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Bridging the gap between chewing and sucking in the hemipteroid insects: new insights from Cretaceous amber

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Abstract

The diversity of feeding apparatuses in insects far exceeds that observed in any other animal group. Consequently, tracking mouthpart innovation in insects is one of the keys toward understanding their diversification. In hemipteroid insects (clade Paraneoptera or Acercaria: lice, thrips, aphids, cicadas, bugs, etc.), the transition from chewing to piercing-and-sucking mouthparts is widely regarded as the turning point that enabled hyperdiversification of the Hemiptera, the fifth largest insect order. However, the transitional process from chewing to piercing-and-sucking in the Paraneoptera was hitherto completely unknown. In this paper, we report a well preserved mid Cretaceous amber fossil of the paraneopteran insect family Archipsyllidae and describe it as *Mydiognathus eviohlhoffae* **gen. et sp. n.** This species has elongate mandibles and styliform laciniae similar to Hemiptera but retains functional chewing mouthparts. A number of morphological characters place the Archipsyllidae as the sister group of the thrips plus hemipterans, which strongly suggests that the mouthparts of *M. eviohlhoffae* represent a transitional condition from primitive chewing to derived piercing-and-sucking mouthparts. The clade composed of Archipsyllidae, thrips, and hemipterans is here named Pancondylognatha, a new supra-ordinal taxon. Based on newly obtained information, we also assess the monophyly of the Paraneoptera, which was called into question by recent phylogenomic analyses. A phylogenetic analysis that includes *Mydiognathus* strongly supports the monophyly of the Paraneoptera.

Key words: Burmese amber, Archipsyllidae, Paraneoptera, Pancondylognatha, Condylgnatha, new genus and species

Introduction

Insects are the most diversified group of Eukaryotes and are highly variable in many traits (Grimaldi & Engel 2005). Feeding habit is one such trait, and insect diets include herbivory, predation, sap feeding, blood feeding, and filter feeding of particulate matter. In many cases, utilization of a new food source was enabled by innovations of the mouthparts, so reconstructing the evolutionary development of insect mouthpart structures is very important in understanding the background to insect diversification (Labandeira 1997). Piercing-and-sucking is a mode of insect feeding that has evolved independently several times, at different levels in the taxonomic hierarchy: family (e.g. mosquitoes), supra-family (e.g. sucking lice) or order (e.g. fleas, lacewing larvae) (Grimaldi & Engel 2005). Generally, the earlier the occurrence of an evolutionary event, the harder it is to trace its transition pattern.

Specialized sucking mouthparts characterize a supra-ordinal clade, the Condylgnatha (Thysanoptera plus Hemiptera), which also represents the second major insect group to acquire novel sucking mouthparts in insect phylogeny (Misof *et al.* 2014), that was preceded only by the very diverse Palaeodictyopteroidea (Labandeira & Phillips 1996). Hemiptera (aphids, cicadas, plant hoppers and true bugs) are by far the most diversified extant order among hemimetabolous insects, and are the fifth largest order of insects (Grimaldi & Engel 2005). Although hemipterans show a wide range of feeding habits (Carver *et al.* 1991; Grimaldi & Engel 2005; Forero 2008), all major lineages possess highly specialized and quite uniform piercing-and-sucking mouthparts, with the mandibles and maxillary laciniae modified as stylets, forming a tube, which lies within a groove of the labium. This feeding apparatus is recognized as one of the key innovations (Müller & Wagner 2003) that enabled Hemiptera to become a

hyperdiverse order (Carver *et al.* 1991; Grimaldi & Engel 2005). The mouthparts of thrips (Thysanoptera) are less specialized than those of Hemiptera but are also fully adapted for piercing-and-sucking and consist of a styliform lacinial tube and a single piercing mandible, even in the most primitive fossil species (Nel *et al.* 2007, 2014).

Psocodea (booklice, barklice and parasitic lice) are generally believed to be the sister group of the Condylgnatha, the two forming a supra-ordinal group known as the Paraneoptera, Acercaria or, informally, the hemipteroid assemblage (e.g. Yoshizawa & Saigusa 2001; Grimaldi & Engel 2005; Misof *et al.* 2014). Psocodeans have a chisel-like lacinia ("the pick"), which is recognized as an intermediate condition between primitive chewing mouthparts, as found in grasshoppers, and the sucking mouthparts of thrips and hemipterans (Yoshizawa & Saigusa 2003). However, apart from lacinial specialization, psocodeans (except for independently specialized sucking lice: Lyal 1985; Yoshizawa & Johnson 2010) have typical mandibles that lack specialization (Badonnel 1934; Yoshizawa 2002). In addition, the lacinial tips of psocodeans are widely separated and placed external to the buccal cavity (Kéler 1966; Hamilton 1981; Yoshizawa 2002), so their function is completely different from that of the laciniae in the Hemiptera and Thysanoptera, which are placed close together within the buccal cavity. These mouthpart distinctions indicate that there are broad morphological and functional differences between the chewing and piercing-and-sucking mouthparts in the Paraneoptera. Some fossil paraneopterans (e.g. Archipsyllidae or *Dichentomum* Tillyard 1926), which are believed to represent ancestral lineages of Paraneoptera, show an anteriorly elongated, somewhat rostrum-like head structure. These lineages may be intermediate between chewing and piercing-and-sucking feeders, but the morphological details of their mouthparts were hitherto poorly known.

In addition to the evolution of the novel feeding apparatus, the Paraneoptera also present a major problem for systematics. A recent phylogenomic analysis (Misof *et al.* 2014) provided a highly resolved insect phylogeny, which is in general overall agreement with morphologically derived phylogenies (e.g. Grimaldi & Engel 2005; Beutel *et al.* 2011; Yoshizawa 2011). The most significant conflict between morphology and phylogenomics concerns the monophyly of the Paraneoptera; phylogenomics places Psocodea as sister group of Holometabola (Misof *et al.* 2014), whereas morphological analysis places Psocodea as sister to Condylgnatha (Yoshizawa & Saigusa 2001; Grimaldi & Engel 2005; Friedemann *et al.* 2014; Beutel *et al.* 2014). Although monophyly of the Paraneoptera was not supported by other molecular phylogenies (Yoshizawa & Johnson 2005; Ishiwata *et al.*, 2011), in all cases including phylogenomics, monophyly of the Paraneoptera could not be rejected statistically. Together with the perennial "Zoraptera problem" (Mashimo *et al.* 2014), monophyly of the Paraneoptera has become one of the remaining controversies in the phylogeny of insect orders (Misof *et al.* 2014). In resolving the "Paraneoptera problem", detailed information on the fossil taxa of Paraneoptera is of special importance because their morphology may indicate ground plan for the broader clade.

Here we report a very well preserved Cretaceous amber fossil of the family Archipsyllidae. Archipsyllidae are an extinct taxon generally considered to represent a stem lineage of Paraneoptera (Grimaldi & Engel 2005) or Psocodea (Huang *et al.* 2008). To date, the family has been known only from impression fossils, so detailed morphological information was unavailable. From the new amber specimen, novel morphological data highly relevant to the paraneopteran phylogeny and evolution can be obtained. We provide a morphological description of the specimen, assigning it to a new genus and species. We then discuss phylogenetic placement of this specimen and the significance of the new morphological information for understanding paraneopteran evolution.

Material and methods

A single piece of Cretaceous amber collected in Myanmar (Burmite) was examined. The amber was polished using Roxite (Iwamoto Mineral Co., Tokyo) after cutting and grinding. Observations were made using an Olympus SZX16 (Olympus Imaging Corporation, Tokyo) binocular microscope and a Zeiss Axiophot (Carl Zeiss AG, Jena) light microscope. Photographs were taken using an Olympus E-M5 (Olympus Imaging Corporation, Tokyo) digital camera attached to the Olympus SZX16 or Zeiss Axiophot. Partially focused photographs were combined using Zerene Stacker (Zerene Systems LLC, WA) to obtain images with a high field of depth.

The phylogenetic placement of the Archipsyllidae was tested by appending morphological data obtained from the new fossil specimen to a matrix previously used to estimate paraneopteran phylogeny (Friedemann *et al.* 2014). A miscoding was corrected, and the interpretation of a couple of character states were modified (see below and Table 1). The maximum parsimony analyses was performed using PAUP*4a142 (Swofford 2002). All characters

were equally weighted, and a branching and bound search was performed. The calculation of tree scores was also performed using PAUP*4a142. Bremer support values were calculated using TreeRot v3 (Sorenson & Franzosa 2007). The character state changes were calculated using MacClade 4 (Maddison & Maddison 2001). Table 1 provides a list of characters and their states, and the analyzed data matrix is deposited at TreeBase (<http://purl.org/phylo/treebase/phylows/study/TB2:S17857>).

