Journal of Paleontology, 86(3), 2012, p. 425–441

0022-3360/12/0086-0425$03.00

MACRUROUS DECAPODA FROM THE LUOPING BIOTA (MIDDLE TRIASSIC) OF CHINA

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ABSTRACT—A large collection of macrurous decapod crustaceans is recorded from the middle–late Anisian (Middle Triassic) Guanling Formation in Yunnan Province, China. A remarkable assemblage of over 20,000 vertebrate, invertebrate, and plant fossils collectively referred to as the Luoping Biota has been collected from quarries in the vicinity of the city of Luoping. Among these, arthropods including the decapods are the most common element although articulated fish and reptiles are also common. The decapods represent new taxa, including *Koryncheiros luopingensis* n. gen. n. sp. within Clytiopsidae, a newly elevated family within Erymoidea; *Tridactylastacus sinensis* n. gen. n. sp. within Glypheidae; and *Yunnanopalinura schrami* n. gen. n. sp. within Palinuridae. A single specimen has been referred to Palinuridae sp. *Koryncheiros luopingensis* exhibits a unique cheliped architecture and the second through fourth chelipeds are subchelate, an extremely rare configuration. *Tridactylastacus sinensis* also exhibits subchelate closures of pereiopods 2–4, but it bears a distinctive subchelate first pereiopod with an intercalated spine between the fingers on the distal margin of the propodus. *Yunnanopalinura schrami* represents the oldest occurrence of Palinuridae and Achelata. Collectively, these expand our knowledge of Chinese decapods significantly in that only six species of fossil decapods have been described previously from the country.

INTRODUCTION

THE LUOPING Biota is an exceedingly well-preserved and abundant assemblage of fossils cropping out in Yunnan Province, southwestern China. The assemblage contains plants, foraminiferans, conodonts, mollusks including ammonites, echinoderms, arthropods, fish, and marine reptiles. Arthropods are estimated to comprise about 94 percent of the approximately 20,000 specimens that have been collected to date. They include myriapods, ostracodes, mysids, conchostracans, limulines, and decapods. Thus far, the decapods that have been examined include shrimp and lobsters. The purposes of this work are to describe the fossil lobsters from the Luoping Biota, to discuss their implications for understanding early Mesozoic radiation of decapods, and to hypothesize on the ecological role played by these organisms. Prior to this work, only six fossil species of decapods have been described from China (Table 1), a country approximately the size of the United States. The supposition that the decapod fauna of the country is underrepresented in the descriptive literature adds even more significance to the Luoping specimens.

The fossiliferous beds containing the Luoping Biota lie within the middle part of Member II of the Guanling Formation, and their stratigraphic relationships are detailed by Zhang et al. (2008) and Hu et al. (2011). The beds are exposed in quarries excavated at the tops of hills that represent karst remnants about 20 km southeast from the city of Luoping (Fig. 1). The age of the beds, based upon conodonts, has been determined to be Pelsonian Substage of the Anisian Stage (early Middle Triassic) (Zhang et al., 2009; Hu et al., 2011).

The early Middle Triassic age of the Luoping decapods is of major significance. Little is known about decapod faunas during this time interval. The oldest decapod crustaceans are known from the Late Devonian of North America (Schram et al., 1978; Feldmann and Schweitzer, 2010), but these represent two of only three documented Paleozoic decapods. The youngest Paleozoic occurrence is *Protoclytiopsis antiqua* Birshtein, 1958, from the uppermost Permian of Siberia (Schram, 1980). The geographic expansion and evolutionary radiation of the Decapoda did not really begin until the Triassic with the recognition of the glypheid lobster species *Litogaster turnbullensis* Schram, 1971, from the Olenekian Stage (Early Triassic) of North America and *Paralitogaster durlachensis* (Förster, 1967b) and *P. limicola* (König, 1920), from the Early Triassic of Europe. All subsequent decapod occurrences are from Middle Triassic or younger rocks. In China, a single species *Sinopemphix guizhouensis* Fenglin, 1975, from Guizhou Province, is the only Middle Triassic decapod known. The species described herein substantially expand the number and variety of taxa that are founders of lineages that became more diverse in the mid and late Mesozoic.

The manner of preservation of the Luoping biota is remarkable. The exquisite preservation of most of the specimens led Hu et al. (2011) to refer to the unit as a Lagerstätte. The specimens, preserved in a uniform micritic limestone similar to the Jurassic Solnhofen Limestone in Bavaria, exhibit fine detail. The fish, marine reptiles, and decapods are typically preserved as fully articulated specimens. Most of the well-preserved fossils are flat and compressed on the surface of bedding planes. Microbial mats blanket many of the decapods and other fossils (Hu et al., 2011) which facilitated rapid burial in an articulated state and thus detailed preservation (Gall, 1990; Briggs and Kear, 1993, 1994; Feldmann and Schweitzer, 2010).

SYSTEMATIC PALEONTOLOGY

Repository.—Specimens are deposited in the Invertebrate Paleontology Collection, Chengdu Institute of Geology and Mineral Resources, Chengdu, Sichuan Province, China, and bear the acronym LPI. Other specimens examined for this study are deposited in the United States National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. (USNM).

Terminology.—Some confusion exists in the terminology applied to chelipeds within the clawed lobsters with regard to the nature of the dactylus and the termination of the

TABLE 1—Systematic list of fossil decapod crustaceans collected, to date, from China. The list of taxa is extracted from Schweitzer et al. (2010) and the present work. The geologic ages of the taxa have been extracted from the original works. Species described herein are indicated in bold face.

Order Decapoda Latreille, 1802
  Infraorder Stenopodidea, Claus, 1872
    Spongicolidae Schram, 1986
      Jilinicaris Schram, Yanbin, Vonk & Taylor, 2000
        J. chinensis Schram et al., 2000
          Late Cretaceous (Santonian); Asia (China)
  Infraorder Caridea Dana, 1952
    Palaemonidae Rafinesque, 1815
      Yongjicaris Garassino, Yanbin, Schram & Taylor, 2002
        Y. zhejiangensis Garassino et al., 2002
          Early Cretaceous (Barremian); Asia (China)
  Infraorder Glypheoidea Winkler, 1882
    Clytiopsidae Beurlen, 1927
      Koryncheiros new genus
        K. luopingensis new species
          Middle Triassic (Anisian), Asia (China)
    Glypheidae Winkler, 1882
      Tridactylastacus new genus
        T. sinensis new species
          Middle Triassic (Anisian), Asia (China)
    Pemphicidae Van Straelen, 1928a
      Sinopemphix Fenglin, 1975
        S. guizhouensis Fenglin, 1975
          Middle Triassic; Asia (China)
  Infraorder Astacidea Latreille, 1802
    Cambaridae Hobbs, 1942
      Palaeocambarus Taylor, Schram & Yan-Bin, 1999
        P. licenti (Van Straelen, 1928b) (=*Astacus spinirostrius* Imiazumi, 1938)
          Cretaceous (Early); Asia (China)
    Cricoidoscelosidae Taylor, Schram & Yan-Bin, 1999
      Cricoidoscelosus Taylor, Schram & Yan-Bin, 1999
        C. aethus Taylor, Schram & Yan-Bin, 1999
          Late Jurassic; Asia (China)
  Infraorder Palinura Latreille, 1802
    Palinuridae Latreille, 1802
      Yunnanopalinura new genus
        Y. schrami new species
          Middle Triassic (Anisian), Asia (China)
      Palinuridae sp.
        Middle Triassic (Anisian), Asia (China)
  Infraorder Brachyura Linnaeus, 1758
    Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929
      Notopocorystes M'Coy, 1849
        N. xizangensis Wang, 1981
          Early Cretaceous (Albian); China (Xizang)

propodus. The terms chelate, pseudochelate, subchelate, and achelate have been applied based upon the relative development of a spine or the fixed finger on the propodus. Examination of chelipeds of numerous lobsters leads us to the conclusion that three grades of termination can be readily defined. *Chelate* chelipeds are those in which the fixed finger and dactylus are of equal or nearly equal length. These might be viewed as ''typical'' claws. *Achelate* chelipeds are those in which the dactylus extends from the distal margin of the propodus and in which there is no occlusal surface. Between these two end members, some chelipeds may be defined as *subchelate*; that is, there is some occlusal surface or structure, such as a prominent protruding spine, on the distal margin of the propodus, but the projection is not nearly as long as the dactylus. Chelae and subchelae are illustrated by Glaessner (1969, p. R418, fig. 235). The term pseudochelate would seem to be nearly synonymous with subchelate and is to be avoided.

Order DECAPODA Latreille, 1802
Infraorder GLYPHEOIDEA Winkler, 1882
Superfamily ERYMOIDEA Van Straelen, 1925
Family CLYTIOPSIDAE Beurlen, 1927

Included genera.—*Clytiopsis* Bill, 1914; *Clytiella* Glaessner, 1931; *Galicia* Garassino and Krobicki, 2002; *Koryncheiros* n. gen.; *Piratella* Assmann, 1927; *Lissocardia* von Meyer, 1851; *Paraclytiopsis* Oravecz, 1962; *Protoclytiopsis* Birshtein, 1958.

Diagnosis.—Subcylindrical carapace without axial intercalated plate, with very deep cervical groove; gastro-orbital groove weak or absent; branchiocardiac and postcervical grooves almost parallel. Rostrum moderately toothed or with granular margins. Pleon with smooth or granular terga and broadly triangular to rounded pleura. Pereiopod 1 with large chelae, often weakly heterochelous; pereiopods 2 and 3 chelate or subchelate; pereiopod 4 chelate or with terminal dactylus; 5 with terminal dactylus. Exopodite of uropod with diaeresis.

Discussion.—Beurlen (1927, p. 100) originally erected Clytiopsinae as a subfamily of Glypheidae and included two genera, *Clytiopsis* Bill, 1914, and *Pseudopemphix* Wüst, 1903, within it. Glaessner (1969) subsequently assigned *Pseudopemphix* to Pemphicidae Van Straelen, 1928. In 1931, Beurlen and Glaessner placed Clytiopsinae in Erymaidae Van Straelen, 1925 (spelling as in Van Straelen) along with Erymainae [sic]. Glaessner (1929) corrected the spelling of Erymaidae to Erymidae. Erymidae, along with Stenochiridae Beurlen, 1928, were assigned to the Tribe Paranephropsidea Beurlen, 1927.

Glaessner (1969) considered Paranephropsidea to be the junior synonym of Erymidae, and he subdivided Erymidae into Eryminae and Clytiopsinae. *Stenochirus*, the only genus within Stenochiridae, was assigned to an uncertain subfamily within Nephropidae Dana, 1852 (Glaessner, 1969, p. R460). Subsequently, De Grave et al. (2009) and Schweitzer et al. (2010) considered Stenochiridae as a family within Nephropoidea, and they included the genera embraced within Eryminae and Clytiopsinae sensu Glaessner (1969) within Erymidae without using subfamilies.

