# Cladoendesis of Parametabola and Systematic Position of the Extinct Taxon Tetrastigmoptera taxon nov.

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**Abstract**—A new circumscriptional name Tetrastigmoptera **taxon n.** is suggested for the extinct taxon comprising the Cretaceous species *Mydiognathus eviohlhoffae* Yoshizawa et Lienhard, 2016 (= *Psocorrhyncha burmitica* Huang et al., 2016) and *Burmopsylla maculata* Liang et al., 2016, described based on well-preserved specimens from Burmese amber, and also some Triassic and Permian species known by less completely preserved specimens. This taxon is known under the typified names Permopsocida and Archipsyllidae. The systematic position of Tetrastigmoptera remains unclear. The formerly expressed opinions about this taxon belonging to Acercaria and about its relationship with Copeognatha and/or Condylognatha are erroneous, caused by wrong notion about the structure of recent insects. The structure and assumed function of the mouth apparatus of Copeognatha, which basically differs from that of Tetrastigmoptera and other chewing insects, is discussed. The phylogenetic significance of such characters as bimotority, presence of tibial spurs, number of tarsomeres, presence of cerci, and some others is discussed. It is demonstrated yet again that the parsimony principle and the taxon/character matrices are totally inconsistent with phylogenetic analysis.

In my book *Insect Systematics and the Principles of Cladoendesis*, soon to be published by the KMK Scientific Press (Kluge, in print), I propose a phylogenetic system of insects mainly based on the morphological and ontogenetic features of recent insects. Most of the extinct taxa are not covered in the book since many characters important for understanding their taxonomic position remain unknown.

One of such taxa is usually considered within the order of psocids (Copeognatha Enderlein, 1903 = Psocoptera Shipley, 1904), either as the suborder Permopsocida Tillyard, 1926 or as the family Archipsyllidae Handlirsch, 1906. Until recently this taxon has been known only by the Permian, Triassic, and Jurassic fossils some of which reveal not only wing venation but also the body shape and leg morphology. More detailed descriptions of two species from this taxon were recently published based on well-preserved inclusions in the Late Cretaceous Burmese amber. One of these species was described twice in 2016, first as *Mydiognathus*

*eviohlhoffae* Yoshizawa et Lienhard, 2016 (= "*Dolichognathus*" nomen nudum) and then, by a team of 17 authors, under the name *Psocorrhyncha burmitica* Huang et al., 2016. The other species described from the Burmese amber is *Burmopsylla maculata* Liang, Zhang et Liu, 2016.

All the authors who described these species from the Burmese amber made the same conclusion that the taxon in question (referred to as Permopsocida and Archipsyllidae) was a sister or an ancestral taxon to Condylognatha, i.e., an intermediate element in the evolutionary lineage from insects with chewing mouthparts to those with a suctorial proboscis (Arthroidignatha, or "Hemiptera"). Correspondingly, they established the taxon Pancondylognatha Yoshizawa et Lienhard, 2016, uniting Archipsyllidae and Condylognatha. To confirm this phylogenetic conclusion, the authors of two papers (Huang et al., 2016; Yoshizawa and Lienhard, 2016) independently performed so called "phylogenetic" analyses using parsimony (PAUP) with arbitrary sets of

characters for arbitrary sets of taxa. Most of the characters selected by these authors were described incorrectly (see section 6); however, even if the correct characters of all the included taxa were used, parsimony-based computations would not prove any statement because the parsimony principle in itself clearly contradicts the theory of evolution (Kluge, 2000).

Thus, opinions about the taxonomic position of this extinct taxon vary from its placement in Copeognatha to convergence with Condylognatha; in both cases the taxon is considered within Acercaria that unite Copeognatha and Condylognatha.

For the taxon currently known under the controversial typified names "Permopsocida" or "Archipsyllidae," I propose a new circumscriptional name Tetrastigmoptera (see section 2). As opposed to phylogenetic analysis based on parsimony and a taxon/character matrix, cladoendesis does not use separate arbitrarily selected facts but unites into a single theory all the known facts relevant to understanding phylogeny. This approach has demonstrated the incorrectness of placement of Tetrastigmoptera in Acercaria (see section 4).

This paper includes the following sections:

The illustrations (Figs. 1–10) were borrowed from my new book *Insect Systematics and the Principles of Cladoendesis* (Kluge, in print).

# 1. CLASSIFICATION AND NOMENCLATURE

In this paper I use the same classification of insects as in my soon-to-be-published book *Insect Systematics and the Principles of Cladoendesis*. The system of Parametabola and the names of higher taxa are as follows (Kluge, 2010, 2012).

1. **Neoptera** Martynov, 1923
1.1. **Idioprothoraca** Kluge, 2012
1.2. **Rhipineoptera** Kluge, 2012
1.3. **Eumetabola** Hennig, 1953
1.3.1. **Parametabola** Crampton, 1938 (= Paraneoptera Martynov, 1923 sensu Martynov, 1938)
1.3.1.1. **Zoraptera** Silvestri, 1913
1.3.1.2. **Acercaria** Börner, 1904 (= Paraneoptera Martynov, 1923 sensu auct.)
1.3.1.2.1. **Panpsocoptera** Crampton, 1938
1.3.1.2.1.1. plesiomorphon **Parapsocida** Tillyard, 1926
1.3.1.2.1.2. **Eupsocida** Tillyard, 1926
1.3.1.2.1.3. **Parasita** Latreille, 1796 (= Anoplura Leach, 1815)
1.3.1.2.1.3.1. **Mallophaga** Nitzsch, 1818
1.3.1.2.1.3.2. **Siphunculata** Latreille, 1825
1.3.1.2.1.3.3. **Rhyncophthirina** Ferris, 1931
1.3.1.2.2. **Condylognatha** Börner, 1904 (= Hemiptera Linnaeus, 1758)
1.3.1.2.2.1. **Thysanoptera** Haliday, 1836
1.3.1.2.2.2. **Arthroidignatha** Spinola, 1850
1.3.1.2.2.2.1 **Hemelytrata** Fallén, 1829
1.3.1.2.2.2.1.1 **Auchenorrhyncha** Dumeril, 1805
1.3.1.2.2.2.1.1.1 **Euhomoptera** Crampton, 1916
1.3.1.2.2.2.1.1.2 **Subtericornes** Amyot et Serville, 1843
1.3.1.2.2.2.1.2 **Heteropteroidea** Schlee, 1969
1.3.1.2.2.2.1.2.1 **Coleorrhyncha** Myers et China, 1929
1.3.1.2.2.2.1.2.2 **Heteroptera** Latreille, 1810
1.3.1.2.2.2.2 **Plantisuga** Dumeril, 1805
1.3.1.2.2.2.2.1 **Psyllaleyroda** Kluge, 2010
1.3.1.2.2.2.2.1.1 **Saltipedes** Amyot et Serville, 1843
1.3.1.2.2.2.2.1.2 **Scytinelytra** Amyot et Serville, 1843
1.3.1.2.2.2.2.2 **Aphidococca** Kluge, 2010
1.3.1.2.2.2.2.2.1 **Gynaptera** Laporte, 1834
1.3.1.2.2.2.2.2.2 **Gallinsecta** De Geer, 1776
1.3.2. **Metabola** Burmeister, 1832

The taxonomic position of Zoraptera is a point of debate: some authors groundlessly consider them to be

close to certain taxa within Idioprothoraca or Rhipineoptera, whereas the morphology of zorapterans shows that they belong to Parametabola (Kluge, 2012).

This classification does not include the commonly accepted taxon Copeognatha Enderlein, 1903 (= Psocoptera Shipley, 1904), i.e., psocids. The taxon Copeognatha is a plesiomorphon ancestral to the holophyletic taxon Parasita; therefore its characteristic is the same as that of the higher taxon Panpsocoptera uniting Copeognatha and Parasita. Instead of the plesiomorphon Copeognatha, the system includes the holophyletic taxon Eupsocida and the plesiomorphon Parapsocida which appears to be ancestral to both Eupsocida and Parasita.

When only the recent insects are considered, the name Thysanoptera Haliday, 1836 fully corresponds by circumscription to the taxon uniting all the thrips, because the taxon Thysanoptera originally (Haliday, 1836) included the known members of the main phylogenetic lineages of thrips: Tubulifera, Stenelytra, and Coleoptrata. However, some extinct insects related to thrips were subsequently found which differ from the taxon uniting only the recent thrips. If these extinct insects are included in analysis, then, according to the rules of circumscriptional nomenclature (Kluge, 1999, 2010), the name Thysanoptera becomes non-monosemantic because it may be equally well assigned either to the taxon uniting thrips and the related taxa discovered after the publication of this name, or to a narrower taxon not including these newly found insects. In this case, in addition to the senior name non-monosemantically corresponding by circumscription to two or more taxa, it is also possible to use junior names monosemantically corresponding to each taxon. In my book *Insect Systematics and the Principles of Cladoendesis* I propose the following classification of thrips with provision for the extinct groups.

1. **Panphysapoda**, or **Thysanoptera** s. l.
1.1. †**Palaeophysapoda**
1.2. **Neothysanoptera**, or **Thysanoptera** s. str.

The taxon **Panphysapoda** Kluge (in print) is characterized by (1) an asymmetrical sucking mouth apparatus without the right mandible; (2) a vesicular arolium and the absence of claws; this is reflected in the name Physapoda Duneril, 1805, a senior synonym of Thysanoptera.

The taxon **Palaeophysapoda** Kluge (in print) comprises the following species known by well-preserved specimens from the Cretaceous ambers: *Jantardachus perfectus* Vishniakova, 1981, *Ja. reductus* Vishniakova, 1981 (the Upper Cretaceous of Taimyr), *Burmacypha longicornis* Zherichin, 2000 (the Upper Cretaceous of Myanmar), and *Moundthrips beatificus* Nel, Azar et Net, 2007 (the Lower Cretaceous of Lebanon) (Vishniakova, 1981; Zherikhin, 2000; Nel et al., 2007). It may also include some other insects described based on wings or impressions not showing the structure of mouthparts or pretarsus.

Here we should clarify some characters of *Jantardachus perfectus* and *Ja. reductus*. The type specimens (holotype of *Ja. perfectus*, holotype and paratype of *Ja. reductus*) are kept at the Paleontological Institute of the Russian Academy of Sciences (Moscow). The descriptions of the genus *Jantardachus* and the species *Ja. perfectus* and *Ja. reductus* mention the presence of both mandibles, curved maxillary laciniae, and a 4-segmented maxillary palp (Vishniakova, 1981: figs. 47*b*, 48*b*). I could not discern the inner stylets (mandibles and maxillae) in any of the three specimens, and it remains unknown whether these species possess both mandibles or only the left mandible, similar to the other known Panphysapoda. The maxillary palp has a large oval distal segment covered with fine setae; proximal to it there is only one visible segment (as in *Moundthrips beatificus*). Some other details mentioned and illustrated in the description are also not discernible in the specimens (Figs. 6, 7).

