

NEW DECAPODS FROM THE NAVIDAD FORMATION (MIOCENE) OF CHILE

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ABSTRACT

A new Miocene decapod fauna is described from the Navidad Formation of coastal Chile. The fauna includes five callianassoid taxa, none of which is preserved sufficiently to identify to species level. New species include *Calappilia?* *chilensis*, *Hepatus spinimarginatus*, *Proterocarcinus navidad*, *Pilumnus cucaoensis*, and *Pinnixa navidadensis*. A possible rhizopine member of the Pilumnidae Samouelle, 1819, is described. *Trichopeltarion levis* Casadío *et al.*, 2004, previously known from the late Oligocene of western Argentina, was also recovered from these rocks. *Calappa circularis* Beurlen, from the lower Miocene Pirabas Formation in Brazil, is herein referred to *Calappilia*. This report greatly increases the known number of fossil decapods from Chile and sets the stage for paleobiogeographic comparison of the decapod faunas of Chile and Argentina.

The Neogene rock sequence in Chile is largely confined to about seven basins along the modern Pacific Ocean (Ceccioni, 1980). These basins have been subject to extreme vertical motion during the Neogene (Martínez-Pardo, 1990) so that rocks have been deposited at depths ranging from shallow, inner shelf to bathyal. One of these, the Navidad Basin, contains a thick succession of richly fossiliferous deposits, the Navidad Formation, that crop out along the coastline for a distance of about 16 km from Boca Pupuya in the south to near San Antonio in the north and inland for a distance of about 2 km (Fig. 1). Although the fauna is overwhelmingly dominated by mollusks, foraminiferans, corals, worm tubes, brachiopods, bryozoans, echinoderms, fish, and whales are also known from the formation (Tavera, 1979). In addition, crustaceans, including barnacles and decapods, have been noted (Philippi, 1887; Tavera, 1979; Chirino-Gálvez, 1993). Collecting in the Navidad Formation by one of us (AE) over a period of about three years and by all the authors in 2004 has resulted in a much larger and more diverse array of decapods than was previously known. It is this collection that forms the basis for this study.

Fossil decapod crustaceans have been known from Chile for many years, but little has been published on them; only four taxa have been recognized in the Navidad Formation. Philippi (1887) described some of the first crabs from Chile and noted that *Cancer tyro* Philippi, 1887, and *Pinnotheres promaucanus* Philippi, 1887, had been collected in the vicinity of Matanzas, within the Navidad Formation. *Cancer tyro* has subsequently been reported from this unit, along with *Cancer* sp., from three other localities (Tavera, 1979). The history of *Cancer tyro* has been controversial as will be discussed below. Suffice it that the original concept of the species is probably embraced within *Chaceon* Manning and Holthuis, 1989 (Casadío *et al.*, 2004). The type specimen of *Pinnotheres promaucanus* has not been identified in the National Museum of Chile, Santiago, and is presumably lost. No specimens resembling the illustration of the type (Philippi, 1887, pl. 50, no. 4) have been collected subsequently. Finally, Chirino-Gálvez (1993), in an unpublished

M.S. thesis, added *Callianassa* sp. and a new species of crab to the list. That material along with the newly collected specimens will be discussed herein.

GEOLOGICAL SETTING

Decapod samples were collected from Neogene marine strata of the Navidad Formation which crops out in the Coastal Cordillera of Central Chile between approximately 33°00'S–34°30'S and 72°W–71°15'W (Fig. 1). The Coastal Cordillera is a subdued mountain range some 40–50 km wide that trends north-south parallel to the Peru-Chile Trench, with most summits varying from 1000 to 2000 m above sea level. At these latitudes this mountain range is largely comprised of Mesozoic granitoid batholithic rocks as well as Paleozoic metamorphic and plutonic basement rocks which are overlain by Cretaceous, Eocene, and Neogene marine rocks (Gana *et al.*, 1996; Wall *et al.*, 1996). Neogene marine sedimentary deposits are widely exposed in this part of the Coastal Cordillera and are represented by the Navidad and La Cueva formations (Brüggen, 1950; Tavera, 1979).

The Navidad Formation was first described by Darwin (1846). The unit consists of a succession of marine sandstone, siltstone, conglomerate, and coquina. Several authors have proposed different divisions for the Navidad Formation (e.g., Ceccioni, 1978; Tavera, 1979; Gana *et al.*, 1996; Wall *et al.*, 1996), of which the most widely accepted division scheme is that of Tavera (1979). He divided the Navidad Formation into the Navidad, Lincanqueu, and Rapel members. Work currently in progress by Lavenu and Encinas (personal commun.) will propose to reorganize these units once again.

The approximately 100-m thick decapod-bearing Navidad Member *sensu* Tavera (1979) overlies the Paleozoic granitic basement and marine Cretaceous rocks of the Punta Topocalma Formation (Ceccioni, 1978) and underlies the Lincanqueu Member. The Navidad Member exhibits a basal coastal conglomerate which is overlain by a succession of interbedded siltstone and sandstone, with minor coquina and conglomerate. Because of the repetitive nature of the sediments within

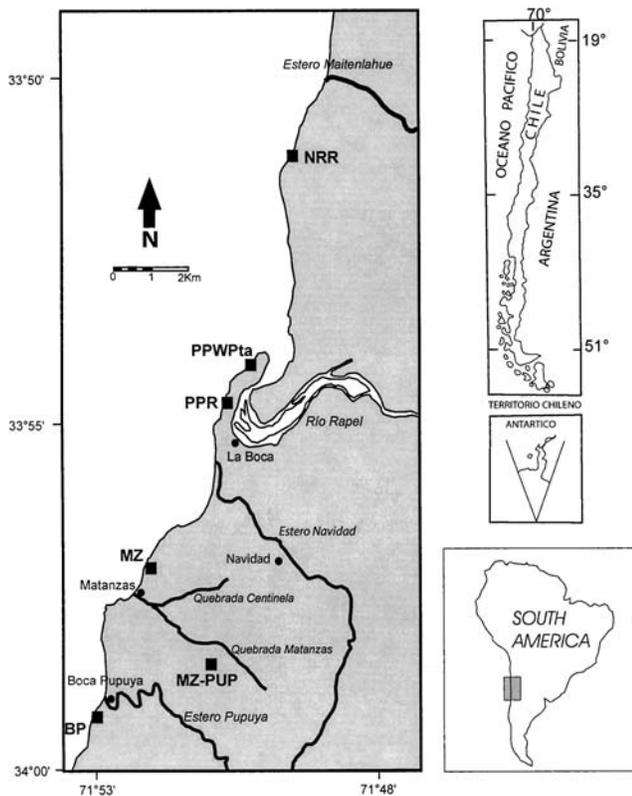


Fig. 1. Location map showing position of decapod collecting localities described in the text.

the Navidad member and the geographically disjunct exposures of limited stratigraphic extent, it is not possible to construct a composite stratigraphic column at this time.

The unit contains a diverse assemblage of fossils, consisting of bivalves, gastropods, foraminifers, shark teeth, leaf impressions, pollen, and crabs (Philippi, 1887; Martínez-Pardo and Valenzuela, 1979; Tavera, 1979; Troncoso, 1991; Troncoso and Romero, 1993; Meón *et al.*, 1994; Finger *et al.*, 2003). Beds overlying the basal conglomerate comprise facies consisting of massive sandstone, interbedded siltstone and sandstone with Bouma cycles, syndimentary breccia, slides, slumps and massive siltstones several meters thick. These facies are interpreted as being generated by alternation of gravity flows with settling of fines deposited in a submarine fan during rapid, major coastal subsidence (Encinas *et al.*, 2003). This interpretation is supported by the presence of benthic foraminifera indicative of deposition at a minimum depth of 1500 m (Finger *et al.*, 2003). The age of the Navidad Member ranges between Tortonian (approximately 11 Ma) and early Pliocene (approximately 5 Ma) according to planktonic foraminifera (K. Finger, personal commun.). Subsequently, the basin shallowed to shelf depths, and deltaic sediments of the Licanheu and Rapel members and La Cueva Formation were deposited during the Pliocene. The basin finally emerged above sea level thereafter.

DECAPOD COLLECTING LOCALITIES AND ABBREVIATIONS

All localities are located near or at the coast approximately 50 km south of San Antonio near the villages of Navidad, Pupuya, and Matanzas (Fig. 1).

NRR.—Located at the the foot of a coastal cliff, about 2 km south of the Estero Maitenlahue and 5 km north of the Rapel River mouth (Fig. 1). Decapod fragments were obtained from silty sandstone blocks at the base of the inaccessible cliff-face. GPS coordinates: WP61, lat. 33°51'18.7"S, long. 71°49.0'32.4"W; WP62, lat. 33°51'26.1"S, long. 71°49'34.1"W.

PPWPta.—Located at the northwestern tip of the coastal cliff just south of the mouth of the Rapel River (Fig. 1). Samples were collected from a 7-m thick siltstone layer that crops out in the coastal cliff and in the wave-cut platform at low tide. Decapods were collected directly from the beds and from concretions. Associated siltstones contain an abundant foraminifer fauna indicating an early Pliocene age and lower bathyal water depths. GPS coordinates: WP59, lat. 33°54.0'22.3"S, long. 71°50.0'17.2"W.

PPR.—Located at the coastal cliff about 500 m northwest of La Boca and about 1 km south of the PPWPta locality (Fig. 1). Samples from WP 64 and WP 66 were collected from concretions situated in a massive sandstone that is overlain by interbedded fine sandstone and siltstone, which bear decapods of WP65. Both beds overlie a siltstone bed that can be laterally correlated with that from locality PPWPta bearing early Pliocene lower bathyal foraminifers. GPS coordinates: WP 64, lat. 33°54.0'48.0"S, long. 71°50'41.1"W; WP 65, lat. 33°55.0'0.0"S, long. 71°50.0'47.2"W; WP66, lat. 33°42.0'52.6"S, long. 71°50.0'44.4"W.

MZ.—About 1 km north of Matanzas, in the coastal cliff (Fig. 1). Decapod samples were obtained from concretions found on a silty sandstone with very abundant leaf impressions that crop out at the base of the cliff. Foraminifers obtained from a well drilled by ENAP at Matanzas indicate an age of approximately 11 Ma (zone N16) and lower bathyal water depths. As the beds transected by the well are directly below the decapod-bearing sandstone layer, the age of approximately 11 Ma is considered as a maximum age for the decapods. GPS coordinates: lat. 33°56.0'53.0"S, long. 71°51.0'56.09"W.

BP.—About 100 m south of Boca Pupuya, located at the coastal cliff (Fig. 1). The sample was collected in a massive sandstone bed underlying a conglomerate. GPS coordinates: WP63, lat. 33°59'22.7"S, long. 71°53'12.4"W.

MZ-PUP.—Foot paths located off the main road between Matanzas and Pupuya; decapods were collected along narrow, dry creek beds where concretions in sandstone and siltstone beds crop out (Fig. 1). The siltstone beds contain abundant foraminifers indicating lower bathyal depths and a late Miocene–early Pliocene age. This bed is probably equivalent to the siltstone from PPWPta. GPS coordinates: WP57, lat. 33°58.0'27.9"S, long. 71°50.0'56.4"W; WP60, lat. 33°58'26.7"S, long. 71°50'55.5"W; WP68, lat. 33°58'38.1"S, long. 71°50'54.4"W.

Institutional Abbreviations.—E, Földtani Intézet (Geological Survey), Budapest, Hungary; In., The Natural History Museum, London, United Kingdom; M., Natural History Museum of Hungary (Természettudományi Múzeum Föld-és Őslénytár), Budapest, Hungary; MHN-UABCS, Museo

de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México; MSNM, Museo Civico di Storia Naturale di Milano, Milano, Italy; SGO.PI., Museo Nacional de Historia Natural, Sección Paleontología, Santiago, Chile; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Infraorder Thalassinidea Latreille, 1831

Superfamily Callianassoidea Dana, 1852

Remarks.—Referral of callianassoid fossils to genera using only the manus and fixed finger of the major cheliped is very difficult. Addition of the carpus is helpful, but the merus is usually necessary to achieve generic placement. The callianassoid material described here is comprised only of broken mani and fixed fingers, with one specimen associated with a carpus, making confident generic placement impossible. However, it is possible to separate the material into two distinctive morphologies that each appear to represent major chelae, not the major and minor chela or male and female chelae of the same taxon.

Because it has been well demonstrated that Miocene rocks typically enclose members of extant genera (Schweitzer, 2001; Schweitzer *et al.*, 2002), in order to attempt placement of the Chilean fossils at the generic level, we primarily investigated the modern records of callianassoids of southern coastal South America. Only six extant callianassoid genera are known from the region: *Neotrypea* Manning and Felder, 1991; *Callichirus* Stimpson, 1866; *Notiax* Manning and Felder, 1991; *Anacalliax* de Saint Laurent, 1973; *Sergia* Manning and Lemaitre, 1993; and *Poti* Rodrigues and Manning, 1992 (Boschi, 2000; Thatje, 2000). In addition, the morphology of other callianassoid taxa was also examined.

Family Callianassidae Dana, 1852

Subfamily Callichirinae Manning and Felder, 1991

Genus *Callichirus* Stimpson, 1866

Type Species.—*Callianassa major* Say, 1818, by original designation.

Fossil Species.—*Callichirus? symmetricus* (Feldmann and Zinsmeister, 1984), Eocene, Antarctica.

Remarks.—One group of Chilean callianassoid fossils exhibits a morphology that is similar to several genera within the Callianassidae Dana, 1852 *sensu stricto*. The shape of the manus of the specimens referred herein to *Callichirus? sp.* is nearly identical to that shown for *Callichirus major* (Say, 1818), illustrated by Manning and Felder (1986, fig. 1c); *Eucalliax jonesi* (Heard, 1989), illustrated by Manning and Felder (1991, fig. 15c, d); and *Calliax lobata* (De Gaillande and Lagardère, 1966), illustrated in Manning and Felder (1991, fig. 15i). All of these taxa, including the new Chilean fossils, exhibit a sinuous proximal margin and a bulbous swelling on the distal margin of the manus, and a stout fixed finger.

However, only the mani of *Callichirus major* narrow distally as in the fossils. Because species of *Callichirus* have already been reported from the high southern latitudes as fossils (Feldmann and Zinsmeister, 1984; Stilwell *et al.*, 1997; Schweitzer and Feldmann, 2000c), members of the genus currently inhabit the coast of Chile (Boschi, 2000; Thatje, 2000), and the morphology of some extant *Callichirus* are similar to the fossils, we questionably place one group of Chilean callianassoid fossils within *Callichirus*.

Callichirus? sp.

Fig. 2D

Material Examined.—Two specimens, SGO.PI.6302 and 6303 from WP62 of the South Mostazal locality.

Description.—Manus not much longer than high, H/L = 0.87, highest proximally, narrowing distally; proximal margin sinuous, with concavities at upper and lower corners, distinctly rimmed; lower margin straight, rimmed; upper margin very weakly convex; distal margin initially oblique to upper margin at about 80 degree angle, then convex and bulbous, with large tubercle bearing forward-directed setal pit on bulbous portion, then followed by very shallow reentrant above fixed finger; outer surface highly vaulted from upper to lower margin, weakly vaulted longitudinally, smooth, with scattered setal pits.

Fixed finger short, stout at base, maintaining height for half of length before narrowing; with weak ridge at base near articulation with manus, ridge extending very short distance onto manus; occlusal surface with blunt spines, row of setal pits parallel to occlusal surface.

Measurements.—Measurements (in mm) taken on specimens of *Callichirus? sp.*: SGO.PI.6302, L = 6.6; H = 5.7; SGO.PI.6303, L = 8.0; H = 7.0.

Family Ctenochelidae Manning and Felder, 1991

Genus *Ctenocheles* Kishinouye, 1926

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

Included Fossil Species.—*Ctenocheles anderseni* Collins and Jakobsen, 2003; *Ctenocheles cookei* (Rathbun, 1935); *C. cultellus* (Rathbun, 1935); *C. dentatus* (Rathbun, 1935); *C. hokoensis* Schweitzer and Feldmann, 2001a; *C. inaequidens* (Pelseneer, 1886); *C. madagascariensis* Secretan, 1964; *C. rupeliensis* (Beurlen, 1939); *C. secretanae* Schweitzer and Feldmann, 2002; *C. sujaku* Imaizumi, 1958; *C. victor* Glaessner, 1947; *Ctenocheles* cfr. *C. cultellus* (Rathbun, 1935) in Vía, 1959, 1969; *Ctenocheles* sp. in Chirino-Gálvez, 1993; *Ctenocheles* sp. in Beschin *et al.*, 1996; *Ctenocheles* sp. in De Angeli, 1995; *Ctenocheles* sp. in Feldmann, 1991; *Ctenocheles* sp. in Feldmann and Duncan, 1992; *Ctenocheles* sp. in Feldmann *et al.*, 1995; *Ctenocheles* sp. in Förster and Mundlos, 1982; *Ctenocheles* sp. in Jenkins, 1972; *Ctenocheles* sp. in Rasmussen, 1971; *Ctenocheles* sp. in Philippe and Secretan, 1971; *Ctenocheles? sp.* in Kato and Karasawa, 1998.

