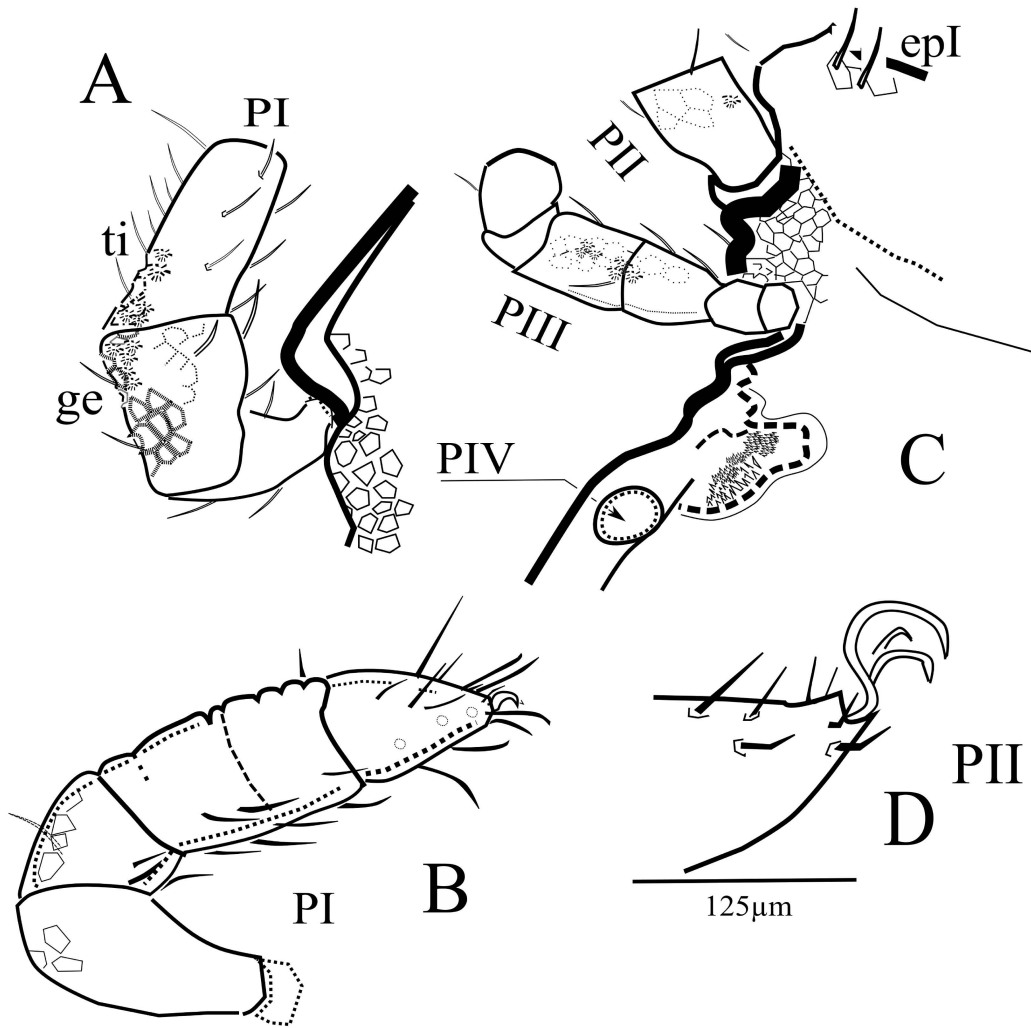


FIGURE 2: *Eunicolina glaesi* n. sp.: A – Genu and tibia, first pair of legs, right side, dorsal view; B – First leg, left side, lateral view; C – Ventral view, detail of the proximal articles of leg I, II and acetabulum of fourth leg (the leg IV is not represented here); D – The tridactylous tip of the tarsus II, lateral view. Abbreviations: *epI*: first epimeral plate; *ge*: genu; *PI*, *PII*, *PIII*, *PIV*: Legs 1 to 4; *ti*: tibia.

