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Research Advances

The Diversity and Phylogeny of Mesozoic Symphyta (Hymenoptera) from Northeastern China

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Objective

Symphyta, as an ancestral and paraphyletic group, are mainly phytophagous lineages. In order to truly elucidate their natural history and the development trends, we need to cover more species, including the extinct and extant species. In general, fossils sometimes appear to be necessary since extinct species usually have the so-called transitional states, which play important roles in their early evolution. It is well known that the Early Cretaceous Yixian Formation and the Middle Jurassic Jiulongshan Formations of Northeastern China have yielded well-preserved insects, including sawflies and some woodwasps. The great morphological diversity of symphytan fossils, especially those transitional character states, will make significant contributions to our understanding of the developmental trends of this basal group, as well as the evolution of hymenopterans.

Methods

The specimens were examined and then photographed, either dry or wetted with 95% ethanol, using a Leica MZ16.5 dissecting microscope (Leica, Wetzlar, Germany) with a Leica DFC500 digital camera attached. The type materials described here are deposited in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, in Beijing, China (Ren Dong, Curator).

Results

(1) Key characters' evolution and changings

As the most basal and ancestral symphytan (sawfly) in Hymenoptera, Xyelidae has a broader diversity in the Mesozoic than in today (Fig. 1B). So far, five fossil genera with eight species of fossil Xyelidae have been described during our study. Another small extinct family Xyelotomidae in Tenthredinoidea was reported to originate from Xyelidae. Gao et al. concluded that the forewing SC vein changed from two-branched to one-branched, to two separate parts, to apical part forming a crossvein, and finally to vestigial in Xyelotomidae from the Early Jurassic to the Early Cretaceous, providing additional evolutionary and transitional evidence. In addition, as another ancient but interesting member in Symphyta, Pamphilioidea is worthy of serious study as well. A Cretaceous xyelydid sawfly was reported with clearly preserved nygmata (Fig. 1C): four on each forewing and two on each hind wing. We summarized the numbers and positions of nygmata occurred in extant and extinct symphytans, concluding that there was a general trend of decreasing number of nygmata during the evolution of hymenopteran wings, and nygmata in the forewing 2rm and hind wing 2+3rm cells were the most stable. The genus *Ferganolyda* in Xyelydidae usually had enormous and heavy head, exaggerated mandibles, and long and thin antennal flagella, which were typical in their relevant males. However, these strange and intriguing structures have raised further controversies. All *Rudisiricius* in Praesiricidae were collected from the Yixian Formation, which possessed larger body size, stronger and more robust mandibles. The most important was their much more exaggerated thick scapes when compared with other praesiricids (Fig. 1D). Moreover, it is interesting that all reported specimens of known Rudisiricinae thus far were definite or possible males, which was also a very enigmatic case for Symphyta. Besides, an unusual praesiricid, with the third antennal segment consisting of tightly connected primary antennomeres (Fig. 1E), provided the flagellar transformations in the early evolution of Hymenoptera. We reviewed the antennal evolution in the lower Hymenoptera and put forward three pathways of antennal transformation during their development.

