

OCCURRENCE OF THE ISOPOD *ARCHAEONISCUS COREAENSIS* NEW SPECIES FROM THE LOWER CRETACEOUS JINJU FORMATION, KOREA

TAE-YOON PARK,^{1,2} GEORGE D. F. WILSON,¹ DONG-CHAN LEE,³ AND DUCK K. CHOI⁴

¹Australian Museum, 6 College Street, Sydney, NSW 2010, Australia, <taeyoon.park@hotmail.com>; <buz.wilson@austmus.gov.au>; ²Present address: Division of Polar Earth System-Science, Korea Polar Research Institute, Incheon 406-840, Korea; ³Department of Heritage Studies, Daejeon Health Sciences College, Daejeon 300-711, Korea, <dclee67@hotmail.com>; and ⁴School of Earth and Environmental Sciences, Seoul National University, Seoul 151-747, Korea, <dkchoi@snu.ac.kr>

ABSTRACT—The fossil isopod crustacean genus *Archaeoniscus* has been known to occur in England, France and Germany during the Upper Jurassic, and in Mexico and Egypt during the Lower Cretaceous. The morphology of this genus is unique in having dorsoventrally compressed body, the cephalon set deeply into the first pereionite, pleon as wide as pereion, and a broad semicircular pleotelson. These features have resulted in placing the classification of the genus in the monotypic family Archaeoniscidae. However, due to the lack of detailed morphological data, suprafamilial classification of this genus has remained unclear, as well as its ecology and lifestyle. Here we report *Archaeoniscus coreaensis* n. sp. from the Jinju Formation, Gyeongsang Basin, Korea. The occurrence of *Archaeoniscus* in the East Asia implies that the genus may have had a worldwide distribution. The Gyeongsang Basin was a Cretaceous backarc basin, which consists of exclusively non-marine sedimentary sequences. The occurrence of this genus, therefore, indicates that *Archaeoniscus* successfully adapted to a freshwater ecosystem as well. Detailed anatomy including antennulae, antennae, pereopods, and uropods was observed from well-preserved multiple specimens, which allows better understanding of the morphology of *Archaeoniscus*. The axial structure in the posterior part of the body, which was previously interpreted as a unique brood pouch characterizing the family, turned out to be a remnant of the hindgut. Females of all isopods and most of the members of the superorder Peracarida have a thoracic ventral brood pouch, modified from the thoracic coxal endites. Based on the morphology of the largely unmodified ambulatory pereopods of *A. coreaensis*, the possibility of *Archaeoniscus* being ectoparasitic is discounted. Instead, the flattened body and the form of limbs of *A. coreaensis* would have been suitable for a benthic lifestyle.

INTRODUCTION

THE MESOZOIC isopod crustacean genus *Archaeoniscus* Milne Edwards, 1843 has been reported from the Upper Jurassic to Cretaceous deposits of England (Ross and Vannier, 2002), Germany (Haack, 1918; Van Straelen, 1928), France (Gaillard et al., 2005), Texas (Wieder and Feldmann, 1992), and Mexico (Feldmann et al., 1998; Vega et al., 2005). Its occurrence from Egypt was also mentioned by Klitzsch et al. (1979). The environments where *Archaeoniscus* is known to have occurred are generally shallow marine-related facies: i.e., shallow continental sea (Wieder and Feldmann, 1992), lagoonal (Feldmann et al., 1998; Gaillard et al., 2005), and freshwater to intermarine environment (Klitzsch et al., 1979; Ross and Vannier, 2002). The paleogeographic distribution of the genus appears to encompass the continental margin environments of the central Atlantic Ocean and the western Tethys Ocean.

This genus, which is classified in the monotypic family Archaeoniscidae Haack, 1918, has a somewhat unique morphology. The phylogenetic position of the Archaeoniscidae within the Isopoda, however, has remained rather elusive. Hessler (1969) wrote that some features of *Archaeoniscus* are reminiscent of the suborder Oniscoidea (now considered to be Oniscidea Latreille, 1802), but he agreed with Haack (1918) that the large pleotelson, the shapes of antennulae, antennae and uropods distinguish *Archaeoniscus* from the Oniscidea. The genus was often considered as a member of the suborder Flabellifera Sars, 1882 (e.g., Van Straelen, 1928; Wieder and Feldmann, 1992; Feldmann et al., 1998). The use of the suborder Flabellifera is no longer recommended (Wägele, 1989; Brusca and Wilson, 1991), and thus Vega et al. (2005) placed the family within the suborder Sphaeromatoidea Wägele, 1989, under the superfamily Sphaeromatoidea Latreille, 1825.

Feldmann et al. (1998) compared the posterior axial structure of *Archaeoniscus* to the brood pouch of the Sphaeromatidae Burmeister, 1834 (e.g., Harrison, 1984); we disagree and discuss this structure below. They also mentioned a resemblance to the ectoparasitic family Cymothoidae Leach, 1814, and suggested *Archaeoniscus* as possible ecological equivalents of the Cymothoidae. Brandt et al. (1999) ruled out the close relationship between the Archaeoniscidae and the Sphaeromatidae, and suggested without supporting arguments that the Archaeoniscidae is a probable ancestor of terrestrial oniscid isopods. The controversial classification of the Archaeoniscidae is partly caused by a lack of detailed morphological data that can be used to infer a phylogenetic position. For example, body parts of *Archaeoniscus*, other than dorsal tergites, have been rarely described or have been misinterpreted; Haack (1918) provided reconstructions with some cephalic appendages, and Vega et al. (2005) also showed a line drawing of a mouth part, but these reconstructions were based on misinterpretations of the anatomy, hence do not advance our understanding of a phylogenetic position for the genus.

This study reports the first record from East Asia of the Mesozoic isopod genus, *Archaeoniscus*, from the non-marine Gyeongsang Basin, Korea, based on a substantial collection amounting to 104 specimens. Along with the occurrences from Europe, North America, and Egypt, this discovery from Korea indicates that *Archaeoniscus* may have had a cosmopolitan distribution. These new specimens of *Archaeoniscus* allowed a detailed description of external anatomy, which will add to evidence for phylogenetic position of the Archaeoniscidae within the Isopoda. Although we do not perform an analysis in this paper, these new data substantially clarify the classification of this clade of fossil isopods.



FIGURE 1—1, index map of Korean peninsula with the dark area indicating the Gyeongsang Basin; 2, detail of rectangle indicated in 1 with road map of the fossil locality area, star indicates the location of the Banryong-ri section.

GEOLOGIC SETTINGS AND FOSSIL LOCALITY

The Cretaceous Gyeongsang Basin occupies in the south-eastern part of the Korean peninsula (Fig. 1) and consists of non-marine sedimentary sequences and volcanic successions (Chough et al., 2000). The non-marine origin of the sedimentary rocks in the Gyeongsang Basin is supported by the occurrence of non-marine fossils such as plants (Yabe, 1905), freshwater mollusks (Yang, 1976, 1979), ostracodes (Paik et al., 1988), and pollen (Choi, 1985; Choi and Park, 1987). Recently, Chough and Sohn (2010) interpreted the locality (area) as a backarc basin, and named it the Gyeongsang Backarc Basin. According to Chough and Sohn (2010) this backarc basin was situated at the western part of the Gyeongsang Volcanic Arc System and began to form during the Hauterivian to Barremian due to the subduction of the proto-Pacific (Izanagi) plate under the Asian continent. The Gyeongsang Backarc Basin is subdivided into the Jinju, Uiseong, and Yeongyang subbasins according to differences in lithology and geographic distribution. Material for this study was collected from the Jinju subbasin where seven formations are recognized, in ascending order: the Nakdong Formation, Hasandong Formation, Jinju Formation, Chilgok Formation, Silla Conglomerate, Haman Formation, and Jindong Formation. The lower three formations are collectively called the Sindong Group (Chang, 1975). The Jinju Formation consists of thick packets of sandstones intercalated in gray to black shale, and with the thickness ranging from 1,000 m to 1,800 m (Chough and Sohn, 2010). The formation is considered to have been deposited in a fluvo-lacustrine environment (Choi, 1986; Chough and Sohn, 2010). Diverse fossils have been reported from the formation, including bivalves, ostracodes, conchostracans, insects, fishes, and some dinosaur and pterosaur teeth (Paik, 2005). Choi (1985) and Choi and Park (1987) reported fossil spores and pollen, and Kim et al. (2002, 2005) described trace fossils. Stromatolites and caddisfly bioherms are also known from this formation (Paik, 2005). Paleontological data from charophytes (Choi, 1987) and palynomorphs (Choi, 1985; Choi and Park, 1987; Yi et al., 1994) suggested that the age of the Sindong Group is

late Neocomian (Hauterivian and Barremian). Recent geochronological research using detrital zircons, however, have suggested a younger age for the Jinju Formation; Lee et al. (2010a) concluded that the strata formed in Aptian to Albian, while Lee et al. (2010b) reported that the youngest detrital zircon age of the Jinju Formation is 106 Ma which is Albian in age.

