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New occurrences of fossil decapod crustaceans (Thalassinidea, Brachyura) from late Pleistocene deposits of Guam, United States Territory

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Abstract

A large collection of fossil decapods has yielded several new occurrences for late Pleistocene deposits of Guam, United States Territory. *Neocallichirus*? sp., *Myra fugax, Thalamita crenata, Rhinolambrus pelagicus, Scylla serrata, Calappa hepatica, Carpilius* sp., *Actaeodes* sp., and several indeterminate chela fragments are herein reported as fossils from Guam for the first time. Emended descriptions and additional illustrations are provided for the previously reported taxa, *Macrophthalmus latreillei* and *Podophthalmus vigil*. *Macrophthalmus guamensis* is herein synonymized with *M. definitus*. *Carcinoplacoides* is herein synonymized with *Libystes*. *Carcinoplacoides flottei* is also synonymous with *Libystes nitidus* and becomes the junior synonym of the latter species. *Myra brevisulcata, M. subcarinata,* and *M. trispinosa* of the Pliocene Miri Formation (Morris and Collins, 1991) are herein synonymized; *M. brevisulcata* becomes the senior synonym. The fauna is unusual because most of the taxa are comprised of many more male than female individuals; the percentage of males within the preserved population ranges from 50 to 89 percent in various species. The late Pleistocene fauna of Guam appears to have been derived from the Tethyan and Indo-Pacific regions, as is typical of Indo-Pacific faunas of Recent oceans (Schweitzer, 2001). Many of the genera and even some species appear to have evolved as early as the Miocene in the western Tethyan area of southern Europe. These findings support the assertion that most decapod genera and many species that first appeared in the Miocene survive into the Recent (Schweitzer, 2001).

Key words: Decapoda, Thalassinidea, Brachyura, Pleistocene, Guam

Introduction

Kesling (1958) described four species of fossil decapod crustaceans from what he considered to be late Pleistocene rocks of Guam. Included in his study were a new species of *Macrophthalmus, M. guamensis,* and a new genus and species, *Carcinoplacoides flottei,* that he placed within the Goneplacidae. In addition, he described two taxa previously reported from the fossil record, *M. latreillei* and *Podophthalmus vigil*. New material collected by one of us (PRS) and Charles Scott-Smith of Guam in conjunction with Gustav Paulay, then of the University of Guam Marine Laboratory, yielded a species of *Mursia* (Schweitzer and Feldmann, 2000). Additionally, these collections contain six previously unreported taxa, *Neocallichirus*? sp., *Myra fugax, Thalamita crenata, Scylla serrata, Calappa hepatica, Carpilius* sp., *Actaeodes* sp., and *Rhinolambrus pelagicus,* as well as specimens of *Podophthalmus vigil, Macrophthalmus latreillei, Macrophthalmus definitus* (=*M. guamensis* Kesling, 1958) and *Libystes nitidus* (=*Carcinoplacoides flottei* Kesling, 1958). Also included

are miscellaneous claw fragments. Examination of specimens of *M. guamensis* indicates that this species is synonymous with the extant *M. definitus.* In addition, *Carcinoplacoides flottei* has been deemed synonymous with *Libystes nitidus.* Thus, at least eleven decapod taxa are now known from late Pleistocene deposits of Guam. Specimens examined are deposited in the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; the American Museum of Natural History (AMNH), New York, New York; and the Zoological Reference Collection (ZRC) of the Raffles Museum, National University of Singapore. Biological specimens mentioned in the text are deposited in the Florida Museum of Natural History (FMNH), University of Florida, Gainesville, Florida.

Geologic Setting

The information on the geology of the area from which the fossils were taken was provided by Gustav Paulay, Florida Museum of Natural History, Gainesville, Florida except where noted otherwise. All of the fossil decapods discussed here were collected from dredging and excavation spoil piles taken from the Inner Harbor area of Apra Harbor on the west coast of Guam. The material was subsequently deposited along beaches of the Orote Peninsula and near the town of Agat, both south of Apra Harbor. Kesling's (1958) material was recovered from these deposits as well. Apra Harbor is a large embayment, bordered by mangroves, and was a silty, reefy habitat before being converted to a military port subsequent to World War II. The corals that previously inhabited the area have been damaged or killed during harbor development (Tracey et al., 1964). The age of the deposits is unknown but is believed to be late Pleistocene (G. Paulay, pers. commun.). The deposits are composed of several facies; however, the crabs appear to have been recovered from a single unit. In their work on the geology of Guam, Tracey et al. (1964) did not place the Apra Harbor deposits within the stratigraphic framework of the deposits of Guam. One of us (PRS) and Charles Scott-Smith wrote a short guidebook entitled *Guam's Fossil Crabs* which includes drawings and a brief discussion of some of the crabs discussed in this report and the associated fauna.

Systematic Paleontology

Order Decapoda Latreille, 1802
Infraorder Thalassinidea Latreille, 1831
Superfamily Callianassoidea Dana, 1852
Family Callianassidae Dana, 1852
Genus *Neocallichirus* Sakai, 1988

Type species: *Neocallichirus horneri* Sakai, 1988.

Discussion: The specimens described here are difficult to assign to a genus based upon their incomplete nature. The specimens are most similar to species of *Neocallichirus* and *Calliax* de Saint Laurent, 1973. Both genera possess meri with serrated lower margins and a longitudinal keel; a carpus somewhat longer than high in most species; and rectangular, unornamented mani. All of these features are present in the Guam material. The carpus in species of *Calliax* appears to be longer than those of species of *Neocallichirus;* in addition, that of species of *Calliax* have a markedly convex proximal margin. In species of *Neocallichirus,* the proximal margin of the carpus is usually less convex; however, the convexity varies considerably among species (Manning and Felder, 1991; Manning, 1993; Felder and Manning, 1995). The material from Guam possesses a markedly convex proximal margin of the carpus. In some species of *Neocallichirus,* the lower margins of the carpus and manus may be serrate (Manning, 1993), a feature not seen in the Guam material. Some species of *Neocallichirus* exhibit an indentation in the distal margin just above the fixed finger, as is present in the Guam material; however, some species do not possess this indentation. Species of *Calliax* also exhibit this indentation as well (Manning and Felder, 1991). Morphological features of the chelipeds are thus not a reliable means by which to assign the new material to either *Neocallichirus* or *Calliax*. *Neocallichirus* is common in waters of the Indo-Pacific (Manning and Felder, 1991), while *Calliax* appears to be a largely Mediterranean and European species (de Saint Laurent and Manning, 1982).

Thus, the specimens are tentatively assigned to *Neocallichirus,* based on the high probability of Indo-Pacific taxa being recovered from Guam, until more complete material is discovered.

Neocallichirus? sp.
(Fig. 1)

Description of material: Merus of cheliped longer than high, highest proximally in some specimens and highest distally in others; proximal margin sinuous; upper margin

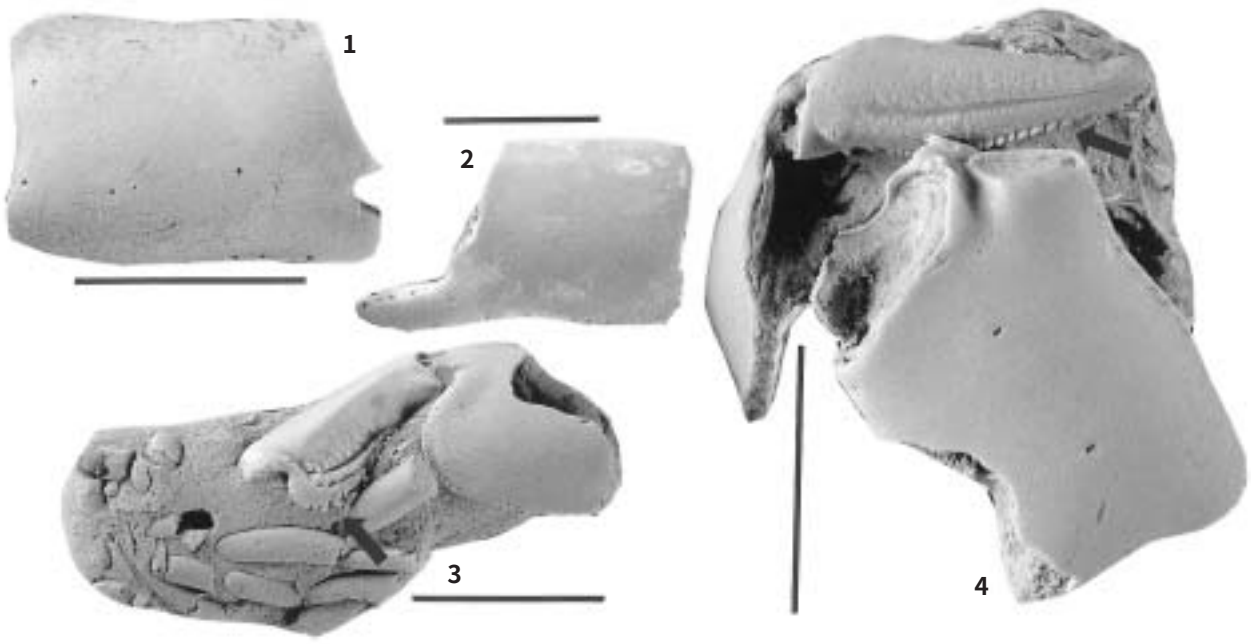


Fig. 1. *Neocallichirus*? sp. 1, outer surface of right manus, USNM 519533. 2, outer surface of left manus, USNM 519536. 3, Merus and carpus of major (?) chela (USNM 519535), arrow indicates serrations on lower margin of merus, which is widest proximally. Note large size of cheliped as compared with remainder of body. 4, Broken chela, focusing on merus, which widens distally (USNM 519534). Arrow indicates serrations on merus. Scale bars equal to 1 cm.

weakly convex, most convex at distal end; lower margin convex, serrate; distal margin slightly concave.

Carpus of cheliped appearing to be slightly longer than high; proximal margin with narrow projection at upper corner facilitating articulation with merus, margin with small, moderately deep notch just below the projection, remainder rounded, convex, projecting proximally, weakly serrate; upper and lower margins weakly convex; distal margin not well known.

Manus of chela rectangular, longer than high, lanceolate in cross-section, appearing to be smooth on inner and outer surfaces; proximal margin weakly convex; upper and lower margins relatively straight; distal margin not well known, articulation with movable finger occupies about two-thirds its height, below articulation a small, distinct notch just above position of fixed finger. Fixed finger narrow, narrowing distally, ovate in cross section, row of setal pits parallel to occlusal surface; finger curves inwards towards inner margin, when viewed from a perspective looking down onto upper margin finger extends at about 70 degree angle to axis of manus.

Movable finger unknown. Remainder of appendages much smaller than chelipeds.

Material examined: USNM 519533-519536; sample lot USNM 517451, 69 specimens; AMNH-FI-47142, 4 mani; ZRC, 2 mani.

Discussion: The material is comprised mainly of broken mani of the chelipeds. Twenty-seven belong to the right chela, and thirty-three to the left. The smaller specimens tend to exhibit greater length relative to the height than do larger specimens, suggesting that the material may contain a mixture of both major and minor chelae. In addition, the form of the merus differs in the two specimens which exhibit meri as described above. Allometric growth might offer an alternative explanation for the differences in relative size of the manus and the merus shape.

