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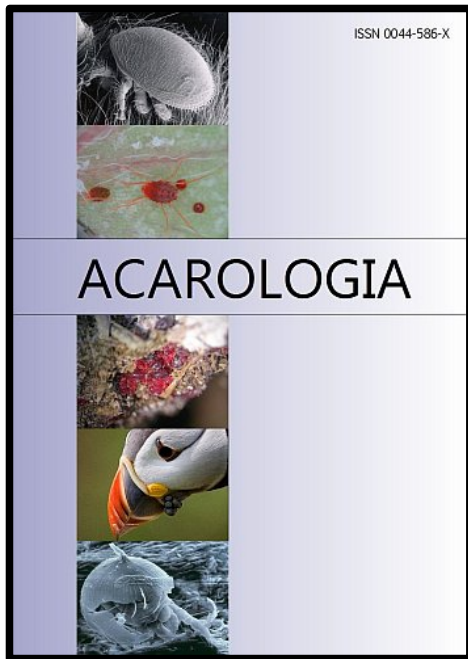
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The labidostommatid palpus: a morphological enigma (Acariformes: Prostigmata)

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ABSTRACT — Hypotheses are reviewed concerning which segments of the primitively five-segmented palpus are coalesced to form the simple, linear, four-segmented form characteristic of labidostommatid mites. Among alternatives, those of either a femurogenu or a tibiotarsus are not based on convincing evidence. Instead, based on ontogeny of the peculiar palpal structure and chaetome of labidostommatids, a case is made that the proximal segment, which bears a single, ventral, postlarval seta, is a basifemur, with the trochanter autapomorphically either coalesced with it or subsumed into the base. Consequently, the second segment is a telofemur, articulating with the third article, which is an unusual, coalescent genuotibia. The phylogenetic significance of various interpretations of segmental coalescence are considered. Ontogenetic studies of palpal musculature and gene expression are needed to provide more substantive evidence.

KEYWORDS — *Labidostoma*; Nicolettiellidae; fundamental setae; palpomeres

INTRODUCTION

The Labidostommatidae is a small but highly distinctive family of free-living, predatory mites that occur from tropical to cool-temperate regions, worldwide. About fifty species have been described and assigned variably to four to nine genera, depending upon whether some genus-groups are treated as subgenera or genera (Kethley 1982, Bertrand 1990). Their morphological attributes are so peculiar, including a unique mixture of derived and primitive traits, that they are placed in their own supercohort (or infraorder), basal in the acariform suborder Prostigmata (Walter *et al.* 2009, Bertrand *et al.* 2012).

A seemingly unremarkable attribute of labidos-

tommatids is their rather ordinarily-shaped, linear palpi, reduced from five to four articles. Among acariform mites, reduction of the number of palpomeres is arguably a progressive trend, reaching its extreme in parasitic and phytophagous lineages of Trombidiformes and in oribatid Astigmata as a whole (Lindquist 1984, Evans 1992, Walter *et al.* 2009, OConnor 2009). Even among free-living acariform mites, four- and even three-segmented palpi are not uncommon: in Trombidiformes such palpi can be found in all major groups (Walter *et al.* 2009), and in Sarcoptiformes - among the Astigmata, Enarthronota, Mixonomata and Brachypylyna (OConnor 2009, Norton and Behan-Pelletier 2009). Usually, reduction in the number of palpomeres to four occurs through the fusion of the femur

and genu, as in Eupodoidea, Tydeoidea, oribatid Mixonomata (Grandjean 1940, 1967, Walter *et al.* 2009), and the trochanter joins this coalescence in the three-segmented state (Grandjean 1965, 1967). Rarely, the palpal trochanter and femur may be fused without affecting articulation of the palpal genu, tibia, and tarsus, as in *Elliptochthonius profundus* Norton (1975).

In all these reductions, phaneres apparently remain with their respective segments. From the plesiomorphic setal complement of 0, 2, 1, 3, 9 setae (+ tarsal solenidion) on the trochanter, femur, genu, tibia and tarsus, respectively (Evans 1992), a reduced four-segmented appendage may present three setae on the second article (see the references above), still leaving the palptrochanter, as the proximal segment, without setae, 'toujour glabre' (Grandjean 1933, Lindquist 1996, Alberti and Coons 1999), whenever it is free. Even among trombidiform mites presenting a strong 'pilosity' (hypertrichy), such as in the Anystidae, the palpal trochanter remains nude (Grandjean 1943).

The labidostommatid palp, however, does have a ventral, postlarval seta on its proximal segment (Grandjean 1942a, b). If this segment is a trochanter, such a state is highly unusual, perhaps unique in the Acariformes (the Halacaroida may be another exception). Moreover, the hypotheses, regarding which of the five palpomeres became fused in labidostommatid mites, are controversial even among multiple contributions by the same authors (see below). This paper aims to reconsider these aspects based on exomorphological evidence, and to draw the attention of acarologists to this tiny but provocative mystery.

NOMENCLATURE.

The genus-group name, *Labidostomma* Kramer, 1879, was originally published with double-m. There is no evidence of a *lapsus calami* in the original publication, where "*Labidostomma*" is the only spelling used (Kramer 1879: p. 13 (twice) and p. 18). The genus name, however, was emended by Oudemans (1904), because "*στομα*" (mouth) should be transliterated to Latin with a single "m". According to the Inter-

national Code of Zoological Nomenclature (ICZN), the correction of a latinization error is an unjustified emendation (ICZN, art. 32.5.2.), and is an available name with its own author and publication date. The only case when an unjustified emendation can replace an original spelling is a prevailing usage of the emendation (ICZN, art. 33.2.3.1.). This is not the case with *Labidostomma*: the original spelling has also been in use since at least 1942 (Grandjean 1942a, b), albeit inconsistently so (see the References). Thus, *Labidostoma* Oudemans, 1904 is a junior objective synonym of *Labidostomma* Kramer, 1879, and we are bound to use the original spelling.

