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The oldest Naibiomorpha: new fossil from NW China with implications for their early evolution

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Abstract

The early morphology and evolution of Naibiomorpha, an extinct infraorder of Sternorrhyncha, remain poorly understood due to scarce fossil material. Herein, we report the oldest known representative of this infraorder: a new specimen of *Dracaphis angustata* from the Tongchuan Formation (Ladinian, Middle Triassic) in Shaanxi Province, NW China, which preserves complete forewing venation. Detailed morphological comparison allows us to refine the diagnostic characters of Naibiomorpha and corroborate its phylogenetic placement. This specimen not only provides a key diagnostic benchmark, but lends support to the "forewing miniaturization hypothesis" within the clade. Integrating our findings with palaeobiogeographic data, we infer a Northern Hemisphere origin for Sternorrhyncha in the Permian, followed by a Triassic diversification that gave rise to both extant lineages (e.g., aphids, whiteflies, and psyllids) and extinct groups such as Naibiomorpha.

Keywords: earliest Naibiomorpha, Sternorrhyncha, Tongchuan Formation, Forewing miniaturization hypothesis

Introduction

The order Hemiptera comprises six suborders: the extinct Paleorrhyncha (archescytinoids), Sternorrhyncha (including modern aphids, scale insects, whiteflies and jumping plant lice), Fulgoromorpha (planthoppers), Cicadomorpha (such as cicadas, froghoppers, leafhoppers and treehoppers), Coleorrhyncha (moss bugs), and Heteroptera (true bugs) (Szwedo et al. 2015; Drohojowska et al. 2020).

Naibiomorpha, an extinct infraorder within the suborder Sternorrhyncha, represents an early-diverging branch that thrived from the Middle Triassic to the Paleocene (Shcherbakov 2007). Its fossils offer key morphological evidence for reconstructing the early evolutionary radiation and groundplan morphology of Sternorrhyncha, prior to the diversification of major extant lineages such as aphids (Aphidomorpha), whiteflies (Aleyrodomorpha), and psyllids (Psylloidea). Recent phylogenetic analyses consistently place Naibiomorpha as a monophyletic group near the base of the sternorrhynchan tree, confirming its status as a basal clade rather than a direct ancestor to any modern group (e.g., Drohojowska et al. 2020; Szwedo 2018).

The oldest known representative of Naibiomorpha is *Dracaphis angustata* (Hong et al. 2009 b), from the Ladinian (Middle Triassic) of Shaanxi Province, NW China (Tab. 1). While previously described specimens preserve distinct somatic features (such as a large body size, large eyes, and two long, slender abdominal processes), the wing venation of these specimens remains incomplete or poorly preserved. This has significantly constrained detailed taxonomic comparison, given the critical diagnostic value of venation characters within this group. This study centers on the first discovery of the oldest Middle Triassic Naibiomorpha fossils with the most completely preserved forewing venation known to date (e.g., *D. angustata*). Through detailed morphological description, we aim to clarify the taxonomic relationships of Naibiomorpha and provide new evidence on the early morphological evolution of Sternorrhyncha.

Geological background

The Ordos Basin is the second-largest sedimentary basin in NW China, spans five

provinces (Shaanxi, Gansu, Ningxia, Inner Mongolia, and Shanxi), with an area of approximately 37×10^4 km^2 (Zhao et al. 2021). This basin is rich in petroleum and natural gas resources, hosting significant deposits of oil shale and sandstone-type uranium (Yang and Zhang 2005; Yang and Deng 2013; Zhang et al. 2009).

The specimen studied here, which obtained from the Ordos Basin, was collected from the Tongchuan Formation at the Qishuihe Section (35°13′80″N, 109°01′50″E), located near Hejiafang Village, Jinsuoguan Town, Tongchuan City, Shaanxi Province, NW China (Fig. 1 A). Stratigraphically, the Tongchuan Formation conformably overlies the Lower–Middle Triassic Ermaying Formation and underlies the Upper Triassic Yanchang Formation (Deng et al. 2018). The lower part of Tongchuan Formation consists primarily of greyish-green to red sandstone, with shale and mudstone interbeds occurring toward the top. Its upper part is characterized by greyish-green to red fine-sandstone and siltstone, interbedded with greyish-green mudstone (Zheng et al. 2018). A distinctive, continuous oil shale bed exceeding 27 m in thickness, marks the top of the formation and is widely recognized as its upper boundary (IGCAGS 1980; Yang et al. 2000).

