

A NEW SPECIES OF *PROTAMPHISOPUS* NICHOLLS (CRUSTACEA, ISOPODA, PHREATOICIDEA) FROM MIDDLE TRIASSIC LUOPING FAUNA OF YUNNAN PROVINCE, CHINA

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ABSTRACT—Fossil isopod crustaceans in the suborder Phreatoicidea have a known stratigraphic range from the Carboniferous to the Jurassic. Until now, all Mesozoic records of this group were thought to occur in fresh water habitats. A new phreatoicidean isopod fossil of the Triassic Luoping marine fauna, Yunnan Province, China, is described. The new species, based on several exceptionally complete specimens, is assigned to the genus *Protamphisopus* Nicholls and the family Amphisopidae Nicholls. This Chinese record is the first report of a Mesozoic-age phreatoicidean isopod outside of Gondwanan terranes, requiring a revision of known biogeographic patterns of the Phreatoicidea. Whether this record is from a marine habitat or is the result of a secondary deposition is not certain. *Sottyella* Racheboef, Schram and Vidal from the Carboniferous (Stephanian) Lagerstätte of Montceau-les-Mines that was assigned to this suborder may be a decapod. Therefore, it has no relationship to this new species.

INTRODUCTION

THE PHREATOICIDEA is a critically important group for understanding the phylogeny of the isopod crustaceans because it is the first isopod group to appear in the fossil record (Wilson and Edgecombe, 2003). More records of this group have come to light recently with new specimens of *Protamphisopus wianamattensis* (Chilton, 1918) being found (Wilson, 2008) and previous records (Borns et al., 1972) being re-investigated (T. Hegna, personal commun., 2010). A recent report of another Paleozoic phreatoicidean (Racheboeuf et al., 2009), however, is not an isopod (discussed below). In this paper, we report a new Triassic fossil crustacean of the isopod suborder Phreatoicidea. The exceptionally well preserved material was recently collected from the Upper Member of the Guanling Formation at Dawazi Village, Luoping County, Yunnan Province, southwestern China. This site, which contains a Middle Triassic marine vertebrate fauna with abundant reptiles and fishes, was recently discovered and described as the Luoping Fauna (Zhang et al., 2008; Sun et al., 2009). Herein we provide a detailed description of the isopod fossils and name the species *Protamphisopus baii* Fu and Wilson n. sp. We assign it to the family Amphisopidae Nicholls, 1943 and discuss the implications of this first marine record of the crown group Phreatoicidea outside of Gondwana.

STRATIGRAPHIC OCCURRENCE

The phreatoicidean isopod fossils were excavated from the upper vertebrate horizon (UVH) in the Upper Member of the Guanling Formation at Dawazi of Luoping, Yunnan, with an age of Pelsonian, Anisian, Middle Triassic (Fig. 1, right) indicated by the index conodont *Nicoraella kockeli* Tatge, 1956 (Sun et al., 2009; Wu et al., 2009; Huang et al., 2009; Zhang et al., 2009).

The Guanling Formation exposed at Luoping can be divided into two members (Huang et al., 2009). Its lower member consists of up to 300 m of siltpelite and pelite intercalated with argillaceous dolostone suggesting a neritic clastic dominant facies. Its upper member consists of marly limestone, dolomitic limestone with chert and limy dolomite suggesting a carbonate platform facies. The upper vertebrate horizon in the Upper Member of the Guanling Formation

mainly consists of thin-bedded marly limestone. The lithology and associated other invertebrate fossils (including crustaceans, echinoderms, gastropods, etc.), as well as paleogeographic analysis, suggest a fossil site situated in a near-shore rather than pelagic sedimentary setting during the Anisian of the Middle Triassic (Fig. 1, left).

METHODS

Isopod fossils were collected during the excavation at Dawazi of Luoping in 2008 while searching for Triassic marine reptile and fish fossils. The overburden above the fossiliferous horizon was removed manually with the assistance of livestock. Fuel-driven jackhammers and rock saws were used in conjunction with man-powered pry bars to disintegrate the rock layers. Layers of the fossiliferous zone were carefully removed; for every layer, fossils were numbered, recorded, photographed, and collected.

The specimens are deposited in the collection of Geological Museum, Peking University, Beijing, China (GMPKU) where they were prepared by mechanical methods under a microscope. Fossils were photographed either as single digital images, or were composited to merge different focal levels. Illustrations were prepared in a vector graphic drawing program (<http://Inkscape.org>) using digital images as templates. In scoring fossil morphology for sex-specific characters, such as the first or fourth pereopod in males, we assumed that specimens of both sexes were represented in the sample; no differences among the specimens were observed that could be attributed to sexual dimorphism. Morphological data were scored using the taxonomic database system DELTA (Dallwitz, 1980; Dallwitz et al., 2000a, 2000b); more detailed information on the database and form of the taxonomic descriptions can be found in Wilson and Keable (2002a, 2002b). Where more than one specimen was used for a measurement, the number was indicated parenthetically. A natural language description was generated using the DELTA tool CONFOR and edited for clarity, such as merging repetitive text. The diagnoses were created from lists of similarities and differences between the two species of *Protamphisopus* using the interactive tool INTKEY, which is part of the DELTA system. The reconstruction (Fig. 8) was

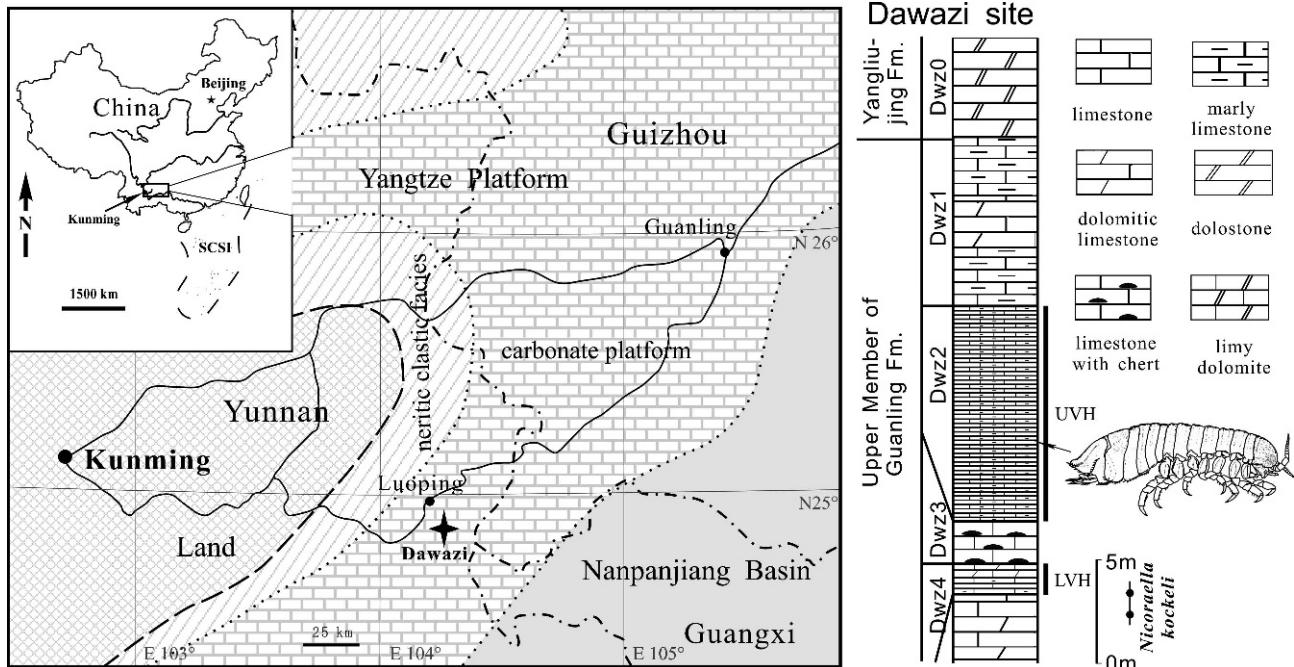


FIGURE 1—(left) Middle Triassic paleogeographic map of eastern Yunnan and western Guizhou, South China, modified from Wang and Zhong (1994) and Feng et al. (1997); (right) The stratigraphic column showing position of the layers bearing *Protamphisisopus* at Dawazi site, Modified from Sun et al. (2009). Abbreviated characters: UVH, upper vertebrate horizons; LVH, lower vertebrate horizons.

created by copying digital images of well preserved parts from all available specimens, and rearranging and resizing them. A drawing was made from the rearranged composite image using a vector graphics editor. The resulting vector graphic was adjusted to account for compression of and lengthening of the specimen (some somites were partially disarticulated). Details were added, based on knowledge of modern phreatoicideans such as *Eophreatoicus* Nicholls, 1926 (see images in Wilson et al., 2009). Explicit authorities, Fu and Wilson, are given for the taxonomic name of the new species. The relationships of *Protamphisisopus* with modern taxa were evaluated using data files generated by the DELTA system and methods described in Wilson (2008).