The family-group containing *Labidostomma* has two names: Nicoletiellidae Canestrini, 1891, derived from *Nicoletiella* Canestrini et Fanzago, 1882, which is a junior objective synonym of *Labidostomma* Kramer, 1879 on the genus level (see Oudemans 1904), and Labidostomidae Oudemans, 1904, which has appeared as Labidostomidae, Labidostommidae, Labidostomatidae, and Labidostommatidae. The name Nicoletiellidae must be abandoned (ICZN, art. 40.2), since it was replaced with the name Labidostomidae before 1961, and since the latter name (with variable spellings) is used prevalently (see References). The family-group name proposed by Oudemans is thus to be used, but not in the original spelling: (1) as this name was derived from the unjustified emendation (see above), it is to be corrected to derive from the type genus name in its original spelling (ICZN art. 35.4.1.); (2) as the stem of this name was originally found not in accordance with the ICZN art. 29.3. (genitive singular of "*στομα*" is "*στοματος*", the stem is "*στοματ-*"), and as it was changed to comply with that article before 1999 (Krantz 1978, p. 233), the version with the correctly found stem is to be used.

Thus, in accordance with ICZN rules, the genus name *Labidostomma* Kramer 1879, the family group category names Labidostommatinae, Labidostomatidae, Labidostommatoidea, and the higher category (supercohort or infraorder) names Labidostommatides or Labidostomatina shall be utilized in this treatment.

MATERIALS AND METHODS

The literature on description and illustration of the palpus of various labidostomatid mites was thoroughly reviewed. Originally studied material included slide preparations of the three nymphal instars and adults of a variety of Labidostommatidae in the Canadian National Collection of Insects and Arachnids. The following data are for a few CNC specimens of special interest to this paper: *Labidostomma* sp. aff. *nepalense* Feider & Vasiliu: Nepal, Kathmandu: one female, Pulchauki, 8000' [ca. 2440 m a.s.l.], 13-VIII-1967, ex forest litter; two females, Godavari, 6000' [ca. 1830 m a.s.l.], 5-VIII-1967, ex dead leaves; two females, Godavari, 5000' [ca. 1525 m a.s.l.], 13-VIII-1967, ex leaf litter. *Labidostomma* sp.: USA, Virginia, Grayson County, Hwy 603 at Fox Creek, 6 km. W. Troutdale, 5-August-1986, coll. E.E. Lindquist, ex mixed deciduous litter, primarily oak and rhododendron. Some reared, slide-mounted material, including four larvae and three protonymphs, without data other than code numbers 92-14 and 92-15, was located and made available from the Field Museum of Natural History, Chicago.

Observations and draft line illustrations of the material were made with compound microscopes equipped with Nomarsky differential interference contrast (DIC) optical systems and drawing tubes. Drawings of slide-prepared mite specimens were finished with the aid of InkScape (v. 0.48 r9654). Stacks of images of those specimens were obtained with a digital camera (Leica DFC420) mounted on a Leica DM5500 microscope under DIC, and combined using Helicon Focus Pro 5.0 (Helicon Soft Ltd.). Drawings of the fossils were made by outlining the video feed from an AmScope (Irvine, California, USA) MU900 digital camera in InkScape (Sidorchuk & Vorontsov 2014).

Notation for palpal setae follows that of Grandjean (1940). In this presentation, we limit usage of 'segment' for a presumed primary or fundamental subdivision of an appendage, equivalent to a podite or podomere or palpomere, and 'article' for a secondary subset, whether fused or subdivided, in general accord with Snodgrass (1952) and (Evans 1992); however, we follow the common usage of

'-segmented' as used in the same references, among others.

HISTORICAL OVERVIEW AND BACKGROUND

Among trombidiform mites, articulation between the infracapitulum wall and the trochanter of the palpus is plesiomorphically a rocking joint, with one dorsal condyle and apposing cotyle; movement takes place along the longitudinal axis of the limb, with the 'rock' occurring alternately, in opposite dorsal-ventral directions, activated by two sets of antagonistic (depressor and levator) muscles originating in the infracapitulum and inserting, respectively, on the ventral and dorsal surfaces of the base of the trochanter (Alberti and Coons 1999). Articulations between the femur and genu, the genu and tibia, and the tibia and tarsus are not condylar, but rather are 'hinge joints', flexible bands in the dorsal cuticle, and pliable arthrodistal cuticle on the ventral side, such that the distal palpomere may be moved in the vertical plane by flexor (depressor) muscles and extended by hydrostatic pressure (levators are absent) (Alberti and Coons 1999, and references therein). In contrast, there is no articulation between the palpal trochanter and femur; even if formed as separate segments, they have no independent movement, with no condyle or hinge joint or pliable cuticle between them (Evans 1992, Alberti and Coons 1999).

