

A new sawfly fossil from the lower Cretaceous of China elucidates antennal evolution in the lower Hymenoptera (Pamphilioidea: Praesiricidae: Archoxyelydinae subfam.n.)

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Abstract. *Archoxyelyda mirabilis* gen.n. and sp.n., is described from the Yixian Formation of Liaoning Province, China. It is placed in the family Praesiricidae based on the loss of forewing Sc. The fossil is placed in Archoxyelydinae subfam.n. based on a modified antennal flagellum (consisting of two distinct multisegmented parts: a thick and tightly connected basal part, and a thin and more loosely articulated distal one). The incompletely preserved genus *Xyelydotes* Rasnitsyn, 1983 is tentatively transferred to Archoxyelydinae. The new material demonstrates a unique feature in the antennal anatomy: the composite third antennomere can be seen to consist of tightly connected primary antennomeres. Antennal evolution in the lower Hymenoptera is reviewed and three hypothetical pathways in their transformation are discussed.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:635EFD90-CA14-402C-BCBF-C77C194F2368>.

Introduction

The superfamily Pamphilioidea includes four families: Pamphiliidae, Megalodontesidae, Praesiricidae and Xyelydidae (Rasnitsyn, 1983). The latter two are extinct families which perhaps form a grade or a stem group of the superfamily (Rasnitsyn, 1988; Grimaldi & Engel, 2005). The earliest fossil records of Pamphilioidea date from the late Early or early Middle Jurassic (Xyelydidae: *Sagulyda* spp., *Ferganolyda* spp.; Rasnitsyn, 1983). Xyelydidae is the most basal and putatively ancestral (paraphyletic) family in the superfamily Pamphilioidea (Rasnitsyn, 1968, 1969, 1980, 1983). Praesiricidae is another extinct family synapomorphic with the extant Megalodontesidae in having lost forewing Sc, R straight from the base to the pterostigma, and mesopseudosternum widely reaching the fore margin of the mesoventropleuron. Praesiricidae is known from the late Jurassic and Early Cretaceous (Rasnitsyn, 1983; Gao *et al.*, 2010). The extant families Pamphiliidae and Megalodontesidae have been recorded since the middle

Jurassic (Rasnitsyn & Zhang, 2004) and Early Cretaceous (Taeger *et al.*, 2010), respectively. So far, 16 genera and 29 species of Pamphilioidea have been recorded as fossils (Taeger *et al.*, 2010).

Recently, a well preserved specimen of an impression fossil was collected from the Yixian Formation (Early Cretaceous) of Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province in northeastern China (Ren *et al.*, 1997, 2010, 2012). The exact age of the Yixian Formation is still debated, with the following three main opinions presented: the late Jurassic (Ren *et al.*, 1997, 2010; Zheng *et al.*, 2003); the late Jurassic–Early Cretaceous (Chen *et al.*, 2004; Wang *et al.*, 2004, 2005) and the Early Cretaceous (Swisher *et al.*, 1999; Zhou *et al.*, 2003). We tentatively consider the age as Early Cretaceous (late Barremian).

Materials and methods

The type specimen of the new species is deposited in the Key Laboratory of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, China.

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The wing venation nomenclature used in this paper (Figs 1C, 3B) is modified after Rasnitsyn (1969, 1980). The specimen was examined under a Leica MZ 12.5× dissecting microscope. The combined photograph of the type specimen of *Xyelydotes sculpturatus* was produced by direct superposition of photographs of the part and counterpart fossil under the respective options in Photoshop CS5 software. The line drawings were obtained CorelDraw Graphic Suite X3, Adobe Illustrator CS2 and Adobe Photoshop CS5 softwares.

Taxonomy

Superfamily Pamphilioidea Cameron

Family Praesiricidae Rasnitsyn

Type genus. *Praesirex* Rasnitsyn

Emended diagnosis. Antennal flagellum heteronomous, with the basal portion, either multisegmented or entire, distinctly thicker and several times longer than any segment in distal portion. Forewing with Sc lost, M + Cu straight or gently curved, not angular and with no posterior appendix (vein stub).