Anatomical abbreviations used in the figures.—*AI*, antennula; *AII*, antenna; *ap*, articular plate; *ba*, basis; *ca*, carpus; *cg*, cervical groove; *co*, coxa; *da*, dactylus; *enp*, endopod; *exp*, exopod; *is*, ischium; *me*, merus; *mnd*, mandible; *mp*, mandibular palp; *mxp*, maxilliped; *pr*, propodus; *pltn*, pleotelson; *pdlr*, pleotelson dorsolateral ridge; *umr*, uropodal median ridge; *ump*, uropodal median plate; *ur*, uropodal ridge; *vmr*, ventral median ridge.

SYSTEMATIC PALAEONTOLOGY

Order ISOPDA Latreille, 1802

Suborder PHREATOICIDEA Stebbing, 1893

Family AMPHISOPIDAE Nicholls, 1943

Genus *PROTAMPHISISOPUS* Nicholls, 1943

Type species.—*Phreatoicus wianamattensis* Chilton, 1918, from Rouse Hill Siltstone Member, Ashfield Shale (Middle Triassic, Anisian) at former brick clay pits, St. Peters, New South Wales, Australia; by monotypy.

Other species.—*Protamphisisopus baii* Fu and Wilson n. sp.

Generic Description (revised from Wilson and Edgecombe, 2003).—Head dorsal surface lateral profile smoothly curved; tubercles absent. Eyes present, projecting anteriorly, approx-

imately round. Mouth field adjacent to posterior margin of head and anterior margin of pereonite 1. Pereon with transverse rounded ridges, occurring toward center of segment, more than one per segment on least some segments. Pereonite 1 dorsal margin in lateral view shorter than on pereonite 2. Pereonites 2–7 coxal articulation free. Pereonites 2–4 without lateral tergal plates. Pleon in lateral view much deeper than pereonites, with large pleurae, basal region of pleopods not visible, pleonite 1 pleura distinctly shallower than pleurae of pleonites 2–5. Pleonite 5 dorsal median ridge absent. Pleotelson vaulted with vertical postero-lateral fields, dorsal surface in lateral view evenly curving, smooth; lateral length less than depth, ventromedial surface anterior to uropods strongly concave; ventral margin length anterior to uropods greater than width of uropodal insertion; postanal ventral surface present; posterolateral margin uninterrupted (without major inflection in margin differentiating apex), margin entire; posterior apex visible in lateral view, posterior apex free (not strongly reflexed and flattened against dorsal surface). Antennula with more than 6 articles (as in most Phreatoicidea), article 4 shorter than article 3, terminal article tubular, shorter than penultimate article, width approximately subequal to ante-penultimate article width, distal articles circular in cross-section. Antenna article 1 not expressed, article 5 longer than article 4, article 6 shorter than articles 4 and 5 combined in length. Mandible palp article 1 present and easily visible, third article relatively linear. Pereopodal coxae not laterally projecting. Pereopod I not sexually dimorphic, male and female pereopods similar (assumed, enlarged propodus of male not observed). Pereopodal basis dorsal ridge produced in cross-section and forming distinct plate, with ridge on lateral face; ischia especially short, less than one third length of bases, but still freely articulated. Pereopod IV similar to anterior pereopods, not prehensile (assumed, prehensile condition of males not observed). Pereopods V–VII basis dorsal ridge distinctly separated from basis shaft, distal margin indented; ischium dorsal ridge without flange.

Uropod protopod not reaching pleotelson apex, dorsomedial ridge produced, plate-like, margin smooth, approximately straight in lateral view; rami flattened on dorsal surface; endopod subequal or longer than exopod, straight-curving dorsally, ventral margin convex-straight proximally.

Discussion.—*Protamphisopus baii* Fu and Wilson n. sp. and new specimens of *P. wianamattensis* (Chilton, 1918) (Australian Museum fossil collection registration number F129871, from Maldon Quarry, near Camden, New South Wales, Australia; figured in Wilson, 2008) add new information that allows a better description for this genus. Perhaps the most surprising aspect of *Protamphisopus* Nicholls, 1943 is its relatively small number of differences from extant phreatoicideans, despite being separated in time by more than 200 my. The description above is relatively detailed because many characters that were marked as “implicit” in the DELTA database (Wilson and Keable, 2002a, 2002b) were scored explicitly where present in the fossils so that the characters that are common in phreatoicideans would be included in the description.

Protamphisopus Nicholls, 1943 is recognizably distinct from extant phreatoicideans and other fossil taxa based on the following characters. The eyes are large, round and protrude anteriorly, a feature that is seen in a few unrelated Phreatoicidae and even in that family not to this degree. Large protruding eyes are also seen in *Palaeophreatoicus* Birstein, 1962, so the Permo-Triassic phreatoicidean clades appear to have had well developed eyes. The pereopods I and IV appear to lack sexual dimorphism (not observed in any specimens of either species to date), which is unlike most living Phreatoicidea. In males of extant species, the propodus of first pereopod is especially enlarged, and the fourth pereopod is shortened and modified to grasp females during precopula. The robust, enlarged first pereopod of males should have fossilised well, but no such limb has been seen in any specimen of either species. Therefore assuming a nearly equal sexual ratio, we infer that males are present in *Protamphisopus* collections but are indistinguishable from females as fossils. The possibility that these specimens could be all one sex is unlikely because none of the extant members phreatoicidean crown group, to which *Protamphisopus* belongs (Wilson and Edgecombe, 2003; see below), are known to have highly distorted sex ratios. This inferred lack of sexual dimorphism suggests that the reproductive strategy in *Protamphisopus* species was different from modern taxa. The bases of all pereopods have dorsal ridges and lateral face ridges. This appears to be a special apomorphy of this genus, because a broad basis with several ridges can be seen distinctly in most specimens where the pereopodal bases are preserved. The ischia of all pereopods appear to be especially short, although not of the same form as seen in the Tanaidacea, one of the potential outgroups to the Isopoda. The pereopodal ischium in this latter group has a largely inflexible articulation with the basis, whereas all Isopoda and Spelaeogryphacea have a more elongate ischium with a fully functional basis-ischium articulation (Wilson, 2009). The pleotelson distal tip is not elaborated or substantially modified in *Protamphisopus*. Several living taxa, such as *Crenisopus* Wilson and Keable, 1999 and *Mesamphisopus* Nicholls, 1943, however, have relatively unmodified pleotelsons, as well.

**PROTAMPHISOPUS BAI FU AND WILSON, NEW SPECIES
(Figs. 2–8)**

Diagnosis.—Head surface pitted; cervical groove straight, extending over dorsal margin of head and connecting medially; antennal notch deep, with posterior extension.

Pleotelson ventral margin anterior to uropods 1.7–1.8 width of uropodal insertion; dorsal surface median ridge present; dorsal surface lateral ridges present, continuous with posterior apex; lateral uropodal ridge curving strongly and extending posteriorly from uropods on pleotelson margin. Posterior apex with one pair of robust setae (assumed on presence of setal sockets). Maxilliped epipod distal tip broadly pointed. Pereopod I subchelate; propodal palm convex. Uropod endopod subequal to protopod length.