As indicated above, a four-segmented palpus of many prostigmatic mites is interpreted to present a femorogenu, as noted by Grandjean (1938b) for the Tydeidae, with the compound segment bearing two, well-separated, dorsal setae. The proximal seta is from a femoral verticil, the distal one from a genual verticil, with the rationale that a single, basic verticil of five setae only includes one, unpaired, dorsal seta (Grandjean 1940). Subsequently, Grandjean (1946) again referred to this femorogenualescence, indicating members of the Labidostommatidae, Eupodidae, Ereyneidae and Tydeidae as examples, and noting the absence of a second (either ventral or lateral) femoral seta on the larva. Grandjean (1946) also noted that, ontogenetically,

the "poil inferieure", or ventral seta, of the palpal femur primitively is postlarval; the larval article is either nude or has one dorsal seta. As mentioned above, Grandjean (1933, 1943) noted that the palptrochanter is always glabrous. However, in seeming contradiction to this pattern, among his studies of the Labidostommatidae, Grandjean (1942a, 1942b) had earlier noted that the basal article of the four-segmented palpus lacked a seta on the larva, but that a ventral one is added on the protonymph, referring to that article as the trochanter (see his Figs 1B, 2C in those papers, respectively).

Subsequent to Grandjean's studies, the identity or construction of the palpal articles (other than the tarsus) in Labidostommatidae was not considered by many authors (e.g., Atyeo and Crossley 1961, Robaux 1977, Bloszyk 1980, and some of the papers by Bertrand and collaborators). Evans (1992) described labidostommatids as having linear palps with four articles, leaving them unnamed. Feider and Vasiliu (1968b) referred to the articles as fémuro-trochanter, genu, tibia, tarsus in their description of *Labidostomma nepalense*, but as femur, genu, tibia, tarsus in that of *Nicoletiella asiatica* (Feider and Vasiliu 1972). In describing nymphs of *Nicoletiella denticulata* (Schrank) and *Eunicolina tuberculata* Berlese, Vistorin (1980b) referred to the palptrochanter, palpfemur, and palptarsus, without naming the penultimate article. Bertrand (1982b) referred to femorogenu, tibia, and tarsus (without naming the proximal article), but later, in his unpublished thesis (Bertrand 1988), he briefly considered the genuotibia as an alternate hypothesis to the femorogenu in segmental coalescence of the labidostommatid palpus, but left this unsettled, with lack of evidence from the reduced chaetome. The first time this interpretation was published seems to have been by Bertrand and Corpuz Raros (1997), who named the penultimate article of the palpus "genuo-tibia", without further comment. Thereafter, labidostommatids were noted by Walter *et al.* (2009) as having a four-segmented palpus "with an unusual fusion of the genu and tibia". However, in descriptions of fossil labidostommatid mites, Dunlop and Bertrand (2011) continued to refer to the penultimate palpal

article as the tibia, while Sidorchuk and Bertrand (2013) referred to the "genu-tibial article" of the palpus, and even distinguished tibial from genual setae on that article in *Labidostomma (Pseudocornutella) electri* Sidorchuk and Bertrand. Whether or not correct, the notion of a coalesced genuotibia has brought attention to this and other palpal characteristics of the Labidostommatidae that until now have not been adequately considered.

OBSERVATIONS

Segmental shapes and articulations

In material available for our study, the form of the palpal articles and their phaneres are closely similar to Grandjean's above-noted illustrations of a larva and adult. Larval labidostommatids are elatostatic (Grandjean 1942b), and have little or no cuticular ornamentation on the surfaces of their bodies and appendages. The basal/proximal palpal article is nude but relatively well developed, cylindrical, nearly as long as wide, without any subsurface indication of subdivision, and about 0.8 as long as the next (second) article. However, there is slight evidence of a weak 'sheath' or sleeve enveloping the base of the cylindrical proximal article of the larvae at hand (Figs 1A, 2A, arrows). The second, third, and apical articles are similar in lengths, none of them showing any break along the length of the segmental wall. The palpi of nymphal instars of any one of our studied labidostommatid species are closely similar to one another, usually with identical form, relative lengths and setation, other than slight gradation in general length, apart from incremental growth of each instar. In contrast to the larva, the cuticular surfaces of nymphal palpi are usually conspicuously striated transversely, and the second and third articles are relatively longer than the basal and apical ones; although the palpal phaneres are more strongly developed, they usually are the same in number, except for the constant addition of a ventral seta on the proximal article in the protonymph (Figs 1A, B; 2A, B). However, the basal article of postlarval instars differs considerably in form from the larval condition: it is inserted in, and slightly enveloped by, a basal annulus devoid of surface pat-