Subfamilies included. Praesiricinae Rasnitsyn (with two genera, *Praesirex* Rasnitsyn and *Turgidontes* Rasnitsyn, both from the lower Cretaceous of Transbaikalia in Russia), Rudisiricinae Gao et al. (with two genera, *Rudisiricius* Gao et al. from the lower Cretaceous of NE China, and

Aulidontes Rasnitsyn from the upper Jurassic of Kazakhstan), and Archoxyelydinae **subfam.n.** (again with two genera, *Archoxyelyda* **gen.n.** from the Lower Cretaceous of NE China, and *Xyelydotes* Rasnitsyn from the lower Cretaceous of Mongolia).

Subfamily Archoxyelydinae subfam.n.

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Type genus. *Archoxyelyda* **gen.n.**

Diagnosis. Antennal flagellum with basal, thick portion multisegmented and tight. Mesopseudosternum remote from fore margin of mesoventropleuron. Forewing with R distinctly angular at Rs base, M + Cu curved.

Genera included. Type genus and, tentatively, *Xyelydotes* Rasnitsyn.

Comments. The new subfamily is included in the Pamphilioidea based on the following pamphilioid synapomorphies: (i) mandibular foramina separated from oral cavity and (ii) ovipositor very short (about as long as a pregenital abdominal segment) and with both gonapophyses (valvulae 1–2) wide apart basally and approaching each other only toward their apices (Fig. 2B). It is further accommodated in the family Praesiricidae based on having forewing Sc lost.

The incompletely preserved genus *Xyelydotes* (Fig. 3) is tentatively included in the subfamily based on its

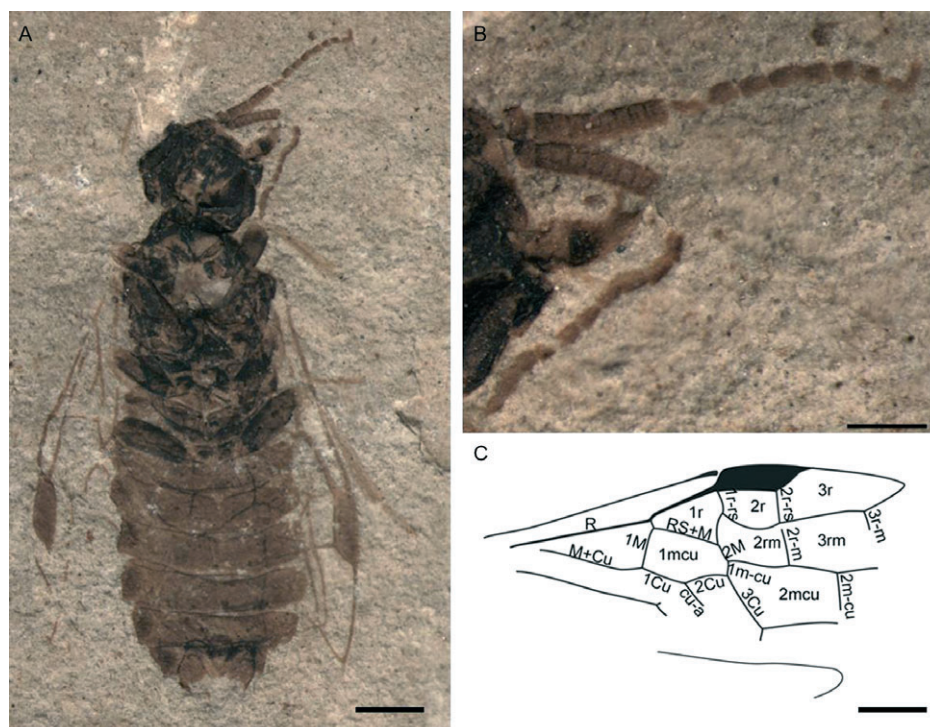


Fig. 1. *Archoxyelyda mirabilis* sp.n., holotype specimen CNU-HYM-LB2012102. (A) Photograph of holotype. (B) Part of the antennae. (C) Reconstruction of right forewing. Scale bars: 1 mm in (A) and (C); 0.5 mm in (B).