The taxon **Neothysanoptera** Kluge (in print) is characterized by (1) an opisthognathous head with antennae positioned at the anterior margin and (2) modified wings with no more than 2 veins looking as longitudinal and no more than 5 veins looking as transverse ones; at least the posterior wing margins bear a regular row of long setae (this is reflected in the name Thysanoptera Haliday, 1836).

In order to provide different names for Neothysanoptera and Panphysapoda, some authors use two different nomenclature systems: one non-typified (circumscriptional), the other typified. The circumscriptional name Thysanoptera is used for Neothysanoptera, and the typified name Thripida, for Panphysapoda (Nel et al., 2012). In the basic format the name Thripida appears as Thrips/fg [f: Thripsides Fallen, 1814; g: *Thrips* Linnaeus, 1758]. According to the rules of rank-based typified nomenclature for higher taxa developed by Rohdendorf

(1977), the same taxon with two ranks (superorder and order) was given two names: superorder Thripidea Fallen, 1814 and order Thripida Fallen, 1814. Since these names are typified, i.e., not linked to specific taxon boundaries, any of them may be used for either Neothysanoptera or Panphysapoda, depending on the ranks of these taxa. Thus, using the names Thysanoptera and Thripida to designate two different taxa is unreasonable, because both names may be equally well applied to either taxon.

## 2. THE NAME OF THE EXTINCT TAXON

The extinct taxon comprising the Cretaceous species *Mydiognathus eviohlhoffae* Yoshizawa et Lienhard, 2016 (= *Psocorrhyncha burmitica* Huang et al., 2016) and *Burmopsylla maculata* Liang et al., 2016, the Triassic species *Archipsylla primitiva* Handlirsch, 1906, the Permian species *Permopsocus latipennis* Tillyard, 1926, and some others is sometimes called "Permopsocida," either with the authorship "Tillyard, 1926" (Martynov, 1926, etc.), or with a new authorship (Huang et al., 2016). In both cases the family Archipsyllidae is considered a subordinate taxon within Permopsocida. Huang and co-authors (2016) attributed their own authorship to the name for no other reason than changing the taxon rank from suborder to order. In reality, however, the name "Permopsocida" was derived from the valid generic name *Permopsocus* Tillyard, 1926 by replacement of the ending by a suffix and ending "-ida"; therefore, it should be regarded as a typified name. Among the several sets of rules proposed by different authors for rank-based typified names of higher zoological taxa, only the rules developed by Rohdendorf (1977) and Rasnitsyn (1980) were introduced into practice. According to these rules, the valid name should be the senior family-group name in the broad sense (i.e., the older of all the typified names), while the ending "-ida" should be given to the order-rank taxon. The senior typified name for the taxon including *Archipsylla primitiva* is Archipsyllidae Handlirsch, 1906; therefore this name in the basic format is **Archipsylla/fg**. If this taxon is given the rank of order, its typified name will be **Archipsyllida** Handlirsch, 1906. The name Archipsyllida may be applied to the taxon in question only if the type species of *Archipsylla*, namely *A. primitiva*, is included in it. However, this species is known by a mere wing fragment (it is not clear if this is a fore or a hind wing). The morphological data provided by this fossil are very scanty; it was even debated which margin was the costal

and which was the anal one. Handlirsch (1906, 1925) interpreted the more convex margin of the wing as the costal one, and for this reason assigned the species to Psylloidea. Enderlein (1909) rotated this wing, so that the cell previously regarded as the pterostigma became the areola postica, and vice versa; according to this new interpretation, he placed the species in the recent subfamily Psyllopsocinae of the family Psoquillidae. Martynov (1926) observed in this wing some differences from the recent psocids and similarity with members of the suborder Permopsocida described by Tillyard (1926). In fact, *A. primitiva* has a very simple wing venation pattern resembling that of many other Neoptera, and it is entirely possible that its taxonomic position will be reassessed in the future.

If it turns out that *A. primitiva* has been erroneously placed into the taxon in question, then the senior typified name for this taxon will be Permopsocida, derived from the generic name *Permopsocus* with the type species *P. latipennis* Tillyard, 1926. However, the latter species was also described based on a single wing (it is unknown whether a fore or a hind one), so that its current taxonomic position may also prove to be wrong.

In view of such uncertainty about the typified name, a circumscriptional name would be the most stable. Since this taxon has had no circumscriptional name until now, I propose the new circumscriptional name **Tetrastigmoptera** taxon n. The original circumscription for this name includes only the species *Mydiognathus eviohlhoffae* (= *Psocorrhyncha burmitica*) and *Burmopsylla maculata*. Other species, such as *Archipsylla primitiva*, *Permopsocus latipennis*, etc., known only by wings, and also the better preserved *Psocidium kansasense* Tillyard, 1926, *Parapsocidium uralicum* Zalessky, 1937, *Dichentomum sojanense* Becker-Migdisova, 1962, *Archipsylla sinica* Huang, Nel, Azar et Nel, 2008, etc. should be only provisionally placed in Tetrastigmoptera, based on incomplete morphological data. Since the name Tetrastigmoptera is circumscriptional, it does not change depending on the taxon rank and can be used for a rankless taxon (Kluge, 1999, 2010).

## 3. CHARACTERISTIC OF TETRASTIGMOPTERA

Clypeus less convex than in Copeognatha. Mouthparts of chewing type ancestral for Hexapoda: mandibles with serrate incisors and asymmetrical chewing

molae; maxillae with lacinia and galea positioned lateral to lacinia; maxillary palps 4-segmented (unlike ancestral 5-segmented ones); labial palps 3-segmented. Labrum, mandibles, maxillary laciniae and galeae, and labium elongate so that whole mouth apparatus extended, all its appendages ending approximately at the same level. Antennae multisegmented. Prothorax small, meso- and metathorax equally well developed. Wings homonomous: fore and hind wings identical in shape and venation and almost identical in size; hind wing only slightly shorter, so that tips of all four wings coincide when wings drawn backwards. Wings without coupling apparatus; in flight each wing pair probably working independently (unlike in all Parametabola). Wings at rest folded in roof-like manner. Each wing with pterostigma limited by curved apical portion of vein $RA$; vein $RS$ forked, diverging from $RA$ proximal to pterostigma; vein $M$ dichotomically divided into 4 branches; vein $Cu_1$ (also termed $CuA$) forked; vein $Cu_2$ (also termed $CuP$) unforked. Each tibia with 2 apical spurs. All tarsi 4-segmented. Female with sclerotized ovipositor (it is unknown whether all components of primary ovipositor are included). Cerci absent.

## 4. DIFFERENT VIEWS ON THE TAXONOMIC POSITION OF TETRASTIGMOPTERA

### 4.1. Placement in Acercaria

It is commonly believed that the Tetrastigmoptera belong to some taxon within Acercaria (Handlirsch, 1906; Enderlein, 1909; Martynov, 1926; Tillyard, 1926; Huang et al., 2016; Liang et al., 2016; Yoshizawa and Lienhard, 2016, etc.). The only arguments for this are the presence of an areola postica (a characteristically shaped cell formed by bifurcation of $Cu_1$) and the absence of cerci (see section 5.6). However, the placement of Tetrastigmoptera in Acercaria is contradicted by the more primitive structure of the maxillae (see section 5.2), homonomous wings without a coupling mechanism (see section 5.3), the presence of two apical spurs on the tibia (see section 5.4), and the 4-segmented tarsus (see section 5.5).

### 4.2. Placement in Arthroidignatha

Handlirsch (1906) assigned the probable member of Tetrastigmoptera to Psylloidea within Arthroidignatha, based on erroneous interpretation of a single wing (see section 2).

### 4.3. Placement in Copeognatha s. str.

Enderlein (1909) assigned this insect directly to Copeognatha, on the sole ground of wing morphology (see section 2). However, Tetrastigmoptera differ from Copeognatha in the presence of 4 branches of vein $M$, whereas in most Copeognatha this vein has no more than 3 branches. Besides, Tetrastigmoptera differ from Copeognatha in the characters differentiating them from the rest of Acercaria (see section 4.1).

### 4.4. Placement in Copeognatha s. l.

Other authors (Martynov, 1926; Tillyard, 1926, etc.) formally placed the members of Tetrastigmoptera into the order Copeognatha (= Psocoptera) but at the same time united them in a special suborder opposed to all the recent psocids. This classification is also unjustified since Copeognatha s. str. (without Tetrastigmoptera), Acercaria, and Zoraptera form a single phylogenetic lineage that differs from Tetrastigmoptera in heteronomous wings with a coupling mechanism (see section 5.3), loss of tibial spurs (see section 5.4), and a reduced number of tarsomeres (see section 5.5).

### 4.5. Uniting with Condylognatha

Based on the supposed relationship between Tetrastigmoptera and Condylognatha, they were united in the taxon Pancondylognatha Yoshizawa et Lienhard, 2016. The reported synapomorphies of Tetrastigmoptera and Condylognatha were the elongated labrum, mandibles, and labium (Huang et al., 2016; Yoshizawa and Lienhard, 2016). In reality, however, insects with a chewing mouth apparatus vary strongly in the proportions of these appendages. Elongation of mandibles and other mouthparts in Tetrastigmoptera is not accompanied by change of function (see section 5.1). Such reversible elongations and shortenings of mouthparts have occurred repeatedly in the evolution of various insects; for instance, in Bittacidae the proportions of the labrum, mandibles, maxillae, and labium are comparable to those in Tetrastigmoptera, whereas in other members of Mecoptera these mouthparts are shorter (Otanes, 1922: figs. 1–61).

Besides the elongated mouthparts, other synapomorphies of Tetrastigmoptera and Condylognatha are believed to be the presence of "paraclypeal lobes" and division of the gena into the anterior (dorsal) and posterior (ventral) lobes (Huang et al., 2016).

According to the cited authors, the "paraclypeal lobes" are sclerotized areas lateral to the articulatory membrane that connects the clypeus to the labrum (whereas the articulatory membrane itself is called the "anteclypeus"). The presence of these sclerites and a membrane between them in Tetrastigmoptera and Thysanoptera (Fig. 1) is believed to be an autapomorphy of Condylognatha, somehow related to the ability for rotation of some mouthparts: "The sclerotized paraclypeal lobes and membranous medial part of the anteclypeus of Permopsocida and Thripida suggest that the ability for rotation of mouthparts to guide the mouthparts to food is a ground plan condition for Condylognatha" (Huang et al., 2016: 7). The cited authors refer to an earlier paper (Nel et al., 2014) in which, contrary to the above, the presence of "paraclypeal lobes" was regarded as the initial state for insects. What was interpreted as "paraclypeal lobes" in Tetrastigmoptera was a pair of large asymmetrical areas outlined by folds (Huang et al., 2016: fig. 2*a–g*). However, this part of the head appears smooth in the photo of another specimen of the same species (Yoshizawa and Lienhard, 2016: fig. 1*c*), suggesting that the folds were simply the result of integument deformation.