Consideration of the genera embraced within Erymidae sensu De Grave et al. (2009) and Schweitzer et al. (2010) reveals that there are two groups within the family that are different enough from one another to warrant separation into distinct families. Erymidae sensu stricto, including *Enoploclytia* M'Coy, 1849; *Eryma* von Meyer, 1840; *Palaeastacus* Bell, 1850; *Pustulina* Quenstedt, 1857; and *Stenodactylus* Beurlen, 1928, possess a separate plate intercalated along the anterior part of the axis of the dorsal carapace. This feature is unique among Decapoda, and taxa possessing it surely warrant placement within their own superfamily, Erymoidea, and family, Erymidae. The remaining genera previously placed within Erymidae, *Clytiella, Clytiopsis, Galicia, Lissocardia, Paraclytiopsis,* and *Protoclytiopsis*, are herein referred to Clytiopsidae within Erymoidea. Species within Clytiopsidae are similar enough to species in Erymidae to warrant placement in the same superfamily; both exhibit long, well-developed cervical grooves, and postcervical and branchiocardiac grooves that are generally parallel to one another. Although not unique to Erymoidea, both families are characterized by species bearing chelate or subchelate pereiopods 1–3. However, clytiopsids lack the intercalated plate, and this is taken to be a sufficiently significant character to warrant separation at the family level.

Genus KORYNCHEIROS Feldmann, Schweitzer and Zhang new genus

Type species.—*Koryncheiros luopingensis* n. sp. by original designation and monotypy.

Diagnosis.—Rostrum triangular, with elevated, beaded rim; rims extend onto dorsal carapace in diverging pattern. Cervical groove distinct, straight, extending anteroventrally at about 70° angle from long axis, bounded posteriorly by row of anteriorly directed fine spines. Postcervical groove and

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branchiocardiac groove diverge posteriorly. Exopod of uropod with arcuate, convex forward diaeresis. Chelipeds heterochelous; manus quadrate; slightly higher distally; fixed finger short, triangular, weakly downturned; dactylus longer than fixed finger, articulates near, but not at, upper distal corner of propodus, lies at nearly 90° to long axis of propodus, upper surface strongly convex so that when occluded against distal margin of manus, entire chela is round-tipped; right chelipeds smaller than left and bearing different termination. Pereiopods 2–4 terminating in subchelate closure with relatively long dactylus closing against distal margin of propodus and triangular fixed finger which is about half the length of movable finger; pereiopod 5 shorter and narrower, termination not known.

Etymology.—The generic name derives from the Greek *korine*, meaning club, and *cheiros*, meaning hand, in reference to the distinctive club-shaped first pereiopod. The gender is masculine.

Discussion.—The Luoping specimens referred to *Koryncheiros luopingensis* new genus and species conform to the diagnosis for the family. The carapace is subcylindrical and exhibits a very deep cervical groove and almost parallel branchiocardiac and postcervical grooves. The rostrum has a granular margin, and the pleon has broadly triangular pleurae. Pereiopod 1 carries large, heterochelous chelae; pereiopods 2–4 are chelate or subchelate; pereiopod 5 apparently has a terminal dactylus; and the exopod of the uropod has a well-developed diaeresis. These are all diagnostic for the family.

KORYNCHEIROS LUOPINGENSIS Feldmann, Schweitzer and Zhang new species
Figures 2, 3

Diagnosis.—Rostrum triangular, with elevated, beaded rim; rims extend onto dorsal carapace in diverging pattern. Cervical groove distinct, straight, extending anteroventrally at about 70° angle from long axis, bounded posteriorly by row of anteriorly directed fine spines. Postcervical groove and branchiocardiac groove diverge posteriorly. Exopod of uropod with arcuate, convex forward diaeresis. Chelipeds heterochelous; manus quadrate; slightly higher distally; fixed finger short, triangular, weakly downturned; dactylus longer than fixed finger, articulates near, but not at, upper distal corner of propodus, lies at nearly 90° to long axis of propodus, upper surface strongly convex so that when occluded against distal margin of manus, entire chela is round-tipped; right chelipeds smaller than left and bearing different termination. Pereiopods 2–4 terminating in subchelate closure with relatively long dactylus closing against distal margin of propodus and triangular fixed finger which is about half the length of movable finger; pereiopod 5 shorter and narrower, termination not known.

Description.—Carapace short, deep. Rostrum triangular, with elevated, beaded rim; sulcate with fine axial ridge. Beaded rims of rostrum extending onto dorsal carapace in diverging pattern, directed posteroventrally, extends from rostrum half the distance to the cervical groove. Between them are rows of widely spaced tubercles more parallel to one another (post-rostral ridge?).

Orbital notch shallow, concave forward. Orbital notch and antennal notch form sinuous anterior carapace margin. Ventral margin of carapace not well preserved. Dorsal margin of carapace weakly arched. Posterior margin straight to weakly concave posteriorly near dorsal margin and moderately convex ventrally, rimmed.

Cephalic region with post or suborbital spinose ridge, two low nodes each bearing a cluster of granules posterior to the orbits at the same level as the end of the post-rostral ridge in the cephalic region. Cervical groove distinct, straight, extending anteroventrally at about 70° angle from long axis, bounded posteriorly by row of anteriorly directed fine spines. Postcervical groove and branchiocardiac groove diverge posteriorly. Branchiocardiac groove curves dorsally abruptly and crosses dorsal margin at nearly right angle. Postcervical groove curves dorsally and diverges from branchiocardiac groove near dorsal midline. Carapace surface with scattered nodes anterior to branchiocardiac groove and uniformly and densely punctate posterior to it.

Pleon with somite 1 shorter than 2; 2–5 about equal in length. Surface with densely spaced punctae; pleurae with V-shaped groove extending from points of articulation to midpoint of pleurae, strongly inflated along inside of the V. Pleurae 2–5 chordate, terminate in acute, postero-ventrally directed tips. Pleuron 6 reduced with laterally directed tip. Telson quadrate, widest proximally, lateral margins convex with three tiny, posterolaterally directed spines in posterior one-third. Exopod of uropod approximately circular with arcuate, convex forward, diaeresis.

Chelipeds heterochelous. Merus of left first pereiopod longer than high; outer surface smooth; upper surface with about 12 moderately strong, distally directed spines; lower surface with row of closely spaced small nodes. Carpus about as long as high, becoming higher distally; upper margin straighter, with a few small nodes; lower margin apparently smooth; outer margin granular. Manus quadrate; slightly higher distally; upper and lower margins mostly smooth, a few spines at distal end of upper margin, diverging slightly distally, outer surface with tiny spines broadly spaced. Fixed finger short, triangular, weakly downturned; outer surface of propodus coarsely granular. Dactylus longer than fixed finger, articulates near, but not at, upper distal corner of propodus, lies nearly at 90° to long axis of propodus, upper surface strongly convex so that when occluded against distal margin of manus, entire unit is round-tipped; occlusal surface with a few blunt denticles. Right chelipeds smaller than left and bearing different termination. Right manus quadrate, as long as high, surface granular. Fixed finger triangular, stout, one-third to two-thirds length of manus, downturned slightly. Dactylus nearly as long as manus, triangular, occludes against fixed finger.

Pereiopods 2–4 similar in form but decreasing in size posteriorly; meri longer than high; carpi about half again as long as high, becoming higher distally; mani longer than high, becoming progressively longer on pereiopods 2–4; each of pereiopods 2–4 terminating in subchelate closure with relatively long dactylus closing against distal margin of propodus and triangular fixed finger which is about half the length of movable finger. Pereiopod 5 shorter and narrower, termination not known.

Basal articles of antennules extend to end of rostrum; flagellae relatively short, slender, about one-third length of antennae. Basal articles of antennae extend beyond rostrum, apparently smooth, inner margin with spine at distal end; flagellae very long, three times as long as those of antennules, stouter than antennules.

Possibly third maxilliped preserved (LPI–41793, 41171); merus longer than high; carpus about as long as high; manus longer than high; dactyl triangular, blunt tipped; entire appendage extending to length of last basal article of antenna.

Etymology.—The trivial name refers to the Luoping Biota from which the specimens were collected.

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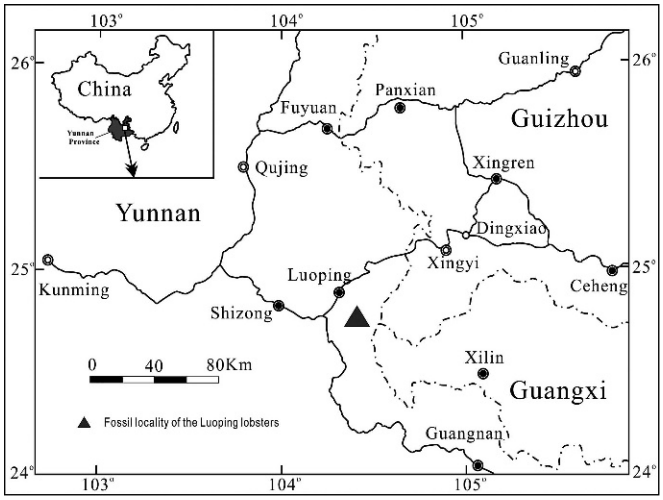

FIGURE 1—Location map showing the site from which decapod crustaceans were collected.

Types.—Holotype, LPI 41171; and paratypes, LPI–40503a, 40505, 40535, 40550, 41793, 40542.

Discussion.—*Koryncheiros* new genus is substantially different from other genera within the family in bearing a rostrum with granular margins that extend onto the anterior part of the carapace as granular ridges and in having a row of anteriorly directed small spines rimming the posterior edge of the cervical groove. Although possession of chelate or subchelate terminations on pereiopods 2 and 3 are considered part of the definitional basis of the Erymoidea, it is unusual to have a similar closure on P4. It is difficult to speculate on just how many taxa contain species with a chelate P4, because the terminations of the walking legs are not commonly preserved. Perhaps the most distinctive aspect of the morphology that distinguishes *Koryncheiros luopingensis* new species from all species within the Clytiopsidae is the club-shaped claw on the left first pereiopod. This form, which is vaguely reminiscent of the claw shape on some raninid brachyurans, is unique in lobsters and lobster-like forms to our knowledge. As contrasted to the raninids, in which the claws are carried more or less in a horizontal plane, the claws of *Koryncheiros luopingensis* n. sp. are carried in a vertical plane. This orientation would facilitate scavenging and capturing live prey on the seafloor as opposed to attacking prey within the water column. The subchelate terminations on pereiopods 2–4 probably served multiple purposes. They may have functioned in grooming behavior, in manipulating food resources, in clinging to items on the seafloor, in clasping during mating, or in maneuvering the egg mass. These behaviors have been attributed to minor claws on extant lobsters (Felder, personal commun. to RMF, 2011) and caridean shrimp (Bauer, 2004).