All material of *Archaeoniscus* was collected from the lower part of the Jinju Formation at the Banryong-ri section (E 128°02'01", N 35°05'51"; Fig. 1) in the Jinju subbasin. The outcrop is exposed along the Gahwa River, which is under influence of sea water; the maximum lateral extent of the exposure during the low tide is about 40 m. The sandstone shows tafoni weathering patterns that are typical of a coastal sandstone landscape. Three upward-fining sequences are recognized from the outcrop (Fig. 2). Each sequence consists of pebbly or medium-grained sandstone with planar cross-stratification at the base, siltstone with bioturbation in various degrees, ripple cross-lamination and parallel lamination with soft sediment deformation structures, and shale or silty shale at the top mostly with parallel lamination, occasionally intercalated with pedogenic carbonates. *Archaeoniscus* specimens were collected from the silty shale and shale layers of all three upward-fining sequences (Fig. 2). The occurrence is rare in the upper two layers, and the majority of the specimens were collected from the lowermost silty shale layers. Insects, conchostracans, and plant debris occur with *Archaeoniscus*. The insect fossils belong to the Order Odonata, the Cixidae and Corixidae of the Order Hemiptera, and the Order Diptera. The occurrences of conchostracans and aquatic insects such as corixids suggest a freshwater environment of the Jinju Formation.

MATERIAL AND METHODS

A total of 104 specimens (see Appendix and online supplemental archive) including various body fragments from the lowermost horizon of the three fossil-occurring horizons (Fig. 2) were used for this study. A histogram of the frequency distribution of body length (Fig. 3) shows that not all specimens

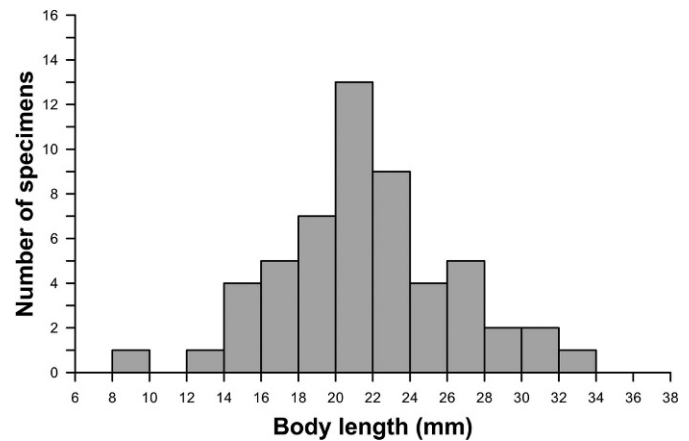
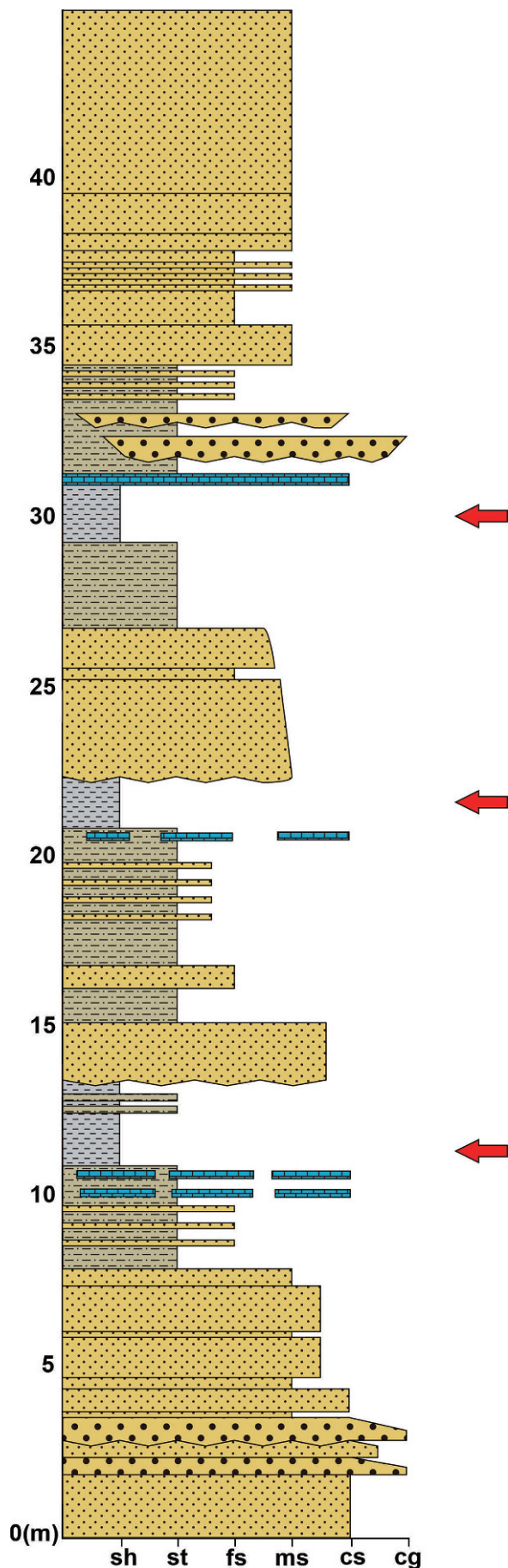


FIGURE 3—Histogram showing the frequency distribution of body length ($n=54$). The total number of this histogram includes some incomplete specimens whose body lengths were extrapolated.

retain the entire length of the body. Body length for those specimens was extrapolated from the width of pereonite 1, the length of pleotelson, or the width of pleotelson, on the basis of the body ratios of the reconstruction (Fig. 4). Line drawings were made by a vector graphic program, Inkscape version 0.48, which is freely downloadable online (www.inkscape.org). All specimens for this study are deposited in the Palaeontology Collection of Australian Museum with registration numbers "AM F."

SYSTEMATIC PALEONTOLOGY

Order ISOPODA Latreille, 1817

Suborder SPHAEROMATIDEA Wägele, 1989

Superfamily SPHAEROMATOIDEA Latreille, 1825

Family ARCHAEONISCIDAE Haack, 1918

Genus ARCHAEONISCUS Milne Edwards, 1843

Type species.—*Archaeoniscus brodiei* Milne Edwards, 1843.

Other species.—*Archaeoniscus aranguthyrum* Feldmann et al. 1998; *Archaeoniscus coreaensis* n. sp. Not *Archaeoniscus: Archaeoniscus texanus* Wieder and Feldmann, 1992.

Diagnosis.—Emended: *Archaeoniscus* is distinguished from other isopods by the following features: oval and dorsoventrally compressed body with the head deeply embedded into the first pereonite; globular eyes that cover the lateral margin of the head; lateral margins of the pereion consisting of broad, overlapping coxal plates that have distinct sutures; anterior four pleonites that extend to lateral margin and are as wide as pereonites; a reduced arcuate pleonite 5 that does not extend to the pleonal lateral margin, and a broad semicircular pleotelson that lacks marginal spines. Although the limbs are not well preserved in most specimens, the antennulae are large and multiarticulate, the mandibles are positioned transversely on the head and have a broad incisor process, the pereopods are ambulatory with distinct coxal dorsal articulations, and the uropodal rami are spine-like, with a narrow parallel-sided protopod.

Remarks.—On the basis of the poorly preserved specimens of *A. brodiei*, Hessler (1969) mentioned, "The broad, oval

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FIGURE 2—The stratigraphic column of the lower part of the Jinju Formation exposed at the Banryong-ri section. The arrows indicate the three horizons bearing the fossils of *Archaeoniscus*. Abbreviations: sh=shale; st=siltstone; fs=fine sandstone; ms=medium sandstone; cs=coarse sandstone; cg=conglomerate.

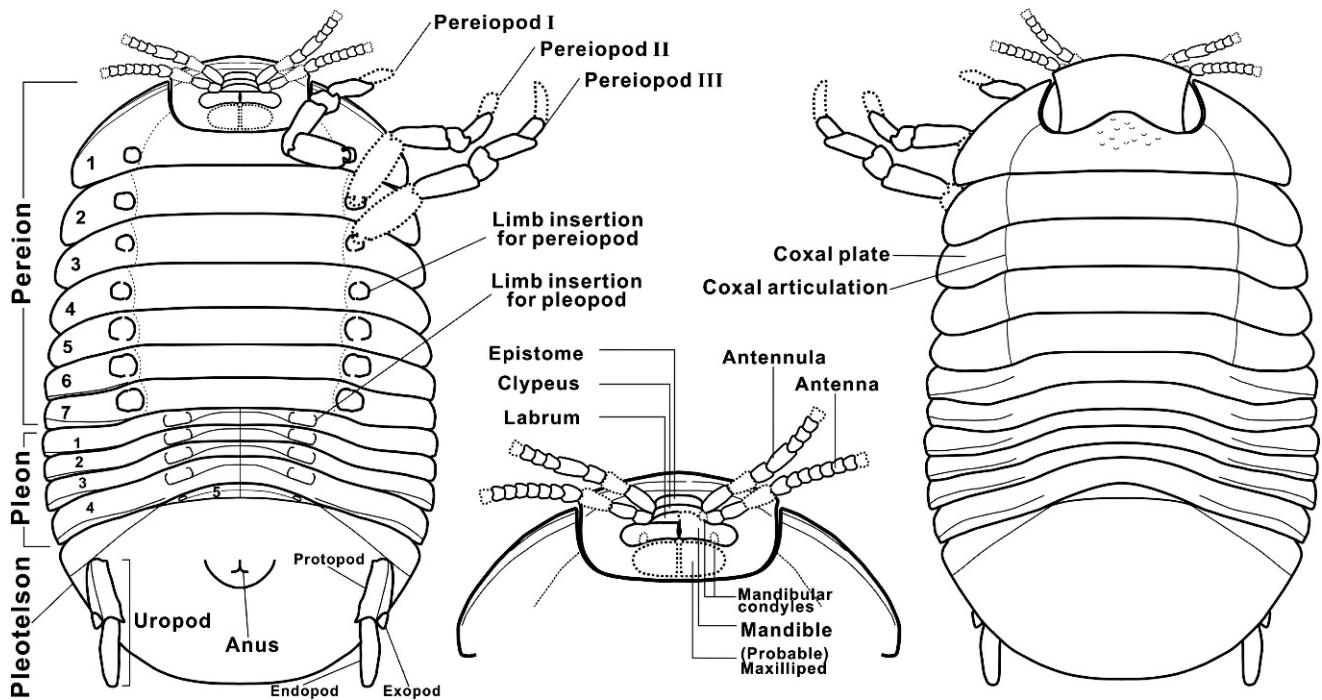


FIGURE 4—Reconstruction of *Archaeoniscus coreaensis* n. sp.; left to right, ventral view; close-up of cephalic region in ventral view; dorsal view, dotted lines represent the presumptive body structure.

body, prominent eyes, absence of defined epimeres, and presence of only 4 free pleonites justifies placement of this monotypic genus in its own family.” The better preserved specimens used in this study, however, show a reduced fifth pleonite. The pereopodal coxae also show dorsal articulation. As a result, we provide the emended diagnosis of *Archaeoniscus*.