The presence of an oblique groove dividing the gena (i.e., the lateral side of the head capsule) into two lobes was regarded as a synapomorphy of Tetrastigmoptera and Condylognatha, proceeding from the assumption that the anterior (dorsal) lobe of the gena was homologous to the mandibular plate (lorum), and the posterior (ventral) lobe, to the maxillary plate in Arthroidignatha (Huang et al., 2016). The cited authors also stated that a groove between these parts of the gena was discernible in certain developmental stages of some Thysanoptera. In reality, however, the mandibular plate of Arthroidignatha is the part of the head wall distal to the mandible base, serving for attachment of the mandible protractor muscle. Due to this function the mandibular plate is usually more or less convex; therefore it is usually separated from the clypeus by a more or less expressed depression or groove. In contrast to Arthroidignatha, the mandibles of Thysanoptera are not protractile and have no protractor muscles, while the head of Thysanoptera has no distinct structure corresponding to the mandibular plates in Arthroidignatha. The same is true of all the other insects including Tetrastigmoptera, in which the mandibles cannot be retracted into the head and, therefore, should not have protractor muscles. The maxillary plate

of Arthroidignatha is actually the maxillary stipes fused with the head wall; similar to the rest of Acercaria, it serves for attachment of the protractor of the maxillary lacinia. In Thysanoptera the maxillary stipes is not fused with the head wall (Fig. 2) and, correspondingly, is not usually called the maxillary plate, even though it lies in the same place and performs the same function. Thus, the mandibular and maxillary plates are present only in Arthroidignatha; besides, they are separated not by a groove but by a fissure leading to the membranous pouch concealing the mandible. By contrast, in Tetrastigmoptera the mandible is not concealed in a pouch but occupies the external position primitive for insects (see section 5.1). The "mandibular plate" and "maxillary plate" of Thysanoptera shown in the diagram (Huang et al., 2016: fig. 4) are actually some arbitrary head areas not outlined in any way, whereas the maxillary stipes is shown by a different color; in the same diagram for Arthroidignatha (under the name "Hemipteran groundpattern"), the "mandibular plate" corresponds to the real mandibular plate plus some arbitrarily selected head area dorsal to it; similarly, the "maxillary plate" corresponds to the real maxillary plate (i.e., the maxillary stipes) plus an arbitrary head area dorsal to it.

Huang and co-authors (2016) justified the placement of Tetrastigmoptera into Acercaria by the following characters, which they believed to be apomorphies of Acercaria.

1. An enlarged clypeus with an enlarged cibarial muscle serving as the pharyngeal dilator. In reality, however, the large and clearly convex clypeus accommodating the enlarged cibarial muscle is typical of Copeognatha and Euhomoptera Crampton, 1916 (= Clypeorrhyncha Sorensen et al., 1995 = Clypeata Shcherbakov, 1996). Enlargement of the cibarial muscles may indeed be related to suctorial specialization; however, it is a paradox that Copeognatha, which do not have the sucking mouth apparatus, possess a very large cibarial muscle, whereas Subtericornes Amyot et Serville, 1843 (= Neurohomoptera Crampton, 1916; = Archaeorrhyncha Sorensen et al., 1995) and some other suctorial Acercaria have a small, non-protruding clypeus with a small cibarial muscle. Besides some taxa within Acercaria, an enlarged convex clypeus accommodating a large cibarial muscle is present in some other insects possessing both a sucking mouth apparatus and a chewing one (for instance, in many termites of the family Termitidae and cockroaches of the family Corydiidae). The clypeus of Tetrastigmo-
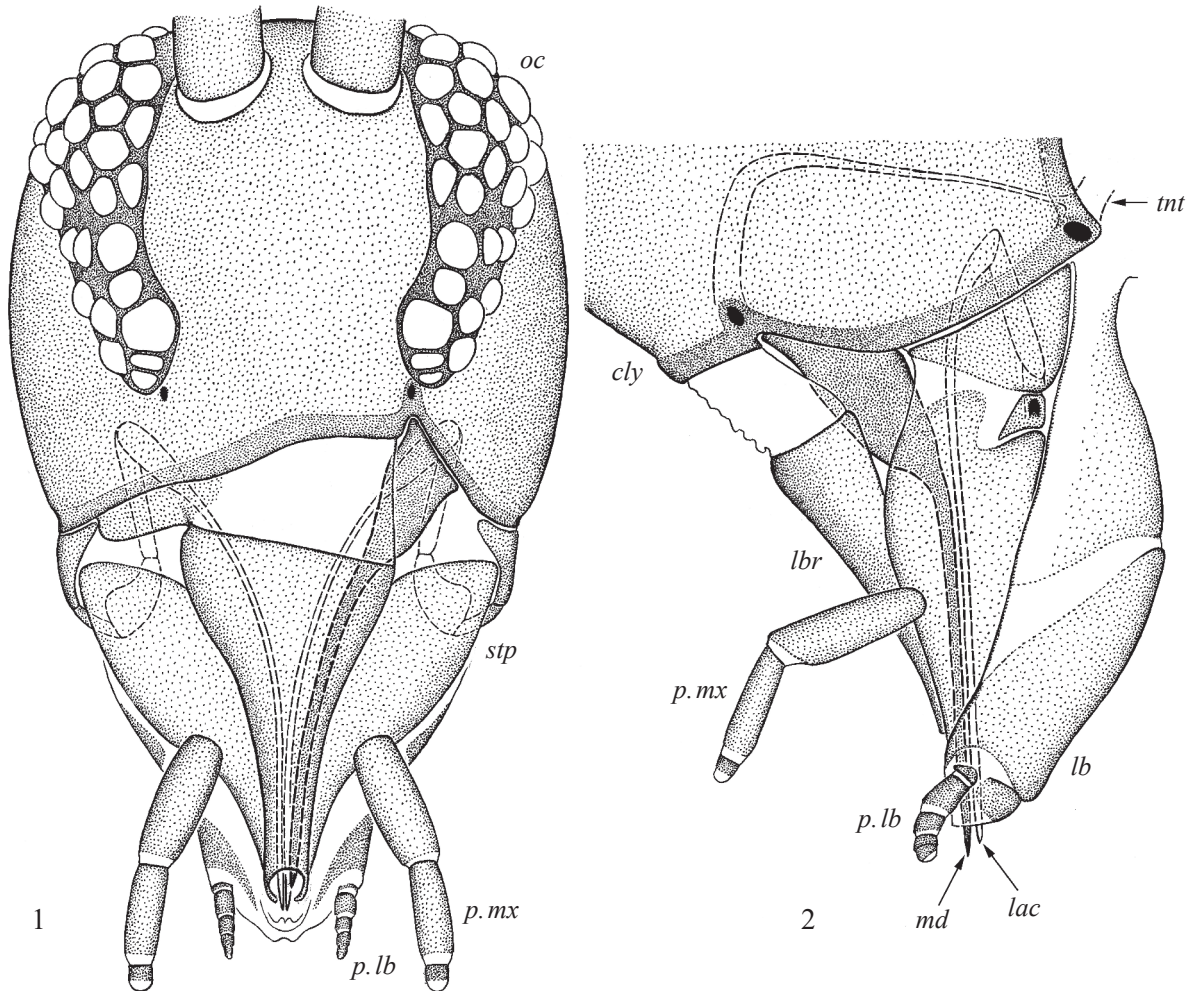
**Figs. 1, 2.** Mouth apparatus of the thrips *Aeolothrips fasciatus* (L., 1758): (1) head in frontal view; (2) mouth apparatus in lateral view (the concealed parts of the left mandible and maxillae are shown in dashed lines; the mandible is punctated); *cly*, clypeus; *oc*, compound eye; *lac*, maxillary lacinia; *lb*, labium; *lbr*, labrum; *md*, mandible; *p. lb*, labial palp; *p. mx*, maxillary palp; *stp*, maxillary stipes; *tnt*, tentorium.

ptera is not enlarged and not convex, and in these features Tetrastigmoptera are clearly differentiated from Copeognatha.

2. Asymmetrical mandibles. In reality, the asymmetry of mandibles observed in Copeognatha is the ancestral condition for Mandibulata (Eucrustacea + Myriapoda + Hexapoda), while the loss of the right mandible in thrips is an autapomorphy of Thysanoptera (see section 5.1).

3. Stylet-like protractile maxillary laciniae. This is indeed an autapomorphy of Acercaria but it is absent in Tetrastigmoptera (see section 5.2).

4. The labial palps reduced to 3 palpomeres or lost. In reality, 3-segmented labial palps are ancestral for Hexapoda, whereas in thrips (belonging to Acercaria) the number of palpomeres is not reduced but, on the contrary, may be secondarily increased (Figs. 1, 2).

5. Similarity in the sclerites and muscles of the cibarial pump in Copeognatha and Thysanoptera. In reality, the pharyngeo-hypophagyngeal apparatus of Copeognatha has specific morphology: the pharyngeal dilator muscle is inserted on a small cibarial sclerite; this sclerite has a projection directed into the pharyngeal cavity; the opposite wall of the pharynx bears a sitophorous sclerite with concavity; a pair of sclerites termed the hypopharyngeal plates is present on the posterior surface of the hypopharynx; there are ligaments extending under the integument of the hypopharynx, from the sitophorous sclerite to the hypopharyngeal plates; muscles

extend from the hypopharyngeal plates to the edge of the occipital foramen. Besides Copeognatha, these morphological details occur in Mallophaga but not in Thysanoptera. To all appearances, the presence of these structures is an autapomorphy of Panpsocoptera: among Panpsocoptera they are clearly expressed in all the Copeognatha (both Parapsocida and Eupsocida) and in all the Mallophaga (both Ischnocera and Amblycera); at the same time, in Rhyncophthirina they have been completely lost due to the development of the rostrum, and in Siphunculata they have changed beyond recognition due to the transformation of the hypopharynx and labium into protractile stylets.

6. The presence of areola postica. This is in fact not an autapomorphy of Acercaria but an ancestral character for Parametabola, since it is expressed not only in some members of Acercaria but also in all the Zoraptera.

7. The wing venation characters considered by the cited authors are related to the debatable homologies of the vein bases.

8. Strong reduction or loss of abdominal sternite I. In reality, abdominal sternite I is reduced or completely lost not only in some members of Acercaria but also in many other insects; at the same time, it is fairly well developed in some Acercaria. For instance, in whiteflies (Scytinelytra) uromere I with a distinct tergite and sternite forms the petiole, whereas in singing cicadas (Stridulantes Latreille, 1825) the muscles extending to abdominal sternite I form the powerful stridulatory apparatus.

9. Loss of cerci. In reality, cerci have been lost not only in Acercaria but also in Metabola (see section 5.6).

10–12. Three more characters mentioned as autapomorphies of Acercaria are unknown for the fossil insects including Tetrastigmoptera; two of them, namely fusion of all the abdominal ganglia and reduction in the number of Malpighian tubules to four, can be found in many taxa besides Acercaria; the third character, related to the sperm morphology, is indicated erroneously.

## 5. REVIEW OF CHARACTERS

### 5.1. Mandibles

There is a widespread but wrong notion that the mandibles of insects were initially monocondylic and only secondarily acquired dicondylic articulation (Hennig,

1981); this idea underlay the establishment of the taxon Dicondylata Boudreaux, 1979 [= Dicondylia Hennig, 1953 (non Dicondylia Haeckel, 1866)], uniting Pterygota and Zygentoma but not including Microcoryphia. In reality, the mandibles of Microcoryphia are functionally dicondylic (Manton, 1964; Kluge, 2000). Besides Pterygota, Zygentoma, and Microcoryphia, dicondylic mandibles are present in many Entognatha, Myriapoda, and Eucrustacea; in all appearances, they are ancestral for Mandibulata (Kluge, 2000).