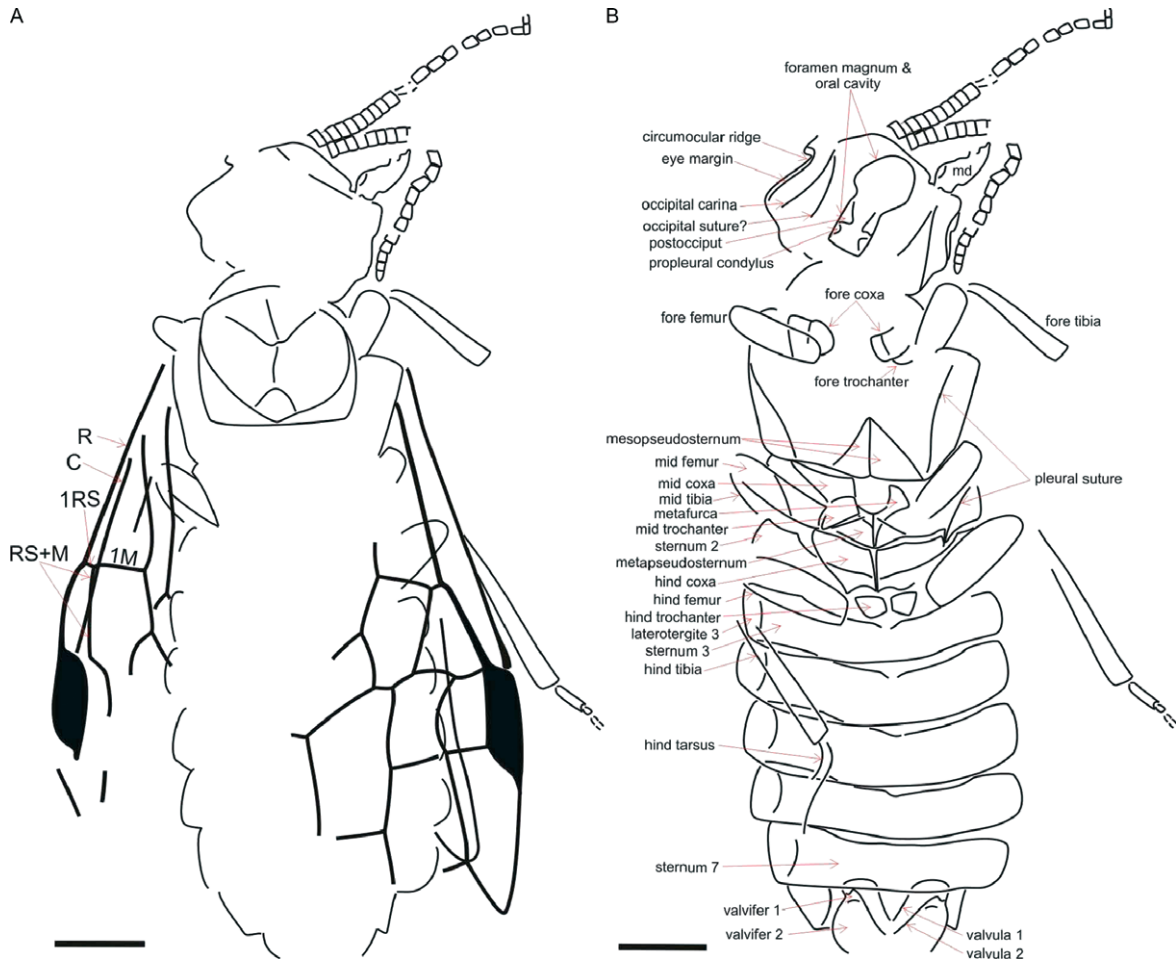


Fig. 2. *Archoxyelyda mirabilis* sp.n., holotype specimen CNU-HYM-LB2012102. (A) Interpretations of dorsal view. (B) Interpretations of ventral view. Scale bars: 1 mm.

symplesiomorphies (forewing R angular at RS base, and mesopseudosternum distant from the fore margin of mesoventropleuron). More reliable attribution depends on discovery of the antenna.