Description.—Head lateral profile of dorsal surface smoothly curved; surface pitted; tubercles absent; setae unknown. Eyes projecting anteriorly; maximum diameter 0.38 head depth ($N = 2$); approximately round; ocelli distinguishable as individual units. Mandibular (genal or cheek) groove smoothly indented. Mandibular notch present. Clypeal notch present.

Pereon.—Pereonite 1 dorsal margin in lateral view shorter than on pereonite 2; shorter than on pereonite 2.

Pleonites.—Pleonites 2–4 respective lengths (observed in lateral view) more than half the length of pleonite 5, 1–4 relative lengths unequal, increasing in length from anterior to posterior. Pleonites 1–5 depth ratio with pereonite 7 depth, respectively: 1.2; 1.5; 2; 1.9; 1.9. Pleonite 5 dorsal median ridge absent (dorsal margin not strongly distinct in lateral view).

Pleotelson.—Dorsal surface setae present but shape unknown, smooth, median ridge present (based on strong margin in specimens GMPKU-P-1972 and GMPKU-P-1971; see Figs. 2–5), lateral ridges continuous with posterior apex. Lateral length 0.42–0.44 body length ($N = 2$), lateral length less than depth, 0.76 depth; depth 1.73 pereonite 7 depth. Ventral surface anterior to uropods strongly concave, ventral margin anterior to uropods 1.7–1.8 width of uropodal insertion ($N = 2$), with single row of simple robust setae (setal sockets present, but setal form unknown), including 4 robust setae altogether (at least), unknown; postanal ventral surface present (partially visible in GMPKU-P-1975; Fig. 7); lateral uropodal ridge curving strongly and extending posteriorly from uropods on pleotelson margin, with 5 robust setae (approximately; setal sockets present, but form unknown). Posterior apex projecting in dorsal view, with one pair of robust setae (setal socket present; seta unknown).

Antennula.—Length 0.09 body length, with 9–10 articles. No articles divisible into one large or two small articles. Article 4 shorter than article 3. Terminal article tubular, shorter than penultimate article. Penultimate article length not distinctly longer than other articles; width approximately subequal to antepenultimate article width. Distal articles in cross-section circular.

Antenna.—Length 0.24 body length. Article 1 not expressed, scale on article 3 not observed. Article 5 longer than article 4, 6 shorter than articles 4 and 5 combined. Flagellum length 0.57 total antenna length, with 11–13 articles.

Mandible.—Palp length 1.8 mandible length (approximately); article 1 easily visible; third article relatively linear, medial surface setae unknown.

Pereopod I.—Length 0.29 body length, subchelate, not sexually dimorphic, male and female pereopods similar (assumed - no enlarged pereopod I observed on any specimen). Dactylus shorter than palm (males and females assumed to be similar), length 0.75 propodal palm length; ventrodistal margin unknown. Propodus length 0.32 pereopod length, 1.6 width; dorsal margin proximal region not protruding (males assumed to be similar to females); propodal palm convex (weakly). Basis length 2.1 width.

Pereopods II–III.—Dactylar claws unknown; propodus articular plate present; basis dorsal ridge in cross-section produced and forming distinct plate; lateral face ridge present.

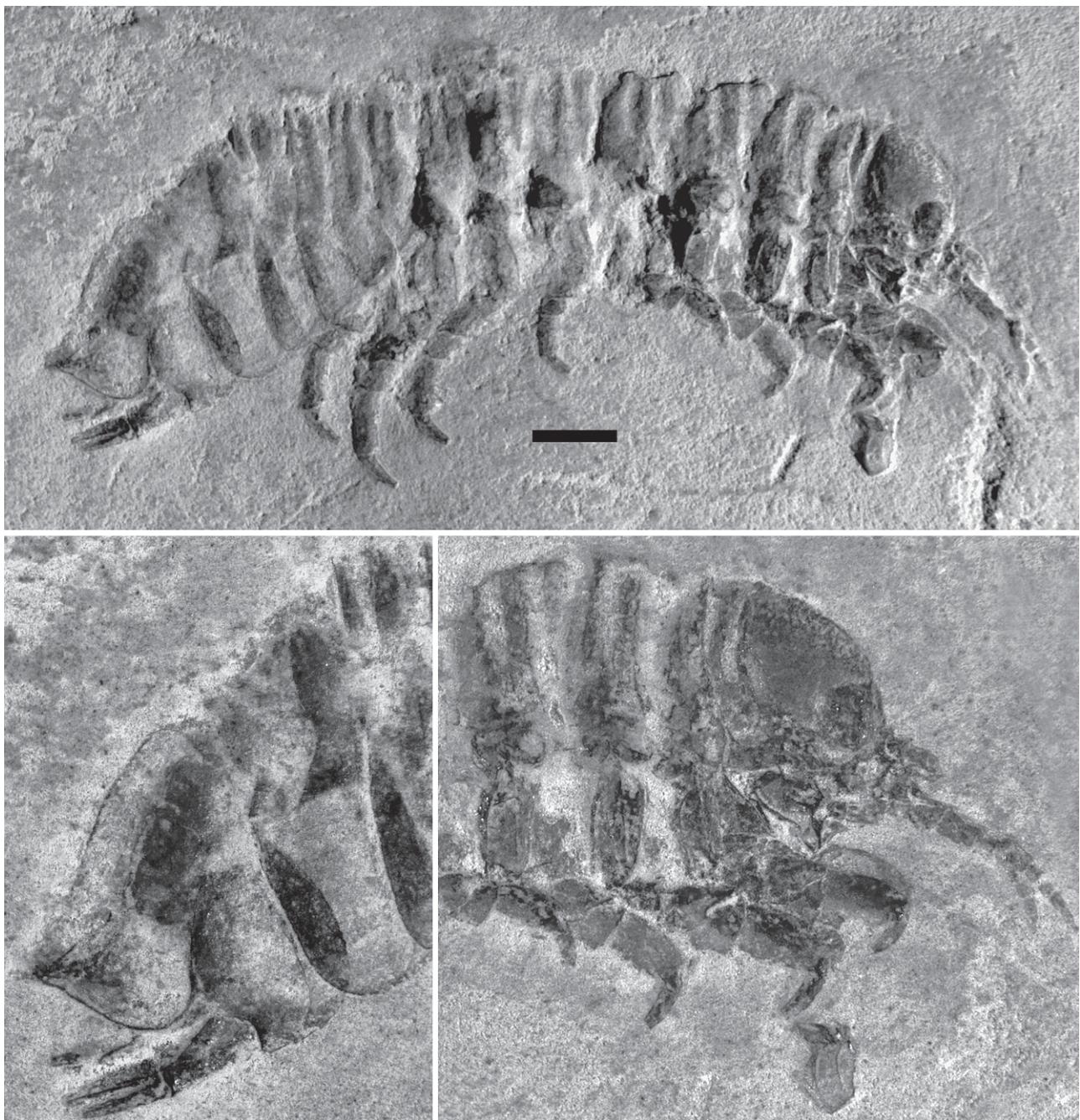


FIGURE 2—*Protamphisopus baai* Fu and Wilson n. sp., in lateral view, photographs of holotype, GMPKU-P-1972 (see Figure 3 for drawings). The whole body (top); the enlargement of pleotelson region (bottom left); the enlargement of head region (bottom right). Scale bar 1 mm.

Pereopod II length 0.3 body length; dactylus length 0.69 propodus length; propodus length 0.2 pereopod length, 1.2 width; carpus length 0.14 pereopod length, 0.65 width; basis length 0.28 pereopod length, 2.1 width. Pereopod III length 2.3 body length; dactylus length 1.0 propodus length; propodus length 0.17 pereopod length; propodus length 1.8 width; carpus length 0.14 pereopod length, 1.0 width; basis length 0.28 pereopod length, length 2.3 width.

Pereopod IV of male.—Simple (not prehensile; assumed); length 0.25 body length; dactylus distal accessory claw unknown; propodus length 0.19 pereopod length, length 1.7 width ($N = 2$); propodus articular plate on posterior side of limb present; basis length 2.4 width; dorsal ridge in cross-section produced and forming distinct plate.

