UTILITY OF PROXY CHARACTERS FOR CLASSIFICATION OF FOSSILS: AN EXAMPLE FROM THE FOSSIL XANTHOIDEA (CRUSTACEA: DECAPODA: BRACHYURA)

CARRIE E. SCHWEITZER

Department of Geology, Kent State University Stark Campus, Canton, Ohio 44720, <cschweit@kent.edu>

ABSTRACT—Diagnoses based upon preservable carapace features are provided for the brachyuran families Carpiliidae, Palaeoxanthopsidae new family, Pseudoziidae, and Zanthopsidae, newly raised to family status. In order to make family and generic level assignments, characters of the dorsal carapace can be used successfully as proxies for soft-part morphology that is not commonly or never preserved in fossils. The identification of carpiliids and pseudoziids in the fossil record yields critical information about the time of divergence of these groups, no later than Eocene, and the relationships between those two families, the Eriphiidae, and the extinct Zanthopsidae. Because the timing of divergence of at least two xanthoid families is now known more accurately, more constrained phylogenetic studies can result. The Eocene to Recent Carpiliidae is restricted to one extant genus and five fossil genera. The Eocene to Recent Pseudoziidae contains the fossil genera *Archaeozius* new genus, *Priabonocarcinus*, and *Santeezanthus* as well as several extant genera; one extant genus, *Euryozius*, also has a fossil record. The Paleocene-Miocene Zanthopsidae embraces five extinct genera including *Neoxanthopsis* new genus. The new family Palaeoxanthopsidae includes four extinct genera, including *Paraverrucoides* new genus and *Remia* new genus and occurs in Maastrichtian-Eocene rocks. New combinations include *Archaeozius occidentalis*, *Harpactoxanthopsis bittneri*, *Harpactoxanthopsis souverbei*, *Neozanthopsis bruckmanni*, *N. carolinensis*, *N. rathbunae*, *N. sonthofensis*, *N. tridentata*, *Ocalina straeleni*, *Palaeocarpilius mississippiensis*, *Palaeocarpilius valrovinensis*, *Paraverrucoides alabamensis*, and *Remia africana*.

INTRODUCTION

THE XANTHOIDEA MacLeay, 1838, embraces a diverse and abundant group of crabs that is well established in modern oceans. The Xanthoidea are excellent indicators of modern biodiversity, inhabiting a broad range of shallow- to deep-water habitats. The group has a robust fossil record extending into the Cretaceous. Some Cretaceous records that were originally believed to have been xanthoids (Schweitzer-Hopkins et al., 1999) have now been referred to a different section in more primitive families (Guinot and Tavares, 2001); however, this study confirms the conclusion of Schweitzer, Feldmann et al. (2002) that xanthoids had in fact appeared by the Cretaceous. In this study, two exclusively fossil xanthoid families are shown to have Cretaceous records in addition to the extant Goneplacidae MacLeay, 1838 (Schweitzer, Feldmann et al., 2002).

Classification of the Xanthoidea has been contentious; Manning and Holthuis (1981) reported that 32 family and subfamily names had been proposed for members of the group at that time (Martin and Davis, 2001). Many more subfamily names have since been created (see for example, Serène, 1984; Ng and Chia, 1994; Ng and Clark, 2000a, 2000b, among many others). Glaessner (1969, p. R515) treated the fossil forms as members of a single family, the Xanthidae MacLeay, 1838, without subfamily designations, remarking that further studies would be required to place fossil xanthids in appropriate subfamilies. Guinot (1978) elevated several subfamilies of the Xanthidae sensu lato to family status, a decision which has generally been accepted and supported by molecular evidence (Serène, 1984; Ng, 1998; Martin and Davis, 2001) and larval studies (Rice, 1980; Martin, 1984; Martin et al., 1985; Clark and Galil, 1988; Clark and Ng, 1998). Paleontologists have also addressed the difficulties in distinguishing among xanthoid groups (Tucker and Feldmann, 1990; Schweitzer, 2000). Wright and Collins (1972) appear to have been the first to elevate the Carpiliidae Ortmann, 1893, to family status (Guinot, 1978). The most recent synthetic work (Martin and Davis, 2001) listed eleven extant xanthoid families, most of which were originally recognized by Guinot (1978) and Serène (1984).

Few biologists consider fossils when reassessing the xanthoids; Guinot (1968a, 1968b, 1978, 1979) has been a notable exception. Fossil xanthoids have yet to be systematically revised within the current framework of relationships within the Xanthoidea, and

attempts to revise the classification of the xanthoid crabs have rarely included fossil evidence. Tucker and Feldmann (1990), Schweitzer (2000), Schweitzer and Feldmann (2001), and Schweitzer, Feldmann et al. (2002) initiated studies on fossil xanthoids, addressing the Carpiliidae; Goneplacidae, Hexapodidae Miers, 1886; Panopeidae Ortmann, 1893; and Pilumnidae Samouelle, 1819. It is clear that all of these families have a fossil record, and the timing of their appearances in the fossil record could be successfully used to address concerns raised in biological studies. For example, Guinot's (1978) assertion that pilumnids and panopeids were more derived than other xanthids, and Martin et al.'s (1985) postulation that pilumnids were least derived among the Xanthoidea, could be tested by the time of appearance of these groups in the fossil record. The approximate time of divergence of xanthoid lineages, the best estimates of the age of common ancestors, and character polarization resulting from knowledge of primitive and derived character states based on timing of appearance in the fossil record, would greatly enhance biological studies using cladistic, genetic, larval, and other data.

Biological classification of the Xanthoidea is largely based upon features of the eyes, antennae, mouthparts, gonopores, gills, internal softparts, and larvae, which are rarely, if ever, fossilized. Occasional occurrences of fossilized eyes and antennae (Schweitzer, Feldmann et al., 2002) are known. The sternum and basal articles of the chelipeds are sometimes preserved, which are of some importance in biological classifications. Biologists rarely use dorsal carapace morphology when describing families, and characters of the dorsal carapace are only occasionally viewed as diagnostic at the family level (but see Ng, 1998). This is unfortunate as the dorsal carapace, with the exception of isolated claw fragments, is the most commonly preserved portion of fossil brachyurans. It is also unfortunate that the dorsal carapace has been found to be quite variable in some families, as in the Pilumnidae (Ng and Clark, 2000a), and thus may not be useful to diagnose taxa in these groups.

However, previous work (Schweitzer, 2000; Schweitzer and Feldmann, 2000a, 2000b, 2000c, 2000d, 2001; Schweitzer and Salva, 2000) has shown that aspects of the dorsal carapace and other hard part morphology in decapods can be successfully used as proxies for unpreserved or non-preservable soft parts. This is a relatively straightforward process. Decapod families as defined
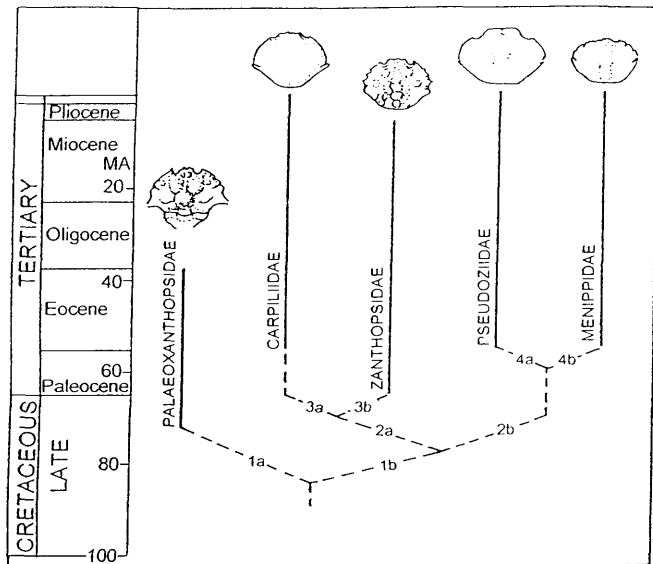
FIGURE 1—Illustrated key to the Carpiliidae, Eriphiidae, Palaeoxanthopsidae, Pseudoziidae, and Zanthopsidae placed with a temporal framework. The key does NOT represent phylogenetic relationships. Drawings of Eriphiidae and Carpiliidae after Ng, 1998. Drawing of Pseudoziidae after Guinot, 1968a.
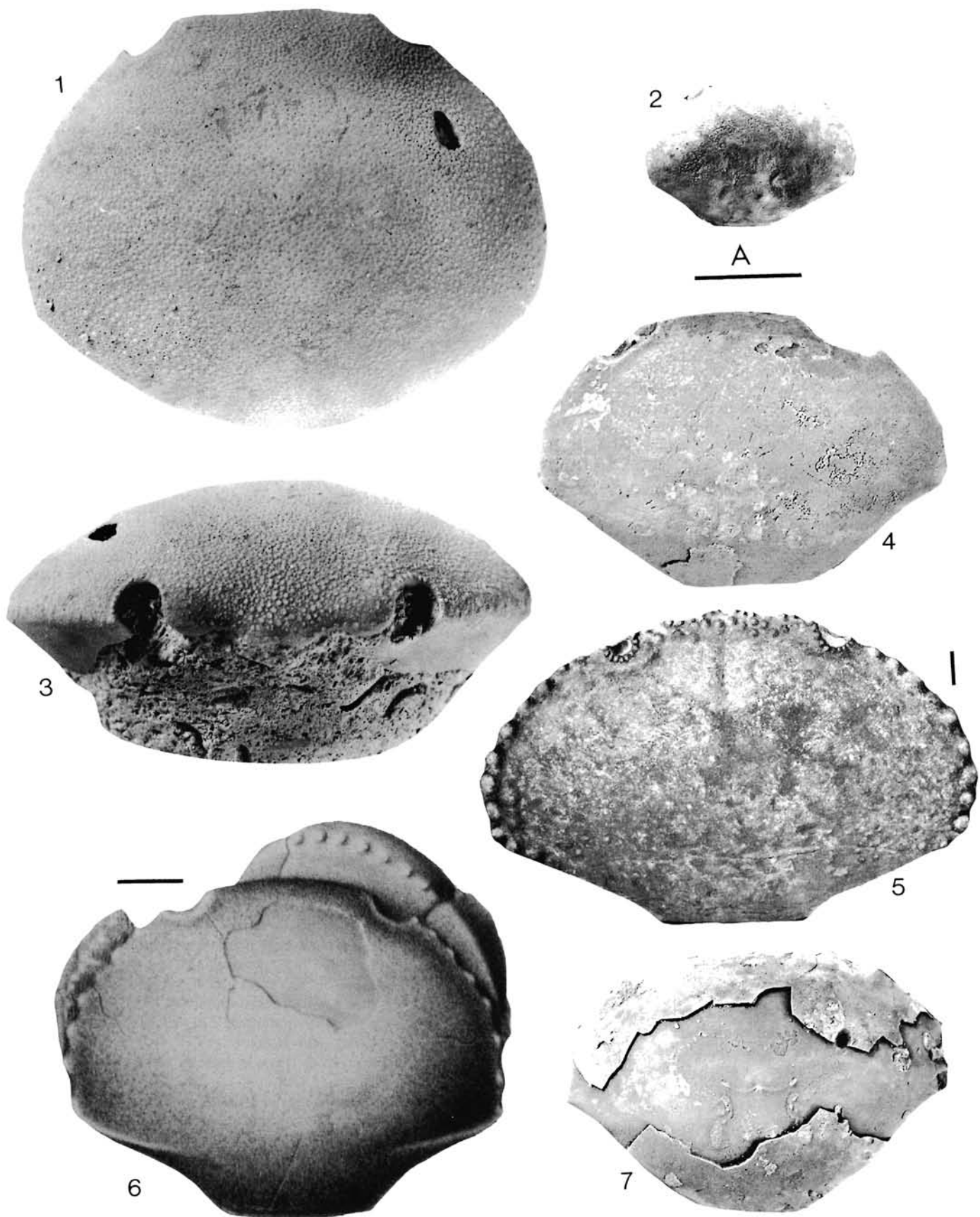
classification used for extant raninids using hard part morphology. The nature of the front, orbits, anterolateral margins, and claws has been shown to successfully differentiate members of the related Atelecyclidae and Cheiragonidae (Schweitzer and Salva, 2000). The length of the protogastric region and the vaulting of the dorsal carapace are diagnostic for some pilumnids and for no other xanthoid family, permitting assignment of some fossils to the family (Schweitzer, 2000), although recent work has also shown the carapace of pilumnids to be quite variable (Ng and Clark, 2000a). Ng (1998) provided many features of the dorsal carapace that are useful at the generic and family level in extant taxa. Thus, the designation of proxy features of the dorsal carapace, sternum, and chelipeds can result in appropriate assignment of fossil forms to families within a modern biological context.

This study addresses four families, including the extinct Zanthopsidae Via, 1959, and Palaeoxanthopsidae new family, and the extant Carpiliidae and Pseudoziidae Alcock, 1898. A key to these families and the closely related extant Eriphiidae MacLeay, 1838 (=Menippidae Ortmann, 1893, see discussion under Systematic Paleontology), is given in Appendix A (Fig. 1). All three extant families have a fossil record extending into the Eocene. Diagnoses for the Carpiliidae and the Pseudoziidae, presented here, are based solely upon hard part morphology. The derivation of these hard part characters was accomplished by examining members of these two families as defined by biologists based upon ventral surfaces, soft part morphology, and molecular data. The diagnoses for the Zanthopsidae and the Palaeoxanthopsidae are in turn based upon the dorsal carapace features that were shown to be important as proxies for soft part data in extant forms.

The fossil record of the Carpiliidae is incontrovertible based upon the distinctive morphology of the appendages and sternum (Guinot, 1968a, 1968b); all of the fossils herein referred to the family display the diagnostic biological features of the family. The record of the Pseudoziidae is a bit more tenuous. None of the exclusively fossil genera herein referred to the Pseudoziidae has preserved sterna or chelae; thus, assignments were based upon proxy features of the dorsal carapace. The use of several proxy characters in combination strengthens placement within the Pseudoziidae. When several proxy characters of the dorsal carapace are considered together, the Pseudoziidae is the only xanthoid family that can embrace these fossil genera.