The type species, *A. brodiei* was originally known from the uppermost Tithonian–Berriasian Purbeck Limestone Group of southern England (Ross and Vannier, 2002). Subsequently, *A. brodiei* was reported from Germany (Haack, 1918; Van Straelen, 1928), and an undescribed species with close affinity to *A. brodiei* occurs in the upper Kimmeridgian strata at Ain, France (Ross

and Vannier, 2002; Gaillard et al., 2005). *Archaeoniscus texanus* Wieder and Feldmann, 1992 was collected from the Upper Cretaceous Austin Chalk, Texas, presumably representing the youngest occurrence of the genus. *Archaeoniscus aranguthyrum* Feldmann, Vega, Applegate and Bishop, 1998 was documented from the middle member of the Tlayúa Formation, Puebla, México, which is middle to late Albian in age. The occurrences of undescribed species of *Archaeoniscus* have been known from the Aptian Abu Ballas Formation, southern Egypt (Klitzsch et al. 1979), and the Tithonian deposits of the Crayssac Lagerstätte at southwest France (Gaillard et al. 2005).

The youngest species, *A. texanus*, is known only from posterior exuviae and is the only supposed species of

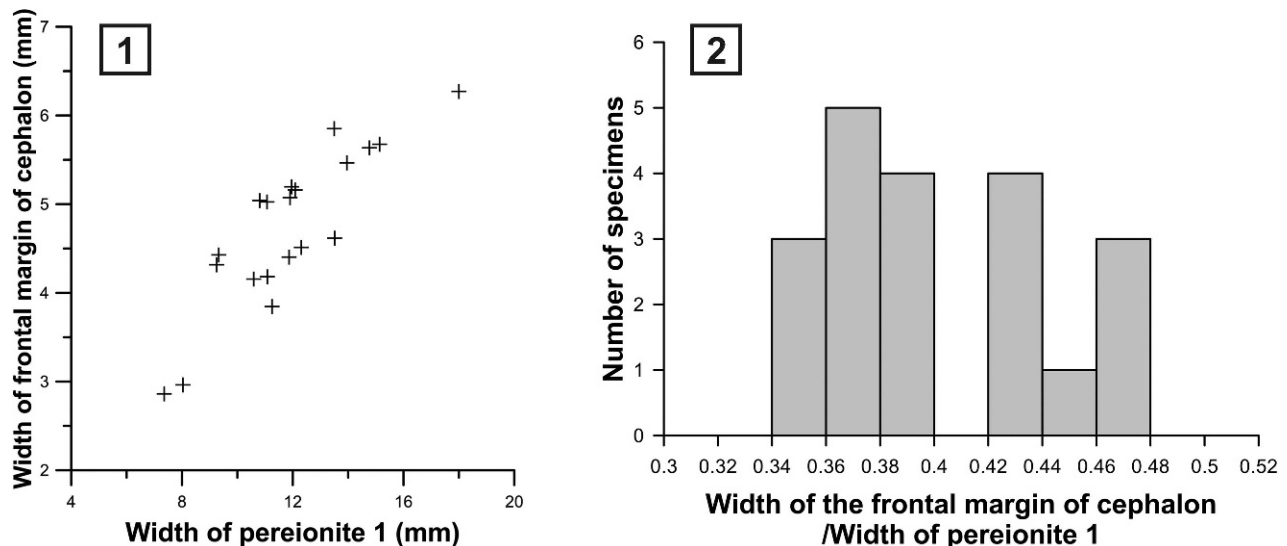


FIGURE 5—Graphs indicating the dimorphism of *Archaeoniscus coreaensis* n. sp. 1, scatter plots of the frontal margin of cephalon width versus the pereonite 1 width; 2, histogram showing the frequency distribution of the ratio of the frontal margin of cephalon width to the pereonite 1 width (n=20). Note the roughly bimodal distribution.

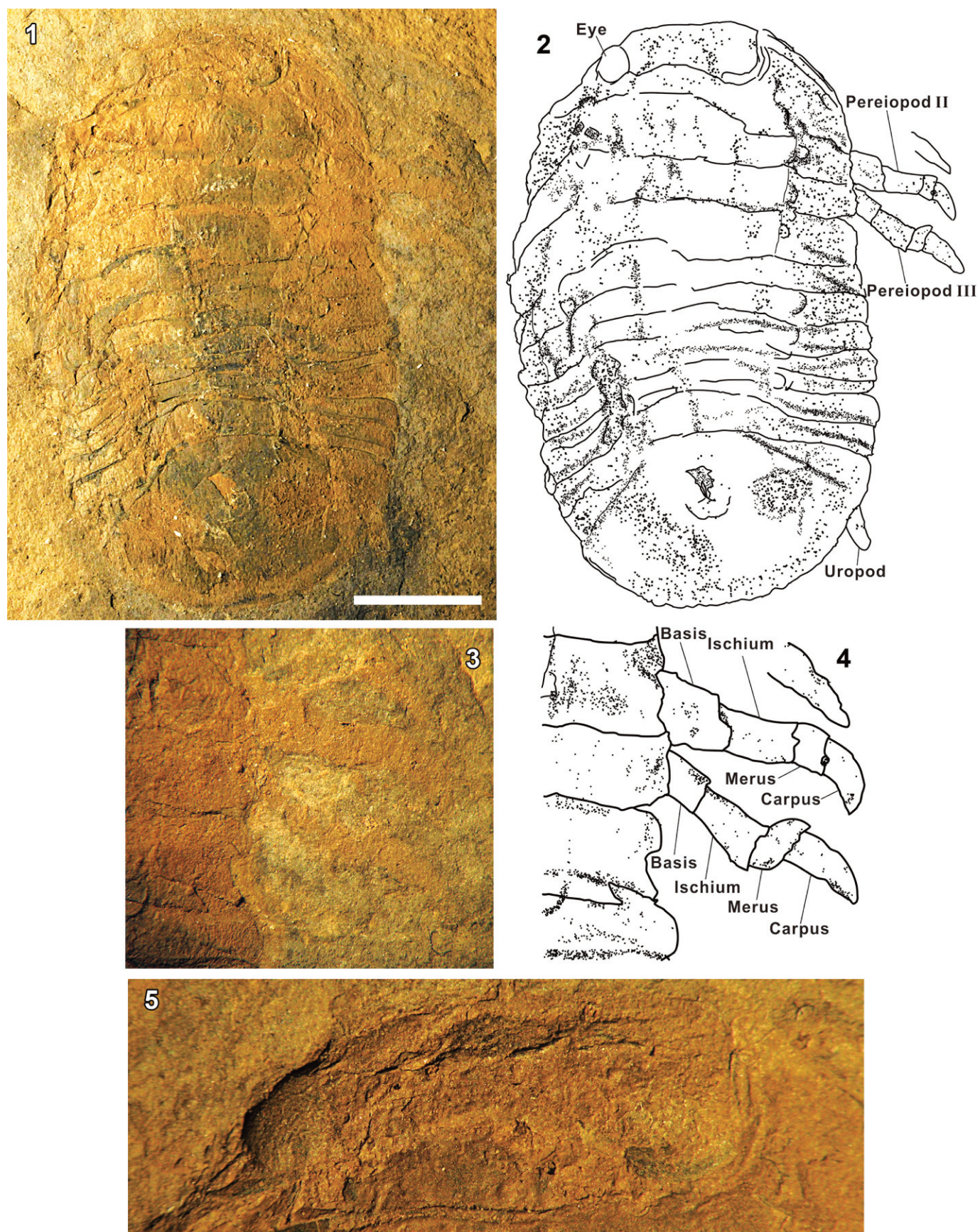


FIGURE 6—*Archaeoniscus coreaensis* n. sp. in dorsal view, holotype, AM F.110499. 1, 2, photograph and drawing of the whole body, respectively; 3, 4, close-up photograph and drawing of the pereopods, respectively; 5, close-up photograph of the cephalon; specimen is slightly skewed. Scale bar is 5 mm.

