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REVISION OF THE CARCINERETIDAE BEURLEN, 1930 (DECAPODA: BRACHYURA: PORTUNOIDEA) AND REMARKS ON THE PORTUNIDAE RAFINESQUE, 1815

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ABSTRACT

All genera previously referred to the Carcineretidae are herein evaluated, and the family is restricted to three genera, *Carcineretes*, *Cancrixantho*, and *Mascaranada*, for which diagnoses are provided. *Ophthalmoplax* and *Longusorbis* are herein removed to the Portunidae, and *Longusorbis eutychius* new species is described from the Eocene Tepetate Formation of Baja California Sur, Mexico, extending the range of that genus across the K/P boundary. The placement of *Ophthalmoplax* into the Portunidae marks the first confirmed notice of the family in Cretaceous rocks, a major range extension for the family. Important characteristics of the Portunoidea are discussed in the context of placement of fossil taxa within the superfamily and its constituent families.

KEY WORDS: Decapoda, Brachyura, Carcineretidae, Portunoidea, Goneplacidae, Eocene, Tepetate Formation, ichnofossils

INTRODUCTION

The composition of the Carcineretidae Beurlen, 1930, has been considered to be heterogeneous for some time (Vega and Feldmann 1991; Feldmann and Villamil 2002; Schweitzer et al. 2002). Feldmann and Villamil (2002) removed several genera from the family, with which we largely concur. In addition, the family has been considered to have become extinct at the end of the Cretaceous, perhaps as a victim of the Chicxulub impact event (Feldmann et al. 1998). Recovery of an Eocene specimen of *Longusorbis* Richards, 1975, from Baja California Sur, Mexico, has spurred a reevaluation of the genera referred to the family and the criteria upon which the family definition is based. Specimens of nearly all genera at some time referred to the Carcineretidae, in addition to members of the Portunoidea and Goneplacoidea, have been examined to facilitate this process.

GEOLOGIC SETTING

The specimens of *Longusorbis eutychius* new species described here were collected from localities in the middle Eocene Tepetate Formation, the geology and paleontology of which have been recently summarized elsewhere (Schweitzer et al. 2002; Schweitzer et al. 2006 [imprint 2005]; Schweitzer et al. 2007). One locality is our Waypoint 39 of other publications, near the village of El Cien, Baja California Sur, Mexico, at lat. 24°19'56.8"N, long. 111°01'06.6"W. Other specimens were collected from Waypoint 37, in Arroyo Conejo, northwest of La Paz, at lat. 24°10'13.9"N, long. 110°55'06.2"W, the same locality at which some of the specimens described by Schweitzer et al. (2002) were collected.

Institutional abbreviations.—**BSP**, Bayerische Staatsammlung für Paläontologie und historische Geologie München (Munich), Germany; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **KSU D**, Kent State University Decapod Comparative Collection, Kent, Ohio; **MHN-UABCS**, Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, Mexico; **PRI**, Paleontological Research Institution, Ithaca, New York; **SDSNH**, San Diego Society of Natural History, San Diego Natural History Museum, California; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **UT**, University of Texas, Austin, Texas.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Carcineretidae Beurlen, 1930

Included genera.—*Carcineretes* Withers, 1922; *Mascaranada* Vega and Feldmann, 1991; questionably *Cancrixantho* Van Straelen, 1934.

Diagnosis.—Carapace quadrate, wider than long, flattened longitudinally and transversely; L/W about 90 percent, widest at position of hepatic region, just posterior to post-orbital angle. Rostrum straight in dorsal view, strongly downturned in anterior view, downturned portion nearly perpendicular to dorsal carapace; frontal width about half maximum carapace width, outermost edges of front are inner-orbital spines. Orbits sinuous, long, with two or three intra-orbital spines and notches; outer-orbital spine triangular, directed forward; fronto-orbital width 90+ percent maximum carapace width. Anterolateral and posterolateral margins confluent, lateral margins with blunt protuberances or very short spines; posterolateral reentrants subtle but present; posterior margin rimmed, nearly straight. Protogastric regions and hepatic regions with transverse keels or swellings; epibranchial regions arcuate; mesobranchial region and cardiac region with transverse ridges; metabranchial region and intestinal region depressed below level of mesobranchial and cardiac regions.

Sternum ovate, slightly wider than long; sternites 1 and 2 fused, no evidence of a suture; sternal suture 2/3 complete; sternite 3 with longitudinal groove extending anteriorly from axis of sterno-abdominal cavity, sternal suture 3/4 incomplete; lateral margin of sternite 4 at high angle to axis; sternal suture 4/5 and 5/6 not parallel, 4/5 at high angle; sternite 8 not visible in ventral view. Male abdomen with concave margins, reaching to about middle of sternite 4, reaching to about middle of coxae of first pereiopods; somites 3-5 fused, may be slight evidence of sutures; somite 3 very wide, completely filling space between coxae of fifth pereiopods; somites 1 and 2 and apparently part of somite 3 not visible in ventral view; somites appearing to lack transverse keels. Chelipeds weakly heterochelate; chelae with keel or keels on outer surface; fingers with keels, lacking black tips. Fourth pereiopod with flattened carpus and merus. Fifth pereiopod with elliptic dactyl and propodus and flattened carpus and merus.

Discussion.—The Carcineretidae was designated as a unique family by Beurlen (1930). The possession of an extremely broad fronto-orbital width (90+ percent the maximum carapace width); a downturned central rostral projection; indistinguishable anterolateral and posterolateral margins lacking well-developed spines; keeled protogastric regions; sternite 8 obscured by the abdomen; male abdomen with somites 3–5 fused with weak evidence of sutures; somite 3 extremely wide and entirely filling space between coxae of fifth pereiopods; somites apparently lacking transverse keels; chelae with keels and lacking black tips on fingers; and elliptic dactyls and propodi of the fifth pereiopods and flattened articles of the fourth and fifth pereiopods is a unique combination of characters, unlike any portunoid, xanthoid, or goneplacoid family. In particular, none of the portunid subfamilies, which generally exhibit paddle-like or flattened articles of the fifth pereiopods, can accommodate the combination of characters exhibited by *Carcineretes*; thus, we retain the family.

However, examination of the various other genera at some time assigned to the Carcineretidae has raised doubt as to their placement in the family; these genera include *Binkhorstia* Noetling, 1881; *Branchiocarcinus* Vega et al., 1995; *Cancrixantho* Van Straelen, 1934; *Icriocarcinus* Bishop, 1988; *Lithophylax* A. Milne Edwards and Brocchi, 1879; *Longusorbis* Richards, 1975; *Mascaranada* Vega and Feldmann, 1991; *Ophthalmoplax* Rathbun, 1935; *Withersella* Wright and Collins, 1972; and *Woodbinax* Stenzel, 1952 (Feldmann and Villamil 2002; van Bakel et al. 2003). Strong justification for reevaluating these taxa and reassigning them to other families arises from the recognition of significant family-level characters exhibited on the sternum and male abdomen (see fig. 6, Schweitzer et al. 2002, for illustration of sternum and abdomen). The overall outline of the sternum, relative size and conformation of sternites and abdominal somites, and the nature of fusion of sternites and abdominal somites are now considered of major importance in assignment of genera to their appropriate family. Often, sterna and somites are not exposed or are not preserved on fossils. However, when they are, these aspects of the ventral architecture are extremely useful in placement. Thus, many of the reassignments discussed below arise from the recognition of the sternum and abdomen as important regions, coupled with the discovery of fossil specimens on which these regions are exposed. In the absence of ventral features, it remains necessary to rely solely on morphological features exhibited on the dorsal carapace.

Schweitzer et al. (2003) reevaluated the family-level placement of *Longusorbis*, concluding that its best placement at that time was within the Carcineretidae. That genus is herein placed within the Portunoidea *sensu lato* discussed below. *Ophthalmoplax* cannot be retained within the Carcineretidae because it is quite different from *Carcineretes* in terms of the dorsal carapace, male abdomen, and sternum (Fig. 1, Table 1). Notable differences include a very wide sternite 3, differing in shape from that of *Carcineretes*; a broad ovate sternum with lateral margins, especially those of sternite 4, at a lower angle than those of *Carcineretes*; sternite 8 visible in ventral view, which is not visible in *Carcineretes*; a sterno-abdominal cavity reaching onto sternite 3, whereas that of *Carcineretes* extends to about the middle of sternite 4; parallel sternal sutures 4/5 and 5/6, whereas those of *Carcineretes* are not parallel; a very elongate male telson, much longer than wide; and a narrow front with two medial spines, instead of a flattened, downturned central rostral spine. *Ophthalmoplax* is herein removed to the Portunidae as discussed below.

Glaessner (1969) placed *Binkhorstia* within the the Dorippidae MacLeay, 1838. Wright and Collins (1972) suggested and later workers (Collins et al. 1995; Fraaye 1996) confirmed placement of *Binkhorstia* and *Withersella* in the Carcineretidae, based upon possession of a quadrate carapace and broad orbits. Van Bakel et al. (2003) later placed *Binkhorstia* within the Torynommidae Glaessner, 1980, based upon their perception that *Binkhorstia* was most similar to *Torynomma* Woods, 1953. Both *Binkhorstia* and *Withersella* possess quadrate, granular carapaces with broad orbits. Both lack the markedly depressed posterior portion of the cephalothorax seen in the Carcineretidae and have very different ornamentation than that seen in carcineretids. The chelae of *Binkhorstia ubaghsi* (Binkhorst, 1857)

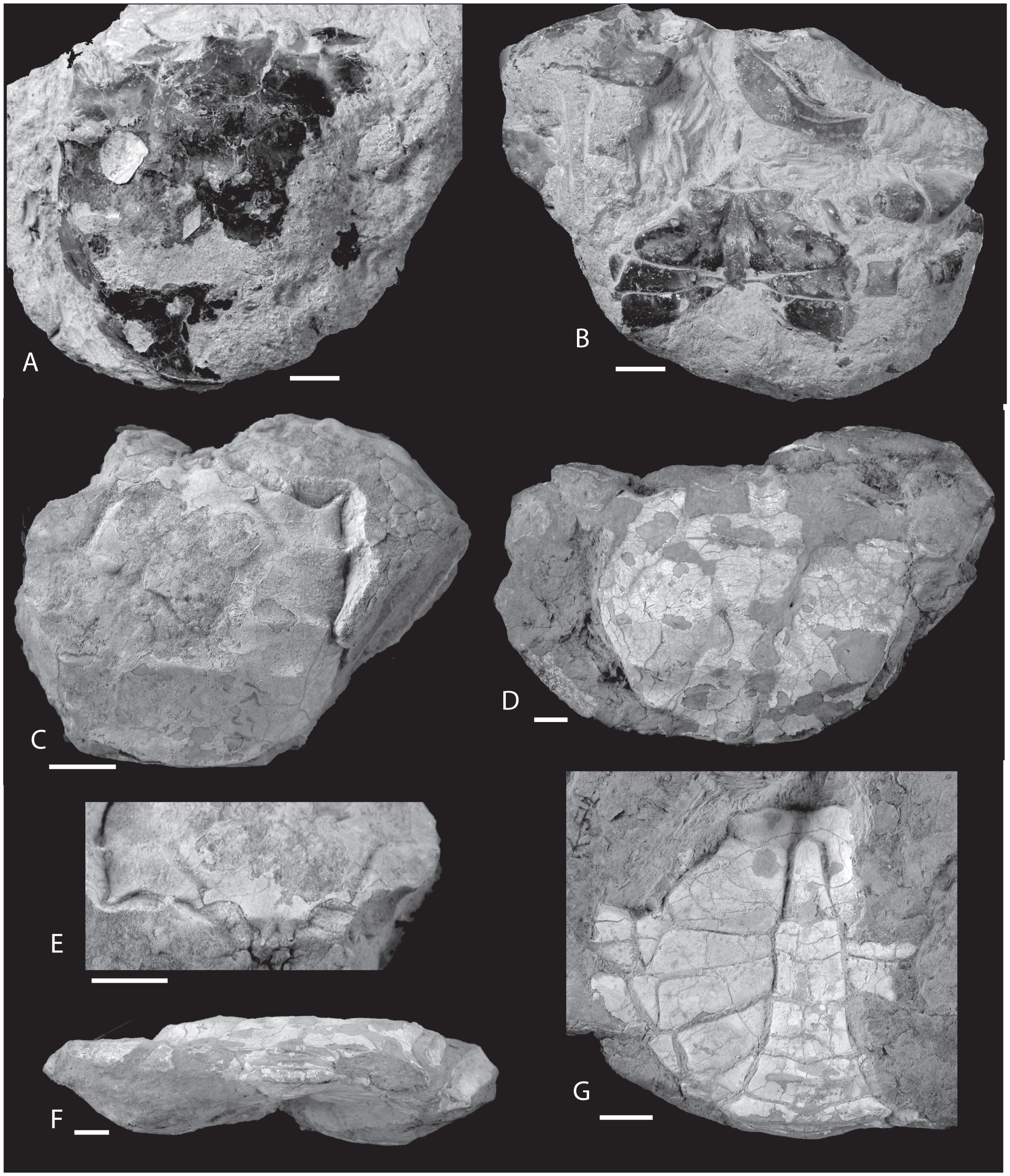

Fig. 1.—*Ophthalmoplax stephensoni* Rathbun, 1935. **A, B,** dorsal and ventral views of holotype, USNM 73793, unwhitened. **C, E,** dorsal and frontal views of paratype, UT 21258, showing the nature of the spines on the anterior and anterolateral margins and the strongly downturned, bifid rostrum. **D, F, G,** dorsal, posterior, and ventral view of paratype, UT 21262, showing the transverse ridges on the abdominal somites and the detail of the sternum and abdomen of a male specimen. Scale bars = 1 cm.

TABLE 1. Important generic and family level characters of species of *Carcineretes* spp., *Ophthalmoplax stephensoni*, and *Longusorbis* spp., each at one time referred to the Carcineretidae.