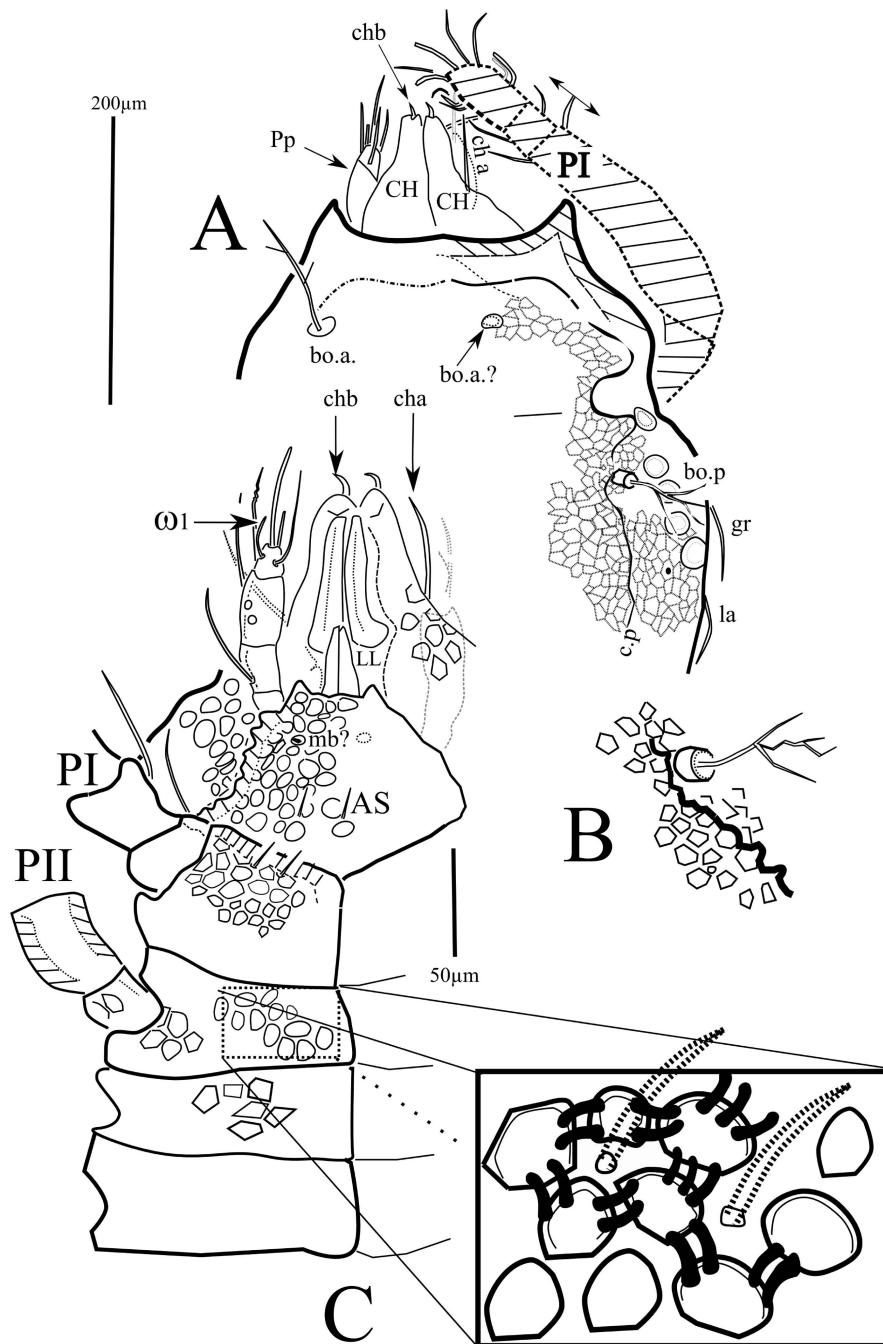


FIGURE 3: . *Eunicolina glaesi* n. sp.: A – Dorsal shield, anterior part; B – Detail of the posterior trichobothrium; C – Ventral view of epimeral plates and detail of ornamentation. Abbreviations: AS: additional posterior seate of the infracapitulum; *bo.a.*, *bo.p.*: anterior and posterior bothridia; *CH*: Chelicera; *cha*, *chb* cheliceral setae; *gr*, *la*: ocular and lateral setae of the dorsal shield; *PI*, *PII*: legs I and II; *Pp*: palp. $\omega 1$: tarsal solenidion of the palp.

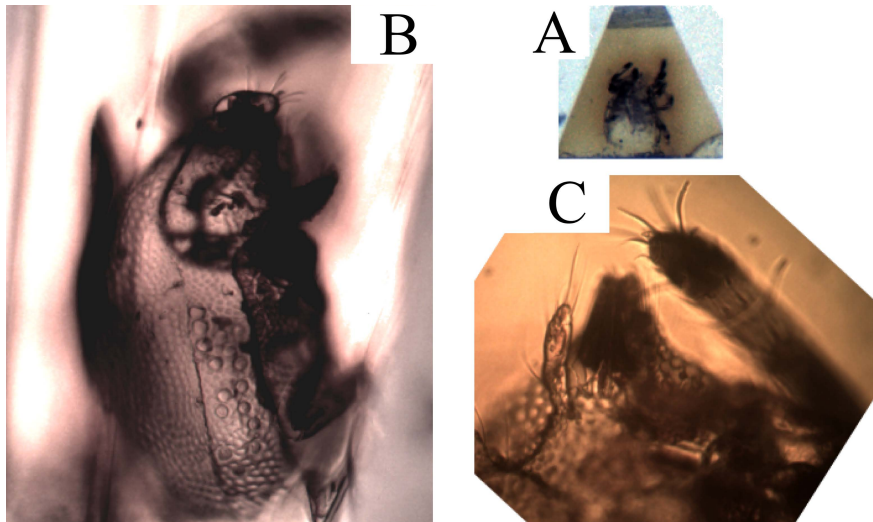


FIGURE 4: *Eunicolina glaesi* n. sp.: A – The holotype piece, CHHC 588-13 (Hoffeins collection); B – Lateral view of the specimen of *Eunicolina glaesi* sp.nov.; C – Ventral view of infracapitulum and leg I.