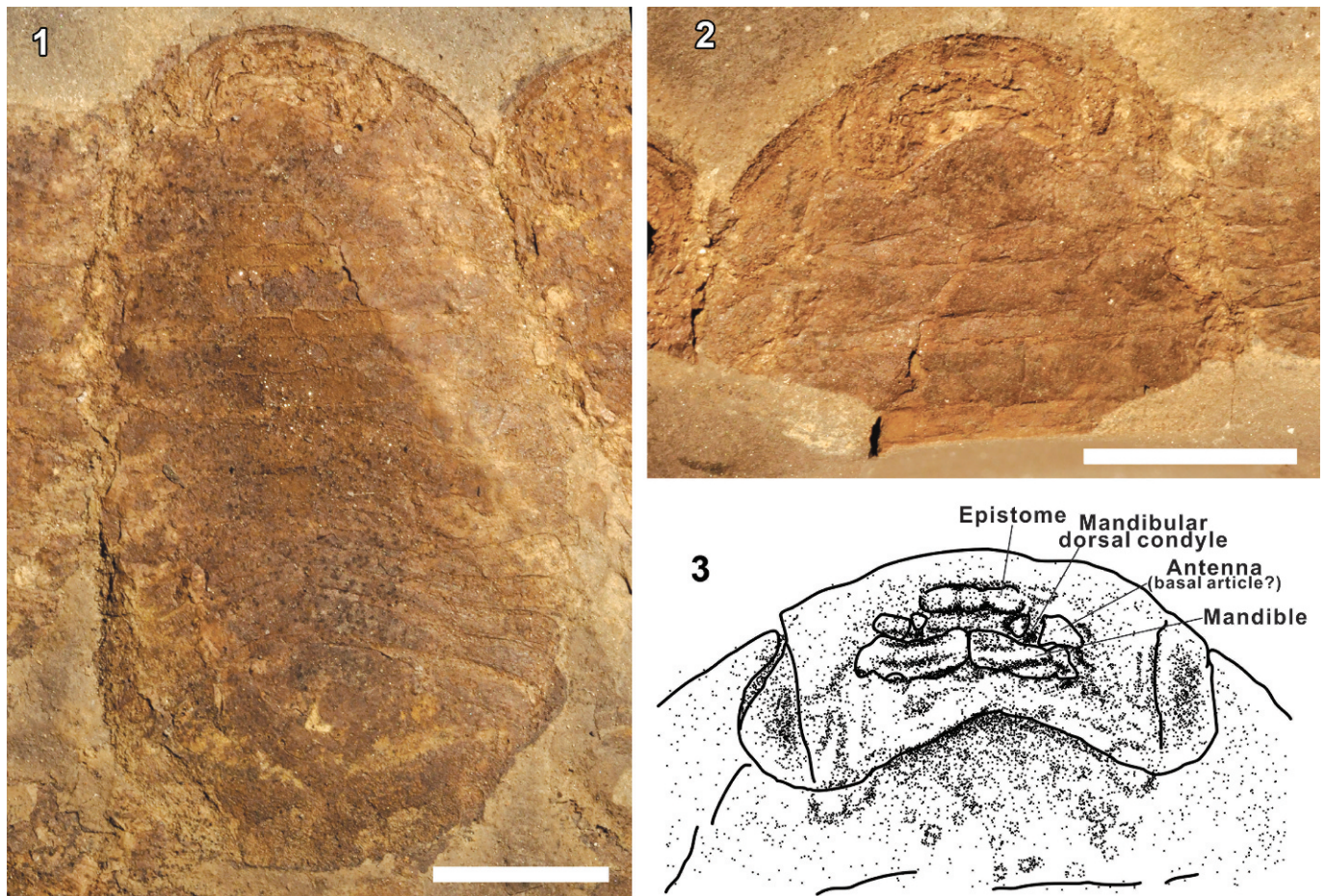


FIGURE 7—*Archaeoniscus coreaensis* n. sp. of part and counterpart relationship. 1, paratype, AM F.110502; 2, paratype, AM F.110503, partial counterpart; 3, drawings of the cephalic region of AM F. 110503; the cephalic region is not in dorsal or ventral view, but is a view from the inside of cephalon. See the preservation section of the text. Scale bars are 5 mm.

Archaeoniscus that has all five subequal pleonites. All other illustrated species of *Archaeoniscus* have four large pleonites with the fifth pleonite reduced or unrecognizable. Feldmann et al. (1998) interpreted the morphology of *A. aranguthyrum* as having five subequal pleonites but all specimens of *A. aranguthyrum* for which the pleonites are recognizable (Feldmann et al., 1998; Vega et al., 2005) appear to have four subequal pleonites. Our inspection of the original images (provided by F. Vega) found that this species has a pleonal conformation similar to the current species, including a trace of the reduced pleonite 5 on the dorsal surface. In *A. texanus*, not only is the fifth pleonite present, it is longer than the other pleonites and participates in the lateral margin of the pleon. Although Wieder and Feldmann (1992) did not reconstruct the appearance of the uropods in *A. texanus*, their photographs (Wieder and Feldmann, 1992; fig. 11) suggest flat limbs that are unlike those of other species of *Archaeoniscus*, which are narrow and rod-like. In addition, *A. texanus* is the only species known from an open marine environment (the Austin Chalk). Given that the anterior body of *A. texanus* is unknown, the evidence for its classification to *Archaeoniscus* is insufficient. We conclude that *A. texanus* does not belong in *Archaeoniscus*. Further study of a complete specimen of *A. texanus* is needed for its correct classification.

As noted by Vega et al. (2005), the occurrence of *Archaeoniscus* is restricted in Europe (England, Germany, and France) during the Upper Jurassic, while it became more worldwide in

the Lower Cretaceous, occurring in North America (Mexico), Africa (Egypt), and the eastern margin of Asia (Korea).

ARCHAEONISCUS COREAENSIS new species Figures 4, 6–14

Diagnosis.—*Archaeoniscus* with pereionites 6 and 7 medial length less than pereionites 2–5; exopod of uropod short, triangular.

Description.—Overall body form broad, suboval in shape; body length showing a unimodal distribution with the length between 20 to 22 mm most frequent (Fig. 3); length approximately 1.6 greatest width (Fig. 4).

Head subrectangular, set deeply into pereionite 1, length less than width, with apparent dimorphism in relative width (Fig. 5); dorsal surface smooth; frontal margin gently rounded anteriorly; submarginal ridges present on ventral surface. Eyes large, entirely covering head lateral margin; round, with ommatidia visible in 16 vertical rows (Fig. 6.5). Partial structures of epistome and clypeus were observed; epistome width one fifth of head width; given the position of mandibular dorsal condyles (Figs. 4, 7), clypeus wider than epistome. Labrum as wide as clypeus, covering anterior inner part of mandible.

Pereionites total medial length approximately 0.48 body length; dorsal surface smooth; coxal articulation to pereionites 1–5 free; coxal articulation for pereionites 6–7 not observed. Pereionite 1 length greater than other pereionites length;

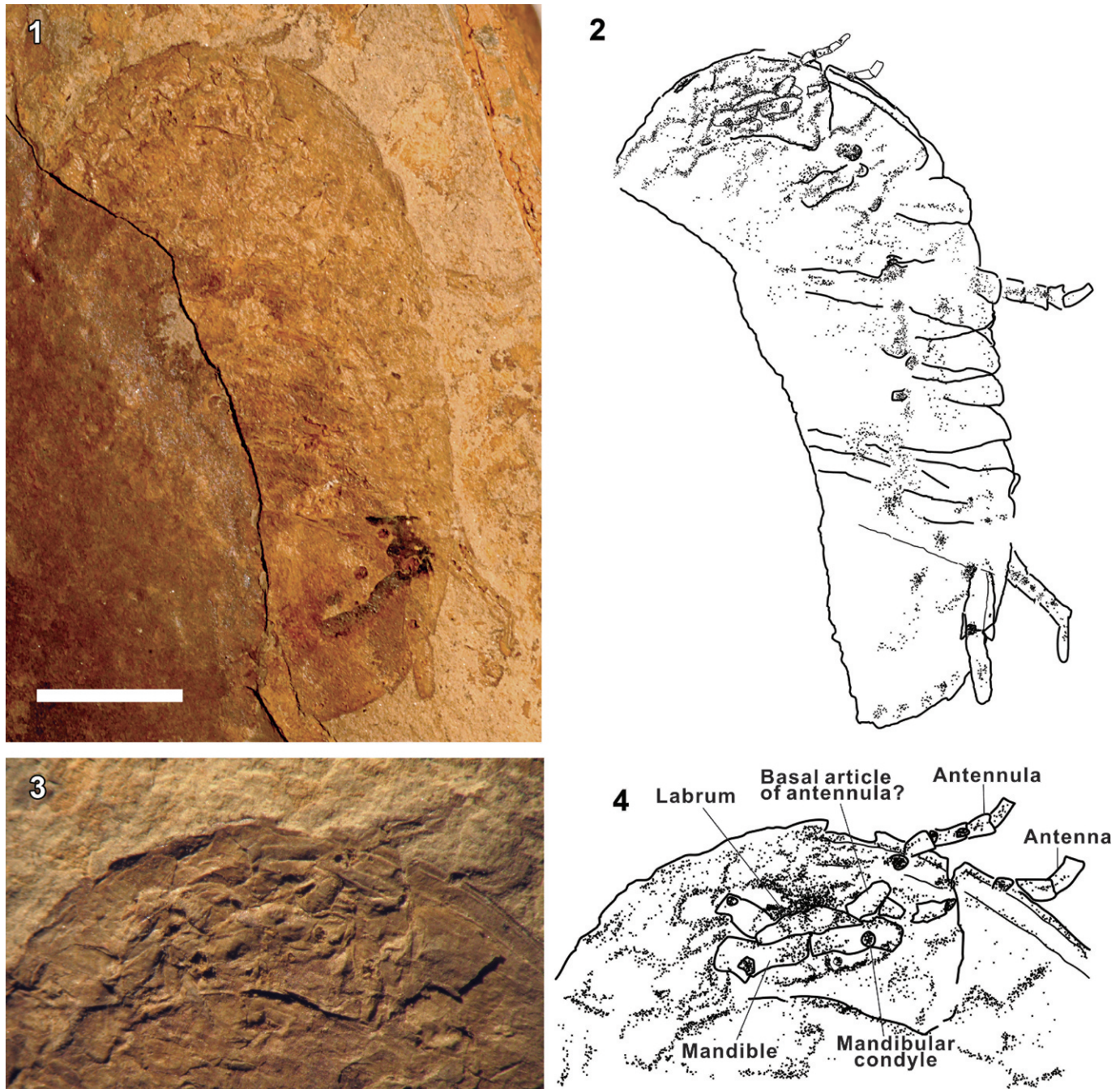


FIGURE 8—*Archaeoniscus coreaensis* n. sp. in ventral view, paratype, AM F.110490. 1, 2, photograph and drawing of the whole body, respectively; 3, 4, close-up photograph and drawing of the cephalic region, respectively. Scale bar is 5 mm.