Carcineretes spp.	*Ophthalmoplax stephensoni*	*Longusorbis* spp.
Sternite 8 covered in ventral view	Sternite 8 clearly visible in ventral view	Sternite 8 covered in ventral view
Sternites 1/2 fused, no suture	Sternites 1/2 fused, no suture, rimmed, concave centrally	Sternites 1/2 fused, no suture
Sternal suture 2/3 complete	Sternal suture 2/3 complete	Sternal suture 2/3 complete
Longitudinal groove in sternite 3	Longitudinal groove in sternite 3	No longitudinal groove in sternite 3
Suture 3/4 incomplete	Suture 3/4 incomplete	Suture 3/4 incomplete
Sternite 3 slightly wider than 1/2	Sternite 3 much wider than 1/2	Sternite 3 slightly wider than 1/2
L/W of sternum (length measured to end of sternite 6) = 0.93	L/W of sternum (length measured to end of sternite 6) = 0.70	L/W of sternum (length measured to end of sternite 6) = 1.03
Outer margin of sternite 4 at high angle, straight	Outer margin of sternite 4 at low angle, sinuous	Outer margin of sternite 4 at high angle, straight
Sternal suture 4/5 and 5/6 not parallel	Sternal suture 4/5 and 5/6 parallel	Sternal suture 4/5 and 5/6 not parallel
Sternal suture 4/5 at high angle	Sternal suture 4/5 at lower angle	Sternal suture 4/5 at high angle
Male abdominal somites 3–5 fused, with faint sutures	Male abdominal somites 3–5 free	Male abdominal somites 3–5 free
Male abdomen extending to position of about mid-coxa 1	Male abdomen extending well beyond mid-coxa 1	Male abdomen extending to position of about mid-coxa 1
Male telson equilateral triangle	Male telson elongate, narrow, rounded tipped	Male telson equilateral triangle
Male somite 6 with straight margin	Male somite 6 with markedly sinuous margin	Male somite 6 with straight margin
Carapace L/W = 0.91	Carapace L/W = 0.91	Carapace L/W = 0.83
Urogastric region narrower than cardiac	Urogastric region much narrower than cardiac and mesogastric	Urogastric region about as wide as cardiac and mesogastric
Widest posterior to outer-orbital angle, at position of hepatic region	Widest at position of first anterolateral spine, about 40 percent the distance posteriorly	Widest posterior to outer-orbital angle, at position of hepatic region
Metabranchial area much depressed	Metabranchial area depressed	Metabranchial area inflated, with oblique ridge parallel to margin
Front simple, steeply downturned	Front with 4 spines, medial two below level of outer two	Front simple, steeply downturned
Fingers without black tips	Fingers without black tips	Fingers with black tips
Weakly heterochelate	Weakly heterochelate	Markedly heterochelate
Paddle-like propodus and dactyl of P5, possibly of P4 also	Paddle-like propodus and dactyl of P5	Paddle-like propodi of P4 and P5

lack the elongate manus and weak keels seen in carcineretids; instead, the mani are short and smooth (van Bakel et al. 2003, fig. 1). The sternum of *B. ubaghsi* is ovate and seems to lack the deep grooves between sternites three and four seen in carcineretids (van Bakel et al. 2003, fig. 1). *Binkhorstia* shares some features with *Longusorbis*, including a flattened dactyl of at least one of the pereiopods and a markedly downturned rostrum that is perpendicular to the upper surface of the carapace. It seems best at this time to follow van Bakel et al. (2003) in placing *Binkhorstia* and the very similar but much more poorly known *Withersella* in the Torynommidae until type material can be examined.

Woodbinax is known only from a fragment of the anterior one-quarter of the dorsal carapace. The development and definition of the protogastric regions, the four-lobed front, and the narrow orbits suggest that it could be a member of the Xanthoidea *sensu lato*, Portunoidea *sensu lato*, or Cancridae Latreille, 1802. The very narrow orbits and fronto-orbital width indicate that it is not allied with the Carcineretidae. Because the specimen is so fragmentary, we herein refer the genus to Brachyura *incertae sedis* until more complete material can be recovered.

Lithophylax was originally described from the green shale of France (in A. Milne Edwards and Brocchi 1879). Based upon the original description of the type material of the sole species, *Lithophylax trigeri* A. Milne Edwards and Brocchi, 1879, which was not illustrated, the specimen appears to have much in common with the Goneplacidae, as was mentioned by the original authors. The species was described as having very broad orbits that slope posteriorly with a well-developed outer orbital spine; a hexagonal carapace with poorly defined carapace regions and little ornamentation; long, smooth claws; and long, thin walking legs (translated from French; A. Milne Edwards and Brocchi, 1879, p. 117). The authors did not mention dorsal carapace ridges or paddle-like or ovate articles of the walking legs which seems to exclude this genus from the Carcineretidae. According to Rathbun (1935), the type specimen has been lost, making it difficult to reevaluate its family-level position. A specimen collected from the Cenomanian of Le Mans and identified as *L. trigeri* is deposited in the collections in Munich (BSP 1988 III 196), and that specimen fits the description of A. Milne Edwards and Brocchi (1879) (Fig. 3.G). It is clear that it is not a member of the Carcineretidae and based upon the elongate orbits, narrow front, and wider than long carapace, is probably allied with either the Goneplacidae or the Portunoidea.

Mascaranada was described from moderately preserved material with well-developed transverse carapace keels and an ovate dactylus of the fifth pereiopod, thus, its placement within the Carcineretidae. At this time, this seems to be the best family-level placement for the genus, although specimens with well-preserved chelae and sterna could help confirm the placement.

Branchiocarcinus is not referable to the family. The sole species of the genus, *Branchiocarcinus cornatus* Feldmann and Vega in Vega et al. 1995, possesses a narrow fronto-orbital width, about half the maximum carapace width; long anterolateral spines; and anterolateral margins that converge anteriorly and are clearly differentiated from the posterolateral margins. These features do not occur in the Carcineretidae and result in an overall very different dorsal carapace shape. The species does possess the transverse ridges typical of the Carcineretidae; however, such ridges are seen in numerous brachyuran families. The incomplete nature of the specimen makes it difficult to speculate on a family designation for the genus; however, the ridges, spines, and Cretaceous age suggest a possible referral to the Orithopsidae Schweitzer et al., 2003.

Genus *Carcineretes* Withers, 1922

Type species.—*Carcineretes woolacotti* Withers, 1922, by original designation.

Other species.—*Carcineretes planetarius* Vega et al., 1997.

Diagnosis.—Carapace quadrate, wider than long, flattened longitudinally and transversely; L/W about 90 percent, widest at position of hepatic region, just posterior to post-orbital angle. Rostrum straight in dorsal view, strongly downturned in anterior view, downturned portion nearly perpendicular to dorsal carapace, dorsal surface of rostrum and surface of downturned portion may be with central tabular regions delineated by grooves; frontal width about 48 percent maximum carapace width, outermost edges of front are inner-orbital spines. Orbits sinuous, long, with two or three intra-orbital spines and notches; outer-orbital spine triangular, directed forward; fronto-orbital width 90+ percent maximum carapace width. Anterolateral and posterolateral margins confluent, lateral margins with blunt protuberances or very short spines where hepatic region and epibranchial region intersect it; posterolateral reentrants subtle but present; posterior margin rimmed, nearly straight. Protogastric regions with transverse keels; hepatic regions with oblique central swelling; epibranchial regions arcuate; urogastric region narrower than mesogastric and cardiac, defined laterally by deep branchio-cardiac grooves; mesobranchial region and cardiac region inflated into almost ridge-like structure continuous across carapace; metabranchial region and intestinal region depressed below level of mesobranchial and cardiac regions.

Sternum ovate, slightly wider than long; sternites 1 and 2 fused, no evidence of a suture; sternal suture 2/3 complete; sternite 3 with longitudinal groove extending anteriorly from axis of sterno-abdominal cavity, sternal suture 3/4 incomplete, notch in margin; lateral margin of sternite 4 at high angle to axis; sternal suture 4/5 and 5/6 not parallel, 4/5 at high angle; sternite 8 not visible in ventral view. Male abdomen with concave margins, reaching to about middle of sternite 4, reaching to about middle of coxae of first pereiopods; somites 3-5 fused, may be slight evidence of sutures; somite 3 very wide, completely filling space between coxae of fifth pereiopods; somites 1 and 2 and apparently part of somite 3 not visible in ventral view; somites appearing to lack transverse keels. Chelipeds weakly heterochelate; chelae with keel or keels on outer surface; fingers with keels, lacking black tips. Fourth pereiopod with flattened carpus and merus. Fifth pereiopod with elliptic dactyl and propodus and flattened carpus and merus.

Discussion.—The family diagnosis is largely based upon the two species of *Carcineretes*, the only well known genus currently referred to the family. The excellent preservation of specimens illustrated by Vega et al. (2001) make it possible to frame a relatively complete diagnosis and differentiate *Carcineretes* from other, superficially similar, taxa.

Genus *Cancrixantho* Van Straelen, 1934
(Fig. 2D)

Type and only species.—*Cancrixantho pyrenaicus* Van Straelen, 1934, by monotypy.

Diagnosis.—Orbits wide, rostrum extremely narrow, eyestalks long, well-calcified; hepatic and branchial regions with transverse ridges. Posterolateral margins with long spines.

Discussion.—The identity and placement of *Cancrixantho* Van Straelen, 1934, has been fraught with problems. According to Via *in* Bataller (1959, p. 71), the original illustration of *Cancrixantho pyrenaicus* Van Straelen, 1934, the type and sole species, was reversed with illustrations of an Eocene species, *Allogoneplax dalloni* Van Straelen, 1934. Examination of the original descriptions of these two taxa (Van Straelen 1934, p. 3, 4) confirms this. A cast of the holotype of *Cancrixantho pyrenaicus* is housed in the Museu Geològic del Seminari de Barcelona, Spain, and it is a cast of the same specimen illustrated by Via *in* Bataller (1959, p. 70). The specimen is quite incomplete and has some similarities with *Carcineretes*, including wide orbits, a narrow rostrum, and ridges on the hepatic and branchial regions. However, the Barcelona cast and the illustrations of Via show indications of spines on the posterolateral margins, not seen in *Carcineretes*. Thus, placement of *Cancrixantho* is enigmatic; we place it in the Carcineretidae provisionally until more and better material can be collected.

Genus *Mascaranada* Vega and Feldmann, 1991

Type and only species.—*Mascaranada difuntaensis* Vega and Feldmann, 1991.

Diagnosis.—Carapace ovate, dorsal carapace regions marked by deep grooves, with transverse ridges; rostrum narrow; fifth pereiopod with elliptic dactylus and propodus.

Discussion.—Problems with placement of *Mascaranada* were discussed above.

Family Portunidae Rafinesque, 1815

Included subfamilies.—Caphyrinae Paul'son, 1875; Carcininae MacLeay, 1838; Carupinae Paul'son, 1875; Podophthalminae Dana, 1851; Polybiinae Ortmann, 1893; Portuninae Rafinesque, 1815; Psammocarcininae Beurlen, 1930 (extinct); Thalamitinae Paul'son, 1875.

Discussion.—The Portunidae as currently defined embraces a wide range of morphology, not only in the dorsal carapace but in the male sternum, male abdomen, and the various articles of the pereiopods, especially one, four, and five. The Carcininae and the Polybiinae previously have been suggested to be polyphyletic (Von Sternberg et al. 1999; Von Sternberg and Cumberlidge 2001; Schubart and Reuschel 2005), but evaluation and revision of the Portunidae is beyond the scope of this paper. However, several observations about the family and the various subfamilies can be made based upon examination of a broad range of species housed in the spirit and paleontological collections at the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Table 2).

The Portunidae is generally described as possessing paddle-like or, rarely, styliform dactyls on the fifth pereiopod (Davie 2002). However, the morphology of the elements of the fifth pereiopod, and in fact that of the fourth pereiopod, is much more variable than that (Table 3). Members of the Podophthalminae, Portuninae, and Thalamitinae, for example, appear to be characterized by broad, ovate dactyls and propodi of the fifth pereiopod, definitely fitting the description of "paddle-like." In those three subfamilies, only the fifth pereiopod displays paddle-like or flattened elements. The fifth pereiopod in the Caphyrinae is quite variable, ranging from ovate to ensiform (Davie 2002). Members of the Polybiinae exhibit the "typical" portunid paddle-like fifth pereiopods, with elliptic meri, carpi, propodi, and dactyli, and the fourth pereiopods can also exhibit somewhat broadened elements as it does in *Polybius*. Exceptions are *Raymanninus* and *Coenophthalmus*. Within the Carupinae, *Carupa* exhibits a more typical elliptic dactyl of the fifth pereiopod. However, the two carupine genera *Catoptrus* A. Milne-Edwards, 1870, and *Libystes* A. Milne-Edwards, 1867, possess lanceolate and ensiform dactyls and moderately broadened propodi of the fifth pereiopod, respectively, but they are not paddle-like as in the previous subfamilies. *Carcinus* Leach, 1814, a member of the Carcininae, is well-known to lack paddle-like fifth pereiopods (Rathbun 1930; Glaessner 1969). However, it is notable that the propodi and dactyls of the fifth pereiopod in the Carcininae may be ovate and oblanceolate in shape, respectively, and that this condition of the propodus applies to the fourth pereiopod and sometimes even the second and third as well. Note the many exceptions to the general rule within many subfamilies.

The Portunidae is described as possessing sternal sutures 4/5, 5/6, 6/7, and 7/8 as interrupted medially, except in the Carcininae in which sternal suture 7/8 is complete (Guinot 1979). However, that feature is extremely variable (Table 4). In all portunid taxa examined herein, sternal sutures 4/5 and 5/6 were interrupted. In several taxa, suture 6/7 was complete, and in the remainder of the taxa, suture 6/7 was interrupted. Sternal suture 7/8 exhibited great variation. In some taxa, suture

TABLE 2. Genera and species within the Portunoidea and Goneplacoidea examined at USNM for this report. * denotes type species of genus.

