

THE GENUS *XANTHILITES* BELL, 1858 AND A NEW XANTHOID FAMILY (CRUSTACEA: DECAPODA: BRACHYURA: XANTHOIDEA): NEW HYPOTHESES ON THE ORIGIN OF THE XANTHOIDEA MACLEAY, 1838

CARRIE E. SCHWEITZER

Department of Geology, Kent State University Stark Campus, 6000 Frank Ave. NW, Canton, Ohio 44720, <cshweit@kent.edu>

ABSTRACT—The xanthoid genus *Xanthilites* Bell, 1858 is herein restricted to contain only the type species *X. bowerbanki* and possibly a second species. *Xanthilites* sensu stricto, *Pulalius*, *Tumidocarcinus*, *Paratumidocarcinus*, and *Baricarcinus* are placed within the Tumidocarcinidae new family within the Xanthoidea. It is hypothesized that the Carpiliidae, Platyxanthidae, Tumidocarcinidae new family, Zanthopsidae, and at least some subfamilies of the Eriphiidae form a natural group and may belong to a discrete superfamily, based upon paleontological and neontological evidence. The earliest documented occurrence in the fossil record for the xanthoid Platyxanthidae is in Eocene rocks, with the referral herein of a fossil species to the family. The two related families, Eriphiidae and Platyxanthidae, are difficult to distinguish from one another in fossil specimens; diagnoses which take into account preservable characters are provided. Moreover, based upon morphological features the Eriphiidae as currently defined may comprise at least two families. Revision of *Xanthilites* has resulted in two new genera, *Jakobsenius* and *Rocacarcinus*, erected for *Xanthilites? cretacea* and *X. gerthi* respectively, both placed within the extinct Palaeoxanthopsidae. The common ancestor of at least some families currently referred to the Xanthoidea may lie within the Palaeoxanthopsidae, which may have embraced “pre-adapted survivor” taxa, surviving the end-Cretaceous extinction event. *Goniocypoda tessieri* is confirmed as a member of the Hexapodidae, extending the range of that family into the Cretaceous; however, the family is not a likely candidate for embracing the ancestral xanthoids. The illustrated specimen of *Menippe frescoensis* retains a barnacle epibiont, very rare in the fossil record of decapods.

INTRODUCTION

SEVERAL RECENT works have considered the fossil Xanthoidea MacLeay, 1838 in an attempt to place the fossils within the context of the group’s most up-to-date neontological classification (Schweitzer, 2000, 2003a, 2003b; Karasawa and Kato, 2003a, 2003b; Karasawa and Schweitzer, 2004; Schweitzer and Karasawa, 2004; Schweitzer et al., 2004). In the course of that work, proxy characters of the dorsal carapace (Schweitzer and Feldmann, 2000a; Schweitzer, 2003a) for many xanthoid families have been defined. These proxy characters of the dorsal carapace track important soft-tissue morphologies that are used taxonomically by biologists but are unavailable to paleontologists. In addition, features employed by biologists (Guinot, 1978; Davie, 2002; Karasawa and Kato, 2003a, 2003b), including the nature of the sternum, abdomen, and the degree of fusion of the articles of the first pereopods, are increasingly important to fossil xanthoid classification as more and better material is collected and as preparation techniques improve to reveal these important features. The proxy characters of the dorsal carapace used here, such as the number and nature of orbital fissures, may not in and of themselves be important for phylogeny, but they do appear to track other features which are undoubtedly phylogenetically important, such as the shape of the male pleopods, the position of gonopores, and the breadth of the sternum, which controls mobility and use of appendages.

The process of reviewing fossil members of the Xanthoidea has demonstrated that the genus *Xanthilites* Bell, 1858 has become a “catch-all” genus for Paleocene and Eocene xanthoid taxa. Förster (1970) first attempted to constrain this problematic genus; his species list has formed the basis of the work on the genus herein. *Xanthilites*, as previously defined (Glaessner, 1969; Förster, 1970), embraced a broad range of carapace morphologies and is herein restricted to the type and possibly one other species. Two species previously referred to *Xanthilites* are herein referred to two new genera in the Palaeoxanthopsidae Schweitzer, 2003a.

Evaluation of *Xanthilites* has prompted an analysis of the fossil record of several other xanthoid families and genera. Morphologically, *Xanthilites* cannot be accommodated by extant families. Tumidocarcinidae n. fam. is erected to embrace that genus as well as *Pulalius* Schweitzer et al., 2000; *Tumidocarcinus* Glaessner,

1960; *Paratumidocarcinus* Martins-Neto, 2001; and *Baricarcinus* Casadío et al., 2004. Through the use of proxy characters and characters of the sternum and male abdomen, diagnoses for the Eriphiidae MacLeay, 1838 and Platyxanthidae Guinot, 1978 that are paleontologically useful have been erected. The Tumidocarcinidae may be closely related to these two families. The geologic record of these families and the timing of their appearance have important implications for the evolutionary history of the Xanthoidea as currently understood.

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations.—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; In., The Natural History Museum, London, United Kingdom; GHUNLPam, Cátedra de Geología Histórica, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina; KSU D, Kent State University Decapod Comparative Collection; MGUH, Geological Museum Copenhagen, Copenhagen, Denmark; RO, Muséum national d’Histoire naturelle, Paris, France; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC.

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Section HETEROTREMATA Guinot, 1977
Superfamily XANTHOIDEA MacLeay, 1838

Included families.—Carpiliidae Ortmann, 1893; Eriphiidae MacLeay, 1838; Goneplacidae MacLeay, 1838; Hexapodidae Miers, 1886; Panopeidae Ortmann, 1893; Palaeoxanthopsidae Schweitzer, 2003a; Pilumnidae Samouelle, 1819; Platyxanthidae Guinot, 1977; Pseudoziidae Alcock, 1898; Pseudorhombilidae Alcock, 1900; Trapeziidae Miers, 1886; Tumidocarcinidae new family; Xanthidae MacLeay, 1838; Zanthopsidae Via, 1959 (after Martin and Davis, 2001; Schweitzer, 2003a, 2003b). The only family without a fossil record confirmed by the author as yet is the Xanthidae.

Family ERIPHIIDAE MacLeay, 1838

(=MENIPPIDAE Ortmann, 1893; see Schweitzer, 2003a, for discussion)

Figure 1

Included subfamilies.—Dacryopilumninae Serène, 1984; Eriphiinae MacLeay, 1838; Menippinae Ortmann, 1893; Oziinae Dana, 1851 (after Ng et al., 2001; Davie, 2002).

Included genera.—For complete list, see Ng et al. (2001).

Included fossil genera.—*Eriphia* Latreille, 1817; *Menippe* de Haan, 1833; *Pseudocarcinus* H. Milne Edwards, 1834; list is currently under study.

Diagnosis.—Carapace wider than long; L/W about 0.70, ranging from 0.65 to 0.76 in measured taxa; shape hexagonal, rectangular, or ovate; dorsal carapace sometimes with granules; epibranchial region often forming an arcuate ridge from last anterolateral spines to axial regions. Frontal margin with four lobes excluding inner-orbital projections, notched medially, about one-quarter maximum carapace width, ranging from 0.17 to 0.31 in measured taxa except *Eriphia* (0.48); fronto-orbital width about 40 percent maximum carapace width, ranging from 0.33 to 0.50 in measured taxa except *Eriphia* (0.72); orbits may be closed (Eriphiinae) but usually open, usually without upper orbital fissures; “antennae typically positioned near orbits and antennules but may be at some distance (Eriphiinae, Dacryopilumninae)” (Davie, 2002, p. 171); anterolateral margins usually with four spines excluding outer-orbital spine but may be entire or with a variable number of spines; posterior width about 40 percent maximum carapace width, ranging from 0.36 to 0.48 in measured taxa except *Eriphia* (0.59); angle of posterolateral margin to posterior margin about 38 degrees in measured taxa except *Eriphia* (48 degrees). Sternum narrow, widest at position of sternite 5; suture between sternites 2 and 3 very distinct; suture between sternites 3 and 4 a shallow groove; longitudinal groove in sternite 4 shallow, extending anteriorly from sterno-abdominal cavity; suture between sternites 4 and 5 at very high angle; male abdomen barely reaching or not reaching posterior end of coxa of pereopod 1; all male abdominal somites free, male abdomen entirely filling space between coxae of fifth pereopods; basis-ischium of first pereopod usually not fused to merus, coxa articulating with basis-ischium (see Table 1 for ratios of measured taxa; diagnosis modified after Guinot, 1978; Ng, 1998; Davie, 2002).

Discussion.—The Eriphiidae has been discussed on several occasions (Guinot, 1977, 1978; Ng, 1998; Martin and Davis, 2001; Ng et al., 2001; Davie, 2002). Guinot (1977, 1978) elevated the Menippinae Ortmann, 1893 (=Eriphiinae) to family status, a position that is currently maintained (Martin and Davis, 2001). It is notable that many of *Eriphia*'s diagnostic features are quite different than those for other members of the family, such as *Menippe* and *Myomenippe* Hilgendorf, 1879, suggesting that perhaps *Eriphia* and some other genera may actually form a distinct family (Ng et al., 2001; Davie, 2002). Herein the Eriphiidae is treated in the sense of Ng et al. (2001) and Davie (2002) as a single family comprised of several distinct subfamilies, listed above, united by the nature of the sternum, male abdomen, and pleopods. The Dacryopilumninae and Eriphiinae are each monotypic (Ng et al.,

2001), while the Menippinae and Oziinae each contain several genera (see Ng et al., 2001, p. 22, for list). The fossils referred herein to the new family Tumidocarcinidae are most closely allied with the Menippinae and the Oziinae, and if those latter two subfamilies were to be removed from the remainder of the Eriphiidae, the Tumidocarcinidae would be most closely related to them and not as closely related to the Eriphiinae and Dacryopilumninae. Because each subfamily within the Eriphiidae and also the Pilumnidae are very distinctive, many of the following comparative discussions must by necessity treat the individual subfamilies within each family (Schweitzer, 2003b).

Several diagnostic features of the Eriphiidae as defined by biologists can be preserved in fossils, such as the nature of the male sternum and abdomen, the first pereopods, and the frontal and anterolateral margins. The Platyxanthidae, composed of only a few extant genera, have features of the sternum, gonopores, gonopods, and general carapace proportions very similar to those of the Eriphiidae (Guinot, 1978). The Platyxanthidae differ from the Eriphiidae in the configuration of the sutures between the sternites, specifically those covered by the abdomen; the nature of the buccal cavity; and the endostome and the epistome (Guinot, 1978). These features are difficult or impossible to observe in fossils. Despite the many similarities, Guinot (1978) maintained the Platyxanthidae as a separate family, and this has been supported in the most recent crustacean classification (Martin and Davis, 2001). In addition, phylogenetic analysis of several xanthoid genera showed that genera within the Platyxanthidae and Eriphiidae were closely related and that the Platyxanthidae appears to be the sister group to the Eriphiidae (Von Sternberg and Cumberlidge, 2001).

Because of the many dorsal and ventral similarities between the two families, differentiation between some members of the Eriphiidae and the Platyxanthidae can be very difficult. The Dacryopilumninae have very widely spaced orbits that are located on the lateral edges of the carapace (Ng et al., 2001; Davie, 2002); thus, they are easily differentiated from platyxanthids. The Eriphiinae also have broadly spaced orbits and very broad fronto-orbital widths, as well as a steeper angle between the posterior and posterolateral margins, than do members of the Platyxanthidae and Menippinae (Table 1). The Eriphiinae (Ng et al., 2001) also lack orbital fissures.

However, differentiating the Platyxanthidae from the Menippinae and Oziinae without benefit of gonopores, antennae, and other rarely fossilized parts is very difficult. There are some dorsal carapace characters with limited utility. The anterolateral margins of the Platyxanthidae are separated into several spines or spined lobes or are weakly lobate with entire margins of each lobe (illustrations in Guinot, 1967; Coelho and Coelho Filho, 1993). The Menippinae have four sharp, well-delimited anterolateral spines, excluding the outer-orbital spine (Ng, 1998); however, the Oziinae have variably ornamented anterolateral margins similar to those of the Platyxanthidae (Davie, 2002). The orbits of members of the Platyxanthidae and the Menippinae clearly are fissured (Ng et al., 2001), whereas the Oziinae have shallow fissures or none at

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FIGURE 1—Representatives of each subfamily of the Eriphiidae MacLeay, 1838, excluding the Dacryopilumninae Serène, 1984. All digital images of plates from Rathbun (1930). 1, *Eriphia gonagra* Fabricius, 1781 (Eriphiinae MacLeay, 1838), dorsal carapace, digital image of plate 222, figure 2; 2, *E. gonagra*, ventral surface, note Y-shaped sternal groove pattern not present in position indicated by arrow, digital image of plate 222, figure 3; 3, *Ozius reticulatus* Desbonne and Schramm, 1867 (Oziinae Dana, 1851), dorsal carapace, digital image of plate 220, figure 2; 4, *Ozius perlatus* Stimpson, 1860, ventral surface, note Y-shaped sternal groove pattern not present in position indicated by arrow, digital image of plate 220, figure 3; 5, *Menippe mercenaria* Say, 1818 (Menippinae Ortmann, 1893), dorsal carapace, digital image of plate 192; 6, *M. mercenaria*, ventral surface, note Y-shaped sternal groove pattern not present in position indicated by arrow, digital image of plate 193, figure 2; 7, *Menippe frescoensis* Remy, 1960, plaster cast of RO3329; arrow indicates presence of a barnacle epibiont. Scale bars = 1 cm.

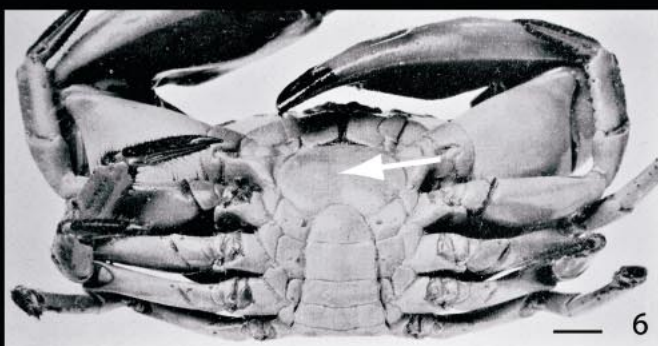
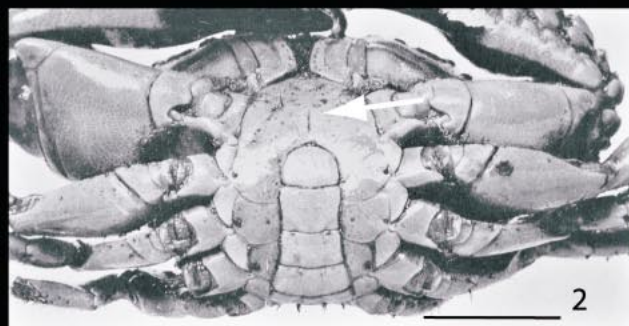


TABLE 1—Carapace ratios calculated for several species referred to the Platyxanthidae Guinot, 1977 and Eriphiidae MacLeay, 1838. Extant platyxanthids measured from Guinot (1967); *Pelaeus chauvini* measured from illustration in A. Milne Edwards, 1863; first four extant Eriphiidae measured from Rathbun (1930); *Menippe rumphii*, *Myomenippe*, and *Eriphia* measured from Ng (1998); *Menippe frescoensis* measured from Remy, 1960. P = Platyxanthidae; E = Eriphiidae; Er = Eriphiinae; M = Menippinae. Angle = angle between posterior margin and posterolateral margin; L/W = length/width; FOW/W = fronto-orbital width/width; F/W = frontal width/width; PW/W = posterior width/width.

