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## EDITED BY

Xing Xu,  
Yunnan University, China

## REVIEWED BY

Yongjie Wang,  
Guangdong Academy of Sciences, China  
Yanhong Pan,  
Nanjing University, China

## \*CORRESPONDENCE

Chen-Yang Cai  
✉ cycai@nigpas.ac.cn

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# Mesozoic *Notocupes* revealed as the sister group of Cupedidae (Coleoptera: Archostemata)

Yan-Da Li<sup>1,2</sup>, Erik Tihelka<sup>1,2</sup>, Shûhei Yamamoto<sup>3</sup>,  
Alfred F. Newton<sup>4</sup>, Fang-Yuan Xia<sup>5</sup>, Ye Liu<sup>6,7</sup>, Di-Ying Huang<sup>1</sup>  
and Chen-Yang Cai<sup>1,2\*</sup>

<sup>1</sup>State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China, <sup>2</sup>Bristol Palaeobiology Group, School of Earth Sciences, University of Bristol, Bristol, United Kingdom, <sup>3</sup>Hokkaido University Museum, Hokkaido University, Sapporo, Japan, <sup>4</sup>Integrative Research Center, Field Museum of Natural History, Chicago, IL, United States, <sup>5</sup>Lingpoge Amber Museum, Shanghai, China, <sup>6</sup>Paleo-diary Museum of Natural History, Beijing, China, <sup>7</sup>Fujian Paleo-diary Bioresearch Centre, Fuzhou, China

Despite encompassing only about 50 extant species, beetles of the suborder Archostemata have a rich fossil history, being known from the Permian and dominating coleopteran assemblages in the Mesozoic before declining in richness towards the Late Cretaceous. Given the limited diversity of extant archostematans, fossils provide a valuable line of evidence for reconstructing the relationships among its constituent families. Here we re-evaluate the phylogenetic position of the Triassic–Cretaceous genus *Notocupes*, the most species-rich archostematan taxon in the fossil record. Exquisitely preserved fossils from the Middle Jurassic Haifanggou Formation (Daohugou; ~165 Ma) and mid-Cretaceous amber (~99 Ma) reveal critical differences from Ommatidae in the presence of separated procoxae and overlapping abdominal ventrites. Our analyses confirm that *Notocupes* is not a member of Ommatidae, but is closely related to Cupedidae. Our fossils reveal that *Notocupes* possessed unique adaptations for protecting their appendages, such as unusual dorsal pronotal grooves for the reception of antennae and epipleural grooves for the reception of legs, shedding light on ecological interactions in Mesozoic saproxylic habitats. The high similarity between Jurassic and Cretaceous *Notocupes* provides an exceptional example of long-term morphological stasis, suggesting a consistent microhabitat for the group.

## KEYWORDS

Archostemata, *Notocupes*, Cupedidae, compression fossils, amber

## 1 Introduction

Archostemata is one of the four extant beetle suborders. While just around 50 extant archostematan species are known in 15 genera (Hörnschemeyer, 2016), the group was considerably diverse in the geological past. Archostematans dominated early Mesozoic fossil beetle assemblages and over 200 extinct species have been described across the world

(Ślipiński et al., 2011). In some analyses, Archostemata (*sensu stricto*, not including stem-group beetles such as Tshekardocoleidae and Permocupedidae) is recovered as the earliest-diverging clade within Coleoptera (Friedrich et al., 2009; Bocak et al., 2014), highlighting its importance for understanding the origin of the present-day diversity of beetles. Because they superficially resemble Permian stem-group beetles (Ponomarenko et al., 2014), archostematans have often been regarded as “living fossils” (Cai and Huang, 2017; Jarzembowski et al., 2020a). This is particularly the case for the families Cupedidae (reticulated beetles) and Ommatidae, which possess elytra with regularly arranged rows of window punctures resembling those found in early beetles from the Permian. Owing to their similar body plans, Cupedidae and Ommatidae have been at times regarded as a single family, Cupedidae *sensu lato* (Ponomarenko, 2000; Kirejtshuk, 2020). However, recent molecular phylogenetic studies indicate that Ommatidae is more closely related to Micromalthidae, rather than Cupedidae *sensu stricto*, and thus “Cupedidae *s.l.*” is not a monophyletic group (McKenna et al., 2015; McKenna et al., 2019). Therefore, in this paper we treat Ommatidae and Cupedidae as separate families. The interrelationships of Cupedidae, Ommatidae, Micromalthidae and the two remaining archostematan families, Crowsoniellidae and the enigmatic Jurodidae, have been historically difficult to elucidate based on morphology, and no molecular data have been available for the latter two. Both Crowsoniellidae and Jurodidae are rare and species-poor in the recent fauna, with Crowsoniellidae known from only three specimens collected in 1973 in Italy (Pace, 1975; Kirejtshuk et al., 2010; Ge et al., 2011), and Jurodidae known from a single Recent specimen found in Far Eastern Russia and scarce Jurassic fossils (Lafer, 1996; Kirejtshuk, 1999; Yan et al., 2014). Since Jurodidae combines characters found in Adephaga, Archostemata and Polyphaga, some authors do not include it within Archostemata and treat it as a taxon of uncertain affinities (Lawrence, 2016).