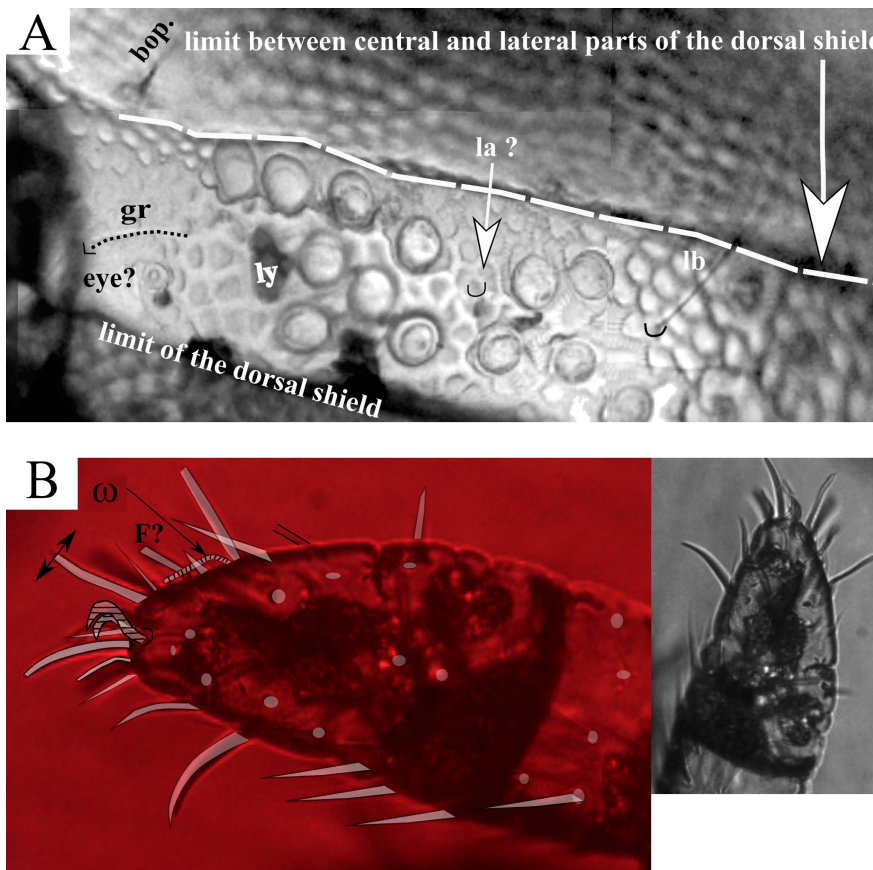


FIGURE 5: *Eunicolina glaesi* n. sp.: A – Oculo-pustular zone. *bo.p.*: trichobthria, *la?*: supposed insertion of the *la* seta; *lb*: seta *lb*; *ly*: post-ocular lyriform organ; B – Detail of the *PI* tarsus showing the bidactylus claw, one of the two tarsal solnidia (ω). *F?*: possible famulus of the tarsus. Some insertions of setae are marked by circles.

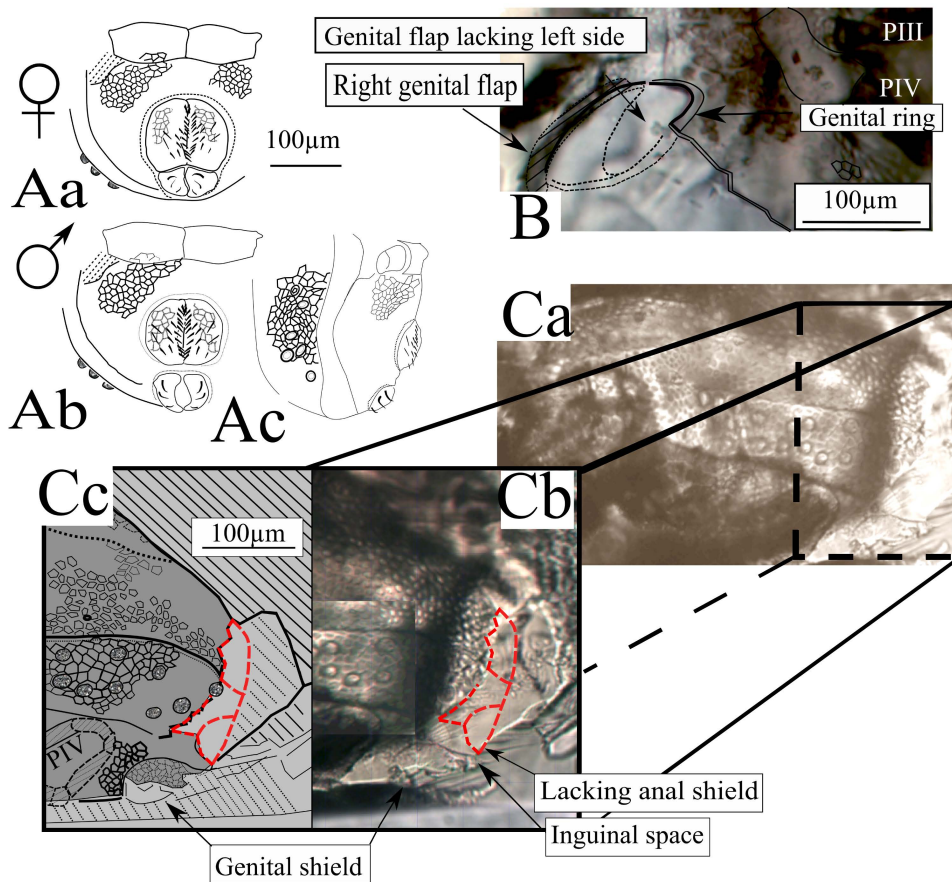


FIGURE 6: Genito-anal area: A – Disposition of genital and anal shields (drawn from the extant species *E. travei*) Aa, Ab: ventral view, female (a), male (b); Ac: male lateral view. *Eunicolina glaesi* n. sp.: B-C – extremity of the opisthosoma, lateral view (B) and interpretation (Ca, Cb, Cc).