The right and left populations each exhibit a wide range of manus sizes; thus, it is not possible to describe the right or left chela as being the major one in the majority of individuals. Because the chelae occur mainly as single fragments, it is impossible to determine if the animal was heterochelous or isochelous. The two specimens which retain portions of other appendages only exhibit one chela. Because the material is quite limited, it seems best to refer it all to one species until more and better preserved material is discovered.

Illustrations of *Callianassa nishikawai* Karasawa, 1993

(Karasawa, 1993; Karasawa and Kishimoto, 1996) indicate that the overall shape of the carpus in that species is nearly identical to that of the material described here. In addition, both the carpus and the merus of that species have serrations on the lower margins as does the material from Guam. *Callianassa nishikawai* has an indentation into the distal margin similar to that of the specimens collected from Guam, and the articulation for the movable finger is very large as in the Guam material. The fixed finger of *Callianassa nishikawai* is slender and curved inward as is the fixed finger of the material from Guam. Karasawa (1993) described *C. nishikawai* as possessing a strong meral hook on the lower margin; however, that hook is not visible in the illustrations. It seems probable that *C. nishikawai* and the Guam material are congeneric.

Karasawa and Goda (1996) described *"Neocallichirus" grandis* from Pleistocene rocks of Japan. The new material shares several features with the Japanese species, including a serrate lower margin of the merus, slender and curved fixed fingers with no dentition on the occlusal surface, and a small indentation positioned on the distal margin above the base of the fixed finger. It seems possible that all three taxa may belong to the same genus.

Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Calappoidea H. Milne Edwards, 1837
Family Calappidae H. Milne Edwards, 1837
Genus *Calappa* Weber, 1795

Type species: *Cancer granulatus* Linnaeus, 1758.

Fossil species: *Calappa costaricana* Rathbun, 1919; *C. earleyi* Withers, 1924; *C. flammea* (Herbst, 1794) (also Recent); *C. granulata* (Linnaeus, 1758) (also Recent); *C. heberti* Brocchi, 1883; *C. lanensis* Rathbun, 1926; *C. lophos* (Herbst, 1785) (also Recent); *C. marmorata* (Herbst, 1790) (also Recent); *C. praelata* Lőrenthey, 1929; *C. protopustulosa* Noetling, 1901; *C. restricta* A. Milne Edwards, 1873; *C. sexspinosa* Morris and Collins, 1991; *C. springeri* Rathbun, 1931 (also Recent); *C. zurcheri* Bouvier, 1899; *C. zinsmeisteri* Feldmann and Wilson, 1988.

Calappa hepatica (Linnaeus, 1758)

Discussion: A few fragments of carapace and cheliped have been recovered that are clearly assignable to *Calappa hepatica,* an extant species now found in waters of Guam. The carapace fragments exhibit the characteristic nodose ornaments of calappids, and the fingers are recurved and armed with teeth as are calappid claws. Specimens of *C. hepatica* are very rarely found as fossils in Guam, although the species is common in the Indo-Pacific (Sakai, 1976). The distribution of the genus in the fossil record suggests that it was primarily a Tethyan and Indo-Pacific form (Schweitzer and Feldmann, 2000).

Material examined: ZRC, a cheliped fragment.

Superfamily Leucosioidea Samouelle, 1819
Family Leucosiidae Samouelle, 1819
Subfamily Philyrinae Rathbun, 1937
Genus *Myra* Leach, 1817

Type species: *Leucosia fugax* Fabricius, 1798.

Fossil species: *Myra amoena* Böhm, 1922; *M. arachnoides* Böhm, 1922; *M. brevisulcata* Morris and Collins, 1991(= *M. subcarinata* Morris and Collins, 1991, and *M. trispinosa* Morris and Collins, 1991); *M. emarginata* Glaessner, 1928; *M. fugax* (Fabricius, 1798); *M. paenitensis* Via, 1941; *M. wenchii* Hu and Tao, 1985.

Discussion: At least two other genera within the Leucosiidae closely resemble *Myra*. *Persephona* Leach, 1817, has been reported to be very similar to *Myra*, but it differs from *Myra* in having a bidentate as opposed to a tridentate anterior margin of the pterygostomial groove (Barnard, 1950; Glaessner, 1969). However, this character is not useful for fossil material. Within *Persephona*, male abdominal somites 3-5 are fused, while in *Myra*, somites 3-6 exhibit fusion. Species of *Persephona* appear to have a somewhat more globular carapace than do members of *Myra*, and the orbits appear to be somewhat more widely spaced and produced further beyond the remainder of the carapace in *Persephona* than in *Myra*.

Members of *Iliacantha* Stimpson, 1871, are also remarkably similar to both *Myra* and *Persephona*, although *Iliacantha* is placed within a different subfamily, the Leucosiinae Samouelle, 1819, based upon features of the maxillipeds and chelae that do not often fossilize. Members of *Myra* exhibit fusion of male abdominal somites 3-6, while *Iliacantha* exhibits fusion of male abdominal somites 3-5. Additionally, the hepatic ridge is globular in most species of *Iliacantha*, while in members of *Myra* it is linear and sharp.

Alphonse Milne Edwards (*in* Sismonda, 1861) reported *Palaeomyra* from Miocene rocks of Northern Italy.

Examination of specimens referred to *Palaeomyra* (M.86.79, M.86.372) deposited in the Natural History Museum of Hungary Paleontological Collection (Természettudományi Múzeum Föld-és Őslénytár), Budapest, Hungary, shows that the new material is not referable to that genus. Members of *Palaeomyra* have two posterior spines, while the new material has three, and *Palaeomyra* possesses granular ornamentation beginning about one-third the distance posteriorly on the carapace and extending to the posterior margin. In the new material, the carapace has little ornamentation.

Fossil occurrences of *Myra* have been reported from the Miocene of Europe, India, and Fiji; the Miocene to Pliocene of Java; the Pliocene of Sarawak, Brunei, and Taiwan; and the Pleistocene of Celebes (Martin, 1880; Böhm, 1922; Via, 1941; Glaessner, 1969; Hu and Tao, 1985, 1996; Solé and Via, 1989; Morris and Collins, 1991; Müller, 1993). Morris and Collins (1991) reported three species of *Myra*, *M. brevisulcata*, *M. subcarinata*, and *M. trispinosa* from the Pliocene Miri Formation of Sarawak and Brunei. Comparison of the descriptions and illustrations of these three taxa indicates that they are very similar in overall shape and carapace morphology. Additionally, the features used to distinguish among the three species are features of ornamentation and development of regions that could be due to individual variation or to preservation. The three species are also known from the same formation. Thus, it seems prudent to synonymize the three species, *M. brevisulcata* becoming the senior synonym. Recent species, numbering sixteen, (Sakai, 1976; Chen and Türkay, 2001), have been recorded from Japan, China, the Indo-Pacific, Hawaii, the Gulf of California, and Panama. The genus clearly displays a Tethyan distribution, perhaps having evolved within the central Tethyan realm in the region of Europe and India during the Miocene and subsequently dispersed throughout the Indo-Pacific.

Myra fugax (Fabricius, 1798)

(Figs. 2, 3)

Description of material: Carapace ovate, longer than wide, about 1.25 times as long as wide, widest about one-third the distance posteriorly on carapace; carapace regions not defined, surface pitted; highly vaulted transversely, moderately vaulted longitudinally.

Rostrum unknown; orbits closely spaced, fronto-orbital width narrow, about one-quarter maximum carapace width; orbits circular, directed forward, with two fissures, orbits situated on anteriorly projecting frontal region. Lateral margins convex, tightly convex anteriorly, more weakly convex posteriorly; margin with small concave indentation anteriorly and distal to the orbits to accommodate the first pereiopods. Lateral margins converging posteriorly into a stout granular spine, spine flanked on each side by smaller, shorter posterolaterally directed granular spines.

Dorsal carapace with little ornamentation; hepatic regions with small ridge parallel to lateral margin and just under the concave indentation which accommodates the pereiopods.

Sternum ovate, longer than wide, widest at position of sternite 5. Sternite 1 tiny, not well known. Sternite 2 triangular, apex of triangle directed forward, lateral margins slightly concave. Sternites 3 and 4 fused; widening posteriorly; lateral margins concave to accommodate coxa of first pereiopods; lower outer corners of sternite 3/4 with short, triangular episternal projections; directed anterolaterally. Sternite 5 directed laterally, widening distally, with long, triangular episternal projections, upper margin weakly concave, lower margin weakly convex. Sternite 6 directed posterolaterally, widening distally, with slender episternal projections. Sternite 7 short, about as wide as long, directed strongly posterolaterally, with short episternal projections. Sternite 8 very small, short, appearing to have small episternal projections.

Abdomen of male long, triangular; lateral margins of entire abdomen nearly straight. Abdominal somites of male with high degree of fusion, somites 3-6 appearing to be fused; telson appearing to be free, triangular.

Coxae of pereiopods becoming progressively smaller posteriorly.

Measurements: Measurements were difficult to obtain because the specimens have suffered extensive damage along the margins of the carapace. Average measurements (in mm) taken on specimens of *Myra fugax* are as follows: maximum length, n=4, 28.1; maximum width, n=8, 26.0; fronto-orbital width, n=5, 5.4.

Material examined: A sample lot of 45 specimens, USNM 517439; USNM 519537-519538; 8 specimens, ZRC; AMNH-FI-47129 and 47130.

Occurrence: This species is relatively uncommon as compared to the other decapod taxa found within the same deposits.

Discussion: The new specimens are referable to *Myra fugax* based upon several characters. Members of *Myra*