Taxon	Family and subfamily	Angle	L/W	FOW/W	F/W	PW/W
<i>Platyxanthus orbigny</i> (H. Milne Edwards and Lucas, 1843), extant	P	38	0.63	0.38	0.13	0.38
<i>Platyxanthus crenulatus</i> A. Milne Edwards, 1879b, extant	P	39	0.7	0.34	0.23	0.41
<i>Homolaspis plana</i> (H. Milne Edwards, 1834), extant	P	39	0.65	0.33	0.2	0.35
<i>Pelaeus armatus</i> Eydoux and Souleyet, 1842, extant	P	39	0.7	0.37	0.21	0.4
<i>Pelaeus chauvini</i> (de Berville, 1857), Eocene	P	38	0.67	0.36	0.19	0.39
<i>Menippe mercenaria</i> (Say, 1818), extant	E, M	38	0.69	0.41	0.25	0.37
<i>Menippe frontalis</i> A. Milne Edwards, 1879b, extant	E, M	35	0.65	0.34	0.22	0.36
<i>Menippe obtusa</i> Stimpson, 1859, extant	E, M	38	0.65	0.42	0.25	0.38
<i>Menippe nodifrons</i> Stimpson, 1859, extant	E, M	37	0.72	0.34	0.26	0.4
<i>Menippe rumphii</i> (Fabricius, 1798), extant	E, M	42	0.7	0.33	0.17	0.4
<i>Myomenippe hardwicki</i> (Gray, 1831), extant	E, M	38	0.74	0.5	0.31	0.48
<i>Eriphia smithii</i> MacLeay, 1838, extant	E, Er	48	0.76	0.72	0.48	0.59
<i>Menippe frescoensis</i> Remy, 1960, Eocene	E, M	38	0.74	0.46	0.26	0.39

all (Ng et al., 2001; Davie, 2002, p. 170, 179; H. Karasawa, personal commun., 2004).

The best feature differentiating all members of the Eriphiidae from the Platyxanthidae in the fossil record is the presence or absence of a deep, Y-shaped groove pattern in the male sternum (Figs. 1.2, 2.4), which is present in the Platyxanthidae but absent in the Eriphiidae. The Y-shaped groove is composed of deep remnants of the suture between the third and fourth sternites and a deep groove extending anteriorly from the sternoabdominal cavity. Interestingly these grooves are also seen in some other fossil forms, such as the Zanthopsidae Via, 1959, and the genus *Lobonotus* A. Milne Edwards, 1864, of the Pilumnidae (Schweitzer et al., 2004). The development of such deep grooves may be a primitive character within the Xanthoidea.

Subfamily MENIPPINAE Ortmann, 1893

Figure 1.5–1.7

Included genera.—See Ng et al. (2001) for complete list.

Included fossil genera.—*Menippe* de Haan, 1833; *Pseudocarcinus* H. Milne Edwards, 1834.

Diagnosis.—Carapace wider than long; L/W about 0.70, ranging from 0.65 to 0.74 in measured taxa; shape hexagonal or ovate; epibranchial region often forming an arcuate ridge from last anterolateral spines to axial regions. Frontal margin with four lobes excluding inner-orbital projections, notched medially, about one-quarter maximum carapace width, ranging from 0.17 to 0.31 in measured taxa; fronto-orbital width about 40 percent maximum carapace width, ranging from 0.33 to 0.50 in measured taxa; orbits open, usually without upper orbital fissures; “antennae typically positioned near orbits” (Davie, 2002, p. 171); anterolateral margins with four spines excluding outer-orbital spine; posterior width about 40 percent maximum carapace width, ranging from 0.36 to 0.48 in measured taxa; angle of posterolateral margin to posterior margin about 38 degrees in measured taxa. Sternum narrow, widest at about position of fifth sternite; suture between sternites 2 and 3 very distinct; suture between sternites 3 and 4 a

shallow groove; longitudinal groove in sternite 4 shallow, extending anteriorly from sterno-abdominal cavity; suture between sternites 4 and 5 at very high angle; male abdomen barely reaching or not reaching posterior end of coxa of pereopod 1; all male abdominal somites free, male abdomen entirely filling space between coxae of fifth pereopods; basis-ischium of first pereopod usually not fused to merus, coxa articulating with basis-ischium (see Table 1 for ratios of measured taxa; diagnosis modified after Guinot, 1978; Ng, 1998; Ng et al., 2001; Davie, 2002).

Genus MENIPPE de Haan, 1833

Figure 1.5–1.7

Menippe DE HAAN, 1833, p. 4, 21.

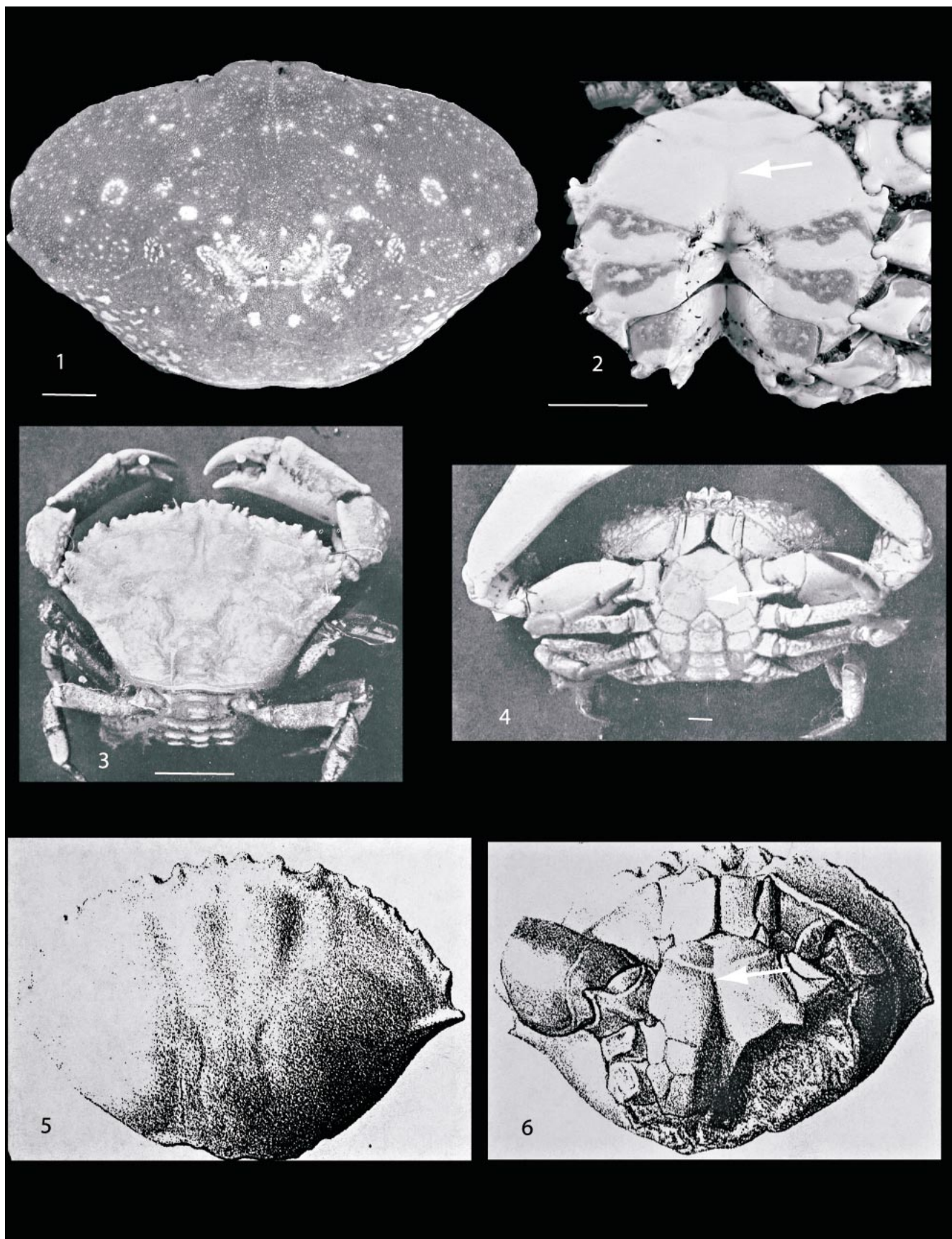
Type species.—*Menippe rumphii* (Fabricius, 1798), subsequent designation by Glaessner, 1929.

Fossil species.—*Menippe frescoensis* Remy, 1960; *Menippe mercenaria* (Say, 1818), still extant.

Material examined.—Cast of RO3329, from the Eocene of Ivory Coast (Remy, 1960).

Discussion.—*Menippe frescoensis* (Fig. 1.7) conforms to the general diagnosis for the family. It possesses a hexagonal carapace; four frontal spines excluding the inner-orbital spines and a median frontal notch; four anterolateral spines; large, stout chelae; the merus of the first pereopod is not fused to the basis-ischium; and the coxa of the first pereopod articulates with the basis-ischium. The features of the pereopods are observable in the holotype, illustrated by Remy (1960); however, I was unable to locate the holotype specimen during a 2001 visit to the Muséum national d'Histoire naturelle, Paris. It lacks the ridge extending posteriorly onto the carapace from the last anterolateral spine, which is the only major way in which it differs from the Menippinae and extant *Menippe*. *Menippe frescoensis* does not possess an anterolateral margin congruent with members of the Platyxanthidae, because it possesses four distinct, broad anterolateral spines as in species of *Menippe*. In addition, the ratios of carapace

FIGURE 2—Representatives of the Platyxanthidae Guinot, 1977. 1, *Homolaspis plana* H. Milne Edwards, 1834, KSU D179, dorsal carapace; 2, *H. plana*, KSU D178, ventral surface, arrow indicates position of weak Y-shaped groove pattern; 3, *Platyxanthus patagonicus* A. Milne Edwards, 1879a, dorsal carapace; digital image of plate 125, figure 1 in Rathbun (1930); 4, *P. patagonicus*, ventral surface, arrow indicates position of Y-shaped groove pattern; digital image of plate 125, figure 2 in Rathbun (1930); 5, *Pelaeus chauvini* (de Berville, 1857), dorsal carapace, digital image of plate XII, figure 1 in A. Milne Edwards (1863); 6, *Pelaeus chauvini*, ventral surface, arrow indicates position of Y-shaped groove pattern; digital image of plate XII, figure 1b in A. Milne Edwards (1863). Scale bars = 1 cm. No scales indicated in originals of A. Milne Edwards (1863).



parameters for *M. frescoensis* are nearly identical to those of extant *Menippe* (Table 1). Thus, I retain *M. frescoensis* within *Menippe*.

When examining only the dorsal carapace, *Menippe frescoensis* is superficially similar to some members of the Portunidae Rafinesque, 1815, such as species of *Minohellenus* Karasawa, 1990. The nature of the fronts and the anterolateral margins, the carapace shape and proportions, and the weakly developed regions are very similar between the two. There are, however, significant differences. The epibranchial region of *Minohellenus* bears a well-developed arcuate ridge extending from the last anterolateral spine (Schweitzer and Feldmann, 2000b), whereas in *Menippe frescoensis*, that area is inflated but not as arcuate and is not confluent with the last anterolateral spine. In addition, species of *Minohellenus* have paddlelike fifth pereopods (Kato and Karasawa, 1994, p. 56), typical of the Portunidae and not the Xanthoidea.

The sternum of *Menippe frescoensis* is quite different from portunid sterna although it is quite similar to xanthoid sterna, especially the Carpiliidae and the Zanthopsidae. The sternum of *M. frescoensis* is narrow and remains narrow throughout its length, whereas portunid sterna are rounded or ovate and markedly widest at about the fifth and sixth sternites. In portunid sterna, the sutures are nearly parallel or are at low angles, and the suture between the fourth and fifth sternites is at a low angle and is not parallel to the sutures between the remainder of the sternites. The broadness of the portunid sternum allows the appendages to project well beyond the lateral margins of the carapace and is an adaptation to the swimming habit which most portunids exhibit. In *M. frescoensis*, the suture between sternites 4 and 5 is at a very high angle, sternites 5–8 are very narrow, and the overall shape of the sternum is rectangular; thus, the appendages do not markedly project laterally, congruent with the benthic habit of species of *Menippe* and most xanthoids.

Menippe frescoensis is the earliest known member of the genus, subfamily, and family, each ranging from Eocene to Recent. The specimen illustrated here is also remarkable in preserving a barnacle epibiont (Fig. 1.7, arrow); epibionts are uncommon and probably under-represented in the fossil record due to the vagaries of preservation of epibionts on decapod cuticle (Feldmann, 2003a, 2003b; Waugh et al., 2004). Only one epibiont was found among 278 fossil crabs in the comparative collection in the Department of Geology at Kent State University (Feldmann, 2003a, p. 1028); thus, the occurrence of an epibiont merits mention due to its rarity and paleoecological significance (Feldmann, 2003b).

Family TUMIDOCARCINIDAE new family Figure 3

Type genus.—*Tumidocarcinus* Glaessner, 1960.

Included genera (all fossil).—*Baricarcinus* Casadío, De Angelis, Feldmann, Garassino, Hetler, Parras, and Schweitzer, 2004; *Paratumidocarcinus* Martins-Neto, 2001; *Pulalius* Schweitzer, Feldmann, Tucker, and Berglund, 2000; *Tumidocarcinus* Glaessner, 1960; *Xanthilites* Bell, 1858, sensu stricto.

Diagnosis.—Carapace wider than long, L/W about 0.80, widest at position of last or penultimate anterolateral spine, about half the distance posteriorly on carapace; carapace markedly vaulted

longitudinally, especially in anterior third; front four-lobed including inner-orbital spines; frontal width about one-quarter maximum carapace width; fronto-orbital width a little less than half maximum carapace width; orbits rimmed, sometimes with very faint, completely fused fissure, circular, directed forward; carapace regions well defined to poorly defined; anterolateral margins with three or four small, blunt spines excluding outer orbital spine or entire and granular; epibranchial regions usually arcuate.

