NEOGENE DECAPOD CRUSTACEA FROM SOUTHERN CHILE

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ABSTRACT

Twelve species of Neogene decapod crustaceans are described from late Miocene and early Pliocene deposits in the Valdivia, Osorno-Llanquihue, and Chiloé basins as well as from Mocha Island, offshore from the Temuco Basin, southern Chile. **New species** of thalassinideans include *Ctenocheles notialis* and *Axianassa? chilensis*. *Axianassa* Schmitt, 1924, has not been reported previously in the fossil record. **New species** of brachyurans include *Trichopeltarion frassinetti*, *Pirulella antipodea*, *Chaceon quadrata*, *Geryon manningi*, *Phenophthalmus mochaensis*, and *Chasmocarcinus chiloeensis*. *Pirulella* and *Phenophthalmus* are **new genera** and *Geryon* Krøyer, 1837, is noted in the fossil record for the first time. Extant congeners are primarily known from lower latitude regions. Only *Chaceon* Manning and Holthuis, 1989, is known from the Chilean coast at present.

Key Words: Brachyura, Chile, Decapoda, Neogene, Thalassinoidea

INTRODUCTION

Neogene marine strata occur at numerous localities along the Chilean forearc (Cecioni 1980; Mordojovich 1981; Encinas et al. 2008b) (Fig. 1). First studied by Darwin (1846), these deposits have been correlated with the Navidad Formation (~34°S), considered to be the reference unit for the marine Neogene of Chile (Cecioni 1980; DeVries and Frassinetti 2003). The first studies generally refer to these units as shallow marine deposits (e.g., Etchart 1973; Cecioni 1978). However, more recent sedimentological and micropaleontological studies indicate that these successions were deposited at bathyal depths (~500-2000 m) during a period of major Miocene subsidence that took place along the Chilean forearc (Gómez 2003; Achurra 2004; Le Roux et al. 2004; Finger et al. 2007; Encinas et al. 2008b).

These deposits contain an abundant and diverse fauna and flora including bivalves, gastropods, decapod crustaceans, echinoids, brachiopods, bryozoans, ostracodes, foraminifers, vertebrates, leaves, and pollen (e.g., d'Orbigny 1842; Darwin 1846; Philippi 1887; Troncoso and Encinas 2006; Finger et al. 2007). Most of the paleontological studies have been performed on mollusks (e.g., Tavera 1979; Covacevich and Frassinetti 1986; Nielsen 2005). Decapod studies, on the other hand, have been scarce (e.g., Philippi 1887; Tavera 1979) until recently.

In 1985, Chirino-Gálvez noted the presence of decapod crustaceans, along with other benthic faunal elements, in a summary of the paleoecology of the area surrounding Valdivia, Chile. Subsequent field work by one of us (RMF) and Chirino-Gálvez yielded extensive collections of fossil decapods from localities extending from Tierra del Fuego to Navidad, west from Santiago. An unpublished M.S. thesis (Chirino-Gálvez 1993) detailed the history of study of fossil decapods in southern South America, summarized the decapod fauna of Chile, and documented the localities from which decapods were known. Subsequent field work by Encinas, Feldmann, and Schweitzer in 2004 in the vicinity of Navidad resulted in the documentation of 12 species of decapods from the Navidad Formation (Feldmann et al. 2005) and three species from Cretaceous and Eocene rocks of the vicinity (Schweitzer et al. 2006a). Those studies documented, for the first time, tenuous connections between the mid-latitude decapod fauna of Chile and Argentina. During the past few years, collections of fossil decapods made by Sven Nielson and one of us (AE) in the area of Isla Chiloé has prompted examination of the fauna surrounding that locality.

In the present contribution, we describe fossil decapods collected from Neogene strata that occur in several different localities of southern Chile (Fig. 2).
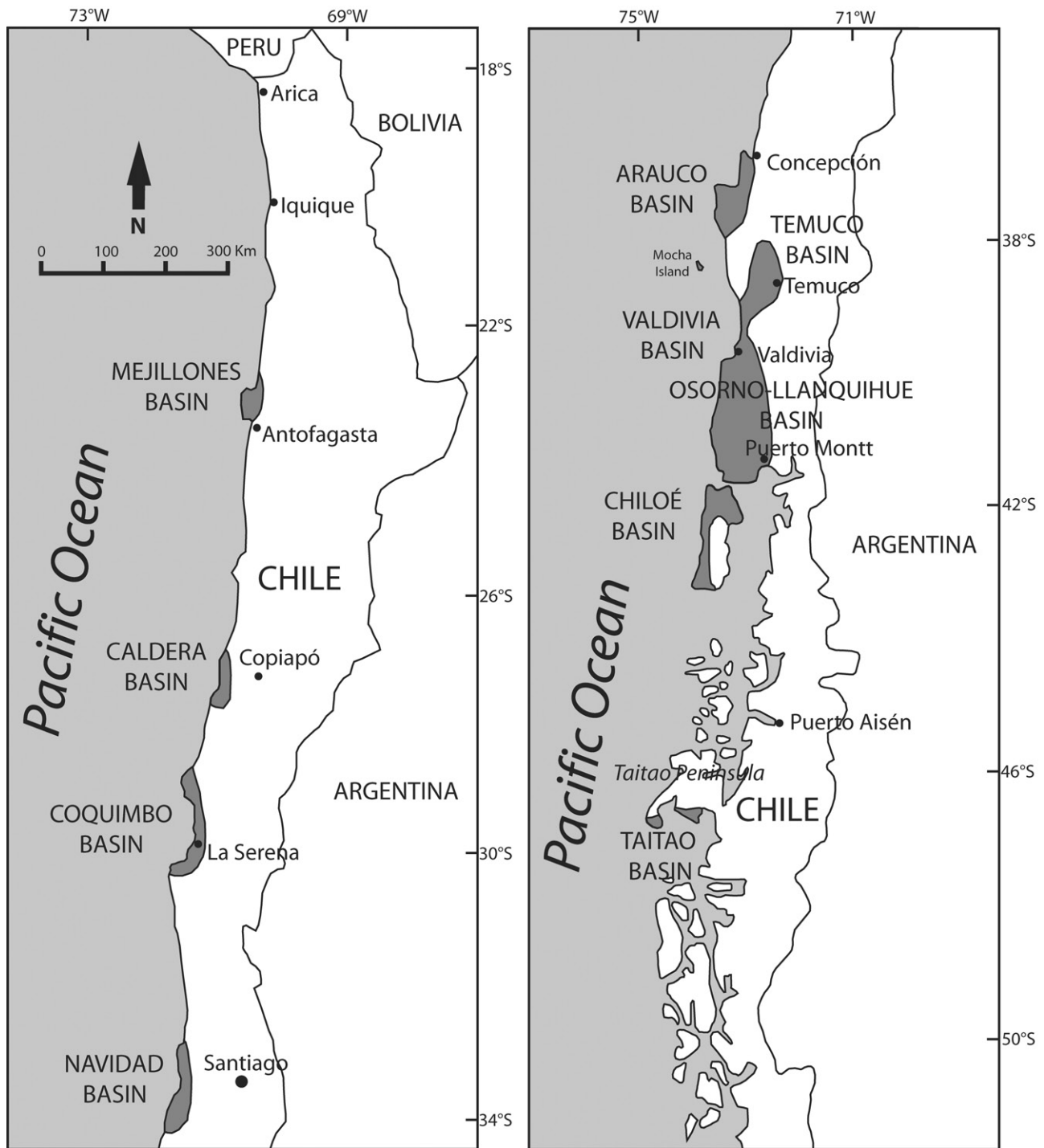
Fig. 1.—Geological map showing the extension of the Neogene marine deposits (dark grey) that crop out along the Chilean forearc. Figure modified from Martínez-Pardo (1990).
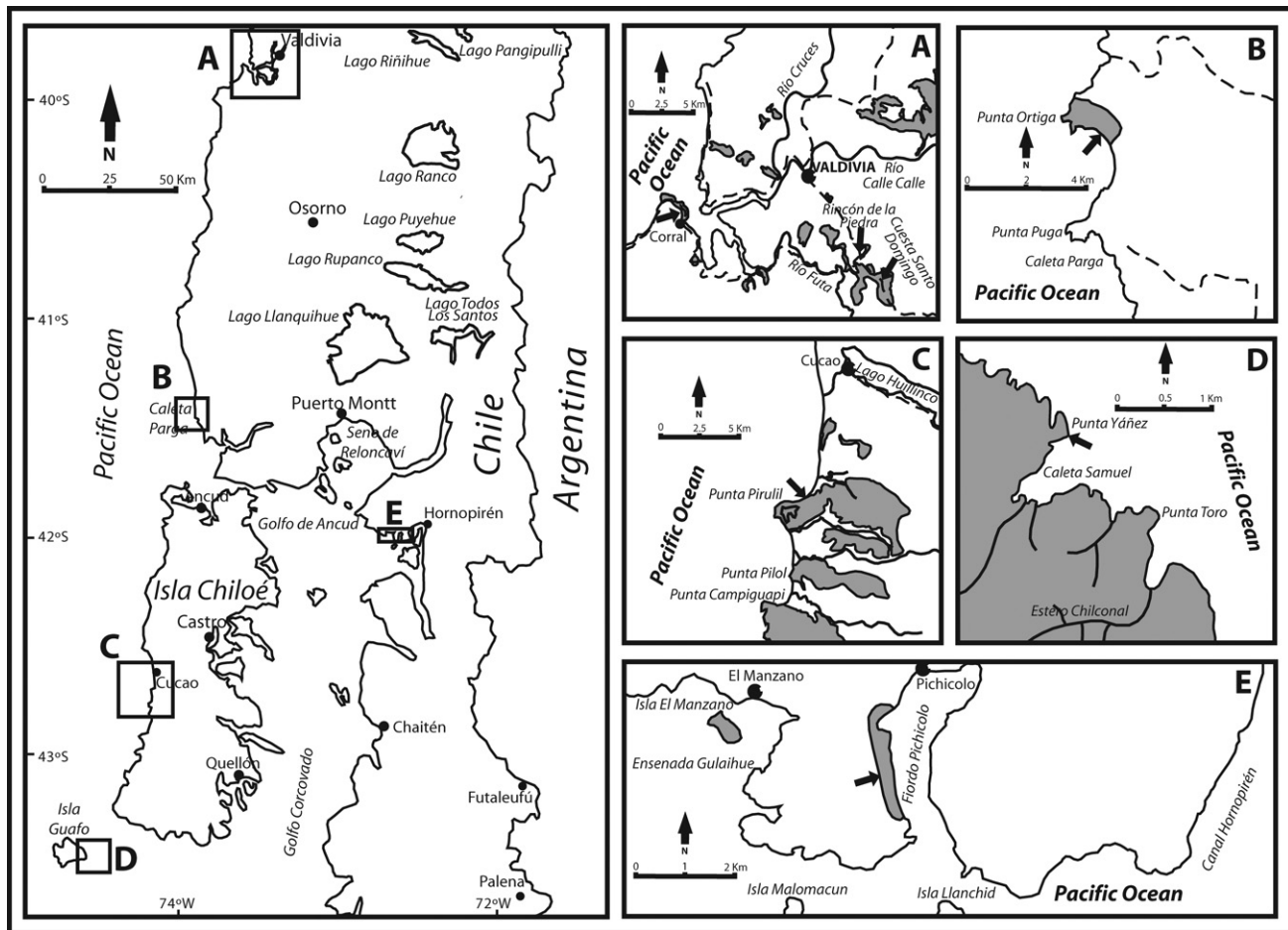
Fig. 2.—Left half: general map of the study area. The insets show the location of the collecting areas described in the text, except Mocha Island which is indicated on Figure 1. Right half: detailed maps of the collecting areas. Decapod collecting localities are highlighted by arrows. Extension of Neogene marine deposits are shown in grey.

DECAPOD SAMPLE LOCALITIES

Decapod specimens have been collected in Neogene strata that crop out in six different localities between Valdivia and Isla Guafo (~40ºS - 43ºS) (Fig. 2). The general lithology and known fauna of crustacean-bearing units as well as the collecting localities for each of these areas are described below.

1) Valdivia. Miocene marine strata that crop out in the Valdivia area (Fig. 2A) were first studied by Brüggen (1950) who correlated this succession with the Navidad Formation. Subsequently, Martínez-Pardo and Pino (1979) defined these deposits as the Santo Domingo Formation after their study of the locality by that name. This unit is exposed in several outcrops of limited dimensions that occur in roadcuts and coastal cliffs around Valdivia. The sedimentary succession consists of a basal breccia overlain by dark-gray sandy siltstones and minor sandstone and breccia (Encinas et al. 2008a). The Santo Domingo Formation contains a rich fossil biota that includes bivalves, gastropods, brachiopods, bryozoans, crustaceans, echinoids, fishes, foraminifers, ostracodes, radiolarians, and leaves (Chirino-Gálvez 1985, and references therein). Benthic foraminifers and trace fossils indicate deposition at lower bathyal depths for this unit (Encinas et al. 2008a). Deposition of this succession took place probably during the late Miocene (see Encinas et al. 2008a, and references therein for discussion).

Crab specimens from this area were collected at the following localities: (1) seventeen specimens were collected from the Cuesta Santo Domingo, which is located along the road between Valdivia and Paillaco, approximately 14 km southwest of Valdivia (lat. 39°57'S, long. 73°06'W); (2) one specimen was collected at Rincon de la Piedra, about 10 km southwest of Valdivia (lat. 39°55'S, long. 73°07'W); and (3) three specimens were collected in a roadcut north of Corral (lat. 39°53'S, long. 73°26'W) (Fig. 2A).

2) Caleta Parga. Brüggen (1950) cited the presence of Miocene marine strata that he assigned to the Navidad Formation in the locality of Caleta Parga on the Pacific

coast west of Puerto Montt (Fig. 2B). Tavera (1965) also correlated these deposits with the Navidad Formation based on the presence of *Turritella ambulacrum* Sowerby, 1846. The succession consists of a basal breccia overlain by dark-gray silty sandstone that contains fossils of bivalves, gastropods, decapods, and lower bathyal foraminifers (K. Finger personal communication). Poorly preserved, partially pyritized decapod claws were collected from this area at Punta Ortiga (lat. 41°26'S, long. 74°08'W) (Fig. 2B).

3) Cucao.—Marine strata assigned to the Lacui Formation (Valenzuela 1982) by Quiroz et al. (2004) occur along the west coast of Chiloé Island south of Cucao (Fig. 2C). The succession consists of sandstone and siltstone beds that locally contain abundant fossils of bivalves, gastropods, foraminifers, scaphopods, cirripeds and decapods (Tavera et al. 1985; Finger et al. 2007). Benthic foraminifers indicate deposition at upper-middle bathyal depths for this succession (Finger et al. 2007). Planktic foraminifers restrict the age of these strata to the Zanclean (early Pliocene, zone N19).

A large number of decapod specimens were collected from the Lacui Formation at the northern part of Punta Pirulil approximately 10 km south of Cucao (lat. 42°42'S, long. 74°08'W) (Fig. 2C). These fossils were found in concretions contained in grey siltstones that are exposed in the tidal platform during low tide.

4) Pichicolo. Marine strata assigned to the Ayacara Formation by Levi et al. (1966) crop out near Hornopiren, east of Chiloé Island (Fig. 2E). The succession consists of rhythmically interbedded sandstone, siltstone, and breccia containing abundant volcanic material and interpreted as deposited by turbiditic currents (Levi et al. 1966). The Ayacara Formation contains microfossils of foraminifers and silicoflagellates (Levi et al. 1966). In contrast, the only macrofauna reported from this succession is a single coral specimen assigned to the genus *Flabellum* Gray, 1849, by Solano (1978), and no crustacean fossils have been reported so far. The age of this unit has been debated. Martínez-Pardo (1961) assigned an Eocene-Miocene age to the Ayacara Formation based upon his study of foraminifera and silicoflagellates obtained from the type section at Ayacara. Subsequently, Martínez-Pardo (1965) assigned a middle Miocene age to the succession of Isla el Manzano (Fig. 2E) based on foraminifera. Rojas (2003) obtained a $^{40}Ar/^{39}Ar$ dating of plagioclase from an ash bed at Isla el Manzano that yielded a similar age of 16.5±0.5 Ma. In contrast, Bourdillón (in Sernageomin 1995) assigned a late Eocene-late Oligocene age to this unit based on planktic foraminifera.