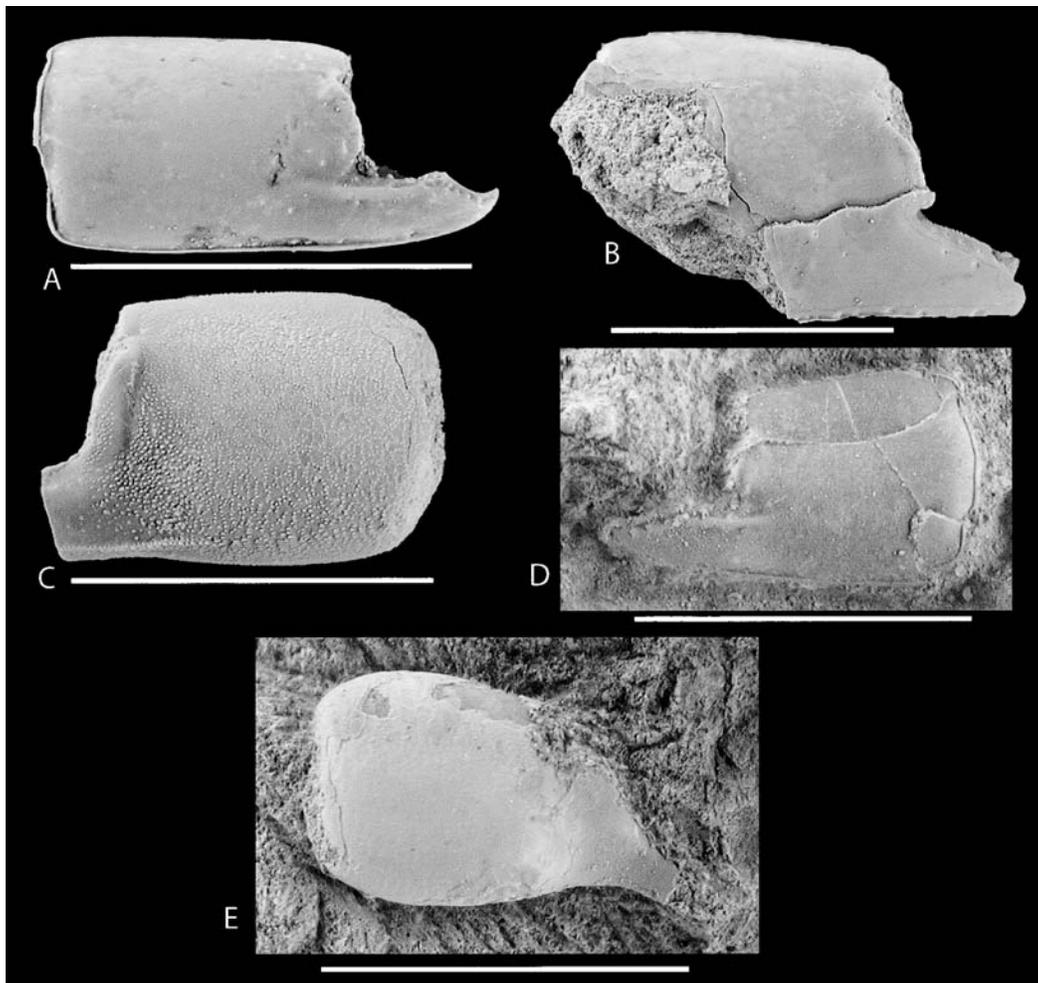


Fig. 2. Callianassoidea. A, *Callianassoidea* sp. 1, outer surface of manus, SGO.PI.6305; B, *Callianassoidea* sp. 2, outer surface of manus, SGO.PI.6308A; C, *Callianassoidea* sp. 3, outer surface of manus, SGO.PI.6309A; D, *Callichirus* sp., outer surface of manus, SGO.PI.6302; E, *Ctenocheles* sp., SGO.PI.6304. Scale bars = 1 cm.

Diagnosis.—"Manus of major cheliped bulbous, longer than high, narrowing distally; fixed finger long and straight or arcuate; occlusal surface of fixed finger with long, needle-like teeth, teeth of variable size, tips curving proximally. Manus of minor cheliped rectangular; fixed finger long, narrow, straight" (Schweitzer and Feldmann, 2001a, p. 186).

Remarks.—Schweitzer and Feldmann (2001a) summarized the known fossil record and the paleobiogeographic distribution of *Ctenocheles*, which is known from both Southern and Northern hemisphere localities in the fossil record. The oldest known occurrence of the genus is from the Late Cretaceous of Madagascar (Secretan, 1964), and fossil occurrences are well-documented for the genus throughout the Cenozoic (Schweitzer and Feldmann, 2001a). The genus is cosmopolitan in modern oceans (Holthuis, 1967; Manning and Felder, 1991). Thus, the new occurrence from the Miocene of Chile does not extend the geographic or geologic range of the genus.

Stenzel (1935) originally described *Callianassa burlsonensis* from middle Eocene rocks of Texas and Mississippi.

Vía (1959, 1969) transferred the species questionably to *Ctenocheles* and questionably referred some specimens from the Eocene of Spain to it. Schweitzer and Feldmann (2001a) included *Ctenocheles* cf. *C. burlsonensis* within the genus. Upon revisiting that issue, we remove *Ctenocheles burlsonensis* from the genus for several reasons. The manus in both the North American type material of *C. burlsonensis* and the Spanish specimens referred questionably to it is quadrate, not bulbous as in other members of *Ctenocheles*. In addition, the fixed finger extends straight from the manus and is not deflexed, as in other members of the genus. These two features are important diagnostic characters of *Ctenocheles*, and thus, *C. burlsonensis* and material questionably referred to it must be removed from the genus. The material referred questionably to *C. burlsonensis* illustrated by Vía (1969, pl. 2, fig. 4) does possess a very long fixed finger as is typical of *Ctenocheles*. Investigation of the Spanish material is currently underway by two of us (RF and CS) and others (P. Artal and B. van Bakel, personal commun.).

Examination of illustrations of *Ctenocheles sujakui* suggest that it may not belong within *Ctenocheles* either.

The manus of that species is less bulbous than other members of the genus, and the fixed finger, where known to be attached to the manus, is not strongly deflexed. Imaizumi (1958, pl. 44, fig. 3) figured isolated fingers that exhibit long, slender teeth typical of *Ctenocheles*; however, these were not connected with a manus. Karasawa and Fudouji (2000) also illustrated a finger similar to the isolated fingers illustrated by Imaizumi (1958). It is possible that there are actually two taxa among the material Imaizumi (1958) referred to *C. sujakui*, but examination of types will be necessary to confirm generic placement of this material. For now, it remains in *Ctenocheles*.

Ctenocheles sp.
Fig. 2E

Material Examined.—SGO.PI.6304 from WP 64 of the Punto Perro Trail locality.

Description of Material.—Manus of major chela longer than high, highest proximally, narrowing distally; bulbous; upper and lower proximal corners rounded; proximal margin straight; upper margin convex, most strongly convex proximally; lower margin convex, achieving maximum convexity centrally; distal margin oblique, at about 120 degree angle to straight line drawn from proximal to distal upper corner, bulbous swelling parallel to it; outer surface moderately vaulted longitudinally; flattened in transverse view up to edges, which are very steep.

Fixed finger narrowing distally, strongly deflexed.

Remainder of major cheliped unknown.

Measurements.—Measurements (in mm) taken on the manus of *Ctenocheles* sp.: length of manus = 7.2; height of manus = 6.0.

Remarks.—The Chilean material is insufficient to refer to a species, although it differs from many previously described members of the genus. Many species and occurrences of *Ctenocheles* in the fossil record are known only from fingers, making comparison with the Chilean material impossible. These include *Ctenocheles victor* and *Ctenocheles* sp. in Rasmussen (1971) and Feldmann and Duncan (1992). The specimen illustrated by Chirino-Gálvez (1993), also from Chile, is known from a finger and a small portion of broken manus; thus, the material described here cannot be compared to it. The manus of *Ctenocheles* sp. in Feldmann (1991) has a more convex lower margin and more bulbous shape than that of the Chilean material. The available illustrations of *C. inaequidens* and *C. rupeliensis* are of poor quality, making comparison with the Chilean specimen very difficult. The Chilean specimen differs from *Ctenocheles sujakui* in possessing a very bulbous manus and deflexed fixed finger. The manus of *C. secretanae* is equidimensional, while it is longer than high in the Chilean specimen illustrated here. Interestingly, the new Chilean material is most similar to the species known from the Eocene of Washington, U.S.A., *C. hokoensis*, which has a nearly identical manus shape to that of the Chilean material. However, because the Chilean material consists of only one incomplete specimen, for now we refer it simply to

Ctenocheles sp. until more complete material can be recovered.

Callianassoidea sp. 1
Fig. 2A

Material Examined.—One illustrated specimen, SGO.PI.6305, from the South Mostazal locality; specimen lot SGO.PI.6307 of three specimens from WP62 of the South Mostazal locality; and a second specimen lot of 24 specimens, SGO.PI.6306, from the South Mostazal locality.

Description.—Carpus of major chela higher than long, L/H = 0.64; proximal margin initially forming a short extension at upper corner to articulate with merus; remainder of proximal margin convex, widest at about mid-height; lower margin continuous with proximal margin and sloping distally; distal margin weakly concave with maximum concavity centrally; upper margin sinuous; outer surface highly vaulted from upper to lower margin.

Manus much longer than high, H/L = 0.61, highest proximally and narrowing distally; proximal margin very weakly convex, rimmed; upper and lower margins straight; lower margin rimmed, rim with setal pits, rim and pits extending onto fixed finger; distal margin initially at oblique angle to upper margin at about 80 degree angle, then extending nearly straight towards fixed finger, with shallow concave reentrant just above fixed finger, large tubercle with forward-directed setal pit just proximal to reentrant; outer surface flattened longitudinally, highly vaulted from upper to lower margin, smooth; inner surface flattened, smooth.

Fixed finger triangular in cross-section; with ridge on outer surface extending about one-fifth the distance proximally onto the manus; occlusal surface with sharp teeth.

Measurements.—Measurements (in mm) taken on specimens of *Callianassoidea* sp. 1: SGO.PI.6307-A, L (length of manus) = 13.5; H (height of manus) = 7.5; SGO.PI.6307-C, L = 11.3; H = 7.6; SGO.PI.6307-B, L = 10.4; H = 6.7. SGO.PI.6307-C, height of carpus = 7.4; length of carpus = 4.7.

Remarks.—*Callianassoidea* sp. 1 does not resemble any of the extant taxa reported from southern South America, nor does it resemble any other callianassoid genus (see illustrations in Glaessner, 1969; Manning and Felder, 1991; Karasawa, 1993; 1997; Schweitzer and Feldmann, 2002). The long manus, which exhibits a length much greater than the height, appears to be unusual for the *Callianassoidea*. Very long mani and relatively small carpi relative to the mani occur in the *Axioida* Huxley, 1879, so it seems possible that with more and better preserved material, *Callianassoidea* sp.1 could be moved to a different superfamily altogether. However, because axioids are uncommon in the fossil record and callianassoids are very common (Glaessner, 1969), for now, we refer these specimens to *Callianassoidea* sp. 1. ?*Callianassa szobensis* Müller, 1984, from the Miocene of Hungary also exhibits a similarly long manus with respect to the height. Unfortunately, it is known only from mani and fingers; that

species warrants a re-examination if more complete material is collected.

Callianassoidea sp. 2
Fig. 2B

Material Examined.—One specimen lot, SGO.PI.6308, of two specimens from the South Mostazal locality.

Description.—Manus of cheliped longer than high, H/L = 0.80, highest near proximal margin, narrowing somewhat distally; proximal margin poorly known; upper margin weakly convex, rimmed, rim with closely-spaced setal pits, giving the appearance of being serrate; lower margin very weakly convex, with setal pits, giving the appearance of being serrate; distal margin initially perpendicular to upper margin, then extending at about 100 degree angle to upper margin, smooth indentation just above fixed finger; outer surface with rows of setal pits paralleling upper and lower margins, remainder smooth; inner surface smooth.

Fixed finger curving inward; narrowing distally; with setal pits parallel to occlusal surface; occlusal surface serrate.

Measurements.—SGO.PI.6308-A, length of manus, 12.5; height of manus, 10.3; SGO.PI.6308-B, 10.7; height of manus, 8.6.

Remarks.—These specimens differ from all others described here. The lack of proximal elements of the cheliped make it impossible to identify the material any more specifically than is done here.

Callianassidae sp. 3
Fig. 2C

Material Examined.—One specimen lot, SGO.PI.6309, of three specimens from the South Mostazal locality.

Description.—Manus of cheliped longer than high, H/L = 0.75; bulbous; proximal margin rounded, confluent with upper and lower margins which are both very weakly convex; distal margin extending at about 100 degree angle to upper margin; outer surface ornamented with fine granules arrayed into scalloped pattern proximally, more randomly arrayed distally; distal margin with bulbous swelling parallel to it; inner surface granular, granules arranged into scalloped pattern, row of granules parallel to lower margin.

Fixed finger with rectangular cross-section, keeled row of granules along lower margin, keel extending onto outer surface of manus; occlusal surface with three granular keels.

Measurements.—SGO.PI.6309-A, length of manus, 10.4; height of manus, 7.9.

Remarks.—The general form and size of the manus is very reminiscent of the Callianassoidea, hence its placement; however, the granular scalloped pattern is unusual for the group. Members of the Laomedidae Borradaile, 1903, sometimes exhibit such ornamentation (Karasawa, 1993; 1997). The lack of the more proximal elements of the cheliped precludes more precise placement of the material.

Infraorder Brachyura Latreille, 1802

Section Heterotremata Guinot, 1977
Superfamily Calappoidea H. Milne Edwards, 1837
Family Calappidae H. Milne Edwards, 1837
Genus *Calappilia* A. Milne Edwards, 1873

Type Species.—*Calappilia verrucosa* A. Milne Edwards in de Bouillé, 1873, by subsequent designation of Glaessner, 1929.

Included Species.—*Calappilia bohmi* Glaessner, 1929; *C. bonairensis* Van Straelen, 1933; *C. borneoensis* Van Straelen, 1923; *C. brooksi* Ross and Scolaro, 1964; *C. circularis* new combination (Beurlen, 1958) as *Calappa*; *C. dacica* Bittner, 1893; *C. dacica* var. *lyrata* Lörenthey and Beurlen, 1929; *C. diglypta* Stenzel, 1934; *C. hondoensis* Rathbun, 1930b; *C. incisa* Bittner, 1886; *C. matzkei* (Bachmayer, 1962) as *Calappa*; *C. mainii* Allasinaz, 1987; *C. maxwelli* Feldmann, 1993; *C. perlata* Noetling, 1885; *C. scopuli* Quayle and Collins, 1981; *C. sexdentata* A. Milne Edwards in de Bouillé, 1876; *C. sitzi* Blow and Manning, 1996; *C. subovata* Beschin, Busulini, De Angeli, and Tessier, 2002; *C. vicentina* Fabiani, 1910; *Calappilia* sp. indeterminate in Roberts, 1956.

Diagnosis.—Carapace ovoid, widest at about midlength; anterolateral margin smooth, lacking prominent lateral spine, posterolateral margin with well-developed spines; surface coarsely nodose; nodes and grooves define carapace regions.

Remarks.—The sole specimen from the Navidad Formation referred to this genus is incomplete. The front is broken, although the orbital rim is present. The anterolateral margin is partially preserved, but the posterolateral margin is broken and cannot be described. The axial regions of the carapace are moderately well preserved as is the branchial region. In terms of the preserved features, the specimen can be assigned to *Calappilia*; however, the placement must be considered tentative. Another calappid crab genus, *Mursia* Leach in Desmarest, 1823, bears characters of the dorsal carapace that are similar to those of *Calappilia*, but the margins are different (Schweitzer and Feldmann, 2000a). The posterior margin of *Mursia* tends to be straight or slightly concave and smooth, whereas that of *Calappilia* is rounded and spinose. The orbits of typical *Calappilia* and of the Navidad specimen are rimmed by a strongly upturned flange. By contrast, the orbital rim, if present on *Mursia*, is not as prominent. The anterolateral margin on *Calappilia* is smooth as it is on the portion of the margin preserved on the Chilean specimen. The anterolateral margin on *Mursia*, is corrugated, nodose, or delicately spinose. Thus, it is prudent to questionably assign the single specimen from the Navidad Formation to *Calappilia* until more complete material is discovered.

Glaessner (1969) cited the range of the genus as middle Eocene to upper Oligocene in the fossil record and Recent, based upon his judgement of synonymy of *Calappilia* with the living genus *Paracyclois* Miers, 1886. Schweitzer and Feldmann (2000a) retained the two genera as distinct, and that view is sustained herein. The range of *Calappilia* has

been extended into the Miocene with records from the Southern Hemisphere. Referral herein of Beurlen's (1958) *Calappa circularis* to *Calappilia*, from the lower Miocene Pirabas Formation in Brazil, represents the only prior South American occurrence of the genus. Feldmann (1993) described *Calappilia maxwelli* from the Pakaurangi Formation, of early Miocene age, on North Island, New Zealand. Jenkins (1972) noted the presence of the genus in Miocene rocks in Australia and in Pleistocene rocks of Australia and South Africa; however, those occurrences have not been published. Thus, the discovery of *Calappilia* in the Navidad Formation would be the second notice in South America and only the third published species in the Southern Hemisphere if confirmed as a member of the genus.

Calappilia? chilensis new species

Fig. 3

Material Examined.—The holotype and sole specimen, SGO.PI.6310, collected from WP68 of the Mat.-Pup. locality.