The ancestral state for Mandibulata includes the presence of the mola, incisor, and kinetodontium (also referred to as lacinia mobilis); the mola and incisor are retained in most Eucrustacea and Hexapoda; among Eucrustacea, the kinetodontium is retained in Peracarida, Thermosbaenacea, and Remipedia; among Hexapoda, a clearly detached kinetodontium is preserved in many larvae of Ephemeroptera (Kluge, 2004: fig. 26C); a non-articulated kinetodontium can be found in many insects (Kluge, 2000). The initial variant of mandibular asymmetry in Mandibulata probably included the mola of the left mandible with the most protruding distal margin and the mola of the right mandible with the most protruding proximal margin (Kluge, 2000: fig. 50D).

The mandibles of Myriapoda have a 4-hinge articulation with the head capsule; therefore, they can perform a variety of movements, not only mincing food but also moving it into the mouth. This structure of the mandibles eliminates the need for other movable mouthparts; correspondingly, Collifera and Chilopoda have no analogues of maxillae, and only Symphyla have a pair of simple maxillae (Kluge, 2000).

Unlike those of myriapods, the mandibles of Hexapoda, being dicondylic and synsclerotized, have only one degree of freedom, i.e., they can only tilt on the axis passing through the two condyles. Therefore the chewing mouth apparatus of insects must always include not only mandibles but also maxillae that perform more diverse movements and can move food particles and bring them into the mouth (see section 5.2).

The mandibles of Condylognatha have lost the ability to bite; instead, they serve for making a hole into which the sucking tube formed by two maxillary laciniae is then inserted. Such a piercing mandible is apically pointed, has no mola and no teeth on the median side; the whole mandible fits in a narrow cleft between the

clypeus and the maxillary stipes and cannot perform lateral movements (Figs. 1, 2).

On the contrary, the mandibles of Tetrastigmoptera totally retain the typical morphology of mandibles in a chewing mouth apparatus: they are positioned openly and can move apart and then close together; the molae are fairly well developed, asymmetrical, and can close together when grinding food; the incisors have medially pointing teeth and can grasp and crack food particles (Huang et al., 2016: fig. 2*f*; Yoshizawa and Lienhard, 2016: figs. 1*c*, 2*a*–*c*).
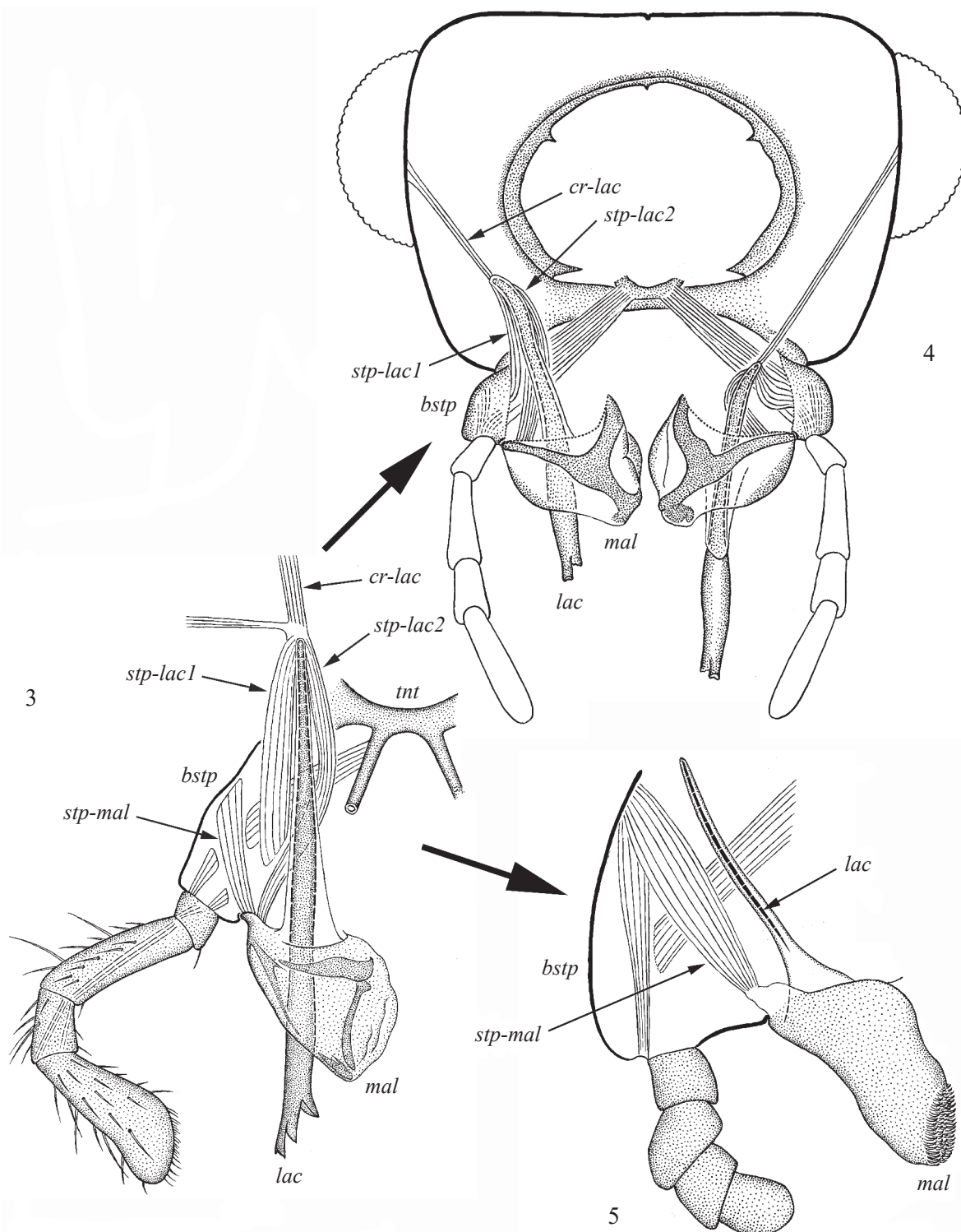
### 5.2. Maxillae

**5.2.1. Structure and function of maxillae in Copeognatha.** The mouth apparatus of psocids (Copeognatha) retains its chewing function; it has the usual chewing mandibles with a mola and an incisor, which can break food particles but cannot move them into the mouth (see section 5.1). Therefore, maxillae capable of holding and moving food particles constitute an essential part of the mouth apparatus in psocids. In the ancestral chewing mouth apparatus of Hexapoda this function of the maxillae is ensured by movable articulation of their proximal segments (coxopodites) to the head; each coxopodite is divided into two movably connected sclerites (cardo and stipes), whereas the laciniae can be brought together to hold food particles. By contrast, the connections of the head, cardo, and stipes have become immovable in psocids, while their laciniae have lost the food grasping function. At the same time, the maxillae of psocids have acquired new structural features due to which they can still perform the same function of holding and moving food particles.

The maxilla has the following structure in all the Copeognatha (Figs. 3, 4). The cardo is lost. The stipes is connected to the head capsule with limited mobility and is subdivided into two lobes: proximal, which may be termed **basistipes**, and distal, which may be termed **mala maxillaris**; the palp is attached to the basistipes, and the lacinia is attached to the mala; the galea is incorporated into the mala and is not discernible as a separate part. The muscles initially extending from the stipes to the tentorium are inserted inside the basistipes, while those extending from the stipes to the palp are also inserted inside the basistipes. The maxillary lacinia is strongly elongated, narrowed, and sclerotized, so that it looks like a shaft basally submerged deep into the head.

The proximal part of the lacinia is concealed in a tubular sheath formed by membranous cuticle that connects the lacinia base to the integument. Due to flexibility of this sheath the lacinia can be protracted and retracted. There are three muscles inserted on the lacinia: the craniolacinial muscle acting as its retractor (Figs. 3, 4: *cr-lac*) and two muscles corresponding to the single ancestral stipito-lacinial muscle: one of them is attached inside the basistipes, the other, inside the mala (Figs. 3, 4: *stp-lac1*, *stp-lac2*). The laciniae are positioned apart and cannot touch one another either in protracted or in retracted state (Fig. 4). Thus, unlike the laciniae of the usual chewing mouth apparatus, the laciniae of psocids cannot grasp food particles and move them into the mouth. Besides the muscles extending to the lacinia, tentorium, and palp, the maxilla may have one more muscle connecting the basistipes to the base of the mala (Fig. 3: *stp-mal*) and most probably corresponding to the initial stipito-galeal muscle of insects. Among Copeognatha, this muscle is present only in members of the plesiomorphon Parapsocida but absent in all the Eupsocida (Fig. 4) (Yoshizawa, 2002). Apart from Parapsocida, this muscle also occurs in chewing lice (Mallophaga) (Fig. 5).

The mala of psocids is commonly mistaken for the galea (Yoshizawa, 2005); however, the true galea cannot serve for attachment of the lacinia and the lacinial muscle. In all appearance, the stipes has split into the basistipes and the mala while the galea has fused with the mala; therefore, the movable articulation between the basistipes and the mala does not correspond to the ancestral place of articulation between the stipes and the galea.

The mala is connected to the basistipes by a movable monocondylic articulation; it lies almost at a right angle to the basistipes with the apex directed medially, so that the apices of the right and left malae may touch one another. The mala apex may be swollen and membranous (Figs. 3, 4), or it may bear denticles curved proximally (Fig. 5). Using this mala, the maxilla can grasp the food particles ground by the mandibles and move them into the mouth. Movements of the mala may be powered by only two muscles inserted on its base: the muscle extending from the basistipes to the mala (the ancestral stipito-galeal muscle retained in Parapsocida and Mallophaga) and the muscle extending from the mala to the proximal end of the retractile lacinia (part of the ancestral stipito-lacinial muscle that is retained in Parapso-

**Figs. 3–5.** Maxillae of Panpsocoptera: (3) *Papuapsocus* sp. (Parapsocida), right maxilla in frontal view (showing section of the stipes); (4) *Metylophorus nebulosus* (Stephens, 1836) (Eupsocida), section of head before the maxillae, frontal view (only the maxillary muscles are shown); (5) *Laemobothrion maximum* (Scopoli, 1763) (Mallophaga), left maxilla; *bstp*, basistipes; *cr-lac*, cranial muscle of lacinia; *lac*, maxillary lacinia; *mal*, mala; *stp-lac1*, stipital muscle of lacinia; *stp-lac2*, malar muscle of lacinia; *stp-mal*, stipito-malar muscle; *tnt*, tentorium.

cida and Eupsocida). Both muscles may act as flexors of the mala, i.e., turn the mala toward the mouth; the reverse movement of the mala may only be powered by the hydraulic mechanism.