Description — The habitus is that of an animal with a rounded body, robust, well-sclerotized, yellow to brown in coloration.

Dimensions and proportions — Body length (c. 580 – 600 μm) is about 1.7 times its maximum width (c. 390 – 400 μm), about as wide as high (Figs 1A, 3B, 3C).

Cuticle ornamentation and cerotegument — The cuticle is ornamented with more or less rounded alveoli: the dorsal shield is covered with a regular polygonal pattern laterally, whereas partitions are more rounded on the central zone of the dorsum, and on the ventral shields. The borders of alveoli are crossed with more or less large costules (Fig. 1C). As in other representatives of the genus, the

polygonal pattern extends onto the articles of the legs and on the chelicerae, but not on the palps.

Dorsal shield — Chaetotaxy as for the genus (Figs 1A, 3A), the dorsal setae are long, (*la* – *le* c. 75 – 100 μm , *da* – *de* c. 75 – 80 μm), anterior setae *ga*, *ge*, and *gm* less visible or broken, their presence revealed only by the mark of insertion. The setae *gr* are short (<40 μm). The trichobothria are similar to those of *E. travei* Coineau, 1964, with 3-4 branches. With more than 100 μm in length, the bothridial setae are longer than the lateral and the dorsal setae (Figs 3A, B). The frontal edge of the dorsal shield bears two cornua. Close to twenty pustules were counted on the lateral fields of the dorsal shield. On each side, the field of the pustules begins at the level of the second coxal plate. In the usual posi-

tion of the lateral eyes, close to the (*gr*) setae, a convex structure (Figs 1A, 1B, star) could be either a pustule or the lateral eye (the usual striation of the lens surface, different from the smooth surface of the pustules, is not visible). No median anterior eye was discernible. The lateral lyrifissure, poorly preserved, may be located between the most anterior pustules. The density of the pustules is maximal behind the supposed lateral eye (Figs 1A, 1B, 5A).

Ventral view — The posterior end of the ventral shield is damaged, hence the anal sclerites were not seen and the genital ones were only partially observable. The infracapitulum (162 μm long, 150 μm wide) is ornamented by alveoli, the pair of setae *mb* is well visible, plus at least one pair of additional posterior setae (*AS* on Fig. 3C). The lateral lips are narrower than the anterior margin of the infracapitulum. The palps (the right palp was well observable in ventral view) are characteristic for the genus (1-1-3-4+ ω), with the palpal solenidion identifiable and the long apical seta (eupathidium?) (45–60 μm long) (Figs 3C & 4C). The chelicerae are partially hidden by the first pair of legs and the palps, and cannot be observed in lateral view. The chelicerae are robust (*c.* 250 μm long) and are strongly sclerotized, the proximal part covered with alveolar ornamentation. Examination in alternate dorsal and ventral views permitted identification of the anterior seta (*chb*) of the fixed digit and the long posterior seta *cha*, whose insertion was not seen (Figs 3A, 3C). The coxisternal area (Fig. 3C) is armoured, sclerotized and ornamented with strong alveoli (Fig. 3C), the epimeral setae are poorly preserved, and only some simple setae were identified on the anterior fringe of the first epimeral plates.

At the level of the fourth epimera, on each side, the integument forms a large cavity, a pit, that receives the basal parts of the legs IV ("*puits tégumentaire*" in Coineau 1964). The cuticle of these hollows is covered with dense villose integument similar to what has been observed in congeneric species (*PT*, Figs 1D, 2C) (*cf.* Coineau 1964; Feider, Vasiliu 1968).

Legs (Figs 1A, 2A, 2D) — The legs are robust and sclerotized, the polygonal pattern ornamentation of the body is continued on the articles and discernible on femora and genua on the first pair of legs. The ar-

ticles of the first pair of legs are thick, and not elongated as in the other genera of labidostommatids. However, asymmetry between right and left legs of the first pair attests that either the fossilisation process or optical properties of amber induced some deformation, the legs of the right side keeping more "natural" proportions. The third leg is missing on the left side. The alveolate ornamentation of the legs is similar to that of the shields, but locally it is resolved in cristules as on the edges of the genu and tibia of leg I (Fig. 2A). The genu, is shorter than the telofemur and the separation of the femora in three articles is functionally reduced to basi- and [mesotelo] femora, due to "ankylosis" of the distal article of the femora (Figs 2A, 2B) already described in the extant species (Coineau 1964).

Tarsi as for the genus, tarsi II, III, IV are tridactylous, and tarsi of legs I bidactylous. The tarsi I are provided with long dorsal setae, and on the left leg, one of the two usual recumbent solenidia (ω) is clearly visible, and a spine which, by both the position and its shape, could be identified as the famulus (Fig. 5B, *F?*).

Differential diagnosis — By the characters described here above, there is no doubt that this specimen belongs to the genus *Eunicolina*. The fossil species is distinct from the extant members of the genus by the supposed absence of frontal eye, reduced lateral eyes and by the lower number of pustules than in modern species. It clearly differs from *E. nova* (Sellnick, 1931b), which has 20 to 35 pustules, by absence of neotrichy; from *E. travei* — by the absence of modified integument near the posterior trichobothria. On the ventral surface of the infracapitulum it clearly differs from both *E. travei* and *E. nova*, these latter species having respectively (*ma*) and (*mb*) and 4-5 or 7 pairs of infracapitular setae, while *E. glaesi* shows two pairs of infracapitular setae: (*mb*) and one other pair with discernible insertion marks.