As far as can be observed, the genital structures of Archipsyllidae are not so highly specialized as in the Hemiptera or Thysanoptera. We therefore adopted more general terms, as used for Orthoptera and Psocodea (Tuxen 1970; Beutel *et al.* 2014), to describe genital morphology. The following abbreviations were used for description of the forewing base articulations. ANWP, MNWP and PNWP: anterior, median and posterior notal wing processes; Tg: tegula; HP: humeral plate; BSc: basisubcostale; BR: basiradiale; 1, 2 and 3Ax: first, second and third axillary sclerites; PMP and DMP: proximal and distal median plates; BA: basianal (Snodgrass 1935; Yoshizawa & Saigusa 2001).

***Mydiognathus* n. gen.**

(Figs 1, 2a–c, 3a–c)

Type species. *Mydiognathus eviohlhoffae* Yoshizawa & Lienhard **n. sp.**

Etymology. Named after elongated mandibles (mydion: small forceps in Greek; gnathos: jaw in Greek).

Diagnosis. This new genus is a representative of Insecta, Neoptera, Paraneoptera, and a member of the family Archipsyllidae Handlirsch, 1906 (= sister clade to Condylognatha). It can be distinguished clearly from the other genera of this family (*Archipsylla* Handlirsch, 1906, *Archipsyllodes* Vishniakova, 1976, *Archipsyllopsis* Vishniakova, 1976 and *Psocopsylla* Özdikmen, 2009 [= *Eopsylla* Vishniakova, 1976, not *Eopsylla* Argyropulo, 1946; see Özdikmen, 2009]) by the following wing venation characters (Figs 1a,b, 3a) (Vishniakova 1976; Huang *et al.* 2008): Sc in forewing with only two sections (near wing base and at the base of pterostigma) in *Mydiognathus* whereas an additional section proximally of the pterostigma between wing margin and R1 in the other genera; basal Cua cross vein (or Cua itself in the sense of Nel *et al.* 2012) in forewing forked from R+M in *Mydiognathus* whereas from M in the other genera; areola postica (ap) in forewing strongly constricted proximally in *Mydiognathus* whereas broadest at the base in the other genera; ap absent in hindwing of *Mydiognathus* whereas present in the other genera as far as known. Apart from these differences, wing venational and other morphological characters are in good agreement with the features previously described for the family, justifying the placement of *Mydiognathus* in the Archipsyllidae. For detailed morphological information see the description of the type species.

***Mydiognathus eviohlhoffae* n. sp.**

(Figs 1, 2a–c, 3a–c)

Description. *Head* (Figs 1a–d, 2a–c). Hypognathous, detached from thorax. Vertex rounded, protruding dorsally; medially concave along occipital suture. Frons bulbous. Frontogenal suture directed backward from anterior tentorial pit along ventral head capsule then strongly curved dorsally, ending between eye and antennal socket. Gena expanded laterally. Eye large; three ocelli, each on a tubercle. Postclypeus not expanded dorsally, not bulged; anteclypeus less sclerotized, with pair of swellings laterally. Antennal socket strongly pedicellate. Antenna filiform, with at least 16 articles; scape nearly cylindrical; pedicel strongly constricted basally, cylindrical distally, with bifurcated tip; flagellum long, far exceeding forewing length, no rupturing mechanism recognizable; flagellomeres annulate except for first one (f1) and basal half of f2. Labrum much longer than wide, apically rounded, covering entire elongated mandibles anteriorly. Mandibles elongate, apically curved inwardly, with two subapical conical teeth; basally broadened, with asymmetrical molar area internally. Maxillae elongate, symmetrical; cardo strip-like, projecting outward posteriorly; stipes bulged posteriorly and laterally; galea clearly separated from stipes, flattened apically and curved internally; lacinia stylet-like, apically curved posterointernally, basally extended deeply into head capsule; palpus four segmented, second and fourth articles especially long, inner surface of terminal article flattened; palpifer well developed. Hypopharynx elongate, apically exceeding base of labial palpus; anterior surface with keel along median line, placed between lacinial stylets. Labium elongate,

medially concave forming groove housing elongated hypopharynx and lacinial stylets; paraglossa present; glossa absent; palpus four segmented (or three if the most basal tiny article represents palpifer).

Thorax (Fig. 1a,b). Prothorax small, detached from mesothorax. Meso- and metathorax fused, analogous in structures, well developed, bulged dorsally; scutum bilobed; scutellum pentagonal in shape; basalare well differentiated from episternum; anapleural suture not visible; posterior margin of epimeron protruding medially.

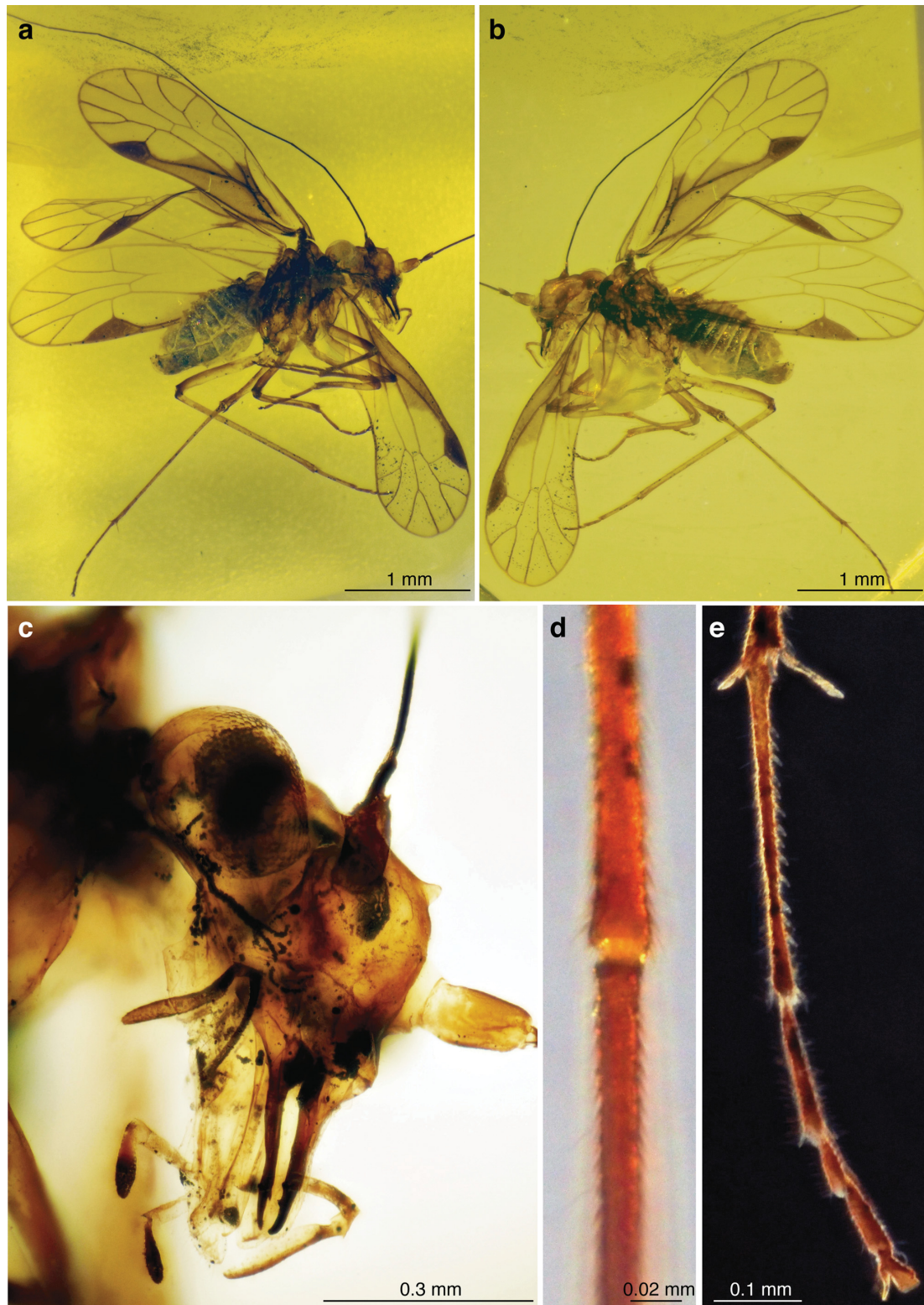


FIGURE 1. Photographs of *Mydiognathus eviohlhoffae*. (a) Habitus, right view. (b) Habitus, left view. (c) Head. (d) Connection between first (top) and second antennal flagellomeres. (e) Right hind tarsus, ventral view.