In order to bend the mala using the muscle extending from the mala to the lacinia, the lacinia has to be rigidly secured. A probable way of accomplishing this is to protract the lacinia with the muscle extending from it to the basistipes (as in the right half of Fig. 4) and set its apex against the substrate. The use of this particular mechanism by psocids is indirectly supported by the fact that in all the species (both Eupsocida and Parapsocida) the protractile maxillary laciniae are equally well developed, shaft-like, and have the same length relative to the maxilla size; unlike in Mallophaga, they are never reduced; the apices of laciniae vary in shape in different species of psocids but always have spikes directed distally; due to these features, the laciniae can probably be set against the substrate and used as support for the muscle extending to the mala.

The maxillae capable of complex movements to scoop food into the mouth are indispensable to insects with chewing mandibles since the one-segmented and dicondylic mandibles have only one degree of freedom and cannot perform such movements themselves (see section 5.1). The maxilla of insects initially has two movably articulated sclerites, the cardo and stipes, and can perform the required scooping movements. In psocids the maxilla has lost its subdivision into the cardo and stipes, but this is compensated for by its subdivision into the basistipes and mala. Both the cardo and the stipes initially have muscles extending from the head endoskeleton, but no such muscles are inserted on the mala. Therefore, the movements of the mala should be powered either by the muscle extending to it from the basistipes, or by a complex mechanism including the protractile lacinia.

Parapsocida retain a complete set of muscles initially present in the insect maxilla; therefore the mala may be powered both by the muscle extending from the basistipes and by that extending from the lacinia (see Fig. 3). The taxon Parapsocida appears to be a plesiomorphon ancestral to both Eupsocida and Parasita (among which the chewing mouth apparatus is retained in Mallophaga).

Eupsocida have lost the muscle extending from the basistipes to the mala, so that the mala can be powered only by the protractile lacinia (see Fig. 4).

On the contrary, Mallophaga have lost the lacinia, and the mala is powered only by the muscle extending to it from the basistipes (see Fig. 5).

The mouth apparatus of Copeognatha may have been the precursor of the piercing-sucking apparatus of Condylognatha, in which the protractile maxillary lacinia form the sucking tube when extended from the head. The mandibles of Condylognatha have lost the chewing function; since their sucking mouth apparatus cannot grind solid food particles, it has no need for movable maxillary malae. As a result, the malae have disappeared, so that the maxilla of Condylognatha consists of the stipes, immovably connected or fused with the head wall, and the protractile lacinia incorporated into the sucking apparatus.

**5.2.2. Essential differences between the maxillae of Tetrastigmoptera and Copeognatha.** Judging by the published drawings and photos of *Mydiognathus eviohlhoffae* (Huang et al., 2016: figs. 1*g*, 2*a–g*; Yoshizawa and Lienhard, 2016: figs. 1*c*, 2*a–c*), Tetrastigmoptera have a regular chewing mouth apparatus differing from the initial one only in the elongated mouthparts. Unlike Copeognatha, Tetrastigmoptera have maxillary galeae of usual structure, lying lateral to the laciniae and extending parallel to them; the laciniae of the left and right maxillae are positioned close together and curved, with their apices facing each other, so that they can hold food particles.

The cited authors believe that the lacinia of *M. eviohlhoffae* has lost its connection with the stipes and can be protracted and retracted as in Copeognatha. However, in the published illustrations the apices of both laciniae are at the same level as the apices of the galeae and mandibles. By contrast, in dead psocids the laciniae are protracted to a varying extent (see Fig. 4). Therefore, the lacinia of *M. eviohlhoffae* is basally articulated with the stipes and cannot be protracted and retracted.

Although the structure of the proximal parts of the maxilla is not exactly clear in the published illustrations of *M. eviohlhoffae*, the authors specified that the maxilla had a well separated cardo and stipes (Huang et al., 2016: 5; Yoshizawa and Lienhard, 2016: 231, fig. 2*a*). Unlike Tetrastigmoptera, all the Acercaria including Copeognatha have lost the subdivision of maxilla into the cardo and stipes.

## 5.3. Wing Coupling

All the Parametabola have an anteromotor wing apparatus: their hind wings are always coupled with the fore ones in flight and move passively. Some members of Parametabola have lost the indirect metathoracic wing muscles while in others these muscles are quite well developed; regardless of this, during flight the hind wings cannot perform independent active movements and only duplicate the movements of the fore wings with which they are coupled.

The mechanisms of coupling of the fore and hind wings vary in different taxa of Parametabola. In some cases two coupling apparatuses are present simultaneously, suggesting that different designs have replaced one another in the course of evolution. In Zoraptera wing coupling is ensured by numerous setae: in the recent members of this taxon the costal margin of the hind wing bears setae that are curved distally and can interlock with the straight setae on the posterior margin of the fore wing; in the extinct *Zorotypus acanthothorax* Engel et Grimaldi, 2002 the coupling setae on the posterior margin of the fore wing are apically hooked (Engel and Grimaldi, 2002: fig. 10). In Copeognatha the costa of the hind wing is secured by a lock positioned at the apex of the claval furrow of the fore wing. Among Panphysapoda (i.e., Thysanoptera s. l.), in Palaeophysapoda the costal margin of the hind wing has a row of setae hooked dorsally and coupling with the bent posterior margin of the fore wing (Fig. 7); in Neothysanoptera (i.e., Thysanoptera s. str.) the hind wing has, besides a regular row of setae, also one ventral hooked seta that is coupled with the robust apical setae on the fore wing clavus (Figs. 8, 9). In Saltipedes one dorsal hooked seta positioned in the middle of the hind wing costa is coupled with the bent margin of the fore wing. In addition, all the Psyllaleyroda (both Saltipedes and Scytinelytra) have a row of non-functional hooked coupling setae proximally on the hind wing costa. In Aphidococca a bundle of hooked setae on the anterior margin of the hind wing is coupled with the bent posterior margin of the fore wing. In Auchenorrhyncha a curved projection of the hind wing is coupled with the bent posterior margin of the fore wing; besides, there is a row of non-functional hooked coupling setae in the proximal part of the hind wing costa. In Heteropteroidea the anterior margin of the hind wing is secured by a lock positioned at the apex of the claval furrow of the fore wing.

It should be noted that the presence or absence of the coupling apparatus is a stable character while the coupling mechanisms are diverse. All the Parametabola have a wing coupling apparatus, regardless of the wing shape and the presence or absence of metathoracic wing muscles; by contrast, wing coupling is absent in all the Neuropteroidea and Mecoptera, also irrespective of the shape and function of the wings.

The authors who discussed the phylogenetic position of Tetrastigmoptera (Huang et al., 2016; Yoshizawa and Lienhard, 2016) mentioned the presence of a certain structure termed the "jugal bar" in various Parametabola, Neuropteroidea, and Hymenoptera. They probably confused different variants of the coupling apparatus (present in Parametabola and Hymenoptera but absent in Neuropteroidea) with the contact sensory apparatus formed by the jugum of the fore wing and the frenulum of the hind wing (present in Neuropteroidea and Mecoptera but absent in Parametabola and Hymenoptera). The jugo-frenate apparatus in Neuropteroidea and Mecoptera has only a sensory function and does not serve for mechanical wing coupling. This misunderstanding may have been related to Tylliard's publications (1918, 1919), in which the jugo-frenate sensory apparatus was erroneously named "wing-coupling apparatus."

Unlike all the Parametabola, Tetrastigmoptera have a bimotor wing apparatus and no coupling between the fore and hind wings. This is related to the presence of identically developed pterostigmata on the two pairs of wings.

## 5.4. Apical Tibial Spurs

The apical tibial spurs are two movably articulated hypoderm-containing setiform processes positioned apically on the inner side of the tibia. During molting the new spur develops inside the spur cuticle of the preceding instar (as opposed to a seta which develops under the cuticle and does not extend into the cavity of the old seta). Such spurs seem to be initially inherent in Neoptera. They are not found in other insects (Odonata, Ephemeroptera, Triplura, and Entognatha): among these taxa, only Zygentoma have a detached dentiform apical projection on the tibia, but this projection is always single, positioned on the outer side of the tibia, and does not resemble a seta. Among Neoptera, spurs are present in some Idioprothoraca, Rhipineoptera, and Metabola but they have been lost in all the Parametabola. Apart
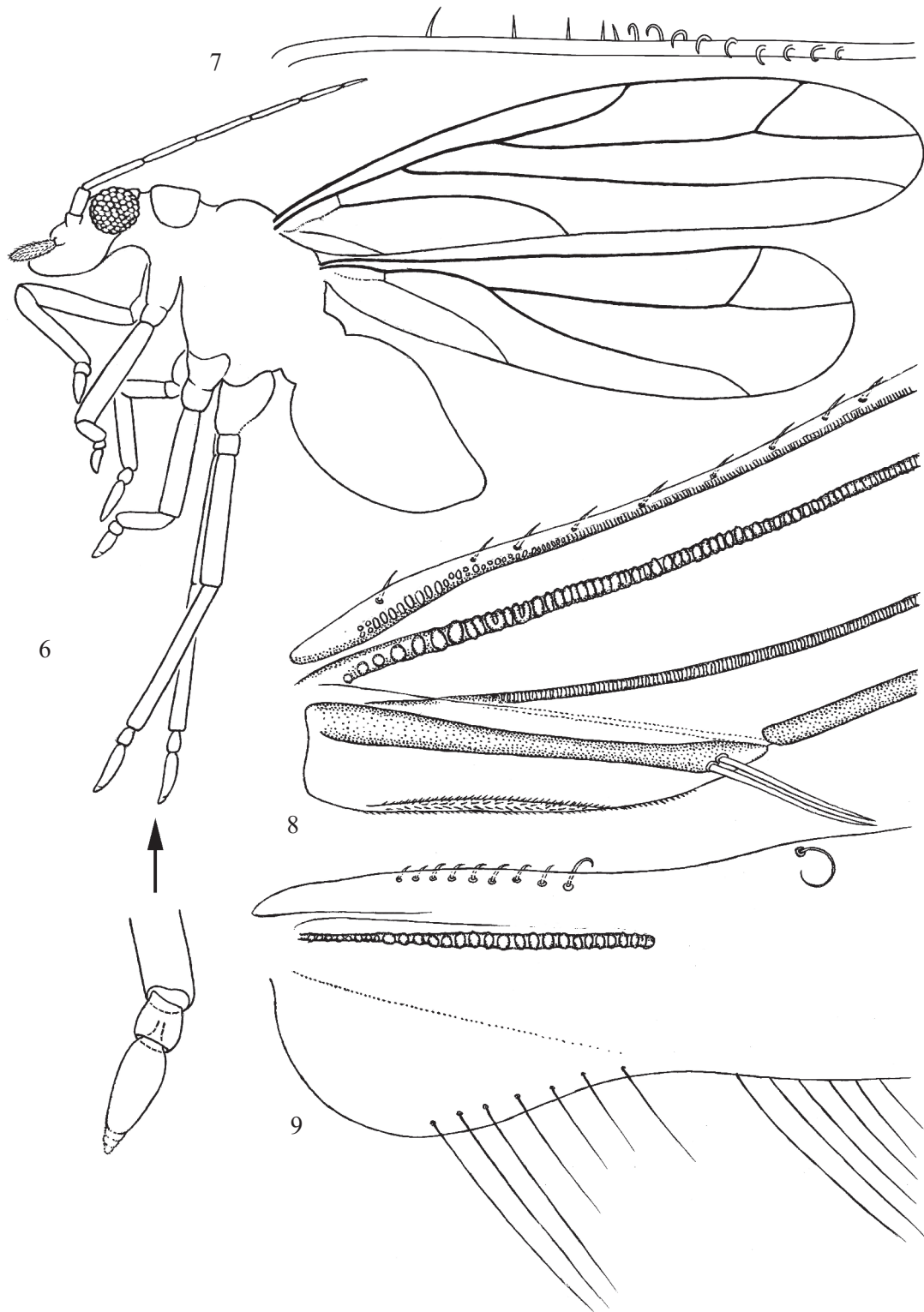
**Figs. 6–9.** Panphysapoda: (6) *Jantardachus reductus* Vishniakova, 1981 (holotype), total view and enlarged hind tarsus; (7) *Jantardachus perfectus* Vishniakova, 1981 (holotype), costal vein of hind wing in dorsal view (with base on the left); (8, 9) *Aeolothrips fasciatus* (L., 1758), bases of the left fore and hind wings in the uncoupled state, ventral view.

