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Revision of *Amydrocarcinus* and *Palaeograpsus* (Decapoda: Brachyura: Xanthoidea) with definition of three new genera

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Abstract. All species referred to *Palaeograpsus* Bittner, 1875, have been reevaluated, resulting in three new genera, *Bittneria*, *Magyarcarcinus*, and *Litograpsus*. *Amydrocarcinus* Schweitzer *et al.*, 2002, and *Magyarcarcinus* new genus are placed within the Goneplacinae MacLeay, 1838, of the Goneplacidae MacLeay, 1838, and constitute some of the earliest occurrences of the family. *Bittneria* new genus, *Carinocarcinus* Lőrenthey, 1898, and *Palaeograpsus sensu stricto* are placed within the Eucratopsinae Stimpson, 1871, of the Panopeidae Ortmann, 1893, and document the first notice of the subfamily in the fossil record. The Pseudorhombilidae Alcock, 1900, and the Eucratopsinae are very difficult to differentiate from one another based upon dorsal carapace characters typically preserved in the fossil record, but the ratios of the frontal width and fronto-orbital width are shown to be useful for this purpose. *Litograpsus* new genus is placed within the Grapsidae MacLeay, 1838, *sensu lato*. *Palaeograpsus guerini* Via, 1959, is placed within *Chasmocarcinus* Rathbun, 1898. The Panopeidae displayed a Tethyan distribution pattern early in its history, and the Pseudorhombilidae has been largely restricted to the Americas since its first occurrence in the Miocene of Argentina (Glaessner, 1933).

Key words: Brachyura, Decapoda, New taxa, Xanthoidea

Introduction

New specimens of *Amydrocarcinus dantei* Schweitzer *et al.*, 2002, have prompted the reevaluation of that genus and species as well as *Palaeograpsus* Bittner, 1875, to which *Amydrocarcinus* is superficially similar. Schweitzer *et al.* (2002) originally placed their new genus *Amydrocarcinus* in the Xanthidae MacLeay, 1838, *sensu lato*. Reevaluation of that placement indicates that it is best placed within the Goneplacidae MacLeay, 1838, as discussed below.

Several authors have begun to address the observation that the Goneplacidae, at least in the fossil record, has become a convenient catch-all taxon within which to place smooth, flattened, xanthoid taxa (Tucker and Feldmann, 1990; Schweitzer, 2000; Schweitzer *et al.*, 2000; Karasawa and Kato, 2003a, b). Recently, the Goneplacidae has been reevaluated by Karasawa and Kato (2003a, b). In that work, they recognized six subfamilies and provided both dorsal carapace characters as well as features of the sternum and abdomen in their diagnoses for those subfamilies. Placement of genera within the Goneplacidae and its constituent subfamilies often depends upon the nature of the eighth sternite. Most subfamilies within the Goneplacidae are characterized by males with the eighth sternite being visible in ventral view and not obscured completely by the abdomen; in a few taxa within the family, the eighth sternite is obscured in males. Unfortunately, the sternum and abdomen of fossil specimens is often missing.

Palaeograpsus has been a catch-all taxon for fossil brachyurans with a smooth, square carapace (P. Müller, pers. com.) and is thus in need of revision. In 1875, Bittner named two species of his new genus, *Palaeograpsus*, of which *P. inflatus* is the type species. *Palaeograpsus* was originally placed within the Grapsidae MacLeay, 1838, probably because it possesses short, spined anterolateral margins and a rectangular carapace, typical of that family. Glaessner (1969) placed *Palaeograpsus* within the Grapsidae but did not refer it to a subfamily; other subsequent authors

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Table 1. All species at one time referred to *Palaeograpsus* and their current generic, subfamily, and family status.

Species	Current Generic Assignment	Current Family and Subfamily Assignment
Palaeograpsus inflatus Bittner, 1875 (type)	*Palaeograpsus sensu stricto*	Panopeidae; Eucratopsinae
Palaeograpsus attenuatus Bittner, 1875	*Bittneria* new genus	Panopeidae; Eucratopsinae
Palaeograpsus bartonensis Quayle and Collins, 1981	*Orthakrolophos* Schweitzer and Feldmann, 2001	Goneplacidae; Chasmocarcininae
Palaeograpsus bittneri Morris and Collins, 1991 (*non P. bittneri* Müller and Collins, 1991a)	*Orthakrolophos* Schweitzer and Feldmann, 2001	Goneplacidae; Chasmocarcininae
Palaeograpsus depressus Quayle and Collins, 1981	*Orthakrolophos* Schweitzer and Feldmann, 2001	Goneplacidae; Chasmocarcininae
Palaeograpsus guerini Via, 1959	*Chasmocarcinus* Rathbun, 1898	Goneplacidae; Chasmocarcininae
Palaeograpsus loczyanus Lőrenthey, 1898a	*Magyarcarcinus* new genus	Goneplacidae; Goneplacinae
Palaeograpsus parvus Müller and Collins, 1991b	*Litograpsus* new genus	Grapsidae *sensu lato*

have maintained placement in the Grapsidae (Beschin *et al.*, 1994; Beschin *et al.*, 1996; De Angeli and Beschin, 2001; Schweitzer and Feldmann, 2001). Reevaluation of *Palaeograpsus* suggests that it belongs within the Xanthoidea MacLeay, 1838, as first indicated by Karasawa and Kato (2001, 2003a), and that each species assigned to it, except the type, is best placed in a different genus (Table 1). Karasawa and Kato (2003a) suggested that *Palaeograpsus sensu stricto* as defined below belongs to the Pseudorhombilidae Alcock, 1900, or the Eucratopsinae Stimpson, 1871, within the Panopeidae Ortmann, 1893. We place the genus within the Eucratopsinae.

Palaeograpsus attenuatus was also named by Bittner (1875); however, that species does not belong to the same genus as the type species. *Palaeograpsus attenuatus* is best placed within the Panopeidae based upon the shape and ornamentation of the dorsal carapace; however, examination of the ventral portion of the carapace will be necessary to confirm placement. We herein assign it to a new genus, *Bittneria*, within the Eucratopsinae.

Schweitzer and Feldmann (2001) erected the new genus *Orthakrolophos* to embrace three species previously assigned to *Palaeograpsus*. At that time, they suggested that *Palaeograpsus loczyanus* Lőrenthey, 1898a, was better allied with the genus *Carcinoplax* H. Milne Edwards, 1852. We concur with the opinion that *P. loczyanus* does not belong to *Palaeograpsus* and herein assign that species to a new genus, *Magyarcarcinus*, within the Goneplacinae MacLeay, 1838, of the Goneplacidae.

Via (1959) erected a new species, *Palaeograpsus guerini*, for Eocene material collected from Spain. Upon examination of illustrations and the original description of that material, we herein transfer that species to the genus *Chasmocarcinus* Rathbun, 1898, within the Chasmocarcininae Serène, 1964, of the Goneplacidae.

In 1991, Müller and Collins (1991a) described a new species they named *Palaeograpsus bittneri* from Eocene rocks of Hungary. Earlier in that same year, *Palaeograpsus bittneri* Morris and Collins, 1991, was described from the Pliocene of Brunei. Thus, *Palaeograpsus bittneri* Müller and Collins, 1991a, is a junior homonym of *Palaeograpsus bittneri* Morris and Collins, 1991, and Müller and Collins (1991b) proposed the replacement name *Palaeograpsus parvus* for their species. *Palaeograpsus bittneri* Morris and Collins, 1991, was referred to *Orthakrolophos* by Schweitzer and Feldmann (2001).