Two fragmentary callianassid claw specimens from this study were collected in a succession of sandstone and siltstone in the western shore of the fiordo Pichicolo (lat. 42°01'S, long. 72°36'W) (Fig. 2E).

5) Guafo island. No stratigraphic studies have been performed in the Neogene of Guafo Island with the exception of a very general stratigraphic column published by Tavera et al. (1985). Frassinetti (1997, 2000) cited the presence of sandstone and siltstone beds containing fossils of bivalves, gastropods, brachiopods, echinoderms, and crustaceans in these strata. He correlated the molluscan fauna of this unit with those of the Guamblin succession (45ºS) and the Tubul Formation of Arauco (37ºS), and based on their similarities suggested a late Pliocene age for the marine succession of Isla Guafo.

A single crab specimen was collected in 1983 by Frassinetti and Covacevich during his trip onboard the R/V Hero at the locality of Punta Yañez (lat. 43°37'S, long. 74°36'W) (Fig. 2D).

6) Mocha Island. Tavera and Veil (1958) reported exposures of the Ranquil Formation on the northern coast of Mocha Island (Fig. 1) and collected numerous invertebrate fossils, including decapod crustaceans (Chirino-Gálvez 1993). Based upon the enclosed fauna, the age of the Ranquil Formation was considered to be Miocene in age.

Institutional Abbreviations.—**BM In,** The Natural History Museum, London, United Kingdom; **KSU,** Department of Geology, Kent State University, Kent, Ohio, U.S.A.; **SGO.PI,** Museo Nacional de Historia Natural, Sección Paleontología, Santiago, Chile; **USNM,** United States National Museum, Smithsonian Institution, Washington, D.C., U.S.A.

SYSTEMATIC PALEONTOLOGY
Infraorder Thalassinidea Latreille, 1831
Superfamily Callianassoidea Dana, 1852
Family Ctenochelidae Manning and Felder, 1991

Ctenocheles Kishinouye, 1926

Type Species.—*Ctenocheles balssi* Kishinouye, 1926, by monotypy.

Included Fossil Species.—*Ctenocheles anderseni* Collins and Jakobsen, 2003; *Ctenocheles chattiensis* Polkowsky, 2004; *Ctenocheles cookei* (Rathbun, 1935), as *Ischnodactylus*; *Ctenocheles cultellus* (Rathbun, 1935), as *Ischnodactylus*; *Ctenocheles dentatus* (Rathbun, 1935), as *Ischnodactylus*; *Ctenocheles falciformis* Collins and Todd in Todd and Collins, 2005; *Ctenocheles hokoensis* Schweitzer and Feldmann, 2001a; *Ctenocheles inaequidens* (Pelseneer, 1886), as *Ischnodactylus*; *Ctenocheles madagascariensis* Secretan, 1964; *Ctenocheles maorianus*, Powell 1949; *Ctenocheles notialis,* new species; *Ctenocheles ornatus* Beschin, De Angeli, Checchi, and Zarantonello, 2005; *Ctenocheles rupeliensis* (Beurlen, 1939), as *Thaumastocheles*; *Ctenocheles secretanae* Schweitzer and Feldmann, 2002; *Ctenocheles sujakui* Imiazumi, 1958; *Ctenocheles valdellae* (Fabiani, 1908), as *Ilia (?)*;*Ctenocheles victor* Glaessner, 1948.

Ctenocheles notialis, new species
(Fig. 3)

Diagnosis.—Major claw with bulbous manus tapering distally into uniformly high, straight fixed finger directed downward at 35° angle from long axis of manus.

Description.—Manus of right, major cheliped ovoid, longer than high; transversely inflated, greatest height appears to be at about midlength. Fixed finger long, broad proximally, tapering rapidly to slender, ovate form with acute tip on lower surface. Finger directed downward at about 35° angle from long axis of manus. Denticles vary in length from about 0.5 mm to 1 mm, pectinate, directed slightly proximally; larger teeth separated by one to four shorter teeth. Terminus of finger curved upward into proximally directed tooth. Other elements missing.

Measurements.—Holotype: length of manus 8.9 mm; height of manus 7.3 mm; thickness > 4.3 mm; length of fixed finger 11 mm. Paratype 1: length of manus 7.7 mm; height of manus 4.3 mm. Paratype 2: length of manus 8.1 mm; length of fixed finger 12.5 mm.

Etymology.—The trivial name is taken from the Latin word *notialis* meaning southern, in reference to the southern latitude from which the specimen was collected.

Types.—The holotype, part and counterpart, SGO.PI. 6554, and three paratypes, SGO.PI. 6555-6557, are deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.—The holotype was collected from the Lacui Formation, early Pliocene, in coastal exposures near Punta Pirulil, south of Cucao, Chiloé Island, Chile at lat. 42°42'S, long. 74°08'W. The paratypes were collected from the Santo Domingo Formation, late Miocene, at Santo Domingo, southwest of CH 207, about 10 km southeast from Valdivia, Chile approximately at lat. 39°53'S, long. 73°10W. This locality is a roadcut near Piedra Blanca.

Discussion.—The bulbous form of the manus of the major claw and the downturned, slender, pectinate fixed finger conforms fully to the morphology of extant and extinct members of *Ctenocheles*. Comparison of the morphology of *C. notialis* with all other fossil species confirms that the specimen from Chiloé is unique. The diagnostic characters noted above represent a plexus of characters that none of the other species possess. The outline of the manus; the height of the fixed finger; the longitudinal profile of the fixed finger, whether straight or curved; the form of the denticles on the occlusal surface; and form of the proximal part of the fixed finger are characters diagnostic of species within the genus. The morphologically most closely related species seems to be *C. maorianus*, originally described as living in soft mud at depths of 19-30 fathoms, and subsequently reported from the Pleistocene of New Zealand (Feldmann and Keyes 1992). The hand is bulbous, the fixed finger lies at an angle of about 30° to the long axis of the manus, and the pectinate denticles are directed slightly proximally. The species differs in that the proximal part of
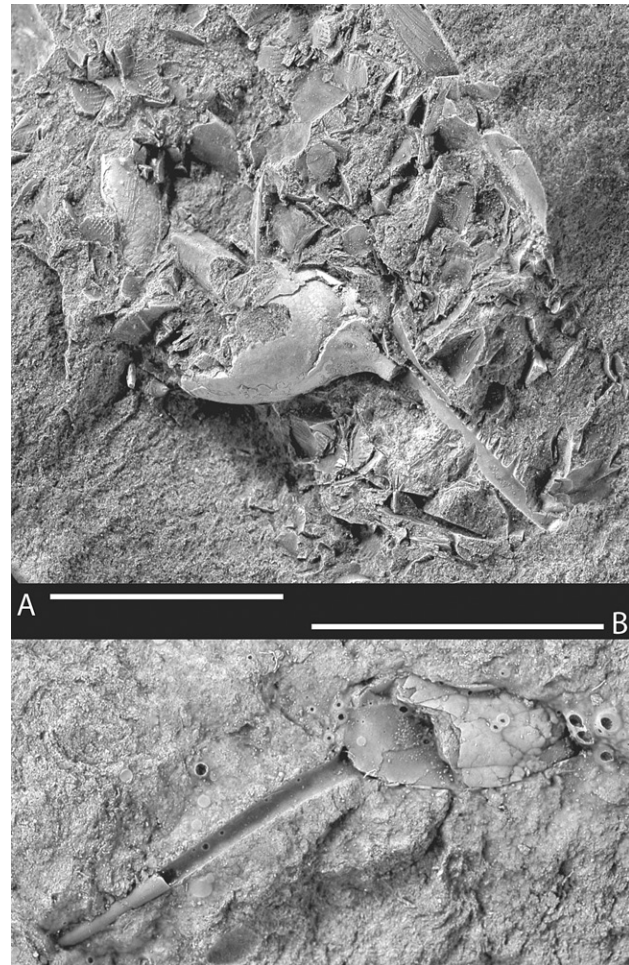

Fig. 3.—*Ctenocheles notialis*, new species. **A**, holotype, SGO.PI. 6554; **B**, paratype, SGO.PI. 6555. Scale bars equal 1 cm.

the fixed finger does not heighten to the same degree in *C. maorianus* that it does in *C. notialis,* and the distal margin of the former species curves more gently and over a greater length of the finger than seen on the latter species. Thus, the specimen from Chiloé represents a new species.

The holotype consists of a broken, corroded major cheliped surrounded by fragments of decapods, probably more fragments of *Ctenocheles*, and fish scales, vertebral centra, other fish parts, and fragments of gastropods. This mass of small fragments forms an ovoid nucleus of a concretion whose long axis is slightly longer than the long axis of the nucleus. Unlike the typical concretions in the Lacui Formation, a mold of a snail with cancellate ornamentation protrudes from one end of the concretion, and the *Ctenocheles* claw extends just to the opposite end of the nucleus. This accumulation of fragments nested within the concretion appears to be a coprolite or regurgitate. The paratypes from the Santo Domingo Formation occur within the matrix of grey, micaceous, sandy siltstone. The presence of the micaceous particles imparts a platy structure to the matrix.
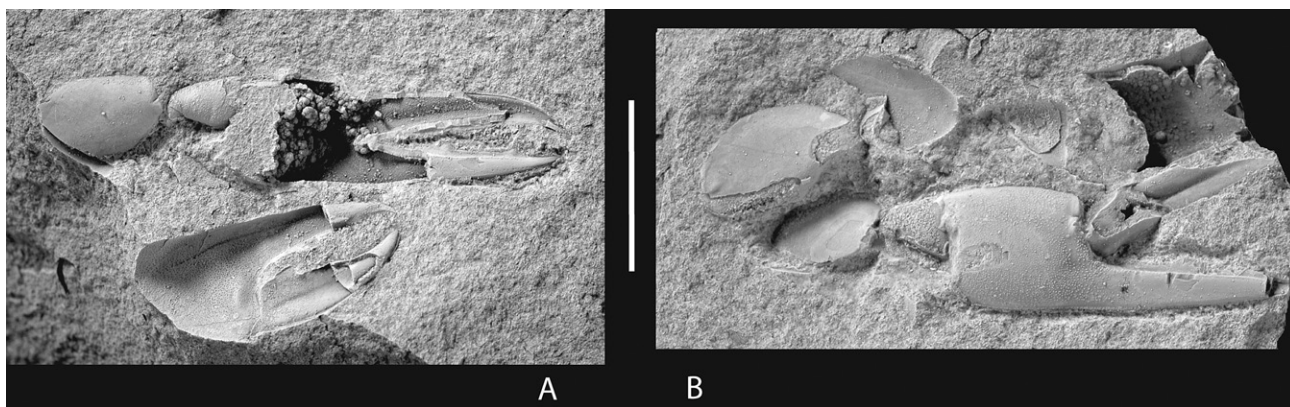
Fig. 4.—*Axianassa? chilensis*, new species. **A**, paratype, SGO.PI. 6559; **B**, holotype, SGO.PI. 6558. Scale bar equals 1 cm.

Family Laomediidae Borradaile, 1903

Included Genera.—*Axianassa* Schmitt, 1924; *Jaxea* Nardo, 1847; *Laomedia* de Haan, 1847; *Laurentiella* LeLoeuff and Intès, 1974 (all have fossil representatives); and *Espeleonaushonia* Juaerro and Martinez-Iglesias, 1997; *Naushonia* Kingsley, 1897 (both lacking a fossil record).

Diagnosis.—See Ngoc-Ho (1997).

Axianassa Schmitt, 1924

Type Species.—*Axianassa intermedia* Schmitt, 1924, by monotypy.

Diagnosis.—See Kensley and Heard (1990).

Discussion.—The specimens can be excluded from most shrimp, lobster, and thalassinidean groups based upon the unusual shape of the carpus. It is very short, and does not extend the entire height of the manus, so that it appears to articulate either with only the upper proximal margin of the manus or with the upper proximal margin and a point part-way along the proximal margin. It does not extend to the lower proximal margin of the manus. The distinctive shape of the carpus, being small, short, triangular, and widening distally, is seen in members of the Laomediidae.

The Laomediidae is not well represented in the fossil record. The existing diagnoses do not list many features that are usually preserved in fossils, but examination of illustrations of species of *Laomedia* (in Ngoc-Ho 1997) and *Axianassa* (in Kensley and Heard 1990), the two most speciose genera in the family, indicate that the carpi are small and widen distally; the meri are ovate; and the mani may be markedly heterochelous. This combination of characters is seen in the specimens described here. The unusual size and shape of the carpus, wherein it is much narrower than both the manus and merus, seems to be characteristic of this family.

Of the six genera currently placed within the Laomediidae, the specimens are best placed within *Axianassa*,

based upon the occurrence of the unusual articulation of the carpus and manus seen in some species of *Axianassa* (illustrations in Kensley and Heard 1990). In addition, members of the Laomediidae, including *Axianassa*, may have strongly heterochelous first pereiopods as seen in the specimens described here. Thus, a questionable referral to *Axianassa*, given the incomplete nature of the material, seems best at this time. *Axianassa* is known from Pacific coastal Panama, coastal Mexico, and the Caribbean in modern oceans (Kensley and Heard 1990).

Within the Laomediidae, only four extinct species are known, including *Jaxea kuemeli* Bachmayer, 1954, from the late Miocene (Tortonian) of Austria (Bachmayer, 1954), *J.* cf. *nocturna* Nardo, 1847, from the Miocene-Pliocene of Spain (Müller 1993), and *Laomedia praestacina* Karasawa, 1989, and *Laurentiella imaizumii* Karasawa, 1993, from the early Miocene of Japan. The one extant species of *Jaxea*, *Jaxea nocturna* Nardo, 1847, has been reported in Pliocene rocks of Italy (De Angeli and Garassino 2006).

Axianassa? chilensis, new species
(Fig. 4)

Diagnosis.—First pereiopods heterochelous; carpus narrow proximally, widening distally, distal margin articulating with upper proximal margin of manus; inner surface of manus of gracile claw with scabrous rows of tubercles; distal margin thickened; inner surface of fixed finger with flattened platform; robust claw with large denticles on fingers.

Description.—First pereiopods heterochelous.

First pereiopod with gracile claw with ovate merus; longer than high; inner surface flattened; distal margin nearly straight. Carpus narrow proximally, widening distally; upper margin nearly straight; lower margin sloping toward lower margin; about as high as long when height measured at highest point; distal margin articulating with upper proximal margin of manus, not entire proximal margin of manus. Manus approximately rectangular, upper and lower margins weakly convex; lower margin with row of setal pits, upper margin with row of tubercles; proximal margin weakly concave; distal margin thickened; inner surface

covered with scabrous ridges of tubercles, tubercles directed distally, ridges oriented parallel to proximal margin. Inner surface of fixed finger with smooth platform on occlusal surface, narrow, sharp teeth on outside edge; inner surface of finger smooth.

Robust claw with granular outer surface of merus, tubercles directed distally; lower margin with rim distally, rim extending onto fixed finger; distal margin with broad, thickened rim. Fixed finger with sharp teeth proximally on occlusal surface. Movable finger stout, high, with stout denticles proximally.

Measurements.—Measurements taken on specimens of *A.? chilensis*, holotype: SGO.PI. 6558: manus length including fixed finger (ML1), >20.0 mm; manus height (MH), 7.4 mm; manus length excluding finger (ML2), 7.9 mm; length of movable finger (MFL), >11.5 mm; carpus length (CL), 4.5 mm; carpus height (CH), 4.0 mm. SGO.PI. 6559 gracile chela: ML1, 22.0 mm; MH, 7.0 mm; ML2, 7.3 mm; MFL, 14.5 mm; CL, 5.2 mm; CH, 3.2 mm; merus length, 8.8 mm; merus height, 5.4 mm. SGO.PI. 6559 robust chela: fixed finger length, 10.8 mm; MFL, 11.0 mm.