from Parametabola, spurs are also absent in some other Neoptera: among Idioprothoraca they are present in Notoptera but absent in Embioptera; among Rhipineoptera they are present in Pandictyoptera, Saltatoria, and many Plecoptera but absent in Spectra and Dermatoptera; in Metabola spurs are present only in adults and pupae but not in larvae; at the same time, in adults of Strepsiptera and Aphaniptera and in some taxa within Eleuterata, Hymenoptera, Diptera, and Lepidoptera one or both spurs may be lost on all the legs or on some leg pairs.

All the Parametabola have lost the apical tibial spurs; they may have only secondary spur-like appendages. The tibia sometimes bears one or several robust apical setae externally resembling spurs. In the leaping hind legs of Auchenorrhyncha and Saltipedes, the apex of the tibia bears transverse rows of spine-like setae or immovable denticles that functionally replace the spurs. All or some of these denticles may become detached and thus transformed into secondary spurs; in particular, in Delphacidae one denticle is modified into a very large movable spur; in Stridulantes numerous secondary spurs are present apically on the hind tibia. In all these cases, the secondary spurs differ from the initial ones, at least in the number which is never equal to two.

As opposed to all the Parametabola, in Tetrastigmoptera the tibia bears two apical spurs of the structure initial for Neoptera (Liang et al., 2016: fig. 3*c*; Yoshizawa and Lienhard, 2016: fig. 1*e*).

### 5.5. Number of Tarsomeres

The initial number of tarsal segments (tarsomeres) in Amyocerata is five. This is indicated by the fact that 5-segmented tarsi can be found in remote phylogenetic lineages of Amyocerata: Triplura (only in Lepidotrichidae), Ephemeroptera (in adults and subimago of many taxa), Idioprothoraca (in Notoptera), Rhipineoptera (in many Raptoriae, all Noeblattariae, primitive Isoptera, extinct primitive members of Saltatoria, many Spectra, extinct primitive members of Dermatoptera), and Metabola (in adults and pupae of most species). The number of tarsomeres is reduced in many taxa of Amyocerata. It should be borne in mind that the number of tarsal segments has never increased in evolution; there are no insects with more than five tarsomeres. In this respect the tarsi differ from other segmented appendages, such as maxillary and labial palps, antennal flagella, and

cerci, in which the number of segments has not only decreased but also increased in the course of evolution.

All the Parametabola have no more than three tarsomeres. It was supposed that the number of tarsomeres was reduced independently in Zoraptera, Copeognatha, and Acercaria (Huang et al., 2016: S3: character 31; Yoshizawa and Lienhard, 2016: 242). This would be a plausible scenario if we only considered the number of tarsomeres in adults, since 3-segmented tarsi have indeed appeared independently in different unrelated taxa of insects; however, Parametabola are characterized by a specific pattern of change in the number of tarsomeres during ontogeny.

In the initial state for Parametabola, the tarsus is 2-segmented in the larva but becomes 3-segmented during the final molt, when the distal tarsomere gets divided in two (Fig. 10). Transition from 3-segmented to 2-segmented tarsus in adults has occurred repeatedly in different lineages of Parametabola as the result of the second larval tarsomere remaining whole during the final molt. The number of tarsomeres was further reduced in some taxa of Parametabola: the tarsus became unsegmented and/or fused with the tibia in Siphunculata, some Mallophaga, larvae and some adults of Thysanoptera, some Heteroptera, and some Plantisuga. The only exception are Subtericornes in which the hind tarsus is 3-segmented not only in adults but also in larvae; in this case, the number of larval tarsomeres probably increased due to advance development of the imaginal state in the leaping hind legs, which may be related to their unusual modification.

In other insects with 3-segmented and 2-segmented tarsi the ontogenetic development of the tarsus may proceed differently from that in Parametabola. In particular, in Embioptera, Plecoptera, Dermatoptera as well as in some members of Raptoriae, Isoptera, Saltatoria, and Spectra the tarsi are 3-segmented, though not only in adults but also in all the larval instars. In some Plecoptera (Chloroperlidae) and some Saltatoria (Tetrigidae and Tridactylidae) the 3-segmented tarsi became 2-segmented not by fusion of two distal segments but, on the contrary, by fusion of two proximal ones. Odonata and Microcoryphia are the only taxa with tarsal segmentation somewhat resembling that in Parametabola. The 1st instar larvae of Odonata have unsegmented tarsi; during the subsequent larval molts the 1st tarsomere is separated before the subdivision of the 2nd and 3rd seg-
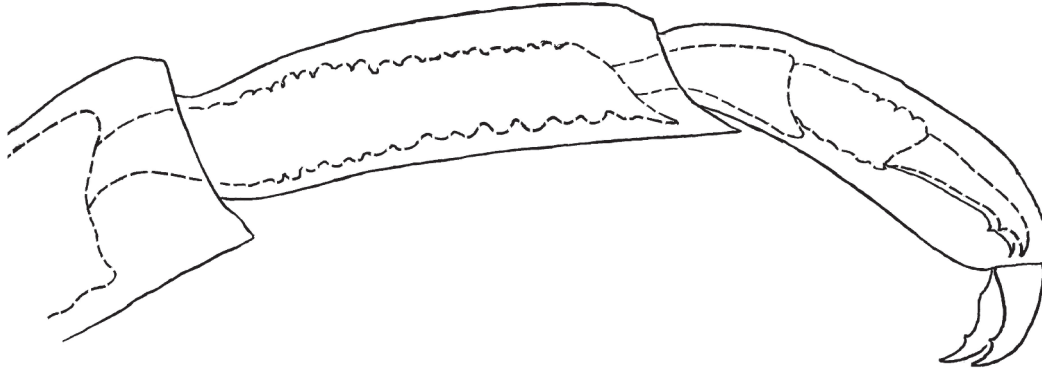
**Fig. 10.** *Elipsocus hyalinus* (Stephens, 1836) (Copeognatha): tarsus of the larva before the final molt; the imaginal tarsus under the larval cuticle is shown in dashed lines.

ments; unlike in Parametabola, in most cases the tarsus becomes 3-segmented before the final molt (Tillyard, 1917). In Microcoryphia the tarsi are 3-segmented or secondarily 2-segmented due to fusion of the two distal segments; unlike in Parametabola, the number of tarsomeres does not change in ontogeny.

Thus, the morphology of the tarsus in Parametabola is a unique autapomorphy indicating holophyly of this taxon. At least Copeognatha and Arthroidignatha include species with characteristic ontogeny of the 3-segmented tarsus. In Zoraptera the tarsi are 2-segmented, which also agrees with the diagnosis of Parametabola.

As opposed to Parametabola, the tarsi of Tetrastigmoptera are 4-segmented (Liang et al., 2016: fig. 3*c*; Yoshizawa and Lienhard, 2016: fig. 1*e*); this fact contradicts the placement of Tetrastigmoptera into Acercaria and their supposed relationship with Copeognatha and/or Condylognatha (see sections 4.1–4.5).

### 5.6. Absence of Cerci

Loss of cerci is the only character shared by Tetrastigmoptera and Acercaria. Besides these two taxa, cerci have been also lost in Metabola (see below).

The name "cerci" is often used for any appendages at the body end of an arthropod. For instance, the "cerci" of Symphyla are paired spinning appendages arising at the posterior margin of the body segment preceding the telson (thus, one pair of "cerci" is replaced by another as new body segments are added). In the taxon Nematophora Verhoeff, 1913 (within Diplopoda), the name "cerci" is used for the spinning appendages at the posterior margin of the telson. In Chilopoda, the "cerci" are the last pair of legs which are directed backwards, not used in locomotion, and sometimes strongly modified. This may be the reason for the widespread but erroneous notion that the cerci of insects also originated from legs. Among Entognatha, members of Collembola and Protura have no structures which could be interpreted as cerci, whereas the "cerci" of Diplura are paired appendages at the end of the tenth (ultimate) abdominal segment. These appendages in Diplura are commonly believed to be homologous to the cerci in Amyocerata. However, my study of the muscles of Campodeidae showed that the muscles moving these appendages initially had ventral insertion, in contrast to the muscles of the true cerci which have dorsal insertion (Kluge, in print). In Japygidae these appendages are transformed into forceps while their muscles are so modified that their initial insertion sites cannot be determined. I propose the term **pseudocaudalii** for the caudal appendages of Diplura. The pseudocaudalii probably originated from some ventral abdominal appendages (but they are not homologous to the jumping furca of Collembola, which is powered by dorsal muscles).

Amyocerata initially possess **caudalii**, i.e., three appendages (two cerci and a paracercus) at the end of the tenth (ultimate) abdominal segment (Kluge, 2004). The muscles extending to the bases of the caudalii originate on the tergite, and the middle element (paracercus) is dorsal to the anal opening; thus, the caudalii, unlike the pseudocaudalii, are initially dorsal. All the Triplura and Ephemeroptera have three caudalii whereas Meta-

pterygota retain only the paired caudalii (cerci) with simplified morphology. The paired cerci with muscles inserted on them are retained in all the Odonata, Idioprothoraca, Rhipineoptera, and Zoraptera but they have been lost in Acercaria and Metabola. Among Parametabola, true cerci (with muscles extending to them from abdominal tergite X) are present in Zoraptera; therefore, loss of cerci cannot be an autapomorphy of Eumetabola but it has occurred independently in Acercaria and Metabola.

The 10th abdominal segment in some Metabola bears paired appendages, or **socii**, which are sometimes mistaken for "cerci." Unlike true cerci, these appendages have no associated muscles. Socii are found only in some taxa and may be specific to a particular sex, and it remains unknown whether their presence is initial for Metabola or they have appeared independently several times.