Pereopods V–VII.—Basis dorsal ridge in cross-section, forming distinct plate, lateral face central ridge present; lateral face ventral ridge present; propodus articular plate on posterior side of limb present. Pereopod V length 0.23 body length; propodus length 0.15 pereopod length; carpus length 0.11 pereopod length; basis length 1.4 width. Pereopod VI length 0.31 body length; propodus length 0.18 pereopod length; carpus length 0.11 pereopod length; basis length 1.6 width; Pereopod VII length 0.34 body length; basis length 1.9 width; dorsal ridge distal margin indented (weakly); ischium dorsal ridge flange absent; carpus length 0.11 pereopod length; propodus length 0.19 pereopod length.

Uropod.—Total length 0.28–0.29 pleotelson length ($N = 2$). Protopod length 1.5 width; length 0.51 uropod total length;

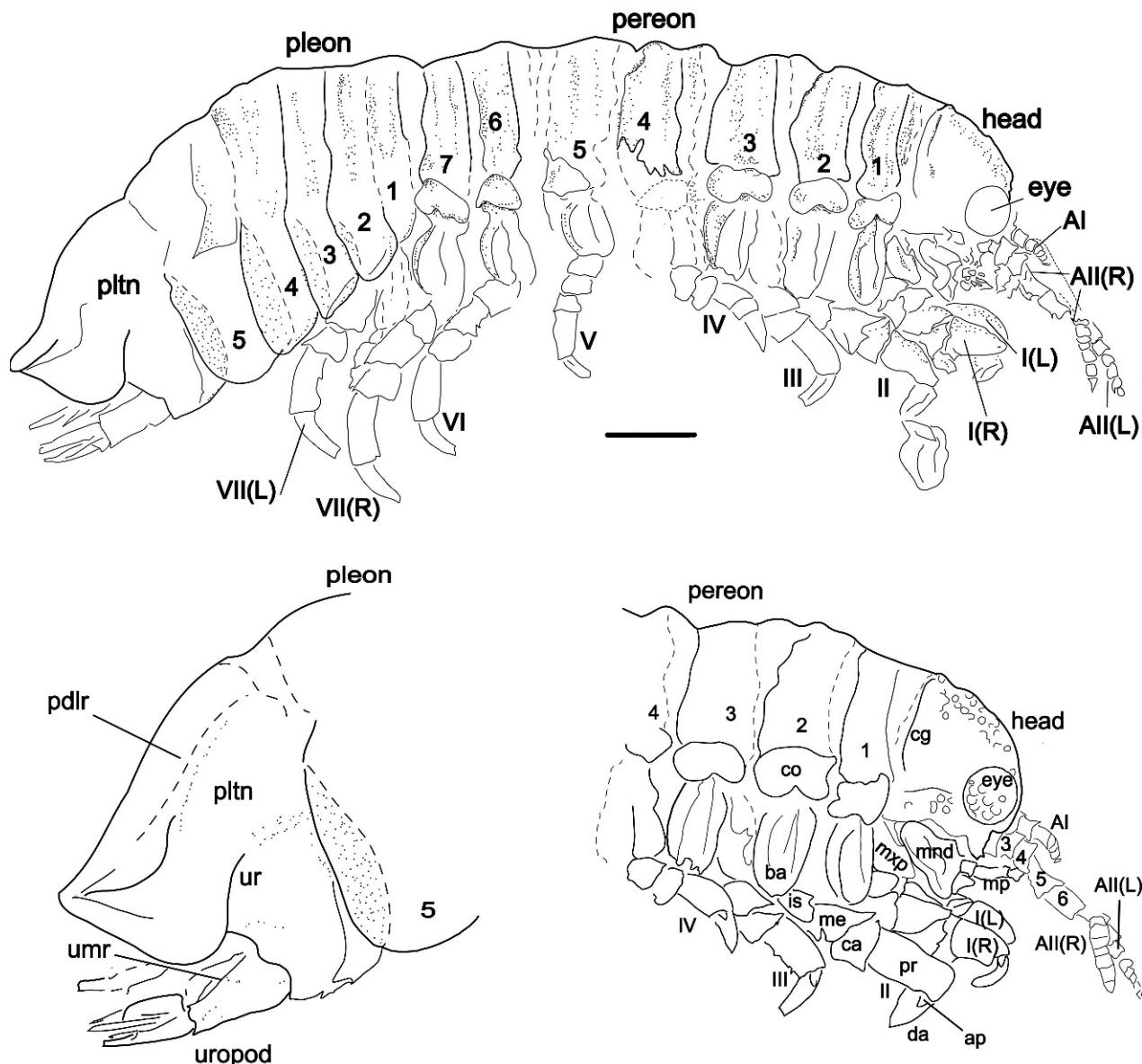


FIGURE 3—*Protamphisopus baii* Fu and Wilson n. sp., in lateral view, drawings of holotype, GMPKU-P-1972 (see Figure 2 for photographs). The whole body (top); the enlargement of pleotelson region (bottom left); the enlargement of head region (bottom right). Scale bar 1 mm. (See anatomical abbreviations in text).

dorsomedial ridge length 0.9 endopod length. Rami cross-sectional shape flattened on dorsal surface only. Endopod subequal to protopod length, longer than exopod, dorsal margin straight; ventral margin convex.

Etymology.—We are pleased to name this species in honor of Prof. Shun-liang Bai of PKU, who has done important paleontological and stratigraphic research in China, and who has brought the pleasure of paleontological studies to many generations of students.

Types.—Holotype, here designated, GMPKU-P-1972 (Figs. 2–3), length 11.4 mm, right lateral presentation, all body somites and right legs present, antenna and antennula incomplete. PARATYPES, 4 specimens designated: GMPKU-P-1971 (Figs. 4–5), length 14.6 mm, similar preservation to GMPKU-P-1972, but left lateral presentation, antenna and antennula more complete, but sections of pereon and pleon missing; GMPKU-P-1973 (Fig. 6), length 15.3 mm, left lateral presentation, good preservation of the antenna and antennula, but pleotelson not complete, and sections of pereon and pleon

missing; GMPKU-P-1975 (Fig. 7), length 14.7 mm, ventral presentation, ventral structure of pleotelson visible but sections of mouthparts, legs and antennula missing.

Preservation.—The types, 5 total, are all in a single block consisting of fine sandy marlstone, embedded on the same discrete horizon. No counterparts are known. The fossils are compressed into the bedding plane, but project above the block surface, and so have some three dimensional features. The holotype (GMPKU-P-1972) and primary paratype (GMPKU-P-1971) are preserved with both external (head and pleotelson) and internal (some pereonites) cuticular surfaces. These specimens show some spreading and disarticulation of the body somites, suggesting some decomposition prior to burial. These complete specimens are not moult casings because isopods have biphasic moulting (Wilson, 2009), which would separate each cuticle into two parts.

Occurrence.—Luoping Fauna (in Yunan Province, China), the Upper Member of the Guanling Formation, Pelsonian of the Anisian, Middle Triassic.

