

## NEW MIOCENE DECAPODA (THALASSINIDEA; BRACHYURA) FROM TIERRA DEL FUEGO, ARGENTINA: PALEOBIOGEOGRAPHIC IMPLICATIONS

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## ABSTRACT

A decapod crustacean fauna of Tierra del Fuego, Argentina, is documented from the middle Miocene Carmen Silva Formation and the early? Miocene Cerro Águila Conglomerate of the Cabo Domingo Group. Three new genera and five new species are named: *Asthenognathus australensis*, new species; *Miotymolus quadratus*, new genus and species; *Mursia fuegiana*, new species; *Pharkidodes agele*, new genus and species; and *Tierrapilumnus edseli*, new genus and species. Compilation of all described species of decapods from late Oligocene to early Pliocene exposures in 18 general localities in Patagonia, southern Argentina, and Chile documents two paleobiogeographic provinces, Argentine and Chilean. Coupled with evidence from the biogeographic patterns of associated mollusks, the faunas from Tierra del Fuego have been assigned to the Argentine Paleobiogeographic Province. Comparison of the distribution of Miocene decapods with that of extant decapods (Boschi 2000) leads to the conclusion that the thermal separation of South Atlantic and South Pacific water in the Miocene was more pronounced than today, so that there is no evidence of a discrete Magellanic Biogeographic Province characterizing the high southern latitude region during the Miocene.

KEY WORDS: Anomura, Argentina, Brachyura, Decapoda, Miocene, paleobiogeography, Thalassinidea

## INTRODUCTION

Decapod crustaceans have been known from Tierra del Fuego, Argentina, since Steinman and Wilckens (1908) noted the presence of *Geryon peruvianus* (d'Orbigny, 1842), in the cliffs of Sierra de Carmen Silva. Subsequently, Aguirre-Urreta (1987) made note of this record in a study of Geryonidae from southern Argentina. Other than those published accounts referring to decapods from the area, the only collecting of decapods from Tierra del Fuego has been anecdotal until recently. In 2007, two of us (SC and MG) studied the exposures of Cenozoic rocks in the area and identified several localities that contained decapod material (Fig. 1). In the following year, three of us (RMF, MG, and CES) visited these localities and made large collections of fossils from several of them. In 2009, two of us (SC and MG) returned to the localities to make more detailed stratigraphic analyses of the sections. The material from these recent field excursions forms the basis for the present study.

The purposes of the study are to describe the geological setting in which fossil decapods occur in Tierra del Fuego, to describe the decapods, and to summarize the

paleobiogeographic distribution of species in southern South America.

## GEOLOGICAL SETTING

The geological evolution of the Austral (or Magallanes) Basin involves three tectonic phases: rift, sag, and foreland stages that were initiated during the Jurassic and ended in the Neogene. By the Late Cretaceous, the uplift of the Fuegian Andes (Olivero et al. 2003) preceded the subsequent origination of the foreland Austral Basin (Biddle et al. 1986).

The northern propagation of the deformation initiated four clastic successions of Late Cretaceous–Danian, late Paleocene–early Eocene, late middle Eocene–late Eocene, and Oligocene–middle Miocene ages; they are thicker toward the fold and thrust belt to the west and south, and thinner with internal truncations toward the foreland in the east and north (Olivero and Malumián 2002, 2008; Ponce et al. 2008).

The late Oligocene–Miocene succession of the Austral Basin in Tierra del Fuego Island, southern Patagonia, lies

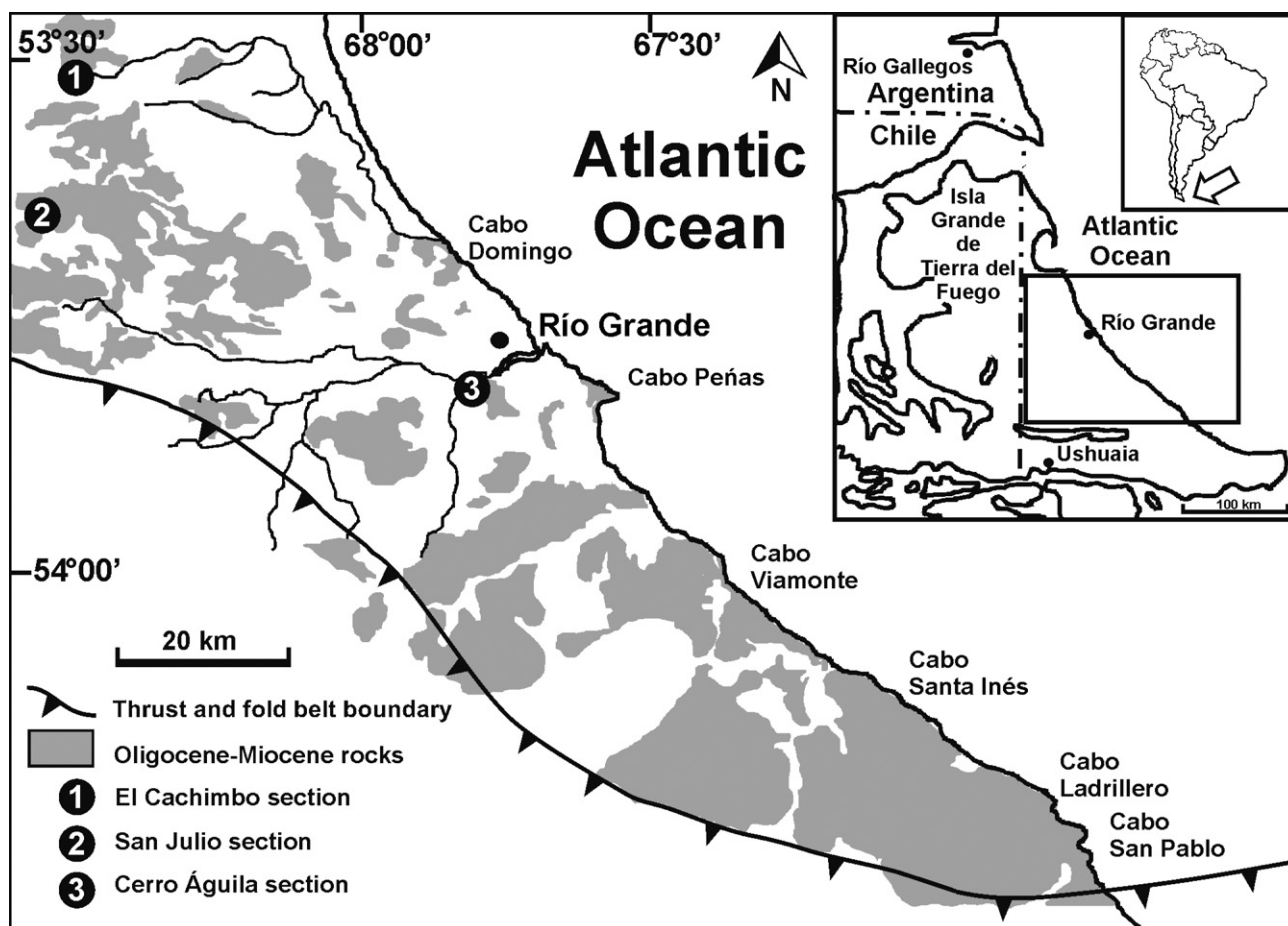


Fig. 1.—Locality map of a part of eastern Tierra del Fuego showing the sites from which fossil decapods were collected.

in front of the fold and thrust belt, and primarily represents the infilling of the youngest foredeep of the foreland basin (Fig. 1). The best outcrops of this sequence are on the cliffs along the Atlantic coast of the island.

Since the early Miocene, sedimentation was represented by primarily unfolded strata developed after the compressive deformation (Malumián and Olivero 2006). This youngest succession of marine and fluvial deposits is mostly included in the upper part of the Cabo Domingo Group (Malumián 1999). This group is partially correlated with shelf deposits of the marine Monte León and Centinela formations in the northern part of the Austral Basin, and with the overlying continental deposits of the Santa Cruz Formation (Malumián 1999; Malumián and Olivero 2006; Olivero and Malumián 2008). The Cabo Domingo Group reflects the typical geometry of a foreland basin fill with thicker packages and a more complete stratigraphic record near the fold and thrust belt, and a less wide-ranging record toward the foreland.

Ponce et al. (2008) recognized five depositional sequences within the late Oligocene–Miocene clastic succession along the Atlantic coast of Tierra del Fuego. The

sequences are constructed of three main architectural elements: hyperpycnal lobe complexes, hyperpycnal channel complexes, and associated hyperpycnal levee complexes, which were interpreted by Ponce et al. (2008) as depositional slope clinoform systems in a mainly deep marine environment. Hyperpycnal flows and their deposits are a formal part of the Walker (1978) classification of deep water deposits. Mulder and Syvitski (1995) and Mulder et al. (2003) differentiate turbidity currents that are generated by the transformation of a submarine slide into a turbulent flow from flows that are generated by processes, such as from hyperpycnal discharge of a river during floods.

#### COLLECTING LOCALITIES

**San Julio Section.**—Middle Miocene Carmen Silva Formation on Cerro Castillo, Estancia San Julio, Lat.  $53^{\circ}39'47.7''\text{S}$ , Long.  $68^{\circ}26'49.3''\text{W}$ , Tierra del Fuego, Argentina, our Waypoint 173 (Fig. 2).

The Carmen Silva Formation of the Cabo Domingo Group at the San Julio section consists of mudstones,

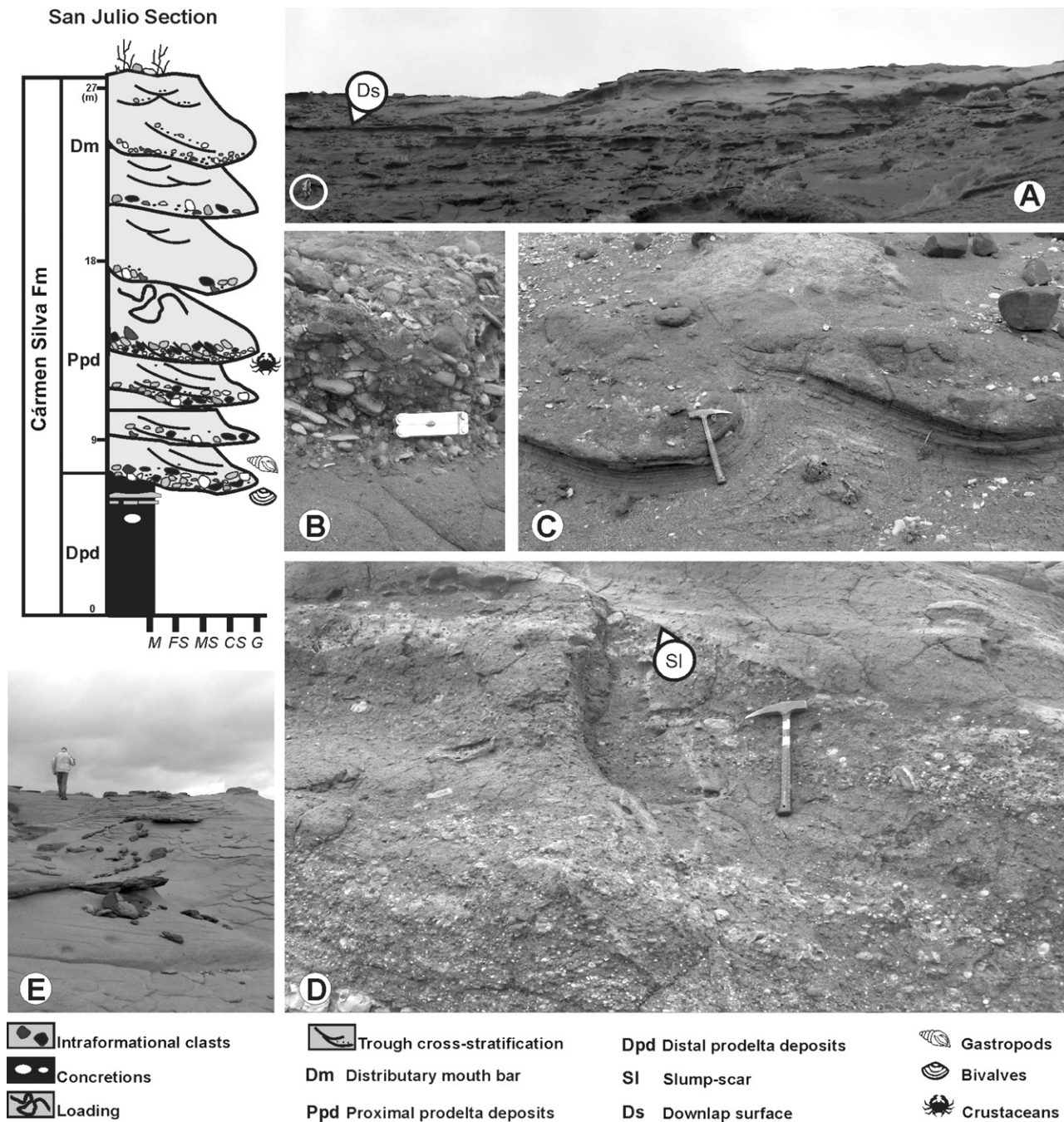


Fig. 2.—Stratigraphic section exposed in the San Julio section. Photographs A–E are referred to in the text. *M* = mud, *FS* = fine sand, *MS* = medium sand, *CS* = coarse sand, *G* = gravel.