Remark — The pustules of *Eunicolina* mites are distributed "on each side from the level of the leg II and extending uninterrupted caudad and absent from a short space of the posterior end of the dorsal shield" (Greenberg 1952), but each species differs by their number (Table 1). Berlese (1911) has

TABLE 1: The tubercles and distributions of the *Eunicolina* species (data from Berlese 1911; Sellnick 1931b; Feider et Vasiliu 1968; Vistorin, 1980; Coineau 1964; Bertrand, 1988)

Species	Number of pustules	Distribution	Habitat
<i>E. tuberculata</i>	ca 28–32. 5–6 anterior, 25 posterior to the eye.	North Italy, Adriatic coast.	fields, natural vegetal cover, shrubs
<i>E. porifera</i>	30. None anterior to the eye.	Virginia (USA)	leaf mold
<i>E. nova</i>	20–35. First four are anterior to the seta <i>gr</i>	East Mediterranean basin, Greece, Romania.	leaf litter, sclerophyllous Mediterranean forest
<i>E. travei</i>	More than 40. More than 7 anterior to the lateral eye.	Mediterranean France	under tree cover, under Mediterranean and temperate climatic conditions, upper layer of litter
<i>E. glaesi</i> n. sp.	18–20. None anterior to the seta <i>gr</i>	Fossil, in Baltic amber	unknown

noted the arrangement of the pustules in two "series" "*tuberculi seriei marginalis 6 numero; marginalibus serie usque ad marginalis posticum producta, ad 25 numero*", i.e a total of 31 pustules, in *E. tuberculata*. *E. travei* presents the largest neotaxy, with more than 40 pustules on each side, in *E. nova* the number of pustules varies from 20 to 35 on each side (Sellnick 1931b; Feider and Vasiliu 1968). The fourth species, the American *E. porifera* Greenberg, 1952, from Virginia, averages 30 pustules on each side (Greenberg 1952).

Etymology — from "*glaesum*", term, used by Pliny the Elder (77) for amber "*.../... certum est gigni in insulis septentrionalis oceani et ab germanis appellari glaesum, itaque et ab nostris ob id unam insularum glaesariam appellatam, .../... nascitur autem defluente medulla pinei generis arboribus .../...*". Translation: It is well established that the amber is a product of islands in the Northern Ocean, that the Germans named "*glaesum*", and that, as a result, one of these islands was nicknamed "*Glaesaria*" by our (legion), .../... (Amber is) formed of a liquid seeping from the interior of a species of pine .../... [adapted from Woolley's translation (1969)].

DISCUSSION

The family Labidostommatidae is homogeneous, and all the species are free-living, robust edaphic hunters, feeding on soft-bodied edaphic organisms, and living under dry tropical, subtropical or temperate climates. The Labidostommatidae have poor abilities of dispersion, with no phoretic behaviour ever recorded. Labidostommatids are protected by a cuticle ornamented with alveolar microsculpture interpreted as an adaptation to heavy rains: this alveolated structure prevents the cuticle from coming into direct contact with water (Alberti 2013). This clade is primitive, and may derive from the most ancient lineages, the older fossil material of which, currently assigned to other primitive Prostigmata (Sphaerolichida and Eupodina) comes from the early Devonian (c. 410 Ma) Rhynie Chert of Scotland (Hirst 1923; Dunlop and Selden 2009).

The genus *Eunicolina* Berlese, 1911 successfully navigated the mid-Eocene-Oligocene transition and later environmental changes. By application of the principle that the life environment of extant organisms allows understanding the life conditions of neighbour extinct species, the discovery of *E. glaesi* n. sp. is congruent with the classic recon-

struction of the European environment during the Eocene (from 54.5 to 33.7 Ma), when Europe was an archipelago under warm and humid, non-seasonal climatic conditions comparable to subtropical climates (Penney 2010). Progressively, these conditions changed to lower winter temperatures and decreased precipitation. During this crisis, contrary to the isolated North American lands, in Europe the land continuity ensured a combination of introgressive Asian elements and the conservation of pre-existing elements of fauna and flora in meridional refugia (Prothero 1994): if numerous "subtropical" species became extinct in Europe, some of them, and among them eunicolinids, have survived under comparable climates, notably in Mediterranean region and South-East Asia (Penney 2010, Wichard *et al.* 2010).

Do the extant eunicoline species result from "recent" speciation or are they relicts?

The three European species of the genus are allopatric. This distribution must be compared with analogous ones, especially of some widespread groups which resisted extinction events since the Oligocene, which have survived to the Miocene Climatic Transition, and whose areas of distribution were fragmented by the uplift of south European mountains (Alpine surrection). Obviously, the isolation facilitated speciation during the Quaternary glacial cycles. Several examples are known among Chelicerata: *Harpactocrates* genus (Araneae, Dysderidae), whose vicariants diversified in peripheral refugia within mountain ranges (Bidegaray-Batista *et al.* 2014), the genus *Euscorpius* (Scorpiones, Euscorpiidae), with isolated populations since the refilling of the Mediterranean Sea and climatic changes (Gantenbein *et al.* 2001, Vachon 1983, Vignoli *et al.* 2007). On the other hand, examples of adaptive radiation are rare in the edaphic clades, notwithstanding ecological opportunity (Losos 2010). Even for more recent and plastic taxa like the *Drosophila* genus, there is no significant support for adaptive radiations when either geographic dispersal or ecological resource shift occurred (Morales-Hojas & Vieira 2012). In stable edaphic communities, the structure of oribatid local faunas seems to be largely driven by the postglacial

dispersal processes (Mumladze *et al.* 2013).