Superfamily GLYPHEOIDEA Winkler, 1882

Diagnosis.—Subcylindrical or flattened carapace; short or long rostrum; cervical groove well-developed, postcervical groove, and branchiocardiac grooves present, variously developed; abdominal somites with triangular, rectangular, or rounded pleural terminations, subrectangular telson; exopodite of uropod with diaeresis; third maxillipeds long, pediform; pereiopod 1 subchelate or chelate, pereiopods 2–4 chelate, subchelate, or achelate; pereiopod 5 with terminal dactylus.

Family GLYPHEIDAE Winkler, 1882

Included genera.—*Cedrillosia* Garassino et al., 2009; *Glyphea* von Meyer, 1835; *Laurentaeglyphea* Forest, 2006 (extant only); *Litogaster* von Meyer, 1847; *Neoglyphea* Forest and de Saint Laurent, 1975 (extant only); *Paralitogaster* Glaessner, 1969; *Squamosoglyphea* Beurlen, 1930; *Trachysoma* Bell, 1858; *Tridactylastacus* n. gen.

Diagnosis.—Subcylindrical carapace, slightly compressed laterally, with longitudinal cephalic carinae; antennae and antennules long, flagellate; short or long rostrum; cervical groove well-developed, oriented at over 70° angle to dorsal surface of carapace, extending from dorsal surface to position beyond half-height of cephalothorax; postcervical groove variable, converging with branchiocardiac groove either dorsally and ventrally or only ventrally; branchiocardiac groove at less than 70° angle to dorsal carapace; hepatic groove sometimes present, inferior groove present; abdominal somites generally smooth, rarely with transverse keels, with triangular or rounded pleural terminations, subrectangular telson; exopodite of uropod with diaeresis; third maxillipeds long, pediform; pereiopod 1 subchelate, pereiopods 2–4 subchelate or achelate, pereiopod 5 with terminal dactylus.

Discussion.—*Tridactylastacus* new genus is placed within Glypheoidea based on the presence of subchelate first pereiopods, with an extra spine between the fingers; subchelate second through fourth pereiopods; and a uropod with a well-developed diaeresis on the exopod. No other superfamily of lobster-like, shrimp-like, or thalassinoid decapod can accommodate this combination of characters. It is unfortunate that only one carapace is preserved of *Tridactylastacus*, because many of the diagnostic features for reptant decapods are located on this area.

The new material is placed within Glypheidae, exhibiting several of the diagnostic characters of the family, including a longer than wide carapace; subchelate pereiopods, with especially strong first pereiopods; an exopod of the uropods with a diaresis; and long, flagellate antennae and antennules. The diaresis of the uropods is serrate, and the pleonites are rounded, both seen in extant glypheids. The pleopods of the new genus are relatively long and extend beyond the pleonites; they also appear to be dimorphic. Extant glypheids have long pleopods also, that extend well-beyond the pleonites (Richer de Forges, 2006).

There are some features of *Tridactylastacus* that do not fit well into the Glypheidae. The dorsal carapace is preserved in only one specimen of *Tridactylastacus*, the holotype, and it is very poorly preserved. Only the rostrum and anterior margin are well-shown. The groove pattern and ornamentation are not discernable. It does appear that the carapace narrows considerably anteriorly, a characteristic of glypheids. The pleonites are rounded in *Tridactylastacus*; they are rounded in the extant genera of Glypheidae, but other extinct genera usually have triangular terminations. Recovery of specimens with a well-preserved carapace could help confirm placement of this genus within Glypheidae.

Other families within Glypheidea cannot accommodate the new genus. Mecochiridae Van Straelen, 1925, have only the first and second pereiopods subchelate, which cannot accommodate the new genus. Pemphicidae Van Straelen, 1928a, is known for certain to have subchelate first pereiopods and is postulated to have subchelate second and third pereiopods. Both pemphicids and mecochirids have triangular pleonal terminations. Chimaerastacidae Amati et al., 2004 have fully chelate pereiopods one through three. Thus, the presence of subchelate terminations on pereiopods one through four, a longer than wide carapace, and rounded pleonal terminations makes Glypheidae the best placement for *Tridactylastacus* at this time.

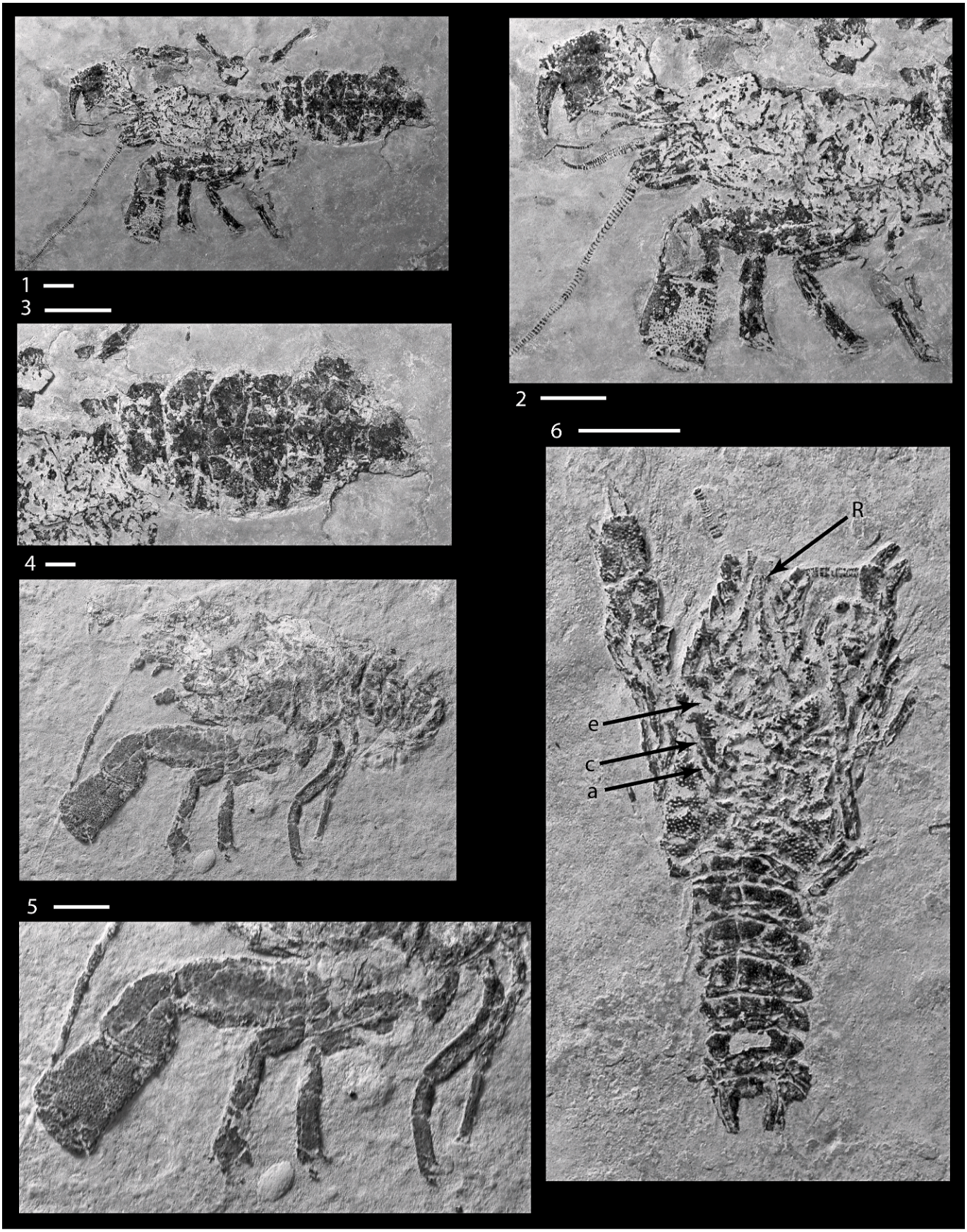

FIGURE 2—*Koryncheiros luopingensis* n. gen. n. sp. unwhitened specimens. *1–3,* holotype LPI–41793, entire animal, closeup of chelipeds, and pleonal somites; *4–5*, paratype LPI–41171, entire animal, closeup of chelipeds; *6,* paratype LPI–40503a, dorsal view of carapace with rostrum (R), cervical groove (e), postcervical groove (c), branchiocardiac groove (a), and pleon. Scale bar=0.5 cm.

