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A NEW SHRIMP (DECAPODA, DENDROBRANCHIATA, PENAEOIDEA) FROM THE MIDDLE TRIASSIC OF YUNNAN, SOUTHWEST CHINA

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ABSTRACT—A new penaeoid shrimp collected from the Middle Triassic Member II of the Guanling Formation in the vicinity of the city of Luxi, Yunnan, southwest China, is a new species, *Aeger luxii* n. sp. The new species possesses prominent spinose third maxillipeds, which is one of the typical characteristics of *Aeger*. The new species differs from the type species, *Aeger tipularius* from the Jurassic Solnhofen Plattenkalk, in having a long, smooth rostrum with no subrostral spines. The new taxon increases the diversity of Chinese decapods, and further expands our knowledge of the phylogeny and evolution of the Mesozoic decapods. The find is the first complete specimen of *Aeger* in the Middle Triassic, and reveals a close biogeographic connection of the marine ecosystem between Eastern and Western Tethys.

INTRODUCTION

THE TRIASSIC Period was a pivotal time in the evolution of decapod crustaceans. Although the record of the order extends back to two species in the Late Devonian (Schram et al., 1978; Feldmann and Schweitzer, 2010), only one other Paleozoic species is known (Birshtein, 1958). However, soon after the end-Permian extinction, decapods underwent a radiation resulting in evolution of a variety of shrimp and lobster species. A compilation of geologic ranges of all known species by two of us (RMF and CES) and based upon the compilation of all known fossil species of decapods (Schweitzer et al., 2010; Feldmann et al., 2012) documents six genera in the Early Triassic, eleven in the Middle Triassic, and ten in the Late Triassic. The record appears to be quite biased geographically. Of the 27 genera, 19 are known only from Europe, two from North America (Van Straelen, 1936; Schram, 1971), two from Madagascar (Garassino and Teruzzi, 1995; Garassino and Pasini, 2002), one from Japan (Karasawa et al., 2003), and four from China (Feldmann et al., 2012). One additional decapod taxon was reported from the Late Triassic of North America (Rinehart et al., 2003); but it was subsequently determined to be considered Arthropoda *insertae sedis* (Schweitzer and Feldmann, 2005).

Prior to Feldmann et al. (2012), only one genus of Triassic decapod was known from China, and this was the only Triassic occurrence in Asia. Continued work on the decapod fauna from the Luoping Biota will expand the number even more as the shrimp from that fauna are described. The purpose of the present study is to describe a new well-preserved decapod found southeast of the city of Luxi, Yunnan Province (Fig. 1). The specimen was collected from finely laminated, micritic limestone of Member II of the Guanling Formation, which possesses a sedimentary environment similar to that of the Luoping Biota (Hu et al., 2011). The age of the fossiliferous beds has been determined to be Anisian (Middle Triassic) on the basis of the conodonts, ammonoids, and bivalves. The discovery of a new, and different, decapod at the new site near Luxi provides an opportunity to further expand the number of these important organisms in China. Thus, the discovery of more and more decapods in China potentially has profound implications for understanding the diversification and geographic radiation of the decapods following the P-Tr mass extinction event.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802
Suborder DENDROBRANCHIATA Spence Bate, 1888
Superfamily PENAEOIDEA Rafinesque, 1815
Family AEGERIDAE Burkenroad, 1963

Included genera.—*Acanthochirana* Strand, 1928; *Aeger* Münster, 1839.

Diagnosis.—Carapace with cervical and hepatic grooves; long or short rostrum compressed laterally, with one subrostral spine or with several suprarostal and some postrostral spines or no rostral spines on the dorsal and ventral rim, sometimes with lateral granules. Hepatic spine present; third maxillipeds long, with multiple thin spines, usually longer than or as long as pereiopods. First three pairs of pereiopods chelate, increasing in length posteriorly, the third pair longest, but not more stout. First pleonal somite overlapping the second, pleonal somite 1 somewhat reduced, shortest among the somites. Pleurae rounded; pleonal hinges with characteristic pattern of extant penaeids. Exopod of uropods with diaeresis.

Occurrence.—Middle Triassic (Anisian)–Upper Cretaceous (Cenomanian).

Remarks.—Aegeridae includes *Acanthochirana* Strand, 1928 and *Aeger* Münster, 1839. It was erected by Burkenroad (1963), and though he provided some comparisons among *Acanthochirana*, *Aeger*, and other shrimp taxa, he did not provide a formal diagnosis for this family. We have examined all species of these two genera from earlier research papers, and summarize a general family diagnosis as presented above. Prior to 2001, *Acanthochirana* and *Aeger* were assigned to Penaeidae (Balss, 1922; Förster, 1967; Förster and Crane, 1984; Glaessner, 1945; Glaessner, 1969; Garassino and Teruzzi, 1990). Schweigert (2001) revised the Late Jurassic decapod species *Aeger tipularius* and placed *Aeger* in Aegeridae. Subsequently, De Grave et al. (2009) and Schweitzer et al. (2010) compiled decapod systematic lists, and placed *Acanthochirana* and *Aeger* in Aegeridae. Species of *Aeger* exhibit variable rostra; some of them have a long, single, subrostral spine;