In this context, the Mediterranean European species of the genus *Eunicolina* result from a paleoendemism, in which the extant species are vicariant: isolation might have resulted from conjunction of a climatic barrier northward (cool climate) and of geographic barrier (mountains) which have interfered in colonizing process. As a result, the European diversity of *Eunicolina* has been limited to the three Mediterranean species, with, from West to East, *E. travei* (occidentally distributed to Alps mountains, France), *E. tuberculata* (Italy) and *E. nova* (Balkan Peninsula, South of Carpathian mountains), a reduction that could have resulted from extinction of the more septentrional species (Fig. 7). However, the enigma of the American species may result from (1) that the unique American record resulted from the post-Columbian introduction of European specimens, which is doubtful, or (2) that the genus *Eunicolina* diversified in Europe and North America. We have no evidence, but this latter hypothesis seems credible when the distribution of the labidostomatid genus *Akrostomma* Robaux, 1977 is taken into consideration: these eu-edaphic mites spend their lives in the deeper soil horizons, in the same place, and are unable to quickly colonize new territories (Bertrand 1988). The genus was discovered from American soils (Robaux 1977), the three others species being European, *A. coraloides* Bertrand & Coineau 1979 (France), *A. coineaui* Bertrand 1983 (Spain), and *A. zangherii* (Lombardini 1943) from Italy described as *Labidostomma zangherii*.

In conclusion, the extant Labidostomatids have successfully passed through the bottlenecks of geological and climatic changes. Since the Mesozoic, these changes may have modified the distributions of labidostomatid lineages, and two scenarios seem likely according to the width of the scale, either temporal or spatial:

i) the previous distribution has been fragmented but its cosmopolitan nature was conserved more or less notwithstanding possible "colateral losses", *i.e.* the widely distributed genus *Labidostomma*, or with failures in recolonization of the lost territories after Tertiary, *i.e.* the genus *Sellnickiella*, restricted now to

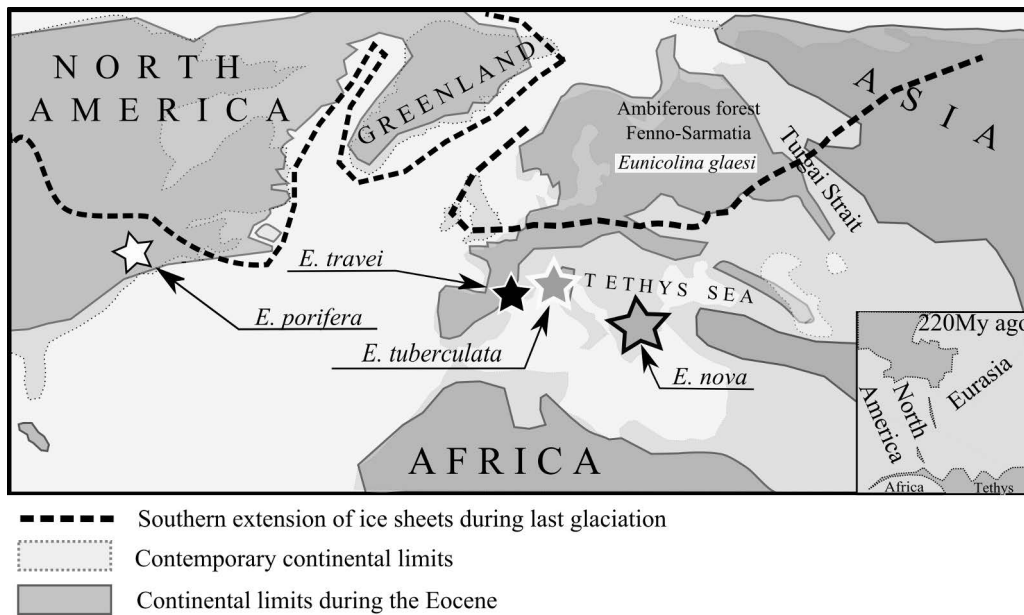


FIGURE 7: Distribution of the fossil *E. glaesi* and of the four extant species of the genus *Eunicolina*, shown on paleogeographic map of Europe (c. 40 Mya) (adapted from maps given by Charbit *et al.* 2007, Swedo, Sontag 2013, Scotese 1997).

the South Hemisphere (Dunlop and Bertrand 2011; Sidorchuk and Bertrand 2013).

ii) the pre-Cenozoic distribution of some lineages has been greatly modified and restricted, leading to disappearance of genera from large parts of their ancestral ranges. Apparently, the members of *Eunicolina* resisted the effects of climate change, at least in Europe, only where sheltered from Quaternary changes, in their restricted Mediterranean milieu. This hypothesis may explain the distribution of the three European species (Vistorin 1978; Bertrand 1989; Pflieger & Bertrand 2011), which can be compared with the European distributions of the genus *Akrostoma* (three species in South Europe, *i.e.* Spaniard, French and Italian), or of the two European species of *Labidostomma* (*Nicolettiella*): the oriental *L. (N.) denticulata* (Schrank, 1776) and the occidental *L. (N.) luteum* Kramer, 1879, isolated by the Alpine chain. The latter species succeeded in (re?)colonizing higher European latitudes by parthenogenetic populations whereas males and females are found in South of France (Grandjean 1942a, Bertrand 1980), while the other common European species are limited to more southern regions (*i.e.* *L. (C.) cornuta*) (Błoszyk 1980).