Institutional abbreviations

Földtani Intézet—Lőrenthey Collection at Földtani Intézet, Budapest, Hungary

M.—Természettudományi Múzeum Föld-és Őslénytár (Natural History Museum of Hungary).

MB.A.—Museum für Naturkunde Berlin Paläontologisches Museum, Humboldt-Universität zu Berlin, Germany

MCZ—Museo Civico ''G. Zannato'' di Montecchio Maggiore (Vicenza), Italy (*non* Museum of Comparative Zoology, Harvard University)

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MHN-UABCS—Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, Mexico

USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC, United States.

Systematics

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Xanthoidea MacLeay, 1838
Family Goneplacidae MacLeay, 1838
Subfamily Chasmocarcininae Serène, 1964
Genus ***Chasmocarcinus*** Rathbun, 1898

Type species.—*Chasmocarcinus typicus* Rathbun, 1898.

Diagnosis.—see Schweitzer and Feldmann, 2001.

Chasmocarcinus guerini (Via, 1959) new combination

Palaeograpsus guerini Via, 1959, p. 391, fig. 18; Via, 1969, p. 317, text-fig. 39, pl. 37, figs. 7–8; Schweitzer and Feldmann, 2001, p. 339.

Diagnosis.—Carapace rectangular to trapezoidal in outline, steep sided; wider than long, L/W about 0.77, widest about one-half to two-thirds the distance posteriorly; carapace regions weakly defined; front rectangular, downturned, notched axially, frontal width about one-quarter maximum carapace width; orbits rectangular, directed forward, fronto-orbital width about half maximum carapace width, frontal width about 40 percent fronto-orbital width; anterolateral and posterolateral margins confluent, anterolateral portion with two small spines; posterolateral reentrants large; posterolateral margin about half the maximum carapace width, fronto-orbital width to posterior width about 1.1.

Discussion.—The diagnosis is taken from drawings (Via, 1959, fig. 18) and photographs (Via, 1969, pl. 37, figs. 7–8) as well as the original description by Via (1959, p. 391); because we have not seen the type material, a detailed description of the species is not possible. Schweitzer and Feldmann (2001) provided a table of carapace length and width ratios for small, rectangular decapods that are easily confused with one another. Comparison of the length to width ratios of *P. guerini* (Table 2) as well as comparison of other carapace characters suggests strongly that *P. guerini* belongs within the genus *Chasmocarcinus*. The carapace ratios are very similar in *P. guerini* and species of *Chasmocarcinus*. Species of *Chasmocarcinus* have an axially sulcate front as does *P. guerini*. The carapace is widest in the posterior portion of the carapace in both *Chasmocarcinus* and *P. guerini*, and the carapace is rectangular to trapezoidal in shape and possesses very steep sides in each. Thus, we place *P. guerini* in *Chasmocarcinus*.

Table 2. Average length and width ratios of the carapace for species of *Chasmocarcinus* and for specimens of *Palaeograpsus guerini*. F/FOW = frontal width/fronto-orbital width; FOW/W = fronto-orbital width/maximum carapace width; FOW/PW = fronto-orbital width/posterior width; L/W = maximum length/maximum carapace width; PW/W = posterior width/maximum carapace width. Values for *Chasmocarcinus* are taken from Schweitzer and Feldmann (2001).

Genus	F/FOW	FOW/W	FOW/PW	L/W	PW/W
Chasmocarcinus spp.	0.41	0.48	1.2	0.72	0.41
Palaeograpsus guerini	0.40	0.53	1.1	0.78	0.48

Only two other fossil species of *Chasmocarcinus* have been recognized, including *C. seymourensis* Feldmann and Zinsmeister, 1984, from the early Eocene of Antarctica, and *C. robertsi* Blow and Bailey, 1992, from Miocene rocks of Virginia. Recent species inhabit Atlantic, Caribbean, and eastern and western Pacific waters (Schweitzer and Feldmann, 2001). The occurrence of *C. guerini* in Eocene rocks of Spain reinforces the Atlantic component of the distribution of the species. The early Eocene occurrence of the Antarctic species suggests that, according to our present knowledge, the genus evolved in that region with subsequent dispersal to the central and northern Atlantic Ocean.

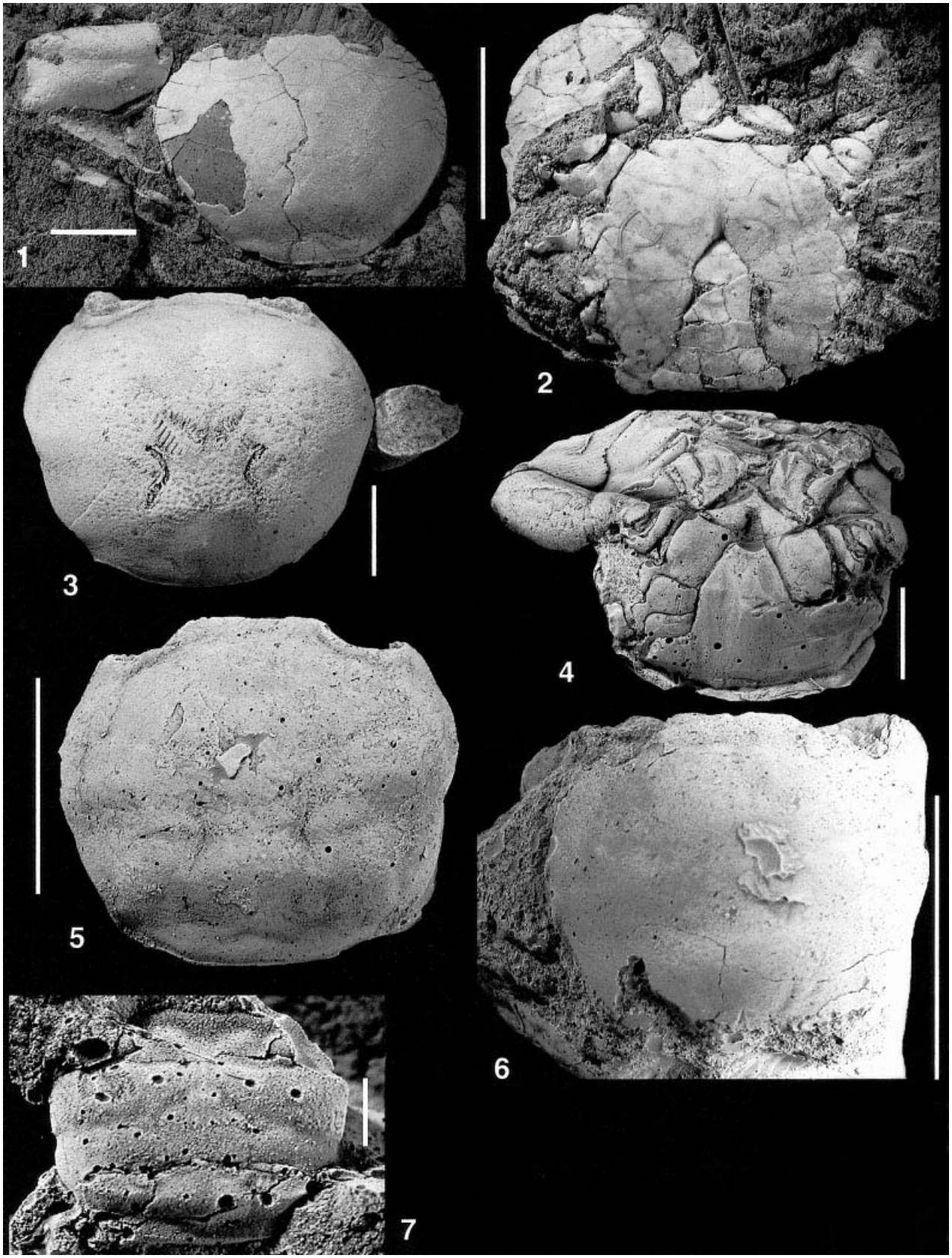
Subfamily Goneplacinae MacLeay, 1838
Genus ***Amydrocarcinus*** Schweitzer, Feldmann, Gonzáles-Barba, and Vega, 2002

Type species.—*Amydrocarcinus dantei* Schweitzer, Feldmann, Gonzáles-Barba, and Vega, 2002.

