MIOCENE FOSSIL DECAPODA (CRUSTACEA: BRACHYURA) FROM PATAGONIA, ARGENTINA, AND THEIR PALEOECOLOGICAL SETTING

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ABSTRACT

Five previously undescribed decapod taxa have been collected from lower upper Miocene rocks of the Puerto Madryn Formation, Península Valdés region, Chubut Province, Patagonia, Argentina. New species include *Osachila valdesensis, Rochinia boschii, Romaleon parspinosus, Panopeus piramidensis,* and *Ocypode vericoncava. Chaceon peruvianus* and *Proterocarcinus latus* are also reported from the unit, in addition to two indeterminate xanthoid species. Assignment of fossil taxa to genera within the Panopeidae Ortmann, 1893, is difficult due to the marked similarity in dorsal carapace characters among several genera. *Panopeus whittenensis* Glaessner, 1980, is herein referred to *Pakicarcinus* Schweitzer et al., 2004. The Puerto Madryn Formation exposed near Puerto Pirámide contains three distinct Facies Associations (1–3), each associated with specific paleoecological and paleoenvironmental conditions, and which recur throughout the section and represent trangressive systems tract (TST) deposits and highstand systems tract (HST) deposits. Within Facies Association 1, near the base of the section at Puerto Pirámide, three paleosurfaces containing invertebrate fossils in life position are exposed and have been carefully mapped in plan view. Because of their sedimentologic, stratigraphic, taphonomic, and paleoecologic features, these three paleosurfaces are considered to be obrution deposits, each preserving a slightly different paleoenvironmental regime in terms of water depth and position with respect to wave base. Paleosurfaces were formed during the waning stages of the transgressive systems tract.

KEY WORDS: Decapoda, Brachyura, Argentina, Miocene, paleoecology, taphonomy

INTRODUCTION

Fossil decapod crustaceans have been known for many years from Península Valdés, Chubut Province, Argentina, but only from anecdotal reports. The Península Valdés area was designated a World Heritage Site largely because of the abundance of modern whales, sea lions, and penguins in the area. Field work in 2002, as well as examination of unstudied material in the Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Argentina, has yielded dozens of new specimens of fossil decapod crustaceans. Many of these fossils belong to previously described taxa as well as to several new decapod taxa. The purposes of the present study are to describe and illustrate the decapod fauna from Miocene rocks of the general region of Península Valdés (Fig. 1) and to describe the paleoecological setting in which the crabs lived. Detailed maps of paleosurfaces within the Puerto Madryn Formation document the distribution of decapods within firm bottom, oyster-dominated communities.

Studies on the fossil decapod Crustacea of Patagonia have increased in recent years, resulting in numerous publications and new species (Aguirre-Urreta 1982, 1987,

1989, 1990, 1992; Aguirre-Urreta and Ramos 1981; Feldmann et al. 1995; Schweitzer and Feldmann 2000b, c, d, 2001; Casadío et al. 2004). Late Cretaceous and Paleocene decapods were reported by Feldmann et al. (1995). There has been some debate about the age of the Centinela Formation, previously thought to be Eocene, from which numerous decapods have been collected (Casadío et al. 2000a; Schweitzer and Feldmann 2000b, c, d, 2001). It is now considered to be late Oligocene to early Miocene (Casadío et al. 2000b; Guerstein et al., in press). A middle Oligocene decapod fauna has recently been described by Casadío et al. (2004) from the Andean foothills near San Carlos de Bariloche, Argentina. Most of the decapods reported herein are early late Miocene in age (Scasso et al. 2001). Thus, fossil decapods are increasingly well known from most epochs of the Cenozoic as well as from the Late Cretaceous in Patagonia.

The decapod fauna of Península Valdés contains the well-known *Chaceon peruvianus* (d'Orbigny 1842) and *Proterocarcinus latus* (Glaessner 1933), which have been described from many localities throughout Patagonia
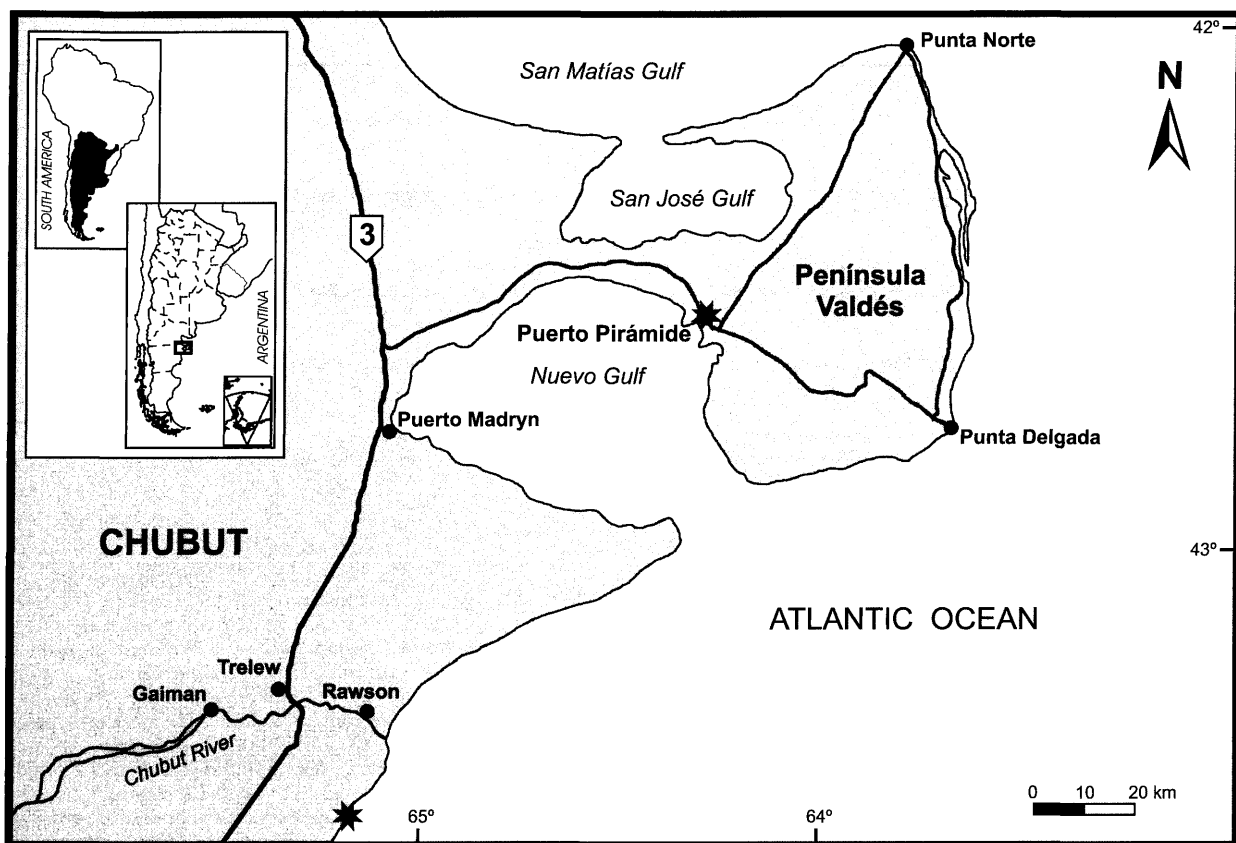
Fig. 1.—Location map for the decapod collecting locales. Star near Puerto Pirámide indicates location of measured section described herein and decapod collecting localities. Star south of Rawson indicates collecting locality in the Gaiman Formation, where some of the decapods described herein were located.

(Feldmann et al. 1995; Schweitzer and Feldmann 2000c; Casadío et al. 2004). In addition to these well-known species, five new species are described herein, as well as two indeterminate members of the Xanthoidea MacLeay, 1838. The new species of *Rochinia* A. Milne Edwards, 1875, is the first report of the genus in the fossil record, and the new species of *Ocypode* Weber, 1795, is the oldest known occurrence of the genus. The new species of *Romaleon* Gistl, 1848, is the fourth Miocene species known, and the new species of *Osachila* Stimpson, 1871a, constitutes only the second known fossil species of the genus.

GEOLOGIC SETTING

A number of transgressive events occurred during the Paleogene and early Neogene in southern South America. These were related mainly to the subsidence of the Atlantic margin of Patagonia. Malumián (1999) recognized five major sedimentary cycles during this interval which were controlled by tectonic events as well as climatic and eustatic changes. The first cycle began with the Maastrichtian marine transgression that covered a large

area of South America. The second event was the middle Eocene transgression, which was represented only south of 40° S. The third cycle was characterized by widespread late Eocene-Oligocene continental deposits, some of which include important anthracogenic intervals. The fourth cycle comprises two of the most important transgressions, both in terms of the area covered and in terms of the quality of the stratigraphic and paleontologic record. The first of these transgressions occurred during the late Oligocene-early Miocene, while the second has been referred to the Tortonian (early late Miocene). Finally, the fifth cycle is related to an important orogenic phase and the uplifting of the Patagonian Cordillera (Malumián 1999).

The fossils studied herein were collected from the Puerto Madryn Formation, exposed near Puerto Pirámide, Chubut Province, Argentina (Fig. 1), which was deposited during the second transgression of the fourth sedimentary cycle of Malumián (1999). This transgression, known in the literature as "Entrerriense" or "Paranense," represents the most widespread of the Cenozoic transgressions of Argentina. In contrast to the transgression during the late Oligocene-early Miocene, it covered mainly the northern area of the country. Its greatest thickness is recorded in the

subsurface of the Chaco-Pampean plains, while sections of not more than 200 m are exposed in the area around Península Valdés (Puerto Madryn Formation); in eastern Entre Ríos, where a thin marine section assigned to the Paraná Formation is exposed; and in Uruguay, where the deposits include the Camacho Formation. Exposures of rocks referred to the "Entrerriense" have been reported in La Pampa (Parras et al. 2000), Córdoba (Bertolino et al. 2000), and other places in the northwestern areas of the country where lacustrine brackish facies are known (Gavriloff and Bossi 1992a, b; Cione et al. 1995; Bossi et al. 1999). These facies probably represent marginal environments.

The rocks deposited during this transgression generally have been assigned a Miocene age. Del Río (1988, 1991) studied the mollusks contained in the Paraná and Puerto Madryn formations, and assigned a middle Miocene age to them. Ostracodes and foraminiferans from the Puerto Madryn Formation in Península Valdés suggest a Miocene age according to García (1970). Malumián and Masiuk (1973) interpreted the age as late Miocene based on the presence of the foraminiferan *Prothelphidium tuberculatum* which is known from the Paris basin and is widely dispersed in the "Entrerriense" deposits in Argentina. Masiuk et al. (1976) referred the Puerto Madryn Formation to the middle-late Miocene. More recently Scasso et al. (2001) used $^{87}Sr/^{86}Sr$ dating to refer the Puerto Madryn Formation to the earliest late Miocene (middle Tortonian, 10 ± 0.3 Ma). These values are close to those reported by Zinsmeister et al. (1981), who published a $^{40}K/^{40}Ar$ age of 9.4 Ma for the uppermost beds of this unit.

Rocks of the equivalent Paraná Formation have been considered to be late Miocene-Pliocene by Frenguelli (1920), Pascual (1965), Gasparini (1968), Delupi de Bianchini and Bianchini (1971), and Scillato Yane (1975). Based on the ostracode content, García (1966, 1969) referred the Paraná Formation to the late Miocene. Zabert and Herbst (1977) and Herbst and Zabert (1987) suggested a late Miocene age based on micropaleontological data. This age was corroborated by Cione (1978) based on fish remains. Martínez (1994) studied the invertebrates of the equivalent Camacho Formation in Uruguay and suggested that a late Miocene age was possible.

The deposits of the Puerto Madryn Formation coincide with the end of the Neogene climatic optimum. The presence of warm water along the Argentine Atlantic coast during the middle Miocene is characterized by a marked diversification of discoasterids and sphenoliths in the calcareous nannoplankton (Malumián 1999) and the disappearance of the *Spirosigmoilinella-Martinottiella* association (Malumián and Náñez 1996). This record of warm water in the South Atlantic is related to an important change in the composition of the faunal associations recorded between the Monte León Formation (early Miocene) and the Puerto Madryn and Paraná formations (early late Miocene). According to del Río (2000), during

the middle Miocene there was a change in the associations of invertebrates as new taxa appeared that were to that time unknown in the South Atlantic. These new taxa constitute 60% of the "Entrerriense" fauna.

Del Río (1990, 1991), del Río and Martínez (1998), and Martínez et al. (1998) analyzed the mollusk assemblages of the Puerto Madryn and Paraná formations. They concluded that 46% of the mollusk genera had modern representatives in the adjacent sea, and 14 of the 143 species recorded in the Miocene are extant. According to del Río (2000), 10% of the genera found in this assemblage became extinct and about 43% are extant, but restricted to tropical areas of the South American continent (20%), to the Caribbean and Indo-Pacific regions (11.2%), to southwestern Africa (9.5%) or are restricted exclusively to the Indo-Pacific region (2.3%). Among the extinct forms there are elements that were distributed only in tropical regions (6.5%) while others were cosmopolitan (3.2%).

Concerning the origin of the "Entrerriense" fauna, del Río (2000) pointed out that 49% of the taxa were austral or cosmopolitan while 51% originated in tropical areas of the Americas before the establishment of the Panamá isthmus. Likewise, some taxa showed an Indo-Pacific distribution prior to the middle Miocene (del Río 2000). The presence of these genera (Caribbean and Indo-Pacific *in* del Río 1988) in the southwestern Atlantic during the mid-Miocene climatic optimum represents, according to del Río (2000), the greatest latitudinal range reached by these taxa. After the early late Miocene their range was restricted to the tropical American regions where they are still extant.

All the fossils studied herein come from the base of the section exposed southeast of Puerto Pirámide, in the Puerto Madryn Formation (Figs. 1, 2). The section is about 90 m thick. Although the base is not exposed there, at other localities the formation unconformably overlies the marine deposits included in the Gaiman Formation (lower Miocene–middle? Miocene). At Puerto Pirámide, the Puerto Madryn Formation is separated from overlying late Pliocene–early Pleistocene conglomerates by an unconformity.

SEDIMENTOLOGY OF THE PUERTO MADRYN FORMATION AT PUERTO PIRÁMIDE

In general, the section exposed at Puerto Pirámide belongs, as suggested by Scasso and del Río (1987) and del Río et al. (2001), to the upper part of a depositional sequence including a transgressive systems tract (TST) and a highstand systems tract (HST). The TST interval is represented by shelf sediments deposited below wave base (Facies Association 1), whereas those of the HST represent tidal channel and tidal flat deposits (Facies Associations 2 and 3) (Fig. 2).

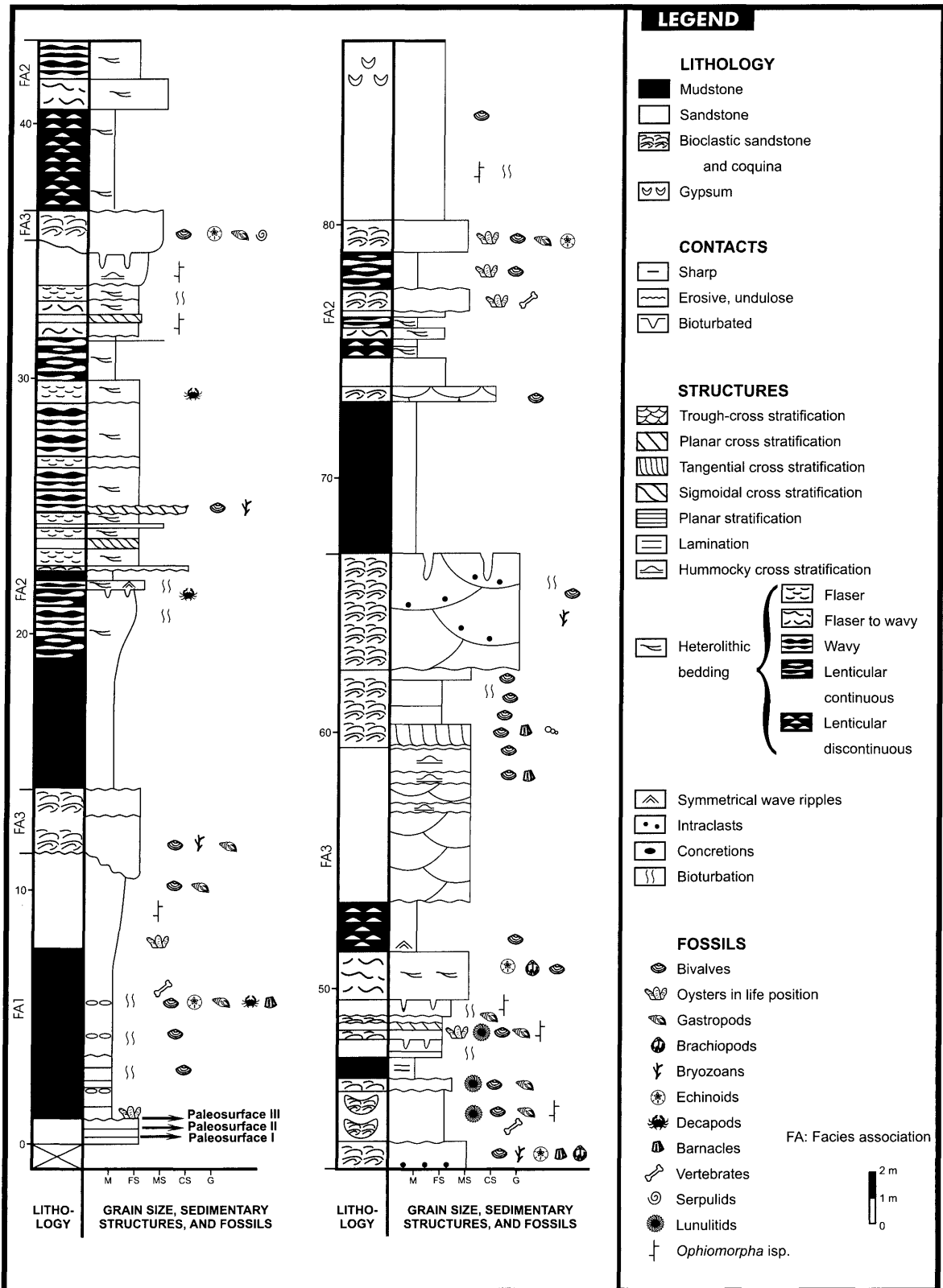Facies Association 1 (FA1).—Inner-outer shelf (8 to 15 m

Fig. 2.—Stratigraphical-sedimentological section and location of the three invertebrate-bearing paleosurfaces (PI, PII, PIII) at the Puerto Pirámide locality, Waypoint 13.

thick). This association comprises a group of lithofacies representing a fining-upward sequence. It includes fine sandstone and massive bioturbated mudrock facies. All three paleosurfaces that yield crabs and that will be discussed in detail below occur in this facies association. The association includes *Rhizocorallium, Rossella, Helicodromites,* and *Curvolithus (Cruziana* Ichnofacies). Invertebrates in life position are frequent. *Ostrea patagonica* is grouped in bunches of up to 30 specimens. Other taxa include isolated specimens or clumps of *Ostrea alvarezi, Aequipecten paranensis, Amusium paris, Mytilus* sp. and *Pachymagas piramidesia* in life position, as well as the crabs *Rochinia boschii* n. sp., *Panopeus piramidensis* n. sp., *Proterocarcinus latus, Osachila valdesensis* n. sp., *Romaleon parspinosus* n. sp., and *Chaceon peruvianus.* Other undetermined bivalves are also common. Articulated fish remains also are present. This facies partially includes the pectinid and oyster assemblage of del Río et al. (2001). The facies grade upwards into a laminated mudrock facies with abundant trace fossils referred to *Zoophycos* and *Glockerichnus (Zoophycos* Ichnofacies). Toward the top there are thin beds containing calcareous concretions with bivalve borings. This facies association is equivalent in part to facies "4a" of Scasso and del Río (1987).