Given the limited diversity of extant archostematan beetles, fossils provide crucial evidence for reconstructing the phylogeny of the group (Tan et al., 2012; Li et al., 2019). The fossil record of archostematans is also important for understanding biotic change in Mesozoic terrestrial ecosystems, namely the conversion from an archostematan-dominated beetle fauna to a polyphagan-dominated one in the late Mesozoic–early Cenozoic (Soriano and Delclòs, 2006; Friedrich et al., 2009).

*Notocupes* Ponomarenko is the most abundant genus of archostematans in Mesozoic deposits. With over 50 extinct species known from the Triassic–Cretaceous it is also one of the most species-rich insect genera in the fossil record (Strelnikova and Yan, 2023). Additional species are assigned to the form genus *Zygadenia* Handlirsch that is reserved for isolated elytra likely belonging to representatives of *Notocupes*. Since the first discovery of a *Zygadenia* elytron by Giebel (1856) from the Cretaceous Purbeck Limestone Group of southern England, the *Notocupes*–*Zygadenia* complex has been reported from Europe, Asia, South America, and Australia (Kirejtshuk, 2020). *Notocupes* has been historically placed into the family Ommatidae (or Ommatinae in Cupedidae *s.l.*), and into the tribe Notocupedini erected by Ponomarenko (Ponomarenko, 1966). Despite its wide distribution, the morphology of *Notocupes* remains

insufficiently known. Most *Notocupes* specimens were described based on compressions from Mesozoic strata, and thus many morphological characters are difficult to interpret or not preserved at all. The morphology of the three *Notocupes* species reported from mid-Cretaceous Burmese amber (Tihelka et al., 2019; Jarzembowski et al., 2020b; Jiang et al., 2020) remains insufficiently described, owing to the challenging optical properties of the amber matrix. Here we report four exquisitely preserved *Notocupes* fossils from Middle–Late Jurassic Daohugou Biota and mid-Cretaceous Burmese amber. With the aid of a range of imaging techniques, including confocal laser scanning microscopy, scanning electron microscopy, and microtomography, we aim to clarify the external morphology of *Notocupes* and evaluate the systematic position of this genus within Archostemata.

## 2 Materials and methods

### 2.1 Fossils and imaging

The three compression fossils photographed herein (Figures 1A–F, 2) originated from Daohugou Village, Ningcheng County, Inner Mongolia, China (~165 Ma). An additional compression fossil (Supplementary Figure 2) originated from Huangbanjigou Village, Shangyuan Township, Beipiao City, Liaoning Province, China (~125 Ma). These specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The Burmese amber specimen BA202101 (Figures 1G, H, 3) originated from amber mines near Noije Bum (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar (~99 Ma), and is deposited in the Lingpoge Amber Museum, Shanghai, China.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Where necessary, compression fossils were moistened with 70% ethanol to improve contrast of morphological characters. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm Argon laser excitation line (Fu et al., 2021). Images under incident light and widefield fluorescence were stacked in Helicon Focus 7.0.2 or Zereine Stacker 1.04. Confocal images were stacked with Helicon Focus 7.0.2. Scanning electron microscopic (SEM) images were obtained with a Hitachi SU 3500 scanning electron microscope, operating with an accelerating voltage of 18 kV and a pressure of 60 Pa. Microtomographic data for BA202101 were obtained with a Zeiss Xradia 520 Versa 3D X-ray microscope at the micro-CT laboratory of NIGP, and analyzed in VGStudio MAX 3.0. Scanning parameters were as follows: isotropic voxel size, 14.096 μm; power, 3 W; acceleration voltage, 40 kV; exposure time, 4 s; projections, 2001. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

The full set of descriptions and figures, along with the new taxonomic acts, will be presented in a separate paper.