(2) Phylogenetic relationships among Symphyta

To date, no matter the phylogeny of Symphyta was

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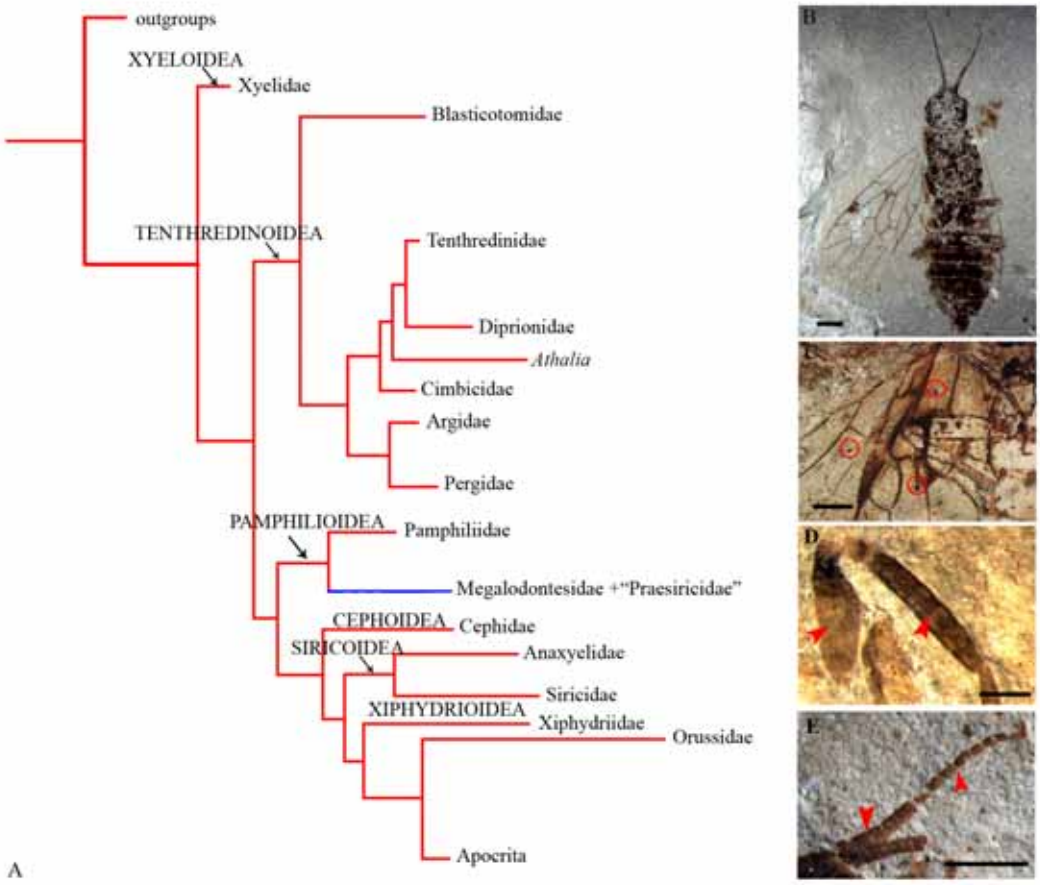

Fig. 1. Interpretations of morphological diversity and phylogeny of Pamphilioidea.
(A), Cladogram of basal Hymenoptera; (B), Photo of habitus (Xyelidae); (C), Nymata on the wings (Xyelydidae); (D), Exaggerate scape of antenna (Praesiricidae); (E), Segmented first flagellomere of antenna (Praesiricidae). Scale bars: 1 mm in (B), (C) and (E); 0.5 mm in (D).

analyzed by using morphological characters, molecular data or more recently, under simultaneous analysis, the paraphyly of Symphyta and the monophyly of each superfamily were both confirmed; however, the relationships among superfamilies of Symphyta were unstable, particularly occurring in Tenthredinoidea, Cephidae, Siricoidea, and Xiphydriidae. Furthermore, the phylogeny of Pamphilioidea was carried out under simultaneous analysis during our research, the results corroborated the monophyly of Pamphilioidea and Pamphiliidae, confirmed that Xyelydidae and Praesiricidae were not monophylum. Additionally, we also suggest that all members of Praesiricidae should be transferred to Megalodontesidae (Fig. 1A).

Conclusion

As aforementioned, our findings from the Middle Jurassic to the Early Cretaceous of northeastern China have enhanced our knowledge of the taxonomic and morphological diversity of Mesozoic Symphyta. Although many interesting and puzzling characters are discovered, some issues still remain unrevealed. It is hoped that more material will be discovered in the future that will help to decipher the functional morphology, evolutionary trend and ecology of these amazing but mysterious symphytans.

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