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Cretaceous beetles of the Jinju Formation (Coleoptera): Archostemata

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Abstract

The beetles from the Lower Cretaceous Lagerstätte in South Korea, Jinju Formation, remain largely unstudied. In the present study, the fossils of suborder Archostemata from the Jinju Formation are described and illustrated, including the complete bodies of *Asiania pax* gen. et sp. nov. and *Brochocoleus sacheonensis* sp. nov., and the isolated elytra of *Brochocoleus* cf. *punctatus*, *Omma* sp. and *Zygadenia cornigera* sp. nov.

Keywords: Coleoptera, Archostemata, Jinju Formation, Lower Cretaceous

Introduction

The beetle suborder Archostemata is currently a small group, including Cupedidae, Ommatidae, Micromalthidae, Crowsoniellidae, and possibly Jurodidae (Hörnschemeyer, 2009, 2016). Compared with their extant fauna, archostematans were more diverse in the Mesozoic fossil record (e.g., Ponomarenko, 1969; Tan & Ren, 2009; Kirejtshuk, 2020). The Permian Archostemata-like fossils are probably the stem groups of the whole Coleoptera (Beutel et al., 2008). Based on their plesiomorphic appearance, Archostemata has once been suggested as the earliest diverging branch among the extant Coleoptera (e.g., Friedrich et al., 2009). However, recent molecular evidences have supported a sister relationship between

Archostemata and Myxophaga (*e.g.*, Zhang *et al.*, 2018; McKenna *et al.*, 2019; Cai *et al.*, 2022). Within Archostemata, Micromalthidae and Crowsoniellidae are monotypic in extant fauna; Cupedidae is relatively common in both extant fauna and fossil record; Ommatidae is species-poor in extant fauna, but had a high level of taxonomic diversity and morphological disparity in the Mesozoic.

The Jinju Formation belongs to the Sindong Group, Gyeongsang Supergroup in the south-eastern part of Korean Peninsula (Chang, 1975; Sha et al., 2012; Kang & Paik, 2013), and is considered to have been deposited in a mainly lacustrine environment (Choi, 1986; Paik et al., 2019; Choi et al., 2021). Based on the U-Pb dating of zircon, the age of the Jinju Formation has been estimated as 112-106 Ma (Albian) (Lee et al., 2010, 2018; Chae et al., 2020). Well-preserved fossils have been discovered in the dark shale of the Jinju Formation (Kim & Huh, 2018). However, the insect (and beetle) fauna of this Lagerstätte has not been extensively studied. The few identified beetles from the Jinju Formation include Coptoclava Ping of Coptoclavidae (Park et al., 2013), Megalithomerus Sohn & Nam and Koreagrypnus Sohn & Nam of Elateridae (Sohn et al., 2019), and Cretosaja Sohn & Nam of Staphylinidae (Sohn & Nam, 2021). An archostematan beetle, Notocupes premeris Lee et al., was also described from the Jinju Formation very recently (Lee et al., 2022).

In his master's thesis, Sam Sik Lee (2016) reported

a variety of beetle fossils from the Jinju Formation. However, the family-level identifications in Lee (2016) were mostly incorrect. We systematically examined the beetle fossils reported by Lee (2016) as well as those in our own collection. The present publication focuses on the Archostemata part of the beetle fauna in the Jinju Formation.

Materials and methods

Materials

The fossils studied herein originated from the Jinju Formation in Sanam-myeon, Sacheon City (35.07°N, 128.06°E), or Jeongchon-myeon, Jinju City (35.12°N, 128.09°E), South Gyeongsang Province, South Korea. The specimens are deposited in Kyungpook National University and Gongju National University of Education.

Imaging

Photographs under incident light were taken with a Sony α 7R IV mirrorless camera equipped with a Canon EF 100mm f/2.8L Macro IS USM lens plus Kenko Extension Tube Set DG (12, 20 and 36 mm). Scanning electron microscopic (SEM) images were obtained with a Hitachi SU5000 field emission scanning electron microscope, operating with an accelerating voltage of 3.0 kV.

Taxonomic treatments and terminology

The family Ommatidae has been treated as a subfamily of Cupedidae *sensu lato* by some authors (*e.g.*, Ponomarenko, 1969; Kirejtshuk, 2020), but recent molecular studies have reaffirmed the familial status of Ommatidae (McKenna *et al.*, 2015, 2019). Here we follow the recent comprehensive textbooks of coleopterology, treating Ommatidae as a separate family (Hörnschemeyer, 2016; Lawrence & Escalona, 2019).

The name *Pareuryomma* Tan *et al.* was proposed as a replacement name for *Euryomma* Tan *et al.* by Tan *et al.* (2012). Dubois *et al.* (2013) claimed that the work by Tan *et al.* (2012) and the names within it are unavailable due to failure to comply with the requirements of ICZN. However, in the taxonomic review of fossil Archostemata, Kirejtshuk (2020) simply adopted the name *Pareuryomma*, as well as other names proposed by Tan *et al.* (2012). For convivence we would continue to use the name *Pareuryomma* in our text, even though it might be nomenclaturally unavailable.

General morphological terminology follows Lawrence and Ślipiński (2013). The homology of elytral veins (longitudinal ridges) among Archostemata is in question, and the terminology for them among different publications is quite chaotic (*e.g.*, Ponomarenko, 1969; Lubkin, 2007; Tan & Ren, 2009; Jarzembowski *et al.*, 2013a; Tihelka *et al.*, 2019). For convenience, in the present publication we follow Kirejtshuk (2020), terming the first primary vein (counted from elytral suture outwards, not including the ridge along elytral suture and the ridge bordering scutellary striole) of Ommatidae as A_1 , the second as Cu, the third as M, and the fourth as R.

Abbreviations

The following abbreviations of collections are used: GNUE—Gongju National University of Education. KNUL—Kyungpook National University, specimens firstly reported by Sam Sik Lee. NSLSS—Number of Specimen used in Lee (2016). The following abbreviations of morphological measurements are used: BL—apparent body length in dorsal view; BW—body width; EL—elytral length; EW—elytral width; HL—head length (excluding neck); HW—head width (including eyes); PL—pronotal length (along the middle); PW—pronotal width.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758 Suborder Archostemata Kolbe, 1908 Family Ommatidae Sharp & Muir, 1912

Asiania pax gen. et sp. nov. (Figs 1–3)

Material. Holotype, GNUE-217012 (GNUE-217012a and GNUE-217012b, part and counterpart).