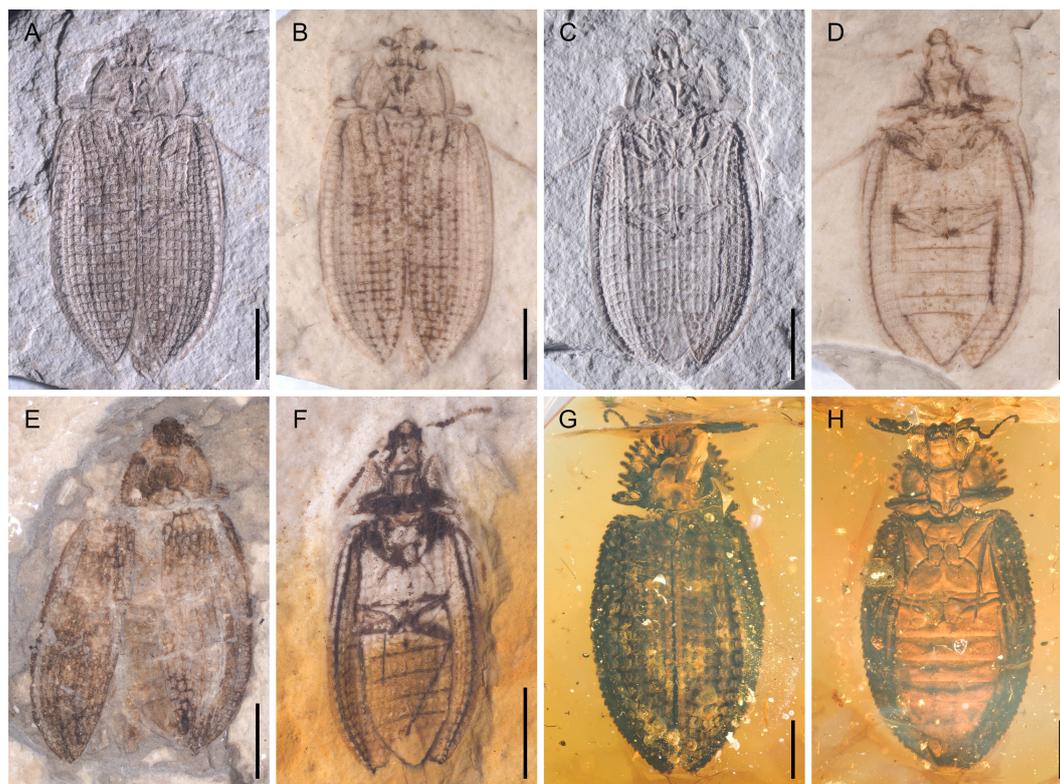


FIGURE 1

General habitus of *Notocupes* spp., under incident light, dry (A, C) or moistened with 70% ethanol (B, D–F). (A, B) NIGP174673a. (C, D) NIGP174673b. (E) NIGP174674. (F) NIGP174675. (G) BA202101, dorsal view. (H) BA202101, ventral view. Scale bars: 5 mm in (E), 3 mm in (A–D), 2 mm in (F–H).

## 2.2 Phylogenetic analysis

To evaluate the systematic placement of *Notocupes*, morphological phylogenetic analyses were performed. The data matrix (Supplementary Data 1, 2) was derived from a previously published dataset (Beutel et al., 2008). The original matrix consists of 90 morphological characters of recent and fossil beetles, including representatives of all archostematan families. Several changes to the scoring of the characters were made. Firstly, head protuberances are important for generic-level identification of Cupedidae (Hörschemeyer, 2009). However, the definition of these protuberances is sometimes unclear for other archostematans. For example, the protuberances P3 were defined as “between P2, on both sides of the median line of the head” in (Hörschemeyer et al., 2006), but in *Tetraphalerus* Waterhouse, the posterior protuberances are situated roughly posteriorly to P2 (Figure 10D in Beutel et al., 2008), making it difficult to determine if they should be coded as P3 or P4. Besides, there might be some miscoding for head protuberances in Beutel et al. (2008). For example, the protuberances P2 for *Omma* Newman were coded as strongly pronounced, but we failed to detect any strongly pronounced protuberances on the head of *Omma* (Figure 16 in Escalona et al., 2020). We therefore excluded characters 6–9 in Beutel et al. (2008) from our analysis. Secondly, Beutel et al. (2008) coded the propleuron as reaching the anterior

margin of prothorax in *Tetraphalerus* and *Crowsoniella* Pace (their character 42). In fact, the propleuron of *Tetraphalerus* does not reach the anterior prothoracic margin (Friedrich et al., 2009; Li et al., 2021), and no separate propleuron is present in *Crowsoniella* at all (Figure 16 in Kirejtshuk et al., 2010); we adapted our character matrix accordingly. Lastly, character 31 in Beutel et al. (2008) was coded as (2) for *Crowsoniella*, which is a non-existent character state and was therefore corrected in our matrix. Thus, our decisive matrix included 86 characters in total.

The problematic family Jurodidae has been considered as a member of Adephaga, Archostemata, or Polyphaga (Ponomarenko, 1985; Lafer, 1996; Kirejtshuk, 1999; Beutel et al., 2008; Hörschemeyer, 2009). Its puzzling combination of characters, seemingly combining states found in three coleopteran suborders, represents a potential source of incongruence in phylogenetic analyses. Hence, we prepared two matrices, one including Jurodidae (represented by the extant *Sikhotealinia* Lafer and the extinct *Jurodes* Ponomarenko), and one excluding the family.

Parsimony analyses were conducted in the program TNT 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016). We experimented with the use of equal and implied weighting. Parsimony analyses have been shown to achieve higher accuracy under a moderate weighting scheme (e.g., when concavity constants,  $K$ , are between 5 and 20) (Goloboff et al., 2018; Smith,

2019). Therefore, we set the concavity constant to 12 in our analyses with implied weighting, as suggested by Goloboff et al. (2018). Most parameters were set as default in the “new technology search”, while the value for “find min. length” was changed from 1 to 100. When multiple most parsimonious trees were obtained, a strict consensus tree was calculated, and a standard bootstrap analysis was implemented with 1,000 pseudoreplicates, where the support values were shown as frequency differences (Goloboff et al., 2003). Settings for the equal weighting approach were identical, employing default parameters. Character states were mapped onto the tree with WinClada 1.00.08. The tree was graphically edited with Adobe Illustrator CC 2017.

