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PENAEOID DECAPODA (DENDROBRANCHIATA) FROM THE LUOPING BIOTA (MIDDLE TRIASSIC) OF CHINA: SYSTEMATICS AND TAPHONOMIC FRAMEWORK

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ABSTRACT—Two new genera, *Anisaeger* and *Distaeger*, and three new species, *Anisaeger brevirostrus*, *A. spiniferus*, and *Distaeger prodigiosus*, extend the range of the Aegeridae (Dendrobranchiata, Penaeoidea) into the Middle Triassic (Anisian) of China. Seven decapod crustacean species are now known from the Luoping biota of southern China. Morphological features of shrimp that are present but rarely mentioned in the neontological literature are recognized as potentially useful in classifying fossil material, including a diaeresis on the exopod of the uropods and multiarticulate flagellae on pleopods. Unusual taphonomic features of the shrimp include fractured cuticle, preservation in lateral, dorsal, and ventral position, and twisted cephalothoraxes.

INTRODUCTION

THE LUOPING Biota, preserved as erosional remnants in a karstic terrane in Yunnan Province, China, has yielded over 20,000 specimens of vertebrate and invertebrate fossil; most numerous among them are the arthropods. Recently, Feldmann et al. (2012) described three new genera and three new species of macrurous decapods from the fossil locality about 20 km southeast from the city of Luoping, approximately N 24°50′, E 104 °30′. Fossils were collected there from Member II of the Guanling Formation of early Middle Triassic age, based upon conodonts (Zhang et al., 2008, 2009; Hu et al., 2010). Details of the occurrence of these decapods were given therein (Feldmann et al., 2012). Subsequently, Huang et al. (2013) described a new species of the dendrobranch shrimp *Aeger* Münster, 1839 from a new locality near the country town of Luxi, Yunnan Province. Thus, the number of decapod crustaceans from the Luoping Biota continues to grow.

Two new genera and three new species of dendrobranch shrimp are described based upon examination of several hundred specimens from the same locality that yielded the previously described lobsters. Although the lobsters were interpreted as having relatively durable cuticle, the shrimp discussed herein are characterized by having very thin cuticle that is readily deformed and oriented in a variety of positions. As a result, the description and interpretation of the morphology of the shrimp is, of necessity, a composite of several specimens; however, fine detail of many parts of the skeletal anatomy is exquisite.

These are among the earliest occurrences of shrimp in the Mesozoic. The Paleozoic record of decapods is sparse. The only occurrence of a Paleozoic shrimp is *Aciculopoda mapesi* Feldmann and Schweitzer, 2010, from the Upper Devonian Woodford Shale of Oklahoma, U.S.A. Thus the Luoping shrimp provide critical information about the range of morphology expressed during the early radiation of the dendrobranchs.

SYSTEMATIC PALEONTOLOGY

Repository.—Specimens in this study are deposited in the Invertebrate Paleontology Collection, Chengdu Institute of Geology and Mineral Resources, Chengdu, Sichuan Province, China, and bear the acronym LPI. Specimen numbers are LPI numbers except one which is an LPV number deposited in the same collection. Comparative specimens examined for this study are deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, U.S.A. (CM), and the United States National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. (USNM).

Order DECAPODA Latreille, 1802
Suborder DENDROBRANCHIATA Spence Bate, 1888
Superfamily PENAEOIDEA Rafinesque, 1815

Included families.—Aegeridae Burkenroad, 1963 (extinct); Aristeidae Wood-Mason *in* Wood-Mason and Alcock, 1891; Benthesicymidae Wood-Mason *in* Wood-Mason and Alcock, 1891; Carpopenaeidae Garassino, 1994 (extinct); Penaeidae Rafinesque, 1815; Sicyonidae Ortmann, 1898; Solenoceridae Wood-Mason *in* Wood-Mason and Alcock, 1891.

Diagnosis.—All five pairs of pereiopods well developed; pereiopods 1–3 chelate, none significantly enlarged. Pleon with posterior part of pleura overlapping anterior part of succeeding one.

Material.—*Aristeus antillensis* A Milne-Edwards and Bouvier, 1909 (Aristeidae), USNM 139787; *Parapenaeus fissurus* Spence Bate, 1881 (Penaeidae), USNM 216125; *Sicyonia penicillata* Lockington, 1878 (Sicyoniidae); USNM 254798; *Psalidopus barbouri* Chace, 1939 (Psalipodopidae Wood-Mason *in* Wood-Mason and Alcock, 1892), USNM 181376, *Macrobrachium olfersi* (Wiegmann, 1836) (Family Palaeomonidae Rafinesque, 1815), USNM 80657; *Lebbeus groenlandicus* (Fabricius, 1775) (Family Hippolytidae Spence Bate, 1888), USNM 27280); *Palaemon xiphias* Risso, 1816 (Family Palaemonidae), USNM 205839; *Glyphocrangon aculeata* A. Milne-Edwards, 1881 (Glyphocrangonidae Smith, 1884), USNM acc. no. 3929; *Pandalus borealis* Krøyer, 1838 (Pandalidae Haworth, 1825), USNM 3914; *Penaeopsis eduardoi* Pérez Farfante, 1977 (Penaeidae), USNM 286960.

Remarks.—The Luoping specimens display characteristics of Dendrobranchiata, Penaeoidea. Features that support placement in Penaeoidea include development of all five pereiopods. This is in contrast with members of the Sergestoidea Dana, 1852, the other dendrobranch superfamily, in which the fourth and fifth pereiopods are often reduced and sometimes absent; however, note that in some genera of Sergestoidea, all five pereiopods are present. In sergestoid shrimp, the rostrum is much reduced, shorter than the eyestalks (Pérez Farfante and Kensley, 1997), whereas it is generally long, at least longer than the eyestalks and sometimes very much longer, in penaeoid shrimp. In the Chinese specimens, the rostrum is about as long as the eyestalks or longer. It appears that the basal articles of the antennules in Sergestoidea are quite long as compared to those in Penaeoidea, so that the flagellae of the antennules begin well anterior to the carapace—two-thirds to the entire length of the carapace anterior to it in most cases. This is not seen in Penaeoidea. In penaeoids, the basal articles are usually about one-quarter to one-third the length of the carapace. In the Luoping specimens, the basal articular arrangement is similar to that in previously described Penaeoidea. However, differentiation based upon the length of the antennal articles does not hold for every genus. As is usual with fossils, a constellation of characters must be used to assign fossil taxa to families and superfamilies.

One of the distinctive characteristics of the Luoping specimens is the presence of multiarticulate pleopods on what appear to be at least pleonal somites 2–5, possibly being absent on somite 1 in *Anisaeger* new genus. These pleopods are biflagellate, and both flagellae are multiarticulate. Such structures are not reported in neontological literature on dendrobranchiate shrimp but are illustrated (Pérez Farfante and Kensley, 1997). Examination of an array of species within Dendrobranchiata confirms the presence of biflagellate multiarticulate pleopods, including in *Aristeus antillensis, Parapenaeus fissurus*, and *Sicyonia penicillata*. Fossils other than Aegeridae displaying multiarticulate pleopods include species of *Antrimpos* Münster, 1839 (Pinna, 1975 [imprint 1974]) and species of Carpopenaeidae within Penaeoidea (Schweigert and Garassino, 2005).

However, pleopod structures with what appear to be fused multiarticulations or remnant but no longer articulating segments occur in some pleocyemate shrimp. For example, in female *Psalidopus barbouri*, the pleopods are flabellate, but the thickened edges show segmentation reminiscent of multiarticulate pleopods in dendrobranchs. The same type of structure is also present only on the outer edge of the pleopods in females of *Macrobrachium olfersi*, on the smaller endopod of the pleopods of *Lebbeus groenlandicus*, and on the outer edges of the pleopod elements of *Palaemon xiphias*, for example. Other pleocyemate shrimps do not show such a structure; examples are *Glyphocrangon aculeata*, and *Pandalus borealis*. Thus, a cursory examination of shrimp suggests that the multiarticulate flagellate pleopods may be confined to Dendrobranchiata but this hypothesis needs far more testing to be confirmed.

Uropods of many shrimp possess a structure on the exopod of the uropod that resembles what is recognized in lobsters as a “diaeresis”, or an articulated joint across the surface (i.e., *Penaeopsis eduardoi*). This structure never appeared in descriptions but did appear in some illustrations (Pérez Farfante and Kensley, 1997). In some taxa, the diaeresis is complete, extending across the entire exopod. In others, it extends one-half, one-third, or one-quarter the distance across the exopod. The structure exists in both dendrobranch and pleocyemate shrimps. The importance of the structure to paleontologists cannot be understated. Such a structure is eminently fossilizable and is present in the extinct penaeoid family Aegeridae. Paleontologists and all workers on lobsters and crayfish have taken the presence or absence of a diaeresis on either the telson or uropodal exopod to be of great phylogenetic importance. This importance has been extended by paleontologists to shrimp and its presence on the uropod has been noted in many fossil forms. Notice of the structure on extant forms helps to demonstrate that Aegeridae is not unusual in possessing the structure and that in fact, it is a common, if underreported, structure in penaeoid shrimp.

Family Aegeridae Burkenroad, 1963

Included genera.—*Acanthochirana* Strand, 1928; *Aeger* Münster, 1839; *Anisaeger* new genus; *Distaeger* new genus.

Diagnosis.—Carapace with long or short rostrum compressed laterally, with one subrostral spine or with several suprarostral and sometimes postrostral spines or no rostral spines at all; hepatic spine present; scaphocerite long; antennular flagellae short or long, basal articles not extending anteriorly more than one-third the length of the carapace; antennar flagellae long; third maxilliped long, usually longer than or as long as pereiopods, with multiple long, thin spines perpendicular to long axis; pereiopods ranging from overall long to overall short; pereiopods 1–3 chelate, may be spinose, 1 to 3 increasing in length posteriorly; pleonal somite 1 overlapping somite 2, somite 1 shorter than other somites; pleura rounded, may be spined or serrate; pleopods with two multiarticulate flagellae each; exopodite of uropod usually with diaeresis; telson with at least one pair of movable spines, may have marginal setae distally.

Remarks.—The name Aegeriidae Stephens, 1829, has been used for an extant family of clear-wing moths. The name is sometimes misspelled in the literature as Aegeridae (i.e., McKay, 1968); however, it was originally spelled Aegeriidae as it was named for the genus *Aegeria* Fabricius, 1807.

When Burkenroad (1963) erected Aegeridae, he provided a comparison of *Aeger* and *Acanthochirana* to other shrimp forms but offered no formal diagnosis for the family. Glaessner (1969) elected to place these two genera within Penaeidae. Thus, we have examined Burkenroad (1963) and other subsequent papers to form a new diagnosis for the family, based primarily upon the type species of the constituent genera.

The new genera and species herein are assigned to Aegeridae although they differ from other members of the family in some regards. However, this may be expectable because, for one, the genus *Aeger* is itself highly variable, and also, there are only four genera including the two new ones within the family. *Anisaeger* is referred to Aegeridae based upon its possession of a short or long rostrum that extends to, or beyond the eyes; a hepatic spine; very long flagellae of the antennules and antennae; apparently spinose or setose third maxillipeds, based upon presence of numerous pits along the margins of several elements of that appendage; two and possibly three chelate appendages; five well-developed pereiopods; very well-developed pleonal somites with rounded pleura very similar in shape to some species of *Aeger*; long multiarticulate flagellae of the pleopods as seen in the type species of *Aeger* (Schweigert, 2001); and a small, sharp telson bearing at least one pair of articulated spines. *Distaeger* is referable to Aegeridae based upon its clear uropodal diaeresis, long, spinose rostrum, third maxilliped with pits to accommodate spines or setae, three chelate pereiopods, very long antennal and antennular flagellae, and long multiarticulate flagellae of the pleopods.