The fine grain-size, trace fossil assemblages, and fossil preservation suggest a relatively low sedimentation rate in an offshore, low-energy environment below fair weather wave base. However, according to taphonomic information, sudden increases in sedimentation rate possibly related to storms are present at the base of this lithologic interval. Facies Association 1 represents sedimentary retrogradation with a rising sea level.

Facies Association 2 (FA2).—Tidal flats (2 to 15 m thick). This association predominates in the middle and upper part of the sequence and includes facies of fine sandstone with mudrock intercalations. Stratification is mostly horizontal, although flaser, wavy, and lenticular bedding are frequent. The facies contains few invertebrate remains, but there are beds with abundant *Skolithos* and *Ophiomorpha.* This facies association partially includes facies "4b" of Scasso and del Río (1987).

The small grain size and available sedimentary structures suggest relatively low energy conditions. The unit was possibly deposited in a sandy to muddy-sandy tidal flat environment. These tidal flats represent the deepest areas of the shelf under tidal influence. This facies association is always associated with Facies Association 3.

Facies Association 3 (FA3).—Large tidal channels (5 to 14 m thick). This association comprises a group of lithofacies clustered to form fining-upward sequences. The geometry of these beds is lenticular with erosive bases. At the bases of these sets there are shell concentrations one to five m thick within a sandy matrix. The beds are massive or with

medium to large scale trough cross stratification. These deposits grade upwards into fine to medium sandstone and mudrock with heterolithic bedding.

The lenticular geometry of the beds, the erosional bases, and the decreasing energy suggested by the grain size and sedimentary structures suggest that these deposits are the result of infilling of tidal channels and tidal sand waves. The great lateral extension of the amalgamated bed sets and the geometry of the individual beds represent the lateral migration of these channels, which would have formed a complex channel system. Shelly, sandy dunes and waves migrated along the deepest parts of these channels, while in other areas with weaker currents small ripples migrated on sandy tidal flats. The presence of mudrock intraclasts suggests that the channels were flanked by fine tidal flat sediments (Facies Association 2).

COLLECTING LOCALITIES

Waypoint 13: Near Puerto Pirámide, Península Valdés, Chubut Province, Argentina, at latitude 42°34'45.3" S, longitude 64°16'16.4" W; Puerto Madryn Formation, lower upper Miocene. All paleosurfaces (Figs. 10–12, Table 3) are from this locality.
Waypoint 16: Punta Pardeles, near Puerto Pirámide, Península Valdés, Chubut Province, Argentina, at latitude 42°37'09.1" S, longitude 64°15'27.0" W; Puerto Madryn Formation, lower upper Miocene.
Waypoint 17: Punta Pardelas, near Puerto Pirámide, Península Valdés, Chubut Province, Argentina, at latitude 42°37'09.7" S, longitude 64°15'13.0" W; Puerto Madryn Formation, lower upper Miocene.

INSTITUTIONAL ABBREVIATIONS

MPEF-PI—Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Parthenopoidea MacLeay, 1838
Family Aethridae Dana, 1851a
Genus *Osachila* Stimpson, 1871a

Type species.—*Osachila tuberosa* Stimpson, 1871a, p. 154, by original designation.

Included extant species.—*Osachila acuta* Stimpson,

1871b; *O. antillensis* Rathbun, 1916a; *O. expansa* Takeda, 1977; *O. galapagensis* Garth, 1946; *O. levis* Rathbun, 1898a; *O. semilevis* Rathbun, 1916a; *O. sona* Garth, 1940; *O. stimpsoni* Studer, 1883.

Included fossil species.—*Osachila tiechi* Studer, 1898, Miocene of Switzerland; *O. valdesensis* new species.

Diagnosis.—Similar to *Hepatus* but narrower, with octagonal carapace, depressed and expanded on lateral margins; surface uneven, typically with 6 prominent swellings; front produced into rostrum (modified from Rathbun 1937).

Discussion.—The diagnosis of Rathbun (1937) remains adequate for characterizing the genus (Guinot 1966, 1967; Williams 1984), and the new species from Argentina conforms closely to that definition. Thus, the new species can be referred to *Osachila* with confidence. The rostrum is broken on all specimens of the new species; however, the front is sulcate and downturned so that there is no doubt that its form would have been much like that of extant species. In addition, the third maxillipeds are well-preserved on two specimens, which permits comparison of this important region with extant forms. As with all modern species, the maxillipeds cover the entire buccal cavity, slope upward steeply to terminate in a narrow, more-or-less triangular anterior margin, and, as with all relatives of *Hepatus*, there is a notch in the margin of the merus of the third maxilliped in which the exopod is situated (Guinot 1966).

Although generic identification is made with reasonable confidence, the placement within a family and superfamily remains contentious. Until recently, *Osachila* was placed within the Hepatinae Stimpson, 1871a, or the Matutinae de Haan, 1841, within the Calappidae H. Milne Edwards, 1837. The history of this classification recently has been summarized by Bellwood (1996) and Schweitzer and Feldmann (2000a). Bellwood conducted a phylogenetic analysis of the calappid genera, elevated subfamilies to family level, placed the Matutidae with the Leucosiidae Samouelle, 1819, in the Leucosioidea, and the Orithyiidae Dana, 1853, with the Dorippidae MacLeay, 1838, in the Dorippoidea MacLeay, 1838. Schweitzer and Feldmann (2000a) concurred with that position and considered the relationship of fossil taxa to the extant taxa considered by Bellwood. However, Guinot (1966, 1967) considered the relationships of several genera, including *Osachila, Hepatus* Latreille, 1802, and *Aethra* Leach *in* Latreille, 1816, and concluded that they formed a distinctive group. She suggested (1966) that the name Hepatinae or Aethrinae be applied and that this subfamily be referred to the Parthenopidae MacLeay, 1838, a position adopted by Sakai (1976). Although she did not state it explicitly, she expressed preference for Aethrinae, probably on the basis of priority. Ng and Rodriguez (1986) subsequently elevat-

ed the parthenopoid subfamilies to the family level, a position supported by Martin and Davis (2001). We support this position and recognize that *Osachila* and its allies have much closer affinities with the Parthenopoidea than with the Calappoidea.

Osachila valdesensis **new species**
(Fig. 3)

Diagnosis.—Carapace transversely ovate; margins broad and dorso-ventrally compressed; anterolateral margin nodose anteriorly and with blunt spines posteriorly. Dorsal carapace surface with pronounced elevations in protogastric and epibranchial regions joined by narrow ridge; elevated regions pustulose and coarsely punctate; depressed areas smooth or finely punctate. Third maxilliped horizontal posteriorly, becoming nearly vertical anteriorly, ischium as long as merus.

Description.—Carapace ovoid, wider than long; moderately vaulted transversely, strongly arched longitudinally; surface smooth, finely punctate; depressions separated by strongly elevated, pustulose, coarsely punctate ridges and swellings.

Front narrow, broken, downturned, axially sulcate; termination not known. Antennal and orbital pits circular, about equal in size; fronto-orbital width less than 30 percent maximum width measured at medial anterolateral spine, orbital rim with two long, closed fissures above margin and one long, closed fissure below margin. Anterolateral margin long, arcuate, becoming more tightly curved posteriorly, sharply defined, upturned; coarsely granular margin anteriorly, separated into five blunt spines posteriorly, spines separated by open or closed fissures. Posterolateral margin short, almost transverse to long axis; scalloped. Posterior margin about as wide as fronto-orbital margin; thickened, granular along rim and deeply pitted below rim.

Frontal region depressed, merging with gastric region which is separated from hepatic region by strongly domed, pustulose, coarsely pitted protogastric regions which form most elevated regions on carapace. Hepatic regions depressed, smooth or finely pitted, extending as rim to anterolateral corner. Strong, elevated, pustulose, coarsely pitted ridge extends posterolaterally from protogastric regions, narrowing then broadening into epibranchial swelling and narrowing to terminate at posterolateral corner. Mesogastric region moderately swollen, pustulose, narrowing posteriorly into urogastric region, bounded laterally by deep, elongate, narrow gastric pits. Cardiac region as broad as posterior margin, broader than long, strongly elevated, pustulose, coarsely pitted, sloping posteriorly into indistinct, depressed, intestinal region. Mesobranchial regions deeply depressed. Metabranchial regions with elevated, central pustulose dome.

Pterygostomial region broad, coarsely pustulose, pitted, with granular ridge and suture bisecting region.
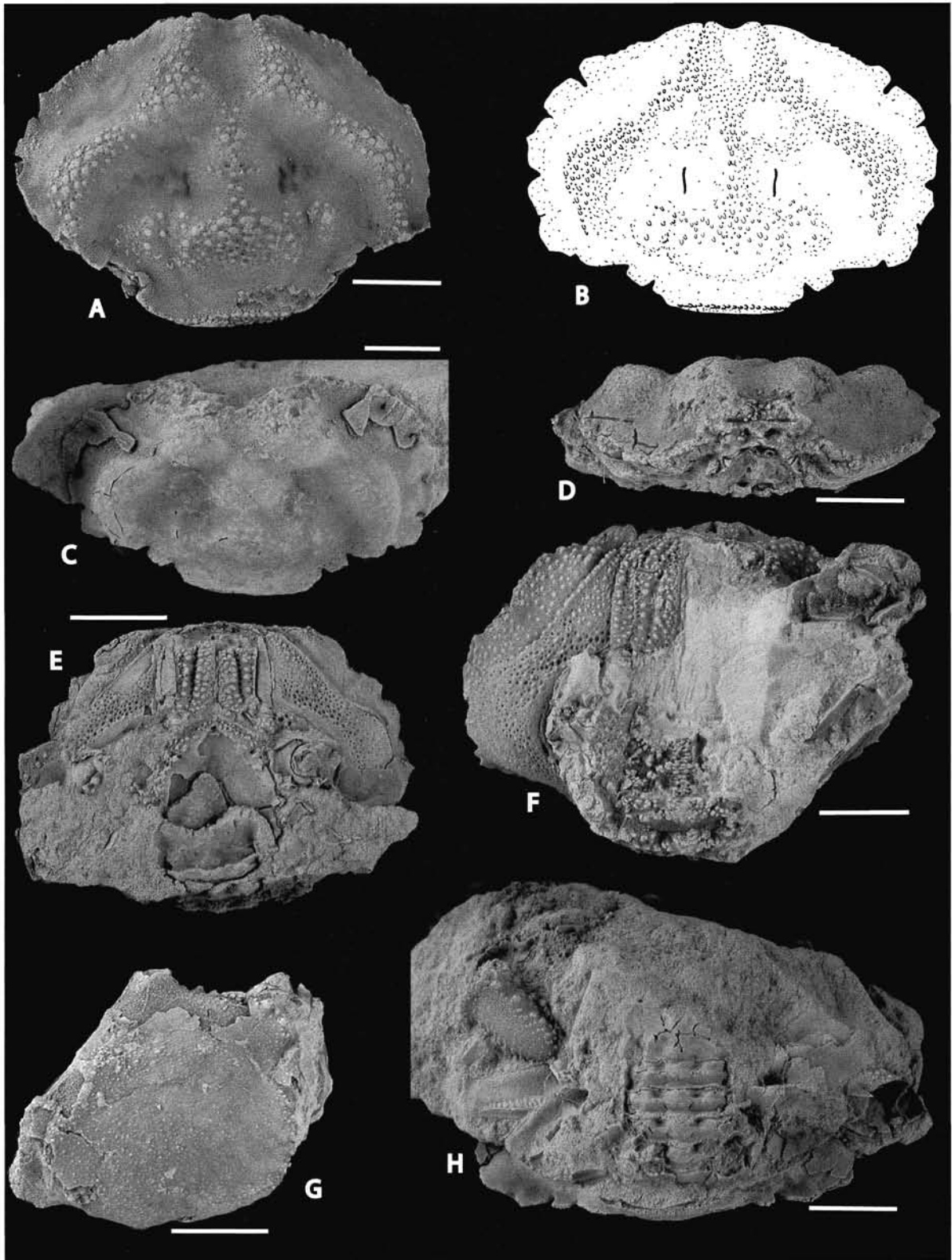
Fig. 3.—*Osachila valdesensis* new species. A, dorsal carapace, holotype, MPEF-PI 1530; B, composite line drawing of dorsal carapace; C, partial dorsal carapace; D, anterior view, paratype, MPEF-PI 1534; E, ventral surface, paratype, MPEF-PI 1534; F, ventral surface, holotype, MPEF-PI 1530; G, portion of major chela, paratype, MPEF-PI 1600; H, ventral surface, paratype, MPEF-PI 1531. Scale bars = 1 cm.

TABLE 1. Measurements, in millimeters, taken on specimens of *Osachila valdesensis* n. sp. Measurements that are minimum values because of breakage of the specimen are denoted by an asterisk (*). L = length; W = maximum width; FOW = fronto-orbital width; PW = posterior width.

Specimen	L	W	FOW	PW
Holotype MPEF-PI 1530	33.2	44.3*	13.6	14.1
Paratype A	27.5	40.0*	12.4*	12.2
Paratype B	30.8	46.2	—	15.2
Paratype C	29.5	45.0	—	15.1*

Epistome narrow, nearly vertical. Buccal frame nearly horizontal posteriorly; inflecting dorsally to become nearly vertical; parallel sided posteriorly, converging to terminate in point below rostrum. Entire buccal area closed by third maxillipeds. Exognath of third maxilliped tapering uniformly anteriorly to terminate at point of inflection; ischium of endognath of third maxilliped quadrate, longer than wide; articulation with merus an arcuate curve. Ischium and merus equal in length. Surface of third maxillipeds with longitudinal rows of pustules and deep pits.

Sternum of female poorly preserved; parallel-sided, deeply depressed axially. Sternites 1–3 fused. Suture of sternite 3 with sternite 4 developed laterally but may not cross entire sternum. Sternum of male unknown.

Abdomen of female generally parallel-sided, slightly narrower across somites 1 and 2; each somite with strong axial and lateral swellings joined by medial, transverse ridge. Somites of equal length. Telson incomplete but appears to be about as long as broad.

Isolated fragments of pereiopods elongate, slender, with rows of spines and granulated surfaces.

Measurements.—Measurements, in millimeters, taken on specimens of *Osachila valdesensis* are given in Table 1.

Etymology.—The trivial name refers to Península Valdés, the site from which the specimens were collected.

Types and occurrence.—The holotype, MPEF-PI 1530 and one paratype, MPEF-PI 1531, were collected from Punta Buenos Aires, at latitude 42°14′40″ S, longitude 64°11′31″ W, Península Valdés, Chubut Province, Argentina. Three paratypes, MPEF-PI 1532–1534 were collected from Waypoint 17. Paratype MPEF-PI 1535 was collected from Waypoint 16. Paratype MPEF-PI 1599 consists of a portion of chela and was collected at Waypoint 13, Paleosurface II.

Discussion.—Guinot (1966) recognized two different groups within the genus based upon, among other things, the conformation of the third maxillipeds. The so-called

"Forme Parthénoxystomienne" (Guinot 1966, p. 753) includes *Osachila stimpsoni* and exhibits short, bluntly terminated meri on the third maxilliped and widely separated efferent canals. The maxillipeds lie essentially in one plane. The other group, consisting of the remaining living species, the so-called American group, possesses long, triangular meri with closely spaced efferent canals; the ischium lies in a distinctly different plane from the merus. *Osachila valdesensis* clearly lies within this latter group.

Although the generic placement of *Osachila valdesensis* is certain, the species bears several morphological features of the cephalothorax and maxillipeds that separate it from other species within the genus. The form of the swollen regions is distinctly different from other known species. The protogastric and epibranchial swellings are the most prominent and are connected by a narrow ridge, or crest. The metabranchial, cardiac, and mesobranchial swellings are somewhat reduced in height. All of these elevations, including the narrow ridge, are strongly pustulose and coarsely pitted whereas the depressed regions of the carapace are generally smooth. The pattern of ornamentation on other species seems to be more uniform. The anterolateral margin of *O. valdesensis* is somewhat less upturned than in most other species and differs from all other species in exhibiting a nodose anterior part and a bluntly spined posterior part. Finally, the pattern of nodes on the third maxillipeds is one of rows of nodes separated by rows of pits. In this character, the species most closely resembles the type species, *Osachila tuberosa*.

Species of *Osachila* have been collected at depths from 24 to 328 m (Rathbun 1937) and on a variety of substrates ranging from sandy mud to coarse and shelly and on reefs (Rathbun 1937; Sakai 1976; Williams 1984). They are distributed on both the Atlantic and Pacific coasts of North America, Central America, and South America, as well as west Africa and Japan. Vernberg and Vernberg *in* Williams (1984) reported that species of *Osachila* collected off Cape Hatteras, North Carolina, died after brief exposure to water with a temperature of 4°C, concluding that their distribution was limited by temperature.

Superfamily Majoidea Samouelle, 1819
Family Pisidae Dana, 1851c
Genus *Rochinia* A. Milne Edwards, 1875

Type species.—*Rochinia gracilipes* A. Milne Edwards, 1875, by monotypy.

Included extant species.—*Rochinia aurorae* (Alcock 1899), as *Sphenocarcinus*; *R. beauchampi* (Alcock and Anderson 1894), as *Anamathia*; *R. bidens* (Sakai 1969); *R. brevirostris* (Doflein 1904), as *Hyastenus*; *R. carbuncula* (Rathbun 1906), as *Sphenocarcinus*; *R. carinata* Griffin and Tranter, 1986; *R. carpenteri* (Thomson 1873), as *Amathia*; *R. confusa* Tavares, 1991; *R. coralliophila*

(Takeda 1980); *R. cornuta* (Rathbun 1898a), as *Anamathia*; *R. crassa* (A. Milne Edwards 1879), as *Amanthia*; *R. crosnieri* Griffin and Tranter, 1986; *R. cuneata* (Wood-Mason *in* Wood-Mason and Alcock 1891), as *Oxypleurodon*; *R. debilis* Rathbun, 1932; *R. fultoni* (Grant 1905) as *Hyastenus*; *R. globulifera* (Wood-Mason *in* Wood-Mason and Alcock 1891), as *Pugettia*; *R. griffini* Davie and Short, 1989; *R. hertwigi* (Doflein 1900), as *Scyramathia*; *R. hystrix* (Stimpson 1871a) as *Amathia*; *R. lowryi* (Richer de Forges 1992), as *Sphenocarcinus*; *R. luzonica* (Rathbun 1916b), as *Sphenocarcinus*; *R. makassar* Griffin and Tranter, 1986; *R. moluccensis* Griffin and Tranter, 1986; *R. mosaica* (Whitelegge 1900), as *Pugettia*; *R. natalensis* Kensley, 1977; *R. nodosa* (Rathbun 1916b), as *Sphenocarcinus*; *R. occidentalis* (Faxon 1893) as *Anamathia*; *R. pulchra* (Miers 1886), as *Anamathia*; *R. riversandersoni* (Alcock 1895), as *Scyramathia*; *R. sibogae* Griffin and Tranter, 1986; *R. soelia* Griffin and Tranter, 1986; *R. strangeri* Serène and Lohavanijaya, 1973; *R. stukiae* (Guinot and Richer de Forges 1986) as *Sphenocarcinus*; *R. suluensis* Griffin and Tranter, 1986; *R. tanneri* (Smith 1883), as ?*Amathia*; *R. tomentosa* Griffin and Tranter, 1986; *R. umbonata* (Stimpson 1871a), as *Scyra*; *R. velutina* (Miers 1886), as *Pugettia*; *R. vesicularis* (Rathbun 1907) as *Scyramathia*. (Species list after Tavares 1991.)

Included fossil species.—*Rochinia boschii* new species.