Etymology. The generic name refers to the continent of Asia, and is feminine in gender. The specific name is the Latin noun "*pax*", meaning peace, used as a noun in apposition.

Diagnosis. Head subquadrate. Neck wide. Elytron with window punctures on explanate epipleuron; elytral veins M and Cu fusing first near elytral apex. Abdomen tergites II–VII with wide median longitudinal groove.

Locality and horizon. Jeongchon-myeon, Jinju City, South Gyeongsang Province, South Korea. Albian (Lower Cretaceous), Jinju Formation.

Description. Body surface covered with tubercles. Head subquadrate; dorsal surface possibly with a pair of prominent posteromedian protuberances. Neck wide. Prothorax widest at middle, slightly wider than long, with rounded lateral edges. Pronotum without clear protuberances or depressions. Procoxae likely contiguous. Elytron with ten longitudinal rows of window punctures on disc; every two cell rows separated by distinctly raised vein; veins Cu and M fusing unambiguously before elytral apex; A₁, Cu+M and R ending independently near

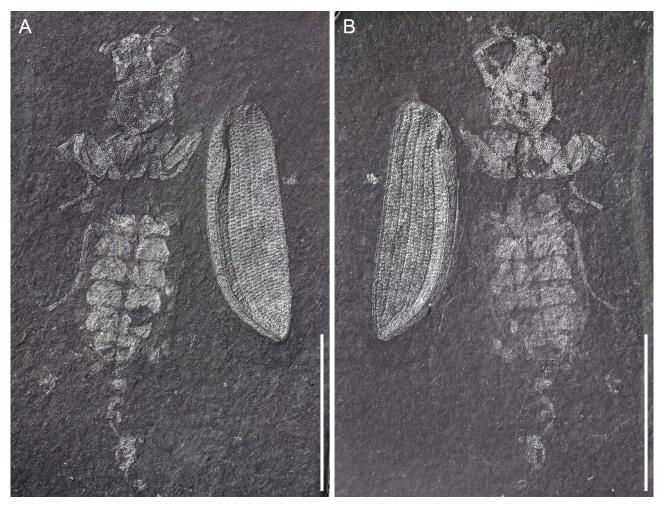


FIGURE 1. *Asiania pax* **gen. et sp. nov.**, holotype, GNUE-217012, under incident light. **A**, GNUE-217012a. **B**, GNUE-217012b. Scale bars = 10 mm.

elytral apex; explanate epipleuron narrow in posterior 2/3, possibly with one row of window punctures, and wider in anterior 1/3, possibly with two or three rows of window punctures. Mesocoxae contiguous. Metacoxae transverse, narrowed laterally, contiguous. Legs moderately long and slender; tibia subequal to femur in length; tarsomeres simple, without ventral lobes. Abdominal tergites II–VII probably weakly sclerotised, with wide median longitudinal groove; tergites II–VI each constricted anteriorly and expanded posteriorly.

Measurements. BL 21.5 mm, PL 3.3 mm, PW 4.1 mm, EL 15.5 mm, EW 4.8 mm.

Remarks. Based on the contiguous procoxae and simple tarsomeres, *Asiania* is placed in Ommatidae, rather than Cupedidae.

In many Ommatidae, the elytral veins are weak, and are hardly traceable near elytral apex. Where the fusions are clear, often A_1 and Cu would fuse first (*e.g.*, Kirejtshuk, 2020: notes on *Diluticupes* Ren and *Monticupes* Ren). This character state also occurs in *Notocupes* Ponomarenko and most Cupedidae (Kirejtshuk *et al.*, 2016). However, in *Asiania*, M and Cu clearly fuse first, which is unknown in other Ommatidae to our knowledge (at least extremely rare). Although a fusion of M and Cu can be seen in the scheme sketch for *Zygadenia* Handlirsch by Ponomarenko (2006), this is likely a mistake, as the fusion of A_1 and Cu is clear even in *Notocupes/Zygadenia* species described by Ponomarenko himself where high-quality photos are available (*e.g.*, Strelnikova & Yan, 2021).

The elytron of *Asiania* has an explanate epipleuron complete to the elytral apex. The presence of window punctures on the epipleuron cannot be confidently confirmed. But based on the width of epipleuron, if window punctures are present, there might be two or three rows of window punctures in the anterior 1/3, and one row of window punctures in the posterior 2/3. *Brochocoleus*like elytra, *e.g.*, those of *Brochocoleus* Hong, *Jarzembowskiops* Kirejtshuk, *Burmocoleus* Kirejtshuk, *Limnomma* Li & Cai and *Stegocoleus* Jarzembowski & Wang, typically have wider explanate epipleura, with at least two window cell rows even in the posterior half (Hong, 1982; Jarzembowski *et al.*, 2016; Liu *et al.*, 2017; Tihelka *et al.*, 2020a; Li *et al.*, 2020a, 2021a). *Polykius* Kirejtshuk and *Notocupes* have narrower explanate

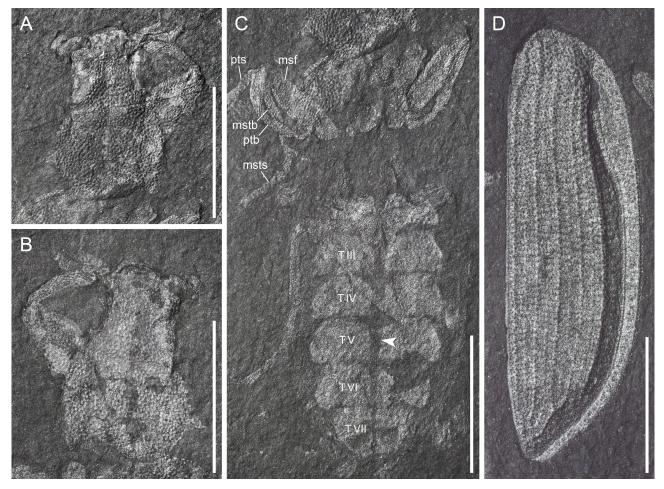


FIGURE 2. Details of *Asiania pax* **gen. et sp. nov.**, holotype, GNUE-217012, under incident light. **A**, GNUE-217012a, head and prothorax. **B**, GNUE-217012b, head and prothorax. **C**, GNUE-217012a, mesothorax, metathorax and abdomen, with arrowhead showing the median groove on abdominal tergites. **D**, GNUE-217012b, elytron. Abbreviations: msf, mesofemur; mstb, mesotibia; msts, mesotarsus; ptb, protibia; pts, protarsus; T III–VII, tergites III–VII. Scale bars = 5 mm.