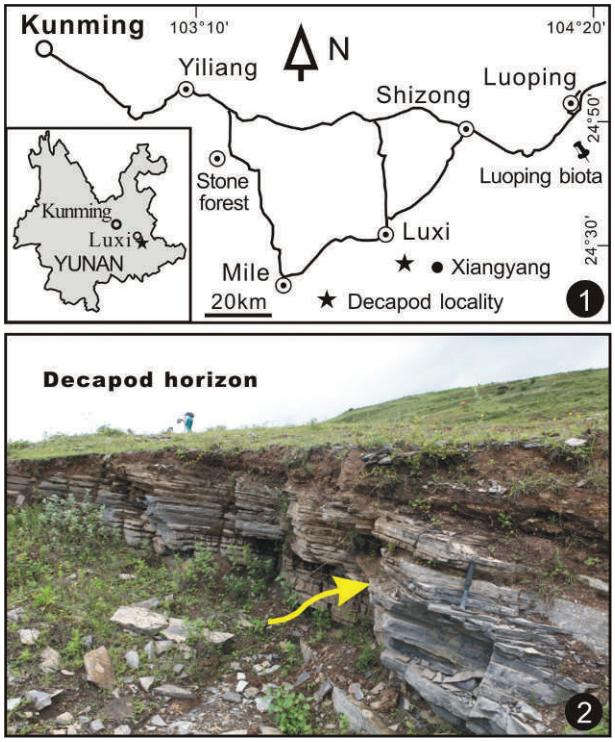

FIGURE 1—Middle Triassic decapod locality and horizon from Luxi County, Yunnan Province, southwest China. *1*, location of the decapod in Luxi County; *2*, field occurrence of the decapod.

some have a subrostral or no subrostral spines with a few suprarostral spines; or some of them have a short rostrum with no supra- or subrostral spines. Species of *Acanthochirana* have a relatively stable short rostrum with multiple suprarostral spines; a very long third maxilliped with spines; and chelate first three pereiopods with spines, the third one longer but not stronger than the first two. A hepatic spine is present in some species (Glaessner, 1945; Förster and Crane, 1984).

Genus AEGER Münster, 1839

Type species.—*Aeger tipularius* Schlotheim, 1822.

Diagnosis.—Rostrum typically long, rarely short as in the type species, laterally granular or smooth. Cephalothorax with cervical, branchiocardiac, and hepatic grooves. Third maxillipeds long, mostly longer than or as long as pereiopods, with multiple thin spines. Five pereiopods, third one longest, first to third chelate, first and second pereiopods with spines, third pereiopods with no spines or spinose chela. Surface of carapace finely granulate. Uropods with diaeresis.

Occurrence.—Middle Triassic to Late Cretaceous (Garassino and Teruzzi, 1990).

Remarks.—*Acanthochirana* Strand, 1928 is very similar to *Aeger*. In both genera, their third maxillipeds bear thin, long, multiple spines; the first three pairs of pereiopods are chelate; and their arrangement of grooves, spines, and keel is rather similar, they can be difficult to distinguish because specimens are typically strongly compressed and poorly preserved.

The typical characteristics to separate *Aeger* and *Acanthochirana* (Förster and Crane, 1984) are the arrangement of the spines on the rostrum (Förster, 1967): whereas *Acanthochirana* usually has a short rostrum and numerous suprarostral spines on the downward curved rostrum, *Aeger* typically has a rostrum that may be short, as in the type species, or long with very few spines on the dorsal and ventral margins. The pereiopods of *Aeger* increase in length from one to three and the third one bears long chelae, fourth and fifth pereiopods thin and long, but species of *Acanthochirana* have a third pereiopod that is longer than the others (Glaessner, 1969). These characters can be used to distinguish between the genera of Aegeridae.

The new species here described is placed in *Aeger* on the basis of the extremely long third maxillipeds with a similar arrangement of the spines to that of *A. spinipes* (Förster, 1967); and a long, slender, smooth rostrum, very similar to *A. spinipes* (Förster, 1967) and *A. elegans* (Münster, 1839; Oppel, 1862). The new species is obviously different from species of *Acanthochirana* in having a very long rostrum.

AEGER LUXII Huang, Feldmann, and Schweitzer new species
Figures 2–4

Type species.—*Aeger luxii* n. sp. by original designation and monotypy.

Diagnosis.—Carapace smooth, long, moderately deep, with thin cuticle. Rostrum long, slightly upturned, unarmed on the rim, laterally smooth. Antennal flagella long. Third maxillipeds long, hypertrophied, longer and more robust than pereiopods, with multiple thin spines. Pereiopods slender, the first or second possesses weak spines. Pleonal somite 1 overlapping somite 2, somite 1 shorter than other somites, somite 6 longest. Pleura subrounded.