Diagnosis.—Pyriform to elongate triangular carapace; rostrum typically bifid; orbits with a weakly expanded eave which may have a preorbital spine or plate, postorbital lobe typically arising from a flattened hepatic swelling, and fused basal antennal article which may be narrow or broad and may or may not bear a lateral tooth; carapace surface with tubercles, nodes or flattened plates (adapted from Griffin and Tranter 1986).

Discussion.—Although there is some debate regarding the systematic position of *Rochinia*, based upon cladistic analyses (Clark and Webber 1991) and larval history (Pohle and Marques 2000), the suprageneric status of *Rochinia* is beyond the scope of this work. Thus, the position that the genus lies within the Pisidae (Martin and Davis 2001), or the Pisinae (Davie 2002) is followed herein.

The morphological features of the carapace that serve to distinguish *Rochinia* from other genera within the Pisidae include the distinctive architecture of the orbits and the carapace ornamentation. The carapace typically bears several elevations in the form of spines or nodes, but the most distinctive form is that of flattened, elevated surfaces on various parts of the carapace, including the metagastric, cardiac, and branchial regions. Most distinctive, however, is the flattened swelling on the hepatic region. This swelling is often triangular in shape and bears an

extension on the anterior corner that forms the postorbital lobe. Alternatively, the postorbital lobe may arise just anterior to the hepatic swelling. Although all genera within the Pisidae bear a postorbital lobe, that lobe typically arises from the general carapace surface rather than from the uniquely swollen surface on the hepatic region, as in *Rochinia*. A second spine, or extension, may arise from the posterodorsal corner of the hepatic swelling.

Although the genus is quite speciose and has a broad distribution in modern oceans, the Atlantic, Indo-west Pacific, and East Pacific (Griffin and Tranter 1986), the new species described below is the first record of the genus in the fossil record, to our knowledge. The discovery extends the range of the genus into the Miocene.

In general, the Majoidea would seem to be underrepresented in the fossil record. The paucity of spider crabs is probably due to several factors. Foremost is that these crabs tend to live out in the open and neither burrow nor bury themselves. Additionally, although the majoids are found in a wide range of depths, many occupy outer shelf and slope environments which are generally under represented in the sedimentary record (Jenkins 1985).

Rochinia boschii **new species**
(Fig. 4)

Diagnosis.—Carapace with prominent, flattened elevations on mesogastric and cardiac regions and seven other elevated regions; fused basal element of antenna with flattened bluntly spined anterior termination.

Description.—Carapace typical size for genus, subtriangular, moderately vaulted longitudinally and transversely; surface with four prominent swellings and an array of sharp spines and two flattened axial prominences.

Front broken, elongate, extending well beyond orbits, apparently with pair of horns. Orbits more or less complete, probably largely concealing eye from dorsal view; prominent supraorbital eave quadrate in outline, apparently lacking spines; postorbital spine extending anteriorly from triangular, prominently elevated and flattened hepatic region bearing postorbital spine on anterior corner and a second spine on upper corner. Base of orbit formed of quadrate basal article of antenna fused to epistome; two or three blunt, flattened teeth extend anterolaterally beneath eyestalks. Lateral margin with smooth, thickened rim extending in smooth arc around branchial regions and merging with weakly projecting, narrow posterior margin.

Frontal region flattened, weakly sulcate axially; rostrum not preserved. Mesogastric region with two axial spines and one axial, flattened protuberance; anterior-most spine small; second spine much larger, base elevated, posterior edge flattened, apex directed anteriorly. Axial protuberance at broadest point of mesogastric region, longer than wide, upper surface generally flattened with two

small spines on anterior end. Metagastric and urogastric regions not differentiated, narrow, depressed. Cardiac region a prominent swelling about as wide as long and bearing a large, strongly elevated prominence with flattened top. Intestinal region poorly defined, bearing prominent axial spine. Protogastric regions poorly defined, sloping laterally toward hepatic regions, bearing weak spine at level of anterior end of metagastric prominence. Epibranchial region swollen, bearing one small centrally located spine and one large spine on posterolateral part of swelling. Remainder of branchial region undifferentiated with a cluster of two small and one larger spines.

Buccal frame quadrate, smoothly rimmed, wider than long. Subhepatic region with row of three small, blunt spines. Remainder of venter and appendages unknown.

Measurements.—Because all the specimens of this species are broken and most are crushed, it is not possible to provide many measurements. The holotype, MPEF-PI 1536, has a length measured from the posterior margin of the carapace to the posterior edge of the orbit of 22.1 mm and a maximum carapace width of 20.2 mm. Paratype MPEF-PI 1538 has a maximum carapace width of 15.6.

Etymology.—The trivial name honors Enrique E. Boschi, CONICET-ENIDEP, Mar del Plata, Argentina, for his elucidation of American decapod zoogeography.

Types and occurrence.—The holotype, MPEF-PI 1536, and paratypes MPEF-PI 1537, 1538, and 1540 were collected from Waypoint 13, Paleosurface II. Paratype MPEF-PI 1539 was collected from Waypoint 17.

Discussion.—Species of Rochinia vary greatly in development of spines, nodes, and flattened elevations. The extant species that most closely resembles R. boschii is R. umbonata (Stimpson 1871a). That species is described as having nine carapace prominences, of which six are large, flattened, and of irregular form (Rathbun 1925, p. 222). Rochinia boschii also has nine general areas of elevations, but only those on the mesobranchial and cardiac regions are clearly developed as broad, flattened areas. The epibranchial regions each have one large and one small spine and, because the larger spines are broken, it is difficult to discern whether or not the termination was flattened. A second distinction between the two species lies in the conformation of the fused basal antennal article. Rathbun (1925, p. 223) described that structure on R. umbonata as being unarmed or bearing a subtle anterior angle whereas the anterior angle is developed into a triangular, flattened process in R. boschii. Thus, although the two species bear many morphological similarities, they are distinct and distinguishable based upon characters customarily used to distinguish species of Rochinia.

Thus far, we know of only four published records of fossil spider crabs from South America. Glaessner (1933) noted the presence of a fragmentary fossil from the Miocene of Santa Cruz Province, Argentina, considered it a new genus and species of Majidae, and commented upon its similarity to Libinia. In that same year, Van Straelen (1933) described the inachid genus Eoinachoides senni from Venezuela. Van Straelen considered the age of the specimen to be late Eocene; however, Feldmann and Schweitzer (2004) have examined some of the type material as well as new material from Venezuela and argued that the age is more likely early Miocene. Eoinachoides sp. cf. E. senni has subsequently been recognized in Oligocene-middle Miocene rocks at Bajo del Gualicho, about 50 km northwest from San Antonio Oeste, in Río Negro Province, Argentina (Aguirre-Urreta 1990). In that same paper, she named a new species of Pisidae, Leurocyclus primigenius Aguirre-Urreta, 1990, from upper Oligocene-lower Miocene rocks at Estancia Tolosa, about 30 km southwest from Rawson, Chubut Province, Argentina.

Neither of these species can be confused with our new species. Eoinachoides senni has a much more rounded outline, less well-developed spines, and a different orbital design, and it is much smaller than our new species. Leurocyclus primigenius is wider than long, has better defined regions, and is ornamented by tubercles rather than large spines and protuberances. Thus, no fossil spider crabs from South America bear even a close resemblance to Rochinia boschii.

Rathbun (1925) recorded R. umbonata from Georgia, USA, to St. Vincent, in the West Indies, in water depths ranging from about 525 to 2600 feet. Boschi (2000) recorded the distribution of R. umbonata in his zoogeographical provinces 11–14, Brazilian, Caribbean, Texan, and Carolinian. Other species of the genus range through the tropical and subtropical regions of North America and South America in both the Atlantic and Pacific oceans and extend into the Magellanic Province in the Atlantic Ocean (Boschi 2000). Thus, the occurrence of R. boschii lies slightly south of that of R. umbonata but well within the range of the genus in modern seas.

Superfamily Cancroidea Latreille, 1802
Family Cancridae Latreille, 1802
Subfamily Cancrinae Latreille, 1802
Genus Romaleon Gistl, 1848

Type species.—Corystes (Trichocera) gibbosula de Haan, 1835.

Included fossil species.—Romaleon dereki Nations, 1975; R. parspinosus new species; R. sakamotoi (Kato 1996), as Cancer; R. sanbonsugii (Imaizumi 1962), as Cancer; R. urbanus (Rathbun 1917), as Cancer.

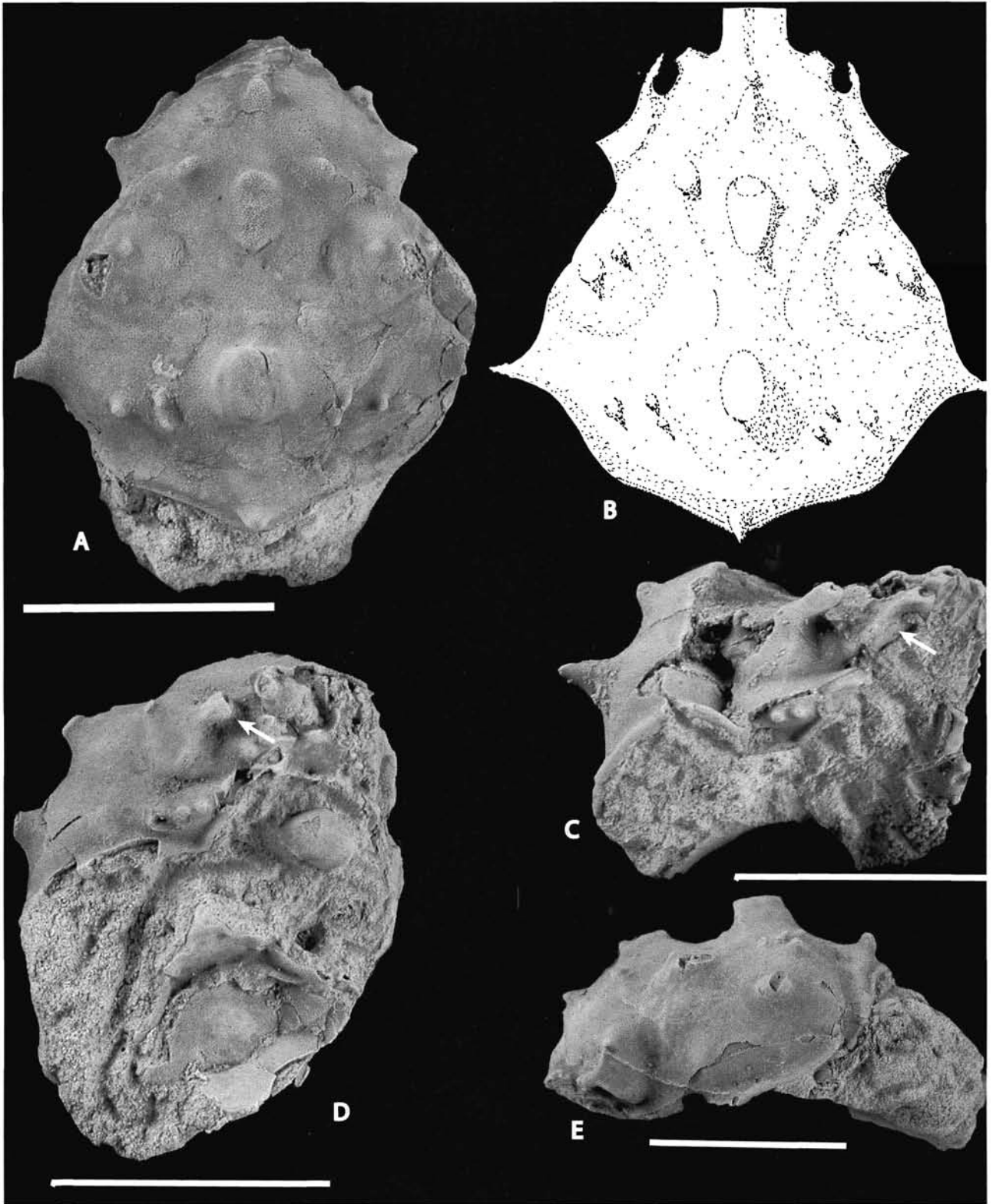Extant species known as fossils only from claw frag-

Fig. 4.—*Rochinia boschii* new species. A, dorsal carapace, holotype, MPEF-PI 1536; B, composite line drawing of dorsal carapace; C, oblique view showing antennal base forming the lower orbital margin, paratype, MPEF-PI 1538; D, oblique view showing orbital region, holotype, MPEF-PI 1536; E, left lateral view of dorsal carapace showing elevations on axial regions diagnostic for *Rochinia*, holotype, MPEF-PI 1536. Scale bars = 1 cm.

ments.—*R. antennarius* (Stimpson 1856), as *Cancer*; *R. branneri* (Rathbun 1926), as *Cancer*; *R. jordani* (Rathbun 1900), as *Cancer*; *R. polyodon* (Poeppig 1836), as *Cancer*.

Diagnosis.—See Schweitzer and Feldmann (2000b).

Discussion.—*Romaleon* Gistl, 1848, was long considered to be a subgenus of *Cancer* Linnaeus, 1758 (Nations 1975); however, Schweitzer and Feldmann (2000b) considered it to be distinct from *Cancer* sensu stricto, based upon the sharp, triangular anterolateral spines separated to their bases and generally curving anterolaterally in species of the genus. Species of *Cancer* have a tightly curved anterolateral margin with anterolateral spines separated by fissures that are often blunt-tipped or granular. The new material conforms well to the diagnosis for *Romaleon* given by Schweitzer and Feldmann (2000b). It possesses nine sharp anterolateral spines including the outer-orbital spine; anterolateral spines separated to their bases and not fissured; one posterolateral spine; granular posterolateral and posterior margins; and five frontal spines, the middle three of which are closely spaced and the axial-most spine being at a slightly lower plane. The new species possesses all of these features. The only major difference is that the new species has spines 4–5, 6–7, and 8–9 paired. Other species of *Romaleon* do not exhibit paired spines. Schweitzer and Feldmann (2000b) erected *Anisospinos* to accommodate specimens collected from the North Pacific that were very similar to *Romaleon* but differed from it in several key features. One of these is the presence of paired spines in *Anisospinos*. However, members of *Anisospinos* have only eight anterolateral spines and no posterolateral spines or rims, as seen in the new species. In addition, the frontal width of *Anisospinos* is much broader than that of the new material, about 30 percent as compared with 17 percent in the new species. The orbits are much larger and more widely spaced in *Anisospinos*, ranging from 40–55 percent of the maximum width; in the new material, it is 37 percent. The frontal spines, including the inner-orbital spines, of *Anisospinos* are evenly spaced, while in the new material, the central three are closely spaced and separated from the inner-orbital spines. The new material is thus much closer to *Romaleon*, differing from it in only one major feature, and is referred to that genus.

Romaleon parspinosus new species
(Fig. 5)

Diagnosis.—Carapace wider than long, L/W = 0.80, widest at position of eighth anterolateral spine; anterolateral margin long, convex, with nine spines including outer-orbital spine; second anterolateral spine smaller than outer-orbital spine; third spine larger than second; fourth and fifth spines paired, about equal in size; spines six and seven paired, six known only from base, seven broad, tri-

angular, directed anterolaterally, largest of all anterolateral spines; spines eight and nine paired, triangular, about equal in size; spine nine directed laterally. Posterolateral margin concave; small, blunt spine posterior to last anterolateral spine; with granular rim.

Description.—Carapace wider than long, L/W = 0.80, widest at position of eighth anterolateral spine, about two-thirds the distance posteriorly on carapace; regions moderately well-marked, either by being inflated or by being bounded by broad, shallow grooves; surface granular; moderately vaulted longitudinally and transversely.

Front projected beyond orbits, 17 percent maximum carapace width, with five spines including inner-orbital spines; inner-most three frontal spines closely spaced, central spine placed slightly lower than lateral two, two lateral spines extending onto carapace in weak, short ridge, lateral spines separated from inner-orbital spines by broad, *U*-shaped indentation. Orbits shallow, not well-known; fronto-orbital width about 37 percent maximum carapace width. Anterolateral margin long, convex, with nine spines including outer-orbital spine; outer-orbital spine directed forward; second anterolateral spine smaller than outer-orbital spine, triangular, directed slightly anterolaterally; third spine larger than second, lower margin longer than upper margin, directed anterolaterally; fourth and fifth spines paired, about equal in size, fourth spine directed anterolaterally, fifth spine curving anteriorly at tip; sixth and seventh spines paired, sixth known only from base, seventh broad, triangular, directed anterolaterally, largest of all anterolateral spines; eighth and ninth spines paired, triangular, about equal in size, eighth spine directed anterolaterally, tip curving anteriorly, ninth spine directed laterally. Posterolateral margin concave; small, blunt spine posterior to last anterolateral spine; with granular rim. Posterior margin narrow, rimmed with granules, about one-quarter maximum carapace width.

Protogastric region pentagonal, apex directed posteriorly, centrally inflated, most inflated of all carapace regions; mesogastric region with very long anterior process, process depressed below level of protogastric regions, region widening and inflated posteriorly, posterior margin very weakly convex; metagastric region poorly developed, inflated; urogastric region not well-differentiated from metagastric, depressed below level of metagastric and cardiac regions; cardiac region bulbous anteriorly, narrowing distally, with two swollen areas positioned anteriorly; intestinal region sloping to posterior margin, poorly differentiated.

Hepatic region broad, depressed below level of protogastric region, weakly inflated centrally. Epibranchial region positioned parallel to posterior margin of hepatic region, extending from posterior margin of protogastric region to anterior-most posterior margin, composed of two swellings; mesobranchial region highly inflated anteriorly, almost to level of protogastric region, less inflated
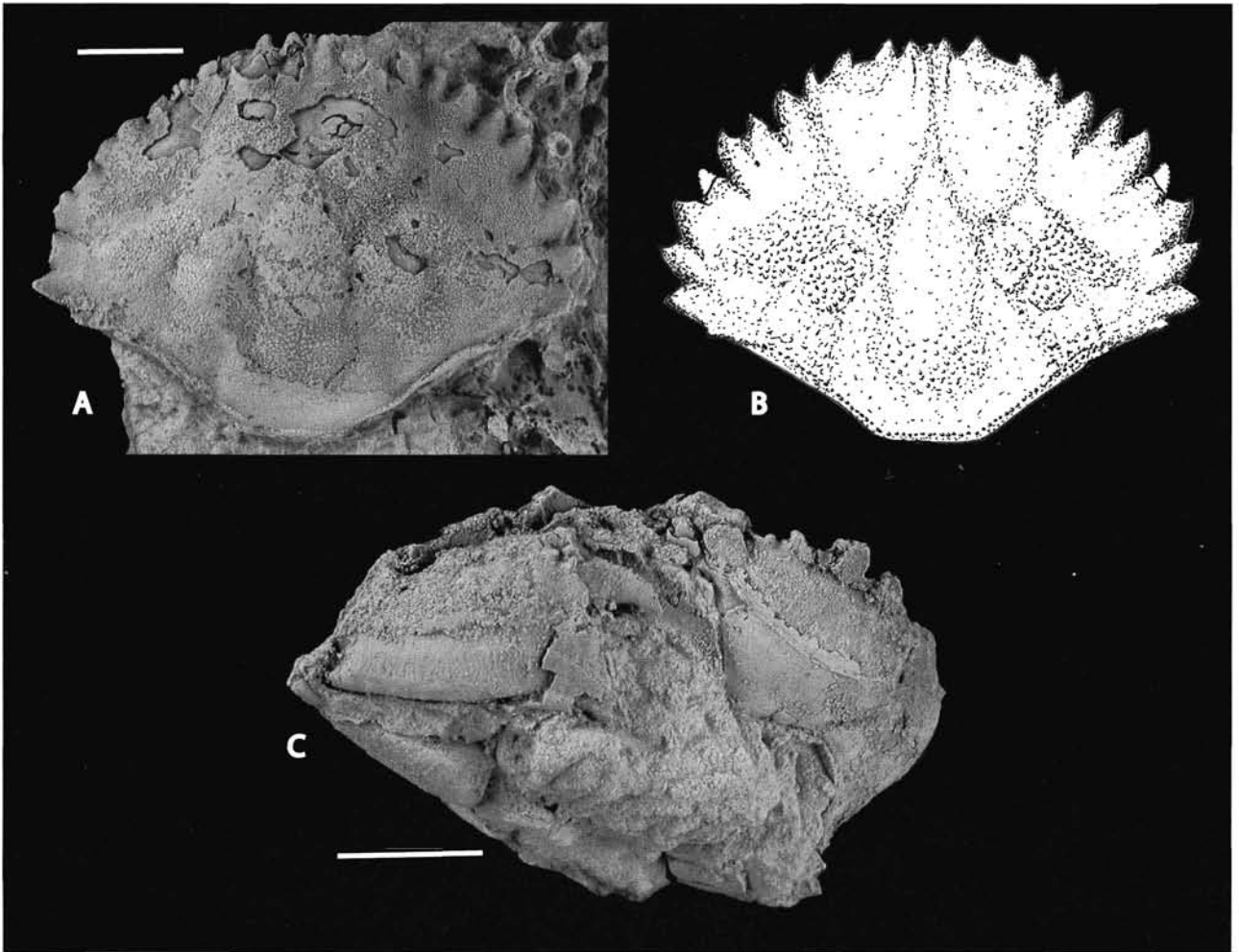
Fig. 5.—*Romaleon parspinosus* new species. A, dorsal carapace, holotype, MPEF-PI 1541; B, composite line drawing of dorsal carapace; C, ventral surface, paratype, MPEF-PI 1543. Scale bars = 1 cm.

posteriorly, aligned parallel to epibranchial; metabranchial region triangular, flattened, merging with intestinal region posteriorly.