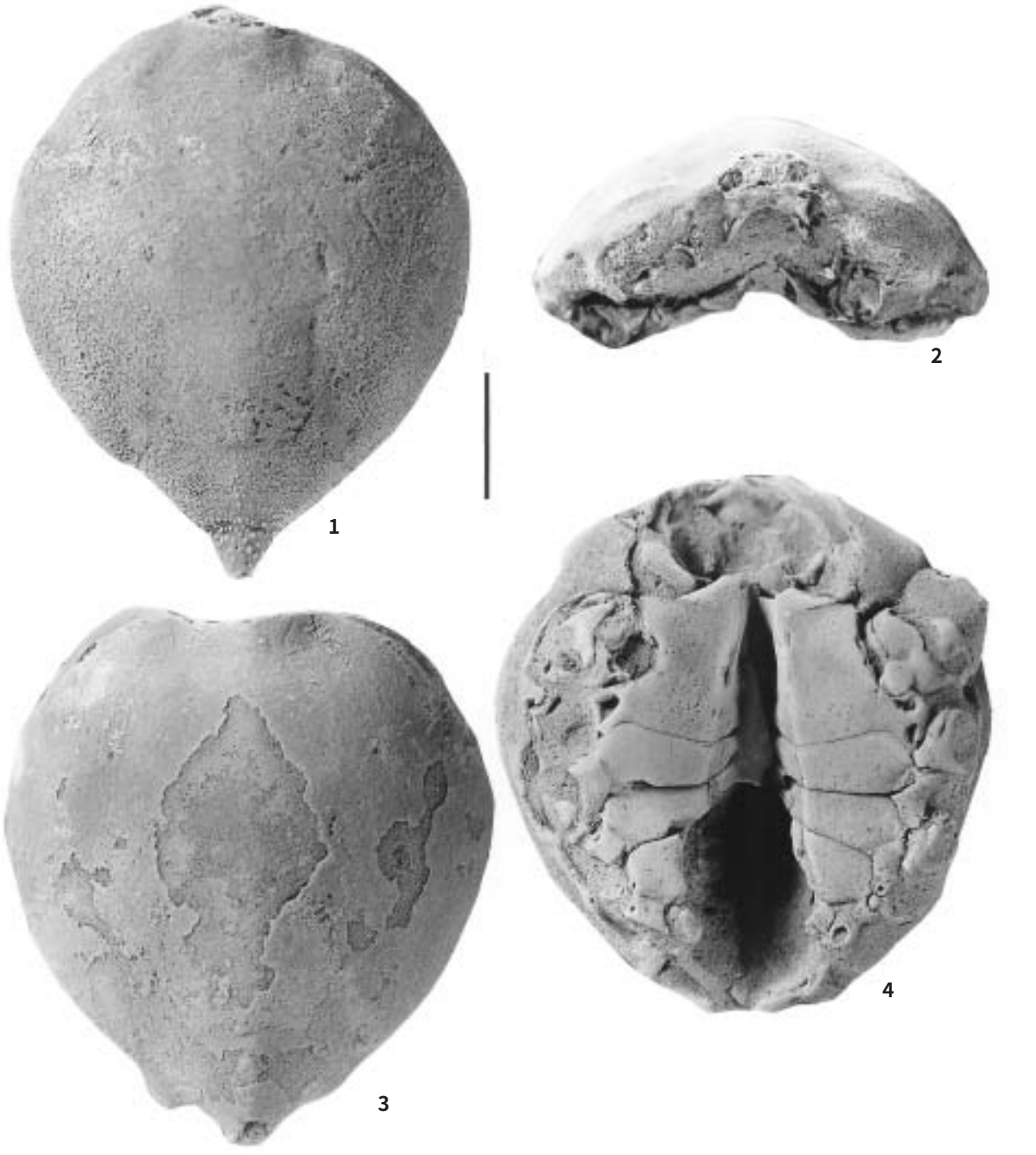


Fig. 2. *Myra fugax* (Fabricius, 1798). 1, dorsal carapace, USNM 519537. 2, anterior view showing tiny orbits, USNM 519537. 3, dorsal carapace, USNM 519538. 4, ventral view of male, USNM 517438. Scale bar equal to 1 cm.

fugax have a sparsely granular carapace that is more densely granulated on the posterior portions of the carapace; the new fossils also possess that feature. Individuals of *Myra fugax* have a large spine posteriorly flanked by two smaller triangular spines, characters that the new material also possesses. Individuals of *M. fugax* have two orbital fissures and hepatic ridges on the dorsal carapace parallel to the lateral margins and the orbits; the new material also has this feature. Thus, the new material is referred to *M. fugax*.

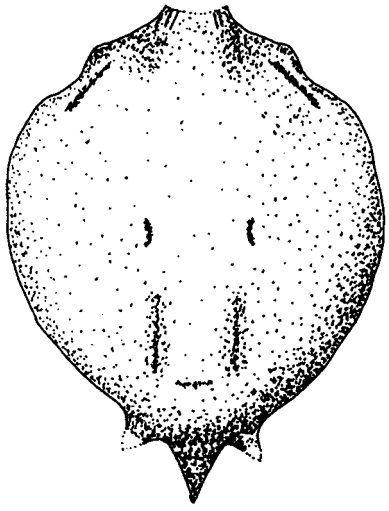


Fig. 3. Line drawing of *Myra fugax,* reconstructed from several specimens.

The fossil material is moderately well-preserved, although the preservation appears to be poorer than for the other decapod taxa found in the same deposits. For example, in almost all of the specimens, the orbits and rostrum are broken and either completely missing or severely damaged. Most of the specimens lack the posterior spines which have been broken off or worn away. The sternum is well-preserved in several specimens, although the abdomen is often broken and somites are usually missing. None of the specimens retains more than the coxae of some of the appendages. Just more than half of the specimens, 12 of 23, appear to be corpses because they retain both the dorsal carapace and the sternum. The dorsal carapace itself is often highly weathered, eroding away the granulation typical of the species. It appears as if the specimens may have been moved by wave or tide activity, causing them to roll like pebbles due to their nearly spherical shape, and eroding the lateral margins of the carapace.

Of the specimens retaining the abdomen, all but one, or 89 percent, appear to be males, because the abdomina are all very narrow. One USNM specimen with a badly damaged abdomen appears to be a female because the abdomen is relatively broad, at least as compared to the other specimens.

Myra fugax has previously been reported from the Miocene to Holocene of Java (Martin, 1880; Van Straelen, 1938); the Pliocene and Pleistocene of Taiwan (Hu and Tao, 1985; 1996); and from Pleistocene deposits of the Ryukyu Group, Okinawa-jima, Japan (Karasawa, Nohara, and Shimoji, 1995). Additionally, Sakai (1976) noted that *M. fugax* is one of the most common leucosid crabs within the Indo-Pacific, which is consistent with its broad geographic distribution within Pleistocene-Holocene deposits of the North Pacific Ocean. A fresh specimen of this species was recently collected from Guam and was examined by one of us (PKLN); it is currently housed in FMNH.

Myra? sp.

Description of material: Merus of pereiopod much longer than high, granular on distal end and becoming smoother at proximal end. Carpus of cheliped very short, slightly longer than high, finely granular. Manus of cheliped longer than high, slightly higher distally, finely granular, bulbous in cross section, most bulbous at position of lower proximal margin; proximal margin nearly straight, at about 80 degree angle to lower margin of manus; lower margin convex; upper margin weakly convex; distal margin with projections that articulate with fingers, at about 120 degree angle to fixed finger. Fixed finger slightly deflexed, appearing to maintain height along at least two-thirds of its length; with small, blunt, spherical tubercles on occlusal surface. Movable finger narrowing distally; with small, blunt tubercles on occlusal surface.

Material examined: Two pereiopod fragments, USNM 517439 and 517440; ZRC, 8 carapace fragments.

Discussion: The pereiopod fragments are consistent with those of leucosid crabs, but because they were not articulated with specimens of *Myra fugax,* and because the specimens of *M. fugax* have no articulated pereiopods for comparison, the fossils are questionably referred to *Myra.* Leucosids typically have very elongate meri of the pereiopods, especially the first; short, equant carpi of the first pereiopods; and claws with elongate fingers with finely developed dentition. The fossil material possesses all of these features; thus, it is questionably referred to the only leucosid genus present in the fauna, *Myra,* until a more definitive placement can be made.

Superfamily Parthenopidae MacLeay, 1838

Family Parthenopidae MacLeay, 1838

Genus *Rhinolambrus* A. Milne Edwards, 1878

Type species: When A. Milne Edwards (1878) erected the genus, he did not designate a type species; this situation is currently under evaluation (S.-H. Tan, personal communication).



Fig. 4. *Rhinolambrus pelagicus* (Rüppell, 1830), dorsal carapace, USNM 519526.

Rhinolambrus pelagicus (Rüppell, 1830)
(Fig. 4)

Description of material: Carapace slightly wider than long, widest at midlength of branchial regions; regions inflated, appearing to have had granular ornamentation but smoothed by abrasion. Rostrum broken; orbits broken, appearing to have been directed anterolaterally; protogastric regions narrow, inflated; mesogastric region flattened anteriorly and more inflated posteriorly; urogastric region narrow, weakly depressed; cardiac region spherical, inflated, much wider than other axial regions. Hepatic region small, inflated; branchial regions not well-differentiated, deep depression lateral to urogastric region. Carapace surface pitted and eroded.

Material examined: 2 specimens (ZRC), 1 specimen (USNM 519526).

Discussion: The specimens are well worn, probably by wave abrasion, but display an arrangement of carapace regions, grooves, and depressions similar to *Rhinolambrus pelagicus*, and they are here referred to that species. Neither the genus nor the species has previously been reported as a fossil from Guam. In modern oceans, the species ranges from Japan southward throughout the waters of the equatorial and tropical west Pacific (Sakai, 1976).

Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Portuninae Rafinesque, 1815

Genus *Scylla* de Haan, 1833

Type species: *Cancer serratus* Forskål, 1775.

Fossil species: *Scylla costata* Rathbun, 1919; *S. hassiaca* Ebert, 1887; *S. laevis* Böhm, 1922; *S. micheleni* A. Milne Edwards, 1860b; *S. molassica* Studer, 1898; *S. ozawai* Glaessner, 1933; *S. serrata* Forskål, 1775 (also Recent).

Scylla serrata (Forskål, 1775)

Material examined: One lot of chela fragments, USNM 517446; ZRC, 2 chela fragments.

Discussion: Fossil specimens of *Scylla serrata* have previously been reported from Pliocene to Pleistocene deposits of the Indo-West Pacific region (Desmarest, 1822; A. Milne Edwards, 1860a; Etheridge and MacCulloch, 1916; Van Straelen, 1928; Das-Gupta, 1924; Karasawa, 1993; Karasawa and Tanaka, 1994), Quaternary alluvium of Malaysia (Idris, 1989), and early Holocene deposits of China (Yang and Wang, 1985). Karasawa (1993) reported another species of *Scylla*, *S. ozawai* (Glaessner, 1933) and specimens referred to *Scylla* aff. *S. serrata* from Miocene rocks of Japan. Hu and Tao (1996) described *Scylla marianae* from the Plio-Pleistocene Mariana Limestone of Guam; however, the fragmental nature of the type specimen makes it difficult to determine if it is in fact distinct from *S. serrata*.

Genus *Thalamita* Latreille, 1829

Type species: *Cancer admete* Herbst, 1803.

Fossil species: *Thalamita* cf. *T. admete* (Herbst, 1803);

T. crenata (Latreille, 1829) (also Recent); *T. fragilis,* Müller, 1979; *T. truncatata* Hu and Tao, 1996; *T. fani* Hu and Tao, 1996.

Discussion: A small number of fossil taxa have been referred to the genus *Thalamita,* and these occurrences suggest a Tethyan origin and distribution. Müller (1984) reported *Thalamita fragilis* Müller, 1979, from Miocene rocks of Hungary; Hu and Tao (1996) described *T. truncatata* and *T. fani* from Miocene rocks of Taiwan; and Karasawa (2000) reported a Pleistocene occurrence of *Thalamita* sp. aff. *T. admete* (Herbst, 1803) from the Ryukyu Islands, Japan.

The genus is typified by possession of a very broad front, widely spaced orbits, and narrow granular ridges on the protogastric and branchial regions of the dorsal carapace. Members of the genus usually have four anterolateral spines excluding the outer-orbital spine, the third of which is usually smallest. The front is usually divided into about six broad, blunt lobes. Species within *Thalamita* are differentiated based upon the relative width of the front, the size of the orbits, the development of carapace regions and ridges, and the size and shape of the anterolateral and frontal spines. Members of the genus *Thalamita* are very similar to species of *Charybdis* de Haan, 1833, but *Charybdis* usually has more closely spaced orbits and a narrower front than *Thalamita.*

Recent species of *Thalamita* are abundant throughout the Indo-Pacific region, and African and Middle Eastern waters (Sakai, 1976). Sakai (1976) reported 21 species of *Thalamita* from Japanese waters, and Ng (1998) reported species of *Thalamita* from the west-central Pacific. Thus, the fossil occurrence of *Thalamita* in Pleistocene-Holocene rocks of Guam is consistent with its Recent distribution.