Taxon	Author	USNM Number(s)
Goneplacidae	MacLeay, 1838	
*Goneplax rhomboides**	(Linnaeus, 1758)	USNM 258116
*Bathyplax typhla**	A. Milne Edwards, 1880	USNM 1001156
Geryonidae	Colosi, 1923	
Chaceon erytheiae	(Macpherson, 1984)	USNM 221963
Geryon longipes	A. Milne Edwards, 1882	USNM 152241
Chaeceon quinquedens	(Smith, 1879)	USNM 5797, 39999
Portunidae	Rafinesque, 1815	
Carcininae	MacLeay, 1838	
Carcinus aestuari	Nardo, 1847	USNM 257965
*Carcinus maenus**	(Linnaeus, 1758)	USNM 119407
*Nectocarcinus integrifrons**	(Latreille, 1825)	USNM 17030
*Portumnus latipes**	(Pennant, 1777)	USNM 221604
Xaiva biguttata	Risso, 1816	USNM 14499
Caphyrinae	Paul'son, 1875	
Caphyra rotundifrons	(A. Milne Edwards, 1869)	USNM 112160
*Coelocarcinus foliates**	Edmondson, 1930	USNM 143987
Lissocarcinus orbicularis	Dana, 1852	USNM 267076, 267078
Carupinae	Paul'son, 1875	
*Carupa tenuipes**	Dana, 1851	USNM 143694
Catoptrus inaequalis	(Rathbun, 1906)	USNM 29661
*Libystes nitidus**	A. Milne Edwards, 1867	USNM 46379
Polybiinae	Ortmann, 1893	
Bathynectes superba	(Costa, 1853)	USNM 186368
Brusinia profunda	Moosa, 1996	USNM 277519
*Coenophthalmus tridentatus**	A. Milne Edwards, 1879	USNM 22050
Liocarcinus arcuatus	(Leach, 1814)	USNM 205810
Macropipus australis	Guinot, 1961	USNM 173102
*Necora puber**	(Linnaeus, 1767)	USNM 121969
*Ovalipes ocellatus**	(Herbst, 1799)	USNM 55556, 185418
*Parathranites orientalis**	(Miers, 1886)	USNM 41075, 120709
*Polybius henslowii**	Leach, 1820	USNM 6777
*Raymanninus schmitti**	(Rathbun, 1931)	USNM 1022063, 1022083, 1000576
Podophthalminae	Dana, 1851	
*Euphylax dovii**	Stimpson, 1862 [1860]	USNM 85535
*Podophthalmus vigil**	(Weber, 1795)	USNM 112121
Portuninae	Rafinesque, 1815	
Portunus sanguinolentus	(Herbst, 1783)	USNM 243950
*Arenaeus cribrarius**	(Lamarck, 1818)	USNM 72191
Cronius ruber	(Lamarck, 1818)	USNM 76854
*Laleonectes nipponensis**	(Sakai, 1938)	USNM 190730
*Lupella forceps**	(Fabricius, 1793)	USNM 1072266
Lupocyclus tugelae	Barnard, 1950	USNM 210826
*Scylla serrata**	(Forskål, 1775)	USNM 112335
Thalamitinae	Paul'son, 1875	
Thalamita crenata	Rüppell, 1830	USNM 111787
Charybdis hellerii	(A. Milne Edwards, 1867)	USNM 93091
Thalamitoides tridens	A. Milne Edwards, 1869	USNM 111813

7/8 appeared to be interrupted, but only by a very tiny space visible when magnified 25 times under a binocular microscope; some taxa exhibiting this condition include *Raymanninus schmitti*, *Polybius henslowii*, and *Liocarcinus arcuatus*. In some taxa, it was very difficult to determine if the suture was complete or interrupted, and if it was interrupted, it was only very briefly so; these include *Parathranites orientalis* and *Portumnus latipes*, for example. In some portunids, the suture 7/8 was interrupted very clearly by a great distance, as in *Euphylax*, *Thalamita*, *Lupella*, and *Libystes* or was clearly interrupted by a short distance, as in *Catoptrus* and *Ovalipes*. Thus, there is considerable variation in this feature.

We also noted several characteristics within the Portunidae that are not commonly reported. Every taxon examined herein exhibited a transverse ridge on the third male abdominal somite, and most also exhibited such ridges on the second male abdominal somite as well. Furthermore, many taxa exhibited such ridges on the first, fourth, and fifth somites. In addition, in many of the portunid taxa, the third male abdominal somite is very markedly wider than the other somites. These abdominal characters are easily visible in fossils retaining the male abdomen. All of the portunid taxa displayed either a clear suture between male sternites 1 and 2, or at least a clearly visible row of setal hairs defining the boundary between those two sternites; it is not known if such a feature would leave visible markings in fossil specimens. In addition, the episternal projections of all of the portunids examined here extended markedly laterally from the sternites themselves. While clearly noticeable, we have not quantified this feature.

We have not exhaustively evaluated the Portunidae; however, we suggest that these variations in characters be used as a starting point for the re-evaluation of the family and its constituent subfamilies. In addition, the extinct Psammocarcininae, members of which bear superficial similarities to *Raymanninus* and *Bathynectes*, and extinct members of various extant subfamilies, must be evaluated in this context.

Subfamily Polybiinae Ortmann, 1893

Included genera.—*Bathynectes* Stimpson, 1871; *Benthochascon* Alcock and Anderson, 1899; *Coenophthalmus* A. Milne-Edwards, 1879; *Falsiportunites* Collins and Jakobsen, 2003 (extinct); *Liocarcinus* Stimpson, 1871 (fossil and extant); *Macropipus* Prestandrea, 1833; *Maeandricampus* Schweitzer and Feldmann, 2002 (extinct); *Megokkos* Schweitzer and Feldmann, 2000 (extinct); *Minohellenus* Karasawa, 1990 (extinct); *Necora* Holthuis, 1987; *Ovalipes* Rathbun, 1898 (fossil and extant); *Ophthalmoplax* Rathbun, 1935 (extinct); *Parathranites* Miers, 1886 (fossil and extant); *Polybius* Leach, 1820; *Portunites* Bell, 1858 (extinct); *Proterocarcinus* Feldmann et al., 1995 (extinct); questionably *Raymanninus* Ng, 2000.

Diagnosis.—Carapace moderately broad; fronto-orbital width usually from about half to three-quarters maximum carapace width; orbits usually moderate sized, often with two fissures; front spined, number and size of spines variable; anterolateral margins with three to five spines including outer-orbital spine; epibranchial ridge arcuate, extending from last anterolateral spine to axial regions; usually with longitudinal branchial ridges parallel to axis; male abdominal somites 3–5 fused, somite three and sometimes others with transverse keels, somite three generally markedly wider than other somites, telson extending to middle or anterior of sternite 4; portion of sternite 8 visible in ventral view; sternal sutures appearing to be incomplete with occasional exception of 7/8; chelae usually keeled; some pereiopods as long as chelipeds; dactylus of fifth pereiopod elliptic, paddle-like in traditional sense (after Glaessner 1969; Davie 2002).

Discussion.—The Polybiinae as currently construed is considered by many to be polyphyletic (Von Sternberg et al. 1999; Von Sternberg and Cumberlidge 2001; Schubart and Reuschel 2005). Indeed, the subfamily embraces a broad range of morphological variation in many aspects of the carapace, sternum, abdomen, and pereiopods considered important at the family and subfamily level. For example, among the specimens recently examined at the United States National Museum, some species exhibited all male somites fused but with very clear sutures (*Raymanninus schmitti*), whereas others possessed male somites 3–5 fused with no evidence of sutures (most). The propodus of the fifth pereiopods of *Raymanninus* is slightly broadened and the dactyls are lanceolate; most other polybiines exhibit paddle-like propodi and dactyls of the fifth pereiopods. The anterolateral margins of polybiines are described as typified by four spines excluding the outer-orbital spine, but *Raymanninus schmitti* possesses only two. Thus, for this paper we use the currently accepted definition of the Polybiinae and its included genera, both fossil and extant, recognizing that revision is overdue.

Genus *Ophthalmoplax* Rathbun, 1935

Type species.—*Ophthalmoplax stephensoni* Rathbun, 1935, by original designation.

Other species.—*Ophthalmoplax brasiliana* (see Feldmann and Villamil 2002); *O. comancheensis* Rathbun, 1935; *O. triambonatus* Feldmann and Villamil, 2002; questionably *O. spinosus* Feldmann et al., 1999.

Diagnosis.—Carapace wider than long, L/W about 0.90, widest at position of last anterolateral spine, about 40 percent the distance posteriorly on carapace; front with two spines centrally set well below level of outer two blunt protuberances or spines which are inner-orbital spines, about 18 percent maximum carapace width measured between inner-orbital spines; orbits extremely broad, sinuous, with two intra-orbital spines and forward directed outer-orbital spine; fronto-orbital width 90 percent maximum carapace width; eyestalks calcified; protogastric regions with transverse ridges; weak transverse ridges on hepatic regions; urogastric region much narrower than cardiac and mesogastric regions; cardiac region with strong transverse keel anteriorly; epibranchial region arcuate; mesobranchial region broadly inflated; metabranchial region depressed; sternites 1/2 fused, no suture apparent, forming triangular unit, rimmed, depressed centrally; sternal suture 2/3 complete; sternite 3 much wider than sternites 1/2, with thickened oblique swellings on either side of axis; sternite 4 with thickened rim parallel to lateral margin, lateral margin sinuous, at low angle to axis; sternal sutures 4/5 and 5/6 parallel; sternal sutures 4/5,

TABLE 3. Important generic and subfamily characteristics of the pereiopods of members of the Portunoidea. P5 = pereiopod five; P4 = pereiopod four. Terminology taken from the illustrations accompanying the definition for "leaf," *Webster's Ninth New Collegiate Dictionary*, 1984, p. 680.

Taxon	P5 Dactylus	P5 Propodus	P4 Propodus	P4 Dactylus
Carcininae				
Carcinus spp.	Ensiform	Oblong flattened	Elongate	Ensiform
Nectocarcinus integrifrons	Lanceolate	Ovate flattened	Ovate flattened	Ensiform
Portumnus latipes	Oblanceolate flattened	Ovate flattened	Ovate flattened	Oblanceolate
Xaiva biguttata	Oblanceolate with acuminate tip	Ovate flattened	Oblong flattened	Ensiform
Caphyrinae				
Caphyra rotundifrons	Ensiform	Elliptic flattened	Oblong flattened	Ensiform
Lissocarcinus orbicularis	Oblanceolate with acuminate tip	Elliptic flattened	Elongate	Lanceolate flattened
Carupinae				
Carupa tenuipes	Elliptic	Obovate flattened	Elongate flattened	Ensiform
Catoptrus inaequalis	Lanceolate	Elongate	Elongate	Ensiform
Libystes nitidus	Sinuous ensiform	Oblong flattened	Rectangular	Ensiform
Polybiinae				
Polybius henslowii	Elliptic	Obovate flattened	Oblong flattened	Lanceolate flattened
Bathynectes superba	Oblanceolate with acuminate tip	Oblong flattened	Elongate	Ensiform
Brusinia profunda	Oblanceolate with acuminate tip	Elliptic flattened	Oblong flattened	Lanceolate
Coenophthalmus tridentatus	Ensiform flattened	Lanceolate flattened	Lanceolate flattened	Ensiform flattened
Liocarcinus arcuatus	Elliptic	Oblong flattened	Elongate	Ensiform
Macropipus australis	Elliptic with acuminate tip	Elliptic flattened		
Necora puber	Oblanceolate with acuminate tip	Ovate flattened	Rectangular flattened	Ensiform
Ophthalmoplax spp.	Ovate	?	?	Oblanceolate
Ovalipes ocellatus	Elliptic	Ovate	Lanceolate	Ensiform
Parathranites orientalis	Elliptic	Oblong flattened	Elongate	Ensiform
Raymanninus schmitti	Lanceolate flattened	Oblong flattened	Flattened rectangular	Ensiform
Podophthalminae				
Podophthalmus vigil	Elliptic	Oblong flattened	Oblong	Ensiform
Euphylax dovii	Elliptic	Oblong flattened	Lanceolate flattened	Oblong flattened
Portuninae				
Portunus sanguinolentus	Elliptic	Oblong flattened	Elongate oblong flattened	Lanceolate
Arenaeus cribrarius	Elliptic	Oblong flattened	Oblong flattened	Lanceolate
Cronius ruber	Elliptic	Cuneate flattened	Elongate rectangular flattened	Ensiform
Laleonectes nipponensis	Ovate with acuminate tip	Cuneate flattened	Ensiform	Ensiform
Lupella forceps	Elliptic	Obovate flattened	Elongate flattened	Ensiform
Lupocyclus tugelae	Elliptic	Obovate flattened	Elongate flattened	Ensiform
Scylla serrata	Elliptic	Cuneate flattened	Oblong flattened	Ensiform
Thalamitinae				
Thalamita crenata	Elliptic	Ovate flattened	Elongate flattened	Ensiform
Charybdis helleri	Elliptic flattened	Oblong flattened	Elongate flattened	Ensiform
Thalamitoides tridens	Elliptic with acuminate tip	Oblong flattened	Elongate oblong flattened	Ensiform

TABLE 4. Important generic and subfamily characteristics of members of the Portunoidea.
♂A3–5 = male abdominal somites 3–5; ♂A = male abdominal somites; ♂A3 = male abdominal somite 3; ♂AP5 = male abdomen covering entire space between coxae of pereiopods 5; T = position to which the telson reaches on the male sternum; S8 = sternite 8 visible in ventral view; 4/5, 5/6, 6/7 = sternal sutures interrupted or complete; 7/8 = sternal suture interrupted or complete; P5 = pereiopod 5; P4 = pereiopod 4; N = Narrow; M = Moderate; W = Wide; Mid-4 = middle of sternite 4; Post-4 = posterior of sternite 4; Ant-4 = anterior of sternite 4; I = interrupted; C = complete; *with slight sutures.

Taxon	♂A3-5 fused	♂A with keels	♂A3 width	♂AP5	T	S8	4/5, 5/6, 6/7	7/8
Carcininae								
Carcinus spp.	Yes	Yes	M	Yes	Mid-4	No	I	C
Nectocarcinus integrifrons	No	Yes	M	Yes	Mid-4	No	4/5, 5/6 I, 6/7C	C
Portumnus latipes	Yes	Yes	N	Yes	Post-4	No	I	C
Xaiva biguttata	Yes	Yes	M	Yes	Ant-4	No	I	C
Caphyrinae								
Caphyra rotundifrons	Yes	?	W	Yes	Post-4	Yes	4/5, 5/6 I, 6/7 C	C
Coelocarcinus foliates	Yes	No	S	?	?	No	4/5 I, 5/6, 6/7 C	I
Lissocarcinus orbicularis	Yes	Yes	M	Yes	Post-4	Yes	4/5, 5/6 I, 6/7C	I
Carupinae								
Carupa tenuipes	Yes	No	W	Yes	Mid-4	Yes	I	C
Catoptrus inaequalis	Yes	No	W	Yes	Mid-4	Yes	I	I
Libystes nitidus	Yes	No	W	Yes	Mid-4	Yes	I	I
Polybiinae								
Polybius henslowii	Yes*	Yes	W	Yes	Mid-4	Yes	I	I
Bathynectes superba	Yes	Yes	W	Yes	Ant-4	Yes	I	C
Brusinia profunda	No	No	M	Yes	Mid-4	Tiny	4/5, 5/6 I, 6/7C	I
Coenophthalmus tridentatus	No	Yes	W	Yes	Ant-4	No		
Liocarcinus arcuatus	Yes	Yes	M	Yes	Mid-4	Yes	I	I
Macropipus australis	Yes	Yes	W	Yes	Ant-4	Yes	I	I
Necora puber	Yes	Yes	W	Yes	Mid-4	Yes	I	I
Ophthalmoplax spp.	No	Yes	W	?	Ant-4	Yes	I	?
Ovalipes ocellatus	Yes*	No	W	Yes	Mid-4	Yes	I	I
Parathranites orientalis	Yes	Yes	W	Yes	Ant-4	Yes	I	C
Raymanninus schmitti	No	Yes	M	Yes	Mid-4	Yes	I	I
Podophthalminae								
Podophthalmus vigil	Yes	Yes	W	Yes	Yes	Yes	I	I
Euphylax dovii	Yes	Yes	M	Yes	Mid-4	Yes	I	I
Portuninae								
Portunus sanguinolentus	Yes	Yes	W	Yes	Post-4	Yes	4/5, 5/6 I, 6/7C	C
Arenaeus cribrarius	Yes*	Yes	W	Yes	Mid-4	Yes	I	I
Cronius ruber	Yes*	Yes	M	Yes	Post-4	Yes	4/5, 5/6 I, 6/7C	I
Laleonectes nipponensis	Yes	Yes	M	Yes	Post-4	Yes	I	C
Lupella forceps	Yes	Yes	W	Yes	Post-4	Yes	I	I
Lupocyclus tugelae	Yes	Yes	W	Yes	Mid-4	Yes	I	I
Scylla serrata	Yes*	Yes	W	Yes	Post-4	Yes	4/5, 5/6 I, 6/7C	C
Thalamitinae								
Thalamita crenata	Yes*	Yes	M	Yes	Post-4	Yes	I	I
Charybdis helleri	Yes	Yes	M	Yes	Post-4	Yes	4/5, 5/6 I, 6/7C	I
Thalamitoides tridens	Yes	Yes	S	Barely	Post-4	Yes	I	C

5/6, and 6/7 incomplete; abdominal locking mechanism on sternite 5; sternite 8 visible in ventral view; male abdomen extending onto sternite 3, sterno-abdominal cavity deep; male abdomen narrow, all somites free, completely filling space between coxae of fifth pereiopods, telson longer than wide; somite 6 longer than wide, with rounded projection centrally in lower margin, somites 2, 3, and 4 with transverse keels, somite 3 markedly wider than other somites. Chelae markedly heterochelous, mani with knobby keels on outer surface, spines on upper margins, fingers without black tips. Pereiopod five with paddle-like propodus and dactyl. Pereiopod four with somewhat broadened articles.