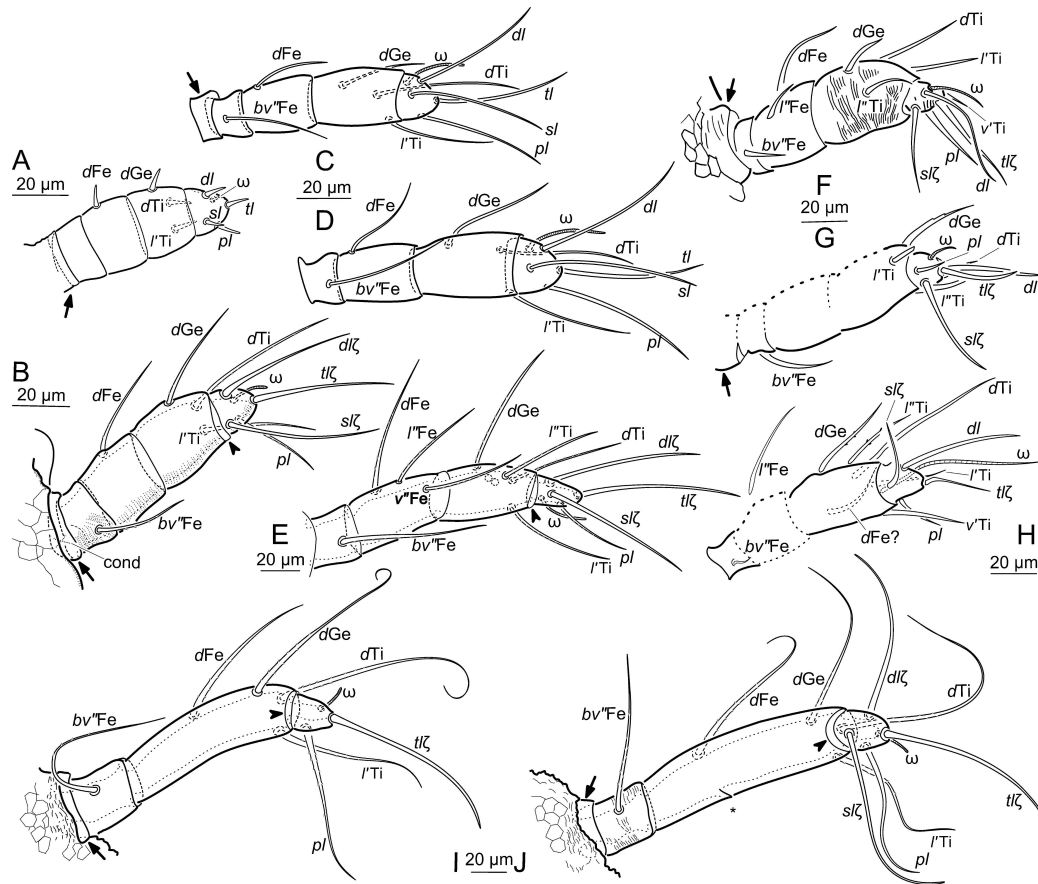


FIGURE 1: Examples of shapes and setations of palpi in Labidostomatidae immatures (A-C) and adults (D-J); arrows point to supposed trochanter or its remnant when present, arrowheads point to areas of arthrodial cuticle at articulations: A — unidentified larva (Field Museum 92-15), ventrolateral view; B — unidentified protonymph (Field Museum 92-14), ventrolateral view; C, D — *Eunicolina nova* Sellnick sensu Feider & Vasiliu, ventral views (modified from Feider & Vasiliu 1968a, Figs 18, 19); C — tritonymph, D — adult female; E — *Labidostomma* sp. aff. *nepalense* Feider & Vasiliu, adult female, ventral view. Note: femoral seta *v''* is variable: unilaterally present in 1 specimen (Pulchauki, 2440 m a.s.l.) absent in other 4 (Godavari, 2 from 1830 m, 2 from 1525 m a.s.l.), position of tibial seta *l''* is variable (observed positions shown with dotted circles); F-H — Baltic amber fossils of *Labidostomma* (*Pseudocornutella*) *electri* Sidorchuk & Bertrand, adult females (modified from Sidorchuk & Bertrand 2013, Figs 3E, G): F — MGCP-Ar 294, right palpus, lateral antiaxial view, G — same as F, left palpus, lateral paraxial view, H — MGCP Ar-97, right palpus, ventral view (modified from Sidorchuk & Bertrand 2013, Fig. 3G); I, J — *Labidostomma* sp. (USA, Virginia), adult female, ventral views of asymmetrically developed palpi: I — right, J — left, asterisk indicates a trace of incomplete femorogenual coalescence.