Thalamita crenata (Latreille, 1829)
(Figs. 5, 6)

Description: Carapace hexagonal, wider than long, L/W about 0.62, widest at position of last anterolateral spine about two-thirds the distance posteriorly on carapace; surface granular; carapace regions poorly defined; flattened transversely and longitudinally.

Frontal margin broad, frontal width about 34 percent maximum carapace width. Antennae situated in very large concavities; antennules situated in smaller, less obvious concavities that appear to be nearly continuous with orbits. Orbits widely spaced, fronto-orbital width about two-thirds maximum carapace width; orbits large, deeply concave, directed slightly anterolaterally, lower

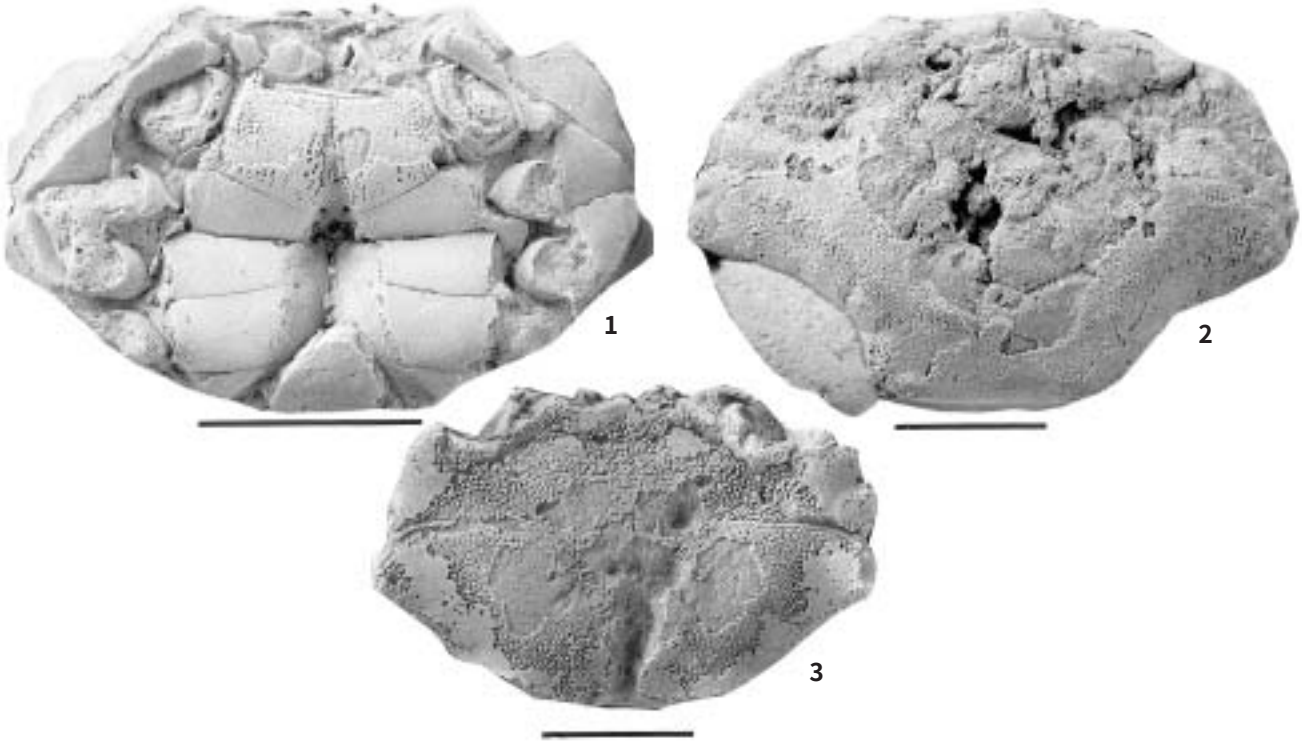


Fig. 5. *Thalamita crenata* (Latreille, 1829). 1, ventral view of male, 507818. 2, dorsal view, USNM 507819. 3, dorsal carapace, USNM 507818. Scale bars equal to 1 cm.

margin of orbits visible in dorsal aspect; orbits with thickened rim and with small, blunt inner and outer orbital spines. Anterolateral margin with four spines excluding outer orbital spine; spines appearing to be broad, blunt, separated by shallow, narrow reentrants. First and second spines similar in size, directed anterolaterally; third spine smallest, directed anterolaterally; fourth spine largest, stout, circular in cross-section, longest and stoutest of all spines, directed laterally. Posterolateral margin concave, entire. Posterior margin weakly concave, entire, about 37 percent maximum width.

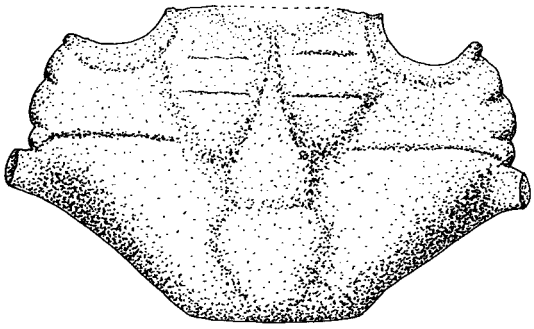


Fig. 6. Reconstruction of *Thalamita crenata,* based upon several specimens.

Frontal region slightly depressed. Protogastric regions weakly inflated, with two granular, linear transverse crests. Mesogastric region narrow anteriorly and widening posteriorly, inflated posteriorly. Urogastric region poorly defined, depressed. Cardiac region poorly defined, weakly inflated. Hepatic region depressed, separated from branchial region by linear, granular ridge, ridge terminating between third and fourth anterolateral spines. Branchial regions inflated axially and anteriorly, and depressed marginally.

Pterygostomial region smoother than dorsal surface. Buccal frame rectangular, wider than long, short. Exopod of third maxiliped narrow, longer than wide. Endopod of third maxilliped smooth, arcuate in shape, arcing axially, with longitudinal groove.

Sternite 1 unknown. Sternites 2-4 fused; sternite 2 narrow, with triangular lateral projections, separated marginally from sternite 3 by narrow reentrant; sternite 3 with convex, rounded lateral margins, directed anterolaterally, wider than long; sternite 4 much wider than long, directed anterolaterally, with large, curved, triangular episternal projections. Sternite 5 much wider than long, upper and lower margins nearly straight, becoming longer laterally; with long, triangular episternal projections, directed slightly anterolaterally. Sternite 6 directed laterally, becoming wider laterally, with small episternal projections. Sternite 7 longest of all sternites, directed posterolaterally, with short episternal projections. Sternite 8 small, directed posterolaterally, triangular in shape.

Abdomen of male narrow, with concave lateral margins, broadest at position of somite 1. Somite 1 free, narrow, widest of all somites. Somites 2-5 appearing to be fused, widest at position of somite 2, narrowest at position of somite 5. Somite 6 free, square. Telson small, bluntly triangular.

Abdomen of mature female broad, lateral margins convex. Somite 1 narrowest of all somites. Somites 2-5 fused, broad, lateral margins weakly convex, widest of all somite units. Somite 6 free, widest posteriorly and narrowest anteriorly, lateral margins convex. Telson much narrower than somites bluntly triangular.

Abdomen of immature female narrow, lateral margins nearly straight; poorly known, somites 2-5 appearing to be fused; somite 6 and telson free.

Chelae typical of genus; fingers long, slender, with blunt tubercles on occlusal surface.

Measurements: Average measurements (in mm) taken on specimens of *Thalamita crenata* are as follows: Maximum length, n=12, 25.6; maximum width, n=11, 41.4; fronto-orbital width, n=15, 27.1; posterior width, n=8, 12.8; frontal width, n=14, 12.3.

Material examined: Four specimens of *Thalamita crenata,* USNM 507818-507821 and a lot of 40 specimens, USNM 507822; AMNH-FI-47138, three males, and AMNH-FI-47139, 1 female.

Discussion: The specimens exhibit rather poor preservation as compared to most other taxa that have been recovered from deposits of similar age in Guam. The frontal margin of the carapace is damaged in most specimens, and the anterolateral spines are damaged in every specimen as well, exhibiting breakage at the tips of the spines. The dorsal carapaces are corroded and worn, perhaps by wave activity, obscuring the details of the dorsal carapace in many specimens. The appendages are preserved only in a few cases where the fingers of one of the chelae remain associated with the carapace. Almost all of the specimens are corpses, exhibiting both the dorsal carapace and the sternum; only two specimens appear to be molts composed only of the dorsal carapace. The majority of the specimens deposited in the USNM are

males, a few are clearly mature females, two specimens appear to be immature females, and two are of unknown gender.

Most members of *Thalamita* have a small protrusion on the posterolateral margin, which the material described here lacks, thus differentiating it from most Recent species of the genus. *Thalamita yoronensis* Sakai, 1969, *T. spinifera* Borradaile, 1903, *T. mitsiensis* Crosnier, 1962, and *T. bouvieri* Nobili, 1906, are each too narrow to accommodate the new material. The fossil species *T. fragilis* has longer anterolateral spines and more forward-directed orbits than does the new material. The new material most closely resembles *Thalamita crenata* (Latreille, 1829) and *T. stimpsoni* A. Milne Edwards, 1861, based upon the shape of the carapace and the width of the front and spacing of the orbits as well as the form of the chelae. The front on the specimens and the chela are diagnostic for *T. crenata* (see Wee and Ng, 1995); thus, the specimens are referred to that species. *Thalamita crenata* is very common in the waters near Dadi Beach and other areas of Guam.

Subfamily Podophthalminae Dana, 1851b

Genus *Podophthalmus* Lamarck, 1801

Type species: *Portunus vigil* Fabricius, 1798.

Fossil species: *Podophthalmus domingensis* Rathbun, 1919; *P. fusiformis* Morris and Collins, 1991; *P. taiwanicus* Hu and Tao, 1996; *P. vigil* (Fabricius, 1798) (also Recent).