Several of the studied xanthoid fossils could not be accommodated in extant families. In the Zanthopsidae, sternal and cheliped characters were available to compare with extant groups as well as characters of the dorsal carapace. Members of the Zanthopsidae do not exhibit a suite of characters that can be embraced by any currently recognized family; thus, the elevation of that group to family status is well justified. Within the Palaeoxanthopsidae, none of the representatives has sterna or basal elements of the chelipeds. However, the dorsal carapace morphology is so distinctive, and so distinctly different from any known family, that a new family must accommodate those genera. The designation and application of proxy characters of the dorsal carapace for fossil xanthoids needs to be extended to other fossil xanthoids that currently are placed within the Goneplacidae, Eriphiidae,

by biologically important, soft-part or molecular features are carefully examined, usually by studying preserved extant material or illustrations in biological papers. By examining the suite of animals that are grouped together by strictly biological means, distinctive features of the dorsal carapace can be identified that characterize the groups. The dorsal carapace features are usually overlooked by biologists for two major reasons. One is that soft-part morphology is more definitive and provides a quick indicator to the question of family status. Often, a biologist need only examine the pleopods to make a family-level designation, thus making the dorsal carapace features superfluous in the diagnosis. Secondly, dorsal carapace morphology can be ambiguous; for example, many xanthoid groups exhibit very similar dorsal carapace morphologies. However, when the taxa referable to a family on biological grounds are examined, a suite of features of the dorsal carapace and other hard-parts that characterizes that group is usually evident. Often an array of characters must be used. For example, possession of a smooth dorsal carapace does not solely distinguish any one family of decapods. But possession of a smooth carapace; round, rimmed, entire orbits; a very long, convex anterolateral margin; and a low angle of the posterolateral to posterior margin does characterize a single family, the Carpiliidae.

Family level designations within the Calappidae sensu lato, using suites of dorsal carapace features as proxies for soft part morphology, were faithful to the designations made with soft part morphology (Bellwood, 1996; Schweitzer and Feldmann, 2000a). Tucker (1998) successfully placed fossil raninid crabs into the

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FIGURE 2—Representatives of the Carpiliidae. 1, *Eocarpilius blowi* Feldmann et al., 1998, dorsal carapace of holotype, CM 36026; 2, *Ocalina straeleni* (Remy and Tessier, 1954), dorsal carapace of holotype, R.03810, from the lower Lutetian of Senegal, photograph provided by the MNHN, Paris; 3, *Eocarpilius blowi* Feldmann et al., 1998, anterior view of holotype, CM 36026; 4, *Proxicarpilius* sp., Eocene of Pakistan, uncataloged material of the University of Michigan; 5, *Ocalina floridana* Rathbun, 1929, dorsal carapace of holotype, USNM 370956, digital image of Rathbun, 1929, pl. 1, fig. 3; 6, *Palaeocarpilius macrocheilus* (Desmarest, 1822), digital image from Glaessner, 1969, p. R519, fig. 328, 1a, From *Treatise on Invertebrate Paleontology*, courtesy of and © 1969, The Geological Society of America and the University of Kansas; 7, *Proxicarpilius* sp., Eocene of Pakistan, uncataloged material of the University of Michigan. Scale bars equal to 1 cm; scale bar A for *1, 2, 3, 4,* and *7*; others for image with which they are associated.

Panopeidae, Pilumnidae, and Xanthidae sensu lato. Only then will the biological affinities within this diverse group of animals be fully illuminated.

SYSTEMATIC PALEONTOLOGY

Repository abbreviations.—USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C.; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; MNHN and R., Muséum national d'Histoire naturelle, Paris; IHNCH, Instituto de Historia Natural de Chiapas, Tuxtla Gutiérrez, Chiapas, México.

Infraorder BRACHYURA Latreille, 1802
Section HETEROTREMATA Guinot, 1977
Superfamily XANTHOIDEA MacLeay, 1838
Family ERIPHIIDAE MacLeay, 1838

Eriphiidae, MACLEAY, 1838.
Menippidae ORTMANN, 1893.
Oziidae DANA, 1851.

Discussion.—No attempt at the enormous task of providing a complete synonymy has been made here; the reader may refer to the sources sited herein. Menippidae has been most widely used (Guinot, 1977, 1978; Serène, 1984; Coelho and Filhol, 1993), even though Holthuis (1978) recognized that Oziidae Dana, 1851, is a senior synonym of Menippidae and recommended its use at that time. It was subsequently recognized that Eriphiidae clearly has priority over Menippidae, and some workers have either used that name or advocated for its use (Ng, 1998; Ng et al., 2001; Ng in Martin and Davis, 2001, p. 53; Davie, 2002). Under the Fourth Edition of the International Code of Zoological Nomenclature (1999), a name that is not a senior synonym but is in prevailing usage may be retained. However, the discovery that Eriphiidae is a senior synonym of Menippidae was made prior to 1999 (see Ng, 1998); thus, the rules of the Third Edition of the Code (1985) apply, which states that the senior synonym must be used, regardless of its prevalence in the literature. Thus, Eriphiidae must be used as the correct family name (P. K. L. Ng, personal commun.).

Family CARPILIIDAE Ortmann, 1893
Figure 2

Type genus.—*Carpilius* Leach *in* Desmarest, 1822.
Included genera.—*Carpilius*; *Eocarpilius* Blow and Manning, 1996; *Holcocarcinus* Withers, 1924; *Ocalina* Rathbun, 1929; *Palaeocarpilius* A. Milne Edwards, 1862; *Proxicarpilius* Collins and Morris, 1978.
Diagnosis.—Carapace wider than long, length about 70–80 percent maximum carapace width, widest about two-thirds to three-quarters the distance posteriorly on carapace; may be ornamented with large, flat nodes; regions moderately to poorly defined; grooves not developed except branchiocardiac groove in some cases. Front usually with bilobed medial projection and blunt inner orbital spines, thus appearing quadrilobed; may be produced into downturned, blunt triangle; frontal width averaging 36 percent maximum carapace width. Orbits circular, entire, rimmed or beaded, directed forward, fronto-orbital width about half to two-thirds maximum carapace width. Anterolateral margin may be entire or with blunt lobes or spines; last spine may be extended onto dorsal carapace as short, low ridge; long, much longer than posterolateral margin, terminating two-thirds to three-quarters the distance posteriorly, convex, tightly curved posteriorly, often very convex posteriorly. Posterolateral margin straight or weakly concave, short, at a very low angle to posterior margin, around 25–30 degrees; posterior margin nearly straight, narrow, averaging about 30 percent maximum carapace width.

Carapace regions may be weakly inflated or not defined. Branchiocardiac groove often defines lateral margins of urogastric region. Chelae large, subequal or heterochelous; outer, upper and lower surfaces generally smooth, upper surface may have blunt nodes; chelipeds much larger than other walking legs; merus fused to basis-ischium; merus and coxa articulating directly. Pereiopods 2–5 narrow, smooth, tubular. Thoracic sternum narrow, rectangular, with subparallel margins; articulation condyle of pereiopods on sternum; male abdominal somites 3–5 fused. (In part after Guinot, 1968a, 1968b, 1978 and Ng, 1998).

Discussion.—The Carpiliidae embraces a small number of crabs with a smooth dorsal carapace, convex anterolateral margins, and an ovate, convex dorsal carapace. Wright and Collins (1972) appear to have been the first to give the group family status, and Guinot (1978, 1979) also designated the group as a family based upon compelling evidence that the group is markedly different from other xanthoids. Most recent work has treated the Carpiliidae as a family (Karasawa, 1993, 1997; Ng, 1998; Schweitzer et al., 2000; Schweitzer, 2000; Martin and Davis, 2001).

Guinot (1968a, 1968b) suggested that the Carpiliidae embraced the extant *Carpilius*, *Euryozius* Miers, 1886, and *Gardineria* Rathbun, 1911 (*non Gardineria* Vaughan, 1907, a scleractinian coral, which is the senior homonym), based upon the dorsal carapace features as well as soft-part anatomy. Sakai (1976) allied numerous genera characterized by smooth dorsal carapaces with *Carpilius*; however, Guinot (1968a, 1968b, 1978) dismissed many of these alliances as based upon superficial characters. Guinot (1978) later restricted the extant group to only *Carpilius*. Serène (1984) suggested that the Carpiliidae was monotypic, embracing only *Carpilius*; Ng (1998) also gave a restricted definition of the family and listed species of *Carpilius* as the only Indo-Pacific representatives. Guinot (1968a), Serène (1984), and Ng (1998) defined the family on dorsal carapace features, characters of the chelipeds, disposition of the male abdomen in *Carpilius* and the form of the first and second male pleopods; however, there is disagreement about the male abdomen in the literature. Serène (1984) and Guinot (1968) described the male abdomen as having two fused somites while Ng (1998) described the male abdomen as always having somites 3–5 fused. The basis for the confusion arises from the visible suture between somites 4 and 5, which suggests that the fusion is not complete. However, although the suture is visible, the segments are immobile and are thus completely fused (P. K. L. Ng, personal commun.). Examination of Recent specimens of *Carpilius convexus* (USNM 25318) shows that somites 3–5 are fused and immobile.

Although Guinot (1968a) included *Euryozius* and *Gardineria* within the Carpiliidae, she noted a few differences between these two genera and *Carpilius* and later removed them from the Carpiliidae (Guinot, 1978). Schweitzer (2000) accepted the placement of *Gardineria* and *Euryozius* in the Carpiliidae; however, it is clear that they are not carpiliids. Guinot (1978) considered *Gardineria* to be a junior synonym of *Euryozius*; this was also discussed by Manning and Holthuis (1981). Ng and Liao (2002) assigned *Euryozius* to the Pseudoziidae, a view with which I concur.

The fossil *Carpilius occidentalis* Schweitzer et al., 2000, exhibits a dorsal carapace morphology that is remarkably similar to that of *Carpilius* and *Euryozius*. *Carpilius occidentalis* exhibits the quadrilobed front; entire orbits; smooth dorsal carapace; convex anterolateral margin; weak ridge extending onto the dorsal carapace from the last anterolateral spine; and nearly entire anterolateral margin typical of *Carpilius*. However, *C. occidentalis* differs from typical *Carpilius* in having two blunt spines near the

anterolateral corner; *Carpilius* has only one. In addition, the anterolateral margin of *C. occidentalis* is shorter than in typical *Carpilius* and other carpiliids and is less convex. The angle between the posterolateral margin and the posterior margin of species of *Carpilius* and other carpiliids is about 25–30 degrees, while that of *C. occidentalis* is about 40 degrees. The posterior margin of *C. occidentalis* is broader than that of *Carpilius*. The orbits of typical *Carpilius* are deeper and more circular than those of *C. occidentalis*, in which the orbits are shallower and broader. Species of *Euryozius* and *Pseudozius* have shorter, less convex anterolateral margins and broader posterior margins than those of typical *Carpilius*, and *Euryozius* and *Pseudozius* have two blunt spines at the anterolateral corners and shallower, less circular orbits than typical *Carpilius*. *Euryozius* and *Pseudozius* share all of these features with *C. occidentalis*. In addition, the angle of the posterolateral margin with the posterior margin in *Euryozius* and *Pseudozius* is about 40–45 degrees, more congruent with that of *C. occidentalis*. Unfortunately, none of the specimens of *C. occidentalis* has preserved sterna, abdomina, or first pereiopods, making it difficult to make a conclusive family-level assignment. However, it seems clear that *C. occidentalis*, from Eocene rocks of the western North American coast, is not referable to *Carpilius*. *Carpilius occidentalis* appears to be most closely allied with *Euryozius* and *Pseudozius* within the Pseudoziidae, and a new genus has been erected to accommodate it, *Archaeozius*, discussed below.

The extant *Liagore* exhibits many similarities with members of the Carpiliidae but may be excluded from the family based on several characters. The front in *Liagore* appears to be distinctly bilobed, not quadrilobed as in the Carpiliidae. The anterolateral margin is much shorter and less convex than in genera within the Carpiliidae. The angle of the posterolateral margin with the posterior margin is much higher, about 42 degrees. The orbits are shallower and less markedly rimmed in *Liagore* than in the Carpiliidae. Thus, that taxon is excluded from the family.

The exclusively fossil genera *Palaeocarpilius* and *Ocalina* were placed within the Carpiliidae based upon features of the dorsal carapace and chelipeds (Guinot, 1968a, 1968b); I concur. Subsequently, *Proxicarpilius*, *Eocarpilius*, and *Harpactoxanthopsis* were referred to the family (Feldmann et al., 1998; Schweitzer et al., 2000; Schweitzer, 2000). *Harpactoxanthopsis* is herein removed to the newly elevated Zanthopsidae Via, 1959. *Proxicarpilius* and *Eocarpilius* exhibit the smooth dorsal carapace; long, convex anterolateral margins; quadrilobed front; entire or weakly spined anterolateral margins; and low angle between the posterolateral and posterior margins typical for the family. *Proxicarpilius* exhibits the weak dorsal carapace ridge at the anterolateral corner and the direct articulation of the coxa with the merus, typical of carpiliids. Guinot (1968a) suggested affinities between *Holcocarcinus* and the carpiliids. I concur; that genus has the long, convex anterolateral margins; smooth dorsal carapace; weakly quadrilobed front extending into a blunt, downturned triangle; ridge at the anterolateral corner; and low angle between the posterolateral and posterior margins typical of the family. *Holcocarcinus* differs from other carpiliids in having two transverse ridges on the dorsal carapace.

Palaeocarpilius is known with certainty from middle Eocene to Oligocene rocks and questionably from the Miocene (Glaessner, 1969). *Eocarpilius* occurs in middle Eocene rocks of North Carolina and Miocene rocks of Europe (Müller, 1984; Feldmann et al., 1998). *Carpilius* occurs in Miocene rocks of Japan (Karasawa, 1993), Pliocene rocks of Barbados (Collins and Morris, 1976); Pleistocene rocks of Jamaica (Collins et al., 1996), and Pleistocene and Holocene rocks of Taiwan (Hu and Tao, 1996). *Holcocarcinus* is known from Eocene rocks of Nigeria (Withers,

1924), and *Proxicarpilius* has been recovered from Eocene localities in Pakistan (Collins and Morris, 1978).

Guinot (1978) considered the family to be a relatively ancient form, its morphological features stabilizing during the Eocene. The family was apparently most diverse and abundant during the Tertiary, as that is the interval from which the most genera are known, and it has declined during the late Tertiary and Quaternary to its present relict status. It is not possible to determine where the family evolved because the Eocene occurrences are not well constrained temporally. The family exhibited a Tethyan distribution, dispersed among epicontinental Europe, the Atlantic and Gulf Coastal Plain of North America, Africa, and the Tethys during the Eocene. Subsequent dispersal during Oligocene and early Miocene time probably occurred via the Central American Seaway and Tethys to result in the relict Tethyan distribution seen in modern species of *Carpilius*, the only extant forms.

Genus CARPILIUS Leach in Desmarest, 1822

Type species.—*Cancer maculatus* Linnaeus, 1758, by original designation, Recent and fossil occurrences.

Other species.—*Carpilius convexus* (Forskål, 1775); *C. corallinus* (Herbst, 1783), as *Cancer*, Recent and fossil occurrences; *Carpilius* sp. Karasawa, 1993 (fossil).