Archoxyelyda gen.n.

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Type species. *A. mirabilis* sp.n.

Diagnosis. Head wider than long, with eyes about half as long as head. Mesopseudosternum triangular, wider than long, nearly as large as mesoscutum. Vein RS + M almost vertical to 1M and much longer than 1Cu, 2M short. Integument without coarse sculpture.

Species included. Type only.

Comments. The diagnosis aims only to differ the genus from *Xyelydotes* which has eyes much smaller and placed far from

the lateral margins of the head, vein RS + M shorter (about as long as 1M) and oblique toward 1M, and mesopleura coarsely areolate (Fig. 3).

Etymology. The generic name is a combination of the Greek prefix 'archo-' (meaning original and primitive) and the genus name *Xyelyda*. The gender is feminine.

Archoxyelyda mirabilis sp.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:EEA2B91E-D730-4C2C-ABBC-A4871719A4E0>

(Figs 1, 2)

Diagnosis. As for genus.

Etymology. The species name refers to the exceptional preservation state of this material.

Material examined. Holotype: CNU-HYM-LB2012102 (Figs 1, 2).

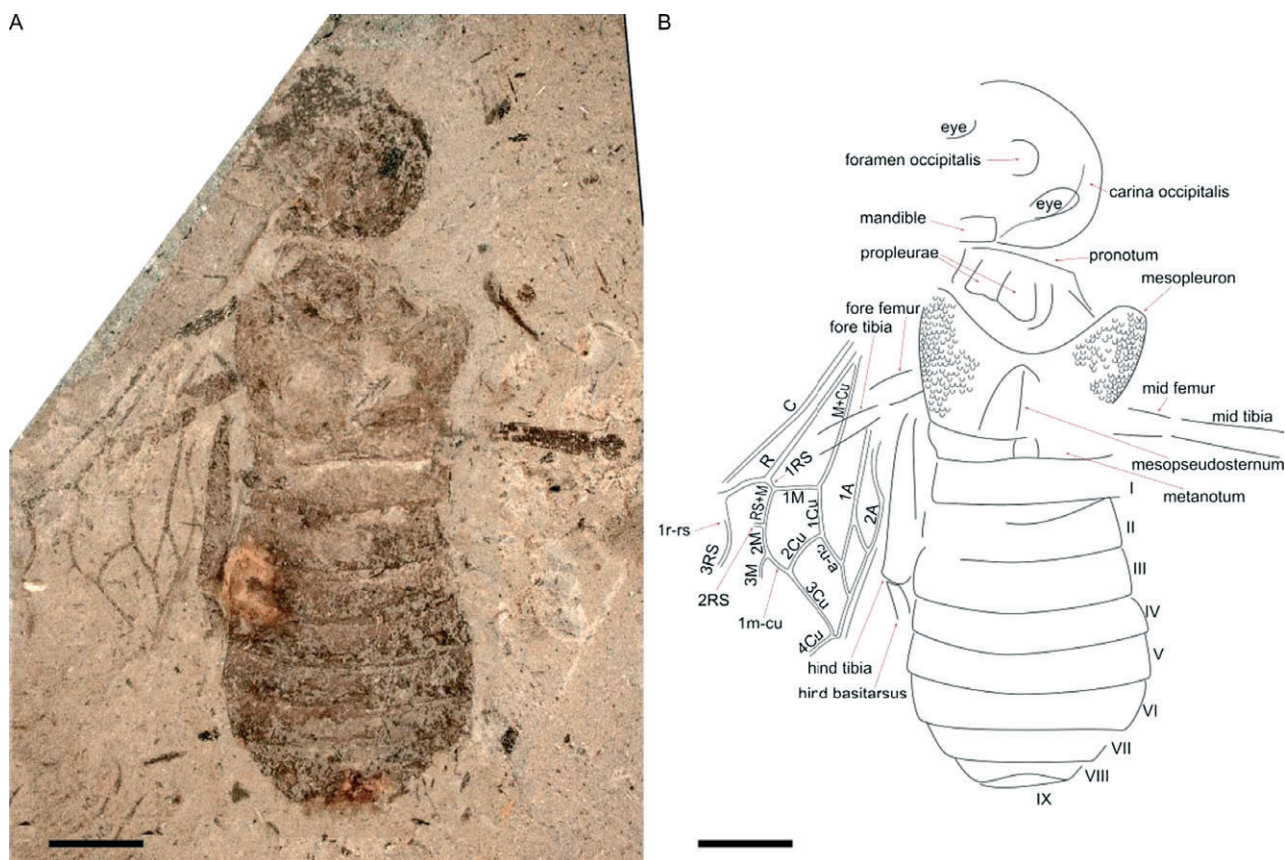


Fig. 3. *Xyelydotes sculpturatus* Rasnitsyn, 1983, holotype specimen PIN 3559/653. (A) Combined photograph of the part and counterpart. (B) interpretation of holotype. Scale bars: 2 mm.

Horizon and locality. Early Cretaceous, Yixian Formation; Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, northeast China.

Description. Colour not reliably known owing to absence of counterpart which might show different colour patterns; as preserved, head, thorax partly and femora much darker than abdomen and pterostigma, flagellum slightly darker and mesonotum much lighter than anywhere in thorax; forewing somewhat infuscate in costal area along veins.