Podophthalmus vigil (Fabricius, 1798)

(Figs. 7, 8)

Description of material: Carapace much wider than long, widest along frontal margin which extends laterally

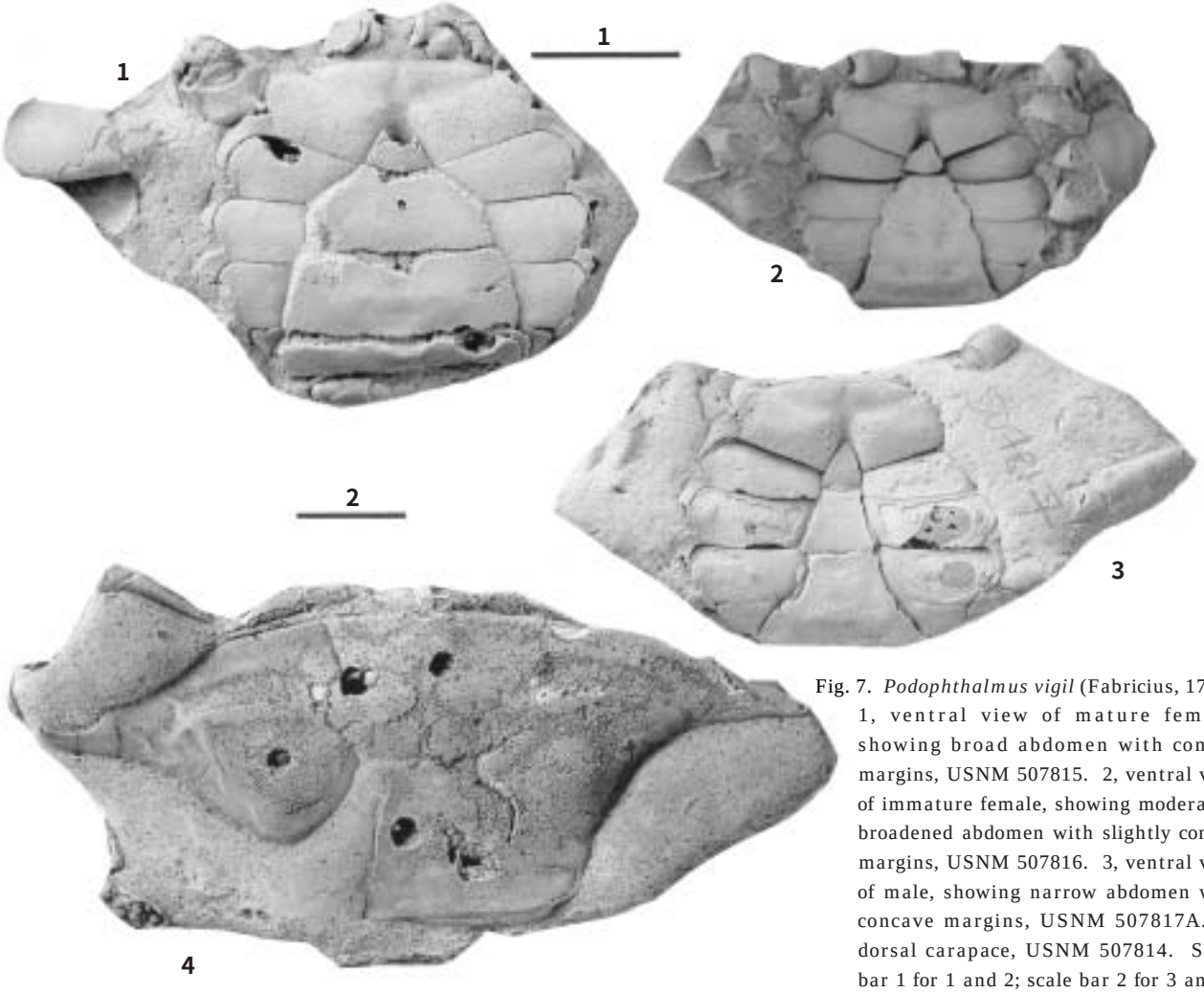


Fig. 7. *Podophthalmus vigil* (Fabricius, 1798). 1, ventral view of mature female, showing broad abdomen with convex margins, USNM 507815. 2, ventral view of immature female, showing moderately broadened abdomen with slightly convex margins, USNM 507816. 3, ventral view of male, showing narrow abdomen with concave margins, USNM 507817A. 4, dorsal carapace, USNM 507814. Scale bar 1 for 1 and 2; scale bar 2 for 3 and 4. Scale bars equal to 1 cm.

into produced, posterolaterally-directed spines; regions poorly defined, ornamented with ridges or spherical inflations; weakly vaulted transversely and longitudinally.

Rostrum very narrow, about 2 percent maximum carapace width; orbits extremely broad, appearing to extend nearly the entire width of the frontal margin of the carapace; lateral margins of carapace arcing and converging posteriorly, entire; posterior margin nearly straight, about one-third maximum carapace width, paralleled by sharp crest.

Protogastric regions weakly inflated, with weak transverse ridge; mesogastric region flattened, widening distally, with narrow anterior projection; urogastric region poorly developed; cardiac region hexagonal in shape, inflated anteriorly, with transverse ridge anteriorly; protogastric and cardiac regions bounded by deep branchiocardiac grooves; intestinal region flattened.

Hepatic region flattened; epibranchial region weakly arcuate, ridge extending from just posterior to lateral spine to distal margin of protogastric region; remainder of branchial region undifferentiated, with spherical swelling lateral to cardiac region, lateral areas of branchial region concave, depressed, sloping to posterolateral margin.

Buccal cavity rectangular, wider than long; third maxillipeds very short.

Sternum nearly circular, widest at position of episternal projections of sternite 5. Sternites 1 and 2 fused,

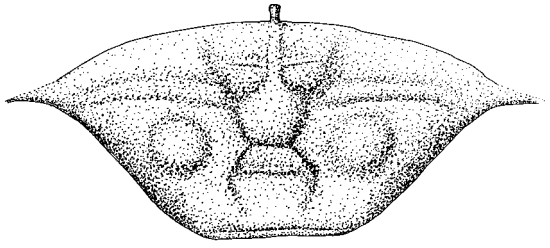


Fig. 8. Reconstruction of *Podophthalmus vigil*, based upon several specimens.

triangular, apex of triangle directed anteriorly, lateral margins slightly concave, posterior margin nearly straight. Sternites 3 and 4 fused; sternite 3 short, wider than long, diamond-shaped, depressed below level of sternite 4; sternite 4 wider than long, longest of all somites, directed anterolaterally with long, sharp, arcuate episternal projections. Sternite 5 directed slightly anterolaterally; wider than long; upper and lower margins straight; with long, arcuate episternal projections. Sternite 6 directed laterally; widest of all sternites; upper margin weakly concave; lower margin weakly convex; with long, arcuate episternal projections. Sternite 8 small, triangular, directed posterolaterally.

Abdomen of male narrow, with concave lateral margins; somites 1-4 and 5-6 appearing to be fused, sutures weakly expressed; abdomen widest at position of somite 1. Somites 1-4 with concave margins; somites 5-6 narrowing anteriorly with straight margins. Telson blunt, triangular, apex directed anteriorly.

Abdomen of mature female broad, cordate, lateral margins of entire abdomen convex; fusion of somites present, somites 1 and 2 appearing to be free; 3/4 and 5/6 appearing to be fused; somites 1 and 2 much wider than long with straight upper and lower margins; somites 3/4 rectangular, with straight margins; somites 5/6 trapezoidal, narrowing anteriorly, lateral margins convex, upper and lower margins nearly straight; telson small, much narrower than other somites, triangular, blunt apex directed forward. Abdomen of immature females similar to abdomen of mature females but with straight lateral margins of abdomen as a whole.

Bases of pereiopods cylindrical; pereiopods becoming smaller posteriorly; meri of pereiopods longer than high.

Measurements: Measurements (in mm) taken on two specimens of *Podophthalmus vigil* are as follows: USNM 507814, maximum length = 22.3; maximum width = 50.6; width of rostrum = 1.1; posterior width = 16.8; USNM 507816, maximum length, 17.3; maximum width ~ 34.0; posterior width = 14.4. Measurements were not taken on the remainder of the specimens because the specimens are badly damaged, making all measurements minimum estimates.

Material examined: Three specimens, USNM 507814-507816 and 120 specimens assigned to USNM 507817; AMNH-FI-47143, 1 excellent male, AMNH-FI-47136, four males, AMNH-FI-47137, three females. ZRC, 9 carapace and cheliped fragments.

Discussion: A total of 141 specimens were examined for this study. Many of the specimens are better preserved than those discussed and illustrated by Kesling (1958). For example, some specimens retain nearly the entire lateral spine extending from the frontal margin of the carapace, all of which were broken in the specimens illustrated by Kesling (1958). However, none of the specimens is complete; thus the line drawing in Figure 7 is based upon several dorsal carapace specimens.

Within the genus *Podophthalmus*, only *P. vigil* has the

extremely attenuated lateral spines extending from the frontal margin, strongly supporting placement of the new material within that species.

Among the 132 USNM and AMNH specimens, 65 percent are males. Twenty-five specimens were not sufficiently well-preserved to determine their gender. Among the male specimens, many are about half as large as the females. This suggests that the females of this species are typically much larger than the males. Additionally, approximately twice as many males are preserved as females, a similar pattern as seen for the other portunid taxon described here, *Thalamita crenata*.

Podophthalmus vigil has previously been reported from the fossil record from Pliocene deposits of Java (Martin, 1883); Pleistocene rocks of Celebes (de Man, 1904); Pleistocene deposits of Taiwan (Hu and Tao, 1996); Pleistocene deposits of Guam (Kesling, 1958) and from the Pleistocene Ryukyu Group, Okinawa-jima, Japan (Karasawa, Nohara, and Shimoji, 1995). *Podophthalmus vigil* is known from Recent occurrences in Japan, the Indo-Pacific, the Red Sea, and Apra Harbor in Guam (Sakai, 1976; Ng, 1998; G. Paulay, pers. commun.). A solely fossil species of *Podophthalmus*, *P. fusiformis* Morris and Collins, 1991, has been reported from Pliocene rocks of Sarawak and another, *P. taiwanicus* Hu and Tao, 1996, is known from the Pleistocene of Taiwan. Other Recent members of the genus are known from Japan (Sakai, 1976); thus, the genus appears to have evolved and dispersed within the Indo-Pacific region as early as the Pliocene.

Subfamily Carupinae Paulson, 1875
(=Catoptrinae Borradaile, 1903)

Discussion: Apel and Spiridonov (1998) discussed the priority of the subfamily name Carupinae over Catoptrinae; that discussion will not be repeated here. The Carupinae contains a small number of genera which exhibit a carapace unlike other portunids in their rectangular shape and entire or weakly spined anterolateral margins. Unlike typical portunids, members of this subfamily possess upcurved and sub-spatuliform dactyls of the last pair of pereiopods as compared to the paddle-like dactyls of typical portunids. Carupines have relatively broad fronts that are either entire with an axial sulcus or spined, whereas most other portunids do not possess entire frontal margins. The carapace regions of members of the Carupinae are poorly developed and they lack the arcuate ridge extending axially from the last anterolateral spine which is typical of most portunids. The last anterolateral spine is often long and well-developed within the Portunidae, which does not appear to be true for the Carupinae. In fact, according to Stephenson (1972), the only character linking this subfamily to the Portunidae are the flattened dactyls of the fifth pereiopods, which do not occur on all members of the subfamily. Apel and Spiridonov (1998) noted that members of the Carupinae generally possess a lobe on the first maxilliped that is typical of portunids. Stephenson and Campbell (1960) suggested that the subfamily had numerous similarities with certain members of the Goneplacidae MacLeay, 1838, and that the Portunidae as currently defined may in fact be a diphyletic group. However, discussion of these matters is beyond the scope of this paper. The Carupinae is herein placed within the Portunidae in agreement with previous workers, most recently Apel and Spiridonov (1998); however, those two authors suggested that the subfamily is very much in need of revision (p. 171).

