

# Phylogenetic analysis of Fulgoroidea based on the morphological characters of the forewing base structure (Hemiptera: Auchenorrhyncha)

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**Abstract:** The forewing base structure of a representative species from 13 families of Fulgoroidea were examined. Results show that these families differ mainly from the characters of various sclerites, the presence or absence of humeral plate, proximal and distal median plate, and the method of connection between each sclerite. The phylogenetic relationships based on forewing structure support the monophyly of Fulgoroidea and also largely support the phylogenetic investigation of Urban & Cryan (2007). Ricaniidae and Flatidae were recovered as sister taxa in agreement with the schemes of Emeljanov (1990) and Song & Liang (2013). Kinnaridae is the most primitive family in Fulgoroidea.

**Key words:** planthopper; phylogeny; morphology; monophyletic group

## 基于翅基片形态的蜡蝉总科系统发育关系分析（半翅目：头喙亚目）

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**摘要:** 研究了蜡蝉总科 13 个科的代表种前翅翅基片形态, 结果显示它们的主要区别在于各骨片的特征, 肩片、近中片和远中片的有无及各骨片间连接方式。基于前翅翅基片形态特征的系统发育研究支持蜡蝉总科的单系性, 并基本支持 Urban & Cryan (2007) 的结果, 但本研究认为蛾蜡蝉科和广蜡蝉科是姐妹群, 这与 Emeljanov (1990) 及 Song & Liang (2013) 的研究结果一致, 此外本研究认为阔蜡蝉科在蜡蝉总科中地位最为原始。

**关键词:** 蜡蝉; 系统发育; 形态; 单系群

## Introduction

Insect wing base structures consist of the lateral notal margin, three axillary sclerites, two median plates and the bases of the wing veins, providing for the complex movements of folding and unfolding, as well as wing control and adjustment during flight (Forbes 1926; Wootton *et al.* 2003; Haas 2006; Muhammad *et al.* 2010; Yoshizawa & Wagatsuma 2012). Due to a quite slow rate of evolution as well as functional constraints, morphological characteristics of this structure may provide important evidence for classification, especially in the higher-level phylogeny of insects, as already used with Polyneoptera (Yoshizawa 2011) and Megaloptera and Neuroptera (Zhao *et al.* 2014).

In Hemiptera, there are previous studies of the morphology of wings in Fulgoroidea (Fennah 1944; Bourgoïn *et al.* 2015) and the phylogeny in some infraorders or

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super-families is based on their wing base structures (Yoshizawa & Saigusa 2001; Ouvrard *et al.* 2008; Yoshizawa & Wagatsuma 2012; Franielczyk & Wegierek 2016; Yoshizawa *et al.* 2017). As a more ancient group in Hemiptera, Fulgoroidea contains a diverse group of phytophagous or fungivorous insects, and the presence of tegula on the mesothorax is one of the most conspicuous features distinguishing them from other super-families in Hemiptera (Bartlett *et al.* 2014; Bourgoin 2022). However, the wing base structure of Fulgoroidea and the phylogeny inferred from this structure have not been thoroughly examined. Meanwhile, the phylogeny of this superfamily remains unsatisfactorily resolved so far (Urban & Cryan 2007; Hamilton 2011; Cryan & Urban 2012). Therefore we describe and compare the forewing base structure of representative species in 13 families in Fulgoroidea as a basis to reconstruct the phylogenetic relationships in Fulgoroidea. The aim of this study is to assess morphological variabilities of wing base structure among families, meanwhile providing important information for the solution of controversial issues in the phylogeny of Fulgoroidea.

## Material and methods

### Material

Dry specimens were used in this study. All specimens were collected from the field by net in recent years and all were placed in a softening cylinder for 1–2 days for wing expansion. *Platypleura kaempferi* (Fabricius) (in Cicadoidea) was selected as the outgroup. Taxa examined here are listed in Table 1.