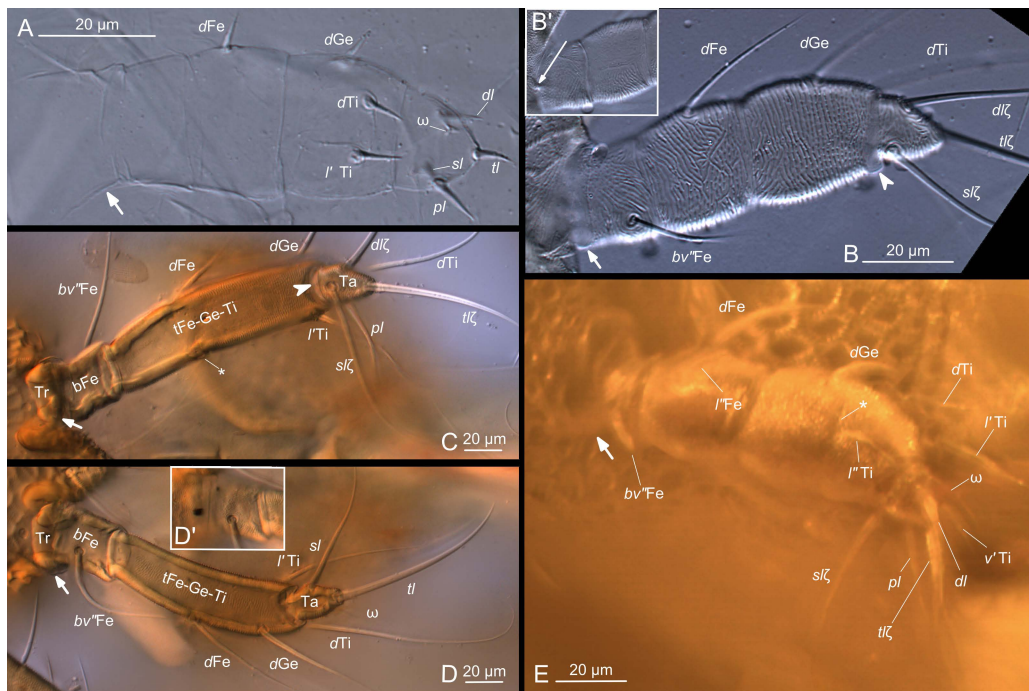


FIGURE 2: Labidostommatid palpi, DIC (A-D) and combined incident and brightfield (E), montaged light micrographs. Only some phaneres, depending on the focus, are labeled. Large arrows point to trochanter or its remnant, arrowheads—to areas of arthrodistal cuticle at articulations: A — unidentified larva (Field Museum 92-15), combined from 14 focal planes (f.p.-s); B — unidentified PN, Field Museum 92-14, 3 f.p.-s; B' — same as B, other 3 f.p.-s, showing dorsal condylo-cotyler articulation at base of palp (thin arrow) and its two proximal articles (note absence of hinges or condyles between them); C, D — *Labidostomma* sp. (USA, Virginia), adult female, ventral view of asymmetrically developed palpi: C — left, asterisk indicates a trace of incomplete femorogenuital coalescence, 15 f.p.-s, D — right, with that coalescence complete, 15 f.p.-s; D' — same as D, other 3 f.p.-s, showing pliable cuticle at proximal and distal articulations of basifemur; E — Baltic amber fossil of *Labidostomma (Pseudocornutella) electri* Sidorchuk & Bertrand, MGCP Ar-294, adult female, setal homologies partly reinterpreted, asterisk indicates a trace of incomplete genuotibial coalescence, 62 f.p.-s.

tern (striae). The annulus in turn is enveloped by strongly ornamented margins of the surrounding infracapitulum (Figs 2B-E).

The palpal articles we have observed typically show no break or change in form along the length of the segmental walls (Figs 1A, B, E, I). In two instances, however, traces of coalescence are present: one, in a form of a partly interrupted segmental wall of an extant, possibly aberrant, specimen (Figs 1J, 2C, asterisks) and one, in a fossil specimen, as a slight constriction and change in cuticular pattern (Fig. 2E, asterisk).

To some extent, the postlarval palpus of labidostomatids conforms with the basic pattern of articulation noted above. That between the infracapitulum and base of the palpus is monocondylar, with a well-developed, dorsal, infracapitular condyle apposing a basal cotyle of the proximal article (Fig. 2B'); this articulation is clear only in partially dissected specimens, and otherwise is obfuscated by enveloping walls of the strongly sclerotized infracapitulum. Notably, the cotyle is located dorsally at the very base of the first article, where the annulus 'blends' or merges with it; the annulus is slightly larger in diameter, ventrally and laterally, than the base of the first article, but appears to mold into the article dorsally (compare Figs 2B, B'). As the cotyle derives plesiomorphically from the trochanter, this condition suggests a coalescence of the trochanter and femur. Significantly, the labidostomatid palpus shows no external indication of a condyle or hinge opposite a strip of transverse soft arthrodial cuticle at the articulation between the first and second article. Such immobility is typical of a joint between the palpal trochanter and femur, but also of one between the elements of a bipartite femur (Grandjean 1954). While the hinge between the third and fourth (apical) articles is typical and dorsal, with the soft arthrodial cuticle ventral (arrowheads on Figs 1, 2), the extent of articulation between the second and third articles is less evident, since a band of soft cuticle is not readily discernible. Also, a rigid condition may be preliminary to a femurogenual fusion, which is common among a variety of early derivative prostigmatans (i.e., Eupodoidea). In this regard, we have ob-

served one adult female of an undetermined species of *Labidostomma* showing palpi asymmetrically with fully and partly coalesced second and third articles, to form an elongate femoro-genuo-tibial article between the short basal and distal articles (Figs 1I, J; 2C, D). The chaetotaxy of one palp is of the prevalent number and position (see below), thus 1-1+3-4, while that of the opposing palp is reduced by two setae, thus 1-1+3-2. In the absence of this form of palpus having been noted previously, either in mites from the same substrate frequently sampled in the Appalachians of the USA (see Materials and Methods), or elsewhere, we cannot exclude the possibility of this individual mite being an aberration.

Setation

The prevalent palpal setation of labidostomatid mites, from proximal to apical article, is 1-1-3-4 (+ solenidion), with the seta on the basal article being protonymphal (Grandjean 1942b, Vistorin 1980b; our Table 1, Figs 1, 2). Although the solenidion was shown by Grandjean to be postlarval (1942b, his Fig. 2C), all four of the larvae at hand have a tiny solenidion (Figs 1A, 2A), which will not be further considered here. Setation of the proximal article is constant, while that of the terminal article may be nearly so, with *Labidostomma asiatica* Feider & Vasiliu being the only exception documented in having one less seta (Table 1). Although Feider and Vasiliu (1969) characterized their genera *Atyeonella*, with six species, and *Sellnickiella*, with five species, as having three palptarsal setae (plus a solenidion), the palpal setation of all species included in those taxa remains undocumented by illustration or specific description. Also, the indication by Feider and Vasiliu (1969), repeated by Robaux (1977), of eight setae on the palpal tarsus of their proposed monobasic genus *Grandjeanellina* (Feider & Vasiliu 1968a) is not substantiated by the original description of the adult female of the type-species, *Eunicolina nova*, by Sellnick (1931), or by Feider and Vasiliu (1968a) who illustrated and specifically stated the typical four setae (and one solenidion) in their subsequent description of all postlarval instars of that species under the name *Grandjeanellina nova* (Sellnick). In contrast, the second and third articles show