The Tongchuan Formation has a total thickness of approximately 596 m and includes a diverse fossil assemblage comprising bivalves, spinicaudatans, ostracods, insects, tadpole shrimps, fish, reptiles, sporopollen and plants (IGCAGS 1980; Wu et al. 2001; Hong 2007, 2009 a, b; Li et al. 2007; Sun and Hong 2011; Zhao et al. 2020). Abundant insects had been recorded in the Tongchuan Entomofauna, such as orders Hemiptera, Mecoptera, Coleoptera, Blattodea, Odonata, Micropterigidae, Glosselytrodea, Orthoptera, Miomoptera and Neuroptera (Fu and Huang 2022; Fu et al. 2021, 2022; Lian et al. 2021, 2023; Xu et al. 2020; Zhang et al. 2021, 2022 a, b, 2024 a, b; Zheng 2017). Despite the high abundance of hemipteran fossils, Naibiomorpha specimens within this order remain exceptionally rare, with only one species reported. The U-Pb dating of the Tongchuan Formation at this section has yielded ages of 238.0 ± 1.0 Ma and 237.4 ± 0.9 Ma, suggesting the fossil insects a latest Ladinian age (Middle Triassic) (Zheng et al. 2018) (Fig. 1 B).

Material and methods

The specimen was examined and photographed in its dry state using a Zeiss Stereo Discovery V16 microscope system under vertical reflected light and polarized light. All images were digitally stacked photomicrographic composites of approximately 50 individual focal planes obtained using the Helicon Focus software. Resulting images were optimized using Adobe Photoshop software. Line drawings and figures were prepared using CorelDRAW 2024 and Inkscape v.1.4.

The nomenclature of forewing venation follows Shcherbakov (2007), special vein abbreviations are explained in Figure 2. The holotype specimen is housed at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS, CAS).

Order Hemiptera Linnaeus, 1758

Suborder Sternorrhyncha Amyot and Serville, 1843

Infraorder Naibiomorpha Szwedo, 2018

Superfamily Naibioidea Shcherbakov, 2007

Revised diagnosis: Forewing: R vein is the longest, extending from the wing apex to the forewing base; M without branches, originated from base of cubitus; CuA with 2–3 branches; claval margin angulate, with simple marginal Pcu+1A.

Type family. Naibiidae Shcherbakov, 2007

Family Dracaphididae Hong, Zhang, Guo et Heie, 2009

Fig. 2 A–C

New material. NIGP [TC-01] (institutional catalog number pending), complete forewing 6.2 mm long, 1.69 mm wide. The top of the lower part of the Tongchuan Formation in the Qishuihe Section (35°13′80″N, 109°01′50″E), Hejiafang Village, Jinsuoguan Town, Tongchuan City, Shaanxi Province, Northwest China (Middle Triassic, latest Ladinian).

Revised diagnosis. Forewing 6.20 mm or longer, rather narrow (length to width ratio about 3.65); Sc weak or invisible; Rs only slightly curved, Rs stem orgina R, R

about 3 times longer than Rs stem; M without branches, originating from base of cubitus; vein CuA continued rather by convex CuA_1, $CuA_1$and CuA_2 usually straight, CuA_1 as long as CuA_2.

Genus *Dracaphis* Hong, Zhang, Guo et Heie, 2009

Type species. *Dracaphis angustata* Hong, Zhang, Guo et Heie, 2009

2009 *Dracaphis angustata*, Hong et al., p. 826.

2011 *D. angustata* Szwedo et al. p.761.

2016 *D. angustata* Szwedo et al. p.216.

2017 *D. angustata* Dagmara et al. p.6.

2017 *D. angustata* Szwedo et al. p.115.

Diagnosis. As for the family.