**Table 1. List of the examined species**

Family	Species	Specimen	Collection information
Fulgoridae	<i>Lycorma delicatula</i> (White)	8♂11♀	2020-10-07, Yangling, Shaanxi
Dictyopharidae	<i>Saigona gibbosa</i> Matsumura	5♂2♀	2021-04-20, Nanling, Guangdong
Ricaniidae	<i>Pochazia discreta</i> Melichar	12♂6♀	2014-07-08, Tiankoushan Mountain, Zhejiang
Flatidae	<i>Flatida marginella</i> Oliver	8♂6♀	2020-08-23, Dongbaling National Nature Reserve, Guangdong
Nogodinidae	<i>Pisacha kwangsiensis</i> Chou & Lu	9♂7♀	2018-05-09, Yinggeling National Nature Reserve, Hainan
Lophopidae	<i>Lacusa fuscofasciata</i> (Stål)	5♂3♀	2017-07-27, Wild Elephant Valley, Yunnan
Eurybrachidae	<i>Loxocephala</i> <i>perpunctata</i> Jacobi	5♂6♀	2010-08-13, Zena Village, Weixi, Yunnan
Cixiidae	<i>Oecleus cucullatus</i> (Noualhier)	15♂13♀	2012-07-18, Huoditang, Shaanxi
Derbidae	<i>Diotrombus politus</i> (Uhler)	6♂8♀	2021-07-25, Mingfeng Town, Suining City, Sichuan

Continued Table 1.

Family	Species	Specimen	Collection information
Delphacidae	<i>Nilaparvata muiri</i> China	15♂12♀	2014-06-23, Taohuachong, Huanggang, Hubei
Tropiduchidae	<i>Catullia subtestacea</i> Stål	9♂8♀	2017-08-07, Chishui, Dehua, Fujian
Kinnaridae	Kinnaridae sp.	4♂6♀	2018-04-28, Diaoluoshan mountain, Yunnan
Issidae	<i>Gergithus reticulatus</i> Matsumura	6♂3♀	2018-04-27–28, Wuzhishan Mountain, Hainan
Cicadidae	<i>Platypleura kaempferi</i> (Fabricius)	17♂23♀	2021-07-19, Suining, Sichuan

### Optical microscope observation

According to the suggestions of Yoshizawa & Saigusa (2001), only parts of the notum and pleurae connected with the forewing base articulation on the right side were removed. Sample processing mainly follows the method of Yoshizawa *et al.* (2017). Morphological characters of the forewing base structure were observed under a Nikon SMZ 1500 stereomicroscope. Figures were drawn using an OLYMPUS PM-10 AD microscope.

### Phylogenetic analysis

Thirty five characters from the forewing base structure were used for cladistic analysis, including binary and multistate characters with the latter treated as ordered. The trait polarity of each feature was determined by outgroup analysis: the ancestral feature was coded “0”, the derivative feature states in the inner group were coded as “1, 2....”. We transformed disordered features into ordered (numerical) features.

TNT ver. 1.5 (Goloboff & Catalano 2016) and WinClada ver. 1.00.08 (Nixon, 2002) software were used for analysis. Some features were automatically merged to obtain a morphology-based phylogenetic tree.

