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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)

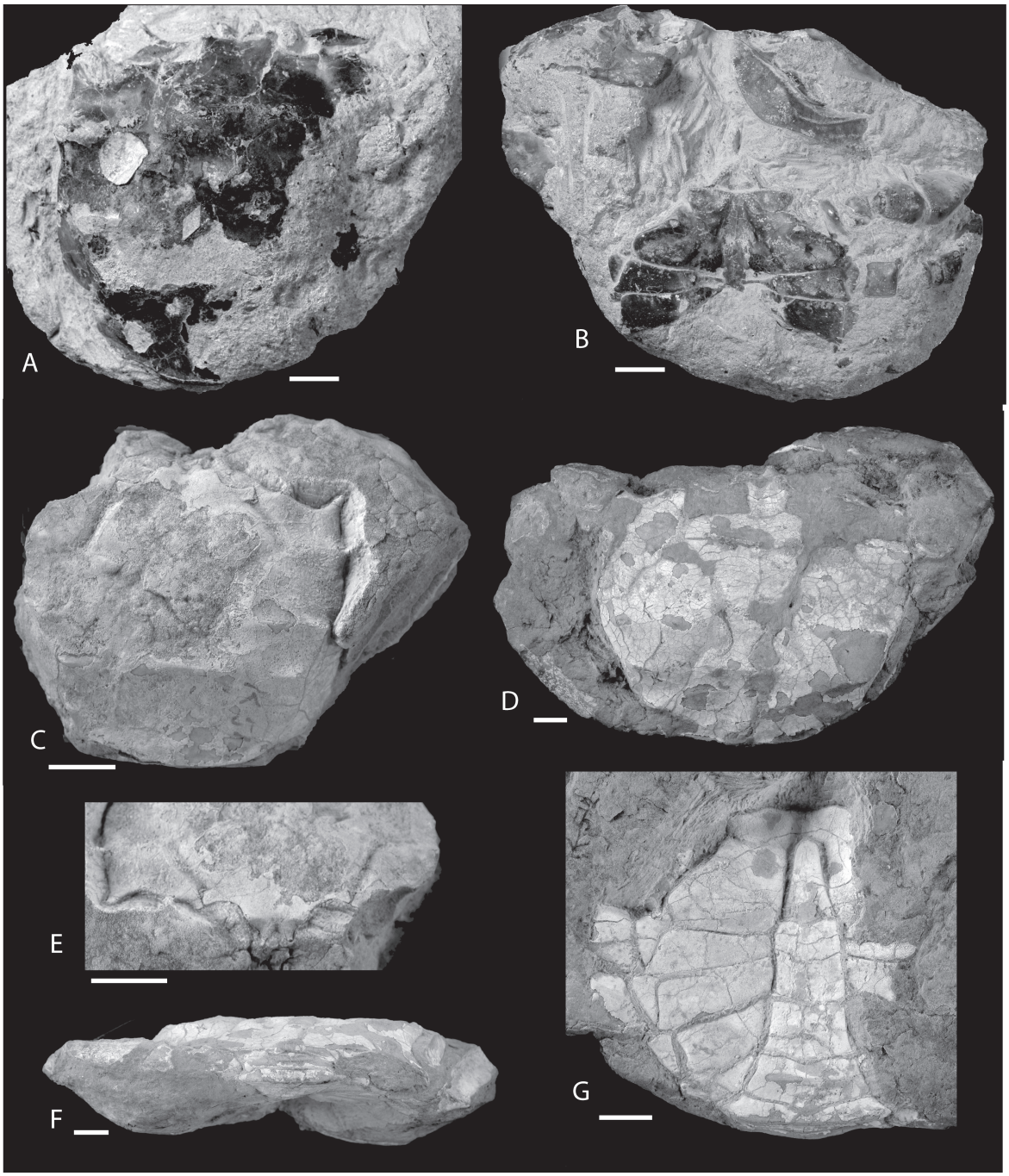

Fig. 1.—*Ophthalmoplax stephensoni* Rathbun, 1935. **A, B,** dorsal and ventral views of holotype, USNM 73793, unwhitened. **C, E,** dorsal and frontal views of paratype, UT 21258, showing the nature of the spines on the anterior and anterolateral margins and the strongly downturned, bifid rostrum. **D, 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 intraorbital 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 thick-

ened 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