Discussion.—*Ophthalmoplax* exhibits numerous characteristics typical of the Portunidae (Tables 3, 4). The possession of long orbits and long, well-calcified eyestalks; keels on the dorsal carapace; a broad, ovate sternum; sternal sutures 4/5, 5/6, and 6/7 interrupted; a small portion of sternite 8 visible in ventral view; episternal projections of sternites 4, 5, and 6 positioned well to the side of the lateral margin of the sternite; a sterno-abdominal cavity reaching to the anterior of sternite 4; keels on male abdominal somites 2–4; a very broad third male abdominal somite; keeled chelae; and paddle-like dactyls and propodi of the fifth pereiopod and somewhat broadened elements of the fourth pereiopod indicate placement within the Portunidae. These features were present in most, but not all, of the Portunidae recently examined (Table 2).

The dorsal carapace of *Ophthalmoplax* as typically described is quite unusual for a portunid. The carapace is usually depicted as *U*-shaped (in the terminology of Bishop 1988). However, that shape is suggested when the lateral sides, which are symmetrically flared outward in *O. stephensoni*, the best known member of the genus, are taken into account. Careful examination of specimens of *O. stephensoni* housed at the University of Texas indicated that when these outwardly-flared lateral sides are regarded in their true position and not part of the dorsal carapace, the dorsal carapace shape of *O. stephensoni* is in fact hexagonal, much like many other extant portunids including *Bathynectes* and *Raymanninus* and also many Geryonidae. The flared lateral sides appear to have increased the volume of the branchial chambers, perhaps an adaptation to low oxygen levels. The inflated branchial regions do not appear to be attributable to deformation due to infestation by bopyrid isopods; the deformation is symmetrical and seen in all specimens of *O. stephensoni*. These types of isopods are known only in certain families within the Decapoda, which do not include any members of the Heterotremata to which *Ophthalmoplax* belongs. *Ophthalmoplax triambonatus* does not exhibit such inflated branchial regions; however, that specimen is tectonically sheared and this may be due to deformation.

Ophthalmoplax is most similar in its morphology to extant *Bathynectes* and *Raymanninus* (Table 5), the former of which is currently placed within the Polybiinae (Rathbun 1930; Manning and Holthuis 1981) and the latter of which was placed within the Portunidae *sensu lato* (Ng 2000) and is seen as problematic (Karasawa and Schweitzer 2006). The only reference to a subfamily placement for *Raymanninus* is an unpublished web forum (http://microscope.mbl.edu/cladeviewer/), which places the genus within the Polybiinae. The main differences between *Ophthalmoplax* and these two extant genera are that in *Ophthalmoplax*, the male abdominal somites are all free, and the fronto-orbital width is much wider with respect to the maximum carapace width than in the two extant genera. *Ophthalmoplax* is most similar to *Bathynectes* because those two taxa share paddle-like elements of the fifth pereiopods, which *Raymanninus* lacks. Thus, we are quite confident of our referral of *Ophthalmoplax* to the Portunidae; however, the subfamily placement is at this time problematic. Ng (2000) did not refer *Raymanninus* to a subfamily when he originally described it and pointed out the many similarities between it and some Geryonidae. Thus, we place *Ophthalmoplax* within the Polybiinae until the Portunidae are revised.

The Portunidae as currently defined are quite variable in carapace shape, ranging from quadrate (*Libystes*, for example), to the typical wider than long, anterolaterally spined blue crabs (*Callinectes*). Other families with broad, ovate sterna and long orbits and eyestalks (Goneplacidae, various fiddler crab and ghost crab families) were considered for placement of *Ophthalmoplax*, but none possesses paddle-like appendages of any sort or stout, keeled, spined chelae, both of which in general characterize the Portunidae. Thus, the Portunidae seems to be the best placement for *Ophthalmoplax* at this time.

Ophthalmoplax spinosus Feldmann et al., 1999, from the Turonian of Colombia may not be referable to the genus. Members of this species possess very long spines on the frontal as well as anterolateral margins of the carapace, features which do not appear to be easily accommodated within *Ophthalmoplax*. However, the specimens of *Ophthalmoplax spinosus* are two-dimensionally flattened and not well-preserved.

This is the first confirmed report of the Portunidae in the Cretaceous.

Ophthalmoplax stephensoni Rathbun, 1935
(Fig. 1)

Ophthalmoplax stephensoni Rathbun, 1935, p. 52, pl. 13, figs. 13–18, pl. 26, fig. 10.

Emended diagnosis.—Carapace equant, slightly wider than long, L/W = 0.90, widest at position of last anterolateral spine, about 40 percent the distance posteriorly on carapace; front axially sulcate, narrowing distally, axially notched; with two central downturned spines; axial spines bordered on either side by blunt projections which form inner-orbital angles; front about 18 percent maximum carapace width; orbits long, sinuous, with two intra-orbital spines; outer intra-orbital spine triangular, robust; anterolateral margin short, with at least two spines excluding outer-orbital spine.

Emended description.—Carapace equant, slightly wider than long,

TABLE 5. Comparison of three genera currently referred to the Polybiinae *sensu lato*. Measurements of *Raymanninus* are based on figures in Ng (2000, fig. 5).

Character	*Raymanninus*	*Bathynectes*	*Ophthalmoplax*
Front axially notched	Yes	Yes	Yes
Dorsal carapace with sharp keels	No	Yes	Yes
Number of anterolateral spines or projections	2	4	3 or so
Frontal width to maximum width	0.26	~0.25	0.18
Fronto-orbital width to maximum width	0.66	~0.50	0.90
Number of orbital fissures	1	2	1
Position of maximum carapace width	0.36	~0.40	0.40
Epibranchial region arcuate or keeled	Yes	Yes	Yes
Anterolateral shorter than posterolateral	Yes	Yes	Yes
Sternal suture 1-2 visible	Yes	Yes	No
Sternal suture 2/3 complete	Yes	Yes	Yes
Sternite 4 with swellings along lateral margins	Yes	Yes	Yes
Episternal projections offset distinctly laterally	Yes	Yes	Yes
Sternite 8 visible in ventral view	Yes	Yes	Yes
Bouton-presson	Yes	?	Yes
Sternal sutures 4/5, 5/6, 6/7 incomplete	Yes	Yes	Yes
Telson longer than wide, rounded tip	No	Yes	Yes
Sterno-abdominal cavity extending onto sternite 3	No	Barely	Yes
Somites with keels	Yes	Yes	Yes
Somite 3 very wide	Yes	Yes	Yes
Male somites 3-5 fused	Yes but with clear sutures	Yes	No
Male abdomen filling entire space between fifth pereiopods	?	Yes	Yes
Chelae with keels	Yes, weak	Yes	Yes
Fingers pigmented	No	Reddish	No
Fifth pereiopod with paddle-like propodus	No	Yes	Yes
Fifth pereiopod with paddle-like dactyl	No	Yes	Yes

L/W = 0.90, widest at position of last anterolateral spine, about 40 percent the distance posteriorly on carapace; regions poorly defined as swollen areas; carapace flattened transversely, moderately vaulted longitudinally.

Front axially sulcate, narrowing distally, axially notched; with two central spines, spines sharply downturned, triangular; axial spines bordered on either side by blunt projections which form inner-orbital angles; front about 18 percent maximum carapace width measured between inner-orbital projections. Orbits long, sinuous, with two intra-orbital spines; inner intra-orbital spine triangular, in same plane as carapace, preceded by oblique fissure; outer intra-orbital spine triangular, directed upwards; outer-orbital spine robust, directed slightly anterolaterally; orbital margin concave, arcuate between orbital spines; fronto-orbital width about 90 percent maximum carapace width.

Anterolateral margin short, with at least two spines excluding outer-orbital spine; first spine sharp, directed slightly upward and anterolaterally, positioned where hepatic ridge intersects margin; at least one and possibly two blunt projections posterior to first spine. Posterolateral margin long, sinuous, with blunt protuberances where it is intersected by branchial ridges; posterolateral reentrants moderately deep. Posterior margin nearly straight, with narrow rim.

Protogastric regions ovate, with central transverse keels continuous across mesogastric region. Mesogastric region poorly defined, widened posteriorly, weakly inflated posteriorly. Urogastric region depressed below level of urogastric and cardiac regions, bounded laterally by deep branchiocardiac groove. Cardiac region very wide anteriorly, with transverse keel, becoming weakly defined and disappearing posterior to keeled area; keeled area with spherical swollen areas laterally. Intestinal area long, not differentiated.

Hepatic region short, wider than long, with transverse keel terminating in anterolateral spine. Subhepatic region short, wider than long, with inflated spherical swelling adjacent to base of mesogastric region. Epibranchial region not well differentiated; marked by sharp, transverse keel. Remainder of branchial region not differentiated, with one short keel posterior and parallel to epibranchial keel, at or just posterior to cardiac keel; short keel just anterior to posterolateral reentrant, positioned along posterolateral margin.

Lateral flanks visible in dorsal view, especially in branchial area, giving carapace a *U*-shaped or equant appearance. Pterygostomial region near orbit particularly robust, providing broad base for orbit. Distal orbital area rather deep, apparently not bounded by spines or a margin on distal-most end. Eyestalks arising from under front, extending distally, apparently well-calcified.

Sternites 1 and 2 fused, no evidence of a suture, rimmed with thickened margin; suture between sternites 2 and 3 complete. Sternite 3 sutured with sternite 4, notches in margin mark suture line, sterno-abdominal cavity extending onto sternite 3. Sternite 4 long, thickened along lateral margins, with spherical inflation about one-third the distance posteriorly along the margin; similarly inflated along inner posterior margin; sterno-abdominal cavity deep; episternal projections long, positioned distinctly distal to lateral margin of sternite. Sternite 5 directed laterally, with marked episternal projections positioned distinctly distal to lateral margin of sternite, sternal locking mechanism present in sterno-abdominal cavity. Sternite 6 directed posterolaterally, episternal projections long, positioned distinctly distal to lateral margin of sternite. Sternite 7 longer than sternites 5 and 6, directed posterolaterally, with robust episternal projection. Sternite 8 clearly visible in ventral view. Sternal sutures 4/5 and 5/6 markedly interrupted, sternal suture 6/7 probably also interrupted. Sternum widest at position of episternal projections of sternite 5.

Male abdomen long, with concave lateral margins, all somites free, entirely filling space between coxae of pereiopods. Somite 1 short, wide; somite 2 longer than somite 1, especially axially, with transverse keel; somite 3 much wider than other somites, transversely centrally keeled; somite 4 longer and narrower than somite 3, with transverse central keel; somite 5 about as long as wide; somite 6 much longer than wide; telson much longer than wide, with rounded tip, extending onto sternite 3.

Chelipeds robust, heterochelous; chelae with keels and large tubercles on outer surface, upper surfaces with spines; fingers with large, blunt denticles on occlusal surfaces.

Pereiopod 5 with paddle-like propodus and dactyl.

Material examined.—*Ophthalmoplax stephensoni*, holotype, USNM 73793; paratype, 73794; UT 21258, 21262.

Measurements.—Measurements (in mm) on specimens of *Ophthalmoplax stephensoni*: USNM 73793 (holotype), maximum carapace width = 76.6; maximum carapace length = 67.3; fronto-orbital width = 65.6. UT 21258, maximum carapace width = 49.5; maximum carapace length = 44.4; frontal width (measured between inner-orbital spines) = 8.2; fronto-orbital width = 47.2; length to position of maximum width (at last anterolateral spine) = 17.8. UT 21262, maximum carapace width = 99.4; maximum carapace length = 86.7; frontal width (measured between inner-orbital spines) = 14.5; fronto-orbital width = 83.0; length to position of maximum width (at last anterolateral spine) = 34.3; width of sternum (measured at episternal projection of sternite 5) = 64.8; length of sternites 3–8 = 57.7.

Discussion.—The additional preparation of specimens deposited in the collections of the University of Texas has made it possible to frame a much more complete description of this species. The sternum and abdomen of UT 21262 (Fig. 1G) is extremely well preserved and permits placement of *Ophthalmoplax* in the Portunidae.