### 3 Systematic paleontology

Order Coleoptera Linnaeus, 1758

Suborder Archostemata Kolbe, 1908

## 3.1 Genus *Notocupes* Ponomarenko, 1964

### 3.1.1 Type species

*Notocupes picturatus* Ponomarenko, 1964

### 3.1.2 Revised diagnosis

Head (Figure 2E) prognathous, nearly as long as wide, narrowing behind eyes and forming distinct neck region. Compound eyes hemispherical, distinctly protruding. Antennae (Figure 2H) moderately long, slightly serrate, extending at most to posterior pronotal apices. Mandibles with horizontal cutting edge, lacking vertically arranged mandibular teeth (Figure 3E). Suture separating mentum and gulamentum present. Weakly impressed grooves on dorsal surface of pronotum for housing antennae at least sometimes present (Figures 2C, G). Pronotal disc broad, often with produced anterior angles, with lateral margins straight or jagged. Prosternum in front of coxae subquadrate, with tarsal grooves along pleurosternal sutures (Figures 2A, 3B, G). Prosteral process well-

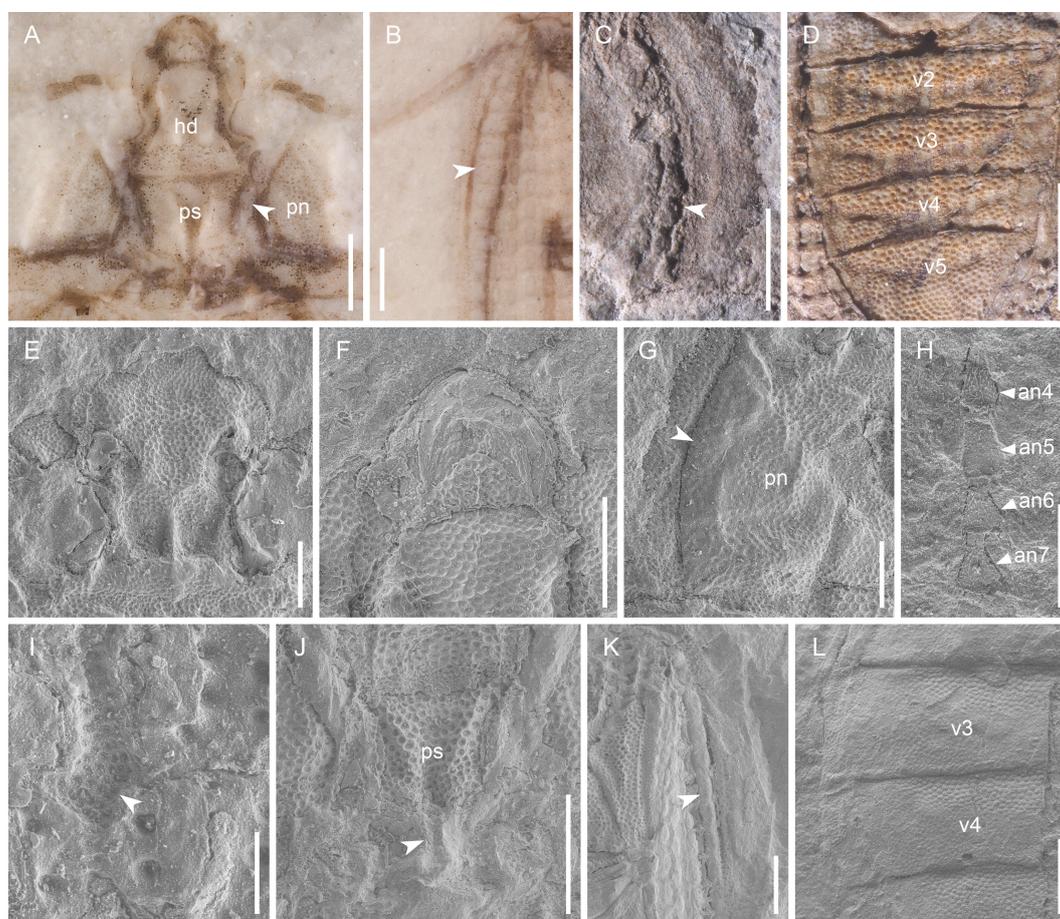


FIGURE 2

Details of *Notocupes* spp. from the Middle Jurassic Daohugou biota, under incident light (A–D) or scanning electron microscopy (E–L). (A) NIGP174673a, head and prothorax, showing the protarsal groove along pleurosternal suture (arrowhead). (B) NIGP174673b, groove on the elytral epipleuron for housing mesotibia and -tarsus (arrowhead). (C) NIGP174674, antenna in the prothoracic antennal groove (arrowhead). (D) NIGP174675, abdomen with overlapping ventrites. (E) NIGP174673a, head. (F) NIGP174673b, mouthparts. (G) NIGP174673a, prothoracic antennal groove (arrowhead). (H) NIGP174673a, antenna. (I) NIGP174673a, scale-covered coniform protuberances on elytron (arrowhead). (J) NIGP174675, prosternum, showing the complete prosternal process (arrowhead). (K) NIGP174675, groove on the elytral epipleuron (arrowhead). (L) NIGP174674, abdomen with overlapping ventrites. an4–7, antennomeres 4–7; hd, head; pn, pronotum; ps, prosternum; v2–5, ventrites 2–5. Scale bars: 1 mm in (A–D, L), 500  $\mu$ m in (E–H, J–K), 200  $\mu$ m in (I).