Diagnosis.—Branchial regions with two small, transversely arrayed nodes on epibranchial region and at least one longitudinal row of three nodes on mesobranchial region.

Description.—Carapace average size for genus, length estimated to be 13 mm, width about 16 mm, outline ovoid; margins poorly known, regions defined by nodes and grooves.

Front broken; orbital rim strongly upturned, margin appears smooth. Anterior part of anterolateral margin sharp, smooth. Posterolateral and posterior margins broken.

Proto gastric regions moderately swollen, bearing small anterior and larger posterior node. Hepatic region with at least one node situated posterior to orbit. Mesogastric region with pair of small nodes adjacent midline and one large axial node posterior to them. Cardiac region elongate, oval; with two axial nodes, anterior node larger. Smaller axial node on intestinal region. Branchial region nodose; two small epibranchial nodes arrayed transversely; longitudinal row of three large mesobranchial spines and possibly a second longitudinal row distal to that; one small metabranchial node. Remainder of carapace surface very finely granulated.

Etymology.—The trivial name refers to Chile, the country from which the specimen was collected.

Remarks.—*Calappilia? chilensis* has been tentatively placed within this genus based upon the similarity of the orbital rim and anterolateral margin with other members of the genus. Because of the fragmentary nature of the material, however, the distinction between it and species of *Mursia* is not clear. *Calappilia? chilensis* differs from other species within the genus in having relatively few rows of large nodes, whereas most species exhibit more rows of smaller nodes. In this regard, the ornamentation is more like some species of *Mursia* but the ornamentation can only be taken to be a more superficial character than the structure of the orbits and the features of the margins. Thus, although the generic placement is questionable, it seems justifiable to erect a new species based on the observation that the morphology is distinctly different from that of other known calappids and

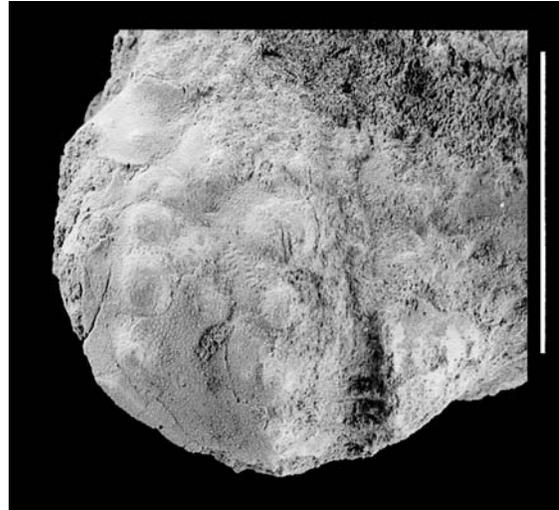


Fig. 3. *Calappilia? chilensis* new species, holotype, SGO.PI.6310. Scale bar = 1 cm.

the paucity of calappids known from the fossil record in southern South America.

Family Hepatidae Stimpson, 1871

Genus *Hepatus* Latreille, 1802

Type Species.—*Calappa angustata* Fabricius, 1798, by original designation.

Diagnosis.—Carapace relatively smooth, much broader than long, broadly obovate, vaulted; rostrum bilobed, extending well beyond orbits, elevated; extremely convex, crenulated or serrated anterolateral margins; posterolateral margin concave, margin beaded, complete; posterior margin narrow.

Included Fossil Species.—*Hepatus bottomsii* Blow, 2003; *H. chiliensis* H. Milne Edwards, 1837; *H. lineatus* Rathbun, 1898b; *H. nodosus* Collins and Morris, 1976; *H. praecox* Collins, Donovan, and Dixon, 1996; *H. spinimarginatus* new species; *Hepatus* sp. in Rathbun, 1918a; *Hepatus* sp. in Collins and Portell, 1998.

Remarks.—When complete material is available, placement of fossils within *Hepatus* is relatively straightforward. The combination of characters in the diagnosis serves to distinguish the genus from all others. However, when the front of the carapace is missing, it is difficult to distinguish *Hepatus* from the totally unrelated cancrinid genus *Metacarcinus* A. Milne Edwards, 1862. Both genera have long, strongly convex, variously crenulate or spined anterolateral margins; similar posterolateral margins although that of *Metacarcinus* may bear a spine; and both have weakly defined carapace regions. However, several characters of the Chilean material could be identified that confirmed placement in *Hepatus*. The front is bilobed and extends slightly in advance of the orbits. The greatest width of the carapace was clearly at the anterolateral corner on the Navidad specimen whereas that on *Metacarcinus* may be in advance of the corner. The anterolateral margin on the

Navidad specimen bears small, upturned nodes which do not resemble the marginal features on any of the known *Metacarcinus* species, although that feature alone would not rule out placement with the cancrids. Finally, the carapace of the Navidad specimen is extremely vaulted whereas cancrids in general tend to be more weakly vaulted. Measurements of relative vaulting were made on two species of *Metacarcinus*, one extant species of *Hepatus*, and the Navidad specimen by determining the ratio of maximum height of the carapace to carapace length. *Metacarcinus novaezelandius* (Jacquinot in Jacquinot and Lucas, 1853), extant of New Zealand; and *M. goederti* Schweitzer and Feldmann, 2000d, from the Oligocene of Alaska, U.S.A., exhibited ratios of 0.198 and 0.177, respectively. *Hepatus epheliticus* (Linnaeus, 1763), extant of eastern U.S.A., and the Navidad specimen had ratios of 0.22 and 0.257 respectively. The position of maximum height was well in advance of midlength in *Hepatus* and near midlength in *Metacarcinus*. The combination of these characters provides sufficient evidence to place the Navidad specimen within *Hepatus*.

Fossil species of *Hepatus* are known exclusively from east coastal U.S.A., the Caribbean region, and Panama in rocks ranging in age from middle Miocene to Pleistocene. Extant species are known from the North and South Atlantic and the East Pacific (Rathbun, 1937; Williams, 1984), all from the Western Hemisphere. Rathbun (1937) reported *H. princeps* (Herbst, 1794) from West Africa, but that occurrence has been recognized as erroneous (Manning and Holthuis, 1981, p. 3).

Hepatus spinimarginatus new species

Fig. 4

Types.—The holotype, SGO.PI.(SA50) was collected by William J. Zinsmeister, Purdue University. Paratype SGO.PI.6322 was collected from WP63 of locality South Boca Pupuya.

Diagnosis.—Front with two prominent, narrow projections; orbits with inner orbital projections and two closed fissures; anterolateral margin with nine or ten distinct, blunt, upturned nodes or spines; posterolateral margin rimmed by very finely beaded elevation.

Description.—Small to moderate size for genus, elongate-ovoid in shape; much wider than long, maximum carapace width of holotype, 48.4 mm; frontal width, 4.5 mm; fronto-orbital width, 15.9 mm; length, 37.5 mm. Maximum width of paratype, 54 mm; length, greater than 35 mm; greatest width at anterolateral corner, about 70% the distance from front; strongly vaulted longitudinally and moderately vaulted transversely; surface punctate.

Front narrow, about 10 percent maximum width, bearing two narrow, elongate projections; orbits directed anteriorly, with prominent inner and outer orbital spines and two closed fissures; fronto-orbital width about one-third maximum width; anterolateral margin strongly and uniformly convex, bearing nine or ten blunt, upturned nodes or spines increasing in size posteriorly, margins of nodes obscured. Posterolateral margin strongly concave, entire, rimmed by

finely beaded elevation. Posterior margin weakly convex, margin broken.

Carapace regions weakly delimited. Protogastric region slightly inflated. Mesogastric and cardiac regions weakly inflated, equally wide, separated by narrow, concave-forward urogastric region. Cardiac region tapering posteriorly to narrow intestinal area.

Carapace surface punctate; punctae large and widely spaced on gastric regions becoming smaller and more densely spaced posteriorly and laterally.

Etymology.—The trivial name alludes to the upturned spines on the anterolateral margin that distinguish the species from its known congeners.

Remarks.—The genus *Hepatus* is not particularly speciose; there are five extant species (Rathbun, 1937), and two of the four formally named species in the fossil record are known from the modern record as well. Thus, prior to the description of *Hepatus spinimarginatus*, only eight species were described. Distinction between species in the literature of living crabs is often based on color patterns and nature of the front; however, the form of the anterolateral and posterolateral margins can serve equally well in distinguishing the taxa. The front on *Hepatus spinimarginatus* bears much more prominent projections, or lobes, than on any other described species. The anterolateral margin of *H. princeps* most closely resembles that of *H. spinimarginatus*, but the spines on the former are more numerous and more closely spaced. The anterolateral margins of the other living and extinct taxa are more finely serrated. *Hepatus spinimarginatus*, *H. princeps*, and the extinct *H. nodosus*, from the middle Miocene of Trinidad, are widest at their anterolateral corners; however, the latter two have nearly straight posterolateral margins and, as the name implies, *H. nodosus* has much more inflated carapace regions. Thus, the Navidad specimen clearly represents a new species.

A single living species of the genus, *Hepatus chiliensis* currently is known off the coast of Chile where it is found in water to a depth of 23 fathoms (Rathbun, 1937). Rathbun (1918a) also reported that species from the Pleistocene of Panama.

Superfamily Portunoidea Rafinesque, 1815

Family Portunidae Rafinesque, 1815

Subfamily Polybiinae Ortmann, 1893

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

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

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

Remarks.—The genus has recently been diagnosed and discussed in detail (Casadío *et al.*, 2004), and that work will not be reiterated here. Examination of the material from the Navidad Formation confirms that the specimens fall within

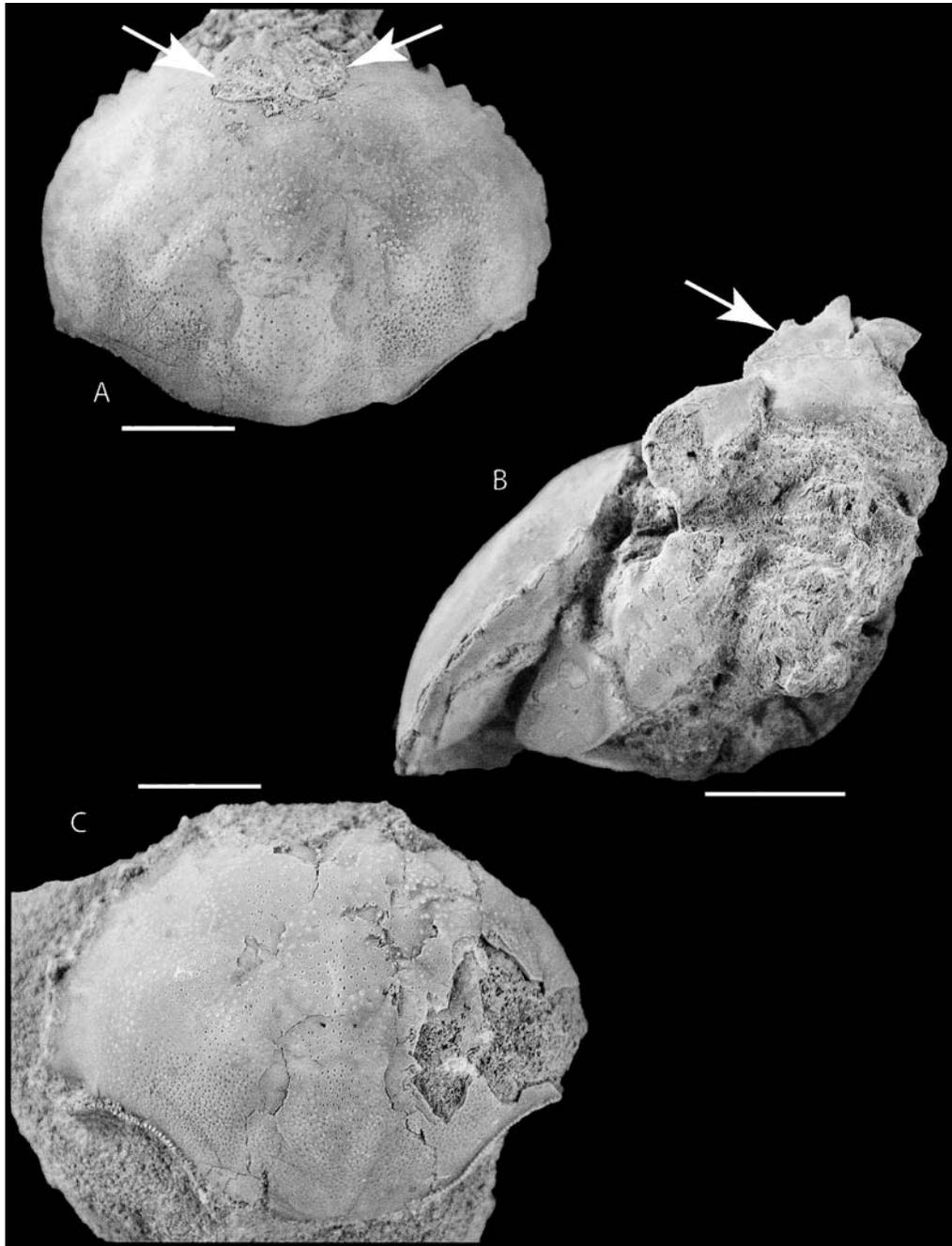


Fig. 4. *Hepatus spinimarginatus* new species. A, holotype, SGO.PI.(SA50), dorsal carapace, arrows indicate bases of barnacle epibionts; B, holotype, SGO.PI.(SA50), lateral view, arrow indicates manus of cheliped; C, paratype SGO.PI.6322, dorsal carapace. Scale bars = 1 cm.

the range of dimensions and morphological features presented therein, so that placement in *Proterocarcinus* can be made with confidence. In that same work, Casadío *et al.* (2004, p. 32) discussed the status of *Lebucarcinus* Bahamonde and Frassinetti, 1980, and concluded that it is a *nomen nudum* (ICZN, 1999, Article 75). Recognition of this condition eliminates nomenclatorial confusion and provides the opportunity to clearly examine the distribution of species of *Proterocarcinus* in Chile as well as in Argentina.

Proterocarcinus navidad new species

Fig. 5

Types.—The holotype, SGO.PI.6323, and paratypes SGO.PI.6324, 6326, and 6327 were collected from WP68 of the Mat-Pup locality. Paratype SGO.PI.6325 was collected from WP60, and paratype SGO.PI.6328 was collected from WP57, both of the Mat-Pup locality. Paratype SGO.PI.6329 was collected from WP 59 of the PPWPta locality.

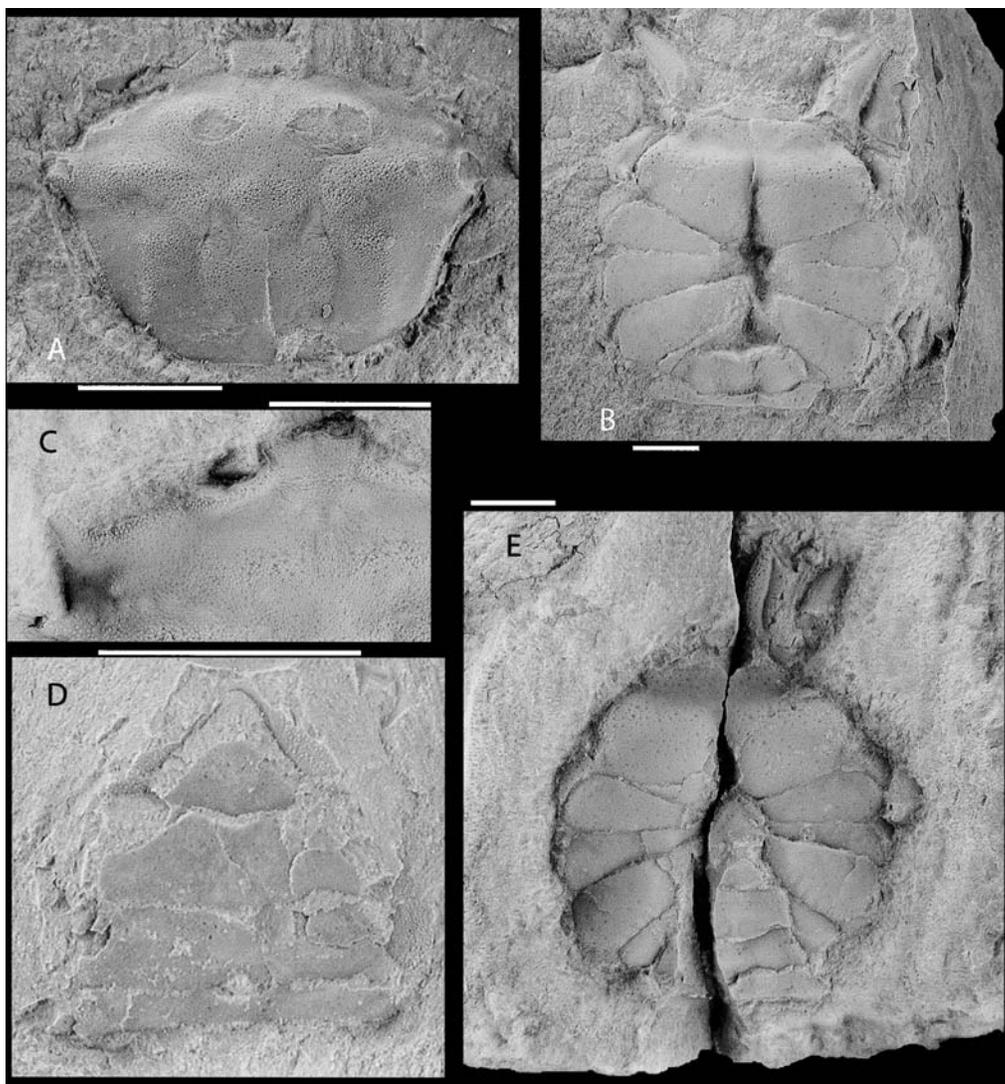


Fig. 5. *Proterocarcinus navidad* new species. A, holotype, SGO.PI.6323, dorsal carapace; B, paratype, SGO.PI.6325, sternum; C, holotype, SGO.PI.6323, close-up of orbits, front, and anterolateral margins showing diagnostic characters of the species; D, paratype, SGO.PI.6326, female abdomen; E, paratype, SGO.PI.6327, male sternum and abdomen. Scale bars = 1 cm.