Family Portunidae incertae sedis

Discussion.—*Longusorbis* is very similar in many regards to the nominate genus of the Carcineretidae, *Carcineretes*; however, those similarities appear to be superficial. In carefully reviewing the well-preserved and illustrated specimens of *Longusorbis* (Richards 1975; Schweitzer et al. 2003), it is clear that there are some major differences between *Longusorbis*, other carcineretids, and taxa previously referred to the Carcineretidae (Table 1). *Carcineretes* exhibits a tabular region in the rostrum, both on the dorsal portion of the rostrum and on the downturned portion; the rostrum on *Longusorbis* is axially sulcate and lacks these tabular regions. *Carcineretes* possesses two orbital fissures and two or three intra-orbital spines, whereas *Longusorbis* possesses an intra-orbital spine and a long, rimmed segment and lacks fissures. The urogastric region of *Carcineretes* is much narrower than the cardiac and mesogastric regions, whereas that same region in *Longusorbis* is the same width as the cardiac and mesogastric regions. Whereas *Carcineretes* exhibits a very depressed metagastric region, that area is inflated into a ridge in *Longusorbis* and is not depressed below the level of the mesogastric and cardiac region. *Carcineretes* exhibits a chela with a keel on the outer surface and keeled fingers that lack black tips (Vega et al. 1997, fig. 4.4), reminiscent of portunid crabs. *Longusorbis* is characterized by stout, smooth chelae with fingers with black tips, more typical of the Xanthoidea MacLeay, 1838, and Goneplacoidea MacLeay, 1838. The fifth pereiopod of *Carcineretes* possesses a paddle-like dactyl, whereas that of *Longusorbis* is lanceolate. In addition, the articles of the pereiopods of *Carcineretes* in general are shorter, and those of the fourth and fifth pereipods are shorter and more flattened, than are the articles of the pereiopods of *Longusorbis*. The male abdomen of *Carcineretes* clearly exhibits fusion of sternites 3–5, whereas those somites in *Longusorbis* are free. The sternum of *Carcineretes* exhibits a longitudinal groove extending anteriorly onto sternite 3, and the sterno-abdominal cavity extends to the anterior of sternite four. In *Longusorbis*, there is no longitudinal groove in sternite 3 and the sterno-abdominal cavity extends to about the middle of sternite 4. Thus, there are several differences between the two genera that are considered to be subfamily or family level characters within the Portunoidea, so we herein remove *Longusorbis* from the Carcineretidae.

The family-level placement for *Longusorbis* is perplexing. Vega and Feldmann (1991) had previously suggested that *Longusorbis* might be better placed within the Xanthidae *sensu lato*. Karasawa and Schweitzer (2006) raised the known subfamilies of the then-family Goneplacidae MacLeay, 1838, to family status within the superfamily Goneplacoidea. *Longusorbis* shares numerous features with the Goneplacoidea, especially the families Goneplacidae *sensu stricto* and Euryplacidae Stimpson, 1871; however, its unique combination of characters precludes placement in the Goneplacoidea. The Goneplacidae is characterized by a subquadrate carapace; very broad orbits; a straight front sometimes with a medial projection; all male abdominal somites free and male abdomen filling the entire space between the coxae of the fifth pereiopod; sternite 8 not visible in ventral view; and robust chelipeds that may have black tips on the fingers. All of these features are shared with *Longusorbis*. However, the orbital margins are entire in the Goneplacidae, and in *Longusorbis*, they are sinuous and ornamented with a spine and thickened

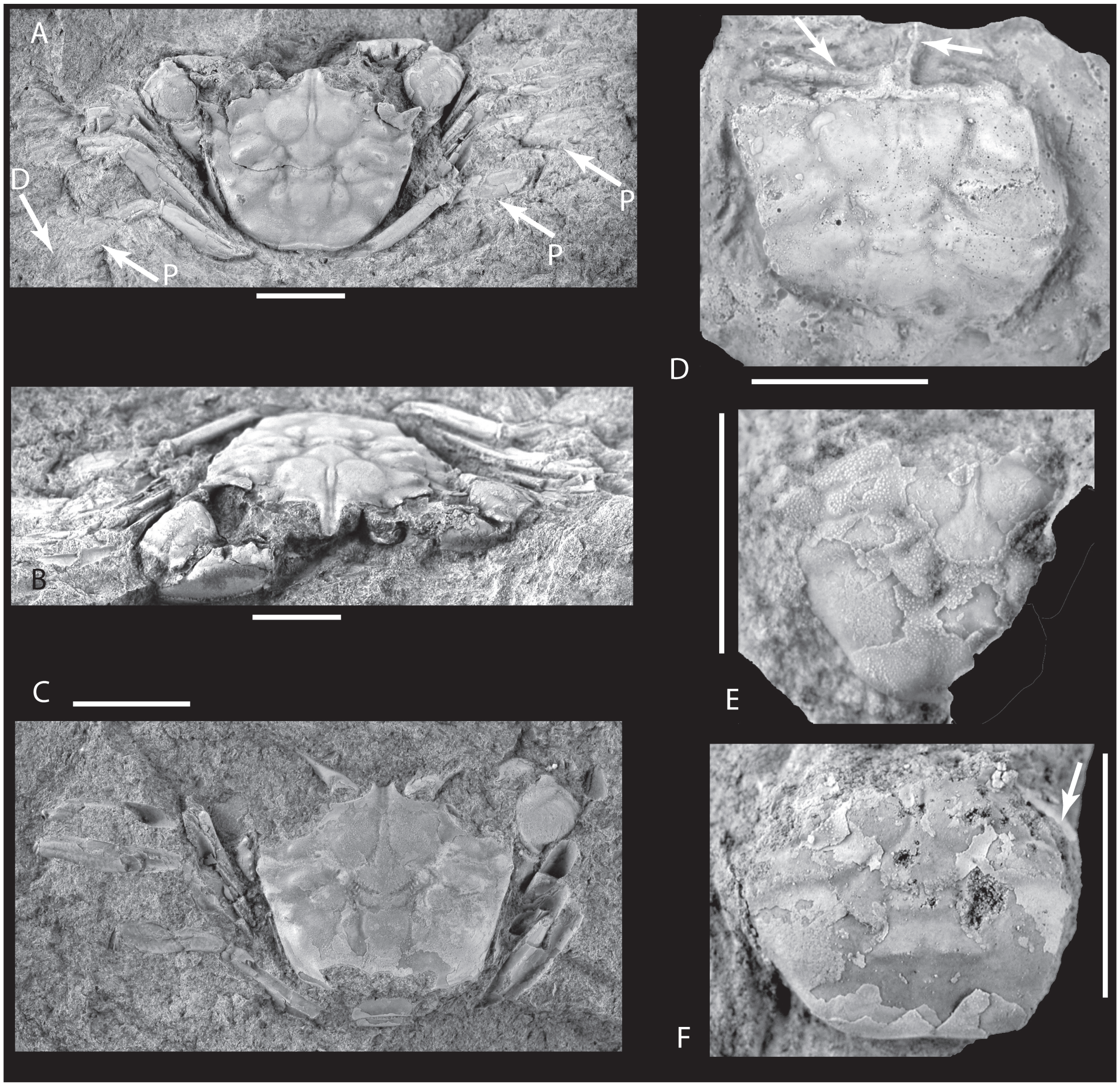

Fig. 2.—**A–C:** *Longusorbis cuniculosus* Richards, 1975. **A,** dorsal and **B,** frontal views of KSU D746 showing of the nature of region development and the strongly downturned, sulcate rostrum. Arrow D indicates styliform dactylus of fifth pereiopod, and arrows P indicate paddle-like propodi of fourth and fifth pereiopods. **C,** dorsal view of PRI 55177, showing well-calcified and well-preserved eyestalks. **D:** *Cancrixantho pyrenaicus* Van Straelen, 1934, plaster cast of holotype, KSU D204, showing the development of regions and the extremely long left eyestalk. Eyestalks indicated by arrows. **E, F:** *Longusorbis eutychius* new species. **E,** Exaflex® cast of holotype (CM 55277) showing dimpled surface of cuticle and relatively smooth mold of the interior of the cuticle. **F,** dorsal view of holotype (MHN-UABCS/Te8/68-413) showing transversely ridged carapace regions. Arrow indicates elongate, transverse orbit. Scale bars = 1 cm.

straight segment. The front in *Longusorbis* is not straight as in the Goneplacidae; it is composed of concave segments laterally and a long, spatulate, downturned projection medially. The sterno-abdominal cavity in the Goneplacidae reaches the anterior of sternite 4, whereas in *Longusorbis*, it reaches to the middle of sternite 4. The sternum of goneplacids is usually broad and ovate; in *Longusorbis*, it is narrow and obovate. *Longusorbis* also possesses a flattened, ovate propodus of the fifth pereiopod and flattened proximal articles of the fourth and fifth pereiopods, not seen in any goneplacids.

The Euryplacidae possess a subquadrilateral carapace, very broad orbits, a well-calcified eyestalk that can be fossilized, an anterolateral margin not well-differentiated from the posterolateral margin; and a male abdomen with all free somites and completely covering the space between the coxae of the fifth pereiopods, all of which are shared with *Longusorbis*. However, the front of members of the Euryplacidae is notched, whereas that of *Longusorbis* possesses a spatulate downturned projection. The orbits of euryplacids possess fissures, which *Longusorbis* lacks. Sternite 8 is visible in ventral view in the euryplacids, which is not true in *Longusorbis*. The sterno-abdominal cavity in the Euryplacidae reaches the anterior of sternite 4, whereas in *Longusorbis* it reaches to the middle of sternite 4. *Longusorbis* also possesses a paddle-like propodus of the fifth pereiopod and flattened proximal articles of the fourth and fifth pereiopods, not seen in most euryplacids (an exception is *Psopheticoides* Sakai, 1969).

Longusorbis shares many similarities with extant portunids, but does not appear to be referable to an existing subfamily. The only portunid subfamily in which sternite 8 is regularly not visible is the Carcininae; however, members of that subfamily possess male somites 3–5 fused, whereas those somites in *Longusorbis* are free. In addition, the sternum of many carcinines is very narrow, much longer than wide, which is not the case in *Longusorbis*. No members of the Carcininae have the extremely broad orbits of *Longusorbis*. *Coenophthalmus*, referred to the Polybiinae although it lacks ovate or paddle-like elements of the fifth pereiopods, has all male somites free and sternite 8 is obscured in ventral view, both characters shared with *Longusorbis* and neither of which is typical of the Polybiinae. *Coenophthalmus* possesses a relatively broad fronto-orbital width, but the orbits themselves are not wide as in *Longusorbis* (Rathbun 1930, pl. 20, USNM 22050). In addition, the sternum of *Coenophthalmus* is broad and ovate, whereas that of *Longusorbis* is narrower and obovate.

Longusorbis also exhibits many similarities with members of the Geryonidae. Members of that family possess all free male somites, although 3–5 may exhibit some degree of fusion; sternite 8 is obscured in ventral view; and the chelae are xanthoid in shape and may have black finger tips; all features shared with *Longusorbis*. However, extant geryonids do not have any flattened or ovate articles of the fifth or fourth pereiopods, as in *Longusorbis*. It is notable that the extinct *Chaceon peruvianus* (d'Orbigny, 1842) has a flattened and rather ovate propodus and a lanceolate dactylus of pereiopod five. Further, the orbits are not broadly spaced and are not themselves broad in the Geryonidae as they are in *Longusorbis*.

Because *Longusorbis* is as different from the various families and subfamilies within the Portunoidea as they are from one another, we suggest at this time that *Longusorbis* represents its own evolutionary grade, probably within the Portunoidea. Its exact family-level position is currently under study by the authors; at this time we are uncertain as to whether it should be placed as a subfamily within the Portunidae or as a unique family within the Portunoidea.

Genus *Longusorbis* Richards, 1975

Type species.—*Longusorbis cuniculosus* Richards, 1975, by monotypy.

Other species.—*Longusorbis eutychius* new species.

Diagnosis.—Carapace wider than long, maximum length ranging from 70 to 80 percent maximum width, widest at position of hepatic region, posterior to outer-orbital angle, about 30 percent the distance posteriorly; lateral margins of carapace converging posteriorly; front interpreted to lie between interior-most orbital notches (Fig. 2B), axially produced into long, blunt-tipped rostrum, rostrum axially sulcate, strongly downturned distally so that distal part is nearly perpendicular to dorsal carapace (Fig. 2B); frontal width about 40 percent maximum carapace width; orbits extremely broad, sinuous, with notches, spines, or blunt protuberances; orbits angling posteriorly; eyestalks apparently well calcified (Fig. 2C); fronto-orbital width about equal to maximum carapace width; mesogastric region merging with rostral sulcus; gastric regions short; branchial regions long; urogastric region about as wide as mesogastric and cardiac regions; epibranchial region arcuate; metabranchial region with inflated oblique ridge parallel to margin; sternum about as long as wide, sternites 1/2 fused, no evidence of suture; sternal suture 2/3 entire; sternal suture 3/4 expressed as a marginal notch and weak groove; sternite 4 long; sternal sutures 4/5 and 5/6 not parallel; sternal suture 4/5 at high angle; sternite 8 not visible in ventral view; male abdomen extending to about middle of sternite 4 and about middle of coxae of pereipods 1; all male abdominal somites free, entirely filling space between coxae of fifth pereiopods; chelae stout, markedly heterochelate, fingers with black tips; meri and carpi of fourth and fifth pereiopods flattened; propodi of fourth and fifth pereiopods elliptic; dactylus of fifth pereiopod narrow, lanceolate (Fig. 2A).

Material examined.—*Longusorbis cuniculosus*: PRI 55177, KSU D746, collected from near Shelter Point (Vancouver Island, British Columbia, Canada; latitude 49°54'21.7"N; longitude 125° 10'41.0")W, late Campanian Northumberland Formation (Schweitzer et al. 2003); *L. eutychius*: MHN-UABCS/Te8/68-413, holotype.

Discussion.—Prior to this report, *Longusorbis* had been known only from one late Campanian locality on Vancouver Island, British Columbia (Richards 1975; Schweitzer et al. 2003). However, the new species described below is clearly congeneric with *Longusorbis cuniculosus*, as discussed. Thus, the geologic range of *Longusorbis* is extended into the Eocene, and the geographic range is extended southward to Baja California Sur. The genus is one of many to survive the Cretaceous-Tertiary boundary event(s) (Schweitzer and Feldmann 2005).

Longusorbis cuniculosus is characterized by a triangular, axially sulcate front; very broad, sinous orbits; an anterolaterally directed outer-orbital spine; a mesogastric region extending into the rostral sulcus; a short hepatic region; an arcuate epibranchial region with a portion paralleling the hepatic region; a maximum width at the position of the hepatic region; orbits angling posteriorly; lateral margins converging posteriorly; and granular carapace ornament (Fig. 2A–C). All of the features are shared by the new species, *Longusorbis eutychius*. *Longusorbis eutychius* differs from *L. cuniculosus* in lacking orbital notches and spines and lacking the spherical swellings on the hepatic, epibranchial, and mesobranchial regions typical of *L. cuniculosus*. *Longusorbis eutychius* also narrows more considerably posteriorly than does *L. cuniculosus*. However, we view these differences primarily in ornament as species-level variations and refer the two species to the same genus.

Unfortunately, the sternum of *L. eutychius* is not preserved; however, the marked similarity in dorsal carapace features makes the referral to *Longusorbis* possible.