The rostra of species of both genera embraced within Aegeridae aside from the new genera are quite divergent. Species of *Aeger* have either a short rostrum with no supra- or subrostral spines or a long rostrum with a single subrostral spine (Fig. 2.1). One of the new species fits into the former description. Species of *Acanthochirana* have a relatively short rostrum with multiple suprarostral spines and postrostral spines (Fig. 2.2). Penaeidae exhibits such intrageneric variation, however, so it is not unknown within Dendrobranchiata to have such variable rostra within a single family and within genera. Within Penaeidae, genera can bear suprarostral spines, suprarostral and subrostral

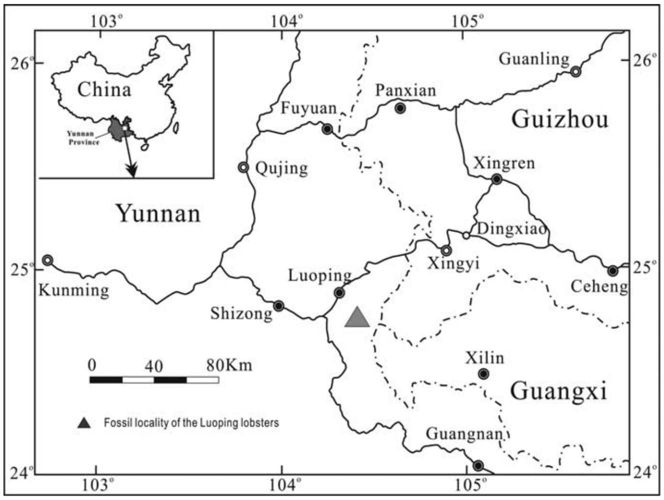

FIGURE *1*—Map and collecting locality.

spines, suprarostral and postrostral spines, or suprarostral, subrostral, and postrostral spines (Pérez Farfante and Kensley, 1997).

Aeger is itself quite variable. The type species, *A. tipularius* (Schlotheim, 1822), has a very long, spinose third maxilliped; spinose first and second pereiopods; a spinose third chela; long multiarticulate flagellae on the pleopods; and a short, entire rostrum (Schweigert, 2001). The best known and most frequently illustrated species of *Aeger*, *A. spinipes* (Desmarest, 1822), was for many years confused with the type species, *A. tipularius*, based upon the revision of the genus by Oppel (1862) (Schweigert, 2001). *Aeger spinipes* (Fig. 2.1) has a very long rostrum with a subrostral spine; weakly spinose first and second pereiopods, and third pereiopods with no spines. Both of these species are known from the Solnhofen-type limestones of Germany. A somewhat older species, *A. marderi* Woodward, 1866, from the Blue Lias of England, of Rhaetian to Sinemurian age, has spinose third maxillipeds and stout chelae on pereiopods 1–3, stouter than those on the later Jurassic species. Woodward (1888) named another species, *A. brodiei*, from rocks of the same general area and stratigraphic level with much more slender pereiopods. Neither of Woodward's species have spinose pereiopods. Garassino and Teruzzi (1990) named several Sinemurian species of *Aeger*; some of these are quite poorly preserved, but of those that retain appendages, the third maxillipeds are spinose and the pereiopods are either short or long, are thin, and appear to lack spines. Species embraced within the genus as it currently stands have pereiopods of variable length, ranging from about as long as the third maxillipeds, as in *A. spinipes*, to very short and much shorter than the third maxillipeds, as in *A. luxii* Huang et al., 2013. This very broad range of variation within *Aeger* suggests that the genus may require revision.

Species of *Acanthochirana* (Fig. 2.2) are more uniform in their morphology. There is some debate over the length of the rostrum, with some authors interpreting it as possibly broken in many examples (Garassino, 1994) and others illustrating it as extending beyond the eyes. It has suprarostral and postrostral spines in all species. The third maxilliped is illustrated as spinose by most authors, and it is as long or longer than most of the pereiopods (Charbonnier and Garassino, 2012, fig. 1C). The first pereiopod is variously spinose or without spines (Münster, 1839; Förster, 1967; Garassino, 1994). Pereiopods appear to increase in length from one to five, and one through three are chelate.

Aegeridae currently resides among the Penaeoidea as discussed above but is similar to some Sergestoidea in regard to the development of the third maxilliped and the pereiopods. In Sergestidae, the third maxilliped can be longer than, or subequal to, the third pereiopod, a condition not seen in extant Penaeoidea but often seen in Aegeridae. In addition, in *Sicyonella* Borradaile, 1910, within Sergestidae Dana, 1852, the third maxilliped is robust, with strong spines or very robust setae (*Sicyonella maldivensis* Borradaile, 1910) (Sergestidae, USNM 260757), as is seen in *Aeger* and *Acanthochirana*. This condition is not reported to our knowledge for extant Penaeoidea, although many taxa are illustrated with what appear to be setose third maxillipeds (Pérez Farfante and Kensley, 1997). *Sergia* Stimpson, 1860, is reported to have stiff setae on pereiopods one through three, as is seen on at least some species of *Aeger. Sergia potens* (Burkenroad, 1940) (Sergestidae, USNM 235081) has such stiff setae on the third maxillipeds. Such stiff setae are not reported for pereiopods of extant Penaeoidea although they are illustrated as setose (Pérez Farfante and Kensley, 1997).

Thus, Aegeridae exhibits an array of characters that clearly places it within Dendrobranchiata but not necessarily clearly within an existing superfamily within that group. For now, we retain it within Penaeoidea based upon the preponderance of features being allied with that superfamily until a phylogenetic analysis based on parsimony or maximum likelihood can be produced.

We note that Aegeridae possess well-developed biflagellar multiarticulate pleopods. These are known for all four genera now assigned to the family. Indeed, such pleopods are known in many fossil taxa currently assigned to Penaeidae, including *Antrimpos* Münster, 1839 (Pinna, 1975 [imprint 1974), and in Carpopenaeidae within Penaeoidea (Schweigert and Garassino, 2005). It appears that most or all extant members of Penaeoidea and Sergestoidea possess such pleopods as well (Pérez Farfante and Kensley, 1997).

Placement of *Anisaeger* and *Distaeger* and their included species within Aegeridae does not extend the geologic range of the family, which was previously known from the Middle Triassic to Cenomanian. *Aeger lehmanni* (Langenhan, 1910) was reported from the upper Muschelkalk (Assmann, 1927) which is Anisian–Ladinian in age, with decapods reported from the Anisian (Garassino et al., 1999). Previously, Aegeridae had been reported from localities in what is now Europe and the Middle East with only one extralimital occurrence, in Mexico (Feldmann et al., 2007). Thus, the new occurrences extend the geographic range considerably.

ANISAEGER new genus

Type species.—*Anisaeger brevirostrus* new species, by original designation.

Other species.—*Anisaeger spiniferus* new species.

Diagnosis.—Carapace small to moderate size, laterally compressed; rostrum short, upturned, and lacking spines to long, upturned, and bearing suprarostral and subrostral spines. Pleon with smooth terga and generally rounded pleural terminations; somites 5 and 6 axially keeled. Telson sharply pointed, with or without articulated spines. Uropodal exopod without diaeresis. Third maxilliped relatively short, setose or spinose. Pereiopods generally short; pereiopods 1–3 with small chelae. Pleopods with a pair of annulated terminal processes.

Etymology.—Derived from a combination of Anisian, the Middle Triassic age from which the specimens were collected, and *Aeger*, the type genus of Aegeridae. The gender is masculine.

Occurrence.—The genus is based upon specimens collected in a quarry 20 km southeast from the city of Luoping, approximately

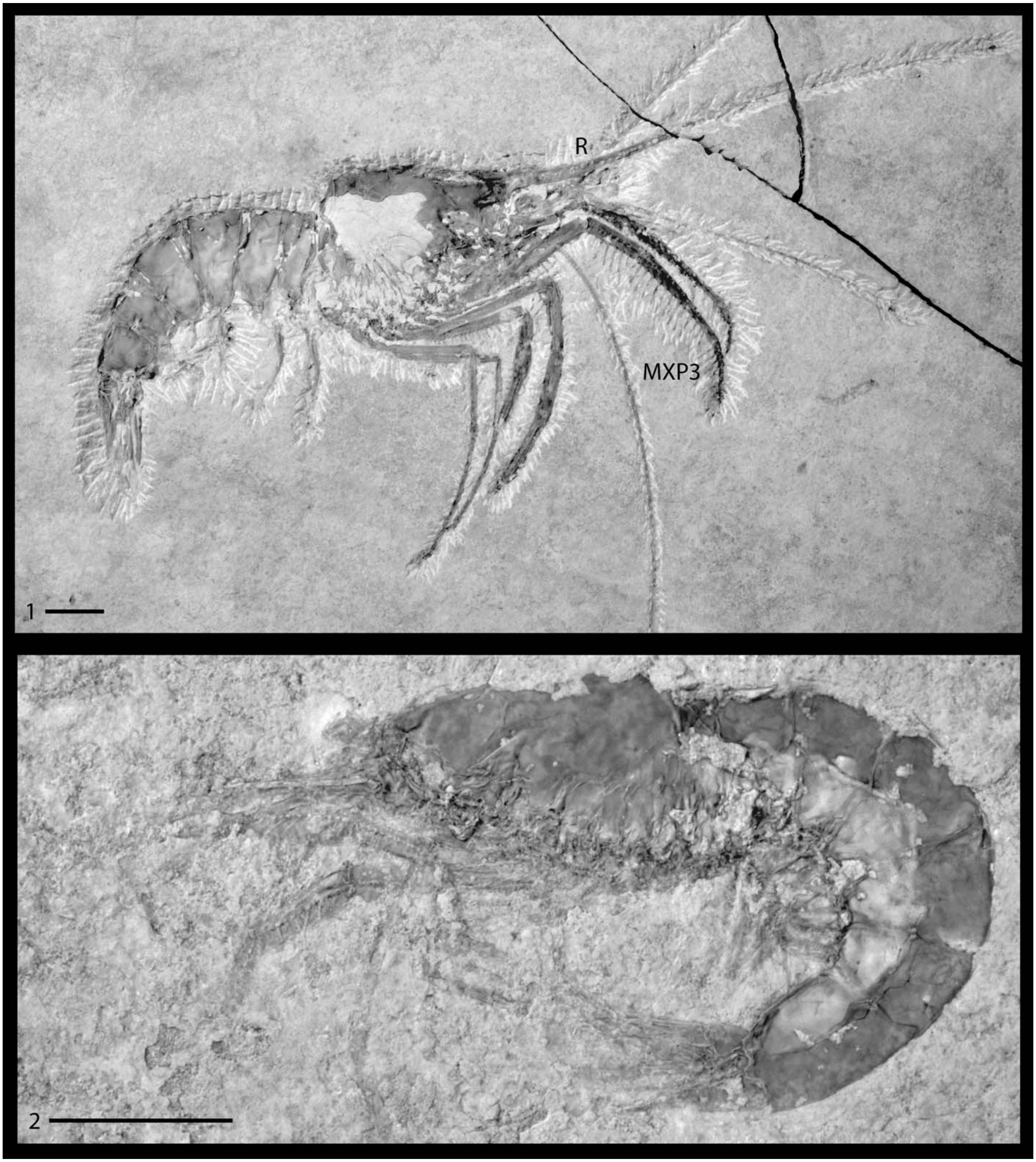

FIGURE 2—Aegeridae Burkenroad, 1963. *1*, *Aeger spinipes* (Desmarest, 1822), CM 33222, R=rostrum, MXP3=maxilliped 3, noting the spines on the third maxilliped; *2*, *Acanthochirana cordata* (Münster, 1839). Note long pleopods on both species. Scale bars=1cm.