Diagnosis.—Rostrum projected well beyond orbits; four short, rounded rostral projections; orbits with deeply convex axial section and weakly concave lateral margin and beaded orbital rim.

Description.—Moderate-sized for genus, maximum width up to 32 mm. Carapace pentagonal to rectangular in outline, wider than long in adults but nearly equant in juveniles; weakly arched transversely and longitudinally; regions moderately well defined as swollen areas, more strongly defined in juveniles.

Front narrow, 17% maximum width, excluding lateral spines, projected well in advance of orbits, slightly downturned with weakly bilobed axis and rounded anterolaterally-directed inner orbital spines. Orbits broad, biconvex, with well-defined beaded orbital rim; fronto-orbital margin 95% maximum width. Two very shallow orbital fissures, innermost separates moderately strongly concave inner margin

from weakly concave distal margin; second fissure near prominent outer orbital spine. Anterolateral margin very short, straight to weakly convex, bounded by anterolaterally directed outer orbital and anterolateral spines. Posterolateral margins straight, converging posteriorly. Posterolateral reentrants long, straight to weakly concave, bounding wide straight posterior margin, 48% maximum width.

Regions of carapace defined as weakly swollen areas with granular surfaces. Frontal areas slightly depressed; two small nodes on juveniles become obscure on adults. Protogastric areas large, transversely elongated, swollen; separated by narrow mesogastric region that remains uniformly narrow to level of anterolateral spine, widening markedly and bearing two subtly elevated nodes. Hepatic regions poorly defined. Metagastric region narrow, depressed. Cardiac region large, transversely ovate, bearing medial transverse elevation. Intestinal region indistinct. Mesobranchial region with a convex forward, well-defined ridge extending from widest

point of mesogastric region to anterolateral spines. Metabranched region with distinct longitudinal ridge extending almost to posterolateral corner.

Sternum circular, as long as wide, sutures distinct, sutures 4/5 and 5/6 incomplete, sutures 6/7 and 7/8 complete; axial depression uniformly narrow. Sternites 1–3 not well exposed, appearing to be fused, triangular. Sternite 4 large, with transverse ridge at midlength at point of inflection where anterior part of sternite is directed dorsally. Sternites 5–7 about equal in size, each sternite narrow axially and broadening distally, with smoothly rounded terminations and posteriorly-directed sharply-pointed episternal projections. Sternite 8 small, poorly exposed. Male abdomen broad at base, narrowing to telson with concave margins; fusion of segments obscured by transverse fractures. Female abdomen broad, margins convex; somites 3–4 and 5–6 apparently fused but sutures visible.

Appendages represented only by fragments.

Etymology.—The trivial name alludes to the Navidad Formation from which the specimens were collected.

Remarks.—*Proterocarcinus navidad* bears all the definitional characters of the genus in terms of the form of the rostrum and rostral spines, length of orbits, development and granulation of regions, possession of transverse and longitudinal ridges, and form of the anterolateral margin. Relative proportions of key dimensions taken on the known species places *P. navidad* within the known range of variation, exhibiting dimensions very close to those of *P. latus*. The ratio of carapace length to carapace width in the genus ranges from 0.71 to 0.89; that of *P. navidad* is 0.79 and that of *P. latus* is 0.76. The range of frontal width to maximum carapace width in the genus is 0.16 to 0.24; that of the new species and that of *P. latus* is 0.17. The fronto-orbital width to total width ranges from 0.70 to 0.95, and that of *P. navidad* is 0.93, whereas that of *P. latus* is 0.95. Thus, the overall shape of specimens within the two species is very similar. However, *Proterocarcinus navidad* can be distinguished from all the other species within the genus in having a rostrum that extends well beyond the orbits, a distinctly biconvex outline of the upper orbital margin, and only two spines on the anterolateral margin.

Preservation of a single juvenile specimen of *Proterocarcinus navidad* makes it possible to add reinforcement to the observation made by Schweitzer and Feldmann (2000b, p. 647) that in some species of decapods, *Chaceon peruvianus* (d'Orbigny, 1842) for example, the carapace morphology of juveniles is more strongly expressed than in the adults. Careful examination of the morphological features critical for species identification confirms that these features are expressed in both juveniles and adults, however.

Presence of a species of *Proterocarcinus* in Chile is significant because it suggests that the Andes Mountains did not form a barrier to dispersal throughout the Cenozoic. It is necessary and important to examine more decapod occurrences in Chile in order to more fully interpret the nature and timing of these connections. To date, it has generally been held that the Cenozoic decapod faunas in the two countries were substantially different and that the Andes did form

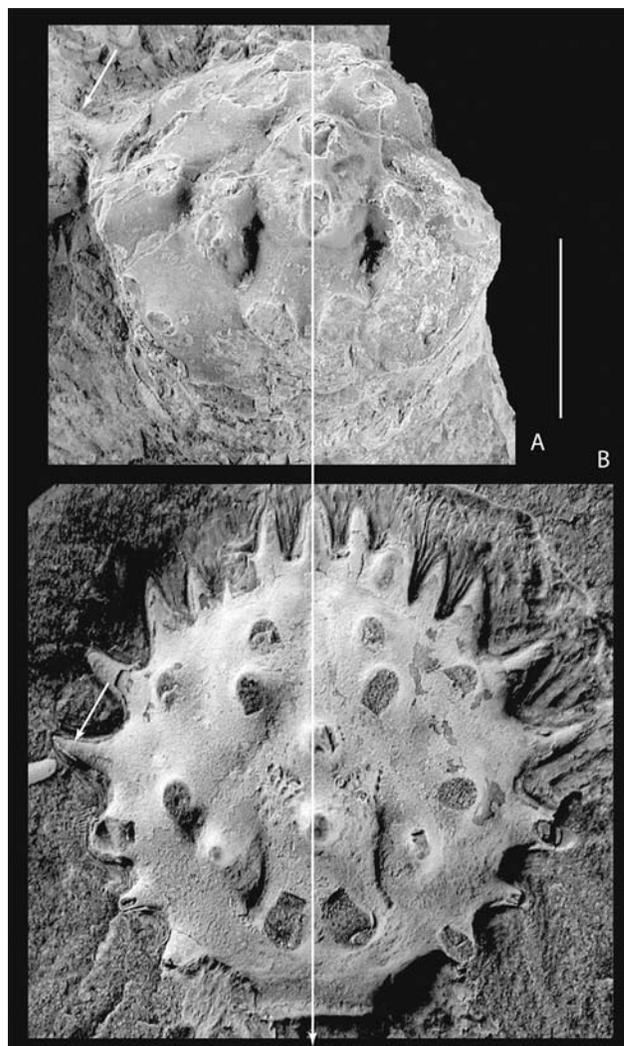


Fig. 6. *Trichopeltarion levis* Casadío, De Angeli, Feldmann, Garassino, Hetler, Parras, and Schweitzer, 2004. A, SGO.PI.6330A, dorsal carapace of Miocene Chilean specimen, arrow indicates position of lateral spine; B, MSNM i25533, paratype, dorsal carapace of well-preserved specimen from Oligocene of Argentina (Casadío *et al.*, 2004), arrow indicates position of same lateral spine as indicated in A. Vertical white line indicates midline of both specimens. Scale bar = 1 cm.

a barrier to dispersal (Feldmann *et al.*, 1995) which, coupled with the thermal barrier of different water sources (Feldmann *et al.*, 1997), resulted in markedly different decapod faunas in the two countries.

Superfamily Cancroidea Latreille, 1802

Family Atelecyclidae Ortmann, 1893

Genus *Trichopeltarion* A. Milne Edwards, 1880

Trichopeltarion A. Milne Edwards, 1880, p. 19.

Trachycarcinus Faxon, 1893, p. 156.

Type Species.—*Trichopeltarion nobile* A. Milne Edwards, 1880, p. 20, pl. 2, by monotypy.

Included Species.—See Schweitzer and Salva (2000) and Salva and Feldmann (2001).

Diagnosis.—See Salva and Feldmann (2001).

Trichopeltarion levis Casadío, de Angeli, Feldmann,
Garassino, Hetler, Parras, and Schweitzer, 2004
Fig. 6

Material Examined.—A specimen lot assigned to SGO.PI.6330 was collected from WP59 of the PPWPta locality.

Diagnosis.—“Carapace ornamented only by very fine pustules; frontal, orbital, and lateral spines simple; posterolateral spines well developed; carapace regions bearing 14 prominent, simple spines” (Casadío *et al.*, 2004, p. 35).

Remarks.—Casadío *et al.* (2004) described extremely well-preserved specimens of a new species of *Trichopeltarion* from the middle Oligocene Río Foyel Formation near Bariloche, Argentina. It should be noted that, in table 3 of that paper, the age of *T. levis* is incorrectly cited as Eocene, rather than middle Oligocene. Casadío *et al.* (2004, table 3) provided a matrix of characters of the dorsal carapace that could be used to distinguish species within the genus, and *Trichopeltarion levis* is the only species exhibiting a circular outline, a generally smooth surface and smooth tubercles, and simple lateral spines. These characters are all present on the single specimen from the Navidad Formation so that, despite the incomplete nature of the specimen, it can be referred confidently to *T. levis*.

As with the new species of *Proterocarcinus*, the occurrence of *Trichopeltarion* in the Navidad Formation provides another link between Chilean and Argentine decapods. This suggests a dispersal pathway from one side of the Andes to the other at the time of, or earlier than, the time of deposition of the Navidad Formation.

Superfamily Xanthoidea MacLeay, 1838

Family Pilumnidae Samouelle, 1819

Included Subfamilies.—Calmaniinae Števcíć, 1991; Eumedoninae Dana, 1853; Galeninae Alcock, 1898; Halimedinae Alcock, 1898; Pilumninae Samouelle, 1819; Rhizopinae Stimpson, 1858 (*sensu* Davie, 2002).

Diagnosis.—Carapace hexagonal, rectangular, or ovate; dorsal carapace smooth or granular, convex; frontal margin entire, bilobate, or multi-lobate; anterolateral margins typically with 1 to 4 spines or lobes but may have 5; gastric regions often long; chelae subequal or very unequal; pereiopods stout, short to moderately long; male abdomen with all somites free, narrow, elongate, sometimes covering most of sternite 4 (after Davie, 2002, p. 392).

Remarks.—The Pilumnidae Samouelle, 1819, as currently recognized is a heterogeneous group (Davie, 2002; Schweitzer, 2005). This has made working with the family in the fossil record very difficult. Although the fossil record of several xanthoid families recently has been revised (Schweitzer and Feldmann, 2001b; Karasawa and Kato, 2003; Schweitzer, 2003; Schweitzer and Karasawa, 2004; Schweitzer *et al.*, 2004; Karasawa and Schweitzer, 2004; Schweitzer, 2005), the Pilumnidae remain in need of

directed attention, currently underway by one of us (CS) and others.

The specimens herein referred to the Pilumnidae are so placed based upon their overall carapace shape; the development of carapace regions; the longitudinal vaulting of the dorsal carapace, especially in the anterior-most one-third; spined anterolateral margins; and free male abdominal somites. No other xanthoid family can accommodate the new material.

The Tumidocarcinidae Schweitzer, 2005, have equant carapaces and well-defined regions, but members of the family are very highly vaulted longitudinally; have four frontal spines; have no orbital fissures or one very faint fissure; and have circular, forward-directed orbits; all of these differ from the features seen in the new Chilean material. In addition, the Chilean material lacks the very deep Y-shaped sternal groove and deep grooves on sternite 4 defined as diagnostic for the Tumidocarcinidae (Schweitzer, 2005).

Some members of the Panopeidae Ortmann, 1893, have ridges on the epigastric and hepatic regions of the carapace as seen in the Chilean specimens. However, *Panopeus* H. Milne Edwards, 1834, and other panopeid taxa that exhibit these features have more poorly developed carapace regions and exhibit fusion of male abdominal somite 5 with somite 4. Somite 5 in the Chilean material is clearly unfused to somite 4. In the Xanthidae MacLeay, 1838; Pseudorhombilidae Alcock, 1900; and the extinct Zanthopsidae Vía, 1959, male abdominal somites 3–5 are fused, excluding the Chilean material from these families as well.

Some members of the Eriphiidae MacLeay, 1838, are superficially similar to the Chilean material, notably *Hypothalassia* Gistel, 1848, of the Eriphiinae MacLeay, 1838; however, the family cannot accommodate the Chilean specimens. All members of the family lack a Y-shaped groove on the sternum (Schweitzer, 2005), which while not deep, is quite evident on the Chilean material. In addition, most taxa within the Eriphiinae lack orbital fissures or have sutured orbital fissures (Ng *et al.*, 2001; Davie, 2002), whereas the Chilean material has two open orbital notches. Members of the other subfamilies within the Eriphiidae (Davie, 2002) have dorsal carapace morphologies altogether different from that of the new specimens and cannot accommodate them.

Members of the Platyxanthidae Guinot, 1977, have well-defined frontal spines; a very narrow front; and a narrow fronto-orbital width (Schweitzer, 2005), all of which exclude the new Chilean material from that family. The Goneplacidae MacLeay, 1838, lack an axial groove on the fourth sternite (Karasawa and Kato, 2003) and generally have much more poorly developed carapace regions than does the Chilean material. The overall carapace shape and ornamentation immediately excludes the new Chilean material from the Carpiliidae Ortmann, 1893; Hexapodidae Miers, 1886; Palaeoxanthopsidae Schweitzer, 2003; and Trapeziidae Miers, 1886. Thus, we are confident in the family-level placement of the material.

The new specimens are Miocene, and thus do not extend the geologic range of the family. Müller (1984) considered that the genus *Pilumnus* Leach, 1816, and its allies extended into the Eocene, and the referral of *Lobonotus* A. Milne

Edwards, 1864, and *Titanocarcinus* A. Milne Edwards, 1864, to the family (Schweitzer *et al.*, 2004; Karasawa and Schweitzer, 2004) confirmed his hypothesis, at least at the family level. These are the oldest confirmed members of the family to date. Extant genera previously have been reported from Miocene rocks of Europe and Japan (Glaessner, 1928; Müller, 1984; Karasawa, 1991; Karasawa and Inoue, 1992) and Plio-Pleistocene rocks of the West Pacific, Europe, and the Caribbean (Risso, 1926; Collins *et al.*, 1996; Collins and Portell, 1998; Kato and Karasawa, 1998; Collins *et al.*, 2003). Because the oldest known genera within the family are members of the Pilumninae Samouelle, 1819, we suggest that all of the other subfamilies are derived from it.

Subfamily Pilumninae Samouelle, 1819

Included Fossil Genera.—*Actumnus* Dana, 1851b; *Lobonotus* A. Milne Edwards, 1864 (extinct); *Pilumnus* Leach, 1816; *Titanocarcinus* A. Milne Edwards, 1864 (extinct). Material referred to *Glabropilumnus* Balss, 1932 (in Moissette and Müller, 1990; Müller, 1996) and *Pilumnopus* A. Milne Edwards, 1863 (in Müller, 1993) must be confirmed as being referable to those genera in order for those genera to have a confirmed fossil record.

Material Examined.—*Actumnus telegdii* (Müller, 1974), M.86.43, M.86.96. *Lobonotus bakeri* Rathbun, 1935, USNM 371574, holotype. *Lobonotus natchitochensis* Stenzel, 1935, USNM 494918, cast of holotype. *Lobonotus mexicanus* Rathbun, 1930b, USNM 371096, holotype; MHN-UABCS/Te3/52-73, 74; MHN-UABCS/Te6/53-17; MHN-UABCS/Te14/50-59. *Lobonotus sculptus* A. Milne Edwards, 1864, In. 28287, holotype. *Pilumnus mediterraneus* (Lörenthey, 1898), M.86.519, 5 specimens in large sample lot. *Titanocarcinus raulinianus* A. Milne Edwards, 1864, identified by P. Müller, E9407.

Diagnosis.—Carapace hexagonal, ovate, or rectangular; dorsal surface convex; carapace smooth, granular, or spinose, often covered with dense setae; regions generally prominent, gastric regions long; anterolateral and posterolateral margins well differentiated from one another; anterolateral margin generally with from 3 to 5 spines, which may be triangular or sharp and needlelike; frontal margin bilobed, entire, or quadrilobed; male abdomen not reaching level of anterior edge of coxae of first pereopods (after Davie, 2002, p. 409).

Remarks.—The included genera are those with fossil records confirmed by us. Other genera have been referred to the family, although usually not placed within a subfamily, but type or other material has not been examined by the authors to confirm these taxa as members of the subfamily.

Genus *Pilumnus* Leach, 1816

Type Species.—*Cancer hirtellus* Linnaeus, 1761, by monotypy.