Diagnosis.—Carapace ovoid, wider than long, L/W = 0.84, regions poorly developed; orbits square, entire; anterolateral margin granular, entire; sternum relatively narrow, sternite 8 obscured by male abdomen, which fills space between coxae of fifth pereiopods, sterno-abdominal cavity not reaching anterior of sternite 4; all male abdominal somites free.

Discussion.—The genus was placed within the Xanthidae *sensu lato* by Schweitzer *et al.* (2002),

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because the male abdomen and sternum are incompletely preserved in the type material. *Amydrocarcinus* cannot be referred to any other family aside from the Goneplacidae, as discussed in part by Schweitzer *et al.* (2002). *Amydrocarcinus* is excluded from the Panopeidae and Pseudorhombilidae Alcock, 1900, of which some members are superficially similar to *Amydrocarcinus*, because the eighth sternite in those two families is not entirely obscured by the abdomen in males. The eighth sternite is obscured by the abdomen in *Amydrocarcinus*. Reconsideration of the genus suggests that it is most likely allied with the Goneplacinae; we herein place it in that subfamily, based upon its ovate, smooth carapace; free male abdominal somites; robust first pereiopods, and slender walking legs (Schweitzer, 2000; Karasawa and Kato, 2003a).

Karasawa and Kato (2003a) synonymized the Carcinoplacinae H. Milne Edwards, 1852, with the Goneplacinae based upon their cladistic analysis of the Goneplacidae. Many features of the dorsal carapace of *Amydrocarcinus* are similar to those of members of the Goneplacinae *sensu* Karasawa and Kato (2003a). Members of the Goneplacinae have poorly defined carapace regions, a straight front without a median notch, and entire orbits, as does *Amydrocarcinus*. *Amydrocarcinus* differs from all other members in the subfamily in lacking anterolateral spines. Members of the Goneplacinae have all male abdominal somites free, as does *Amydrocarcinus*. Male goneplacines and *Amydrocarcinus* have the eighth sternite completely obscured by the male abdomen.

Amydrocarcinus cannot be placed into any other subfamily of the Goneplacidae. The Mathildellinae Karasawa and Kato, 2003a, cannot embrace *Amydrocarcinus* because members of the subfamily have a flattened carapace, a front with a shallow median notch, orbital fissures, and an anterolateral margin with five spines. *Amydrocarcinus* has none of these features. Members of the Euryplacinae Stimpson, 1871, have a straight front with a shallow median notch, orbital fissures, male abdominal somites 4–6 much narrower than somite 3, and the sternoabdominal cavity reaching the anterior of sternite 4. *Amydrocarcinus* demonstrates none of these features. *Amydrocarcinus* is immediately eliminated from the Carinocarcinoidinae Karasawa and Kato, 2003a, because it lacks the dorsal carapace carinae typical of the subfamily and all abdominal somites of males are free, whereas in the Carinocarcinoidinae male abdominal somites 3–5 are fused. *Amydrocarcinus* cannot be referred to the Chasmocarcininae or Trogloplacinae Guinot, 1986, because it lacks the supplementary plate in sternite 8 typical of those subfamilies. The circular carapace of *Cycloplax* Guinot, 1969a, is reminiscent of that of *Amydrocarcinus*, but in *Cycloplax*, a portion of the eighth sternite is clearly visible in ventral view; thus, it is not allied with *Amydrocarcinus*.

Karasawa and Kato (2003a) recognized four genera within the Goneplacinae with fossil records. To these must be added *Icriocarcinus* Bishop, 1988 (Schweitzer *et al.*, 2002; Karasawa and Kato, 2003b), known from the Maastrichtian of Baja California (Bishop, 1988). Only two goneplacine genera have Paleogene records, *Carcinoplax* H. Milne Edwards, 1852, and *Psopheticus* Wood-Mason, 1892. *Psopheticus* is known from Paleogene (upper Oligocene) rocks of Taiwan (Hu and Tao, 1996). The middle Eocene occurrences of *Amydrocarcinus dantei*, the sole species of the genus, and *Magyarcarcinus* new genus are thus some of the earlier occurrences of the subfamily.

Karasawa (1993) reported that *Carcinoplax* was one of the Indo-west Pacific genera which has tropical and subtropical distributions. The genus decreases in number of extant species from low latitudes to high latitude areas and seems to be tropical in origin and to have had the South China Seas as its center of dispersal based upon the distribution of its present species (Karasawa, 1993). However, the occurrences of *Icriocarcinus* from the late Cretaceous and *Amydrocarcinus* from the Eocene of Baja California suggests that the subfamily may have originated in the western portion of the Tethyan realm.

Amydrocarcinus dantei Schweitzer, Feldmann, Gonzáles-Barba, and Vega, 2002

Figure 1.1, 1.2

Emendation to diagnosis.—Front with blunt, low protuberance axially, weakly sulcate on either side of axial protuberance. Anterolateral and anteriormost posterolateral margins with tiny, closely spaced

⬅ **Figure 1.** *Amydrocarcinus* and fossil species, some originally referred to *Palaeograpsus sensu lato*. **1.** *Amydrocarcinus dantei* Schweitzer *et al.*, 2002, MHN-UABCS Te 14/66-61. **2.** *A. dantei*, MHN-UABCS Te 14/66-60, ventral surface of male, note that at bottom left corner, coxa of pereiopod 5 touches abdomen. **3.** *Magyarcarcinus loczyanus* (Lőrenthey, 1898a), cast of dorsal surface of holotype, E283. **4.** *M. loczyanus*, cast of ventral surface of holotype, E283. **5.** *M. loczyanus*, cast of MCZ 1520. **6.** *Bittneria attenuatus* (Bittner, 1875), cast of holotype, MB.A.663. **7.** *Litograpsus parvus* (Müller and Collins, 1991b), cast of holotype, M91-227. All scale bars = 1 cm, except for *Litograpsus*, in which scale bar = 1 mm.

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spines. Male sternite 8 obscured by abdomen. Sternoabdominal cavity not reaching level of base of coxae of first pereiopods.

Emendation to description.—Frontal margin with blunt, low protuberance axially, weakly sulcate on either side of axial projection; orbits deepest distally; eyestalks often preserved, short. Anterolateral margin short, with tiny, closely spaced spines, merging smoothly with posterolateral margin; posterolateral margin with tiny, closely spaced spines on anteriormost half.