Etymology.—The trivial name is derived from Chile, the country from which the material was collected.

Types.—The holotype, SGO-PI. 6558, and two paratypes, SGO-PI. 6559 and 6560, are deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.— The holotype and one paratype, SGO.PI. 6559, were collected from the Lacui Formation, early Pliocene, in coastal exposures near Punta Pirulil, south of Cucao, Chiloé Island, Chile at lat. 42°42'S, long. 74°08'W. One paratype, SGO.PI. 6560, was collected from the Santo Domingo Formation, late Miocene, at Santo Domingo, southwest of CH 207, about 10 km southeast from Valdivia, Chile approximately at lat. 39°53'S, long. 73°10'W. This locality is a roadcut near Piedra Blanca.

Discussion.—The specimens are fragmentary, but because they retain portions of the merus and carpus, we refer them to a new species. More complete material, including complete meri and possibly portions of the carapace, could confirm the generic placement in *Axianassa*. This would mark the most southerly occurrence of the genus in the Americas.

Infraorder Brachyura Latreille, 1802
Superfamily Cancroidea Latreille, 1802
Family Atelecyclidae Ortmann 1893

Trichopeltarion A. Milne-Edwards, 1880

Trichopeltarion A. Milne-Edwards, 1880:19.
Trachycarcinus Faxon, 1893:156.

Type Species.—*Trichopeltarion nobile* A. Milne-Edwards, 1880.

Included Fossil Species.—*Trichopeltarion berglundorum* Schweitzer and Feldmann, 1999; *Trichopeltarion*

decorus (Rathbun, 1945), as *Trachycarcinus*; *Trichopeltarion frassinetti,* new species; *Trichopeltarion granulosa* Schweitzer and Salva, 2000; *Trichopeltarion greggi* Dell, 1969; *Trichopeltarion huziokai* (Imaizumi , 1951), as *Trachycarcinus*; *Trichopeltarion inflatus* (Kato, 1996), as *Trachycarcinus*; *Trichopeltarion levis* Casadío et al., 2004; *Trichopeltarion merrinae* Schweitzer and Salva, 2000.

Diagnosis.—See Salva and Feldmann (2001).

Discussion.—*Trichopeltarion* is a distinctive genus whose species have complex marginal spines, often with a very large spine at the junction of the anterolateral and posterolateral margins. The genus embraces individuals that are pentagonal in outline and others that are nearly circular, and ornamentation of the carapace varies from granular to coarsely nodose, giving them quite a different appearance. However, Salva and Feldmann (2001) illustrated a range from one morphotype to the other in the growth series of a single species. This observation reinforces the unity of the genus despite the broad range of forms.

Extant species of *Trichopeltarion* typically inhabit outer sublittoral to bathyal water depths (Sakai 1976; Guinot 1989; Salva and Feldmann 2001), which is consistent with the interpretation of the Neogene rocks of the Chilean coast in this area being deposited at bathyal depths.

Trichopeltarion levis Casadío et al., 2004
(Fig. 5)

Trichopeltarion levis Casadío, De Angeli, Feldmann, Garassino, Hetler, Parras, and Schweitzer, 2004:35.
Trichopeltarion levis Casadío et al., 2004 in Feldmann et al., 2005:438.

Studied Specimens.—Three specimens, SGO.PI. 6561-6563, deposited in the National Museum of Natural History, Santiago, Chile, were collected from the Santo Domingo Formation at Santo Domingo, southwest of CH 207, about 10 km southeast from Valdivia, Chile approximately at lat. 39°53'S, long. 73°10'W.

Diagnosis.—See Casadío et al. (2004:35).

Description of Material.—Carapace ovoid, moderately vaulted transversely and longitudinally; margins spinose; regions tumid and bearing coarse nodes.

Front broken, downturned weakly and axially sulcate. Upper orbital margin poorly preserved, slightly elevated, with two (?) supraorbital spines. Anterolateral margin convex, with four long, dorsally granular spines; spines radiate from anterolaterally directed to laterally directed; last spine defines anterolateral corner. Posterolateral margin convex, short, bearing two smaller, blunt, coarsely granular spines. Posterior margin appears to be broken.

Carapace regions defined as nodose swellings separated by smooth depressed grooves. Axial regions narrow. Mesogastric region elongate, triangular, with large axial node posteriorly, a smaller node anterior to it, and depressed in anterior half. Mesogastric and urogastric regions not differentiated; transversely ovoid, bearing prominent axial node. Cardiac region with two posterodorsally directed, blunt, granular nodes arrayed transverse to longitudinal axis. Intestinal area not seen. Epigastric and protogastric regions not well separated from one another, broad, elevated, bearing large boss posteriorly and smaller one at midlength; longitudinal
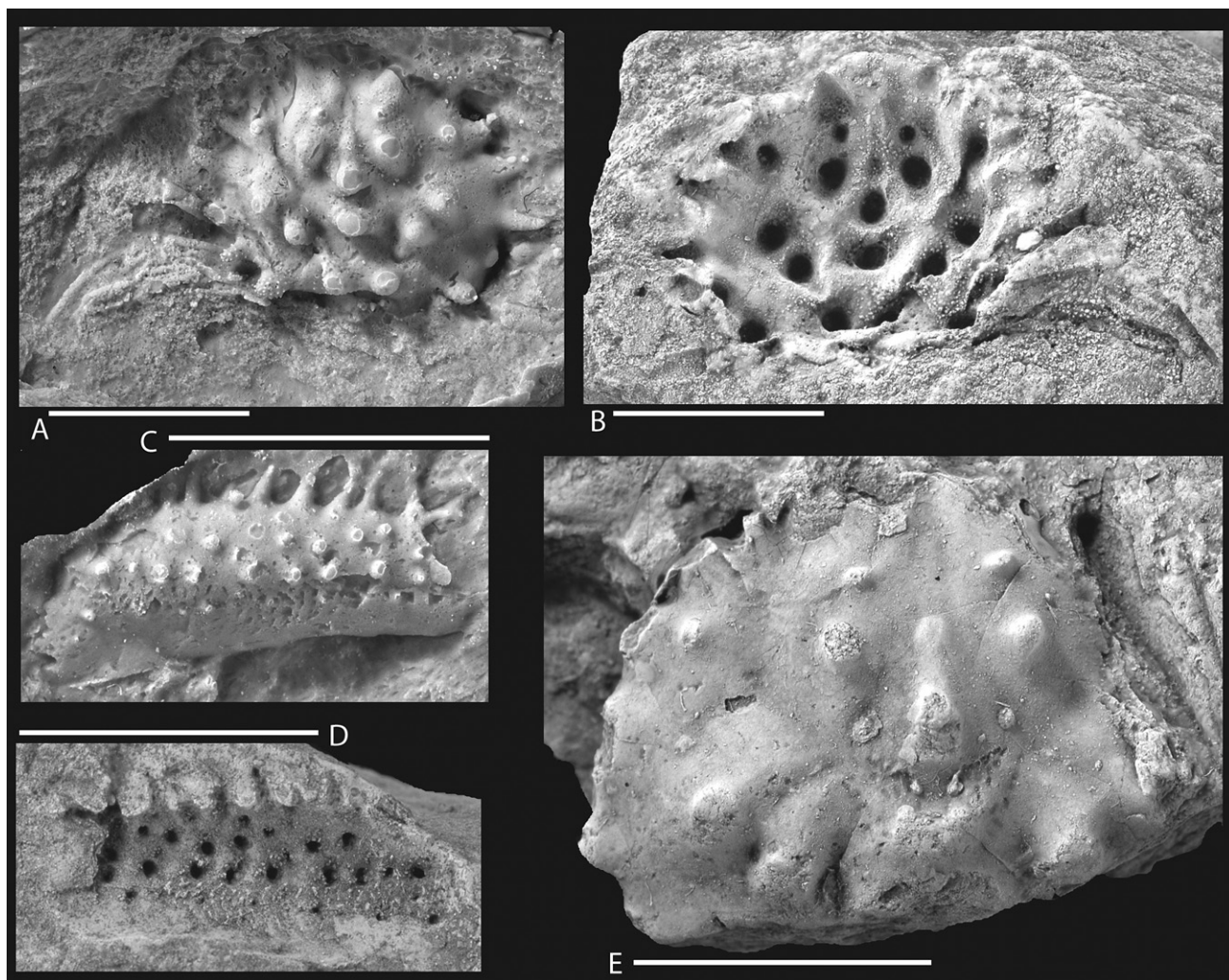
Fig. 5.—*Trichopeltarion levis* Casadío et al., 2004. **A**, latex cast of SGO.PI. 6561; **B**, mold of the exterior of SGO.PI. 6561; **C**, latex cast of SGO.PI. 6563; **D**, mold of the exterior of merus; **E**, partial carapace, SGO.PI. 6562. Scale bars equal 1 cm.

axis of regions converge slightly toward front. Hepatic region weakly elevated, with central node. Branchial regions undifferentiated, bearing large, granular node at level of posterolateral corner and smaller node situated posteriad and axiad of large node.

Cervical groove a concave forward arc around mesogastric region, curving anterolaterally around posterior margin of hepatic region. Branchiocardiac region not expressed.

A single appendage article, interpreted to be the right merus of first pereiopod, three times as long as high; upper surface with at least eight elongate, sharp spines directed upward and distally; outer surface with about 16 blunt nodes arrayed in two longitudinal rows; lower surface appears smooth. Proximal articles of two other appendages on left side of holotype appear to be pereiopods 4 and 5; however, they are too poorly preserved to characterize.

Ventral surface of carapace, abdomen, and other appendages not preserved.

Measurements.—Measurements, taken on the most complete specimen, SGO.PI. 6561, include carapace length = 13.1 mm; width excluding spines, 14.0 mm; width including last anterolateral spine, 21.4 mm. Specimen SGO.PI. 6562 margins not sufficiently preserved. SGO.PI. 6563 merus length of preserved part 12.7 mm; height, excluding spines, 4.8 mm.

Discussion.—The specimens referred to this species match the description and the morphological character of the type specimen in all essential regards. The spinulation on the lateral margins and the number and degree of development of the nodes on the carapace regions precisely match those of the type specimen. The only feature that differs from that of the type specimen is that the lateral spines on the Santo Domingo material are not smooth, but are coarsely granular or finely spined. This difference is probably attributable to exfoliation of the exocuticle on the specimens from the type locality near Bariloche, Argentina, and from the Navidad Formation.

Another apparent difference is that the posterior margin on the most complete specimen from the Santo Domingo

Formation appears to lie at the level of the last posterolateral spines, whereas that of the type specimen is drawn out beyond the last posterolateral spines. The Santo Domingo specimen is a mold of the exterior, and examination of the cast prepared from the specimens reveals that the posterior margin is deformed and is folded anteriorly beneath the carapace. This is documented by noting that the two cardiac spines are rotated to point posteriorly and, at first examination, appear to overhang the posterior margin. This is a taphonomic rather than a true morphologic feature. For this reason, it is not possible to precisely characterize the posterior margin of the Santo Domingo material.

Trichopeltarion frassinetti, new species
(Fig. 6)

Diagnosis.—Carapace circular, rostral region with axial spine larger and extended farther anteriorly than lateral rostral spines; rostral region extends anteriorly beyond remainder of fronto-orbital margin; orbits with complex spinose array; carapace regions granular, generally lacking stronger nodose ornamentation.

Description.—Carapace with circular outline; width, 35.2 mm, nearly equal length, 37.9 mm; moderately vaulted longitudinally, less so transversely; regions defined as nodose swellings separated by distinct, smooth grooves.

Rostrum narrow, extends in advance of orbits, trifid with longer axial and shorter lateral spines directed parallel to long axis; frontal width, 4.3 mm, 12% maximum width. Orbits large, directed anteriorly; inner orbital angle a complex elevation bearing long, upturned medial and two smaller lateral spines; inner orbital structure separated by prominent sulcate reentrant from large, upturned supraorbital spine bearing spinelets; second reentrant separates supraorbital spines from outer orbital complex of prominent broadly triangular spine bearing smaller spinelets; fronto-orbital width, 22.9 mm, 65% maximum width. Anterolateral margin convex, with at least three prominent spines, excluding outer orbital spine, the largest of which is the anteriormost one, and several smaller spines situated between major ones. Posterolateral margin straighter, with at least one prominent complex spine. Posterior margin straight, broadly rimmed.

Frontal region axially sulcate, bounded by lateral elevations bearing row of three nodes on either side of midline. Axial regions narrow, widest at cardiac region, 26.7% maximum width; Mesogastric region arises at level of base of orbits as long, slender elevation broadening at midlength to pentagonal posterior part. Metagastric region wider than long, quadrate, prominently swollen. Urogastric region well defined, narrower, shorter, less swollen than metagastric region. Cardiac region pentagonal with apex directed posteriorly, elevated, with axial and lateral swellings. Intestinal region not well preserved. Protogastric and epigastric regions a single ovoid swelling bounded laterally by circumgastric groove separating it from small, circular hepatic region. Branchial regions a series of low swellings not readily distinguished from one another except for prominent elongate swelling lying adjacent metagastric and urogastric regions.

Cervical groove well defined axially, less so laterally; deeply concave around mesogastric and protogastric regions, becoming straight and directed anterolaterally posterior to hepatic region. Branchiocardiac groove deep, well defined along margins of metagastric, urogastric, and cardiac regions; less well defined along posterior margin of cardiac region; obscure laterally.

Entire surface of regions bears moderately coarse to coarse nodes separated from one another by distance of about 2 mm. Surface between
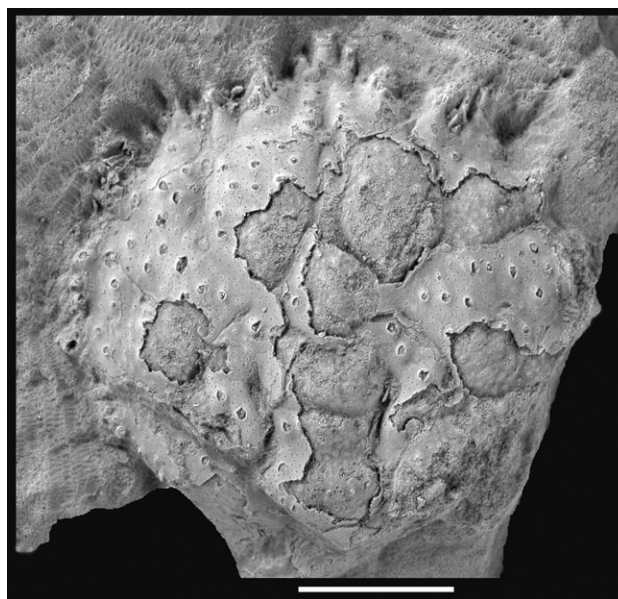

Fig. 6.—*Trichopeltarion frassinetti*, new species, SGO.PI. 6564. Scale bar equals 1 cm.

nodes and carapace grooves finely and uniformly punctate.

Remainder of exoskeleton not preserved.

Etymology.—The trivial name recognizes Daniel Frassinetti, Sección Paleontología, Museo Nacional de Historia Natural, as one of the collectors of the type specimen and for providing access to the collections of the museum and facilitating the loan of specimens.

Holotype.—The holotype and sole specimen, SGO.PI. 6564, is deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.—The holotype was collected at Punta Yáñez, field location #031083, on Isla Guafo, by V. Covacevich and D. Frassinetti, on the cruise of R/V Hero, October, 1983.

Discussion.—Members of the genus *Trichopeltarion* are characterized by having a front bearing three spines, an orbital margin with complex spines separated by prominent gaps, and a margin with compound spines. These, and other characteristics defined by Salva and Feldmann (2001), are all exhibited by the single specimen from Isla Guafo so that it can be referred to the genus with confidence.