## 6. INADEQUACY OF THE SO CALLED "PHYLOGENETIC ANALYSIS" BASED ON PARSIMONY

No phylogenetic analysis using parsimony (PAUP) can provide arguments in support of any phylogenetic hypothesis, because the very idea of parsimony is incompatible with the existing theory of evolution (Kluge, 2000). Researchers certainly have a right to disagree with the conventional theory; but in this case they are expected to express their views and to act according to the theory they believe to be true. By contrast, the authors using the parsimony principle still claim to accept the Darwinian theory of evolution and the Hennigian principle of phylogenetic analysis based on apomorphies, which have no place for the parsimonious evolution model.

The so called "phylogenetic analysis" based on parsimony begins with compiling the taxon/character matrix. This approach already complicates further analysis because the design of such a matrix contradicts the hierarchical principle of the phylogenetic system. Since the diversity of actual characters follows a certain hierarchy determined by the actual phylogeny, the only way to fit these characters in the Procrustean bed of a rectangular matrix is to twist their descriptions. As a result, most characters included in such matrices are either incorrect or make no phylogenetic sense.

Two teams of researchers (Huang et al., 2016; Yoshizawa and Lienhard, 2016) have performed such phylogenetic "analyses" to determine the taxonomic position of Tetrastigmoptera. Their taxon/character matrices were compiled independently but based on the same limited set of literature sources, which led to similar erroneous results. The mistakes made by the cited authors were to a certain extent to be expected since they stemmed from some widespread but erroneous notions; this is why I feel compelled to consider some of them below.

### 6.1. The Smaller Matrix

A team of 17 co-authors (Huang et al., 2016) compiled the taxon/character matrix including only 16 arbitrarily selected recent and extinct insect species and only 60 arbitrarily worded characters. This matrix and the character descriptions can be found in Supplements S3 and S4 to the cited paper, where they are presented in a barely legible form; in order to study the data, I had to perform tedious work of copying, converting, and manual text editing. Of the 60 characters included in the matrix, about 2/3 turned out to be either incorrect or meaningless. Some of them are considered below under the same numbers as in the original paper.

1. Head opisthognathous / not opisthognathous. In reality, the head position in insects shows complete transition from prognathous to hypognathous to opisthognathous; in some cases the head position is related to important morphological details (such as the presence of the postgenal bridge in Heteroptera), while in other cases it is variable (for instance, in cockroaches the head is hypognathous at rest and prognathous during feeding).

6. Position of anterior tentorial pits. For the recent Thysanoptera it is described as shifted dorsally in Supplement S3 and as frontal in S4. For *Southia*, it is erroneously described as shifted dorsally; in fact it is ventral as in all the Subtericornes.

7. The cited authors considered similarity between Tetrastigmoptera and *Southia* (representing Arthroidignatha) in the position of the ocelli on the anterior head wall; however, in Tetrastigmoptera this position corresponds to the ancestral state for insects, whereas in *Southia* it is related to a specific head shape, which is an autapomorphy of Subtericornes and is absent in the other Arthroidignatha.

8. Ocelli positioned close together / far apart. This feature is indeed used as a diagnostic character for some taxa but it is variable or has an intermediate state in other taxa; therefore it cannot be entered in the matrix for all the insects.

9. Clypeus divided / not divided into the ante- and postclypeus by a furrow. In Supplement S3 the clypeus is described as divided in some Arthroidignatha (Cicadoidea but not Aphidoidea), some Copeognatha, and all Thysanoptera; in S4 it is described as divided in both species of Copeognatha and the only species of Arthroidignatha included in the matrix. It is not clear what structures are referred to as "anteclypeus" and "postclypeus": in different species (including Aphidoidea) the clypeus may have various transverse grooves or furrows. In case of Thysanoptera, the cited authors use the term "anteclypeus" for the articulatory membrane between the clypeus and the labrum, rather than for the part of the clypeus separated by a furrow.

10. The "postclypeus" is erroneously described as very large in *Thrips* and *Southia*. In reality, the clypeus in *Thrips* is small and not protruding (similar to the rest of Thysanoptera; see Figs. 1, 2); in *Southia* and other Subtericornes, the clypeus is strongly reduced in size.

11. The presence of separated paraclypeal lobes is erroneously indicated as a synapomorphy of Tetrastigmoptera, Thysanoptera, and Arthroidignatha (see section 4.5).

12. The membranous median part of the clypeus is erroneously indicated as a shared character of Tetrastigmoptera and Thysanoptera (see section 4.5).

13. The elongate labrum (at least twice as long as wide) is indicated as a synapomorphy of Tetrastigmoptera, Thysanoptera, and Arthroidignatha. Among Tetrastigmoptera, this character is given not only for *Psocorrhyncha* but also for three other fossil species in which the labrum proportions are unknown. In reality, however, the labrum of Thysanoptera and Arthroidignatha may be less than twice as long as wide (see Fig. 1). Strong elongation of the labrum has occurred independently in different insect taxa, for instance, in Diptera and Aphaniptera not included in this analysis.

14. The left mandible of Thysanoptera is correctly described as stylet-like in Supplement S3 but it is listed as not stylet-like in Table S4.

15. The right mandible of Thysanoptera is described as stylet-like, though in fact it is completely absent.

17. The lacinia of Tetrastigmoptera is erroneously described as detached from the stipes (see section 5.2.2).

21. In Table S4, the presence of the separate cardo and stipes is indicated for *Southia* and *Moundthrips*; the former is clearly erroneous since in all the Arthroidignatha the cardo and stipes are incorporated into the head wall, while for the latter species there are no such data in the description (Nel et al., 2007).

22. Gena subdivided / not subdivided into two parts. This character is based on incorrect homologization of some parts of the head capsule and the maxilla (see section 4.5). Table S4 includes 3 states (0, 1, and 2), whereas only 2 states (0 and 1) are described in Supplement S3.

23. Five segments in the maxillary palp are erroneously indicated for *Xyela*; in fact, the number of segments is secondarily increased to seven.

27. No more than two segments in the labial palp are erroneously indicated for Thysanoptera; in fact, there may be more segments (see Figs. 1, 2).

30. Pearman's organ: 2 states of this character (0 and 1) are given in Supplement S3, but 3 states (0, 1, and 2) are given in Table S4.

31. Number of tarsomeres. This character refers only to the number of tarsomeres in adults without regard to their ontogeny, so that it fails to reveal the synapomorphy of Zoraptera, Copeognatha, and Condylognatha (see section 5.5).

32. The presence of paired tarsal plantulae is erroneously indicated for *Eusthenia* and *Periplaneta*; in reality paired plantulae are absent in all the Plecoptera and Pandictyoptera. In Supplement S3, loss of paired plantulae is regarded as an apomorphy of Eumetabola. In reality, however, paired projections (plantulae) on tarsomeres may appear in various unrelated insects that step on the whole tarsus (i.e., many beetles); yet they are absent in most insects.

37. The fringe on the posterior wing edge is indicated as present in *Moundthrips*, whereas the absence of a fringe is mentioned in the taxon's description (Nel et al., 2007).

39. Hind wing not much smaller / much smaller than fore wing. This character is interpreted in a very arbitrary way. In particular, the hind wing is equally diminished in Hymenoptera (including *Xyela*) and in Copeognatha (including *Burmacompsocus* and *Libanomphientomum*); yet it is described as large in *Xyela* but as small in *Burmacompsocus* and *Libanomphientomum*.

40. The common stem $R + M + CuA$ is erroneously described as absent in *Xyela*; in reality this stem is present in all the Hymenoptera.

45. Vein $M$ in *Eusthenia* is erroneously taken to have more than 4 branches (in reality it is 2-branched as in most other Plecoptera); in *Zorotypus* it is erroneously described as 3-branched (in reality it is unbranched).

46. Vein $RP$ in *Xyela* is erroneously described as unforked (in reality it is forked, as opposed to Neohymenoptera Grimaldi et Engel, 2005).

52. The presence of a "jugal bar" is indicated for Eumetabola. If this term is taken to mean a certain structure associated with the jugal area of the wing, then its presence is erroneously indicated for *Xyela* (and Hymenoptera as a whole), both members of Copeognatha, and *Southia* (and Parametabola as a whole). Alternatively, if this term refers to any apparatus (not necessarily in the jugal area) coupling the fore and hind wings in flight, then its absence is erroneously indicated for *Thrips* (see section 5.3). In any case, this "jugal bar" cannot be an ancestral character of Eumetabola (see section 5.3).

53. The presence of abdominal sternite I is erroneously indicated for *Xyela*, in which it is absent, similar to the rest of Hymenoptera.

54. Abdominal segment I not very narrow / very narrow. This character is interpreted in a very arbitrary way; in Supplement S3 the authors describe this character as variable even among the members of Copeognatha known to them, and also mention *Lachesilla* that is not included in Table S4.

55. Abdominal tergites IX and X in females of Thysanoptera are described as reduced. In reality, they are not reduced but enlarged as compared with those of most other insects.

57. The presence of an ovipositor is erroneously indicated for *Eusthenia*; in fact, the ovipositor has been lost in all the Plecoptera.

58. The presence of a gonangulum not fused with tergum IX is erroneously indicated for *Eusthenia* (which, as in all the Plecoptera, have lost not only the gonangulum but the whole ovipositor), whereas its absence is erroneously indicated for Acercaria and Odonata in Supplement S3. In reality, a fully functional ovipositor with a clearly separated gonangulum is retained in some Acercaria and in some Odonata (Kluge, 2000: fig. 62).

59. The presence of gonostyli is erroneously indicated for *Eusthenia* and *Xyela*. In reality, both sexes of *Eusthenia*, as well as other Plecoptera, have no structures homologous or analogous to gonostyli. True gonostyli are absent in *Xyela*, similar to the rest of Metabola (Kluge, 2003); however, the gonoforceps or volsellae, present in Hymenoptera and derived from the phallic complex, are regarded as derivatives of the gonostyli by some authors.

*6.2. The Larger Matrix*

Two other authors (Yoshizawa and Lienhard, 2016) compiled the taxon/character matrix with 33 taxa (including some high-rank taxa and some random species) and 118 chaotically arranged random characters, and on this basis built the similarity dendrogram (Yoshizawa and Lienhard, 2016: fig. 6). In a different similarity dendrogram based on the same matrix, generic names were used instead of the names of higher taxa (Yoshizawa and Lienhard, 2016: fig. 5): for example, the name of the order Odonata was replaced with an invalid generic name *Ictinus*, the name of the order Hymenoptera, with the generic name *Xyela*, the nonexistent taxon Coccina, with the generic name *Coccus*, and so on. In some cases such replacement has considerably changed the meaning, since many characters are correct for the given genus but incorrect for the whole order. The line containing the characters of *Embidopsocus* is shifted one column left; this must have affected the results of calculations. More than a half of the characters in the matrix are either incorrect or meaningless. They are listed below under the same numbers as in the original paper.

4. In the table the mandibles of Hymenoptera are described as not elongated, as opposed to the elongated ones in *Mydiognathus*; in reality, the mandibles in some Hymenoptera are elongated to the same degree as in *Mydiognathus*. In the dendrogram the order Hymenoptera is replaced with the genus *Xyela*, in which the mandibles are indeed not elongated.