Description. Forewing 6.20 mm long, 1.69 mm wide, appearing rather narrow (length/width ratio 3.65). Main stem (R+Rs+M+Cu) stronger than other veins; Sc weak or invisible; vein R longest, extending from wing base to apex; Rs branches from R, Rs leaving near base of R–R1, stem R about 3 times longer than vein Rs; M without branches, originating from base of cubitus, and extending about halfway to lateral margin; veins CuA_1 and CuA_2 with convex base and straight, both similar in length, with CuA_2 equal in length to stem CuA; CuP week, long and straight.

Discussion

The taxonomic position of the superfamily Naibioidea has undergone substantial revision. It was initially placed within the infraorder Aphidomorpha, which traditionally comprised three superfamilies: Triassoaphidoidea, Lutevassoaphididae, and Naibioidea (Szwedo et al. 2015). This placement, however, was contested, with alternative hypotheses aligning Naibioidea with Coccidomorpha (Shcherbakov 2007). To resolve this systematic uncertainty, Szwedo et al. (2018) erected the new infraorder Naibiomorpha to accommodate Naibioidea and its constituent families (Dracaphididae, Naibiidae, and Sinojuraphididae).

Subsequently, within the modern phylogenetic framework established by Drohojowska et al. (2020) Naibiomorpha is recognized as an entirely extinct infraorder within Sternorrhyncha. It was positioned as the sister group to Aphidomorpha (true aphids), rather than a lineage within it (Drohojowska et al. 2020). Consequently, Naibiomorpha and Aphidomorpha represent two distinct evolutionary branches that diverged from a common ancestor approximately 250 million years ago (Szwedo et al. 2015) (Fig. 3).

The new fossil exhibits a forewing venation pattern of R+Rs+M+Cu, which is typical of *Dracaphis angustata* Hong et al. 2009 b. Previously specimens of this species preserve complete body outlines, yet their forewing venation remains incomplete or obscured (Hong et al. 2007). As comparative studies of basal Sternorrhyncha and Aphidomorpha (e.g., Lutevanaphididae, Boreoscytidae, etc.) heavily rely on venation characters (Shcherbakov 2007; Szwedo and Nel 2011; Szwedo et al. 2015), the complete venation presented in this new material effectively addresses a critical gap. Although the new fossil shows general similarity to members of Naibiinae and Coccavinae, key venation characters distinguish it from these groups (see comparison below). Notably, the minor venational differences observed between the new fossil and the holotype of *D. angustata* are interpreted here as taphonomic artifacts, likely resulting from compression and vein obscuration in the holotype. Given its morphological consistency and origin from the same deposit, we assign the new specimen to *D. angustata*, thereby complementing the species diagnosis.

Pincombeomorpha is characterized by Rs originating anterior to the pterostigma and by M and CuA forming a short common stalk. Aphidomorpha is defined by the lack of fusion between M and Rs and by M typically having three branches. Naibiomorpha is diagnosed by an unbranched M vein that originates near the base of the cubitus (Shcherbakov 2007; Szwedo and Nel 2011; Szwedo et al. 2015) (Fig. 3).

The new specimen of *D. angustata* not only represents the oldest fossil record of Naibiomorpha but also provides critical diagnostic characters for understanding the early divergence of this infraorder. Another Triassic species, *Coccavus supercubitus* from Kyrgyzstan (Middle Triassic), can be distinguished from *D. angustata* by key

venational features, most notably its distinctly three-branched CuA vein. This morphological distinction indicates that by the Middle Triassic, the three major stem groups of Sternorrhyncha (Aphidomorpha, Naibiomorpha and Pincombeomorpha) were already clearly differentiated. They likely originated from a common ancestor during the Early Permian (Cisuralian) and thereafter followed independent evolutionary trajectories: some lineages gave rise to extant crown groups (aphids, whiteflies and psyllids), while Naibiomorpha ultimately went extinct.