N 24°50′, E 104 °30′, Yunnan Province, China. The fossils were collected from Member II of the Guanling Formation of early Middle Triassic age.

Remarks.—Although the genus exhibits sufficient characters to place it within Aegeridae, as discussed above, it differs sufficiently from both *Aeger* spp. and *Acanthochirana* spp. to warrant recognition as a distinct genus. Species within *Anisaeger* differ from species of *Aeger* and from *Acanthochirana*, the only other genera in the family, in having relatively short appendages, including the third maxilliped. Species of *Aeger* are typified by a very long, well-developed, spinose third maxilliped. The third maxilliped of *Acanthochirana* is somewhat shorter, closer in size and length to that of the new species. Those of *Anisaeger* are certainly well-developed and obvious but are not as large or nearly as long as seen on *Aeger* or *Acanthochirana*. It has setal pits or pits that would have embraced movable spines, but the spines are not preserved.

The pereiopods of species in *Anisaeger* are much smaller and shorter than in species of *Aeger*, again closer in size to those of *Acanthochirana*, but are still more slender and shorter than even species of the latter genus. Species of *Aeger* are quite variable in the development of the first through third pereiopods. The first and second can be spinose, which they are in the type species, *A. tipularius* (Schlotheim, 1822). Other species of *Aeger* do not express these types on spines on the pereiopods. Species of *Acanthochirana* may possess spinose first pereiopods. The new genus does not exhibit such spines on the pereiopods and the pereiopods are relatively short. In addition, the chelae are small and weakly developed. In fact, they are difficult to discern. A diaeresis has been reported on the exopod of the uropod on species of *Aeger* and *Acanthochirana*; however, we did not detect any evidence of a diaeresis on either of the new species of *Anisaeger*. Examination of extant specimens shows that the diaeresis in shrimp is present but more weakly developed than that of lobsters, so if preservation is less than optimal, it may not be preserved or easily discerned.

Anisaeger brevirostrus new species
Figures 3–7

Diagnosis.—Carapace with well developed postorbital and hepatic spines and rostrum shorter than or equal to length of eye; pleon generally smooth with keel on somites 5 and 6; lacking serrations on posterior margins of pleura of somites 5 and 6.

Description.—Carapace longer than high (all measurements in mm given in Tables 1–3), carapace height about half to three-quarters length measured at mid-length; dorsal surface weakly convex, ventral margin of carapace smoothly convex, carapace generally smooth; rostrum upturned, slender, keeled, no supra- or subrostral spines (40718, 41833) (all specimen numbers are LPI-numbers unless otherwise noted), does not extend beyond eyes (Fig. 3.1, 3.2, 3.5). Frontal margin a concave arc from base of rostrum to lower edge of orbit, then proceeding straight posteroventrally. Posterior margin weakly concave dorsally, convex ventrally, narrowly rimmed. Endophragmal skeleton with thoracic pleurites absent, apparently very thin; intrapleurite ribs strong (40478, 40491) (Fig. 7.2). Postorbital spine slender, directed anterodorsally (40718) (Fig. 4.2); cervical groove shallow, extending from about mid-height of orbit anteroventrally at about 30° angle (measure 40855, 40718) to level of scaphocerite, with strong hepatic spine at ventral termination (40718) (Fig. 4.1, 4.2).

Terga of somites uniformly smooth. First pleonal somite narrower than second, high, pleuron concave forward, convex posteriorly, terminating in sharp to narrowly rounded point, overlapping somite 2 slightly (Figs. 3, 5). Pleuron of second somite with nearly straight or slightly convex anterior margin, slightly convex or nearly straight posterior margin, rounded termination (Figs. 3, 5). Third somite pleuron slightly longer than wide, anterior margin rounded, posterior margin nearly straight, termination rounded (Figs. 3, 5). Fourth somite with pleuron about as long as wide, ovoid (Figs. 3, 5). Fifth somite with rounded pleuron wider than long, circular, pleura become wider posteriorly from 1–5, margins of all pleura with narrow rim, with dorsal crest in posterior half of somite 5 and spine which overlaps anterior portion of somite 6 (Figs. 1, 5). Somites 4 and 5 with rounded notch at point of articulation between terga and pleura on posterior margin (Fig. 5.1). Sixth somite with dorsal keel on posterior two-thirds, terminating in small spine (Fig. 6.2, 6.3). Telson uniformly straight sided, triangular, axially keeled (41315), small bases for one pair of articulating spines near base of telson (41315), ventral lateral margins of telson with setal pits, 32 pits over a distance of 1.32 mm (41315) or about 24 pits per mm (Fig. 6.2, 6.5). Uropods longer than telson; exopod and endopod weakly convex on inner and outer surfaces; no evidence of diaeresis on exopod, exopod with narrow thickened rim on outer margin; both elements longitudinally keeled; basal element of uropod with moderate to strong spine on posterolateral corner (41315) (Fig. 6.2, 6.4, 6.5).

Eyes rectilinear, weakly convex distally, longer than wide, on stalks, stalk length=2.7 mm, stalk height 0.7 mm at base, 0.9 mm high distally (LPV-10767) (Figs. 3.2, 3.5, 4.1, 4.2). Basal elements of antennules long, slender, antennular flagellae paired, longer than carapace. Antennal bases with distal basal element longer than high, rectilinear, flagella long, at least three times the length of the carapace (Figs. 3.1, 4.4). Female pleopods flabellate basally, distal basal element long, rounded termination, much longer than wide, generally uniformly wide for entire length, length of distal basal element=3.6, height of distal basal element=6.1 (40065); male pleopods rectilinear (40523), longer than wide, approximately twice as long as wide; two multi-articulate flagella of approximately the same length per pleopod in both males and females, flagella are very long (40792) and apparently about the same length; pleopods appear to be more or less the same throughout all somites in males and females although some have longer flabellate segments in females than others (see esp. 40065) (Fig. 5.3, 5.4).

Scaphocerite blade long, tapers to sharp termination, extends beyond basal elements of antennules, axially keeled, widest at base (Figs. 3.5, 4.4, 6.1, 6.3). Third maxilliped (41491) moderately long, pediform; ischium long, slender (L=2.1 mm, H=0.3); merus longer than high (L=1.7 mm, H=0.7), at least six setal pits along lower margin; carpus (L=1.3 mm, H=0.5); propodus (L=0.6 mm, H=0.5), ovate, with setal pits along lower margin (41392); dactylus (L=1.1 mm) tapers to sharp termination, with setal pits along lower margin (Fig. 7.3).

Pereiopods slender, not particularly long, first two pairs apparently shortest, third apparently longest, fourth and fifth apparently most slender, pereiopods folded posteroventrally underneath the carapace, third maxilliped directed generally anteriorly (Fig. 7). Two pairs definitely chelate, pereiopods 2 and 3, possibly all three anterior pairs chelate but no one specimen having all three pairs of chelae preserved. Specimens exhibiting two chelate terminations have posterior-most chela largest. In all cases propodus long, fingers relatively short. Specimen 40748 has anterior-most chela with tiny fingers and posterior-most chelae with longer fingers and slightly stouter propodus; 41392 has slightly stouter posterior-most cheliped. Pereiopods 4 and 5 with long, slender terminal dactyls. Specimen 40864 with anterior chelate pair longer and more slender and posterior chelate pair slightly shorter but stouter; fingers long and slender on anterior pair of chelae. Specimen 40850 has domal occlusal surfaces on fingers of pereiopod 3?, apparently smooth on pereiopod 2?

Etymology.—Reflects the short rostrum characteristic of the species.

Types.—The holotype is LPI-41833, and paratypes include 32271, 40065, 40447, 40456, 40458, 40478, 40491, 40511, 40523, 40549, 40556, 40579A, 40579B, 40703, 40718, 40739, 40748, 40751, 40758, 40767, 40792, 40793, 40848, 40850, 40855, 40864, 41315, 41388, 41392, 41491, 41765, 41803, 41833b, and LPV-10767.

Occurrence.—The specimens were collected in a quarry 20 km southeast from the city of Luoping, approximately N 24°50′, E 104 °30′, Yunnan Province, China. The fossils were collected

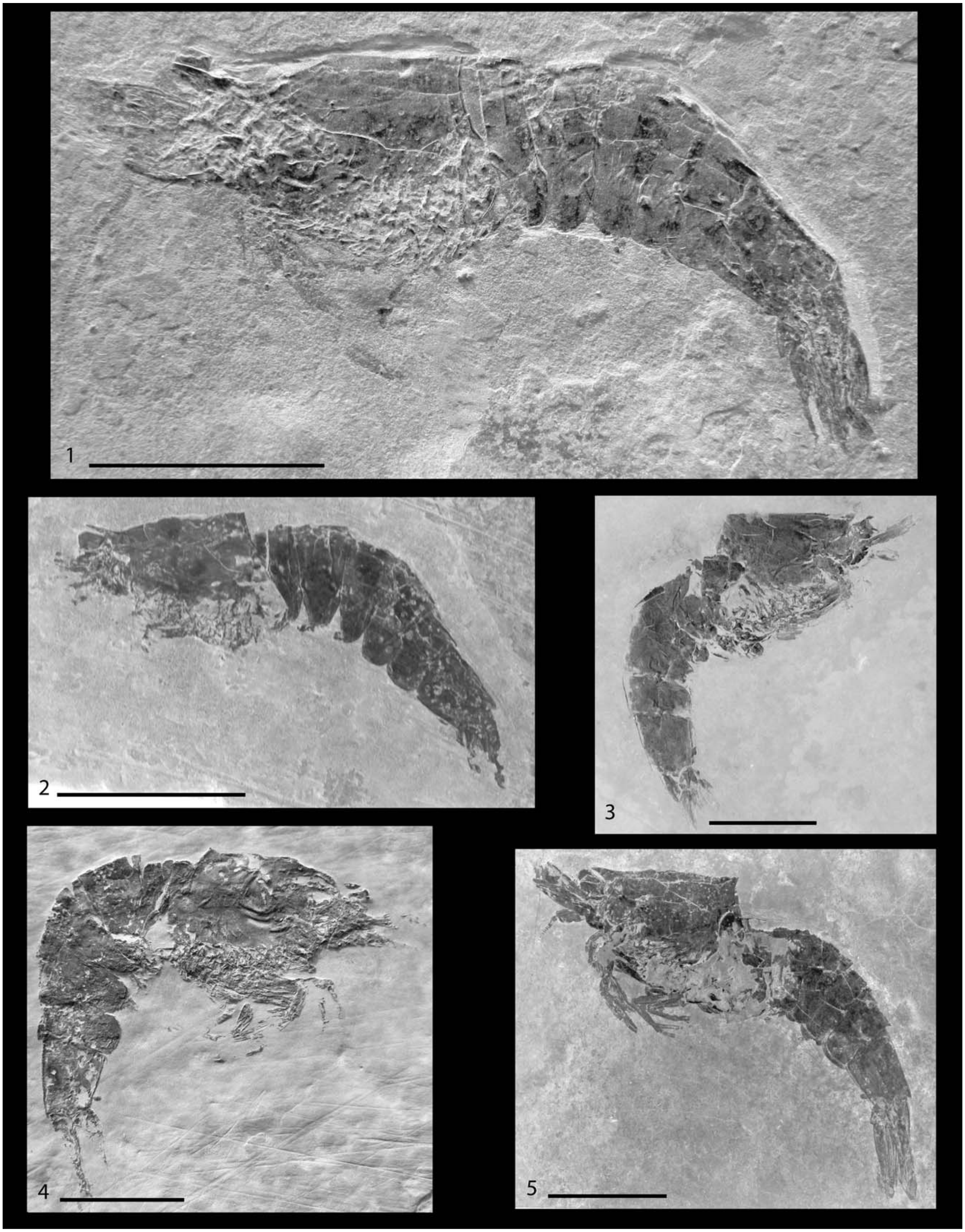

FIGURE 3—*Anisaeger brevispinus* n. gen. n. sp. *1*, LPI-41833, holotype, left lateral view; *2*, LIP-40556, paratype, left lateral view; *3*, LPI-40855, paratype, right lateral view; *4*, LPI-41388b, paratype, right lateral view; *5*, LPI-40751, paratype, left lateral view. Scale bars=1 cm.