sandstones, and conglomerates that, according to the fossil content, are middle Miocene in age (Codignotto and Malumián 1981). The lower part of the San Julio section is comprised of seven meters of laminated mudstones and fine-grained sandstones that crop out in small scarps. These beds pass upwards into tuffaceous sandstones with gently undulating, low angle cross-lamination. This part

of the section records deposition in a distal prodelta environment. The middle part of the section is composed of sandstones and minor conglomerates. The latter consists of more than 80% pebbles with sandy matrix. Conglomerates include intraformational clasts of laminated mudstone, igneous rocks, common reworked trace fossils and well-preserved corals, *Flabellum* cf. *F. cuneiforme wailesi*



Conrad, 1855; mollusks, *Nucula (Leionucula) grandis* Malumián, Camacho, and Gorroño, 1978; *Neilo doellojuradoi* Malumián, Camacho, and Gorroño, 1978; *Glycymeris cuevensis* (Ihering, 1897); *Cucullaea fueguensis* Malumián, Camacho, and Gorroño, 1978; unnamed species of *Swiftopecten Bernardi*, 1858; *Modiolus ameghinoi* Ihering, 1897; *Pteromyrtea crucialis* (Ihering, 1907); *Fasciculicardia freti* (Ihering, 1907); *Pleuromeris sylvia* (Ihering, 1907); *Retrotapes fuegoensis* del Río, 1997; *Turritella sylvia* (Ihering, 1907); unnamed species of *Penion* Fischer, 1884; unnamed species of *Calyptraea* Lamarck, 1799; *Calyptraea merriami* (Ortmann, 1899); *Struthiochenopus santacruzensis* (Ihering, 1907); *Perissodonta fuegensis* (Ihering, 1907); new species of *Polinices* Montfort, 1810; *Polinices santacruzensis* Ihering, 1907; *Falsilunatia puntarenasensis* (Ihering, 1907); *Buccinanops nordenskjoldi* (Steinmann and Wilckens, 1908); *Austrocominella fuegensis* (Ihering, 1907); *Trophon? nordenskjoldi* (Steinmann and Wilckens, 1908); *Ocenebra? iheringi* (Steinmann and Wilckens, 1908); *Miomelon castilloensis* del Río and Martínez, 2006; *Adelomelon cannada* (Ihering, 1907); *Acteon argentinus* Ihering, 1907; brachiopods, *Pachymagas* cf. *P. venter* Ihering, 1903; and crabs. The conglomerates are frequently sharp based, and the gravels are organized into gently-inclined beds that pinch-out in the downdip direction and interfinger with sandy beds (Fig. 2D). Upward through the succession, conglomerates are up to a few decimeters thick and many are inverse-graded and composed of well-rounded and imbricated clasts (Fig. 2B). The sandstones that underlie the conglomerates frequently show load deformation (Fig. 2C). The deposits forming the middle part of the San Julio section record sedimentation occurring in a proximal prodelta environment, along a subaqueous slope, where the flux of sediment was influenced by gravity and exceptional fluvial discharges, generating avalanches of coarser material. The upper part of the studied section comprises clinofolds (Fig. 2A) of sandstones and minor conglomerates. The topset beds are mainly composed of sandstones and matrix-supported conglomerates showing trough cross-stratification and are interpreted as distributary mouth bar deposits.

**El Cachimbo Section.**—Middle Miocene Carmen Silva Formation at Puesto Cachimbo, Estancia Sara, Lat. 53°29'41.9"S, Long. 68°31'45.6"W, Tierra del Fuego, Argentina, our Waypoint 172 (Fig. 3).

The Carmen Silva Formation of the Cabo Domingo Group at the El Cachimbo section consists of mudstones, sandstones, and conglomerates that according to the foraminiferal content are middle Miocene in age (Codignotto and Malumián 1981; Malumián and Olivero 2006). The lower part of the succession comprises more than 15 m of mudstones (Fig. 3A) that contain a low diversity assemblage of foraminifera (Codignotto and Malumián 1981), mollusks, e.g., *Neilo* cf. *N. ornata* (Sowerby, in Darwin, 1846), and *Turritella sylvia* Ihering, 1907; and crabs. The crabs are preserved in calcareous concretions near the top

of the mudstones. Based upon the fossil content and the lithology, Codignotto and Malumián (1981) proposed that this part of the section records deposition in a distal prodelta environment. Overlying the mudstones are up to 15 m of interbedded, chaotic, mostly sandy, matrix-supported conglomerates and sandstones. Conglomerates form chaotic meter-thick beds and are poorly sorted, with sub-angular to sub-rounded intraformational clasts of laminated mudstones (Fig. 3C). Pumicite pebbles and mollusk shells are commonly dispersed in the beds (Fig. 3D). Among the species identified are *Neilo* cf. *N. ornata*, *Arca (Neonavicula)* cf. *N. patagonica* (Ihering, 1897), *Glycymeris cuevensis* (Ihering, 1897), unnamed species of *Ostrea* (Linnaeus, 1758), *Zygochlamys geminata* (Sowerby, in Darwin, 1846), *Pleuromeris elegantoides* (Ortmann, 1902), *Turritella sylvia*, *Cirsotrema rugulosa* (Sowerby, in Darwin, 1846), unnamed species of *Polinices*, unnamed species of *Penion*, and *Adelomelon cannada* (Ihering, 1907). Matrix-supported conglomerates and sandstones are arranged into lenses up to two meters thick. Several intercalated pebbly sandstones show pebble alignments. Conglomerates and sandstones were deposited by avalanching and mass-flow processes in a lower delta front. The upper part of the section consists of heterolithic beds (Fig. 3B) composed of centimeter-thick alternation of medium-grained sandstone and siltstone. Sandstone beds have sharp lower bases, load-casts, and unidirectional and climbing ripple laminations. These beds are followed by sandstones and minor clasts and matrix supported conglomerate lenses containing mollusk shells (Fig. 3A). Heterolithic beds are interpreted as the deposits generated by dilution of non-cohesive sediment-gravity flow after deposition of the gravel fraction. The conglomerate lenses record major gravity-flow events probably originated during exceptional fluvial discharges. Deposits forming the upper part of the El Cachimbo section record sedimentation occurring in a prodelta or delta toe environment.

**Cerro Águila Section.**—Late lower–middle Miocene Cabo Domingo Group (Cerro Águila Conglomerate), about 50 m west from the bridge on Route 3 crossing Río Grande and about 8 km southwest from the town of Río Grande, Lat. 53°50'14.3"S, Long. 67°47'35.4"W, Tierra del Fuego, Argentina, our Waypoint 171(2) (Fig. 4).

The lower part of the Cerro Águila section comprises six meters of fine-grained sandstones and laminated mudstones containing a cool water, heterotrophic dinocyst association (Guerstein et al. 2008). Guerstein et al. (2008) recognized a regressive trend with the best representation of outer neritic and oceanic dinocyst species in the lower part of the section and maximum frequencies of taxa that inhabited coastal paleoenvironments toward the top of the mudstones. Guerstein et al. (2002) included this part of the section in the Cabo Peñas Formation and indicated that the age of these rocks is late Eocene–earliest Oligocene. Mudstones of the Cabo Peñas Formation are followed by six meters of sandstones and prominent conglomerate facies

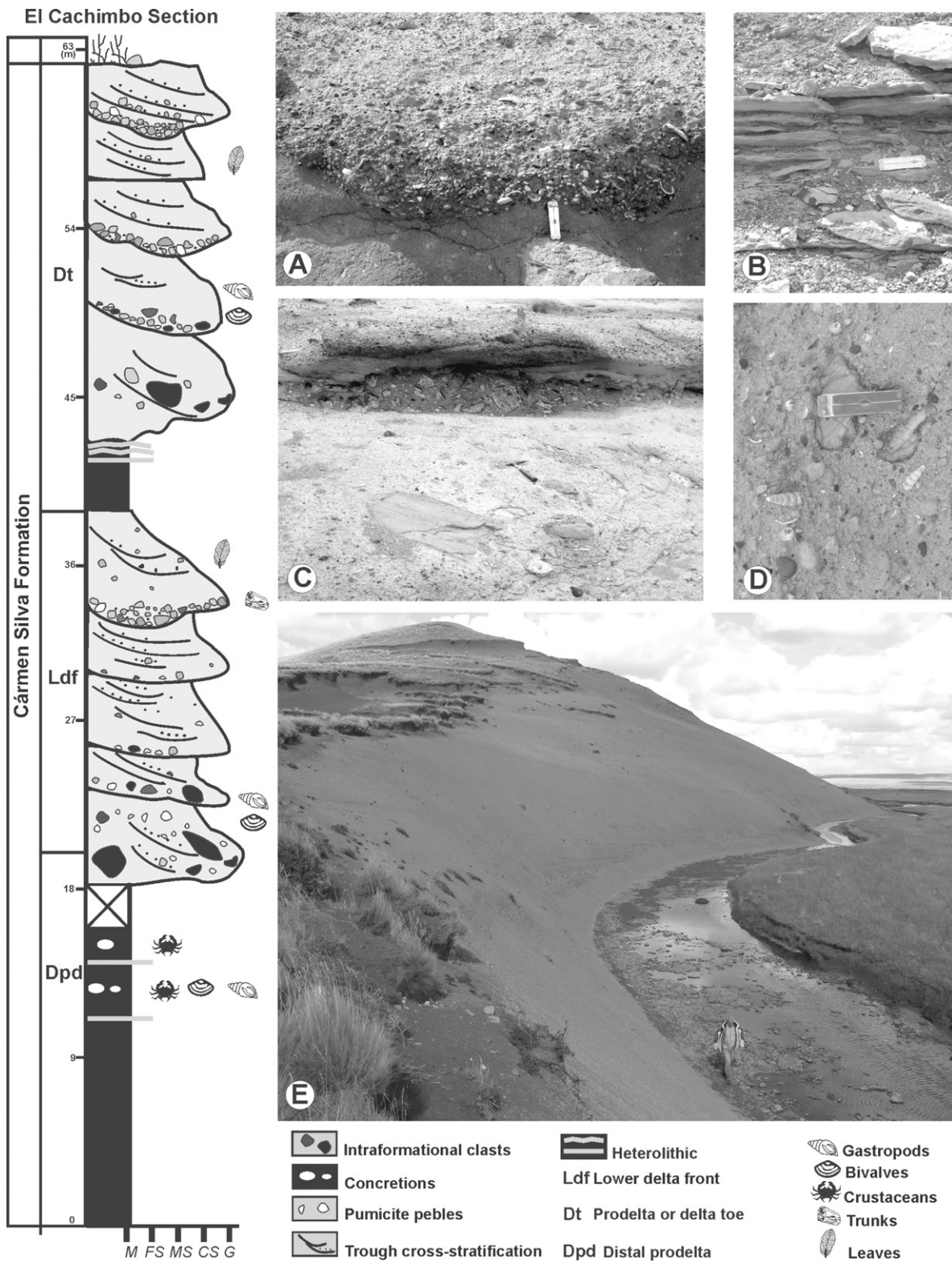


Fig. 3.—Stratigraphic section exposed in the El Cachimbo Section. Photographs A–E are referred to in the text. *M* = mud, *FS* = fine sand, *MS* = medium sand, *CS* = coarse sand, *G* = gravel.