The genus *Trichopeltarion* exhibits a range of morphology from having strongly nodose regions and long lateral spines, as seen in *T. levis*, to having a carapace with more subtle regional development ornamented with granules rather than coarse nodes and shorter lateral spines with well developed spinelets. In addition to these differences, there is a range of outlines from pentagonal and longer than wide to nearly circular. This shape difference not only

characterizes different species but also has been documented as an ontogenetic variant. Salva and Feldmann (2001) examined several specimens of *Trichopeltarion fantasticum* Richardson and Dell, 1964, from Castlepoint, New Zealand, and observed that the small individuals were elongate and pentagonal, whereas the larger individuals were nearly circular. It is also noteworthy that the strength of the ornamentation on individuals within this species diminishes with increase in size. The circular outline and subdued carapace ornamentation on *T. frassinetti* suggests that it is a fully mature individual.

T. frassinetti most closely resembles *T. nobile*, type species of the genus from the Caribbean, and *T. fantasticum* known from the Pacific Ocean surrounding New Zealand and *T. greggi* from the Miocene and Pliocene of New Zealand. However, none of these previously described species exhibit the combination of characters seen on the new species. The rostrum on *T. nobile* does not project as far forward as that of the new species, and the medial rostral spine is shorter than the lateral spine on the type species. Furthermore, the orbital spine complex on the type species is not as prominent as the spines on the anterolateral margin. The development and complexity of orbital spines on *T. frassinetti* more closely resembles the array on *T. fantasticum*, but the latter species bears more strongly developed nodes on the metagastric and cardiac regions than on the new species. The surface ornamentation on *T. greggi* is quite similar to that of *T. frassinetti*; however, the medial rostral spine is about equal in size to that of the lateral spines on the former whereas the medial spine is much longer and stronger than the lateral spines on *T. frassinetti*. The spines developed along the lateral margins of *T. greggi* also appear to be more complex than seen on the new species; however, the margins of *T. frassinetti* are not well preserved and some are missing altogether. Thus, this comparison is problematic. Examination of other species within the genus confirm that outline of the carapace, lateral spinulation, and carapace ornamentation are different enough that detailed comparison is not necessary.

Family Cheiragonidae Ortmann, 1893

Included genera.—*Erimacrus* Benedict, 1892; *Karasawaia* Vega et al., 2008; *Montezumella* Rathbun, 1930; *Pirulella,* new genus; *Stintonius* Collins, 2002; *Telmessus* White, 1846.

Pirulella, new genus

Diagnosis.—As for species.

Etymology.—The genus name is derived from Punta Pirulil, the type locality.

Discussion.—The Cheiragonidae is diagnosed by an axially sulcate front that is either bifid or with four spines. The new genus possesses four spines. Species are as long

as wide or slightly longer than wide; the new genus is about as wide as long. The carapace of the new genus is granular, rectangular posteriorly, and possesses carapace regions typical of cheiragonids. It differs from other cheiragonids in appearing to lack an orbital groove or fissure and in having more subdued ornamentation overall.

Other families cannot accommodate the new genus. The Corystidae Samouelle, 1819, although having the same general carapace regions, are much longer than wide and are highly vaulted transversely; the new genus is very flattened. Atelecyclidae have a trifid front. The overall carapace proportions and nature of the front and orbits are unlike those in the Goneplacoidea MacLeay, 1838, or Xanthoidea MacLeay, 1838. Thus, placement within the Cheiragonidae seems most parsimonious.

Superficially, the new genus is similar to members of *Montezumella*; however, species of *Montezumella* have a much broader fronto-orbital width, scabrous ornamentation over the entire carapace; short, serrate spines on the front; small, rounded swellings adjacent to the urogastric region; and a mesogastric region with a more sinuous anterior process. *Stintonius* has larger anterolateral spines and a smoother carapace than does the new genus. *Karasawaia* has much more prominent spines and ridge-like ornamentation on the cardiac and protogastric ridges, absent on the new genus. The new genus is most similar to *Erimacrus*, from which it differs in lacking posterolateral spines. It also appears to have less prominent lateral spines than those seen in *Erimacrus*, although because the margins are damaged in the sole specimen, they may be larger than they appear.

Members of the Cheiragonidae are well known from Central America from Eocene to the present and the Pacific rim today. *Montezumella* is recorded from Eocene through Miocene occurrences of Central America and northern South America (Schweitzer and Salva 2000; Portell and Collins 2002). *Karasawaia* has been reported from Eocene rocks of southern Mexico (Vega et al. 2008). Extant species of *Erimacrus* and *Telmessus* are found in the North Pacific. *Telmessus* extends as far south as California in the East Pacific, and is found in Japan in the West Pacific (Rathbun 1930; Sakai 1976). *Erimacrus* ranges from Alaska to southern Japan in the West Pacific (Rathbun 1930; Sakai 1976).

Pirulella antipodea, new species
(Fig. 7)

Diagnosis.—Carapace hexagonal, length about 96% maximum carapace width, widest at position of last anterolateral spine about 55% the distance posteriorly on carapace; carapace flattened transversely and longitudinally, ornamented with coarse granules overall; orbits very shallow, directed anterolaterally, no immediate evidence of fissures; outer-orbital spine triangular, directed forward; fronto-orbital width about 48% maximum carapace width;

posterolateral margin entire; arcuate reniform swellings parallel lateral margins of cardiac region.

Description.—Carapace hexagonal, slightly wider than long, length about 96% maximum carapace width, widest at position of last antero-lateral spine about 55% the distance posteriorly on carapace; carapace flattened transversely and longitudinally, ornamented with coarse granules overall.

Front poorly preserved, axially sulcate, sulcus bounded by two small spines; inner orbital angle a triangular spine, remainder of front appearing to have been a concave arc between inner spine and inner-orbital spine but not known for certain; frontal width about 27% maximum carapace width. Orbits very shallow, small, rimmed, directed anterolaterally, no immediate evidence of fissures; outer-orbital spine triangular, directed forward; fronto-orbital width about 48% maximum carapace width. Anterolateral margins poorly preserved, with large spine at termination, spine stout with circular base, directed anterolaterally; unknown if other spines present. Posterolateral margin much longer than anterolateral margin; initially straight, then convex where intersected by epibranchial arc, then sinuous and generally weakly convex to posterolateral corner. Posterior margin with weak posterolateral reentrant; posterior margin nearly straight; reentrants and margin rimmed.

Epigastric regions small, equant, weakly inflated, protogastric region pentagonal, broad; hepatic regions short, rectangular, with swelling along lateral margin. Mesogastric region with long, narrow anterior process, terminating between protogastric regions, widened posteriorly. Urogastric region depressed below level of other regions, lateral sides concave. Cardiac region rounded-triangular, most inflated anteriorly, merging posteriorly with flattened intestinal region; arcuate reniform swellings parallel to lateral margins of cardiac region.

Epibranchial regions arcuate, extending from just posterior to last anterolateral spine; arcing sharply anteriorly, then sharply posteriorly to terminate at anterolateral edge of cardiac region. Remainder of branchial region broadly inflated laterally and centrally, flattened somewhat posteriorly.

Measurements.—Measurements taken on the dorsal carapace of SGO.PI. 6565: maximum width = 41.8 mm; maximum length = 40.0 mm; fronto-orbital width = 19.4 mm; frontal width = 11.4 mm; length to position of maximum width = 22.1 mm.

Etymology.—The trivial name is derived from the Latin adjective *antipodean* meaning opposite end in reference to the occurrence in the high southern latitudes whereas extant and fossil cheiragonids are distributed in the Northern Hemisphere.

Types.—The holotype, and sole specimen, SGO.PI. 6565, is deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.— The holotype was collected from the Lacui Formation, early Pliocene, in coastal exposures near Punta Pirulil, south of Cucao, Chiloé Island, Chile at lat. 42°42'S, long. 74°08'W.

Superfamily Portunoidea Rafinesque, 1815
Family Geryonidae Colosi, 1923

Chaceon Manning and Holthuis, 1989

Type species.—*Geryon fenneri* Manning and Holthuis, 1984, by original designation.
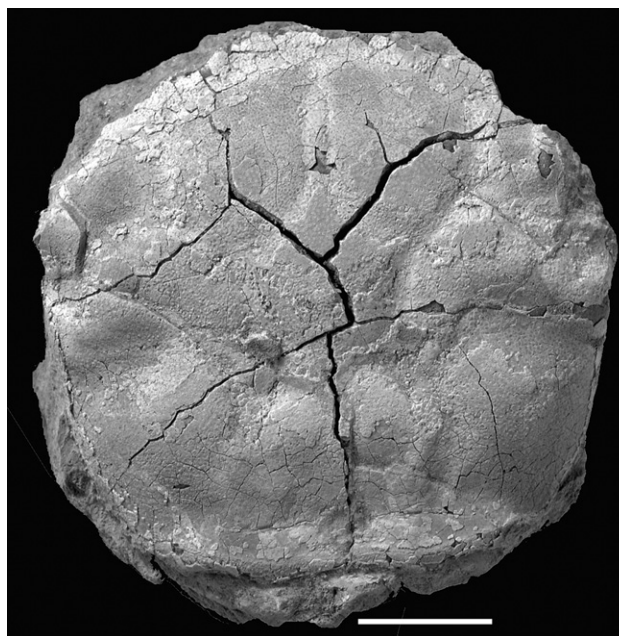

Fig. 7.—*Pirulella antipodea*, new species, SGO.PI. 6565. Scale bar equals 1 cm.

Included fossil species.—*Chaceon heimertingensis* (?) (Bachmayer and Wagner, 1957), as *Geryon*; *Chaceon helmstedtense* (Bachmayer and Mundlos, 1968), as *Coeloma* (?);*Chaceon matsushimai* Kato and Koizumi, 2001; *Chaceon miocenicus* Fraaije et al., 2005; *Chaceon peruvianus* (d'Orbigny, 1842), as *Portunus*; *Chaceon quadrata*, new species.

Chaceon quadrata, new species
(Fig. 8)

Diagnosis.—Carapace nearly as long as wide, regions recognizable as subtle swellings; front with blunt, triangular teeth; medial pair closely spaced and separated by triangular axial reentrant; orbits directed slightly anterolaterally; dactyli of cheliped with longitudinal sulci on inner and outer surfaces.

Description.—Carapace large, quadrate or subtly hexagonal, wider, 68.9 mm, than long, 65.8 mm; L/W = 0.96; weakly vaulted transversely, or strongly vaulted longitudinally particularly in anterior third; regions defined as subtle swollen areas bordered by shallow, smooth grooves.

Front projected in advance of orbits; 32% maximum width measured at about midlength; bearing four blunt nodes and prominent triangular medial notch. Orbits crushed, arcuate reentrants, directed anterolaterally, appearing to bear two shallow fissures; bounded laterally by acute post-orbital spine; fronto-orbital width 60% maximum width. Anterolateral margin shorter than posterolateral margin, weakly convex, with two short spines, the posteriormost largest, and situated at termination of cervical groove. Posterolateral margin smoothly convex, with one weak swelling at level of epibranchial region. Posterolateral corner with thick rim and long, weakly concave outline. Posterior margin 17.8 mm wide, strongly
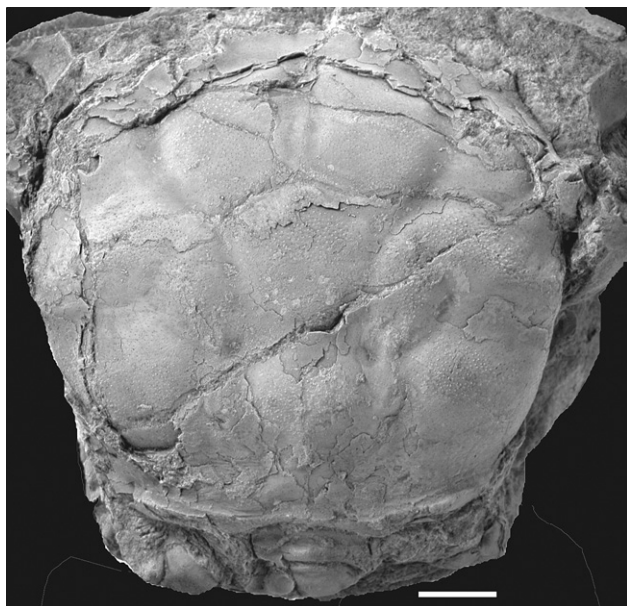
Fig. 8.—*Chaceon quadrata*, new species, SGO.PI. 6566. Scale bar equals 1 cm.

rimmed, strongly concave.

Frontal region weakly sulcate, bounded by small, well-defined epibranchial swellings posterior to medial rostral nodes. Anterior process of mesogastric region a narrow, subtle swelling broadening into pentagonal region posteriorly. Mesogastric region the broadest axial region, bounded posteriorly and laterally by cervical groove which curves laterally at level of maximum width of mesogastric as sinusoidal curve to base of spine at anterolateral corner. Metagastric and urogastric regions not differentiated, narrow, with concave lateral margins defined by broad, arcuate depression ending posteriorly by circular pit. Cardiac region circular, elevated, narrowing posteriorly to weakly elevated intestinal region.

Protogastric regions distinct swellings, slightly longer than wide, separated from triangular hepatic swellings by broad groove. Branchial regions with transversely swollen epibranchial region, longitudinally swollen mesobranchial region, and weakly swollen circular metabranchial region.

Surface of carapace with uniformly closely spaced fine granules and setal pits.

Abdominal somites 1 and 2 as wide as posterior margin; axial part transversely arched and rimmed posteriorly; lateral parts smoothly depressed with quadrate outlines. Remainder of abdomen not exposed.

Chelipeds unequal; the right larger than the left. Merus of chelipeds large; longer, 27.3 mm, than high, 17.7 mm, with prominent downturned spine at distal end of lower margin; inner surface not exposed. Carpus longer, 20.7 mm, than high, 17.2 mm; outer surface granular; lower and inner surface partially broken or obscured; distal margin with weak marginal rim. Propodus of right cheliped at least 49 mm long, poorly preserved. Manus of right propodus 32.8 mm long, 18.0 mm high; proximal margin with prominent rim along propodus-carpus articulation; articulation oriented at about 50° angle to long axis of dactylus; outer surface granular; fixed finger appears darkened, broken near base. Dactylus broad, darkened, and coarsely granular on upper surface narrowing toward occlusal surface; inner and outer surfaces with longitudinal sulci; denticles not visible, tip broken. Other elements of appendages too poorly exposed to describe.

Etymology.—The trivial name alludes to the nearly quadrate outline of the type specimen.

Holotype.—The holotype and sole specimen, SGO.PI. 6566, is deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.—The holotype was collected from the Santo Domingo Formation in a roadcut north of Corral, Chile (lat. 39°53'S, long. 73°26'W) (Fig. 2).

Discussion.—Placement within the Geryonidae and the genus *Chaceon* is based upon the overall outline, being quadrate or weakly hexagonal and wider than long, as well as possession of a front bearing four blunt nodes that projects beyond the orbital margins, relatively broad orbits, and an anterolateral margin that has at least three spines, including the outer orbital spine. The posterior margin is straight and the carapace regions, although visible, are weakly developed. The chelipeds are unequal and are similar to those observed on genera within the Portunidae. The definition of *Chaceon* (Manning and Holthuis 1989) indicated that the genus was further characterized by possession of five anterolateral spines, including the outer orbital spine. The anterolateral margins are poorly preserved on this new species and the number of spines cannot be determined with certainty. Examination of species within the genus does confirm that the development of anterolateral spines can vary considerably, and, for example, those of *C. crosnieri* Manning and Holthuis, 1989, are reduced to the point that at least one of them could be overlooked. Anterolateral spines two, three, and four are described as obsolete in adult *Chaceon ramosae* Manning, Tavares, and Albuquerque, 1989. Another point of comparison that cannot be confirmed with certainty is that the meri of the chelipeds in all Geryonidae bear subdistal dorsal spines. That region on the sole fossil specimen referred to this family has what appears to be broken spine bases in the appropriate position, but confirmation of their form is not possible.