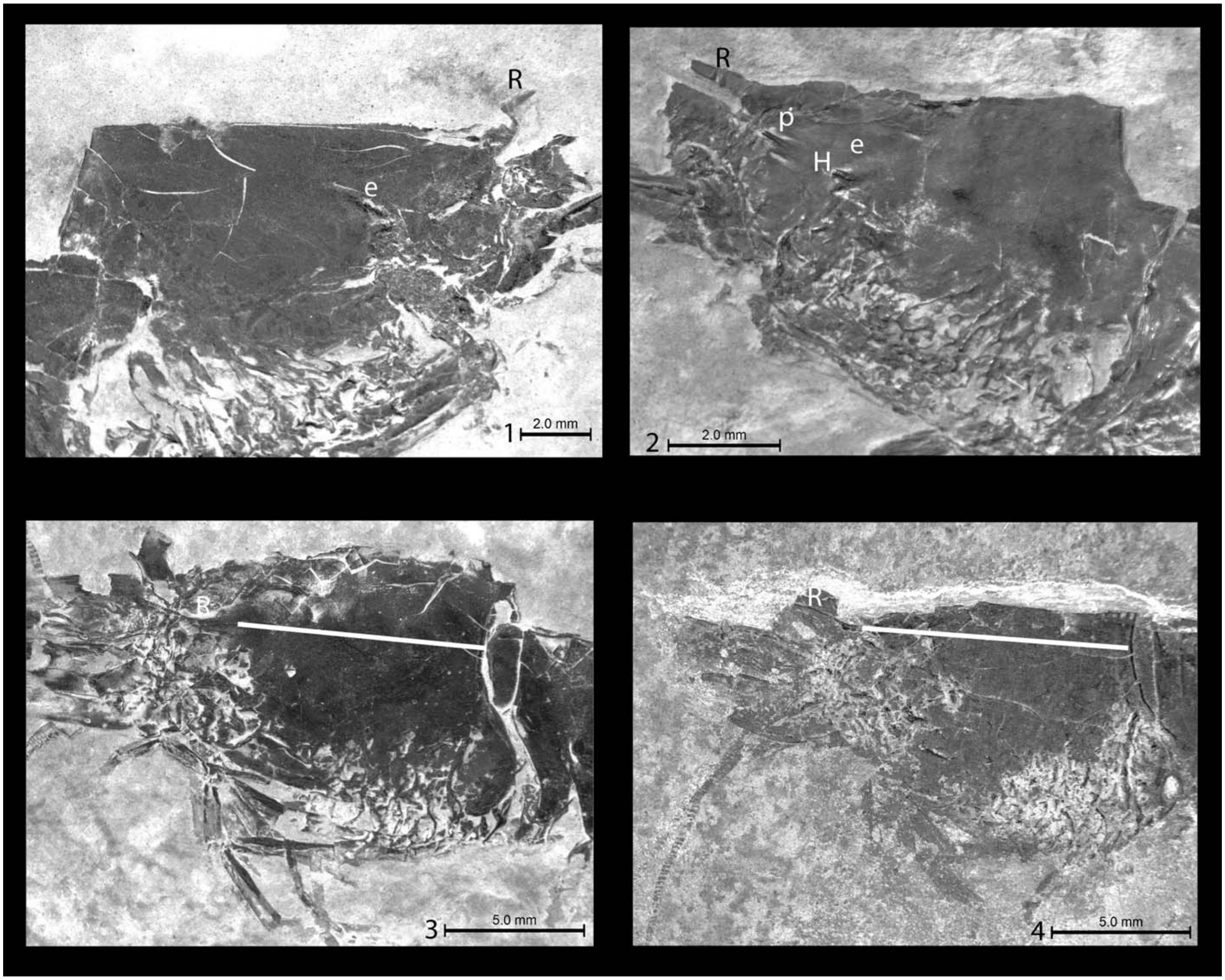

FIGURE 4—*Anisaeger brevispinus* n. gen. n. sp. *1*, LPI-40855, paratype, right lateral view of carapace; *2*, LPI-40718, paratype, left lateral view of carapace; *3*, LPI-40456, paratype, left lateral view of carapace and pereiopods; *4*, LPI-41833, paratype, left lateral view of carapace. R= rostrum; e=cervical groove; p=postantennal spine; H=hepatic spine. White line on *3* and *4* indicates approximate position of midline of dorsal carapace. Scale bars as labeled.

from Member II of the Guanling Formation of early Middle Triassic age.

Remarks.—Distinctions between the two species of *Anisaeger* are based largely on the development of the rostrum, which is short in *A. brevirostris* and long and spinose in *A. spiniferus* and the presence or absence of serrations on the terminal pleonal pleurites, which *A. spiniferus* possesses. *Anisaeger brevirostrus* is far more common that *A. spiniferus*. These features, rostrum length and serrations on the pleonal somites, do not appear to be explainable by sexual dimorphism. One family within Penaeoidea, Aristeidae, has sexually dimorphic rostra. The new specimens do not fit the diagnosis for this family, and there are no indications of dimorphism in the nature of the pleopods, which are moderately preserved in the new specimens.

Descriptions of the two species represent composites of characters taken from numerous specimens owing to the nature of preservation. Thus, specimen numbers and figure numbers are included throughout the description. Crushing and distortion of cuticle has resulted in features of the carapace being obscured. Thus, features such as postorbital and hepatic spines as well as development of the cervical groove may be observed on some specimens but not on others. Because most of the specimens are preserved with both carapace and pleon present, it is possible to assign specimens to one of the two species, based upon their diagnostic characters, with reasonable confidence.

The distortion of the specimens interferes with study of the specimens of both species in the taking of measurements (Tables 1–5). When looking at the various measurements of the pleonal somites, patterns are difficult to discern. There is no real pattern in which specific somites are longer than others. This seems to be due to the taphonomy of the specimens discussed below, the ways in which the somites overlap one another, and difficulty in determining the boundaries between individual somites due to these issues. Thus, the measurements, especially of the pleonal somites, must be taken as approximations of their lengths. It is also difficult to determine the numbering of the pereiopods. Thus, whereas it is clear that some specimens have two chelate appendages, it is difficult to determine which two they are. We are reasonably certain that on some specimens, pereiopods one and two are chelate, and that oneother specimens two and three are chelate, based upon lengths of the appendages and the numbers of appendages anterior and posterior to them. However,

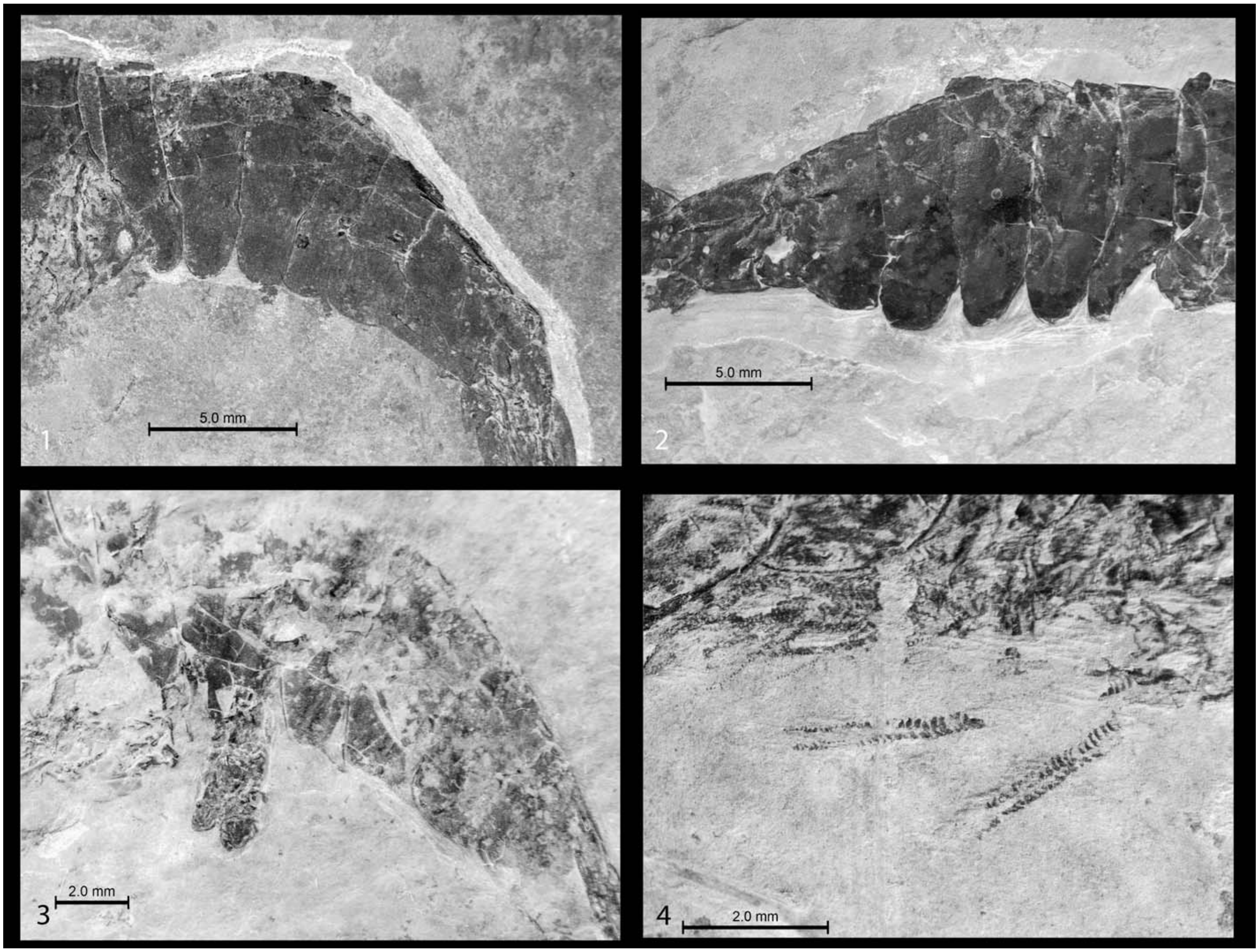

FIGURE 5—*Anisaeger brevispinus* n. gen. n. sp. *1*, LPI-41833, holotype, pleon; *2*, LPI-40758, paratype, dorsal and right lateral view of pleon showing axial keels on somites 5 and 6; *3*, LPI-40065, paratype, pleon showing long bases of pleopods on somite 2; *4*, LPI-40792, paratype showing annulated pleopods. Scale bars as labeled.

the taphonomy of the specimens makes it difficult to be absolutely certain of this interpretation.

ANISAEGER SPINIFERUS new species
Figures 8, 9

Diagnosis.—Carapace with slender, postorbital spine triangular, hepatic spine needle-like; rostrum elongate bearing three suprarostral and one subrostral spine; pleura smooth, with dorsal keel on somite 6; pleura of somites 4–6 with serrate posterior margins.

Description.—Carapace short (Tables 4, 5; all measurements in mm), generally fractured and/or wrinkled, generally smooth overall; dorsal surface gently arched; posterior margin concave dorsally, convex ventrally, rimmed; anterior and ventral margins of carapace obscure. Rostrum long, with at least three basal suprarostral spines (LPI-33315), one subrostral spine (40455, LPI-33315), and three non-basal suprarostral spines (40455), length ranging from one-quarter to one half carapace length (Figs. 8, 9.1–9.3). Postorbital spine triangular; cervical short, inclined anteroventrally at about 45° angle, deep; hepatic spine situated at base of cervical groove, spine needle-like. Endophragmal skeleton with thoracic pleurites present separating intrapleurites (Figs. 8.3, 9.4).