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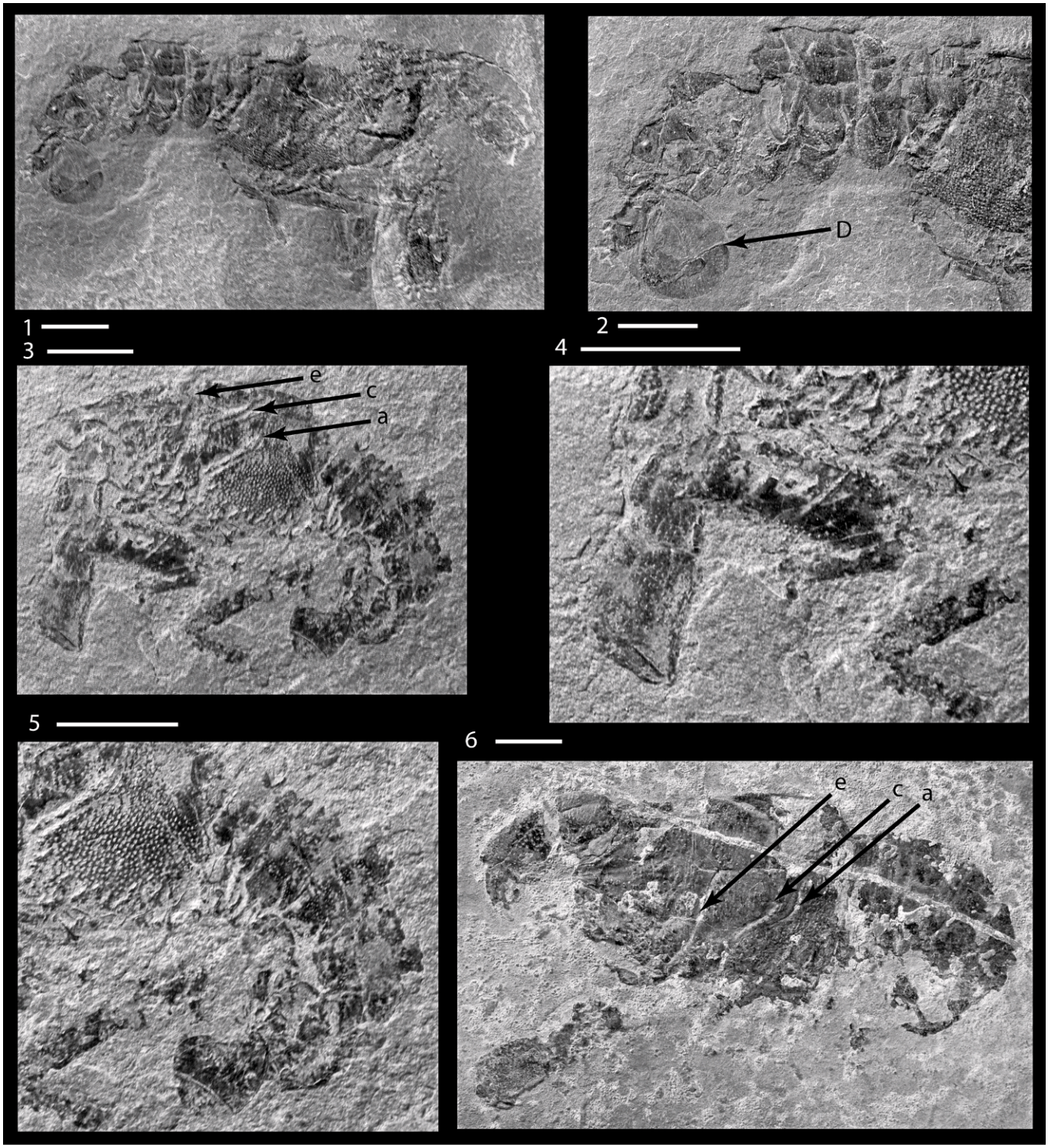

FIGURE 3—*Koryncheiros luopingensis* n. gen. n. sp. unwhitened specimens. *1, 2,* paratype LPI–40505, entire animal, exopod of uropod with clear diaresis (D); *3–5,* paratype LPI–40550, entire animal showing groove pattern including cervical groove (e), postcervical groove (c), and branchiocardiac groove (a), chelate first pereiopod, and pleon with well preserved uropods; *6*, paratype LPI–40535, entire animal showing cervical (e), postcervical (c), and branchiocardiac (a) grooves. Scale bars=0.5 cm.

Tridactylastacus n. gen. of Middle Triassic age is one of the oldest known taxa within Glypheidae. *Litogaster turnbullensis* Schram, 1971 is older, reported from latest Olenekian (Early Triassic) rocks of Idaho, U.S.A. (Perry and Chatterton, 1979). *Paralitogaster durlachensis* (Förster, 1967) is also Early Triassic in age. Four species of *Litogaster* are Middle Triassic in age (Glaessner, 1929). All other species within Glypheidae are younger than the new taxon from China. Within the Superfamily Glypheoidea, *Chimaerastacus* Amati et al., 2004, the only member of its family, is Middle Triassic in age. Within Mecochiridae, two species of *Pseudoglyphea* Oppel, 1861, are Middle Triassic in age (Assmann, 1927, Théobald, 1953), and the remaining members are younger. Most members of Pemphicidae are Middle Triassic in age (Glaessner,

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1969), and Platychelidae is almost entirely Late Triassic in age (Glaessner, 1969). Thus, it appears that Glypheoidea, based on current evidence, originated in the Early Triassic (1 family, Glypheidae; 2 continents, North America and Europe), radiated substantially by the Middle Triassic (4 families, Chimerastacidae, Glypheidae, Mecochiridae, and Pemphicidae; 3 continents, Asia, Europe, North America), and explosively by the Jurassic (see Glaessner, 1969).

Genus TRIDACTYLASTACUS Feldmann, Schweitzer and Zhang new genus

Type species.—*Tridactylastacus sinensis* new species by original designation and monotypy.

Diagnosis.—Rostrum with rounded tip and axial keel, cephalothorax longer than wide, narrowed anteriorly; antennae and antennules long, flagellate; pleonal pleurae rounded; telson with straight termination; exopod of uropod with serrate diaresis, exopod with spines anterior to diaresis and serrate distal to diaresis; first pereiopods slightly heterochelous, subchelate, merus with spines on upper and lower margins, manus with spines on upper distal margin and with stout spine above position of fixed finger on distal margin yielding the appearance of possessing three fingers, movable finger with beaded occlusal surface; second through fourth pereiopods subchelate, fifth pereiopod termination unknown, shortest of all pereiopods; pleopods apparently dimorphic, either ovate with lanceolate tip or styliform and axially keeled, extending well beyond pleurae in either case.

Etymology.—The genus name is derived from the Greek words *dactylos*, meaning finger, *astakos*, meaning lobster, and *trion*, meaning three, in reference to first pereiopods which appear to have three fingers. The gender is masculine.

Discussion.—The new material warrants a new genus for several reasons. Two other genera within Glypheidae, *Paralitogaster* and *Trachysoma*, are known to have subchelate pereiopods 1 through 4, as in *Tridactylastacus*. However, *Tridactylastacus* is easily distinguished from *Paralitogaster* because *Paralitogaster* has spines along the axis of the carapace, long spines on the lower margin of the manus, and sharply triangular terminations of the pleonites. The new genus lacks these features. *Paralitogaster* lacks the distinctive triangular spine between the fixed and movable fingers of the first pereiopod present in *Tridactylastacus*. *Trachysoma* is not a well-known taxon despite being reported from several localities; its pleonites have triangular terminations and its rostrum is long and sharp, whereas the pleonites and the rostrum of *Tridactylastacus* are bluntly rounded. *Squamosoglyphea* and *Pseudoglyphea*, the latter of which at this time is placed in the Mecochiridae, both possess chelae very similar to those of *Tridactylastacus*. The three genera all exhibit the tooth intercalated between the fingers; however, the former two have narrow, triangular terminations on the somites, and pereiopod 4 is not known to be subchelate in either *Squamosoglyphea* and *Pseudoglyphea*. *Glyphea* is quite speciose as it is currently defined, and at least one referred species has subchelate pereiopods 4. Typically, the genus is characterized by some combination of pereiopods 1–3 subchelate: either 1, 2, 1 and 2, or all three. The chelae do not exhibit the intercalated spine between the fingers in *Glyphea*.

TRIDACTYLASTACUS SINENSIS Feldmann, Schweitzer and Zhang new species

Figures 4–6

Diagnosis.—Rostrum with rounded tip and axial keel, cephalothorax longer than wide, narrowed anteriorly; antennae and antennules long, flagellate; pleurae rounded; telson with straight termination; exopod of uropod with serrate diaresis, exopod with spines anterior to diaresis and serrate distal to diaresis; first pereiopods slightly heterochelous, subchelate, merus with spines on upper and lower margins, manus with spines on upper distal margin and with stout spine above position of fixed finger on distal margin yielding the appearance of possessing three fingers, movable finger with beaded occlusal surface; second-fourth pereiopods subchelate, fifth pereiopod termination unknown, shortest of all pereiopods; pleopods apparently dimorphic, either ovate with lanceolate tip or styliform and axially keeled, extending well beyond pleurae in either case.

Description.—Cephalothorax apparently narrow anteriorly, wider posteriorly, overall longer than wide. Rostrum long, bluntly rounded, axially keeled, keel extending onto cephalothorax. Anterior margin of cephalothorax extending from either side of rostrum in a margin perpendicular to rostrum, rimmed. Possibly some antennal articles or acicles present (LPI–40546).

Antennules with robust basal articles that are also long and extend relatively far in advance of animal; two basal articles observable, longer than wide, then composed of 14 or so rings before bifurcating into two fine flagellae composed of multiple rings (LPI–41545). Antennae longer than antennules and flagella composed of stouter rings, basal article proximal to flagella stout, long (LPI–41545).

Narrow pleonal somite 1, much higher than long, terga with rims on anterior and posterior margins, with posteriorly directed pleurite; somites 2–4 about same width, wider than somite 1, higher than long, somites 2 and 3 with articulating ring that is triangular in shape in lateral view, with broad, rounded pleurite that curves slightly posteriorly; somite 4 of same form as 3, with smoothly rounded pleurite (LPI–41674), tergae with rims on anterior and posterior margins; somites 5 and 6 seem to be about the same size as 2–4 (LPI–41671), somite 5 with short blunt rounded pleurae, somite 5 shorter than somite 4, but with articulating ring of same size and shape, very highly rounded pleura, overlapping somite 6; somite 6 appearing to be rather short, with blunt, rounded pleurae with tiny spines on the margin, somite 6 shorter than other somites, with short, rounded pleura (LPI–41674) (LPI–40140).

Telson appearing to be square, short, shorter than uropods by far, lateral margins convex proximally, becoming weakly concave near distal end, appearing to have straight distal margin (LPI–41672); exopod of uropod broadly rounded, with small spines on outer margin of outer-most unit anterior to diaeresis and large spine just anterior to diaeresis, diaeresis extending diagonally arranged across exopod so that it arises about two thirds the distance along the outer margin of exopod and ends along inner margin near the base, margin of diaresis finely serrate, inner margin and margin distal to diaeresis of exopod very finely serrate (LPI–41677); endopod concave on outer margin, with convex inner margin, with weak keel axially, margins very finely serrate (LPI–41675).