Male sternites 1 and 2 fused with no evidence of suture; very clear, deep, continuous suture between sternites 2 and 3; sternites 3 and 4 with notch in lateral margins where suture intersects it, suture becoming increasingly shallow, becoming a shallow groove at midlength, completely interrupted axially; left and right sternal sutures between sternites 3 and 4 merge with deep groove extending anteriorly from sterno-abdominal cavity, forming prominent, Y-shaped groove pattern; suture between sternites 3 and 4 oriented at high angle; sternite 4 with very clear, longitudinal grooves near lateral margins, which appear to be episternal projections from sternite 3 fused with and prominent on sternite 4.

Male abdomen barely reaching or not quite reaching posterior margin of coxae of first pereopods; all male abdominal somites free; male abdomen completely occupying space between coxae of fifth pereopods; sternite 8 not visible.

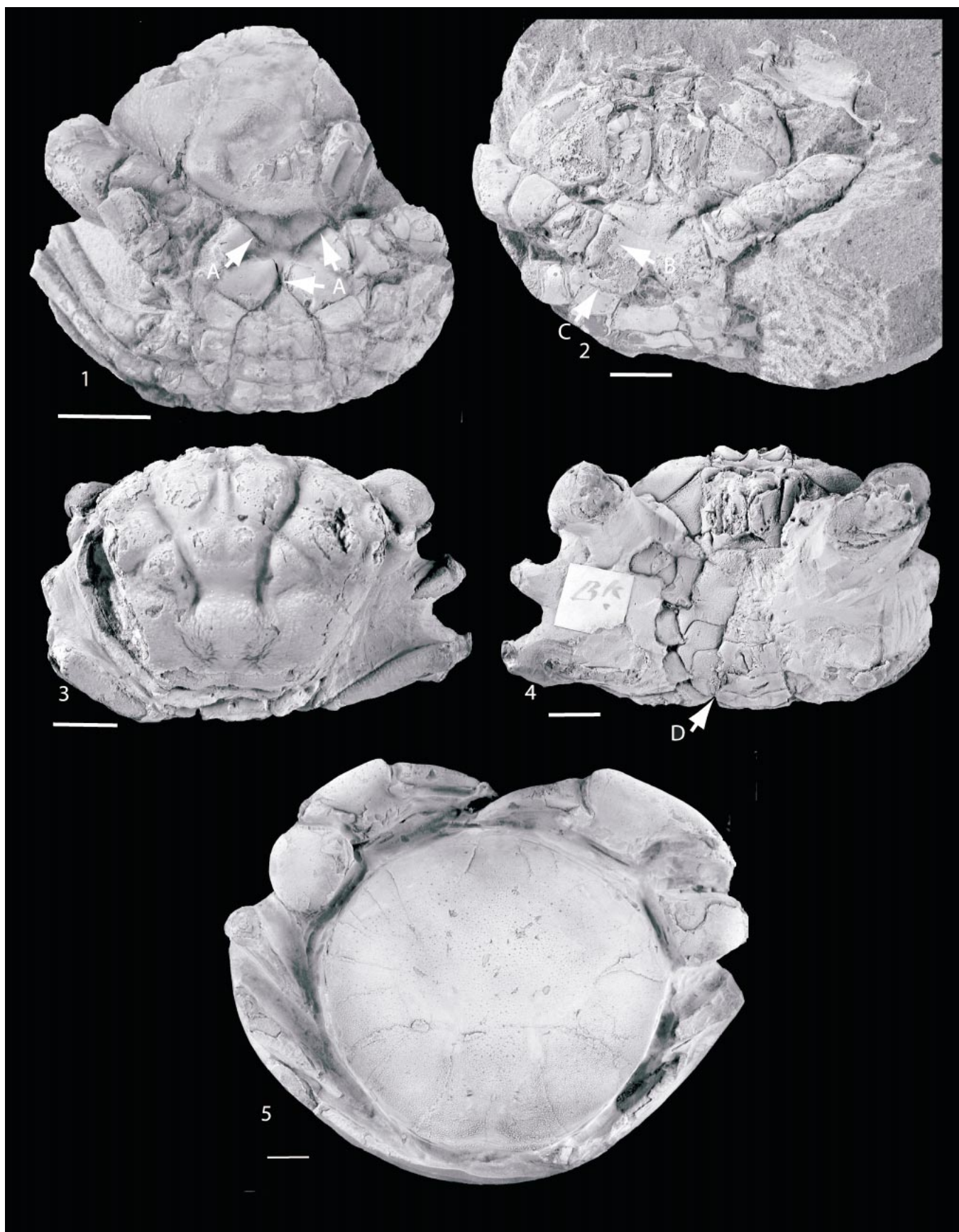
Chelae subequal to very unequal; mani stout; fingers with black tips; coxae of first pereopods articulating with basis-ischium, basis-ischium not fused to merus; other pereopods slender.

Etymology.—The family is named for the Southern Hemisphere genus *Tumidocarcinus* which is represented by abundant, well-preserved dorsal carapace material; well-preserved ventral portions of the carapace; and male, female, immature female, and feminized male abdomina (Feldmann, 1998), providing a nearly unprecedented sample from which to describe both dorsal and ventral carapace features in a fossil taxon.

Material examined.—*Pulalius vulgaris* (Rathbun, 1926), USNM 508355–508357; *P. dunhamorum* Schweitzer et al., 2000, CM 45844, CM 45383; *Xanthilites bowerbanki* Bell, 1858, In. 46369, 46380, 43488, 59087; CM 38700; cast of MGUH 2483, referred to *Xanthilites cretaceus* by Collins and Jakobsen (1994) and now referred to *Jakobsenius* new genus.

Discussion.—Prior to this discussion, *Tumidocarcinus* and *Xanthilites* were placed within the Xanthidae sensu lato (Glaessner, 1969). Reassessment of species of *Xanthilites* has prompted a reevaluation of its family-level placement and that of the closely related genera *Pulalius* and *Tumidocarcinus*. *Xanthilites* and *Pulalius* are nearly identical in the shape and relative proportions of the dorsal carapace and dorsal carapace regions, the male sternum, and the male abdomen (Fig. 3.1–3.4). However, *Xanthilites* has distinctly developed regions and deeper dorsal carapace grooves than *Pulalius*, features which clearly differentiate the two genera. Casadío et al. (2004) discussed the similarities among *Pulalius*, *Tumidocarcinus*, *Paratumidocarcinus*, and *Baricarcinus*; these four genera along with *Xanthilites* form a natural group. Because these five genera exhibit major differences as compared with existing xanthoid families in the nature of the sternum and male abdomen, features which are diagnostic at the family and subfamily levels (Guinot, 1967, 1969, 1978; Davie, 2002), as well as

FIGURE 3—Representatives of the Tumidocarcinidae new family. 1, *Pulalius dunhamorum* Schweitzer et al., 2000, USNM 508357, arrows indicate three components of Y-shaped groove; 2, *P. dunhamorum*, USNM 508356, arrow B indicates groove where episternite 3 is fused to sternite 4, arrow C indicates high angle of sternal suture 3–4; 3, *Xanthilites bowerbanki* Bell, 1858, CM38700, dorsal carapace; 4, *X. bowerbanki*, CM38700, note that all male abdominal somites are free and that male abdomen completely covers space between coxae of fifth pereopod (arrow D); 5, *Tumidocarcinus giganteus* Glaessner, 1960, KSU D180, dorsal carapace. Scale bars = 1 cm.



characters of the dorsal carapace, a new family, the Tumidocarcinidae n. fam., must accommodate them. The new family is best allied with the Eriphiidae and the Platyxanthidae, which Guinot (1978) acknowledged to be very closely related to one another.

The male sternum and abdomen of *Xanthilites*, *Tumidocarcinus*, and *Pulalius*, the only genera among the five to have preserved sterna, are very similar to one another and form a distinctive morphological group. These three genera have prominent grooves marking the fusion of the episternites of sternite 3 with sternite 4 and a prominent Y-shaped groove pattern on the male sternum (Fig. 3.1, 3.2). Very few other xanthoids have prominent episternal grooves on sternite 4; these include the Platyxanthidae, and some eriphiids and Xanthidae s.s. (see illustrations in Rathbun, 1930; genera within Xanthidae s.s. in that work include *Chlorodiella* Rathbun, 1897; *Xanthias* Rathbun, 1897; *Paraxanthias* Odhner, 1925, for example), although the grooves are not nearly as distinct as on the fossils referred to the Tumidocarcinidae. Only the Platyxanthidae (Fig. 2), Palaeoxanthopsidae (Fig. 4), Zanthopsidae (discussed below), and *Lobonotus* have the Y-shaped groove pattern similar to that seen in the fossils referred to the Tumidocarcinidae. However, they differ from the Tumidocarcinidae in other important regards as discussed below. Thus, the combination of characters displayed by the Tumidocarcinidae is unique.

The Tumidocarcinidae differ from the Platyxanthidae and the Eriphiidae in several important regards in addition to the sternal differences discussed above (Table 2). The dorsal carapace in the Tumidocarcinidae is not particularly similar to members of either the Eriphiidae or Platyxanthidae, although it is notable that within these two families, the dorsal carapace shape, ornamentation, and relative proportions are extremely variable (illustrations in Rathbun, 1930; Guinot, 1967; Davie, 2002). The Tumidocarcinidae possess four frontal spines, including the inner-orbital spines, rather than six as in the Platyxanthidae and the Eriphiidae. The dorsal carapace of the Tumidocarcinidae displays a length to width ratio of approximately 0.8, whereas the Eriphiidae and the Platyxanthidae have ratios of approximately 0.7 or slightly less. The dorsal carapace is markedly vaulted longitudinally in the anterior third of the carapace in the Tumidocarcinidae; such prominent vaulting is not present in the Eriphiidae or Platyxanthidae.

Even more distinctions from the Eriphiidae can be made at the subfamily level. The fronto-orbital width of the Tumidocarcinidae is about half the maximum carapace width, as compared to approximately 40 percent or less in the Menippinae and Oziinae of the Eriphiidae. In the Eriphiinae and Dacryopilumninae of the Eriphiidae, it is 70 percent or more. The Dacryopilumninae and the Eriphiinae of the Eriphiidae have very broad fronto-orbital widths and completely closed orbits, not seen in tumidocarcinids. In the Menippinae of the Eriphiidae, the orbits are fissured, and the suture between sternites 3 and 4 is very indistinct, whereas that suture in tumidocarcinids is deep and well marked. Members of the Oziinae of the Eriphiidae have a notched merus of the third maxilliped, which is not evident in tumidocarcinids.

In the Platyxanthidae, the suture between the second and third sternites is indistinct and interrupted medially, whereas in *Pulalius*, *Tumidocarcinus*, and *Xanthilites* it is very deep, clear, and uninterrupted (Fig. 3.2). Platyxanthids have two clearly defined orbital fissures, whereas tumidocarcinids have no such fissures or

one very completely fused, barely discernible fissure. The fronto-orbital width of the Tumidocarcinidae is about half the maximum carapace width, as compared to approximately 40 percent or less in platyxanthids.

The genera here referred to the Tumidocarcinidae n. fam. cannot be accommodated in any of the other currently recognized xanthoid families. The Pilumnidae Samouelle, 1819, as currently understood, is a heterogeneous group in terms of dorsal carapace morphology united by the shape of the male gonopods 1 and 2 and by the presence of unfused somites in the male and female abdomina throughout life (Ng and Clark, 2000a). They are a difficult group to work with in the fossil record because the gonopods are never preserved. However, some features serve to distinguish the Pilumnidae from the Tumidocarcinidae, and as in the Eriphiidae, the pilumnids must be considered at the subfamily level because of their heterogeneity. In most pilumnids, the male abdomen extends nearly to the anterior margin of sternite 4 (Davie, 2002), a condition not seen in the fossils referred to the Tumidocarcinidae. In the Rhizopinae Stimpson, 1858, part of sternite 8 is visible in males, a very important xanthoid character and one that differentiates it from the Tumidocarcinidae. The Calmaniinae Števcic, 1991 and the Eumedoninae Dana, 1853 have distinctive, unusual carapace shapes (Davie, 2002) that immediately exclude the fossils referred to the Tumidocarcinidae. The Halimedinae Alcock, 1898 have an extremely elongate telson, not seen in the fossils referred to the Tumidocarcinidae. The Tumidocarcinidae displays some similarities with the Pilumnoidinae Guinot and MacPherson (1987). The Pilumnoidinae exhibit a narrow male sternum and male abdominal somites free and completely covering the eighth sternite (Guinot and MacPherson, 1987); both are features of the Tumidocarcinidae. However, members of the Pilumnoidinae lack the deep grooves on the fourth sternite resulting from fusion of the episternal projections and the deep Y-shaped groove pattern on the sternum. Further, the sternum of Tumidocarcinidae is broader than that of the Pilumnoidinae. The front of the Pilumnoidinae projects markedly beyond the orbits, often in a triangular projection, that is not present in the Tumidocarcinidae. Schweitzer (2000) had previously allied *Pulalius* with *Galene* de Haan, 1833, within the Galeninae Alcock, 1898, of the Pilumnidae (Ng, 1998; Ng and Clark, 2000b; Davie, 2002). However, the sternum of *Galene* lacks marked episternal projections expressed on sternite 4, and the sutures between sternites 3/4 and 4/5 are nearly parallel and not oriented at a very high angle (Guinot, 1967; personal commun., 2003), not seen in the Tumidocarcinidae. *Galene* remains as a pilumnid. The extinct *Lobonotus* has deep grooves on the male sternum but is clearly a pilumnid based upon other features of the sternum (Schweitzer et al., 2004); thus, *Lobonotus* is not placed within the Tumidocarcinidae.

Portions of sternite 8 are visible in males of the Pseudorhombilidae and the Panopeidae; in addition, male abdominal somites 3–5 are fused in each, differentiating them from the Tumidocarcinidae. Within the Goneplacidae sternal and abdominal features are quite variable (Karasawa and Kato, 2003a), but the Tumidocarcinidae are easily differentiated from the Goneplacidae because members of that heterogeneous family lack a deep groove extending anteriorly from the sterno-abdominal cavity, the sternum is broad, and the carapace is generally flattened and poorly ornamented. In the Xanthidae s.s. male abdominal somites 3–5 are

FIGURE 4—Representatives of the Palaeoxanthopsidae Schweitzer, 2003a. 1, *Rocacarcinus gerthi* (Glaessner, 1960), n. gen. and comb., GHUNLPam 7019, note markedly notched front; 2, *R. gerthi*, GHUNLPam 7010; 3, *R. gerthi*, GHUNLPam 7048; 4, *Jakobsenius cretacea* (Seegerberg, 1900), n. gen. and comb., plaster cast of MGUH 2483; 5, *Lobulata lobulata* (Feldmann et al., 1995), GHUNLPam 7047, ventral view, note Y-shaped sternal groove pattern. Scale bars = 1 cm.