Terga and pleura only differentiated by articulations, not well-differentiated from one another by ornamentation; margins of pleura rimmed. First somite narrow, with straight anterior margin, concave anterior margin of pleuron, convex posterior margin of pleuron, sharp termination directed anteroventrally. Somite two angular, weakly concave anteriorly, weakly convex posteriorly, sharp termination. Somite three triangular, longest of all somites, posterior margin serrate. Somite four with rounded posterior margin, margin posteriorly serrate, with sharp termination. Somite five serrate, very bulbous and rounded with marked notch just above rounded posterior margin, posteroventral corner acute (Fig. 9.6). Somite six with dorsal keel and dorsal posterior terminal spine. Telson slender, triangular, shorter than uropods. Endopod of uropods with keel, lanceolate (Figs. 8, 9.5, 9.6).

Eye appears square; scaphocerite two-thirds length of carapace, lanceolate, axially keeled; antennal and antennular bases slender, antennal flagellum long, much longer than carapace. Preserved portion of pereiopods uniform in size and shape (Fig. 9.4). Pleopods proximally styliform, may have other portions extending ventrally from styliform portions (Figs. 8.1, 9.6).

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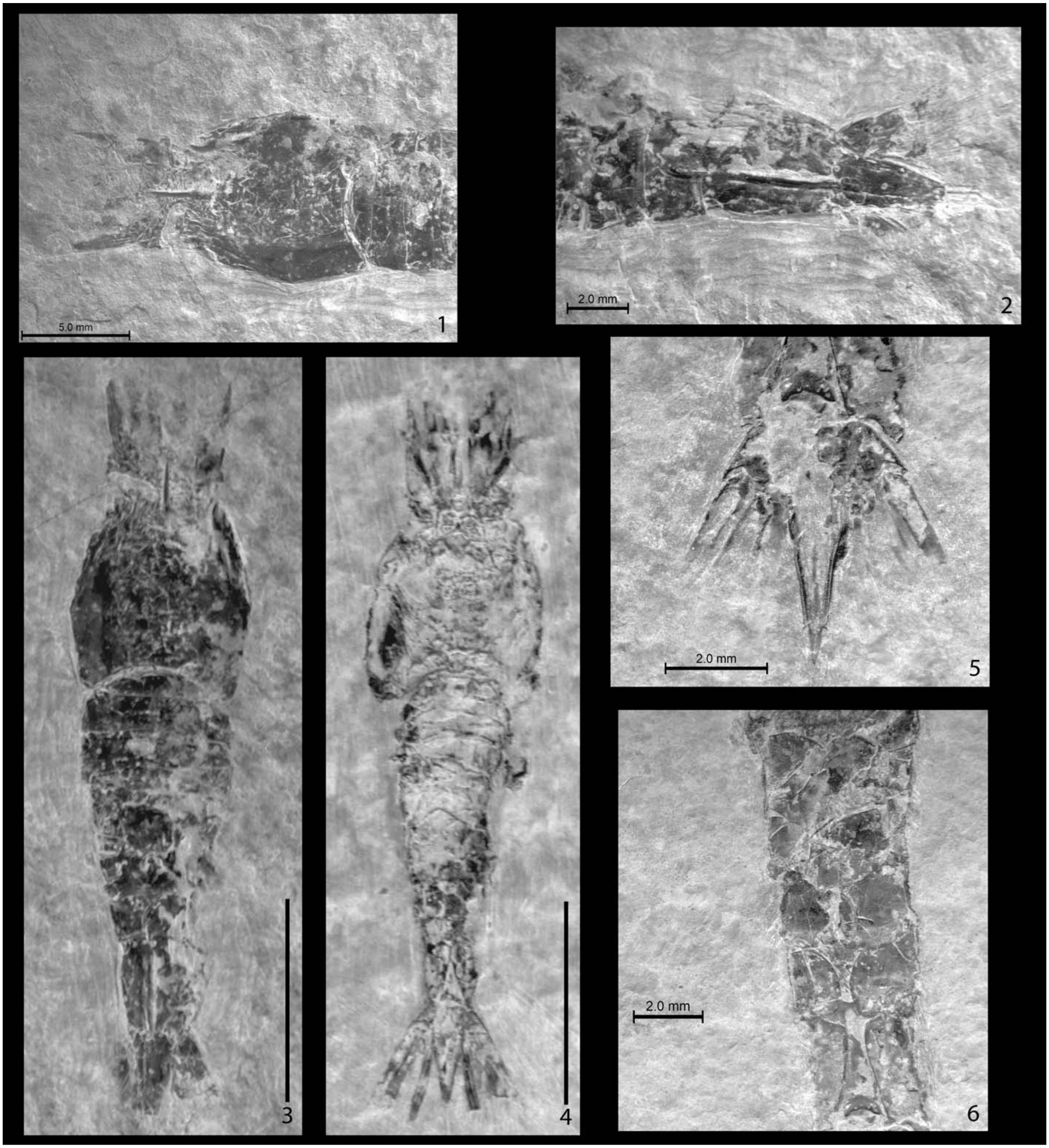

FIGURE 6—*Anisaeger brevispinus* n. gen. n. sp. *1*, LPI-40767, paratype, dorsal view of carapace and scaphocerites; *2*, LPI-40767, paratype, dorsal view of posterior pleon, showing dorsal keel on somites 5 and 6, telson, and uropods; *3*, LPI-40767, paratype, dorsal view; *4*, LPI-4073, paratype, ventral view; *5*, LPI-41315, paratype, ventral view of telson and uropods, showing movable spines and tiny setal pits on ventral surface of telson; *6*, LPI-41315, paratype, ventral view of pleon showing overlap of somites ventrally. Scale bars=1 cm or as labeled.

Etymology.—Alludes to the spinose nature of the rostrum.

Types.—The holotype is LPI-40455, and paratypes include LPI-40474, LPI-33315, LPI-33316.

Occurrence.—The genus is based upon specimens collected in a quarry 20 km southeast from the city of Luoping, approximately N 24°50′, E 104 °30′, Yunnan Province, China. The fossils were collected from Member II of the Guanling Formation of early Middle Triassic age.

Remarks.—The development of a spinose rostrum that is considerably longer than the eye and the presence of serrated margins on the pleonal pleura of somites 4–6 serve to distinguish *A. spiniferus* from *A. brevirostrus*. Pleonal somite one is narrower

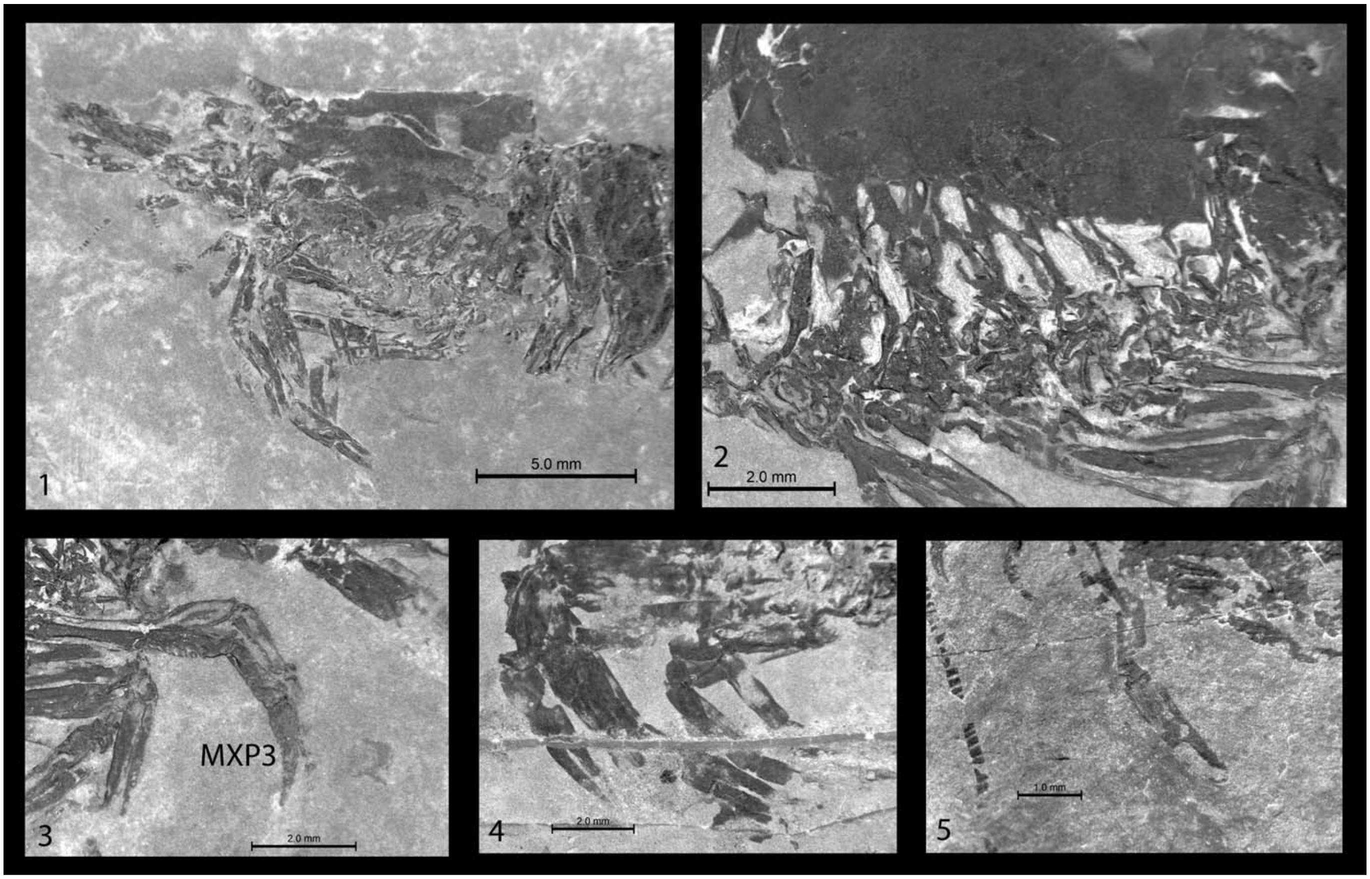

FIGURE 7—*Anisaeger brevispinus* n. gen. n. sp. *1*, LPI-40864, paratype, carapace and appendages; *2*, LPI-41491, paratype, endophragmal skeleton; *3*, LPI-41491, paratype showing the third maxilliped (MXP3), note tiny bases for movable spines or setae; *4*, LPI-40850, paratype, close-up of appendages, anterior-most with possible chela; *5*, LPI-41392, paratype, appendages including what appear to be two chelae. Scale bars as labeled.

TABLE *1*—Measurements (in mm) taken on the carapace and anterior appendages of specimens of *Anisaeger brevispinus* n. gen. n. sp. Specimen numbers in row one are LPI numbers.

	40556	41833	40751	10767	41765	41392	40758	41388b
Carapace length excluding rostrum	7.0	9.4	9.8	7.0	6.2	6.2	11.0	9.0
Carapace length including rostrum	8.2	10.3	10.9	–	7.6	5.5	10.0	–
Carapace height	4.6	–	5.8	–	–	3.0	–	7.0
Length of scaphocerite	–	5.1	4.7	3.0	–	3.2	5.0	–
Width of base of scaphocerite	–	1.0	–	0.9	–	–	–	–
Length of antennal flagellum	–	>31.3	–	–	>14.4	>16.9	–	>43.2
Antennal base length	–	–	1.1	–	2.5	1.3	–	–
Antennal base height	–	–	0.7	–	0.5	–	–	–
Length of antennular flagellum	–	–	–	–	>16.7	–	–	–
Antennular base length	–	–	–	–	3.4	–	–	–
Antennular base height	–	–	–	–	0.8	–	–	–

TABLE *2*—Measurements (in mm) taken on pereiopods of *Anisaeger brevispinus* n. gen. n. sp. Specimen numbers in column one are LPI numbers. P=pereiopod.