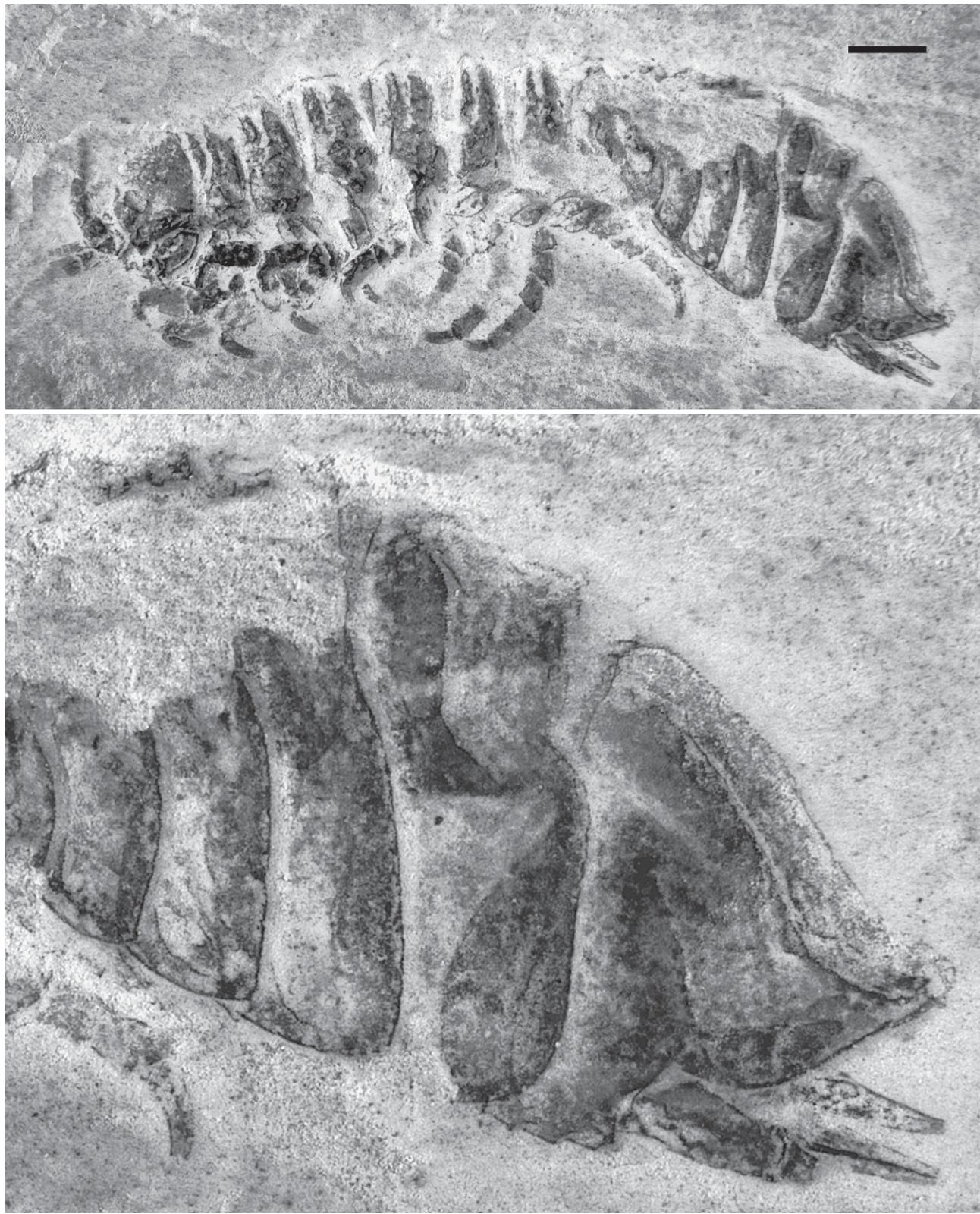


FIGURE 4—*Protamphisopus baii* Fu and Wilson n. sp., in lateral view, photographs of paratype, GMPKU-P-1971 (see Figure 5 for drawings). The whole body (top); the enlargement of pleotelson region (bottom). Scale bar 1 mm.

Species comparison.—The exceptional preservation of these fossils provided detailed data on the morphology, which allowed the creation of a detailed reconstruction of the species (Fig. 8). *Protamphisopus baii* Fu and Wilson n. sp. and *P.*

wianamattensis (Chilton, 1918) differ in several distinctive characters, as follows (*P. wianamattensis* character states indicated parenthetically). The head surface is pitted (granular). The cervical groove on the head is more or less linear

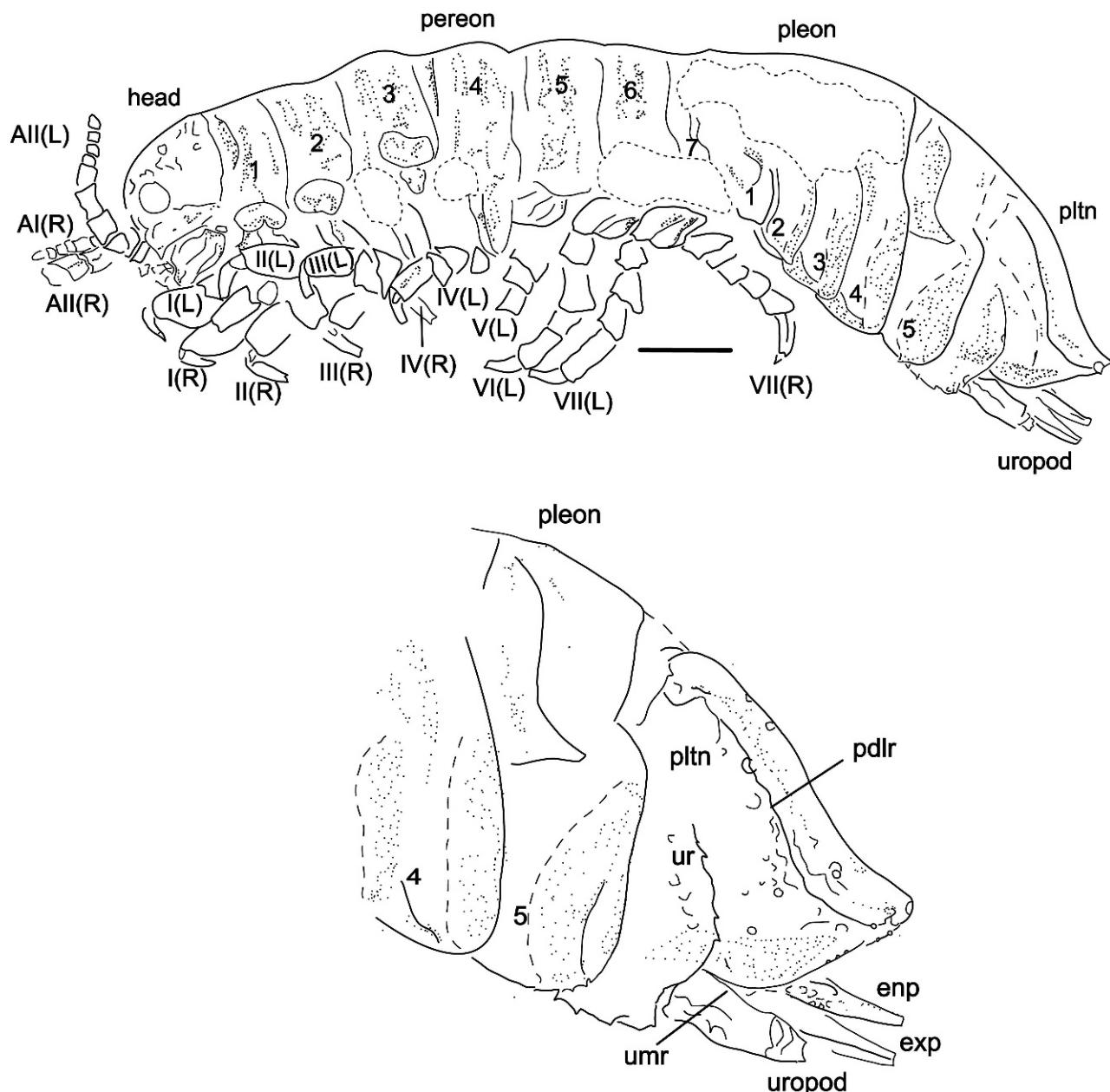


FIGURE 5—*Protamphisopus baii* Fu and Wilson n. sp., in lateral view, drawings of paratype, GMPKU-P-1971 (see Figure 4 for photographs). The whole body (top); the enlargement of pleotelson region (bottom). Scale bar 1 mm.

(smoothly curved) and extends over dorsal margin of head and connects medially (extending just above antero-lateral margin of pereonite 1). The pleotelson dorsal surface median ridge is present (absent), the lateral ridges are continuous with posterior apex (absent). The lateral uropodal ridge curves strongly and extending posteriorly on pleotelson margin from uropods (appears to terminate at pleotelson margin near uropods). The uropodal endopod is subequal to protopod length (endopod appears to be longer than protopod).