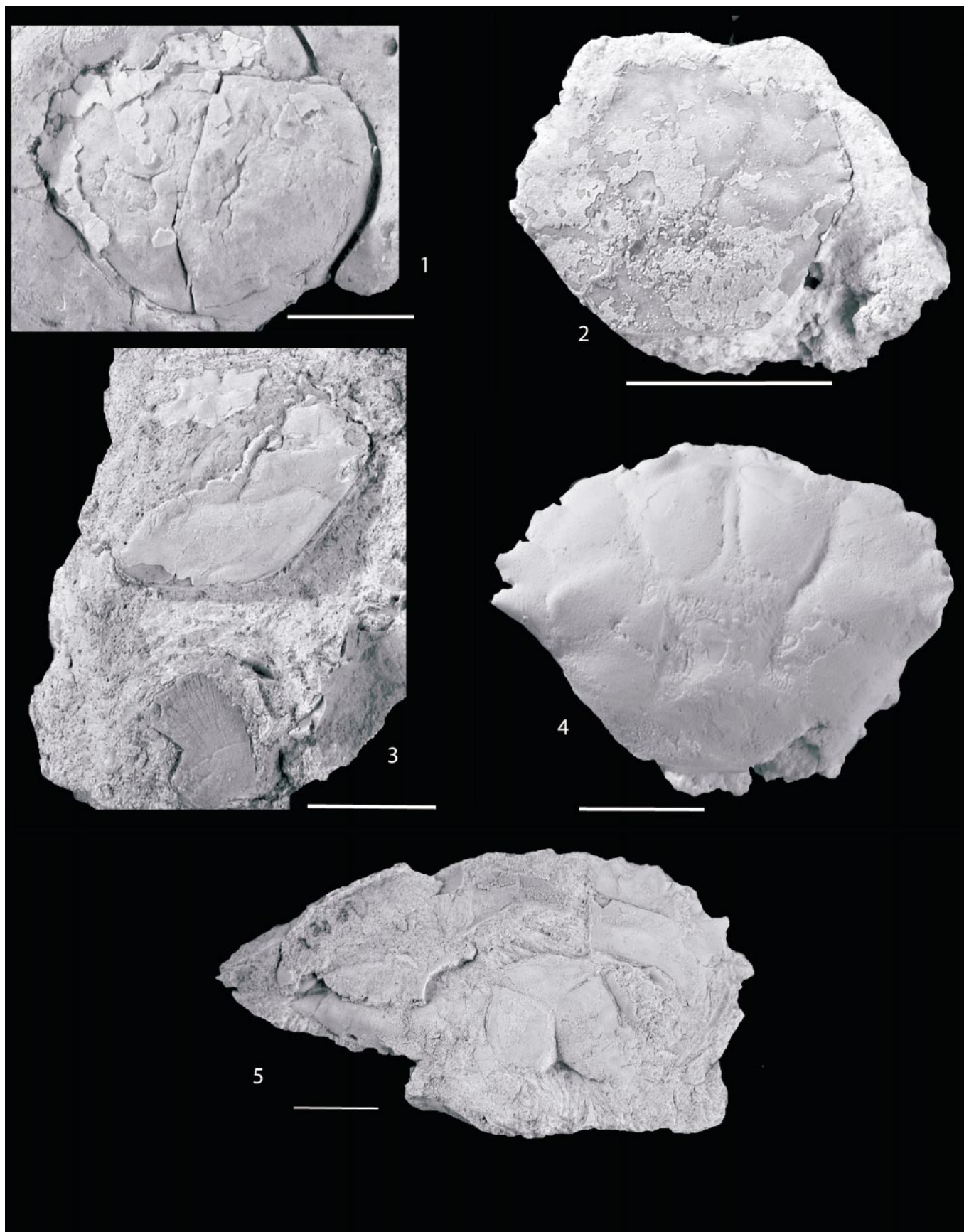


TABLE 2—Matrix of important characters among the Tumidocarcinidae; Platyxanthidae; and Eriphiinae, Menippinae, and Oziinae of the Eriphiidae. Dacryopilumninae of the Eriphiidae not included due to their distinctive orbital characters.

Character	Tumidocarcinidae	Platyxanthidae	Eriphiinae	Menippinae/ Oziinae
Fusion of male somites	none	none	none	none
Y-shaped sternal groove pattern	present	present	absent	absent
Suture between sternites 1 and 2	deep, uninterrupted	indistinct, interrupted	deep, uninterrupted	deep, uninterrupted
Groove between sternites 3 and 4	marginally notched, well-marked	well-marked	shallow, indistinct	shallow, indistinct
Episternal markings on sternite 4	very deep, well-marked	well-marked	not well-marked	not well-marked
Anterior sterno-abdominal groove	very deep	deep	shallow or not present	shallow or not present
Orbital fissures	absent	present	absent	present/absent
Frontal spines	four	six	six	six

fused, differentiating them from the Tumidocarcinidae. In the Trapeziidae usually male abdominal somites 3–5 are fused; in addition, the smooth carapace and broad fronto-orbital width in this family excludes members of the Tumidocarcinidae. The Carpiliidae exhibit very distinctive features of the sternum, abdomen, and articulation of the articles of the first pereopods (Schweitzer, 2003a), which clearly differentiate them from the Tumidocarcinidae. Within the Hexapodidae there is always fusion of at least some of the male abdominal somites; in addition, the dorsal carapace shape and relative proportions are very distinctive (Schweitzer and Feldmann, 2001a), excluding the fossils referred to the Tumidocarcinidae from that family.

The Pseudoziidae exhibit some features of the sternum and male abdomen that are quite similar to the Tumidocarcinidae, but the pseudoziid sternum is markedly wide and the sutures between sternites 3/4 and 4/5 are nearly parallel and oriented at a low angle (Ng and Liao, 2002), not seen in the Tumidocarcinidae. In addition, the dorsal carapace of pseudoziids is much wider than long, while tumidocarcinids are not much wider than long, and the dorsal carapace regions of pseudoziids are poorly defined or not defined, while in most Tumidocarcinidae, the regions are well defined.

The extinct Palaeoxanthopsidae (Fig. 4) and Zanthopsidae exhibit dorsal carapace ornamentation and relative proportions quite different from the Tumidocarcinidae (Schweitzer, 2003a). However, there are many similarities between the sternum and abdomen of the zanthopsids and the fossils referred to the Tumidocarcinidae. For example, the zanthopsids have a deep, Y-shaped groove pattern on the sternum, the sternum is narrow, and the male abdomen just reaches the level of the posterior end of the coxae of the first pereopods. However, sternite 4 of the zanthopsids lacks the deep episternal markings and male abdominal somites 3 and 4 are fused, neither of which are seen in the fossils referred to the Tumidocarcinidae. Few sterna of the Palaeoxanthopsidae are known. A newly prepared specimen of *Lobulata lobulata* (Feldmann et al., 1995) (Fig. 4.5) has a deep Y-shaped groove as in the Tumidocarcinidae, but it lacks the episternal grooves on sternite 4 typical of the Tumidocarcinidae.

The Tumidocarcinidae display an amphitropical distribution with a strong Southern Hemisphere component. *Pulalius* and *Xanthilites* have Eocene records (Bell, 1858; Schweitzer et al., 2000) from the Pacific Northwest of North America and England, respectively. *Tumidocarcinus* is known from Eocene to Miocene rocks of New Zealand (Glaessner, 1960; Feldmann, 1998); Casadío et al. (2004) have previously excluded an Eocene Antarctic species (Aguirre-Urreta et al., 1995) from *Tumidocarcinus*. *Pulalius* is also known from Oligocene rocks of the Pacific Northwest of North America (Rathbun, 1926; Schweitzer, 2000; Schweitzer et al., 2000). *Baricarcinus* has been reported from late Oligocene rocks near San Juan de Bariloche, Patagonia, Argentina (Casadío et al., 2004), and *Paratumidocarcinus* is recorded from Miocene rocks of Brazil (Martins-Neto, 2001).

A species of *Progeryon* Bouvier, 1922 was described by Ng and Guinot (1999, p. 687, fig. 1c) as having a deep and V-shaped suture between sternites 3 and 4, and the illustration shows the suture to be continuous with the groove extending anteriorly from the sterno-abdominal cavity, forming a Y-shaped structure similar to that seen in the genera herein referred to the Tumidocarcinidae. The family-level placement of *Progeryon* has been contentious. Bouvier (1922) placed the genus in the Galenidae. Balss (1957) and Guinot (1969) moved it to the Geryonidae; however, Manning and Holthuis (1989) excluded it from the Geryonidae Colosi, 1923, suggesting that it may belong in a new family with *Paragalene* Kossmann, 1878. Ng and Guinot (1999) retained *Progeryon* in the Geryonidae but suggested that it was actually closer to the Carcinoplacinae of the Goneplacidae MacLeay, 1838. The work of Karasawa and Kato (2003b) showed *Progeryon* to be allied with the Goneplacidae, but the specific relationship of the genus to the Goneplacidae, which is heterogeneous s. Karasawa and Kato (2003a, 2003b), was not resolved. The family-level placement of *Progeryon* and *Paragalene* should continue to be investigated.

Genus XANTHILITES Bell, 1858 Figure 3.2, 3.3

Xanthilites BELL, 1858, p. 17, pl. II, figs. 2–6 (listed in the captions as *Xantholites* [sic]).

Pseuderiphia REUSS, 1859, p. 54, pl. 18, figs. 4–6.

Type species.—*Xanthilites bowerbanki* Bell, 1858, by original designation.

Other species.—Questionably *Xanthilites interpunctus* Schaffhäutl, 1863.

Diagnosis.—Carapace wider than long, L/W about 0.80, widest at position of last anterolateral spine, a little less than half the distance posteriorly on carapace; carapace vaulted longitudinally, most strongly in anterior one-third of carapace; carapace regions well defined by deep grooves.

Frontal width about one-quarter maximum carapace width, front with four spines including inner-orbital spines; fronto-orbital width a little less than half maximum carapace width, orbits without fissures, rimmed; anterolateral margin with four spines, not including outer-orbital spine; posterior margin entire, relatively straight; posterior margin very weakly concave centrally, about same relative width as fronto-orbital width.

Carapace regions tumid, ornamented by fine granules; epibranchial region arcuate, comprised of two components, one component arcing anteriorly from base of anterolateral spine, second component triangular, aligned alongside urogastric region.

Male sternites 1 and 2 fused with no evidence of suture; very clear, deep, continuous suture between sternites 2 and 3; sternites 3 and 4 with notch in lateral margins where suture intersects it, the suture becoming increasingly shallow and becoming a shallow groove at midlength, completely interrupted axially; left and right

TABLE 3—Species originally or at some time referred to *Xanthilites* and their current generic and family designation. List based on that of Förster (1970).

Species	Current generic designation	Current family
<i>X. bowerbanki</i> (type)	<i>Xanthilites</i>	Tumidocarcinidae
<i>X. alabamensis</i> Rathbun, 1935	<i>Paraverrucoides</i> Schweitzer, 2003a	Palaeoxanthopsidae
<i>X. bavaricus</i> Lörenthey, 1898	unknown	Xanthoidea sensu lato
<i>Colpocaris bullata</i> von Meyer, 1863, referred to <i>Xanthilites</i> by Glaessner (1969)	<i>Colpocaris</i>	Xanthoidea sensu lato
<i>X. cretacea</i> Segerberg, 1900	<i>Jakobsenius</i> new genus	Palaeoxanthopsidae
<i>Menippe frescoensis</i> Remy, 1960, referred to <i>Xanthilites</i> by Förster (1970)	<i>Menippe</i>	Eriphiidae
<i>X. gerthi</i> Glaessner, 1930	<i>Rocarcinus</i> new genus	Palaeoxanthopsidae
<i>X. interpunctus</i> (Schafhäütl, 1863), originally referred to <i>Cancer</i> Linnaeus, 1758	<i>Xanthilites</i> ?	Tumidocarcinidae
<i>X. macrodactylus</i> Van Straelen, 1925	unknown	Xanthoidea sensu lato
<i>X. macrodactylus pyrenaicus</i> Artal and Via, 1988	<i>Coeloma</i> ?	Goneplacidae?
<i>X. pentagonalis</i> Yokoyama, 1911	<i>Branchioplax</i> Rathbun, 1916	Goneplacidae
<i>X. rathbunae</i> Withers, 1924	too fragmental to assign	unknown
<i>X. traubi</i> Förster, 1970	too fragmental to assign	unknown
<i>X. verrucoides</i> Collins and Rasmussen, 1992	<i>Verrucoides</i> Vega et al., 2001	Palaeoxanthopsidae
<i>Zanthopsis vulgaris</i> Rathbun, 1926, referred to <i>Xanthilites</i> by Förster (1970)	<i>Pulalius</i> Schweitzer et al., 2000	Tumidocarcinidae
? <i>Xanthilites</i> sp. Fraaye and Summesberger, 1999	unknown (fragmental)	unknown

sternal sutures between sternites 3 and 4 merge with deep groove extending anteriorly from sterno-abdominal cavity, forming Y-shaped groove pattern, pattern less prominent than in other members of family; suture between sternites 3 and 4 oriented at high angle to midline; sternite 4 with longitudinal grooves near lateral margins, which appear to be episternal projections from sternite 3 fused with and prominent on sternite 4, grooves fainter than on other members of the family.

Male abdomen barely reaching or not quite reaching level of posterior margin of coxae of first pereopods; all male abdominal somites free, male abdomen completely occupying space between coxae of fifth pereopods (Fig. 3.4, arrow D); sternite 8 not visible.

Material examined.—*Xanthilites* [sic] *bowerbanki*, CM 38700, from the Eocene London Clay of Sheppey, England.

Discussion.—The genus *Xanthilites* has become a catchall genus for Paleocene and Eocene xanthoid taxa that are wider than long and have well-developed anterolateral spines (Table 3). *Xanthilites* is herein restricted to the type species, *X. bowerbanki*, and questionably *X. interpunctus*, as discussed below. No other species referred to the genus displays dorsal carapace or ventral characters congruent with those of *X. bowerbanki*.