TABLE 1: Palp setation in Labidostommatidae.

setal formula*	species, life instar	reference
0-1-3-4 (no solenidion)	<i>Labidostomma luteum</i> Kramer, 1879, L	Grandjean 1942b
0-1-3-4	Labidostommatid L (4 specimens), Field Museum 92-15	new observations
1-1-2-4	<i>Nicoletiella romanica</i> Feider & Vasiliu, 1968c, AD	Feider & Vasiliu 1968c
1-1-3-3	<i>Nicoletiella asiatica</i> Feider & Vasiliu, 1972, AD	Feider & Vasiliu 1972
1-1-3-4	prevalent postlarval chaetotaxy, for examples: <i>L. luteum</i> Kramer, 1879, PN-AD <i>L. nepalense</i> Feider & Vasiliu 1968b, PN Labidostommatid Field Museum 92-14, PN <i>Nicoletiella denticulata</i> (Schrank), nymph <i>Eumicolina nova</i> Sellnick, 1931 TN, AD <i>E. tuberculata</i> Berlese, 1911, AD <i>L. vialeae</i> Bertrand, 1982, AD <i>Sellnickiella balticae</i> Sidorchuk & Bertrand, 2013, AD	Grandjean 1942b; Vistorin 1980b; Sellnick 1931; Feider & Vasiliu 1968a, b; Bertrand 1982; Sidorchuk & Bertrand 2013; new observations
1-2-3-4	<i>Mahunkiella multisetosa</i> (Shiba, 1969), AD <i>M. coreana</i> Feider & Vasiliu 1972	Feider & Vasiliu 1972
1-2-3-4	<i>L. nepalense</i> Feider & Vasiliu 1968b, TN	Feider & Vasiliu 1968b
1-3-3-4	<i>L. nepalense</i> Feider & Vasiliu 1968b, AD	Feider & Vasiliu 1968b
1-2-5-4	<i>L. corsicum</i> Bertrand, 1982a PN-AD	Bertrand 1982b
1-2 to 3-4-4	<i>Labidostomma</i> sp. aff. <i>nepalense</i> , AD	new observations
1-2-6-4 (or 1-2-5-4?)	<i>L. (Pseudocornutella) electri</i> Sidorchuk & Bertrand, 2013	Sidorchuk & Bertrand 2013; new observations

* from proximal segment to distal, constantly present tarsal solenidion omitted

considerable variability, as follows.

Second article — Generally, the larva and protonymph present the typical, full complement of one seta (d), with no further ontogenetic additions (Grandjean 1942b, Vistorin 1980b). Exceptionally, one seta (l'') may be added in the deuto- or tritonymph, and another one (v'') in the adult of *Labidostomma nepalense* Feider & Vasiliu (Table 1). Of these additional setae, we have observed l'' to be also consistently present among five adults of *Labidostomma* sp. aff. *nepalense*), while v'' is asymmetrically present in one of those females (Fig. 1E).

Third article — According to observations in literature, this article shows the greatest variability, with up to 6 setae being present (see Table 1). The three setae in common are generally interpreted as tibial d , l' and v' (Bertrand 1982b). When a fourth seta is present, it occupies a lateral antiaxial position (Figs 2E, F, H). Five setae are known only in one modern species, *Labidostomma corsicum* Bertrand, beginning with the protonymph (Bertrand 1982a).

Bertrand (1982b) regarded this condition as a plesiomorphic retention of a complete verticil of setae, d, l', l'', v', v'' .

The richest complement, six setae, has been reported from Eocene Baltic amber fossils of *Labidostomma (Pseudocornutella) electri* (Sidorchuk & Bertrand 2013, their Fig. 4). However, this formula was inferred from a group of specimens, where several palps clearly had two setae on the second article and five on the third, but only one had six setae attributable to it (specimen MGCP Ar-97, their Fig. 4G). This is possibly an asymmetrical variant with an additional seta on one palpus, similar to that noted above for the second article of *Labidostomma* sp. aff. *nepalense*. Alternatively, as the specimen does not show the second article well, and as the seta labeled Ge2 on Sidorchuk and Bertrand's Fig. 4G does not clearly show an alveolus, it is possibly of femoral origin (our Fig. 1H), such that the setal formula may be 1-2-5-4 as in *L. corsicum* Bertrand 1982a, rather than the interpreted 1-2-6-4.

Also, the seta labeled Ge1 in their figure may be of tibial rather than genual origin, and we think it may be possible to homologize the other setae on these palpi, see Figs 1F–H, 2E. One of us (E.A.S.) restudied the type series of *L. electri* with improved optics, but failed to obtain any additional information: uncertainty is caused by imperfect preservation and the positions of the fossil specimens, and the question remains, pending finds of further ones.

Interpretations: Palpal article coalescence alternatives in Labidostommatidae

Palpal tibiotarsus — A fused tibiotarsus (leaving separate trochanter, femur, genu), is not supported by chaetome attributes or by number of setae on the apical segment of labidostommatids. Although a fused tibiotarsus is encountered among some families of free-living Prostigmata, these are among more derivative members of the Eleutherengona. None of the relatively early-derivative families of trombidiform mites with linear palpi presents such a palpal form, and the palpal tarsus maintains its integrity (Grandjean 1954). The argument presented by Atyeo (1960) for a fused tibiotarsus in Bdellidae and Cunaxidae is not supported by general muscular or chaetome patterns of the palpal segments for the Prostigmata. Also, the interpretation by Zacharda (1980) of the four-segmented palpus in Rhagidiidae having a fused tibiotarsus is not supported by evidence, and their palpus was subsequently viewed as having a fused femorogenu (Lindquist and Zacharda 1987, Baker 1990).