Included Fossil Species.—*Pilumnus cucaoensis* new species; *P. fookimensis* Collins, Lee, and Noad, 2003; *P. hirtellus* (extant); *P. hirtellus* var. *villosa* Risso, 1826; *P. mediterraneus* (Lörenthey, 1898); *P. olivellai* Müller,

1993; *P. subequus* Rathbun, 1919 (claws only); *Pilumnus* sp. cf. *P. sayi* Rathbun, 1897 in Collins, Donovan, and Dixon, 1996 (extant; claws only); *Pilumnus* aff. *P. pannosus* Rathbun, 1896 in Collins and Portell, 1998 (extant; claws only); *Pilumnus* aff. *P. spinosissimus* Rathbun, 1898a in Collins and Portell, 1998 (extant; claws only); *Pilumnus* sp. in Glaessner, 1928; *Pilumnus* sp. in Karasawa, 1990; *Pilumnus* sp. in Kato and Karasawa, 1998 (claws only). Those species that are also extant are so marked.

Diagnosis.—Carapace subquadrilateral or ovate, not much wider than long, generally covered with setae; vaulted longitudinally, especially anteriorly; regions moderately to well defined; anterolateral margin generally not longer than posterolateral, with three to five spines; front usually about one-third maximum carapace width, axially notched, separated from orbit by deep notch or fissure; orbits usually with two orbital notches or fissures; chelipeds stout; sternal suture 2/3 continuous; sternal suture 3/4 shallow, continuous; sternal sutures 4/5 and 5/6 interrupted medially; male abdominal somites free (modified from Rathbun, 1930a).

Remarks.—The new material is referred to *Pilumnus* based upon its possession of all of the diagnostic features for the genus, subfamily, and family *sensu* Rathbun (1930a) and Davie (2002). The generic diagnosis above is based upon their and our observations. The new species is warranted based upon its possession of five needlelike anterolateral spines, whereas most other species of the genus have three spines, which may not be needlelike in shape; the very sharp ridge on the hepatic region; and the longer anterolateral margins than are typical for the genus, which are slightly longer than the posterolateral margins in the new species.

The Chilean material is similar to the pilumnine species *Lobonotus* in several features of the dorsal carapace but cannot be referred to that genus. The sternum of the Chilean material differs significantly from species of *Lobonotus* in lacking the very deep Y-shaped sternal groove and deep grooves on sternite 4 typical of that genus. Karasawa and Schweitzer (2004) referred *Glyphithyreus bituberculatus* Collins and Jakobsen, 2003, to *Titanocarcinus*, a genus so similar to *Lobonotus* that many authors have suggested that the two may be synonymous (Collins and Morris, 1978; Schweitzer *et al.*, 2002; Schweitzer *et al.*, 2004). *Titanocarcinus bituberculatus* (Collins and Jakobsen, 2003) exhibits a sternum nearly identical to that of *Lobonotus*; thus, the Chilean material cannot be referred to *Titanocarcinus*.

Rathbun (1919, p. 177) referred a dactyl, or movable finger, to *Pilumnus* sp. and considered it to be lower Miocene in age, although in her introductory remarks, she noted that the unit from which the specimen was recovered was considered by some to be Oligocene in age (p. 159). Glaessner (1929) considered the specimen to be Oligocene, and the range of the genus has been reported as Oligocene to Recent, apparently based upon his publication, ever since (Glaessner, 1969; Collins *et al.*, 2003). The earliest dorsal carapace material known from the genus has been reported from the Miocene of Europe (Müller, 1984) and Chile (this report), and chela material has been reported from the Miocene of Europe (Glaessner, 1928). The genus

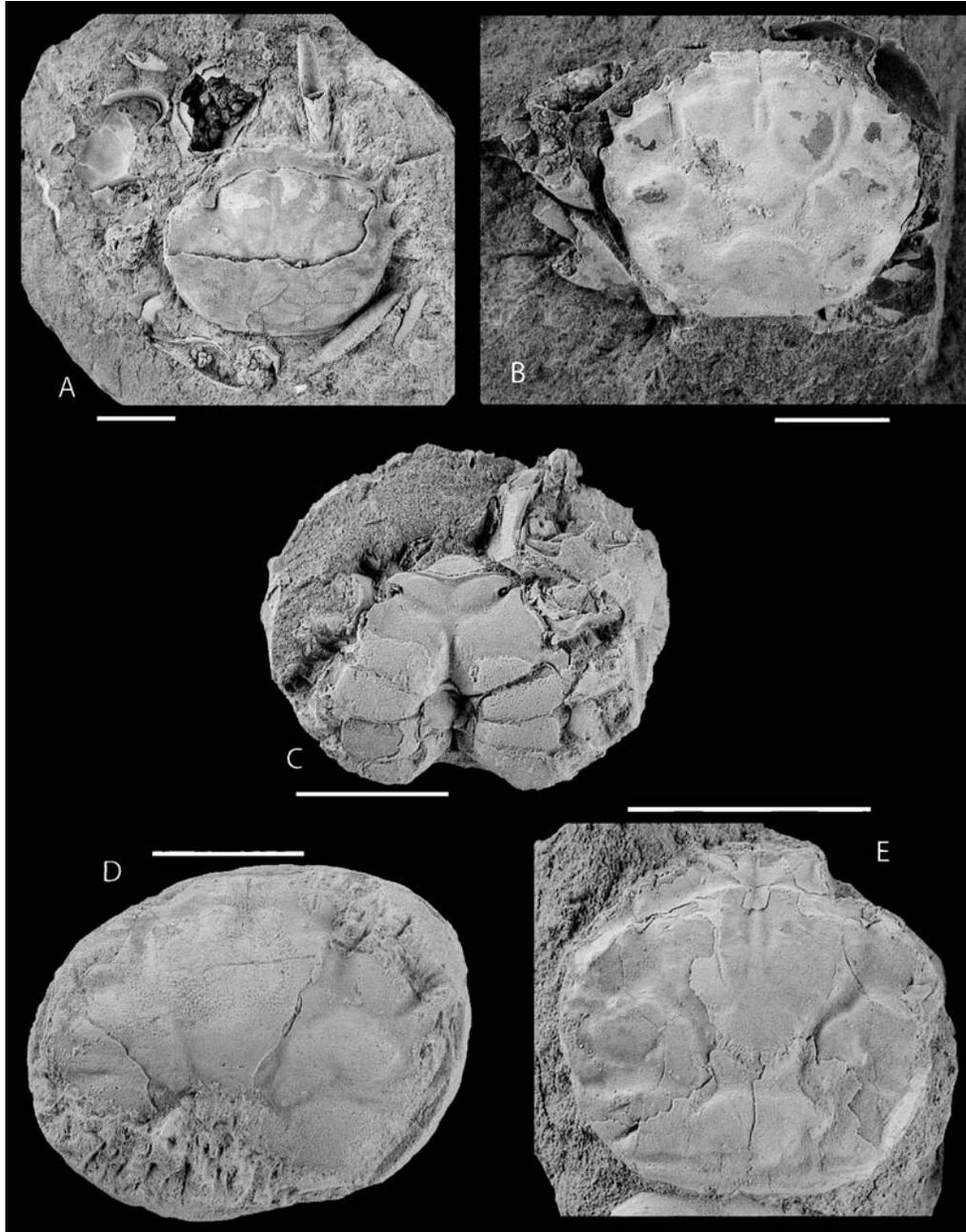


Fig. 7. *Pilumnus cucaoensis* new species. A, holotype SGO.PI.6331, dorsal carapace and appendages; B, paratype, SGO.PI.6332, dorsal carapace; C, paratype, SGO.PI.6333, male sternum and abdomen; D, paratype, SGO.PI.6334, partial dorsal carapace; E, paratype, SGO.PI.6335, dorsal carapace. Scale bars = 1 cm.

has also been noted from the Pleistocene of Europe, the Caribbean, Japan, and Sabah in Malaysia (Risso, 1826; Collins *et al.*, 1996; Collins and Portell, 1998; Kato and Karasawa, 1998; Collins *et al.*, 2003). Because Rathbun (1919) considered that her specimen was Miocene, and because the earliest dorsal carapace material is Miocene in age, we consider that the range of the genus is Miocene to Recent. Thus, the new species is one of the earliest known species of the genus and is the first notice of the genus in the southern hemisphere in the fossil record. *Pilumnus* is cosmopolitan in modern oceans (Glaessner, 1969), and

extant species inhabit coastal South America as far south as Peru (Rathbun, 1930a).

Pilumnus cucaoensis new species

Fig. 7

Types.—The holotype, SGO.PI.6331, and paratypes SGO.PI.6336–6339 were collected from Feldmann locality on Chiloe Island. Paratypes SGO.PI.6332, 6333, and 6340–6343 were collected from Nielsen locality on Chiloe

Island. Paratype SGO.PI.63335 was collected from WP57, paratype SGO.PI.6335 from WP68, and paratype SGO.PI.6344 from a location without waypoint, all of the Mat-Pup locality.

Diagnosis.—Carapace not much wider than long, regions well defined by grooves and densely granular; front axially notched, deep notch between front and inner-orbital angle; orbits oblique, directed anterolaterally, with two open fissures; epigastric and hepatic regions ornamented by granular ridges; anterolateral margin with 5 spines, penultimate spine circular in cross-section; last spine smaller, ornamented with sharp tubercles; sternal suture 2/3 clear, continuous; sternite 4 with axial groove, forming Y-shaped groove with shallow sternal sutures 3/4; male abdominal somites 4/5 free.

Description.—Carapace not much wider than long, L/W about 87 percent; widest about 40 percent the distance posteriorly on carapace; moderately vaulted longitudinally, especially in anterior one-third; weakly vaulted transversely; regions well defined by grooves and densely granular on elevated regions.

Front axially notched, with very slight, blunt projections on either side of notch; slightly produced beyond orbits; extending weakly sinuously to inner-orbital angle, which is not produced into a spine or projection, frontal width about one-third maximum carapace width. Marked notch between front and inner-orbital angle. Orbits shallow, oblique, directed anterolaterally; broadly rimmed; with protuberance just distal to inner-orbital angle; one open orbital fissure at about two-thirds the distance distally from inner-orbital angle; second open fissure just proximal to outer-orbital angle; outer-orbital angle produced into small spine, sometimes with small spine at base; fronto-orbital width about 60 percent maximum carapace width.

Anterolateral margin convex, very tightly arced posteriorly; with 5 spines excluding outer-orbital spine; first two spines smallest, first directed forward, sharp; second directed anterolaterally, stouter than first; third spine triangular, broad based, stoutest of all anterolateral spines, directed anterolaterally; penultimate spine longest of known spines, attenuated, round in cross-section, directed anterolaterally, granular on upper surface; fifth spine shorter than penultimate spine, broad, ornamented with small, sharp tubercles, length of anterolateral margin measured from outer-orbital angle to position of last anterolateral spine about 110 percent length of posterolateral margin.

Posterolateral margin convex, ornamented with small beads; posterolateral reentrant small; posterior margin nearly straight, with beaded rim, ridge parallel to it just anterior to margin, width about 40 percent maximum carapace width.

Frontal region axially sulcate; epigastric regions equant, with sharp anterior ridge. Protogastric regions widened anteriorly; with weak ridge along distal half of anterior edge; moderately inflated. Mesogastric region with long anterior process terminating at anterior edge of epigastric regions, widened posteriorly, best defined posteriorly by cervical groove. Urogastric region depressed below level of proto-

Table 1. Measurements (in mm) taken on the dorsal carapace of specimens of *Pilumnus cucaoensis* new species. W = maximum carapace width; L1 = maximum carapace length; L2 = length to position of maximum width on carapace; FOW = fronto-orbital width; FW = frontal width; PW = posterior width.

Specimen Number	W	L1	FOW	FW	PW	L2
SGO.PI.6335	14.6	13.5	9.9	5.2	5.5	7.2
SGO.PI.6334	26.2	21.5	15.4	7.6	11.8	13.8
SGO.PI.6332	26.6	22.8	15.8	8.5	9.2	10.3
SGO.PI.6342	33.5	28.4	21.4	12.1	—	13.4
SGO.PI.6343	27.3	23.5	16.2	8.6	9.3	11.3
SGO.PI.6340	24.5	21.6	15.0	8.0	—	9.8
SGO.PI.6341	25.3	22.0	15.8	8.6	—	9.8
SGO.PI.6338	22.0	19.6	14.0	8.8	—	8.4
SGO.PI.6337	26.8	23.0	—	—	—	11.5
SGO.PI.6336	29.1	24.7	16.4	7.1	—	10.5
SGO.PI.6339	23.2	20.2	14.0	6.7	—	9.6
SGO.PI.6331	29.4	25.7	16.0	8.7	14.0	12.5

gastric and cardiac regions, with concave margins, well defined laterally by branchiocardiac groove. Cardiac region broadest of axial regions, widest anteriorly and narrowing posteriorly; with short, arcuate projections extending laterally from anterior-distal corner and arcing posteriorly; with three tubercles arranged in triangular pattern, apex directed posteriorly. Intestinal region poorly defined, depressed below level of cardiac region.

Hepatic regions inflated; equant; with very sharp, granular, oblique ridge situated on anterior edge, parallel to anterolateral margin. Epibranchial region arcuate, inflated; ovate, nearly straight segment extending axially from last anterolateral spine; second, triangular segment arcing posteriorly, terminating alongside urogastric region. Flattened, triangular area positioned posterior to epibranchial region, base of triangle along posterolateral margin, apex at about half the distance axially. Mesobranchial region inflated, markedly-so about two-thirds the distance distally to the posterolateral margin to almost form a longitudinal ridge. Metabranchial region narrow, linear, parallel to posterior margin, terminating at edge of intestinal region.

Sternites 1 and 2 fused, suture not visible. Sternal suture 2/3 clear, continuous, straight. Sternal suture 3/4 notched at margins, shallow across sternum. Sternite 4 long, with axial groove connecting to sternal suture 3/4, forming Y-shaped groove on sternum. Suture between sternites 4 and 5 incomplete, at high angle, sternite 5 directed anterolaterally. Sternite 6 directed anterolaterally, sternal suture 5/6 incomplete. Sternite 7 directed posterolaterally; sternite 8 not known. Sterno-abdominal cavity reaching just to posterior margin of coxae of first pereopods.

Male abdominal somites 5, 6 and telson free, somite 5 not fused to somite 4.

Chelae of pereopods 1 heterochelous; mani longer than high, stout, smooth; fingers black.

Measurements.—Measurements (in mm) taken on the dorsal carapace of *Pilumnus cucaoensis* new species are presented in Table 1.

Etymology.—The trivial name is derived from the locality at which most of the specimens were collected, Cucao, on Chiloe Island, Chile.

Remarks.—Two specimens were collected from the Navidad Formation, and the remainder were recovered from the Lacui Formation near Cucao, Chiloe. Although many of the specimens are preserved as carcasses, retaining the sternum and portions of the appendages, only one specimen retains portions of the abdomen. In several cases, the sternum is well-preserved and exposed, but the abdomen is missing. This is unusual and suggests that the abdomen may have been more poorly calcified than the sternum or that the abdominal holding mechanism may not have been well developed in this species, allowing it to be quickly disarticulated from the remainder of the animal.

?Subfamily Rhizopinae Stimpson, 1858

Diagnosis.—Carapace wider than long, subrectangular, smooth; anterolateral and posterolateral margins often confluent; anterolateral margins convex, often with small spines or entire; front broad and square or narrow, bilobed, and deflexed; orbits shallow; male abdomen with all somites free, usually not covering entire space between coxae of fifth pereopods (after Davie, 2002).

Remarks.—The Rhizopinae embraces a group of relatively small, rectangular pilumnid crabs. Many were originally placed within the Goneplacidae (Serène, 1964; Sakai, 1976), but more recent revisions have placed them as a subfamily of the Pilumnidae (i.e., Ng, 1985, 1987; Ng and Huang, 2001; Davie, 2002). The vast majority of the taxa found within the group are Indo-Pacific or South Pacific in distribution (Rathbun, 1909; Serène, 1964; Sakai, 1976; Ng, 1985, 1987; Ng and Huang, 2001; Davie, 2002); thus, this occurrence, if confirmed, would lie outside the general geographic distribution of the group.

In the Chilean specimen, the rectangular carapace, broad frontal width, lack of well-developed posterolateral reentrants, distinctly longitudinally vaulted dorsal carapace, and moderately defined dorsal carapace regions all suggest placement in the Rhizopinae. However, because the specimen is a mold of the interior, and because the front is damaged, we cannot place the specimen in the subfamily or in a genus and species with certainty. Recovery of fossils preserving some carapace material and especially the ventral portion of the carapace could confirm the systematic status of this material.

Tiny, rectangular dorsal carapaces are typical of many types of crabs, especially of the superfamily Xanthoidea and the Pinnotheridae de Haan, 1833. Many such genera previously have been reported from the fossil record, and their morphology has recently been summarized (Schweitzer and Feldmann, 2001b). However, the specimen under discussion here cannot be accommodated by any of these taxa characterized by tiny, rectangular outlines. The Hexapodidae Miers, 1886, which have a relatively good fossil record including occurrences in South America (Feldmann *et al.*, 1995; Schweitzer and Feldmann, 2001b), cannot accommodate the Chilean specimen. Hexapodids have a relatively narrow fronto-orbital width with respect to

the maximum carapace width (usually 50 percent or less) (Schweitzer and Feldmann, 2001b), while in the Chilean specimen it occupies nearly three-quarters of the maximum carapace width. The posterior width in hexapodids is always larger than the fronto-orbital width, while in the Chilean material, those widths are the same.