	P2? propodus length including finger	P2? propodus length excluding finger	P2? propodus height	P2? dactylus length	Carapace length excluding rostrum	Carapace length including rostrum	P3? propodus length including finger	P3? propodus length excluding finger	P3? propodus height	P3? dactylus length
40447	3.5	2.7	0.6	–	8.1	–	2.3	–	0.4	–
40748	1.7	1.3	0.4	–	6.6	7.4	–	–	–	–
41392	–	–	–	–	6.1	–	2.3	1.2	0.5	–
40864	3.3	1.9	0.8	1.5	~8.2	–	3.7	2.7	1.1	1.6
40850	4.4	2.1	1.0	2.0	~13.4		4.3	2.2	1.0	–
							Carpus length	Carpus height		
40751	4.4	2.9	0.7	–	11.1	–	1.1	0.5	–	–

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TABLE 3—Measurements (in mm) taken on pleonal somites and telson and uropodal elements of *Anisaeger brevispinus* n. gen. n. sp. Specimen numbers in row one are LPI numbers.

	40848	41833	40854	40703	40556	40550	40751	40855	41388b
Length of first pleonal somite	2.5	1.9	–	–	1.7	1.9	–	–	–
Length of second pleonal somite	4.5	3.5	–	–	3.0	2.9	–	–	5.6
Length of third pleonal somite	~5.9	4.0	–	–	3.9	3.6	3.3	4.5	4.3
Length of fourth pleonal somite	–	–	–	–	3.6	4.3	2.9	4.3	4.3
Length of fifth pleonal somite	–	2.6	–	–	2.7	4.1	3.4	4.2	2.9
Length of sixth pleonal somite	5.5	5.9	–	–	4.5	5.0	5.4	6.0	5.7
Length of telson	4.9	6.5	5.8	4.6	–	~5.0	4.9	6.0	–
Width at base of telson	1.8	1.7	–	1.6	–	–	~1.7	–	–
Length of exopod of uropods	5.6	6.4	7.9	5.7	–	–	6.0	–	–
Width of exopod of uropods	1.3	–	–	1.3	–	–	–	–	–
Length of endopod of uropods	–	–	–	5.5	–	–	–	–	–
Width of endopod of uropods	–	–	–	0.7	–	–	–	–	–

and has straight margins, whereas that of *A. spiniferus* has straight margins dorsally and convex margins ventrally. Although the form of the hepatic and postorbital spines are described as somewhat different, the nature of preservation of specimens makes distinction of the two species on this basis problematic.

DISTAEGER new genus

Type species.—*Distaeger prodigiosus* new species, by original designation and monotypy.

Diagnosis.—As for type species.

Etymology.—Derived from the Latin *disto*, meaning to be separate, to differ, and *Aeger*, the type genus of Aegeridae. The gender is masculine.

Occurrence.—The genus is based upon specimens collected in a quarry 20 km southeast from the city of Luoping, approximately N 24°50′, E 104 °30′, Yunnan Province, China. The fossils were collected from Member II of the Guanling Formation of early Middle Triassic age.

Remarks.—*Distaeger* differs sufficiently from the other three genera within Aegeridae to warrant a separate genus. The third maxillipeds in *Distaeger* are about as long as the first and second pereiopods and more robust than all of the other appendages, different than in the other three genera within the family. Critically, the maxillipeds preserve large pits for spines or setae that appear to have been forward-directed but lack the structures themselves. The pereiopods are smooth and lack spines or setae or pits to accommodate them. The third pereiopods are longest, although the fourth and fifth are also longer than the first and second pereiopods. The rostrum is extremely long, constituting 40 percent of the carapace length. The exopods of the uropods exhibit a clear diaeresis. Such a combination of characters is not seen in any of the other three genera within Aegeridae. Within *Acanthochirana*, the rostrum is short, barely extending beyond the eyes where known. In *Anisaeger*, the third maxillipeds and pereiopods are short and slender and the exopod of the uropod lacks a diaeresis. *Aeger* is more variable, but all known species have spinose third maxillipeds that are longer than the first pereiopods, whereas those of *Distaeger* are about the same length as the first and second pereiopods and only exhibit pits for either spines or setae.

DISTAEGER PRODIGIOSUS new species
Figures 10, 11

Diagnosis.—Carapace longer than high; rostrum very long, 40 percent length of carapace, with one basal suprarostral spine and one subrostral spine at midlength; uropodal exopod with diaeresis; ventral lateral margins of telson with setal pits, appearing to extend entire length of telson; third maxilliped about as long as first and second pereiopods, with spine bases or setal pits along propodal and dactyl ventral margin; pereiopods 1–3 chelate, third pereiopod longest, fourth and fifth longer than first and second, pereiopods without spines; pleopods apparently with multiarticulate flagellae.

Description.—Carapace longer than high, carapace height measured at mid-length (~27.00 mm) about 62 percent length excluding rostrum (43 mm); dorsal surface weakly convex, posterior and ventral margins of carapace obscure, carapace generally smooth; rostrum long, slender, upturned, sinuous, concave upward proximally and straightening near tip, one basal suprarostal spine and one subrostral spine positioned at about midlength (Fig. 11.1), extends well beyond eyes, rostral length 28.7 mm, 40 percent carapace length (Fig. 10.2).

Posterior margin and ventral margin with very narrow, smooth rim; carapace thin, crushed. Endophragmal skeleton visible beneath carapace cuticle which is draped over it. No carapace ornamentation visible.

Terga of somites uniformly smooth. First pleonal somite (length [L]=3 mm) narrower than second, high, pleuron concave forward, weakly convex posteriorly, with acute, anteroventrally directed tip, overlapping somite two slightly. Pleuron of second somite with slightly convex anterior margin, L=~5 mm, nearly straight posterior margin, ventral margin nearly straight, directed anteroventrally. Third somite pleuron longer than high, L=17 mm, anterior margin sinuous, broken, ventral margin smoothly

TABLE 4—Measurements (in mm) taken on the carapace and anterior appendages of specimens of *Anisaeger spiniferus* n. gen. n. sp. Specimen numbers in row one are LPI numbers.

	40455	40474	33315	33316
Carapace length excluding rostrum	7.0	6.2	3.0	8.3
Carapace length including rostrum	13.3	8.1	6.1	12.2
Length of scaphocerite	5.0	3.5	3.4	4.5
Width of base of scaphocerite	1.1	–	–	1.3
Length of antennal flagellum	–	–	>5.3	–
Length of antennular flagellum	–	–	>9.8	>8.6

TABLE 5—Measurements (in mm) taken on pleonal somites and telson and uropodal elements of *Anisaeger spiniferus* n. gen. n. sp. Specimen numbers in row one are LPI numbers.

	40455	40474	33315	33316
Length of first pleonal somite	0.3	0.7	–	1.4
Length of second pleonal somite	1.5	1.9	–	2.6
Length of third pleonal somite	2.7	2.5	1.1	2.7
Length of fourth pleonal somite	2.0	3.3	0.9	4.1
Length of fifth pleonal somite	1.2	1.6	1.1	2.7
Length of sixth pleonal somite	2.0	3.7	2.2	4.3
Length of telson	1.7	4.3	2.3	4.1
Width at telson base	–	–	0.5	–
Length of exopod of uropods	–	–	2.9	–

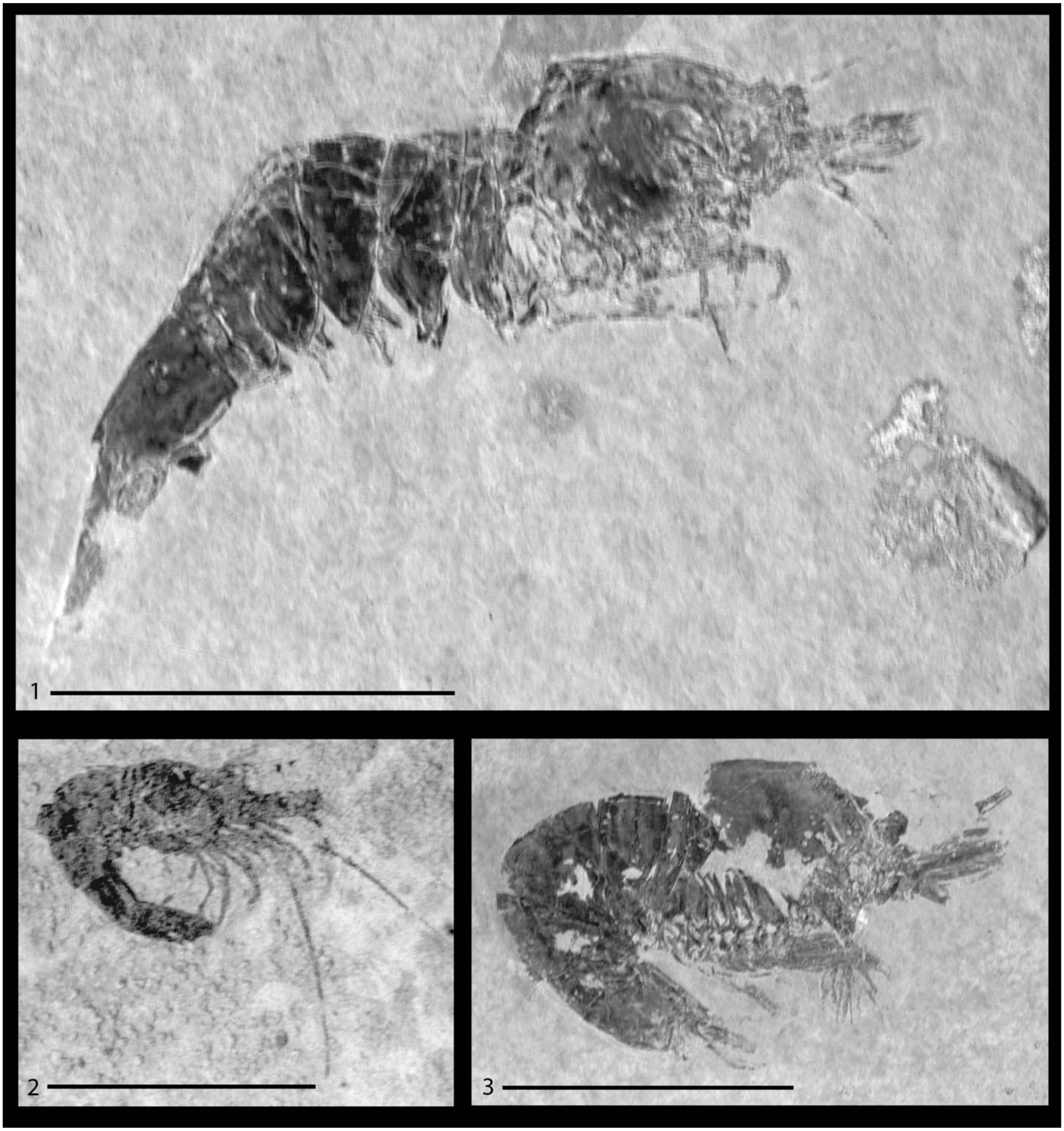

FIGURE 8—*Anisaeger spiniferus* n. gen. n. sp. *1*, LPI-40474, paratype, right lateral view; *2*, LPI-33315, paratype, right lateral view; *3*, LPI-40455, holotype, right lateral view. Scale bars=1 cm.

rounded, posterior margin straight. Fourth somite with pleuron about as long as wide, L=6 mm, ovoid. Fifth somite with rounded pleuron wider than long, L=9 mm, circular, pleura become wider posteriorly from 1–5, margins of all pleura with narrow rim. Somites 4 and 5 with rounded notch at point of articulation between terga and pleura on posterior margin. Somite 6 apparently rectangular, broadly rounded ventral margin, L=12.3 mm. Telson uniformly straight sided, triangular, ventral lateral margins of telson with setal pits, appearing to extend entire length of telson; axially keeled, L=11.6 mm, width at base=3 mm.