Male sternum broad, obovate, widest at position of episternal projections of fourth sternite. Male sternites 1 and 2 fused, no suture visible; sternites 3 and 4 fused, suture visible only laterally; sternite 4 longest of all sternites, with episternal projections, directed anterolaterally; sternite 5 with episternal projections, directed anterolaterally; sternite 6 with episternal projections, directed laterally; sternite 7 narrowest of all sternites, with blunt episternal projections, directed posterolaterally; sternite 8 obscured. Sternoabdominal cavity not reaching level of base of coxae of first pereiopods.

Male abdomen with concave lateral sides; somite 1 poorly known; somite 2 short, touching coxae of fifth pereiopods; somite 3 broadest of all somites, touching coxae of fifth pereiopods; somites 4–6 becoming increasingly narrower; somite 6 about as long as wide; telson a blunt triangle.

Material examined.—MHN-UABCS Te 27/61-1, was collected from the Eocene Tepetate Formation, at Curva al Sur del Rancho San Agustin, kilometer 75 of Route 1, Baja California Sur, Mexico, lat. N24°09′34.7″ long. W110°54′27.0″, northwest of La Paz. Four additional specimens, MHN-UABCS Te 14/66-60, Te 14/66-61, Te 14/66-62, Te 14/66-63, were collected in Arroyo El Conejo, at approximately lat. N24°10′, long. W110°55′, northwest of La Paz, Baja California Sur, Mexico.

Occurrence.—Both the genus and species are known only from the Eocene Tepetate Formation, Baja California Sur, Mexico; see additional localities in Schweitzer *et al.* (2002).

Discussion.—The new material permits placement within a family and subfamily within the Xanthoidea based upon the excellent preservation in Te 14/66-60 of the sternum and male abdomen as discussed above. The excellent preservation of the anterolateral margin of Te 14/66-61 shows minute spines, which were not visible in the type material. Many new specimens were collected from the Arroyo Conejo locality, nearly all of them corpses, suggesting that the animals were living in the environment and were quite numerous.

Genus ***Magyarcarcinus*** new genus

Figure 1.3–1.5

Palaeograpsus loczyanus Lőrenthey, 1898a, p. 69, pl. 4, fig. 6; Beschin *et al.*, 1996, p. 31, fig. 15.3, fig. 16.2; Schweitzer and Feldmann, 2001, p. 339.

Type species.—*Palaeograpsus loczyanus* Lőrenthey, 1898a, by monotypy.

Diagnosis.—Carapace steep-sided, nearly circular, L/W about 0.88, widest about 40 percent the distance posteriorly; surface smooth, regions poorly marked; front straight, about one-third maximum carapace width; fronto-orbital width about 70 percent maximum carapace width; orbits entire, rimmed; anterolateral margin entire, thickened into a rim; posterolateral margin about 38 percent maximum carapace width; epibranchial ridge weak, arcuate; posteriormost branchial and intestinal regions continuous, forming a flattened shelf; sternite 8 apparently not visible in ventral view.

Description.—Carapace steep-sided; nearly circular, not much wider than long, L/W about 0.88, widest about 40 percent the distance posteriorly on carapace; surface smooth; moderately vaulted transversely, markedly vaulted longitudinally; regions poorly marked.

Front straight, about one-third maximum carapace width; fronto-orbital width about 70 percent maximum carapace width; orbits circular, entire; directed forward, rimmed; anterolateral margin entire, convex, thickened into a distinctive, weakly granular rim, boundary between anterolateral and posterolateral margin marked by a weak concavity; posterolateral margin weakly convex; posterolateral corner with small, shallow reentrant; posterior margin short, about 38 percent maximum carapace width; fronto-orbital width to posterior width about 1.9.

Protogastric, epigastric, hepatic, and anterior mesogastric regions indistinguishable from one another; posteriormost mesogastric region weakly marked by shallow grooves; urogastric and cardiac regions marked by weak branchiocardiac grooves; urogastric depressed, cardiac weakly inflated, pentagonal in shape, apex directed posteriorly; intestinal region flattened; branchial regions with broad, gentle epibranchial ridge extending weakly arcuately from anterolateral margin to urogastric region, remainder of branchial region weakly inflated; flattened posteriorly, continuous with flattened intestinal region.

Third maxillipeds arcuate, convex axially, relatively short; bases and merus stout; sternum ovate, sutures between 2/3 and 3/4 marked.

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Etymology.—The term ''Magyar'' means Hungarian in the Hungarian language; we honor Imre Lőrenthey and Pál Müller, Földtani Intézet, Budapest, Hungary, both Hungarian students of paleontology who have made significant contributions to the study of fossil decapods. Note: Lőrenthey's first initial is ''E'' in literature written in German, because his first name in those publications was written in the German form, Emerich (P. Müller, pers. com.).

Material examined.—Lőrenthey's holotype material, E282, a dorsal carapace labeled as ''cotype,'' and E283, portions of chelipeds labeled as ''part of holotype,'' deposited in Földtani Intézet; MCZ 1520.

Occurrence.—The type and sole species is known from upper Eocene rocks in Hungary (Lőrenthey, 1898a) and Italy (Beschin *et al.*, 1998).

Discussion.—Lőrenthey (1898a) erected *Palaeograpsus loczyanus* for Eocene material collected in Hungary. The species has some similarities with the type and sole species of *Palaeograpsus*, but it differs from it in several important ways. The two species are alike in possessing a straight front, a broad fronto-orbital width, an equant carapace, and an epibranchial ridge. However, in *P. inflatus*, the type species of *Palaeograpsus*, the orbits are fissured and the anterolateral margin has two small spines. Neither of these features is seen in *P. loczyanus*. The anterolateral margin of *P. inflatus* is short and nearly straight, while in *P. loczyanus*, the anterolateral margin is convex and thickened. The epibranchial ridge of *P. inflatus* is much more inflated and straighter than that of *P. loczyanus*. In addition, the epibranchial ridge of *P. inflatus* is positioned quite a bit further anteriorly on the carapace than in *P. loczyanus*. The carapace regions of *P. inflatus* are much better developed than those of *P. loczyanus*. Thus, it is clear that the two species are not congeneric; in fact, their carapaces are markedly different in many fundamental aspects. *Palaeograpsus loczyanus* is therefore placed within the new genus *Magyarcarcinus*.

Magyarcarcinus has several superficial similarities with *Amydrocarcinus*. The sole species of both genera have rimmed, entire orbits; straight fronts; a fronto-orbital width to maximum carapace width ratio 0.67–0.70; frontal width to maximum carapace width ratio of about 30 percent; carapace length to width ratio of about 0.85; weakly defined carapace regions; depressed intestinal and posteriormost branchial regions; arcuate third maxillipeds; and stout first pereiopods. It is not possible to ascertain whether the eighth sternite is obscured by the abdomen in *Magyarcarcinus*, because unfortunately, in the holotype, that portion of the fossil has been destroyed, apparently with a rock saw or other tool (Fig. 1.4). Thus, we have provisionally allied *Magyarcarcinus* with *Amydrocarcinus* in the same subfamily.

These two apparently closely related genera, based upon their occurrences in Baja California and southern Europe, clearly display a Tethyan distribution, typical of many Eocene decapod taxa (Karasawa, 1993; Schweitzer, 2001; Schweitzer *et al.*, 2002).