Xanthilites interpunctus has had a convoluted history. It was originally referred to *Cancer* Linnaeus, 1758, and was later placed within *Xanthilites* (Glaessner, 1929). The original material is fragmental, and based upon the original illustration (Schafhäütl, 1863, fig. 1), it is not possible to determine the specimen's generic placement. Förster (1970, p. 250, abb. 4) published a drawing of *X. interpunctus*, clearly based upon a different, more complete specimen. As drawn, that specimen looks very much like the specimen of *X. cretacea* Segerberg, 1900, illustrated by Collins and Jakobsen (1994), and is only in a broad sense similar to Schafhäütl's original illustration of *X. interpunctus*. Unfortunately, there is no specimen number given for Förster's (1970) illustrated specimen. Further complicating the matter, Glaessner (1929) synonymized *X. bavaricus* Lörenthey, 1898 with *X. interpunctus*. Examination of Lörenthey's illustration (1898, pl. XI, fig. 2) suggests that it is only superficially similar to Schafhäütl's holotype of *X. interpunctus*. Unfortunately, Lörenthey's (1898) material, which was deposited in the Bayerische Staatssammlung in Munich, was apparently destroyed during World War II, according to the late R. Förster (P. Müller, personal commun., 2003). For now, I questionably refer *X. interpunctus* to the genus, and *Xanthilites bavaricus* is best retained as a separate species until material referable to the species can be examined.

Several species previously referred to *Xanthilites* have already been removed from the genus (Table 3).? *Xanthilites rathbunae* Withers, 1924 and *X. traubi* Förster, 1970 are fragmental and cannot be assigned with confidence to any family. *Colpocaris* von Meyer, 1863 was previously synonymized with *Xanthilites* (Glaessner, 1969), but examination of the illustration in von Meyer (1863, pl. 16, fig. 15) suggests that it should remain a distinct genus. The various dorsal carapace swellings of *Colpocaris bullata* von Meyer, 1863 are quite distinctive and are unlike *Xanthilites* s.s., or for that matter, any other species previously referred to *Xanthilites*. Type material needs to be examined to make a family-level placement for *Colpocaris*. *Xanthilites cretacea* was questionably referred to the genus; herein, *X. cretacea* is referred to *Jakobsenius* n. gen. described below.

Xanthilites macrodactylus was described by Van Straelen (1925) from the Montien (Paleocene) of France. That species as illustrated clearly does not belong within *Xanthilites*, due to the extremely produced, bifurcated front; broad, quadrate orbits; large penultimate anterolateral spine; and small circular swellings on the dorsal carapace. However, because the only illustrations are of poor quality, type material will need to be examined to determine the proper placement of this strange form.

Family PLATYXANTHIDAE Guinot, 1977

Figure 2

Included genera.—*Homolaspis* A. Milne Edwards, 1863; *Pelaeus* Eydoux and Souleyet, 1842 (fossil and extant); *Platyxanthus* A. Milne Edwards, 1863 (list from Guinot, 1978).

Diagnosis.—Carapace hexagonal, wider than long, length about two-thirds maximum carapace width, ranging from 0.63 to 0.70; front with four spines excluding inner-orbital projections or nearly straight with central notch, frontal width about 0.2 maximum carapace width, ranging from 0.13 to 0.24; orbits with fissures, usually two, fronto-orbital width about 0.36 maximum carapace width, ranging from 0.33 to 0.38. Anterolateral margins moderately convex; many possible configurations, either with numerous blunt spines, or with broad, bluntly spinose lobes separated by fissures, or with broad, entire lobes separated by fissures; last anterolateral spine extending posteriorly and axially onto dorsal carapace; angle of posterolateral to posterior margin about 38 degrees; posterior width about 0.38 maximum carapace width, ranging from 0.36 to 0.41. Carapace regions poorly defined, protogastric and hepatic regions weakly inflated. Chelae stout, smooth, coxa of first pereopod articulating with merus, merus not fused to basis-ischium. Sternum relatively straight or rather wide,

sternal sutures 4–5 and 5–6 not continuous; suture between sternites 2 and 3 complete; suture between sternites 3 and 4 deep, well developed laterally but becoming a shallow groove axially, merging with long groove extending anteriorly from sterno-abdominal cavity to form deep, Y-shaped groove pattern; all male abdominal somites free, male abdomen barely reaching or not reaching level of posterior margin of coxae of first pereopods. Male pleopod 1 stout; male pleopod 2 long, with an elongated proximal article and a developed flagellum (after Guinot, 1978; Coelho and Coelho Filho, 1993).

Material examined.—*Homolaspis plana* (H. Milne Edwards, 1834), USNM 65034; *Platyxanthus orbigny* (H. Milne Edwards and Lucas, 1843), USNM 40412.

Discussion.—The diagnostic features of the Platyxanthidae are very similar to those of the Eriphiidae; however, those features have been considered to be plesiomorphic (Guinot, 1978). The family status of the Platyxanthidae is supported by adult morphology (Guinot, 1978; Coelho and Coelho Filho, 1993) and larval morphology (Clark and Galil, 1988). Martin and Davis (2001) maintained the family status in their update of the Crustacea. Differences between the Platyxanthidae, the Eriphiidae, and the Tumidocarcinidae have been discussed above.

Guinot (1967, 1978) suggested that *Pseudocarcinus chauvinii* de Berville, 1857 (later referred to *Menippe* by A. Milne Edwards, 1863) (Fig. 2.5, 2.6) may be referable to the extant genus *Pelaeus*, based upon the striking similarities between these taxa; I concur. The carapace proportions are nearly identical between *Pseudocarcinus chauvinii* and the Platyxanthidae and differ slightly from those for the Eriphiidae (Table 1). In addition, the last anterolateral spine of *Pseudocarcinus chauvinii* is longest, sharp, and projects laterally; the last anterolateral spine in *Pelaeus* also bears this configuration which is not seen in the Eriphiidae. The formal referral of *Pseudocarcinus chauvinii* to *Pelaeus* constitutes the first documented fossil occurrence of the Platyxanthidae, extending its stratigraphic range into the Eocene (A. Milne Edwards, 1865), suggesting that the Xanthoidea was diverse and well established by that time.

Family PALAEOXANTHOPSIDAE Schweitzer, 2003a

Figure 4

Included genera (all fossils).—*Jakobsenius* n. gen.; *Lobulata* Schweitzer, Feldmann, and Gingerich, 2004; *Palaioxanthopsis* Beurlen, 1958; *Paraverrucoides* Schweitzer, 2003a; *Remia* Schweitzer, 2003a; *Rocacarcinus* n. gen.; *Verrucoides* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001.

Emendation to diagnosis.—Carapace widest just over half to two-thirds the distance posteriorly on carapace. Orbits with two fissures or faint sutures. Carapace regions may be moderately to weakly swollen; V-shaped groove outlining gastric regions may be moderately or very deeply incised. Sternum with no evidence of suture between sternites 2 and 3; left and right sutures between sternites 3 and 4 merging with deep groove extending anteriorly from sterno-abdominal cavity forming a prominent Y-shaped groove pattern; suture between sternite 3 and 4 oriented at high angle; sternite 4 with very large episternal projection extending laterally beyond margin of sternite 4. After Schweitzer (2003a).

Discussion.—Since the family was erected, several new genera have been referred to it, based upon study of several Atlantic taxa previously referred to *Lobonotus* and *Xanthilites*. Some of the diagnostic characters display a broader range of variation than was originally reported (Schweitzer, 2003a); however, the family is still quite tightly constrained morphologically. The diagnosis is herein emended to reflect the range of variation in carapace ornamentation seen in members of the family. Recent preparation of the sternum of a specimen of *Lobulata lobulata* (Fig. 4.5) adds

TABLE 4—Measurements (in mm) taken on the dorsal carapace of specimens of *Rocacarcinus gerthi* (Glaessner, 1930). W1, maximum carapace width; L1, maximum carapace length; L2, length to position of maximum width; FOW, fronto-orbital width; FW, frontal width; PW, posterior width.

Specimen number	W1	L1	L2	FOW	FW	PW
GHUNLPam 7010	15.7	13	7.1	8.9	4.3	6.8
GHUNLPam 7019	29.4	24.4	13.9	14.8	7.6	N/A
GHUNLPam 7048	23.8	17.3	10.2	13	6.8	N/A

sternal details previously unknown. It is probable that the specimen is a male, due to the narrow sterno-abdominal cavity and lack of obvious gonopores, but the lack of the abdomen makes this impossible to confirm. Recovery and description of aspects of the male abdomen are still sorely needed for this family.

Genus ROCACARCINUS new genus

Figure 4.1–4.3

Xanthilites BELL, 1858 (part). GLAESSNER, 1930, p. 5; FELDMANN ET AL., 1995, p. 12.

Type species.—*Xanthilites gerthi* Glaessner, 1930.

Diagnosis.—Carapace wider than long, L/W about 0.80, widest at position of last anterolateral spine a little more than half the distance posteriorly on carapace; frontal width about 27 percent maximum carapace width, width broad, V-shaped axial notch, front downturned, medial two spines project well beyond orbits, inner-orbital angles very weak, blunt projection; orbits circular, projected forward, with flared rim and two clear orbital fissures positioned near outer-orbital angle, outer-orbital spine triangular, projecting anterolaterally; fronto-orbital width just over half maximum carapace width. Anterolateral margin with four anterolateral spines not including triangular outer-orbital spine; first spine nearly straight, very weakly projected; second and third anterolateral spines quadrate with triangular, pointed tips, edges serrate; last spine longer, needlelike, directed laterally; deep fissures separating each anterolateral spine; carapace with upturned anterolateral margins when viewed anteriorly. Posterolateral margin weakly concave; posterior margin weakly concave.

Carapace regions developed as broad swellings; epigastric regions circular, more or less prominently swollen; hepatic region with broad central swelling; urogastric region markedly depressed; epibranchial region well developed, arcuate, composed of two swellings; remainder of branchial region undifferentiated, with weak oblong swelling parallel to epibranchial region, continuous with weak transverse ridge on cardiac region.

Sternum of female longer than wide; suture between sternites 2 and 3 continuous, deep; suture between sternites 3 and 4 deep laterally, becoming a narrow groove medially, interrupted at axis; sternite 4 with weakly developed grooves from fusion of episternite 3 to sternite 4, long groove extending from sterno-abdominal cavity onto sternite 4; female abdomen reaching level of base of coxae of first pereopods.

Etymology.—The generic name is derived from the Greek *karkinos*, meaning crab, and the name of the formation from which much of the material was collected, the Roca Formation of southern Argentina (Feldmann et al., 1995). The gender is masculine.

Material examined.—GHUMLPam 7019, 7010, 7048.

Measurements.—Measurements (in mm) of the dorsal carapace are presented in Table 4.

Occurrence.—The genus is known only from Maastrichtian (Cretaceous) and Danian (Paleocene) rocks of Patagonia, Argentina (Glaessner, 1930; Feldmann et al., 1995).

Discussion.—The type specimen and other material referred to *Xanthilites gerthi* differ significantly from *X. bowerbanki*; it is

herein placed within *Rocacarcinus*. *Rocacarcinus gerthi* (Glaesner, 1930) has a projected, downturned front that is very weakly quadrilobed; neither of these features is seen in *Xanthilites* s.s. The anterolateral margins of *Xanthilites* s.s. have weak spines and lack the strong, rectangular anterolateral spines separated by fissures and scalloped appearance seen in *R. gerthi*. The carapace of *R. gerthi* is much less vaulted than that of *Xanthilites* s.s., and the regions of *R. gerthi* are much more poorly delineated than in *Xanthilites* s.s. *Rocacarcinus gerthi* has two orbital fissures, while *Xanthilites* s.s. lacks orbital fissures. Thus, the two species are clearly not congeneric.

The new genus, *Rocacarcinus*, is monospecific and is placed within the Palaeoxanthopsidae, based upon its overall carapace proportions; two orbital fissures; deeply axially notched and prominently four-lobed front; rectangular anterolateral spines separated by fissures, the first of which is a nearly straight segment; long, attenuated last anterolateral spines; arcuate epibranchial region; and transverse swellings on the cardiac and branchial regions which form a weak but nearly continuous ridge. The upturned, crispate anterolateral margins of *Rocacarcinus* are seen in other genera within the family, notably *Paraverrucoides* Schweitzer, 2003a, and *Lobulata* Schweitzer et al., 2004.

Rocacarcinus differs from other paleoxanthopsids in lacking prominent spherical swellings on the dorsal carapace, a deep groove separating the protogastric regions from the hepatic regions, and in having the position of maximum width only a little more than half the distance posteriorly rather than at about two-thirds the distance posteriorly. The nearly continuous branchial and cardiac ridges are very much more weakly developed in *Rocacarcinus* than in other genera within the family. In addition, the buccal frame and maxillipeds appear to be significantly shorter in *Rocacarcinus* than in *Lobulata*, which is the only genus of the Palaeoxanthopsidae for which well-preserved ventral carapace regions are known. Collection of a male sternum of *Rocacarcinus gerthi* could help to reinforce the family placement of the taxon.

Genus JAKOBSENIUS new genus

Figure 4.4

Xanthilites BELL, 1858 (part). SEGERBERG, 1900, p. 375, pl. 9, figs. 19, 20; COLLINS AND JAKOBSEN, 1994.

Type species.—*Xanthilites cretacea* Segerberg, 1900.

Diagnosis.—Carapace wider than long, L/W about 0.75, widest at position of last anterolateral spine, about 60 percent the distance posteriorly on carapace; flattened transversely and moderately vaulted longitudinally, especially in anterior third; front poorly known, downturned, appearing to have had four spines, about 30 percent maximum carapace width; orbits angular, directed forward, with two clear orbital fissures positioned near outer orbital spine, fronto-orbital width a little over half maximum carapace width. Anterolateral margin with four spines excluding small outer orbital spine; first spine barely developed, almost a straight segment, second and third spines rectangular with triangular tips; last spine needlelike, sharp, directed laterally; all spines separated by broad fissures. Posterolateral and posterior margins nearly straight, posterior margin about 40 percent maximum carapace width, rimmed.

Epibranchial regions slightly swollen, rectangular; protogastric region bounded by relatively deep grooves on outer margin; hepatic region with longitudinal central swelling; axial regions flattened; epibranchial region arcuate, composed of two parts, outermost part a nearly straight, ridgelike segment, inner part a triangular swelling; remainder of branchial region undifferentiated, with very weak swelling along central posterolateral margin.

Etymology.—The genus commemorates Mr. Sten L. Jakobsen, Geological Museum Copenhagen, Denmark, for his contribution

to our understanding of Paleogene crabs from northern Europe. The gender is masculine.

Material examined.—Plaster cast of MGUH 2483 produced from Exaflex® mold.

Measurements.—Measurements (in mm) taken on a cast of MGUH 2483: carapace width, 37.2; carapace length, 27.6; fronto-orbital width, 19.2; frontal width, 10.8; posterior width, 15.6; length to position of maximum width, 16.3.

Occurrence.—The genus is known from Cretaceous rocks of Sweden and Danian rocks of Denmark (Collins and Jakobsen, 1994).