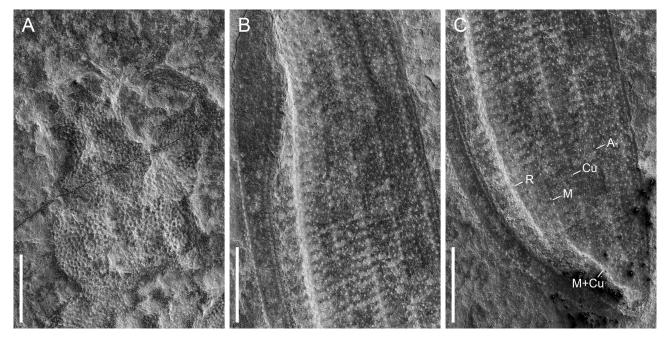


FIGURE 3. Details of *Asiania pax* **gen. et sp. nov.**, holotype, GNUE-217012a, under scanning electron microscopy. **A**, Head and prothorax. **B**, Basal part of elytron. **C**, Apical part of elytron. Scale bars = 2 mm.

epipleura, but with only one window cell row along the full length (Kirejtshuk, 2020; Strelnikova & Yan, 2021; Li et al., 2023a). The epipleura of Pareuryomma have two window cell rows in the anterior part, and narrow posteriorly with one window cell row, but the narrowing appears to be more gradual compared with that in Asiania (Tan et al., 2006).

The abdominal tergites of the specimen are preserved as a carbonaceous film, while the ventral side of its abdomen is preserved only as a weak impression. The carbon film representing the tergites is clearly split along the midline, which we interpret as a well-developed median groove on the tergites. Such a wide groove on abdominal tergites is absent in extant ommatids (Hünefeld et al., 2011: fig. 3; Escalona et al., 2020: fig. 75), and has not been reported in other fossil ommatids.

Genus Brochocoleus Hong, 1982

Brochocoleus sacheonensis sp. nov. (Fig. 4)

Material. Holotype, KNUL-1111-01 (NSLSS 1033), originally placed in Tenebrionidae by Lee (2016).

Etymology. The specific name refers to the type locality, Sacheon.

Diagnosis. Brochocoleus sacheonensis can be separated from other body fossils of Brochocoleus sensu Kirejtshuk (2020) based on the following characters: from Br. planus Ponomarenko by the smaller size; from Br. cossyphus Ponomarenko and Br. alatus Ponomarenko by the transverse prothorax, of which the lateral edges are not strongly converging anteriorly; from Br. rostratus Ponomarenko and also Br. planus by the less elongate head.

Locality and horizon. Sanam-myeon, Sacheon City, South Gyeongsang Province, South Korea. Albian (Lower Cretaceous), Jinju Formation.

Description. Body surface covered with tubercles. Head subquadrate. Compound eyes prominent. Temple present, short. Neck wide. Pronotum strongly transverse, possibly explanate; anterior angles slightly produced; lateral edges possibly serrate. Procoxae contiguous. Elytra

B

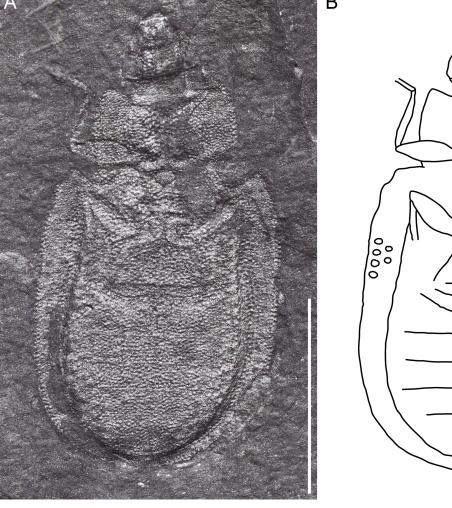


FIGURE 4. Brochocoleus sacheonensis sp. nov., holotype, KNUL-1111-01. A, Photo under incident light. B, Interpretive drawing of ventral side. Scale bars = 5 mm.

with explanate epipleuron developed along full length; explanate epipleuron with at least two rows of window punctures at least in anterior half; lateral sides serrate. Mesoventrite with well-developed transverse suture. Mesocoxae contiguous. Metaventrite with discrimen and well-developed transverse suture. Metacoxae transverse, narrowed laterally, contiguous. Legs moderately long and slender; tarsomeres likely simple (as seen in fore leg). Abdomen with five ventrites; ventrites 5 about 1.6 times as long as 4, apically broadly rounded.

Measurements. BL 11.0 mm, BW 5.8 mm; HL 1.8 mm, HW 1.7 mm, PL 1.6 mm, PW 3.4 mm, EL 7.2 mm.

Remarks. Lee (2016) originally placed this specimen in Tenebrionidae. However, the general appearance of this specimen, and especially the explanate elytral epipleura with window punctures (Fig. 4; see also Lee, 2016: fig. 51), clearly show an affinity to the *Brochocoleus*-like taxa of Ommatidae.

Brochocoleus was a quite problematic and heterogeneous genus, once including various species with widened elytral epipleura. The revision by Kirejtshuk (2020) partly alleviated the taxonomic confusion related to these taxa, although some problems remain. Particularly, those species having elytral epipleura without clear window punctures were removed from *Brochocoleus* and returned or transferred to *Diluticupes* and *Odontomma* Ren *et al.* (Kirejtshuk, 2020).