anterior margin depressed rearward to embrace head; middle part of anterior margin projecting forward, forming a sigmoidal shape; dorsal surface of middle part weakly tuberculate; two submarginal ridges present on anterolateral margin of ventral side, seemingly continuous from ventral ridges of head; coxal plate 1 occupying almost half of tergite of pereonite 1, encompassing lateral margin of eyes; posterolateral margin more angular than those of pereonites 2–5. Pereonites 2–5 of similar shape with somewhat rounded lateral margin, subequal in length and width; dorsal surface smooth; straight dorsal tergite flanked laterally by coxal plates that are moderately curved rearward with the curvature posteriorly diminishing. Pereonites 6 and 7 medial length slightly less than pereonites

1–5, intermediate in shape between pereonites 2–5 and pleonites; posterolateral margin more angular than those of pereonites 2–5; lateral part possessing dorsal ridges running from supposed boundary of coxal articulation, reaching anterior to the posterolateral corner.

Pleonites total medial length about 0.14 body length; dorsal surface smooth. Pleonites 1–3 relative width subequal, lengths less than pereonite 7. Pleonite 4 width approximately 0.96 pleonite 3 width; medially longer than pleonites 1–3. Pleonites 1–4 possessing dorsal ridges similar to ridges of pereonites 6 and 7, reaching anterior to the posterolateral corner; posterolateral corner angular. Pleonite 5 reduced, arcuate, seemingly fused to pleotelson; anterior and lateral margin

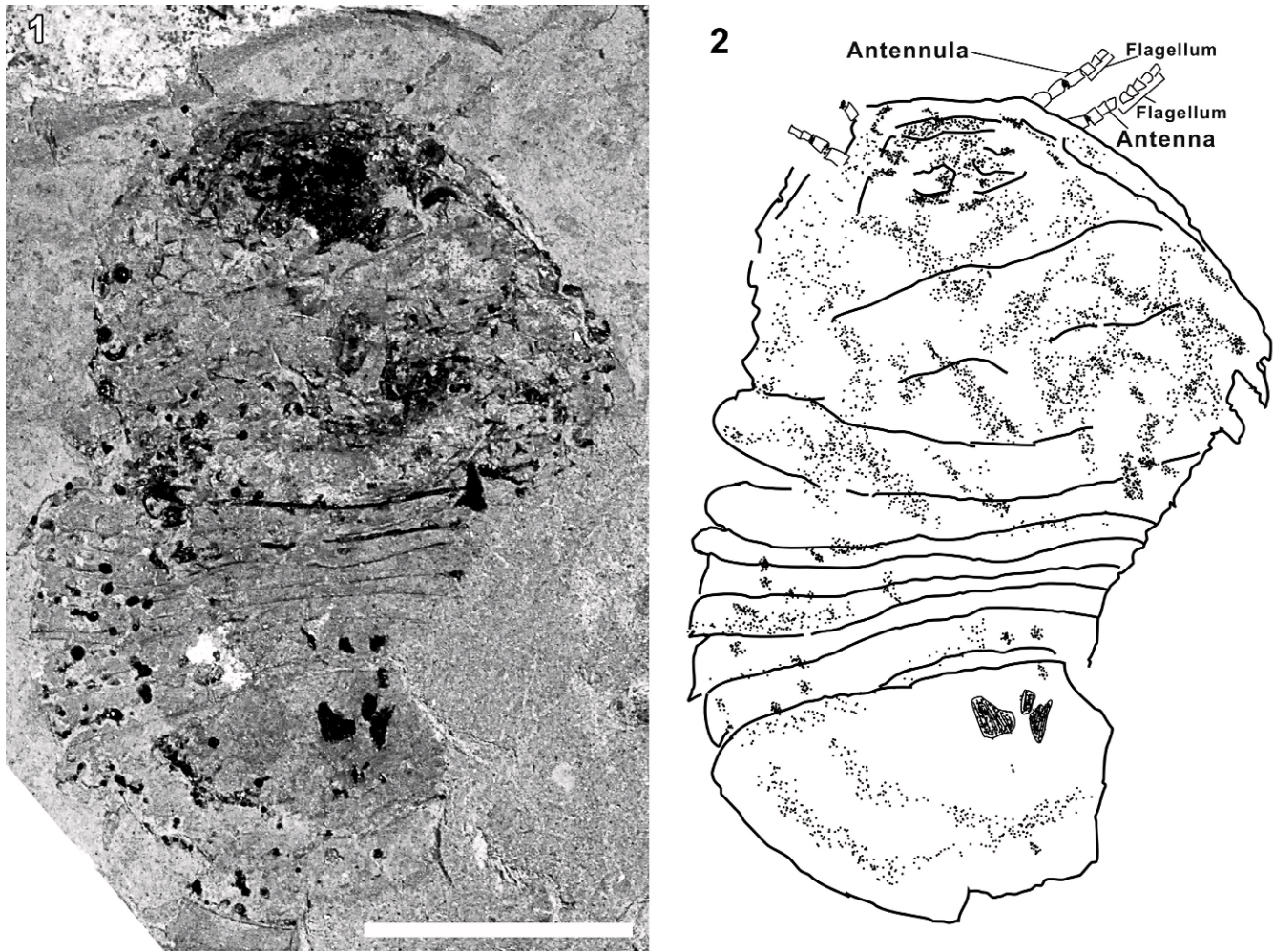


FIGURE 9—*Archaeoniscus coreaensis* n. sp. in ventral view, paratype, AM F.110440. 1, 2, photograph and drawing of the whole body, respectively. Note flagellae of the antennulae and antennae. Scale bar is 5 mm.

completely enclosed by pleonite 4; relative width about one third of maximum body width; often dorsally covered by pleonite 4, hence not observable. Pleopod I–IV limb insertions subrectangular to suboval in outline; pleopod V insertion small, oval in outline; a ridge-like structure adaxially running from posterolateral adaxial corner of each limb insertion to meet the axial midline of pleon.

Pleotelson posteriorly semicircular, broad, median length 0.5 maximum width; dorsal surface smooth; anterior margin weakly rounded, with a median indentation adjacent to pleonite 5; weakly vaulted axial ridge extending posteriorly from anterior margin of pleonite 5, meeting somewhat posterior to the anterolateral corner of pleotelson. Anus (Fig. 14, also visible in Figs. 6, 12) located anterior to pleotelson center at the level of uropodal articulation; posterior margin of anus semicircular; in most cases only posterior part of anal plates preserved, expressed as a short groove bifurcating posteriorly.

Antennula (Figs. 4, 8, 9) inserting to anterolateral margin of clypeus; article 1 longest; article 2 not preserved, inferred in reconstruction (Fig. 4); presumptive article 3 short; subsequent 2 or 3 articles connected to flagellum, of which three articles were observed (more articles are likely because terminal article was not observed).

Antenna (Figs. 4, 8, 9) inserting to lateral margin of clypeus; article 1 short; article 2 twice long as article 1; article 3 not

preserved but inferred in reconstruction (Fig. 4); subsequent articles connected to flagellum, of which five articles were observed (more articles are likely because terminal article was not observed).

Mandible subrectangular; moderately thicker adaxially; more heavily sclerotized than other appendages; incisor process with truncate edge; mandibular palp or molar process not observed.

Pereiopod I (Figs. 4, 10) basis, ischium, merus, and carpus observed; ischium as long as, but thinner than basis; merus short, about one third of ischium; carpus thin, twice long as merus.

Pereiopod II (Figs. 4, 6) ischium, merus, and carpus observed; ischium as long as the ischium of pereiopod I; merus length about one third of ischium; carpus thin, twice long as merus.

Pereiopod III (Figs. 4, 6, 11) ischium, merus, carpus, propodus, and dactylus observed, carpus incompletely preserved; ischium 1.1 length of the ischium of pereiopod II; merus about two fifths long as ischium; carpus almost as thick as merus, two third long as ischium; propodus thinner than carpus, as long as merus; dactylus thinner, but longer than propodus.

Other pereiopods not preserved well enough to be described.