Key for identification of fossil Labidostommatidae (fossil taxa are noted "†")

1. Idiosoma with at least one pair of lateral pustules, with or without eyes. Famulus of tarsus I simple or complex, with lateral and central branches ("bracts" and central "fruit" according to Grandjean 1941) . . 3 — Without lateral pustules; lateral eyes and unpaired frontal eye usually present. Famulus long, simple or bifid, without a "fruit". (Extant species were described from South Hemisphere). Genus *Sellnickiella* Feider & Vasiliu, 1969. Type species: *Labidostomma brasiliensis* Sellnick, 1922. 2
2. Famulus bifid (Extant species collectively "Gondwanan" in distribution).....Subgenus *Sellnickiella*. One fossil species from Baltic amber, *S. balticae*† Sidorchuk & Bertrand, 2013. — Famulus simple (described from South America)Subgenus *Dicatriella*. Feider & Vasiliu, 1970 Type species: *Dicatriella covarubiasi* Feider & Vasiliu, 1970.
3. Cuticle dense and heavily sclerotized, retic-

ulation with very thick walls, chelicerae strong and stout, with several denticulations (serrate) on the fixed digit, eyes reduced or lacking. Body shape fusiform, small species (<800 µm) (described from Europe and North America).....

.....Genus *Akrostomma*
Robaux, 1977. Type species: *A. grandjeani* Robaux, 1977.

— Reticulation of the cuticle usually with fine walls, chelicerae not as above, eyes usually present, some species are blind or with reduced eyes. Body fusiform or not, often large species (800 to 1500 µm)..... 4

4. With a pair of large lateral pustules, each larger than four lengths of the lateral eye (the subgenus was described from Asia (Japan) and South Hemisphere: New Zealand, Australia, and Peru).....

.....Genus *Labidostomma*
Kramer, 1879 (pars: subgenus *Atyeonella* Feider & Vasiliu 1969 (ex genus *Atyeonella* Feider & Vasiliu 1969). Type species *Labidostomma fictiluteum* Atyeo & Crossley, 1961 (see Bertrand 1990a, Feider & Vasiliu 1969).

— With pustules not larger than three lengths of the lateral eye.....5

5. Multiple pustules (close to or more than 20) present laterally and posterolaterally on dorsal shield, each uniporous; body heavily sclerotized, articles of legs with polygons, a hollow with villose ornamentation present posterior to coxae IV (extant species noted from Europe and North America).....

.....Genus *Eunicolina*
Berlese, 1911. Type species *E. tuberculata* Berlese, 1911: *E. glaesii*† nov. sp.

— Not as above, pustules mostly one pair (rarely 2 to 4 pairs) and the only or anterior pustule is multiporous; entire body heavily sclerotized or with softer sclerotization on the dorsal shield; leg articles with fine striations; hollow with a floor of villosities near the coxa IV is absent (cosmopolitan). Genus *Labidostomma* Kramer, 1879. Type species (the only species originally assigned to the genus) *Labidostomma luteum* Kramer, 1879 (pars: subgenera *Labidostomma*, *Cornutella*, *Pseudocornutella*†,

and *Nicoletiella*; see Remark).....6

6. Famulus with a "fruit", rounded or needle like. With or without latero-frontal projections (cornua). Frontal eye usually overlooking the chelicerae...7

— Famulus regressive, often hidden by dorsal setae of the tarsus, spinelike. Cornua present or lacking. Frontal eye subterminal, or overlooking the chelicerae, (cosmopolitan).....

.....Subgenus *Labidostomma*. Type species *Labidostomma luteum* Kramer, 1879.

Note: Two entities with this subgeneric diagnosis: (i) with cornua and lateral file of lateral pores on the dorsal shield not underlined by a thickened cuticle drawing a line: *L. luteum* group, (including *L. denticulatus* Schrank, 1777); (ii) without cornua and with dorso-lateral pores confined to a cuticular gutter: *L. integrum* group (including species similar to *L. integrum* Berlese, 1918).

7. Seta *la* inserted between eye and pustule. No additional pustules present. Cornua lacking. Penultimate segment of palp with five or more setae.....

.....Subgenus *Pseudocornutella*† Sidorchuk & Bertrand, 2013. Type species *Labidostomma (Pseudocornutella) electri*† Sidorchuk & Bertrand, 2013.

— Seta *la* inserted posterior to pustule; additional pustules present or absent. Cornua present or absent. Penultimate palp segment typically with three setae.....8

8. One pair of multiporous pustules in the unique species of this subgenus. Ornamentation vanished in the central zone of the dorsal shield. Anterior eye projected forward by a "collar" anterior to the setae (*ga*) and the anterior trichobothria, cornua absent. Elongate hollow present on the ventral shield at the level of the legs IV. All leg segments have alveolar ornamentation. Only one neotrichous species described from Peru.....