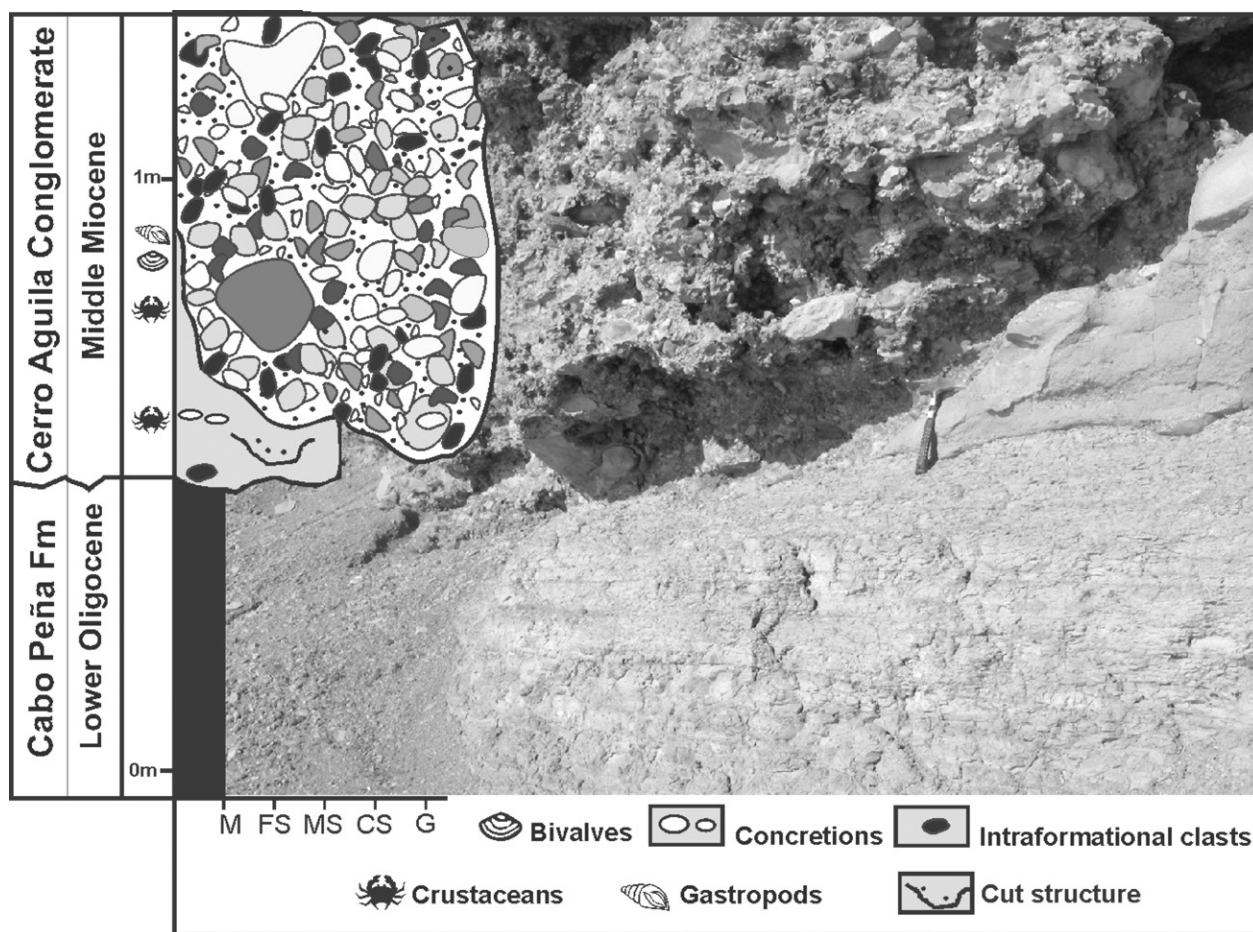


Fig. 4.—Stratigraphic section exposed in the Cerro Águila Section along the Río Grande.

that are an unnamed part of the Cabo Domingo Group. A major unconformity separates the Cabo Peñas Formation from the coarse-grained sandstones and conglomerates of the upper part of the Cerro Águila section (Fig. 4) that were placed in the early Miocene by Codignotto and Malumián (1981) or late early Miocene by Olivero and Malumián (2008). Sandstones show multiple internal erosion surfaces with intraformational boulders of laminated mudstone (major diameter <0.40 m) and calcareous concretions containing well preserved decapod crustaceans discussed below; gastropods, *Perissodonta fuegina* (Ihering, 1907); *Valdesia collaris* (Sowerby, in Darwin, 1846); *Turritella sylvia*; and bivalves, *Panopea ibari* Philippi, 1887; and unnamed species of *Nucula* Lamarck, 1799. Conglomerates are clast supported and exhibit a channel-shaped geometry. A distinguishing feature in the conglomeratic deposits is the abundance of basalt clasts, reworked trace fossils, and concretions containing fossils. The basaltic clasts mark a compositional break between this part of the Oligocene–Miocene succession and the underlying units (Ponce et al. 2008). The sandstones with multiple reactivation

surfaces were produced by hyperpycnal flows and the conglomerates are interpreted as contemporaneous residual conglomerate facies, segregated at the base of channels. Equivalent conglomerates cropping out 30 km to the southeast were considered by Ponce et al. (2008) to be the result of the dilution of a cohesive flow that evolved into gravelly, high density turbidity currents. Hyperpycnal flows are generated during exceptional fluvial discharges, and in foreland basins, like the Austral Basin, the regions adjacent to the orogen were characterized by very steep slopes lacking a well-developed shelf which facilitated the acceleration of the flows. A remarkable record of hyperpycnal flow deposits was described by Ponce et al. (2008) in the Oligocene–Miocene succession cropping out along the Atlantic coast of Tierra del Fuego from Cabo San Pablo to Cabo Viamonte.

#### SYSTEMATIC PALEONTOLOGY

**Institutional Abbreviations.**—CADIC-PI, Centro Austral de Investigaciones Científicas—Paleontología Invertebrados; Ushuaia, Tierra del Fuego, Argentina; CM, Carnegie

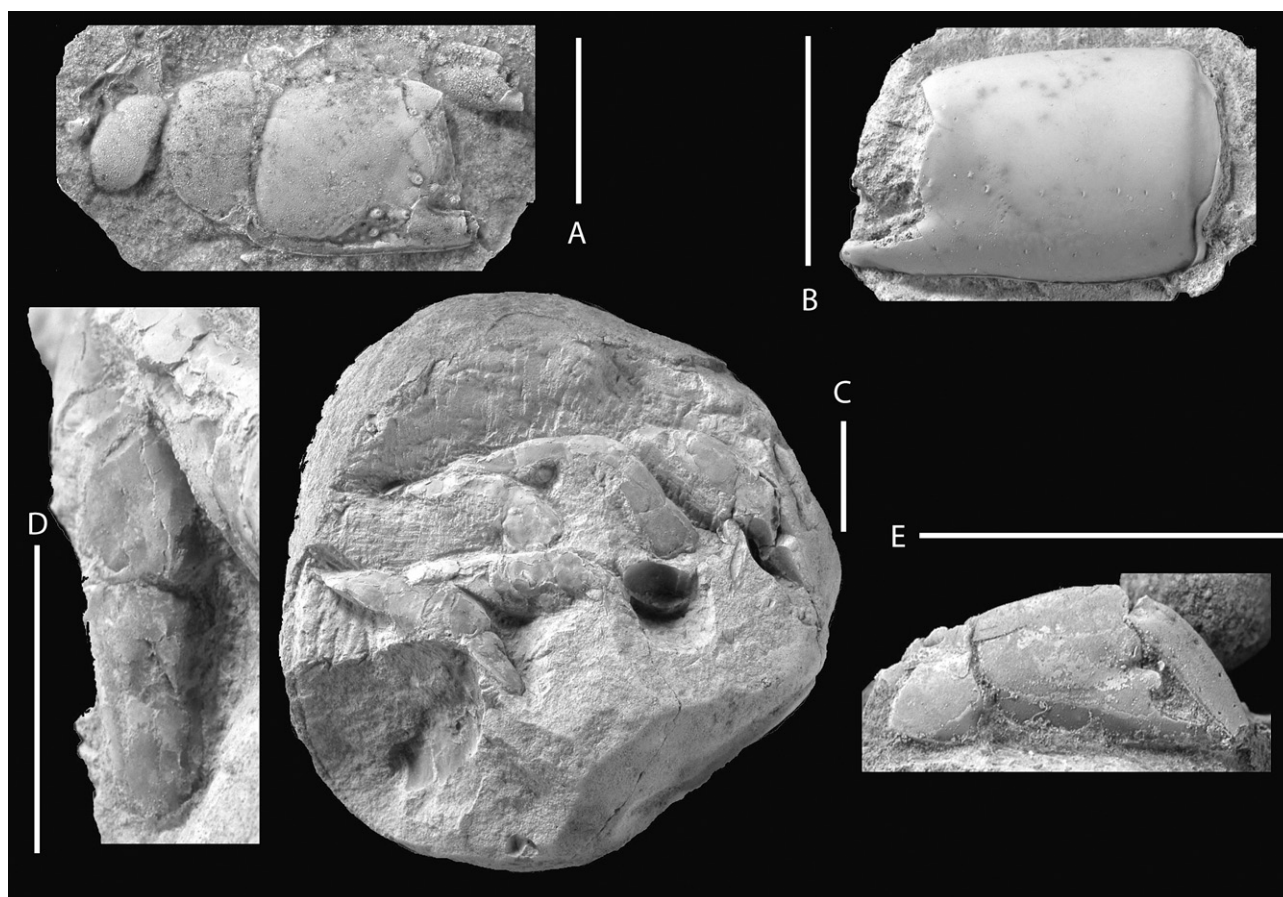


Fig. 5.—Callianassidae. **A**, outer surface of right major cheliped, Form A, CADIC PI 102; **B**, outer surface of left chela interpreted as major, Form B, CADIC PI 103; **C**, imbricate abdomina of several callianassids, CADIC PI 101; **D**, abdominal somite 6 and telson of one individual, CADIC PI 101; **E**, outer surface of right chela interpreted as minor, Form B, CADIC PI 104. Scale bars = 1 cm.

Museum of Natural History, Pittsburgh, Pennsylvania, USA; **Riksm**, Naturhistoriska riksmuseets, Stockholm, Sweden.

Order Decapoda Latreille, 1802  
 Infraorder Thalassinidea Latreille, 1831  
 Superfamily Callianassoidea Dana, 1852

Family, genus, and species indeterminate  
 (Figs. 5A–E)

**Description of Abdomina.**—Abdomina long, at least 30 mm, straight or curved downward at somite 5; cuticle very thin. Terga smooth, pleura very short, ventral margins straight where visible. Somites about equal length, ~ 12 mm; telson longer, 7.4 mm, than wide, 5.8 mm, tapering posteriorly to blunt, rounded termination, weakly rimmed and with swollen area proximally.