Family Panopeidae Ortmann, 1893
Subfamily Eucratopsinae Stimpson, 1871

Figure 2.1, 2.3, 2.5

Included fossil genera.—*Bittneria* new genus; *Carinocarcinus* Lőrenthey, 1898b; *Palaeograpsus sensu stricto* Bittner, 1875.

Diagnosis.—Carapace wider than long, L/W ranging from 0.73–0.93, point of maximum carapace width about 40–50 percent the distance posteriorly on carapace; carapace flattened, regions moderately well-marked to weakly defined; front bilobed, ranging from 30 to 43 percent maximum carapace width; orbits with two fissures or notches, fronto-orbital width about 63–81 percent maximum carapace width; anterolateral margin with 3–5 spines including outer-orbital spine; sternum wide, triangular in shape, comparatively large portion of sternite 8 visible in ventral view; male abdominal somites 1, 2, and 3 not covering entire space between fifth pereiopods; male abdominal somites 3–5 fused, sutures may be evident. Pereiopods 2–5 long. Male genital openings coxal but penis often lies in a more or less elongate sternal (coxo-sternal) position. Male gonopod 1 with several, sometimes complex, apical extensions. Gonopod 2 short, curved. Diagnosis in part based upon descriptions and observations from Rathbun (1918) and Davie (2002).

Discussion.—Members of the Eucratopsinae and the Pseudorhombilidae Alcock, 1900, are very difficult to differentiate from one another. The dorsal carapace regions, the ornamentation of the anterolateral margin, and the shape and size of the pereiopods are similar to one another in both groups. Schweitzer (2003b) demonstrated that proxy characters of the dorsal carapace in the Xanthoidea could be successfully used to place fossil taxa within extant families primarily defined on soft-part features. Using several commonly used characters of the dorsal carapace, sternum, and abdomen that are typically preserved in fossils, the Eucratopsinae and Pseudorhombilidae differ in only a few major ways (Tables 3, 4). The fronto-orbital width to maximum carapace width ratio and the frontal width to maximum carapace width ratio in the Eucra-

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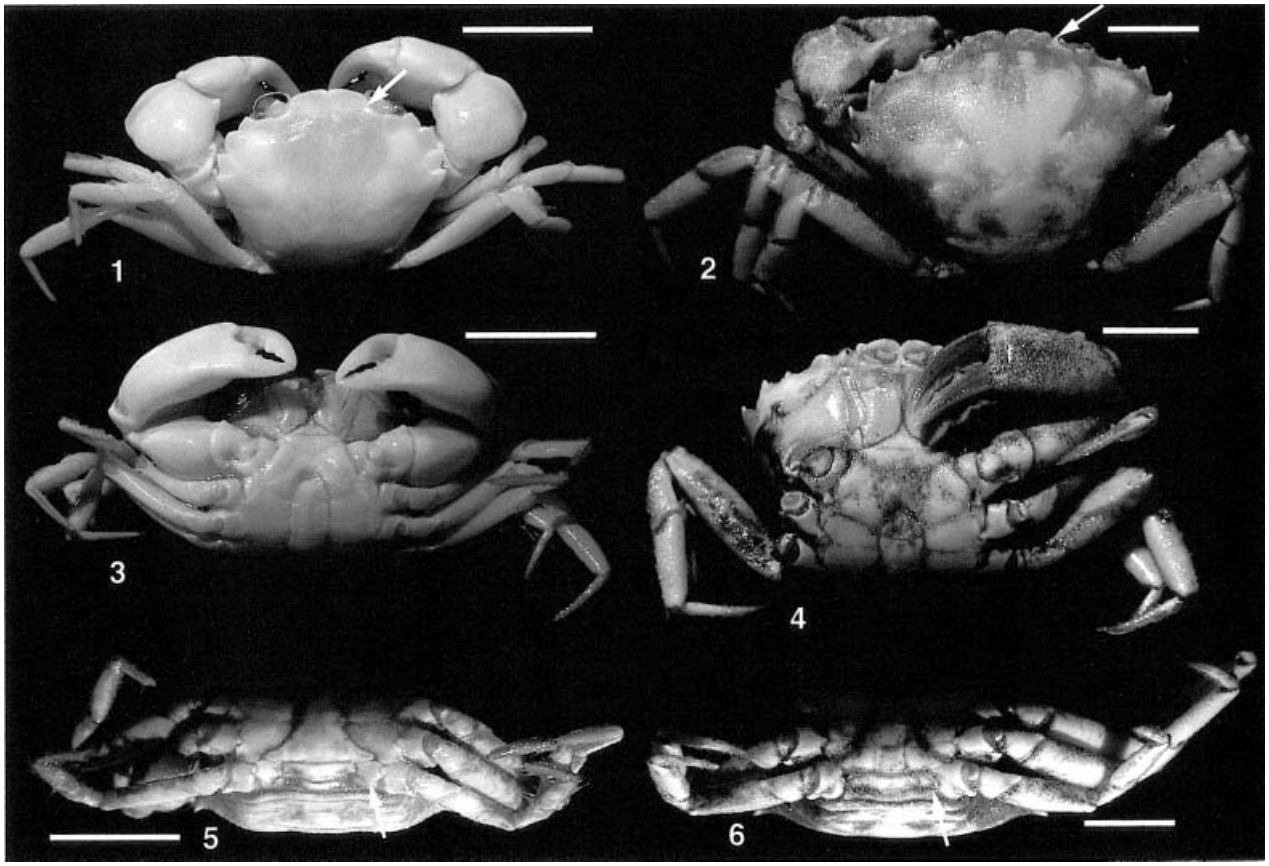


Figure 2. Comparison of Eucratopsinae (E) with Pseudorhombilidae (P), highlighting important differences. **1.** *Eucratopsis crassimanus* (Dana), USNM 45950, arrow indicates lack of intraorbital spine on orbital margin (E). **2.** *Euphrosynoplax campechiensis* Vazquez-Bader and Garcia, USNM 267608, arrow indicates intraorbital spine on orbital margin (P). **3.** *Eucratopsis crassimanus* (Dana), male, USNM 45950, ventral surface (E). **4.** *Euphrosynoplax campechiensis* Vazquez-Bader and Garcia, male, USNM 267608, ventral surface (P). **5.** *Cyrtoplax spinidentata* (Benedict), USNM 82158, male, arrow indicates large portion of somite 8 visible and abdomen not touching coxae of fifth pereiopods (E). **6.** *Euphrosynoplax campechiensis* Vazquez-Bader and Garcia, male, USNM 267608, arrow indicates that very little of somite 8 is visible and that somite 3 of the abdomen does touch the coxae of the fifth pereiopods. Scale bars equal to 1 cm.

topsinae is consistently higher than in the Pseudorhombilidae, although each set of ratios shows a small amount of overlap. At present, use of these ratios appears to be the best means of distinguishing the two taxa in the fossil record, because the major differences between extant forms are in the morphology of the pleopods (Hendrickx, 1998).

Other dorsal carapace characters which might serve to differentiate between members of the Eucratopsinae and Pseudorhombilidae include some features of the orbits. In pseudorhombilids, the orbit is weakly rimmed and has an intraorbital projection positioned just posterior to the edge of the front (Figure 2.1, 2.2). This projection is not seen, or is very weak, in eucratopsines. In addition, the orbits are more sinuous in pseudorhombilids, being weakly but noticeably convex between the two orbital fissures (Figure 2.1, 2.2). This sinuosity is much less noticeable in members of the eucratopsines.