The Chilean specimen cannot be accommodated in the Asthenognathinae Stimpson, 1858, of the Pinnotheridae, which is also known from South America (Schweitzer and Feldmann, 2001b; Casadío *et al.*, 2004). Taxa in that subfamily have distinctly trapezoidal carapaces, well-developed posterolateral reentrants, and small orbits (Schweitzer and Feldmann, 2001b); none of these is possessed by the Chilean specimen. The Chasmocarcininae Serène, 1964, of the Goneplacidae MacLeay, 1838, have trapezoidal carapaces, well-developed posterolateral reentrants, and a narrow posterior width (Schweitzer and Feldmann, 2001b), differing in all these regards from the Chilean specimen.

Rhizopinae genus and species indeterminate
Fig. 8A

Material Examined.—SGO.PI.6345.

Description.—Carapace rectangular, wider than long, L/W about 0.80; flattened transversely; markedly vaulted longitudinally, especially anteriorly; lateral margins steep.

Front broad, almost half maximum carapace width, appearing to have been slightly sinuous; orbits not well known, directed forward; fronto-orbital width about 70 percent maximum carapace width. Anterolateral and posterolateral margins confluent; anterolateral portion with thickened rim, rim produced into two or three small, blunt spines; posterolateral portion smoothly convex; posterolateral reentrant very reduced; posterior margin straight, about 75 percent maximum carapace width.

Carapace regions not well defined; protogastric region weakly inflated, bounded posteriorly and laterally by moderately deep grooves; hepatic area flattened; mesogastric region with long anterior process, widened posteriorly, with muscle scars on widened portion; urogastric region depressed, with concave margins; cardiac region triangular, apex directed posteriorly, with two large tubercles on anterior portion situated on either side of axis, possibly a third at posterior-most apex of triangle.

Epibranchial region transversely inflated, extending from anterolateral angle to lateral margin of mesogastric region; remainder of branchial region with blunt, domed central swelling.

Measurements.—Measurements (in mm) taken on SGO.PI.6345: maximum carapace width = 9.4; maximum carapace length = 7.6; fronto-orbital width = 6.4; frontal width = 4.4; posterior width = 6.8.

Occurrence.—Collected from the Navidad Formation, exposed in a roadcut at the 4700 meter sign, north of Matanzas, Chile, on June 20, 1993.

Remarks.—The bases for the tentative systematic placement of the specimen have been discussed above.

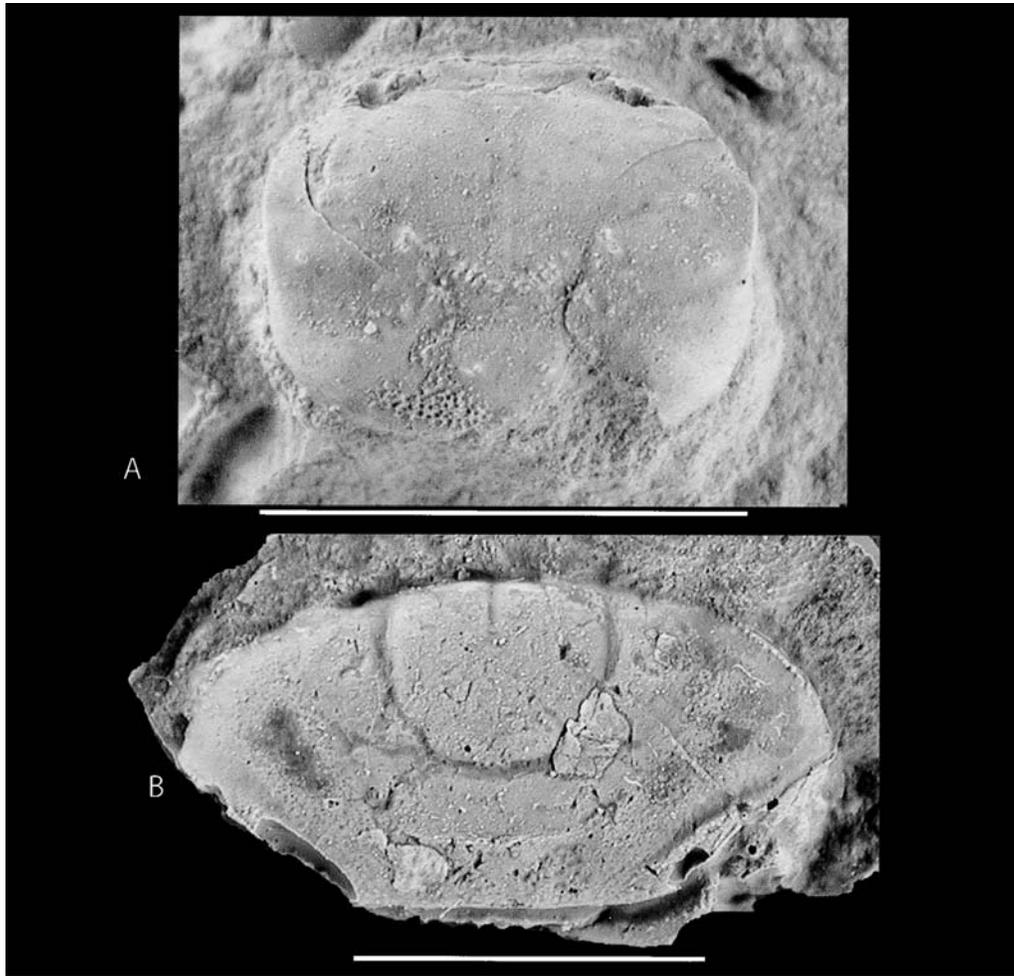


Fig. 8. A, Rhizopinae, genus and species indeterminate, SGO.PI.6345; B, *Pinnixa navidadensis* new species, silicone cast of mold of exterior of dorsal carapace, holotype, SGO.PI.6346. Scale bars = 1 cm.

Section Thoracotremata Guinot, 1977
 Superfamily Pinnotheroidea de Haan, 1833
 Family Pinnotheridae de Haan, 1833

Fossil Genera.—*Asthenognathus* Stimpson, 1858; *Globihexapus* Schweitzer and Feldmann, 2001b (extinct); *Pinnixa* White, 1846 *sensu lato*; ?*Pinnotheres* Bosc, 1802; *Tetrias* Rathbun, 1898b; *Viapinnixa* Schweitzer and Feldmann, 2001b (extinct); *Xenophthalmus* White, 1846.

Remarks.—Vía (1969) considered that the species referred by Rathbun (1932) to *Parapinnixa* Holmes, 1894, *P. miocenica* Rathbun, 1932, was a member of *Pinnixa*. We concur; thus, *Parapinnixa* has no fossil record. All of the fossil occurrences of *Pinnotheres* thus far have been questionable (Glaessner, 1929; Feldmann *et al.*, 1999). Nyborg (2002) and Schweitzer (2005) referred *Globihexapus* to the Pinnotheridae.

Subfamily Pinnotherelinae Alcock, 1900
 Genus *Pinnixa* White, 1846, *sensu lato*

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

Fossil Species.—*Pinnixa faba* Dana, 1851a (*in* Zullo and Chivers, 1970) (extant); *P. galliheri* Rathbun, 1932; *P. miocenica* Rathbun, 1932; *P. montereyensis* Rathbun, 1932; *P. navidadensis* new species; *Pinnixa* sp. *in* Zullo and Chivers (1970). Birshstein (1956) described *Pinnixa heckeri* from the Paleogene of Russia; it may be a hexapodid.

Diagnosis.—Carapace small, hexagonal, much wider than long, cuticle usually firm; front narrow, with axial notch; frontal and anterolateral margins confluent and arcuate; posterolateral reentrants large; posterior margin straight; cardiac region often with transverse ridge on cardiac region or extending across entire carapace; all male abdominal somites free; chelipeds moderate in size; third pereiopod longest of pereiopods; fourth pereiopods shorter than third pereiopods but stouter (after Rathbun, 1918b; Manning and Felder, 1989).

Remarks.—Female members of the Pinnotherelinae Alcock, 1900, are often commensal, living inside pelecypods, annelid and sipunculid worm tubes and burrows, sea urchins and holothurians, callianassoid burrows, or living directly in mud (Rathbun, 1918b; Manning and Morton, 1987; Manning and

Felder, 1989; Davie, 2002). Males, however, are generally free-living both in the subfamily and the family in general (Davie, 2002). Members of this subfamily are typically very small, and because females often live inside other animals, would not be expected to preserve well in the fossil record. Thus, it would be expected that most fossil occurrences in each would be of male individuals. *Pinnixa*, *sensu lato*, has a modest fossil record, including occurrences in Oligocene rocks of Central Asia and Miocene rocks of California (Glaessner, 1969). These fossil specimens are flattened and poorly preserved, making them difficult to identify, but their small size, possession of five pereopods, and rectangular carapace suggest that *Pinnixa*, *sensu lato*, is a reasonable assignment for them.

The Chilean material described here is much better preserved than most other pinnothereline material thus far known from the fossil record. Details of the dorsal carapace can be described and suggest that the specimen is best referred to *Pinnixa*, *sensu lato*. The carapace of the fossil specimen described here is much wider than long and has arcuate frontal and anterolateral margins, large posterolateral reentrants, and a ridge on the cardiac region, all features of *Pinnixa*, *sensu lato*. The ridge on the cardiac region is quite reminiscent of that seen in extant species of the genus known from coastal Chile, illustrated by Garth (1957), and in the *Pinnixa cristata* Complex (Manning and Felder, 1989), known from both North and South America. Recent workers have often erected new genera to embrace extant species formerly assigned to *Pinnixa*, *sensu lato*; however, the bases for these new genera are often details of the male abdomen and third maxilliped (Manning and Morton, 1987; Campos and Wicksten, 1997, for example) which are not preserved in the fossils at hand. Thus, we refer the specimen to *Pinnixa*, *sensu lato*, until material including the ventral aspects of the carapace can be recovered. The diagnosis above is intended to be useful for *Pinnixa*, *sensu lato*, and includes characters likely to be preserved in fossils.

Many species of *Pinnixa* live in the burrows of callianassoids, which may explain the presence of the genus in the Chilean deposits. Three different taxa within the Callianassoidea are described from the same formation as the new species of *Pinnixa*, including *Callichirus*?. *Callichirus* is known to house members of *Pinnixa* in extant habitats in southern North America and South America (Manning and Felder, 1989). We suggest that individuals of *P. navidadensis* may have been living commensally with the taxa of callianassoids described. A problem with this interpretation is that the specimen of *P. navidadensis* is larger than the callianassoid claws themselves; thus, observation of burrow structures and more callianassoid material would be necessary to test this observation.

Morris and Collins (1991) and Collins *et al.* (2003) referred several fossil species to *Pinnixa*, including *P. aequipunctata* Morris and Collins, 1991; *P. microgranulosa* Collins, Lee, and Noad, 2003; and *P. omega* Morris and Collins, 1991. All three of these species exhibit a rectangular carapace, not hexagonal as in *Pinnixa*, *sensu lato*, and the carapace in all three species is not much wider than long, while it is markedly wider than long in *Pinnixa*,

sensu lato. We suggest that these species are better referred to another pinnotherid genus such as *Tetrias* Rathbun, 1898b, which is rectangular and has deep grooves defining the protogastric and mesogastric regions (Rathbun, 1918b, pl. 39, fig. 4, 5; Sakai, 1976, pl. 202, fig. 2, 3), as in these three species. Examination of type material will be necessary to place these three species within a genus; however, they are not referable to *Pinnixa*, *sensu lato*.

Pinnixa navidadensis new species

Fig. 8B

Types.—The holotype and sole specimen, SGO.PI.6346, is a mold of the exterior of the carapace and was collected from the Matanzas locality. Carapace morphology was described from a silicone cast of this mold.

Diagnosis.—Carapace hexagonal, width about twice the length, widest about half the distance posteriorly on carapace; hepatic region arcuate, parallel to protogastric region; branchial region arcuate, parallel to hepatic region, cardiac region with transverse ridge about two-thirds the distance posteriorly on region.

Description.—Carapace hexagonal, width about twice the length, widest about half the distance posteriorly on carapace; regions moderately defined by grooves; flattened longitudinally and transversely; lateral sides convex.

Rostrum and orbits not known. Entire frontal and anterolateral margins of carapace confluent, arcuate; anterolateral margin bordered anteriorly by rim of granules. Posterolateral margin short, straight, rimmed, converging posteriorly. Posterolateral reentrants very large, with thick rim, rim widening as it approaches posterior margin. Posterior margin straight, about one-third maximum carapace width.

Epigastric regions weakly inflated. Protogastric regions best developed of all carapace regions, bounded by moderately deep grooves, with convex lateral margins, widest anteriorly, narrowing distally. Mesogastric region with short, narrow anterior process, widened posteriorly, somewhat inflated posteriorly, bounded on distal margin by deep cervical groove. Urogastric region absent. Cardiac region large, hexagonal, separated into two portions by transverse ridge about two-thirds the distance posteriorly on region, anterior portion longer than posterior portion. Intestinal region not well differentiated.

Hepatic region arcuate, parallel to protogastric region, moderately inflated; just distal to posterior end are situated a pair of large, broad swellings adjacent to cardiac region. Branchial region arcuate, parallel to hepatic region, longest along lateral margins, narrowing axially, not differentiated.

Some fragments of abdomen, pterygostomials, and antennal bases preserved but insufficient to describe.

Measurements.—Measurements (in mm) taken on the cast the dorsal carapace of *Pinnixa navidadensis*: length of dorsal carapace, 8.4; width of dorsal carapace, 15.5; posterior width, 5.1; length to position of maximum width of carapace, 3.8.

Etymology.—The trivial name is derived from the village of Navidad, Chile, which is near to where the specimen was collected.

Remarks.—The new species differs from most other species within *Pinnixa* in having well-defined protogastric, hepatic, and branchial regions that are arcuate and parallel one another. In addition, the cardiac ridge in members of the genus that possess it tends to extend onto the branchial region, whereas it does not in *Pinnixa navidadensis*. The extant species known from coastal Chile, *P. bahamonde* Garth, 1957; *P. chilensis* Garth, 1957; *P. transversalis* (H. Milne Edwards and Lucas, 1842); and *P. valdiviensis* Rathbun, 1907, are each similar to the new species in some regards. All exhibit a granular anterior portion of the anterolateral margin (Garth, 1957). *Pinnixa transversalis* and *P. valdiviensis* each possess a cardiac ridge, but in *P. transversalis* it extends onto the branchial regions and in *P. valdiviensis*, it is medially interrupted. Thus, although the new species appears to be related to the extant Chilean species, it is a distinct species from each.