Chela longer than high, manus with keels on outer surface, fixed finger with granular keel extending onto it from manus.

Measurements.—Measurements (in mm) taken on the holotype of *Romaleon parspinosus* new species: maximum length, 36.7; maximum width, 46.1; fronto-orbital width, 17.2; frontal width, 8.0; posterior width, 11.2; length to point of maximum width, 23.9.

Etymology.—The trivial name is derived from the Latin words "par," meaning paired, and "spinosus," meaning spiny, in reference to the paired anterolateral spines, unique in the genus.

Types.—Holotype, MPEF-PI 1541; paratypes, MPEF-PI 1542–1543, MPEF-PI 1601.

Occurrence.—MPEF-PI 1541 and 1542 are fromWaypoint 17, and MPEF-PI 1543 is from Waypoint 16. MPEF-PI 1601 was collected from Waypoint 13, Paleosurface II.

Discussion.—The new species is represented by a reasonably complete dorsal carapace and two fragmental specimens. *Romaleon parspinosus* differs from all other species of the genus in possessing paired anterolateral spines 4–5, 6–7, and 8–9. *Romaleon antennarius* Stimpson, 1856, has a broader carapace, a broader posterior width, less inflated carapace regions, and more equant spines than does *R. parspinosus*. *Romaleon branneri* (Rathbun 1926) has much more concave posterolateral margins and a more coarsely granular dorsal carapace than does the new species. *Romaleon jordani* (Rathbun 1900) has more attenuated, longer anterolateral spines than does *R. parspinosus*. *Romaleon polyodon* (Poeppig 1836) has more concave posterolateral margins and a more ovate carapace than does the new species.

Extant species of *Romaleon* primarily inhabit the coastal waters of western North America and Central America (Nations 1975; Boschi 2000). One extant species, *R. polyodon*, currently inhabits coastal Argentina, Chile, and Central America (Boschi 2000), and *R. gibbosulus* occurs in Japan (Sakai 1976). The oldest occurrences of *Romaleon* are the middle Miocene *R. dereki* from California, and the middle Miocene *R. sakamotoi* and *R. sanbonsugii* from Japan (Kato 1996; Schweitzer and Feldmann 2000b). Only one other fossil dorsal carapace of the genus is known, *R. urbanus*, from the Pliocene of California (Rathbun 1917; Schweitzer and Feldmann 2000b). It is thus difficult to determine where the genus arose as the Miocene occurrences are not sufficiently constrained; however, it is notable that another Miocene member of the subfamily, *Notocarcinus* Schweitzer and Feldmann, 2000b, was recovered from the Centinela Formation (then thought to be Eocene, Casadío et al. 2000a) of Argentina. This is the first report of an Atlantic coastal fossil occurrence of *Romaleon*.

Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Polybiinae Ortmann, 1893
Genus *Proterocarcinus* Feldmann, Casadío, Chirino-Gálvez, and Aguirre Urreta, 1995

Type species.—*Proterocarcinus lophos* Feldmann, Casadío, Chirino-Gálvez, and Aguirre Urreta, 1995, by monotypy.

Other species.—*Proterocarcinus latus* (Glaessner 1933), as *Archaeogeryon; Proterocarcinus corsolini* Casadío, De Angeli, Feldmann, Garassino, Hetler, Parras, and Schweitzer, 2004.

Proterocarcinus latus (Glaessner 1933)
(Fig. 6)

Archaeogeryon Latus (Glaessner 1933, p. 23, pl. V, figs. 4, 5
Lebucarcinus tyro (Philippi 1887). Bahamonde and Frassinetti, 1980, p. 276, figs. 1–7. non *Cancer tyro* Philippi, 1887.
Coeloma (Coeloma) latum (Glaessner). Aguirre Urreta, 1987, p. 471.
Proterocarcinus latus (Glaessner). Schweitzer and Feldmann, 2000c, p. 644, fig. 7.

Diagnosis.—*Proterocarcinus latus* was recently diagnosed (Schweitzer and Feldmann 2000c, p. 644) and that diagnosis will not be repeated here.

Material examined and occurrence.—Five specimens were collected from Waypoint 13, MPEF-PI 1561–1564 and MPEF-PI 1602, all from Paleosurface II. Eight specimens from Waypoint 16, MPEF-PI 1565–1572, and five specimens from Waypoint 17, MPEF-PI 1573–1577.

Discussion.—The specimens referred to in this study conform closely to the original description of the species and to specimens that subsequently have been referred to the species.

The systematic position of the species has been a point of contention in that it was originally placed in *Archaeogeryon*, in the Geryonidae, by Glaessner (1933), subsequently referred to *Coeloma*, also in the Geryonidae, by Aguirre Urreta (1987), and finally placed in *Proterocarcinus* by Schweitzer and Feldmann (2000c). The latter authors referred *Proterocarcinus* to the Portunidae, based upon presence of well-developed transverse ridges on the carapace and paddle-like dactyli on the fifth pereiopods. Casadío et al. (2004) concluded that the specimen selected by Bahamonde and Frassinetti (1980) as the neotype of *Cancer tyro* Philippi, 1887, did not conform either to Philippi's description or illustration of *C. tyro*. For that, and other reasons, Casadío et al. (2004) concluded that the genus *Lebucarcinus* Bahamonde and Frassinetti, 1980, was invalid and, further, the specimen they selected as the holotype was, in fact, referable to *Proterocarcinus*. It is interesting to note that, although she retained *Lebucarcinus tyro* as a valid taxon, Aguirre Urreta (1987) placed the genus in the same family with *Coeloma*, the Geryonidae.

In addition to material from Puerto Pirámide, noted in this study, representatives of the species have a broad distribution in Argentina and Chile. Aguirre Urreta (1987) recognized material referred to *Coeloma (Coeloma) latum* at seven localities ranging from as far north as Puesto Picavea in the Gran Bajo del Gualicho, Río Negro Province to as far south as Río Seco, in Santa Cruz Province, in rocks ranging in age from late Eocene to late Miocene. Schweitzer and Feldmann (2000c) extended the geographic range still farther south by recognition of the species in the Centinela Formation at Estancia 25 de Mayo in southwestern Santa Cruz Province. They noted an age of middle Eocene for the Centinela formation, based upon a $^{40}Ar/^{39}Ar$ date on volcanic tuff (Casadío et al. 2000a). That age has subsequently been called into question based upon $^{87}Sr/^{86}Sr$ dating of oyster shells and palynomorphs from the formation (Guerstein et al., in press). Those results yielded a late Oligocene to early Miocene age.

Occurrences of the species in Chile, as *Lebucarcinus tyro*, are from Miocene rocks at the mouth of Río Rapel in O'Higgins Province and at Punta del Fraile, in Biobio Province. Aguirre Urreta (1987) noted the species at Puerto San José on Península de Valdés, very near Puerto Pirámide.

Family Geryonidae Colosi, 1923
Genus *Chaceon* Manning and Holthuis, 1989

Type species.—*Geryon fenneri* Manning and Holthuis, 1984, by original designation.
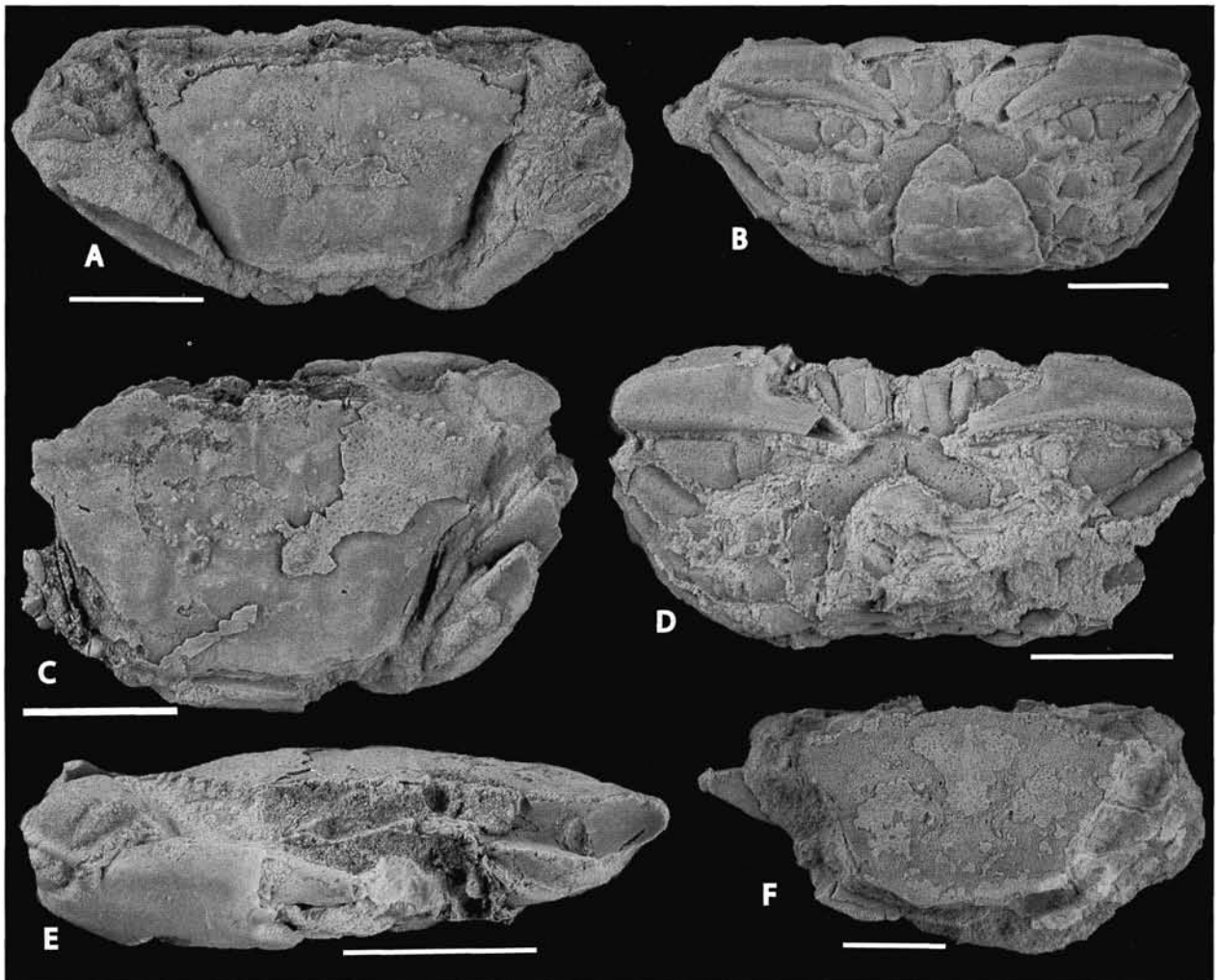
Fig. 6.—*Proterocarcinus latus* (Glaessner 1933). A, dorsal carapace, MPEF-PI 1577; B, ventral surface of carapace, MPEF-PI 1575; C, dorsal carapace, MPEF-PI 1573; D, ventral surface of carapace, MPEF-PI 1574; E, anterior view showing chela, MPEF-PI 1573; F, dorsal carapace, MPEF-PI 1576. Scale bars = 1 cm.

Included fossil species.—*Chaceon matsushimai* Kato and Koizumi, 2001; *C. peruvianus* (d'Orbigny 1842), as *Portunus*.

Chaceon peruvianus (d'Orbigny 1842)
(Fig. 7)

Portunus peruvianus d'Orbigny, 1842, p. 107, pl. 6, fig. 17.
Podopilumnus peruvianus (d'Orbigny). McCoy, 1849, p. 166.
Carcinus peruvianus (d'Orbigny). A. Milne Edwards, 1860, p. 269, pl. 8, figs. 1-c.
Cancer patagonicus Philippi, 1887, p. 213, pl. 50, fig. 1, Hatcher, 1897, p. 337.
Geryon? Peruvianus (d'Orbigny). Ortmann, 1900, p. 381; Ortmann, 1902, p. 255, pl. 38, fig. 6; Steinmann and Wilckens, 1908, p. 70.
Geryon peruvianus (d'Orbigny). Rovereto, 1921, p. 25; Frenguelli, 1927, p. 205, figs. 1(a–b), 11(a–b); Glaessner, 1929, p. 182; Aguirre-Urreta, 1987, p. 464, pl. 1, pl. 2, figs. A–C, pl. 3, figs. A–E, pl. 4, fig. B.

Archaeogeryon peruvianus (d'Orbigny). Glaessner, 1933, p. 22, pl. 5, figs. 1–2; Camacho, 1966, p. 477, pl. 16.13, figs. a–b; Glaessner, 1969, p. R524, figs. 332, 5a–b; De La Fuente, 1977, p. 310; Morris, 1980, p. 1; Briggs et al., 1985, p. 203, pl. 9.2.10 A–B.
Chaceon peruvianus (d'Orbigny). Schweitzer and Feldmann, 2000c, p. 648, figs. 9.1–3, 10.1–4.

Material examined and occurrence.—Specimens MPEF-PI 1578–1583 were collected from Waypoint 17. Specimens MPEF-PI 1584–1591 and 1603–1607 were collected from Waypoint 13. Specimens of *Chaceon peruvianus* occur on all three Paleosurfaces. Specimens MPEF-PI 1592–1598 were collected from Waypoint 16.

Discussion.—*Chaceon peruvianus* is undoubtedly the best known species of fossil crab from South America. Originally described by d'Orbigny (1842), J.B. Hatcher and R. Hauthal collected 16 specimens from southern Patagonia that were subsequently described by Ortmann
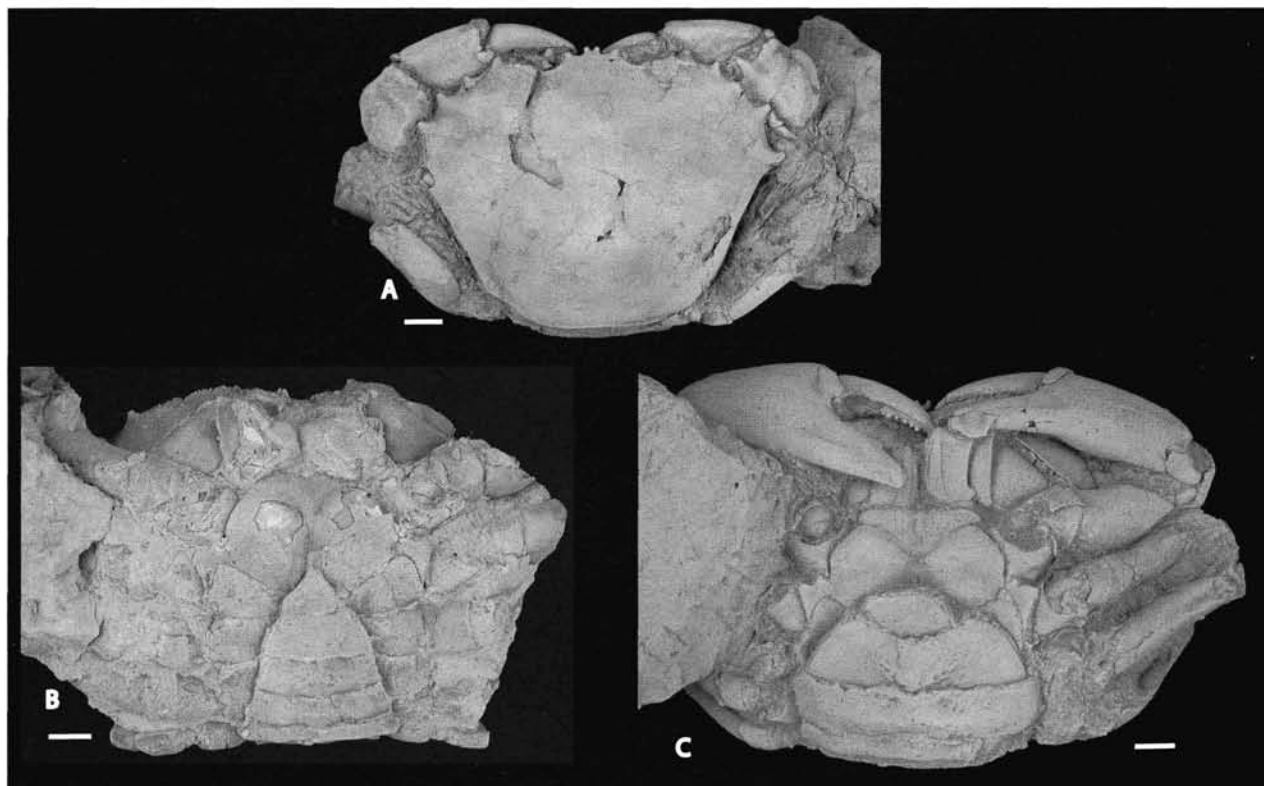
Fig. 7.—*Chaceon peruvianus* (d'Orbigny 1842). A, dorsal carapace, MPEF-PI 1593; B, ventral surface of male, MPEF-PI 1595; C, ventral surface of female, MPEF-PI 1593. Scale bars = 1 cm.

(1900) in his description of invertebrates collected by the Princeton Expedition to Patagonia (Schweitzer and Feldmann 2000c). Subsequently, Glaessner (1933) discussed the specimens of *C. peruvianus* in the collections of the British Museum (Natural History) and compiled a list of localities from which the species had been collected in Patagonia. That list included Puerto Pirámide. In the course of studying additional specimens that formed the basis for the work by Schweitzer and Feldmann, all the above-mentioned specimens have been examined by us so that the confirmation of identification is certain.

The specimens collected from the three localities at Puerto Pirámide are interpreted to be corpses preserved in their living position. Although some of the specimens are partially destroyed by wave erosion on the wave-cut benches upon which they are exposed, all of them were found with the carapace surface upward and with the sternum, abdomen, and appendages present and in life position. Both female (Fig. 7A, C) and male (Fig. 7B) specimens are represented.