DISCUSSION

Relationships of Protamphisopus to other phreatoideans.—A preliminary phylogenetic analysis, similar to that done by Wilson and Edgecombe (2003) and Wilson (2008), was conducted on data generated by the DELTA system. We can confirm that *Protamphisopus baii* Fu and Wilson n. sp. (Fig. 8) and *P. wianamattensis* (Chilton, 1918) have a sister

group relationship, supporting our generic classification of this new species. Unlike earlier analyses that had fewer data, this analysis did not find a close relationship between *Phreatoicopsis* and *Synamphisopus*, but instead located *Protamphisopus* among the genera of the Amphisopidae *sensu stricto*. The new data also changed relationships of the extant taxa. The detailed results are not reported here because ongoing studies by one of us (GDFW) will add to the database additional species (e.g., *Eophreatoicus* spp.), as well as Jurassic fossil phreatoicids from Carapace Nunatak in Antarctica (Borns et al., 1972; T. Hegna, pers. comm.). If these latter fossils can be assigned to *Protamphisopus*, as suggested in the original publication, this genus will have a stratigraphic range of more than 80 my, from Anisian in the Triassic (238 my) to the base of the Upper Jurassic (156 my). Members of the Palaeophreatoicidae (e.g., *Hesslerella* and *Palaeophreatoicus*) appear to be more divergent from modern forms compared to

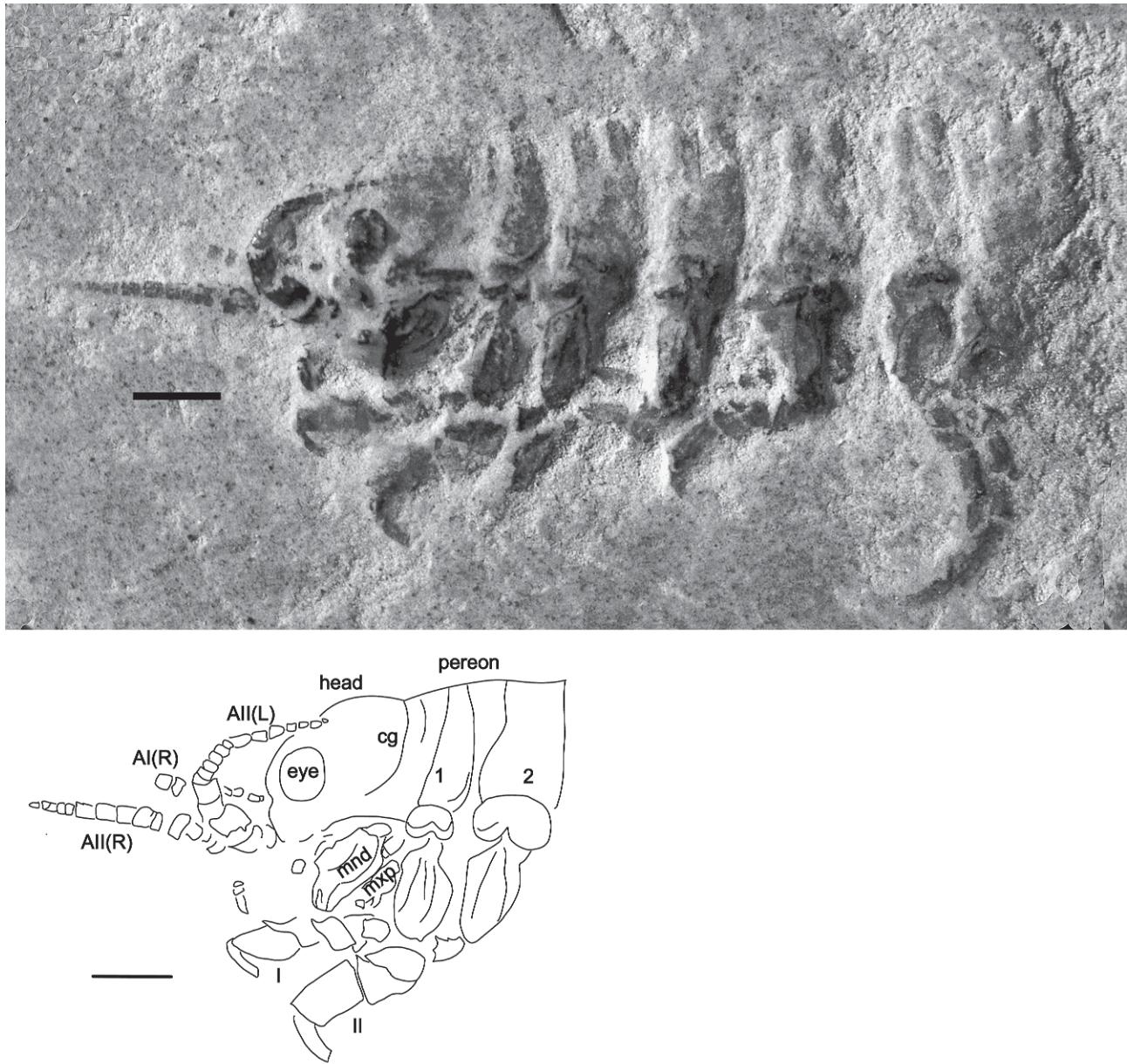


FIGURE 6—*Protamphisopus baii* Fu and Wilson n. sp., in lateral view, paratype, GMPKU-P-1974. Photograph of the anterior region (top); line drawing of the head region (bottom). Scale bar 1 mm.

Protamphisopus, which is a member of the crown group of the Phreatoicidea (Wilson and Edgecombe, 2003). Despite this growing diversity of ancient phreatoicideans, the suborder as a whole is substantially modified from what might be considered a basally-derived isopod and is not likely to represent the ancestral isopod (Wilson, 2009).

Racheboeuf et al. (2009) recently described *Sottyella montcellensis*, a supposed phreatoicidean from the Carboniferous (Stephanian) Lagerstätte of Montceau-Les-Mines. Their discussion did not indicate why they considered this fossil to be a phreatoicidean and described features that were not present in the fossil (i.e., the head was missing). The fossil's classification as a member of the Phreatoicidea, or even as an isopod, is not well supported owing to poor preservation and overall lack of features (no head and no pleotelson). The illustrations of this fossil (Racheboeuf et al., 2009: their fig. 2(1–3) and fig. 3(5–7)) show that legs, which were preserved,

do not have an isopod character: the ischium appears to be short relative to the basis with an inflexible articulation, a pattern that is found in other peracarids or in other malacostracans, but not in the Isopoda (Wilson, 2009). The configuration of the leg segments suggest that *S. montcellensis* might be a decapod crustacean, such as *Palaeocaris secretanae* Schram, 1984 that was illustrated in the same publication. We conclude that this fossil is not an isopod, and bears no relationship to *Protamphisopus* or the Paleozoic phreatoideans, *Palaeophreatoicus* or *Hesslerella*.

Habitat classification and biogeography.—*Protamphisopus wianamattensis*, as well as the undescribed Jurassic phreatoidean from Antarctica are well established as occurring in fresh-water facies (Wilson and Edgecombe, 2003; Borns et al., 1972). The finding of *P. baii* Fu and Wilson n. sp. in marine facies raises the possibility that this genus retained the shallow marine habit of the Paleozoic phreatoideans (Schram, 1974,