Uropod (Figs. 4, 8, 12) total length approximately 0.7 pleotelson length; inserting to pleotelson ventrolaterally,

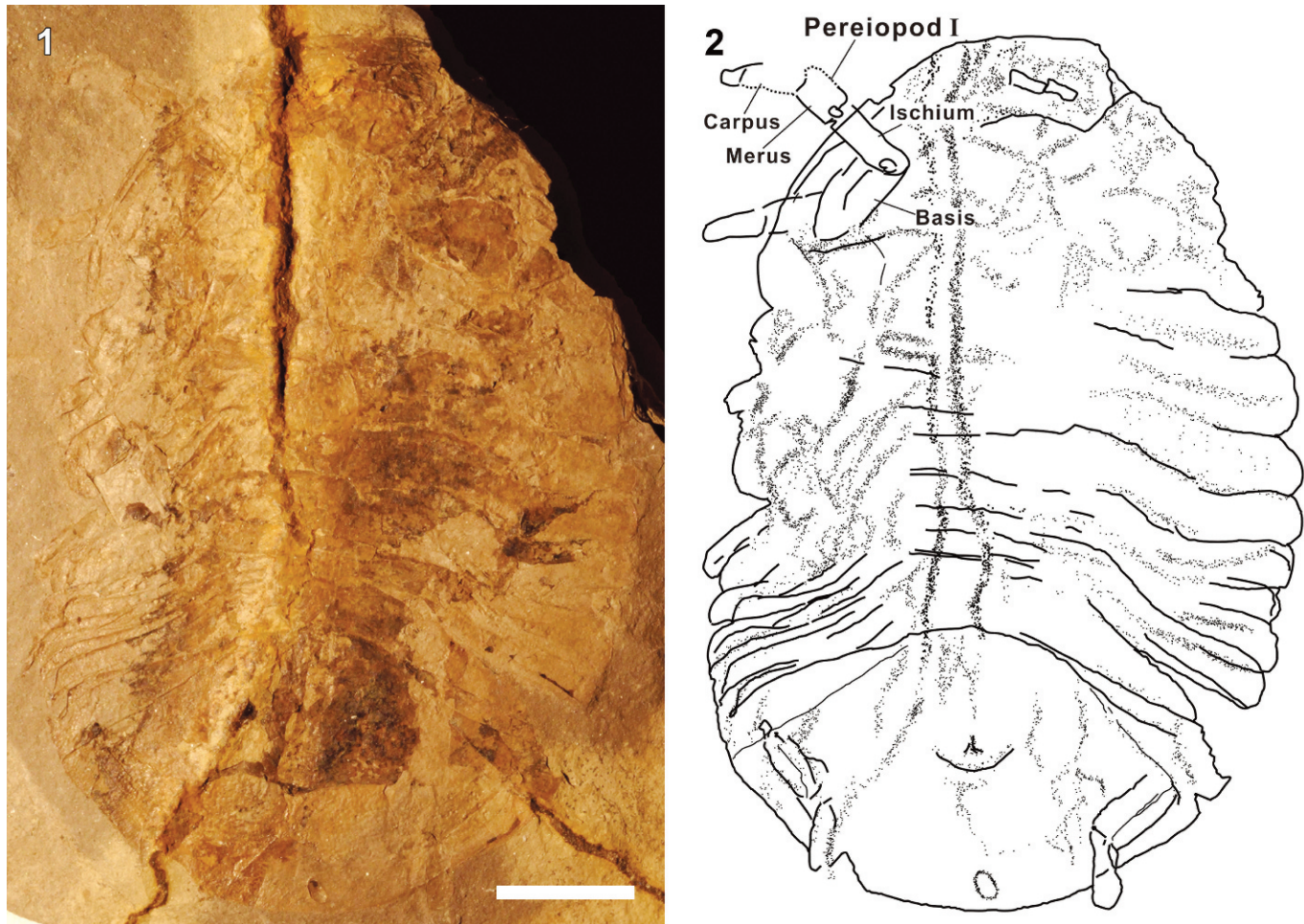


FIGURE 10—*Archaeoniscus coreaensis* n. sp., paratype, AM F.110487. 1, 2, photograph and drawing of the whole body, respectively. This is the largest individual in the collection. Scale bar is 5 mm.

approximately one protopod width away from the lateral margin of pleotelson; protopod insertion at the transverse ridge of pleotelson. Protopod width 0.5 length, length 0.47 uropod total length, not extending beyond pleotelson distal margin with ridge running through the entire length, seemingly dividing protopod into endopod-side and exopod-side, distomedial margin bearing a short subtriangular spine-like projection medial to the endopod. Endopod suboval in outline, length 1.1 protopod length, extending beyond the pleotelson. Exopod small, subtriangular in outline, as long as wide; length 0.2 protopod length. Articulating condyle between protopod and exopod not observed. Position of the uropod in multiple specimens (e.g., Figs. 8, 10, 12, 14.1) relative to body axis indicates that its rotational axis is normal to the body plane.

Etymology.—Referring to the Latin name of Korea, the country from which the specimens were collected.

Types.—Holotype, here designated, AM F.110499 (Fig. 6), length 22.8 mm, dorsal presentation, body slightly skewed, all body somites and part of right pereiopods 2 and 3 preserved. Paratypes, 17 specimens designated, all of which are illustrated in this study: AM F.110430, AM F.110432, AM F.110440, AM F.110445, AM F.110473, AM F.110487, AM F.110490, AM F.110495, AM F.110502, AM F.110503, AM F.110504, AM F.110505, AM F.110516, AM F.110517, AM F.110520, AM F.110522 and AM F.110523.

Material examined.—A total of 104 specimens (see Appendix) including body fragments preserved on 52 blocks of shale and siltstone. Some specimens are parts and counterparts.

Preservation.—Some fossils are compressed into the bedding plane, while others retain a weak convexity, with some three dimensional features. In the specimens completely compressed into the bedding plane, the dorsal features and ventral features are both expressed in the fossils (e.g., Figs. 10, 13.1). In some specimens retaining a weak convexity, the splitting into part and counterpart result in the splitting the fossil elements into two; the part and counterpart do not have mould-and-cast relationship. Even though fossils retained some convexity, observing the genuine dorsal or ventral surface is less frequent. For instance, the paratype and its counterpart (AM F.110502, 110503; Fig. 7) show the view from the inside of the cephalon: e.g., ventral half of the mandible on one side and the dorsal half on the other side.

Occurrence.—The lower part of the Jinju Formation (late Aptian to Albian?) at the Banryong-ri section, Gyeongsang Basin, Korea.

Remarks.—*Archaeoniscus coreaensis* n. sp. is most similar to *A. aranguthyrum* Feldmann et al. 1998 in having shorter pereionites 6 and 7 than *A. brodiei* Milne Edwards, 1843. This new species is distinguished from *A. aranguthyrum* by having short and triangular exopod of uropod; the latter species has a more elongate spine-like exopod. Both species also have a

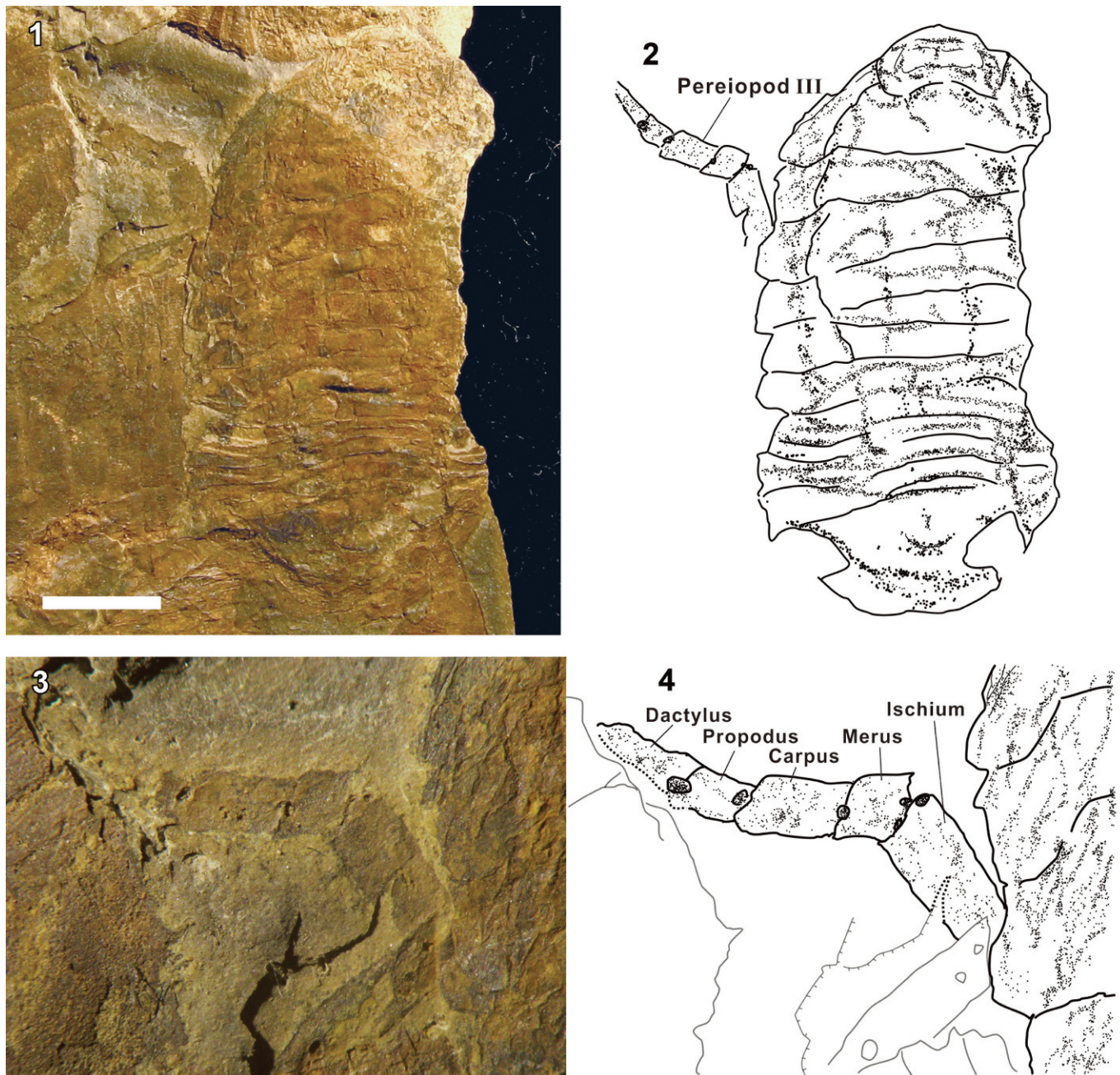


FIGURE 11—*Archaeoniscus coreaensis* n. sp. in dorsal view, paratype, AM F.110504. 1, 2, photograph and drawing of the whole body, respectively; 3, 4, close-up view of the pereopod III, photograph and drawing, respectively. Scale bar is 5 mm.