Superfamily Xanthoidea MacLeay, 1838
Family Panopeidae Ortmann, 1893

Diagnosis.—Carapace usually hexagonal, transversely

hexagonal to transversely ovate, sometimes subcircular; dorsal carapace regions more or less defined; frontal margin usually bilobed, may extend beyond orbits; anterolateral and posterolateral margins usually distinct from one another, posterolateral margins clearly converging toward posterior margin; anterolateral margins convex, with 2–4 spines or lobes; endostomial ridges absent or confined to posterior part of buccal cavity, not reaching anterior buccal frame; chelipeds with fingers pointed or spoon-tipped; ambulatory legs without dactylo-propodal articulation; portion of sternite 8 visible between abdomen and coxae of fifth pereiopods; male abdomen with segments 3–5 fused, immovable, sutures sometimes visible; female abdomen with all somites free; male genital openings coxal or coxo-sternal; female openings sternal; sternal sutures 2–3 and 3–4 very evident, 3–4 interrupted medially, sternite 4 sometimes with medial groove extending anteriorly from sterno-abdominal cavity; male first gonopod slender to stout, slightly curved to straight, apex with complex lobes or folds, often with spines or long setae; second gonopod short, less than a quarter the length of the first gonopod (modified after Davie 2002, p. 372).

Discussion.—Guinot (1978) elevated the Panopeinae Ortmann, 1893, to family status and separated it into two groups, one in which taxa have a "xanthoid facies" and a

male genital opening in a coxal position, now placed within the Panopeinae, and those genera with a "goneplacid facies" and male genital openings either coxal or coxosternal (p. 275–276), placed within the Eucratopsinae Stimpson, 1871a. Taxa belonging to the family were also described as having a portion of sternite 8 visible in dorsal view; abdomen separated from the coxae of the fifth pereiopods by part of sternite 8; and a reunion of sternite 8 with the posterior border of the carapace (Guinot 1978, p. 276). There are few characters that are diagnostic for the dorsal carapace of members of the family, other than the very broad features used by Davie (2002). However, each subfamily has a very distinctive dorsal carapace morphology that is not easily confused with the other. Davie (2002) provided a diagnosis for the family and for the Eucratopsinae. Members of the Panopeinae were reviewed by Martin and Abele (1986) although they did not provide a diagnosis for the subfamily.

The material described below is referred to the Panopeidae based upon its clear resemblance to the dorsal carapace of members of the genus *Panopeus* H. Milne Edwards, 1834. No other xanthoid family can accommodate the constellation of characters exhibited by the new material.

Subfamily Panopeinae Ortmann, 1893

Fossil genera.—*Eurypanopeus* A. Milne Edwards, 1880, claws only (in Collins and Portell 1998; Collins, Donovan, and Dixon 1996; Morris 1993); *Hexapanopeus* Rathbun, 1898b, claws only (in Collins, Donovan, and Dixon 1996); *Laevicarcinus* Lőrenthey in Lőrenthey and Beurlen, 1929; *Lophopanopeus* Rathbun, 1898b; *Micropanope* Stimpson, 1871a, claws only (in Collins and Portell 1998; Morris 1993); *Neopanope* A. Milne Edwards, 1880, claws only (in Collins and Portell 1998); *Panopeus*; *Sereneopeus* Collins, 2002.

Diagnosis.—Carapace wider than long, length usually about two-thirds to three-quarters maximum carapace width but can be nearly equidimensional; regions fairly well delimited, sometimes with transverse, discontinuous ridges or with granules on anterior half; anterolateral margins convex, usually shorter than posterolateral margins but can be equivalent or slightly longer, usually with four spines excluding outer-orbital spine, outer-orbital spine usually coalesced with first anterolateral spine, remainder of anterolateral spines usually well-delineated; angle between anterolateral and posterolateral margin usually between 100 and 120 degrees but sometimes higher, especially in fossil forms; fronto-orbital width more than half maximum carapace width; front between 0.25–0.40 maximum carapace width, with median notch, separated from inner orbital rim by a notch, may be produced beyond orbits; orbital margin with two open notches. Chelipeds

unequal in males and females; merus with superior subterminal tooth; carpus with tooth at inner angle; fingers acute. Male genital openings coxal (after Rathbun 1930; Davie 2002).

Discussion.—Members of the subfamily are united in possession of coxal male genital openings (Davie 2002). The diagnosis above is based upon the diagnosis given by Rathbun (1930) for *Panopeus*. Many other species of the genus are defined in terms of their differences with *Panopeus* (see Rathbun 1930; Martin and Abele 1986); thus, the general diagnosis for the dorsal carapace of *Panopeus* had merely to be modestly modified to accommodate other genera within the subfamily. In cases in which "usually" modifies the character, there are only one or two genera that do not fit the general pattern (Table 2 and discussion below). Genera within the Panopeinae are typically distinguished from one another based upon the morphology of the male pleopods (Martin and Abele 1986). Unfortunately, pleopods are not preserved in fossils; thus, features of the dorsal carapace must be used.

One of the features of members of *Panopeus* that distinguishes them from other genera within the subfamily is the distinctly trilobed male first pleopod with a bifid lateral tooth (Martin and Abele 1986). Rathbun (1930) provided a detailed description of the dorsal carapace of *Panopeus* that is quite useful to paleontologists, and the new material conforms in all regards to that description. Unfortunately, the characters used by biologists to define genera within the family are not significantly different than those used to define *Panopeus*. For example, Rathbun's (1930) diagnoses for *Lophopanopeus, Neopanope,* and *Hexapanopeus,* and Martin and Abele's (1986) diagnosis for *Dyspanopeus* Martin and Abele, 1986, are not appreciably different from that of *Panopeus*. Many of these diagnoses list a few features of the anterolateral margin or front as being distinctive, but otherwise that the genus is like *Panopeus*. Many of these so-called distinctive features are very difficult to quantify. For example, *Lophopanopeus* was described as essentially like *Panopeus* except that the regions are areolated and the front is sinuous (Rathbun 1930, p. 319).

To facilitate referral of fossils to genera within the subfamily, we compared the various length and width ratios and anterolateral margin characteristics of the dorsal carapace of members of the subfamily. Twenty-six illustrations in Rathbun (1930) were measured, representing 21 species in 11 genera (Table 2). With two exceptions, all extant species measured were listed by Martin and Abele (1986) as belonging to the subfamily and at least one species of each of their listed genera was examined. Perusal of the various ratios and angle measures for *Lophopanopeus, Panopeus, Dyspanopeus, Eurypanopeus,* and *Rhithropanopeus* shows remarkable overlap between and among genera. *Micropanope* stands apart from these five genera only in having broader fronto-orbital width/width and

TABLE 2. Measurements taken on genera and species placed within the Panopeinae Ortmann, 1893, sensu Guinot (1978) and Martin and Abele (1986). † indicates fossil taxa; * indicates species not referred to by Martin and Abele (1986). L = length; W = maximum width; FOW = fronto-orbital width; F = frontal width; LMW = length to maximum width; A = length of anterolateral margin; P = length of posterolateral margin; Angle = angle between posterolateral and posterior margins. FOW = fronto-orbital width; PW = posterior width.

Species	L/W	FOW/W	F/W	LMW/L	A/P	Angle	Ornament
Lophopanopeus bellus Stimpson, 1860	0.7	0.47	0.3	0.33	0.8	125°	Granular
Lophopanopeus frontalis (Rathbun 1893)	0.73	0.55	0.36	0.36	0.87	109°	Smooth
Lophopanopeus leucomanus (Lockington 1877)	0.77	0.66	0.3	0.5	0.92	100°	Granular
†*Laevicarcinus egerensis* Lőrenthey in Lőrenthey and Beurlen, 1929	0.75	0.6	0.32	0.37	0.64	112°	Ridges
Panopeus herbstii H. Milne Edwards, 1834	0.79	0.61	0.33	0.5	0.58	115°	Ridges
Panopeus herbstii forma *obesa* Rathbun, 1930	0.76	0.89	0.38	0.43	0.65	118°	Ridges
Panopeus simpsoni Rathbun, 1930	0.74	0.63	0.34	0.5	0.67	105°	Ridges
Panopeus herbstii forma *crassa* Rathbun, 1930	0.7	0.55	0.34	0.45	0.6	110°	Ridges
Panopeus chilensis H. Milne Edwards and Lucas, 1844	0.74	0.51	0.32	0.51	0.86	112°	Ridges
Panopeus occidentalis no. 1, Saussure, 1857	0.74	0.56	0.3	0.55	0.82	112°	Ridges
Panopeus occidentalis no. 2, Saussure, 1857	0.65	0.55	0.33	0.46	0.74	105°	Ridges
Panopeus turgidus no. 1 Rathbun, 1930	0.77	0.69	0.31	0.56	0.82	115°	Ridges
Panopeus turgidus no. 2 Rathbun, 1930	0.87	0.63	0.3	0.42	0.86	110°	Ridges
†*Panopeus piramidensis* new species	0.8	0.66	0.33	—	0.63	115°	Weak ridges
†*Panopeus wronai* Müller, 1984	0.88	0.51	0.31	0.31	0.89	135°	Ridges
†*Panopeus granulineatus* Müller and Collins, 1991	0.69	0.5	0.29	0.55	—	118°	Ridges
†*Panopeus prosakrolophos* Schweitzer, 2000	0.75	0.66	0.33	0.5	0.55	130°	Ridges
†*Panopeus torus* Schweitzer, 2000	0.75	0.6	0.33	0.5	0.66	120°	Granular ridges
Neopanope packardii (Kingsley 1879)	0.95	0.56	0.39	0.37	1	98°	Weak ridges
Dyspanopeus sayi (Smith 1869a)	0.77	0.59	0.41	0.36	0.8	105°	Uknown
Dyspanopeus texanus (Stimpson 1859)	0.85	0.6	0.45	0.4	0.9	105°	Unknown
Hexapanopeus angustifrons (Benedict and Rathbun 1891)	0.74	0.48	0.3	0.59	1.11	110°	None

							TABLE 2. CONT.
Species	L/W	FOW/W	F/W	LMW/L	A/P	Angle	Ornament
*Hexapanopeus schmitti Rathbun, 1930	0.91	0.63	0.4	0.66	1	110°	None
Eurypanopeus abbreviatus (Stimpson, 1860)	0.69	0.5	0.31	0.55	0.78	108°	None
Eurypanopeus depressus (Smith, 1869a)	0.77	0.64	0.41	0.53	0.78	108°	Ridges
Eurytium limosum (Say, 1818)	0.63	0.72	0.33	0.41	0.94	110°	Smooth
Micropanope sculptipes Stimpson, 1871a	0.68	0.74	—	0.46	0.86	108°	Large granules
Micropanope lobifrons no. 1, A. Milne Edwards, 1881	0.71	0.79	0.58	0.53	0.6	111°	Large granules
Micropanope lobifrons no. 2, A. Milne Edwards, 1881	0.75	0.8	0.5	0.47	0.75	112°	Large granules
Metopocarcinus truncatus Stimpson, 1860	0.9	0.76	0.41	0.5	0.53	128°	Smooth
*Lophoxanthus lamellipes Stimpson, 1860	0.66	0.79	0.47	0.52	0.5	145°	Smooth
Rhithropanopeus harrisii (Gould, 1841)	0.79	0.63	0.32	0.4	0.88	120°	Ridges

frontal width/width ratios. *Neopanope* stands apart from the group of five genera in being nearly as long as wide and in having equal anterolateral and posterolateral margins, a lower angle between the anterolateral and posterolateral margins, and a slightly broader front. *Hexapanopeus* is nearly as long as wide, has a longer anterolateral margin than posterolateral margin which is unique among the taxa measured, and the point of maximum width is positioned further posteriorly than it is in other members of the subfamily. *Eurytium* has nearly equal anterolateral and posterolateral margins and a broader front than other members of the subfamily. Clearly, the relative width of the front is a variable feature within the group.

The fossil species of *Panopeus* differ from the extant ones only in the angle of the anterolateral margin and the posterolateral margin; it is higher in the fossils. The only extant genera that have high angles, *Metopocarcinus* and *Lophoxanthus*, are smooth and highly aberrant from the typical panopeine facies; the fossils are clearly not referable to those genera. *Metopocarcinus* is nearly as long as wide and displays broader fronto-orbital and frontal widths than other members of the subfamily. It also has anterolateral margins only half as long as the posterolateral margins, and the angle between those two margins is comparatively high. In addition, *Metopocarcinus* is smooth; has a very produced front; has deep-set, obliquely directed orbits; and lacks anterolateral spines. No other genus in the subfamily displays these features. *Lophoxanthus* is very similar to *Metopocarcinus* except that it is much wider than long and has an even higher angle between the anterolateral and posterolateral margins and has two anterolateral spines, differentiating it from every other member of the subfamily.

What of the five genera that are similar to one another, *Lophopanopeus, Panopeus, Dyspanopeus, Eurypanopeus,* and *Rhithropanopeus*? Possession of ridges, granules, or smooth ornamentation can be a help, as in distinguishing *Panopeus* from *Lophopanopeus*, but this study shows that it would be difficult to distinguish among these five in the fossil record. What is the resolution to this problem? It is clear that fossil taxa can be assigned to the Panopeinae with relative ease; the diagnosis provided above works well to define members of the subfamily. Generic-level placements, however, will probably always be problematic to some extent and will rely on comparison of fossil material to various species within panopeine genera to find a good match. This is problematic at the generic level, of course, but in the larger scheme, fossils can be referred with confidence to the subfamily, thus establishing a geological record for the subfamily, which is useful for evolutionary and phylogenetic analyses.

Panopeus is well-represented in the fossil record, as discussed below. The other extant genera known from the fossil record are represented only by claws and claw fragments. *Eurypanopeus, Hexapanopeus, Lophopanopeus,*

Micropanope, and *Neopanope* are all known from claw fragments, primarily from Pliocene and Pleistocene deposits of North America and the Caribbean (Rathbun *in* Oldroyd 1925; Rathbun 1926; Collins, Donovan, and Dixon 1996; Collins and Portell 1998; Morris 1993). An exclusively fossil genus, *Laevicarcinus,* clearly belongs to the subfamily, based upon its carapace shape, development of carapace regions, ridged ornamentation, and the length and width ratios and angles presented in Table 2. In fact, the characters of *Laevicarcinus* completely overlap with those of *Panopeus* spp. and are quite similar to those of *Eurypanopeus* and *Rithropanopeus.* We maintain *Laevicarcinus* as a separate genus because of its lobate anterolateral margin, anterolateral spines separated by grooves extending onto the dorsal carapace; straight posterolateral margins, and more angular carapace than other members of the subfamily.

Budapanopeus Müller and Collins, 1991, was referred to the Panopeidae, but the shape of the carapace of material housed in Hungary, M.91-155 (Hungarian Museum of Natural History) and EK-17 (Hungary Geological Institute), the highly vaulted carapace, and the weak anterolateral spines suggest that it might better be placed with the Pilumnidae.

The referral of several fossil species of *Panopeus* and of *Laevicarcinus,* all based upon the dorsal carapace, to the subfamily gives it a well established Eocene record. Clearly, the common ancestor of the Panopeinae and Eucratopsinae existed and the divergence of these two lineages occurred before that time.

Genus *Panopeus* H. Milne Edwards, 1834

Type species.—*Panopeus herbstii* H. Milne Edwards, 1834, by subsequent designation of Fowler, 1912.

Fossil species.—*Panopeus baldwini* (Kooser and Orr 1973), as *Lophopanopeus; P. bessmanni* Collins and Jakobsen 2004[2003]; *P. capanemaensis* Martins Neto, 2001; *P. granulineatus* Müller and Collins, 1991; *P. nanus* Portell and Collins, 2004; *P. olearis* (Rathbun 1926), as *Lophopanopeus; P. prosakrolophos* Schweitzer, 2000; *P. piramidensis* new species; *P. soledadensis* (Rathbun 1926), as *Pilumnoplax; P. torus* Schweitzer, 2000; *P. viai* Müller, 1993; *P. wronai* Müller, 1984; questionably *P. lauensis* Rathbun, 1945, based upon a fragment of carapace.

Fossil species known from claw fragments only.— *Panopeus* sp., see Rathbun, 1918, 1919, 1923; Withers, 1924; *P. antepurpureus* Rathbun, 1918; *P. estellensis* Rathbun, 1935; *P. herbstii* (also extant); *P. jerseyensis* Roberts, 1956; *P. rugosus* A. Milne Edwards, 1880, in Collins, Donovan, and Dixon, 1996 (also extant); *P. tridentatus* Rathbun, 1918.

Diagnosis.—Carapace wider than long, length usually about two-thirds to three-quarters maximum carapace width; regions fairly well delimited, sometimes with transverse, discontinuous ridges or with granules on anterior half; anterolateral margins convex, shorter than posterolateral margins, with four spines excluding outer-orbital spine, outer-orbital spine coalesced with first anterolateral spine, remainder of anterolateral spines usually well-delineated; angle between anterolateral and posterolateral margins between 100 and 120 degrees, especially in fossil forms; fronto-orbital width more than half maximum carapace width; front about 30 percent maximum carapace width, with median notch, separated from inner orbital rim by a notch, may be produced beyond orbits; orbital margin with two open notches. Chelipeds unequal in males and females; merus with superior subterminal tooth; carpus with tooth at inner angle; fingers acute. Male genital openings coxal (after Rathbun 1930; Davie 2002).

Discussion.—Members of the genus *Panopeus* have been reviewed on many occasions (Benedict and Rathbun 1891; Rathbun, 1930; Manning and Holthuis, 1981; Williams, 1983; Martin and Abele, 1986; Williams and Boschi, 1990). It is a speciose genus that is well known from the western Atlantic region (Boschi, 1964; Williams, 1984). Species within the genus are differentiated based upon the number, shape, and fusion of the anterolateral spines; the number and development of transverse dorsal carapace ridges; and the ornamentation of the chelipeds (Williams 1983).

The new material described below is best placed within *Panopeus,* based upon dorsal carapace material, as are other fossil species including *Panopeus baldwini, P. granulineatus, P. olearis, P. prosakrolophos, P. soledadensis, P. torus,* and *P. wronai. Lophopanopeus, Dyspanopeus,* and *Eurytium* cannot accommodate the new material or the other fossil species based upon dorsal carapace material because they each have ridges on the dorsal carapace regions; in *Lophopanopeus,* those regions are smooth or granular. *Neopanope* has a very low angle between the anterolateral and posterolateral margins, which cannot accommodate the new material or any of the other fossil species. *Micropanope* has granular ornamentation and lacks ridges, excluding the new material and the other fossil species from it. *Eurypanopeus* and *Rithropanopeus* are the only other viable options for the new material and other fossil species, as each completely overlaps with *Panopeus* in terms of carapace ratios, angle, and ornamentation as discussed above (Table 2). We opt to refer the fossils to *Panopeus,* the nominate genus of the subfamily, until other means are discovered to differentiate among these three genera.

In addition to the similarity of the new fossil material to extant species of *Panopeus,* extant species of the genus are well-known from coastal Argentina, Uruguay, Brazil, Chile, and Central America (Rathbun 1930; Garth 1957;

Williams 1983, 1984; Williams and Boschi 1990; Boschi 2000). Thus, placement of the new material described here in *Panopeus* seems most judicious at this time.