Species within *Chaceon* are distinguished from one-another, from the standpoint of carapace characters, on the basis of the conformation of the frontal area, the nature of the spinulation on the anterolateral margin, overall outline, and degree of development of recognizable carapace regions. *Chaceon quadrata* most closely resembles *Chaceon eldorado* Manning and Holthuis, 1989, in these regards. Both species have a frontal area that is projected well beyond the orbits and the medial two rostral spines are blunt and more closely spaced to one another than they are to the lateral rostral spines. Two of the anterolateral spines on *C. eldorado* are substantially reduced to tiny elevations so that they are not obvious and, given the amount of crushing of the margins on *C. quadrata*, spines of this size could readily be overlooked. The length/width ratio of a male *C. eldorado* is 0.91, whereas that of the new species is 0.95. In this regard, it is interesting to note that Manning and Holthuis indicate that this ratio in species of *Chaceon* ranges from 0.5 to 0.67; however, measurement of illustrations of several species they assign to the genus have ratios varying from 0.75 to 0.91, and 1.01 in *C. ramosae*,

described by Manning et al. (1989). Thus, these dimensions are not necessarily good generic descriptors. The two species can be distinguished because the orbits are directed forward in *C. eldorado* and anterolaterally in *C. quadrata*. Also, the fronto-orbital width of the extant species is 52% the maximum width and 60% in the new species.

Chaceon quadrata differs from the common South American fossil species of *Chaceon, C. peruvianus*, in several ways. The new species is more quadrate, with a L/W ratio of 0.95, as opposed to 0.82 for *C. peruvianus*. The individual spines on the front of *C. peruvianus* are narrower and more discrete than they are on the new species. The fronto-orbital width on *C. peruvianus* is 52% the carapace width and 60% on *C. quadrata*. Further, the orbits are directed forward in the former species and more laterally in the new species. Additionally, the anterolateral spines on *C. peruvianus* are much more strongly developed than they are on the new species. Thus, the two species cannot be confused with one another. The other fossil species assigned to the genus differ significantly from the new species as well. *Chaceon heimertingensis*, from the late Oligocene of Germany, is questionably referred to the genus because, although it has the proper overall outline and anterolateral spine development, it is not well preserved. It is much wider than long. *Chaceon helmstedtense*, also from the Oligocene of Germany, has much stronger development of anterolateral spines; *C. matsushimai*, from the Plio-Pleistocene of Japan, has a well rounded outline; and *C. miocenicus*, from the Miocene of Denmark, is transversely and longitudinally much less inflated than the new species and the regions are less well defined. Thus, *C. quadrata* is unique.

Extant species of *Chaceon* are considered deep-sea organisms. Manning and Holthuis (1989) recorded a range of depths from which different species had been collected from 120 to over 2800 meters. Presence of *C. quadrata* in Neogene sediments of the Chilean coast is consistent with independent determinations of bathyal depositional depths cited above.

Geryon Krøyer, 1837

Type Species.—*Geryon tridens* Krøyer, 1837, by monotypy.

Included Species.—*Geryon longipes* A. Milne-Edwards, 1882; *Geryon manningi,* new species; *Geryon trispinosus* (Herbst, 1803), as *Cancer* (=*Geryon tridens* Krøyer).

Diagnosis.—Carapace typically hexagonal, wider than long, with three anterolateral teeth, including outer orbital tooth. Frontal teeth small, set close to midline. Orbits rounded with inner tooth on suborbital margin. Branchial regions not inflated. Chelipeds like portunids, merus and carpus with distal or subdistal spines.

Discussion.—When Manning and Holthuis (1989) erected *Chaceon*, they restricted the genus *Geryon* to those forms bearing only three anterolateral spines. As such, the number

of extant species known was two. To our knowledge no fossil representatives have been correctly assigned to *Geryon* until now. The Geryonidae are represented in the Western Hemisphere only by species of *Chaceon* (Boschi 2000) so that the discovery of a fossil *Geryon* defines the earliest occurrence of a genus which is now confined to the eastern Atlantic in the Northern Hemisphere.

The fossil Geryonidae is commonly represented in the Neogene of South America by *C. peruvianus*, discussed above and exhibiting five anterolateral spines, and by *Archaeogeryon fuegianus* Colosi, 1923. This latter species has not been studied in detail by us, but it appears to be a geryonid, based upon illustrations by Aguirre-Urreta (1987). Possession of four anterolateral spines and orbits that are wider than those seen in *Geryon* species exclude it from *Geryon*. Thus, the addition of a species to *Geryon* adds a third genus to the list of South American occurrences.

Geryon manningi, new species
(Fig. 9)

Diagnosis.—Carapace moderately vaulted longitudinally, primarily in the anterior third; anterolateral margin with three spines increasing in size posteriorly; outer frontal spines reduced to swellings; suborbital margin smooth, complete, terminating axially in small, blunt spine; carapace regions moderately well defined.

Description.—Carapace hexagonal; wider, 49.5 mm, than long, 41.1 mm; width measured at position of last anterolateral spine but excluding spine; moderately vaulted transversely, more so longitudinally, particularly in anterior third; regions well developed and delimited by relatively broad, shallow grooves.

Front generally straight to biconcave, 23% maximum width measured at about midlength, with two small, short, upturned spines adjacent to midline and subtle spine at frontal corners; margin beaded. Front not projected beyond orbits. Orbits large, fronto-orbital width 63% maximum width, directed forward and upward, with distinct medial projection on biconcave upper margin; rim beaded. Lower orbital margin complete, projected well in advance of upper margin, terminating axially in a small, blunt spine.

Anterolateral margin short, convex, with three equally-spaced spines including small outer orbital spine; posteriormost spine longest, directed laterally. Posterolateral margin smoothly convex. Posterolateral corners with wide, weakly concave reentrant. Posterior margin 34% maximum width, nearly straight.

Frontal region weakly depressed between orbits. Epigastric regions barely discernable. Mesogastric region pyriform, arising posterior to level of orbits; posterior part of region with two low, broad swellings. Mesogastric and urogastric regions not differentiated; bounded laterally by concave branchiocardiac grooves. Cardiac region pentagonal, swollen, well defined laterally by branchiocardiac grooves. Intestinal region short, not well defined.

Protogastric regions prominent, with transverse swelling at level of domed swelling on hepatic region. Posterior margin of hepatic and protogastric regions defined by broad, convex-forward cervical groove which curves in smooth concave-forward arc around mesogastric region. Epibranchial region strongly inflated transverse ridge bounded anteriorly by cervical groove and posteriorly by convex-forward lateral extensions of branchiocardiac groove. Mesogastric and metagastric regions swollen, not differentiated.
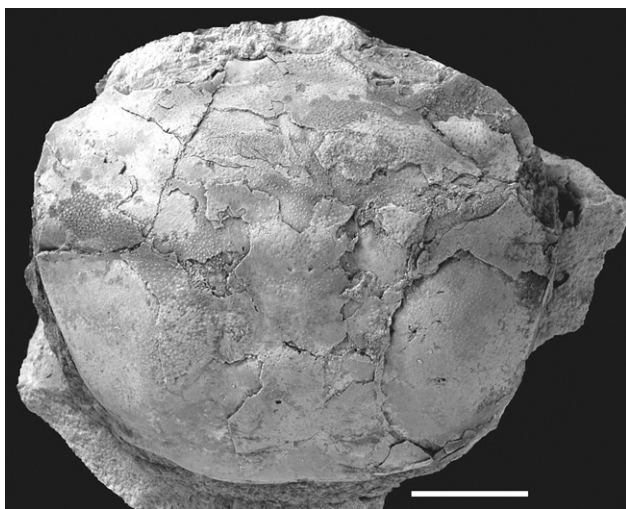
Entire surface finely and uniformly granular.

Fig. 9.—*Geryon manningi*, new species, SGO.PI. 6567. Scale bar equals 1 cm.

Etymology.—The trivial name honors the late Dr. Raymond Manning, who, with L. B. Holthuis, clarified our understanding of the Geryonidae, facilitated the work of RMF and CES at the Smithsonian Institution until his death, and provided them with new insights into the systematics of decapods.

Holotype.—The holotype and sole specimen, SGO.PI. 6567, is deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.— The holotype was collected from the Lacui Formation, early Pliocene, in coastal exposures near Punta Pirulil, south of Cucao, Chiloé Island, Chile at lat. 42°42'S, long. 74°08'W.

Discussion.—Placement within *Geryon* is based upon the close correspondence between the diagnostic characters of the species and those of the genus (Manning and Holthuis 1989:51). Examination of illustrations of the two extant species indicates that the relative proportions of the carapace of the holotype match those of the living forms and differ from some of the relative proportions of species of *Chaceon*. The length/width ratio of *G. manningi* is 0.83, whereas it is 0.82 on *G. trispinosus* and 0.87 on *G. longipes*. The frontal width/width ratio is 0.23 on the new species, 0.22 on the type species, and 0.26 on *G. longipes*. The fronto-orbital width/width ratio of *G. manningi* is 0.61, and it is 0.62 on *G. trispinosus* and 0.61 on *G. longipes*. Thus, there are no significant differences in relative proportions between the extant and fossil representatives of *Geryon*.

The frontal region of the new species most closely resembles that of *G. longipes* in that the front does not extend beyond the orbits and the lateral frontal spines are reduced to subtle projections. The front of the type species extends beyond the orbits and the frontal spines are

somewhat more strongly developed. The form of the anterolateral spines on *G. manningi* are relatively blunt as they are on *G. trispinosus*, but they diminish in size anteriorly on the former to a much greater degree than on the two extant species. Therefore, *G. manningi* can be placed within the genus with certainty, but it can be readily distinguished from other members of the genus.

Family Macropipidae Stephenson and Campbell, 1960

Proterocarcinus Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995

Type Species.—*Proterocarcinus lophos* Feldmann et al., 1995, by monotypy.

Included Species.—*Proterocarcinus corsolini* Casadío et al., 2004; *Proterocarcinus latus* (Glaessner, 1933), as *Archaeogeryon*; *Proterocarcinus lophos* Feldmann et al., 1995; *Proterocarcinus navidad* Feldmann et al., 2005.

Diagnosis.—See Feldmann et al. (2005).

Proterocarcinus navidad Feldmann, Schweitzer, and Encinas, 2005
(Fig. 10)

Material Studied.—Five specimens, SGO.PI. 6568-6572, were studied from the Miocene Lacui Formation at Punta Pirulil, near Cucao, Chiloé, Chile, and 22 specimens, SGO. PI. 6773-6594, were studied from the Santo Domingo Formation in the vicinity of Valdivia, Chile. The specimens are deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.— Five specimens studied herein, were collected from the Lacui Formation, Miocene, in coastal exposures near Punta Pirulil, south of Cucao, Chiloé Island, Chile at lat. 42°42'S, long. 74°08'W. Eighteen specimens were collected from the Santo Domingo Formation at Santo Domingo, southwest of CH 207, about 10 km southeast from Valdivia, Chile approximately at lat. 39°53'S, long. 73°10W. One additional specimen was collected from the Santo Domingo formation at La Piedra, a roadcut near Piedra Blanca, about 8 km southeast from Valdivia, Chile at approximately lat. 39°S, long. 73°10'W. Three other specimens were collected from the same unit at Corral, 12 km west southwest from Valdivia approximately at lat. 39°53'S, long. 73°26'W.

Discussion.—*Proterocarcinus navidad* is most readily distinguished from other members of the genus because it bears only two anterolateral spines, the outer orbital spine which is very prominent and the spine defining the posterior termination of the anterolateral margin. Other members of the genus exhibit three or four spines on this margin. Further, the orbital margin is divided into a deeply indent-

ed inner segment that is separated from a nearly straight outer segment by a shallow fissure. In other regards the species is similar to the other known species.

Proterocarcinus navidad is the only species within the genus that is known from Chile. All others are found on the eastern side of the Andes in Argentina where it is quite widespread. Comparison of specimens collected from the type localities near Matanzas with those from the region of Valdivia and Cucao certainly confirm placement within the species. The form of the orbits and the presence of only two spines on the anterolateral margin in addition to the general conformation of the carapace regions makes placement within *P. navidad* certain.

Proterocarcinus navidad seems to be a much more common member of the Santo Domingo Formation than of the Lacui Formation. In the latter unit at Punta Pirulil, only five relatively complete specimens were collected whereas 21 nearly complete specimens were collected from the Santo Domingo Formation. Although this difference might be attributable to collecting bias, that is not thought to be the case. A large number of concretions were collected at Punta Pirulil and the overwhelming majority contained specimens of *Pilumnus cucaoensis* Feldmann et al., 2005. Collections of decapods from the Santo Domingo Formation were strongly dominated by *P. navidad* The manner of preservation of specimens from the two formations is quite different, owing in all probability to the different nature of the enclosing sediment. In the Lacui Formation at Punta Pirulil, *P. navidad*, along with the other decapods, is preserved as inflated specimens with well preserved cuticle. The mean width of the specimens is about 37 mm; specimens range from a width of 30.1 mm to 41.4 mm. In the Santo Domingo Formation the specimens are typically crushed flat, the calcitic material within the cuticle has been leached out, and what remains of the cuticle is typically shattered into small fragments. The mean width of the specimens in this formation is about 25 mm with specimens ranging from a width of 8.3 mm to 34.7 mm. The distribution of sizes in the Santo Domingo Formation suggests that three age classes may be present. The widths of two specimens lie between 8 and 10 mm, three specimens range from 14–19 mm, and 16 specimens range from 23–35 mm. This latter size is the only one represented in the Lacui Formation. Thus, although the manner or preservation of specimens in the Santo Domingo Formation is less good, the sample may more closely represent the population structure of the unit than that seen in the Lacui Formation.

The manner of occurrence of the species in the two formations is also different. At Punta Pirulil, *P. navidad* occurs within carbonate-cemented concretions enclosed in soft, grey shale. In the Santo Domingo Formation at La Piedra and Santo Domingo, the specimens occur in the matrix of micaceous silty sand, whereas they occur in limonite-cemented concretions at the Corral locality. It is possible that the micaceous sediments of the Santo Domingo Formation are water-laid sediments of volcanic
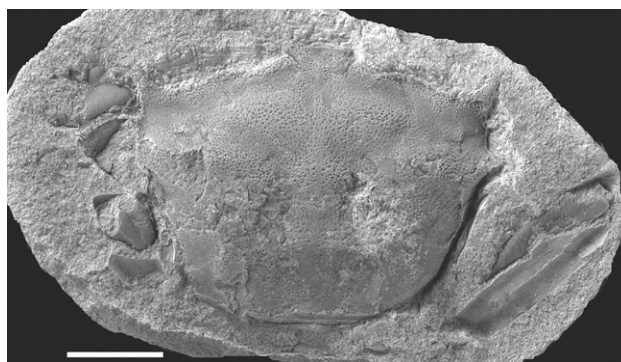

Fig. 10.—*Proterocarcinus navidad* Feldmann et al., 2005, SGO.PI. 6568. Scale bar equals 1 cm.

origin, similar perhaps to those described by Crawford et al. (2008) from Argentina. Rapid deposition of these volcanic sediments could kill the benthic fauna indiscriminately and bury them rapidly. These same sediments would lower the pH of the sediments which may account for the loss of calacaeous material in the cuticle and subsequent flattening of the carapace. It is notable that the specimens studied by Crawford et al. (2008) from the Monte Leon Formation were not flattened; thus, the occurrences are not identical. Preservation of the specimens in the Monte Leon Formation likely occurred under more normal marine conditions where the pH was high enough that carbonate material was preserved and the original convexity of the carapaces was retained.