Longusorbis eutychius, **new species**
(Fig. 2E, F)

Description.—Carapace wider than long, length about 70 percent maximum carapace width, widest at position of outer-orbital angle, about 30 percent the distance posteriorly; regions moderately defined by grooves; carapace very weakly vaulted both transversely and longitudinally; carapace surface finely granular in all areas where cuticle is preserved including orbital rim and branchial regions.

Front interpreted to lie between interior-most orbital notches, axially produced into triangular or blunt tipped-projection, axially sulcate; frontal width about 42 percent maximum carapace width. Orbits extremely broad; with broad, granular rim; sinuous; angling posteriorly to blunt outer-orbital spine which is directed anterolaterally; fronto-orbital width occupying maximum carapace width. Lateral margins converging posteriorly, sinuous, appearing to have been rimmed. Posterior margin rimmed, weakly concave centrally, about 42 percent maximum carapace width.

Protogastric regions equant, weakly inflated. Mesogastric region with long anterior process, process extending into rostral sulcus where it narrows considerably, with concave lateral margins; broadened posteriorly, with rounded posterior margin. Urogastric region somewhat narrower than either posterior portion of mesogastric region or anterior portion of cardiac region, with concave lateral margins, raised transversely. Cardiac region pentagonal, apex directed posteriorly, with two transversely inflated swellings anteriorly, small swelling at apex. Intestinal region weakly inflated, narrow. Hepatic region short, very wide, paralleling orbital rim, giving it a ridge-like appearance. Epibranchial region composed of two segments; anterior-most segment ridge-like, parallel and about as long as hepatic region; inner segment triangular, apex directed obliquely at cardiac region; two segments taken together yield arcuate appearance for entire region. Mesobranchial region broadly inflated, equant; metabranchial region triangular, inflated, shorter than wide.

Remainder of carapace and appendages unknown.

Measurements.—Measurements (in mm) taken on the holotype and sole specimen of *Longusorbis eutychius*: maximum carapace width = 17.0; maximum carapace length = 11.6; fronto-orbital width = 17.0; posterior width = 7.0; length to position of maximum width = 3.2.

Type.—The holotype and sole specimen is deposited in the Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, Mexico (MHN-UABCS/Te8/68-413). A cast of the holotype is deposited in the Carnegie Museum of Natural History, Pittsburgh, PA (CM 55277).

Etymology.—The trivial name is derived from the Greek word *eutychia*, meaning good luck, referring to the chance finding of a single, but readily identifiable, specimen of *Longusorbis* in Eocene rocks, spurring the re-evaluation of the genus and the family Carcineretidae.

Occurrence.—WP 39.

Discussion.—The specimen is not well preserved, but the details visible in both the part and counterpart make it possible to frame a relatively complete description of the dorsal carapace of *Longusorbis eutychius*. The new species extends both the geographic range of *Longusorbis* to the southern Pacific coast of North America and the geologic range into the Eocene.

Superfamily Goneplacoidea MacLeay, 1838
Family Goneplacidae MacLeay, 1838

Discussion.—Bishop (1988, p. 247) originally placed *Icriocarcinus* Bishop, 1988, within the Carcineretidae, based upon its shape, long eyestalks, transverse ridges, and carapace region development, allied with *Longusorbis* among other genera. Later, it was suggested that *Icriocarcinus* might be better placed among the Xanthidae *sensu lato* (Vega and Feldmann 1991; Vega et al. 1997), and it was finally assigned to the Goneplacidae (Schweitzer et al. 2002). Schweitzer et al. (2002) provided several lines of reasoning for placing *Icriocarcinus* within the Goneplacidae, and we concur with their decision. Most compelling among these reasons is the similarity of *Icriocarcinus* with the extant *Ommatocarcinus* White, 1851, and other goneplacid genera, which we expand upon here.

Icriocarcinus possesses most of the diagnostic characters of the Goneplacidae *sensu stricto* (Karasawa and Schweitzer 2006). These characters include broad orbits; a broad fronto-orbital width that may encompass the entire anterior margin of the carapace; a very narrow front that may be widened distally; a male abdomen filling the entire space between the coxae of the fifth pereiopods and with all somites free; a broad, ovate sternum with sternite 8 not visible in ventral view, and a sterno-abdominal cavity reaching the anterior of sternite 4. *Icriocarcinus* possesses black tips on the fingers and obovate propodi on the fifth pereiopods, not typical of many extant goneplacids. However, the overwhelming majority of the characters clearly allies *Icriocarcinus* with such extant genera as *Goneplax* Leach, 1814, and *Ommatocarcinus*; thus, we are confident in referring it to the Goneplacidae. *Ommatocarcinus* is known from fossils and is extant in the western Pacific Ocean (Jenkins 1975).

The similarities between *Icriocarcinus* (Fig. 3A–D) and *Ommatocarcinus* (Fig. 3E, F) are particularly striking. Both genera possess a trapezoidal dorsal carapace in which the position of maximum width occurs at the outer-orbital angle; extremely broad orbits and apparently well-calcified eyestalks that are readily fossilized; spiny or granular ornamentation of the orbital margin; a narrow front that widens distally; an arcuate epibranchial region positioned quite far anteriorly on the dorsal carapace; well-developed posterolateral reentrants; a broad, ovate sternum, a sterno-abdominal cavity reaching to the anterior of sternite 4; all male somites free and male abdomen covering the space between the coxae of the fifth pereiopods; long, spined meri of the chelipeds; long, keeled mani of the chelipeds; long fingers of the chelae with blunt denticles on the occlusal

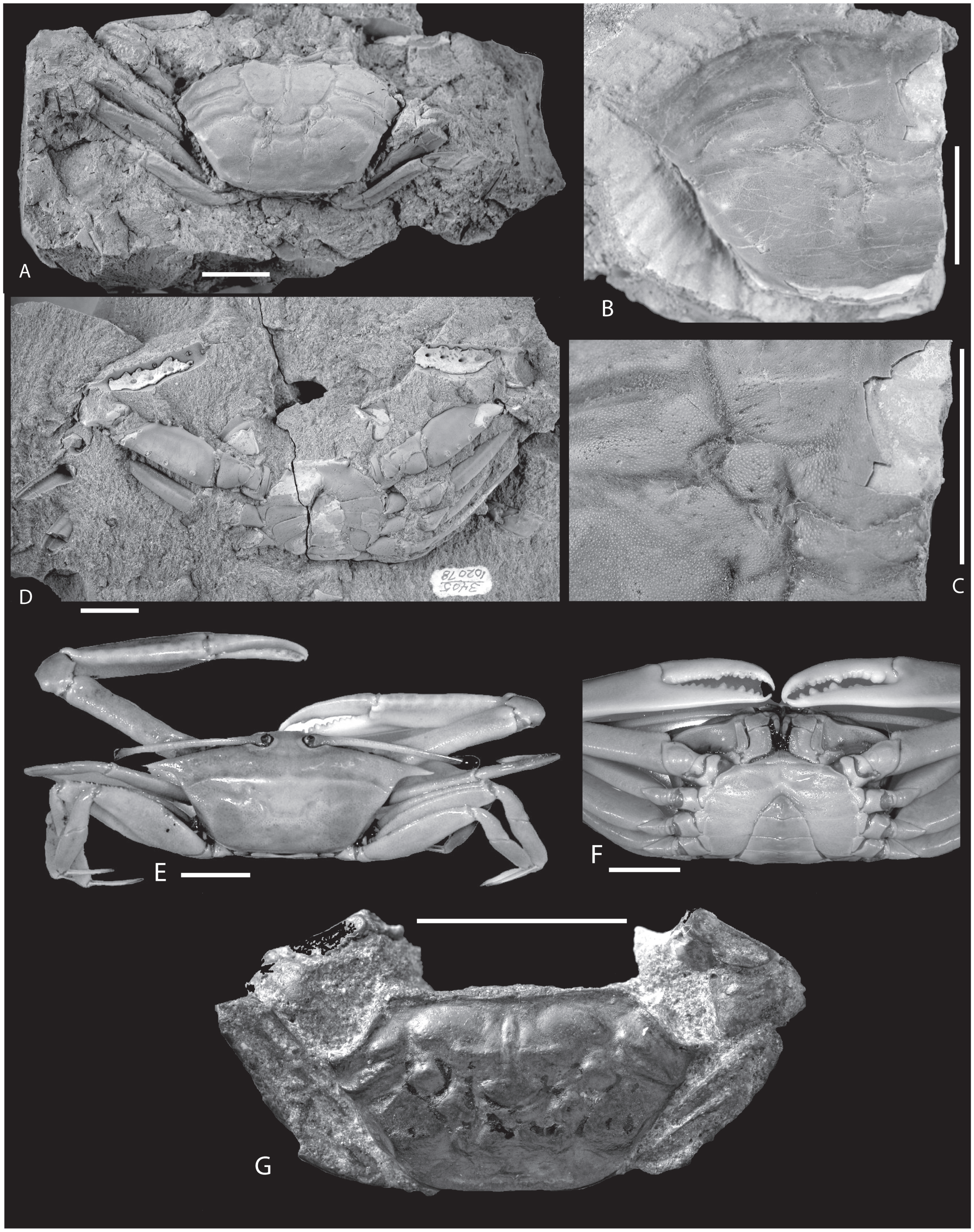

Fig. 3.—**A–D:** *Icriocarcinus xestos* Bishop, 1988. **A,** dorsal view of holotype, SDSNH 26038, showing a complete dorsal carapace from which the cuticle has been exfoliated. **B–D,** SDSNH 102078, collected from the Point Loma Formation on College Boulevard at SDSNH Locality 3405; **B,** dorsal carapace showing two intra-orbital spines; **C,** enlarged view of the dorsal carapace showing the contrast in surface texture and groove development seen on the cuticular surface as opposed to that on the exfoliated specimens; **D,** ventral surface. **E, F:** *Ommatocarcinus macgillivrayi* White, 1851, CBM-ZC 2042, deposited in the Natural History Museum and Institute, Chiba, Japan. **E,** dorsal carapace, note extremely long eyestalks; **F,** ventral surface. **G:** *Lithophylax trigeri* A. Milne Edwards and Brocchi, 1879, dorsal carapace, BSP 1988 III 196. Scale bars = 1 cm.

TABLE 6. Measurements (in mm) taken on the dorsal carapace of *Icriocarcinus xestos* Bishop, 1988. L = maximum carapace length measured from base of front; W = maximum carapace width measured between bases of outer-orbital spines; FOW = fronto-orbital width; PW = posterior width measured from outer edge of posterolateral reentrant; L2 = length from base of front to position of maximum width; FW = width of base of front.

Specimen Number	L	W	FOW	PW	L2	FW
SDSNH 26038 (Holotype)	21.0	33.5	33.5	21.1	6.7	-
SDSNH 26113 (Paratype)	20.0	35.2	35.2	-	5.0	1.5
SDSNH 102078	24.2	42.6	42.6	24.0	5.7	2.3
KSU D309	20.1	35.0	35.0	-	5.5	1.9

surfaces; and flattened ischia of pereiopods 2–5 (after Jenkins 1975). These similarities are especially compelling, given that *Icriocarcinus* is Late Cretaceous in age, and *Ommatocarcinus* is known from the Miocene to Holocene (Jenkins 1975). Thus, there is very strong evidence that *Icriocarcinus* is indeed a member of the Goneplacidae, perhaps particularly closely related to *Ommatocarcinus* and related genera.

Genus *Icriocarcinus* Bishop, 1988

Type species.—*Icriocarcinus xestos* Bishop, 1988, by monotypy.

Diagnosis.—As for species.

Icriocarcinus xestos Bishop, 1988
(Fig. 3A–D, 4)

Icriocarcinus xestos Bishop, 1988, p. 247, fig. 2, fig. 3A–D. Schweitzer et al., 2002, p. 21.

Emended diagnosis.—Carapace wider than long; regions defined by deep grooves; front long, extremely narrow, widening slightly distally; fronto-orbital width occupying maximum carapace width; orbits sloping obliquely and posteriorly; two intra-orbital spines; male abdomen with all somites free; filling entire space between coxae of fifth pereiopods; somite 3 widest of all somites, with transverse keel.

Emended description.—Carapace wider than long, maximum length measured at base of front about 60 percent maximum carapace width measured at base of outer-orbital spines which are positioned one-quarter to one-third the distance posteriorly; regions well-defined by deep grooves; carapace flattened transversely, moderately vaulted longitudinally. Front long, extremely narrow, weakly downturned, widening slightly distally, spatulate tip. Eyestalk well-calcified, extending longitudinally from beneath front. Orbits extremely wide, fronto-orbital width occupying entire frontal margin of carapace; appearing to be a short orbital fissure where groove defining lateral margin of protogastric region intersects margin; orbit with two intra-orbital spines, one at about half the distance distally to outer-orbital angle from axis, other spine about half the distance distally between the first intra-orbital spine and outer-orbital spine, both intra-orbital spines blunt, directed anterolaterally; outer-orbital spine long, sharp, directed laterally at base, curving anterolaterally at tip; orbital margin sinuous, sloping posteriorly so that outer-orbital angle is one-quarter to one-third the distance posteriorly. Lateral margins sinuous, with weak indentations where grooves separating regions intersect them, with three large tubercles along margin of metabranchial region. Posterolateral reentrants large. Posterior margin rimmed, very weakly concave centrally.

Protogastric regions trapezoidal, narrow end oriented posteriorly. Mesogastric region with long, straight, anterior process terminating well before front; mesogastric widening posteriorly, three-sided, with concave lateral margins and very convex posterior margin. Metagastric region about as wide as posterior-most mesogastric region, anterior margin very concave, posterior margin nearly straight, lateral margins converging slightly posteriorly. Urogastric region depressed below level of metagastric region, much wider than long, well-defined laterally by grooves. Cardiac region well defined anteriorly and laterally by deep grooves, weakly inflated anteriorly, flattening posteriorly, becoming weakly inflated into spherical swelling at posterior tip. Intestinal region poorly differentiated.

Hepatic region shorter than wide, with transverse swelling bearing a central spherical node. Epibranchial region wider than high, parallel to hepatic region, with central node; spherical mesobranchial region positioned between epibranchial and mesogastric regions. Metabranchial region very large, inflated towards lateral margin, flattening toward posterior margin.

Specimens with preserved cuticle covered with very fine, scale-like granules, granules occasionally merging to form scabrous ridges; exfoliated specimens with very broad, flattened grooves between smooth carapace regions.

Sternum about as wide as long. Sternites 1 and 2 fused, forming triangular unit, no evidence of suture. Sternite 3 broader than sternite 2, suture 2/3 complete, surface of sternite 3 broadly concave. Sternite 4 long, sternal suture 3/4 expressed as a notch in margin and shallow depression extending toward axis; sterno-abdominal cavity extending to anterior end; marked episternal projection. Sternite 5 directed laterally, sternite 6 directed posterolaterally, both with episternal projections. Sternite 7 about as long as wide. Sternite 8 not visible in ventral view.