Description.—The specimen is strongly compressed laterally and slightly convex on the surface of the rock, some diagnostic features are not well preserved. The entire length of the specimen is approximately 55 mm.

Cephalothorax (Fig. 3A) narrow anteriorly, wider posteriorly, overall longer than high. Carapace cuticle very thin, some missing. Endophragmal skeleton displaced ventrally and visible below carapace. Ventral margin of carapace not well preserved. Dorsal margin of carapace slightly arched. Greatest convexity in anterior one third of carapace, and slightly convex downward to anterior and posterior.

Rostrum (Fig. 4A) long, slender, smooth; distal tip sharp, and slightly concave upward; thick proximally, becoming slender distally. Proximal upper margin of rostrum relatively convex.

Antenna (Fig. 4A) clearly preserved beneath rostrum, with robust scaphocerite. Scaphocerite longer than wide, flagellum extending beyond scaphocerite. Short, indistinct, disjointed annular segments of antennular flagella (Fig. 4B) present on either side of the rostrum.

Because the specimen is compressed, thoracic appendages from right and left side are visible.

Third maxillipeds (Fig. 4B) both preserved, pediform, very pronounced, equal in size, gradually becoming more slender from basal to distal end; many tiny spines along both sides of maxilliped, especially clear at distal end; spines appear to project from sockets. Merus is very much longer than high, wider near carpus than at basis; carpus slightly longer than high, upper margin straight, lower margin slightly convex; propodus much longer than high, becoming narrower distally. Dactylus longer than high, becoming slightly narrower distally, proximal margin straight, distal margin subrounded, with clear spines around both sides of the distal end.

First and second pereiopods (Fig. 3A) compressed, approximately equal in size, slender, with some tiny spines along second pereiopod, distal elements missing; third through fifth pereiopods missing.

Pleon (Fig. 3B) comprising 6 somites; laterally compressed so right and left sides of somites overlap one another. Somite 1 shorter than others; 2–5 approximately equal in length; somite 6 longest. Dorsal margin of pleon moderately convex upward with highest point at somite 3. Articulation of each somite not clear along dorsal margin, but outlines of pleura are distinct. Somite 1

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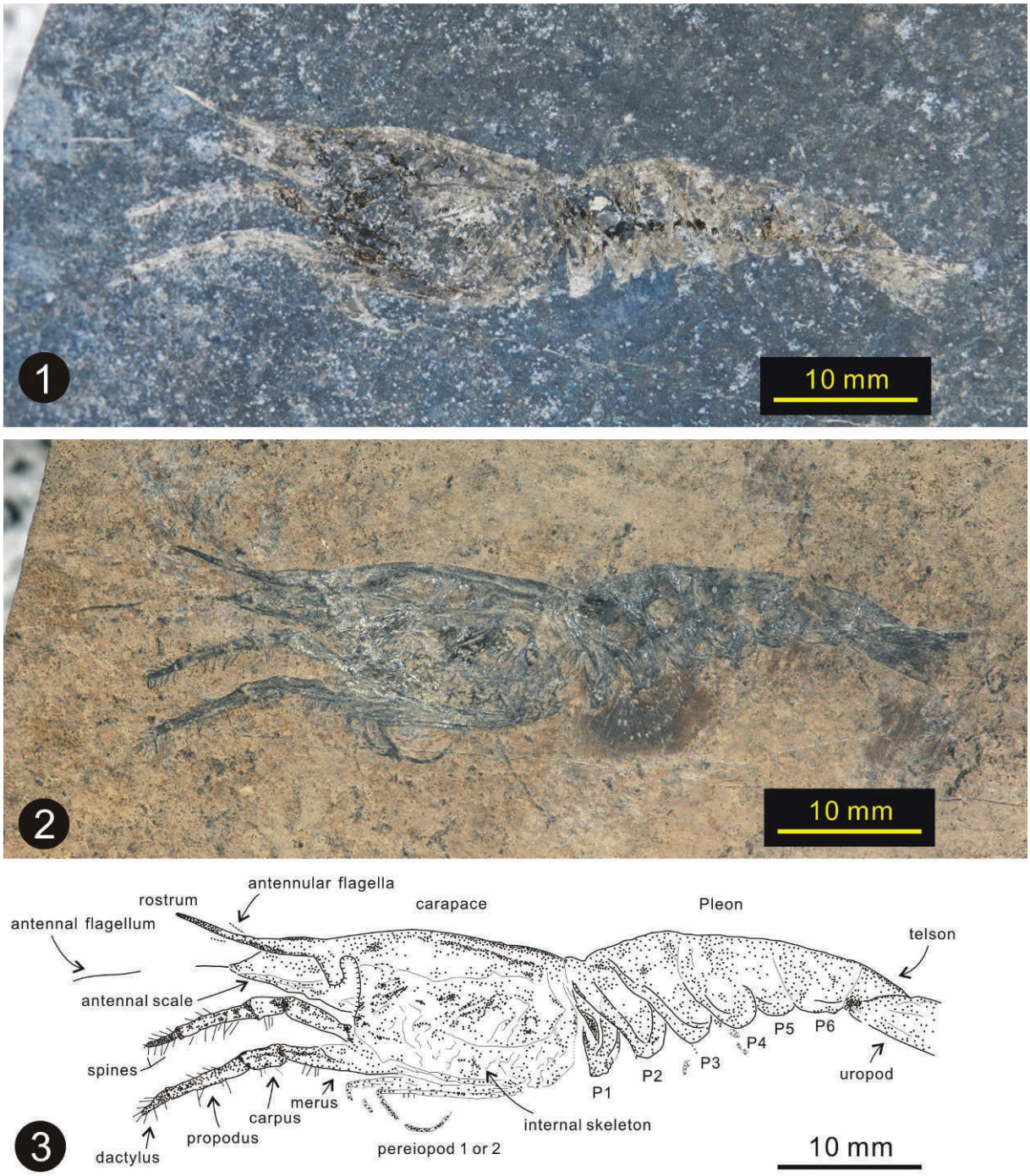