Examination of some of the species previously referred to *Panopeus* suggests that they do not belong to the genus. *Panopeus vicentinus* Bittner, 1875, has well-developed carapace grooves and overall development of regions typical of members of the Dynomenidae Ortmann, 1892, specifically *Diaulax* Bell, 1863, or *Polycnemidium* Reuss, 1859, or possibly the Etyiidae Guinot and Tavares, 2001. Examination of type material will be necessary to confirm placement of this species within a genus and family. Collins and Jakobsen (1994) and Jakobsen and Collins (1997) moved *P. incertus* and *P. subellipticus* to *Titanocarcinus* and *P. incertus* to *Cyclocorystes*. Schweitzer (2000) removed *P. incertus* Segerberg, 1900, from the genus; that taxon probably belongs to the Dromiidae, possibly allied with *Dromiopsis*. *Panopeus faxoensis* Fischer-Benzon, 1866, and *P. subellipticus* Segerberg, 1900, definitely display a xanthoid-like appearance, but it appears that they may be better referred to the Dynomenidae or the Palaeoxanthopsidae Schweitzer, 2003. *Panopeus subellipticus* (Segerberg 1900, fig. 9.14a) greatly resembles *Remia* Schweitzer, 2003 of the Palaeoxanthopsidae. However, the type material of the Segerberg and Fischer-Benzon material will need to be examined to make confident family and generic-level referrals. None appears to belong to the Panopeidae. Schweitzer (2000) suggested that *Panopeus kempi* Quayle and Collins, 1981, was not a member of the genus, and Collins (2002) subsequently placed it within the genus *Sereneopeus* Collins, 2002.

Panopeus whittenensis Glaessner, 1980, was described from Eocene rocks of Australia; Schweitzer (2000) maintained placement within *Panopeus* although noting the lack of narrow dorsal carapace ridges diagnostic for *Panopeus*. The species must be removed from the genus and probably also the family. It closely resembles *Pakicarcinus* Schweitzer et al., 2004, known from Eocene rocks of Pakistan and we herein erect the new combination, *Pakicarcinus whittenensis*. Both *Pakicarcinus orientalis* and *Panopeus whittenensis* have quadrate carapaces, sharp anterolateral spines; ridge-like epibranchial regions, ridge-like cardiac and mesobranchial regions, and very depressed intestinal and metabranchial regions. Examination of the holotype of *Panopeus? lauensis* Rathbun, 1945 (USNM 498427), indicates that it is too fragmental to positively identify.

Panopeus piramidensis new species
(Fig. 8)

Diagnosis.—Carapace small, L/W about 0.80; protogastric, epigastric, and hepatic regions with very weak ridges; second anterolateral spine largest; fourth anterolateral spine very reduced.

Description.—Carapace wider than long, L/W about 0.80, widest at position of last anterolateral spine; flattened in transverse section, weakly vaulted in longitudinal section; regions appearing to have been relatively smooth. Front appearing to have been nearly straight, with small axial notch, axially sulcate, not extending beyond orbits, directed downward, notched between rim of orbits, front about one-third maximum carapace width; orbits directed weakly anterolaterally, rimmed, two open notches in upper orbital margin, fronto-orbital width about two-thirds maximum carapace width. Anterolateral margin shorter than posterolateral margin, convex; with four spines excluding outer-orbital spine; outer-orbital spine and first anterolateral spine coalesced into straight segment; second anterolateral spine largest, sharp, directed anterolaterally, upper margin short, lower margin long and concave; third anterolateral spine directed anterolaterally, smaller than second spine, triangular, upper margin shorter than lower margin; fourth spine very reduced, developed as blunt protuberance posterior to third spine, separated from third spine by groove in dorsal carapace. Posterolateral margin convex, entire, small reentrant at posterolateral corner; posterior margin nearly straight, about 40 percent maximum carapace width.

Frontal area smooth. Epigastric regions trapezoidal, with ridged inflation anteriorly. Protogastric region pentagonal, flattened, well defined by grooves, appearing to have had weak row of granules along anterior-most margin. Mesogastric region triangular; with long anterior process, terminating at midlength of epigastric region; region well defined by grooves. Urogastric region very short, anterior margin concave, posterior margin and lateral margins nearly straight. Cardiac region broadly triangular, apex directed posteriorly, with pair of small swellings anteriorly and one small swelling at posterior apex of triangle. Intestinal region flattened, not well-differentiated. Hepatic region square, with weak ridge of granules anteriorly; epibranchial region arcuate, extending from bases of third and fourth anterolateral spines, arcing anteriorly, terminating at margin of urogastric region; remainder of branchial region not differentiated, poorly preserved in all specimens.

Remainder of carapace, ventral aspect, and appendages unknown.

Measurements.—Measurements (in mm) taken on the dorsal carapace of specimens of *Panopeus piramidensis*: MPEF-PI 1545, width, 13.5; fronto-orbital width, 8.6; frontal width, 4.4. MPEF-PI 1547, width, 13.2; length, 9.7. MPEF-PI 1546, width, 16.6; fronto-orbital width, 10.4. MPEF-PI 1548, width, 11.9; length, 9.6; fronto-orbital width, 7.8; posterior width, 4.7.

Types.—The holotype, MPEF-PI 1545, and paratypes MPEF-1547, MPEF-PI 1546, and MPEF-PI 1548. MPEF-1547 contains three specimens and MPEF-PI 1548 contains two specimens.
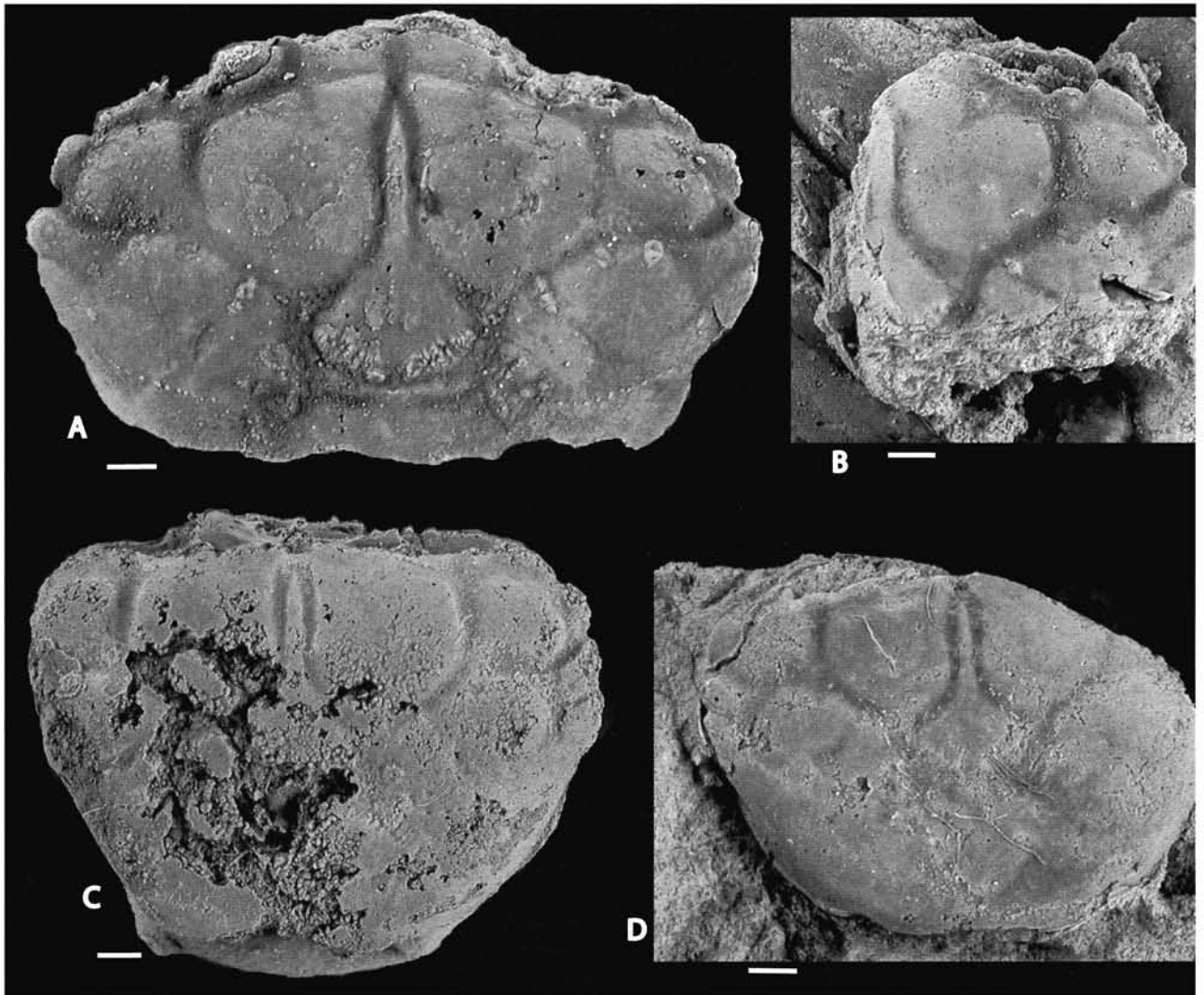
Fig. 8.—*Panopeus piramidensis* new species. A, partial dorsal carapace, holotype, MPEF-PI 1545; B, partial dorsal carapace, paratype, MPEF-PI 1546; C, dorsal carapace, paratype, MPEF-PI 1547; D, partial dorsal carapace, paratype, MPEF-PI 1548. Scale bars = 1 cm.

Occurrence.—Waypoint 13, Paleosurface II.

Etymology.—The trivial name is derived from the charming village of Puerto Pirámide, near the collecting locality of the type material and where the authors were housed during the field season.

Discussion.—The weak ridges on the dorsal carapace of the new material distinguish it from all other fossil species of the genus and most extant species as well. The new species is very small in size as well, much smaller than other fossil species of the genus. Numerous extant species of *Panopeus* are known from the eastern coast of South America as are several species of *Hexapanopeus*. However, the equidimensional anterolateral and posterolateral margins and more posteriorly positioned point of maximum width of *Hexapanopeus* preclude assignment of

the new species to that genus. Interestingly, extant species of both *Panopeus* and *Hexapanopeus* are known from Brazilian and more northerly waters, suggesting that warm waters extended further south during the time in which *P. piramidensis* lived.

Superfamily Xanthoidea *incertae sedis*
Xanthoidea family, genus and species indeterminate 1
(Fig. 9A)

Description of material.—Carapace wider than long, L/W about 0.74, widest at position of third anterolateral spine about 42 percent distance posteriorly on carapace; regions moderately well-marked by broad grooves; moderately vaulted longitudinally and transversely.

Front bilobed, axially notched and sulcate, about 30

percent maximum carapace width, very slightly produced beyond orbits. Orbits shallow, directed forward, fronto-orbital width about half maximum carapace width. Anterolateral margins with at least four spines and possibly five, excluding outer-orbital angle; first anterolateral spine and outer-orbital angle coalesced into straight segment; second anterolateral spine broadest, longest, and best developed; third spine second-largest, triangular; fourth spine tiny, a blunt projection; fifth spine, if present, very small blunt projection; anterolateral margin as long as or longer than posterolateral margin. Posterolateral margin weakly convex.

Epigastric regions small, equant, transversely ridged; protogastric regions pentagonal, apex directed posteriorly, bounded by broad grooves; mesogastric region with long anterior process, widened distally, posterior margin convex; urogastric region relatively long, with convex margins, depressed below level of mesogastric and cardiac regions; cardiac region elongate-pentagonal in shape, apex directed posteriorly. Hepatic region about as wide as long, inflated; subhepatic triangular, flattened; epibranchial region composed of two segments, arcuate, extending from base of fourth and fifth anterolateral spines to lateral margin of urogastric region; remainder of branchial region undifferentiated, inflated.

Measurements.—Measurements (in mm): maximum length, 27.3; maximum width, 35.3; fronto-orbital width, 18.6; frontal width, 10.1; length to position of maximum width, 11.6.

Material examined.—MPEF-PI 1549.

Occurrence.—Waypoint 16.

Discussion.—The single specimen is very poorly preserved. It differs from genus and species 2 in having an anterolateral margin that is the same length as or longer than the posterolateral margin, a much longer urogastric region, and a more elongate cardiac region. It differs from *Panopeus piramidensis* in lacking the weak ridges on the epigastric, protogastric, and hepatic regions, and in having anterolateral margins as long as or longer than the posterolateral margins; much longer urogastric region; much smaller epigastric regions; and a much shorter frontal region of the carapace.

It is not possible to place the specimen into a family, based upon its poor preservation. The front is damaged; the orbits are corroded; the anterolateral and posterolateral margins are strongly weathered; the posterior margin is missing; and the entire ventral aspect of the carapace is not preserved. The long anterolateral margins suggest possible placement within the Pilumnidae or Xanthidae, but better material will need to be collected to provide a more complete evaluation of this taxon.

Xanthoidea family, genus and species indeterminate 2
(Fig. 9B, D)

Description of material.—Carapace wider than long, L/W about 0.78, widest about 42 percent distance posteriorly on carapace; dorsal carapace severely eroded and pitted, regions difficult to discern, surface granular where cuticle is preserved; fronto-orbital width about half maximum carapace width; anterolateral margin appearing to have had at least four blunt spines; posterolateral margin weakly convex. Hepatic region inflated, about as wide as long; subhepatic region flattened.

Third maxillipeds longer than wide. Sternum longer than wide, widest at position of sternite 5, granular; sternites 1–2 fused; distinct suture between sternites 2 and 3; sternites 3 and 4 fused, distinct sutures between them, interrupted medially; sternite 4 very long, with episternal projections, directed anterolaterally; sternite 5 directed anterolaterally, with episternal projections, sternite 6 directed laterally, narrower than sternite 5.

Measurements.—Measurements (in mm): maximum length, 37.9; maximum width, 48.9; fronto-orbital width, 24.1; length to maximum width, 16.8.

Material examined.—MPEF-PI 1550.

Occurrence.—Waypoint 16.

Discussion.—The specimen is superficially similar to Xanthoidea family, genus and species indeterminate species 1 in its fronto-orbital width to width ratio, length to width ratio, inflated hepatic regions, spined anterolateral margin, and convex posterolateral margin, but it is too incompletely preserved to confidently assign the two specimens to the same taxon. The well-defined sutures between sternites 2–3 and 3–4 suggest it is not a member of the Eriphiidae, but it is not possible to refer the specimen to a family at this time.

Section Thoracotremata Guinot, 1977
Superfamily Ocypodoidea Rafinesque, 1815
Family Ocypodoidea Rafinesque, 1815 *sensu lato*

Fossil genera.—*Macrophthalmus* Desmarest, 1823; *Hemiplax* Heller, 1865; *Ocypode* Weber, 1795; *Uca* Leach, 1814 (all are also Recent).

Diagnosis.—Carapace long, subquadrilateral to pentagonal, dorsal carapace regions typically indistinct; anterolateral margins straight, often confluent with posterolateral margins; front narrow, deflexed; interantennular septum broad; third maxilliped typically completely closing buccal cavity, exopod visible; chelipeds unequal in males, equal or unequal in females; thoracic sternum broad poste-
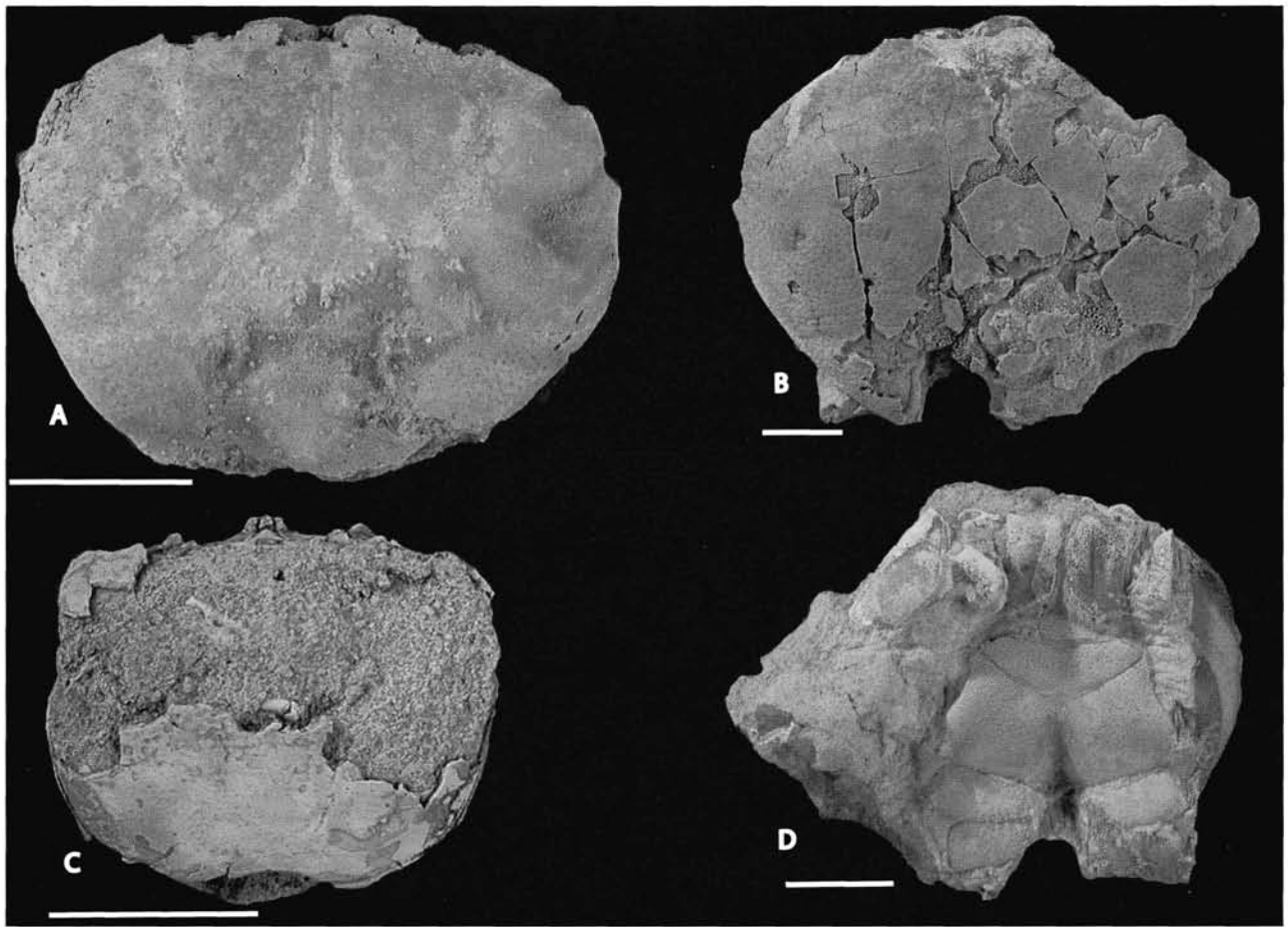
Fig. 9.—Xanthoidea and Ocypodidae. A, Xanthoidea family, genus and species indeterminate 1, MPEF-PI 1549; B, Xanthoidea family, genus and species indeterminate 2, dorsal carapace, MPEF-PI 1550; C, *Ocypode vericoncava* new species, holotype, MPEF-PI 1551; D, Xanthoidea family, genus and species indeterminate 2, ventral surface, MPEF-PI 1550. Scale bars = 1 cm.

riorly; male genital openings sternal (after Davie 2002).

Discussion.—The new material is referred to the Ocypodidae based on the rectangular carapace that is not much wider than long; broad orbits; narrow, deflexed front; straight lateral margins; and well-developed posterolateral reentrants. The extremely narrow front, broad orbits, and rectangular carapace taken together are diagnostic only for this family. Members of the Grapsidae MacLeay, 1838, also have rectangular carapaces, but members of that family have broad fronts and anterolateral spines, neither of which the new material possesses.

Recently, Kitaura et al. (2002) suggested that the subfamilies of the Ocypodidae be elevated to family status, which would result in movement of some genera to families other than the Ocypodidae *sensu stricto*. Their work was based upon molecular studies and evaluation of that decision is beyond the scope of this work. Thus, we refer to the family *sensu lato* in this work.

Fossil ocypodes are uncommon. Glaessner (1969) listed only a few ocypode genera with fossil records, and all

but one occurrence was in Miocene or younger rocks. Of the genera he referred to the family, *Loerentheya* Beurlen *in* Lőrenthey and Beurlen, 1929, has since been referred to the Retroplumidae Gill, 1894 (Beschin et al. 1996). *Sandomingia* Rathbun, 1919, is closely allied with *Podophthalmus* Lamarck, 1801, of the Portunidae based upon its carapace shape and broad orbits; the two genera may be synonymous. In any case, *Sandomingia* is clearly not an ocypode.