Palpal genuotibia — Coalescence of the palpal genu and tibia (in the absence of fusion among other segments) is otherwise unknown among acariform mites. So unique a fusion may seem questionable, but there are morphological and chaetotactic indications that it may have occurred. The third palpal article in Labidostommatidae is not distinguished by particularly greater length, by any break along length of the segmental wall, or generally by any surface pattern differentiation. However, an antiaxial line breaks the ornamentation of that article about its mid-length in the fossil *Labidostomma electri* (Fig. 2E, asterisk). The chaetotaxy of this article (from three to five setae among extant species)

can be attributed to one verticil, in the absence of evidence of more than one seta being inserted in a clearly dorsal position. However, the clearly dorsal seta is usually inserted at mid-level, more proximally than other setae on the third article (Figs 1, 2). When more than three setae are present, the lateral antiaxial seta also may be quite proximal, as in *L. corsicum* Bertrand (his 1982b, Fig. 2b) and in *L.(P.) electri* Sidorchuk & Bertrand (their Figs 3E, 4D; our Figs 1F, H, 2E). The lateral antiaxial seta, however, is variably more distal in our specimens of *Labidostomma* sp. aff. *nepalense* (Fig. 1E). A similar difference in position also is common on the palpal tibia among the families of related eupodoid mites (Baker 1990, Fig. 4a). This difference in insertion is insignificant in the labidostommatid larval instar (Figs 1A, 2A). A genuotibial coalescence becomes more convincing if one of the more distal setae may be interpreted as dorsal (as one of the tibial setae could be). The seta usually otherwise denoted as *l'* is a possible contender, partly because of its dorso-lateral insertion and partly because of the anterolateral 'twist' of the dorsal surface apically, from the second to the fourth articles (see Figs 1, 2).

Palpal femorogenu — A coalescence of the palpal femur and genu, as noted by Grandjean (1946), would not be surprising in that this consolidation has been commonly observed among a variety of trombidiform mites. Yet, based on our observations, this hypothesis does not seem to be supported by morphological evidence among labidostommatid mites. The second article is not distinguished by particularly greater length, or by any break along the length of the segmental wall, or by any surface pattern differentiation. Its nearly invariant chaetotaxy, usually of one dorsal seta (if another seta or two are present, they are not dorsal), provides no indication of a second verticil of setae.

Palpal femoral consolidation — The coalescence of a primitively bipartite basi- and telo-femur into an entire femur is in accord with the generalization by Grandjean (1954), that the palpal femur is always entire among acariform mites: "Je ne connais aucun exemple, chez les Acariens actinochitineux, de fémur palprien divisé". However, are labidostommatids exceptional? Their legs have tripartite

femora, in which partition is postlarval (Grandjean 1942b, 1954); perhaps a divided palpfemur may be serially correlated with divided leg femora. A single dorsal seta on the palp (telo)femur of the larva, followed ontogenetically by a single ventroproximal seta on the palp (basi)femur, may support this notion, in that the basal part of the palpal femur may often have a postlarval seta. Nevertheless, a bipartition of the palpal femur is in itself so unique among acariform mites as to initiate doubt about this interpretation. For example, the basic palpal configuration of bdellid and cunaxid mites was interpreted by Atyeo (1960) to include an incomplete division between a long basifemur and short telofemur. However, the basal part of such subdivided segments of legs and palpi of acariform mites (including labidostommatids) is typically of short to moderate length (Alberti and Coons 1999), and Grandjean (1938a) viewed the same bdellid structures as a long, entire femur and a short, immovable genu. The latter immobility would accord with a frequent tendency towards femorogenual consolidation (see above).

Palpal trochantero-femur — An interpretation in general accord with that of Feider and Vasiliu (1968a, 1968b, 1972) is the ontogenetic reduction of the true trochanter in adulthood, leaving the femur, genu, tibia, and tarsus as intact, articulating elements. This point of view was based on the ontogeny of palpal structure in *Eunicolina* (= *Grandjeanellina*) *nova* (Sellnick), in which they (Feider and Vasiliu 1968a) noted and illustrated *five* articles, including a nude trochanter basally, on each of the three nymphal instars, and four articles with a coalesced "fémuro-trochanter" in adults, the basal article having the ventral seta previously on the femur (their Figs 16-18, our Fig. 1C). Like those of Vistorin (1980b), our observations of the palpus of all nymphal instar and adult examples of a variety of labidostommatids do not indicate such differences between nymphs and adults. However, material of *E. nova* was not available for study.