Explanate elytral epipleura with at least two rows of window punctures can be found in Brochocoleus, Jarzembowskiops, Burmocoleus, Limnomma, Pareuryomma and Stegocoleus. The specimen KNUL-1111-01 can be excluded from the abnormal Stegocoleus by the clearly coplanar abdominal ventrite and contiguous procoxae, from Pareuryomma by the wider body and short temples (temples prominent in Pareuryomma), from Limnomma by the absence of non-tuberculate region in abdominal ventrite 5, widened basal region of explanate epipleura and wider head, and from Burmocoleus by the wider neck and transverse prothorax (prothorax subglobular in Burmocoleus). While we have reservations about the validity of Jarzembowskiops, KNUL-1111-01 can be separated from Jarzembowskiops as currently defined by the wider head (especially the part in front of eyes).

In the type species of *Brochocoleus*, *Br. punctatus* Hong, only the elytron is well preserved (Hong, 1982). Kirejtshuk (2020) characterised *Brochocoleus* as having long temples, probably based on the species reported by Ponomarenko (1994). However, the drawings in Ponomarenko (1994) could possibly be misleading, as the boundary between the temples and neck might not be clearly illustrated. Actually, the shape of head and prothorax of KNUL-1111-01 is quite similar to that of the paratype of *Brochocoleus alatus* (PIN No. 3559/6057) (this paratype may not necessarily be conspecific to the holotype of *Br. alatus*). As such, here we decide to place KNUL-1111-01 in genus *Brochocoleus*.

Brochocoleus cf. punctatus

(Fig. 5A)

Material. GNUE-217013.

Locality and horizon. Jeongchon-myeon, Jinju City, South Gyeongsang Province, South Korea. Albian (Lower Cretaceous), Jinju Formation.

Measurements. EL 9.9 mm, EW 3.6 mm.

Remarks. The elytron specimen GNUE-217013 is strongly similar to the holotype of the type species of *Brochocoleus*, *Br. punctatus* (Hong, 1982: fig. 73). There might be some subtle differences between the two specimens. For example, the median cell row of explanate epipleuron only contains five window punctures in the holotype of *Br. punctatus*, while the median cell row of explanate epipleuron is longer in GNUE-217013, with at least nine window punctures. Nevertheless, such a character is not very stable and may even varies within a specimen (*e.g.*, Tihelka *et al.*, 2020a: fig. 5C; Li *et al.*, 2021a: fig. 6A). Thus, we here classify the specimen GNUE-217013 as *Brochocoleus* cf. *punctatus*.

Genus Omma Newman, 1839

Omma sp.

(Fig. 5B)

Material. KNUL-1111-02 (NSLSS 1068), originally placed in Cupedidae by Lee (2016).

Locality and horizon. Sanam-myeon, Sacheon City, South Gyeongsang Province, South Korea. Albian (Lower Cretaceous), Jinju Formation.

Measurements. EL 10.5 mm, EW 3.7 mm.

Remarks. Although not very well preserved, the elytron specimen KNUL-1111-02 has a general appearance reminiscent of genus Omma Newman. No trace of window punctures is detected on the epipleuron. The lateral elytral margin of KNUL-1111-02 is serrated. While the elytral margin of extant Omma lacks distinct serration (Escalona et al., 2020), serration similar to that of KNUL-1111-02 can be observed in some fossil species of Omma from Burmese amber, i.e., O. forte Li & Cai and O. manukvani Kirejtshuk. As noted by Escalona et al. (2020) and Li et al. (2021b), the characters of Omma are largely plesiomorphic, and it is quite difficult to confidently identify an adpression body fossil as Omma, not to mention the isolated elytron. Nevertheless, KNUL-1111-02 is here provisionally placed in Omma before further evidence is available.

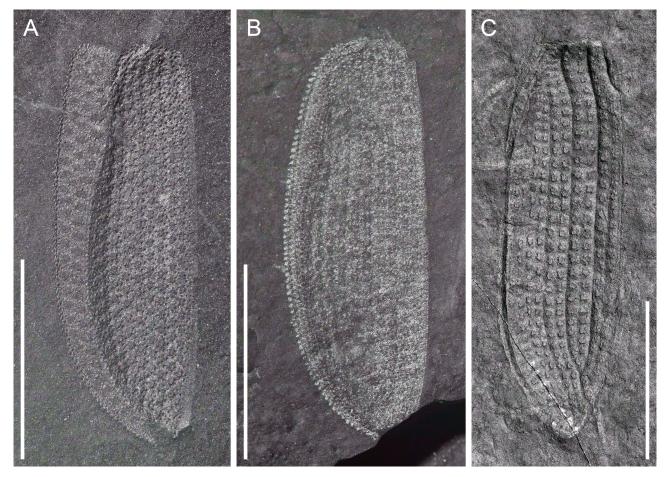


FIGURE 5. Isolated archostematan elytra from Jinju Formation. A, *Brochocoleus* cf. *punctatus*, GNUE-217013. B, *Omma* sp., KNUL-1111-02. C, *Zygadenia* sp., GNUE217014a. Scale bars = 5 mm.

Family incertae sedis

Genus Zygadenia Handlirsch, 1906

Zygadenia cornigera sp. nov. (Fig. 6)

Material. Holotype, GNUE-217011.

Etymology. The specific name refers to its distinctly produced apex of elytral disc.

Diagnosis. Typical *Zygadenia* appearance, with apex of elytral disc distinctly produced, covering or interrupting explanate epipleuron.

Locality and horizon. Jeongchon-myeon, Jinju City, South Gyeongsang Province, South Korea. Albian (Lower Cretaceous), Jinju Formation.

Description. Elytron with ten longitudinal rows of window punctures on disc and one row of window punctures on explanate epipleuron; apex of elytral disc distinctly produced, covering or interrupting explanate epipleuron; every two cell rows on disc separated by distinctly raised vein; veins A_1 and Cu fusing before elytral apex.

Measurements. EL 13.9 mm, EW 4.8 mm.