To date, *Ocypode* has been reported from fossil occurrences only from Pleistocene rocks of Florida and Morocco (Rathbun 1935; Secretan 1959; Glaessner 1969; Portell et al. 2003). A claw fragment referred to *Ocypode* sp. (M.86.269) is housed in the Hungarian Museum of Natural History (Müller 1978). *Uca*, another member of the subfamily Ocypodinae, has a fossil record in lower Miocene rocks of Brazil (Brito 1972; Martins Neto 2001); and Pliocene and Pleistocene rocks of North and Central America, the Caribbean, and the Indo-Pacific (Rathbun 1926; Glaessner 1969; Morris 1993; Collins and Portell 1998). Glaessner (1969) reported both *Macrophthalmus*,

of the Macrophthalminae Dana, 1851b, as also having fossil records Miocene to Recent fossil records; see Karasawa and Kato (1992) and Schweitzer et al. (2002) for a summary of fossil occurrences of *Macrophthalmus*. *Hemiplax* is known from questionably Pliocene rocks of New Zealand and from Pleistocene deposits of New Zealand and Australia (Glaessner 1969). Thus, this report of a species of *Ocypode* from Miocene rocks of Argentina is seminal for several reasons: it is the oldest known occurrence of *Ocypode*; it one of the oldest occurrences of its subfamily; and it is one of the few ocypodes known in the fossil record. Interestingly, the two oldest occurrences for the subfamily are in South America.

Secretan (1975) described the genus and species *Archaeocypoda veronensis* from Monte Bolca, Italy; examination of the paratype no. 104 and 103, cass. 40, scat. 13, deposited in the Museo Civico di Storia Naturale, Verona, Italy, suggests that it is not an ocypode (RF and CS). The rounded carapace, deep orbits, and relatively broad front suggest that it may be a member of the Dorippidae MacLeay, 1838.

Subfamily Ocypodinae Rafinesque, 1815
Genus *Ocypode* Weber, 1795

Type species.—*Cancer ceratophthalmus* Pallas, 1772, by subsequent designation of Latreille (1810).

Fossil species.—*Ocypode quadrata* (Fabricius 1787) (also extant); *O.* cf. *O. africana* de Man, 1881; *O. vericoncava* new species.

Diagnosis.—Carapace somewhat wider than long, subquadrilateral; dorsal carapace regions typically indistinct; anterolateral margins confluent with posterolateral margins to form straight lateral margins, posterolateral reentrant present; front narrow, deflexed, with concave margins; orbits large, shallow, with sinuous upper margins; fronto-orbital width almost equal to maximum width of carapace; chelae heterochelous; pereiopods 2–4 long, pereiopod 5 shorter; male abdomen narrow (after Glaessner 1969; Davie 2002).

Discussion.—The new material is referred to *Ocypode* based upon its carapace that is not much wider than long; broad orbits; narrow front; and nearly straight lateral margins. Members of *Uca* have clearly differentiated anterolateral and posterolateral margins and a hexagonal carapace, which cannot accommodate the new material.

Ocypode vericoncava new species
(Fig. 9C)

Diagnosis.—Carapace rectangular, slightly wider than

long; front about 10 percent carapace width; antennular fossae positioned just below front; considerable gap between antennular fossae and orbits. Orbits ovate in anterior view, constricted centrally, highest laterally, narrowed axially, with triangular inner sub-orbital spine which is visible in dorsal view; orbits with sinuous upper margin, fronto-orbital width about 85 percent maximum carapace width. Posterior margin with concave reentrant axially.

Description.—Carapace rectangular, slightly wider than long, L/W about 0.86, flattened longitudinally and transversely. Front very narrow, about 10 percent maximum carapace width, depressed below level of dorsal carapace, lateral margins concave. Antennular fossae positioned just below front; considerable gap between antennular fossae and orbits. Orbits ovate in anterior view, constricted centrally, highest laterally, narrowed axially, with triangular inner sub-orbital spine which is visible in dorsal view; in dorsal view, orbits with sinuous upper margin, fronto-orbital width about 85 percent maximum carapace width.

Anterolateral and posterolateral margins confluent to form continuous lateral margin, lateral margins parallel to one another anteriorly, converging posteriorly, with posterolateral reentrant. Posterior margin with concave reentrant axially. Cuticle smooth where preserved.

Pterygostomial region smooth, groove extending from inner orbital angle, arcing posteriorly and continuing in oblique straight segment to intersect lateral margin. Mandibles smooth, widened axially at occlusal surface.

Measurements.—Measurements (in mm) taken on the dorsal carapace of *Ocypode vericoncava* new species: maximum carapace width, 20.7; maximum carapace length, 17.8; fronto-orbital width, 16.9; frontal width, 1.9.

Etymology.—The trivial name is derived from the Latin word *concavus*, meaning concave, and referring to the concave nature of the posterior margin which is especially marked in this taxon, and the Latin word *veris*, meaning old, in referrence to the species being the oldest known in the genus to date.

Type.—MPEF-PI 1551, holotype.

Occurrence.—Waypoint 17.

Discussion.—The specimen is poorly preserved dorsally; thus, it is not possible to provide a description of the dorsal carapace regions. However, the outline of the carapace and the orbital, frontal, and antennular regions are reasonably well-preserved. Thus, the holotype is adequately preserved so that subsequent specimens will be referable to the species.

The new species is much older than either of the other reported fossil occurrences of *Ocypode*, *O.* cf. *O. africana* de Man, 1881 (Secretan 1959) and *O. quadrata*, both
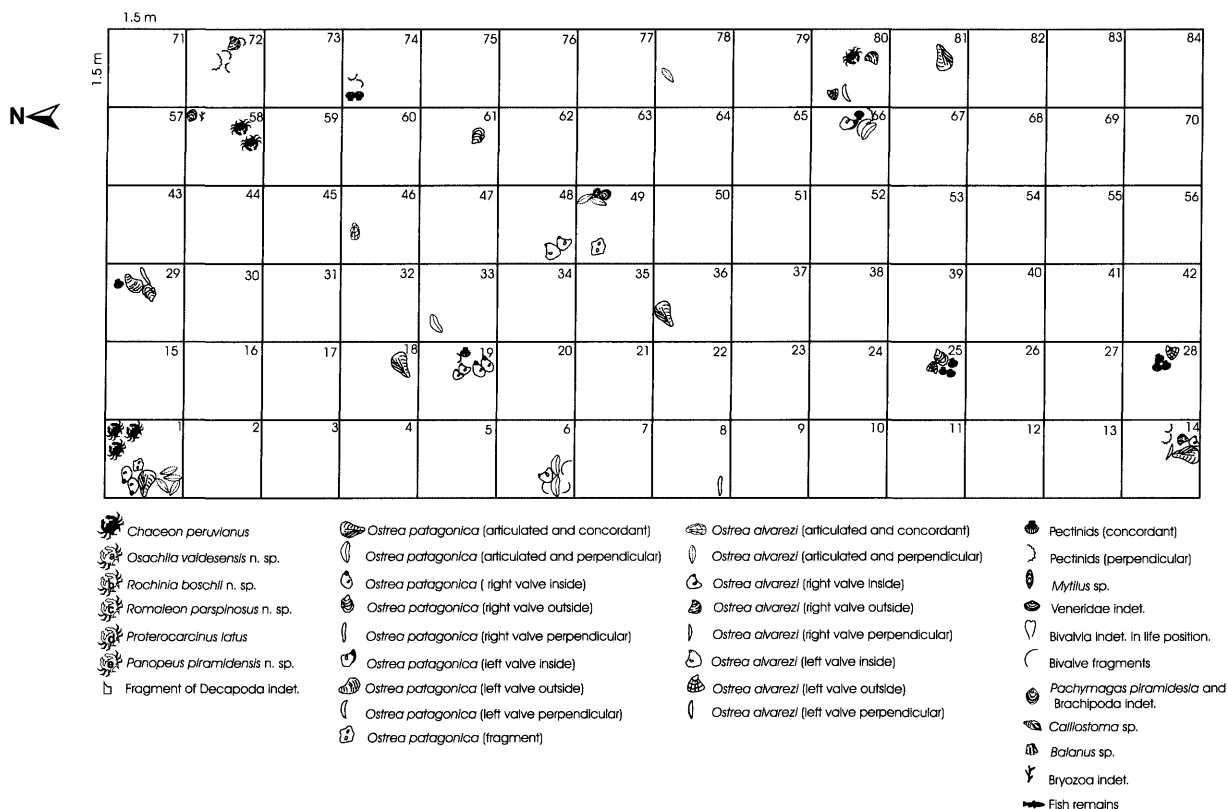
Fig. 10.—Map of Paleosurface I, following grid system of 1.5 m². Detailed information about Paleosurface I is found in Table 3.

Pleistocene. Secretan's (1959) material is quite fragmental; thus, direct comparisons cannot be made.

TAPHONOMY AND PALEOECOLOGY OF OYSTER AND DECAPOD CONCENTRATIONS

Taphonomic and paleoecologic studies of marine invertebrate fossil assemblages within a well-defined sedimentological context provide critical information for the reconstruction of paleoenvironmental conditions and relative sea-level changes. We present the results of a taphonomic and paleoecologic study based on three paleosurfaces present in the lowest part of the Puerto Pirámide section (Facies Association 1), cropping out along the coastline of Nuevo Gulf during low tide (Figs. 1, 2). The section has a rich marine invertebrate fauna consisting mainly of articulated crabs and oysters. The recognition of bounding surfaces is used in order to determine the geological history from a sequence stratigraphic point of view. This approach permits reconstruction of relative sea level changes and paleoenvironmental conditions during the late Miocene in southern Patagonia.

Methods

The three paleosurfaces considered in this study (from bottom to top, Paleosurface I: lat. 42°35'43"S, long. 64°15'30"W; Paleosurface II: lat. 42°35'38"S, long. 64°15'31"W and, Paleosurface III: lat. 42°35'48"S, long. 64°15'27"W), were measured, described, and carefully mapped in plan view on field maps to record the precise location of all fossil specimens (Figs. 10–12). The total area included is 1165.5 m²; 189 m² (9 m wide by 21 m long) for Paleosuface I (Fig. 10); 247.5 m² (15 m wide by 16.5 m long) for Paleosurface II (Fig. 11); and 679.5 m² (15 m wide by 37.5 m long plus 3 m wide by 39 m long) for Paleosurface III (Fig. 12). The paleosurfaces were mapped using a 1.5 m grid system. All of the exposed macroscopic fossils were noted, and their exact positions (relative to North and to the horizontal) were registered. As a result, 733 individuals were recorded, and most of them were collected. In the laboratory, the fossils were cleaned using standard mechanical and chemical methods. The field data supplemented observations made in the laboratory.

On each paleosurface, stratigraphic features (lateral extent, association with significant surface, and position within depositional sequence), sedimentologic features

TABLE 3. Stratigraphic, sedimentologic, paleoecologic, and taphonomic features of the three paleosurfaces (=levels) at the Puerto Pirámide locality.

	PI	PII	PIII
Location	S 42° 35' 43"/ W 64° 15' 30"	S 42° 35' 38"/ W 64° 15' 31"	S 42° 35' 48"/ W 64° 15' 27"
Mapped area	189 m^2	247.5 m^2	679.5 m^2
Number of individuals	79	237	417

STRATIGRAPHIC FEATURES

	PI	PII	PIII
Lateral extent	continuous	continuous	continuous
Geometry	solitary individuals and clusters	solitary individuals and clusters	clusters
Association with significant surface	below maximum flooding surface	below maximum flooding surface	below maximum flooding surface
Position within depositional sequence	within transgressive system tract	within transgressive system tract	within transgressive system tract

SEDIMENTOLOGIC FEATURES

	PI	PII	PIII
Close-packing	dispersed to loosely packed	dispersed to densely packed	dispersed to densely packed
Size sorting	poorly sorted	bimodal	well sorted
Type of matrix	fine-grained muddy sandstone	fine-grained muddy sandstone	fine-grained muddy sandstone
Associated physical and biogenic structures of the bed	massive bed with *Cruziana* ichnofacies	massive bed with *Cruziana* ichonofacies	massive bed with *Cruziana* ichnofacies

PALEOECOLOGIC FEATURES

	PI	PII	PIII
Taxonomic composition	*Chaceon peruvianus* *Ostrea patagonica* *Ostrea alvarezi* *Amusium paris* *Aequipecten paranensis* Pectinidae indet. *Pachymagas piramidesia* Bryozoan indet.	*Chaceon peruvianus* *Rochinia boschii* n. sp. *Panopeus piramidensis* n. sp. *Proterocarcinus latus* *Osachila valdesensis* n. sp. *Romaleon parspinosus* n. sp. *Ostrea patagonica* *Ostrea alvarezi* *Mytilus* sp. *Argopecten?* sp. *Dinocardium* sp. Veneridae indet. Pectinidae indet. *Pachymagas piramidesia* Brachiopoda indet. *Calliostoma* sp. Bryozoan indet. *Balanus* sp. Fish remains	*Ostrea patagonica* *Chaceon peruvianus*
Life habits	mostly epifaunal and semi-infaunal suspension feeders	mostly epifaunal and semi-infaunal suspension feeders	mostly epifaunal and semi-infaunal suspension feeders
Ontogenetic age	mostly adults	mostly adults	mostly adults
Original mineralogy and microarchitecture	calcite	calcite	calcite

TAXONOMIC FEATURES

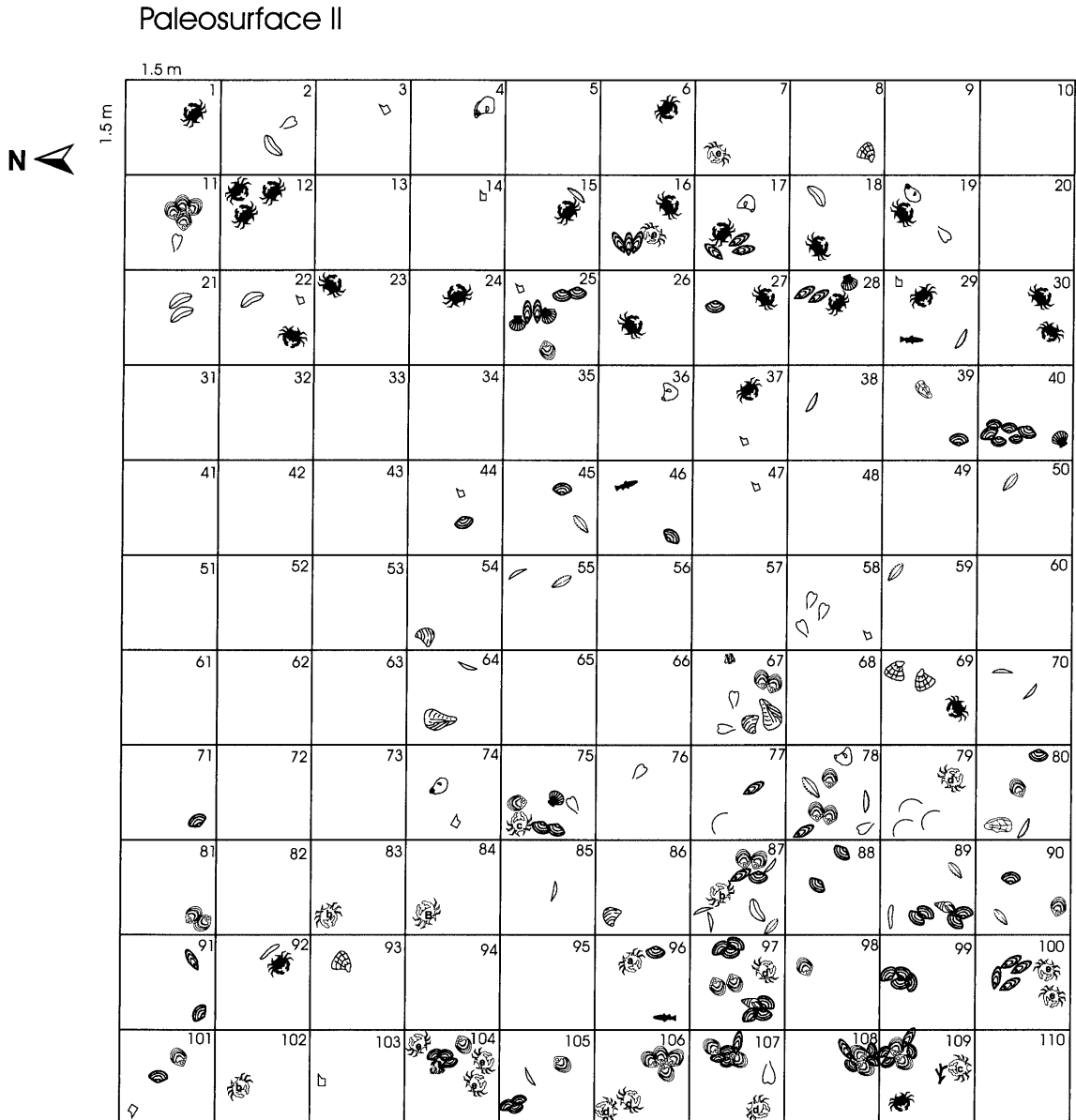|	PI	PII	PIII
Orientation	some edgewise in life position and others concordant in life position	some edgewise in life position and others concordant in life position	mostly edgewise in life position
Fragmentation	very low to none	very low to none	very low to none
Abrasion	very low (unabraded)	very low (unabraded)	very low (unabraded)
Disarticulation	very low (mostly articulated)	very low (mostly articulated)	very low (mostly articulated)
Encrustation	low	moderate	low
Bioerosion	moderate	moderate	high
Preserved mineralogy and microarchitecture	original	original	original

Paleosurface II

Fig. 11.—Map of Paleosurface II, following grid system of 1.5 m². Detailed information about Paleosurface II is found in Table 3. Explanation of symbols is given in Figure 10.

(close packing and size sorting of the bioclasts, type of matrix and associated physical and biogenic sedimentary structures), paleoecological features (taxonomic composition, life habits, ontogenetic age spectrum, original mineralogy, and microarchitecture), and taphonomic features (orientation, fragmentation, abrasion, disarticulation, encrustation, bioerosion, and preserved mineralogy and microarchitecure) were noted (Table 3), following Kidwell (1991). Close packing and size sorting were estimated following the semiquantitative categories for coarse bioclastic fabrics of Kidwell and Holland (1991). Geometry of

concentrations and orientation of specimens follows terminology proposed by Kidwell et al. (1986). Chi-square independence tests were used to ascertain whether there was an azimuthal preferred orientation of the specimens on each paleosurface.