Uropods longer than telson; exopod and endopod weakly convex on inner and outer surfaces; anterolaterally directed diaeresis-like structure near tip of exopod of uropod (Fig. 11.6); exopod with narrow thickened rim on outer margin, L=16 mm; basal element of uropod with moderate to strong spine on posterolateral corner, L=19 mm, width about 5 mm.

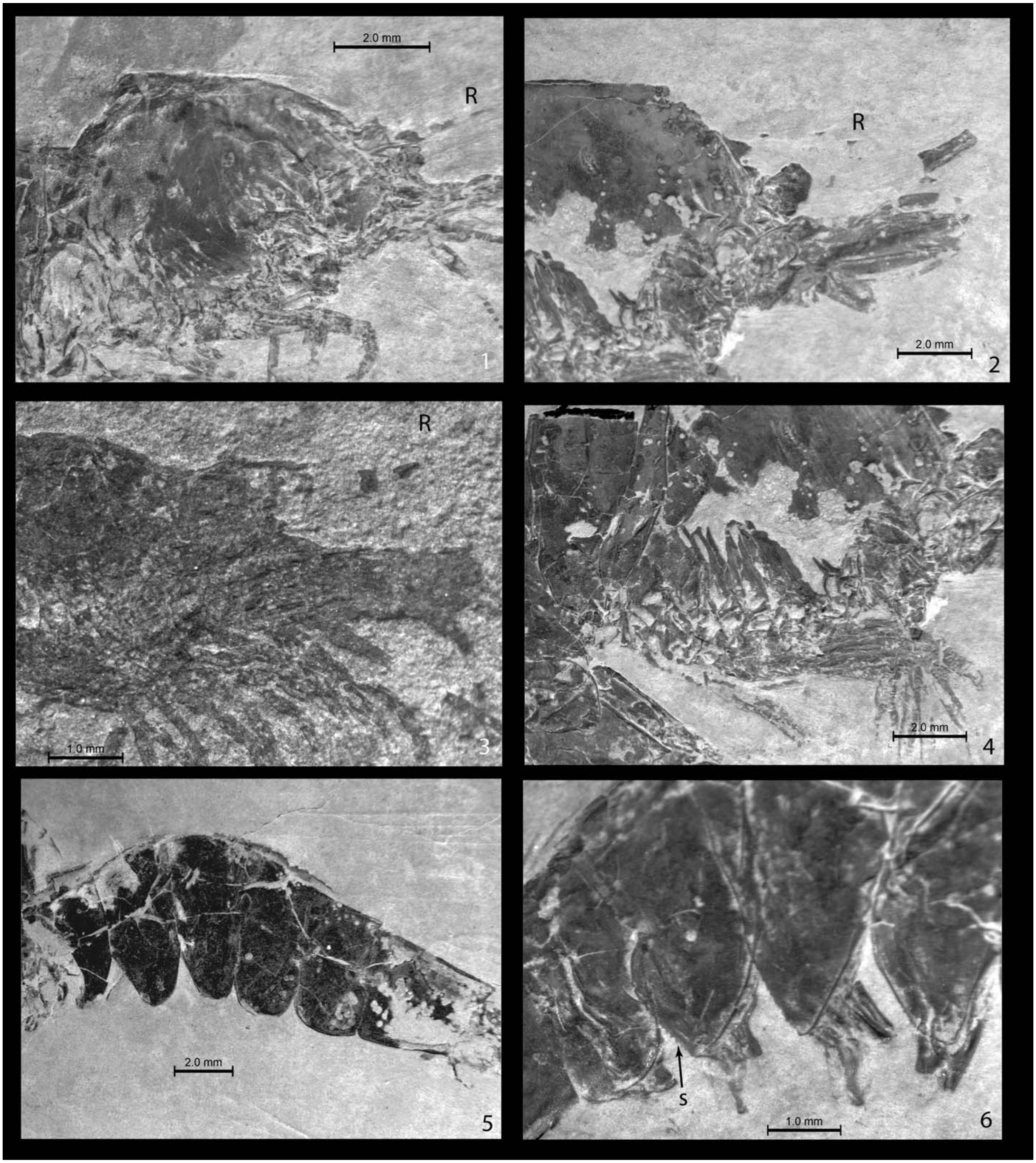

FIGURE 9—*Anisaeger spiniferus* n. gen. n. sp. *1*, LPI-40474, paratype, carapace showing rostrum (R); *2*, LPI-40455, holotype, carapace showing rostrum (R), scaphocerite, and eye; *3*, LPI-33315, paratype, showing rostrum (R); *4*, LPI-40455, holotype, endophragm and appendages; *5*, LPI-33316, paratype, pleon; *6*, LPI-40474, paratype, pleon indicating serrations on somite. Scale bars as labeled.

Basal element of antennule slightly longer than high, L=2.9, height (H)=2.7, with serrate distal margin, ventral distal spine; second basal element, punctate, discrete row of punctae along upper surface, single row of punctae arcuate and subparallel to distal margin, rectangular, ventral spine at about half length; third basal element poorly exposed ventrally, apparently rectangular, higher than long, punctate (Fig. 11.2); antennular flagellae paired, longer than carapace, at least 31 mm. Antennular stylocerite

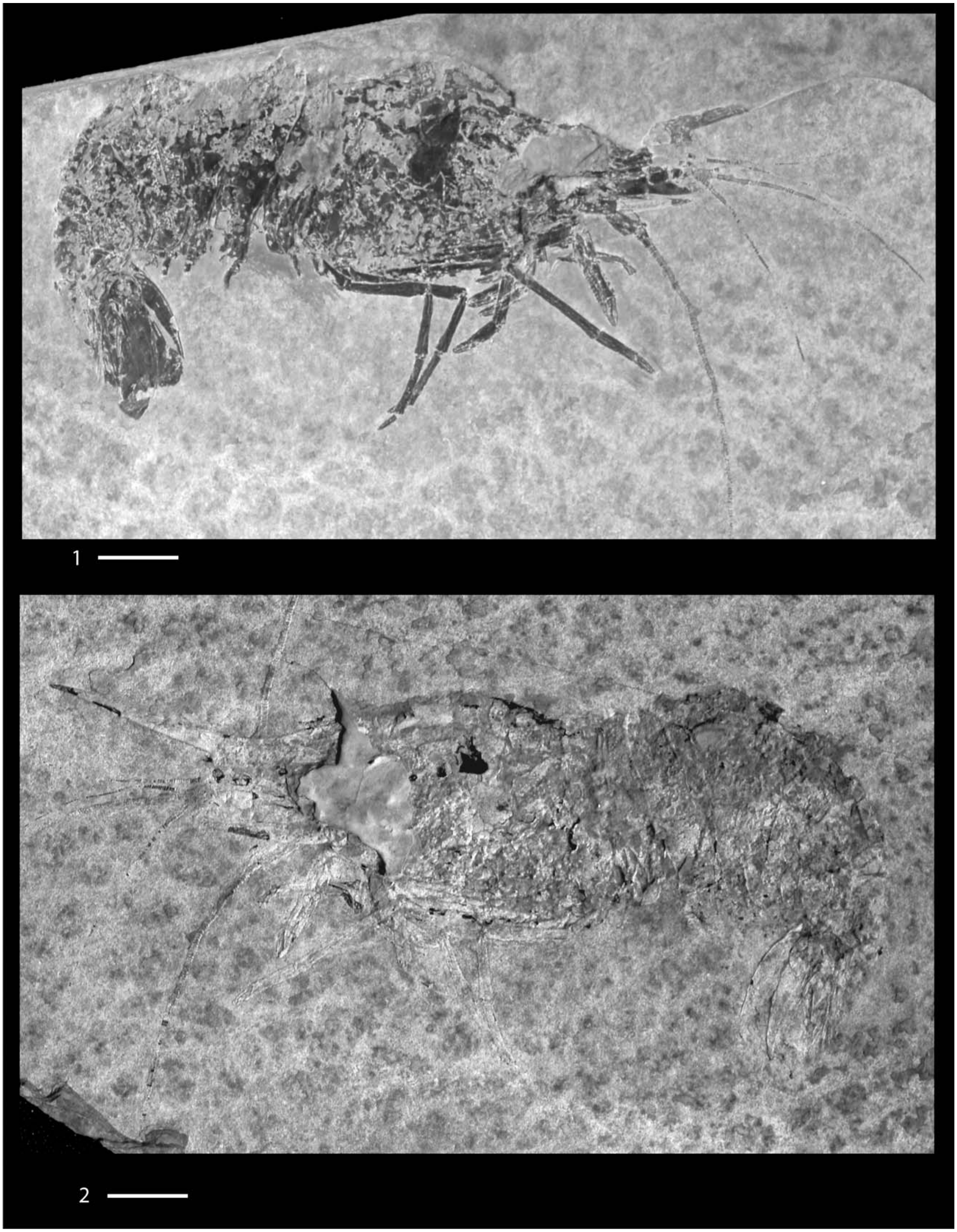

FIGURE 10—*Distaeger prodigiosus* n. gen. n. sp. *1*, LPI-41666A, holotype part, right lateral view; *2*, LPI-41666B, holotype counterpart. Scale bars=1 cm.

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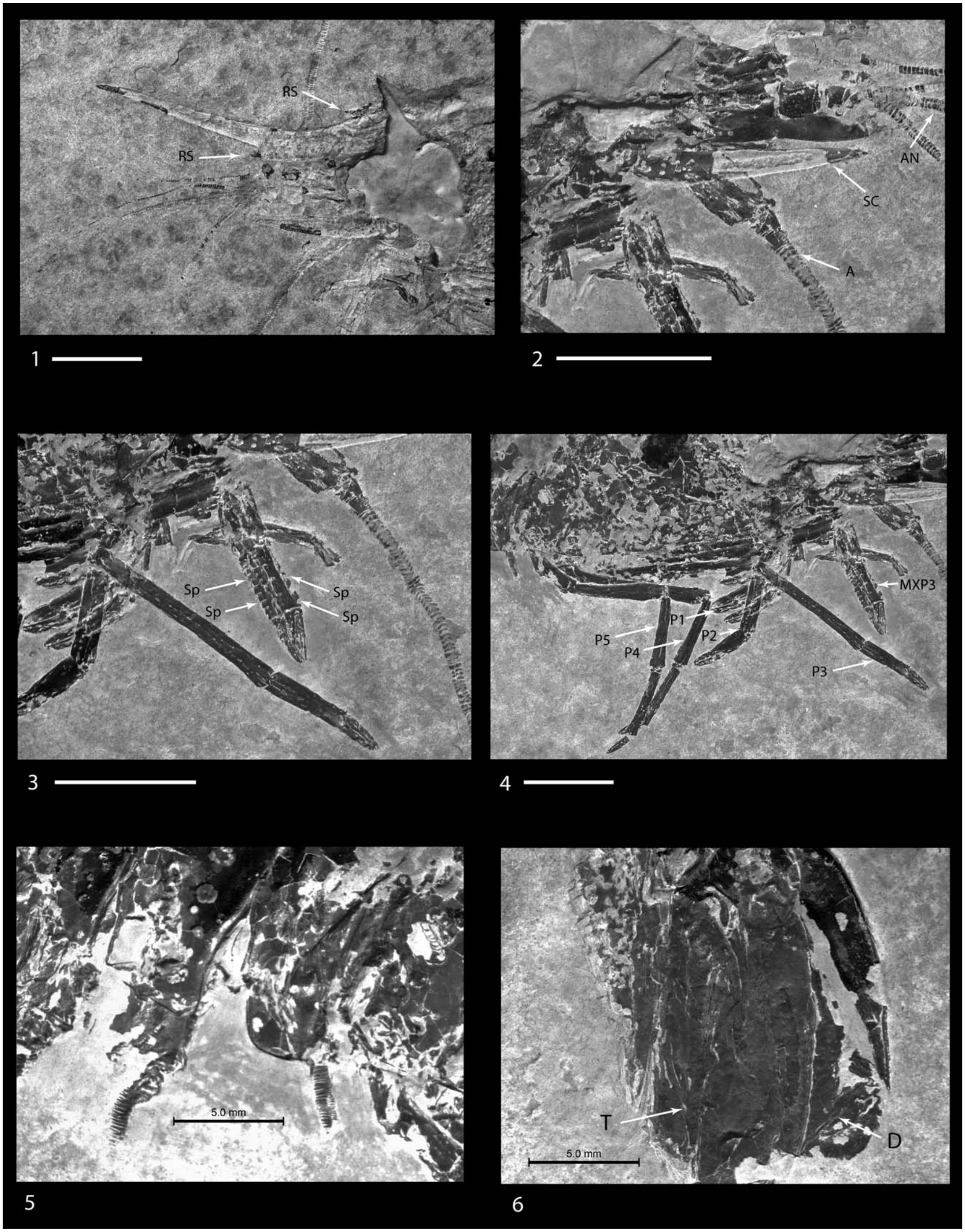