**Description of Cheliped Form A.**—Major claw with merus longer, 7.3 mm, than high, 3.9 mm; margins smooth, upper margin weakly convex, lower margin nearly straight,

articulating with carpus at upper corner of proximal carpus margin; outer surface smooth. Carpus higher, 11.0 mm, than long, 6.2 mm, highest distally; upper margin weakly convex, sloping downward proximally; lower margin rimmed, curves upward and merges with proximal margin in smooth curve; proximal margin sinuous; distal margin weakly concave; lower distal corner acute; outer surface smooth. Manus nearly square, 12.6 mm high, ~ 11.7 mm long; proximal margin weakly convex, perpendicular to long axis; dorsal margin straight, slopes gently distally; lower margin convex, rimmed; distal margin incomplete, sinuous, with small spine just above base of fixed finger. Fixed finger with rimmed lower margin.

**Description of Cheliped Form B.**—Major claw with manus longer, 12.8, 11.8, 11.6 mm, than high, 10.7, 8.2, 9.5 mm respectively; upper and lower margins straight, smooth, converge slightly distally; lower margin very weakly rimmed; proximal margin straight, perpendicular to long axis of manus; distal margin curved with shallow re-entrant at



mid-height; outer surface generally smooth, convex, with 2 rows of about 7 setal pits, one row at level of fixed finger and another 1/3 height from lower margin. Fixed finger short uniformly tapering with single, strong tooth near proximal end of finger.

Minor claw with manus longer, 4.6 mm, than high, 3.6 mm; highest distally; upper margin straight, smooth, tapers proximally; lower margin straight, proximal margin weakly convex, distal margin sinuous with prominent node near origin of fixed finger. Fixed finger nearly straight, about 1/2 length of manus, tapering distally. Dactylus stout, upper surface convex; outer surface with row of setal pits above sulcate midline. Dactylus closes downward on fixed finger. Occlusal surfaces not exposed.

**Material Examined.**—CADIC PI 101 (abdomen), 102 (Form A), 103–105 (Form B).

**Occurrence.**—CADIC PI 101 was collected from the Cerro Águila section, and CADIC PI 102–105 were collected from the San Julio section.

**Discussion.**—Callianassids have been common elements of decapod faunas of all ages and places since the Mesozoic. Notable in this fauna is CADIC PI 101, with several individuals preserved in imbricated fashion. This suggests that the individuals or molts were swept up by currents and deposited somewhere other than their area of habitation.

Infraorder Anomura MacLeay, 1838  
Superfamily Lithodoidea Samouelle, 1819  
Family Lithodidae Samouelle, 1819

Genus and species indeterminate  
(Figs. 6A–D)

**Description of Material.**—Carpus of cheliped longer than high, becoming higher distally; proximal margin concave; upper margin oblique; lower margin obliquely sloping downward, with at least four forward-directed spines; inner surface weakly inflated, ornamented with large tubercles; distal margin concave.

Manus of major cheliped rhomboid in cross-section. Upper surface with stout, forward-directed spines. Inner surface convex distally, flattening proximally, ornamented with short spines. Fixed finger very stout, with broad lower margin; movable finger appearing to have been relatively stout; both ornamented with short, stout spines.

**Material Examined.**—CADIC PI 106–108.

**Occurrence.**—Cerro Águila section.

**Discussion.**—The specimens appear to be referable to the Lithodidae based upon the stout chelae with broad fingers and ornamentation of either spines or stout tubercles. Paguroids may also exhibit similar ornamentation but often do not exhibit such stout fingers of the manus. Many

lithodid taxa are known from Tierra del Fuego in modern oceans (MacPherson 1988) and in fact are an economically viable fishery there. Recovery of more elements of the appendages or a carapace could help to confirm placement of these specimens.

Infraorder Brachyura Linnaeus, 1758  
Section Cyclodorippoidea Ortmann, 1892

**Discussion.**—As understanding of the primitive crabs has evolved during the last decade, the concept of Podotremata has been variously interpreted. Martin and Davis (2001) argued that the Section Podotremata was a heterogeneous grouping and revised the classification to include the Section Dromiacea De Haan, 1833, to include dromiids, homolodromiids, and homolids. The Raninoidea De Haan, 1841, and the Cyclodorippoidea Ortmann, 1892, were considered to be superfamilies within the Section Eubrachiura, Subsection Raninoidea. Ng et al. (2008) continued to use Section Podotremata to embrace all these groups, whereas De Grave et al. (2009) recognized three sections to include both fossil and extant members of the “podotremes,” Dromiacea, Raninoidea, and Cyclodorippoidea. Although these relationships remain in contention, we follow the classification of De Grave et al. at this time.

Superfamily Cyclodorippoidea Ortmann, 1892  
Family Cyclodorippidae Ortmann, 1892

**Discussion.**—The Cyclodorippidae has been examined in detail by Tavares (1993, 1996), and diagnoses and keys to identification of genera provide a clear understanding of the nature of the group. His diagnosis of the family (1993:264) includes several characters potentially useful in assigning fossils to the taxon. They include subcircular to subpentagonal carapace outline; presence of orbits; endostome generally elongate, narrowing anteriorly and reaching anterior margin of the carapace; and spermatheca expressed as a simple opening at the extremity of sternal suture 7/8.

Tavares (1993:265) subdivided the family into two subfamilies of which the Cyclodorippinae are characterized by having a fronto-orbital width that is about half the total width of the carapace, a condition seen in *Tymolus* Stimpson, 1858, and *Corycodus* A. Milne-Edwards, 1880. The combination of family and subfamilial characters, particularly that of the conformation of the fronto-orbital region, support placement of the new genus described herein within the Cyclodorippinae. The Xeinostomatinae Tavares, 1992, exhibit a fronto-orbital width greater than half the carapace width (Tavares 1993).

#### *Miotymolus*, new genus

**Type Species.**—*Miotymolus quadratus*, new species, by original designation.



**Etymology.**—The generic name is derived from the Greek *Meiotikos* = lessening, the root word of Miocene, denoting the age of the rocks from which the specimen was collected, and the generic name *Tymolus*. The gender is masculine.

**Diagnosis.**—Carapace large for family, quadrate, slightly longer than wide; broadest across metabranchial region. Regions well defined, tumid; rostrum with very small axial spine and prominent lateral rostral spines; fronto-orbital margin less than half maximum carapace width; frontal region depressed below remainder of carapace surface. Flanks concave in anterior half of carapace.

**Discussion.**—The morphology of the frontal region, expressed as a nearly cylindrical forward extension of the carapace and lying at a level below the overall carapace surface, is similar to that seen in *Tymolus*. However, the quadrate form of the carapace and the large size as compared to species of *Tymolus* suggest that the specimens from Tierra del Fuego represent a unique genus. The quadrate outline and the projection of the fronto-orbital region are defined by the angle at which the anterior margin slopes away from the fronto-orbital region. These characters distinguish the genus from other members of the family and yet are consistent with the definitional bases for the family.

*Miotymolus quadratus*, new species  
(Figs. 7A–D)

**Diagnosis.**—As for genus.

**Description.**—Carapace quadrate, longer, 40 mm, than wide, 38.6 mm; widest in metabranchial region. Dorsal surface weakly arched transversely and longitudinally with highest elevation in mesogastric region; flanks steep, prominent, weakly concave. Regions well defined, inflated.

Rostrum narrow, 13% maximum width, with small central spine; defined laterally by large, forward-directed lateral rostral spines. Lateral rostral spines bear fine corrugations on outer surface. Orbits narrow, deeply concave dorsally, bounded axially by lateral rostral spines, laterally by short, triangular supraorbital spine directed anterolaterally toward strong outer orbital spine nearly as long as lateral rostral spine. Lower lateral corner defined by very prominent lower orbital spine extending anteriorly well beyond tips of rostral spines. Fronto-orbital margin 21% maximum width. Anterior margin slopes posterolaterally to form 67° angle with midline, with small spine at midlength and bounded on outer angle by small anterolaterally-directed spine; anterolateral margin bearing prominent hepatic spine at about mid length. Remainder of lateral margin nearly straight with slight indentation at level of branchiocardiac groove. Posterolateral corner smoothly rounded. Posterior margin not well preserved.

Frontal region smooth, depressed below general carapace surface, extending in advance of remainder of carapace as

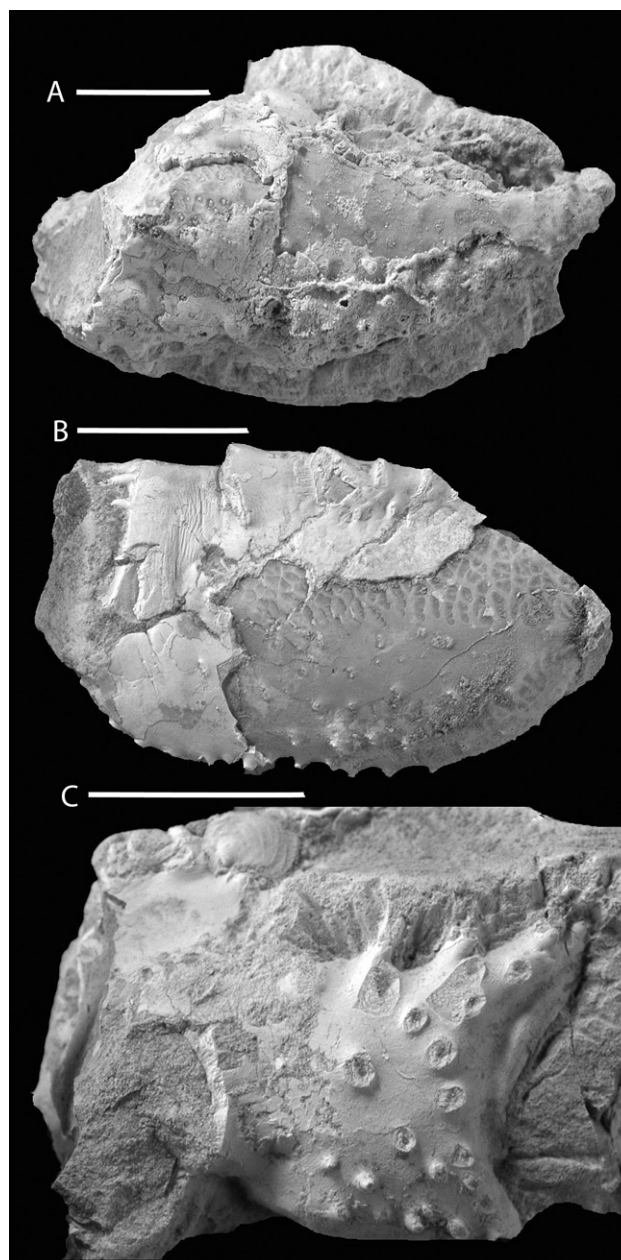


Fig. 6.—Lithodidae. **A**, inner surface of chela, CADIC PI 106; **B**, element of cheliped, CADIC PI 107; **C**, carpus of cheliped, CADIC PI 108. Scale bars = 1 cm.

nearly cylindrical projection. Mesogastric region quadrate with weakly defined anterior projection, the widest axial region, 36% maximum width, well defined posteriorly and laterally by cervical groove; posterior margin of mesogastric region with large, arcuate nodose field of gastric muscle scars; anterior projection of mesogastric region with prominent keel on mold of interior of carapace which is more subtly expressed on cuticle surface; keel extends about half the length of anterior projection which becomes less well developed anteriorly and terminates before reaching frontal