Several characters of the ventral surface may be used to distinguish between members of the Eucratopsinae and Pseudorhombilidae. In the Eucratopsinae, the fusion of male abdominal somites 3–5 is nearly complete, with sutures sometimes evident, whereas in the Pseudorhombilidae, the fusion may be much weaker, with clearly evident sutures and sometimes with notches in the abdominal margin at the suture (Hendrickx, 1998). Degree of fusion, however, is quite difficult to observe in fossils where the abdomen cannot be moved so as to determine the degree of fusion. In addition, disarticulation of the animal upon burial can also make the abdomen appear as if the fusion was more weak than it was in life, because the somites can break apart along weak sutures. The ex-

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Table 3. Characters of the Eucratopsinae that may be observed in fossils. Included genera are based upon Martin and Abele (1986) and Davie (2002). The important characters differentiating the Eucratopsinae and the Pseudorhombilidae are highlighted in bold. Angle = angle of posterior margin to posterolateral margin; front = whether front is straight or bilobed; orbits = number of orbital notches or fissures; ABD 1 = whether or not male abdomen covers entire space between coxae of fifth pereiopods; ABD 2 = presence or absence of male abdominal somites 3–5 fused and sometimes having discernable sutures. Abbreviations: L = maximum carapace length; W = maximum carapace width; FOW = fronto-orbital width; FW = frontal width; LMW = length to position of maximum width; PL = length from front to posteriormost end of protogastric region.

	Homoioplax Rathbun, 1914	*Tetraplax* Rathbun, 1901	*Panoplax* Stimpson, 1871	*Cyrtoplax* Rathbun, 1914	*Glyptoplax* Smith, 1870	*Eucratopsis* Smith, 1869
L/W	0.93	0.81	0.74	0.73	0.74	0.87
FOW/W	**0.75**	**0.81**	**0.67**	**0.57**	**0.63**	**0.73**
FW/W	**0.43**	**0.35**	**0.37**	**0.30**	**0.37**	**0.33**
LMW/L	0.46	0.44	0.40	0.50	0.50	0.40
Angle	69	54	55	58	57	65
PL/L	0.38	0.52	0.45	0.50	0.50	0.38
Front	bilobed	bilobed	bilobed	bilobed	bilobed	bilobed
Orbits	2	2	2	2	2	2
ABD 1	not	not	not	not	not	not
ABD 2	present	present	present	present	present	present

Table 4. Characters of the Pseudorhombilidae that may be observed in fossils. Included genera are based upon Hendrickx, 1998. Some genera included by Hendrickx (1998) were not observed. Abbreviations and characters are the same as those outlined in Table 3. The important characters differentiating the Eucratopsinae and the Pseudorhombilidae are highlighted in bold.

	Euphrosynoplax Guinot, 1969b	*Bathyrhombila* Hendrickx, 1998	*Pseudorhombila* H. Milne Edwards, 1837	*Oediplax* Rathbun, 1893	*Chacellus* Guinot, 1967
L/W	0.72	0.72	0.74	0.74	0.76
FOW/W	**0.59**	**0.53**	**0.59**	**0.51**	**0.53**
FW/W	**0.31**	**0.32**	**0.30**	**0.26**	**0.29**
LMW/L	0.49	0.55	0.41	0.50	0.50
Angle	52	60	54	55	56
PL/L	0.52	0.50	0.52	0.44	0.42
Front	bilobed	bilobed	bilobed	bilobed	bilobed
Orbits	2	2	2	2	2
ABD 1	not	not	not	not	not
ABD 2	present	present	present	present	present

posed portion of the eighth sternite is much larger in eucratopsines than in pseudorhombilids, where only a tiny portion of sternite 8 is visible in ventral view (Figure 2.5, 2.6).

Karasawa and Kato (2003a) reported that the male abdomen does not fill the entire space between the pereiopods in *Palaeograpsus inflatus*, the type and sole species. In the Eucratopsinae, the first three abdominal somites do not touch the coxae of the fifth pereiopods and thus do not fill the entire space between the pereiopods, leaving a large portion of sternite 8 visible (Figure 2.5). In the Pseudorhombilidae, the male abdominal somites 1 and 2 do not cover the entire space between the fifth pereiopods (Guinot, 1969a; Hendrickx, 1998). Note, however, that in observing members of the Pseudorhombilidae in the National Museum of Natural History (*Chacellus pacificus* Hendrickx, acc. no. 381784; *Euphrosynoplax campechiensis* Vazquez-Bader and Garcia, USNM 267608; *Oediplax granulata* Rathbun, USNM 136650; *Chacellus filiformis* Guinot, USNM 151477, 250196; *Euphrosynoplax clausa* Guinot, USNM 298321), the male abdominal somite 3 does in fact touch the coxae of the fifth pereiopods, although a portion of sternite 8 is visible (Figure 2.6). Thus, paleontologists must be very careful to try to observe male abdominal somites 1–3, if possible, when attempting to differentiate between the Eucratopsinae and the Pseudorhombilidae

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in fossil specimens. Whether the male abdomen touches the coxae of the fifth pereiopods, and whether a portion of somite 8 is exposed in males, are two different characters and must be observed separately.

The fronto-orbital width to maximum carapace width and frontal width to maximum carapace width ratios in *Palaeograpsus* fall well within the bounds of those typical of the Eucratopsinae and are far greater than those found in the Pseudorhombilidae (see Table 4). Thus, placement of *Palaeograpsus* in the Eucratopsinae is well warranted.

Genus ***Palaeograpsus*** Bittner, 1875

Type species.—*Palaeograpsus inflatus* Bittner, 1875, by order of precedence in the original descriptive paper.

Included species.—Only the type species is included.

Diagnosis.—Carapace square, not much wider than long, L/W about 0.90, widest about two-thirds the distance posteriorly on carapace; front axially sulcate, about 30 percent maximum carapace width; orbits circular, rimmed, directed forward, fronto-orbital width about two-thirds maximum carapace width; anterolateral and posterolateral margins confluent, weakly convex; with two small, sharp spines anteriorly; posterior margin nearly straight; protogastric regions broadly inflated; epibranchial regions and posteriormost mesogastric region swollen, forming a continuous ridge across carapace; branchio-cardiac groove outlining cardiac region; cardiac region inflated; central branchial region inflated, branchial inflations together with cardiac inflation forming a discontinuous ridge transversely across carapace; intestinal region flattened; male abdominal somites 3 and 4 fused, possibly 4 fused to 5 as well.

Material examined.—E9440, deposited in Földtani Intézet, illustrated by Lőrenthey and Beurlen, 1929, note that this illustration is a composite of two specimens (P. Müller, pers. com.); MCZ 1507, 1509, 1511, 1513, identified by Beschin, Busulini, De Angeli, and Tessier (pers. com.); MCZ 1521 (Beschin *et al.*, 1996); Földtani Intézet 209, identified and illustrated by Lőrenthey (1898a).

Discussion.—Because only the illustrations of the type material (Bittner, 1875, pl. II, fig. 11) as well as non-type material were examined, only a diagnosis is provided including the most obvious, well-illustrated aspects of the carapace. It should be stated that the illustrations in Bittner (1875) are remarkably accurate for specimens that have been observed by the authors; thus, we have every reason to believe that his illustrations of *P. inflatus* are similarly accurate. However, a complete description of the genus must await examination of type material. In particular, the sternites and abdominal somites must be examined in order to confirm the family placement of the genus.