5. The presence of a separate cardo is indicated for Thysanoptera; in reality, the separate sclerites occurring at the maxilla base in thrips (see Fig. 2) do not correspond to the cardo; unlike the true cardo, they are not movable and have no muscles connecting them to the tentorium.

6. The lacinia is described as absent in Siphunculata (under the incorrect name "Anoplura") and as present in Amblycera and Ischnocera; in reality, all the three taxa have the same character state: the lacinia is either absent or vestigial (see Fig. 5).

7. The lacinia is described as detached from the stipes for all the members of Copeognatha, Mallophaga, and Arthroidignatha but not for Thysanoptera. In reality, the lacinia has the same morphology in Thysanoptera and Arthroidignatha: it is separated from the stipes but reconnected to it (or to the head wall with which the stipes has fused) by a secondary lever passing inside the head from the base of the lacinial pouch to the integument (see Figs. 1, 2).

8. The laciniae of Amblycera and Ischnocera are described as elongate and stylet-like, whereas in reality they are either absent or strongly reduced.

12. Since the presence of the "jugal bar" is indicated for members of Hymenoptera, Copeognatha, and Condylognatha, I assume that this term refers to the apparatus coupling the wings in flight, even though in these insects the actual coupling apparatus is not associated with the jugal area (see section 5.3); in this case the indication of the "jugal bar" is erroneous for *Nevrorthus* (belonging to Neuropteroidea-Birostrata), because the wings of all the Neuropteroidea remain uncoupled in flight. The presence of the "jugal bar" is also incorrectly indicated for *Liposcelis* which has no wings.

14. In the table the larval eyes of Hymenoptera are erroneously described as disintegrate or internal (in reality they are compound with a single ommatidium, if present at all), and those of Scytinelytra, as well developed (in reality they are internal). In the dendrogram the order Hymenoptera is replaced with the genus *Xyela*, whose larvae have lost their eyes due to development in plant tissues.

15. The external wing buds are erroneously described as absent in Hymenoptera and Birostrata (under the incorrect name "Neuroptera"); in reality, protoptera (external wing buds) are present in all the Metabola at the last preimaginal instar which is commonly called the pupa. In the same entry, the external wing buds are erroneously described as present in Scytinelytra; in reality, this is the only taxon in which protoptera are absent at all the development stages and wings are formed during one molt.

16. The presence of the pupal stage is erroneously indicated for Thysanoptera; if the dormant nymphs of thrips can be called "pupae," this term should also apply to exactly the same stages in Gallinsecta, for which no pupae are indicated.

17. The presence of compound eyes at preimaginal stages is erroneously indicated for Zoraptera, Scytinelytra, and Gallinsecta; in reality, compound eyes appear in these insects only during the final molt.

18. The presence of ocelli at immature stages is erroneously indicated for Zoraptera; in reality, larvae of Zoraptera have neither ocelli nor eyes.

20. The presence of tegulae is indicated for Odonata and all the other insects except Heteropteroidea; in reality, it is hardly possible to determine any homologous parts in the wing articulation mechanisms of Odonata and other insects.

20–39. These characters, pertaining to the wing articulation apparatus, are interpreted differently by different researchers. Such taxa as *Tettigonia*, *Locusta*, Hymenoptera, Birostrata, and Zoraptera have been well studied in this respect, and the fact that the corresponding characters are listed as unknown shows lack of thoroughness on the part of the cited authors.

40. The lateral hypopharyngeal arm is described as present in some Arthroidignatha and in Saltatoria. In reality, however, the hypopharynx of all the Arthroidignatha has uniform modified morphology and includes the salivary pump whose muscles are inserted on special lateral sclerites; nothing of the kind is present in Saltatoria.

43. The presence of abdominal sternite I is arbitrarily indicated for different taxa: for instance, this sternite is described as present in Hymenoptera (where it is always absent), and as absent in Cicadidae (where this sternite serves for attachment of the enormous muscles of the stridulatory apparatus).

44. Number of axonemes in spermatozoans: the list of characters includes 4 states (0, 1, 2, and 3) while the matrix includes only 2 states (0 and 1) quite arbitrarily assigned to different taxa.

45. The gonangulum is erroneously described as fused with tergum IX in Odonata, Scytinelytra, various Auchenorrhyncha, Heteroptera, and Coleorrhyncha; in reality, the ovipositor in these taxa is fairly well developed, functional, and has a detached gonangulum. At the same time, the gonangulum is described as separate in Plecoptera, Neuropteroidea, and Zoraptera; in reality, in Neuropteroidea the gonangulum is either fused with tergite IX or lost, whereas in all the Plecoptera and Zoraptera both the ovipositor and gonangulum have been completely lost.

48. The symmetry / asymmetry of the male genitalia is characterized as unknown for the studied member of of the genus *Mydiognathus*, although the genitalia of this species are described and illustrated in the same paper.

51. The number of ommatidia in the first-instar larva is given based on a single publication on Heteroptera, without comparison with other taxa.

52. The number of tarsomeres in the first-instar larva is described as unknown for most taxa (though it is well known); the tarsi of all the Heteroptera are described as 1-segmented, whereas in fact the first-instar larvae of most Heteroptera have 2-segmented tarsi.

55. The presence of metathoracic scent glands is erroneously indicated for Coleorrhyncha.

56. The morphology of the labium is described as unknown for Rhynchophtyrina and Siphunculata (in reality, the labium is absent in Rhynchophtyrina and protractile, stylet-like in Siphunculata). The proboscis of Psyllina is erroneously described as 3-segmented (in reality it is 2-segmented); the proboscis morphology in Scytinelytra is reported as unknown (although it is clearly 3-segmented in this taxon); the proboscis of Aphidina is erroneously described as 3-segmented (in reality 4-segmented in most members); that of Coleorrhyncha is erroneously described as 4-segmented (in reality 3-segmented).

59. The number of flagellomeres is erroneously described as not greater than 4 in Odonata (there are usu-

ally 5) and as greater than 4 in Hymenoptera (in fact the number varies among different members of the taxon). In fig. 5 the order Hymenoptera is replaced by the genus *Xyela*, in which the number of flagellomeres is indeed greater than 4.

60–69. These characters are probably restricted to the genitalia of Panpsocoptera and incomparable with other insects; such terms as "mesomere," "anterodorsal extension of ventral plate," and "posterior end of basal plate" are not applicable to most insects.

70. This is the same as character 18; the presence of paired ocelli in larvae is again erroneously indicated for Zoraptera.

72. It is not clear what is meant by the "ventral metasternal process": since the whole metasternum lies ventrally, any of its processes may be called "ventral."

76. The structure referred to as pedicel in this entry ("proximal abdomen pediculate by reduction of the 1st and 2nd segments") has essentially different morphology in Saltipedes and Scytinelytra. The absence of a pedicel is indicated for Hymenoptera, although most of these insects are Apocrite with a pediculate abdomen. In fig. 5 the order Hymenoptera is replaced by the genus *Xyela*, where the abdomen is indeed sessile.

77. Broad and closely adjacent hind coxae are indicated for Saltipedes and Scytinelytra; in reality, the hind coxae have essentially different morphology in these taxa, whereas wide and contiguous hind coxae also occur in Copeognatha and many other insects.

78. An organ named "proboscis" is indicated for Rhynchophthirina (apparently this is the rostrum formed by the head capsule), Siphunculata (it is unknown what the authors mean), Thysanoptera (also unknown), and various Arthroidignata (probably this is the articulate proboscis formed by the labium). In addition, according to the authors, the proboscis is shifted posteriad and positioned between the coxae in Scytinelytra and Gynaptera but not shifted in the various Auchenorrhyncha and in Coleorrhyncha; in reality the proboscis has the same position in all these taxa.

79. The posterior part of the head capsule is erroneously described as membraneous in all the Plantisuga; in reality, the head is desclerotized only in some larvae and in neotenic forms.

81. The ovipositor is described as simplified only in Mallophaga and Rhynchophthirina and as not simplified in all the other taxa, including Plecoptera, Zoraptera, Gallinsecta, etc., in which the ovipositor has been completely lost.

84. The fusion of the "pronotum" and fore coxae is indicated for Rhynchophthirina and Siphunculata. In reality, all the legs including the fore ones are quite mobile, and their coxae are movably articulated to the body in both taxa.

85. The anterior tentorial pits are described as positioned frontally or dorsally in an arbitrary way; for example, they are described as shifted dorsally in Thysanoptera, Saltipedes, Gallinsecta, Cercopidae, Cixiidae, Delphacidae, Fulgoridae, Coleorrhyncha (in which they lie on the ventral side), and Heteroptera (in which they are totally absent).

86. The fusion of the head and thorax is indicated for Gallinsecta; in reality, the head is not fused with the thorax in adult males, whereas indistinct separation of the head in larvae and neotenic females is observed in these and some other Plantisuga.

87. The body and head are described as flattened or not flattened for different taxa in a totally arbitrary manner.

88. The hind femora are arbitrarily described as enlarged or not enlarged in different taxa (for instance, enlarged in Amblycera and Ischnocera but not enlarged in Zorapera).

90. The presence of no more than two ommatidia in the compound eyes is erroneously indicated for Gallinsecta, in which males have a greater number of ommatidia.

91. The labial palps are erroneously described as absent in *Caecilius* and Amblycera.

93. The aristate antennal flagellum is erroneously indicated for Odonata and Cicadidae; their larvae have a regular segmented flagellum, while in adults the antennae are reduced in size but retain the same set of segments.

96. The unicondylar / dicondylar mandibular and lacinial stylets. This character appears obscure since the mandibular and lacinial stylets differ in origin and can-

not have a common character; besides, the lacinial stylet has no condyles.

97. Pedunculate eggs are indicated for some arbitrarily chosen taxa.

99. The coronal (= median epicranial) suture is arbitrarily described as absent in some taxa and present in others. In reality, this is the suture along which cuticle is ruptured during molting; therefore it is present in all the larvae and may also be more or less expressed in adults.

100. The presence of a special kind of parempodia, believed to be primitive for Heteroptera, is erroneously indicated for Saltipedes.

101. The number of tarsal segments in Odonata is erroneously described as greater than 3 (in reality, there are 3 segments).

102–118. These are some details of the pretarsus morphology which are described for certain taxa but are incomparable with the corresponding data for other insects.

107. The claw teeth are arbitrarily described as present in some taxa and absent in others; in reality, such teeth occur in certain species within many of the considered taxa.

## 7. CONCLUSIONS

The extinct taxon Tetrastigmoptera had existed at least since the Permian till the Late Cretaceous. It is not closely related either to psocids (Copeognatha) or to thrips (Thysanoptera), and does not belong to Acercaria at all. Even if this taxon is related to Parametabola, it forms a lineage external to all the recent Parametabola including Zoraptera. It is possible that Tetrastigmoptera developed with complete metamorphosis and thus the taxon belongs to Metabola. It is also possible that Tetrastigmoptera belong to the taxon Eumetabola uniting Metabola and Parametabola, but at the same time do not belong to either Metabola or Parametabola.

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