### Terminology

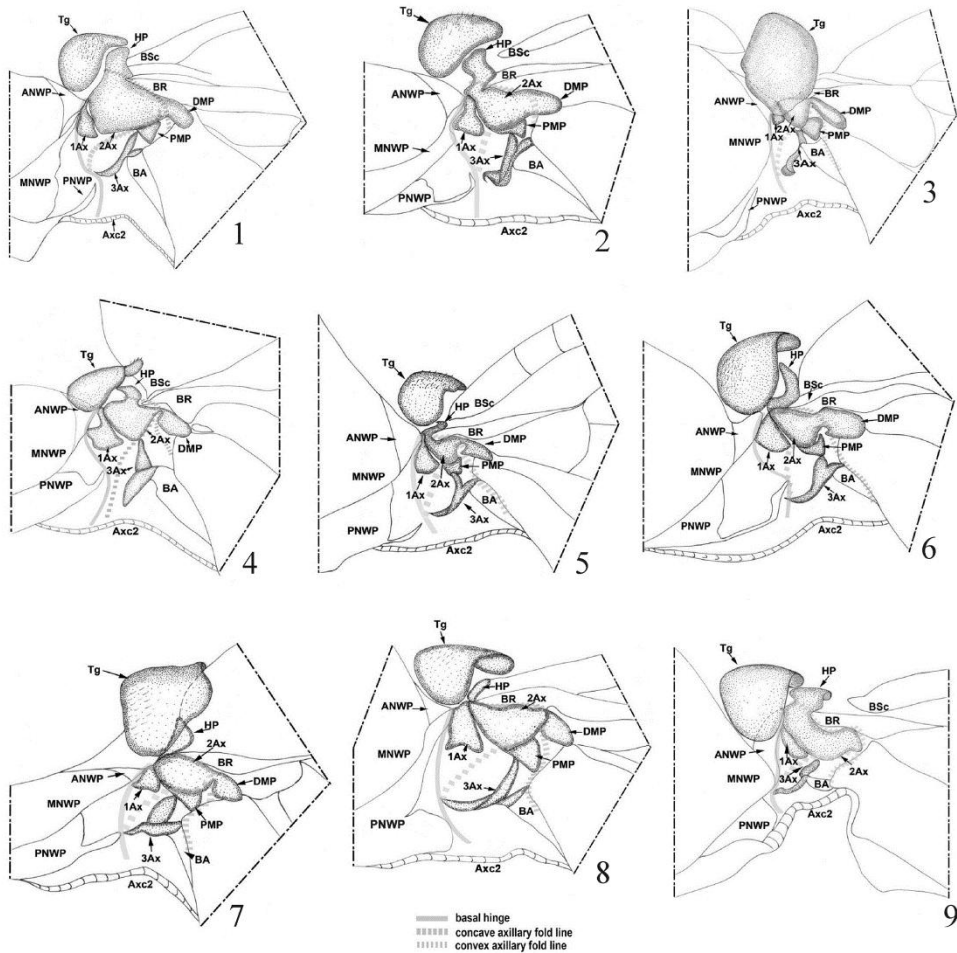
The terminology of the forewing base sclerites follows that of Brodsky (1994) and Matsuda (1970). The terminology of the folding lines follows that of Wootton (1979). The following abbreviations are used in the text and figures: ANWP — anterior notal wing process; MNWP — median notal wing process; PNWP — posterior notal wing process; 1Ax, 2Ax, 3Ax — first, second and third axillary sclerites; Axc2 — axillary cord; BA — basalare; BR — basiradiale; BSc — basisubcostale; PMP — proximal median plate; DMP — distal median plate; HP — humeral plate; Tg — tegula.

### Taxonomy

#### General morphology of forewing base structure of Fulgoroidea (Figs 1–14)

The notum has three principal wing processes: ANWP, MNWP, and PNWP. The apex of the ANWP is almost always adjacent to the head or anteroproximal margin of the body of 1Ax, forming the anterior-most articulation between the notum and axillary region (= the