Head: Head $c. 1.2\times$ as wide as long, slightly narrowed anteriorly ($1.1\times$ as wide behind eyes as before them). Clypeus short, with fore and hind margins almost straight and parallel except that fore margin very slightly emarginated medially. Oral cavity (well traceable along its margins; cf. Fig 2B) isolated from mandibular orifices with lower clypeal parts, and lacking sclerotized bridge between it and occipital foramen (postoccipital sclerites disconnected). Eyes (discernible from circumocular ridge only, cornea lost) in lateral position, $0.45\times$ as long as head. Occipital carina parallel to eye margin and forming an angle with occipital suture. Mandible long triangular, $2.5\times$ as long as wide, almost straight, acute, with inner margin undulate and bearing ill-preserved subapical tooth, and outer margin emarginated subbasally. Antennal

scape not preserved, pedicel slightly wider than flagellum basally, with length less than half of width, flagellum with basal $c. 9$ antennomeres tightly connected to each other and markedly transverse (apical one less transverse), jointly about $0.4\times$ as long as head width, with following some 10–12 antennomeres less tightly connected, elongate or (subapical) subquadrate, growing gradually shorter and narrower apicad, $0.7\times$ (subbasal one) to $0.5\times$ (subapical one) as wide as antennomeres in basal group (Fig 1B).

Thorax: Prothoracic structure poorly known except that pronotum short with widely and shallowly incurved hind margin, mesonotum with median mesoscutellar sulcus and notauli present, mesoscutellum short. Dorsal structures posterior to mesoscutellum not observable. Mesopseudosternum triangular, nearly as large as mesoprescutum (space between notauli) and well distant of the fore margin of mesoventropleuron. Metafurca as preserved less developed than in living Pamphiliidae and more similar to that in Xiphydriidae (e.g. Rasnitsyn, 1969: figs 191 and 193).

Legs: Coxae trapezoid, femora short (metafemur shorter than mesonotum length), not particularly wide (metafemur length less than three times their width), with fore and mid femora narrower than hind. Tibiae comparatively narrow and long, hind tibiae a little longer than fore tibiae and $1.6\times$ as long as