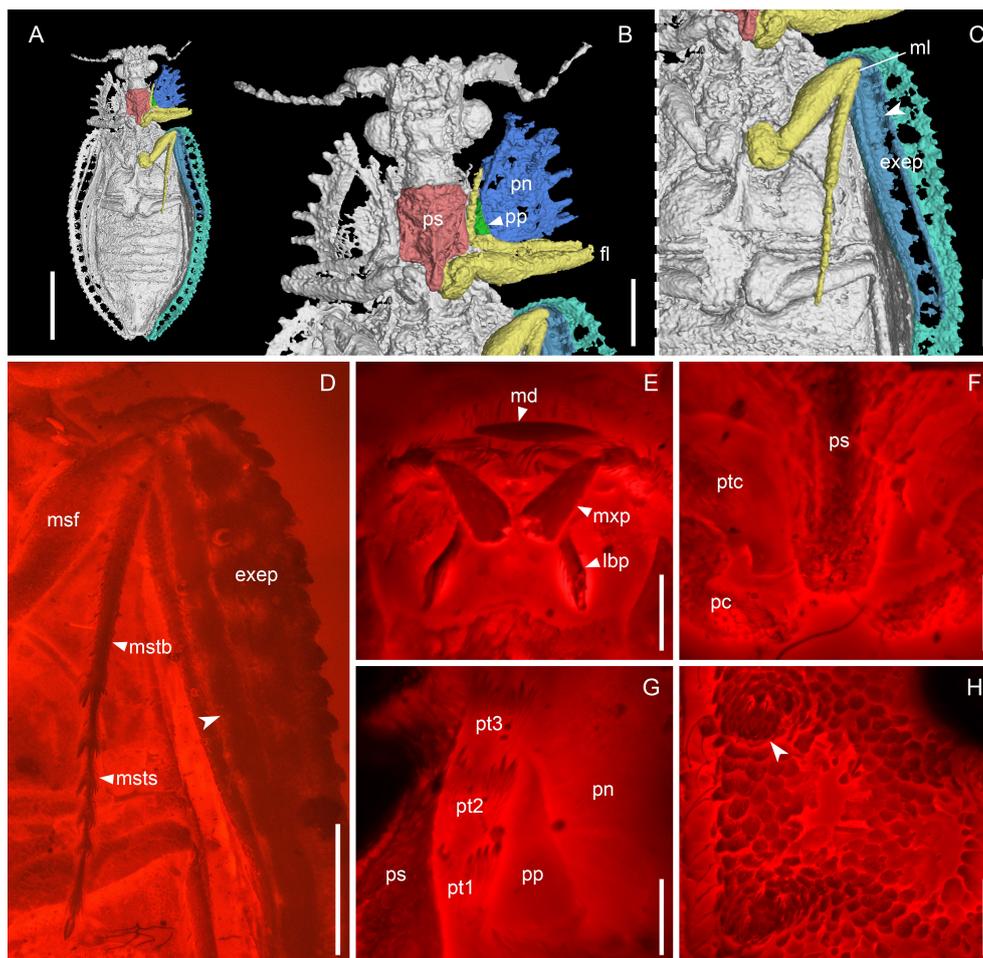


FIGURE 3

*Notocupes* sp., BA202101, in mid-Cretaceous amber from Myanmar. (A–C) X-ray microtomographic reconstruction, ventral view, with groove on the elytral epipleuron for housing mesotibia and -tarsus highlighted in (C) (arrowhead). (D) Groove on the elytral epipleuron, ventral view, under widefield fluorescence. (E–H) Confocal images. (E) Mouthparts, ventral view. (F) Prothorax, ventral view. (G) Protarsus in the protarsal groove, ventral view. (H) Elytron, dorsal view, showing the scale-covered coniform protuberances (arrowhead). exep, explanate epipleuron; fl, fore leg; lbp, labial palp; md, mandible; ml, mid leg; msf, mesofemur; mstb, mesotibia; msts, mesotarsus; mxp, maxillary palp; pc, procoxa; pn, pronotum; pp, propleuron; ps, prosternum; pt1–3, protarsomeres 1–3; ptc, prothrochanter. Scale bars: 3 mm in (A), 1 mm in (B–D), 200  $\mu$ m in (E–H).

developed, extending beyond middle of procoxae (Figures 2J, 3B, F). Procoxae narrowly separated by prosternal process. Elytra elongate, with ten longitudinal rows of window punctures on disc and one row of window punctures on explanate epipleuron, sometimes with raised veins with coniform protuberances (elytral spines; Figures 2I, 3H), veins A1 and CuA fused before elytral apex. Anterior portion of explanate elytral epipleura at least sometimes with grooves for housing mesotibiae and mesotarsi (Figures 2B, K, 3C, D). Tarsi 5-segmented, elongate; tarsomeres not emarginate or ventrally lobed (Figures 3D, G). Abdominal ventrites overlapping (Figures 1H, 2D, L).