FIGURE 2—*Aeger luxii* n. sp. Overview of the Middle Triassic decapod, holotype D2239-F73; entire animal showing the rostrum, antenna, the prominent third maxilliped, cephalothorax, abdomen, and uropods. *1*, field photograph of the Luxi shrimp after processing by opposite phase in photoshop; *2*, the specimen after preparation; *3*, line sketch of the shrimp with structures interpretation. Scale bars=10mm.

higher than long, in lateral view with subtriangular pleura, part of pleopod 1 basis is preserved. Somites 2 and 3 also higher than long, with subrounded pleura. Somites 4 and 5 with smoothly rounded pleura, somite 4 higher than 5. Somite 6 rather long, with blunt rounded pleura.

Pleopods with poorly preserved basal elements. Uropod (Fig. 3B) with straight sided exopod with blunt termination. Part of telson (Fig. 3B) covered by uropod; upper margin straight.

Etymology.—The species name refers to Luxi County where the specimen was collected.

Types.—The holotype is D2239-F73. The holotype and sole specimen, D2239-F73, is deposited in the Chengdu Institute of Geology and Mineral Resources, Chengdu, Sichuan Province. The single specimen is from southeastern Luxi County, Yunnan Province, southwest China. The thin fossiliferous layer containing the decapod lies within Member II of the Guanling Formation. Measurements (in mm) of the holotype of *Aeger luxii* n. sp. are shown in Table 1.

Occurrence.—Member II of Guanling Formation, Middle Triassic; Luxi, Yunnan, southwest China.

Remarks.—The specimen described here is not well preserved. The carapace structures are difficult to interpret. The hepatic

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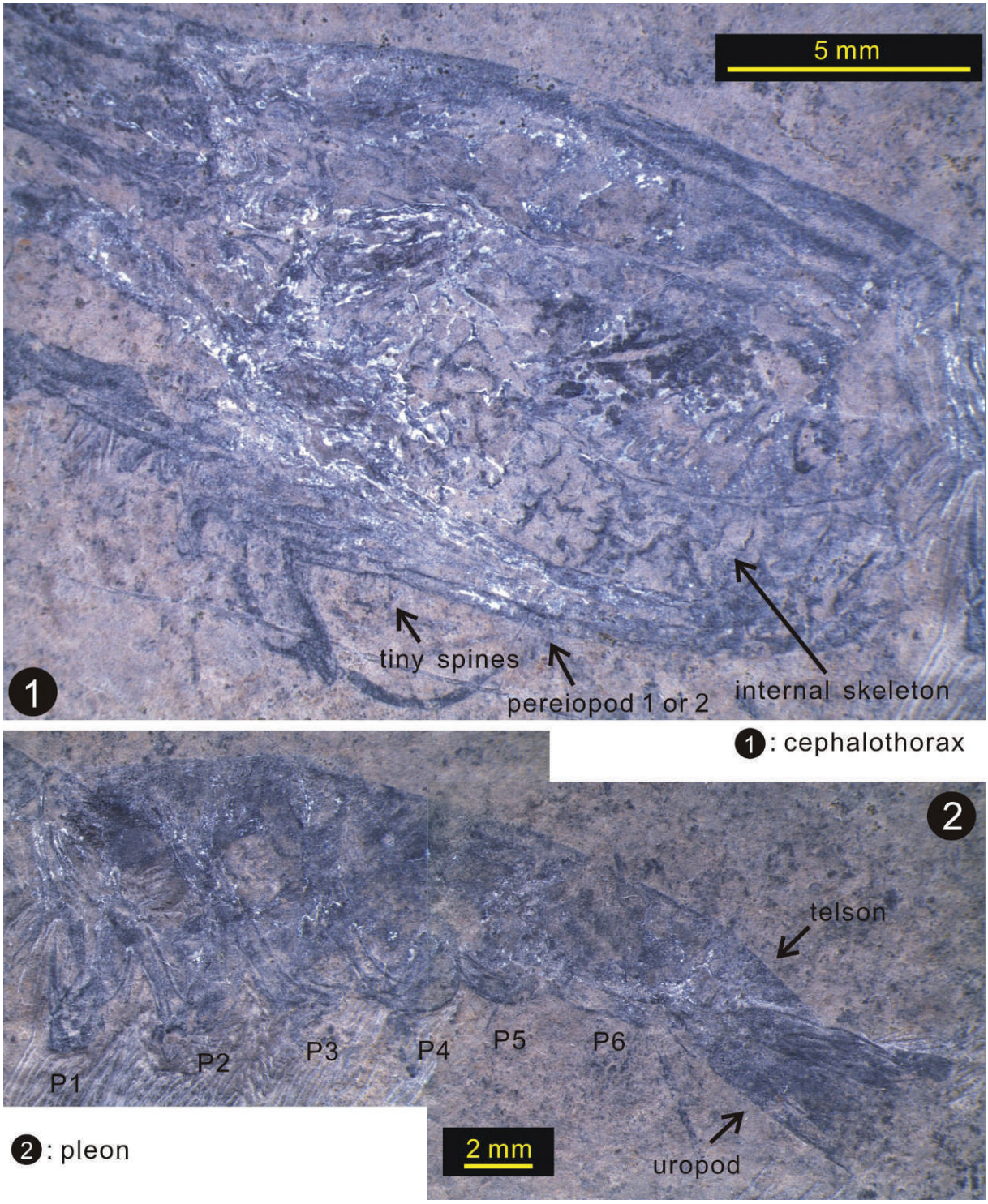