Diagnosis.—Carapace wider than long, length about three-quarters maximum width, widest about one-half to two-thirds the distance posteriorly on carapace; carapace with undefined regions, smooth; front lobate, two inner orbital lobes, two axial lobes or one broad, fused central lobe, about 22 percent maximum carapace width; orbits circular, rimmed, entire, fronto-orbital width about 45 percent maximum carapace width; anterolateral margin entire with large protuberance at anterolateral corner, protuberance extending onto anterolateral margin as blunt ridge; posterolateral margin straight or weakly concave, angle between posterolateral margin and posterior margin about 25 degrees; posterior margin straight, narrow, about 28 percent maximum carapace width; heterochelous, meri of chelae articulating directly with coxa; merus of first pereiopod fused to basis-ischium; sternum narrow, with parallel lateral margins; male abdominal somites 3–5 fused.

Discussion.—*Carpilius* is the only extant member of the family. Three species are known in modern oceans, two of which also have fossil records. A carapace referred to *C. corallinus* was reported from Pliocene rocks of Barbados (Collins and Morris, 1976), and claws referred to that species have been reported from Pleistocene rocks of Jamaica (Collins et al., 1996). Schweitzer et al. (2002) reported *Carpilius* sp. dactyls in Pleistocene deposits of Guam. *Carpilius convexus* has been reported from subfossils from Taiwan (Hu and Tao, 1996). Karasawa (1993) reported chelae from Miocene rocks of southwest Japan referable to *Carpilius* sp.

Genus EOCARPILIUS Blow and Manning, 1996
Figure 2.1, 2.3

Type species.—*Eocarpilius carolinensis* Blow and Manning, 1996, by original designation.

Other species.—*Eocarpilius anomala* (Rathbun, 1935), as *Menippe*; *E. antiquus* (Glaessner, 1928), as *Carpilius*; *E. blowi* Feldmann et al., 1998.

Diagnosis.—Carapace ovate, length about 75 percent carapace width, widest about one-half to two-thirds the distance posteriorly on carapace; carapace with undefined regions, punctate; front quadrilobed including inner orbital spines, about thirty percent maximum carapace width; orbits circular, rimmed, entire, fronto-orbital width about 60 percent maximum carapace width; anterolateral margin entire with small protuberance at anterolateral corner; lacking ridge at anterolateral corner extending onto dorsal
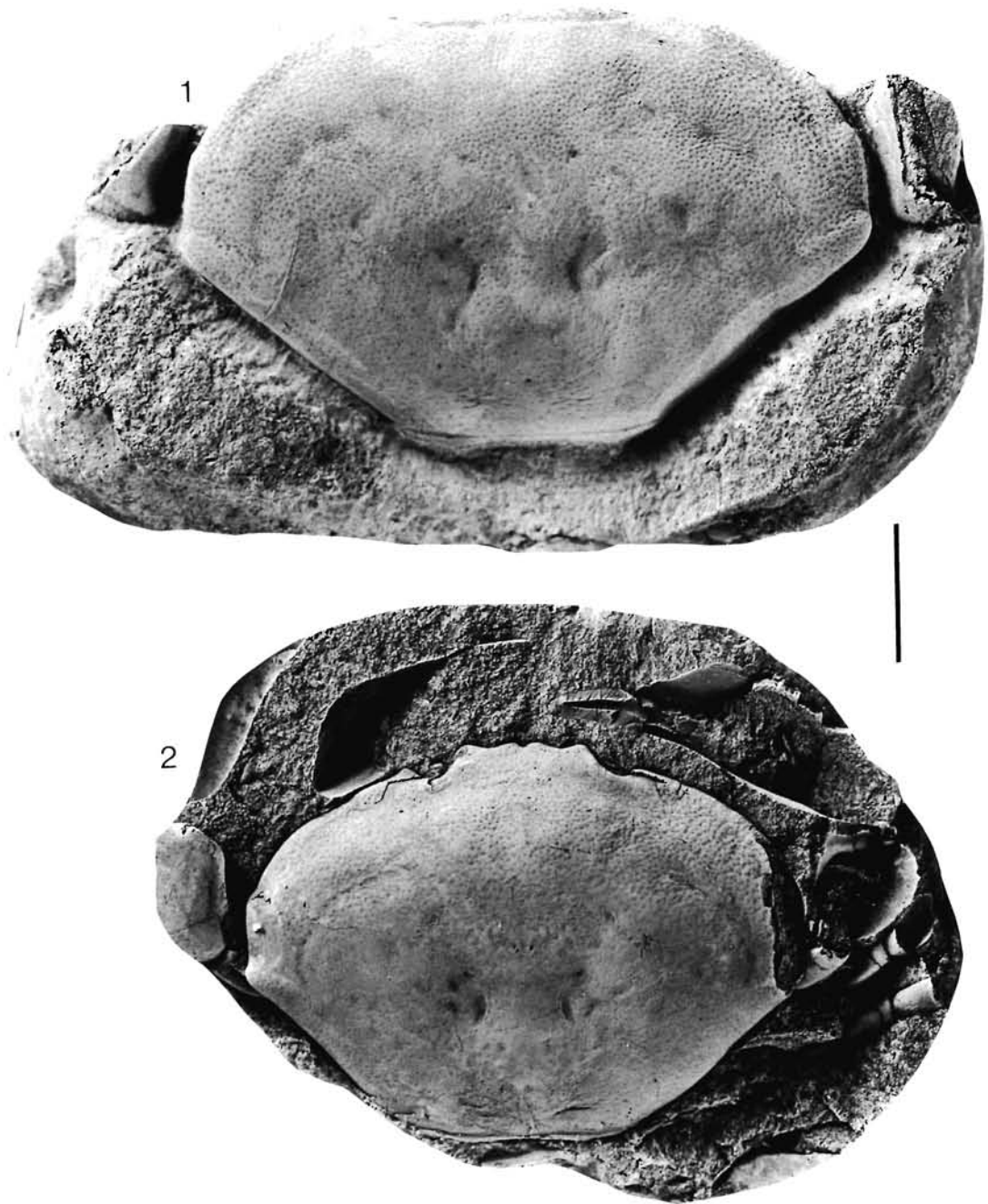
FIGURE 3—*Archaeozius occidentalis* (Schweitzer et al., 2000), fossil member of the Pseudoziidae. *1*, dorsal carapace of holotype, CM 45847; *2*, dorsal carapace of paratype, CM 45848. After Schweitzer et al., 2000. Scale bar equal to 1 cm.

maximum carapace width; regions poorly defined or not defined, gastric grooves defining cardiac and other gastric regions weakly developed, epigastric regions may be weakly developed but often indistinct. Front nearly straight or weakly quadri-lobed, axially notched, can be markedly deflexed, all four lobes extending the same distance anteriorly, front about 30 percent maximum carapace width; orbits shallow, ovoid, weakly rimmed; fronto-orbital width about half maximum carapace width. Anterolateral margin entire with small spines at anterolateral corner or weakly lobed with shallow notches or fissures separating lobes; extending to about midlength. Posterolateral margin sinuous or nearly straight,

angle of posterolateral to posterior margin 40–45 degrees. Posterior margins 30 percent to half maximum carapace width. All male abdominal somites free. Fusion of the basis-ischium with merus incomplete, remnants of suture visible; coxa appearing to articulate directly with merus (after Ng and Wang, 1994).

Discussion.—The placement of *Pseudozius* and related genera has been debated for nearly a century. Ng and Wang (1994) summarized the various family-level placements of *Pseudozius*, and Ng and Liao (2002) elevated Alcock's (1898) alliance Pseudozioida to family status. Fossil Pseudoziidae are not easily differentiated from fossil carpiliids; however, some features are especially

carapace; posterolateral margin at about 25 degree angle to posterior margin; posterior margin narrow, straight, about 33 percent maximum carapace width; heterochelous, mani of chelae with smooth outer surface; merus of major cheliped articulating directly with ischium.

Discussion.—*Eocarpilius* is known from the Eocene of North America and the Miocene of Europe (Feldmann et al., 1998). The genus, as do most genera in the family, exhibits a Tethyan distribution and appears to have dispersed eastward via ocean currents to epicontinental Europe.

Genus HOLCOCARCINUS Withers, 1924

Type species.—*Holcocarcinus sulcatus* Withers, 1924, by original designation.

Diagnosis.—Carapace ovate, wider than long; carapace regions not developed, with two transverse ridges, one extending between first anterolateral protuberances, second extending between protuberances at anterolateral corner; front broad, depressed, triangular; orbits circular; anterolateral margin entire except for small protuberances where transverse ridges intersect margin; posterolateral margin at about 30 degree angle to posterior margin, posterior margin about 31 percent maximum carapace width.

Discussion.—The sole species of the genus is known from middle Eocene rocks of Nigeria.

Genus OCALINA Rathbun, 1929
Figure 2.2, 2.5

Type species.—*Ocalina floridana* Rathbun, 1929, by original designation.

Other species.—*Ocalina straeleni* (Remy and Tessier, 1954), as *Palaeocarpilius*.

Diagnosis.—Carapace ovate, wider than long, widest about three-quarters the distance posteriorly on carapace, regions poorly defined, surface ornamented with numerous broad, low swellings; front about one-third maximum carapace width, weakly quadrilobed, ornamented with large tubercles; orbits circular, entire, rimmed with small tubercles, fronto-orbital width about half maximum carapace width; anterolateral margin convex, especially tightly curved posteriorly, ornamented with about nine large tubercles; posterolateral margin with two or three weak tubercles just posterior to anterolateral corner, weakly concave, at about 25 degree angle to posterior margin; posterior margin straight, about 31 percent maximum carapace width; branchiocardiac groove well-developed lateral to urogastric and cardiac regions.

Discussion.—Remy and Tessier (1954) described *Palaeocarpilius straeleni* from Eocene rocks of Senegal. Guinot (1968a) noted that *P. straeleni* more closely resembled *Ocalina* than *Palaeocarpilius*. In *Ocalina* and *P. straeleni*, the carapace is transversely wider than in typical *Palaeocarpilius*. In *Ocalina* and *P. straeleni*, tubercles situated on the dorsal carapace parallel some of the anterolateral projections, a feature not present in typical *Palaeocarpilius*. In typical *Palaeocarpilius*, the ridge extending from the last anterolateral spine onto the dorsal carapace is well-developed and long, while in *Ocalina* and *P. straeleni*, it is poorly-developed or not present. Thus, *P. straeleni* is herein assigned to *Ocalina*. The two known species of *Ocalina* are known from Eocene rocks, and the genus exhibits a Tethyan distribution based upon its occurrences in Florida and Senegal.

Genus PALAEOCARPILIUS A. Milne Edwards, 1862
Figure 2.6

Type species.—*Cancer macrocheilus* Desmarest, 1822, by subsequent designation (=*P. macrocheilus* var. *coronata* Bittner, 1886).

Other species.—*Palaeocarpilius anodon* Bittner, 1875; *P.*

aquilinus Collins and Morris, 1973; *P. aquitanicus* A. Milne Edwards, 1862; *P. bispinosus* Satsangi and Changkakoti, 1989; *P. brodkorbi* Lewis and Ross, 1965; *P. ignotus* A. Milne Edwards, 1862; *P. intermedius* Stubblefield, 1927; *P. klipsteini* (von Meyer, 1862), as *Cancer*; *P. laevis* Imaizumi, 1939; *P. mississippiensis* (Rathbun, 1935), as *Harpactocarcinus*; *P. rugifer* Stoliczka, 1871, *P. simplex* Stoliczka, 1871; *P. valrovinensis* de Gregorio, 1895, as *Harpactocarcinus*.

Diagnosis.—Carapace wider than long, widest three-quarters or more the distance posteriorly on carapace, smooth, regions not defined; front downturned, blunt-triangular, about 40 percent maximum carapace width; orbits small, rimmed, circular, entire, fronto-orbital width about 60 percent maximum carapace width; anterolateral margin very convex, long, usually with numerous spines or blunt projections but may have only a few spines near anterolateral corner; well-developed ridge extending onto dorsal carapace from last anterolateral spine; posterolateral margin at about 32 degree angle to posterior margin, posterior margin about 33 percent maximum carapace width; merus of major cheliped articulating directly with ischium.

Discussion.—The concept of *Palaeocarpilius* has changed little since Glaessner (1929); species reported since then are noted here. *Harpactocarcinus mississippiensis* Rathbun, 1935 and *Harpactocarcinus valrovinensis* de Gregorio, 1895, are reassigned to *Palaeocarpilius* A. Milne Edwards, 1862. Each of these species possesses the smooth carapace, lobate anterolateral margins, and down-turned, bluntly triangular front characteristic of *Palaeocarpilius*; thus, their placement within that genus is made with confidence. The genus exhibits a Tethyan distribution.

Genus PROXICARPILIUS Collins and Morris, 1978
Figure 2.4, 2.7

Type species.—*Proxicarpilius planifrons* Collins and Morris, 1978, by original designation.

Other species.—*Proxicarpilius minor* Collins and Morris, 1978.