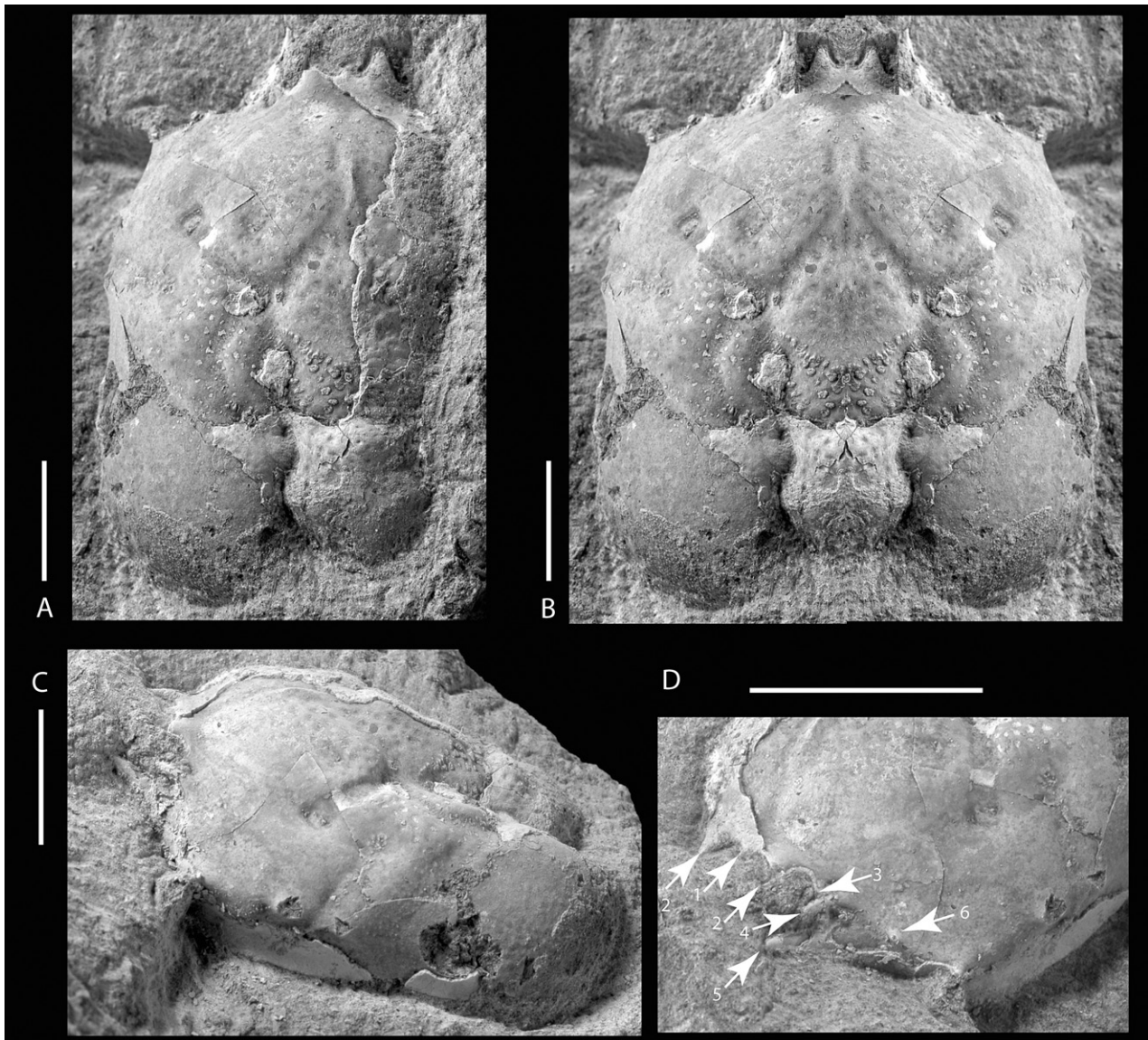


Fig. 7.—*Miotymolus quadratus*, new genus and species. **A–C**, CADIC PI 109, holotype, dorsal carapace (**A**) and oblique left lateral views (**C**), as well as a composite image in which most of the left side and the right rostral spines have been mirrored (**B**); **D**, paratype CADIC PI 110, showing array of spines in anterior region. 1 = central rostral spine, 2 = lateral rostral spine, 3 = small supraorbital spine, 4 = outer orbital spine, 5 = lower orbital spine, 6 = small spine on anterior margin. Scale bars = 1 cm.

region. Progastric and hepatic regions moderately swollen, separated by subtle depression. Cervical groove crosses midline as straight element, curves anteriorly as straight element nearly parallel to midline, and terminates in oblique element before reaching margin.

Metagastric and urogastric regions not differentiated, defined laterally by concave grooves and bearing a central axial dome. Cardiac region nearly as broad as mesogastric region, triangular, weakly swollen laterally, bounded posteriorly and laterally by branchiocardiac groove which extends antero-laterally from midlength of metagastric/urogastric region approximately parallel to cervical groove and

becoming faint laterally.

Epibranchial region bounded by cervical and branchiocardiac grooves, flattened with shallow depression medially. Mesobranchial region small, reniform, elongate parallel to midline. Metabranchial region large, circular, inflated.

Cuticle surface, where preserved, with uniformly spaced, small pits on elevated regions and tiny, densely packed nodes on elevated regions and in grooves.

Ventral surface, abdomen, and appendages not preserved.

**Etymology.**—The trivial name, *quadratus*, from the Latin word for four-sided, alludes to the quadrate outline of the



carapace

**Types.**—The holotype, CADIC PI 109, and paratype CADIC PI 110.

**Occurrence.**—The holotype and paratype were collected in March, 2008, from the Cerro Águila section.

**Discussion.**—The specimens were preserved in immature, medium sandstone concretions, with grains of quartz, biotite, a ferromagnesian mineral (possibly augite), and rock fragments cemented by iron which weathers to a yellowish-red color on the exterior. The concretions are enclosed within a conglomerate layer about 4 m thick, concentrated in the lower 2 m of the unit. The cuticle of the specimens is extremely fragile and has been lost over most of the surface of the holotype and paratype. Where preserved, the fine detail of the surface is revealed, whereas the surface of the mold of the interior or the cuticle does not show these structures.

The occurrence of *Miotymolus quadratus* in Tierra del Fuego is significant because it suggests the Cyclodorippidae had an amphitropical distribution in the Miocene, and the origin of the family most likely predated that time. The family presently has a broad geographic range extending from northern Japan, through the Indian Ocean, and south to Tasmania in the Indo-West Pacific region (Tavares 1993) and on both sides of the Americas from the United States to northern Brazil (Tavares 1996). The extant specimens studied from the Indo-West Pacific were collected at depths ranging from 90–1200 m. All extant forms are small (Davie 2002; Poore 2004) and typically inhabit soft, sandy and muddy substrates (Davie 2002). Fossil Cyclodorippidae reported from the Miocene of Japan and Alaska, U.S.A. (Imiazumi 1952; Takeda and Tomida 1984; Conkle et al. 2006) are all referred to *Tymolus* and all are larger than the extant forms. Schweitzer (2001) described *Xeniosoma? antiqua* based upon a tiny specimen from the late Eocene of Washington state, U.S.A.

Section Eubrachyura de Saint Laurent, 1980  
Superfamily Calappoidea De Haan, 1833  
Family Calappidae De Haan, 1833

*Mursia* Leach in Desmarest, 1823

**Type Species.**—*Mursia cristiata* H. Milne-Edwards, 1837.

**Included Fossil Species.**—See Schweitzer et al. (2010).

**Discussion.**—The tightly convex anterolateral margin, narrow front, rimmed orbits, rows of tubercles on the dorsal carapace, and pairs of tubercles on the anterior portion of the mesogastric region clearly place the new species within *Mursia*. The straight, entire posterolateral margin of the new species eliminates it from other calappid genera with extensive fossil records such as *Calappa* Weber, 1795, and *Calappilia* A. Milne-Edwards in de Bouillé,

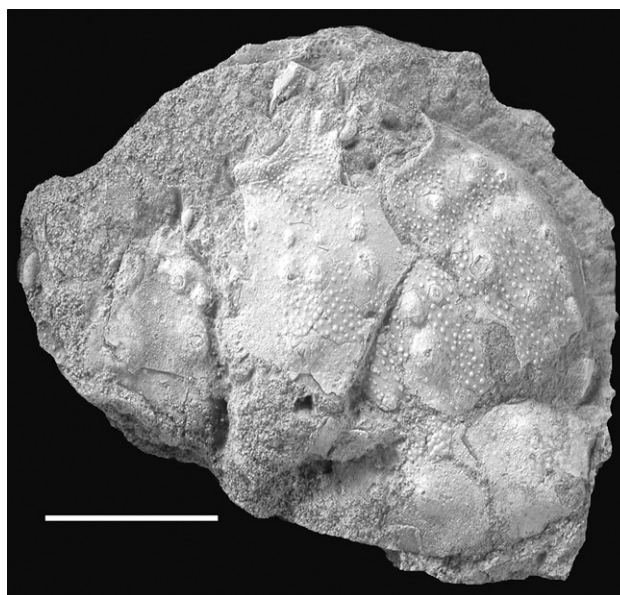


Fig. 8.—*Mursia fuegiana* new species, holotype CADIC PI 111, dorsal carapace. Scale bar = 1 cm.

1873, each of which have spiny flanges on the posterolateral margins. The calappoid genera (sensu Schweitzer et al. 2010), *Hepatus* Latreille, 1802, and *Osachila* Stimpson, 1871, have already been reported from southern South America, but they are each characterized by either much smoother carapaces or very distinctive ornamentation unlike that of *Mursia* spp.

*Mursia* has an extensive fossil record and is widespread in modern oceans (Schweitzer and Feldmann 2000a). Occurrences of the genus were hypothesized to be in generally temperate areas or in deep water (outer-shelf to slope) (Schweitzer and Feldmann 1999). More recent reports corroborate this finding (Galil 2001; Takeda and Galil 2005). Fossil occurrences of *Mursia* are previously unknown from the southern Hemisphere, but extant species are reported from Australia and the South Atlantic (Schweitzer and Feldmann 1999).

***Mursia fuegiana*, new species**  
(Fig. 8)

**Diagnosis.**—Carapace with two pairs of tubercles on anterior extension of mesogastric region; lateral regions with two longitudinal rows and one short row of tubercles.

**Description.**—Carapace ovate, about 37 mm in width, ornamented with tubercles of varying sizes, larger tubercles arranged into rows.

Front narrow, axially sulcate. Orbits forward-directed, closely-spaced, rimmed, with small outer-orbital spine; fronto-orbital width about 13.6 mm, about 37 % maximum carapace width.

Anterolateral margin long, tightly convex, with eight

rounded projections; last largest, directed posterolaterally. Posterolateral margin straight. Posterior margin unknown.

Post-frontal margin weakly inflated; mesogastric region with long anterior process, ornamented with two pairs of tubercles anteriorly and one large tubercle posteriorly; remainder of axial regions unknown. Protogastric and hepatic regions with two longitudinal rows of tubercles that extend onto branchial regions and one short row between longer rows; tiny granules interspersed between rows.

**Etymology.**—The trivial name refers to Tierra del Fuego, where the specimen was collected, and in recognition of it being the first species of *Mursia* known from southern South America.

**Type.**—The holotype and sole specimen is CADIC PI 111.

**Occurrence.**—Cerro Águila section.

**Discussion.**—*Mursia fuegiana* is differentiated from all other species of the genus in having two pairs of tubercles on the anterior portion of the mesogastric region. All other species have one pair. The occurrence of *M. fuegiana* in Argentina extends the geographic range of the genus to include much of the Southern Hemisphere.

Superfamily Portunoidea Rafinesque, 1815

Family Macropipidae Stephenson and Campbell, 1960

*Archaeogeryon* Colosi, 1924

*Archaeogeryon* Colosi, 1924:250.

*Proterocarcinus* Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995:9.

**Type Species.**—*Archaeogeryon fuegianus* Colosi, 1924, by monotypy.

**Included Species.**—*Archaeogeryon corsolini* (Casadío, De Angeli, Feldmann, Garassino, Hetler, Parras, and Schweitzer, 2004), as *Proterocarcinus*; *A. fuegianus* Colosi, 1924; *A. lophos* (Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995), as *Proterocarcinus*; *A. latus* Glaessner, 1933; *A. navidad* (Feldmann, Schweitzer, and Encinas, 2005), as *Proterocarcinus*.