FIGURE 3—Closeup of *Aeger luxii* n. sp. *1*, cephalothorax with clear internal skeleton and some tiny spines along beneath pereiopods 1 or 2, scale bar=5mm; *2*, pleonal somites and uropod, pleopods with poorly preserved basal elements, scale bar=2mm.

spine is absent. The first two spinose pereiopods lack chelae. All the pleopods are lost, with the exception of some poorly preserved basal elements. The exopod of the uropod is truncated distally, so the diaeresis can not be confirmed.

The new species can be assigned to *Aeger* on the basis of the prominent third maxilliped and long, slender, smooth rostrum. Other diagnostic elements are not available for study. Among the species of *Aeger*, *A. brodiei* Woodward, 1888, from the Lower Lias of Wilmcote, Warwickshire, U.K., is very similar to *A. luxii*. The rostrum has a similar shape with a long, slender, smooth margin. The third maxilliped also possesses an extremely long, spinose outline. However, in *A. brodiei*, the sixth pleonal somite is nearly the same size as the others. In *A. luxii*, the pleonal somites are of different sizes, with the sixth somite the longest. Moreover, each pleuron of the new species has a different shape. The new species clearly differs from *A. tipularius* (Schlotheim,

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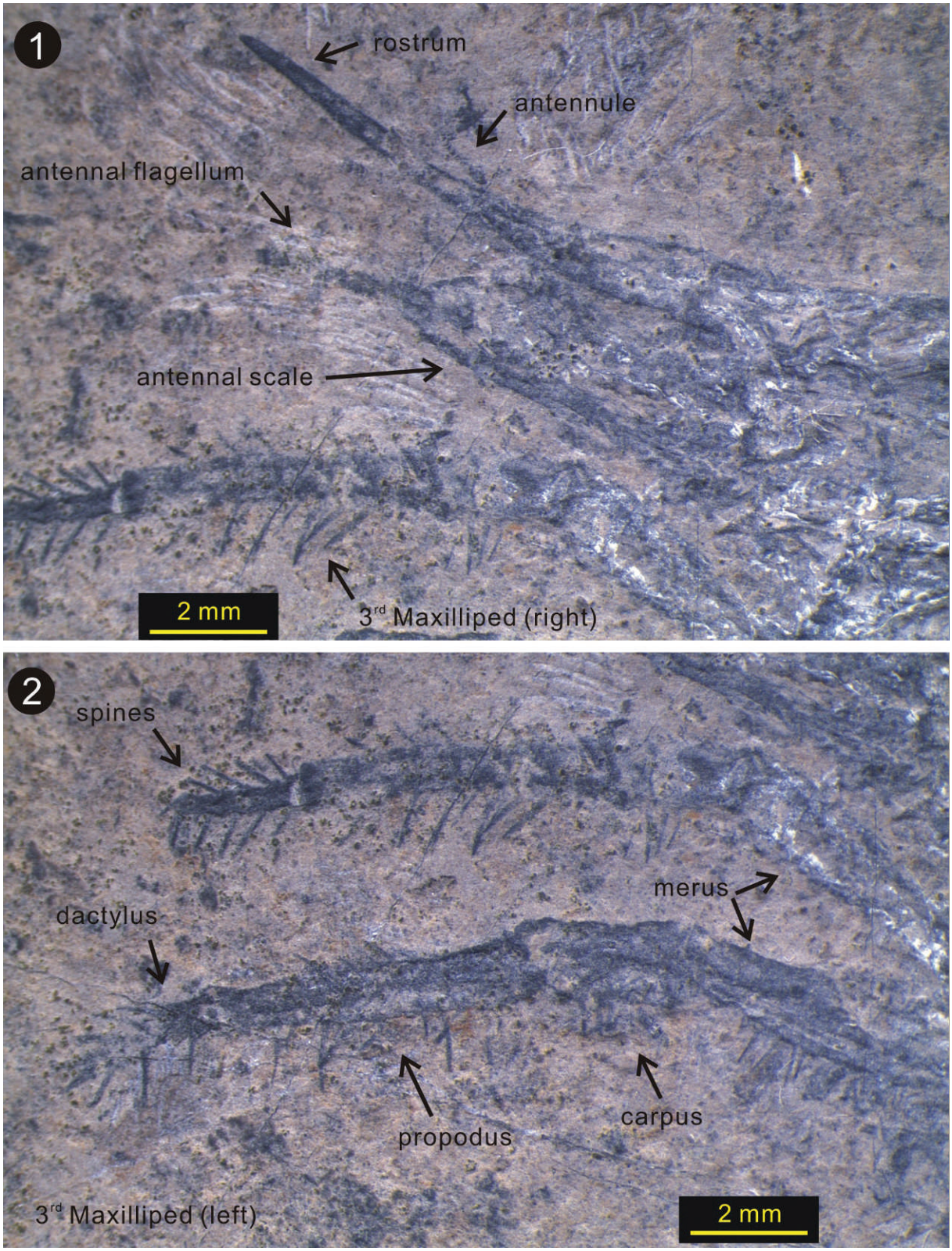