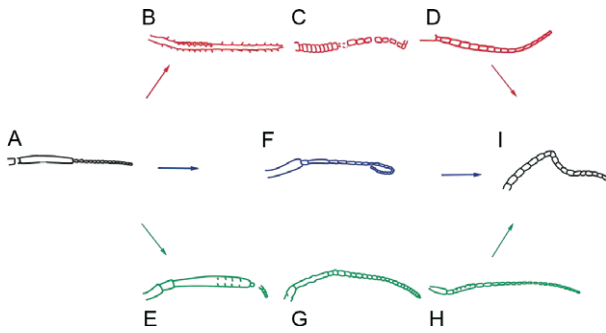


Fig. 4. Antennae of various sawflies. (A) *Platyxyela unica* Wang *et al.* 2012 (Xyelidae, orig.). (B) *Xyela julii* (Brébisson, 1818) (Xyelidae, early pupa after Rasnitsyn, 1968, fig. 54). (C) *Archoxyelyda mirabilis* sp.n. (Xyelidae, orig.). (D) *Brachysyntexis brachyura* Rasnitsyn (1968) (Anaxyelidae, after Rasnitsyn, 1969, fig. 102). (E) *Xyelotoma macroclada* Gao, Ren & Shih, 2009 (Xyelotomidae, orig.). (F) *Rudisircius belli* Gao, Rasnitsyn, Ren & Shih, 2010 (Praesiricidae, after Gao *et al.*, fig. 2b). (G) *Cephalcia fasciipennis* (Cresson, 1880) (Pamphiliidae, pupa, after Eidt, 1969, fig. 30). (H) *Caenolyda reticulata* (Linnaeus, 1758) (Pamphiliidae, orig. based on Taeger *et al.*, 2010, pl. 5, fig. 2). (I) *Microrhyssus minus* Rasnitsyn, 1968 (Paroryssidae, after Rasnitsyn, 1968, fig. 33).

hind femur. Hind basitarsus short (*c.* 1.5× as long as its tibia is wide apically), otherwise tarsal structure unknown.

Abdomen (only contour and ventral aspect preserved): wider than mesonotum, sterna narrow, parallel-sided, with fore margin indented medially, laterotergites not wide, with medial margin rounded. Ovipositor as preserved (very incompletely) typical of Pamphilioidea: very short, with stylets (valvula 1 and valvula 2) widely separated basally and meeting only at their apices.

Wings: Forewing with pterostigma sclerotized. Sc lost. R distinctly angular at Rs base. First abscissa of RS short and inclined toward wing tip. Cell 2r widens strongly and 3r moderately, 2r-m coincides with 2r-rs and is more or less inclined, 3r-m separated from apex of cell 3r by less than its length. RS + M long, vertical to 1M and subparallel to 1Cu, 2M some 0.3× as long as RS + M. 1m-cu about 0.3× as long as 3Cu, 2m-cu at midlength of cell 3rm. M + Cu straight in basal half, bend apically. Cell 1m-cu about 1.8× as long as wide, with cu-a near its midlength. Hind wing not distinctive as preserved (Fig. 1C).

Measurements: Body length (except antenna) 9.4 mm, head width 2.0 mm, length without mandible 1.6 mm, third antennomere as preserved 0.9 mm, mandible 1.9 mm long, forewing length up to end of cell 3r 6.5 mm, fore tibia length 1.3 mm, hind tibia as preserved 1.7 mm.

Discussion

Archoxyelyda mirabilis sp.n. demonstrates unusual antennal morphology that forces us to revisit an old problem of the flagellar transformation in the early evolution of Hymenoptera. The problem arose from the observation that the oldest

(Triassic) Hymenoptera (all belonging to the family Xyelidae), and many Jurassic hymenopterons, possessed unusual antennae with an enlarged (disproportionally long and thick) third antennomere mounted with an ordinary flagellum, a series of antennomeres of usual length and width (Fig. 4A). These paleontological observations initiated a series of publications (Rasnitsyn, 1968, 1969, 1980, 1988, 1996, 2002, 2006) which demonstrated the enlarged third antennomere being the ground plan character state of Hymenoptera.

The above hypothesis suggests that the xyelid-like antenna experienced transformation along different trajectories (coloured in Figs 5, 6) during the course of evolution of the order, resulting in a third antennomere that is not remarkably different from the remaining antennomeres, as observed in most Hymenoptera (black in Figs 5, 6). Different pathways of transformation has left few traces in the antennal morphology of extant taxa. The relevance of *A. mirabilis* in the present context is that it provides new test of the hypothesis and permits its further refinement.