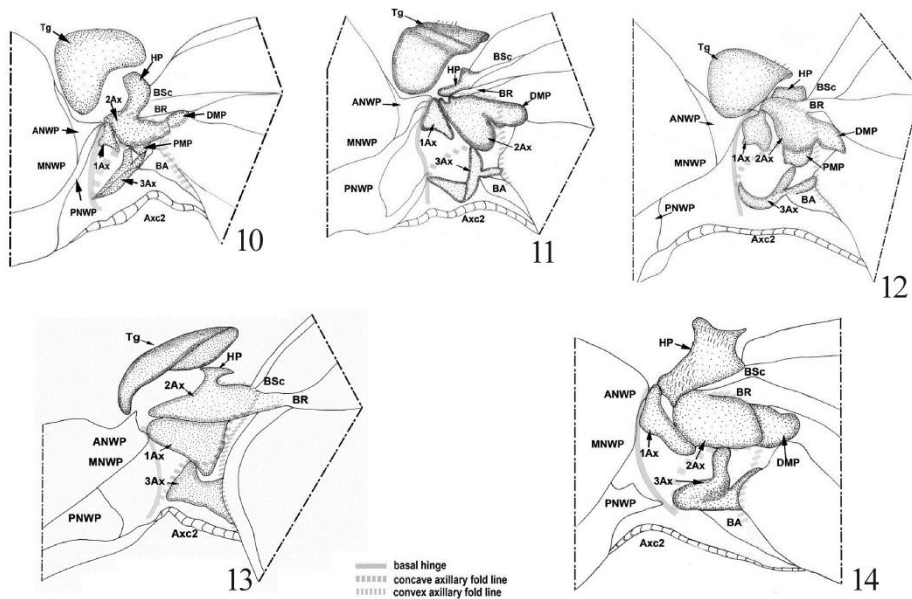
basal hinge) (Figs 1–14). MNWP is usually fused to the notum, and in a few species to 1Ax. PNWP usually extends from the posterolateral corner of the notum, tapering, rather than loosely articulating to or toward the proximal lobes of 3Ax, which forms the posterior end of the basal hinge (Figs 1–7, 11). PNWP is generally separate from 1Ax (Figs 1–7, 9, 12–14) except in a few species (Figs 8, 10, 11).



Figures 1–9. Forewing base structure. 1. *Lycorma delicatula* (in Fulgoridae); 2. *Saigona gibbosa* (in Dictyophacidae); 3. *Pochazia discreta* (in Ricaniidae); 4. *Flatida marginella* (in Flatidae); 5. *Pisacha kwangsiensis* (in Nogodinidae); 6. *Lacusa fuscofasciata* (in Lophopidae); 7. *Loxocephala perpunctata* (in Eurybrachidae); 8. *Oecleus cucullatus* (in Cixiidae); 9. *Diostrombus politus* (in Derbidae).

Tg is always elevated above the other sclerites and consistently enlarged. It has a broad extension encircling the outer margin and only has a small attachment to the body wall. The front margin is usually covered with a few sparse bristles on the surface. In most species the Tg is slightly wider in middle and raised (Figs 1, 2, 5–13), this roof-like structure covers forewing articulation and probably plays a protective role, although its structure obviously differs in shape in different species.

HP is usually irregular in shape and almost entirely hidden by Tg, and is a group of small basal sclerites with anterodistal corner rounded (Figs 1, 2, 7–12) or sharp-pointed (Figs 4–6, 13, 14).



Figures 10–14. Forewing base structure. 10. *Nilaparvata muiroi* (in Delphacidae); 11. *Catullia subtestacea* (in Tropiduchidae); 12. Kinnaridae sp. (in Kinnaridae); 13. *Gergithus reticulatus* (in Issidae); 14. *Platyleura kaempferi* (in Cicadoidea).

The axillary region consists of three axillary sclerites (1Ax, 2Ax and 3Ax), two median plates (PMP and DMP) and some basal sclerites of the veins (BSc, BR and BA predominantly). 4Ax is apparently absent in Fulgoroidea.

Three regions are generally recognized in 1Ax, including the head, neck, and body regions. The head and neck regions are often absent in some planthopper species, and the outer margin of 1Ax is connected with 2Ax.

2Ax is usually triangular, flat and sclerotized. The front end of the outer margin is often fused with HP and BR, and posteriorly fused with DMP, forming a deep depression in some species or like a small indentation (Figs 3–7, 11, 12). The distal end of the inner margin is connected to PMP or the anterior lobe articulates of 3Ax. 2Ax forms a side-by-side articulation to PMP along the concave axillary fold line. However, 2Ax articulates with the anterior lobe of 3Ax along the concave axillary fold line because of the reduced or less sclerotized PMP (Figs 4, 9, 11, 14).