Földtani Intézet 209 is in almost all regards very similar to the illustration of the type species (Bittner, 1875, pl. II, fig. 11), except that the fronto-orbital width occupies nearly the entire maximum width of the carapace, 92 percent. It is possible that the species displays allometric growth with regard to the relative width of the fronto-orbital margin, a condition seen in other brachyurans including the Etyiidae Guinot and Tavares, 2001 (Wright and Collins, 1972) and the Portunidae Rafinesque, 1815 (Schweitzer and Feldmann, 2000).

Genus ***Bittneria*** new genus

Figure 1.6

Type species.—*Palaeograpsus attenuatus* Bittner, 1875, by monotypy.

Diagnosis.—Carapace hexagonal, wider than long, L/W = 0.85; front with median notch, about 36 percent maximum carapace width; orbits directed forward, fronto-orbital width about 64 percent carapace width; anterolateral margin with three or four small spines; posterolateral margin entire, posterolateral reentrants at posterolateral corner; posterior margin about 35 percent maximum carapace width; regions generally indistinct; epibranchial regions ridgelike, extending from posterolateral spine to axial regions; branchial region with transverse ridge centrally, crossing axis to form continuous ridge across cardiac region; both ridges arcing weakly anteriorly.

Etymology.—The genus name honors Alexander Bittner, a nineteenth century decapod paleontologist who has contributed much to our understanding of fossil crabs.

Material examined.—MB.A.663, holotype, deposited in Museum für Naturkunde Berlin Paläontologisches Museum Humboldt-Universität zu Berlin; MCZ 1423, 1424.

Occurrence.—*Bittneria* is known from Eocene rocks of Italy (Bittner, 1875; Beschin *et al.*, 1994).

Discussion.—The new genus accommodates *Palaeograpsus attenuatus*, which cannot be retained in *Palaeograpsus sensu stricto*. *Palaeograpsus sensu stricto* is characterized by a carapace that is in many ways very similar to that of *P. attenuatus* but in *Palaeograpsus*, the anterolateral margin is extremely short with one spine; in *P. attenuatus* the anterolateral margin is long, with several spines. The ridges of *Palaeograpsus* ex-

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hibit different development as well. The epibranchial-mesogastric ridge in *Palaeograpsus* is continuous across the carapace and the two lateral segments of the ridge converge posteriorly, whereas the epibranchial ridge of *P. attenuatus* is not continuous, does not extend onto the mesogastric region, and arcs anteriorly. The branchial ridge of *P. attenuatus* is continuous across the cardiac region and arcs anteriorly, while the branchial ridge of *Palaeograpsus* is a discontinuous series of spherical inflations and does not extend across the cardiac region. The carapace of *P. attenuatus* narrows distally and the posterolateral margins converge distally, while in *Palaeograpsus*, the lateral margins are nearly straight and converge only a small amount. Thus, it is clear that *P. attenuatus* must be removed to a new genus, *Bittneria*.

Bittneria exhibits many superficial similarities to *Carinocarcinus* Lőrenthey, 1898b. Both have transverse ridges on the dorsal carapace, a hexagonal carapace, and spined anterolateral margins, and nearly identical fronto-orbital width to maximum carapace width and frontal-width to maximum carapace width ratios. However, *Carinocarcinus* is wider proportionally than *Bittneria*; the L/W of *Carinocarcinus* is about 0.73 as compared to 0.85 in *Bittneria*. The front of *Carinocarcinus* appears to be straight, while in *Bittneria* it is notched. The anterolateral spines of *Carinocarcinus* are large and triangular in shape, while those of *Bittneria* are very small. Thus, the two are clearly distinct, but may be closely related.

Karasawa and Kato (2003a) suggested that *Carinocarcinus* be referred to the Pseudorhombilidae, but based upon the broad fronto-orbital width to maximum carapace width and frontal width to maximum carapace width ratios in both *Bittneria* and *Carinocarcinus*, we place these two genera within the Eucratopsinae.

Family Pseudorhombilidae Alcock, 1900

Figure 2.2, 2.4, 2.6

Included genera.—*Bathyrhombila* Hendrickx, 1998; *Chacellus* Guinot, 1969b; *Euphrosynoplax* Guinot, 1969b; *Nanoplax* Guinot, 1967 (extant and fossil); *Oediplax* Rathbun, 1893; *Pseudorhombila* H. Milne Edwards, 1837 (extant and fossil) (list from Hendrickx, 1998). Unless otherwise marked, genera are solely extant.

Diagnosis.—Carapace wider than long, L/W ranging from 0.72–0.76, point of maximum carapace width about 40–55 percent the distance posteriorly on carapace; carapace flattened, regions moderately well marked to weakly defined; front bilobed, ranging from 26–32 percent maximum carapace width; orbits with two fissures or notches, orbital rim sinuous, convex between fissures, marked protuberance on inner orbital rim; fronto-orbital width about 53–59 percent maximum carapace width; anterolateral margin with 3-5 spines including outer-orbital spine; sternum wide, tiny portion of sternite 8 visible adjacent to articulation condyle of coxa of fifth pereiopod, visible in posterior or dorsal view; male abdominal somites 1 and 2 not covering entire space between fifth pereiopods, somite 3 usually touching coxa of fifth pereiopod; male abdominal somites 3–5 fused, often weakly, sutures may be quite obvious. Diagnosis based in part on descriptions and observations from Rathbun (1918), Guinot (1969b), and Hendrickx (1998).

Discussion.—Hendrickx (1998) recognized the family Pseudorhombilidae Alcock, 1900, for xanthoid crabs in which the eighth male abdominal somite is visible and the male abdomen is clearly separated from the coxae of the fifth pereiopods (p. 635). The dorsal carapace, sternal, and abdominal characters of the Pseudorhombilidae are remarkably consistent among included genera. There is very little variation in the various dorsal carapace ratios (Table 4) and in the development of dorsal carapace regions. Genera within the family are distinguished from one another based upon the nature of the outer-orbital and anterolateral spines, the male pleopods, and the third maxillipeds (Hendrickx, 1998). Of these features, only the nature of the outer-orbital and anterolateral spines, and in relatively rare cases the third maxillipeds, may be preserved as fossils.

At this time, *Pseudorhombila patagonica* Glaessner, 1933, is known from Miocene rocks of Santa Cruz Province, Argentina, and *Nanoplax* was reported from late Pleistocene rocks of Jamaica (Collins and Donovan, 1997). They are the only fossils of the family known.

It is notable that in a parasitized specimen of *Chacellus filiformis* (USNM 250196), the eighth sternite is totally obscured by the male abdominal somites. The specimen exhibits parasitic castration, described in Miocene crabs from New Zealand (Feldmann, 1998), in which the male abdomen becomes broadened to mimic that of a female. Because the exposure of the eighth sternite is such an important character in xanthoid classification, this phenomenon is worthy of note.

Section Thoracotremata Guinot, 1977
Superfamily Grapsoidea MacLeay, 1838
Family Grapsidae MacLeay, 1838 *sensu lato*
Genus ***Litograpsus*** new genus

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Type species.—*Palaeograpsus parvus* Müller and Collins, 1991b (= *Palaeograpsus bittneri* Müller and Collins, 1991a, *non Palaeograpsus bittneri* Morris and Collins, 1991), by monotypy.