### 3.1.3 Remarks

*Notocupes* has sometimes been treated as a junior synonym of *Zygaenia* (e.g., Ponomarenko, 2000; Kirejtshuk, 2020). The name

*Zygaenia* Handlirsch was proposed based on an isolated elytron. As elytra with similar morphology may belong to different taxa (Strelnikova and Yan, 2021), we here reserve *Notocupes* for complete body fossils of unambiguous systematic assignment, following the practice of Ponomarenko and Ren (2010).

*Notocupes* differs from Ommatidae primarily by its horizontal cutting edge of mandibles, separated procoxae and overlapping abdominal ventrites, and differs from Cupedidae primarily by its relatively short prosternal process (not reaching posterior end of procoxae) and simple tarsomeres. *Notocupes* may deserve a new familial status. However, the morphology and phylogenetic placement of the genera historically associated with *Notocupes*, including *Notocupoides* Ponomarenko, *Rhabdocupes* Ponomarenko, and *Eurydicton* Ponomarenko, are not currently clear. Thus, *Notocupes*, along with these genera, is temporarily left in Archostemata, without a familial attribution.

## 4 Discussion

### 4.1 Exceptional fossils illuminate the morphology of *Notocupes*

#### 4.1.1 Compression fossils and amber inclusions provide a complementary view of *Notocupes* morphology

Traditionally, *Notocupes* has been placed in the family Ommatidae (or Ommatinae in Cupedidae *s.l.*), primarily based on the length of its antennae and contiguous procoxae (Ponomarenko, 1964). However, our examination of exceptionally preserved *Notocupes* compressions from Daohugou and amber from northern Myanmar revealed a suite of morphological characters that are not diagnostic for Ommatidae, but correspond well to Cupedidae *s. s.*

Some beetles possess a transverse suture between the posterior tentorial pits, separating the submentum and gula, while in others (including all extant Ommatidae) this suture is reduced, and the submentum and gula are fused into a single gulamentum. Though this suture was not explicitly described, the line drawings by Ponomarenko (Ponomarenko, 1969) suggested the presence of a distinct suture separating the submentum and gula in *Notocupes* and closely related genera. Our observations, in contrast, showed no suture between the posterior tentorial pits, but a suture separating the mentum and gulamentum (Figure 1H).

The Ommatidae + Micromalthidae clade is characterized by vertically arranged mandibular teeth (Hörschemeyer, 2009; Li et al., 2020b; Tihelka et al., 2020b), while in Cupedidae the mandibles have a horizontal cutting edge. Similar to cupedids, *Notocupes* also possesses a horizontal mandibular cutting edge (Figure 3E).

In Ommatidae, the procoxae are contiguous (except for the aberrant genus *Stegocoleus* Jarzembowski & Wang which gained this character independently; Jarzembowski and Wang, 2016; Li et al., 2020a; Tihelka et al., 2020a), and the prosternal process is reduced, not reaching the posterior half of the procoxae. In the *Notocupes* specimen from Burmese amber we examined, the prosternal process is relatively well-developed, extending beyond the middle of procoxae, though not reaching the posterior end of procoxae (Figures 2J, 3B, F). The procoxae are completely separated by the prosternal process, which are similar to Cupedidae and contradictory to previous descriptions of this genus based on compression fossils (Ponomarenko, 1964; Tan and Ren, 2009). We suppose that the contiguous procoxae reported by previous researchers could have been a taphonomic artefact caused by distortion during the fossilization processes. Indeed, the elongate prosternal process has also been inexplicitly noted by Ponomarenko (in Jarzembowski et al., 2015), and recently reported by Lee et al. (2022).

In most ommatids, the abdominal ventrites are coplanar and separated by wide grooves (Beutel et al., 2008) (Figure 4A in Yamamoto, 2017; Figures 71–74 in Escalona et al., 2020). In most cupedids, the abdominal ventrites are overlapping (Beutel et al., 2008; but see Kirejtshuk et al., 2016). *Notocupes* has overlapping

abdominal ventrites (Figures 1H, 2D, L) which are discordant with a placement in Ommatidae (Ponomarenko, 1969; Ponomarenko, 2006; Ponomarenko and Ren, 2010; Tan et al., 2012; Strelnikova, 2019). Notably, Kirejtshuk (2020) transferred *Ovatocupes alienus* Tan & Ren, a species reported from the Yixian Formation, into *Notocupes*. However, it was originally placed in Cupedidae based on its separated procoxal cavities and overlapping abdominal ventrites (Tan and Ren, 2006).

#### 4.1.2 New potential apomorphies of *Notocupes*

Curiously, *Notocupes* possesses a pair of weak grooves on the dorsal surface of the pronotum. In NIGP174674 and the holotype of *N. denticollis* (likely also in the holotype of *N. ohmkuhnlei*), the antennae are positioned within these grooves (Figure 2C). This character is unusual, as most beetles with antennal grooves have ventral ones, not dorsal ones (Lawrence and Ślipiński, 2013). This character represents a potential apomorphy of *Notocupes*, provided its presence can be confirmed in other early members of the genus.