Discussion.—Segerberg (1900) referred two xanthoid specimens questionably to *Xanthilites*. Those specimens, as well as another figured by Collins and Jakobsen (1994), are herein placed within a new genus, *Jakobsenius*. *Jakobsenius cretacea* (Segerberg, 1900) is not a member of *Xanthilites* s.s. because it possesses a downturned front, orbits with two fissures, and quadrate anterolateral spines separated by broad fissures, none of which is present in *Xanthilites* s.s. These features, especially the possession of orbital fissures and the nature of the anterolateral margin, are very distinctive and easily separate the species into different genera. In addition, *J. cretacea* has a broader fronto-orbital width to width ratio than that seen in *Xanthilites* s.s.

Jakobsenius is placed within the Palaeoxanthopsidae based upon its two orbital fissures, quadrate anterolateral spines separated by fissures and separated from outer-orbital spine by a straight segment, a long, attenuated last anterolateral spine that is directed laterally, a position of maximum width about 60 percent the distance posteriorly on carapace, a deep groove outlining the outer margins of the protogastric regions, and epibranchial regions arcuate. *Jakobsenius* differs from other paleoxanthopsids in lacking well-developed swellings on the dorsal carapace regions and especially on the branchial regions which are flattened. Other paleoxanthopsids have at least some degree of swelling in this area.

Jakobsenius is similar to *Rocacarcinus* n. gen. described above but differs from it in several important aspects. The first anterolateral spine of *Jakobsenius* is not really a spine at all but a nearly straight segment separated from the second anterolateral spine by a fissure; in *Rocacarcinus* the first anterolateral spine is well developed. The position of maximum carapace width in *Rocacarcinus* is a little less than half the distance posteriorly, while in *Jakobsenius* it is about 60 percent the distance posteriorly. The epibranchial region of *Jakobsenius* has a very distinctive transverse ridge beginning just proximal to the last anterolateral spine. Such a ridge is not seen in *Rocacarcinus*, and dorsal carapace ornamentation is an important feature at the generic level within the family. The dorsal carapace of *Jakobsenius* is much more vaulted longitudinally than in *Rocacarcinus*, which has a relatively flattened carapace longitudinally. *Rocacarcinus* possesses spherical, swollen epigastric regions which are absent in *Jakobsenius*.

Family HEXAPODIDAE Miers, 1886

Included genera.—*Goniocypoda* Woodward, 1867 (fossil only); *Hexapinus* Manning and Holthuis, 1981; *Hexaplex* Doflein, 1904; *Hexapus* de Haan, 1833 (fossil and extant); *Lambdophallus* Alcock, 1900; *Latohexapus* Huang, Hsueh, and Ng, 2002; *Paeduma* Rathbun, 1897; *Palaeopinnixa* Via, 1966 (fossil); *Parahexapus* Balss, 1922; *Pseudohexapus* Monod, 1956; *Spiroplax* Manning and Holthuis, 1981; *Stevea* Manning and Holthuis, 1981 (fossil and extant); *Thaumastoplax* Miers, 1881; *Tritoplax* Manning and Holthuis, 1981; all are extant only unless otherwise marked.

Diagnosis.—See Schweitzer and Feldmann (2001a).

Discussion.—The family has recently been treated (Schweitzer and Feldmann, 2001a; Huang et al., 2002); those discussions need



FIGURE 5—Representatives of the Hexapodidae Miers, 1886. 1, *Goniocyropa tessieri* Remy in Remy and Tessier, 1954, plaster cast of specimen designated as RO3884, cotype; 2, *G. tessieri*, plaster cast of specimen designated as RO3884, cotype. Scale bars = 1 cm.

not be repeated here. *Globihexapus* Schweitzer and Feldmann, 2001a was removed to the Pinnotheridae by Nyborg (2002); I concur.

Genus GONIOCYPODA WOODWARD, 1867

Goniocyropa WOODWARD, 1867, p. 529–531, pl. XXI, fig. 1.

Included species.—See Schweitzer and Feldmann (2001a); *Goniocyropa tessieri* Remy in Remy and Tessier, 1954 is herein confirmed as a member of the genus.

Diagnosis.—See Schweitzer and Feldmann (2001a).

Occurrence.—Maastrichtian to Eocene of the Tethyan region (Schweitzer and Feldmann, 2001a).

GONIOCYPODA TESSIERI Remy in Remy and Tessier, 1954
Figure 5

Goniocyropa tessieri REMY IN REMY AND TESSIER, 1954, p. 190, pl. XI, fig. 4, text-fig. 1b.

Description.—Carapace rectangular, weakly ornamented; posterolateral reentrant well developed; point of maximum width of dorsal carapace just anterior to posterolateral reentrants; lateral margins ridged; posterior margin about 75 percent maximum carapace width.

Material examined.—RO3884, holotype, comprised of two specimens, and casts of the material prepared by the author.

Occurrence.—Maastrichtian rocks of Senegal (Remy in Remy and Tessier, 1954).

Discussion.—The placement of *Goniocypoda tessieri* in the Hexapodidae had been questioned based upon the poor illustrations of the material (Schweitzer and Feldmann, 2001a). Examination of the type material confirms that the material is hexapodid in nature (Fig. 2.1, 2.2). All of its carapace features fall well within the diagnosis for the Hexapodidae and for *Goniocypoda* (Schweitzer and Feldmann, 2001a). Thus, the genus and family are confirmed as extending into the Maastrichtian.

DISCUSSION

General.—The fossil Xanthoidea has received little directed attention until recently, with some notable exceptions (see Schweitzer, 2003b for a summary). Recent work on the fossil Xanthoidea has resulted in the definition of several new families (Schweitzer, 2003a) and subfamilies (Karasawa and Kato, 2003a). Because the group has had a convoluted and difficult history in the biological literature, this revision should not be surprising (Schweitzer, 2003b). Biologists working with extant xanthoids have recently (in the last decade or less) elevated various subfamilies, alliances, or tribes of the older literature to family status; for example, the Pseudorhombilidae elevated by Hendrickx (1998), and the Pseudoziidae, elevated by Ng and Liao (2002). New subfamilies also have been recognized by Ng and Clark (2000b) and Karasawa and Kato (2003a). The large number of fossil xanthoid genera that have yet to be reevaluated within the context of the current biological classification of the Xanthoidea may result in additional elevations of subfamilies to family status and the creation of new subfamilies and families.

Origins of the Xanthoidea s.l.—Based upon the referrals herein, the extant xanthoid families now known from the Eocene or earlier include the Carpiliidae, Eriphiidae, Goneplacidae, Hexapodidae, Panopeidae, Pilumnidae, Pseudoziidae, and Trapeziidae (Schweitzer, 2003a, 2003b; Schweitzer and Karasawa, 2004; Schweitzer et al., 2004). In addition, there are three extinct xanthoid families known from the Eocene—the Palaeoxanthopsidae, Tumidocarcinidae, and Zanthopsidae.

Those families known from pre-Eocene occurrences include the Carpiliidae, Goneplacidae, Hexapodidae, Palaeoxanthopsidae, Panopeidae, and Zanthopsidae (Schweitzer, 2003a, 2003b; Karasawa and Schweitzer, 2004). Of these, the Goneplacidae, Hexapodidae, and Palaeoxanthopsidae are known from the Cretaceous; however, some of these Cretaceous families may not be good candidates for embracing the forms ancestral to extant xanthoids. The Goneplacidae is known from at least one confirmed Cretaceous occurrence. The extinct Late Cretaceous *Icriocarcinus* Bishop, 1988, from Pacific coastal Baja California (Schweitzer et al., 2002), is nearly identical to the extant *Ommatocarcinus* White, 1852. Such conservatism is usually seen in ecological generalists or eurytopic taxa (Harries et al., 1996). The marked conservatism in at least this particular goneplacid lineage suggests that some Goneplacidae may not be the best candidate for embracing the ancestral xanthoids. However, it must be cautioned that this family as currently construed (Karasawa and Kato, 2003a, 2003b) is quite heterogeneous, so that it is probably best to look at individual taxa within the group when attempting to reconstruct ancestry within the Xanthoidea.

The Hexapodidae, now known with certainty from the Cretaceous, comprise a very specialized family, with small, rectangular carapaces and reduced numbers of pereopods and sternites, adaptations for living in worm tubes (Schweitzer and Feldmann, 2001a). Such conserved specialization suggests that the family is unlikely to have given rise to the other xanthoids, and in fact,

other authors have considered them to be very specialized goneplacids (Manning and Holthuis, 1981). In addition, conserved specialization across a major mass extinction event is likely very unusual, especially since the family was known from the tropical and equatorial Atlantic Ocean, proximal to the Chicxulub impact site. Perhaps the lineage survived as refugium species (Kauffman and Harries, 1996) and thus repopulated during the post-Cretaceous recovery.

The referral of two additional genera to the Palaeoxanthopsidae brings the total number of genera embraced by the family to seven. The family was well established by Late Cretaceous time and was successful well into the Paleogene. The family inhabited the proto-Atlantic Ocean, ranging from localities as far north as Denmark to those in southern South America. The relatively small size of the Atlantic Ocean during the Late Cretaceous undoubtedly contributed to the rapid expansion of the family throughout that basin. Interestingly, the Chicxulub Impact occurred in the very region that also saw the evolution and radiation of the Palaeoxanthopsidae. The family survived into the Paleocene and Eocene within the region as new and different genera, although their post-Cretaceous numbers were reduced (two known genera). However, other decapod families that existed in the region during the Late Cretaceous, including the Carcineretidae Beurlen, 1930 and Dakoticancridae Rathbun, 1917 (Feldmann et al., 1998; Bishop et al., 1998), became extinct by the end of the Cretaceous, with last records in the Maastrichtian. Perhaps the Palaeoxanthopsidae embraced some “preadapted survivors” (Kauffman and Harries, 1996), taxa with adaptations facilitating survival during rapid environmental changes and catastrophic events. This apparent ability to adapt to new conditions contributed to the group’s successful survival of the end-Cretaceous event, and this very adaptability makes the group a good candidate for continued investigation into the origins of at least some of the Xanthoidea. The subsequent extinction of the family may be a pseudoextinction, because the Palaeoxanthopsidae may have given rise to many of the extant lineages comprising the Xanthoidea.

Affinities within the Xanthoidea s.l.—Any investigation into the origins of the Xanthoidea is bound to be impeded by a vexing problem: there is no good definition for the superfamily (D. Guinot, personal commun., 2003). The superfamily embraces crabs that are, in general, wider than long and have well-marked gastric, hepatic, and branchial regions (usually); an arcuate epibranchial region; four to six frontal spines, including the inner orbital spines; and anterolateral margins generally with spines or lobes but that may be entire. All xanthoids are heterotremes, but there is marked variability in the location of the male genital openings among members of the group (Guinot, 1978). In addition, there is broad variability in the group in the nature of a large number of characters of the sternum and male abdomen (Guinot, 1978). For example, in the Xanthidae s.s., the sternum is very narrow and straight, reminiscent of crabs generally thought to be more primitive, such as the Calappidae H. Milne Edwards, 1837 and Parthenopidae MacLeay, 1838. Other groups, such as the Goneplacidae and Hexapodidae, have broad, ovate sterna; still others have sternal shapes of intermediate width and degree of ovateness. Even more variation exists in the nature of the fusion of male sternites and abdominal somites, size and visibility of the eighth sternite, and numerous other characters.

There are several possible resolutions to the problem of the definition of the Xanthoidea. Von Sternberg and Cumberlidge (2001) have already suggested that the Xanthoidea as currently understood is polyphyletic. It has been suggested that the Goneplacidae should be placed in a distinct superfamily (d’Udekem d’Acoz, 1999; Collins et al., 2003); if such a move is made, the Hexapodidae must go with them (but see Guinot, 1969, who considered the Hexapodoidea as a separate superfamily). Along these

lines, Collins et al. (2003) placed the Goneplacidae, Hexapodidae, and Pilumnidae within the Goneplacoidea, but did not provide an explanation of the relationships they perceived among the three families.

It seems possible that the Xanthidae s.s., characterized by very narrow sterna, very well-marked regions (usually), and concave posterolateral margins into which the last pereopods fit (Davie, 2002), may be best placed in a superfamily separate from some of the other families with which they are now associated, and possibly as an evolutionary descendant of the Dynomenidae (Wright and Collins, 1972), which originated in the Late Jurassic, or the Late Cretaceous Etyiidae Guinot and Tavares, 2001. That superfamily could well contain other xanthoid families; for example, Wetzter et al. (2003) showed that the Panopeidae, now known to extend into the Paleocene (Karasawa and Schweitzer, 2004), may have affinities with the Xanthidae s.s. They also suggested that the current concept of the Xanthoidea may not be a viable, monophyletic group, due to weak bootstrap support (Wetzter et al., 2003). Investigation of such hypotheses in terms of the fossil record is ongoing.

Schweitzer (2003a) suggested that the Carpiliidae, Zanthopsidae, and Eriphiidae were closely related based upon paleontological and neontological evidence. The close relationship of the Platyxanthidae with the Eriphiidae, and the marked similarity in sternal features between the Platyxanthidae and the Tumidocarcinidae, suggest that these five families comprise a natural group and might warrant a separate superfamily. As all have fossil records extending into the Eocene, it is likely that they share a common ancestor that is pre-Eocene and that the families diverged sometime during the Paleocene or early Eocene (Schweitzer, 2003a). In their analysis of mitochondrial DNA, Wetzter et al. (2003) showed that the Carpiliidae may be closely related to the Eriphiidae (=Menippidae in their paper), adding to the mounting evidence for this close relationship. Schweitzer and Feldmann (2001b) suggested that the origin of the Xanthoidea may lie in a common ancestor of the group with the Portunoidea Rafinesque, 1815, based upon the similarity in dorsal carapace shape and ornamentation of Paleocene and Eocene xanthoids and portunoids. A recent analysis of several heterotreme and thoracotreme brachyurans based upon 16S rDNA shows that several species of *Menippe* (Eriphiidae) cluster with members of the Cancridae Latreille, 1802 and Portunidae Rafinesque, 1815 (Schubart et al., 2000; Schram, 2001). This supports the hypothesis of Schweitzer and Feldmann (2001b) that early xanthoids may be derived from a common ancestor of the Portunoidea and Xanthoidea and possibly the Cancridae as well. As more Eocene and Paleocene occurrences are studied (in progress by the author and others), these hypotheses about the origins of the lineages of the Xanthoidea can be tested.