Regarding the infraorder's taxonomic composition, our detailed comparison of forewing venation challenges the current inclusion of *Sinojuraphis* (Huang and Nel 2008) within Naibiomorpha. The venation of *Sinojuraphis*—characterized by a 2-branched M vein and a distinct basal separation of veins M and Cu, differs significantly from the diagnostic pattern observed in core Naibiomorphans. Therefore, we propose the taxonomic revision of *Sinojuraphis* and recommend its removal from Naibiomorpha to reflect a more accurate phylogeny (Fig. 4, green circle).

Current palaeogeographic reconstructions indicate that Naibiomorpha likely originated in northern Laurasia, a scenario consistent with a Northern Hemisphere origin hypothesis for Sternorrhyncha (Szwedo and Nel 2011; Szwedo et al. 2015). Despite this shared early history, the evolutionary fates of these lineages diverged markedly. Naibiomorpha remained geographically confined to Laurasia and eventually became extinct. In contrast, aphids achieved a nearly global distribution in temperate zones, while whiteflies and scale insects radiated into tropical and subtropical regions worldwide. This stark disparity in evolutionary success suggests that differential capacities for co-evolution with host plants and for exploiting newly available ecological niches were probably critical factors determining the long-term survival or extinction of major sternorrhynchan lineages (Fig. 4).

With the venational supplement of *Dracaphis*, Naibiomorpha exhibits a clear macroevolutionary trend toward miniaturization. Its earliest and largest known representative, *D. angustata* from the Middle Triassic, attained a forewing length of up to 6.20 mm. Other younger species such as the Middle Jurassic *Panirena tenella*, the Early Cretaceous *P. sukatshevae*, and the Paleogene *Naibia zherichini* (~1 mm)

are markedly smaller in forewing length (Fig. 4). We propose that the evolutionary trajectory of this clade aligns with a “forewing miniaturization hypothesis”, driven bythe need to evade efficient aerial predators, particularly early birds. Although advantageous as a short-term survival strategy, it consequently led to the degeneration of flight capability and a severely constrained ecological niche. Ultimately, this extreme specialization entrapped the clade in an “adaptive trap”, resulting in its extinction.

Conclusions

This study provides, for the first time, the complete forewing venational data for the Middle Triassic naibiomorphan hemipteran of *Dracaphis angustata*. Its derived morphological traits provide definitive evidence for recognizing Naibiomorpha as a distinct clade, which also establishing a key diagnostic benchmark for this stem group. Integration of these morphological and palaeogeographic evidence supports a Northern Hemisphere origin and a Triassic diversification of Sternorrhyncha. This synthesis reveals two divergent evolutionary trajectories within Sternorrhyncha: certain lineages gave rise to extant crown groups (e.g., aphids, whiteflies, and psyllids), whereas Naibiomorpha ultimately faced extinction during the Paleogene.

Acknowledgements

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333 **Figure captions**

334 **Figure 1**. Fossil locality in the Qishuihe Section of Jinsuoguan Town, Tongchuan
335 City, Shaanxi Province, China. **A,** Location map of Jinsuoguan Town; **B**, stratigraphic
336 column of the Tongchuan Formation (modified after of Zheng et al. 2018).

337 **Figure 2**. *Dracaphis angustata* Hong et al. 2009, new material; holotype NIGP TC-
338 01. **A**, Holotype under oblique illumination; **B**, Holotype imaged with transmitted
339 brightfield light; **C**, line drawing. Scale bars = 1 mm.

340 **Figure 3**. Temporal range and phylogenetic relationships of the Naibiomorpha and
341 related groups in the Permian and Triassic. Circles with asterisks indicate figured taxa,
342 empty circles do not represent a figured taxon. The lower right insert presents the
343 relationships of the Permian and Triassic lineages (modified after Szwedo et al. 2011,
344 2015; based on data from Shcherbakov 2007, 2010; Heie and Wegierek 2011;
345 Drohojowska et al. 2020).
346 **Figure 4**. Palaeogeographic distribution and forewing venation of Naibiomorpha
347 (modified after Scotese et al. 2016; based on data from Hong et al. 2009 b,
348 Shcherbakov 2007 and Huang et al. 2008).

349

350 **Tab 1.** Fossil records of Naibiomorpha with forewings' information.

351