Results

The three paleosurfaces are each composed of massive fine-grained muddy sandstone, with biogenic sedimentary
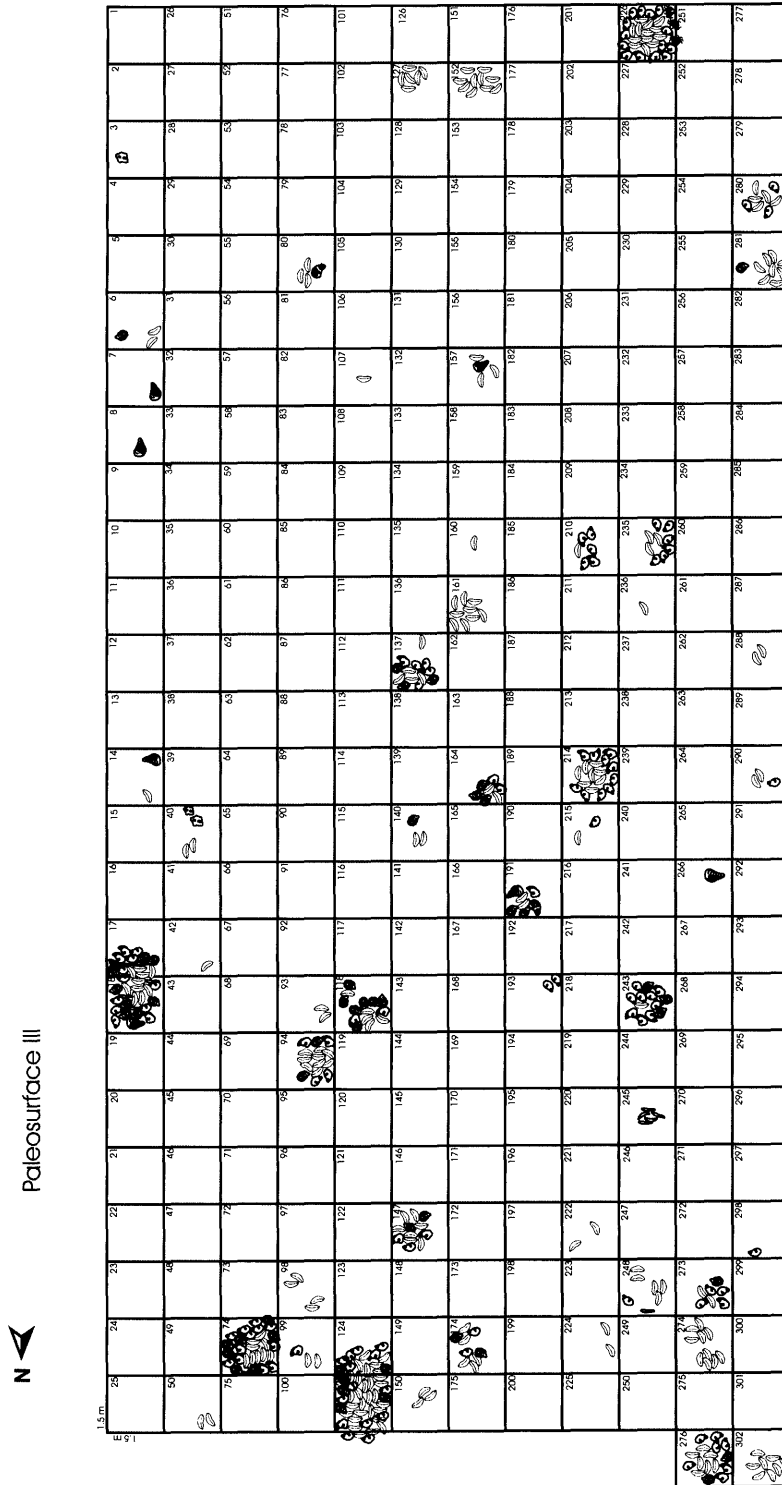
Paleosurface III

Fig. 12.—Map of Paleosurface III, following grid system of 1.5 m². Detailed information about Paleosurface III is found in Table 3. Explanation of symbols is given in Figure 10.

structures represented by the ichnogenera *Rhizocorallium, Rossella, Helicodromites,* and *Curvolithus.*

Paleosurface I (Fig. 10) is at the top of a continuous bed (0.30 m thick) of massive fine-grained muddy sandstone with a buried bottom and sharp top. The specimens are solitary individuals or are grouped in clumps. The fossils are poorly sorted and dispersed to loosely packed, with most of the bioclasts separated from one another by more than one body diameter. Seventy-nine specimens were documented on Paleosurface I: six decapods, 69 bivalves (44 oysters, 21 pectinids, and four bivalves indet.), three brachiopods, and one bryozoan. A total of eight taxa were recorded. Among these taxa, one decapod (*Chaceon peruvianus*), five bivalves (*Ostrea patagonica, Ostrea alvarezi, Amusium paris, Aequipecten paranensis,* and Pectinidae indet.), one articulated brachiopod (*Pachymagas piramidesia*), and one bryozoan (Bryozoa indet.) are present. This paleosurface is oyster-dominated: the bivalves represent 87.4% (oysters 55.7% and 31.7% other bivalves) of the identified specimens, decapods 7.6%, brachiopods 3.8%, and bryozoans 1.3% (Figure 13A). All of the brachiopods, 36% of the bivalves, and the bryozoan are perpendicular to stratification, and all of the crabs are concordant, with a NE-SW azimuthal orientation. The degree of disarticulation is low. Of the six crabs, three are completely articulated and three have a complete cephalothorax without appendages. Thirty-eight percent of the oysters are articulated, without a statistically significant ventral margin azimuthal orientation. The isolated valves have a preference for a convex-up position and a long-axis NE-SW azimuthal orientation (P <0.005). Most of the isolated valves are right valves. Most of the other bivalves, all of the brachiopods, and the only bryozoan are articulated. The degree of abrasion and fragmentation is low, and only two of 44 oysters are fragmented. The degree of encrustation is low: *Ostrea patagonica* and the pectinids have *Balanus* sp. and cheilostemate bryozoans as encrusters, and *Ostrea alvarezi* has brachiopods as encrusters. The bioerosion is moderate. The articulated and disarticulated specimens of *Ostrea patagonica* and *O. alvarezi* have borings assigned to *Gastrochaenolites* isp. (attributed to the bivalve *Litophaga* sp.), sponges (*Entobia* isp.) and polychaetes (*Maeandropolydora* isp.). On specimens in life position, the borings are preferentially on the exterior of the left valve.

Paleosurface II (Fig. 11) is at the top of a continuous bed (0.20 m thick) of fine-grained muddy sandstone with sharp upper and lower contacts. Most of the specimens are solitary individuals or are grouped in clumps. The packing is dispersed in some areas to densely packed in others, and the size sorting is bimodal, with a distinctive second mode. Two hundred and thirty-seven individuals were registered: 54 decapods, 142 bivalves (47 oysters, 21 mytiloids, five pectinids, 69 veneroids), 33 brachiopods, three vertebrate fragments, two gastropods, two barnacles, and one bryozoan. At least 19 taxa were recorded. Among these taxa,

six decapods (*Chaceon peruvianus, Rochinia boschii* n. sp., *Panopeus piramidensis* n. sp., *Proterocarcinus latus, Osachila valdesensis* n. sp., and *Romaleon parspinosus* n. sp.), seven bivalves (*Ostrea patagonica, O. alvarezi, Argopecten?* sp., *Dinocardium* sp., *Mytilus* sp., Veneridae indet. and Pectinidae indet.), two brachiopods (*Pachymagas piramidesia* and Brachiopoda indet.), one gastropod (*Calliostoma* sp.), one bryozoan (Bryozoa indet.), one cirripede (*Balanus* sp.), and one fish are present. This level is crab and oyster-dominated. The bivalves represent 59.9% (oysters 19.8% and other bivalves 40.0%) of the identified specimens, decapods 22.8%, brachiopods 13.9%, vertebrates 1.3%, barnacles and gastropods 0.8%, and algae and bryozoans 0.4% (Fig. 13B). All of the crabs are concordant with stratification and have preferred NE-SW and NW-SE azimuthal orientations (P <0.0001). Thirty-eight percent of the oysters, 50% of the other bivalves, and 83% of the brachiopods are perpendicular to the stratification. The articulated oysters have their ventral margin in a preferred NE-SW and NW-SE azimuthal orientation (P <0.001). The degree of disarticulation is low. Of 54 crabs, 25 are completely articulated, 17 have a complete cephalothorax without appendages, and 12 are decapod fragments, mostly hands. Sixty-one and one-half percent the specimens of *Ostrea patagonica* and 29.4% of the specimens of *O. alvarezi* are articulated. When the specimens are disarticulated, the right valves lie in both convex-down and convex-up positions. Most of the other bivalves, brachiopods, and multielement skeleton specimens (bryozoans, barnacles, and vertebrates) are articulated. The degrees of fragmentation and abrasion are low. The degree of encrustation is moderate: *Ostrea patagonica* have *Balanus* sp. and cheilostemate bryozoans as encrusters, and *O. alvarezi* has serpulids as encrusters. Bioerosion is moderate. Articulated and disarticulated specimens of *Ostrea patagonica* and *O. alvarezi* have bivalve (*Gastrochaenolites* isp.) and sponge borings (*Entobia* isp.).

Paleosurface III (Fig. 12) is at the top of a continuous bed (0.40 m thick) of fine-grained muddy sandstone with a sharp bottom and top. Individuals form clusters of up to 29 specimens. The packing is dispersed in some sectors and densely packed in others, and the sediment is well sorted. Four hundred and seventeen specimens were registered: 414 bivalves and three decapods. Two species were recorded: one decapod (*Chaceon peruvianus*) and one bivalve (*Ostrea patagonica*). This paleosurface is oyster-dominated, oysters represent 99.3% and crabs only 0.7% (Fig. 13C). Fifty-three percent of the oysters are perpendicular to stratification with a highly preferred ventral margin, E-W and N-S azimuthal orientation (P <0.001), and the three crabs are concordant and have a NW-SE orientation. The degree of disarticulation is low: the three crabs are completely articulated and 55% of the oysters are articulated. When disarticulated, the right valves outnumber the left valves (74% of the valves are right valves) and they lie in both convex-down and convex-up positions.
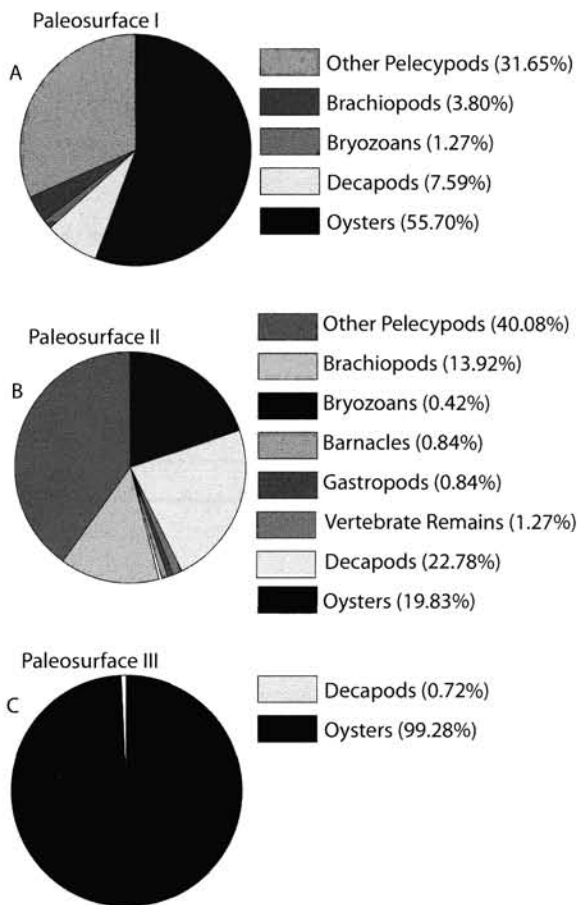
Paleosurface I

A

Other Pelecypods (31.65%)

Brachiopods (3.80%)

Bryozoans (1.27%)

Decapods (7.59%)

Oysters (55.70%)

Paleosurface II

B

Other Pelecypods (40.08%)

Brachiopods (13.92%)

Bryozoans (0.42%)

Barnacles (0.84%)

Gastropods (0.84%)

Vertebrate Remains (1.27%)

Decapods (22.78%)

Oysters (19.83%)

Paleosurface III

C

Decapods (0.72%)

Oysters (99.28%)

Fig. 13.—Relative abundance of fossils in the three paleosurfaces. A, Paleosurface I; B, Paleosurface II; C, Paleosurface III.

The abrasion and fragmentation is minimal; only three of 414 oysters are fragmented. The encrustation of the fossils on Paleosurface III is low, and *Balanus* sp. and cheilostemate bryozoans are the most common encrusters. Bioerosion is high. Most articulated specimens of *Ostrea patagonica* have borings of *Gastrochaenolites* sp., especially on the ventral margin.

Discussion

The faunal composition and the fossil preservation suggest that the three beds are obrution deposits in which specimens were smothered by sudden sedimentation within their habitats. This type of deposit comprises individual bedding-planes, on which benthic organisms are preserved in an articulated, but not-aligned, fashion (Seilacher 1992). The low degree of disarticulation, abrasion, and fragmentation; the moderate to high degree of bioerosion; and the lithological coherence between the

specimen filling and the sediment observed in thin sections indicate no taphonomic reworking.

The disarticulation of bivalved skeletons typically occurs rapidly, and clusters of intact brachiopod or bivalve shells may mark rapidly smothered seafloors (Brett and Baird 1986). Furthermore, the presence of articulated, multielement skeletons offers proof of rapid sediment influx in nearly all environments (Brett and Baird 1986). The low degree of disarticulation of the bivalves and brachiopods on the three paleosurfaces, the presence of many shells in growth position in clusters forming bunches, the presence of so-called "butterflied" bivalves on Paleosurface II, and the presence of articulated crabs suggest normally low energy conditions, with a short high-energy interlude during which the fauna was smothered and buried by sediments, with minimal post-mortem disturbance. There are no preservational features diagnostic of mechanical abrasion indicative of highly agitated environments.

The degree of encrustation and boring of the oysters indicates that from Paleosurface I to Paleosurface III there was an increase in the residence time of shells on the sea floor and an overall low rate of sedimentation at the time of formation of the three paleosurfaces. The low rate of sedimentation is also suggested by the high degree of bioturbation of the layers. The three paleosurfaces were formed below fair weather wave base in an offshore, low-energy environment, where abrasion, fragmentation, and disarticulation play a relatively minor role. The surfaces represent relatively undisturbed relics of the former community. The concentrations are interpreted as having formed by biological processes, including a high rate of production of biogenic hard parts and gregarious settling behavior (especially on Paleosurface III), and low rates of sedimentation. The abundance of oriented right valves as contrasted with left valves of the oysters is indicative of sorting and the influence of currents, probably storm flows.

When the paleoecological and taphonomic features are taken into account, it is possible to infer that the paleosurfaces formed in slightly different positions in the offshore environment (Fig. 14). Paleosurface I, with low faunal diversity and fewer articulated individuals, could have been formed in the shallow bathymetric range, near fair weather wave base. Paleosurface II could have occupied an intermediate position, and Paleosurface III, with highly bored and articulated oysters forming clusters, reflects quieter, offshore environments with respect to storm influence.

Because of the dependence of fossil preservation upon rates of sedimentation and environmental energy, different types of skeletal concentrations occur predictably at several locations in depositional sequences (Brett 1995). According to the sedimentologic, stratigraphic, paleoecological, and taphonomic features described above, the crab and oyster-dominated concentrations of the upper
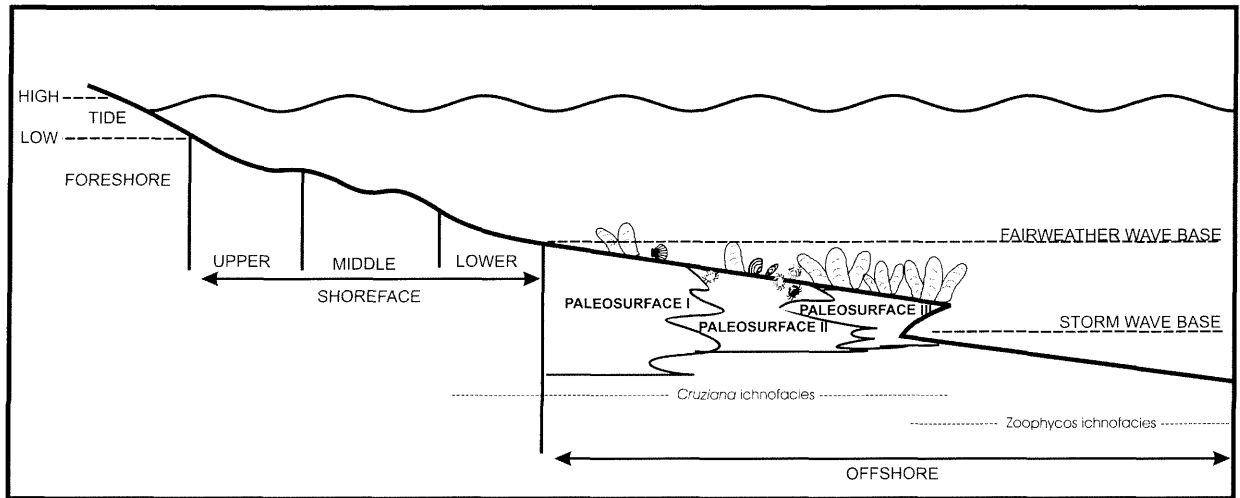
Fig. 14.—Position of the three paleosurfaces with respect to fair weather wave base and storm wave base.

Miocene Puerto Madryn Formation suggest that these paleosurfaces formed during the last stages of a transgressive systems tract. The paleosurfaces developed immediately below the maximum flooding surfaces, which are represented by laminated mudrock facies of the *Zoophycos* ichnofacies, representative of more distal environments. Shell concentrations in this position of the sequence are characterized by medium to high faunal diversity and high bioturbation, are poorly sorted and dominated by mollusks and brachiopods, and moderate to high biogenic alteration (Fürsich and Pandey 2003). This position in the sequence is where obrution deposits are most frequently recognized, due to infrequent major depositional events and protection from later reworking because of the deep (and deepening) position of the sea floor (Brett 1995).

CONCLUSIONS

Description of five new species of brachyurous decapod crustaceans brings to 11 the total number of described crabs from the Puerto Madryn Formation in the Península Valdés region, Chubut Province, Argentina. In addition, at least two other species of crabs, all xanthoids, are known but are too poorly preserved to permit identification. Thus, this is one of the most robust Miocene faunas known from the Southern Hemisphere and it has resulted in several important taxonomic records. The species of *Osachila* reported herein is only the second report of the genus in the fossil record, and the new species of *Rochinia* is the second fossil record of the genus. *Ocypode vericoncava* n. sp. is the oldest known fossil occurrence of the genus, and the new species of *Romaleon* is the first fossil record of the genus on the Atlantic coast. Reevaluation of the Panopeinae and the genus *Panopeus* suggests that members of the subfamily

are difficult to distinguish from one another and that many species assigned to *Panopeus* are better placed in other genera.

The lower upper Miocene Puerto Madryn Formation belongs to the upper part of a depositional sequence including a transgressive systems tract (TST) and a highstand systems tract (HST). Deposits of the TST interval were deposited below wave base, whereas deposits of the HST accumulated in tidal channels and tidal flats. Deposits of each type recur throughout the section exposed near Puerto Pirámide.

The occurrence of crabs and oysters on three paleosurfaces broadly exposed on wave-cut benches in the lowermost part of the Puerto Madryn Formation exposed near Puerto Pirámide permitted detailed mapping of their distribution along with that of other megainvertebrates exposed on the same surface. The results document patchy distribution of the dominant crab, *Chaceon peruvianus*, and the dominant oyster, *Ostrea patagonica*, as well as sporadic distribution of the other megafauna. The three paleosurfaces are interpreted to represent three successively deeper and more distal surfaces lying between fair weather base and storm wave base. The distribution of organisms, primarily the oysters, becomes progressively more clustered from Paleosurface I to Paleosurface III. The sediment becomes better sorted from Paleosurface I to III, although all surfaces are composed of fine-grained muddy sandstone. The fauna uniformly consists of suspension-feeding, mostly epifaunal and semi-infaunal organisms. Faunal diversity is highest on Paleosurface II and lowest on Paleosurface III. The fauna is primarily preserved in life position, there is little abrasion and fragmentation, most multi element remains are articulated, and bioerosion is moderate to high. This combination of taphonomic conditions suggests that the organisms were preserved in their life habitats and that little, if any, postmortem movement occurred. Detailed analysis of fossil

decapods and their paleoecological setting in the Puerto Madryn Formation has therefore provided an unusual opportunity to describe the ecological setting that the decapods inhabited during life.

ACKNOWLEDGMENTS

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