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LITERATURE CITED

- Alcock, A. 1898. Materials for a Carcinological Fauna of India. No. 3. The Brachyura Cyclometopa. Part I. The Family Xanthidae.—Journal of the Asiatic Society of Bengal 67 (pt. 2 no. 1): 67–233.
- . 1900. Materials for a Carcinological Fauna of India. No. 6. The Brachyura Catametopa, or Grapsoidea.—Journal of the Asiatic Society of Bengal 69 (pt. 2, no. 3): 279–456.
- Allasinaz, A. 1987. Brachyura Decapoda oligocenici (Rupeliano) del Bacino Ligure Piemontese.—Bollettino Museo reg. Scienze Naturale di Torino 5(2): 509–566.
- Bachmayer, F. Von. 1962. Die Calappiden (Crustacea, Decapoda) aus den tertonischen Ablagerungen des Wiener Beckens.—Annalen des Naturhistorischen Museum der Wiener 65: 39–46.
- Bahamonde, N. N., and D. Frasinetti. 1980. *Lebucarcinus* n. gen. del Mioceno de Chile (Crustacea, Decapoda, Brachyura).—Boletim de Museo Nacional de Historia Natural, Chile (Santiago) 37: 275–279.
- Balss, H. 1932. Über einige systematisch interessante Xanthidae (Crustacea Decapoda Brachyura) der Harmsschen Reisen nach dem Sundaarchipel.—Zeitschrift für Wissenschaftliche Zoologie 142(2): 510–519.
- Beschin, C., A. Busulini, A. De Angeli, and G. Tessier. 2002. Aggiornamento ai crostacei eocenici di cava “Main” di Arzignano (Vicenza-Italia settentrionale) (Crustacea, Decapoda).—Studi e Ricerche, Associazione Amici del Museo Zannato Montecchio Maggiore (Vicenza) 2002: 7–28.
- , ———, ———, ———, and S. Ungaro. 1996. Crostacei eocenici di “Cava Rossi” presso Monte di Malo (Vicenza-Italia settentrionale).—Studi Trentini di Scienze Naturali Acta Geologica 73: 7–34.
- Beurlen, K. 1939. Neue Decapoden-Krebse aus dem ungarischen Tertiär.—Palaeontologische Zeitschrift 21(2): 135–160, pl. 7.
- . 1958. Contribuição à Paleontologia do Estado do Pará. Crustáceos decápodes da Formação Pirabas. 1 – (Arthropoda – Crustacea).—Boletim do Museu Paraense Emilio Geoldi, Nova Série, Geologia 5: 1–47, 5 pls.
- Birshstein, Y. A. 1956. The decapod Crustacea of the Ferganian Paleogene.—Bulletin of the Moscow Society for Natural Research, new series, volume 61, Geological Section 31 (1–3): 74–96. [Translated by Israel Program for Scientific Translations, Jerusalem, 1961.]
- Bittner, A. 1886. Neue Brachyuren des Eocäns von Verona.—Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien 94: 44–55.
- . 1893. Decapoden des pannonischen Tertiärs.—Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien 102: 10–37.
- Blow, W. C. 2003. New brachyuran crabs (Crustacea: Decapoda) from the Upper Pliocene Yorktown Formation of southeastern Virginia.—Proceedings of the Biological Society of Washington 116: 168–189.
- , and R. B. Manning. 1996. Preliminary descriptions of 25 new decapod crustaceans from the middle Eocene of the Carolinas, U.S.A.—Tulane Studies in Geology and Paleontology 29: 1–26.
- Borradaile, L. A. 1903. On the classification of the Thalassinidea.—Annals and Magazine of Natural History 7: 534–551.
- Bosc, L. A. G. 1802. Histoire naturelle des Crustacés, contenant leur description et leurs mœurs; avec figures dessinées d’après nature. Deterville, Paris.
- Boschi, E. E. 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces.—Revista de Investigación y Desarrollo Pesquero 13: 7–136.
- Bouillé, R. de. 1873. Paléontologie de Biarritz et de quelques autres localités des Basses Pyrénées.—Compte Rendu Travaux Congrès Scientifique de France, 39e Session à Pau 1: 1–24, pls. 3–8.
- . 1876. Paléontologie de Biarritz et des autres localités des Basses Pyrénées. Vironese, Pau, France.
- Brüggen, J. 1950. Fundamentos de la Geología de Chile. Instituto Geográfico Militar, Santiago, Chile. 374 pp.
- Campos, E., and M. K. Wicksten. 1997. A new genus for the Central American crab *Pinnixa costaricana* Wicksten, 1982 (Crustacea: Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 110: 69–73.
- Casadio, S., A. de Angeli, R. M. Feldmann, A. Garassino, J. L. Hetler, A. Parras, and C. E. Schweitzer. 2004. New decapod crustaceans (Thalassinidea, Galatheoidea, Brachyura) from the middle Oligocene of Patagonia, Argentina.—Annals of Carnegie Museum 73: 25–47.
- Ceccioni, G. 1978. Petroleum possibilities of the Darwin’s Navidad Formation near Santiago, Chile.—Publicación Ocasional del Museo Nacional de Historia Natural, Chile 25: 3–18.
- . 1980. Darwin’s Navidad embayment, Santiago Region, Chile, as a model of the southeastern Pacific shelf.—Journal of Petroleum Geology 2–3: 309–321.
- Chirino-Gálvez, L. 1993. Cenozoic crabs from Chile.—Master’s Thesis, Kent State University, Kent, Ohio. 280 pp. [Unpublished.]
- Collins, J. S. H., S. K. Donovan, and J. L. Dixon. 1996. Crabs and barnacles (Crustacea: Decapoda & Cirripedia) from the late Pleistocene Port Morant Formation of southeast Jamaica.—Bulletin of the Mizunami Fossil Museum 23: 51–63, pls. 12–18.
- , and S. L. Jakobsen. 2003. New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark.—Bulletin of the Mizunami Fossil Museum 30: 63–96.
- , C. Lee, and J. Noad. 2003. Miocene and Pleistocene crabs (Crustacea, Decapoda) from Sabah and Sarawak.—Journal of Systematic Palaeontology 1: 187–226.
- , and S. F. Morris. 1976. Tertiary and Pleistocene crabs from Barbados and Trinidad.—Palaeontology 19: 107–131.
- , and ———. 1978. New Lower Tertiary crabs from Pakistan.—Palaeontology 21: 957–981.
- , and R. W. Portell. 1998. Decapod, stomatopod, and cirripede Crustacea from the Pliocene Bowden shell bed, St. Thomas Parish, Jamaica.—Contributions to Tertiary and Quaternary Geology 35: 113–127.
- Dana, J. D. 1851a. *Crustacea Grapsoidea*, (*Cyclometopa*, *Edwardsii*): *Conspectus Crustacearum quae in Orbis Terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae Foederatae Duce, lexit et descriptis*

- J. D. Dana.—Proceedings of the Academy of Natural Sciences of Philadelphia 5: 247–254.
- . 1851b. On the classification of the Cancroidea.—American Journal of Science and Arts 12(34): 121–131.
- . 1852. Macrourea. *Conspectus Crustaceorum & Conspectus of the Crustacea of the Exploring Expedition under Capt. C. Wilkes, U. S. N.*—Proceedings of the Academy of Natural Sciences of Philadelphia 7: 175–177.
- . 1853. On the Classification and Geographical Distribution of Crustacea from the Report on Crustacea of the United States Exploring Expedition, under Captain Charles Wilkes, U.S.N., during the years 1838–1842. C. Sherman, Philadelphia. Pp. 1395–1592, 1 map.
- Darwin, C. 1846. Geological Observations in South America. Smith, Elder and Co., London. 279 pp.
- Davie, P. J. F. 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda—Anomura, Brachyura. Pp. 1–641 in A. Wells and W. W. K. Houston, eds. *Zoological Catalogue of Australia*, Vol. 19.3B. CSIRO Publishing, Melbourne, Australia.
- De Angeli, A. 1995. Crostacei dell'Eocene Superiore di "Fontanella" di Granconca (Vicenza-Italia Settentrionale).—Studi e Ricerche, Associazione Amici del Museo Civico "G. Zannato," Montecchio Maggiore IV: 7–24.
- Desmarest, A.-G. 1823. Malacostracés, Malacostraca.—*Dictionnaire des Sciences Naturelles* 28: 158–425.
- Encinas, A., K. Finger, S. Nielsen, M. Suárez, D. Peterson, and J. Le Roux. 2003. Evolución Tectono – Sedimentaria de la cuenca neógena de Navidad (33°40'S–34°15'S), Chile central.—X Congreso Geológico Chileno, Concepción, Chile.
- Fabiani, R. 1910. I crostacei terziarii del Vicentino.—*Bolletino Museo Civico Vicenza* 1: 1–40, 2 pls.
- Fabricius, J. C. 1798. *Supplementum Entomologiae Systematicae*. C. G. Proft et Storch, Hafniae (Copenhagen). 572 pp.
- Faxon, W. 1893. Preliminary descriptions of new species of Crustacea: Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission Steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N., Commanding, VI.—*Bulletin of the Museum of Comparative Zoölogy at Harvard College* 24(7): 149–220.
- Feldmann, R. M. 1991. Decapod Crustacea from the Tapui Glauconitic Sandstone (Bortonian: middle Eocene) in the Waitaki Valley, South Island, New Zealand.—*New Zealand Journal of Geology and Geophysics* 34: 17–22.
- . 1993. Additions to the fossil decapod crustacean fauna of New Zealand.—*New Zealand Journal of Geology and Geophysics* 36: 201–211.
- , M. Aguirre-Urreta, L. Chirino-Gálvez, and S. Casadío. 1997. Paleobiogeography of Cretaceous and Tertiary decapod crustaceans from southern South America: the link with Antarctica. Pp. 1007–1016 in C. A. Ricci, ed. *The Antarctic Region: Geological Evolution and Processes*. Terra Antarctica Publication, Siena, Italy.
- , S. Casadío, L. Chirino-Gálvez, and M. Aguirre-Urreta. 1995. Fossil decapod crustaceans from the Jaguel and Roca formations (Maastrichtian-Danian) of the Neuquén Basin, Argentina.—*The Paleontological Society Memoir* 43 (Supplement to *Journal of Paleontology* Volume 69): 1–22.
- , and P. W. Duncan. 1992. Eocene decapod crustaceans from Snowdrift Quarry, South Otago, New Zealand.—*New Zealand Journal of Geology and Geophysics* 34: 455–461.
- , T. Villamil, and E. G. Kauffman. 1999. Decapod and stomatopod crustaceans from mass mortality Lagerstätten: Turonian (Cretaceous) of Colombia.—*Journal of Paleontology* 73: 91–101.
- , and W. J. Zinsmeister. 1984. First occurrence of fossil decapod crustaceans (Callianassidae) from the McMurdo Sound region, Antarctica.—*Journal of Paleontology* 58: 1041–1045.
- Finger, K., A. Encinas, S. Nielsen, and D. Peterson. 2003. Microfaunal indications of Late Miocene deep-water basins off the central coast of Chile. X Congreso Geológico Chileno, Concepción, Chile.
- Förster, R., and R. Mundlos. 1982. Krebse aus dem Alttertiär von Helmstedt und Handorf (Niedersachsen).—*Palaeontographica Abt. A* 179: 148–184, pls. 1–3.
- Gaillande, D. de, and J.-P. Lagardère. 1966. Description de *Callianassa (Callichirus) lobata* nov. sp. (Crustacea Decapoda Callianassidae).—*Recueil des Travaux de la Station Marine d'Endoume* 40(56): 259–265.
- Gana, P., R. Wall, and A. Gutiérrez. 1996. Mapa geológico del área de Valparaíso – Curacaví. Región de Valparaíso y Metropolitana. Mapa n° 1, escala 1: 100.000. Sernageomin. Santiago, Chile.
- Garth, J. S. 1957. The Crustacea Decapoda Brachyura of Chile.—*Reports of the Lund University Chile Expedition 1948–49* 29: 1–125, appendices A–C, pls. I–V.
- Gistel, J. 1848. *Naturgeschichte des Thierreiches für höhere Schulen* bearbeitet. Hoffman, Stuttgart. i–xvi, 1–220, pls. 1–32.
- Glaessner, M. F. 1928. Die Dekapodenfauna des österreichischen Jungtertiärs.—*Jahrbuch der Geologischen Bundesanstalt (Reichsanstalt)* Wien 78: 161–219, pl. 3, 4.
- . 1929. *Fossilium Catalogus; I: Animalia, Editus a J. F. Pompeckj, pars 41: Crustacea Decapoda*. W. Jüнк. Berlin.
- . 1933. New Tertiary crabs in the collection of the British Museum.—*Annals and Magazine of Natural History*, series 10(12): 1–28, pls. 1–6.
- . 1947. Decapod Crustacea (Callianassidae) from the Eocene of Victoria.—*Proceedings of the Royal Society of Victoria* 59: 1–7.
- . 1969. Decapoda. Pp. R400–R566, R626–R628 in R. C. Moore, ed. *Treatise on Invertebrate Paleontology*, Pt. R, Arthropoda 4. Geological Society of America and University of Kansas Press, Lawrence.
- Guinot, D. 1977. Propositions pour une nouvelle classification des Crustacés, Décapodes, Brachyours.—*Compte Rendu Académie des Sciences de Paris, Série D*. 285: 1049–1052.
- de Haan, W. 1833–1850. Crustacea. Pp. i–xviii, i–xxxii, ix–xvi, 1–243, pls. A–J, L–Q, 1–55, circ. tab. 2 in P. F. von Siebold, *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit*. J. Müller et Co., Lugduni-Batavorum (Leiden).
- Heard, R. W. 1989. *Calliax jonesi*, n. sp. (Decapoda: Thalassinidea: Callianassidae) from the northwestern Bahamas.—*Gulf Research Reports* 8: 129–136.
- Herbst, J. F. W. 1782–1804. Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten, volume 2 (1791–1796). i–viii, iii, iv, 1–225, pls. 22–46.
- Holmes, S. J. 1894. Notes on West American Crustacea.—*Proceedings of the California Academy of Science, Series 2*, 4: 563.
- Holthuis, L. B. 1967. A survey of the genus *Ctenocheles* (Crustacea: Decapoda: Callianassidae), with a discussion of its zoogeography and its occurrence in the Atlantic Ocean.—*Bulletin of Marine Science* 17: 376–385.
- Huxley, T. H. 1879. On the classification and the distribution of the crayfishes.—*Proceedings of the Zoological Society of London* 1878: 752–788.
- Imaizumi, R. 1958. An interesting crustacean remain, *Ctenocheles sujakai* n. sp. from the Paleogene of Kyushu, Japan.—*Transactions and Proceedings of the Palaeontological Society of Japan, New Series* 32: 299–304, pl. 44.
- International Commission of Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature*. Fourth Edition. International Trust for Zoological Nomenclature, London, England.
- Jacquinet, H., and H. Lucas. 1853. Voyage au Pole Sud et dans l'Océanie sur les Corvettes L' Astrolabe et La Zelee. *Zoologie* 3, Crustacés. Gide et Baudry, Paris.
- Jenkins, R. J. F. 1972. Australian fossil decapod Crustacea: faunal and environmental changes. Ph.D. dissertation, University of Adelaide, Adelaide, Australia. [Unpublished.]
- Karasawa, H. 1990. Decapod crustaceans from the Miocene Mizunami Group, Central Japan, Pt 2. Section Oxyryncha, Cancridae, and Brachyryncha.—*Bulletin of the Mizunami Fossil Museum* 17: 1–33, pls. 1–8.
- . 1991. Decapod crustaceans from the Miocene Mizunami Group, Central Japan. Part 3. Decapod crustacean assemblage, paleoecology, with descriptions of two species.—*Bulletin of the Mizunami Fossil Museum* 18: 1–18.
- . 1993. Cenozoic decapod Crustacea from southwest Japan.—*Bulletin of the Mizunami Fossil Museum* 20: 1–92, 24 pls.
- . 1997. A monograph of Cenozoic stomatopod, decapod, isopod, and amphipod Crustacea from West Japan.—*Monograph of the Mizunami Fossil Museum* 8: 1–81, 30 pls.
- , and Y. Fudouji. 2000. Palaeogene decapod Crustacea from the Kishima and Okinoshima groups, Kyushu, Japan.—*Paleontological Research* 4: 239–253.