There is a distinct groove along the propleurosternal suture in *Notocupes*, which functions for housing the protarsi, as clearly shown in the amber specimen BA202101 and other compression fossils (Figures 2A, 3B, G). This protarsal groove is also preserved in some previously noted amber and compression fossils of *Notocupes* (e.g., Plate II, Figure 2 in Tan et al., 2006; Figure 1 in Jarzembowski et al., 2020b). Grooves for housing the protarsi are also present in the majority of extant Cupedidae (except for *Priacma* LeConte and *Paracupes* Kolbe) and Crowsoniellidae. However, in Cupedidae, the protarsal groove runs along the notopleural and notosternal sutures; and in *Crowsoniella*, the propleuron is reduced or fused with other sclerites, and the protarsal groove runs along the apparent notosternal suture (Figure 16 in Kirejtshuk et al., 2010). Notably, such prothoracic grooves for housing tarsi are absent in Ommatidae (Lawrence, 1999).

A groove is also present in the anterior portion of the elytral epipleura of *Notocupes*, most clearly shown by the amber specimen BA202101 (Figures 3C, D). The position and length of this groove suggest that it housed the mesotibia and mesotarsus. Similar structures are also preserved in our newly discovered compression *Notocupes* fossils from Daohugou (Figures 2B, K). However, it would be hard to correctly interpret them without the aid of amber fossils. The groove for housing legs in elytral epipleura is, to our knowledge, reported in beetles for the first time, and may represent a further apomorphy of *Notocupes*.

### 4.2 Systematic placement of *Notocupes* and the evolution of Archostemata

#### 4.2.1 Phylogeny of Archostemata

We integrated our updated understanding of *Notocupes* morphology into a formal phylogenetic analysis to evaluate the placement of the genus within Archostemata. The result was generally consistent with Beutel et al. (2008), except for the position of Ademosynidae and Schizophoridae. Our analyses have consistently recovered a monophyletic Archostemata, including the

extinct family Catiniidae, albeit with low support (Figure 4). The monophyly of Archostemata including Catiniidae was unaffected by the exclusion of Jurodidae (Supplementary Figure 1). The relationships among archostematan families remained almost the same regardless of the analytical approach used or the dataset analyzed. Ommatidae appears to be the earliest-diverging archostematan family in the present analyses, though with extremely low support. Our analyses, regardless of the weighting used or the dataset analysed, supported three archostematan clades, (i) Ommatidae, (ii) Crowsoniellidae, Micromalthidae, and Catiniidae, and (ii) *Notocupes* and Cupedidae, although the support values were not high (bootstrap values = 23–52).

### 4.2.2 Systematic placement of *Notocupes*

Regardless of the analytical method used or the inclusion of Jurodidae, *Notocupes* was always recovered as sister to Cupedidae (bootstrap values = 34–52). Cupedidae excluding *Notocupes* was strongly supported as monophyletic (bootstrap values = 88–92). *Notocupes* shares with Cupedidae the apomorphic arrangement of the abdominal sterna with both taxa possessing overlapping ventrites (character 62: 1). Both taxa also share the presence of scale-like setae (3: 1). *Notocupes* differs from Cupedidae in possessing a distinctly developed mentum: (35: 0) and possessing prosternal grooves for tarsomeres (40: 1). Besides these characters, *Notocupes* differs from Cupedidae by its relatively short prosternal process not reaching posterior end of procoxae and simple tarsomeres.

Based on the previous discussions, we conclude that *Notocupes* differs substantially from Ommatidae in morphology. Since a potential inclusion of *Notocupes* in Cupedidae would necessitate a dramatic revision of the latter’s diagnosis, we prefer to temporarily leave *Notocupes* without familial attribution, before more information is available for the possibly associated *Notocupoides*, *Rhabdocupes* and *Eurydicton*.

### 4.3 Paleobiology and evolutionary significance

Extant members of Cupedidae and Ommatidae are associated with decaying wood, although some adults have been reported to feed on pollen (Crowson, 1962; Atkins, 1963; Evans, 2014; Escalona et al., 2020). A saproxylic mode of life may also be expected in *Notocupes*. The relatively flattened habitus of *Notocupes* suggests that the beetles may have occupied narrow spaces such as crevices under bark, while the presence of sharp spines in some species suggest the beetles also occurred in open habitats, such as on tree trunks. Species from Burmese amber, fossils previously placed into the genus *Amblomma*, and NIGP174673, possessed dentate lateral edges of the prothorax or (and) sharp spines on elytra (Tan and Ren, 2009; Tihelka et al., 2019; Jiang et al., 2020) that may have fulfilled a defensive function or alternatively played a role in bark mimesis. Color patterns preserved in some Cretaceous *Notocupes*/