FIGURE 4—Closeup of *Aeger luxii* n. sp. *1*, slightly upward concave rostrum and antenna; *2*, third maxilliped with prominent spines along both sides of the distal end. Scale bars=2mm.

1822) (Fig. 5), *A. spinipes* (Desmarest, 1822), *A. insignis* (Oppel, 1862), *A. muensteri* (Garassino and Teruzzi, 1990), and *A. robustus* (Garassino and Teruzzi, 1990), as they have one ventral spine on the rostrum which *A. luxii* lacks. *Aeger luxii* differs from *A. rostrospinatus* (Garassino and Teruzzi, 1990), which bears upper and lower margin spines on the rostrum; and from *A. brevirostris* (Van Straelen, 1922), *A. elongatus* (Garassino and Teruzzi, 1990), *A. foersteri* (Garassino and Teruzzi, 1990), and *A.*

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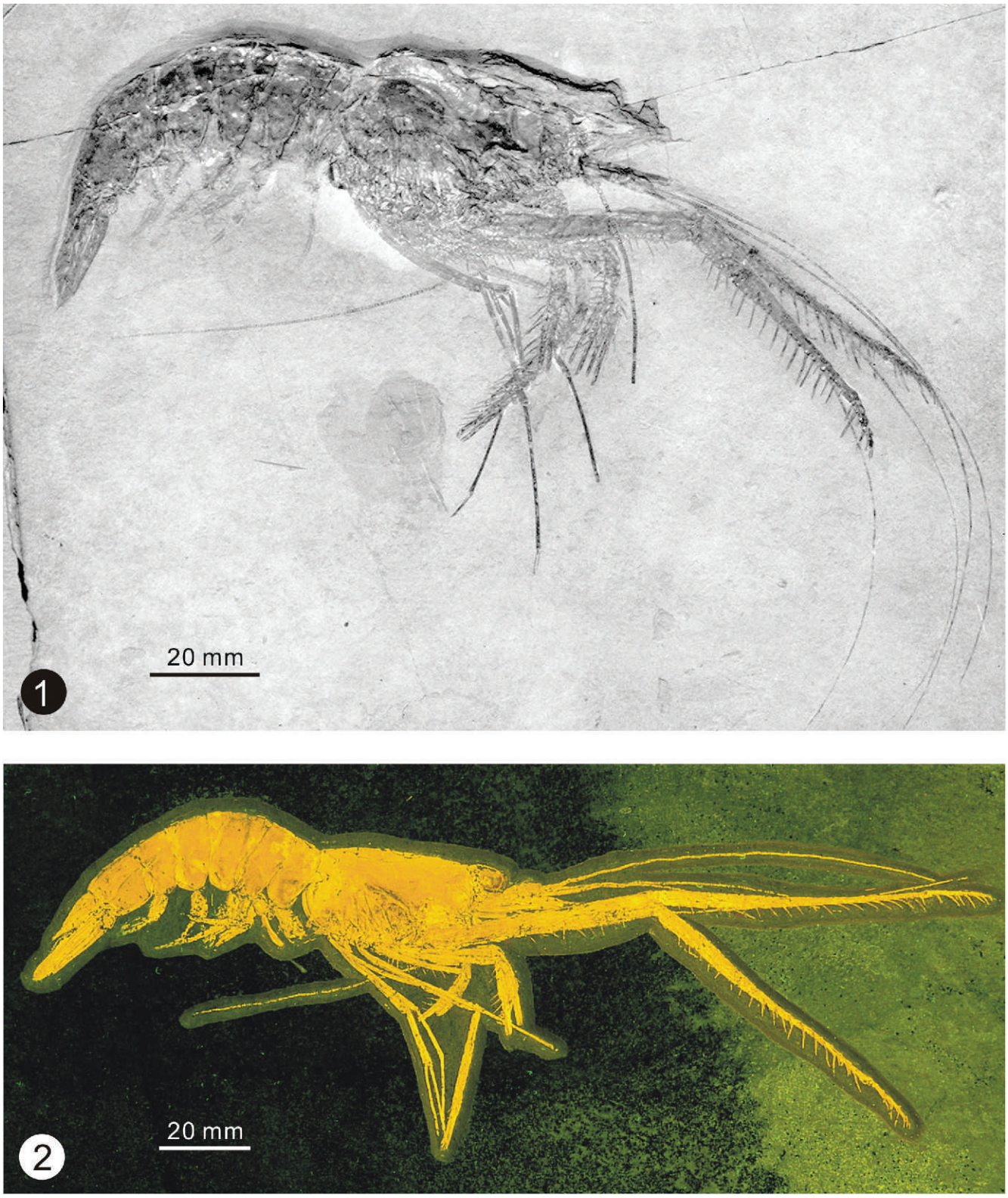