The pathways of transformation, as described in the aforementioned publications, are as follows:

- 1 Direct separation of the compound third antennomere into its constituent antennomeres as a result of a heterochrony, i.e. the early pupal segmentation, which has equal sized antennomeres (Fig. 4B), is retained in the imago (Fig. 4C–I). This pathway (yellow in Figs 5, 6) is rather uncommonly realized. The condition in *Archoxyelyda* might represent an intermediate stage in this transformation series. A few other examples are shown by Rasnitsyn (2006, fig. 14 a, d).
- 2 Simple size reduction resulted in the enlarged third antennomere looking like an ordinary flagellomere (Fig. 4A–F, I). This trajectory (red in Figs 5, 6) seems to occur more frequently, as indicated by a number of examples (Rasnitsyn, 2006, fig. 10 d, 11 c, d, 12 d, e, 13, 14 b).
- 3 Combination of (1) and (2), that is, the compound third antennomere is growing smaller, and simultaneously its constituent primary subunits become more and more clearly delimited (Fig. 4A–E, G–I) until they are finally totally separated. This transformation series (blue in Figs 5, 6) is rather uncommon (Rasnitsyn, 2006, fig. 9c, d).

Archoxyelyda mirabilis provides evidence for an occurrence of evolutionary trajectory C–I (Fig. 4) which otherwise has only previously been supported by the example of *Syntexyela media* (Rasnitsyn, 1963) (cf. Rasnitsyn, 2006, fig. 14a) whose preservation state is inferior to that of *A. mirabilis*.

Other pathways of transformation of the heteronomous xyelid-like flagellum cannot be ruled out at present. It is hoped that more material will be discovered that will help to decipher the complicated pattern of antennal evolution in early Hymenoptera. As it is, *Archoxyelyda mirabilis* not only increases our knowledge of the taxonomic and morphological diversity of Mesozoic Hymenoptera, but also makes an important contribution to our understanding of their early morphological evolution.