.....Subgenus *Pselistoma* Bertrand, 1990 (Type species: *Labidostomma (Pselistoma) legendrei* Bertrand, 1990b).

— At least one pair of multiporous pustules close to the lateral eye. If multiple pustules are present, additional pustules are uniporous. Anterior eye not

as above, cornua present 9

9. Additional pustules present or absent. Cornua more or less developed, sharpened or blunted distally. Frontal eye in terminal position above chelicerae. Genua of legs I clearly shorter than tibia I. Chelicerae with proximal seta inserted on a short tubercle. Penultimate palp article with 3 setae.....Subgenus *Nicoletiella* Feider & Vasiliu 1969. Type species: *Nicoletiella cornuta* Canestrini et Fanzago, 1882 (1877): *L. (N.) paleoluteum*† Dunlop & Bertrand, 2011

— With a single pair of large multiporous pustules. Distinct cornua, directed forward, and distally sharpened. Frontal eye usually present, distinct, not overlooking chelicerae. Genua of legs I longer than tibia. Proximal cheliceral seta may arise atop a long tube with alveolar ornamentation or on a short and rounded tubercle (in *L. glymma* Grandjean, 1942a). Penultimate palp article with 3 setae, exceptionally with 5.....Subgenus *Cornutella*. Feider & Vasiliu 1969 Type species: *Nicoletiella cornuta* Canestrini et Fanzago 1882 (as defined, *Cornutella* is a junior objective synonym of *Nicoletiella*, see Remark)

Remark — The taxonomy within Labidostomatidae is highly problematic, with two main issues: (i) the lack of well-established diagnoses for genera and subgenera (ii) the confusion with type species of several genus-groups. (i) In the current state of knowledge, Labidostomatidae (ca 50 species) includes at least five well-defined genera: *Eunicolina*, *Labidostomma*, *Akrostomma*, *Sellnickiella*, and *Atyeonella* (the latter was previously considered a subgenus of *Labidostomma*, see Bertrand (1990a). The use of subgenera have helped in the identification of the species as a useful but limited tool and more recent descriptions of species allow now a better overview of the diversity (Feider and Vasiliu 1969; Bertrand 1990; Pflieger and Bertrand 2011). This diversity pointed out some problems, notably the definition of the genus *Labidostomma* which needs to be revised: this genus aggregated an heterogeneous assemblage of species which cannot be readily assigned to any subgenus, whereas

some emergent species-groups are obvious (*i.e.* the groups "*cornuta*", "*luteum*", "*integrum*"), each readily defined by morphology, even if it is sometimes difficult to characterize the apomorphies, synapomorphies or possible convergence induced by adaptation.

(ii) The second problem has been caused by re-assigning type species of the genus *Labidostomma*, as well as those of the subgenera *Nicoletiella* and *Cornutella*, during the XIX-XXth centuries. Especially much confusion arose since Feider and Vasiliu's "Critical review of Nicoletiellidae" in 1969, where they proposed several new genus-groups and changed type species of the old ones. Up to date, there is no satisfying correction following the ICZN rules and respecting the species groups defined by morphology. Feider and Vasiliu (1969, p. 205) proposed as the type for the genus and the subgenus *Nicoletiella* Canestrini et Fanzago, 1882, *L. luteum* Kramer 1879, the sole species of *Labidostomma* as '*Nicoletiella lutea* Kramer 1879'. For the newly proposed subgenus *Cornutella*, they (*op. cit.*) proposed *Nicoletiella cornuta* Canestrini et Fanzago 1882 as the type species (as '*Nicoletiella (Cornutella) cornutum* Canestrini et Fanzago 1877' dated from the date of proposed name *Nicoletia* which was a junior homonym allowing confusion with a thysanuran name). *Labidostomma* Kramer, 1879 ended up with '*L. integrum* Berlese 1887' for the "type" species (*op. cit.*). Such type designation discords with the Principle of Coordination of genus-group names (ICZN, art. 43), and even with the general provisions of the Code in the section concerning types in the genus group (see especially art. 67.2): the ICZN prescriptions rule that *N. cornuta* should be the type species of the genus-group *Nicoletiella*, being the unique species originally included in this genus (Canestrini et Fanzago 1877, p. 52). In the genus *Labidostomma*, *L. luteum* is the type species by monotypy, as there was no other species included in this genus, or even mentioned alongside, originally (see Kramer 1879, pp. 13-16). Regarding the problem created for the subgenus *Cornutella*, it is deemed to be suppressed as a junior objective synonym of *Nicoletiella* as defined to date. The easiest decision would be to re-define the respective group of species under a new

name, with its own type species. If the name *Cornutella* is to be kept (by the application to, and subsequent decision of the International Commission on the Zoological Nomenclature), the type species should be chosen among the originally included nominal species (ICZN art. 67.2.). The oldest (Feider and Vasiliu, 1969, p. 205) is *Acarus denticulatus* Schrank, 1776, but it is closer to *L. luteum* than to *L. cornuta*. Notwithstanding the choice of the replacement type species for *Cornutella*, proper fixation requires the adequate description of type material and/or designation of a neotype, and following the rules of the abovementioned application to the Commission.

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Note: the title of this paper was inspired by a popular song "*Before the summer turns to winter - Before the dreams will turn to snow- I see the yellow leaves are falling- And soon I know I have to go*" (Tolkii, Timo Tapio).


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