distomedial spine on the protopod, although that of *A. aranguthyrorum* is approximately twice as long as in *A. coreaensis* n. sp. Feldmann et al. (1998) described *A. aranguthyrorum* with five free pleonites, although their published images and additional unpublished images provided by Vega indicate that this species has only four free pleonites that contribute to the lateral margin of the pleon. We find that *A. coreaensis* n. sp. has five pleonites, but the fifth pleonite is a small arcuate plate at the anterior margin of the pleotelson. Images of *A. aranguthyrorum* indicate that this is the case as well. Part of the confusion regarding the pleonites arises from the overlapping of the lateral margins of the pleonites, plus the presence of a ridge on the pleotelson that overlaps the insertion of the uropods. *Archaeoniscus coreaensis* n. sp. also differs from *A. aranguthyrorum*

in that the coxal articulations of pereonites 6–7 are not observable, whereas they are visible in images of the latter species. Given the number of specimens at our disposal, we suspect that this difference could be real. The relative width of the head shows a possible dimorphism. The ratio of the width of the cephalic margin to the maximum width of the first pereonite displays a roughly bimodal distribution (Fig. 5). This could be attributed to sexual dimorphism; Feldmann et al. (1998) suggested that the morph with broader head represented the male, based on their identification of specimens with a “brood pouch” as female. Such dimorphism is also shown by *Archaeoniscus brodiei*; specimens of both morphs are preserved in one block recovered from Germany (Haack, 1918, pl. 4, fig. 7). The small number of specimens available for such measurement in

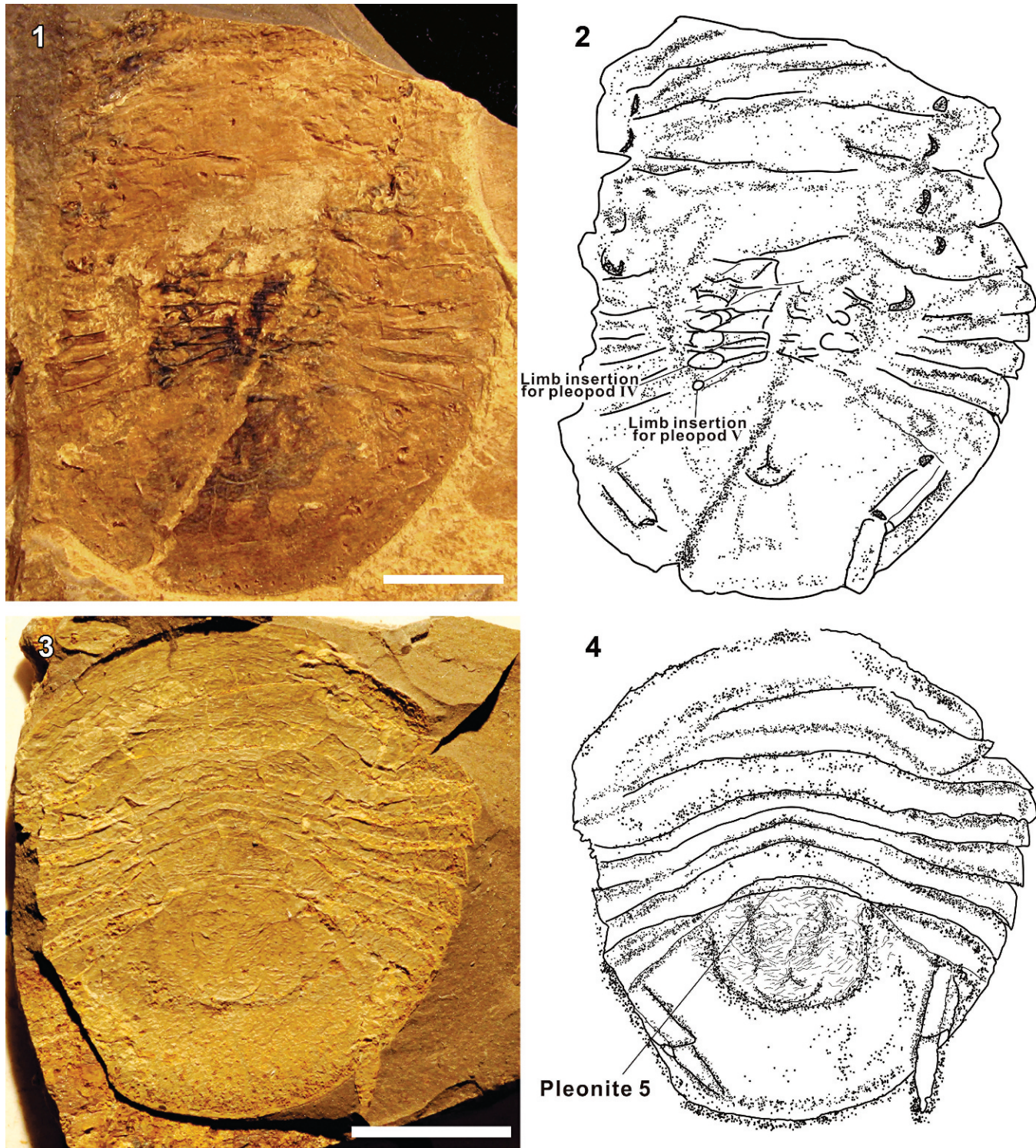


FIGURE 12—Posterior part of *Archaeoniscus coreaensis* n. sp. in ventral view. 1, 2, paratype, AM F.110445, photograph and drawing, respectively; note the pleopod limb insertions; 3, 4, paratype, AM F.110445, photograph and drawing, respectively. Scale bars are 5 mm.

our study (Fig. 5, $n=20$), however, leave the door open for morphological variability rather than dimorphism. Taphonomic effects also cannot be discounted.

DISCUSSION

Ecology.—Apart from *A. texanus*, which we consider misclassified, the occurrences of *Archaeoniscus* are usually related to continental marginal marine habitats: i.e., lagoonal

environment (Feldmann et al., 1998; Gaillard et al., 2005), or freshwater to intermarine environment (Klitzsch et al., 1979; Ross and Vannier, 2002). The latter study was unclear whether *Archaeoniscus brodiei* was marine, freshwater, or terrestrial, although a non-aquatic existence seems less probable. Given the geological settings of the Jinju Formation and the associated fauna, *A. coreaensis* n. sp. must have inhabited in a fluvo-lacustrine environment. This is the first report of