FIGURE *11*—*Distaeger prodigiosus* n. gen. n. sp., LPI-41666, holotype. *1*, enlargement of rostrum on counterpart showing rostral spines (LPI-41666B); *2*, frontal region of part showing antennules, antenna, and scaphocerite (LPI-41666A); *3*, enlargement of anterior region of part showing setal pits on third maxilliped (LPI-41666A); *4*, pereiopods and maxilliped 3 preserved on LPI-41666A; *5*, enlargement of anterior pleura on part showing flabellate proximal and annulated distal ends of pleopods (LPI-41666A); *6*, telson and right uropods preserved on part showing diaeresis on exopod of uropod (LPI-41666A). Abbreviations: A=antenna; AN=antennule; D=diaeresis; MXP3=maxilliped 3; P1–P5=pereiopods; RS=rostral spine; SC=scaphocerite; SP=setal pits; T=telson. Scale bars=1 cm on *1*–*4*, others as labeled.

TABLE 6—Measurements (in mm) taken on third maxilliped and pereiopods of *Distaeger prodigiosus* n. sp. (LPI-41666A). Abbreviations: I=Ischium; M=Merus; C=Carpus; P=Propodus; D=Dactylus; L=Length; H=Height.

	IL	ML	MH	CL	CH	PL	PH	DL	DH
Third Maxilliped						11.2	2.7	3.8	2.3
Pereiopod 1								3.5	0.8
Pereiopod 2				6.8	1.7	6.7	1.8	3.1	0.8
Pereiopod 3		10.0	1.0	15.5	1.3	14.1	1.8	3.4	0.7
Pereiopod 4	4.6	11.4	2	8.3	1.3	7.9	1.1		
Pereiopod 5		11	2	8.3	1.8	7.9	1.4	3.1	0.9

lanceolate, extends distally beyond antennular base, surface smooth (Fig. 11.2). Antennal bases with distal basal element longer than high, L=10 mm, H=3.3, rectilinear; flagella long, L=54 mm (Fig. 11.). Scaphocerite long, L=15.2, width at base 3.3 mm, slender, lanceolate, smooth, longer than antennal base (Fig. 11.2).

Pleopods flabellate basally, rounded termination, longer than wide, generally uniformly wide for entire length. One multiarticulate flagellum present on pleopods two through five; pleopod one indicates a pair of flagellae; pleopods appear to be more or less the same throughout all somites (Fig. 11.5).

Third maxilliped moderately long (measurements in Table 6), pediform; merus longer than high, smooth; carpus broken; propodus long, slender, upper and lower margins scalloped from presence of forwardly directed setal pits; dactylus tapers to sharp termination, with setal pits along lower margin; third maxilliped directed generally anteroventrally (Fig. 11.3).

Pereiopods slender, first two pairs shortest, third longest, fourth and fifth most slender, of equal length (Fig. 11.4). First three pairs chelate. Pereiopod one short; chelae moderately stout, smooth. Pereiopod 2 more slender than pereiopod 1, chela more slender than chela of pereiopod 1, occlusal surfaces with very fine denticles set in herringbone pattern. Pereiopod 3 very long, very slender, with setal pits extending along outer surface of carpus and propodus, chela very slender, fingers edentulous. Pereiopods 4 and 5 very long, slender, carpus, propodus, and dactylus punctuate along outer surface.

Etymology.—The Latin word *prodigiosus* means wonderful, large, alluding to the large size and good preservation of the type specimen.

Type.—The holotype consists of a part (LPI-41666A) and counterpart (LPI-41666B) of a single specimen.

Occurrence.—The specimens were collected in a quarry 20 km southeast from the city of Luoping, approximately N 24°50′, E 104 °30′, Yunnan Province, China. The fossils were collected from Member II of the Guanling Formation of early Middle Triassic age.

Remarks.—The new species is known from only one, very well preserved specimen.

TAPHONOMY

Observations.—The presentation of the shrimp from the Luoping Biota poses some perplexing taphonomic problems. Shrimp are generally laterally compressed so that, upon death, they tend to lie on the substrate with either the right or left side parallel to the bedding planes. As a result, the general aspect of fossil shrimp is the lateral view. This orientation is almost invariably seen regardless of the unit from which specimens are collected. As just one example, Figure 2 illustrates two specimens from the Solnhofen Limestone in Bavaria. Both of the specimens are preserved in lateral aspect as would be expected. This is the attitude of nearly all specimens collected from the Solnhofen-type limestone sites (G. Schweigert, personal commun. to RMF, 2012). As another example, Pinna (1975 [imprint 1974]) and Garassino (1994) illustrated Triassic shrimps from Italy, and all are in lateral position, although some are somewhat twisted and disarticulated as seen in the Luoping shrimp as described below. None is illustrated in dorsal or ventral view. Observation of specimens in the "normal" lateral aspect facilitates recognition and description of morphological features. When specimens are preserved in some other orientation, description can be problematic.

The shrimp from the Luoping biota are only sometimes preserved in the typical lateral aspect. Rather, specimens may be oriented in such a way as to expose the lateral aspect of one side along with a substantial portion of the opposite side suggesting that a shear force had plastically deformed the remains (Fig. 5.2). The majority of the specimens observed tend to be complete but deformed. That is, the cephalothorax and pleon are preserved together, although the pleon may be somewhat displaced (Fig. 3.5). Partial remains of pereiopods are often preserved as well and, in some cases, pleopods are also visible (Fig. 5.4). In several cases, the cephalothorax and pleon are deformed to different degrees. The cephalothorax may be strongly deformed whereas the pleon is presented in "normal" lateral aspect (Fig. 4.3).

In addition to the rotation out of the typical lateral aspect, some specimens are preserved in dorsal or ventral aspect (Fig. 6). This is an extremely uncommon position for shrimp to be preserved. The specimens in which these orientations are observed tend to have the carapace and pleon in perfect alignment suggesting that the position was original and not the product of shearing and rotation.

The cuticle of most shrimp is relatively thin and weakly calcified. Thus, the cuticle is soft, flexible, and readily susceptible to plastic deformation. That the cuticle of the Luoping shrimp exhibits these properties is indicated by observing that one part of the exoskeleton, such as a pleonal pleuron may be observed despite its lying below an adjacent pleuron (Fig. 5.4). Further, in many of the specimens studied, the surface of the cuticle is wrinkled (Fig. 3.4). This manner of deformation from the original form is rarely observed in lobsters and crabs in which the cuticle is more strongly calcified and tends to be brittle.

Although the cuticle is thin and pliable, some specimens exhibit fractured and displaced bits of cuticle, apparently resulting from brittle deformation (Figs. 3.5, 4.1, 9.4). Fractures attributable to brittle deformation resulted in straight or intersecting breaks and displacement of cuticle elements only a millimeter or two. Because the shrimp were collected from discrete bedding planes and because they are common on those bedding planes, it is reasonable to suggest that, although not observed directly in the field, specimens exhibiting plastic and brittle deformation occurred on the same bedding planes.

None of the specimens observed bore any evidence of predation or scavenging and none was invested with epibionts. Rather, the carapace material was clean, and any breaks and displacement or loss of parts of the specimens could be attributed to collecting and preparation damage.

Interpretation.—Based upon the observations on the Luoping shrimp, the following interpretation of the taphonomic history is suggested. The shrimp were judged to be gregarious, based upon the large number and relatively close proximity of specimens preserved. Absence of epibionts suggests that the shrimp were either swimmers or exhibited efficient cleaning mechanisms. Possession of spinose or setose third maxillipeds and/or pereiopods suggests a benthic habit in which those appendages could be used for feeding on soft sediment or grooming. Upon death, the specimens were rapidly buried so that scavenging of remains did not efficiently reduce the numbers of potentially preservable individuals. Preservation of the shrimp as relatively intact corpses or molts also suggests very rapid burial, as decay experiments indicate rapid disarticulation even after only several days of decay (Plotnick, 1986). Partial remains with bite marks or other evidence of scavenging or predation were not observed. Although most of the specimens came to rest lying on one side or the other, some few were oriented with the dorsal or ventral surface parallel to the substrate. This orientation, although unlikely and only rarely observed, probably was made possible by the large scaphocerites being extended laterally to stabilize the individuals in this otherwise unstable orientation.

Although many of the specimens were preserved with the pleon rotated away from the carapace, there is no clear evidence that the specimens represent molts rather than corpses. The articular membranes securing the pleon to the carapace are extremely thin and would have been subject to dissociation with only slight decomposition (Plotnick, 1986). Similarly, some specimens have the endophragm exposed and displaced ventrally relative to the carapace. As with the displacement of the pleon, this position could readily result from decomposition of the corpse. The presence of so many specimens exhibiting complete remains including appendages, within the limits of preservation, suggests death and rapid burial of individuals. The large number of individuals on discrete bedding planes suggests that their death might represent a short duration, toxic event.

Upon death and burial, the overlying sediment, while not yet completely dewatered and lithified, shifted and resulted in the shear forces that deformed the corpses. This event was possibly in the form of subaqueous slumping on an irregular seafloor and did not reflect a large displacement. Whether the specimens were deformed as plastic or brittle objects may have been a result of the rate of displacement of the sediment or the degree of flexibility of the individual specimen.

Future work.—Several questions remain unanswered. If one interprets the deformation of specimens to be the result of overlying sediment exerting a shear force on the specimens, it could be hypothesized that the specimens would exhibit a preferred orientation such that the same forces would have acted on numerous specimens in close proximity. If the specimens displaying brittle deformation as opposed to plastic deformation do occur in close proximity to one another, suggesting that different shear forces were involved, it might be possible to test whether the cuticle of the various individuals represents different stages of the molt cycle and, therefore, different degrees of calcification. Finally, if the accumulation of a large number of individuals on discrete bedding planes represents a short term event, geochemical examination of the sediment might provide confirming evidence. These studies, and others, related to the occurrence of the Luoping shrimp, must await further studies.

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