Family Portunidae Rafinesque, 1815

Included genera.—*Euphylax* Stimpson, 1862 (extinct and extant); *Pheophthalmus,* new genus (extinct); *Podophthalmus* Lamarck, 1801 (extinct and extant); *Psygmophthalmus* Schweitzer et al., 2006b (extinct); *Sandomingia* Rathbun, 1919 (extinct); *Saratunus* Collins et al., 2003 (extinct).

Diagnosis.—See Karasawa et al. (2008).

Discussion.—The Podophthalminae has been well summarized recently (Schweitzer et al. 2006b; Karasawa et al. 2008). The new genus is most similar to *Podophthalmus* in overall shape and in having the widest portion of the carapace at the orbital margins and in having one anterolateral spine. However, no species of *Podophthalmus*, and no species of any genus within the Podophthalminae, possesses the spined orbital margins seen in *Pheophthalmus mochaensis,* new species.

The new occurrence reported herein is Miocene in age from coastal Chile. The other reported occurrences of the subfamily are generally Miocene in age or younger and mostly Caribbean or Indo-Pacific in distribution. Thus, the new genus is outside the general known distribution for the subfamily, although still Pacific in distribution. The occurrence
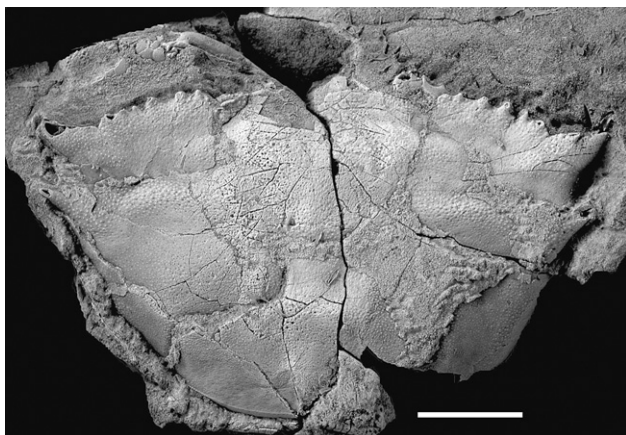
Fig. 11.—*Pheophthalmus mochaensis*, new species, SGO.PI. 6595. Scale bar equals 1 cm.

of another extinct genus within this family suggests that its peak diversity occurred during the Miocene-Pliocene time and that the remaining extant species are relicts of its former diversity.

Karasawa and Kato (2003) moved *Ommatocarcinus zanquieyi* Via, 1959, to the podophthalmine *Euphylax*. Subsequently, Karasawa et al. (2008) erected a new genus for a species that had been referred originally to the goneplacid genus *Ommatocarcinus* White, 1852, later placed within the podophthalmine genus *Euphylax*, and then removed from that genus. They placed the resulting new taxon, *Viaophthalmus zariquieyi* (Vía, 1959), within the Podophthalminae with reservations. Examination of some taxa of Goneplacidae illustrated by Castro (2007) suggests that they are superficially similar to *Viaophthalmus*. *Viaophthalmus* is characterized by very long orbital margins that are oriented obliquely posteriorly, produced outer-orbital spines, a carapace that is about as wide as long, transverse keels on the dorsal carapace, sternite 8 clearly visible in males, and an anteriorly produced front. These features are seen in several genera well-illustrated by Castro (2007), notably *Singhaplax* Serène and Soh, 1976; *Neogoneplax* Castro, 2007; and *Microgoneplax* Castro, 2007. However, *Viaophthalmus* has fused abdominal somites 3-5; whereas those somites are free in typical genera within the Goneplacidae. Thus, we retain *Viaophthalmus* within the Podophthalminae. Notably, the genera discussed by Castro are Indo-Pacific, whereas *Viaophthalmus* is from the Eocene of Spain.

Pheophthalmus, new genus

Type species.—*Pheophthalmus mochaensis,* new species, by monotypy.

Diagnosis.—as for species.

Description.—as for species.

Etymology.—The genus name is derived from the Greek words *pheos*, meaning spiny plant, and *ophthalmos*, meaning eye, in reference to the spiny orbital margins in this taxon. The gender is masculine.

Pheophthalmus mochaensis, new species
(Fig. 11)

Diagnosis.—Carapace wider than long, widest at position of outer-orbital spines; upper orbital margins serrate proximally, bearing about nine spines distally including outer orbital spine; outer-orbital spine long, extending anterolaterally.

Description.—Carapace wider than long, length about 60% maximum carapace width measured at bases of outer-orbital spines; carapace narrowing distally, flattened transversely and longitudinally.

Front missing, appearing to have been narrow, widening distally. Orbits very broad, fronto-orbital width occupying 97% maximum carapace width; upper orbital margins serrate proximally, bearing about nine spines distally including outer orbital spine; outer-orbital spine long, extending anterolaterally.

Anterolateral and posterolateral margins confluent; anterolateral portion bearing one spine; posterolateral portion weakly convex, with beaded rim posteriorly. Posterior margin weakly convex, rimmed.

Protogastric regions weakly inflated, short, narrow; hepatic region wider than long, very short, with swellings proximally and distally along orbit. Axial regions poorly marked; mesogastric region with long anterior process; urogastric region depressed below level of mesogastric and cardiac regions, with concave lateral margins; cardiac region poorly marked, with transverse crest centrally. Intestinal region not well known.

Epibranchial region arcuate, ridge-like, positioned very far anteriorly; consequently, remainder of undifferentiated branchial regions very long, weakly inflated.

Chelipeds appearing to have been short.

Measurements.—Measurements taken on the dorsal carapace of the holotype and sole specimen of *P. mochaensis*: maximum carapace width, 53.2 mm; maximum carapace length, 31.7 mm; fronto-orbital width, 51.8 mm.

Etymology.—The trivial name is derived from the type locality, La Mocha.

Type.—The holotype, and sole specimen, SGO.PI. 6595, is deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.—The holotype was collected from the north coast of Mocha Island from rocks assigned to the Ranquil Formation which, based upon enclosed fossils, is Miocene in age.

Discussion.—The holotype and sole specimen of *P. mochaensis* has very well-preserved orbital margins with obvious spines and serrations. This combination of characters is unique within the subfamily. Its occurrence on an island might account for divergence of the morphology of this taxon from other members of the subfamily. It is also one of the oldest occurrences of the family.
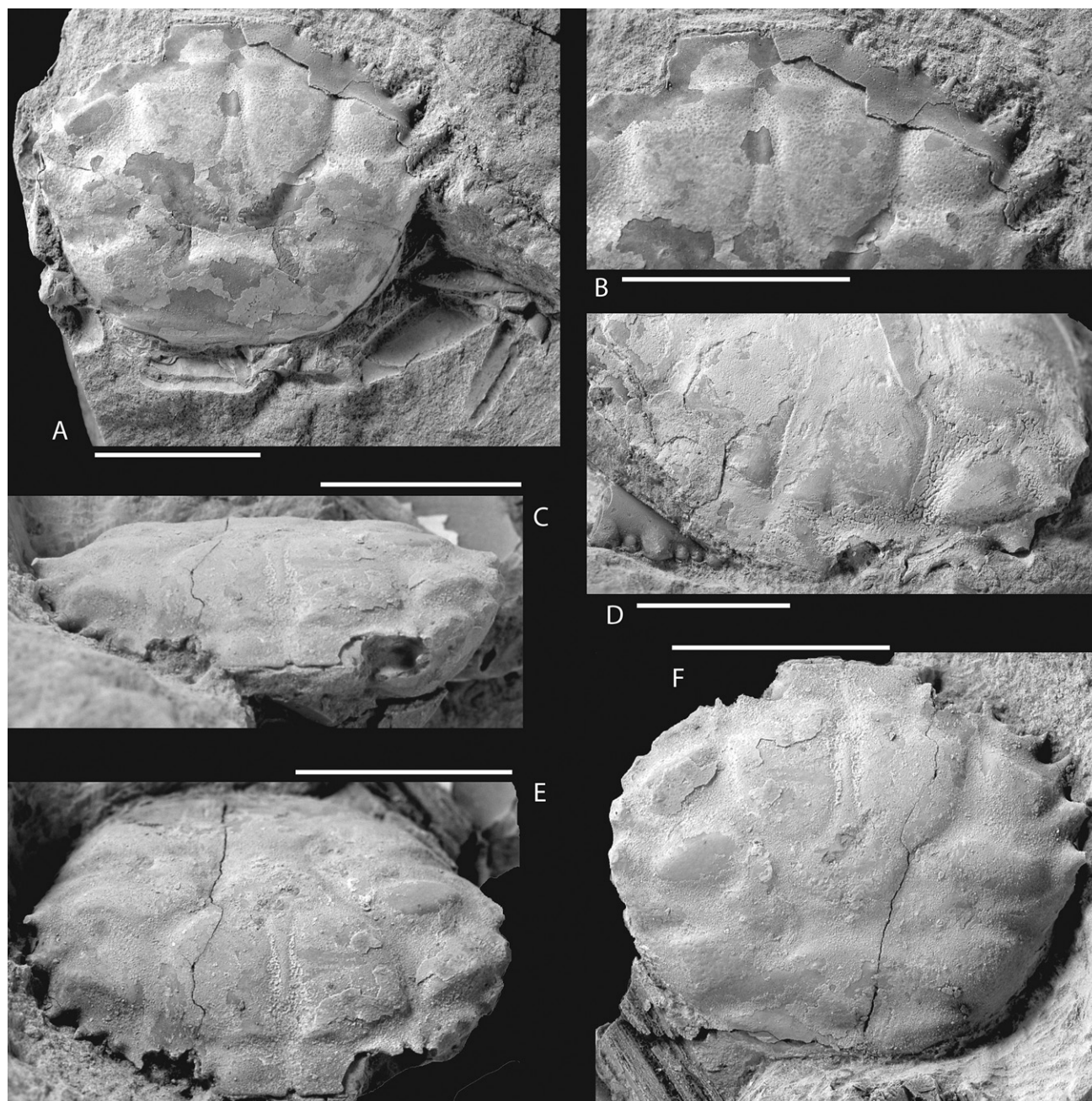
Fig. 12.—*Pilumnus cucaoensis* Feldmann et al., 2005. **A**, SGO.PI. 6596; **B**, close-up of right anterolateral corner of SGO.PI. 6596 showing details of spines; **C**, **E**, **F**, frontal, oblique frontal, and dorsal views of SGO.PI. 6597; **D**, oblique view of left anterolateral part of SGO.PI. 6598. Scale bars equal 1 cm.

Superfamily Xanthoidea MacLeay, 1838
Family Pilumnidae Samouelle, 1819

Pilumnus Leach, 1816

Included Fossil Species.—*Pilumnus cucaoensis* Feldmann et al., 2005; *Pilumnus fookimensis* Collins et al., 2003; *Pilumnus hirtellus* (Linnaeus, 1761); *Pilumnus hirtellus* var. *villosa* Risso, 1826; *Pilumnus mediterraneus* (Lörenthey, 1898); *Pilumnus olivellae* Müller, 1993; *Pilumnus pannosus* Rathbun, 1898; *Pilumnus sayi* Rathbun, 1897; *Pilumnus spinossimus* Rathbun, 1898; *Pilumnus subequus* Rathbun, 1919; *Pilumnus villosissimus* (Rafinesque, 1814); *Pilumnus* sp. in Förster, 1979; *Pilumnus* sp. in Karasawa, 1990; *Pilumnus* sp. in Kato and Karasawa, 1998.
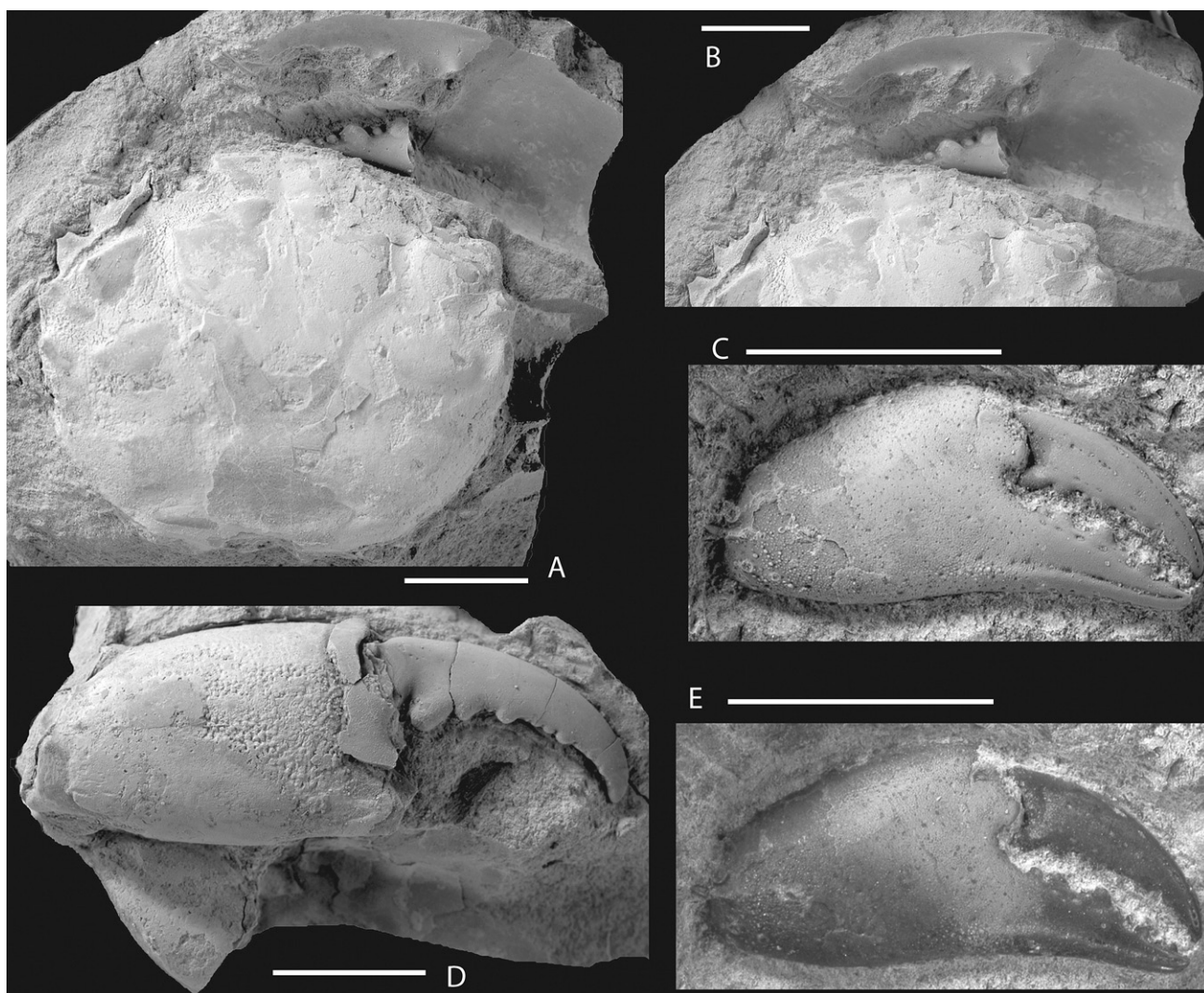
Fig. 13.—*Pilumnus cucaoensis* Feldmann et al., 2005. **A**, dorsal view of SGO.PI. 6598 showing mold of right cheliped; **B**, close-up of right cheliped of SGO.PI. 6598 showing preserved tip of fixed finger; **C**, **E**, whitened and unwhitened views of right cheliped, SGO.PI. 6600; **D**, relatively large right cheliped, SGO.PI. 6599. Scale bars equal 1 cm.

Pilumnus cucaoensis Feldmann, Schweitzer, and Encinas, 2005
(Figs. 12–14)

Material Studied.—The holotype, SGO.PI. 6331 and the 28 specimens studied herein, SGO.PI. 6596-6623, and deposited in the National Museum of Natural History, Santiago, Chile, were collected from the Lacui Formation at Punta Pirulil, near Cucao, Chiloé, Chile, and one specimen was studied from the Santo Domingo Formation in the vicinity of Valdivia, Chile.