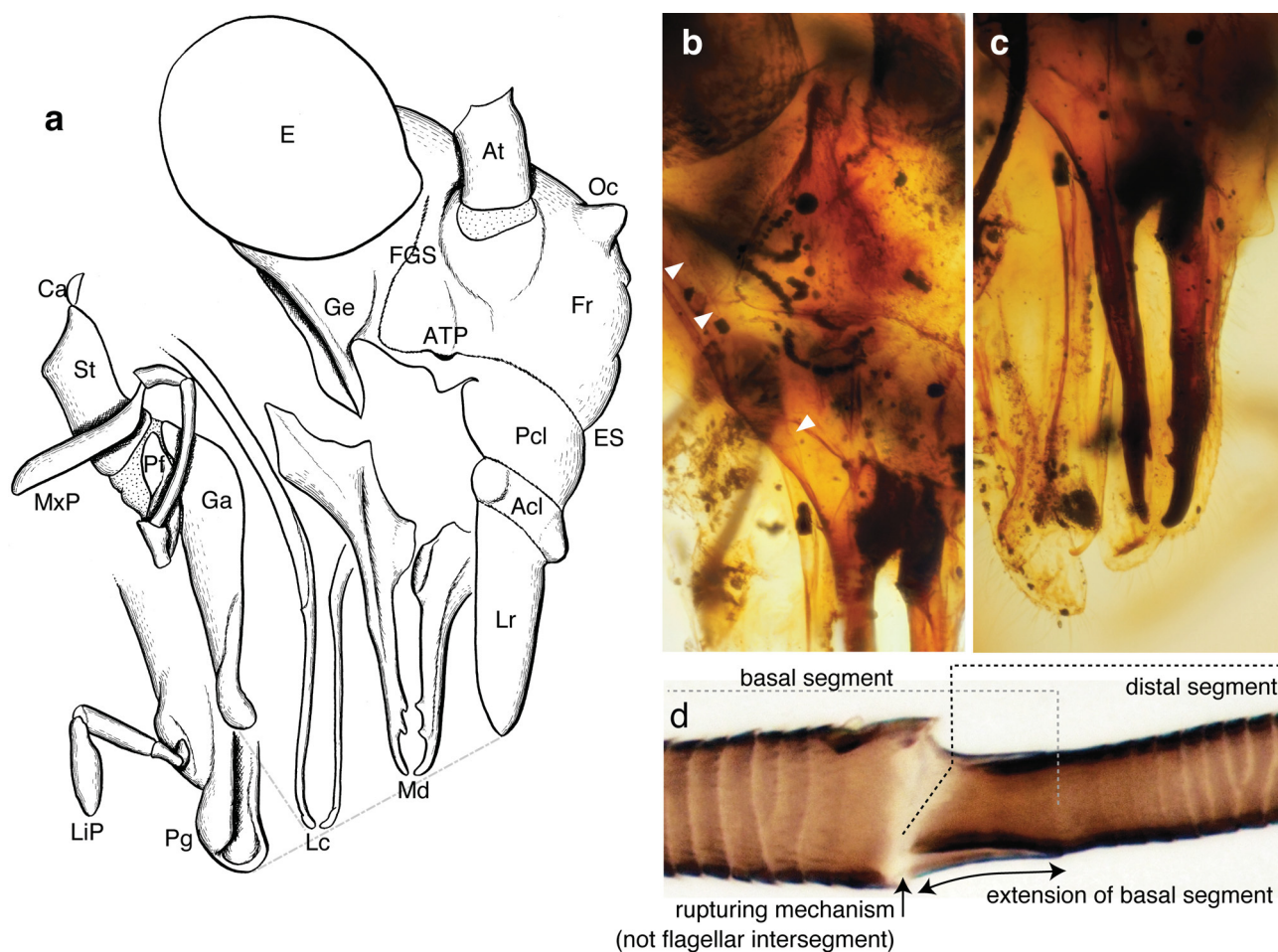


FIGURE 2. Key head structures of *Mydiognathus eviohlhoffae* (a–c) and *Neotroglia aurora* (d). (a) Head. Dotted gray lines indicate alignment of mouthpart structures against the labrum (Lr) or lacinia (Lc, only for galea: Ga) (Acl: anteclypeus; At: antenna; ATP: anterior tentorial pit; Ca: cardo; E: eye; ES: epistomal suture; FGR: frontogenal suture; Fr: frons; Ga: galea; Ge: gena; Lc: lacinia; LiP: labial palpus; Lr: labrum; Md: mandible; MxP: maxillary palpus; Oc: ocellus; Pcl: postclypeus; Pf: palpifer; Pg: paraglossa; St: stipes). (b) Head, magnified. White arrowheads indicate the internally expanded lacinial base. (c) Tip of the mouth, magnified. (d) Antennal flagellum of *Neotroglia aurora* (Psocodea: Trogiomorpha: Prionoglarididae), showing the rupturing mechanism observed in extant Psocodea.

Wings (Figs 1a,b, 3a). Membrane and veins of both wings evenly covered by microtrichia; margins setose. Forewing transparent with broad blackish brown region anteroproximally; Sc short, ending on anterior margin; pterostigma darkly pigmented but not significantly thickened; nodus and nodulus (fore- and hindwings coupling mechanism) absent; venation as indicated for family (Vishniakova 1976; Huang *et al.* 2008) and genus (see above); bases of Cu veins obscure. Hindwing slightly smaller and very similar to forewing, but areola postica absent.

Forewing base articulations (Fig. 3b,c). Tips of ANWP and MNWP invisible. PNWP narrow and long, tightly articulated with 3Ax. Tg well developed. HP and BSc fused. BSc and 2Ax separated by BR. First axillary sclerite hardly visible. Anterior region of 2Ax strongly swollen, divided into two sclerites; posterior region small and triangular, articulated with 3Ax. Proximal and distal arms of 3Ax short, anterior arm long. PMP deeply concave, distal margin strongly sclerotized, anteroproximal region broadly membranous, fused to BA posteriorly and distally. DMP small, located next to 2Ax.

Legs (Fig. 1a,b,e). All legs analogous in structures; hind leg significantly longer than other legs but no specialization detected (e.g. for jumping). Coxae well developed, no specialization on internal surface of hind coxae. Tibiae with two well-developed tibial spurs distally. Tarsi four segmented; pretarsal claws symmetrical, without preapical tooth, with well-developed arolium between them.