Genus Libystes A. Milne Edwards, 1867

Libystes A. Milne Edwards, 1867, p. 285; A. Milne Edwards, 1868, p. 84; Alcock, 1900, p. 304-305; Tesch, 1918, p. 111-178; Stephenson and Campbell, 1960, p. 85-86; Crosnier, 1962, p. 13-14; Seréne, 1966, p. 989; Stephenson, 1972, p. 29; Sakai, 1976, p. 324; Dai and Yang, 1991, p. 200; Apel and Spiridonov, 1998, p. 174.

Carcinoplacoides Kesling, 1958, p. 235, pl. III, figs. 1-4; pl. V, fig. 8; pl. VII, figs. 4-5; pl. XII, figs. 19-23; Glaessner, 1969, p. R526.

Type species: *Libystes nitidus* A. Milne Edwards, 1867.

Other species: *Libystes alphonsi* Alcock, 1900; *L. edwardsi* Alcock, 1900; *L. lepidus* Takeda and Miyake, 1970; *L. paucidentatus* Stephenson and Campbell, 1960; *L. vietnamensis* Tien, 1969; and *L. villosus* Rathbun, 1924.

Discussion: Kesling (1958) erected a new genus, *Carcinoplacoides*, to accommodate fossil decapods with a rectangular carapace; entire anterolateral margins; and a broad, smooth front. His material lacked preserved pereiopods. He considered the new genus to be related to the Carcinoplacinae H. Milne Edwards, 1852, of the Goneplacidae, a group characterized by rectangular, smooth carapaces. Kesling noted that *Carcinoplacoides* was allied with *Carcinoplax* H. Milne Edwards, 1852, but differed from *Carcinoplax* in lacking anterolateral teeth. He also compared *Carcinoplacoides* with *Cryptolutea* Ward, 1936, noting numerous similarities but

differentiating the two based upon the strongly convex transverse aspect of the carapace and the presence of fused somites in the male abdomen of *Carcinoplacoides*. However, species of *Carcinoplax* may lack anterolateral spines, which *Carcinoplacoides* possesses, and members of *Cryptolutea* have seven free abdominal somites while those of *Carcinoplacoides* are fused (Ng and Davie, 1991). Thus, the original comparisons of *Carcinoplacoides* with these genera were not valid.

In fact, *Carcinoplacoides* is clearly synonymous with the aberrant portunid genus *Libystes*. Members of *Libystes* are diagnosed by possession of a rectangular carapace; a front which occupies one-third or less the maximum carapace width, is square, and weakly sulcate axially; shallow orbits with entire upper margins; entire or spinose anterolateral margins; a carapace that is much wider than long, smooth, relatively well-vaulted longitudinally and flattened transversely; and slender pereiopods (Stephenson and Campbell, 1960; Apel and Spiridonov, 1998). The abdomen and fifth pereiopods agree well with those of *Libystes*. The material referred to *Carcinoplacoides* possesses all of these features and is thus synonymized with *Libystes*; *Carcinoplacoides* becomes the junior synonym. Interestingly, Kesling (1958) discussed *Libystes* in some detail (p. 233) but refrained from assigning the specimens to it.

Libystes is referred to the Portunidae based upon its possession of fifth pereiopods that are considered to be portunid-like, that is, flattened or paddle-shaped. The fifth pereiopods are paddle-like in some species of *Libystes* but are lanceolate in others (Stephenson and Campbell, 1960; Apel and Spiridonov, 1998). The fossil material does not retain any aspect of the fifth pereiopods; thus, it is impossible to confirm placement within the Portunidae based upon that character. The genus is here maintained within the Portunidae in agreement with Stephenson and Campbell (1960) and other subsequent workers; however, it is suggested that the possession of paddle-like dactyls on the fifth pereiopod may be an example of convergence. *Libystes* may not be a legitimate portunid. Further research on all members of the genus and all members of the Carupinae, perhaps including molecular studies, will be necessary to fully resolve family placement of these taxa. Validity of some of the species of the genus is also in question. *Libystes alphonsi* is regarded by some as a junior synonym of *L. nitidus* (see Tesch, 1918; Edmondson, 1954), and Apel and Spiridonov (1998) suggested that *L. alphonsi*, *L. lepidus*, and *L. villosus* may each be synonymous with *L. nitidus*.

Libystes nitidus A. Milne Edwards, 1867
(Fig. 9)

Libystes nitidus A. Milne Edwards, 1867, p. 285; Alcock, 1900, p. 304-305; Tesch, 1918, p. 177-178; Balss, 1922, p. 113; Sakai, 1939, p. 371-372; Stephensen, 1946, p. 168-169, figs. 45C-F; Barnard, 1954, p. 99-100, figs. 2a-e; Edmondson, 1954, p. 222, fig. 4; Stephenson and Campbell, 1960, p. 13; Crosnier, 1962, p. 14-15, figs. 5-10; Serène, 1965, p. 992-994; Sakai, 1976, p. 324, pl. 110.

Carcinoplacoides flottei Kesling, 1958, p. 235, pl. III, figs. 1-4; pl. V, fig. 8; pl. VII, figs. 4-5; pl. XII, figs. 19-23.

Emendation to Description: Carapace vaulted longitudinally, flattened transversely with steep lateral margins, carapace length about 60 percent maximum carapace width. Fronto-orbital width about 60 percent maximum carapace width; orbits square, upper orbital margin sinuous. Front broad, with shallow axial sulcus, frontal width about one-quarter maximum carapace width. Anterolateral margins entire or with a few very small, blunt nodes. Posterior width about 60 percent maximum carapace width.

Sternites 1-4 fused in males and females, little trace of suture lines, sternite 4 directed strongly anterolaterally; sternites 5 and 6 directed anterolaterally; sternite 7 directed posterolaterally; sternite 8 tiny, directed posterolaterally; all sternites with well-developed episternal projections.

Male abdomen broadest at position of somite 2; somites 1-5 fused; somite 6 slightly wider than long; telson small, triangular.

Female abdomen broadest at position of somites 1 and 2; somites 1, 2, and 3 much wider than long; somite 4 longer, about 3 times as long as somite 1; somites 5 and 6 appearing to be fused; telson very small, about one-fifth as wide as sternite 1, triangular, with concave lateral margins.

Measurements: Measurements (in mm) taken on the dorsal carapace of specimens of *Libystes nitidus*. USNM 518974, maximum width (W1) = 17.5; frontal width (W2) = 5.1; fronto-orbital width (W3) = 10.4; posterior width (W4) = 11.0; length (L) = 11.3. USNM 518975, W1 = 20.5; W3 = 11.5; W4 = 12.2; L = 12.5. USNM 518976, W1 = 20.7; W3 = 11.8; W4 = 10.8. USNM 518977, W1 = 21.2; W2 = 5.8; W3 = 11.9; W4 = 12.8; L = 13.2.

Material examined: Five specimens, USNM 518974-518978, 519523; USNM 519524, sample lot of 94 specimens; AMNH-FI-47134, eight females, AMNH-FI-

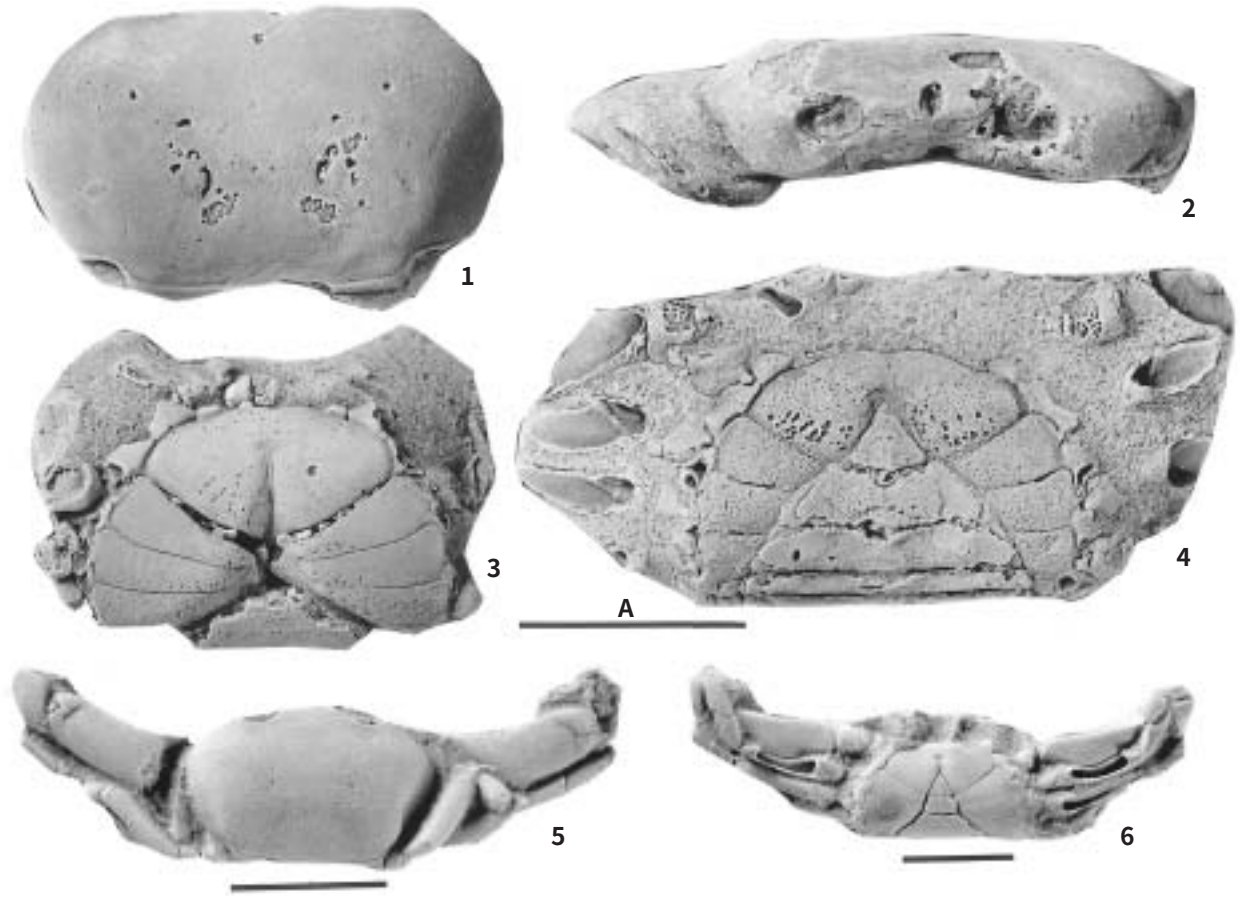


Fig. 9. *Libystes nitidus* A. Milne Edwards, 1867. 1, dorsal carapace, USNM 518975. 2, anterior view showing orbits, USNM 518977. 3, ventral view of male, USNM 518976. 4, ventral view of female, USNM 518978. 5, dorsal carapace and appendages, USNM 519523. 6, ventral view of male and appendages, USNM 519523. Scale bar A for 1-4; all scale bars equal to 1 cm.

47135, ten males. ZRC, 41 carapace and chela fragments.