Remarks. The specimen of Zygadenia cornigera sp. nov. shows a typical appearance of Notocupes/Zygadenia. It has ten rows of window punctures on disc and one row of window punctures on explanate epipleuron, with veins A₁ and Cu fusing near elytral apex, which are diagnostic for the genus. The apex of elytral disc is distinctly produced in Z. cornigera, covering or interrupting the explanate epipleuron, which is an extremely rare state in Zygadenia or Notocupes. Typically when preserved, the elytral apex of Zygadenia or Notocupes should be simple, with explanate epipleuron being complete towards the posterior end. A somewhat similarly produced elytral apex can also be found in Z. alexrasnitsyni Strelnikova & Yan, but its protrusion seems to be more gentle compared with that of Z. cornigera. Zygadenia cornigera can be additionally separated from Z. alexrasnitsyni by the absence of cell triplets at the base of field IV (interspace between M and Cu) (Strelnikova & Yan, 2021).

A recent study has removed *Notocupes* from Ommatidae, and suggested a close affinity to Cupedidae (Li *et al.*, 2023b). However, the isolated elytra classified

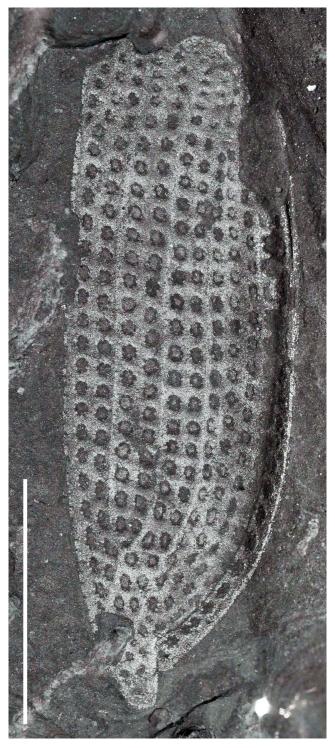


FIGURE 6. *Zygadenia cornigera* **sp. nov.**, holotype, GNUE-217011, under incident light. Scale bar = 5 mm.

in *Zygadenia* may actually include members from both *Notocupes* and other unrelated lineages (Strelnikova & Yan, 2023). The biological affinity of *Z. cornigera* is further uncertain due to the unusually produced apex of elytral disc. Hopefully the discovery of complete body fossils with similar elytral form will clarify its systematic position in the future.

Concluding remarks

Extensive studies have been conducted on the Mesozoic archostematan fossils from Asia in the past decades, especially on those from Central Asia (Ponomarenko, 1964, 1966, 1969), Mongolia (Ponomarenko, 1994, 1997), Northeast China (e.g., Tan & Ren, 2009; Jarzembowski et al., 2013a, b, 2015; Yan et al., 2014; Cai & Huang, 2017), and Burmese (Myanmar) amber (e.g., Jarzembowski et al., 2017; Yamamoto, 2017, 2021; Li et al., 2019, 2020b, 2021c, 2021d; Tihelka et al., 2020b; Li & Cai, 2021; Song et al., 2022). Most archostematan fossils discovered from the Cretaceous Jinju Formation in Korea belong to the common and widespread genera (Brochocoleus, Omma, and Notocupes/Zygadenia). Nevertheless, the new genus reported here, Asiania gen. nov., suggests that the palaeodiversity of Archostemata has not been fully documented and requires further study.

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References

Beutel, R.G., Ge, S.Q. & Hörnschemeyer, T. (2008) On the head morphology of *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera. *Cladistics*, 24, 270–298.

https://doi.org/10.1111/j.1096-0031.2007.00186.x

Cai, C.Y. & Huang, D.Y. (2017) Omma daxishanense sp. nov., a fossil representative of an extant Australian endemic genus recorded from the Late Jurassic of China (Coleoptera: Ommatidae). Alcheringa, 41, 277–283.

https://doi.org/10.1080/03115518.2016.1225251

Cai, C.Y., Tihelka, E., Giacomelli, M., Lawrence, J.F., Ślipiński,
A., Kundrata, R., Yamamoto, S., Thayer, M.K., Newton,
A.F., Leschen, R.A.B., Gimmel, M.L., Lü, L., Engel, M.S.,
Bouchard, P., Huang, D.Y., Pisani, D. & Donoghue, P.C.J.
(2022) Integrated phylogenomics and fossil data illuminate
the evolution of beetles. *Royal Society Open Science*, 9,

211771.

https://doi.org/10.1098/rsos.211771

- Chae, Y.U., Lim, J.D., Kim, C.B., Kim, K.S., Ha, S.J. & Lim, H.S. (2020) Detrital zircon U-Pb ages of the uppermost Jinju Formation in the Natural Monument No. 534 'Tracksite of pterosaurs, birds, and dinosaurs in Hotandong, Jinju', Korea. *Journal of the Korean Earth Science Society*, 41, 367–380. https://doi.org/10.5467/JKESS.2020.41.4.367
- Chang, K.H. (1975) Cretaceous stratigraphy of Southeast Korea. Journal of the Geological Society of Korea, 11, 1–23.
- Choi, B.D., Jia, B.Y., Huh, M., Jung, J.Y. & Wang, Y.Q. (2021) Taxonomy, biostratigraphic and paleoecological aspects of non-marine ostracod fauna from the Jinju Formation (Albian) of the Gyeongsang Basin, South Korea. *Cretaceous Research*, 127, 104944.

https://doi.org/10.1016/j.cretres.2021.104944

Choi, H.I. (1986) Fluvial plain/lacustrine facies transition in the Cretaceous Sindong Group, south coast of Korea. *Sedimentary Geology*, 48, 295–320.

https://doi.org/10.1016/0037-0738(86)90034-5

- Dubois, A., Crochet, P.A., Dickinson, E.C., Nemésio, A., Aescht, E., Bauer, A.M., Blagoderov, V., Bour, R., De Carvalho, M.R., Desutter-Grandcolas, L., Frétey, T., Jäger, P., Koyamba, V., Lavilla, E.O., Löbl, I., Louchart, A., Malécot, V., Schatz, H. & Ohler, A. (2013) Nomenclatural and taxonomic problems related to the electronic publication of new nomina and nomenclatural acts in zoology, with brief comments on optical discs and on the situation in botany. *Zootaxa*, 3735, 1–94. https://doi.org/10.11646/zootaxa.3735.1.1
- Escalona, H.E., Lawrence, J.F. & Ślipiński, A. (2020) The extant species of the genus *Omma* Newman and description of *Beutelius* gen. nov. (Coleoptera: Archostemata: Ommatidae: Ommatinae). *Zootaxa*, 4728, 547–574. https://doi.org/10.11646/zootaxa.4728.4.11
- Friedrich, F., Farrell, B.D. & Beutel, R.G. (2009) The thoracic morphology of Archostemata and the relationships of the extant suborders of Coleoptera (Hexapoda). *Cladistics*, 25, 1–37.