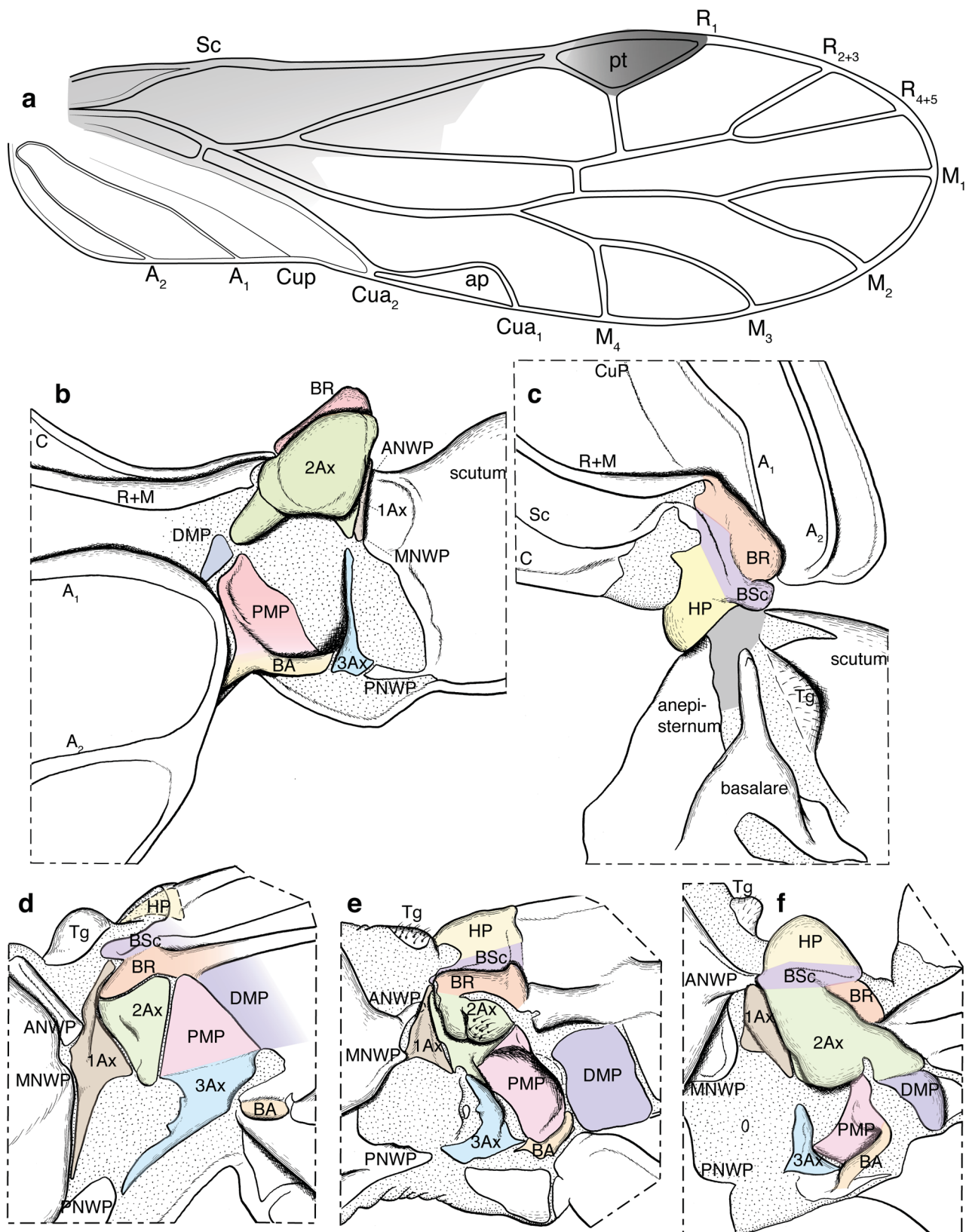


FIGURE 3. Illustrations of key wing structures in *Mydiognathus eviohlhoffae* (a–c) and other insect orders (d–f). (a) Forewing (composite drawing reconstructed from distal half of right forewing and basal half of left forewing). (b) Left forewing base articulation. (c) Right forewing base articulation. Forewing base articulation d–f: (d) *Alloperla* sp. (Plecoptera), (e) *Longivalvus nubilus* (Psocodea), (f) *Petalolyma bicolor* (Hemiptera).

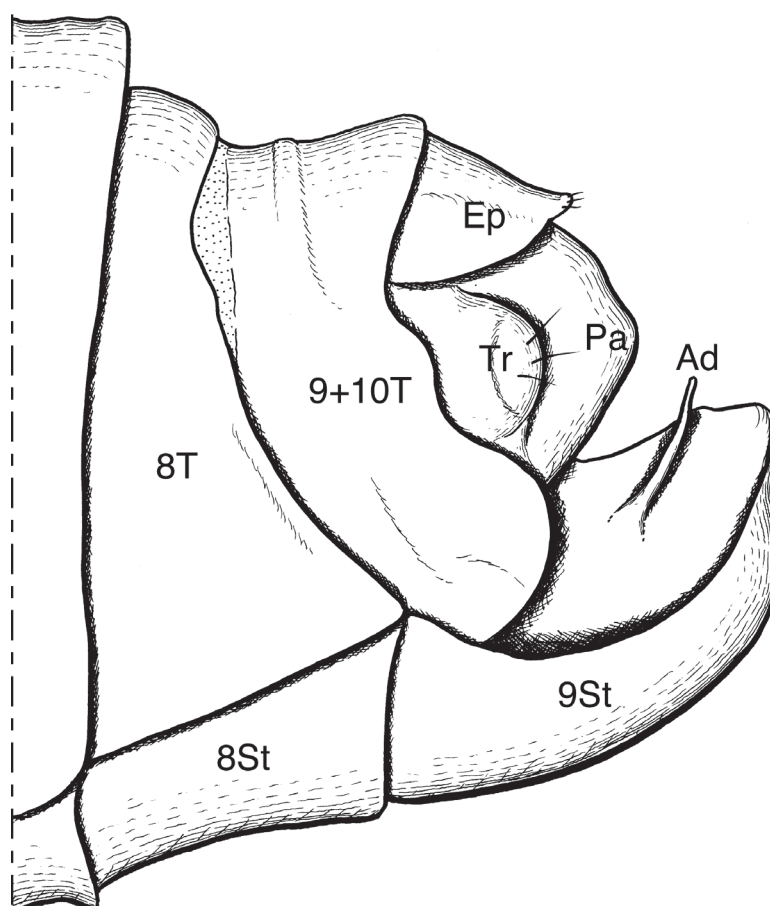


FIGURE 4. Male terminalia of *Mydiognathus eviohlhoffae* (St: sternite; T: tergite; Ad: aedeagus; Ep: epiproct; Pa: paraproct; Tr: trichobothria).

Abdomen (Figs 1a,b, 4). Weakly sclerotized, tergum and sternum well differentiated. First abdominal tergite clearly differentiated from second segment; sternite 1 not clearly differentiated. Terminal segments well sclerotized. Epiproct convex dorsally, pointed posteriorly. Paraproct rounded posteriorly, with swollen trichobothrial field. Ninth sternum strongly protruding posteriorly, genital chamber broadly open dorsally. Aedeagus pointed apically.

Lengths (seen from right side, in mm). Body 2.12; antennal flagellomere f1 0.60, f2 0.56, f3 0.61; forewing 2.38, hindwing 2.20; hind femur 0.68, hind tibia 1.26, hind tarsus t1 0.38, t2 0.16, t3 0.05, t4 0.06.

Holotype. Male. Embedded in Burmite, early Cenomanian (Upper Cretaceous, ca. 99 Mya: Shi *et al.* 2012), Hukawng Valley, northern Myanmar (to be deposited in State Museum of Natural History in Stuttgart, Germany, under specimen ID SMNS Bu-174).

Etymology. The specific epithet honours Evi Ohlhoff, wife of Rainer Ohlhoff (who made the specimen available for study) and codiscoverer of the specimen.

Phylogeny

Based on the above observations, morphological data of *Mydiognathus* were appended to the matrix previously used by Friedemann *et al.* (2014) to estimate paraneopteran phylogeny. Two specializations observed in *Mydiognathus* could not be incorporated into the matrix. Definitions of these character states were therefore modified as follows (see Table 1):

Character 4 shape of mandible: (0) not stylet; (1) stylet was interpreted as follow: mandible elongate (1); not elongate (0).

The state of this character for *Mydiognathus* was coded as 1 (Figs 1c, 2a,c).

Character 28 anterior axillary fold line: (0) not forked; (1) forked, and proximal branch running through the distal portion of 2Ax was interpreted as follow: 2Ax not divided (0); 2Ax divided (1).

This interpretation attributes the fork of the folding line to division of 2Ax. Although it is impossible to observe the wing folding lines directly in fossil specimens, the divided condition of 2Ax, as observed in Thysanoptera and Hemiptera, could clearly be seen in *Mydiognathus* (Fig. 3b).

Equally weighted parsimony analysis of 118 morphological characters (Friedemann *et al.* 2014) yielded 54 trees (tree length = 197, consistency index = 0.69, retention index = 0.85), and *Mydiognathus* was unambiguously placed within the Paraneoptera (Figs 5–6) with Bremer support value = 6, the second best supported branches within the tree. Within the Paraneoptera, *Mydiognathus* was always placed to the stem of the Condylgnatha, with Bremer support value = 2. The strict consensus of 54 trees is presented in Figs 5–6. Based on this result, we propose a new supraordinal taxon as follow.