**Diagnosis.**—Carapace transversely ovoid to hexagonal, wider than long, 0.60–0.76 times as long as wide; front narrow, downturned, bearing four spines including outer-orbital spines; orbits extremely wide, rimmed, bearing two orbital fissures, one at about midlength and the other near the outer orbital corner; fronto-orbital width to width ratio 0.68–0.95; anterolateral margin short, with two to five spines including outer-orbital spines; epibranchial ridge elevated, granular, terminating at anterolateral corner; branchial region swollen, with longitudinal ridge parallel to long axis of cardiac region; first pereopods isochelous; propodus and dactylus of fifth pereopod paddle-like (modified from Casadío et al. 2004).

**Discussion.**—Assignment of species to *Archaeogeryon* has had a complex history that has resulted in confusion. Colosi (1924) originally described the genus, with *Archaeogeryon fuegianus* as the type species. He compared *Archaeogeryon* to *Geryon*, Krøyer, 1837, the type genus of the Geryonidae Colosi, 1924. Since then, *Archaeogeryon* has been placed in the Geryonidae and two other species, *Archaeogeryon peruvianus* (d'Orbigny, 1842), and *Archaeogeryon latus* were also assigned to it. Subsequently, Aguirre-Urreta (1987) reviewed the record of the Geryonidae as it was known from the Cenozoic deposits of Patagonia. She assigned *A. peruvianus* to *Geryon* and *A. fueguianus* and *A. latus* to *Coeloma* (*Coeloma*) A. Milne-Edwards, 1865, a placement that has not been used by other authors (i.e., Schweitzer et al. 2010). Aguirre-Urreta also placed *Lebucarcinus tyro* (Phillippi, 1887) within the Goneplacidae. *Lebucarcinus* is a genus based upon a neotype (Bahamonde and Frassinetti 1980) because the holotype of *Cancer tyro* Phillippi, 1887, was lost.

Subsequent to Aguirre-Urreta (1987), Feldmann et al. (1995) erected a new genus and species, *Proterocarcinus lophos*, to accommodate a specimen from the Danian Roca Formation in Río Negro Province, Argentina. They assigned *Proterocarcinus* to the Portunidae, based on the conformation of the carapace, orbits, and first pereopods. Later, Schweitzer and Feldmann (2000b) referred *Archaeogeryon latus* to *Proterocarcinus*. Presence of a paddle-like fifth pereopod on a specimen of *P. latus* strengthened the assignment to the Portunidae.

Schweitzer and Feldmann (2000b) assigned *Geryon peruvianus* to *Chaceon* Manning and Holthuis, 1989, and attempted to clarify the relationships between *Proterocarcinus latus* and *Chaceon peruvianus*. Conformation of the ridges and regions of the carapaces of the latter two species is remarkably similar, as is the morphology of the sterna and abdomina; however, the morphology of the orbits is markedly different as is the nature of the anterolateral margins. Orbits on all adult geryonids, including *Chaceon* spp., span about 60–70% of the maximum width of the carapace, whereas the fronto-orbital width of *Proterocarcinus* spp., as well as *Archaeogeryon fuegianus*, is typically from 68–95% the maximum carapace width. Members of the Geryonidae are diagnosed by having five anterolateral spines, whereas *Proterocarcinus* spp. possess two to four. Schweitzer and Feldmann (2000) also documented an ontogenetic change in *C. peruvianus* that resulted in juvenile *C. peruvianus* closely resembling adult *P. latus*.

Subsequently, two other species, *Proterocarcinus corsolini* Casadío et al., 2004, and *P. navidad* Feldmann et al., 2005, were included in *Proterocarcinus*. *Proterocarcinus navidad* was a replacement name for *Lebucarcinus tyro*, based upon the conclusions that the taxon was named for a specimen that did not resemble Phillippi's description and illustrations and that the specimen was collected a great distance from the type locality of *Cancer tyro*. A full discussion of these arguments is presented by Feldmann et al. (2005).



Although the genus and species *A. fuegianus* has been considered valid by the authors throughout their work in Patagonia, no specimens were collected that resembled *A. fuegianus* as described by Colosi (1924) until now. The specimens collected from the vicinity of Rio Grande, Tierra del Fuego, Argentina, bear a striking superficial resemblance to *Proterocarcinus latus*; however, they exhibit five anterolateral spines, and the spines alternate in size. The outer orbital spine, the third spine, and the fifth spine, situated at the anterolateral corner are strong, and the two intervening spines are substantially smaller (Figs. 9A, 9D). This arrangement is precisely the one illustrated by Colosi (1924:252) for *Archaeogeryon fuegianus*. Thus, we consider that the new specimens are referable to the latter species.

Species of *Proterocarcinus* have been distinguished on the basis of number of anterolateral spines as well as degree of development of carapace regions and ridges. The specimen of *A. fuegianus* is nearly indistinguishable from *Proterocarcinus* spp. in terms of generic level characters, such as regions, orbital development, and the nature of the sternum and abdomen. The major difference is in the number of anterolateral spines. Based upon these observations, there is no significant difference between the two genera. Thus, we herein consider *Proterocarcinus* Feldmann et al., 1995, to be the junior subjective synonym of *Archaeogeryon* Colosi, 1924.

The synonymy of these two species requires clarification of the family placement. *Archaeogeryon* has historically been placed within the Geryonidae, and presence of five anterolateral spines is consistent with the definition of the Geryonidae (Manning and Holthuis 1989). However, presence of five spines is not confined to that family. The conformation of the orbits in the Tierra del Fuego specimens and the ratios of frontal width to total width and fronto-orbital width to total width strongly support placement in the Portunoidea, specifically, the Macropipidae. In addition, *Proterocarcinus* spp. possess paddle-like fifth pereopods and unfused male abdominal somites, characteristics typical of the Macropipidae.

Because both *Chaceon* and *Archaeogeryon* are common in Cenozoic deposits of southern South America, it is important to note that the morphology of the sternum and abdomen does not serve to distinguish the two genera (Schweitzer and Feldmann 2000b; Feldmann et al. 2005; Casadío et al. 2005). The female sternum in both genera is broader than that of the male, the male abdomen is unfused in both, and the tip of the telson extends to about the midpoint of sternite 4. This pattern is consistent with other taxa within the Portunoidea, of which both taxa are members.

*Archaeogeryon fuegianus* Colosi, 1924  
(Figs. 9A–D)

**Diagnosis.**—Carapace transversely ovoid to hexagonal, wider than long; front narrow; frontal width to width

ratio 0.16–0.20, downturned, bearing four spines including outer orbital spine; orbits extremely wide, bilobed, upper orbital rim coarsely beaded, bearing two orbital fissures, one at about midlength and the other near the outer orbital corner; fronto-orbital width-to-width ratio 0.68–0.89; anterolateral margin short, with five spines including outer orbital spines; second and fourth anterolateral spines markedly smaller than outer orbital, medial, and last anterolateral spines; epibranchial ridge elevated, granular, terminating at base of last anterolateral spine; branchial region swollen, with longitudinal branchial ridge diverging slightly posteriorly.

**Material Examined.**—CADIC PI 112-122; CM 56199 (cast of CADIC PI 119), Riksm Ar. 42191, 42194, and 42204, and CM 56120–56123.

**Occurrence.**—San Julio (CADIC PI 112, 116, 117, 120–122; CM 56122, 56123), Carmen Silva (Riksm Ar. 42191), and Cerro Águila (CADIC PI 113–115, 118, 119; Riksm Ar. 42194 and 42204; CM 56120–56121) sections.

**Discussion.**—As discussed above, the morphology of the specimens at hand corresponds closely to the description and illustrations of Colosi (1924) so that placement within the species can be made with confidence. The most striking feature of the species is the possession of five anterolateral spines that alternate in degree of development. The second and fourth anterolateral spines may be relatively long and slender or reduced to small spines or swellings (Figs. 9A, 9D). Regardless, they are always smaller than the spines that bound them. Possession of five anterolateral spines distinguishes *A. fuegianus* from all other species within the genus, and the number of spines has been taken to be one of the distinguishing features of species within the genus-group.

The species that is morphologically most similar to *A. fuegianus* is *A. latus*. The former species has five anterolateral spines, rather than four, less distinctly granular carapace ridges, and a more strongly bilobed orbit than seen on *A. latus*. The upper orbital margin in both species is nearly perpendicular to the longitudinal axis whereas it slopes posterolaterally in both *A. corsolini* and *A. navidad*. Both of these species exhibit carapace granulation that is much reduced. Thus, there is no difficulty in distinguishing them from the other two species, *A. fuegianus* and *A. latus*. *Archaeogeryon lophos*, from the Danian Roca Formation, has four anterolateral spines of equal development and a granulated transverse epibranchial ridge, but the longitudinal branchial ridge lacks pronounced granulations.

Of the approximately 30 specimens of *A. fuegianus* collected from localities in Tierra del Fuego, 13 were completely enough preserved to provide useful measurements (Table 1), and nine had sufficiently complete abdomina to permit determination of gender. Of those, six were males and three were females.

Several of the specimens are preserved with all but the

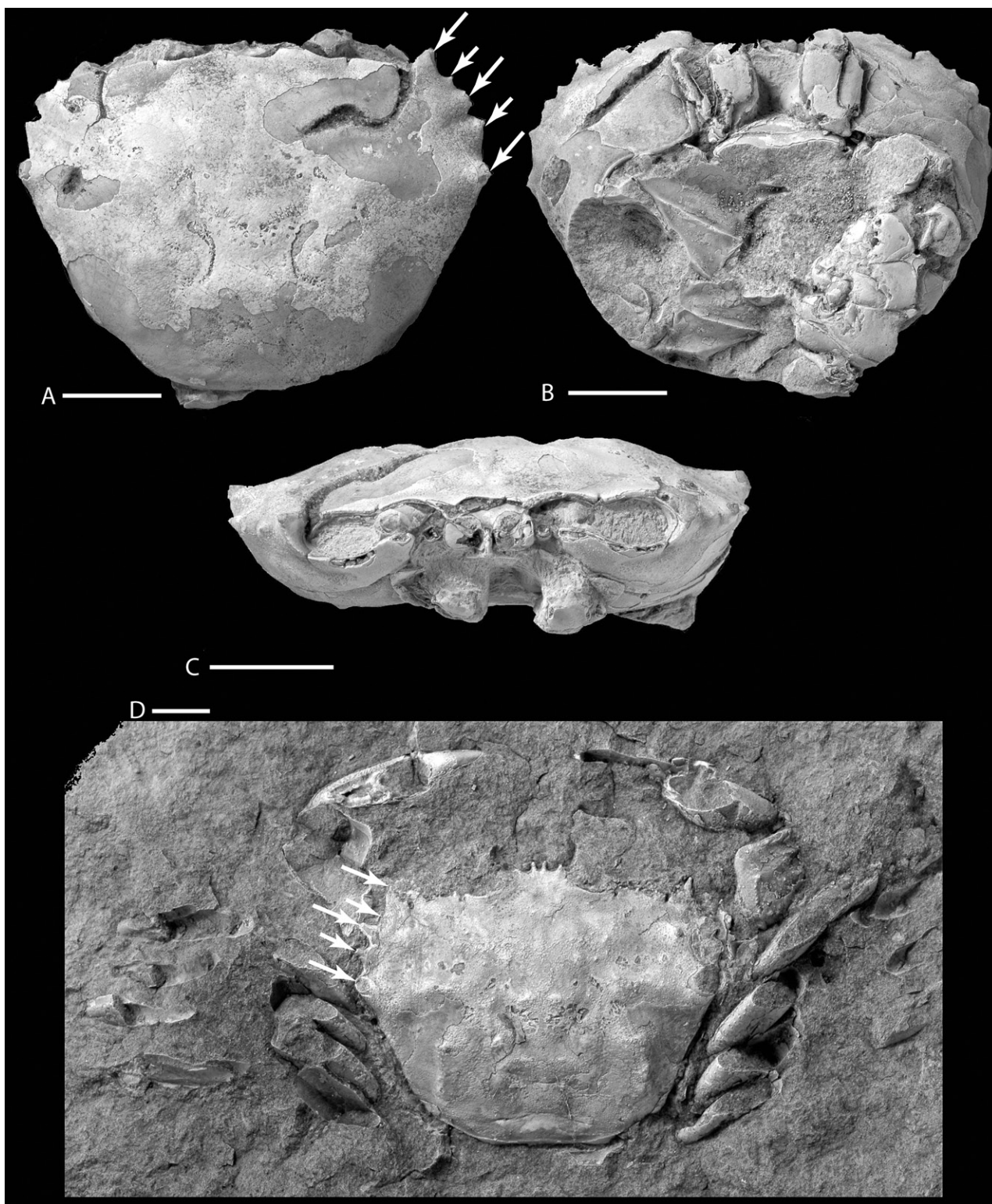


Fig. 9.—*Archaeogeryon fuegianus* Colosi, 1924. A–C, CADIC PI 112, dorsal carapace showing alternating long and short anterolateral spines with corresponding long and short arrows as well as bioexcavation on anterior right corner (A), ventral surface (B), and anterior view showing broadly bilobed orbits (C); D, CADIC PI 113, also showing alternating long and short anterolateral spines with corresponding long and short arrows and 4 distinct frontal spines corresponding well to original drawing and description on Colosi (1924). Scale bars = 1 cm.