Discussion: Of the extant species of *Libystes,* three are characterized by having the anterolateral margin entire, without teeth or denticulations, including *L. nitidus, L. alphonsi,* and *L. villosus.* As noted above, the validity of *L. alphonsi* and *L. villosus* are doubtful or uncertain. From the descriptions of these latter two species by Alcock (1900), Tesch (1918), Rathbun, (1924), Edmondson (1951) and Takeda and Miyake (1970), both have quadrilateral carapaces, not ellipitical ones as in other species, and *L. villosus* possesses numerous dense setae on the pereiopods.

The series of specimens of *Carcinoplacoides flottei* examined here are remarkably consistent in their carapace shape; all are transversely ovate, have entire anterolateral margins that may be granular or smooth, and a finely granular or smooth dorsal carapace surface. Weathering of the carapace may contribute to the range between smooth and granular. Because of the doubtful validity of *L. aphonsi* and *L. villosus,* the specimens from Guam are best referred to *L. nitidus sensu lato.* It seems likely that what is now regarded as extant *L. nitidus* is actually a complex of several species, but resolution of that issue is beyond the scope of this paper. *Carcinoplacoides flottei* is herein synonymized with *L. nitidus* and the new specimens are referred to *L. nitidus. Libystes nitidus* has a very broad Indo-West Pacific distribution (see Apel and Spiridinov, 1998) and its presence in Guam is thus not surprising.

The specimens are moderately well-preserved, but lack some of the fine detail that may have been present on the dorsal carapace. The specimens have a polished appearance; thus, it is likely that they were subjected to a good deal of wave abrasion as fossils before collection. Of the four specimens for which gender can be determined, half are males and half are females, the only taxon of the Guam material to have an equal ratio of males to females. None of the specimens retains more than broken proximal

elements of the pereiopods; however, the sterna and abdomina are quite well-preserved.

Portunidae, genus and species indeterminate

Material examined: 2 lots of chela fragments, USNM 517448-517449.

Superfamily Xanthoidea Macleay, 1838
Family Carpiliidae Ortmann, 1893
Genus *Carpilius* Desmarest, 1822

Type species: *Carpilius maculatus* (Linnaeus, 1758).

Fossil species: *Carpilius occidentalis* Schweitzer et al., 2000.

Carpilius sp.
(Fig. 10.1)

Discussion: The specimen is only a chela fragment, but it has a well-preserved pollex and basal molariform tooth, making its positive identification possible. The short finger and very large, flattened tooth is diagnostic for members of the genus. Two extant species, *C. convexus* (Forskål, 1775) and *C. maculatus* are currently present in Guam, and from the form of the tooth, the fossil is most likely to be *C. maculatus*.

Material examined: ZRC, 1 chela fragment.

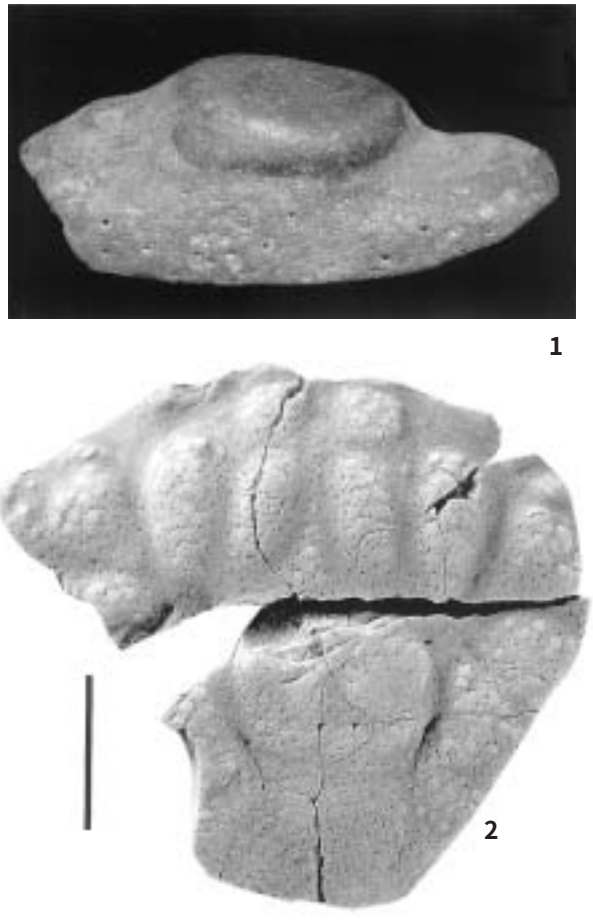


Fig. 10. 1, fragment of finger of *Carpilius* sp., showing large molariform tooth, ZRC specimen. 2, *Actaeodes* sp., fractured and weathered dorsal carapace, USNM 517447. Scale bars equal to 1 cm.

Family Xanthidae Macleay, 1838
Genus Actaeodes Dana, 1851b

T*ype species*: *Zozymus tomentosus* H. Milne Edwards, 1834.

Actaeodes sp.
(Fig. 10.2)

Discussion: The dorsal carapace is badly damaged and smoothed by weathering, and the front, orbits, lateral margins and posterior margin are broken. However, the epigastric, protogastric, hepatic, and cardiac regions display the pronounced inflations typical of the genus; note especially the bilobed nature of the protogastric region. To date, only a single specimen of this taxon is known to have been recovered as a subfossil from Guam. The extant species *A. tomentosus* is common near Dadi Beach in Guam, and the present fossil may belong to this species.

Material examined: USNM 517447.

Section Thoracotremata, Guinot, 1977
Superfamily Ocypodoidea Rafinesque, 1815
Family Ocypodidae Rafinesque, 1815
Subfamily Macrophthalminae Dana, 1851a
Genus *Macrophthalmus* Latreille in Desmarest, 1822

Type species: *Gonoplax transversus* Latreille, 1817.

Fossil species: *Macrophthalmus aquensis* A. Milne Edwards and Brocchi, 1879 (=*M. vindobonenesis* Glaessner, 1924); *M. definitus* Adams and White, 1848 (=*M. guamensis* Kesling, 1958) (also Recent); *M. depressus* Rüppell, 1830 (also Recent); *M.* (*Euplax*) *granulosus* de Man, 1904; *M. incisus* (Desmarest, 1822); *M.* (*Mareotis*) sp. aff. *M. japonicus* de Haan, 1835; *M.* (*Tasmanoplax*) *latifrons* (Haswell, 1882) (also Recent); *M.* (*Euplax*) *latreillei* (Desmarest, 1822) (also Recent); *M.* (*Euplax*) *leptophthalmus* H. Milne Edwards, 1852 (also Recent); *M.* (*Hemiplax*) *major* Glaessner, 1960; *M.* (*Mareotis*) *setosus* H. Milne Edwards, 1852 (also Recent); *M.* (*Mareotis*) *viai* Karasawa and Inoue, 1992; *M.* (*Mareotis*) *wilfordi* Morris and Collins, 1991.

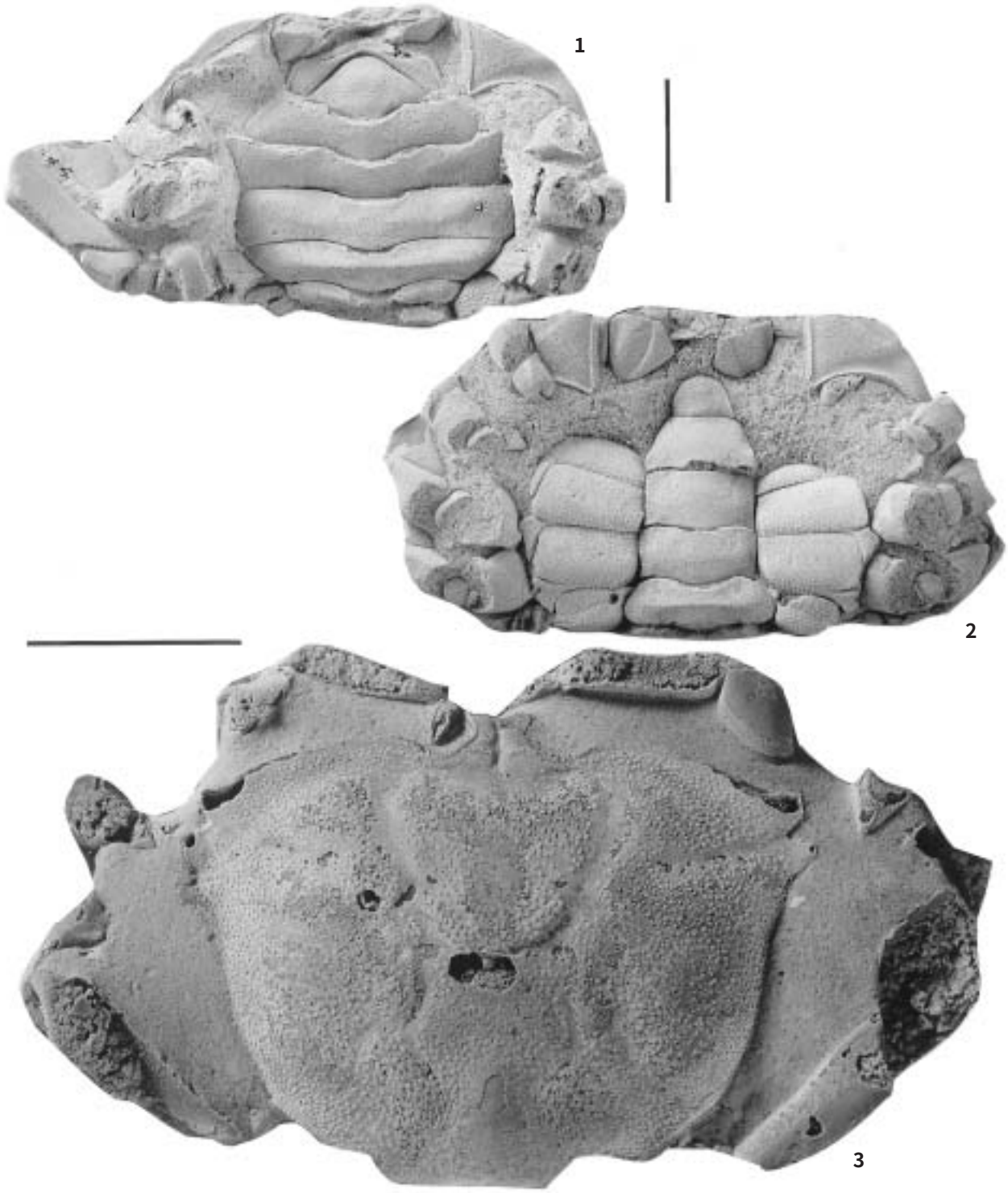


Fig. 11. *Macrophthalmus* (*Euplax*) *latreillei* (Desmarest, 1822). 1, ventral surface of mature female, USNM 517444. 2, ventral view of male, USNM 517443A. 3, dorsal carapace, USNM 517442. Scale bars equal to 1 cm.

Discussion: Fossil species of *Macrophthalmus* (not necessarily identified to subspecies) have been reported from Miocene rocks of Europe (Glaessner, 1924; Via, 1980; Müller, 1984, 1993, 1998) and Japan (Karasawa and Inoue, 1992), the Miocene-Pliocene of New Zealand (Glaessner, 1960), and from middle Pleistocene rocks of Brunei (Morris and Collins, 1991). Several authors have considered the genus to have arisen within the Tethyan region during the Miocene with subsequent dispersal throughout the Indo-Pacific (Remy, 1952; Kesling, 1958; Via, 1969, 1980); however, fossil evidence accumulated since their work has led Karasawa and Inoue (1992) to concur with Barnes (1968) speculation that the genus in fact arose within the Indo-Pacific with subsequent dispersal to the Mediterranean region via the Tethys Seaway. Because Miocene fossils of *Macrophthalmus* occur in both Europe and the Indo-Pacific, it is difficult to resolve this problem.