Diagnosis.—Carapace ovate, wider than long, length about three-quarters maximum width, widest about two-thirds the distance posteriorly on carapace; front downturned, bluntly triangular in shape, about 40 percent maximum carapace width; orbits circular, rimmed, entire, fronto-orbital width about two-thirds maximum carapace width; anterolateral margin with four spines or protuberances including outer orbital spine; outer orbital spine triangular; next anterolateral spine very small, blunt; last two spines triangular, sharp, very weak ridge extending onto dorsal carapace from last anterolateral spine; posterolateral margin at about 32 degree angle to posterior margin, about 31 percent maximum carapace width; outer surface of manus of chelae with longitudinal ridges.
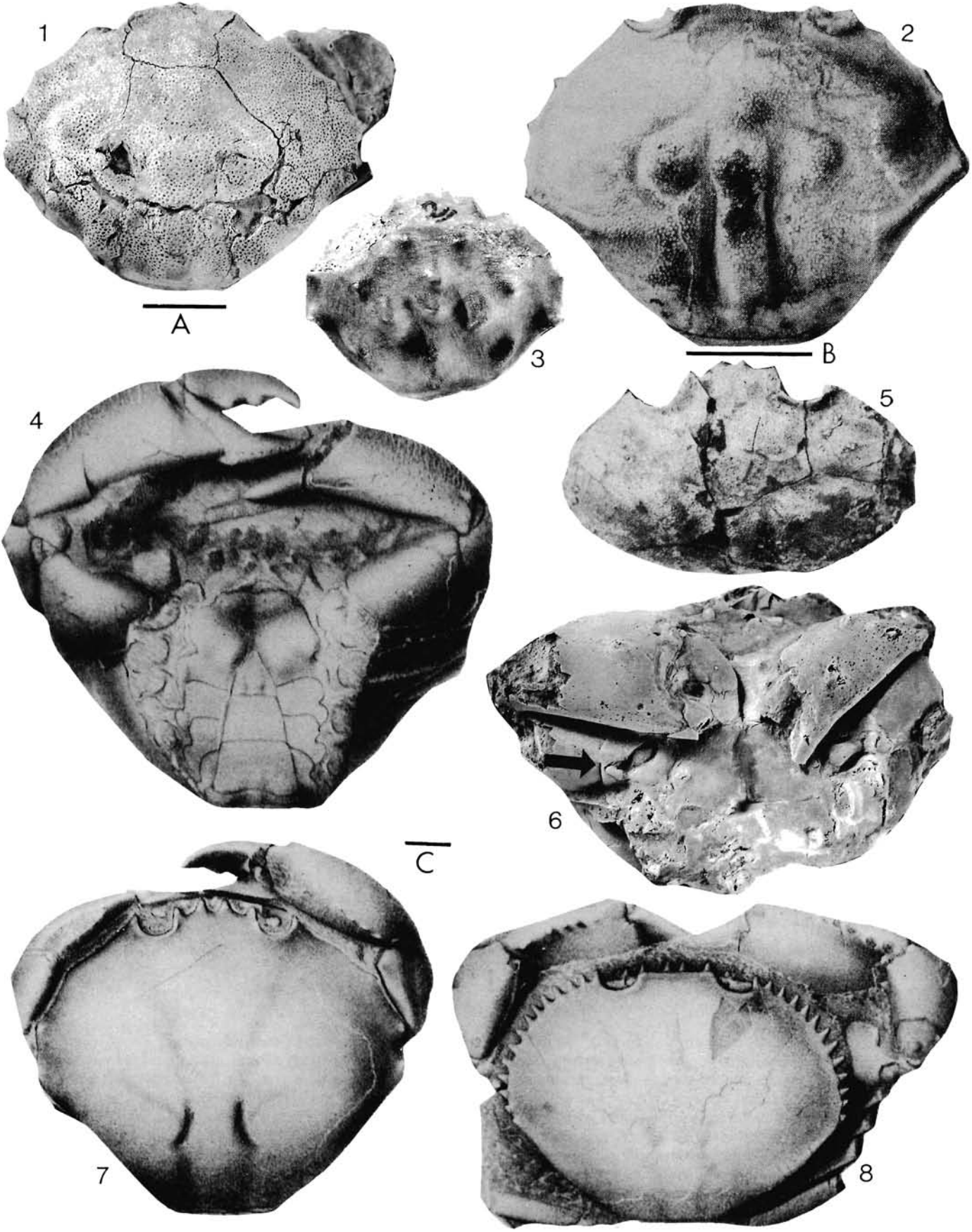
Discussion.—The two species are known from Eocene rocks of Pakistan (Collins and Morris, 1978).

Family PSEUDOZIIDAE Alcock, 1898

Type genus.—*Pseudozius* Dana, 1851.

Included genera.—*Archaeozius* new genus (fossil), *Euryozius* Miers, 1886 (Recent and fossil); *Flindersoplax* Davie, 1989; *Planopilumnus* Balss, 1933; *Platychelonion* Crosnier and Guinot, 1969; *Priabonocarcinus* Müller and Collins, 1991 (fossil); *Pseudozius*; *Santeexanthus* Blow and Manning, 1996 (fossil). All are Recent only (Ng and Liao, 2002) unless otherwise marked; *Platychelonion* and *Planopilumnus* are aberrant in terms of their dorsal carapace shape and ornamentation, although they have been placed within the family (Ng and Liao, 2002) based upon abdominal and soft part features. The following diagnosis does not embrace those two genera.

Diagnosis.—Carapace wider than long, length about 65 percent

useful. The angle of the posterolateral margin with the posterior margin is markedly higher in pseudoziids, and the anterolateral margin is shorter and less convex in pseudoziids than in carpiliids. The posterior margin of the pseudoziids is much wider than that of carpiliids, and the orbits are more circular with better developed rims in carpiliids as compared to pseudoziids. The four-lobed front in pseudoziids differs from that of carpiliids, in which the middle two lobes usually extend anteriorly beyond the two lateral lobes. In the pseudoziids, all four lobes extend anteriorly the same distance. If male abdomina are preserved, the fusion of the somites is also diagnostic; pseudoziids exhibit no fusion of somites while carpiliids have somites 3–5 fused. In the first pereiopods of Carpiliidae, the basis-ischium is fused to the merus, while in pseudoziids, this fusion is incomplete.

The dorsal carapace of *Planopilumnus* and *Platychelonion* differs markedly in many ways from the other members of the family. These genera have well-ornamented carapaces that exhibit carapace width and length ratios that differ from the other genera within the family. In these two genera, the length is about 75 percent the maximum carapace width as opposed to 65 percent in the other pseudoziid genera. The fronto-orbital width in these two genera is about 64 percent, rather than 43 percent, the maximum width, and the frontal width is about 33 percent the carapace width rather than 25 percent. The dorsal carapace of *Planopilumnus* and *Platychelonion* is angular as in other pseudoziids, and the orbits are small and shallow as in other pseudoziids. Thus, these two genera do not fit the diagnosis above. This example illustrates some of the difficulties in relating fossil to extant taxa.

According to Guinot (1968a), *Pseudozius* and *Euryozius* (which are now placed within the Pseudoziidae) display primitive characters, such as the lack of fusion of abdominal somites as well as character states of other soft-part features; derived features such as the enlargement of the sternum; and intermediate features such as the near fusion of the basis-ischium with the merus (p. 330). Members of the Carpiliidae exhibit derived features including the fusion of male abdominal somites and fused basis-ischium with the merus, and more primitive features such as the narrow, straight sternum. Dorsal carapace features of the two families are gradational. The front of pseudoziids is less distinctly quadrilobed than those of the Carpiliidae; however, making a firm distinction between "more" and "less" quadrilobed is not easy. Similarly, the anterolateral margins are convex in both families, but they are much more convex and much longer in the Carpiliidae, a feature that is easier to quantify. In many ways the distinction between the Pseudoziidae and Carpiliidae is gradational; however, the many characters of soft parts, hard parts, and molecular features now employed demonstrates that the two can be differentiated into separate families (Ng and Liao, 2002). The presence of both families in Eocene rocks suggests that they diverged before that time, and as mentioned above, *Archaeozius*, which displays characters intermediate between the two families, may be close to the common ancestor of the two families.

Pseudozius is Indo-Pacific and *Euryozius* is Indo-Pacific and East Atlantic (Guinot, 1968a) in modern oceans. The fossil forms exhibit a primarily Tethyan distribution based upon Eocene occurrences in Hungary (*Priabonocarcinus*) and east-coastal North America (*Santeexanthus*) and Miocene occurrences in Japan (*Euryozius*). Ancestors of *Archaeozius* may have reached west-coastal North America via the Central American Seaway or via the North Pacific gyre. The oldest occurrences, *Archaeozius* and *Santeexanthus*, are both middle Eocene, so it is difficult to speculate on where the family originated. The Recent occurrences in the Indo-Pacific and eastern Atlantic may be relics of the Tethyan distribution.

Genus ARCHAEOZIUS new genus
Figure 3

Type species.—*Carpilius occidentalis* Schweitzer, Feldmann, Tucker, and Berglund, 2000.

Diagnosis.—Carapace wider than long, length about 70 percent maximum width, widest at about 60 percent distance posteriorly; smooth; regions not defined. Front quadrilobed, about one quarter maximum carapace width. Orbits shallow, incompletely circular, weakly rimmed, fronto-orbital width about 43 percent maximum carapace width. Anterolateral margin convex, tightly arched posteriorly, terminating about 60 percent the distance posteriorly on carapace; two blunt protuberances, one at anterolateral corner and other just anterior to anterolateral corner. Posterolateral margin nearly straight, at about 40 degree angle to posterior margin; posterior margin straight, about 40 percent maximum carapace width. Branchiocardiac groove moderately incised.

Etymology.—The genus name is derived from the genus name *Ozius*, from which the family name is derived, and the prefix *archaeo*, meaning "old," in reference to its fossil status.

Discussion.—The new genus differs from all members of the Eriphiidae, with members of which it shares superficial similarities in carapace ornamentation and shape. Eriphiids typically have six spines or protuberences on the frontal margin including the inner orbital spines, while *Archaeozius* has four, and eriphiids have moderately- to well-developed carapace regions, which *Archaeozius* does not have. Eriphiids often have three to five well-defined spines on the anterolateral margin, which *Archaeozius* lacks.

Archaeozius differs from all Carpiliidae in possessing shorter, less convex anterolateral margins; shallower, less markedly rimmed, and more incomplete orbits; a much steeper angle between the posterolateral and posterior margins; and a broader posterior margin than carpiliids. These major differences between *Archaeozius* and the Carpiliidae exclude it from that family.

Archaeozius possesses several features typical of the Pseudoziidae. The length of the anterolateral margins, the angle of the posterolateral margin to the posterior margin, the position of maximum width, the shape of the orbits, and the length of the posterior margin all conform to the diagnosis for the family. *Archaeozius* differs

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FIGURE 4—Representatives of the Zanthopsidae Via, 1959. *1*, dorsal carapace of *Zanthopsis leachii*, CM 38715a; *2*, *Neozanthopsis americanus* new comb. (Rathbun, 1928), holotype, USNM 369607, digital image from Rathbun, 1928, pl. 2, fig. 3; *3*, dorsal carapace, *Zanthopsis multispinosa* Remy, 1960, holotype, R.03788, Eocene of Ivory Coast, photograph provided by the MNHN, Paris; *4*, *Harpactoxanthopsis quadrilobatus* (Desmarest, 1822), ventral view, digital image from Glaessner, 1969, p. R516, fig. 326,10b, From *Treatise on Invertebrate Paleontology*, courtesy of and © 1969, The Geological Society of America and the University of Kansas; *5*, *Neozanthopsis americanus* new comb. (Rathbun, 1928), holotype, USNM 369607, digital image from Rathbun, 1928, pl. 2, fig. 6; *6*, ventral view of *Zanthopsis leachii*, CM 38715b, arrow indicates articulation of merus and basis-ischium with no fusion; *7*, *Harpactoxanthopsis quadrilobatus* (Desmarest, 1822), ventral view, digital image from Glaessner, 1969, p. R516, fig. 326,10a, From *Treatise on Invertebrate Paleontology*, courtesy of and © 1969, The Geological Society of America and the University of Kansas; *8*, *Harpactocarcinus punctulatus* (Desmarest, 1822), dorsal carapace, digital image from Glaessner, 1969, p. R518, fig. 327,1a, From *Treatise on Invertebrate Paleontology*, courtesy of and © 1969, The Geological Society of America and the University of Kansas. Scale bars equal to 1 cm. Scale bar A for *1, 3*; scale bar B for *2, 5*; scale bar C for *4, 6–8*.

from all other pseudoziids in possessing a markedly quadrilobed front; other members of the family have smoother or less lobate fronts. The carapace of *Archaeozius* is more highly vaulted anteriorly than other members of the family, and the last anterolateral protuberance is stouter than in other members of the family. The width of the posterior margin of *Archaeozius* is exactly intermediate between that of the pseudoziids and the carpiliids. *Archaeozius* displays features more like pseudoziids than carpiliids, hence its placement in the Pseudoziidae. However, its intermediate form suggests that it may be close to the common ancestor of the Carpiliidae and the Pseudoziidae. Unfortunately, the oldest known carpiliid is middle Eocene, and the oldest pseudoziids as reported here are middle Eocene, so timing constraints cannot help to resolve the problem.

The only known occurrence of *Archaeozius* is in middle Eocene rocks questionably referred to the Aldwell Formation in Washington, USA (Schweitzer et al., 2000).

Genus EURYOZIUS Miers, 1886

Gardineria RATHBUN, 1911, p. 236. (*non Gardineria* VAUGHAN, 1907).

Type species.—*Xantho bouvieri* A. Milne Edwards, 1869.
Fossil species.—*Euryozius angustus* Karasawa, 1993; *E. bidentatus* Karasawa, 1993.
Diagnosis.—Carapace ovate, wider than long, length about 60 percent width, widest about half the distance posteriorly on carapace, regions poorly defined or not defined, smooth; frontal margin nearly straight or medially notched, about 30 percent maximum carapace width; orbits shallow, weakly rimmed, ovate, fronto-orbital width about half to 60 percent maximum carapace width; anterolateral margin entire with two small, sharp spines at anterolateral corner, convex, as long as or shorter than posterolateral margin; posterolateral margin nearly straight, at approximately 40 degree angle to posterior margin; posterior margin straight, about 47 percent maximum carapace width.
Discussion.—*Euryozius* has a limited distribution in modern oceans, occurring in the Indo-Pacific region. The two fossil species are known from Miocene rocks of southwest Japan (Karasawa, 1993).

Genus PRIABONOCARCINUS Müller and Collins, 1991

Type species.—*Priabonocarcinus gallicus* Müller and Collins, 1991, by original designation.
Diagnosis.—Carapace ovoid, wider than long, L/W about 0.7, widest about half the distance posteriorly on carapace; dorsal surface smooth; front downturned, blunt triangular in shape, axially notched; orbits circular, rimmed, entire, fronto-orbital width about half maximum carapace width; anterolateral margin nearly entire, with two small projections including one at anterolateral corner, projection at anterolateral corner extending onto dorsal carapace as weak ridge, anterolateral margin terminating about half the distance posteriorly on carapace; posterolateral margin making approximately 35 degree angle with posterior margin, posterior width about 40 percent maximum carapace width.
Discussion.—*Priabonocarcinus* is herein referred to the Pseudoziidae because of its shallow, ovate orbits; smooth carapace; short anterolateral margins, entire or with "rudimentary" spines (Müller and Collins, 1991, p. 78); and high angle of the posterolateral margin to the posterior margin. *Priabonocarcinus* differs from other members of the family by having a distinctly rounded front and a somewhat less broad posterior margin. The genus is monotypic, known only from late Eocene rocks of Hungary.

Genus SANTEEXANTHUS Blow and Manning, 1996

Type species.—*Santeexanthus wardi* Blow and Manning, 1996.
Diagnosis.—Carapace about two-thirds as long as wide, widest about half the distance posteriorly on carapace; smooth; regions not defined. Front appearing to be nearly straight and axially notched, about 30 percent maximum carapace width. Orbits shallow, ovate, rimmed, fronto-orbital width about two-thirds maximum carapace width. Anterolateral margin weakly convex, with two blunt spines at anterolateral corner, terminating about half the distance posteriorly on carapace, last anterolateral spine extends posteriorly on carapace as blunt, short ridge. Posterolateral margin nearly straight, making about a 40 degree angle to posterior margin, which is straight, about one-third carapace width. Branchiocardiac groove moderately incised.
Discussion.—One species is known from middle Eocene rocks of North Carolina (Blow and Manning, 1996). *Santeexanthus* is placed within the Pseudoziidae because of its relatively straight front with a central notch; limited development of regions; shallow, ovate orbits which are weakly rimmed; short, lobate anterolateral margins with two small spines at the anterolateral corner and lobes separated by shallow fissures; and high angle between the posterolateral and posterior margins. The relative proportions of *Santeexanthus* are almost identical to those of *Euryozius*, except that *Santeexanthus* has narrower posterior margins. *Santeexanthus* remains a separate genus because of its punctate dorsal surface, weak ridge that extends posteriorly on the dorsal carapace from the last anterolateral spine, and narrow posterior margin.