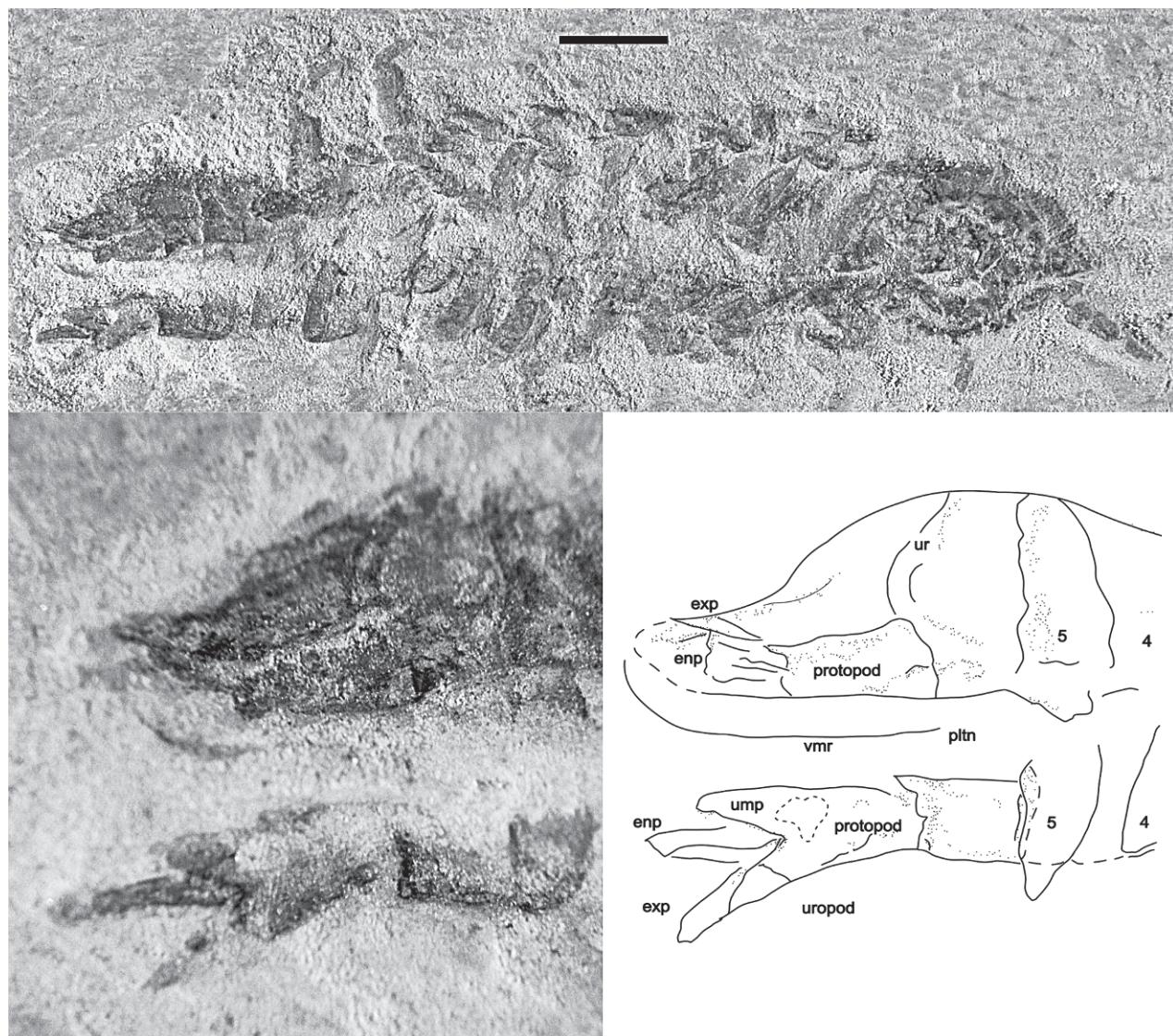


FIGURE 7—*Protamphisopus baiei* Fu and Wilson n. sp., in ventral view, paratype, GMPKU-P-1975. Photograph of the whole body (top); an enlargement of pleotelson region (bottom left); line drawing of pleotelson region (bottom right). Scale bar 1 mm.

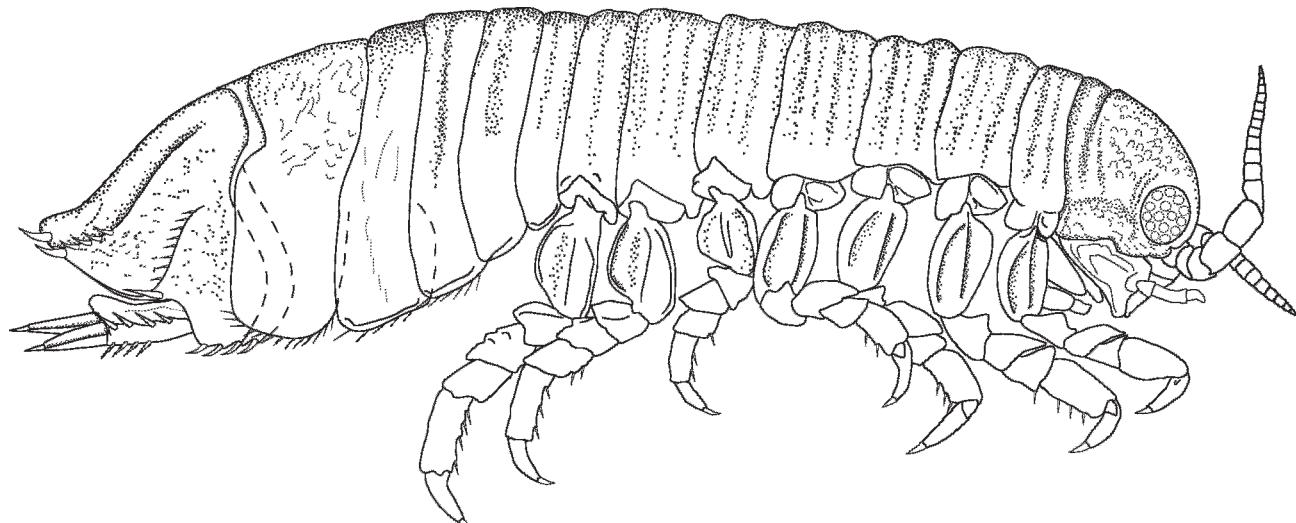


FIGURE 8—Reconstruction of *Protamphisopus baiei* Fu and Wilson n. sp., based primarily on the holotype GMPKU-P-1972 but with details from the paratypes.

1977). Because *Protamphisopus* is a member of the phreatoicidean crown group (Wilson and Edgecombe, 2003), all of which live in fresh water (Wilson, 2008), assigning *P. baii* to a marine habitat might suggest a secondary introduction into marine waters, rather than being marine as in the Paleozoic isopod species. Considering the near-shore sedimentary setting of the fossil site, however, the possibility that the specimens were washed into a marine setting from nearby fresh-water habitats cannot be fully excluded. Although the excellent preservation of the fossils might argue against transport, phreatoicideans have robust bodies and might survive displacement into a marine lagoon. Several extant species live within a few metres of the ocean (Nicholls, 1942; Wilson and Keable, 2002a) so these fossils coming from an exogenous source is not as unlikely as it seems. This possibility needs a detailed taphonomic and sedimentary investigation for corroboration.

The new phreatoicidean isopod species described herein is an important member of the Middle Triassic Panxian-Luoping *Mixosaurus panxianensis* Fauna, one of the best preserved Triassic marine vertebrate faunas in the world (older than those known in Europe and North America). It is a representative of the rapid evolutionary radiation in the Middle Triassic that occurred during the biotic recovery after the end-Permian Mass Extinction, along with the global sea level maximum on both stage and period scale (Jiang et al., 2009). The isopod fossils appear relatively abundant on the fossiliferous layer at Luoping (5 specimens on a single large block) compared to the marine reptiles and fishes, although rare compared to *P. wianamattensis* in Australia, which occurs at much higher densities. The marine reptile and fish composition of the Panxian-Luoping fauna shows a strong western Tethyan paleobiogeographic affinity, indicated by cognates (e.g., *Mixosaurus*, *Placodus*, *Nothosaurus* and *Lariosaurus*) of southwestern China to Europe (Jiang et al., 2006a, 2006b, 2006c, 2007, 2008). These finds suggest a Middle Triassic fauna distributed along the northern coastline of the Paleotethys. But the new phreatoicidean isopod taxon reported here reveals a potential Australian paleogeographic affinity. This raises the question of the paleogeographic position and history of South China Terrane, which needs further detailed study and fossil evidence.