Subgenus *Euplax* H. Milne Edwards, 1852

Macrophthalmus (*Euplax*) *latreillei* (Desmarest, 1822) (Fig. 11)

Material examined: USNM 517441-51742; three large lots of specimens, USNM 517443-517445. USNM 517443 is comprised of 43 male specimens, USNM 517444 is composed of 25 female specimens, and USNM 517445 contains all specimens and specimen fragments of indeterminable gender. AMNH-FI-47131, 1 male, AMNH-FI-47132, 1 female, AMNH-FI-47133, three males. ZRC, 100 carapace and cheliped fragments.

Discussion: Of the specimens of *Macrophthalmus* (*Euplax*) *latreillei* deposited in the USNM and AMNH examined for this report, about 54 percent are males, 31 percent are females, and the remainder are of indeterminable gender. The specimens are well-preserved, often retaining both the dorsal carapace and the ventral surface. However, most do not possess the appendages and only one (AMNH-FI-47131) has a preserved chela. The specimens exhibit similar preservation to those described by Kesling (1958) and thus further description is unnecessary. However, note that USNM 517441a retains the fifth pereiopod, which was not illustrated by Kesling (1958).

In addition to the deposits of Guam, fossil occurrences of *Macrophthalmus latreillei* have been reported from Holocene deposits of Aichi Prefecture, Japan (Karasawa and Matsuoka, 1991), Pleistocene deposits of the Ryukyu Group, Okinawa-jima, Japan (Karasawa, Nohara, and Shimoji, 1995) and Quaternary alluvium from Sabah, Malaysia (Idris, 1989).

Subgenus *Mareotis* Barnes, 1967

Macrophthalmus (*Mareotis*) *definitus* Adams and White, 1848 (= *Macrophthalmus guamensis* Kesling, 1958) (Fig. 12)

Material examined: USNM 519527-519529; 43 males specimens, USNM 519530; 24 female specimens, USNM 519531; 14 specimens of indeterminate gender, USNM 519532; AMNH-FI-47140, three males; AMNH-FI-47141, three females.

Discussion: Kesling (1958) reported two species of *Macrophthalmus* from Guam, *M. latreillei* and a new species, *M. guamensis.* Kesling (1958) differentiated *M. guamensis* from *M. latreillei* because *M. guamensis* is widest at the mid-length of the carapace instead of along the frontal margin as in *M. latreillei. Macrophthalmus guamensis* is here identical to *M. definitus* Adams and White, 1848. *Macrophthalmus definitus* is characterized by small adult size, with an average adult width of only 15 mm, and a transversely narrow carapace. In addition, members of the species possess a transverse ridge on the third abdominal somite in both males and females and granules on the protogastric region (Barnes, 1967, 1970; Komai et al., 1995). The specimens corresponding to Kesling's *M. guamensis* possess all of these features. Thus, it seems probable that both species are synonymous, *M. definitus* being the senior synonym. *Macrophthalmus definitus* is a wide-ranging species in modern oceans, occurring in Phuket of the Indian Ocean, Japan, Solomon Islands, and Australia. The occurrence of two species of *Macrophthalmus* in the same deposits is not surprising, because numerous species of modern *Macrophthalmus* can be found living in the same area (Komai et al., 1995).

Discussion

Among several of the taxa discussed here, males are preferentially preserved. In most cases there are at least twice as many males as females within the sample collections, and the percentage of males to females ranges from 50 to 89 percent of the specimens retaining abdomina. The ratio of males to females does not appear to be due to a collecting bias skewed to larger specimens,

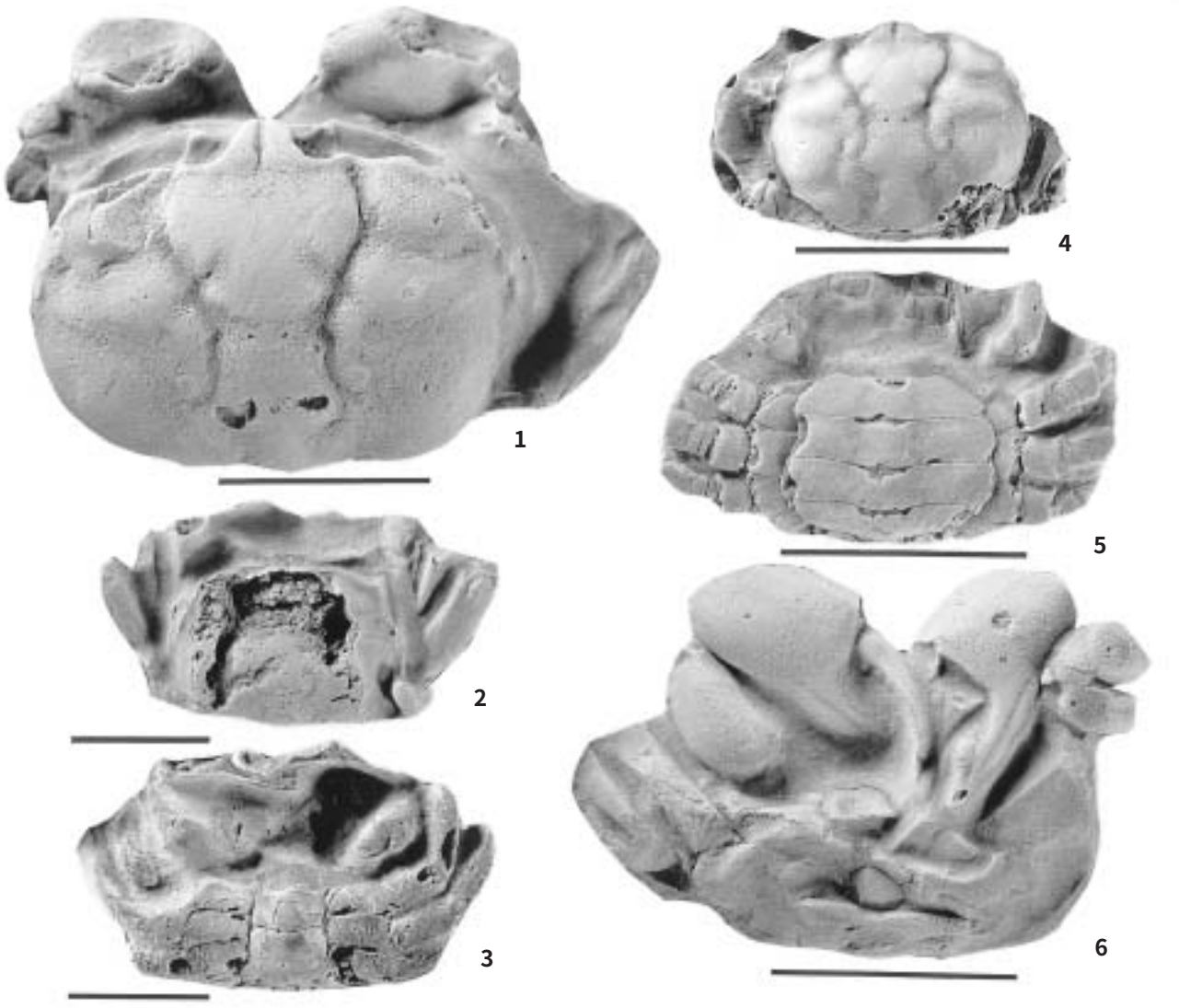


Fig. 12. *Macrophthalmus* (*Mareotis*) *definitus* (Adams and White, 1848) (=*M. guamensis* Kesling, 1958). 1, oblique view of dorsal carapace showing rostrum and orbits, USNM 519527. 2, dorsal carapace with well-preserved eyestalks, USNM 519529. 3, venter of male, USNM 519529. 4, dorsal carapace of female, USNM 519528. 5, venter of female, USNM 519528. 6, ventral view with isochelous first pereiopods, USNM 519527. Scale bars equal to 1 cm.

as the females of *Macrophthalmus latreillei* are typically larger than the males. One of us (PRS) reports that preservational and collecting biases may have been present; females occur as damaged specimens more often than do males and were thus not collected as often. The reason for this is not clear; it might be expected that males would be damaged more frequently due to aggressive behavior during reproductive cycles. It is possible that environmental factors may have played a role, but there are none known to the authors that could contribute to such a discrepancy in numbers of males and females.

Many of the specimens occur together in one mass or concretion (Fig. 13), suggesting that accumulation of decapods in this region was a result of one or more mass mortality events. Kesling (1958) asserted that submarine landslides may have been responsible for the accumulation of large numbers of crabs. Typhoons or tsunamis may also provide a logical explanation for the large number of crab carapaces found in Guam.

Of the decapods collected from the localities discussed here, *Macrophthalmus latreillei* is the most common taxon collected. The remainder of taxa occur with lower frequencies, listed in descending order of frequency (most



Fig. 13. Specimen with three crabs preserved (USNM 519525A), illustrating a possible mass mortality event resulting from a tsunami or other cataclysmic event. Scale bar equal to 1 cm.

common to rarest): *M. latreillei, Podophthalmus vigil, Libystes nitidus, Myra fugax, Macrophthalmus definitus, Thalamita crenata, Neocallichirus*? sp., *Scylla serrata, Rhinolambrus pelagicus, Calappa hepatica, Mursia* sp., *Carpilius* sp., and *Actaeodes* sp. Of these, *Scylla serrata* and *Calappa hepatica* are known from chela and carapace fragments only. *Mursia* sp. was described by Schweitzer and Feldmann (2000).

All of the fossil taxa reported from Guam display Tethyan or Indo-Pacific distribution patterns. The first fossil occurrences of *Myra* and *Thalamita* occur in Miocene rocks of the western Tethys in southern Europe, and the taxa subsequently dispersed to the Indo-Pacific region, where they are found as Neogene and Holocene fossils as well as in Recent oceans. *Macrophthalmus* either evolved in the Indo-Pacific or the Mediterranean region of the Tethys; its area of origin cannot be successfully resolved at this time. However, the occurrence in Japan appears to be the oldest yet known (Karasawa and Inoue, 1992); however, poor stratigraphic control on European occurrences makes this difficult to confirm. *Podophthalmus* and *Rhinolambrus* are known from fossil occurrences only within the Indo-Pacific. *Libystes* is known only from modern oceans and has an Indo-Pacific distribution; known *Neocallichirus* also exhibit an Indo-Pacific distribution (Manning and Felder, 1991). Fossil *Calappa* species exhibit a broad distibution that could easily have resulted in their dispersal to the Indo-Pacific; in fact, modern *Calappa* are nearly always found in tropical to subtropical waters (Schweitzer and Feldmann, 2000). Derivation from the Tethyan and Indo-Pacific regions is typical of Indo-Pacific faunas of Recent oceans (Schweitzer, 2001). These findings also support the assertion that most decapod taxa that appeared in the Miocene survive into the Recent (Schweitzer, 2001).

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