https://doi.org/10.1111/j.1096-0031.2008.00233.x

- Hong, Y.C. (1982) Mesozoic fossil insects of the Jiuquan Basin in Gansu Province. Geological Publishing House, Beijing, 187 pp. [In Chinese]
- Hörnschemeyer, T. (2009) The species-level phylogeny of archostematan beetles—where do *Micromalthus debilis* and *Crowsoniella relicta* belong? *Systematic Entomology*, 34, 533–558.

https://doi.org/10.1111/j.1365-3113.2009.00476.x

Hörnschemeyer, T. (2016) Archostemata Kolbe, 1908. Introduction and phylogeny. In: Beutel, R.G. & Leschen, R.A.B. (Eds), Handbook of Zoology, Arthropoda: Insecta, Coleoptera, beetles, Vol. 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). 2nd Edition. Walter de Gruyter, Berlin, pp. 41–43.

https://doi.org/10.1515/9783110373929-008

Hünefeld, F., Marvaldi, A.E., Müller, B., Lawrence, J.F. & Beutel,

R.G. (2011) The male postabdomen of the "ancestral" archostematan beetle *Tetraphalerus bruchi* Heller, 1913 (Ommatidae) and its phylogenetic significance. *Arthropod Structure & Development*, 40, 146–158. https://doi.org/10.1016/j.asd.2010.12.003

Jarzembowski, E.A., Yan, E.V., Wang, B. & Zhang, H.C. (2013a) Brochocolein beetles (Insecta: Coleoptera) from the Lower Cretaceous of northeast China and southern England. *Cretaceous Research*, 44, 1–11. https://doi.org/10.1016/j.cretres.2013.03.003

- Jarzembowski, E.A., Yan, E.V., Wang, B. & Zhang, H.C. (2013b) Ommatin beetles (Insecta: Coleoptera) from the Lower Cretaceous of northeast China and southern England. *Terrestrial Arthropod Reviews*, 6, 135–161. https://doi.org/10.1163/18749836-06021062
- Jarzembowski, E.A., Wang, B., Zhang, H.C. & Fang, Y. (2015) Boring beetles are not necessarily dull: new notocupedins (Insecta: Coleoptera) from the Mesozoic of Eurasia and East Gondwana. *Cretaceous Research*, 52, 431–439. https://doi.org/10.1016/j.cretres.2014.03.006
- Jarzembowski, E.A., Wang, B. & Zheng, D.R. (2016) An amber double first: a new brochocolein beetle (Coleoptera: Archostemata) from northern Myanmar. *Proceedings of the Geologists'Association*, 127, 676–680.

https://doi.org/10.1016/j.pgeola.2016.11.005

Jarzembowski, E.A., Wang, B. & Zheng, D.R. (2017) A new reticulated beetle (Coleoptera: Cupedidae) with aedeagus preserved from mid-Cretaceous amber of Myanmar. *Cretaceous Research*, 80, 86–90.

https://doi.org/10.1016/j.cretres.2017.08.015

- Kang, H.C. & Paik, I.S. (2013) Review on the geological ages of the formations in the Gyeongsang Basin, Korea. *Journal of the Geological Society of Korea*, 49, 17–29. [In Korean] https://doi.org/10.14770/jgsk.2013.49.1.17
- Kim, J.Y. & Huh, M. (2018) Dinosaurs, birds, and pterosaurs of Korea: A paradise of Mesozoic vertebrates. Springer Nature, Singapore, 320 pp.

https://doi.org/10.1007/978-981-10-6998-7

Kirejtshuk, A.G. (2020) Taxonomic review of fossil coleopterous families (Insecta, Coleoptera). Suborder Archostemata: superfamilies Coleopseoidea and Cupedoidea. *Geosciences*, 10, 73.

https://doi.org/10.3390/geosciences10020073

Kirejtshuk, A.G., Nel, A. & Kirejtshuk, P.A. (2016) Taxonomy of the reticulate beetles of the subfamily Cupedinae (Coleoptera, Archostemata), with a review of the historical development. *Invertebrate Zoology*, 13, 61–190. https://doi.org/10.15298/invertzool.13.2.01

Lawrence, J.F. & Escalona, H.E. (2019) Archostemata Kolbe, 1908. In: Ślipiński, A. & Lawrence, J.F. (Eds), Australian beetles. Vol. 2. Archostemata, Myxophaga, Adephaga, Polyphaga (part). CSIRO Publishing, Clayton, pp. 1–3.

Lawrence, J.F. & Ślipiński, A. (2013) Australian beetles. Vol. 1. Morphology, classification and keys. CSIRO Publishing, Clayton.

https://doi.org/10.1071/9780643097292

Lee, S.B., Nam, G.S. & Li, Y.D. (2022) A new species of *Notocupes* (Coleoptera: Archostemata) from the Lower Cretaceous (Albian) Jinju Formation in South Korea. *Cretaceous Research*, 140, 105357.

https://doi.org/10.1016/j.cretres.2022.105357

Lee, S.S. (2016) Systematic classification of the Cretaceous Coleoptera fossils from the Jinju formation of Sindong Group in Gyeongsang Basin, Korea. Kyungpook National University, Daegu. [In Korean]

https://www.riss.kr/link?id=T14439160

- Lee, T.H., Park, K.H., Chun, J.H. & Yi, K.W. (2010) SHRIMP U-Pb zircon ages of the Jinju Formation and Silla conglomerate, Gyeongsang Basin. *Journal of the Petrological Society of Korea*, 19, 89–101. [In Korean] https://www.riss.kr/link?id=A82317538
- Lee, T.H., Park, K.H. & Yi, K.W. (2018) Nature and evolution of the Cretaceous basins in the eastern margin of Eurasia: a case study of the Gyeongsang Basin, SE Korea. *Journal of Asian Earth Sciences*, 166, 19–31. https://doi.org/10.1016/j.jseaes.2018.07.004
- Li, Y.D. & Cai, C.Y. (2021) Revisiting the morphology of the Cretaceous ommatid beetle *Clessidromma palmeri* (Coleoptera: Archostemata: Ommatidae). *Papéis Avulsos de Zoologia*, 61, e20216195.