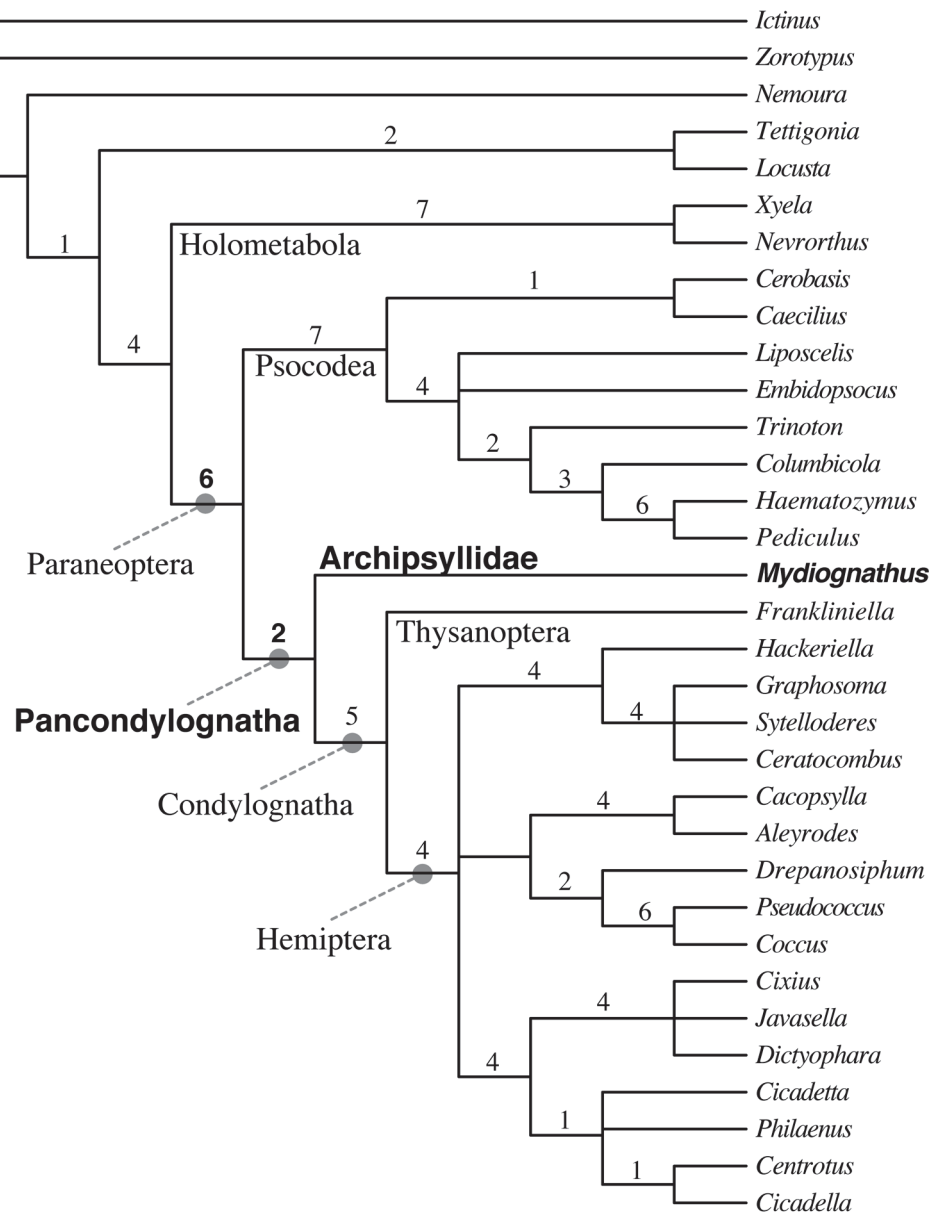


FIGURE 5. Strict consensus of the most parsimonious trees estimated from the data matrix of 118 morphological characters, showing placement of Archipsyllidae: *Mydiognathus*. Numbers above branches are Bremer support values.

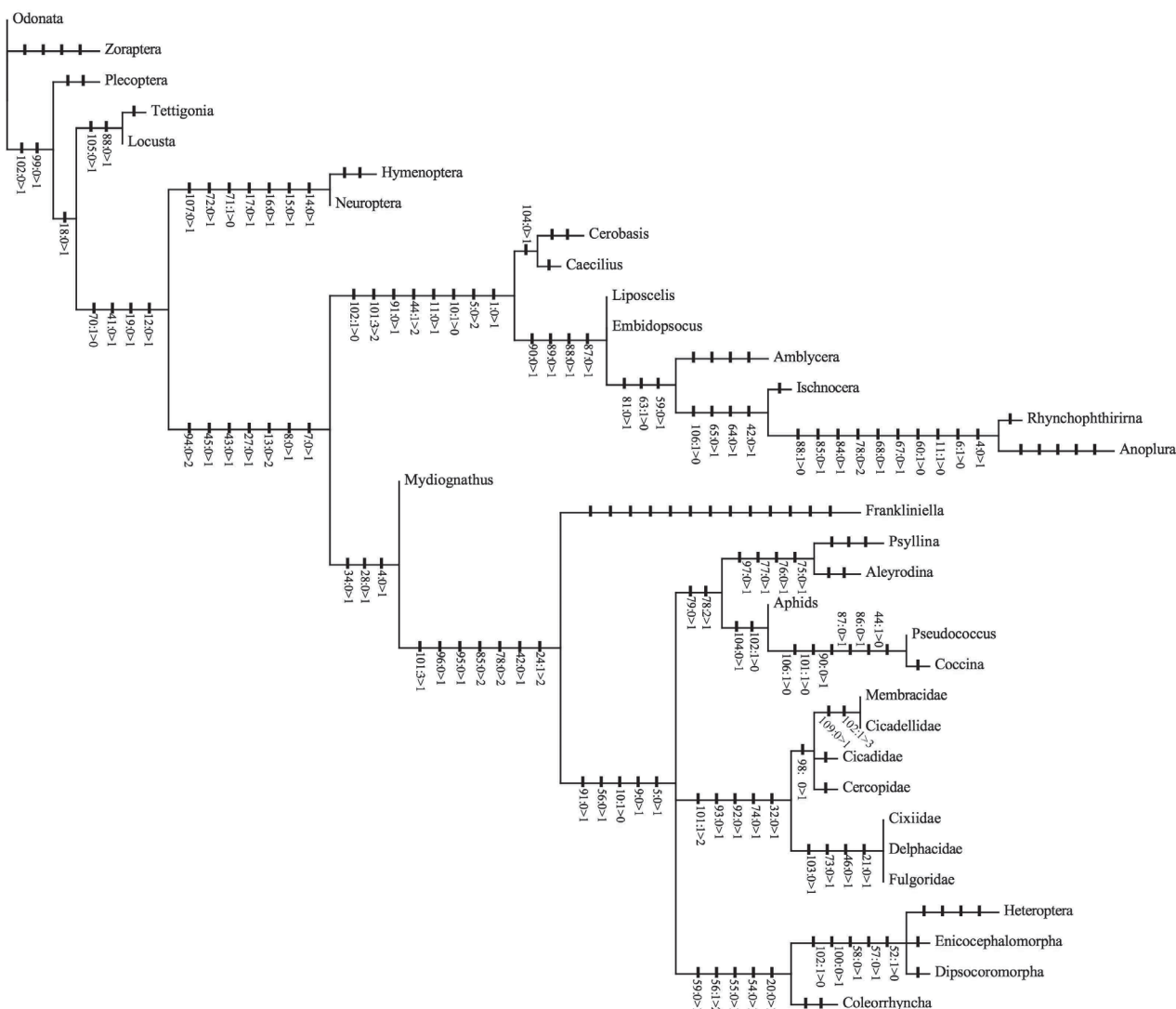


FIGURE 6. The most parsimonious reconstruction of the morphological characters used for phylogenetic estimation. Numbers before colon indicate character number (see Table 1), and character state changes are indicated after colon. Autapomorphies on the terminal branches are omitted from the figure.

TABLE 1. Characters used for phylogenetic analysis and states coded for *Mydiognathus*.

1. Rupturing mechanism at the base of the antennal flagellum: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
2. Exposure of mouthparts: (0) largely or completely exposed; (1) left mandible enclosed in a pouch formed by anteclypeal wall, labrum, stipes, and hypopharynx; (2) bases of mandibular and maxillary stylets articulate inside head with mandibular and maxillary plates. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
3. Right mandible: (0) present; (1) reduced. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
4. Shape of mandibles: (0) not elongated; (1) elongated. Character state interpretation modified (see “Phylogeny”); State 1 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.92$.
5. Cardo: (0) present; (1) strongly reduced or absent; (2) fused with stipes. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
6. Lacinia: (0) absent; (1) present. State 1 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
7. Insertion of lacinia: (0) on stipes; (1) detached from stipes. State 1 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.86$.
8. Lacinia: (0) not elongate and stylet-like; (1) elongate and stylet-like. State 1 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
9. Labial rostrum: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
10. Labial palps: (0) absent or strongly reduced; (1) comprising at least 2 segments. State 1 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.88$.
11. Cibarial water-vapour uptake apparatus: (0) absent; (1) present. “?” is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.80$.