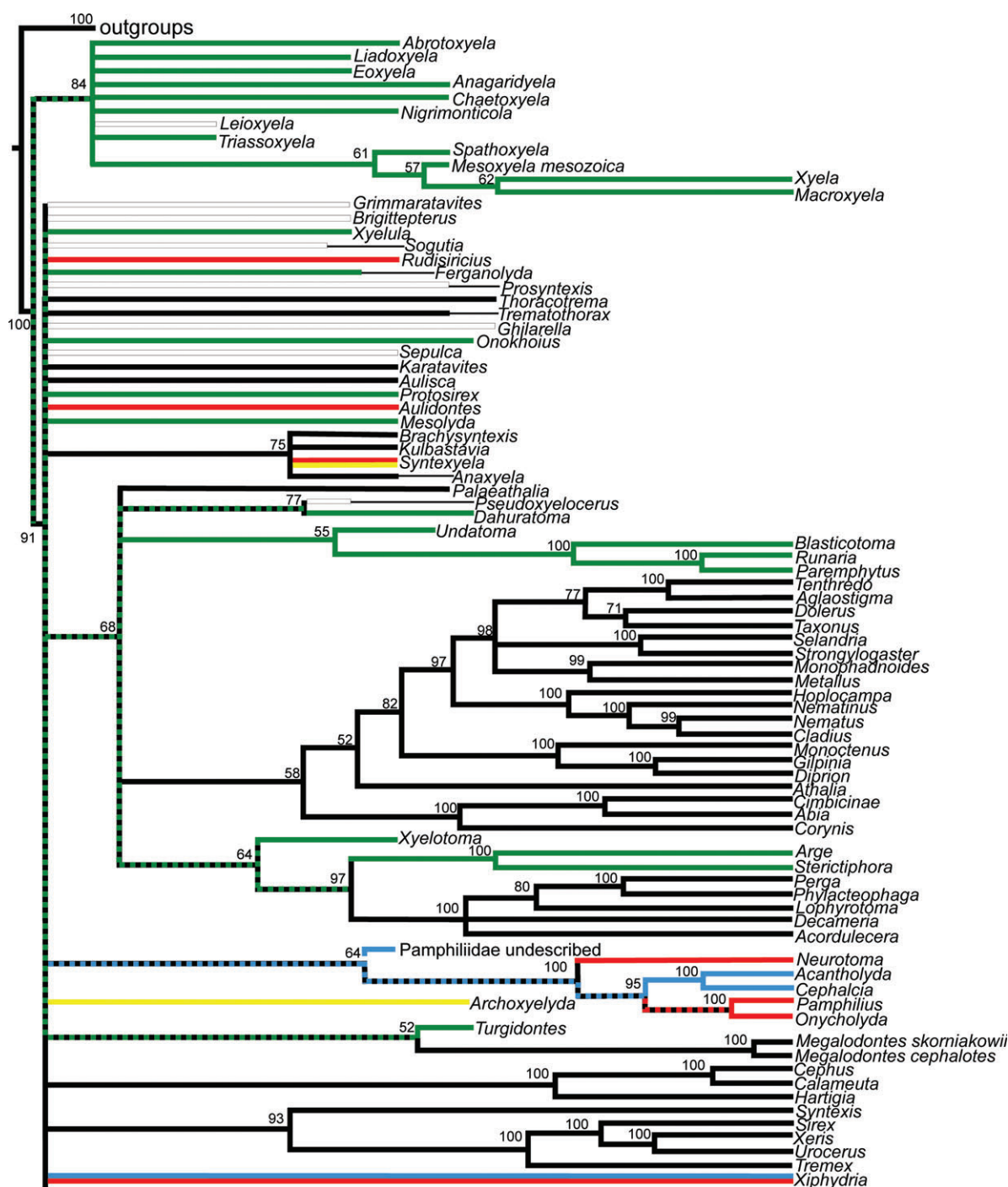


Fig. 5. Cladogram of basal Hymenoptera after Ronquist *et al.* (2012, fig 7, slightly modified), with flagellar character states mapped. Dashed lines are according Rasnitsyn's (1968, 1969, 1980, 1983, 1988, 1996, 2002, 2006) hypothesis of flagellar transformation. Line colours: black, homonomous flagellum; green, xyelid-like (Fig. 4A); yellow, *Archoxyelyda*-like (Fig. 4C); blue, *Caenolyda*-like (Fig. 4H); red, *Rudisircius*-like (Fig. 4F); blank (white), flagellum unknown. Double/triple lines refer to multistate branches.

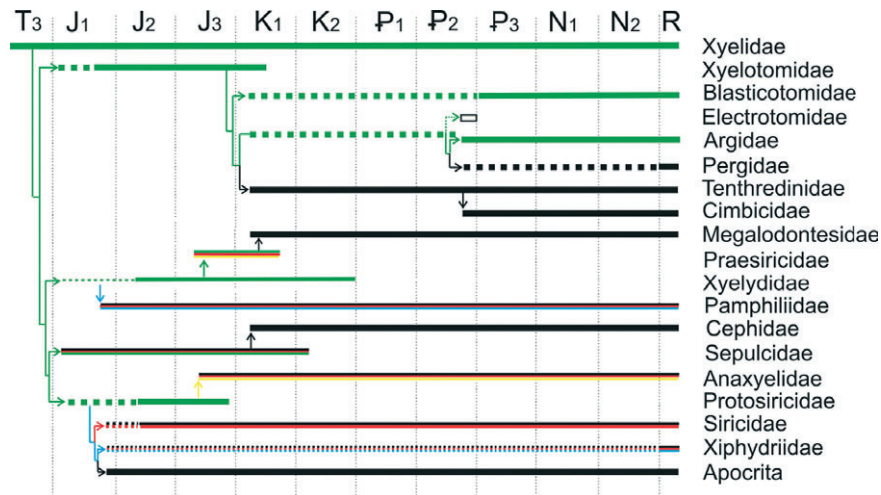


Fig. 6. Noncladistic cladogram of basal Hymenoptera after Rasnitsyn (2002, fig 331, partial, modified), with flagellar character states mapped. Colours as in Fig. 5; dashed lines are hypothetical. Stratigraphic symbols: T₃, Upper Triassic; J₁, J₂, J₃, Lower, Middle and Upper Jurassic; K₁, K₂, Lower and Upper Cretaceous; P₁, Paleocene; P₂, Eocene; P₃, Oligocene; N₁, Miocene; N₂, Pliocene; R, present time (Holocene).

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