FIGURE 5—*Aeger tipularius*. *1*, holotype of *Aeger bronni* Oppel, 1862, BSP (Bayerische Staatsammlung für Paläontologie und historische Geologie, München) AS I 959=*A. tipularius*; *2*, *A. tipularius*, SMNS (Staatliches Museum für Naturkunde, Stuttgart) 65538, ultra-violet illumination. Scale bars=20 mm.

macropus (Garassino and Teruzzi, 1990), all of which have short rostra with upper marginal spines. The new species lacks rostral spines of any kind. The new species prominently differs from species of *Aeger spinipes* (CM 3320, 3583, 33075, 33222, and 33438) in the Carnegie Museum of Natural History of Pittsburgh (Fig. 6). The rostrum exhibits one subrostral spine and some lateral granules, and robust spinose third maxillipeds with an enlarged point at the base of the spines. Even more distinctive,

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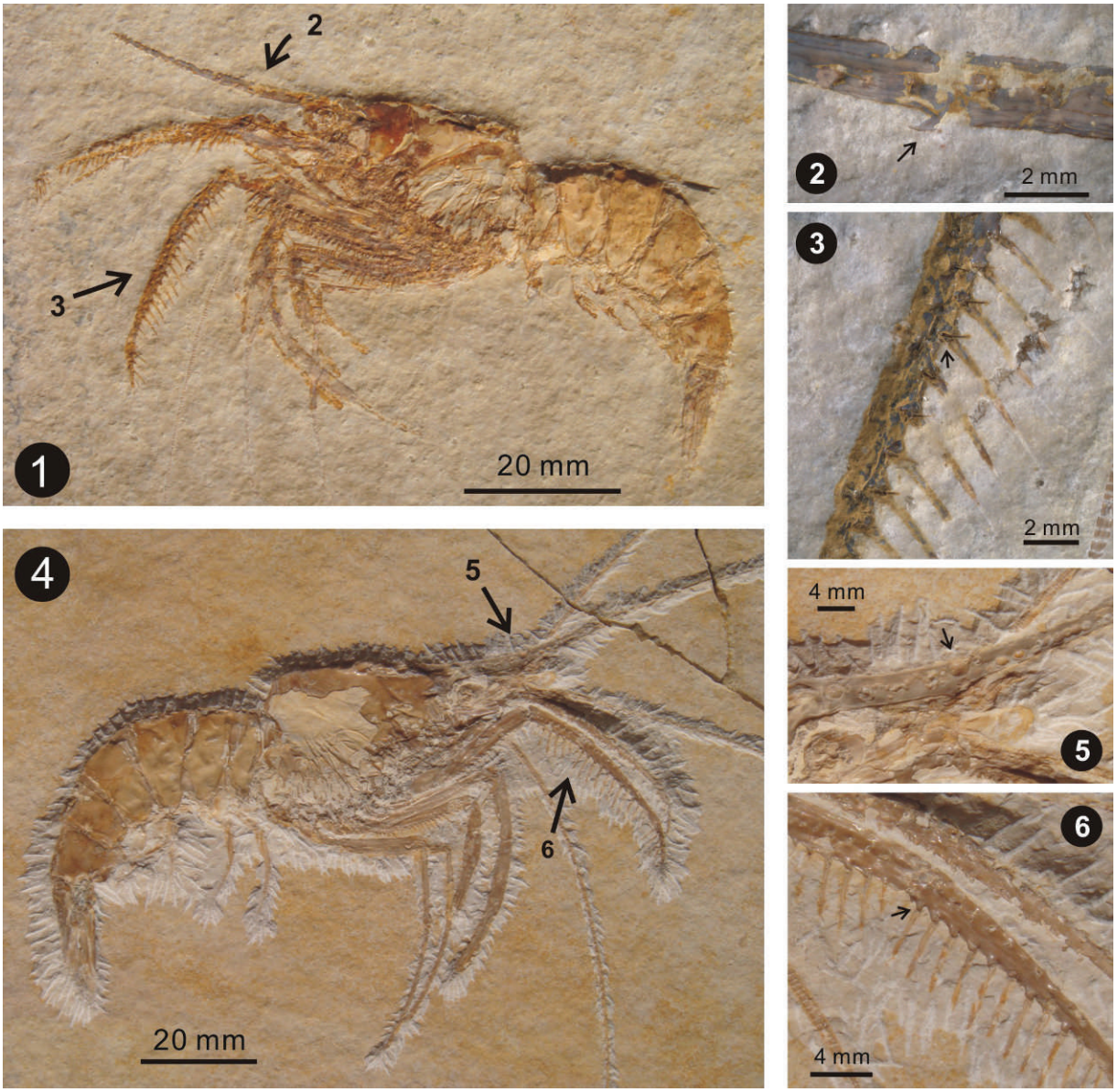