First pereiopods subequal, one appearing to be slightly smaller and shorter (L = 0.5 of top, 0.6 of bottom, LPI–41676) than the other. Merus much longer than high, upper and lower margins straight, upper margin with short forward directed spines, lower margin with tiny spines that are curved forward, becoming somewhat higher distally, possibly with parallel ridges longitudinally; carpus slightly longer than high, becoming higher distally, proximal margin rounded, rounding into convex lower margin. Manus longer than high, becoming slightly higher distally; proximal margin straight; upper margin weakly convex; lower margin weakly concave; distal

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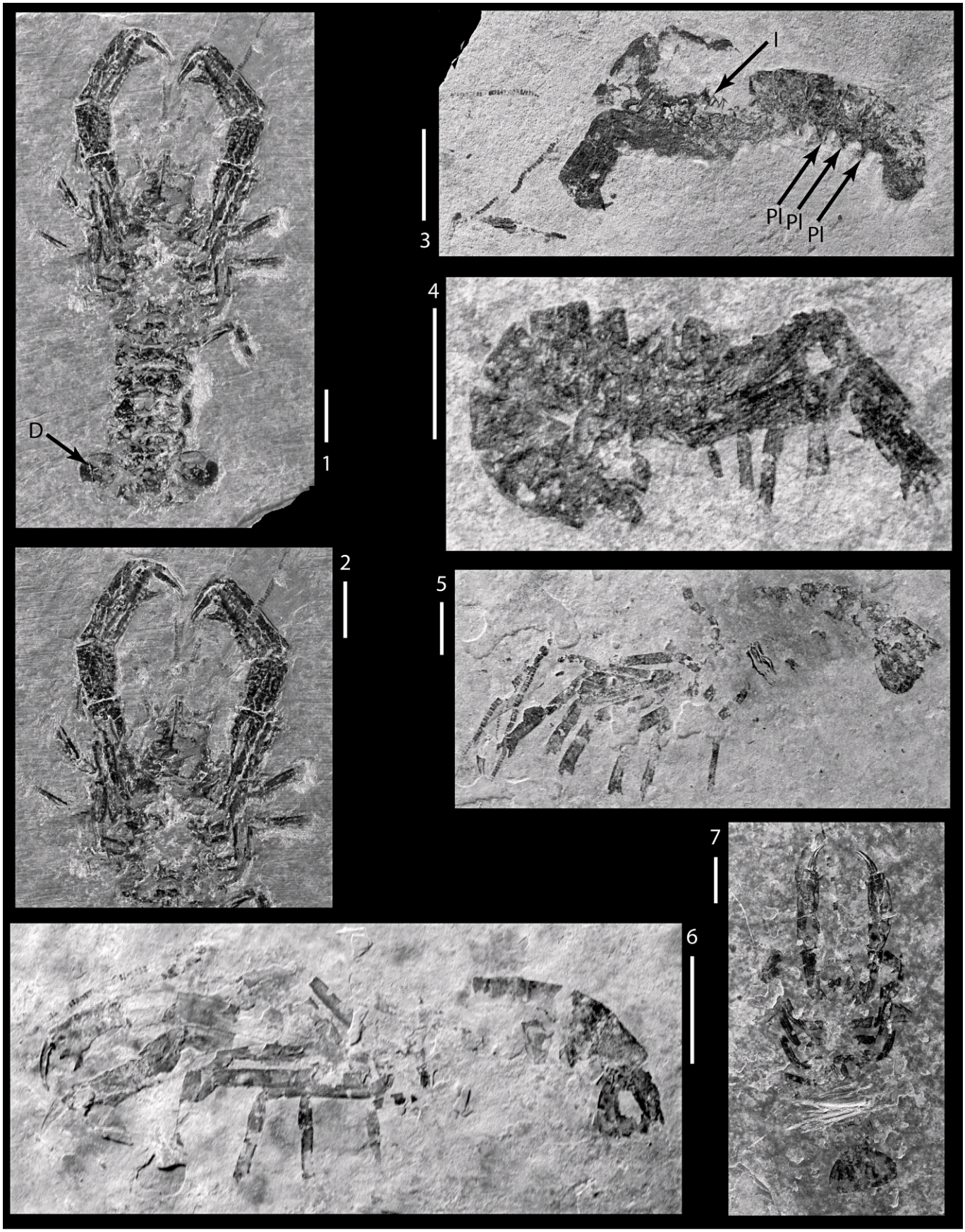

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margin extending straight, on distal margin a little over half the distance from upper margin a triangular tooth. Fixed finger a more slender triangular spine that may be same size as triangular tooth or larger, slightly curved upward, may possess some tiny spines at base along distal margin between triangular tooth and fixed finger. Outer surface of manus may have been ornamented with some ridges; manus in dorsal view with a triangular spine about 80 percent the distance along inner upper margin is projected anteriorly, two small spines follow it to tip of upper margin. Movable finger long, higher at base, with a weak triangular projection at base in some specimens, with beads along entire occlusal surface, curved downward, can be very much longer than fixed finger in some specimens (LPI-40546).

Second through fifth pereiopods long, slender, becoming shorter posteriorly so that fifth is shortest. Second pereiopod shorter than first; basis arcuate, about as long as high, proximal margin straight, upper margin convex and longer than lower margin, lower margin very short, distal margin concave; ischium about as long as high, proximal margin at about 70° angle to lower margin, upper and lower margins diverging slightly so that height increases slightly distally, upper margin with short spines, distal margin weakly concave; merus much longer than high, upper and lower margins nearly straight, lower margin with distally directed spines (LPI–40503b); carpus slightly longer than high, proximal margin sinuous, with projection at upper corner for articulation with merus, upper and lower margins weakly convex, distal margin nearly straight; manus rectangular, longer than wide, widening distally, upper margin convex, lower margin concave; fixed finger very short, small spines proximal to it on lower margin of manus (LPI–41670); movable finger longer, at least twice as long as fixed finger, slender.

Third pereiopod smaller still, shorter than second pereiopod; basis arcuate, about as long as high, proximal margin straight, upper margin convex and longer than lower margin, lower margin very short, distal margin concave; ischium about as long as high, proximal margin at about 70° angle to lower margin, upper and lower margins diverging slightly so that height increases slightly distally, upper margin with short spines, distal margin weakly concave; merus long; manus longer than high, of same form as that of second pereiopod but more slender; fixed finger short, triangular, strongly downcurved; movable finger long, slender, extending straight from manus (LPI–41675, LPI–40503b).

Fourth pereiopod shorter than third and more slender; manus very long, subchelate, fixed finger very short triangular spine, movable finger longer, more slender (movable finger on LPI–41764, LPI–40503b).

Fifth pereiopod shorter than other pereiopods (LPI–40503).

Pleopods appear to be dimorphic. Pleopods of somites 2 through 4 large, ovate with lanceolate tip, extending well beyond pleurae (LPI–41548). Pleopods of somites 2 through 4 triangular, pleopod 5 styliform, axially keeled, all extending well beyond pleurae (LPI–41672).

Types.—The holotype LPI–40546, and paratypes include LPI–40140, 40503b, 41446, 41545, 41548, 41670, 41671, 41672, 41674, 41675, 41676, 41677, and 41764.

Measurements.—Measurements (in mm) of chelae are presented in Table 2. LPI–41677, length of exopod of uropod = 2.9 mm; width = 2.0 mm.

Etymology.—The trivial name is derived from the stem *Sino-*, meaning pertaining to China, in reference to the location from where the specimens were collected.

Discussion.—The specimens of this species are preserved in various stages of fragmentation. Thus, the description above is pieced together from numerous specimens, which are indicated throughout the description. Only one specimen retains the dorsal carapace, the holotype, suggesting that either most of the specimens are molts, that the material was transported from a different environment, or that the carapace was attached to the rest of the animal by easily degraded tissue. The species was apparently relatively common, as it is by far the most common of the three lobster species described here although less common than the shrimp that are known from the same unit and that are yet to be studied by the authors.

Infraorder PALINURA Latreille, 1802
Family PALINURIDAE Latreille, 1802

Included fossil genera.—*Archaeocarabus* M'Coy, 1849; *Archaeopalinurus* Pinna, 1974; *Astacodes* Bell, 1863; *Jasus* Parker, 1883 (also Holocene); *Justitia* Holthuis, 1946 (also Holocene); *Linuparus* White, 1847 (also Holocene); *Palaeopalinurus* Bachmayer, 1954; *Palinurina* Zu Münster, 1839; *Palinurus* Weber, 1795 (also Holocene); *Panulirus* White, 1847 (also Holocene); *Phalangites* Münster, 1839 (possibly larval form of *Palinurina*); *Rugafarius* Bishop, 1985; *Yunnanopalinura* new genus.

Diagnosis.—Subcylindrical or subrectangular carapace, with variously developed spines or other ornamentation, rostrum usually very small or absent; eyes usually protected by large supraocular spines (horns); antennae very large, thick, antennal scale absent, antennal bases usually with spines; pereiopods 1–5 usually without chelae, first pereiopods almost always same length or only slightly longer than other pereiopods; rarely, first pereiopods longer and stouter or same length but stouter than other pereiopods; abdominal somites well developed; rounded subrectangular telson; telson, endopodite and exopodite soft and flexible in their posterior half, being strongly chitinized in the basal part (after Davie, 2002).

Material examined.—*Palinurellus wieneckii* (De Man, 1881), USNM 107345; *Puerulus angulatus* (Bate, 1888), USNM 104636 (males and females); *Jasus paulensis* (Heller, 1862), USNM 228796 (males and females); *Projasus parkeri* (Stebbing, 1902), USNM 221819 (males and females); *Sagmariasus verreauxi* (H. Milne-Edwards, 1851), USNM 240250 (female), 240252 (male); *Palinurus elephas* (Fabricius, 1787), USNM 151684 (female); *Panulirus argus* (Latreille, 1804), USNM 13996 (female).

Discussion.—Palinuridae has a well-recognized, relatively robust fossil record. Members of the family are easily recognized by their stout antennae, general lack of chelae on any

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FIGURE 4—*Tridactylastacus sinensis* n. gen. n. sp. unwhitened specimens. *1, 2,* holotype LPI–40546, entire animal including chelipeds, pleon, and rounded pleurites and diaresis (D) of exopod of uropod, closeup of first pereiopods, antennae, and antennules; *3*, paratype LPI–41672, entire animal with weakly heterochelous first pereiopods, internal skeleton (I), and pleon with styliform pleopods (Pl) extending beyond pleurae; *4*, paratype LPI–41446, entire animal with pleon; *5,* paratype LPI–41677, pleon and pereiopods, showing subchelate nature of pereiopods 2 and 3; *6,* paratype LPI–41545, entire animal excluding carapace, showing pleon and telson, antennae, and chelipeds with movable finger, fixed finger, and intercalated spine; *7,* paratype LPI–40140, specimen showing telson and pleonite 6 as well as chelipeds. Scale bars=0.5 cm.