Family ZANTHOPSIDAE Via, 1959
Figure 4

Xanthopsinae VIA, 1959, p. 50. McCOY (1849) erected the genus *Zanthopsis*, the nominal genus for the family. Subsequent authors, including BELL (1858), GLAESSNER (1929), and VIA (1959), misspelled the genus name as *Xanthopsis*; thus, VIA (1959) erected the subfamily "Xanthopsinae." GLAESSNER (1969, p. R522) considered the latter spelling with an "X" to be a "nomen vanum." Thus, the spelling of the family name is corrected to reflect the original spelling of the nominal genus.

Included genera.—*Zanthopsis* McCoy, 1849; *Harpactocarcinus* A. Milne Edwards, 1862; *Harpactoxanthopsis* Via, 1959; *Martinetta* Blow and Manning, 1997; *Neozanthopsis* new genus.
Diagnosis.—Carapace wider than long, length about 81 percent maximum width, widest about one half to two thirds the distance posteriorly on carapace; may be ornamented with large nodes, sometimes arranged on raised ridges; regions moderately to poorly defined; surface may be punctate; grooves generally very shallow except branchiocardiac. Front quadrilobed including inner orbital spines, frontal width about 27 percent maximum width. Orbits circular or rectangular, entire, rimmed, directed forward, fronto-orbital width about half maximum carapace width. Anterolateral margin with three to five blunt lobes or with numerous small spines; last spine may extend onto dorsal carapace as long, low ridge, usually about as long as or slightly longer than posterolateral margin; convex, often tightly curved posteriorly. Posterolateral margin sinuous or weakly convex; posterior margin nearly straight, 30–40 percent maximum carapace width.
Carapace regions weakly inflated or not defined; branchial regions may have rows of large tubercles, sometimes arranged on rows. Branchiocardiac groove defining lateral margins of urogastric region. Chelae large, subequal or weakly heterochelous, outer surface smooth or with large nodes, upper and lower margins with numerous small spines; chelipeds much longer than walking legs. Ischium of major cheliped articulating with coxa. Sternum narrow, broadest anteriorly at position of fourth sternite, narrowing distally, merus not fused completely to ischium. Male abdominal somites exhibiting fusion of at least somites 4 and 5 and probably 3–5.
Discussion.—Via (1959) erected the Xanthopsinae to embrace

Zanthopsis and *Harpactocarcinus* as well as his new *Harpactoxanthopsis*. He suggested at that time that the subfamily was intermediate in position between the Carpiliinae and the Menippinae (=Eriphiidae) (Via, 1959, p. 51). Since that time, both the Carpiliidae and the Eriphiidae (=Menippidae) have been elevated to family status (Wright and Collins, 1972; Guinot, 1978; Karasawa, 1993; Ng, 1998; Schweitzer et al., 2000; Schweitzer, 2000; Martin and Davis, 2001). *Zanthopsis, Harpactoxanthopsis,* and *Harpactocarcinus* have been recognized by several authors as belonging together as a discrete unit (Via, 1959; Guinot, 1968a, 1978; Glaessner, 1969). Glaessner (1969) suggested that *Tumidocarcinus* should be included in that group; however, that genus is markedly different and belongs within the Pilumnidae. Via (1959) suggested erecting a new subfamily to contain the three genera, a view which Glaessner (1969) supported but did not formalize. *Martinetta* was originally compared closely to *Harpactocarcinus*, to which it is clearly related. Because the members of the Zanthopsinae as defined by Via (1959), plus *Martinetta* and the new genus *Neozanthopsis*, comprise a distinctive unit that cannot be embraced by any other brachyuran family, the subfamily is herein raised to family status.

The Zanthopsidae bear some resemblance to both the Carpiliidae and the Eriphiidae; however, neither family can embrace the members of the Zanthopsidae. Affinities between the carpiliids *Palaeocarpilius* and *Harpactocarcinus, Harpactoxanthopsis,* and *Zanthopsis* have been based upon their four-lobed front, convex anterolateral margins, convex carapace, and relatively smooth carapace (except *Zanthopsis*) (Guinot, 1968a, 1978; Schweitzer et al., 2000).

One of the primary features separating the Carpiliidae from the fossil genera now placed within the Zanthopsidae is the fusion of the basis-ischium and merus, within the Carpiliidae (Guinot, 1968a, 1968b). This arrangement has been observed in fossil forms now included within the Carpiliidae, including *Palaeocarpilius* and *Ocalina* (Guinot, 1968a, 1968b) and *Proxicarpilius* sp. However, examination of specimens of *Zanthopsis leachi* indicates that the merus and basis-ischium are not fused. Further, in authentic carpiliids, the coxa of the major cheliped articulates directly with the merus (Guinot, 1968a, 1968b), a configuration not present in specimens of *Zanthopsis leachi*. Typical carpiliids have a narrow, rectangular abdomen, with subparallel lateral margins (Guinot, 1968a). Members of the Zanthopsidae in which the sternum could be observed have a sternum that is broadest anteriorly at the position of the fourth sternite and narrows distally. Thus, the features of the pereiopods and sternum, which have been considered by biologists to be phylogenetically important at the family level, clearly exclude the Zanthopsidae from the Carpiliidae.

The Eriphiidae differs from the Zanthopsidae in having all somites of the male abdomen free. Members of the Zanthopsidae have at least some degree of fusion of the somites of the male abdomen. In addition, eriphiids have moderately to well-developed carapace regions and relatively deep grooves, which the members of the Zanthopsidae lack.

As first suggested by Via (1959) and as reiterated by Guinot (1968a, 1968b), the Zanthopsidae is closely related to both the Carpiliidae and the Eriphiidae. Wright and Collins (1972) suggested that *Caloxanthus* A. Milne Edwards, 1864, was ancestral to the Carpiliidae; however, examination of type material will be necessary to test this hypothesis. Typical Carpiliidae as defined here do not appear until the Eocene, and the fossil record of the Eriphiidae probably extends into the Eocene (Remy, 1960). It appears that these three families diverged from one another sometime in the Paleocene, based upon occurrences of the Zanthopsidae, but the timing of the divergence of these families must await further work on xanthoid fossils and Paleocene occurrences.

The Zanthopsidae appeared first during the Paleocene, as *Zanthopsis* has been reported from Paleocene-Miocene rocks. The Paleocene occurrences are known from epicontinental European localities, and subsequent Eocene occurrences are in epicontinental and coastal Europe and North America. The other included genera, *Harpactocarcinus, Harpactoxanthopsis, Martinetta,* and *Neozanthopsis* new genus, are known only from Eocene rocks.

Genus ZANTHOPSIS McCoy, 1849
Figure 4.1, 4.3, 4.6

Cycloxanthus H. Milne Edwards in D'ARCHIAC, 1850.
Xanthopsis BELL, 1858, p. 10 (*nomen vanum*).

Type species.—*Cancer leachii* Desmarest, 1822.
Included species.—*Zanthopsis bispinosa* Bell, 1858; *Z. dufourii* (H. Milne Edwards in d'Archiac, 1850), as *Cycloxanthus; Z. errans* Woods, 1922; *Z. hendersonianus* Rathbun, 1926; *Z. jacobi* Van Straelen, 1925; *Z. leachii* (Desmarest, 1822); *Zanthopsis milleri* Roberts, 1955; *Z. multispinosa* Remy, 1960; *Z. nodosa* McCoy, 1849; *Zanthopsis peytoni* Stenzel, 1934; *Z. unispinosa* McCoy, 1849.

Diagnosis.—Carapace length about 80 percent maximum width, ovate to nearly circular in shape; regions poorly to moderately defined; branchiocardiac groove well-developed; front with four blunt spines including inner orbital spines; orbits circular, entire, fronto-orbital width about half maximum carapace width; anterolateral margin with four or five blunt spines including outer-orbital spine; branchial regions with discrete swellings arranged in rows, rows may be situated on raised ridges; other regions not ornamented with swellings; "antennulae infolded obliquely; chelae massive, heterochelous, propodus tuberculate dorsally and exteriorly; male abdominal somites 3–5 fused" (Glaessner, 1969, p. R522).

Description.—Carapace not much wider than long, L/W approximately 0.83, ranging from 0.76–0.94; ovate to nearly circular; widest about two-thirds distance posteriorly on carapace; regions moderately to poorly defined; grooves shallow except branchiocardiac which is well-developed. Front with four blunt spines including inner orbital spines, about 28 percent maximum carapace width, ranging from 24–34 percent; not projected much beyond orbits. Orbits circular, entire, directed forward, fronto-orbital width about 53 percent maximum carapace width, ranging from 46–59 percent. Anterolateral margin convex; with four or five small, blunt spines including outer orbital spine, tightly curved toward anterolateral corner; posterolateral margin entire, relatively straight to very weakly convex. Posterior margin entire, nearly straight, about 40 percent maximum carapace width.

Protogastric regions inflated, unornamented; mesogastric region inflated distally; metagastric region well defined, inflated; urogastric region inflated; cardiac region inflated, spherical or bilobed in shape. Branchiocardiac groove deep. Hepatic region flattened, unornamented. Branchial region with rows of large, inflated, discrete swellings, arranged in rows, rows parallel or slightly oblique to axis, nodes may be situated on raised ridge; rows positioned adjacent to axis (inner-most) with two or three discrete swellings, posterior-most swelling often linear; rows positioned adjacent to lateral margins (outer-most) usually with two discrete, spherical swellings.

Discussion.—For nearly a century, decapod workers commonly placed nodose, xanthoid crabs, often those with well-developed dorsal carapace regions, into *Zanthopsis*. Consequently, the genus eventually contained species of quite different morphologies. Schweitzer et al. (2000) discussed some of these problems and suggested the referral of several species of *Zanthopsis* to other genera. *Zanthopsis* is herein restricted to only those species conforming to the diagnosis and description presented here, which

TABLE *1*—Species originally assigned to *Zanthopsis* and their current generic placement.

Original name	Current generic designation	Relevant reference
Zanthopsis africana Remy and Tessier, 1954	*Remia* new genus	this paper
Zanthopsis bartholomaensis Rathbun, 1919	*Eriosachila* Blow and Manning, 1996	Schweitzer, Feldmann et al., 2002
Zanthopsis bittneri Lörenthey, 1898	*Harpactoxanthopsis* Via, 1959	this paper
Zanthopsis brasiliana Maury, 1930	*Palaeoxanthopsis* Beurlen, 1958	Beurlen, 1958
Zanthopsis bruckmanni von Meyer, 1862	*Neozanthopsis* new genus	this paper
Zanthopsis carolinensis Rathbun, 1935	*Neozanthopsis* new genus	this paper
Z. lutugini Likharev, 1917	*Harpactoxanthopsis*	Via, 1969
Zanthopsis rathbunae sensu Kooser and Orr, 1973 (junior synonym of *Z. rathbunae* Maury, 1930)	*Eriosachila orri* (nomen novum was created)	Schweitzer and Feldmann, 2000a
Zanthopsis rathbunae Maury, 1930	*Eriosachila*	Schweitzer and Feldmann, 2000a
Zanthopsis sonthofenensis von Meyer, 1862	*Neozanthopsis* new genus	this paper
Zanthopsis sternbergi Rathbun, 1926	*Xandaros* Bishop, 1988	Bishop, 1988
Zanthopsis terryi Rathbun, 1937	*Eriosachila*	Blow and Manning, 1996
Zanthopsis tridentata von Meyer, 1862	*Neozanthopsis* new genus	this paper
Zanthopsis vulgaris Rathbun, 1926	*Pulalius* Schweitzer et al., 2000	Schweitzer et al., 2000

are based upon the type and very similar species. Study of specimens of *Z. leachii*, *Z. unispinosa*, *Z. dufourii*, and *Z. nodosa* indicates that there is a gradation in morphologies among these taxa, suggesting that they may be synonymous.

Several species originally assigned to *Zanthopsis* have been formally reassigned to other genera herein or by other authors (Table 1). Discussion of reassignments made in other papers will not be reiterated here. *Zanthopsis africana* Remy and Tessier, 1954, is herein placed in the new genus *Remia*, as discussed below. *Zanthopsis bittneri* Lörenthey, 1898, is placed within *Harpactoxanthopsis*, because of the lack of nodes on the dorsal carapace which are diagnostic for *Zanthopsis*. *Zanthopsis bruckmanni* von Meyer, 1862; *Z. carolinensis* Rathbun, 1935; *Z. sonthofenensis* von Meyer, 1862; and *Z. tridentata* von Meyer, 1862, are referred to the new genus *Neozanthopsis* discussed below, due to their lack of swellings on the carapace and possession of a weak ridge extending from the anterolateral margin onto the carapace.

As defined here, *Zanthopsis* exhibits a modified Tethyan distribution. The genus was not restricted to low latitude areas, as are many Tethyan taxa, but based upon its distribution pattern, it appears to have dispersed via the Tethyan Seaway. The oldest occurrences appear to be Paleocene (Van Straelen, 1925; Glaessner, 1969), and *Z. leachii* and *Z. unispinosa* are known from the lower Lutetian (middle Eocene) of northern Europe. Species are reported from middle Eocene rocks of northern Europe (*Z. nodosa*, *Z. dufourii*, *Z. bispinosa*) and from Eocene rocks of Texas (*Z. peytoni*); Peru (*Z. errans*); the Atlantic coast of the United States (*Z. milleri*); the Middle East (*Z. nodosa*) (Withers, 1932); and California (*Z. hendersonianus*). *Zanthopsis hendersonianus* is also known from Oligocene rocks of Oregon. The genus appears to have arisen in the northern Atlantic and Tethyan region and subsequently dispersed both east and west, perhaps via the Tethys, into the Middle East and the Americas respectively. The Central American Seaway was open during this time (Bice et al., 2000); facilitating dispersal to the west coast of North America and to Peru.

Genus HARPACTOCARCINUS A. Milne Edwards, 1862
Figure 4.8

Type species.—*Cancer punctulatus* Desmarest, 1822.

Included species.—*Harpactocarcinus achalzicus* Bittner, 1882; *H. jacquoti* A. Milne Edwards, 1865; *H. ovalis* A. Milne Edwards, 1862; *H. punctulatus* (Desmarest, 1822) (=*H. macrodactylus* A. Milne Edwards, 1862); *H. rotundatus* A. Milne Edwards, 1862.