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REFERENCES

- BIRSTEIN, Y. A. 1962. *Palaeophreatoicus sojanensis* gen. et sp.nov. and some problems of phylogeny and distribution of Isopoda. *Paleontologicheskii Zhurnal*, 3:65–80.
- BORNS, H. W. J., B. A. HALL, H. W. BALL, AND H. K. BROOKS. 1972. Mawson Tillite, Victoria Land, East Antarctica: Reinvestigation continued. *Antarctic Journal of the United States*, 7:106–107.
- CHILTON, C. 1918. A fossil isopod belonging to the fresh-water genus *Phreatoicus*. *Journal of Proceedings of the Royal Society of New South Wales*, 51:365–388.
- DALLWITZ, M. J. 1980. A general system for coding taxonomic descriptions. *Taxon*, 29: 41–46.
- DALLWITZ, M. J., T. A. PAYNE, AND E. J. ZURCHER. 2000a. User's guide to the DELTA editor. <http://delta-intkey.com/>, accessed March 2010.
- DALLWITZ, M. J., T. A. PAYNE, AND E. J. ZURCHER. 2000b. User's guide to the DELTA system: a general system for processing taxonomic descriptions. Edition 4.12, December 2000. CSIRO, Canberra, 158 p.
- FENG, Z.-Z., Z.-D. BAO, AND S.-W. LI. 1997. Lithofacies paleogeography of Early and Middle Triassic of South China. Petroleum Industry Press, Beijing, 222p.
- HUANG, J.-Y., K.-X. ZHANG, Q.-Y. ZHANG, T. LU, C.-Y. ZHOU, AND J.-K. BAI. 2009. Conodont stratigraphy and sedimentary environment of the Middle Triassic at Daaozi Section of Luoping County, Yunnan Province, South China. *Acta Micropalaeontologica Sinica*, 26(3):211–224.
- JIANG, D.-Y., L. SCHMITZ, R. MOTANI, W.-C. HAO, AND Y.-L. SUN. 2007. The mixosaurid ichthyosaur *Phalarodon* cf. *P. fraasi* from the Middle Triassic of Guizhou Province, China. *Journal of Paleontology*, 81(3): 602–605.
- JIANG, D.-Y., L. SCHMITZ, W.-C. HAO, AND Y.-L. SUN. 2006c. A new mixosaurid ichthyosaur from the Middle Triassic of China. *Journal of Vertebrate Paleontology*, 26(1):60–69.
- JIANG, D.-Y., M. W. MAISCH, W. C. HAO, Y.-L. SUN, AND Z.-Y. SUN. 2006a. *Nothosaurus yangtuanensis* n. sp. (Reptilia, Sauropterygia, Nothosauridae) from the middle Anisian (Middle Triassic) of Guizhou, southwestern China. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2006:257–276.
- JIANG, D.-Y., M. W. MAISCH, Z.-Y. SUN, Y.-L. SUN, AND W.-C. HAO. 2006b. A new species of *Lariosaurus* (Reptilia, Sauropterygia) from the middle Anisian (Middle Triassic) of Guizhou, southwestern China. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 242:19–42.
- JIANG, D.-Y., R. MOTANI, W.-C. HAO, O. RIEPPEL, Y.-L. SUN, A. TINTORI, Z.-Y. SUN, AND L. SCHMITZ. 2009. Biodiversity and sequence of the Middle Triassic Panxian Marine Reptile Fauna, Guizhou Province, China. *Acta Geologica Sinica*, 83(3):451–459.
- JIANG, D.-Y., R. MOTANI, W.-C. HAO, O. RIEPPEL, Y.-L. SUN, L. SCHMITZ, AND Z.-Y. SUN. 2008. First record of Placodontoidea (Reptilia, Sauropterygia, Placodontia) from the eastern Tethys. *Journal of Vertebrate Paleontology*, 28(3):904–908.
- LATREILLE, P. A. 1802. *Histoire Naturelle Générale et Particulière des Crustacés et Insectes*. F. Dufart, Paris, 3, 467 p.
- NICHOLLS, G. E. 1926. A description of two genera and species of Phreatoicidea, with a discussion of the affinities of the members of this family. *Journal of the Royal Society of Western Australia*, 12(19):179–210, pls.125–128.
- NICHOLLS, G. E. 1943. The Phreatoicoidea. Part I. The Amphisopidae. *Papers and Proceedings of the Royal Society of Tasmania*, 1942:1–145.
- RACHEBOEUF, P. R., F. R. SCHRAM, AND M. VIDAL. 2009. New malacostracean Crustacea from the Carboniferous (Stephanian) Lagerstätte of Montceau-Les-Mines, France. *Journal of Paleontology*, 83(4):624–629.
- SCHRAM, F. R. 1974. Paleozoic Peracarida of North America. *Fieldiana Geology*, 33(6):95–124.
- SCHRAM, F. R. 1977. Paleozoogeography of late Paleozoic and Triassic Malacostraca. *Systematic Zoology*, 26(4):367–379.
- STEBBING, T. R. R. 1893. *A History of Crustacea—Recent Malacostraca*. Kegan Paul, Trench, Trübner and Co. Ltd., London, 466 p.
- SUN Z.-Y., A. TINTORI, D.-Y. JIANG, M. RUSCONI, C. LOMBARDO, W.-C. HAO, AND Y.-L. SUN. 2009. A New Perleidiform (Actinopterygii, Osteichthyes) from the Middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geologica Sinica*, 83(3):460–470.
- WANG Z.-H. AND D. ZHONG. 1994. Triassic conodont biostratigraphy from different facies in eastern Yunnan, western Guizhou and northern Guangxi. *Acta Micropalaeontologica Sinica*, 11(4): 379–412. (In English with Chinese abstract)
- WILSON, G. D. F. 2008. Gondwanan groundwater: subterranean connections of Australian phreatoicidean isopods (Crustacea) to India and New Zealand. *Invertebrate Systematics*, 22:301–310.
- WILSON, G. D. F. 2009. The phylogenetic position of the Isopoda in the Peracarida (Crustacea: Malacostraca). *Arthropod Systematics and Phylogeny*, 67(2):159–198.
- WILSON, G. D. F. AND G. D. EDGECOMBE. 2003. The Triassic isopod *Protamphisopus wianamattensis* (Chilton) and comparison with extant taxa (Crustacea, Phreatoicidea). *Journal of Paleontology*, 77(3):454–470.

- WILSON, G. D. F. AND S. J. KEABLE. 1999. A new genus of phreatoicidean isopod (Crustacea) from the north Kimberley region, Western Australia. *Zoological Journal of the Linnean Society*, 126:51–79.
- WILSON, G. D. F. AND S. J. KEABLE. 2002a. New genera of Phreatoicidea (Isopoda, Crustacea) from Western Australia. *Records of the Australian Museum*, 54:41–70.
- WILSON, G. D. F. AND S. J. KEABLE. 2002b. New Phreatoicidea (Crustacea, Isopoda) from Grampians National Park, with revisions of *Synamphisopus* and *Phreatoicopsis*. *Memoirs of Museum Victoria*, 59:457–529.
- WILSON, G. D. F., C. L. HUMPHREY, D. J. COLGAN, K.-A. GRAY, AND R. N. JOHNSON. 2009. Monsoon-influenced speciation patterns in a species flock of *Eophreatoicus* Nicholls (Isopoda; Crustacea). *Molecular Phylogenetics and Evolution*, 51:349–364.
- WU F.-X, Y.-L. SUN, W.-C. HAO, D.-Y. JIANG, G.-H. XU, Z.-Y. SUN, AND A. TINTORI. 2009. New Species of *Saurichthys* (Actinopterygii: Sautichthyidae) from Middle Triassic (Anisian) of Yunnan Province, China. *Acta Geologica Sinica*, 83(3):440–450.
- ZHANG Q.-Y, C.-Y. ZHOU, T. LU, T. XIE, X.-Y. LOU, W. LIU, Y.-Y. SUN, AND X.-S. JIANG. 2008. Discovery and significance of the Middle Triassic Anisian Biota from Luoping, Yunnan Province. *Geological Review*, 54(4): 523–526 (in Chinese with English abstract).
- ZHANG, Q.-Y., C.-Y. ZHOU, T. LU, T. XIE, X.-Y. LOU, W. LIU, Y.-Y. SUN, J.-Y. HUANG, AND L.-S. ZHAO. 2009. A conodont-based Middle Triassic age assignment for the Luoping Biota of Yunnan, China. *Science in China, Series D: Earth Sciences*, 52(10):1673–1678.

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