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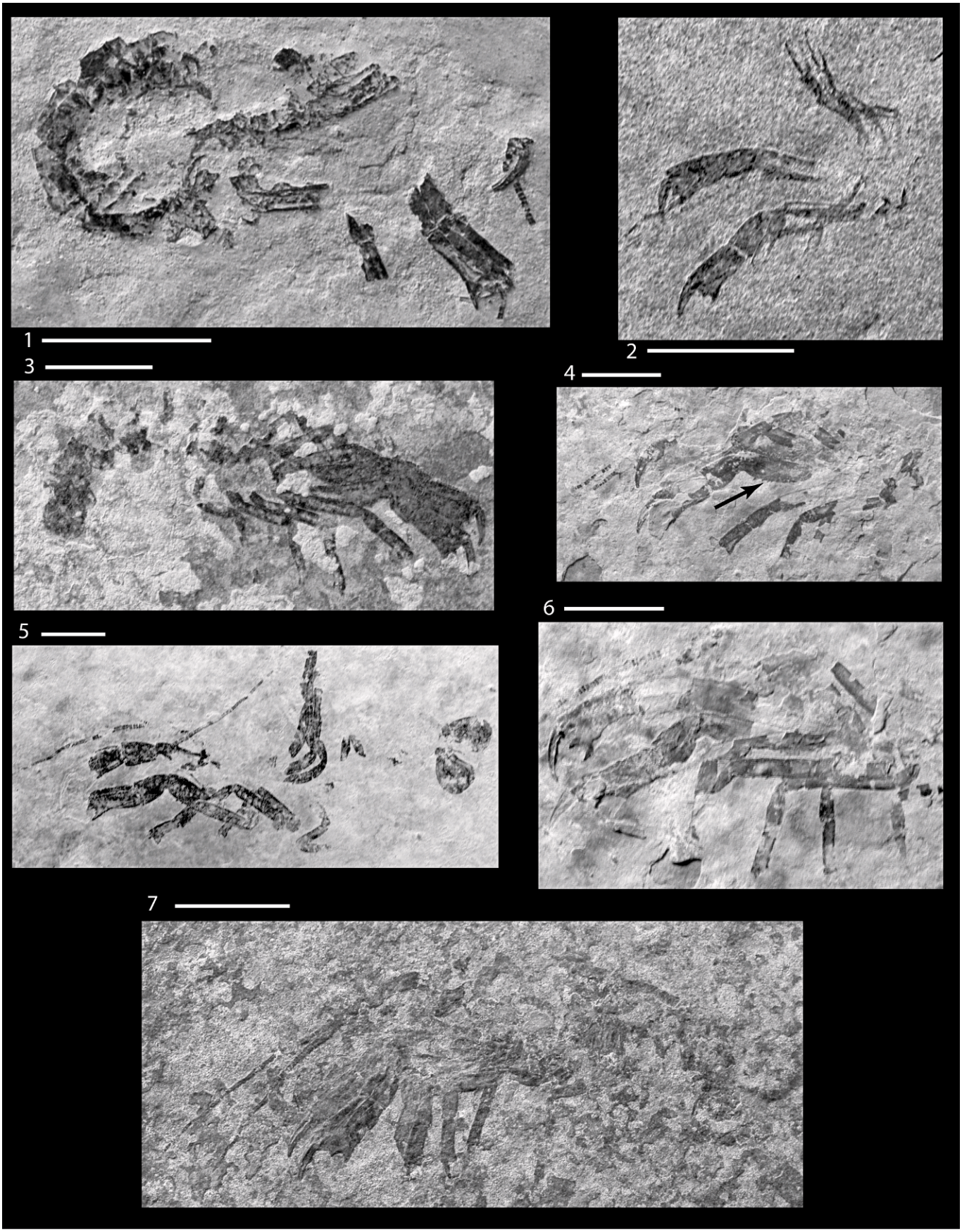

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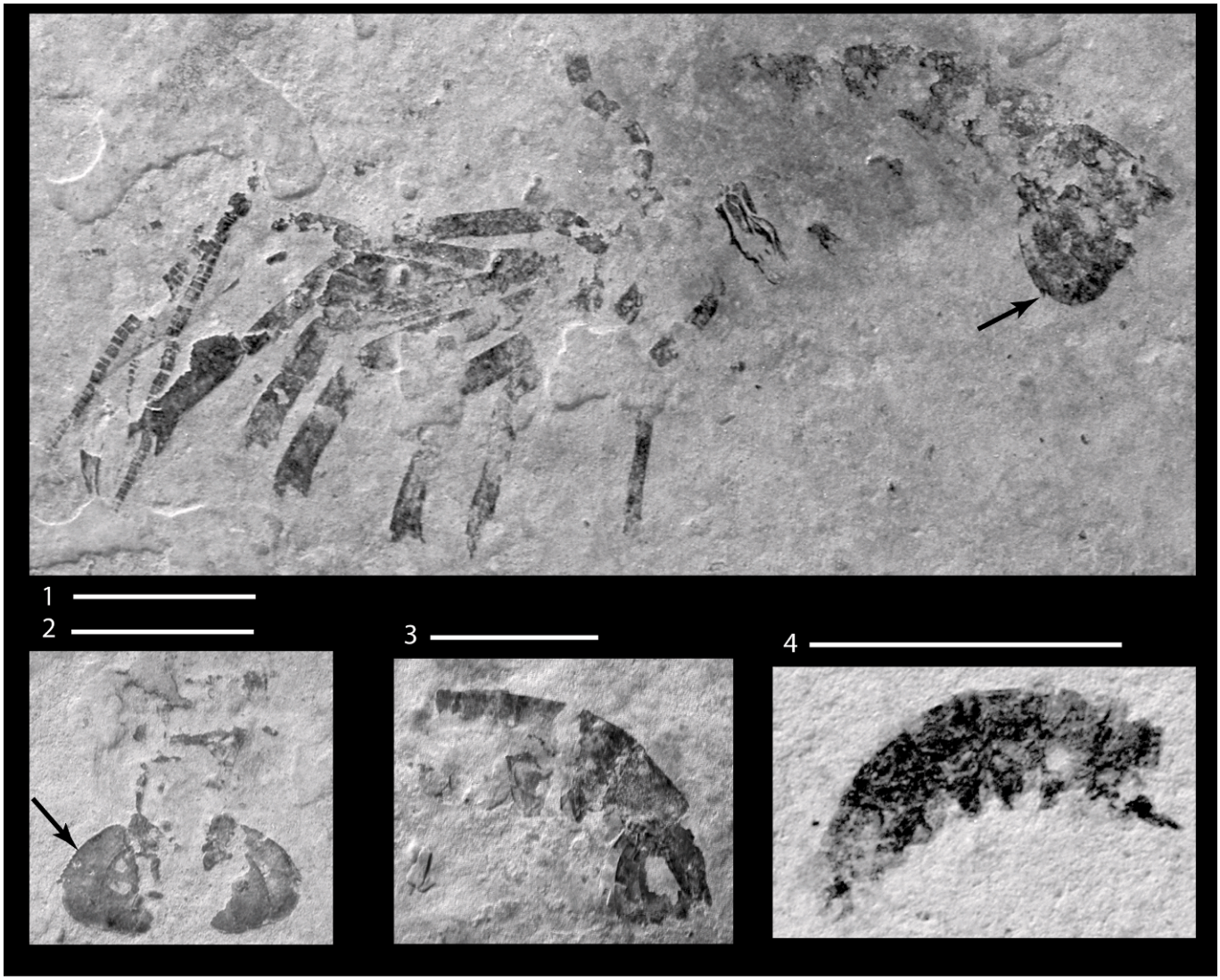

FIGURE 6—*Tridactylastacus sinensis* n. gen. n. sp. unwhitened specimens. *1,* paratype LPI–41677, telson showing spine (arrow) on outer margin of exopod of uropod, subchelate nature of pereiopods 2–4; *2,* paratype LPI–41677, uropods, note serrate outer margin of left exopod (arrow); *3,* paratype LPI–41670, pleon showing ovate pleopods extending beyond pleurae; *4,* paratype LPI–41671, pleon showing styliform pleopods extending beyond pleurae. Scale bars=0.5 cm.

pereiopods, and subrectangular carapaces with ridges or spines. Most extant genera possess rather slender first pereiopods that are similar in size and length to the other pereiopods. Exceptions are the males of *Justitia longimanus* (H. Milne Edwards, 1837), in which the first pereiopods are very large and even subchelate; and *Palibythus* Davie, 1990, and *Palinurellus* Von Martens, 1878. The latter two genera are composed of species in which the first pereiopods are about the same length as the other pereiopods but are more robust (Holthuis, 1991). They had been for some time placed in a separate family, Synaxidae Bate, 1881, but phylogenetic evidence has placed them among Palinuridae (Tsang et al., 2009).

The new material from Luoping has several characters that strongly suggest placement within Palinuridae; these include stout antennae with very large, spinose basal elements; more slender antennules with long whiplike flagellae; five achelate, tuberculate pereiopods; a granular dorsal carapace with no evidence of carapace grooves; and what appear to be ridges on the distal ends of the uropods suggestive of soft terminations. However, some features of the specimens seem somewhat problematic. The first pereiopods are very stout, not typical of most extant palinurids. Perhaps more important, and more vexing given the preservational style of the material, is the nature of the uropods. The exopod of the uropod appears to

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FIGURE 5—*Tridactylastacus sinensis* n. gen. n. sp. unwhitened specimens. *1,* paratype LPI–40503b, partially preserved animal with portions of pleon and first pereiopods; *2,* paratype LPI–41676, subequal chelipeds; *3,* paratype LPI–41548, partial animal with ovate pleopods extending beyond pleurites; *4,* paratype LPI–41670, pereiopods, merus of chelipeds with spines on lower margin (arrow) and pereiopod 2 subchelate; *5,* paratype LPI–41675, pereiopods showing pereiopods 2 and 3 subchelate; *6,* paratype LPI–41545, first pereiopods and antennae; *7,* paratype LPI–41764, specimen showing pereiopods 2–4 subchelate. Scale bars=0.5 cm.