Diagnosis.—Carapace wider than long, length approximately 80 percent maximum width; carapace regions poorly to not defined, surface punctate; branchiocardiac groove well defined along lateral margins of urogastric region; front about one-quarter maximum carapace width, with four sharp spines including inner orbital spine; orbits shallow, circular or rectangular in shape, fronto-orbital width about half maximum carapace width; anterolateral margin with between 8 and 15 sharp spines.

Description.—Carapace wider than long, length approximately 80 percent maximum width, ranging from 0.74–0.85 in specimens measured; ovate; punctate; widest about two-thirds the distance posteriorly on carapace; regions poorly defined; grooves absent to poorly defined except for branchiocardiac groove, which is well defined along lateral margins of urogastric and cardiac regions; longitudinally markedly vaulted, especially posteriorly, weakly vaulted transversely. Front with four sharp spines including inner orbital spines, frontal width about one-quarter maximum carapace width, 0.23–0.26 in specimens measured; orbits circular or rectangular, directed forward, shallow, rimmed; fronto-orbital width about half maximum carapace width, 0.44–0.55 in specimens measured. Anterolateral margins with numerous triangular spines, ranging in number from 8–15; posterolateral margin entire, slightly thickened anteriorly; posterior margin narrow, about as wide as front, nearly straight, about 30 percent maximum carapace width.

Discussion.—*Harpactocarcinus* is herein restricted to those species with a punctate carapace, poorly developed regions, anterolateral margins with numerous sharp spines, and a relatively narrow posterior margin. This diagnosis excludes several species that have previously been referred to the genus (Table 2). Via (1959) previously erected *Harpactoxanthopsis*, for *Harpactocarcinus quadrilobatus* Desmarest, 1822, discussed below. Glaessner (1960) erected *Tumidocarcinus* to contain *Harpactocarcinus tumidus* Woodward, 1876. Herein, *Harpactocarcinus rathbunae* and *Harpactocarcinus souverbiei* are placed within *Neozanthopsis* new genus and *Harpactoxanthopsis* respectively.

Harpactocarcinus is easily distinguished from *Zanthopsis* because the former possesses between eight and 15 spines on the anterolateral margin; species of *Zanthopsis* only possess four. In addition, species of *Zanthopsis* have well-developed swellings on the dorsal carapace, while species of *Harpactocarcinus* have a smooth dorsal carapace. *Harpactocarcinus* is most similar to *Harpactoxanthopsis* but differs from that genus in its possession of eight to15 spines on the anterolateral margin. *Harpactocarcinus* differs from *Neozanthopsis*, because *Neozanthopsis* possess a

TABLE 2—Species originally assigned to *Harpactocarcinus* and their current generic designation.

Original name	Current generic designation	Relevant reference
Harpactocarcinus mississippiensis Rathbun, 1935	*Palaeocarpilius* A. Milne Edwards, 1862	this paper
Harpactocarcinus quadrilobatus Desmarest, 1822	*Harpactoxanthopsis* Via, 1959	Via, 1959
Harpactocarcinus rathbunae Stenzel, 1934	*Neozanthopsis* new genus	this paper
Harpactocarcinus souverbiei A Milne Edwards, 1862	*Harpactoxanthopsis* Via, 1959	this paper
Harpactocarcinus tumidus Woodward, 1876	*Tumidocarcinus* Glaessner, 1960	Glaessner, 1960
Harpactocarcinus valrovinensis de Gregorio, 1895	*Palaeocarpilius*	this paper

well-developed ridge extending from the last anterolateral spine onto the dorsal carapace. *Harpactocarcinus* lacks this ridge.

Harpactocarcinus as now defined embraces only Eocene taxa known from Europe. The genus evolved and was apparently endemic to that region, unlike *Zanthopsis* which was widely dispersed during the Eocene.

Genus HARPACTOXANTHOPSIS Via, 1959
Figure 4.4, 4.7

Type species.—*Cancer quadrilobatus* Desmarest, 1822 (=*Xanthopsis kressenbergensis nomen nudum* von Meyer, 1846; see Glaessner, 1929).

Other species.—*Harpactoxanthopsis bittneri* (Lőrenthey, 1898), as *Zanthopsis*; *H. lutugini* (Likharev, 1917), as *Xanthopsis*; *H. souverbiei* (A. Milne Edwards, 1862), as *Harpactocarcinus*; *H. villaltae* Via, 1959.

Diagnosis.—Carapace about 80 percent as long as wide, ovate; regions poorly defined; branchiocardiac groove usually well-defined along lateral margins of urogastric region. Front with four blunt spines including inner orbital spine; anterolateral margin convex, with five spines excluding outer orbital spine.

Description.—Carapace length 74–86 percent carapace width; ovate. Front with four blunt spines including inner orbital spines, 24–27 percent maximum carapace width; not projected beyond orbits. Orbits circular, entire, weakly rimmed, directed forward; fronto-orbital width 44–51 percent maximum carapace width. Anterolateral margins convex, usually with four anterolateral spines excluding outer orbital spine; posterolateral margin entire, straight, weakly concave, or weakly convex. Posterior margin entire, narrow, nearly straight, posterior margins about 30 percent maximum carapace width.

Carapace regions poorly defined, punctate; branchiocardiac groove usually well-defined along lateral margins of urogastric region. Chelae subequal, massive.

Discussion.—Via (1959) erected *Harpactoxanthopsis* to embrace species with not more than four anterolateral spines, reduced development of carapace regions, and a front with four spines (p. 54). He included *Cancer quadrilobatus* Desmarest, 1822, and *Xanthopsis kressenbergensis* von Meyer, 1862, as well as a new species, *H. villaltae*. Glaessner (1929) had previously synonymized *X. kressenbergensis* with *Cancer quadrilobatus*, which at that time was referred to *Harpactocarcinus*. That synonymy stands; thus, *X. kressenbergensis* is a junior synonym of *Harpactoxanthopsis quadrilobatus*. Lőenthey (1898) described *Zanthopsis bittneri* from Eocene rocks of Hungary; it cannot be embraced by *Zanthopsis* as defined here. Because *Zanthopsis bittneri* possesses a smooth dorsal carapace, an anterolateral margin with blunt spines, and a front with four spines, it is herein placed within *Harpactoxanthopsis*.

Harpactoxanthopsis is very similar to *Zanthopsis*, but differs in possession of a smooth dorsal carapace. Species of *Zanthopsis* always possess large nodes and sometimes possess inflated ridges on the dorsal carapace. *Harpactoxanthopsis* differs from *Harpactocarcinus* because members of *Harpactocarcinus* have eight to 15 spines on the anterolateral margin.

All of the species now referred to *Harpactoxanthopsis* are known from Eocene rocks of central and northern Europe. *Zanthopsis*, *Harpactocarcinus*, and *Harpactoxanthopsis* are closely related genera; they evolved and dispersed within the same geographic area. However, their distinctive dorsal carapace features allow them to be readily distinguished from one another.

Genus MARTINETTA Blow and Manning, 1997

Type species.—*Martinetta palmeri* Blow and Manning, 1997.

Diagnosis.—Carapace wider than long, length about 70 percent carapace width; front quadrilobed, extending beyond orbits, about one quarter maximum width; orbits small for family, appearing to be circular, rimmed, fronto-orbital width about 34 percent maximum carapace width; anterolateral margin long, with about 15 spines, last spine longest; posterior width narrow; protogastric and mesogastric regions inflated; dorsal surface punctate (after Blow and Manning, 1997, p. 172–173).

Discussion.—Blow and Manning (1997) erected the genus to accommodate new material recovered from the Eocene Santee Limestone of South Carolina. *Martinetta* may be differentiated from other genera within the family except *Harpactocarcinus* by its possession of about 15 anterolateral spines. *Martinetta* is distinguishable from *Harpactocarcinus*, to which it is quite similar, by several means. Blow and Manning (1997, p. 172) reported that the orbits were "v-shaped," small, and weakly rimmed. However, the rim on *Martinetta* appears to be just as well developed, if not better developed, than species of *Harpactocarcinus*. The orbits are indeed smaller than those of *Harpactocarcinus* and are much more closely spaced. The front of *Martinetta* is produced well beyond the orbits, a condition not seen in *Harpactocarcinus*. In *Martinetta*, the anterolateral margin is longer and less convex than that of *Harpactocarcinus*. Blow and Manning (1997, p. 172) also noted that the major chela in the two genera differed and that *Martinetta* has inflated protogastric regions which *Harpactocarcinus* lacks. Thus, *Martinetta* is retained as a monotypic genus. *Martinetta* probably arose from *Harpactocarcinus*-like stock, which could have easily reached the east coast of North America from European *Harpactocarcinus* populations.

Genus NEOZANTHOPSIS new genus
Figure 4.2, 4.5

Type species.—*Harpactocarcinus americanus* Rathbun, 1928, by original designation.

Other species.—*Neozanthopsis bruckmanni* (von Meyer, 1862), as *Zanthopsis*; *N. carolinensis* (Rathbun, 1935), as *Zanthopsis*; *N. rathbunae* (Stenzel, 1934), as *Harpactocarcinus*; *N. sonthofenensis* (von Meyer, 1862), as *Zanthopsis*; *N. tridentata* (von Meyer, 1862), as *Zanthopsis*.

Diagnosis.—Carapace length about 81 percent maximum width; front with four short, blunt spines including inner orbital spine, about 30 percent maximum carapace width; fronto-orbital width about 52 percent maximum carapace width; anterolateral margin entire or with three or four blunt spines; last anterolateral spine extending onto carapace as oblique ridge. Carapace regions developed as broad swellings.

Description.—Carapace wider than long, length 77–86 percent maximum width; ovate; widest about two-thirds distance posteriorly on carapace; regions moderately defined as broad swellings, grooves not well-developed. Front with four short, blunt spines including inner orbital spines; 25–33 percent maximum carapace width; front not projected beyond orbits. Orbits circular, entire, rimmed, may be very shallow, directed forward; fronto-orbital width about 46–60 percent maximum carapace width. Anterolateral margin convex, entire or with three to four blunt spines excluding outer orbital spine; spine usually positioned posteriorly, often separated from outer-orbital angle by entire segment. Last spine largest, extends onto dorsal carapace as well-developed oblique ridge, ridge oriented obliquely and posteriorly from anterolateral margin, terminating about half the distance across the branchial region, may terminate in round tubercle. Posterolateral margin weakly convex or nearly straight. Posterior margin straight, about 31 percent maximum carapace width.

Regions moderately developed as broad swellings. Protogastric region composed of one or two broad swellings; mesogastric region weakly inflated posteriorly, anterior projection flattened; urogastric region narrow, weakly inflated; cardiac region elongate, weakly inflated. Hepatic region small, weakly inflated. Epibranchial region inflated anterior to oblique ridge, comprised of two swellings, one adjacent to anterolateral margin, other a discrete swelling on either side of urogastric region. Mesobranchial and metabranchial regions not differentiated, weakly inflated.

Chelae appearing to be heterochelous, stout, with relatively smooth outer surfaces.

Etymology.—The genus name is a combination of the generic name *Zanthopsis*, upon which the family name is based, and *neo*, meaning "new," in reference to the type species of the genus which is found in the "New World," North America.

Discussion.—All of the species here referred to *Neozanthopsis* were originally assigned to *Zanthopsis*, with one exception (see above). All of these taxa exhibit an oblique ridge extending from the last anterolateral spine, regions defined as broad swellings, weak carapace grooves, and an anterolateral margin with no spines or blunt, small spines; all are features unique to the new genus. These features separate *Neozanthopsis* from the other genera discussed herein and in fact all other decapod genera.

Neozanthopsis exhibits a distribution similar to that of *Zanthopsis*; occurrences are known from the Eocene of central Europe and from the Atlantic and Gulf Coastal Plain of North America. It is not possible to determine where the genus originated, as ages for the fossils are not sufficiently precise.

Family PALAEOXANTHOPSIDAE new family
Figures 5, 6

Type genus.—*Palaeoxanthopsis* Beurlen, 1958, by original designation (*non Palaeoxanthops* Karasawa, 1993).

Other genera.—*Paraverrucoides* new genus; *Remia* new genus; *Verrucoides* Vega, Cosma et al., 2001.

Diagnosis.—Carapace length about three-quarters carapace width, widest about two-thirds the distance posteriorly on carapace; deep, v-shaped groove separates gastric regions from hepatic and branchial regions; regions often with large, spherical swellings; anterolateral margin long, with four or five spines, last spine longest, directed laterally or posterolaterally.

Description.—Carapace wider than long, length about three-quarters carapace width, widest about two-thirds the distance posteriorly on carapace; regions defined by grooves; deep, v-shaped groove separates gastric regions from hepatic and branchial regions; regions often with large, spherical swellings. Front about 20 percent maximum carapace width, quadrilobed, sometimes

with medial two lobes projecting well beyond orbits. Fronto-orbital width about half maximum carapace width; orbits rectangular, with two fissures or faint sutures, sometimes rimmed, outer orbital angle projected as a triangular spine. Anterolateral margin relatively long, straight to weakly convex; with a straight segment followed by three spines or with four spines not including outer orbital spine; spines sharp, triangular, separated from one another by notches or fissures; last spine longest, directed laterally or posterolaterally; posterolateral margin convex; posterior margin concave, narrow, about one-quarter carapace width.

Epigastric regions weakly inflated. Protogastric regions inflated, sometimes with distinct, large tubercles; mesogastric region with long anterior process, widened posteriorly, often with large swelling posteriorly; urogastric region depressed, ill-defined; cardiac region inflated, sometimes with a small tubercle; intestinal region depressed, sometimes markedly so. Hepatic region strongly inflated or weakly inflated with distinct tubercle. Branchial regions with two large or one large and one small swelling at same level as last anterolateral spine; one or two large swellings situated posteriorly on branchial region.

Discussion.—Beurlen (1958) erected *Palaeoxanthopsis* to embrace *Zanthopsis cretacea* Rathbun, 1902, which as he rightly observed, differs markedly from authentic *Zanthopsis*. *Palaeoxanthopsis cretacea* possesses well-developed carapace regions and grooves, rectangular orbits with two fissures, an extremely long last anterolateral spine, and a completely different arrangement of carapace nodes than authentic *Zanthopsis*; thus, Beurlen's (1958) new genus was warranted. *Palaeoxanthopsis* is markedly different from all other known xanthoid crabs, and in fact, crabs of any family. The ovate-hexagonal shape of the carapace, quadrilobed front, spined anterolateral margins, and the development of carapace regions suggest an alliance with the Xanthoidea; however, no xanthoid families can accommodate it. Members of the Carpiliidae have generally smooth carapaces with regions that are ill-defined or not defined; entire, circular orbits; and shallow or non-existent grooves, which cannot embrace *Palaeoxanthopsis*. Members of the Trapeziidae Miers, 1886, have very smooth carapaces that are about as long as wide, which cannot accommodate *Palaeoxanthopsis*. In the Xanthidae and Eriphiidae, the dorsal carapace has better defined regions and usually quantitatively more regions than seen in *Palaeoxanthopsis*; in addition, the carapace ornamentation and the configuration of the last anterolateral spine is unlike any other xanthid or eriphiid. The Hexapodidae have very small, smooth, rectangular carapaces, thus excluding *Palaeoxanthopsis*. Within the Goneplacidae, taxa are characterized by broad, relatively straight fronts and flattened carapaces, neither of which can accomodate *Palaeoxanthopsis*.