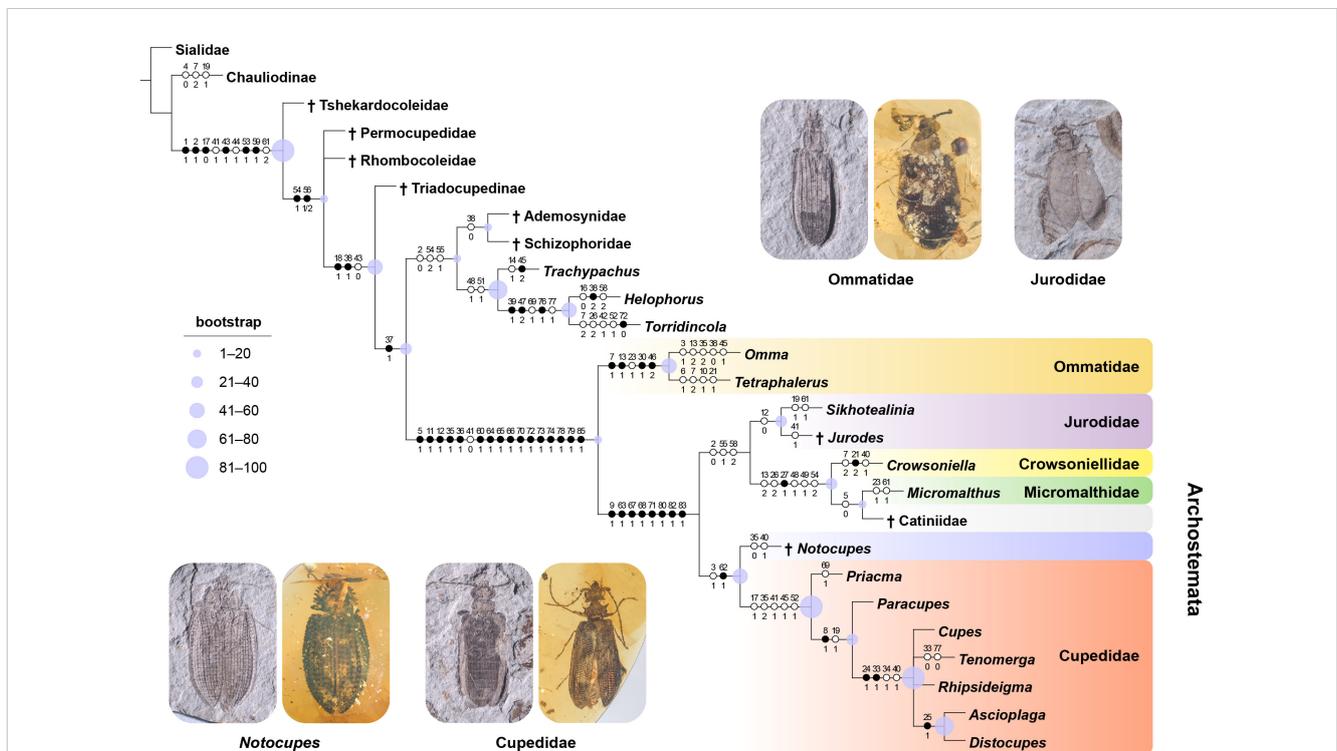


FIGURE 4  
 Strict consensus tree of three equally shortest trees from TNT implied weighting parsimony analysis, with all taxa included. The equal weighting analysis produced exactly the same topology. Black circles indicate nonhomoplasious changes; white circles indicate homoplasious characters; numbers above the branches of the strict consensus tree indicate character numbers. The insets show representatives of Archostemata from Daohugou and Burmese amber.

*Zygadenia elytra* (Jarzembowski et al., 2015; Strelnikova and Yan, 2021) (Supplementary Figure 2) may have served as disruptive camouflage, breaking up the beetle's outline and concealing them from visual predators. Grooves along the pleurosternal suture for housing the protarsi, grooves on the dorsal surface of the pronotum for housing the antennae, and epipleural grooves represent further morphological adaptations for life in confined space or may have served a protective function.

The more than 80 Myr range of the *Notocupes*–*Zygadenia* complex in the fossil record, from the Middle Triassic (Bathonian) to the Late Cretaceous (Coniacian), makes *Notocupes* a prime example of morphological, and probably also ecological, conservatism in Mesozoic archostematan. The morphology of Middle Jurassic *Notocupes* from Daohugou corresponds astonishingly well to that of the mid-Cretaceous one from Burmese amber. The prothoracic protarsal grooves and the epipleural mesotibial and -tarsal grooves remained almost unchanged for at least 66 Myr. Even some fine structures, such as the scale-covered coniform protuberances on elytra, persisted at least in some of the lineages. This high-level of morphological stability might suggest the group managed to track an almost consistent microhabitat (Marín et al., 2018; Cerca et al., 2020), in spite of the dramatic climatic changes over geological timescale. Nevertheless, some other pressures may have also played a role in conserving some characters.

*Notocupes* highlights ancestral character states with respect to Cupedidae, facilitating future comparative work on the latter family. Our study highlights the importance of examining fossils representing different types of preservation, such as compressions and amber inclusions, to shed light on controversial characters that may be distorted by taphonomic processes and build a more accurate evolutionary picture of extinct insect groups.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

## Author contributions

Y-DL and C-YC conceived the study. D-YH, C-YC, F-YX and YL acquired and processed the fossils. Y-DL acquired and processed the photomicrograph data. Y-DL, ET and C-YC drafted the manuscript, to

which SY and AFN contributed. All authors commented on the manuscript and gave final approval for publication.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1015627/full#supplementary-material>

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