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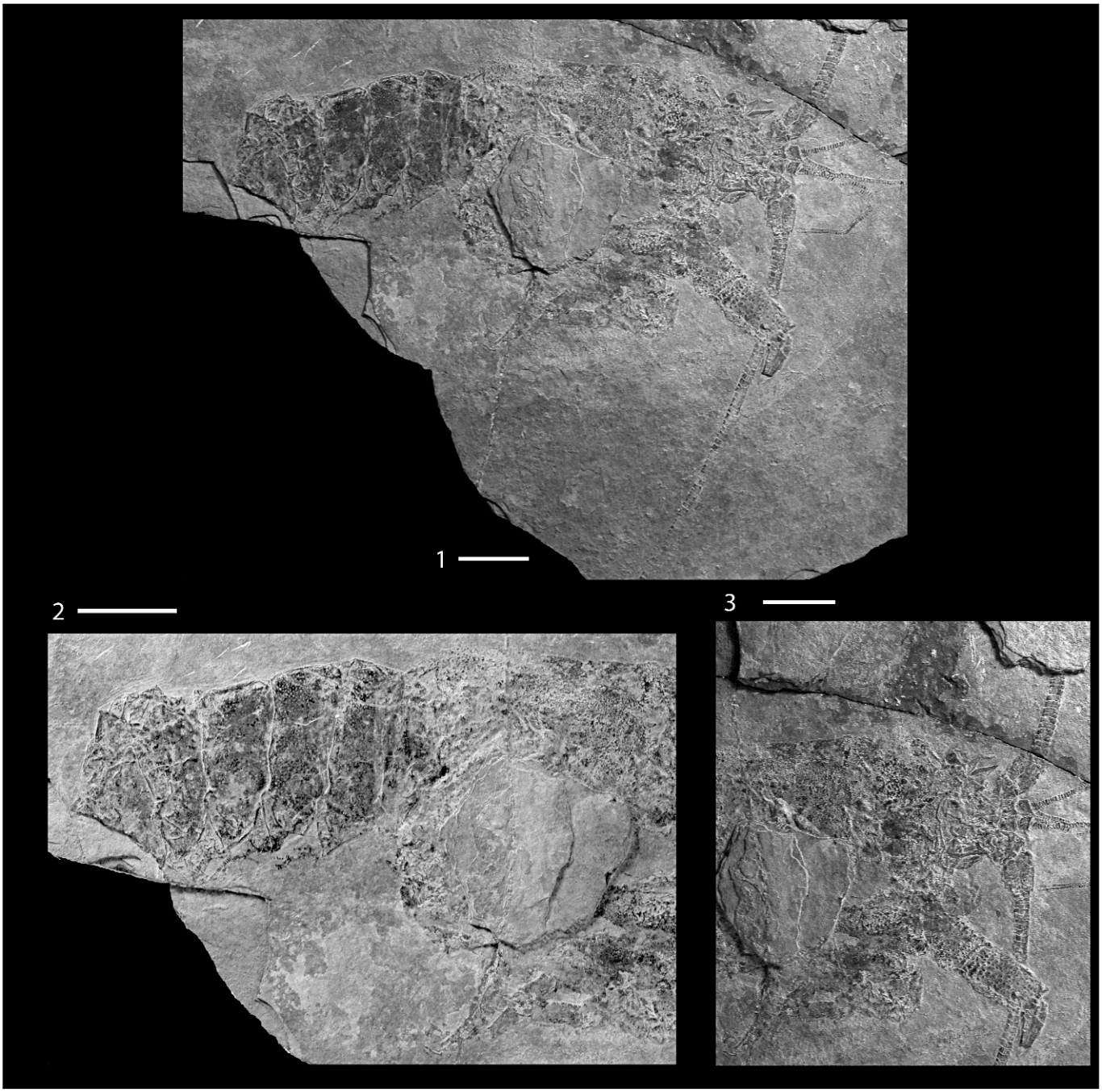

FIGURE 7—*Yunnanopalinura schrami* n. gen. n. sp. holotype LPI–40169. *1,* entire animal, showing long antennae, stout first pereiopod, and partially preserved carapace and pleon; *2,* pleon, note triangular and posteriorly directed pleurites of somites 2–5; *3,* anterior carapace, note stout antennal bases and stout first pereiopod, atypical of Palinuridae. Scale bars=1 cm.

lie on top of the endopod, not the usual state in living material. The exopod also exhibits what appears to be a diaresis, which arcs across the exopod in a convex forward manner. Anterior to the diaresis, the exopod appears to be calcified and pitted; posterior to the diaresis, the exopod exhibits the ridges typical of the softened distal end of palinurids. The structure interpreted as the endopod exhibits these ridges distally as well. The anterior end of the telson is well-calcified, and the posterior part is not preserved.

Examination of illustrations of *Palinurellus* spp. as well as specimens in the USNM indicates that, as mentioned, the first pereiopods are robust. Further, the telson and uropodal elements of species in this taxon are calcified anteriorly to a greater extent than seen in other palinurids. The calcification extends further posteriorly, and seems to terminate in a convex-forward arc across the entire element in both the exopod and endopod of the uropods and in the telson. In other palinurids, the calcification seems to be more confined to the outer edges of these elements.

Thus, we suggest the following. The Luoping specimens are referable to Palinuridae based upon the features listed above. The possession of a stout first pereiopod, whereas uncommon in Palinuridae, is present in some extant taxa and can be accommodated. The exopod of the uropod may not exhibit a diaresis in the strict sense but rather a boundary between the calcified and soft portions of the cuticle, which in the

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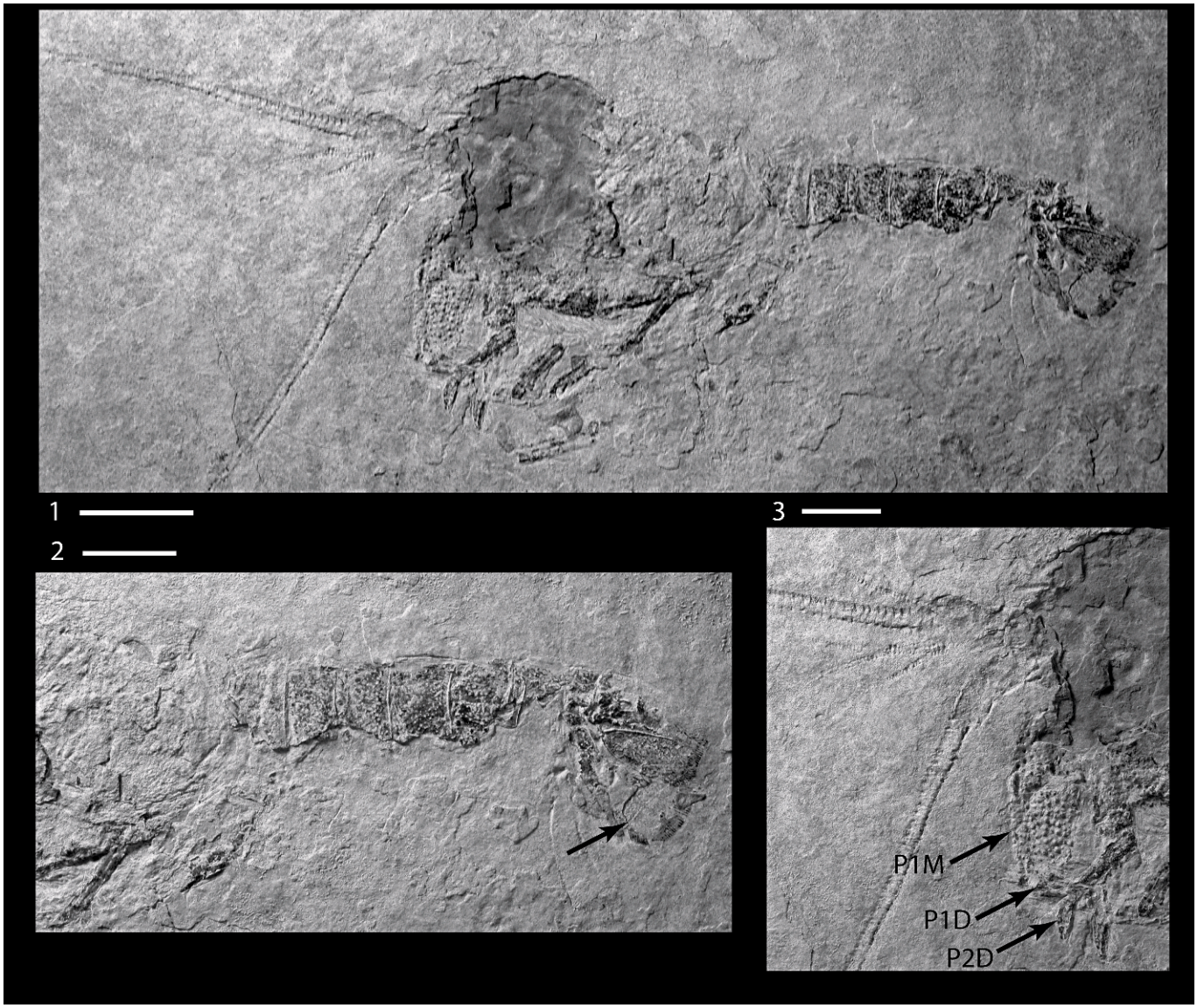

FIGURE 8—*Yunnanopalinura schrami* n. gen. n. sp. paratype LPI–41667, unwhitened specimen. *1,* entire animal showing long antennae and antennules, pereiopods, preserved posterior portion of carapace, and pleon; *2,* pleon with telson and uropods, arcuate boundary between calcified and uncalciifed portion of exopod visible (arrow); *3,* bases of antennae and stout manus (P1M) and long dactylus (P1D) of first pereiopod as well as second pereiopod (dactylus, P2D, indicated with arrow). Scale bars=1 cm.

compressed state of the fossil, appears as a diaresis. This is the most parsimonious explanation for the fossil specimens. Placement within other Triassic families, or families of any age, is contraindicated based upon the lack of carapace grooves and lack of chelae or subchelae on any pereiopods. Thus, placement other than Palinuridae would require a new family, and the possession of so many key features of Palinuridae suggests that placement in that family is more parsimonious.

Palinurellus was considered to have been a primitive form within the Palinuridae (Davie, 1990) but more recent phylogenies have shown it to have a more derived position (Tsang et al., 2009). Tsang et al. (2009) suggested that *Palinurellus* might be a transitional form between the two traditionally recognized groups within the Palinuridae, the Silentes and the Stridentes. Whereas our new form seems to bear some similarities to *Palinurellus*, the material is too poorly preserved to make more direct comparisons at this time. The site of a stridulating device is not exposed on the Luoping material.

This Anisian (Middle Triassic) occurrence is the oldest known of the Palinuridae and the Achelata. The next oldest occurrence is *Archaeopalinurus* Pinna, 1974, known from Norian (Late Triassic) rocks of Italy.

Genus YUNNANOPALINURA Feldmann, Schweitzer and Zhang new genus

Type species.—*Yunannopalinura schrami* new species, by original designation and monotypy.

Diagnosis.—Carapace granular, without distinct grooves or ridges; antennules with long, whip-like flagellae; antennae with stout, spinose basal articles, long; pereiopods 1–5 achelate, first pereiopod stout, granular, stouter than other pereiopods; exopod of uropod well-calcified anteriorly, well calcified portion terminating in convex forward arc, soft and ridged posteriorly; endopod of uropod soft and ridged posteriorly; telson well-calcified anteriorly.