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REFERENCES

- AGUIRRE-URRETA, M. B., S. MARENSSI, AND S. SANTILLANA. 1995. A new Eocene crab (Crustacea, Decapoda) from Seymour Island, Antarctica. *Antarctic Science*, 7:277-281.
- ALCOCK, A. 1898. The family Xanthidae: the Brachyura Cyclometopa, Pt. I, Material for a carcinological fauna of India, No. 3. *Journal of the Asiatic Society of Bengal*, 67(II:1):67-233.
- ALCOCK, A. 1900. Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. *Journal of Asiatic Society of Bengal*, 69, 2(3):279-456.
- ARTAL, P., AND L. VIA. 1988. *Xanthilites macrodactylus pyrenaicus* (Crustacea, Decapoda) nueva subespecie del Ilerdiense medio del Pirineo de Huesco. *Batalleria*, 2:57-61.
- BALSS, H. 1922. Decapoda Brachyura (Oxyryncha und Brachyryncha) und geographische Übersicht über Crustacea Decapoda: Crustacea VII, p. 70-110, figs. 1-5. In W. Michaelsen, Beiträge zur Kenntnis der Meeresfauna Westafrikas (Hamburg), 3 (3).
- BALSS, H. 1957. Decapoda, VIII: Systematik, p. 1505-1672, figs. 1131-1199. In H. G. Bronn, Klassen und Ordnungen des Tierreichs, Band 5, Abteilung 1, 7(12).
- BELL, T. 1858. A monograph of the fossil malacostracous Crustacea of Great Britain, Pt. I, Crustacea of the London Clay. *Palaeontographical Society Monograph*, London, 44 p.
- BEURLEN, K. 1930. Vergleichende Stammesgeschichte Grundlagen, Methoden, Probleme unter Besonderer Berücksichtigung der höheren Krebse. *Fortschritte Geologie und Palaeontologie*, 8:317-586.
- BEURLEN, K. 1958. Contribuição a paleontologia do Estado do Pará, Crustaceos decápodos da Formação Pirabas. *Boletim Museum Paraense Emilio Goeldi, n. s. (geol.)*, 5:2-48, 4 pls.
- BISHOP, G. A. 1988. Two crabs, *Xandaros sternbergi* (Rathbun, 1926) n. gen., and *Icriocarcinus xestos* n. gen., n. sp., from the Late Cretaceous of San Diego County, California, USA, and Baja California Norte, Mexico. *Transactions of the San Diego Society of Natural History*, 21: 245-257.
- BISHOP, G. A., R. M. FELDMANN, AND F. J. VEGA. 1998. The Dakoticancridae (Decapoda, Brachyura) from the late Cretaceous of North America and Mexico. *Contributions to Zoology*, 67:237-255.
- BOUVIER, E.-L. 1922. Observations complémentaires sur les Crustacés décapodes (Abstraction faite les Carides) provenant des Campagnes de S. A. S. le Prince de Monaco. Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert 1er Prince Souverain de Monaco, 62:1-106, pls. 1-6.
- CASADÍO, S., A. DE ANGELI, R. M. FELDMANN, A. GARASSINO, J. L. HETLER, A. PARRAS, AND C. E. SCHWEITZER. 2004. New decapod crustaceans (Thalassinidea, Brachyura) from the late Oligocene of Patagonia, Argentina. *Annals of Carnegie Museum*, 73:25-47.
- CLARK, P. F., AND B. S. GALIL. 1988. Redescriptions of *Tetralia cavimana* Heller, 1861 and *Trapezia cymodoce* Herbst, 1799: first stage zoeas with implications for classification within the superfamily Xanthoidea (Crustacea Brachyura). *Proceedings of the Biological Society of Washington*, 101:853-860.
- COELHO, P. A., AND P. A. COELHO FILHO. 1993. Proposta de classificação da família Xanthidae (Crustacea, Decapoda, Brachyura) através da taxonomia numérica. *Revista Brasileira de Zoologia*, 10(4):559-580.
- COLLINS, J. S. H., AND S. L. JAKOBSEN. 1994. A synopsis of the biostratigraphic distribution of the crab genera (Crustacea, Decapoda) of the Danian (Palaeocene) of Denmark and Sweden. *Bulletin of the Mizunami Fossil Museum*, 21:35-46, 1 pl.
- COLLINS, J. S. H., AND H. W. RASMUSSEN. 1992. Upper Cretaceous-

- Lower Tertiary decapod crustaceans from west Greenland. Grønlands Geologiske Undersøgelse Bulletin, 162:1–46.
- COLLINS, J. S. H., C. LEE, AND J. NOAD. 2003. Miocene and Pleistocene crabs (Crustacea, Decapoda) from Sabah and Sarawak. *Journal of Systematic Paleontology*, 1:187–226.
- COLOSI, G. 1923. Una specie fossile de Gerionide (Decapodi brachiuri). *Bolettino della Società dei Naturalisti in Napoli*, 35(series 2, vol. 15), 37:248–255.
- DANA, J. D. 1851. On the classification of the Cancroidea. *American Journal of Sciences and Arts*, 12(34):121–131.
- DANA, J. D. 1853. On the classification and geographical distribution of Crustacea from the report on Crustacea of the United States Exploring Expedition, under Captain Charles Wilkes, U.S.N., during the years 1838–1842. C. Sherman, Philadelphia, p. 1395–1592, 1 map.
- DAVIE, P. J. F. 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda–Anomura, Brachyura, 641 p. *In* A. Wells and W. W. K. Houston (eds.), *Zoological Catalogue of Australia*, 19.3B. CSIRO Publishing, Melbourne, Australia.
- DE BERVILLE, P. 1857. Note sur une nouvelle espèce de Crustacés fossiles trouvé dans le Calcaire Grossier inférieur. *Bulletin de la Société Géologique de France*, série 2, 14:108–117, pl. 2.
- DE HAAN, W. 1833–1850. Crustacea, p. i–xvii, i–xxxii, ix–xvi, 1–243, pls. A–J, L–Q, 1–55, circ. tab. 2. *In* P. F. Von Siebold, *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit, J. Müller, Lugduni-Batavorum (=Leiden)*.
- DESBONNE, I., AND A. SCHRAMM. 1867. Crustacés de la Guadeloupe d'après un manuscrit du. . . I. Desbonne comparé avec les échantillons de Crustacés de sa collection et les dernières publications de MM. H. De Saussure et W. Stimpson. I. Partie. Brachyures. Published by the authors, 60 p., 8 pls.
- DOFLEIN, F. 1904. Brachyura. *In* *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*, 6. Verlag von Gustav Fischer, Jena, 314 p. + atlas, pls. 1–38.
- D'UDEKEM D'ACOSTA, C. 1999. Inventaire et distribution des Crustacés de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25N. Service du Patrimoine Naturel, Institut d'Écologie et de Gestion de la Biodiversité, Paris, 383 p.
- EYDOUX, F., AND L. F. A. SOULEYET. 1842. Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette la Bonite, commandée par M. aillant, etc., *Zoologie*, p. xxxvii–334, atlas, pls. 1–101. Crustacés, 1, 2nd partie, p. 219–250, pls. 1–3.
- FABRICIUS, J. C. 1781. *Species insectorum exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adiectis observationibus, descriptionibus*. C. E. Bohnii, Hamburg, viii + 552 p.
- FABRICIUS, J. C. 1798. *Supplementum Entomologiae Systematicae*. Proft et Storch, Hafniae (=Copenhagen), 572 p.
- FELDMANN, R. M. 1998. Parasitic castration of the crab, *Tumidocarcinus giganteus* Glaessner, from the Miocene of New Zealand: coevolution within the Crustacea. *Journal of Paleontology*, 72:493–498.
- FELDMANN, R. M. 2003a. The Decapoda: new initiatives and novel approaches. *Journal of Paleontology*, 77:1021–1039.
- FELDMANN, R. M. 2003b. Interpreting ecology and physiology of fossil decapod crustaceans. *Contributions to Zoology*, 72:111–117.
- FELDMANN, R. M., F. J. VEGA, AND T. VILLAMIL. 1998. Cretaceous extinction of the Tethyan crab family Carcineretidae: a victim of the impact? *Geological Society of America Abstracts with Programs*, 39:A286.
- FELDMANN, R. M., S. CASADÍO, L. CHIRINO-GALVEZ, AND M. AGUIRRE-URRETA. 1995. Fossil decapod crustaceans from the Jaguel and Roca formations (Maastrichtian–Danian) of the Neuquén Basin. *The Paleontological Society Memoir* 43 (supplement to *Journal of Paleontology*, 69), 22 p.
- FÖRSTER, R. 1970. Zwei neue brachyure Krebse aus dem Paläozän des Haunsberges nördlich von Salzburg. *Mitteilungen Bayerischen Staatssammlung Paläontologische und Historische Geologie*, 10:241–252.
- FRAAYE, R. H. B., AND H. SUMMESBERGER. 1999. New crustacean records from the Late Campanian of the Gschliefgraben (Cretaceous, Austria). *Beiträge zur Paläontologie*, 24:1–6.
- GLAESSNER, M. F. 1929. Crustacea Decapoda, p. 1–464. *In* J. F. Pompeck (ed.), *Fossilium Catalogus I: Animalia*, Pt. 41. W. Junk, Berlin.
- GLAESSNER, M. F. 1930. Neues Krebsreste aus der Kreide. *Jahrbuch der Preussischen Geologischen Landesanstalt zu Berlin*, 51:1–7, pl. 1.
- GLAESSNER, M. F. 1960. The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. New Zealand Department of Scientific and Industrial Research, New Zealand Geological Survey, *Palaeontological Bulletin*, 31:5–79.
- GLAESSNER, M. F. 1969. Decapoda, p. R400–R566, R626–R628. *In* R. C. Moore (ed.), *Treatise on Invertebrate Paleontology*, Pt. R, Arthropoda 4. Geological Society of America and University of Kansas Press, Lawrence.
- GRAY, J. E. 1831. Description of a new genus, and some undescribed species of Crustacea, p. 39–40. *In* J. E. Gray (ed.), *The Zoological Miscellany*. Treuttel, Wurtz, London.
- GUINOT, D. 1967. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyours. IV. Observations sur quelques genres de Xanthidae. *Bulletin du Muséum national d'Histoire naturelle*, Paris, second series, 39(4):695–727.
- GUINOT, D. 1969. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyours. VII. Les Goneplacidae (suite et fin). *Bulletin du Muséum national d'Histoire naturelle*, Paris, second series, 41(3):688–724.
- GUINOT, D. 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyours. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences (Paris)*, series D, 285:1049–1052.
- GUINOT, D. 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyours. *Bulletin Biologique de la France et de la Belgique*, 112(3):209–292.
- GUINOT, D., AND E. MACPHERSON. 1987. Révision du genre *Pilumnoides* Lucas, 1844, avec description de quatre espèces nouvelles et création de *Pilumnoidinae* subfam. nov. (Crustacea Decapoda Brachyura). *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4th serie, 9, section A, no. 1:211–247.
- GUINOT, D., AND M. TAVARES. 2001. Une nouvelle famille de crabes du Crétacé, et al notion de Podotremata Guinot, 1977 (Crustacea, Decapoda, Brachyura). *Zoosystema*, 23:507–546.
- HARRIES, P. J., E. G. KAUFFMAN, AND T. A. HANSEN. 1996. Models for biotic survival following mass extinction, p. 41–60. *In* M. B. Hart (ed.), *Biotic Recovery from Mass Extinction*. Geological Society Special Publication No. 102. The Geological Society, London.
- HENDRICKX, M. E. 1998. A new genus and species of "goneplacid-like" brachyuran crab (Crustacea: Decapoda) from the Gulf of California, Mexico, and a proposal for the use of the family Pseudorhombilidae Alcock, 1900. *Proceedings of the Biological Society of Washington*, 111:634–644.
- HILGENDORF, F. 1879. Die von Herrn W. Peters in Moçambique gesammelten Crustaceen, bearbeitet von Herrn Dr. F. Hilgendorf. *Mitteilungen. Berliner Deutsches Akademie Wissenschaften Berlin*, 1878:782–851, pls. 1–4.
- HUANG, J.-F., P.-W. HSUEH, AND P. K. L. NG. 2002. Crabs of the family Hexapodidae (Decapoda: Brachyura) from Taiwan, with description of a new genus and new species. *Journal of Crustacean Biology*, 22:651–660.
- KARASAWA, H. 1990. Decapod crustaceans from the Miocene Mizunami Group, Central Japan, Pt. 2, Section Oxryncha, Cancridea, and Brachyryncha. *Bulletin of the Mizunami Fossil Museum*, 17:1–33, pls. 1–8.
- KARASAWA, H., AND H. KATO. 2003a. The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records. *Paleontological Research*, 7(2):129–151.
- KARASAWA, H., AND H. KATO. 2003b. The phylogeny, systematics and fossil record of the Goneplacidae MacLeay (Crustacea, Decapoda, Brachyura) revisited. *Contributions to Zoology, Mesozoic and Cenozoic Decapod Crustaceans*, 72(2–3):147–152.
- KARASAWA, H., AND C. E. SCHWEITZER. 2004. Revision of the genus *Glyphithyreus* Reuss, 1859 (Crustacea, Decapoda, Brachyura, Xanthoidea) and recognition of a new genus. *Paleontological Research*, 8(2):143–154.
- KATO, H., AND H. KARASAWA. 1994. *Minohellenus macrocheilus* sp. nov. (Decapoda: Crustacea) from the Oligocene Ashiya Group, Kyushu, Japan. *Bulletin of the Kitakyushu Museum of Natural History*, 13:51–58.
- KAUFFMAN, E. G., AND P. J. HARRIES. 1996. The importance of crisis progenitors in recovery from mass extinction, p. 15–39. *In* M. B. Hart