Male abdomen with concave lateral margins, all somites free; filling entire space between coxae of fifth pereiopods; somite 3 widest of all somites, with transverse keel.

Chelae long, weakly heterochelous. Merus of cheliped much longer than high, with spines on upper margin; carpus about as long as high; manus of cheliped much longer than high, with two or three keels on inner and outer surfaces; upper surface with spines; fingers long; occlusal surfaces with blunt tipped, black teeth and tips; movable finger with spines on upper surface. Pereiopods 2-5 with long, flattened ischia. Pereiopod five with obovate propodus and lanceolate dactylus.

Measurements.—Measurements (in mm) on the dorsal carapace of specimens of *Icriocarcinus xestos* are presented in Table 6.

Material examined.—SDSNH 26038 (holotype); SDSHN 26040, 26101, 26202, 26113 (paratypes); SDSHN 50548, 102078; KSU D309, 310.

Discussion.—Specimens of *Icriocarcinus xestos* exhibit a range of preservation styles. One style is with the cuti-

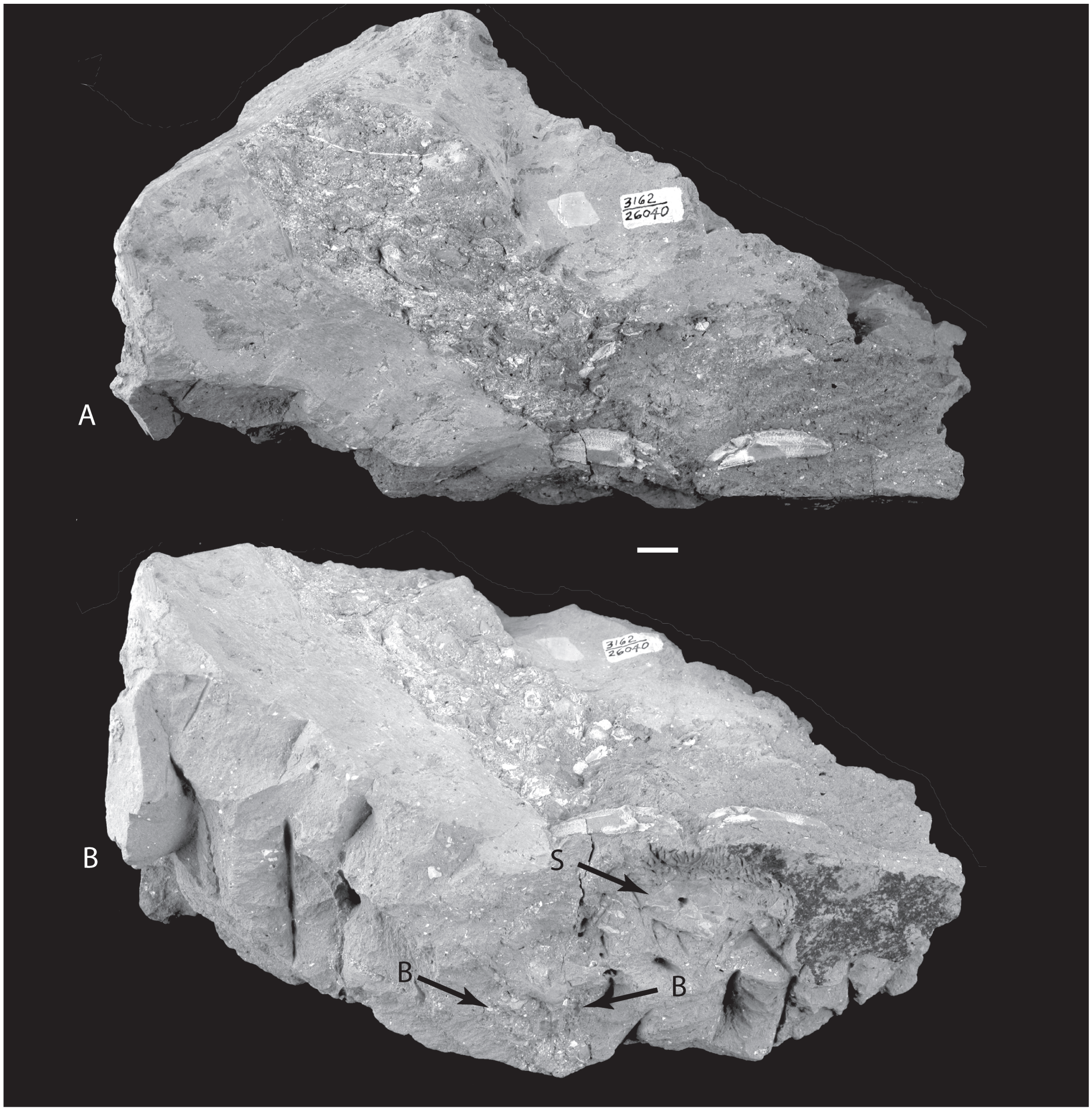

Fig. 4.—*Icriocarcinus xestos* Bishop, 1988. **A,** transverse and **B,** oblique views of paratype, SDSNH 26040, preserved within a complex, sand-filled burrow. The position of the specimen is shown by the claws and the sternum (S), seen in the oblique view (B). The lower continuation of the burrow (B) is also visible on the oblique view.

cle completely exfoliated, so that the dorsal carapace surface appears smooth and the grooves appear very deep. The other style is with preserved cuticle, which exhibits small granules that can become very closely spaced to appear like wrinkles or scabrous ridges. In this style of preservation, the grooves are still apparent but are not as deep as in specimens lacking cuticle.

As discussed above, *Icriocarcinus* is morphologically quite similar to *Ommatocarcinus*. It is also noteworthy that species of both genera are burrowers that produce complex burrow structures. Both fossil and extant members of *Ommatocarcinus* are known as burrowers (Jenkins 1975). Jenkins (1975) described exposed burrows, containing well-preserved remains of *Ommatocarcinus corioensis* (Cresswell, 1886) from the lower Miocene-Pliocene Port Campbell Limestone, southeastern Australia and Tasmania. The burrows are exposed on bedding planes, and single burrows may extend for a distance of over a meter. As described and illustrated (Jenkins 1975, pl. 8), the burrows are branching structures in which horizontal elements dominate over vertical ones. The exposed surfaces of the burrows seem to be either smooth or pelleted.

One paratype of *Icriocarcinus* recovered from the

Point Loma Formation was found preserved in a well-defined burrow structure (Fig. 4). That burrow, originally illustrated by Bishop (1988, fig. 3D), appears to be relatively short and contains a complete specimen of *Icriocarcinus xestos* within it. The burrow is constructed in a grey mudstone containing sand-sized particles of shell fragments and organic debris. The burrow is filled with fine sandy sediment with large fragments of mollusks. If the burrow is oriented with the preserved crab in a horizontal position, the uppermost part of the burrow descends into the sediment at a 60º angle to a depth of about 3.5 cm, at which point the burrow continues into the sediment at a 35º angle to a depth of about 8 cm. The structure is broader in the upper segment with a maximum measurable dimension of 4 cm, whereas the lower segment has a maximum measurable dimension of about 2.5 cm. These measurements provide relative sizes but the cross-section of the burrow and the maximum diameter cannot be determined because the structure is viewed along the broken section. The crab appears to be positioned within a chamber more than 10 cm wide and 4.5 cm high. The sediment filling the chamber is darker in color but otherwise similar to the mudstone in which the burrow is constructed.

Examination of the lower surface of the specimen, however, indicates that the structure is more complex. On this surface, the sternum of the animal is exposed along with a continuation of the sand-filled burrow structure (Fig. 4). The downward extension of the burrow structure is ovoid with a maximum diameter of 5 cm and a minimum diameter of 3.5 cm. Thus, as in the case of the burrows of *Ommatocarcinus*, the burrow of *Icriocarcinus xestos* is complex.

Ichnofossils in the Point Loma Formation have been studied previously (Kern and Warme 1974). Burrow structures were recognized not unlike the one described above in addition to two observations that are relevant to this study. Kern and Warme noted (1974, p. 896, fig. 6) that when the burrows passed from sandy sediment into muddy sediment, the burrow angle decreased from being vertically dominated to becoming horizontally dominated. Further, they noted that the burrows were pellet-lined in the sandy sediment, and would likely be referred to *Ophiomorpha*; whereas the same burrow in muddy sediment was smooth and unlined, so that it would be referred to the ichnogenus *Thalassinoides*. The burrow in which *Icriocarcinus xestos* was preserved is steep at the top, becoming more gently sloping downward and is sand-filled. Perhaps the structure originated in sandy sediment, ultimately penetrating muddy sediment.

The environment of deposition of the Point Loma Formation has been interpreted to be at bathyal depths at which mudstones were deposited by relatively slow processes of sedimentation whereas the sandstones were accumulated rapidly by grain-flow processes (Kern and Warme 1974). Interpretation of water depth as well as the downslope accumulation of sediments was based upon the mixing of sublittoral and bathyal foraminiferans (Sliter 1968 in Kern and Warme 1974). Thus, *Icriocarcinus* may have inhabited water deeper than, or as deep as, that in which *Ommatocarcinus* has been reported. Sakai (1976) recorded *O. macgillivrayi* White, 1851, from depths up to 100 m, and Jenkins (1975) reported the same species at depths of 274 m. Another species, *O. fibriophthalmus* Yokoya, 1933, was collected at a depth of 146 m (Sakai 1976).

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LITERATURE CITED

ALCOCK, A.W., AND A.R.S. ANDERSON. 1899. Natural history notes from H.M. Royal Marine survey ship "Investigator," commander T.H. Heming, R.N., commanding. Ser. III, No. 2. An account of the deep-sea Crustacea dredged during the surveying-season of 1897–1898. Annals and Magazine of Natural History (7)3:1–27, 278–292.

VAN BAKEL, B.W.M., J.W.M. JAGT, R.H.B. FRAAIJE, AND Y. COOLE. 2003. New data on the crab *Binkhorstia ubaghsii* (Late Maastrichtian; NE Belgium, SE Netherlands). Contributions to Zoology, 72:85–89.

BARNARD, K.H. 1950. Descriptive Catalogue of South African Decapod Crustacea (Crabs and Shrimps). Annals of the South African Museum, 38:1–837, figs. 1–154.

BATALLER, J.R. 1959. Primer suplemento a la "sinopsis de las especies nuevas del Cretáceo de España." Boletín del Instituto Geológico y Minero de España, 70:1–77.

BELL, T. 1858. A Monograph of the Fossil Malacostracous Crustacea of Great Britain, Pt. I, Crustacea of the London Clay. Monograph of the Palaeontographical Society, London, 10(1856), viii + 44 pp., 11 pls.

BEURLEN, K. 1930. Vergleichende Stammesgeschichte Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. Fortschrift Geologie und Paläontologie, 8:317–586.

BINKHORST, J.T. VON. 1857. Neue Krebse aus der Maestrichter Tuffkreide. Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens, 14:107–110, pl. 6, 7.

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.

COLLINS, J.S.H., R.H.B. FRAAYE, AND J.W.M. JAGT. 1995. Late Cretaceous anomurans and brachyurans from the Maastrichtian type area. Acta Palaeontologica Polonica, 40(2):165–210.

COLLINS, J.S.H., AND S.L. JAKOBSEN. 2003. New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark. Bulletin of the Mizunami Fossil Museum, 30:63–96, 8 pls.

COLOSI, G. 1923. Une specie fossile de Gerionide (Decapodi brachiuri). Bolettino della Societá dei Naturalisti in Napoli, 35 (series 2, vol. 15), 37:248–255.

COSTA, O.G. 1853. Addizioni a' Decapodi Brachyuri. Pp. 14–15, *in* Fauna del Regno di Napoli. Stamperia di Antonio Cons, Napoli.

CRESSWELL, A.W. 1886. Notes on some fossil crabs from the Miocene rocks of Corio Bay. Victorian Naturalist, 3:86–91.

DANA, J.D. 1851. On the classification of the Cancroidea. American Journal of Science and Arts, (2)12(34):121–131.

———. 1852. Conspectus Crustaceorum, etc. Conspectus of the Crustacea of the Exploring Expedition under Capt. Wilkes, U.S.N., including the Crustacea Cancroidea Corystoidea. Proceedings of the Academy of Natural Sciences of Philadelphia, 6:73–86.

DAVIE, P.J.F. 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda—Anomura, Brachyura. *In* Zoological Catalogue of Australia, Vol. 19.3B (A. Wells and W.W.K. Houston, eds.). CSIRO Publishing, Melbourne, Australia, 641 pp.

EDMONDSON, C.H. 1930. New Hawaiian Crustacea. Occasional Papers of the Bernice P. Bishop Museum, 9(10):1–18, pl. 1.

FABRICIUS, J.C. 1793. Entomologia Systematica Emendata et Aucta Secundum Classes, Ordines, Genera, Species adjectis Synonymis, Locis, Observationibus, Descriptionibus. Hafniae, 2:1–519.

FELDMANN, R.M., S. CASADÍO, L. CHIRINO-GÁLVEZ, AND M. AGUIRRE-URRETA. 1995. Fossil decapod crustaceans from the Jagüel and Roca formations (Maastrichtian-Danian) of the Neuquén Basin. The Paleontological Society Memoir 43, ii + 22 pp.

FELDMANN, R.M., F.J. VEGA, AND T. VILLAMIL. 1998. Cretaceous extinction of the Tethyan crab family Carcineretidae: a victim of the impact? GSA Abstracts with Programs, 1998:A286.

FELDMANN, R.M., AND T. VILLAMIL. 2002. A new carcineretid crab (Upper Turonian, Cretaceous) of Colombia. Journal of Paleontology, 76:718–724.

FELDMANN, R.M., T. VILLAMIL, AND E.G. KAUFFMAN. 1999. Decapod and stomatopod crustaceans from mass mortality Lagerstatten: Turonian (Cretaceous) of Colombia. Journal of Paleontology, 73:91–101.

FORSKÅL, P. 1775. Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål. Mölleri: Hafniae, 164 pp.

FRAAYE, R.H.B. 1996. Late Cretaceous swimming crabs: radiation, migration, competition, and extinction. Acta Geologica Polonica, 46:269–278.

GLAESSNER, M.F. 1969. Decapoda. Pp. R400–R533, R626–R628, *in* Treatise on Invertebrate Paleontology, Pt. R4(2) (R.C. Moore, ed.). Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas.

———. 1980. New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. Transactions of the Royal Society of South Australia, 104:171–192.

GUINOT, D. 1961. Caractères et affinités de *Macropipus australis* sp. nov., Crustacé Décapode Brachyoure de la côte sud-ouest Africaine. Bulletin de l'Institut royal des Sciences naturelles de Belgique, 37(26):1–13, pls. 1, 2.