12. Jugal "bar": (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
13. Abdominal ganglia: (0) more than two separate ganglia; (1) two separate ganglia; (2) one single ganglionic mass. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
14. Eyes of immature stages: (0) persist; (1) disintegrate or pulled back proximally into cerebrum. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
15. External wing buds: (0) present; (1) absent. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
16. Pupal stage: (0) absent; (2) present. "?" is adopted for *Mydiognathus*: $ci = 0.5, ri = 0.5$.
17. Appearance of compound eyes: (0) before ultimate immature stage; (1) in ultimate immature stage. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
18. Ocelli of immature stages: (0) present; (1) absent. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
19. Cerci of immature stages: (0) present; (1) absent. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 1$. Although immature stage of this fossil is known, absence of the cercus in adult clearly shows its absence in immature stages.
20. Tegulae of the forewing: (0) present; (1) absent. State 0 is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
21. Size and shape of tegulae: (0) small; (1) enlarged, with broad extension encircling the entire margin. State 0 is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
22. Attachment of tegulae to body wall: (0) narrow; (1) broad. State 0 is adopted for *Mydiognathus*: $ci = 0.5, ri = 0$.
23. HP and BSc: (0) separated from each other; (1) connected with each other. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
24. BSc: (0) distant from 2Ax; (1) closely adjacent with the anteroproximal corner of 2Ax; (2) fused with anteroproximal part of 2Ax. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
25. BR and HP + BSc: (0) fused with each other; (1) separated from each other. State 0 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
26. BR and 2Ax: (0) separated from each other; (1) fused. State 1 is adopted for *Mydiognathus*: $ci = 0.5, ri = 0$.
27. 2Ax: (0) nearly flat; (1) anterior region inflated. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
28. 2Ax: (0) divided; (1) not divided. (Character state interpretation modified: see "Phylogen") State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
29. Position of PMP: (0) distad 2Ax; (1) posterodistad 2Ax. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
30. PMP: (0) nearly flat; (1) deeply concave. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
31. PMP: (0) almost evenly sclerotized; (1) distal margin sclerotized more strongly than its other regions. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
32. PMP: (0) well sclerotized; (1) reduced, often completely membranous. State 0 is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
33. DMP: (0) not divided; (1) divided into 2 sclerites. State 0 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
34. DMP: (0) distant from 2Ax; (1) placed next to 2Ax, articulating along a convex hinge. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
35. DMP: (0) large; (1) reduced in size. State 1 is adopted for *Mydiognathus*: $ci = 0.5, ri = 0$.
36. Distal arm of 3Ax and DMP: (0) articulating with each other; (1) not articulating with each other. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
37. Anterior arm of 3Ax: (0) present; (1) absent. State 0 is adopted for *Mydiognathus*: $ci = 0.5, ri = 0$.
38. 3Ax and BA: (0) separate from posterior margin of forewing base; (1) attached to posterior margin of forewing base. State 0 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
39. BA and PMP: (0) separate from each other; (1) fused with each other. State 1 is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
40. Lateral hypopharyngeal arm (0) present; (1) absent. "?" is adopted for *Mydiognathus*: $ci = 0.5, ri = 0.88$.
41. Ovarioles: (0) not polytrophic; (1) polytrophic; (2) telotrophic; (3) panoistic. "?" is adopted for *Mydiognathus*: $ci = 0.75, ri = 0.92$.
42. Maxillary palps: (0) present, with four segments or more; (1) absent or reduced number of segments. State 0 is adopted for *Mydiognathus*: $ci = 0.33, ri = 0.82$.
43. Abdominal sternite 1: (0) present; (1) absent. State 1 is adopted for *Mydiognathus*: $ci = 0.5, ri = 0.8$.
44. Number of axonemes in spermatozoans: (0) zero; (1) one; (2) two; (3) three. "?" is adopted for *Mydiognathus*: $ci = 0.75, ri = 0.83$.
45. Gonangulum: (0) not fused with tergum IX; (1) fused with tergum IX. "?" is adopted for *Mydiognathus*: $ci = 0.5, ri = 0.8$.
46. Pretentorium: (0) absent or if present not connecting internal extremities of mandibular lever and corpotentorium; (1) unites internal extremities of mandibular lever and corpotentorium. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
47. Lacinial gland: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 0.5, ri = 0$.
48. Male genitalia: (0) symmetrical, or if asymmetrical, asymmetry not involving pregenital segments; (1) asymmetrical, this asymmetry often involving pregenital segments. "?" is adopted for *Mydiognathus*: $ci = 0.5, ri = 0$.
49. Accessory salivary glands generally: (0) not tubular; (1) of the tubular type. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
50. Number of eye trichobothria of first instars: (0) one or absent; (1) two. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 0$.
51. Number of ommatidia in first-instar larvae: (0) 4-5; (1) more than five. "?" is adopted for *Mydiognathus*: $ci = 0.5, ri = 0$.
52. Number of tarsomeres in first-instar larvae: (0) one; (1) two. "?" is adopted for *Mydiognathus*: $ci = 1, ri = 1$.
53. Forewings: (0) completely uniform or if differentiated, not forming a distinct corium-clavus and membrane; (1) forewing

- divided into a distinct corium-clavus and membrane. State 0 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0$.
54. Cephalic trichobothria: (0) absent in adults; (1) present in adults. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 55. Metathoracic scent gland system: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 56. Labium: (0) not tubular; (1) tubular labium with three segments; (2) tubular labium with four segments. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 57. Insertion of tubular labium: (0) posteriorly on the head, (1) anteriorly on the head. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 58. Dorsal abdominal glands in immature stages: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 59. Number of antennal flagellomeres: (0) more than 4, (1) 4 or less. State 0 is adopted for *Mydiognathus*: $ci = 0.33$, $ri = 0.75$.
 60. Articulations between the mesomere, anterodorsal extension of ventral plate and posterior end of basal plate: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.5$.
 61. Length of basal apodeme of the phallic organ: (0) short; (1) long, longer than basal plate. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
 62. Third posterodorsal corner of basal plate: (0) not extended; (1) extended posteriorly. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
 63. Basal apodeme of the phallic organ: (0) present; (1) absent. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 64. Width of basal apodeme: (0) narrow; (1) as broad as or broader than basal plate. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 65. Ventral plates 1: (0) separated; (1) partly fused anteriorly. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 66. Ventral plates 2: (0) separated or partly fused; (1) completely fused. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
 67. Mesomere of the aedeagus: (0) rounded posteriorly; (1) pointed posteriorly. "?" is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.5$.
 68. Posteromedian part of basal plate: (0) membranous; (1) sclerotized. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 69. Anterior end of mesomere: (0) articulated with basal plate; (1) articulated with paramere. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
 70. Paired ocelli in nymphs or larvae: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 71. Intrinsic antennal muscles (Mm. scapopedicellares) in immature stages: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 72. Ventral metasternal process: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 73. Sensory plate organs of pedicel: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 74. Evan's organ: (0) absent, (1) present. "?" is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.86$.
 75. Ductus ejaculatorius: (0) normal; (1) modified as a sperm pump. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 76. Proximal abdomen pediculate by reduction of the 1st and 2nd segment: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 77. Hind coxae: (0) normally developed; (1) broad, closely adjacent. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 78. Proboscis: (0) absent; (1) shifted posteriorly between bases of procoxae; (2) not shifted posteriorly between bases of procoxae. State 0 is adopted for *Mydiognathus*: $ci = 0.67$, $ri = 0.94$.
 79. Posterior parts of the head capsule: (0) sclerotized; (1) membranous. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 80. Connective tissue occluding occipital foramen: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0$.
 81. Ovipositor simplified: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.5$.
 82. Spiracular glands: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0$.
 83. Extension of the occipital apodeme reaching into the thorax: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0$.
 84. Pronotum and procoxae: (0) not fused; (1) fused. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 85. Position of anterior tentorial pits: (0) frontal side of head; (1) absent; (2) shifted dorsally. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 86. Fusion of head and thorax: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 87. Body and head: (0) not flattened; (1) dorsoventrally flattened. State 0 is adopted for *Mydiognathus*: $ci = 0.25$, $ri = 0.67$.
 88. Hind femora: (0) not enlarged; (1) enlarged. State 0 is adopted for *Mydiognathus*: $ci = 0.33$, $ri = 0.6$.
 89. Meso- and metanotum: (0) not fused; (1) fused. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 90. Compound eyes: (0) not reduced; (1) only 2 ommatidia or less. State 0 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.86$.
 91. Labial palp: (0) present; (1) absent. State 0 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.88$.
 92. Complex tymbal acoustic system: absent (0); present (1). State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 93. Aristate antennal flagellum: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.86$.
 94. Malpighian tubules: (0) more than six; (1) six; (2) four or less. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 95. Labrum: (0) not narrowed; (1) narrowed. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 96. Mandibular and lacinial stylets: (1) unicondylar; (0) dicondylar. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 97. Pedunculate eggs (with stalk): (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 98. Gut with filter chamber containing Malpighian tubules: (0) absent; (1) present. "?" is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
 99. Coronal (= median epicranial) suture: (0) absent; (1) present. State 1 is adopted for *Mydiognathus*: $ci = 0.33$, $ri = 0.33$.