Localities and Stratigraphic Position.—Twenty-seven specimens studied herein, were collected from the Lacui Formation, Miocene, in coastal exposures near Punta Pirulil, south of Cucao, Chiloé Island, Chile at lat. 42°42'S,

long. 74°08'W. One other specimen was collected from the Santo Domingo Formation at Corral, 12 km west southwest from Valdivia approximately at lat. 39°53'S, long. 73°26'W.

Discussion.—This species was recently described (Feldmann et al. 2005), based upon specimens collected from Chiloé Island by Feldmann and Luis Chirino-Gálvez in 1991, and by Sven Nielsen. Additional specimens were collected from the Navidad Formation along creek beds between Matanzas and Pupuya. Because the focus of that work was primarily on the Navidad Formation, little reference was made to the occurrences on Chiloé Island.

Only two minor additions can be made to the original description of the species. Excellent preservation of the cuticle surface on the frontal region of one specimen
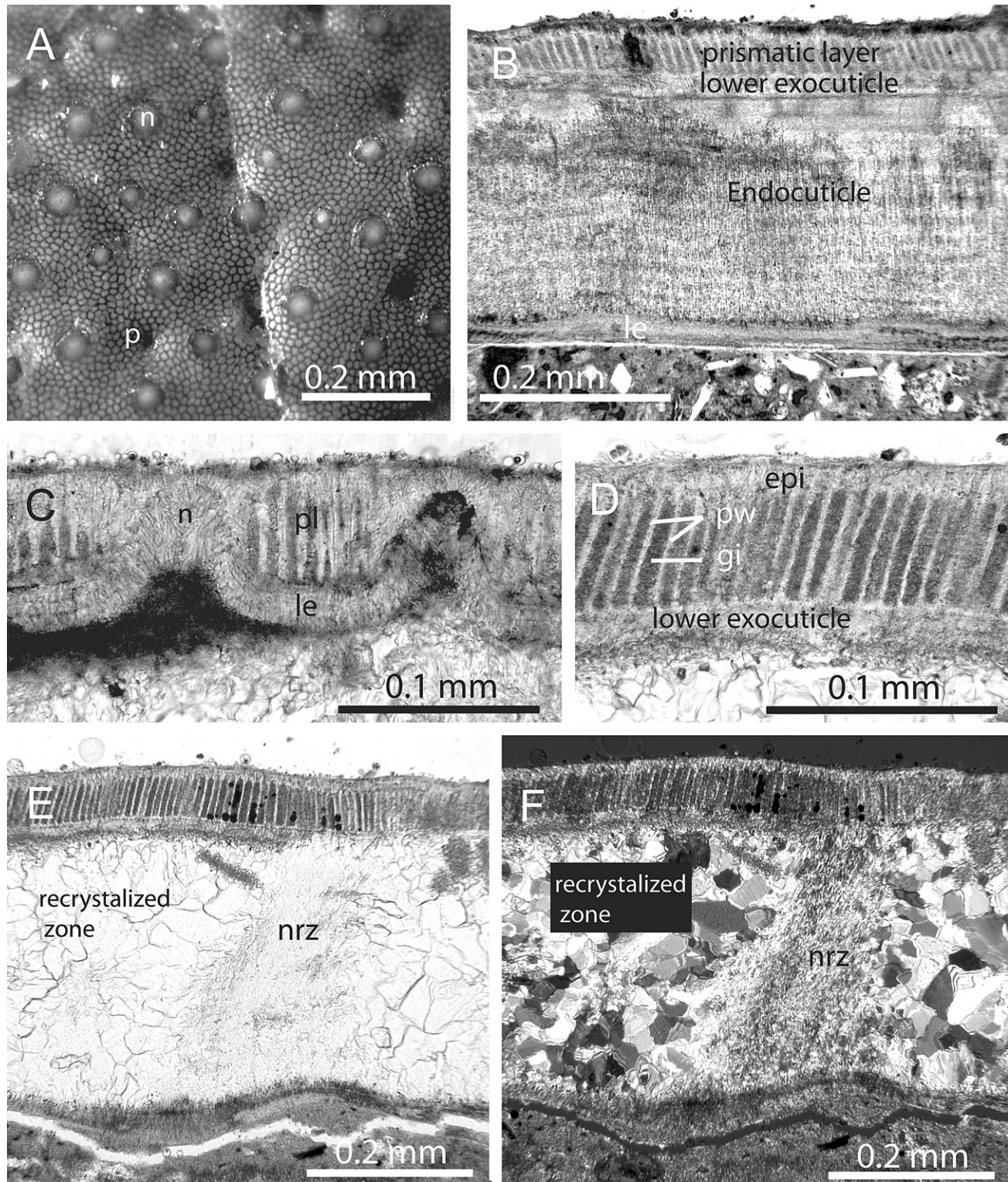
Fig. 14.—Details of cuticle of *Pilumnus cucaoensis* Feldmann et al., 2005. **A**, external surface of well-preserved cuticle; **B**, thin section of entire cuticle thickness showing cuticular layers, plane polarized light; **C**, upward projection of lower exocuticle into prismatic layer to produce nodes, plane polarized light; **D**, prismatic layer, plane polarized light; **E**, **F**, plane polarized and cross polarized view of recrystallized and non-recrystallized regions within the endocuticle. **epi**, epicuticle; **gi,** granular interior of prism; **le,** lower exocuticle; **n,** node; **nrz,** non-recrystallized zone; **p,** pit; **pl,** prismatic layer; **pw,** prism wall. Scale bars as indicated on figure.

documented a very finely beaded margin of the front and the upper orbital margin. Additionally, a single specimen preserved a very long last anterolateral spine that was slender and curved slightly upward. Presence of this spine had been noted but its length could not be determined from the type series.

In the vicinity of Punta Pirulil south of Cucao, where specimens of this species were collected from the Lacui Formation, *P. cucaoensis* was overwhelmingly the most common decapod, and likely the most common of all the fossils. It is difficult to count the number of specimens accurately because many are fragments, and some are counterparts that have not been matched with the part. Nevertheless, 29 specimens are nearly complete carapaces and at least twice as many partial specimens are also present in the collections. The second most common decapod, *Proterocarcinus navidad* is represented by five reasonably complete specimens and an equal number of fragmentary remains. The other taxa reported from the area are represented by from one to three specimens.

In the Santo Domingo Formation where *P. navidad* is the dominant fossil decapod, only one specimen of *P. cucaoensis* has been identified, suggesting that either the environmental conditions did not favor its survival there or that the manner of preservation in the Santo Domingo Formation, with a relatively low pH, reduced the preservational potential of the species. The former would seem to be the more likely possibility.

Of the specimens representing *P. cucaoensis*, 27 were complete enough to permit characterizing the range of sizes of the individuals. The maximum width of the specimens, excluding the anterolateral spine, was 34.9 mm and the minimum width was 20.8. The length-to-width ratio varied from 0.77 to 0.89, with a mean value of 0.83. Because only one of the measured specimens, a male, exposed the ventral as well as dorsal surface, it was not possible to determine the ratio of males to females.

The specimens in the Lacui Formation were all preserved within spherical to ovoid, carbonate concretions. The concretions varied in size from a minimum diameter that just encircled the carapace and preserved legs to a maximum of more than three times the maximum width of the enclosed carapace. This is in marked contrast to the size of concretions encircling *Chasmocarcinus chiloeensis,* new species, described below, which varied from a minimum of 6.5 to a maximum of 7.5 times the carapace width. The concretions enclosing *P. cucaoensis* did not contain any molluscan or other animal remains; however, a few did preserve carbonaceous woody fragments.

The specimens were typically preserved with at least the proximal parts of the appendages present, suggesting that they represented corpses rather than molts. Of the complete carapaces, only one showed evidence of having been crushed following burial. All of the fragments comprising the dorsal carapace were present, but they had been fractured and separated.

The cuticle on carapaces was either preserved with endocuticle and exocuticle on the specimen, or the exocuticle was separated from the endocuticle and preserved on the counterpart. The cuticle on chelipeds was not exfoliated and appeared to be much more strongly calcified than that of the carapace.

The exposed surface of the cuticle on the carapace of *P. cucaoensis* is interspersed with low nodes (~16 per 0.5 mm^2) and shallow pits (~3 per 0.5 mm^2). The nodes are greater in width than height (Fig. 14A). The shallow pits, each containing a central canal, appear to penetrate the cuticular surface (Fig. 14A). As currently exposed, the surface would appear to retain some the original epicuticle (the upper-most calcified layer in crustaceans) based on the presence of a recognizable crystalline layer (Fig. 14D) above the prismatic layer of the exocuticle (Figs. 14B–C). In thin section, the exocuticle preserves a clearly developed prismatic layer (Figs. 14B–F), the walls of which are amber in color. Interprismatic areas are filled with a darker granular material (Fig. 14D). The epicuticle, as preserved, is translucent to the point that the exocuticular prisms are visible through the surface of the cuticle (Fig. 14A), despite lacking a surficial expression. Underlying the prismatic layer of the exocuticle is an additional amber colored horizon (Figs. 14C–D). Laminations in this layer are narrower than those of what is certainly endocuticular (Fig. 14B). Preservation is similar to that of the exocuticle, and the horizon remains distinct from the endocuticle throughout the sectioned material suggesting this layer is exocuticular in origin and is referred to herein as the lower exocuticle.

The endocuticle varies in fidelity of preservation between almost completely recrystallized (Figs. 14E–F), to well preserved showing a delicate, fibrous texture (Figs. 14B, 14F). Within the well-preserved regions both laminations and pore canals, original to the cuticle, remain recognizable. The spatial distribution of these two structures is similar to that of the mineralized and unmineralized portions of the endocuticle observed in extant decapod cuticle. This suggests that the well-preserved areas are those that were calcified during life and the poorly preserved areas lacked original calcification and were infilled during diagenesis following decay of the organic cuticular component.

At the base of the endocuticle is an horizon of finer laminations and contrasting crystalline fabric (Fig. 14B). Crystal orientations are similar to that of the endocuticle. This, in combination with the fine crystallization would suggest that it is part of the endocuticle and does not represent secondary calcification of the uncalcified membranous layer observed in living decapods.

The nodes visible on the surface of the cuticle are constructed from the upward projections of the lower exocuticle that reach the elevation of the epicuticle. In these regions the prismatic layer of the exocuticle is absent, or reduced to a very thin laminar layer (Fig. 14C). Pits were not successfully sectioned axially, but it appears that the basal exocuticle is deflected upward and the epicuticle is
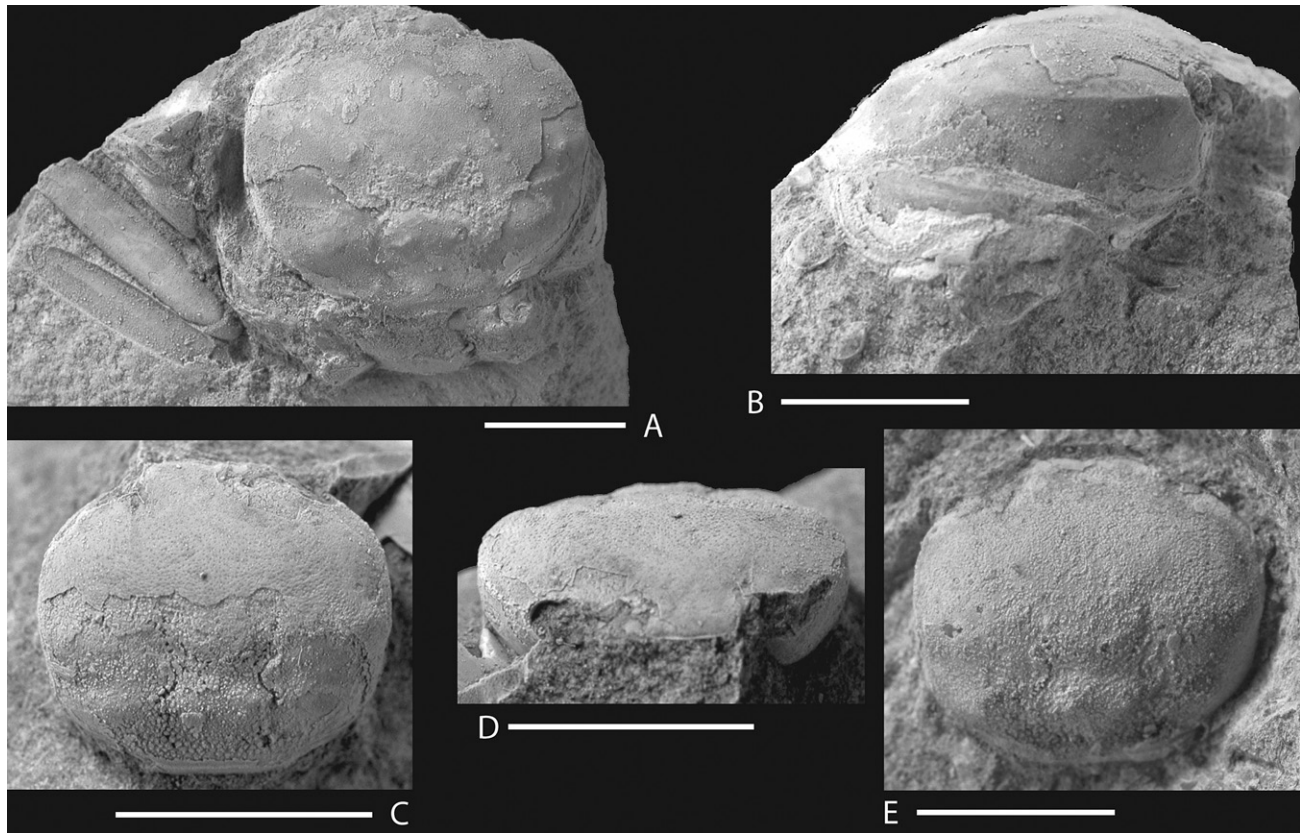
Fig. 15.—*Chasmocarcinus chiloeensis*, new species. **A**, **B**, dorsal and right lateral view of holotype, SGO.PI. 6624; **C**, **D**, dorsal and frontal view of paratype, SGO.PI. 6625; **E**, dorsal view of paratype, SGO.PI. 6626. Scale bars equal 0.5 cm.

deflected downward. The extent that the prismatic layer of the exocuticle is influenced is unclear.

Superfamily Goneplacoidea MacLeay, 1838
Family Chasmocarcinidae Serène, 1964
Subfamily Chasmocarcininae Serène, 1964

Included Genera.—*Chasmocarcinus* Rathbun, 1898; *Collinsius* Karasawa, 1993; *Falconoplax* Van Straelen, 1933; *Gillcarcinus* Collins and Morris, 1978; *Mioplax* Bittner, 1884; *Orthakrolophos* Schweitzer and Feldmann, 2001b.

Discussion.—Placement of small, generally quadrate, more or less smooth crabs within families is difficult when only the dorsal carapace is preserved. Schweitzer and Feldmann (2001b) provided points of comparison between the Hexapodidae Miers, 1886; Asthenognathinae Stimpson, 1858, within the Pinnotheridae de Haan, 1833; and the Chasmocarcininae. The primary points of discrimination visible on the carapace were overall carapace shape, form of the front, presence or absence of a lateral ridge, development of posterolateral reentrants, and ratios defining the relative dimensions of the front, fronto-orbital margin, and posterior margin. These points of comparison

are quite useful in characterizing the genera within the various groups; however, one of the points requires modification. The Chasmocarcininae were indicated to lack a lateral ridge, whereas that is not always the case. For example, *Chasmocarcinus mississippiensis* Rathbun, 1931, possesses a distinct anterolateral ridge (Felder and Rabalais 1986), quite similar to that possessed by the material from Cucao. *Chasmocarcinus chacei* Felder and Rabalais, 1986, also possesses an anterolateral ridge, although it is not as well developed as on *C. mississippiensis*. A ridge is indicated in the diagnosis of the genus (Schweitzer and Feldmann 2001b:338). Both of these species have fronto-orbital widths that are greater than is seen on other extant forms and, for that matter, on fossils assigned to genera within the subfamily (Table 1). In other regards, the Cucao specimens conform to the characters of the subfamily and can be placed there with confidence. Representatives of the Hexapodidae have a rostrum that widens distally, much wider posterior margins, and fronto-orbital widths that are much less than the posterior width. The taxa within the Asthenognathinae bear a short, tapering, downturned front; and have a broader posterior margin.