3Ax often consists of three lobes, e.g. the anterior, proximal and distal lobes, with its central region plate-like, sclerotized. The distal lobe of 3Ax articulates with BA. In some species, e.g. *Saigona gibbosa*, *Pisacha kwangsiensis*, *Oecleus cucullatus* and *Catullia subtestacea*, the proximal lobes of the 3Ax has a certain angle of turn. But 3Ax does not exist completely in Fulgoroidea (Figs 3, 4, 9, 13).

PMP is roughly triangular or irregularly quadrilateral in shape, and evenly sclerotized,



Table 3. Axillary characters and their states in Fulgoroidea

Species	IAX	2AX	3AX	MNWP/	PNWP	Tg	Anterodistal	Hip						
	Head	Neck	Body	Surface	Anterior lobe	Proximal lobe	Distal lobe	MNWP/	PNWP	Extended sclerite of	Surface	Degree of ossification	Anterodistal corner	Hip/2AX
<i>L. delicatula</i>	Present	Present	Irregular	Concave	Connect to PMP	Unfolded	Present	Separated	With extension	With bristles	Sclerotized	Sclerotized	Smoothly rounded	Completely fused
<i>S. gibbosa</i>	Present	Present	Irregular	Concave	Connect to PMP	With fold	Present	Separated	With extension	With bristles	Sclerotized	Sclerotized	Smoothly rounded	Completely fused
<i>P. discreta</i>	-	Present	Nearly quadrilateral	Not concave	Connect to PMP	Unfolded	-	Fused	With extension	With bristles	Sclerotized	Sclerotized	-	-
<i>F. marginella</i>	Present	Present	Irregular	Not concave	Connect to 2AX	Unfolded	-	Fused	With extension	With bristles	Sclerotized	Sclerotized	Acutely pointed	Completely fused
<i>P. kwangstenis</i>	Present	Present	Nearly quadrilateral	Not concave	Connect to PMP	With fold	Present	Fused	With extension	With bristles	Sclerotized	Sclerotized	Acutely pointed	Completely fused
<i>L. fuscifasciata</i>	-	-	Triangular	Not concave	Connect to PMP	Unfolded	Present	Fused	With extension	With bristles	Sclerotized	Sclerotized	Acutely pointed	Completely fused
<i>L. perpunctata</i>	-	-	Nearly quadrilateral	Not concave	Connect to PMP	Unfolded	Present	Fused	With extension	With bristles	Sclerotized	Sclerotized	Acutely pointed	Partly fused
<i>O. exallatus</i>	-	-	Nearly quadrilateral	Not concave	Connect to PMP	With fold	Present	Fused	No extension	With bristles	Weakly sclerotized	Weakly sclerotized	Smoothly rounded	Partly fused
<i>D. politus</i>	-	-	Irregular	Not concave	Connect to 2AX	Unfolded	-	Fused	No extension	Smooth	Sclerotized	Sclerotized	Smoothly rounded	Completely fused
<i>N. nairi</i>	-	-	Irregular	Not concave	Connect to PMP	Unfolded	Present	Fused	No extension	With bristles	Weakly sclerotized	Weakly sclerotized	Smoothly rounded	Completely fused
<i>C. subretacea</i>	-	-	Triangular	Not concave	Connect to 2AX	With fold	Present	Fused	With extension	With bristles	Sclerotized	Sclerotized	Smoothly rounded	Partly fused
Kimariidae sp.	Present	-	Irregular	Not concave	Connect to PMP	Unfolded	Present	Fused	No extension	With bristles	Weakly sclerotized	Weakly sclerotized	Smoothly rounded	Partly fused
<i>G. reticulatus</i>	-	-	Irregular	Not concave	Connect to JAX	-	-	Fused	No extension	Smooth	Sclerotized	Sclerotized	Acutely pointed	Completely fused
<i>P. kaempferi</i>	Present	-	Irregular	Not concave	Connect to 2AX	Unfolded	Present	Fused	No extension	-	-	-	Acutely pointed	Partly fused