- , and K. Inoue. 1992. Decapod crustaceans from the Miocene Kukinaga Group, Tanegashima Island, Kyushu, Japan.—*Tertiary Research* 14: 73–96, 3 pls.
- , and H. Kato. 2003. The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records.—*Paleontological Research* 7: 129–151.
- , and C. E. Schweitzer. 2004. Revision of the genus *Glyphithyreus* Reuss, 1859 (Crustacea, Decapoda, Brachyura, Xanthoidea) and recognition of a new genus.—*Paleontological Research* 8: 143–154.
- Kato, H., and H. Karasawa. 1998. Pleistocene fossil decapod Crustacea from the Boso Peninsula, Japan.—*Natural History Research Special Issue No. 5*: 1–31.
- Kishinouye, K. 1926. Two rare and remarkable forms of macrurous Crustacea from Japan.—*Japanese Journal of Zoology* 11: 63–70.
- Latreille, P. A. 1802–1803. Histoire naturelle, générale et particulière, des crustacés, des Arachnides, des Myriapodes, et des Insectes, etc. *Annals I. Atlas*. Roret, Paris.
- . 1831. Cours d'Entomologie, ou de l'histoire naturelle des Crustacés, des Arachnides, des Myriapodes, et des Insectes, etc. *Annals I. Atlas*. Roret, Paris.
- Leach, W. E. 1816. A tabular view of the external characters of four classes of animals which Linné arranged under Insecta: with the distribution of the genera composing three of these classes into orders &c. and descriptions of several new genera and species.—*Transactions of the Linnean Society of London* 11: 306–400.
- Linnaeus, C. von. 1761. *Fauna Svecica sistens animalia Sveciae regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per classes & ordines, genera & species, cum differentiis specierum, synonymis auctorum, nominibus incolarum, locis natalium, descriptionibus insectorum*. L. Salvii, Stockholmiae. 578 pp., 3 pls.
- . 1763. *Genera Morborum*. C. E. Steiner, Upsaliae. 7 pp.
- Lórenthey, E. 1898. Beiträge zur Decapodenfauna des Ungarischen Tertiärs.—*Természetről Füzetek* 21: 1–131, pls. 1–9.
- , and K. Beurlen. 1929. Die fossilen Decapoden der Länder der Ungarischen Krone.—*Geologica Hungarica, Series Palaeontographica, Fasciculus 3*: 1–421, pl. 1–16.
- MacLeay, W. S. 1838. On the Brachyurous Decapod Crustacea brought from the Cape by Dr. Smith. Pp. 53–71 in A. Smith, ed. *Illustrations of the Annulosa of South Africa; Being a Portion of the Objects of Natural History Chiefly Collected during an Expedition into the Interior of South Africa, under the Direction of Dr. Andrew Smith, in the Years 1834, 1835, and 1836; Fitted Out by "The Cape of Good Hope Association for Exploring Africa."* Smith, Elder, & Co., London.
- Manning, R. B., and D. L. Felder. 1986. The status of the callianassid genus *Callichirus* Stimpson, 1866 (Crustacea: Decapoda: Thalassinidea).—*Proceedings of the Biological Society of Washington* 99: 437–443.
- , and ———. 1989. The *Pinnixa cristata* Complex in the Western Atlantic, with descriptions of two new species (Crustacea: Decapoda: Pinnotheridae).—*Smithsonian Contributions to Zoology* 473: 1–26.
- , and ———. 1991. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea).—*Proceedings of the Biological Society of Washington* 104: 764–792.
- , and L. B. Holthuis. 1981. West African brachyuran crabs (Crustacea: Decapoda).—*Smithsonian Contributions to Zoology* 306: 1–379.
- , and ———. 1989. Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae).—*Proceedings of the Biological Society of Washington* 102: 50–77.
- , and R. Lemaitre. 1993. *Sergio*, a new genus of ghost shrimp from the Americas (Crustacea: Decapoda: Callianassidae).—*Nauplius, Rio Grande* 1: 39–43.
- , and B. Morton. 1987. Pinnotherids (Crustacea: Decapoda) and leptonaceans (Mollusca: Bivalvia) associated with sipunculan worms in Hong Kong.—*Proceedings of the Biological Society of Washington* 100: 543–551.
- Martínez-Pardo, R. 1990. Major Neogene events of the southeastern Pacific: the Chilean and Peruvian record.—*Palaeogeography, Palaeoclimatology, Palaeoecology* 77: 263–278.
- , and M. Valenzuela. 1979. Discoasterídeos de la Formación Navidad (emend. Etchart, 1973), en Punta Perro, Provincia De San Antonio, Chile.—*II Congreso Geológico Chileno* 3: H77–H101, 1 pl.
- Meón, H., T. Torres, and R. Martínez-Pardo. 1994. Sporopollinic análisis in the Navidad Formation near Navidad (Chile).—*7° Congreso Geológico Chileno I*: 488–490.
- Miers, E. J. 1886. Report of the Brachyura collected by H. M. S. *Challenger* during the years 1873–1876. Pp. 1–362 in C. Wyville Thomson and J. Murray, eds. *Report of the Scientific Results of the Voyage of H. M. S. Challenger during the years 1873–1876, Zoology Vol. XVII*. Challenger Office, published by Order of Her Majesty's Government, Edinburgh; first reprinting, 1965, Johnson Reprint Corporation, New York.
- Milne Edwards, A. 1862–1865. Monographie des Crustacés fossiles de la famille Cancériens.—*Annales de Science Naturelle, Zoologie, série 4*, 18(1862): 31–85, pls. 1–10; 20(1863): 273–324, pls. 5–12; série 5, 1(1864): 31–88, pls. 1–10; 3(1865): 297–351, pls. 5–13.
- . 1873. Descriptions des quelques crustacés nouveaux ou peu connus provenant du Musée de M. C. Godeffroy.—*Journal of the Museum Godeffroy* 1: 77–88.
- . 1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea, 1877, '78, '79, by the United States Coast Survey steamer "Blake". . . VIII.—*Bulletin of the Museum of Comparative Zoölogy at Harvard College* 8: 1–68.
- Milne Edwards, H. 1834–1837. Histoire naturelle des Crustacés. Vol. 1 (1834), 468 p.; Vol. 2 (1837), 532 p.; Atlas. Librairie Encyclopedique de Roret, Paris.
- , and H. Lucas. 1842–1844. Crustacés. Pp. 1–37, pls. 1–17 in A. d'Orbigny. *Voyage dans l'Amérique méridionale (le Brésil, la république orientale de l'Uruguay, la république Argentine, Patagonie, la république du Chili, la république de Bolivia, la république de Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, 6(1)*. Ve. Levrault, Strasbourg.
- Moissette, P., and P. Müller. 1990. Crustacés décapodes des faciès Marmotiques du Messinien d'Oranie (Algérie Occidentale).—*Geobios* 23(6): 737–747.
- Morris, S. F., and J. S. H. Collins. 1991. Neogene crabs from Brunei, Sabah and Sarawak.—*Bulletin of the British Museum of Natural History (Geology)* 47: 1–33.
- Müller, P. 1974. Decapoda (Crustacea) fauna a budapesti miocénból 2.—*Földtani Közlöny* 102(3): 275–287, pls. 1–3.
- . 1984. Decapod Crustacea of the Badenian.—*Institutum Geologicum Hungaricum, Geologica Hungarica, Series Palaeontologica* 42: 1–317.
- . 1993. Neogene decapod crustaceans from Catalonia.—*Scripta Musei Geologici Seminarii Barcinonensis* 225: 1–39.
- . 1996. Middle Miocene decapod Crustacea from southern Poland.—*Prace Muzeum Ziemi* 43: 3–14, pls. 1–2.
- Ng, P. K. L. 1985. On a new species of pilumnid crab, *Rhizopa yangae*, sp. nov. from Singapore, with notes on the genus *Rhizopa* Stimpson, 1858 (Decapoda: Brachyura: Pilumnidae).—*Journal of Natural History* 19: 627–633.
- . 1987. The Indo-Pacific Pilumnidae II. A revision of the genus *Rhizopa* Stimpson, 1858, and the status of the Rhizopinae Stimpson, 1858 (Crustacea, Decapoda, Brachyura).—*Indo-Malayan Zoology* 4: 69–111, pl. 1.
- , and J.-F. Huang. 2001. The Indo-Pacific Pilumnidae XV. On two rare species of Rhizopinae (Decapoda, Brachyura) from Taiwan.—*Crustaceana* 74: 1379–1385.
- , C.-H. Wang, P.-H. Ho, and H.-T. Shih. 2001. An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda).—*National Taiwan Museum Special Publication Series, Taipei, Taiwan* 11: 1–86, 8 pls.
- Noetling, F. 1885. Die Fauna des samländischen Tertiärs. J. H. Neumann, Berlin.
- Nyborg, T. G. 2002. Fossil decapod crustaceans from the early to middle Miocene Astoria Formation, Washington and Oregon, U. S. A.—*Master's Thesis, Kent State University, Kent, Ohio*. [Unpublished.]
- D'Orbigny, A. 1842. *Voyage dans l'Amérique méridional, 1826–1833 (III)*. Géologie et Paléontologie. Paris, France.
- Ortmann, A. E. 1893. Abtheilung: Brachyura (Brachyura genuina Boas), II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Die DecapodenKrebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei Liu-Kiu-Inseln gesammelten und zur im Strassburger Museum aufbewahrten Formen, VII. Theil.—*Zoologische Jahrbücher, Abtheilung für Systematik, Geographie, und Biologie der Thiere* 7: 411–495, pl. 17.

- Pelseneer, P. 1886. Notice sur les crustacés décapodes du Maestrichtien du Limbourg.—Bulletin du Musée royal d'Histoire naturelle de Belgique 4(III): 161–175.
- Philippe, M., and S. Secretan. 1971. Crustacés Décapodes du Burdigalien des Courennes (Vaucluse).—Annales de Paléontologie, Invertébrés 56: 117–134, pls. A–C.
- Philippi, R. A. 1887. Los Fósiles cuaternarios y terciarios de Chile. Imprenta Brockhaus, Leipzig. 256 pp., 58 pls.
- Quayle, W. J., and J. S. H. Collins. 1981. New Eocene crabs from the Hampshire Basin.—Palaeontology 24: 733–758.
- Rafinesque, C. S. 1815. Analyse de la nature, ou tableau de l'Univers et des corps organisés. L'Imprimerie de Jean Barravecchia, Palermo, Italy.
- Rasmussen, H. W. 1971. Echinoid and crustacean burrows and their diagenetic significance in the Maastrichtian-Danian of Stevns Klint, Denmark.—Lethaia 4: 191–216.
- Rathbun, M. J. 1896. Description of a new genus and four new species of crabs from the West Indies.—Proceedings of the U. S. National Museum 14: 141–144.
- . 1897. List of the Decapod Crustacea of Jamaica.—Annals of the Institute of Jamaica 1: 3–46.
- . 1898a. The Brachyura of the Biological Expedition to the Florida Keys and the Bahamas in 1893.—Bulletin of the Laboratory of Natural History, State University of Iowa 4: 250–294, pls. 1–9.
- . 1898b. The Brachyura collected by the United States Fish Commission steamer *Albatross* on the voyage from Norfolk, Virginia, to San Francisco, California, 1887–1888.—Proceedings of the United States National Museum 21: 567–616, pls. 41–44.
- . 1907. South American Crustacea.—Revista Chilena de Historia Natural 11: 45–50, pls. 2–3.
- . 1909. New crabs from the Gulf of Siam.—Proceedings of the Biological Society of Washington 22: 107–114.
- . 1918a. Decapod crustaceans from the Panama region.—United States National Museum Bulletin 103: 123–184, pls. 54–66.
- . 1918b. The Grapsoid Crabs of America.—United States National Museum Bulletin 97: 1–461.
- . 1919. West Indian Tertiary decapod crustaceans. Pp. 159–184, pls. 1–9 in T. W. Vaughan, ed. Contributions to the Geology and Paleontology of the West Indies. Carnegie Institution of Washington, Washington, D.C.
- . 1930a. The cancrioid crabs of America of the families Euryalidae, Portunidae, Atelecyliidae, Cancridae, and Xanthidae.—United States National Museum Bulletin 152: 1–609.
- . 1930b. Fossil decapod crustaceans from Mexico.—Proceedings of the United States National Museum 78: 1–10, pls. 1–6.
- . 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain.—Geological Society of America Special Paper 2: 1–160.
- . 1932. Fossil pinnotherids from the California Miocene.—Journal of the Washington Academy of Sciences 22: 411–413.
- . 1937. The oxytomatous and allied crabs of America.—United States National Museum Bulletin 166: 1–278.
- Risso, A. 1826. Histoire Naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes. F.-G. Levrault, Paris, 5 volumes.
- Roberts, H. B. 1956. Early Tertiary decapod crustaceans from the Vincentown Formation in New Jersey.—Bulletin of the Wagner Free Institute of Science 31: 5–12, pl. 2.
- Rodrigues, S. de A., and R. B. Manning. 1992. *Poti gaucho*, a new genus and species of ghost shrimp from southern Brazil (Crustacea: Decapoda: Callianassidae).—Bulletin of Marine Science 51: 9–13.
- Ross, A., and R. J. Scolaro. 1964. A new crab from the Eocene of Florida.—Quarterly Journal of the Florida Academy of Sciences 27: 97–106.
- Samouelle, G. 1819. The Entomologist's Useful Compendium, or An Introduction to the Knowledge of British Insects. Thomas Boys, London. 496 pp.
- Saint Laurent, M. de. 1973. Sur la systématique et la phylogénie des Thalassinidea: définition des familles des Callianassidae et des Upogebiidae et diagnose de cinq genres nouveaux (Crustacea Decapoda).—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris (series D) 277: 513–516.
- Sakai, T. 1976. Crabs of Japan and the Adjacent Seas. Kodansha, Ltd., Tokyo, Japan.
- Salva, E. W., and R. M. Feldmann. 2001. Re-evaluation of the family Atelecyliidae (Decapoda: Brachyura).—Kirtlandia 52: 9–62.
- Say, T. 1818. An account of the Crustacea of the United States, Part 5.—Journal of the Academy of Natural Sciences of Philadelphia 1 (part 2, number 1): 235–253.
- Schweitzer, C. E. 2001. Paleobiogeography of Cretaceous and Tertiary decapod crustaceans of the North Pacific Ocean.—Journal of Paleontology 75: 808–826.
- . 2003. Utility of proxy characters for classification of fossils: an example from the fossil Xanthoidea (Crustacea: Decapoda: Brachyura).—Journal of Paleontology 77: 1107–1128.
- . 2005. The genus *Xanthilites* Bell, 1858 and a new xanthoid family (Crustacea: Decapoda: Brachyura: Xanthoidea): new hypotheses on the origin of the Xanthoidea MacLeay, 1838.—Journal of Paleontology 79: 277–295.
- , and R. M. Feldmann. 2000a. New species of calappid crabs from western North America and reconsideration of the Calappidae *sensu lato*.—Journal of Paleontology 74: 230–246.
- , and ———. 2000b. New fossil portunids from Washington, USA, and Argentina, and a re-evaluation of generic and family relationships within the Portunoidea Rafinesque, 1815 (Decapoda: Brachyura).—Journal of Paleontology 74: 636–653.
- , and ———. 2000c. *Callichirus? symmetricus* (Decapoda: Thalassinidea) and associated burrows, Eocene, Antarctica. Pp. 335–347 in R. M. Feldmann and J. D. Stillewell, eds. Paleobiology and Paleoenvironments of Eocene rocks, McMurdo Sound, East Antarctica. American Geophysical Union Antarctic Research Series Volume 76, Washington D.C.
- , and ———. 2000d. Re-evaluation of the Cancridae Latreille, 1802 (Decapoda: Brachyura) including three new genera and three new species.—Contributions of Zoology 69: 223–250.
- , and ———. 2001a. New Cretaceous and Tertiary decapod crustaceans from western North America.—Bulletin of the Mizunami Fossil Museum 28: 173–210.
- , and ———. 2001b. Differentiation of the fossil Hexapodidae Miers, 1886 (Decapoda: Brachyura) from similar forms.—Journal of Paleontology 75: 330–345.
- , and ———. 2002. New Eocene decapods (Thalassinidea and Brachyura) from Southern California.—Journal of Crustacean Biology 22: 938–967.
- , and P. D. Gingerich. 2004. New Decapoda (Crustacea) from the middle and late Eocene of Pakistan and a revision of *Lobonotus* A. Milne Edwards, 1864.—The University of Michigan Contributions from the Museum of Paleontology 31: 89–118.
- , G. González-Barba, and F. J. Vega. 2002. New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods.—The Paleontological Society Memoir 59 (Supplement to Journal of Paleontology, 76): 1–43.
- , and H. Karasawa. 2004. Revision of *Amydrocarcinus* and *Palaeograpsus* (Decapoda: Brachyura: Xanthoidea) with definition of three new genera.—Paleontological Research 8: 71–86.
- , and E. W. Salva. 2000. First recognition of the Cheiragonidae (Decapoda) in the fossil record and comparison of the family with the Atelecyliidae.—Journal of Crustacean Biology 20: 285–298.
- Secretan, S. 1964. Les Crustacés décapodes du Jurassique Supérieur et du Crétacé de Madagascar.—Mémoires du Muséum national d'Histoire naturelle, Nouvelle Série, Série C, Sciences de la Terre 14: 1–223.
- Serène, R. 1964. Goneplacidae et Pinnotheridae. Papers from T. Mortensen's Pacific Expedition 1914–1916. 80.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 126: 181–282, pls. 16–24.
- Stenzel, H. B. 1934. Decapod crustaceans from the middle Eocene of Texas.—Journal of Paleontology 8: 38–56, pls. 6–7.
- . 1935. Middle Eocene and Oligocene decapod crustaceans from Texas, Louisiana, and Mississippi.—The American Midland Naturalist 16: 379–400.
- Števičić, Z. 1991. Note on some rare and aberrant Australian crabs.—Beagle, Records of the Northern Territory Museum of Arts and Sciences 8: 121–134.
- Stillewell, J. D., R. H. Levy, R. M. Feldmann, and D. M. Harwood. 1997. On the rare occurrence of Eocene callianassid decapods (Arthropoda) preserved in their burrows, Mount Discovery, East Antarctica.—Journal of Paleontology 71: 284–287.
- Stimpson, W. 1858. *Crustacea Ocyopodoidea: prodromus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum*

- Pacificum Septentrionalem, a Republica Federata missa, Cadwaladara Ringgold et Johanne Rodgers Ducibus, observavit et descripsit, Pars V.*—Proceedings of the Academy of Natural Sciences of Philadelphia 1858: 93–110.
- . 1866. Descriptions of new genera and species of Macrurous Crustacea from the coasts of North America.—Proceedings of the Chicago Academy of Sciences 1: 46–48.
- . 1870–1881. Brachyura, Pt. 1. Pp. 150–156 in L. F. de Pourtalès, ed. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida. Bulletin of the Museum of Comparative Zoölogy at Harvard College, 2.
- Straelen, V. Van. 1923. Description de Crustacés décapodes nouveaux des terrains tertiaires de Borneo.—Koninklijke Akademie van Wetenschappen (Netherlands). Afdeling Natuurkunde 26: 489–492.
- . 1933. Sur des crustacés décapodes de l'Eocene supérieur de l'Ile Bonaire.—Bulletin du Musée royal d'Histoire naturelle de Belgique 9(23): 1–4.
- Tavera, J. 1979. Estratigrafía y paleontología de la Formación Navidad, provincia de Colchagua, Chile (Lat. 30°50'–34°S).—Boletín del Museo Nacional de Historia Natural Chile 36: 5–176.
- Thatje, S. 2000. *Notiax santarita*, a new species of the Callianassidae (Decapoda, Thalassinidea) from the Beagle Channel, southernmost America.—Crustaceana 73: 289–299.
- Troncoso, A. 1991. Paleomegafauna de la Formación Navidad, Miembro Navidad (Mioceno), en el área de Matanzas, Chile central occidental.—Boletín del Museo Nacional de Historia Natural de Chile 42: 131–168.
- , and E. J. Romero. 1993. Consideraciones acerca de las Coníferas del Mioceno de Chile central occidental.—Boletín del Museo Nacional de Historia Natural de Chile 44: 47–71.
- Vía, L. 1959. Decápodos fósiles del Eoceno español.—Boletín del Instituto geológico y minero de España 70: 331–402, 7 pls.
- . 1969. Crustáceos Decápodos del Eoceno español.—Pirineos, Revista del Instituto de Estudios Pirenaicos 91–94: 1–479, 39 pls.
- Wall, R., P. Gana, and A. Gutiérrez. 1996. Mapa geológico del área de San Antonio – Melipilla. Sernageomin, Santiago, Chile. 19 pp.
- White, A. 1846. Notes on four new genera of Crustacea.—Annals and Magazine of Natural History 18(118): 176–178, pl. 2.
- Williams, A. B. 1984. Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington.
- Zullo, V. A., and D. D. Chivers. 1970. Pleistocene symbiosis: pinnotherid crabs in pelecypods from Cape Blanco, Oregon.—The Veliger 12: 72–73, pl. 5.

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