https://doi.org/10.11606/1807-0205/2021.61.95

- Li, Y.D., Liu, Z.H., Jarzembowski, E.A., Yin, Z.W., Huang, D.Y. & Cai, C.Y. (2019) Early evolution of Cupedidae revealed by a mid-Cretaceous reticulated beetle from Myanmar (Coleoptera: Archostemata). *Systematic Entomology*, 44, 777–786. https://doi.org/10.1111/syen.12355
- Li, Y.D., Tihelka, E., Yamamoto, S., Huang, D.Y. & Cai, C.Y. (2020a) A close affinity of the enigmatic genus *Stegocoleus* with *Lepidomma* revealed by new fossil evidence (Coleoptera: Archostemata: Ommatidae). *Palaeoentomology*, 3 (6), 632–640.

https://doi.org/10.11646/palaeoentomology.3.6.15

- Li, Y.D., Yamamoto, S., Huang, D.Y. & Cai, C.Y. (2020b) A miniaturized ommatid beetle in mid-Cretaceous Burmese amber (Coleoptera: Archostemata: Ommatidae). *Papéis Avulsos de Zoologia*, 60, e20206063. https://doi.org/10.11606/1807-0205/2020.60.63
- Li, Y.D., Tihelka, E., Pang, H., Huang, D.Y. & Cai, C.Y. (2021a) *Limnomma*, a new genus of Ommatidae from the Middle Jurassic Daohugou beds (Coleoptera, Archostemata). *Deutsche Entomologische Zeitschrift*, 68, 299–308. https://doi.org/10.3897/dez.68.71880
- Li, Y.D., Huang, D.Y. & Cai, C.Y. (2021b) New species of Omma Newman from mid-Cretaceous Burmese amber (Coleoptera, Archostemata, Ommatidae). Deutsche Entomologische Zeitschrift, 68, 341–348. https://doi.org/10.3897/dez.68.74174
- Li, Y.D., Huang, D.Y. & Cai, C.Y. (2021c) Revisiting the morphology and systematic placement of the enigmatic

Cretaceous ommatid beetle *Bukhkalius lindae* (Coleoptera: Archostemata: Ommatidae). *Papéis Avulsos de Zoologia*, 61, e20216128.

https://doi.org/10.11606/1807-0205/2021.61.28

Li, Y.D., Yamamoto, S., Huang, D.Y. & Cai, C.Y. (2021d) New species of *Paraodontomma* from mid-Cretaceous Burmese amber with muscle tissue preservation (Coleoptera: Archostemata: Ommatidae). *Papéis Avulsos de Zoologia*, 61, e20216153.

https://doi.org/10.11606/1807-0205/2021.61.53

- Li, Y.D., Tihelka, E., Newton, A.F., Huang, D.Y. & Cai, C.Y. (2023a) New species of *Notocupes* (Coleoptera: Archostemata) from the Middle Jurassic Daohugou beds, with discussion on the generic circumscription. *Palaeoentomology*, 6 (4), 398–415. https://doi.org/10.11646/palaeoentomology.6.4.11
- Li, Y.D., Tihelka, E., Yamamoto, S., Newton, A.F., Xia, F.Y., Liu, Y., Huang, D.Y. & Cai, C.Y. (2023b) Mesozoic Notocupes revealed as the sister group of Cupedidae (Coleoptera: Archostemata). Frontiers in Ecology and Evolution, 11, 1015627.

https://doi.org/10.3389/fevo.2023.1015627

Liu, Z.H., Tan, J.J., Ślipiński, A., Jarzembowski, E.A., Wang, B., Ren, D. & Pang, H. (2017) *Brochocoleus zhiyuani*, a new species of brochocolein beetle (Coleoptera: Ommatidae) from the Cretaceous amber of Myanmar. *Annales Zoologici*, 67, 79–85.

https://doi.org/10.3161/00034541ANZ2017.67.1.009

- Lubkin, S.H. (2007) *Taxonomic studies on Paleozoic and Mesozoic* beetles, with phylogenetic interpretation based on elytral venation and structure. Cornell University, Ithaca, NY.
- McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, A., Maddison, D.R. & Farrell, B.D. (2015) The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, 40, 835–880.

https://doi.org/10.1111/syen.12132

McKenna, D.D., Shin, S.G., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath, A., Escalona, H.E., Friedrich, F., Letsch, H., Liu, S.L., Maddison, D., Mayer, C., Misof, B., Murin, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E.V., Zhou, X., Ślipiński, A. & Beutel, R.G. (2019) The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences, USA*, 116, 24729–24737.

https://doi.org/10.1073/pnas.1909655116

Paik, I.S., Kim, H.J., Kim, S.Y., Lee, J.E., So, Y.H. & Lee H.I. (2019). Fossil-bearing deposits in the Jinju Formation at Jinju: Occurrences, paleoenvironments and stratigraphic implications. *Journal of the Geological Society of Korea*, 55, 513–530. [In Korean]

https://doi.org/10.14770/jgsk.2019.55.5.513

Park, T.Y.S., Kim, Y.H. & Nam, K.S. (2013) Preliminary research on the aquatic coleopteran, *Coptoclava* from the Early Cretaceous Jinju Formation. *Journal of the Geological Society* of Korea, 49, 617–624. [In Korean] https://doi.org/10.14770/jgsk.2013.49.6.617

Ponomarenko, A.G. (1964) New beetles of the family Cupedidae from the Jurassic of Karatau. *Paleontologicheskii Zhurnal*, 2, 49–62. [In Russian]