Diagnosis.—as for species.

Description.—as for species.

Etymology.—The genus name is derived from the genus name *Grapsus*, commonly used as a stem in the superfamily, and the Greek word *litos*, meaning simple, in reference to the relatively unornamented carapace of the taxon, unusual among the Grapsoidea.

Discussion.—The specimen referred to *Palaeograpsus* by Müller and Collins (1991a, b) cannot be accommodated by the genus as restricted herein. The rectangular carapace; extremely broad fronto-orbital width, which is equal to the maximum carapace width; concave, rounded frontal region; transverse ridge formed by the cardiac region and broad branchial ridges; and orbits positioned at the lateral margins of the carapace differentiate it from all eucratopsines and pseudorhombilids. The aforementioned features of the dorsal carapace best ally the species with the Grapsidae *sensu lato*, specifically, members of the Grapsidae *sensu stricto* and the Sesarmidae Dana, 1851. Thus, we have placed the species within the Grapsidae *sensu lato*; because the material consists only of a dorsal carapace, more definitive family-level placement cannot be made.

The species is referred to a new genus, *Litograpsus*, because the above-mentioned characters do not permit placement into any known genus. The lack of multiple transverse ridges on the dorsal carapace excludes the species from many grapsid genera. Many grapsoids have anterolateral spines or serrations, which *L. parvus* lacks. *Litograpsus parvus* has a rounded frontal margin, while other grapsoids have a much more angular frontal margin that often flares distally, a condition not seen in *L. parvus*.

The Grapsoidea are not well represented in the fossil record, probably because of their predominantly near-shore habitat which is not conducive to preservation. Glaessner (1969) reported an Eocene to Recent range for the Grapsidae *sensu lato*, the Eocene occurrences including *Palaeograpsus sensu lato*, *Daranyia* Lőrenthey, 1901, and *Varuna* H. Milne Edwards, 1830. Although all of the species of *Palaeograpsus* known by Glaessner (1969) have now been removed from the Grapsidae, *Litograpsus* is known from the Eocene of Hungary, and *Daranyia* and *Varuna* are clearly grapsoids. Thus, the Eocene to Recent range still holds, at least for the superfamily Grapsoidea. The subfamilies employed by Glaessner (1969) have now been raised to family status (Martin and Davis, 2001), and the family-level position of these fossil taxa has yet to be confirmed. Karasawa and Kato (2001) reviewed all fossil records of the superfamily and removed several genera from it.

Litograpsus parvus (Müller and Collins, 1991b) new combination

Figure 1.7

Palaeograpsus bittneri Müller and Collins, 1991a, p. 89, text-fig. 5i; pl. 8, figs. 11, 12, 15 (*non Palaeograpsus bittneri* Morris and Collins, 1991).

Palaeograpsus parvus Müller and Collins, 1991b, p. 140.

Diagnosis.—Carapace slightly wider than long; front concave, broad, broadly rimmed; fronto-orbital width equal to maximum carapace width; transverse branchial ridges and cardiac region forming nearly continuous transverse ridge across carapace.

Description.—Carapace rectangular, slightly wider than long, L/W = 0.89; regions poorly defined; moderately vaulted longitudinally and transversely.

Front very broad, frontal width about half maximum carapace width, projecting beyond orbits, broadly rimmed; entire frontal area concave, weak epigastric swellings positioned adjacent to orbits. Orbits large, circular, directed laterally, positioned at lateral margins of carapace so that fronto-orbital width is equal to maximum carapace width. Lateral margins sinuous, with small indentations where transverse grooves intersect it, posterolateral reentrant large. Posterior margin nearly straight, posterior width about half maximum carapace width. Protogastric regions small, weakly inflated; mesogastric region very poorly defined, confluent with urogastric region; cardiac region most inflated of all carapace regions, ovate; intestinal region flattened, depressed below level of cardiac region. Hepatic regions broad, bounded posteriorly by transverse grooves. Branchial regions undifferentiated, with broad transverse ridge on line with cardiac region, forming a nearly continuous transverse ridge across carapace.

Remainder of carapace unknown.

Measurements.—Measurements (in mm) taken on a cast of the dorsal carapace of M.91-227: maximum carapace width, 4.7; maximum carapace length, 4.2; fronto-orbital width, 4.7; frontal width, 2.5; posterior width, 2.5.

Material examined.—Holotype, M.91-227; cast of holotype.

Occurrence.—The species is known from Eocene rocks of Hungary (Müller and Collins, 1991a, b).

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Evolutionary implications

The assignment of two middle Eocene fossil genera to the Eucratopsinae marks the first notice of that subfamily in the fossil record. The Panopeinae Ortmann, 1893 has a well-defined fossil record extending into the middle Eocene, based upon occurrences of *Panopeus* H. Milne Edwards, 1834, and *Laevicarcinus* Lőrenthey *in* Lőrenthey and Beurlen, 1929 (Glaessner, 1969; Schweitzer, 2000). Thus, the divergence of these two subfamilies of the Panopeidae must have occurred before that time. It is becoming increasingly clear that the divergence of the various families and subfamilies of the Xanthoidea occurred before the middle Eocene, and probably after the Cretaceous, in which there are few xanthoid fossils (Schweitzer *et al.*, 2002; Schweitzer, 2003a, b).

The Eocene occurrences of members of the Panopeidae display a clear geographic pattern. The Tethyan occurrence of the eucratopsines known from the fossil record and the Eocene panopeine occurrences known from the Tethyan and Pacific slope of North America suggest that the family arose in the Tethyan region and was dispersed via the Tethys Sea and the Central American Seaway as has been suggested for many decapod taxa (Schweitzer, 2001; Schweitzer *et al.*, 2002). The two known fossil members of the Pseudorhombilidae are from the Pleistocene of the Caribbean and the Miocene of South America, suggesting that the family arose in the central and South Atlantic Ocean. Extant members of the family are known from the east and west coasts of the Americas, probably dispersing to the Pacific via the Central American Seaway which was still open during the early Miocene (Bice *et al.*, 2000).

Currently, three genera of the Grapsoidea are known with some level of certainty from the middle Eocene of Europe. The Grapsoidea belong to the Section Thoracotremata Guinot, 1977, considered to be the most advanced group of crabs. In this group, which also includes the Pinnotheridae de Haan, 1833, the pea crabs, and the Ocypodoidea Rafinesque, 1815, the fiddler and ghost crabs, the genital openings are on the sternites in both males and females. The thoracotreme crabs, in general, have a very poor fossil record; for example, only one crab taxon from Central America belongs to this group (Schweitzer *et al.*, 2002). A similar pattern was observed for the North Pacific (Schweitzer, 2001). Eocene occurrences of the Thoracotremata include members of the Grapsoidea and the Pinnotheridae (Schweitzer and Feldmann, 2001). Other crabs, belonging to the sections Podotremata Guinot, 1977, and Heterotremata Guinot, 1977, have genital openings on the appendages in both males and females, and on the sternum in females and the appendages in males, respectively. Both the Podotremata and the Heterotremata, which includes the Xanthoidea, are well represented in the fossil record. The documented presence of thoracotremes in the middle Eocene strongly suggests that the divergence between these major crab lineages must have occurred before that time, even though most fossil thoracotreme specimens are Miocene or younger.

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