## Phylogenetic analyses (Fig. 15)

The parsimonious analysis of the forewing base dataset yielded two trees, the strict consensus tree is shown in Fig. 15. (tree length = 75; consistency index = 0.59; retention index = 0.66), in which the monophyly of Fulgoroidea is supported. Kinnaridae is the most primitive family in Fulgoroidea. Relationships recovered suggest several major lineages, including: (1) Delphacidae + Cixiidae; (2) Derbidae + Issidae; (3) (Tropiduchidae + (Lophopidae + Eurybrachidae)); (4) Fulgoridae + Dictyopharidae; (5) (Nogodinidae + (Flatidae + Ricianiidae)).

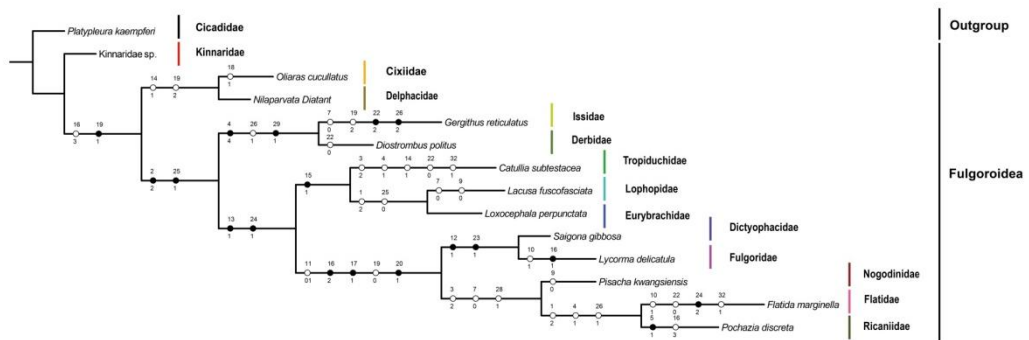


Figure 15. Phylogenetic relationships of Fulgoroidea based on forewing base characters.

## Discussion

Yoshizawa & Saigusa (2001) suggested 1Ax connected proximally to ANWP and MNWP, and distally connects to 2Ax in *Oliarus angusticeps* Horváth, 1892 (in Cixiidae). Franielczyk & Wegierek (2016) thought that in *Cixius nervosus* (Linné, 1758) the 1Ax has four clearly defined edges, the proximal edge connected with ANWP, the two distally located edges form a wall parallel to 2Ax, and the fourth one was directed to the process of the notum, MNWP. This research confirms the relationship between 1Ax/notum and 1Ax/2Ax suggested by Yoshizawa & Saigusa (2001) and Franielczyk & Wegierek (2016) in Cixiidae.

The morphological characters of 2Ax in this study are consistent with the descriptions of Yoshizawa & Saigusa (2001) who thought 2Ax in Fulgoromorpha are irregular and comprised of a few elements: the upper, proximal part of 2Ax fuses with humeral plate without clear boundaries, the distal part passes smoothly into the DMP and at the bottom almost links 3Ax and PMP; 2Ax and PMP articulate with each other along a concave hinge, whereas 2Ax and DMP articulate along a convex hinge; and reduction of PMP is unique and almost membranous or absent in Fulgoromorpha. However, Franielczyk and Wegierek (2016) suggested 2Ax has two arms with different lengths and a small indentation is between the two arms. Here we think the structure of 2Ax in Cixiidae needs to be studied further for 2Ax exhibits an irregular triangle in this study.