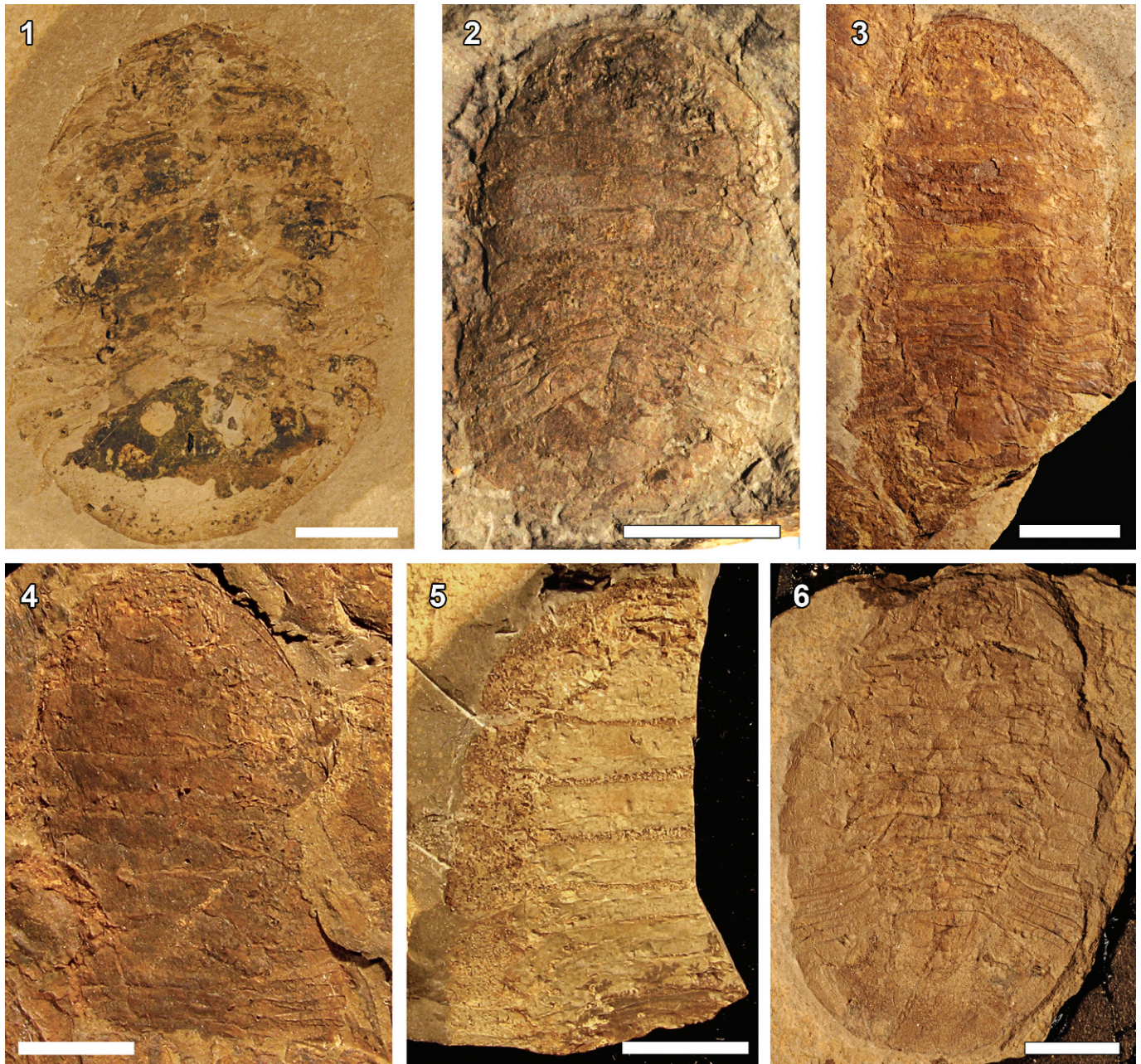


FIGURE 13—*Archaeoniscus coreaensis* n. sp. 1, paratype, AM F.110430; 2, paratype, AM F.110495; 3, paratype, AM F.110503; 4, paratype, AM F.110505; 5, paratype, AM F.110517; 6, paratype, AM F.110522. Scale bars are 5 mm.

Archaeoniscus occurring in an exclusively freshwater environment, indicating that *Archaeoniscus* also adapted to a freshwater ecosystem.

Brood pouch of Feldmann et al. (1998).—Some but not all specimens of *Archaeoniscus* display an axial structure in the posterior part of the body. Some specimens of *A. brodiei* have paired ridges (see Haack, 1918, pl. 4, fig. 7; Vega et al., 2005, pl. 1, fig. 4), while some others possess a raised, broad ridge (Ross and Vannier, 2002). The length of this structure is also variable; in a specimen illustrated by Haack (1918, pl. 4, fig. 7), the long paired ridges extend from the central part of the pleotelson up to the posterior margin of pereion, while the structure appears only in the posterior part of the pleon, reaching the anterior margin of the pleotelson in the one illustrated by Ross and Vannier (2002, pl. 1, fig. 1). This

structure may be an expression of a ventral structure that became pronounced during preservation process, although the pronounced paired ridges of some specimens could have accompanied a modification of the dorsal tergites. Feldmann et al. (1998) interpreted the ridge-like structure of *A. aranguthyrum* as a brood pouch, comparing it to the brooding structures of the Sphaeromatidae. They also noted that the presence of the brood pouch on the pleon could be an important character for the family Archaeoniscidae.

All isopods and most of the members of the superorder Peracarida are characterized by the thoracic ventral brood pouch in female, formed by the oostegites, which are modification of the thoracic coxal endites (Brusca and Brusca, 1990). Internal brood pouches occur in the Sphaeromatidae but no species has one posterior to pereionite 5 (Harrison,

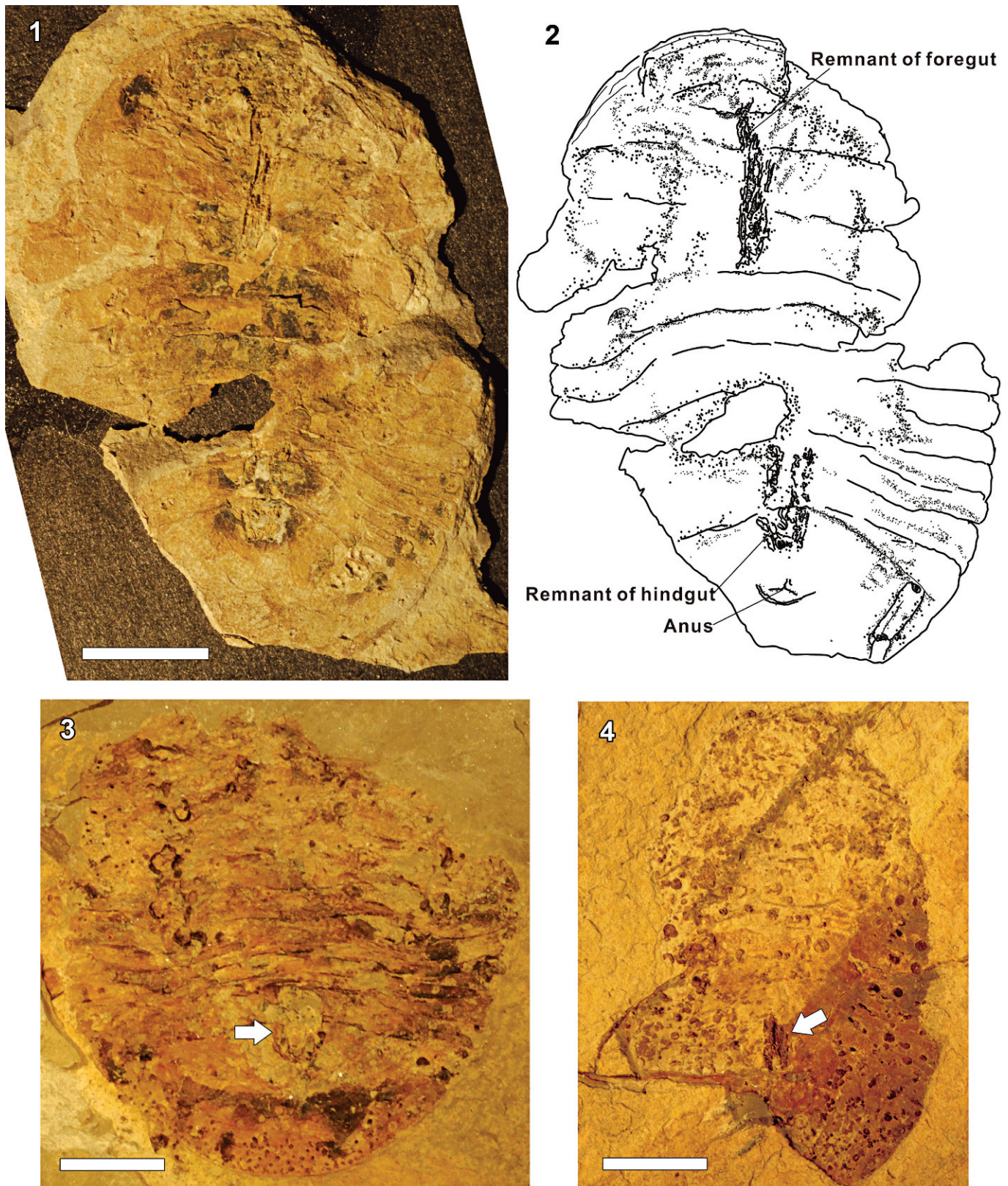


FIGURE 14—*Archaeoniscus coreaensis* n. sp. 1, 2, paratype, AM F.110523, photograph and drawing, respectively, showing remnants of foregut and hindgut; 3, paratype, AM F.110473; 4, paratype, AM F.110432. The white arrows indicate the remnant of hind gut. Scale bars are 5 mm.

1984). These pouches are also paired and not positioned axially (Harrison, 1984). The supposed position of the brood pouch in the pleon of *A. aranguthyrorum* would be too exceptional to be justified as a character grouping the family

Archaeoniscidae. Instead, the structure in *A. aranguthyrorum* is likely the remnant of the hindgut. Several specimens of *A. coreaensis* n. sp. preserve the gut-remnants of foregut and the hindgut (Fig. 14), and the position of the hindgut-remnant is

similar to that of the brood pouch in Feldmann et al. (1998). We interpret the brood pouch in *A. aranguthyrum* and the paired ridges in *A. brodiei* as impressions of the hindgut. Because this is a more mundane expression of internal anatomy, it cannot be regarded as a character for the family Archaeoniscidae.

Lifestyle of Archaeoniscus.—Feldmann et al. (1998) proposed that species of *Archaeoniscus* could have been ectoparasites on fishes, based on the occurrence of fish fossils in the same horizon with *A. aranguthyrum* and on the broad, cymothoid-like shape of this species. A clear association between fossil fish and isopods might allow one to make this claim (i.e., Wilson et al., 2011) but this association was not observed for *A. aranguthyrum*. We can now discount this possibility because our information on the anterior limbs clearly shows mostly unmodified ambulatory limbs rather than the hook-like limbs that characterize the Cymothoidae. Although the pattern of the lifestyle for *Archaeoniscus* remains unclear, the form of the limbs and the flattened body of *A. coreaensis* argues for a benthic existence, perhaps similar to extant Serolidae or other Sphaeromatidea. The broad, articulated coxae suggest a lifestyle similar to *Plakarthrium* Chilton, 1883, which lives epiphytically on marine algae (Wilson et al., 1976).

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad data package
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