100. Parempodia on unguitactor plate: (0) absent; (1) elongate and setiform, inserted in an alveolus. "?" is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.5$.
101. Number of tarsal segments: (0) one; (1) two; (2) three; (3) more than three. State 3 is adopted for *Mydiognathus*: $ci = 0.3$, $ri = 0.61$. Coding for *Cerobasis* (Psocodea: Trogiomorpha) has changed from 2 to 3 (Friedmann et al. 2014).
102. Arolium: (0) absent; (1) present; (2) eversible; (3) bilobed. State 1 is adopted for *Mydiognathus*: $ci = 0.33$, $ri = 0.5$.
103. Sticky terminal lip of arolium: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0.67$.
104. Pulvilli: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 0.33$, $ri = 0.6$.
105. Euplantulae: (0) absent, (1) present. State 0 is adopted for *Mydiognathus*: $ci = 0.33$, $ri = 0.33$.
106. Number of claws: (0) one; (1) two; (2) reduced into spoon-shaped plates; (3) main claw plus accessory claw. State 1 is adopted for *Mydiognathus*: $ci = 0.75$, $ri = 0.67$.
107. Claw teeth: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 0.33$, $ri = 0.33$.
108. Protuberance with microtrichia on distolateral side of the pretarsus: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
109. Sensorial setae on mesal side of arolium: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 1$.
110. Adhesive claw setae: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
111. Eversible structure between tibia and tarsus: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 0$, $ri = 0$.
112. Tibial thumb-like process: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
113. Empodial paronychium: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
114. Tarsal apophysis on the ventral side of the tarsus: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
115. Two dorsal capitate setae: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
116. Flag-like sensilla on the 1st tarsal segment: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
117. Fingerlike process below claw: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 1$, $ri = 0$.
118. Ventral brush: (0) absent; (1) present. State 0 is adopted for *Mydiognathus*: $ci = 0.5$, $ri = 0$.

Proposal of Pancondylognatha new supraorder

This supraorder is proposed for the clade composed of Archipsyllidae and Condylgnatha (Fig. 5). Apomorphies defining the supraorder are as follows: the labrum narrows apically; the mandible is elongated; the labium is elongated, deeply concave medially and envelops the elongated lacinia (Figs 1c, 2a–c); 2Ax divided; DMP located close to 2Ax (Fig. 3b,c).

Discussion

Around 30 insect orders are currently recognized and, in most cases, there are big morphological gaps among them. Fossils may well be expected to fill such gaps. However, almost all amber fossil insects have been assigned to extant orders, families or even genera (Penny 2010). Conversely, most insect fossils that cannot be assigned to extant orders are known only from impression fossils, and usually only limited morphological information can be obtained from them. Early Cretaceous ambers are an exception to this rule, and contain several exquisitely preserved insect families that are typically found as impression fossils in late Paleozoic to mid Mesozoic that become extinct soon after their mid Cretaceous last appearances (Labandeira 2014). The paraneopteran family Archipsyllidae was one such example, which was known only from impression fossils and cannot be assigned to any extant lineage (Vishniakova 1976; Huang *et al.* 2008). Their wing venation has been well documented, but other key characters for understanding insect evolution and phylogeny (e.g. mouthparts, wing base, genitalia) are little known, even from the best preserved fossils (Huang *et al.* 2008). The present discovery from mid-Cretaceous amber represents an extremely rare case where an intermediate condition between supraordinal insect groups can be observed in detail (Figs 1, 2a–c, 3a–c). The youngest fossils of Archipsyllidae known to date are from the early Cretaceous in impression material (*Archipsyllodes* and *Archipsyllopsis*) (Vishniakova 1976). The discovery of the new fossil reveals the survival of Archipsyllidae until the mid Cretaceous. Judging from its placement at the stem of Condylgnatha and also from the age of this lineage (Misof *et al.* 2014), Archipsyllidae might have originated around 340 Mya, showing that this clade survived for at least 240 million years (Fig. 7).

There is almost universal agreement for the placement of the Archipsyllidae in the Paraneoptera (Carpenter 1992; Grimaldi & Engel 2005; Huang *et al.* 2008). The present examination and phylogenetic analyses undoubtedly confirm this assumption (Figs 5–6) on the basis of the styliform lacinia detached from stipes (Fig.

2a,b), and the complete absence of a cercus (Figs 1a,b, 4) in *Mydiognathus* (Kristensen 1991; Grimaldi & Engel 2005; Beutel *et al.* 2014). As far as could be observed, apomorphic forewing base articulations characteristic for Paraneoptera were confirmed in *Mydiognathus* (Fig. 3b–f): the HP and BSc united; the anterior region of 2Ax strongly swollen; the PMP placed posterior to the 2Ax; the PMP concave and outer region strongly sclerotized; the 3Ax not articulated with the DMP; and the BA fused with the PMP (Yoshizawa & Saigusa 2001). Supports from the wing base are especially important because this character system is widely recognized as very reliable in estimating the higher level phylogeny of insects (Hörschemeyer 2002; Yoshizawa 2011; Friedrich *et al.* 2014; Misof *et al.* 2014; Zhao *et al.* 2014).

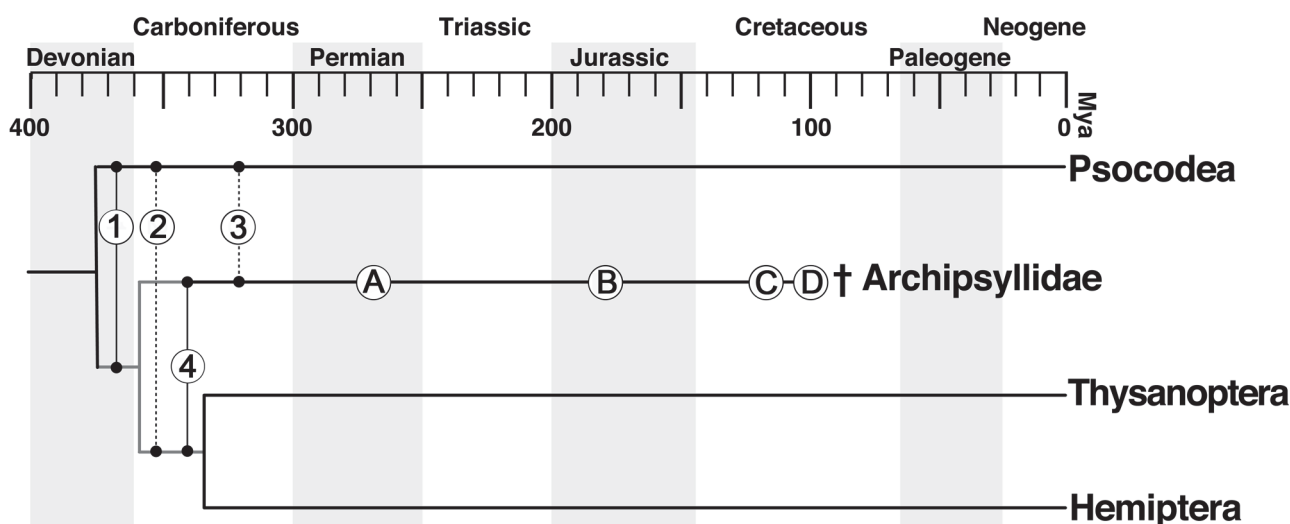


FIGURE 7. Phylogeny and chronology of Paraneoptera including the placement of Archipsyllidae. Gray branches indicates uncertainty of divergence age (Misof *et al.* 2014). A–D indicate age of known fossils of Archipsyllidae (A: *Psocopsylla* (monotypic); B: *Archipsylla* (5 species known, oldest record indicated); C: *Archipsyllodes* and *Archipsyllopsis* (both monotypic); D: *Mydiognathus*). Numbers connecting branches indicate their supposed synapomorphies as follow: (1) Synapomorphies of Paraneoptera listed previously (e.g. Yoshizawa and Saigusa 2001; Grimaldi and Engel 2005; Beutel *et al.* 2014) except for (2). (2) Reduction of labial palpus (two segments or less) and reduction of tarsal segments (three segments or less) have been accepted as paraneopteran synapomorphies, but are excluded by recent studies of Archipsyllidae (Huang *et al.* 2008; present study). (3) Enlarged clypeus and antennal rupturing mechanism were considered as synapomorphies of Archipsyllidae and Psocodea (Huang *et al.* 2008) but are excluded by the present study. (4) Elongated mandible, elongated and grooved labium, and several forewing articulation apomorphies support placement of Archipsyllidae sister to Condylgnatha (these clades together compose the new supraordinal taxon Pancondylgnatha).