- Ponomarenko, A.G. (1966) Beetles of the family Cupedidae, Lower Triassic of Soviet Central Asia. *Paleontologicheskii Zhurnal*, 4, 47–68. [In Russian; translation in *International Geology Review*, 9, 957–973.]
- Ponomarenko, A.G. (1969) Historical development of archostomatan beetles. *Trudy Paleontologicheskogo Instituta*, 125, 1–240. [In Russian]
- Ponomarenko, A.G. (1994) New Mesozoic cupedid beetles from Mongolia. Brochocoleini and Notocupedini. *Paleontologicheskii Zhurnal*, 28, 83–93. [In Russian; translation in *Paleontological Journal*, 28, 102–115.]
- Ponomarenko, A.G. (1997) New beetles of the family Cupedidae from the Mesozoic of Mongolia. Ommatini, Mesocupedini, Priacmini. *Paleontologicheskii Zhurnal*, 31, 45–55. [In Russian; translation in *Paleontological Journal*, 31, 389– 399.]
- Ponomarenko, A.G. (2006) On the types of Mesozoic archostematan beetles (Insecta, Coleoptera, Archostemata) in the Natural History Museum, London. *Paleontologicheskii Zhurnal*, 40, 86–94. [In Russian; translation in *Paleontological Journal*, 40, 90–99.]

https://doi.org/10.1134/S0031030106010102

- Sha, J.G., Pan, Y.H., Wang, Y.Q., Zhang, X.L. & Rao, X. (2012) Non-marine and marine stratigraphic correlation of Early Cretaceous deposits in NE China, SE Korea and SW Japan, non-marine molluscan biochronology, and palaeogeographic implications. *Journal of Stratigraphy*, 36 (2), 357–381. https://doi.org/10.19839/j.cnki.dcxzz.2012.02.015
- Sohn, J.C. & Nam, G.S. (2021) New fossil genus and species of carrion beetle (Coleoptera, Silphidae) from the Lower Cretaceous Jinju Formation, South Korea. *Journal of Asia-Pacific Entomology*, 24, 584–587. https://doi.org/10.1016/j.aspen.2021.05.003

Sohn, J.C., Nam, G.S., Choi, S.W. & Ren, D. (2019) New fossils of Elateridae (Insecta, Coleoptera) from Early Cretaceous Jinju Formation (South Korea) with their implications to

Junju Formation (South Korea) with their implications to evolutionary diversity of extinct Protagrypninae. *PLoS One*, 14, e0225502. https://doi.org/10.1371/journal.pone.0225502

Song, Z.Y., Zhao, X.Y., Jarzembowski, E.A. & Xiao, C.T. (2022) Overview of and taphonomic bias in Archostemata (Insecta: Coleoptera) from Cretaceous amber. *Palaeontographica Abteilung A*, 323, 119–137. https://doi.org/10.1127/pala/2022/0131 Strelnikova, O.D. & Yan, E.V. (2021) Redescriptions of beetles of the *Notocupes* generic complex (Coleoptera: Archostemata: Ommatidae) from the Lower Cretaceous of Buryatia. *Palaeoentomology*, 4 (5), 499–514. https://doi.org/10.11646/palaeoentomology.4.5.15

Strelnikova, O.D. & Yan, E.V. (2023) Redescriptions of the Triassic *Notocupes* beetles (Archostemata: Ommatidae) from Kyrgyzstan and South Kazakhstan. *Palaeoentomology*, 6 (2), 174–190.

https://doi.org/10.11646/palaeoentomology.6.2.9

- Tan, J.J. & Ren, D. (2009) Mesozoic archostematan fauna from China. Science Press, Beijing, 347 pp. [In Chinese with English summary]
- Tan, J.J., Ren, D., Shih, C.K. & Ge, S.Q. (2006) New fossil beetles of the family Ommatidae (Coleoptera: Archostemata) from the Jehol Biota of China. *Acta Geologica Sinica*, 80, 474–485. https://doi.org/10.1111/j.1755-6724.2006.tb00266.x
- Tan, J.J., Wang, Y.J., Ren, D. & Yang, X.K. (2012) New fossil species of ommatids (Coleoptera: Archostemata) from the Middle Mesozoic of China illuminating the phylogeny of Ommatidae. *BMC Evolutionary Biology*, 12, 113. https://doi.org/10.1186/1471-2148-12-113
- Tihelka, E., Huang, D.Y. & Cai, C.Y. (2019) New notocupedin beetle in Cretaceous Burmese amber (Coleoptera: Archostemata: Ommatidae). *Palaeoentomology*, 2 (6), 570–575. https://doi.org/10.11646/palaeoentomology.2.6.5
- Tihelka, E., Huang, D.Y. & Cai, C.Y. (2020a) New data on Ommatidae (Coleoptera) from mid-Cretaceous Burmese amber. *Cretaceous Research*, 106, 104253. https://doi.org/10.1016/j.cretres.2019.104253
- Tihelka, E., Huang, D.Y. & Cai, C.Y. (2020b) A new genus and species of Micromalthidae from Burmese amber (Coleoptera: Archostemata). *Earth and Environmental Science Transactions* of the Royal Society of Edinburgh, 111, 39–46. https://doi.org/10.1017/S1755691019000185
- Yamamoto, S. (2017) A new genus of Brochocoleini beetle in Upper Cretaceous Burmese amber (Coleoptera: Archostemata: Ommatidae). Cretaceous Research, 76, 34–39. https://doi.org/10.1016/j.cretres.2017.04.008
- Yamamoto, S. (2021) The extant telephone-pole beetle genus *Micromalthus* discovered in mid-Cretaceous amber from northern Myanmar (Coleoptera: Archostemata: Micromalthidae). *Historical Biology*, 33, 941–948. https://doi.org/10.1080/08912963.2019.1670174
- Yan, E.V., Wang, B., Ponomarenko, A.G. & Zhang, H.C. (2014) The most mysterious beetles: Jurassic Jurodidae (Insecta: Coleoptera) from China. *Gondwana Research*, 25, 214–225. https://doi.org/10.1016/j.gr.2013.04.002
- Zhang, S.Q., Che, L.H., Li, Y., Liang, D., Pang, H., Ślipiński, A. & Zhang, P. (2018) Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications*, 9, 205.

https://doi.org/10.1038/s41467-017-02644-4