TABLE 1. Measurements and ratios determined on specimens of *Archaeogeryon fuegianus* Colosi, 1924.

L = carapace length, W = maximum carapace width, FW = frontal width; FOW = fronto-orbital width, FOW/W = ratio of fronto-orbital width to carapace width, FW/W = ratio of frontal width to carapace width.

SPECIMEN	L	W	FW	FOW	FOW/W	FW/W
CADIC PI 112	34.9	46.5	~ 7.7	31.4	0.68	0.17
CADIC PI 113	38.2	52.1	8.7	37.7	0.72	0.17
CADIC PI 114	37.6	51.6	-	41.8	0.81	-
CADIC PI 115	27.2	36.9	6.1	30.0	0.81	0.17
CADIC PI 116	>36	48	-	32.8	0.68	-
CADIC PI 117	41.7	51.2	10.0	39.8	0.78	0.20
CADIC PI 120	20.1	25.2	5.2	20.4	0.81	0.21
CADIC PI 121	46.6	59.5	9.5	46.8	0.79	0.16
CADIC PI 122	> 45	61.1	-	43.7	0.72	-
Riksm. 42119a	56.0	73.1	-	53.4	0.73	-
Riksm. 42204	38.7	45.3	10.2	34.5	0.76	0.23
Riksm. 42794	40.4	47.6	9.5	34.8	0.73	0.20

distal parts of the pereiopods articulated. Chelipeds are attached in some (Fig. 9D). The remainder preserves the sternum and often the abdomen and basal elements of the pereiopods along with the carapace. This suggests that the specimens represent corpses, rather than molts. A single specimen, CADIC PI 112, is preserved with the third maxillipeds extended away from the dorsal carapace (Fig. 9C). This posture has previously been interpreted to indicate that the organism was suffocating and was gasping for oxygenated water (Crawford et al. 2008). Crawford et al. (2008) suggested that, in the occurrence within the Monte León Formation, Santa Cruz Province, the animals were smothered by volcanic ash which fouled the gill surfaces. In the Monte León Formation, all the specimens of *A. la-tus* observed exhibited this posture, whereas only a single specimen in the Cabo Domingo Group assumed this posture. The other specimens were preserved with the third maxillipeds in the normal closed position.

Cuticle is present on several of the specimens. Two of the specimens show evidence of scavenging. Elongate, sinuous excavations, 1–1 ½ mm in width, penetrate the cuticle (Fig. 9A). One trace originates near the right outer orbital corner and extends across the hepatic and protogastric regions, whereas the other arises at the posterolateral margin and crosses the metabranchial region. The organism responsible for the excavations is not known.

Family Geryonidae Colosi, 1924  
*Chaceon* Manning and Holthuis, 1989

**Type Species.**—*Geryon fenneri* Manning and Holthuis, 1984.

**Included Fossil Species.**—*Chaceon heimertingensis* (Bachmayer and Wagner, 1957), as *Geryon*; *C. helmstedtense*

(Bachmayer and Mundlos, 1968), as *Coeloma* (?); *C. matsushitai* Kato and Koizumi, 2001; *C. miocenicus* Fraaije, Hansen and Hansen, 2005; *C. ottnangensis* (Bachmayer, 1953), as *Geryon*; *C. peruvianus* (d'Orbigny, 1842), as *Portunus*.

*Chaceon peruvianus* (d'Orbigny, 1842)  
(Figs. 10A–B)

**Diagnosis.**—The species has recently been diagnosed and discussed by Schweitzer and Feldmann (2000b) and Casadio et al. (2005), and will not be repeated here.

**Studied Specimen.**—CADIC PI 152, collected in March, 2008, and Riksm Ar. 42199a, collected in May, 1908.

**Occurrence.**—The specimens were collected from the Cerro Águila section.

**Discussion.**—The nearly complete specimen of carapace, Riksm Ar. 42199a, bears all the characteristics of the species seen in other Argentine specimens.

The cheliped specimen, CADIC PI 152, consists only of the outer surface of the distal rim of the propodus and the fixed finger of the right cheliped. A prominent protuberance along the distal rim is situated just below the presumed point of insertion of the dactylus and is separated from fixed finger by a shallow re-entrant. The fixed finger is stout, inflated, and tapers uniformly to its termination. The denticles are molariform, and the innermost two are elongate and exhibit weakly corrugated surfaces. The outermost seven are smaller, appear to be more equidimensional, and vary in size, but they do not appear to show any obvious pattern of size variation. The tips of all the denticles are blackened. Placement in *C. peruvianus* is

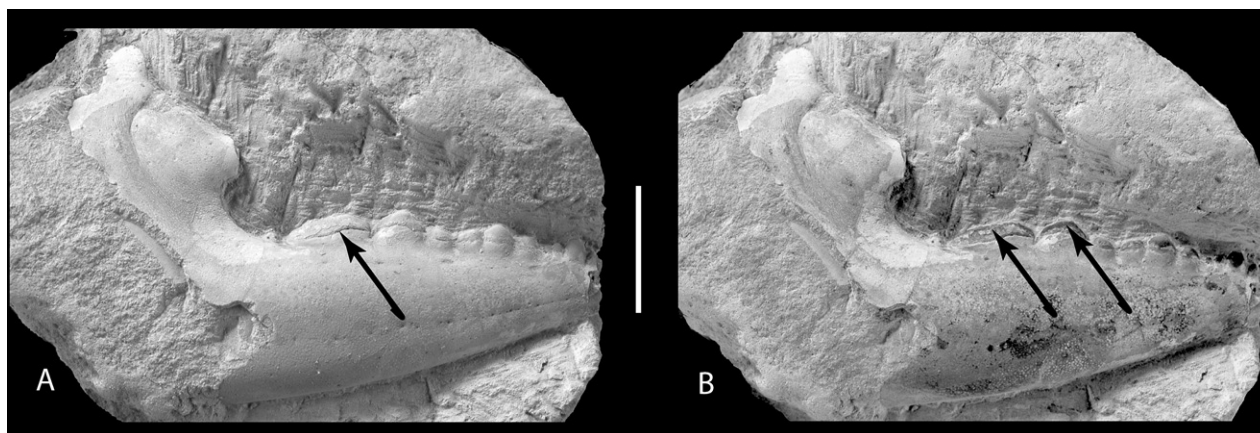


Fig. 10.—*Chaceon* sp. A, B, Fixed finger of right cheliped (A) whitened, and (B) unwhitened. Arrows point to line of separation between heavily calcified upper surface of denticles and remainder of finger. Scale bar = 1 cm.

based upon the possession of the prominent swelling on the distal margin of the manus, the generally strong, smooth outer surface of the finger, and the form of the denticles. These features appear to be identical to those illustrated on more complete specimens of the species (e.g., Casadío et al. 2005).

Although *C. peruvianus* is common and often abundant in other Miocene occurrences in Argentina, the species is represented only by one partial carapace and a single claw fragment in the studied collection. Aguirre-Urreta (1987) noted that Steinman and Wilckens (1908) reported the species from Tierra del Fuego, possibly Riksm Ar. 42199a which was collected in 1908, although she apparently did not study the material and confirm the identification. Thus, it appears that *C. peruvianus* is less common in southernmost Argentina than it is farther north in Patagonia.

The claw specimen is interesting because it exhibits the initial separation of the blackened tips of the denticles from the rest of the fixed finger. Mutel et al. (2008) demonstrated that the tips of the denticles on *Callinectes sapidus* Rathbun, 1896, were more densely calcified than the lower part of the denticles and that, during the process of degradation, the tips of the denticles could separate from the fingers. Examination of the single finger of *C. peruvianus* confirms that observation because a clear line of separation can be observed between the tips of the proximal two denticles and the lower part of the denticles, although complete separation has not occurred.

Superfamily Xanthoidea MacLeay, 1838  
Family Pilumnidae Samouelle, 1819

**Diagnosis.**—See recent works for the most current diagnoses for this family (Davie 2002; Poore 2004; Karasawa and Schweitzer 2006).

**Discussion.**—The new xanthoid crab from Tierra del Fuego is referred to the Pilumnidae for several reasons. It possesses all of the key diagnostic features of the family

that can be observed in fossil specimens, including a wider than long carapace; bilobed front; a front occupying one-third the maximum carapace width; a fronto-orbital width of about half the maximum carapace width; a spinose anterolateral margin with four large spines not including the poorly developed outer-orbital protuberance; all male abdominal somites free; and chelae small with fingers with black tips. It differs from other pilumnids in being only moderately vaulted longitudinally.

Other families to which the new genus bears superficial resemblance within the Xanthoidea sensu stricto and sensu lato cannot accommodate the new genus. The Panopeidae Ortmann, 1893, and Xanthidae MacLeay, 1838, sensu stricto have fused male abdominal somites 3-5. Members of the Tumidocarcinidae Schweitzer, 2005, bear one or no orbital fissures, whereas the new genus bears two and a four-lobed front. In addition, tumidocarcinids are quite inflated, especially longitudinally, whereas the new genus is only moderately inflated. The new genus does possess the Y-shaped groove pattern seen in tumidocarcinids, Zanthopsidae Vía, 1959, and Platyxanthidae Guinot, 1977. However, zanthopsids possess male abdominal somites 3-5 fused and with distinct swellings on somite 3 which are absent in the new genus. Platyxanthids have very narrow fronts and fronto-orbital widths, and poorly defined carapace regions. Thus, the best placement for the new genus is within the Pilumnidae.

Subfamily Pilumninae Samouelle, 1819

**Discussion.**—The only subfamily within the Pilumnidae that can accommodate the new genus is the Pilumninae. Other subfamilies have unusually shaped carapaces (Eumetoninae Dana, 1853; Calmaniinae Števcíć, 1991) or are generally rectangular (Rhizopinae Stimpson, 1858) (Poore 2004; Karasawa and Schweitzer 2006). Extant genera considered referable to the subfamily are based upon Ng et al. (2008).



***Tierrapilumnus*, new genus**

**Type Species.**—*Tierrapilumnus edseli*, new species, by monotypy.

**Diagnosis.**—As for species.

**Description.**—As for species.

**Etymology.**—The generic name is derived from the Spanish word “tierra,” meaning land and part of the name Tierra del Fuego, where the specimens were collected, and the genus name *Pilumnus*, the type genus for the family and a common stem for generic names within the family. The gender is masculine.