In 1935, Rathbun described *Xanthilites alabamensis* from Eocene rocks of Alabama. That species differs markedly from authentic *Xanthilites* because it possesses large, spherical nodes on the dorsal carapace, an extremely long last anterolateral spine, a short hepatic and protogastric region, and a different overall pattern of development of regions than seen in authentic *Xanthilites*; thus, *X. alabamensis* must be removed from that genus. In fact, no known genus can accommodate *X. alabamensis*, so a new genus has been erected for it herein, *Paraverrucoides*. This new genus possesses features that are remarkably similar to those of *Palaeoxanthopsis*, necessitating their placement within the same family. Vega, Cosma et al. (2001) described *Verrucoides* to embrace a Paleocene form from Greenland (Collins and Rasmussen, 1992) and an Eocene species from México. That species is also remarkably similar to *Palaeoxanthopsis*. Thus, *Palaeoxanthopsis*, *Paraverrucoides*, and *Verrucoides* form a distinctive unit embraced by the new family.

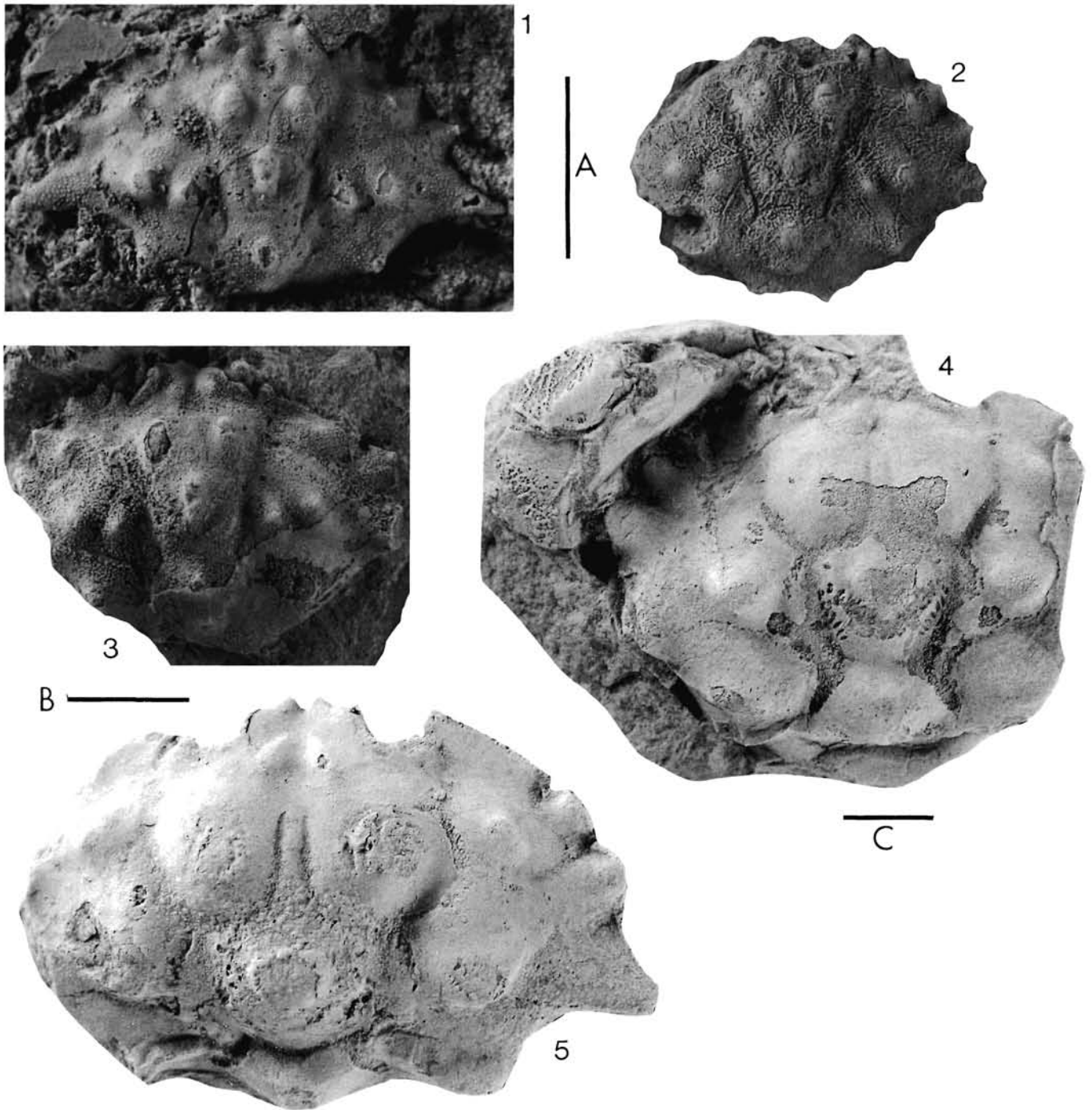Remy and Tessier (1954) described *Xanthopsis africana* from

FIGURE 5—Representatives of the Palaeozanthopsidae new family. *1, Verrucoides stenohedra* Vega, Cosma et al., 2001, paratype IHNCH 3470; *2, V. stenohedra*, paratype IHNCH 3472; *3, V. stenohedra*, holotype IHNCH 3469; *4, Palaeoxanthopsis cretacea* (Rathbun, 1902), USNM 73709a; *5,* dorsal carapace, *P. cretacea*, USNM 73709b. Scale bars equal to 1 cm. Scale bar A for *1, 2*; scale bar B for *3, 5*; scale bar C for *4*.

Maastrichtian rocks of Sénégal. That species cannot be accommodated within *Zanthopsis* as discussed above. The new genus erected for that species, *Remia*, displays all of the diagnostic features of the new family and is thus placed within it. *Remia* differs somewhat from other members of the family because it is not much wider than long, almost equidimensional, and the anterolateral margin is slightly shorter in *Remia* than in other members of the family. However, its possession of key characters of the

front, orbits, anterolateral margins, and dorsal carapace ornamentation indicate its placement in the Palaeoxanthopsidae.

The Palaeoxanthopsidae ranges from the Cretaceous (Maastrichtian) to the Eocene. *Palaeoxanthopsis* is known from Maastrichtian rocks of Brazil and México (Rathbun, 1902; Maury, 1930; Beurlen, 1958; Vega, Feldmann et al., 2001) and the sole species of *Remia* was collected from Maastrichtian rocks of Sénégal (Remy and Tessier, 1954). *Verrucoides* is known from the
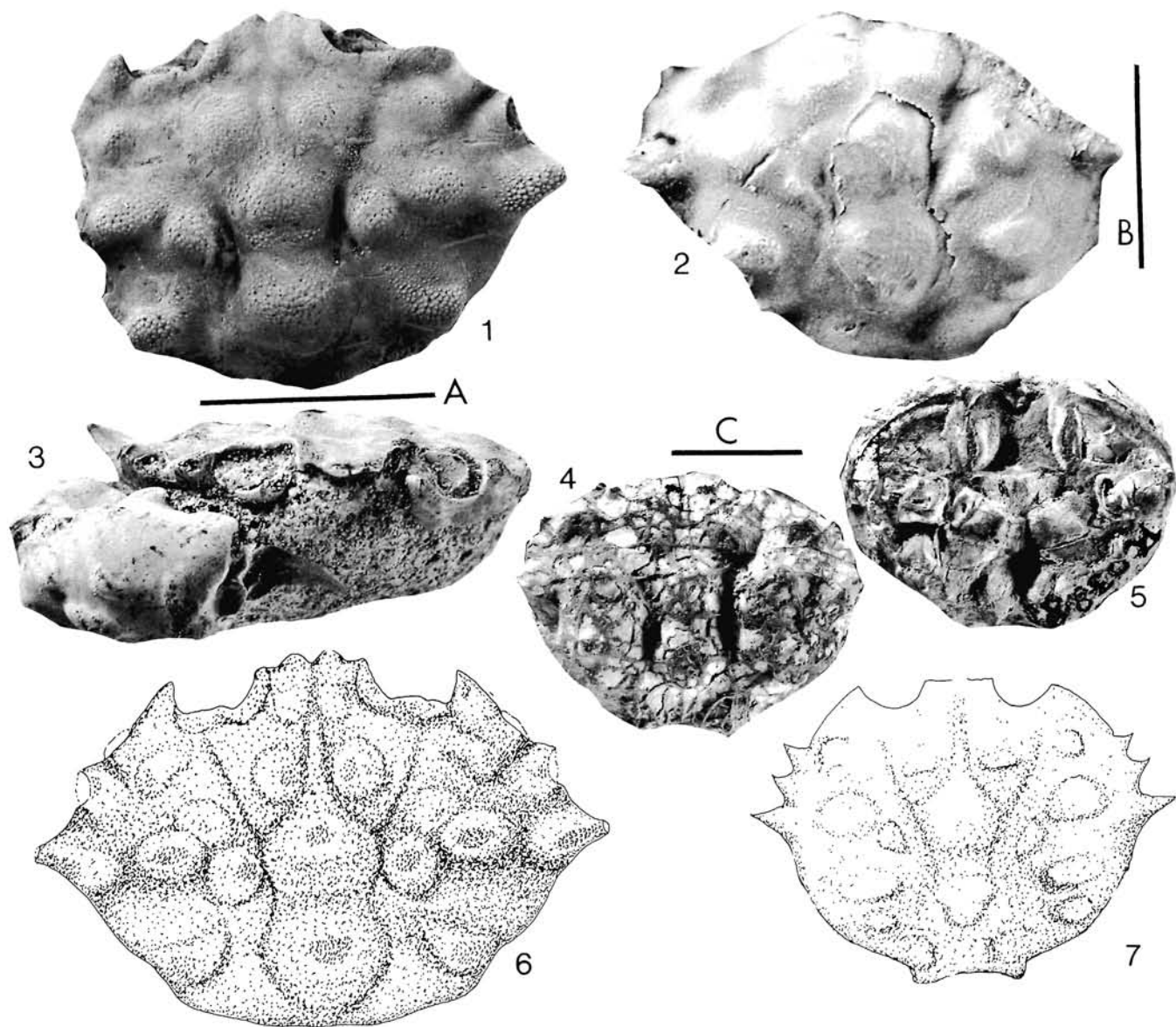
FIGURE 6—Representatives of the Palaeozanthopsidae new family. *1, Paraverrucoides alabamensis* new comb. (Rathbun, 1935), dorsal carapace, USNM 371708; *2, Remia africana* new comb. (Remy and Tessier, 1954), R.03332, epoxy cast of external mold; *3, Paraverrucoides alabamensis* new comb., anterior view showing orbits and upturned last anterolateral spine, USNM 371708; *4, R. africana* new comb., holotype, R.03885, dorsal carapace with mud-cracking, photograph provided by MNHN, Paris; *5, R. africana*, new comb., holotype, R.03885, ventral surface, photograph provided by MNHN, Paris; *6*, reconstruction of *Paraverrucoides alabamensis*; *7*, reconstruction of *Remia africana*, front, orbits and anterior-most anterolateral margins conjectural. Scale bars equal to 1 cm. Scale bar A for 1, 3; scale bar B for 2; scale bar C for 4, 5.

Paleocene of Greenland (Collins and Rasmussen, 1992) and the Eocene of southeastern México (Vega, Cosma et al., 2001). *Paraverrucoides* is known only from the Eocene of the Gulf Coastal Plain of North America. The family appears to have evolved in the relatively narrow central Atlantic area during the Maastrichtian and subsequently dispersed northward to México and the Gulf Coast and to Greenland, either following the continental shelf or via ocean surface currents. The family appears to follow a pattern of evolution seen for many decapod families, that of appearance in the Cretaceous, with subsequent extinction. In this case, the group appears to have experienced a radiation during the Paleocene and Eocene subsequent to appearance in the Cretaceous, and extinction by the end of the Eocene, a pattern that is under investigation by the author.

Genus PALAEOXANTHOPSIS Beurlen, 1958
Figure 5.4, 5.5

Parazanthopsis VEGA, FELDMANN, GARCÍA-BARRERA, FILKORN, PIMENTEL, and AVENDAÑO, 2001, p. 323, fig. 4.

Type species.—*Xanthopsis cretacea* Rathbun, 1902, by original designation.

Other species.—*Palaeoxanthopsis meyapaquensis* (Vega, Feldmann, García-Barrera, Filkorn, Pimentel, and Avendaño, 2001), as *Paraxanthopsis*.

Diagnosis.—Carapace wider than long, about three-quarters as long as wide, widest at position of last anterolateral spine, about

two-thirds the distance posteriorly on carapace; regions well-defined, inflated, often with large swellings; highly vaulted longitudinally and moderately vaulted transversely. Front projected beyond orbits, triangular, axially notched, with spines on either side of notch; inner orbital spine small, blunt; frontal width about 20 percent maximum carapace width. Orbits square, directed forward and weakly axially, with two fissures, outer-orbital spine triangular, projected weakly axially, fronto-orbital width about half maximum carapace width. Anterolateral margins long, convex; with straight segment followed by three spines; first two spines short, triangular, directed anterolaterally; last spine long, stout, attenuated, directed posterolaterally. Posterolateral margins short, sinuous, convex. Posterior margin unknown.

Epigastric regions square, weakly inflated; protogastric regions long, inflated posteriorly; mesogastric region with long anterior process, with large spherical swelling posteriorly; urogastric region narrow, depressed; cardiac region with large central swelling; intestinal region poorly defined, depressed well below level of cardiac region. Hepatic region with large central swelling; epibranchial region arcuate, with very large, high central swelling; remainder of branchial region undifferentiated, with two transverse ridges, the anterior-most with a central triangular swelling directed posteriorly.

Discussion.—Schweitzer, Feldmann et al. (2002) synonymized *Parazanthopsis* with *Palaeoxanthopsis*; that discussion need not be repeated here. The type species is known from Maastrichtian rocks of Brazil, and *P. meyapaquensis* has been reported from Maastrichtian rocks of Chiapas, México.

Genus PARAVERRUCOIDES new genus
Fig. 6.1, 6.3, 6.6

Type species.—*Xanthilites alabamensis* Rathbun, 1935, by original designation.