- (ed.), Biotic Recovery from Mass Extinction. Geological Society Special Publication No. 102. The Geological Society, London.
- KOSSMANN, R. 1878. Kurze Notizen über einige neue Crustaceen sowie über neue Fundorte einiger bereits beschriebenen. *Archiv für Naturgeschichte*, 44(1):251–258.
- LATREILLE, P. A. 1802–1803. *Histoire naturelle, général et particulière, des crustacés et des insectes*. Vol. 3. DuFart, Paris, 468 p.
- LATREILLE, P. A. 1817. *Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc.* Vol. 10. Déterville, Paris, 404 p.
- LINNAEUS, C. VON. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (tenth edition). Vol. 1. Laurentii Salvii, Stockholm, 824 p.
- LÓRENTHEY, E. 1898. Über die Brachyuren der palaeotologischen Sammlung des bayerischen Staates. *Természetráji Füzetek*, 21:134–152, pls. 10, 11.
- MACLEAY, W. S. 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith, p. 53–71, pls. 2–3. *In* *Illustrations of the Annulosa of South Africa; being a portion of the objects of Natural History Chiefly Collected during an Expedition into the Interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835, and 1836; Fitted out by "The Cape of Good Hope Association for Exploring Africa."* Smith, Elder, London.
- MANNING, R. B., AND L. B. HOLTHUIS. 1981. West African brachyuran crabs (Crustacea Decapoda). *Smithsonian Contributions to Zoology*, 306, 379 p.
- MANNING, R. B., AND L. B. HOLTHUIS. 1989. Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae). *Proceedings of the Biological Society of Washington*, 102:50–77.
- MARTIN, J. W., AND G. E. DAVIS. 2001. An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County Science Series*, no. 39:1–124.
- MARTINS-NETO, R. G. 2001. Review of some Crustacea (Isopoda and Decapoda) from Brazilian deposits (Paleozoic, Mesozoic, and Cenozoic) with descriptions of new taxa. *Acta Geologica Leopoldensia*, XXXIV(52/53):237–254.
- MIERS, E. J. 1881. On a collection of Crustacea made by Baron Hermann Maltzam at Goree Island, Senegambia. *Annals and Magazine of Natural History*, series 5, 8:204–220, 259–281, 364–377, pls. 13–16.
- MIERS, E. J. 1886. Report of the Brachyura collected by H. M. S. Challenger during the years 1873–1876, p. 1–362. *In* C. W. Thomson and J. Murray (eds.), *Report of the Scientific Results of the Voyage of H. M. S. Challenger during the years 1873–1876*, Zoology. Johnson Reprints, New York.
- MILNE EDWARDS, A. 1862–65. *Monographie des Crustacés fossiles de la famille Cancériens*. *Annales de Science Naturelle, Zoologie*, series 4, 18(1862):31–85, pls. 1–10; 20 (1863): 273–324, pls. 5–12; series 5, 1 (1864):31–88, pls. 1–10; 3(1865):297–351, pls. 5–13.
- MILNE EDWARDS, A. 1879a. Description de quelques Crustacés nouveaux. *Bulletin de la Société Philomatique de Paris*, series 7, 3:103–110.
- MILNE EDWARDS, A. 1879b. Études sur les Xiphosures et les Crustacés de la région mexicaine. *In* *Missions scientifiques au Mexique et dans l'Amérique Centrale. Recherches Zoologique de la Faune Amérique Centrale et Mexique, Mission scientifique au Mexique et dans l'Amérique centrale, Recherches zoologiques*, fifth part. Vol. 1, 368 p., 61 pls.
- MILNE EDWARDS, H. 1834–1837. *Histoire naturelle des Crustacés*. Vol. 1 (1834), 468 p.; Vol. 2 (1837), 532 p.; atlas. Librairie Encyclopedique de Roret, Paris.
- MILNE EDWARDS, H., AND H. LUCAS. 1843. Crustacés, p. 1–37, pls. 1–17. *In* A. D'Orbigny, *Voyage dans l'Amérique méridionale (le Brésil, la république orientale de l'Uruguay, la république Argentine, la Patagonie, la république du Chili, la république de Bolivia, la république du Pérou)*, exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, 6(1). Pitois-Levrault, Paris.
- MONOD, TH. 1956. Hippidea et Brachyura ouest-africains. *Mémoires de l'Institut Français d'Afrique Noire*, 45:1–674.
- NG, P. K. L. 1998. Crabs, p. 1046–1155. *In* K. E. Carpenter and V. H. Niem (eds.), *The Living Marine Resources of the Western Central Pacific*, Vol. 2. Cephalopods, Crustaceans, Holothurians, and Sharks. Food and Agriculture Organization of the United Nations, Rome.
- NG, P. K. L., AND P. F. CLARK. 2000a. The eumedonid file: a case study of systematic compatibility using larval and adult characters (Crustacea: Decapoda: Brachyura). *Invertebrate Reproduction and Development*, 38:225–252.
- NG, P. K. L., AND P. F. CLARK. 2000b. The Indo-Pacific Pilmunidae XII. On the familial placement of *Chlorodiella bidentata* (Nobili, 1901) and *Tanaocheles stenochilus* Kropp, 1984 using adult and larval characters with the establishment of a new subfamily, Tanaocheilinae (Crustacea: Decapoda: Brachyura). *Journal of Natural History*, 34:207–245.
- NG, P. K. L., AND D. GUINOT. 1999. On a new species of deep-water crab of the genus *Progeron* (Decapoda, Brachyura, Geryonidae) from Hawaii. *Crustaceana*, 72:685–692.
- NG, P. K. L., AND L. M. LIAO. 2002. On a new species of *Euryozius* Miers, 1886 (Crustacea: Decapoda: Brachyura: Pseudoziidae) from the Philippines, with notes on the taxonomy of the genus. *Proceedings of the Biological Society of Washington*, 115:585–593.
- NG, P. K. L., C.-H. WANG, P.-H. HO, AND H.-T. SHIH. 2001. An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Special Publication Series*, Taipei, Taiwan, 11: 1–86, 8 pls.
- NYBORG, T. G. 2002. Fossil decapod crustaceans from the early to middle Miocene Astoria Formation, Washington and Oregon, U. S. A. Unpublished M.S. thesis, Kent State University, Kent, Ohio, 224 p.
- ODHNER, T. 1925. *Monographierte Gattungen der Krabbenfamilie Xanthidae*. I. Göteborgs Kungliga Vetenskaps-och Vitterhets-Samhälles Handlingar, 29(1):1–92, figs. 1–7, pls. 1–5.
- ORTMANN, A. 1893. *Abtheilung: Brachyura (Brachyura genuina Boas), II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen*, VII. Theil. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie, und Biologie der Thiere*, 7:411–495, pl. 17.
- RAFINESQUE, C. S. 1815. *Analyse de la nature, ou tableau de l'univers et des corps organisés*. L'Imprimerie de Jean Barravecchia, Palermo, Italy, 224 p.
- RATHBUN, M. J. 1897. A revision of the nomenclature of the Brachyura. *Proceedings of the Biological Society of Washington*, 11:153–167.
- RATHBUN, M. J. 1916. Description of a new genus and species of fossil crab from Port Townsend, Washington. *American Journal of Science*, 41:344–346.
- RATHBUN, M. J. 1917. New species of South Dakota Cretaceous crabs. *Proceedings of the United States National Museum*, 52:385–391.
- RATHBUN, M. J. 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America. *United States National Museum Bulletin*, 138, 155 p.
- RATHBUN, M. J. 1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. *United States National Museum Bulletin*, 152, 609 p.
- RATHBUN, M. J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America Special Paper*, 2, 160 p.
- REMY, J. M. 1960. Études paléontologiques et géologiques sur les falaises de Fresco (Cote d'Ivoire). 2. Crustacés. *Annals of the Faculty of Science of the University of Dakar*, 5:55–64, 1 pl.
- REMY, J. M., AND F. TESSIER. 1954. Décapodes nouveaux de la partie Ouest du Sénégal. *Bulletin de la Société Géologique de France*, 6(4): 185–191, pl. 11.
- REUSS, A. 1859. Zur Kenntnis fossiler Krabben. *Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematische-Naturwissenschaftliche Classe*, 17:1–90, pls. I–XXIV.
- SAMOUELLE, G. 1819. *The Entomologist's Useful Compendium, or an Introduction to the Knowledge of British Insects*. Thomas Boys, London, 496 p.
- SAY, T. 1817–1818. An account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia*, 1(1–2): 1817: 57–63, 65–80, 97–101, 155–160, 161–169, pl. 4; 1818: 235–253, 313–316, 317–319, 374–380, 381–401, 423–441.
- SCHAFHÄUTL, K. E. 1863. Südbayerns Lethaea geognostica. Der Kressenberg und die südlich von ihm gelegenen Hochalpen geognostisch betrachtet in ihren Petrefacten + Atlas zu Südbayerns Lethaea geognostica, Einhundert Tafeln und 2 Karten. Verlag Von Leopold Voss, Leipzig, 472 p.

- SCHRAM, F. R. 2001. Phylogeny of decapods: moving towards a consensus. *Hydrobiologia*, 449:1–20.
- SCHUBART, C. D., J. E. NEIGLE, AND D. L. FELDER. 2000. Use of the mitochondrial 16S rDNA gene for phylogenetic and population studies of Crustacea. *Crustacean Issues*, 121:817–830.
- SCHWEITZER, C. E. 2000. Tertiary Xanthoidea (Crustacea: Decapoda: Brachyura) from the west coast of North America. *Journal of Crustacean Biology*, 20:715–742.
- SCHWEITZER, C. E. 2003a. Utility of proxy characters for classification of fossils: an example from the fossil Xanthoidea (Crustacea: Decapoda: Brachyura). *Journal of Paleontology*, 77:911–932.
- SCHWEITZER, C. E. 2003b. Progress on the fossil Xanthoidea MacLeay, 1838 (Decapoda, Brachyura). *Contributions to Zoology*, 72(2–3):181–186.
- SCHWEITZER, C. E., AND R. M. FELDMANN. 2000a. New species of calappid crabs from western North America and reconsideration of the Calappidae sensu lato. *Journal of Palaeontology*, 74:230–246.
- SCHWEITZER, C. E., AND R. M. FELDMANN. 2000b. New fossil portunids from Washington, U.S.A., and Argentina and a reevaluation of generic and family relationships within the Portunoidea Rafinesque (Decapoda: Brachyura). *Journal of Paleontology*, 74:636–653.
- SCHWEITZER, C. E., AND R. M. FELDMANN. 2001a. Differentiating fossil Hexapodidae Miers (Decapoda: Brachyura) from similar forms. *Journal of Paleontology*, 75:330–345.
- SCHWEITZER, C. E., AND R. M. FELDMANN. 2001b. Combining paleontological and biological criteria within the Xanthoidea (Decapoda): toward a new view of decapod systematics, evolution, and paleobiogeography. Geological Society of America 2001 Annual Meeting Abstracts with Programs, 33(6):A-378.
- SCHWEITZER, C. E., AND H. KARASAWA. 2004. Revision of *Amydrocarcinus* and *Palaeograpsus* (Decapoda: Brachyura: Xanthoidea) with definition of three new genera. *Paleontological Research*, 8(1):71–86.
- SCHWEITZER, C. E., R. M. FELDMANN, AND P. D. GINGERICH. 2004. New decapods (Crustacea) from the Eocene of Pakistan and a revision of *Lobonotus* A. Milne Edwards, 1864. University of Michigan Contributions from the Museum of Paleontology, 31(4):89–118.
- SCHWEITZER, C. E., R. M. FELDMANN, G. GONZÁLES-BARBA, AND F. J. VEGA. 2002. New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. *The Paleontological Society Memoir* 76 (supplement to *Journal of Paleontology*, 76), 43 p.
- SCHWEITZER, C. E., R. M. FELDMANN, A. B. TUCKER, AND R. E. BERGLUND. 2000. Eocene decapod crustaceans from Pulali Point, Washington. *Annals of Carnegie Museum*, 69:23–67.
- SEGERBERG, K. O. 1900. De anomura och brachyura dekapoderna inom Skandinavien Yngre krita. *Geologiska Föreningens Stockholm, Förhandlingar* 22:347–394, pl. 9.
- SERÈNE, R. 1984. Crustacés Décapodes Brachyours de l'Océan Indien occidentale et de la Mer Rouge. Xanthoidea: Xanthidea et Trapeziidae. *Faune Tropicale*, 24:1–400, pls. 1–48.
- ŠTEVČIĆ, Z. 1991. Note on some rare and aberrant Australian crabs. *Beagle, Records of the Northern Territory Museum of Arts and Sciences*, 8:121–134.
- STIMPSON, W. 1858. Crustacea Ocypodoidea: Prodromus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit W. Stimpson, Pt. V. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 10: 93–110.
- STIMPSON, W. 1859. Notes on North American Crustacea, No. I. *Annals of the Lyceum of Natural History of New York*, 7:49–93, pl. 1.
- STIMPSON, W. 1860. Notes on North American Crustacea, in the Museum of the Smithsonian Institution. No. II. *Annals of the Lyceum of Natural History of New York*, 7:176–246, pls. 2, 5.
- VAN STRAELEN, V. 1925. Description de Brachyours montiens du Comings. *Bulletin de la Société Belgique de Géologie*, 34:58–62.
- VEGA, F. J., T. COSMA, M. A. COUTIÑO, R. M. FELDMANN, T. G. NYBORG, C. E. SCHWEITZER, AND D. A. WAUGH. 2001. New middle Eocene decapods (Crustacea) from Chiapas, Mexico. *Journal of Paleontology*, 75:929–946.
- VIA, L. 1959. Decápodos fósiles del Eocene español. *Boletín Instituto Geológico y Minero de España*, 70:331–402.
- VIA, L. 1966. *Pinnixa (Palaeopinnixa) mytilicola* nuevo braquiuro fósil en el mioceno marino des Valles (Barcelona). *Acta Geologica Hispanica*, 1:1–4.
- VON MEYER, H. 1863. Tertiaere Decapoden aus den Alpen, von Oeningen und dem Taunus. *Palaeontographica (Stuttgart)*, 10:147–178, pls. 16–19.
- VON STERNBERG, R., AND N. CUMBERLIDGE. 2001. Notes on the position of the true freshwater crabs within the brachyrhynch Eubranchyura (Crustacea: Decapoda: Brachyura). *Hydrobiologia*, 449:21–39.
- WAUGH, D. A., R. M. FELDMANN, R. S. CRAWFORD, S. L. JAKOBSEN, AND K. B. THOMAS. 2004. Epibiont preservational and observational bias in fossil marine decapods. *Journal of Paleontology*, 78(5):961–972.
- WEITZER, R., J. W. MARTIN, AND S. E. TRAUTWEIN. 2003. Phylogenetic relationships within the coral crab genus *Carpilius* (Brachyura, Xanthoidea, Carpiliidae) and of the Carpiliidae to other xanthoid crab families based on molecular sequence data. *Molecular Phylogenetics and Evolution*, 27:410–421.
- WHITE, A. 1852. Descriptions of some new species of Annulosa, p. 387–395. In J. MacGillivray (ed.), *Narrative of the Voyage of H. M. S. "Rattlesnake" During the Years 1846–1850*. Vol. 2, appendix. Boone, London.
- WITHERS, T. 1924. Some Cretaceous and Tertiary decapod crustaceans from Jamaica. *Annals and Magazine of Natural History*, series 9, 13: 81–93, pls. II–IV.
- WOODWARD, H. 1867. On a new genus of shore-crab, *Goniocypoda Edwardsi*, from the lower Eocene of Hampshire. *Geological Magazine*, 4: 529–531.
- WRIGHT, C. W., AND J. S. H. COLLINS. 1972. *British Cretaceous Crabs*. Palaeontographical Society Monograph, London, 114 p.
- YOKOYAMA, M. 1911. Some Tertiary fossils from the Miike Coalfield. *Journal of the Collections of Science, Imperial University of Tokyo*, 27:1–16, 3 pls.