Etymology.—The genus name is based upon Yunnan Province, the location where the specimens were collected,

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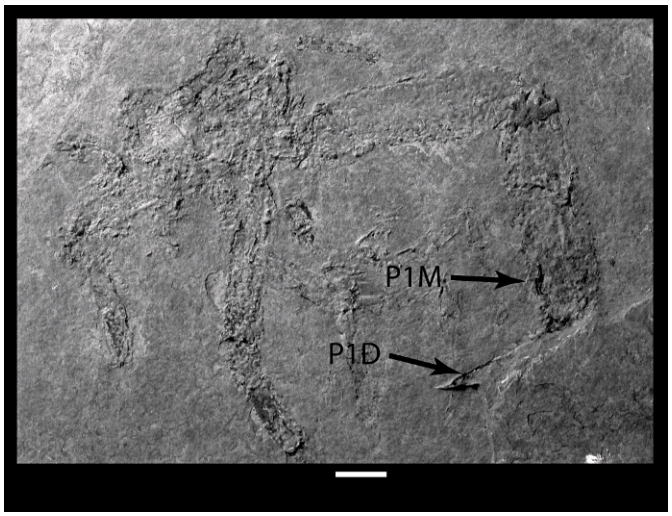

FIGURE 9—Palinuridae sp., specimen 2987. Long manus (P1M) and dactylus (P1D) of first pereiopod indicated with arrows. Scale bar=1 cm.

and *Palinurus*, the type genus of the family to which the new genus belongs. The gender is feminine.

Discussion.—*Yunnanopalinura* n. gen. differs from all other palinurids in having a very robust first pereiopod. As mentioned, those of *Palinurellus* and *Palibythus* are larger than the other pereiopods, but they are not as robust as those seen in *Yunnanopalinura*. Another difference with most known palinurids is that the antennules have very long flagellae; in extant palinurids, they are shorter.

YUNNANOPALINURA SCHRAMI Feldmann, Schweitzer and Zhang new species
Figures 7, 8

Diagnosis.—Carapace granular, without distinct grooves or ridges; antennules with long, whip-like flagellae; antennae with stout, spinose basal articles, long; pereiopods 1–5 achelate, first pereiopod stout, granular, stouter than other pereiopods; exopod of uropod well-calcified anteriorly, well calcified portion terminating in convex forward arc, soft and ridged posteriorly; endopod of uropod soft and ridged posteriorly; telson well-calcified anteriorly.

Description.—Antennules with first basal article about as wide as long; second article stout, wider than long; third article about as wide as long but longer along inner surface so that distal margin is at angle; followed by two multi-articulate flagellae, flagellae long, slender, narrowing distally.

Antennae stout; first basal article not well known; second basal article slightly wider than long; third basal article longer than high, upper margin longer than lower margin, lower margin with two forward directed spines, upper margin with several short forward directed spines near distal margin; distal margin short; flagellae stout, composed of stout rings.

Anterior portion of carapace and rostral area preserved but difficult to interpret. Dorsal carapace ornamented with scattered, large tubercles arrayed into very poorly aligned rows. Carapace outline known for posterior one third; upper and lower surfaces convex; posterior margin concave from upper margin, then sweeping convexly posteriorly into lower margin, appearing to have been rimmed. No evidence of grooves apparent.

First pereiopod stout; merus long, ornamented with tubercles; carpus longer than high, upper surface weakly convex, lower surface convex, distal margin weakly concave, outer surface ornamented with stout, somewhat forward directed tubercles; propodus longer than high, narrowing distally, rectangular, ornamented with stout tubercles overall, distal margin ornamented with large tubercles, ornamented with forward directed tubercles; dactylus triangular, longer than high, coming to sharp point distally, appearing to articulate with entire distal margin of propodus.

Other pereiopods poorly preserved, elements of 2–5 present. Pereiopod 2 may be somewhat larger than 3–5, dactyls of 2 and 3 appear to be oblanceolate, terminal; manus of pereiopod 2 with small spines on lower margin. Merus of pereiopod 4? very long, much longer than high.

Pleonal somites with rectangular tergites, appearing to have been pitted or possibly ornamented with tubercles because cuticular surface as preserved is covered with evenly distributed pits. Somite 1 poorly known. Somites 2–5 similar in shape; tergites appear smooth, posterior margins rimmed; pleurites have distinctive shape, anterior margin of pleurite convex, with corresponding large swelling on surface, then arcing convex forward, and then directed posteriorly in triangular sharp pleurite, posterior margin of pleurite has concavity where anterior margin has bulge; somites overlap succeeding somite slightly. Somite 6 appearing to be longer than others.

Base of exopod of left uropod short, wider than long; exopod of left uropod lying on top of left endopod, appearing to be broadly ovate, calcified anteriorly, with axial ridge on calcified portion, calcified portion terminating in convex-forward arc which begins about three quarters the distance posteriorly along outer margin and terminates along posterior margin; exopod posterior to calcified portion with parallel ridges; inner margin of exopod serrate on posterior two-thirds of length.

Endopod of uropod more rectangular, more or less parallel sided along distal two-thirds of length, with ridges distally.

Telson well-calcified anteriorly.

Etymology.—The trivial name honors Frederick R. Schram, who has described some of the only other known fossil decapods from China and some of the oldest known fossil decapods.

Types.—The holotype is LPI–40169, and one paratype is LPI–41667.

Measurements.—The length of holotype, LPI–40169, is about 84 mm, excluding the telson and uropods and antennae; carapace length, 51 mm; abdominal somites 1–6, 33 mm; length of manus of pereiopod 1, 11 mm; length of dactylus of pereiopod 1, 8 mm. The paratype, LPI–41667, measures 9.1 cm in length, excluding the antennae; carapace length, 40 mm; abdominal length including uropods and telson, 51 mm;

TABLE 2—Measurements (in mm) taken on the first pereiopods of *Tridactylastacus sinensis* n. gen. n. sp.

Specimen number	Length of manus	Height of manus	Length of dactylus	Length of fixed finger
LPI–41545 (left)	4.4	2.1	1.9	—
LPI–41545 (right)	3.9	2.4	2.3	—
LPI–41678 (right)	3.2	2.6	2.9	—
PI–41549	3.6	2.2	2.8	0.3

https://doi.org/10.1666/11-113.1 Published online by Cambridge University Press

antennae about 70 mm long; length of manus of pereiopod 1, 17 mm; length of dactylus of pereiopod 1, 8 mm; length of manus of pereiopod 2, 10 mm; length of dactylus of pereiopod 2, 4 mm.

Discussion.—The two specimens of *Yunnanopalinura schrami* n. sp. are each incomplete. Little is known about the cephalothorax, for example, of this taxon due to the poor preservation of that part of the animal. The pereiopods, antennae, and antennules are all well-preserved, and the pleon, uropods, and telson are moderately preserved also.

Palinuridae sp.
Figure 9

Description of material.—First pereiopod long, stout. Merus longer than high, stout, granular overall, lower and upper margins nearly parallel, lower margin may have had spines. Carpus longer than high, highest distally; proximal margin short, upper margin weakly convex, lower margin nearly straight, appearing to have had spines, distal margin straight. Manus longer than high, proximal margin straight, granular; upper and lower margins arcuate, possibly with spines; distal margin poorly known. Dactyl very long, about as long as manus, narrowing distally and terminating in sharp tip.

Second pereiopod moderately stout. Merus longer than high, granular, upper and lower margins parallel; carpus longer than high; manus rectangular, granular on outer surface, lower margin with small spines; dactyl long, slender, sharp-tipped.

Flagellae of antennae very stout.

Measurements.—Measurements (in mm) taken on large palinurid specimen are presented here. First pereiopod: dactyl length, 2.5 cm; merus length, 4 cm; height, 12 mm; manus length, 3 cm; height, 13 mm; carpus length, 19 mm, height, 12 mm. Second pereiopod: dactyl length, 12 mm, height, 3 mm; manus length, 15 mm, height, 5 mm; carpus length, 12 mm, height, 5 mm; merus length, 22 mm, height, 6 mm.

Material examined.—Specimen LPI 2987.

Discussion.—This specimen appears to belong to a different taxon than *Yunnanopalinura schrami* because of its much larger size and the very much larger dactyl of the first pereiopod. The dactyl is equal in length to the manus, whereas in *Y. schrami* it is much shorter. A large specimen in the possession of a private collector shows a similarly long dactyl. This suggests that future collection will yield a new species.

ECOLOGICAL IMPLICATIONS

Decapods have played a major role as low-level predators and scavengers in a wide range of marine environments. They have been considered key components in the so-called Mesozoic Marine Revolution (Vermeij, 1977, 1987). Recently, Schweitzer and Feldmann (2010) examined the potential for decapods as durophagous predators. They suggested that the range of behaviors and morphological features exhibited within the order argued for inclusion of a broader range of taxa within the spectrum of potential predators than had previously been considered. The predatory behavior certainly had evolved at least by the Triassic (Schweitzer and Feldmann, 2010). The lobsters in the Luoping Biota provide evidence of a broad spectrum of feeding behaviors.

The claw morphology observed on the lobsters in the Luoping Biota certainly supports an active role in predation for these organisms. *Koryncheiros luopingensis* n. gen. n. sp. bears unusual claws in that the dactylus closes on the end of the propodus. The claw is oriented more or less in the vertical plane which suggests that the organism would be more efficient at preying on benthic epifauna and infauna rather than on pelagic creatures. It is possible that this species was adapted to extracting food from the substrate by capturing live prey and by scavenging. In contrast, *Tridactylastacus sinensis* n. gen. n. sp. carries the large, toothed subchelae in a generally horizontal plane. This position would be conducive to preying on pelagic as well as benthic epifauna. Scavenging would also provide additional food resources. Decapods in general seem to be opportunistic feeders (Schweitzer and Feldmann, 2010). The first pereiopods on *Yunnanopalinura schrami* n. gen. n. sp. do not seem adapted to grasping in the same manner as the glypheoids but their stout design would permit them to use the pair of first pereiopods to grasp prey. Although not preserved on the Chinese specimens, palinurids in general have strong mandibles to facilitate durophagous predation (Schweitzer and Feldmann, 2010).

The sediment on which the lobsters lived was fine grained and probably not firm. Therefore, it is likely that the animals did not burrow actively but instead sought cover by burying themselves just below the sediment-water interface. All the specimens were preserved on sediment surfaces; none was preserved in burrow structures. Some of the specimens, particularly those preserving dissociated appendages, were probably molted remains which may not have lived precisely at the site of burial. Providing sediment cover for the individuals may have been facilitated by use of pereiopods 2–5 along with motion of the pleon.

ACKNOWLEDGMENTS

This work was supported by the Chinese Geological Survey (no. 1212011140051, 1212011120621 and 1212010610211). NSF grant EF-0531670 supported examination of extant macrurous decapods at the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A., and R. Lemaitre and K. Reed provided access to the collections at that institution for comparative work. Careful reviews by G. Schweigert, Staatliches Museum fur Naturkunde, Stuttgart, Germany, and an anonymous review provided valuable additions to the manuscript. Editorial guidance by S. Hageman was much appreciated.

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ACCEPTED 8 NOVEMBER 2011