This phylogenetic study largely supports the analysis of Urban & Cryan (2007) insofar as the families Delphacidae and Cixiidae, Fulgoridae and Dictyopharidae, and Lophopidae and Eurybrachidae are recovered as sister taxa. The character states of 16 is that PNWP and 3Ax are separated or loosely connected (CI = 100, RI = 100), strongly supporting Lophopidae and



Eurybrachidae as sister groups. The character states of MNWP fused or separated into notum (CI = 100, RI = 100) strongly supports the Fulgoridae and Dictyopharidae as sister groups. However, this current study places Ricaniidae sister to Flatidae, supporting the results of Emeljanov (1990) and Song & Liang (2013). Kinnaridae is the most primitive family in Fulgoroidea.

DMP of Fulgoroidea is clearly visible and well sclerotized. However, DMP is not present in *Diostrombus politus* and *Gergithus reticulatus*. So we speculate that it may be completely fused and homologous to 2Ax, but further verification will be needed. This study discusses the phylogenetic relationships among Fulgoroidea based on their forewing base structure only. We acknowledge the phylogenetic relationships in Fulgoroidea need further study.

#### Characters and their state used for phylogenetic analysis

1. Tg: (0) absent; (1) present.
2. Size of Tg: (1) small; (2) enlarged, with broad extension encircle the entire margin.
3. Ossification degree of Tg: (1) weakly sclerotized; (2) well sclerotized.
4. Surface of Tg: (1) smooth, without dents on surface; (2) with dents on surface.
5. Bristle on Tg: (1) with bristles at front edge only; (2) with bristles at front end; (3) with bristles on surface; (4) smooth, without surface.
6. HP: (0) present; (1) absent.
7. HP and BR + BSc: (0) fused; (1) separated.
8. Anterodistal corner of HP: (0) acutely pointed; (1) smoothly rounded.
9. HP and 2Ax: (0) partly fused; (1) completely fused.
10. HP and 1Ax: (0) partly fused; (1) completely separated.
11. Shape of ANWP: (0) nearly triangular; (1) nearly trapezoidal.
12. Articulation between ANWP and 1Ax: (0) almost at a point; (1) along long margin of neck of 1Ax; (2) along long margin of body of 1Ax.
13. MNWP: (0) fused to notum; (1) separated from notum.
14. PNWP: (0) without extended sclerite; (1) with extended sclerite.
15. PNWP and 1Ax: (0) separated; (1) partly fused.
16. PNWP and 3Ax: (0) separated; (1) loosely connected.
17. Width of head of 1Ax: (0) hardly recognized owing to absence of neck; (1) narrower than neck; (2) almost as wide as neck; (3) absent.
18. Length of neck of 1Ax: (0) absent; (1) as long as the head of 1Ax.
19. Body of 1Ax: (0) irregular; (1) near quadrilateral; (2) triangular.
20. Posterior margin of body of 1Ax: (0) convex; (1) relatively straight; (2) concave.
21. Transition from body to neck in 1Ax: (0) hardly recognized owing to absence of neck; (1) recognized by abrupt change of width.
22. Articulation between 1Ax and 2Ax: (0) at proximal-cranial point of 2Ax; (1) along proximal margin of 2Ax.
23. 2Ax and 3Ax: (0) partly fused; (1) fused by PMP; (2) separated.
24. 2Ax: (0) smooth; (1) concave.
25. 2Ax and contact between BR: (0) 2Ax fused to BR completely; (1) 2Ax partly fused to BR; (2) separated.
26. 2Ax and BSc: (0) in close proximity; (1) widely separated by basiradiale.
27. Number of 3Ax lobes: (0) three; (1) two; (2) one.
28. PMP: (0) reduced and completely membranous; (1) well sclerotized.
29. Shape of PMP: (0) irregular quadrilateral; (1) nearly triangular.
30. DMP: (0) present; (1) absent.

31. DMP and 2Ax: (0) partly fused; (1) completely fused.
32. HP front fork: (0) present; (1) absent.
33. 3Ax: (0) well sclerotized; (1) weakly sclerotized.
34. HP: (0) with bristle on surface; (1) smooth without bristle.
35. 3Ax: (0) with bristle on the surface; (1) smooth without bristle.

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