In contrast to its placement in Paraneoptera, there are conflicting opinions about the position of the Archipsyllidae within the Paraneoptera. In recent studies, Archipsyllidae are generally placed in Psocodea (e.g. Smithers 1972; Vishniakova 1976; Carpenter 1992; Ansorge 1996), although this assignment is not based on any shared apomorphy but on plesiomorphic or superficial similarities. Therefore, the most conservative view about the placement of this family would be the stem lineage of Paraneoptera (Grimaldi & Engel 2005). In contrast, a study of well-preserved impression fossils of *Archipsylla* suggested its placement in the Psocodea (Huang *et al.* 2008) based on the following apomorphies: bulbous and protruding postclypeus and presence of the rupturing mechanism in the antennal flagellomeres, both recognized as psocodean autapomorphies (Seeger 1975; Grimaldi & Engel 2005). However, the present study clearly suggests that these are misinterpretations of the impression fossils (Huang *et al.* 2008): the protruding head part is the frons, not the clypeus (Fig. 2a), and no clear rupturing mechanism in flagellomeres was observed in *Mydiognathus* (Figs 1d, 2d). The annulated flagellum, clearly observed in *Mydiognathus* as well as in *Archipsylla* (Huang *et al.* 2008), is the only apomorphy potentially uniting Archipsyllidae and Psocodea (Fig. 7). However, this feature is only observed in some Psocodea (Troctomorpha and some Trogomorpha) (e.g. Lienhard 1998). Furthermore, annulated flagellomeres are also observed in Thysanoptera (Mound & Masumoto 2009) and Hemiptera (Bromley *et al.* 1980; Akimoto 1983) and this feature cannot be regarded as an autapomorphy of the Psocodea but as highly homoplastic or as belonging to the paraneopteran ground plan. The placement of Archipsyllidae in the Psocodea clade (Huang *et al.* 2008) is therefore unjustified.

The phylogenetic tree estimated here (Figs 5–6), resulting from the first numerical cladistic analysis of Archipsyllidae based on extensive morphological data, provides additional insights into the phylogenetic relationships of this enigmatic lineage. The following character states (including characters not scored for the phylogenetic analyses) observed in *Mydiognathus* are apomorphic and shared with Condylgnatha (= Thysanoptera plus Hemiptera) (Figs 1c, 2a–c): the labrum narrows apically; the mandible is elongated; and the labium is elongated, deeply concave medially and envelops the elongated lacinia. These features strongly suggest that this archipsyllid is close to the Condylgnatha. The mouthpart modifications observed in *Mydiognathus* may actually represent autapomorphic specializations, as observed in Palaeodictyopteroidea (Labandeira & Phillips 1996) and *Pseudopolycentropus* (Mecoptera: Ren *et al.* 2009). However, the complicated and composite mouthpart modifications shared by Condylgnatha and *Mydiognathus* (Figs 5–6) strongly imply that these are homologous changes. In addition, the wing base apomorphies of *Mydiognathus* (2Ax divided and DMP located close to 2Ax: Fig. 3b,c) also support its placement close to the Condylgnatha (Yoshizawa & Saigusa 2001), although one wing-base autapomorphy of Condylgnatha (fusion between BSc and 2Ax: Fig. 3f) could not be confirmed in *Mydiognathus* (Fig. 3b,c). The combination of these apomorphies shared by Condylgnatha and Archipsyllidae is used to define the new taxon Pancondylgnatha for them. Establishment of this supraordinal taxon allows preservation of the well-defined name Condylgnatha for the two orders with piercing-and-sucking mouthparts. Establishment of a new order for the Archipsyllidae also may be justified, but the phylogenetic placement of other fossil insects potentially belonging to the Pancondylgnatha should be clarified prior to its establishment.

The modified mouthparts in *Mydiognathus* are of special interest. The asymmetrical molars at the inner base of the mandibles (Fig. 2a–c), very similar to those of psocodeans, clearly show that *Mydiognathus* is a chewing feeder. It is also evident from the detached condition of the elongated lacinia (Fig. 2a,b) that this structure can be protracted and retracted as in Psocodea and Condylgnatha. These features, in addition to the phylogenetic placement of *Mydiognathus* (Fig. 5–6), clearly show that elongation of the mandible and the styliform lacinia of Condylgnatha first evolved in a chewing feeder. The flat postclypeus without dorsal extension also probably suggests that they lack considerable sucking activity. This is quite different in the case of the Lepidoptera, wherein elongation of mouthparts, specifically the maxillary galeae, was exclusively related to fluid feeding from the beginning (Krenn 2010). The vertically and symmetrically arranged and inwardly curved tips of the mandibles (Figs 1c, 2a,c) suggest that these organs functioned to grasp food, rather than to cut or extricate it from a substrate as in Psocodea. The very long basal extension of the lacinia (Fig. 2a,b) clearly demonstrates that this structure could be projected forwards for some distance. The curved lacinial tips (Figs 1c, 2a,c) therefore might function to hook and collect distantly located food to be efficiently retrieved by the mouth. The internally flattened, terminal segment of the maxillary palpus (Figs 1c, 2a) also might help the laciniae to secure food. Because the molars are widely separated from the tip of the mandibles (Figs 1c, 2a–c), the protraction and retraction of the laciniae might also transport food to the molar region. Further studies are needed to clarify the feeding habits of these insects, but it is probably safe to say from their elongated mouthparts that they utilized food sources occurring in interstices or inaccessible spaces, such as seeds.

One such food source is pollen. Judging from the insect phylogenomic tree (Misof *et al.* 2014) and the placement of Archipsyllidae proposed here, the origin of the Pancondylgnatha can be assumed to be mid Devonian (Fig. 7), which is about synchronous with the origin of the spermatophytes (Jiao *et al.* 2011). A cluster of tiny pollen-like particles was observed at the inner tip of the right galea (Fig. 2c); however, they are too small to be pollen grains (less than 1 μm). *Mydiognathus* has none of the specializations of the mouthparts generally observed in other pollen feeding insects, such as dense bristles or other hair-laden structures facilitating pollen harvesting (Krenn *et al.* 2005) (Figs 1c, 2a–c). Therefore, the pollen feeder hypothesis is less likely.

The present analysis also addresses to the controversy over the monophyly of the Paraneoptera (= Acercaria or informally known as hemipteroid assemblage). Recent molecular and genomic phylogenetic analyses have cast doubt on the monophyly of the Paraneoptera (Yoshizawa & Johnson 2005; Ishiwata *et al.* 2011; Misof *et al.* 2014). Morphologically, monophyly of the Paraneoptera has been supported by many apomorphies, such as an enlarged postclypeus, an elongated lacinia detached from stipes, reduction or absence of the labial palpus, three or fewer tarsal segments, absence of a cercus, presence of abdominal trichobothria, four Malpighian tubules, and a single abdominal ganglion (Kristensen 1991; Grimaldi & Engel 2005; Beutel *et al.* 2014). The four segmented labial palpus (Figs 1c, 2a) and four segmented tarsus (Fig. 1a,b,e) of *Mydiognathus*, clearly show that reduction of labial palps and tarsal segments occurred independently in the Psocodea and Condylgnatha, removing two potential

synapomorphies of the Paraneoptera (2 in Fig. 7). However, elongation of lacinia (Figs 1c, 2a–c) and absence of a cercus (Figs 1a,b, 4), which are confirmed in *Mydiognathus*, still suggest the monophyly of the Paraneoptera, as do the forewing base articulation structures of *Mydiognathus* (Fig. 3b,c) (Yoshizawa & Saigusa 2001). The Bremer support value for the monophyly of the Paraneoptera also was high (6) even after the inclusion of *Mydiognathus* into the phylogenetic analysis (Fig. 5–6). Acceptance of the non-monophyly of Paraneoptera implies convergent evolutions of many morphological apomorphies. Given that no molecular analysis, including phylogenomics, could statistically reject the monophyly of the Paraneoptera (Yoshizawa and Johnson 2005; Ishiwata *et al.* 2011; Misof *et al.* 2014), the monophyly of this clade remains a well-founded and highly likely hypothesis. Further morphological analyses, including fossil data, will be the key to resolving the "Paraneoptera problem".

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