———. 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyoures. Compte Rendu Académie des Sciences, Paris, Série D, 285:1049–1052.

———. 1979. Morphologie et phylogenèse des brachyoures. Mémoires du Muséum National d'Histoire Naturelle, nouvelle série, Série A, 112:1–354.

HERBST, J.F.W. 1782–1804. Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten, volume 1 (1782–1790), pp. 1–274, pls. 1–21; volume 2 (1791–1796), pp. 1–225, pls. 22–46; volume 3 (1799–1804), pp. 1–66, pls. 47–50.

HOLTHUIS, L.B. 1987. *Necora*, new genus of European swimming crabs (Crustacea Decapoda Portunidae) and its type species *Cancer puber* Linnaeus, 1767. Zoologische Mededelingen (Leiden), 61:1–14.

JENKINS, R.J.F. 1975. The fossil crab *Ommatocarcinus corioensis* (Cresswell) and a review of related Australasian species. Memoirs of the National Museum of Victoria, 36:33–62.

KARASAWA, H. 1990. Decapod crustaceans from the Miocene Mizunami Group, Central Japan, Pt. 2, Oxyrhyncha, Cancridea, and Brachyrhyncha. Bulletin of the Mizunami Fossil Museum, 17:1–34, pls. 1–8.

KARASAWA, H., AND C.E. SCHWEITZER. 2006. A new classification of the Xanthoidea sensu lato (Crustacea: Decapoda: Brachyura) based on phylogenetic analysis and traditional systematics and evaluation of all fossil Xanthoidea sensu lato. Contributions to Zoology, 75(1/2):23–72.

KERN, J.P., AND J.E. WARME. 1974. Trace fossils and bathymetry of the Upper Cretaceous Point Loma Formation, San Diego, California. Geological Society of America Bulletin, 85:893–900.

LAMARCK, J.B.P.A. 1818. Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la zoologie. Tome 5. Déterville, Paris, 612 pp.

LATREILLE, P.A. 1802–1803. Histoire naturelle, générale et particulière, des crustacés et des insectes. Volume 3, Dufart, Paris, France, 467 pp.

———. 1825. Encyclopédie Méthodique. Histoire Naturelle. Entomologie, ou Histoire naturelle des Crustacés, des Arachnides et des Insectes, Vol 10, part 1. Paris, 344 pp.

LEACH, W.E. 1814. Crustaceology. *In* The Edinburgh Encyclopedia (D. Brewster, ed.), 7:383–437, pl. 221.

———. 1815-1875. Malacostraca Podophthalmata Britanniae. London: 1–124 + pl. 1–45.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Edition 10, volume 1. Laurentii Salvii, Homiae (Stockholm), 824 pp.

———. 1767. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Edition 12, volume 1, part 2, p. 533–1327. Laurentii Salvii, Homiae (Stockholm).

MACLEAY, W.S. 1838. On the brachyurous Decapod Crustacea brought from the Cape by Dr. Smith. Pp. 53–71, 2 pls, *in* Illustrations of the Annulosa of South Africa; consisting chiefly of Figures and Descriptions of the Objects of Natural History Collected during an Expedition into the Interior of South Africa, in the Years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa" (A. Smith, ed.). Smith, Elder, and Co., London.

MACPHERSON, E. 1984. Crustáceos decápodos del Banco Valdivia (Atlántico sudoriental). Resultados Expediciones Cientificas (supplement to Investigación Pesquera, Barcelona), 12:39–105.

MANNING, R.B., AND L.B. HOLTHUIS. 1981. West African brachyuran crabs (Crustacea: Decapoda). Smithsonian Contributions to Zoology, 306:1–379.

MIERS, E.J. 1886. Report on the Brachyura collected by H. M. S. Challenger during the years 1873–1876. Pp. 1–362, *in* Report of the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876, Zoology (C.W. Thomson and J. Murray, eds.). Johnson Reprints, New York.

MILNE EDWARDS, A. 1867. Descriptions de quelques espéces nouvelles de Crustacés Brachyoures. Annales de la Societé Entomologique de France, 4:263–288.

———. 1869. Description de quelques Crustacés Nouveaux de la famille des Portuniens. Nouvelles Archives du Museum National d'Histoire Naturelle, Paris, 5:146–160, pls. 6–7.

———. 1870. Note sur le *Catoptrus*, nouveau genre appartenant a la division des Crustacés Brachyures catometopes. Annales de la Science Naturelle (Zoologie), (5)13:80–86.

———. 1879-1881. Études sur les Xiphosures et les Crustacés Podophthalmaires. Mission Scientifique au Mexique et dans l'Amérique Centrale, Recherches Zoologiques. cinquième partie. Imprimerie National, Paris, 368 pp., 60 pls.

———. 1882. Rapport sur les travaux de la Commission chargée par M. Le Ministre de L'Instruction Publique d'étudier la faune sous-marine dans les grandes profoundeurs de la Méditerranée et de l'Océan Atlantique. Archives des Missions Scientifiques et Litteraires, Paris (3)9:1–59.

MILNE EDWARDS, A., AND P. BROCCHI. 1879. Note sur quelques Crustacés fossiles apartenant au groupe des Macrophthalmiens. Bulletin de la Société Philomatique de Paris, 3:113–117.

MOOSA, K.M. 1996. Crustacea Decapoda: Deep-water swimming crabs from the South-West Pacific, particularly New Caledonia (Brachyura, Portunidae). Pp. 503–550, *in* Résultats des Campagnes MUSORSTOM, vol. 15 (A. Crosnier, ed.). Mémoires du Muséum national d'Histoire naturelle (A) 168.

NARDO, G.D. 1847. Sinonimia moderna delle specie registrate nell'-opera intitolata : Descrizone de Crostacei, de Testacei e de Pesci che abitano le lagune e golfo veneto rappresentati...dall'Abate Chiereghini: i-xi + 1–127.

NG, P.K.L. 2000. The deep-water swimming crabs of the genus *Benthochascon* (Decapoda: Brachyura: Portunidae), with description of a new genus for the American *B. schmitti*. Journal of Crustacean Biology, 20 (sp. no. 2):310–324.

NOETLING, F. 1881. Über einige Brachyuren aus dem Senon von Mastricht und dem Tertiär Norddeutschlands. Zeitschrift der deutschen Geologischen Gesellschaft (Berlin), 33:357–371.

D'ORBIGNY, A. 1842. Voyage dans l'Amérique méridional, 1826–1833 (III). Géologie et Paláontologie, Paris, France.

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.

PAUL'SON, O.M. 1875 [reprint 1961]. Studies on Crustacea of the Red Sea with notes regarding other seas. Part I. Podophthalmata and Edriophthalmata (Cumacea). The Israel Program for Scientific Translations, Jerusalem, 164 pp., 21 pls.

PENNANT, T. 1777. British Zoology, Volume 4: Crustacea Mollusca Testacea. B. White, London.

PRESTANDREA, N. 1833. Su di alcuni nuovi crustacei dei mari di Messina. Effemeridi Scientifiche e Letterarie per La Sicilia, April 1833:3–14.

RAFINESQUE, C.S. 1815. Analyse de la Nature, ou Tableau de l'Univers et des corps organisée. L'Imprimerie de Jean Barravecchia, Palermo, Italy, 224 pp.

RATHBUN, M.J. 1898. The Brachyura collected by the U.S. Fish Commission steamer Albatross on the voyage from Norfolk, Virginia, to San Francisco, California, 1887–1888. Proceedings of the United States National Museum, 21:567–616, pls. 41–44.

———. 1906. The Brachyura and Macrura of the Hawaiian Islands. U.S. Fish Commission Bulletin for 1903, Part III:829–930, pls. III–XXIV.

———. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. United States National Museum Bulletin 152, 609 pp.

———. 1931. New crabs from the Gulf of Mexico. Journal of the Washington Academy of Science, 21:125–128.

———. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. Geological Society of America, Special Paper 2, 160 pp.

RICHARDS, B.C. 1975. *Longusorbis cuniculosus*: a new genus and species of Upper Cretaceous crab; with comments on the Spray Formation at Shelter Point, Vancouver Island, British Columbia. Canadian Journal of Earth Sciences, 12:1850–1863.

RISSO, A. 1816. Histoire naturelle des Crustacés des environs de Nice. Paris: 1–175 + pl. 1–3.

RÜPPELL, E. 1830. Beschreibung und Abbildung von 24 Arten kurzschänzigen Krabben, also Beitrag zur Naturgeschichte des rothen Meeres. H. L. Brönner, Frankfurt am Main, 28 pp., pls. 1–6.

SAKAI, T. 1938. On three systematically interesting crabs from Japan, one of which is new to science. Annotated Zoology of Japan, 17(3–4):301–301, pl. 16.

———. 1969. Two new genera and twenty-two new species of crabs from Japan. Proceedings of the Biological Society of Washington, 82:243–280.

———. 1976. Crabs of Japan and the Adjacent Seas. Kodansha Ltd., Tokyo, 773 pp., 251 pls.

SCHUBART, C.D., AND S. REUSCHEL. 2005. Molecular phylogenetic relationships of cancroid and portunoid crabs (Decapoda: Brachyura) do not reflect current taxonomy. Book of Abstracts, Sixth International Crustacean Congress, Glasgow, Scotland, UK, 18–22 July, 2005:7.

SCHWEITZER, C.E., AND R.M. FELDMANN. 2000. New fossil portunids from Washington, USA, and Argentina, and a re-evaluation of generic and family relationships within the Portunoidea Rafinesque, 1815 (Decapoda: Brachyura). Journal of Paleontology, 74:636–653.

———. 2002. New Eocene decapods (Thalassinidea and Brachyura) from Southern California. Journal of Crustacean Biology, 22:938–967.

———. 2005. Decapod crustaceans, the K/P event, and Palaeocene recovery. Pp. 17–53, *in* Crustacea and Arthropod Relationships (S. Koenemann and R.A. Jenner, eds.). Taylor and Francis Group, New York.

SCHWEITZER, C.E., R.M. FELDMANN, J. FAM, W.A. HESSIN, S.W. HETRICK, T.G. NYBORG, AND R.L.M. ROSS. 2003. Cretaceous and Eocene Decapod Crustaceans from Southern Vancouver Island, British Columbia, Canada. NRC Research Press, Ottawa, Ontario, Canada, 66 pp.

SCHWEITZER, C.E., R.M. FELDMANN, G. GONZALEZ-BARBA, AND V. ĆOSOVIĆ. 2007. Decapod crustaceans (Brachyura) from the Eocene Tepetate Formation, Baja California Sur, Mexico. Annals of Carnegie Museum, 76:15–28.

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, 59 (Supplement to Journal of Paleontology, 76), 43 pp.

SCHWEITZER, C.E., G. GONZÁLES-BARBA, R.M. FELDMANN, AND D.A. WAUGH. 2006 [imprint 2005]. Decapoda (Thalassinidea, Paguroidea) from the Eocene Bateque and Tepetate formations, Baja California Sur, México: Systematics, Cuticle Microstructure, and Paleoecology. Annals of Carnegie Museum, 74(4):275–293.

SMITH, S.I. 1879. The stalk-eyed crustaceans of the Atlantic coast of North America north of Cape Cod. Transactions of the

Connecticut Academy of Arts and Sciences, 5(1):27–136.
STENZEL, H.B. 1952. Decapod crustaceans from the Woodbine Formation of Texas. United States Geological Survey Professional Paper, 242:212–217.
STERNBERG, R. VON, AND N. CUMBERLIDGE. 2001. Notes on the position of the true freshwater crabs within the brachyrhynchan Eubrachyura (Crustacea: Decapoda: Brachyura). Hydrobiologia, 449:21–39.
STERNBERG, R. VON, N. CUMBERLIDGE, AND G. RODRIGUEZ. 1999. On the marine sister groups of the freshwater crabs (Crustacea: Decapoda: Brachyura). Journal of Systematic and Evolutionary Research, 37:19–38.
STIMPSON, W. 1862 [read 1860]. Notes on North American Crustacea, in the Museum of the Smithsonian Institution. No. II. Annals of the Lyceum of Natural History, 7:176–246, pl. II, V.
———. 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L.F. de Pourtalès, Assistant, United States Coast Survey. Bulletin of the Museum of Comparative Zoology, 2:109–160.
VAN STRAELEN, V. 1934. Contribution à l'étude des crustacés décapodes fossiles de la Catalogne. Géologique Pays Catalans, 3:1–6.
VEGA, F.J., AND R.M. FELDMANN. 1991. Fossil crabs (Crustacea, Decapoda) from the Maastrichtian Difunta Group, northeastern Mexico. Annals of Carnegie Museum, 60:163–177.
VEGA, F.J., R.M. FELDMANN, P. GARCÍA-BARRERA, H. FILKORN, F. PIMENTEL, AND J. AVENDAÑO. 2001. Maastrichtian Crustacea (Brachyura: Decapoda) from the Ocozocuautla Formation in Chiapas, southeast Mexico. Journal of Paleontology, 75:319–329.
VEGA, F.J., R.M. FELDMANN, A.C. OCAMPO, AND K.O. POPE. 1997. A new species of Late Cretaceous crab (Brachyura: Carcineretidae) from Albion Island, Belize. Journal of Paleontology, 71:615–620.
VEGA, F.J., R.M. FELDMANN, AND F. SOUR-TOVAR. 1995. Fossil crabs (Crustacea: Decapoda) from the Late Cretaceous Cárdenas Formation, east-central Mexico. Journal of Paleontology, 69:340–350.
WEBER, F. 1795. Nomenclator entomologicus secundum entomologian systematicum ill. Fabricii, adjectis speciebus recens detectis et varietatibus. C.E. Bohn, Chiloni et Hamburgi, 171 pp.
WHITE, A. 1851. Descriptions of some new species of Annulosa. Pp. 387–395, *in* Narrative of the Voyage of H.M.S. 'Rattlesnake' During the Years 1846–1850, Volume 2, Appendix 6 (J. Macgillivray, ed.). Boone, London.
WITHERS, T.H. 1922. On a new brachyurous crustacean from the Upper Cretaceous of Jamaica. Annals and Magazine of Natural History, 10:534–541.
WOODS, J.T. 1953. Brachyura from the Cretaceous of central Queensland. Memoirs of the Queensland Museum, 13(1):50–57.
WRIGHT, C.W., AND J.S.H. COLLINS. 1972. British Cretaceous Crabs. Palaeontographical Society Monograph, 114 pp., 22 pls.
YOKOYA, Y. 1933. On the distribution of the decapod crustaceans inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S.S. Sôyô-Maru, during the years 1923–1930. Journal of the College of Agriculture of the Imperial University of Tokyo, 12:1–226.