Palptrochanter subsumption — In this interpretation, the trochanter of the palpus becomes diminished and integrated into the annulus at the base of the palpus, rather than being integrated with

the femur. Although the observations of *Eunicolina nova* by Feider and Vasiliu (1968a) noted above for nymphs (in distinction to adults) may be used to support this viewpoint, such postlarval ontogenetic distinction of the basal structure of the palpi has not been supported by our observations or those of other authors, on other species of labidostommatids. However, a small, unornamented basal ring-like structure may be readily visible on postlarval instars, especially in dorsal view. It is, at most, half as long as wide, devoid of setae, much as illustrated in figures 1B and 3B by Grandjean (1942a), 12 by Feider et al. (1975), 4C by Bertrand (1982a), in the striking SEM fig. 2 by Vistorin (1980a), and in some of our specimens (large arrows in our Figs 1, 2). Apart from the case of a possibly aberrant adult with three-segmented palps, where the ring-like structure looks like a more fully formed segment (Figs 2C, D), it appears to be an annulus around the base of the palpus rather than a basal article of the palpus itself, and it may be as well developed in adults as in the nymphal instars (Figs 1B, F, J; 2B, E). A similar basal annulus is not shown in Grandjean's figure of the labidostommatid larva, and it is not discernible on the larvae at hand (Figs 1A, 2A). However, may the basal sheath we have observed in the larva be subsumed into the annulus in postlarval instars?

Concomitant coalescences — This interpretation would involve three simultaneous or consequential conditions: subsumption of the palptrochanter, retention of a bipartite femur, and genuotibial coalescence. If the first two conditions have been met, then coalescence of the genu and tibia follows (logically, if not consequentially), to account for the constitution of the third article. Each of these three conditions is singular among modifications of the primitively linear, five-segmented palpus of acariform mites.

DISCUSSION

The notion, that the first, well-formed article of the postlarval labidostommatid palpus may be part (or all) of the femur (whether the trochanter is incorporated, as a "fémuro-trochanter" or is subsumed

into a basal annulus), is supported by two series of observations. First, the protonymphal addition of a basiventral seta is typical of the palpfemur in oribatid, various endeostigmatic, and bdellid mites (Grandjean 1937, 1938a, b, 1946). Second, as noted above, the labidostommatid palpus shows no external indication of articulation (condyle, hinge, soft arthroal cuticle) between the first and second articles. Although a lack of independent movement is typical between the palpal trochanter and femur among free-living prostigmatic mites with palpal articles delineated, it is also typical of a bipartite femur (Evans 1992, Alberti and Coons 1999, see above background).

Alternative significances of article coalescences and the basiventral seta of the labidostommatid palpus

Palpal genuotibia — If the coalescence of two palpal segments is demonstrably genuotibial, rather than any of the other options considered above, that attribute would not necessarily be correlated with the trochanter and its seta, but in itself would appear to be uniquely apomorphic among the Acariformes, in the absence of other apparent coalescences or reductions.

Palpfemoral bipartition — If the labidostommatid palpal configuration actually includes retention of a bipartite femur, this would be a remarkably plesiomorphic exception to Grandjean's generalization (1954), all the more so if combined with apomorphic coalescences of a genuotibia and subsumed trochanter. Among acariform mites, there is no evidence of a secondary regression to bipartition from an entire state (Grandjean 1954); and this condition would be further unlikely, in view of reductions of other palpal segments by subsumption or coalescence.

Palpal trochantero-femur — If fine structure indicates that the proximal articulating article is actually a coalesced trochantero-femur, then the Labidostommatidae may be characterized by that unique coalescence, which is otherwise not found among prostigmatans retaining a linear four-segmented palpus, as well as by the apomorphic presence of a single, postlarval (protonymphal),

ventral femoral seta (instead of a plesiomorphic, fundamental larval, dorsal femoral seta) on that segment.

Palpal trochanter — If the proximal articulating article of the labidostommatid palpus is truly the trochanter, then the family Labidostommatidae is uniquely characterized by the presence of a post-larval (protonymphal) ventral seta on that segment. This attribute would be arguably autapomorphic, in not being found among other early-derivative members of the Acariformes (both Trombidiformes and Sarcoptiformes).

An unlikely possibility is that the basal article is a trochanter that bears a displaced femoral seta. We are not aware of such setal displacements or transpositions on palpomeres, or even on the legs among other prostigmatans or, for that matter, among acariform mites in general (although some rare examples of a transposed solenidion on the legs are known).

The palpal structure of the relatively early derivative aquatic superfamily Halacaroidea is noteworthy in that adult females of the monogeneric family Pezidae are presented as having a palpal 'trochanter' with a dorsal seta, followed by an elongated article with eight setae, then a 'genu' with four or five setae, and an apical, short 'tibiotalar' with four to six setae (Harvey 1990). No rationale was presented as to why the four-segmented condition of the palpus involves a coalesced tibiotarsus instead of another segmental coalescence. Further, no attempt was made to identify palpal setae based on verticil aspects. Larval material was not available, and setation of the protonymphal palpus was not presented. In any case, the condition in Pezidae involves a clearly dorsal seta on the basal palpomere, rather than the ventral seta on that palpomere of postlarval instars of labidostommatids.

CONCLUSIONS

Whether apomorphies or plesiomorphies, a resolution of issues concerning the labidostommatid palpus is relevant to further defining the Labidostommatidae. These observations may also stimulate

reviews of palpal structure among other basal lineages of trombidiform mites, which in turn may test several of the generalities of Grandjean. While our observations support Grandjean's positions of the palptrochanter being consistently nude and the palptarsus maintaining its integrity, they may present an exception to the palpfemur being entire. Until fine structure and embryogenetic studies can provide additional data, an interpretation of the palpal article configuration in Labidostomatidae as being an extraordinary combination of apomorphic subsumption of the trochanter, autapomorphic coalescence of the genu and tibia, and 'autopleiomorphic' retention of a bipartite femur, seems persuasive and challenging.

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