FIGURE 6—Well-preserved specimen of *Aeger spinipes* from the Carnegie Museums of Pittsburgh, note the form of rostrum and the accessory on the third maxillipeds (arrows point). *1*, entire animal, long antennules and antennae, concave upward rostrum, prominent third maxillipeds, specimen number CM 33075, scale bar=20 mm, numbered arrows indicate locations of magnified views; *2,* closeup of long subrostral spine rostrum, scale bar=2 mm; *3*, closeup of distinctive long spines third maxillipeds with short, small hairs attached at the base of the spines, scale bar=2 mm; *4*, entire animal, extremely long antennules and antennae, concave upward rostrum with side granules, prominent third maxillipeds, third pereiopods with long chelae, fourth and fifth pereiopods thin and long, specimen number CM 33222, the rostrum exhibits one broken subrostral spine and some lateral granules and the long third maxillipeds possess a strong enlarged point at the base of the spines, scale bar=20 mm; *5*, closeup of subrostral spine and lateral granules, scale bar=4 mm; *6*, closeup of third maxilliped, scale bar=4 mm.

there are short fine hairs attached at the base of the spines (Förster, 1967; Oppel, 1862). The new species has a smooth rostrum with no sub- or suprarostral spines, and much more slender spines on the third maxillipeds.

PALEOBIOGEOGRAPHY

More than twenty species have been included in *Aeger* (Schweitzer et al., 2010). It ranges from Middle Triassic to Upper Cretaceous, and is known for the very beautiful material from the Late Jurassic Solnhofen Plattenkalk. There are four species of *Aeger* in the Triassic: three Late Triassic species: *A. gracilis* Förster and Crane, 1984, from the Rhaetian of Somerset, England preserving three-dimensional carapaces and pleons; *A. straeleni* Glaessner, 1929, from the Carnian of Austria, and *Aeger* sp. (Glaessner, 1965; Pinna, 1974) from the Norian of Italy. They are strongly compressed and preserved in shales, except for the material from Somerset. One species is from the Middle Triassic of Thuringia, Germany, *A. lehmanni* (Langenhan, 1910). However, this species is difficult to identify with certainly because the sole specimen lacks its carapace, and there are only remains of the pleon and part of one maxilliped. Thus far, the new material from Yunnan, China, is the most complete specimen of *Aeger* in the Middle Triassic. Therefore, this discovery can reliably confirm the first appearance of *Aeger* in the Middle Triassic.

Aeger has been described mainly from Western Tethys regions (Italy, Spain, United Kingdom, France, and Germany). It is best known from the Jurassic Solnhofen-type limestones in

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TABLE 1—Measurements (in mm) of *Aeger luxii* n. sp., holotype specimen; L=left, R=right.

Character	Length (in mm)
Total length of specimen	45.3
Rostrum	9.9
Carapace length	17.6
3rd maxilliped (dactylus) (R)	2.2
3rd maxilliped (dactylus) (L)	2.0
3rd maxilliped (propodus) (R)	5.1
3rd maxilliped (propodus) (L)	5.5
3rd maxilliped (carpus) (R)	2.5
3rd maxilliped (carpus) (L)	2.6
3rd maxilliped (merus) (R)	4.8
3rd maxilliped (merus) (L)	5.2
Pleon	27.7
Tail fan	6.5
Telson (visible part)	2.3

Germany. The earliest reported species in Western Tethys, *Aeger lehmanni* from Thuringia, Germany, is based on a fragmentary and uncertain specimen. The new taxon here described is the first occurrence in Eastern Tethys. The discovery confirms that a very close biogeographic connection existed between Eastern and Western Tethys during the Middle Triassic. This connection is further documented by comparison of the marine fish genera between the South China Block (Luoping biota and Panxian fauna) and the Western Tethys area (Monte San Giorgio and other sites in the Alps) (Lombardo et al., 2011; López-Arbarello et al., 2011).

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