Diagnosis.—Carapace wider than long, length about 70 percent maximum width, widest at position of last anterolateral spine about half the distance posteriorly on carapace. Regions moderately defined by grooves, ornamented with large swellings. Front quadrilobed, about 20 percent maximum carapace width; orbits rimmed, with two entirely sutured fissures; anterolateral margin with four spines including outer orbital spine, last spine longest, directed laterally. Epibranchial region composed of base of last anterolateral spine, two large swellings, and one small swelling. Branchial regions with spinelike swelling.

Description.—Carapace wider than long, length about 70 percent maximum width, widest at position of last anterolateral spine about half the distance posteriorly on carapace. Regions moderately defined by grooves; most with large, granular swellings. Moderately vaulted longitudinally and transversely, anterolateral margins thin and crispate.

Front lobate; with bilobed central projection and blunt innerorbital spines, thus appearing quadrilobed; projected beyond orbits; about 20 percent maximum carapace width. Orbits rimmed, with completely sutured fissures, lower orbital margin with prominent spine just distal to inner orbital angle, fronto-orbital width about half maximum carapace width. Anterolateral margins with four spines including outer orbital spine; last longest, attenuated distally, directed laterally and vertically. Posterolateral margin sinuous, posterior margin not well known.

Epigastric regions weakly inflated. Protogastric regions with spherical inflation centrally. Mesogastric region with long anterior process; pentagonal posteriorly; inflated posteriorly. Urogastric region depressed. Cardiac region bluntly triangular; inflated. Intestinal region depressed; not well differentiated.

Hepatic regions weakly defined, with central inflation. Epibranchial regions differentiated from remainder of branchial region; composed of base of last anterolateral spine which extends

onto carapace, two large granular swellings, and small, weakly inflated swelling. Remainder of gastric region undifferentiated, with large central inflation directed posterolaterally.

Outer surface of manus with large, blunt, tubercles. Sternum narrow, ovate, widest at position of sternite 5.

Etymology.—The genus name is derived from *Verrucoides* and the Greek "para," meaning near, in reference to the similarity of the new genus to *Verrucoides*.

Discussion.—The above description is based upon the type specimen, USNM 371708, and numerous paratypes in USNM 371699 and 337411. The taxon is unique among brachyurans due to its distinctive dorsal carapace ornamentation. Unfortunately, very few sterna were preserved, so that the description of that aspect of the animal is incomplete.

Genus REMIA new genus

Diagnosis.—As for species.
Description.—As for species.
Etymology.—The name is a patronym honoring Jean-Marcel Remy, who contributed significantly to the knowledge of African fossil decapod crustaceans.

Discussion.—The material assigned to *Xanthopsis africana* cannot be accommodated by *Zanthopsis* as discussed above. Neither can any known genera accommodate it. The new genus is most similar to the three other genera within the Palaeoxanthopsidae, but differs from them in several important ways as discussed above. The degree of development of regions and the ornamentation of the regions is most reminiscent of that of *Verrucoides*; however, *Remia* has two ridge-like tubercles on the branchial region instead of one in addition to the differences listed above. *Remia* is similar to *Palaeoxanthopsis* in possessing two ridge-like tubercles on the branchial regions, but differs from *Palaeoxanthopsis* because *Palaeoxanthopsis* has a huge, posterolaterally directed last anterolateral spine. The last anterolateral spine of *Remia* is much smaller and directed laterally.

Remia africana is the sole species within the genus.

REMIA AFRICANA (Remy and Tessier, 1954)
new combination
Figure 6.2, 6.4, 6.5, 6.7

Xanthopsis africana REMY AND TESSIER, 1954, p. 187, pl. XI, fig. 1.

Diagnosis.—Carapace ovate, about three-quarters as wide as long; grooves deep and broad; regions with discrete, large swellings; last anterolateral spine needle-like, directed laterally; posterior margin narrow, about one-quarter maximum carapace width; intestinal region very broad, depressed.

Description.—Carapace ovate, wider than long, L/W = 0.78, widest at position of last anterolateral spine; regions well defined, some with large, discrete swellings; grooves broad and moderately deep; moderately vaulted longitudinally and weakly vaulted transversely.

Front not well-known, produced weakly beyond orbits, about 20 percent maximum carapace width; orbits shallow, small, directed forward, not well-known, fronto-orbital width about half maximum carapace width. Anterolateral margin appearing to have three spines; margin with convex, entire segment anteriorly which is followed by two small, anterolaterally directed spines; third anterolateral spine longest, stout, circular in cross-section, directed laterally. Posterolateral margin sinuous, convex just posterior to last anterolateral spine, concave at posterolateral corner; posterior margin concave, about one quarter maximum carapace width.

Epigastric regions weakly inflated, circular. Protogastric regions inflated, widest anteriorly, with transverse linear swelling about three-quarters the distance posteriorly; mesogastric region with

long anterior process, inflated posteriorly; urogastric region depressed, with concave lateral margins; cardiac region inflated anteriorly, triangular with blunt apices, apex directed posteriorly, two small swellings anteriorly and one at posteriormost apex of triangle; intestinal region broad, depressed, extending laterally to posterolateral margin. Branchiocardiac groove well-developed, broad, deep. Hepatic regions with spinose inflation positioned near base of first anterolateral spine. Epibranchial region arcuate, extending from base of last anterolateral spine, arcing anteriorly, terminating at urogastric region, comprised of two distinct swellings, one located just lateral to mesogastric region, second larger and positioned at base of last anterolateral spine. Remainder of branchial region inflated, undifferentiated, with two transverse, linear swellings, anterior-most longest and widest.

Sternum nearly circular, widest at position of sternite 5; sternites 1–3 fused; sternite 4 appearing to be weakly fused to sternite 3, directed anterolaterally; sternite 5 directed laterally; sternite 6 directed posterolaterally; remainder of sternites unknown. Male abdomen narrow. Remainder of ventral surface and appendages unknown.

Measurements.—Measurements (in mm) taken on the holotype, RO3885: width = 26.6; length = 20.7; fronto-orbital width = 13.2; frontal width = 5.9; posterior width = 7.3.

Material examined.—The holotype, RO3885, and a paratype, RO3332, are housed in the Muséum national d'Histoire naturelle, Paris.

Occurrence.—The specimens were collected from Maastrichtian rocks of Sénégal.

Discussion.—The holotype is damaged and lacks details of the front and orbits. Additionally, the dorsal carapace surface appears to have been abraded and much of the dorsal ornamentation is subdued. Further, the holotype specimen itself is cracked over the entire surface; the cracks appear to be from the process of dewatering and drying and look much like mud cracks. The specimens in the paratype lot also are damaged in the frontal and orbital areas; thus, it is nearly impossible to describe the front and orbits of this taxon. The holotype specimen best shows the overall size of the animal, but the paratype specimen yields much more information on the ornamentation and the development of carapace grooves and regions.

Genus VERRUCOIDES Vega, Cosma, Coutiño, Feldmann,
Nyborg, Schweitzer, and Waugh, 2001
Figure 5.1–5.3

Type species.—*Xanthilites verrucoides* Collins and Rasmussen, 1992, by original designation.

Other species.—*Verrucoides stenohedra* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001.

Diagnosis.—Carapace wider than long, length about three quarters maximum width, widest at position of last anterolateral spine, about two-thirds the distance posteriorly on carapace; regions moderately defined; moderately vaulted transversely and strongly vaulted longitudinally. Front about one-quarter maximum carapace width, with four small spines including inner orbital spines, not projected much beyond orbits. Orbits square, directed weakly anterolaterally, with two fissures, outer-orbital spine small, directed forward, fronto-orbital width about half maximum carapace width. Anterolateral margin with four spines excluding outer-orbital spine; first three spines with straight sides and triangular tips, separated by u-shaped fissures; last anterolateral spine long, attenuated, directed posterolaterally. Posterolateral margin nearly straight; posterior margin narrow, concave, with short spines at posterolateral corner.

Epigastric regions small, inflated; protogastric regions with prominent inflated tubercle centrally; mesogastric region ill-defined; metagastric region with ovate tubercle centrally; urogastric

region depressed; cardiac region with small, central tubercle; intestinal region narrow, depressed. Hepatic regions with small tubercles near anterolateral margin; branchial regions not differentiated; two spherical tubercles anteriorly; spiniform tubercle posteriorly and near posterolateral margin.

Discussion.—The genus is known from Paleocene rocks of Greenland (Collins and Rasmussen, 1992) and Eocene rocks of Chiapas, México (Vega, Cosma et al., 2001).

BIOLOGICAL AND PALEONTOLOGICAL SIGNIFICANCE

The results of this work have many implications for phylogenetic and evolutionary studies of the Xanthoidea. First, the superfamily exhibits a Cretaceous record (see also Schweitzer and Feldmann, 2001; Schweitzer, Feldmann et al., 2002), which can serve as an important benchmark in rooting characters and designating primitive versus advanced character states. Second, at least two extant xanthoid families have Cretaceous records, the Goneplacidae and Hexapodidae (Schweitzer and Feldmann, 2001; Schweitzer, Feldmann et al., 2002), and at least three families have first records during the Eocene, the Carpiliidae, Hexapodidae, and Pseudoziidae. The extant Goneplacidae and Hexapodidae were widespread by the Eocene (Glaessner, 1969; Schweitzer and Feldmann, 2001; Schweitzer, 2001). In addition, it is likely that the Eriphiidae, Panopeidae and Pilumnidae have Eocene records (Remy, 1960; Schweitzer, 2000). Genetic, larval, phylogenetic, and other studies must take this timing into account, as it yields information about the time of divergence of taxa. Further, as discussed below, this work has even more direct implications for the appearance and evolution of several xanthoid families.

Guinot (1968a) discussed the affinities between *Euryozius*, *Gardineria*, and *Carpilius* (the former two have been synonymized) as discussed above and postulated that they must have a common ancestor. She also discussed the similarities between the carpiliid and eriphiid brachyuran forms (Guinot, 1968a, 1968b). *Archaeozius occidentalis* new combination has many morphological features of the dorsal carapace that are intermediate between the Pseudoziidae and the Carpiliidae as discussed above, and in fact, there has been considerable debate over the generic constitution of the Carpiliidae (i.e., Guinot, 1968a, 1968b, 1978; Sakai, 1976; Serène, 1984). Many forms now assigned to the Eriphiidae and to the Pseudoziidae have at various times been placed within the Carpiliidae and vice versa because of similarities in various morphological features. Larval development is similar in eriphiids and carpiliids as well (J. Martin, personal commun.). In a phylogenetic analysis of freshwater crabs, von Sternberg and Cumberlidge (2001) found that extant members of the Carpiliidae and Eriphiidae as well as representatives of other xanthoid families belong to a monophyletic group, at least in their neighbor-joining phylogeny (fig. 4). However, other analyses in that same paper (von Sternberg and Cumberlidge, 2001, figs. 2, 3) do not show xanthoids as a monophyletic group. In light of the majority of the evidence, it seems reasonable to suggest that the three families, the Carpiliidae, Eriphiidae, and Pseudoziidae, are closely related and share a common ancestor.

Further, the Zanthopsidae, newly raised to family status, exhibits numerous similarities with the Carpiliidae; thus, paleontologists have found it difficult to distinguish between carpiliids and zanthopsids. In fact, some debate has occurred in the paleontological literature over the placement of species within genera in these two families. For example, some species originally assigned to *Harpactocarcinus* are now referred to *Palaeocarpilius* (de Gregorio, 1895; Rathbun, 1935). *Harpactoxanthopsis* was formerly placed within the Carpiliidae based upon its smooth carapace and other features (Feldmann et al., 1998; Schweitzer et al., 2000; Schweitzer, 2000). Careful examination of genera of the Carpiliidae and those now referred to the Zanthopsidae shows that they

share many features. The regions of members of both families are poorly defined; they have quadrilobed fronts; entire, rimmed, circular orbits; entire or spined anterolateral margins; similar length/width ratios; narrow, linear sterna; and fusion of abdominal somites. Guinot (1968a) also discussed these affinities. Because of these many similarities, it seems reasonable to suggest that these two families are closely related. Thus, it is suggested that the Carpiliidae, Eriphiidae, Pseudoziidae, and Zanthopsidae share a common ancestor.

Guinot (1968a, 1968b) suggested that the fusion of the merus and ischium in the major cheliped of the Carpiliidae was a derived feature as was the fusion of abdominal somites 3–5 in male carpiliids. The Zanthopsidae exhibits some fusion of abdominal somites in males but lacks the fusion of the ischium with the merus in the major cheliped. Synapomorphic features for the Zanthopsidae include the markedly quadrilobate front and the highly vaulted, convex dorsal carapace. These important phylogenetic features are readily observable in fossil carpiliids and zanthopsids as early as the Eocene and Paleocene respectively. In addition, features of the dorsal carapace that serve as proxies for the soft-part synapomorphies of the pseudoziids can be observed in fossils as old as Eocene. The fossil record of the Eriphiidae is probably at least Eocene (Remy, 1960). This suggests that the appearance of the common ancestor of these families and the divergence of the lineages of these four families occurred in pre-Eocene time because well-documented synapomorphic characters existed by Eocene time. Cladograms generated for xanthoid families should be evaluated within this context in the future because the timing of divergence is now more tightly constrained.

As of now, all four of the xanthoid families described herein are known to have Eocene records, and two are known to extend into the Cretaceous. With all of the first occurrences of extant families being Eocene records, it becomes rather difficult to root characters and define primitive and advanced states. The Paleocene is therefore a crucial time interval to be studied. Did the xanthoids begin to diverge during the Paleocene, or was the event part of the "Eocene radiation" of brachyurans (Glaessner, 1969; Schram, 1986)? Were the brachyurans affected by the end-Cretaceous event? If so, did they rebound during the Paleocene or Eocene? Directed study of Paleocene rocks is sorely needed to address these important questions.

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APPENDIX A

Key to the Carpiliidae, Eriphiidae, Palaeoxanthopsidae, Pseudoziidae, and Zanthopsidae. An illustrated key, superimposed on a geologic time scale, is found in Figure 1.

1a. Cervical groove well-defined, U-shaped . . . . . Palaeoxanthopsidae
1b. Cervical groove poorly defined or not present 2
2a. Fusion between some male abdominal somites, usually 3–4 or 3–5 3
2b. All male abdominal somites free and unfused 4
3a. Basis-ischium of first pereiopod completely fused to merus with few to no vestiges of suture . . . . Carpiliidae
3b. Basis-ischium of first pereipod not fused to merus . . Zanthopsidae
4a. Basis-ischium of first pereipod incompletely fused to merus, some remnants of suture visible; merus appearing to articulate directly with coxa . . . . .Pseudoziidae
4b. Basis-ischium of first pereiopod not fused to merus; coxa articulating with basis-ischium . . . . .Eriphiidae