Philippi (1887) described two species that he referred to *Pinnotheres* Bosc, 1802, *Pinnotheres promaucanus* Philippi, 1887, from Matanzas, and *Pinnotheres araucanus*

TABLE 1. Ratios of measurements taken on specimens from all known fossil species within the Chasmocarcininae. Abbreviations as in Table 2.

Number	L/W	FOW/W	FW/W	PW/FOW	PW/W	Source
Chasmocarcinus cylindricus Rathbun, 1918						
USNM 24551	0.75	0.30	0.12	0.83	0.25	From photo
Chasmocarcinus guerini (Via, 1959)						
KSU 189	0.85	0.64	0.26	0.69	0.44	Barcelona 20099
Chasmocarcinus robertsi Blow and Bailey, 1992						
USNM 468599	0.72	0.47	0.14	1.15	0.54	From photo
Chasmocarcinus seymourensis Feldmann and Zinsmeister, 1984						
USNM 365455	0.80	0.48	0.18	1.19	0.57	Recorded measurements
Chasmocarcinus chiloeensis, new species						
Holotype	0.80	0.67	0.31	1.06	0.32	Recorded measurements
Falconoplax kugleri Van Straelen, 1933						
KSU 546A	0.82	0.39	---	0.91	0.36	Brussels I.G. 9932
KSU 546B	0.80	0.62	---	---	---	Brussels I.G. 9932
KSU 44	0.79	---	---	---	0.39	Paris R 53027
KSU 118	0.83	0.37	0.13	1.10	0.40	Berlin uncatalogued Uncatalogued
KSU 507	0.79	0.43	0.11	0.74	0.32	Vienna 1938 (No 200 I 83)
Falconoplax bicarinella Collins and Morris, 1976						
BM In 61353	0.85	0.55	---	0.85	0.47	From photo
Collinsius simplex Karasawa, 1993						
KSU 11256	0.90	0.53	0.16	0.71	0.38	Chiba uncatalogued
KSU 11270	0.80	0.54	0.22	0.98	0.53	From specimen
Gillcarcinus amphora Collins and Morris, 1978						
BM In 61559	0.91	0.46	0.14	0.80	0.37	From photo
Mioplax socialis Bittner, 1884						
Unnumbered	0.88	0.62	0.27	0.81	0.50	From illustration
Orthakrolophos depressus (Quayle and Collins, 1981)						
BM In 61735	0.81	0.50	0.19	---	---	From photo
Orthakrolophos bartonensis (Quayle and Collins, 1981)						
BM In 61733	0.95	0.55	0.19	---	---	From photo
Orthakrolophos bittneri (Morris and Collins, 1991)						
BM In 61987	0.75	0.45	---	1.0	0.45	From photo

Philippi, 1887, from the area of Lebu. Examination of the descriptions and the drawings of these taxa confirms that they are not referable to *Chasmocarcinus* and, certainly, are not to be confused with the species described below. Philippi's taxa are much wider than long and both have a straight fronto-orbital margin, whereas the species described herein is nearly equant and bears a front that projects well beyond the orbits. Bahamonde and Frassinetti (1980) indicated that the types of some of Philippi's taxa had been lost, presumably in an earthquake. A careful search by one of us (RMF) for the specimens upon which Philippi based the new species of pinnotherids also failed to locate the material. Thus, the descriptions and illustrations are all that remain for comparison.

Chasmocarcinus Rathbun, 1898

Type Species.—*Chasmocarcinus typicus* Rathbun, 1898, by original designation.

Included Fossil Species.—*Chasmocarcinus chiloeensis,* new species; *Chasmocarcinus guerini* (Vía, 1959), as *Palaeograpsus*; *Chasmocarcinus robertsi* Blow and Bailey, 1992; *Chasmocarcinus seymourensis* Feldmann and Zinsmeister, 1984.

Diagnosis.—As in Schweitzer and Feldmann (2001b:338).

Discussion.—Ratios of measurements on one or more specimens of all fossil species within the Chasmocarcininae (Table 1), coupled with morphological characters of the carapace, confirm placement within *Chasmocarcinus*. *Chasmocarcinus chiloeensis* has a greater fronto-orbital width-to-width ratio and a greater frontal width-to-width ratio than any of the other taxa assigned to the subfamily and, for that matter, greater ratios than all but *C. guerini*. The posterior width-to-width ratio on the new species is similar to that determined on other fossil representatives of the genus; only that of *Mioplax socialis* Bittner, 1884, is comparable. However, *M. socialis* is readily distinguished from species of *Chasmocarcinus* because the former bears a dentate anterolateral margin. Further, the front on the specimens from Cucao is rectangular, axially notched, slightly downturned, and it extends well beyond the orbits. The new specimens have a much narrower posterior width than members of *Falconoplax* and a much greater fronto-orbital width. Thus, the only genus within the family with features that can accommodate the new specimens is *Chasmocarcinus*. In other groups, *Asthenognathus* species are known from southern South America and have carapaces with a similar shape to those of *Chasmocarcinus* (Schweitzer and Feldmann 2001b), but the new specimens can be excluded from *Asthenognathus* due to their greater length-to-width ratio, greater fronto-orbital width, and much narrow posterior width.

Chasmocarcinus chiloeensis, new species
(Fig. 15)

Diagnosis.—Frontal area and fronto-orbital margin very broad for genus; anterolateral margin bears well defined, finely granular ridge; metagastric region very weakly defined posteriorly and laterally by subtly cervical groove which becomes obscure laterally.

Description.—Carapace small, length about 80% maximum carapace width; well calcified except for posterolateral edges; outline weakly hexagonal, maximum width about 87% the distance posteriorly on carapace just anterior to posterolateral reentrant; transversely weakly arched, longitudinally strongly arched particularly in anterior third; surface generally smooth.

Front broad, 31% maximum width attained at about midlength; straight, downturned, with narrow, smooth rim, axially sulcate, projected in advance of orbits. Lateral margins of front smoothly rounded and merging into smoothly concave, forward directed orbit with finely granulated rim; outer orbital corner acutely angled; fronto-orbital margin about 70% maximum carapace width. Anterolateral margin smoothly convex; defined by sharply delineated, granular inflection distinctly separating carapace surface from smooth, vertical flanks. Posterolateral margins weakly convex; margin smoothly

rounded into posterolateral flanks. Posterolateral corner with distinct reentrant. Posterior margin about 32% maximum width and about equal to fronto-orbital width, slightly sinuous, with broad, posteriorly sloping, smooth rim.

Cervical groove a subtle hemispherical arc around posterior and lateral margins of nearly obscure mesogastric region; metagastric and urogastric regions narrow, indistinct, depressed below mesobranchial and cardiac regions, bounded laterally by prominent, arcuate branchiocardiac grooves. Cardiac region pentagonal with apex directed posteriorly; bearing two circular bosses at widest part of region. Intestinal region not defined.

Lateral regions not clearly defined. Epibranchial region a faint swelling between undifferentiated protogastric and hepatic regions and weakly inflated mesobranchial region.

First three somites of abdomen free, otherwise not preserved.

Ocular peduncle short, narrow medially, flared terminally; ocular surface not preserved.

Cheliped partially represented; appears to be smoothly inflated with short, nearly edentulous, black-tipped fixed finger. Other pereiopods fragmentary, slender, laterally compressed.

Measurements.—Measurements, in mm, taken on specimens of *C. chiloeensis* are given in Table 2. Ratios of measurements are given in Table 1.

Etymology.—The trivial name refers to the Grand Island of Chiloé, Chile, from which the specimen was collected.

Types.—Holotype, SGO.PI. 6624, and paratypes, SGO. PI. 6625-6627, are deposited in the National Museum of Natural History, Santiago, Chile.

Occurrence.—The specimens were collected from the Lacui Formation, Miocene, in coastal exposures near Punta Pirulil, south of Cucao, Chiloé Island, Chile at lat. 42°42'S, long. 74°08'W.

Discussion.—*Chasmocarcinus chiloeensis* is readily distinguished from other species within the genus on the basis of its relatively broad front and fronto-orbital width which exceed that of other known species (Table 1). In this regard, the new species has dimensions most like those of *C. guerini*; however, that species lacks the distinctive anterolateral ridge. This feature is morphologically quite similar to that of the extant *C. mississippiensis*.

As with the other decapods from the Lacui Formation, these specimens are preserved within small, spherical, carbonate-cemented concretions. One of the three specimens assigned to this species has fragments of a left cheliped and some of the left pereiopods preserved, and another has some of the right pereiopods, suggesting that the specimens are corpses, rather than molted specimens. Some of the exocuticle is missing on each of the specimens. The surface of the exocuticle is very finely punctate whereas the exposed endocuticle exhibits a granular texture, possibly resulting from increased calcification around tegumental glands. Nodes developed on the cardiac and epibranchial regions are more clearly expressed on the surface of the endocuticle in areas where the exocuticle has exfoliated. Separation of the cuticular layers commonly occurs in this fashion (Waugh et al. 2004). Some, or all, of the exocuticle

TABLE 2. Measurements, in mm, taken on specimens of *Chasmocarcinus chiloeensis*.

L = Carapace length; W = Maximum carapace width; FOW = Fronto-orbital width; FW = Frontal width; PW = Posterior width.
* = specimens lacking part of dorsal carapace.

Number	L	W	FOW	FW	PW
SGO.PI. 6624	12.0	~15.0	10.0	4.6	4.9
SGO.PI. 6625	6.7	7.5*	5.6	2.8	3.1
SGO.PI. 6627	9.0	9.6*	6.4	3.4	---
SGO.PI. 6626	7.6	8.6*	~6.6	3.3	3.6

may be retained on the counterpart of the specimen, but the counterpart was not always collected.

One of the specimens, SGO.PI. 6625, is preserved beside a well preserved tellinid bivalve exhibiting what appears to be the original concentric color markings. Another specimen, SGO.PI. 6626, is associated with some highly nacreous bivalve fragments, reminiscent of nuculid bivalves. A tiny calcareous, tubular fossil is associated with the third specimen, SGO.PI. 6627, that may be a scaphopod.

Superfamily Pinnotheroidea de Haan, 1833
Family Pinnotheridae de Haan, 1833

Pinnixa White, 1846, sensu lato

Type species.—*Pinnotheres cylindricum* Say, 1818, by monotypy.

Included fossil species.—See Feldmann et al. (2005).

Discussion.—Feldmann et al. (2005) recently discussed the fossil record for *Pinnixa* sensu lato. It need not be repeated here. The report of *Pinnixa navidadensis* from Pliocene rocks in Chile extends its geologic record but not its geographic record.

Pinnixa navidadensis Feldmann, Schweitzer,
and Encinas, 2005
Fig. 16

Emendation to diagnosis.—Front narrow, about 10% maximum carapace width. Orbits small, circular, closely spaced, directed forward; fronto-orbital width about 25% maximum carapace width; orbits positioned on anterior margin of carapace.

Description of Material.—Carapace ovate, wider than long, length about half maximum carapace width, widest about 35% the distance posteriorly on carapace; dorsal surface flattened transversely and longitudinally; flanks steep, at right angles to dorsal carapace; carapace ornamentation unknown due to poor preservation of cuticle.

Front poorly known, narrow, about 10% maximum carapace width. Orbits small, circular, closely spaced, directed forward; fronto-orbital width about 25% maximum carapace width; orbits positioned on anterior

margin of carapace, anterior margins merging with anterolateral margins; anterior and anterolateral flanks steep, at 90º angle to dorsal carapace, lower edge rimmed, upper edge rimmed forming rim along edge of dorsal carapace, upper rim diminishing at anterolateral corner.

Posterolateral margin more flattened, flank at 20º or so angle to dorsal carapace, lower edge rimmed, upper edge with broad ridge marking edge of dorsal carapace, at least one appendage issuing from under posterolateral margin. Posterolateral margin merging smoothly into posterior margin; posterior margin rimmed, about half maximum carapace width.

Epigastric regions weakly inflated, situated at base of frontal margin. Protogastric regions marked by deep grooves on lateral margins, forming marked U-shaped groove on mid-anterior portion of carapace. Mesogastric region with 2 inflations posteriorly, narrowing anteriorly, terminating between epigastric regions; groove bounding posterior edge of mesogastric region deep. Cardiac region with transverse ridge. Intestinal region oriented at steep angle to remainder of dorsal carapace. Hepatic and branchial regions not well differentiated, a groove paralleling lateral margins of protogastric regions about central on hepatic regions.

Eye short, apparently reasonably well-calcified. Remainder of carapace and appendages unknown.

Measurements.—Measurements taken on specimens of *P. navidadensis* are presented here. Specimens CGO.PI. 6628 and SGO.PI. 6629 are listed respectively: maximum width, 24.4 mm, 21.7 mm; maximum carapace length, 11.7 mm, 11.3 mm; length to position of maximum carapace width, 4.1 mm, 4.0 mm; fronto-orbital width, unknown, 5.7 mm; posterior width, 11.8 mm, 10.7 mm; frontal width, unknown, 2.4 mm.

Material examined.—Two specimens, SGO.PI. 6628 and 6629, are deposited in the Natural History Museum, Santiago, Chile.

Occurrence.— The specimens were collected from the Lacui Formation, early Pliocene, in coastal exposures near Punta Pirulil, south of Cucao, Chiloé Island, Chile at lat. 42°42'S, long. 74°08'W.

Discussion.—The new specimens agree in all ways with the original specimen described from the Navidad Formation. They add new information because they have reasonably preserved orbits and front, which indicate that the orbits were small and directed forward and that the front was narrow. The new specimens are also quite a bit larger than the holotype specimen.
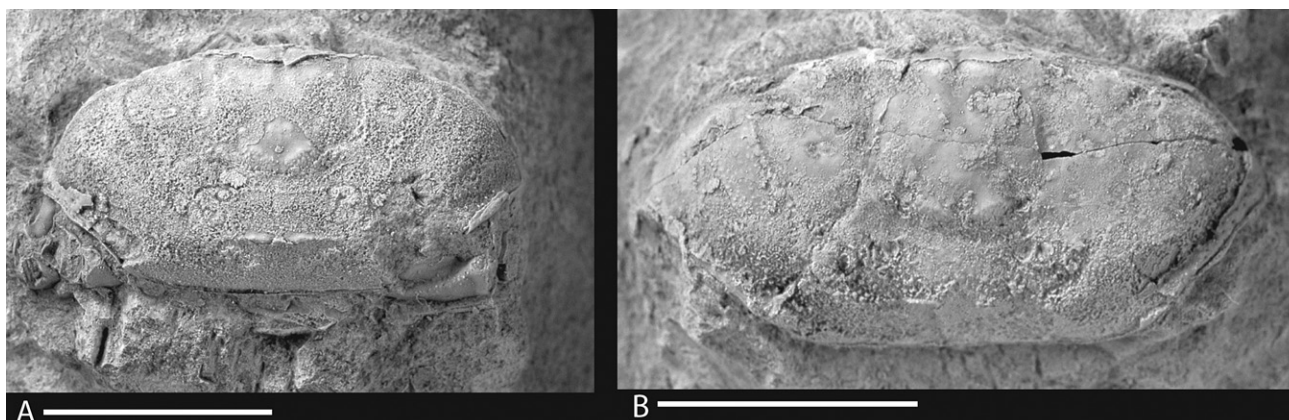
Fig. 16.—*Pinnixa navidadensis* Feldmann et al., 2005. **A**, SGO.PI. 6629;. **B**, SGO.PI. 6628. Scale bars equal 1 cm.

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