**Discussion.**—*Tierrapilumnus* fits all of the diagnostic characters for the family. However, it possesses a complex of characters that is not seen in any existing genera. For example, the bilobed front with an axial notch and beaded rim is seen in some species of *Pilumnus* Leach, 1815, but members of that genus possess only three anterolateral spines, not four. Other genera are generally smooth with poorly defined carapace regions and lobate anterolateral margins, such as *Glabropilumnus* Balss, 1932; *Lentilumnus* Galil and Takeda, 1988; and *Gorgonaria* Galil and Takeda, 1988. Some genera possess only three anterolateral spines, rather than four, including *Serenolumnus* Galil and Takeda, 1988, and *Xlumnus* Galil and Takeda, 1988. *Pilumnopeus* A. Milne-Edwards, 1867, has abdominal somites 3 and 4 fused in males, whereas those somites are free in *Tierrapilumnus*. In other regards, however, *Pilumnopeus* is similar to *Tierrapilumnus* in having an anterolateral margin with four spines and beginning with a relatively straight segment and in having a bilobed front. *Actumnus* Dana, 1851, has a strongly vaulted carapace (Poore 2004), not seen in *Tierrapilumnus*. *Lobopilumnus* A. Milne-Edwards, 1880, is relatively wide and has moderately developed regions as in *Tierrapilumnus*, but the chelae are ornamented with very large tubercles, whereas those of *Tierrapilumnus* are smooth.

Thus, because it embraces a unique combination of characters, we erect a new genus and species to accommodate the new material. The combination of a broad, relatively flattened carapace; four anterolateral spines excluding the outer-orbital projection as well as a straight segment preceding the first anterolateral spine; a bilobed front that is straight other than the axial notch; moderately defined carapace regions; all somites of the male abdomen free; and smooth chelae differentiates *Tierrapilumnus* from all other genera within the subfamily.

***Tierrapilumnus edseli*, new species**

(Figs. 11A–F)

**Diagnosis.**—Carapace broad, relatively flattened; four anterolateral spines excluding the outer-orbital projection, straight segment preceding the first anterolateral spine;

straight bilobed front with axial notch; moderately defined carapace regions; all somites of male abdomen free; chelae with smooth surface.

**Description.**—Carapace wider than long, broadly hexagonal, maximum width about 78% maximum length, maximum width positioned about half the distance posteriorly at position of penultimate anterolateral spine; carapace flattened transversely and moderately vaulted longitudinally.

Front axially notched, otherwise straight, edge beaded, front about one-third maximum carapace width. Orbits directed forward, broadly rimmed, rim beaded; two short, closed fissures in outer one-third; eyestalks short, eye spherical, apparently well-calcified; fronto-orbital width about 55% maximum carapace width.

Anterolateral margin tightly convex, initially directed forward; with four spines not including small outer-orbital protuberance and tiny spinelets on anterior-directed segment; first spine small, granular, triangular, directed anterolaterally; second spine larger, longer, directed anterolaterally, with spinelets on upper and lower margins; third spine about same size as first, granular, directed anterolaterally; last spine smaller than second and third but larger than first; direct laterally. Posterolaterally margin weakly convex. Posterior margin with widely granular rim, weakly concave centrally.

Epigastric regions small, equant, with transverse keel anteriorly which is especially strong on mold of interior but not particularly strong on cuticular surface. Progastric regions weakly inflated; hepatic regions strongly inflated, with anterior transverse keel parallel to anterolateral margin.

Mesogastric region with long anterior process terminating at anterior end of epigastric regions, widening posteriorly, anterior margins of widened portion nearly straight, directed posterolaterally, posterior margin strongly convex, mold of interior with strong muscle scars along posterior margin, posterior margin with pair of pores.

Urogastric region short, wider than long, lateral margins concave, surface flattened. Cardiac region pentagonal, apex directed posteriorly, wider than long, with two swellings anteriorly and one at apex, swellings most acute on mold of interior.

Epibranchial region arcuate, composed of two segments; first ovate, parallel to transverse axis; second ovate, directed at cardiac region. Mesobranchial region broadly inflated laterally, becoming more weakly inflated adjacent to cardiac region. Metabranchial region transversely linear, parallel to posterior margin of carapace.

Sternum ovate, longer than wide. Sternite 3 completely separated from sternites 1 and 2. Sternite 3–4 separated by notch at margins and deep groove otherwise. Sternite 4 long, wide, with deep groove axially extending anteriorly from sterno-abdominal cavity forming Y-shaped groove pattern with grooves separating sternites 3 and 4. Sternite 5 directed anterolaterally; sternite 6 directed laterally;

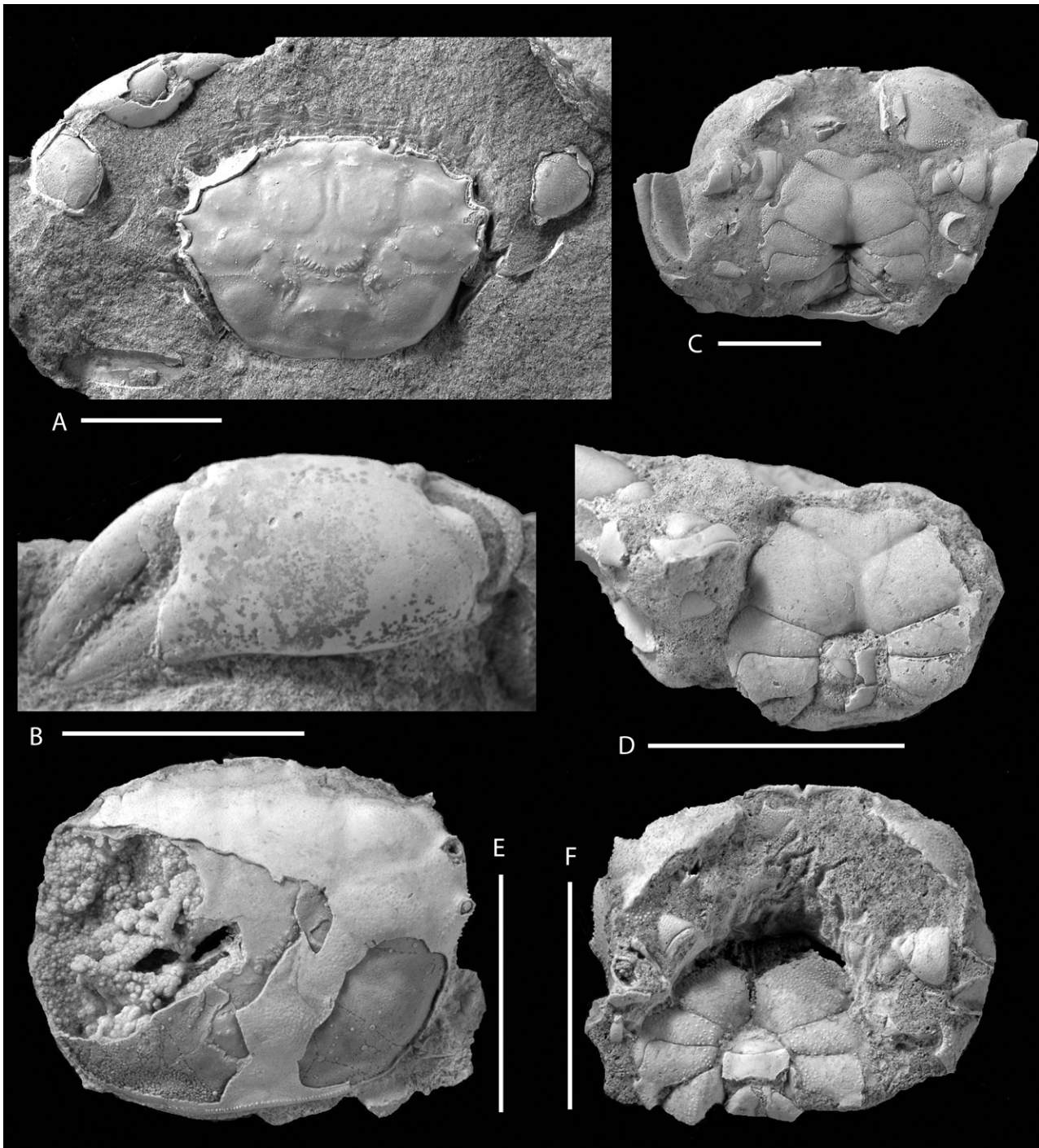


Fig. 11.—*Tierrapilumnus edseli*, new genus and species. A, C, dorsal carapace (A) and chela (C) of holotype, CADIC PI 123; B, sternum of paratype CADIC PI 124; D) sternum and male abdomen of paratype CADIC PI 125; E–F, dorsal carapace and male sternum of paratype CADIC PI 126. Scale bars = 1 cm.

sternite 7 directed posterolaterally. Sternite 8 unknown. All male abdominal somites free.

Left first cheliped with manus longer than high, smooth; fixed finger downturned slightly, shorter than smooth dactylus; denticles not well exposed.

**Measurements.**—Measurements (in mm) taken on *Tierrapilumnus edseli* are given in Table 2.

**Etymology.**—The trivial name honors Dr. Edsel Brussa, late of the Universidad Nacional de La Pampa, Santa Rosa, Argentina, who studied graptolites and was our friend.



**TABLE 2.** Measurements (in mm) taken of *Tierrapilumnus edseli*, new genus and species, on Tierra del Fuego.

L = maximum carapace length; W = maximum carapace width; FOW = fronto-orbital width; FW = frontal width; L2 = length from front to position of maximum width.

Specimen Number	L	W	FOW	FW	L2
CADIC PI 123 for 171-1	17.0	22.1	11.4	6.4	7.1
CADIC PI 127 for 171-2	14.0	17.9	10.2	6.2	7.2
CADIC PI 128 for 171-3	12.0	15.2	8.8	5.8	6.3
CADIC PI 130 for 173-1	15.0	19.4	10.7	6.0	8.3
CADIC PI 131 for 173-2	13.2	17.8	-	-	-
CADIC PI 132 for 173-3	-	17.8	9.4	-	-
CADIC PI 133 for 173-4	-	18.1	9.8	5.7	-
CADIC PI 126 for 173-5	15.3	18.8	10.2	6.2	7.4

**Types.**—The holotype is CADIC PI 123, and paratypes include CADIC PI 124–147. Additional material is CM 56124–56127.

**Occurrence.**—The holotype, CADIC PI 123, and CADIC PI 127–129 were collected from the Cerro Águila section; specimens CADIC PI 124, 134–147 and CM 56124–56127 were collected from the El Cachimbo section, and specimens CADIC PI 125, 126, 130–133 were collected from the San Julio section.

**Discussion.**—Pilumnid crabs are not known today from the Magellanic Province, but they are known from provinces directly to the north on both the east and west coasts of South America (Boschi 2000) as well as in South Africa (Barnard 1950), Australia (Davie 2002; Poore 2004), and New Zealand (McLay 1988). Nearly all fossil occurrences of the Pilumnidae are from the northern Hemisphere, specifically, Europe. Occurrences of *Pilumnus* include several Pacific species, with the Miocene *Pilumnus cucaoensis* Feldmann et al., 2005, being the closest geographically to Tierra del Fuego and the only other occurrence of the family in the southern hemisphere (Feldmann et al. 2005).

Section Thoracotremata Guinot, 1977  
Superfamily Pinnotheroidea De Haan, 1833

**Included Families.**—Pinnotheridae De Haan, 1833; Aphanodactylidae Ahyong and Ng, 2009.

**Diagnosis.**—As for family.

Family Pinnotheridae De Haan, 1833

**Included Fossil Genera.**—*Pinnotheres* Bosc, 1802; *Globihexapus* Schweitzer and Feldmann, 2001; *Pharkidodes*, new genus; *Pinnixa* White, 1846; *Viapinnixa* Schweitzer and Feldmann, 2001; *Zaops* Rathbun, 1900.

**Diagnosis.**—Davie (2002:429) recently diagnosed the

family, following the diagnosis of Barnard (1950). The essential elements relative to fossil pinnotherids include a more or less round or oval carapace that is weakly calcified and bears a smooth or finely dentate anterolateral margin. The front is narrow and the orbits are small. To that combination of characters, Rathbun (1918) noted that the male abdomen was very narrow.

#### *Pharkidodes*, new genus

**Type Species.**—*Pharkidodes agele* by original designation.

**Etymology.**—The generic name is the Greek word *pharkidodes*, meaning wrinkled, in reference to the wrinkled cuticle pattern that defines the regions on the carapace. The gender is feminine.

**Diagnosis.**—Carapace quadrate, width about 89% length; front deeply sulcate, downturned, weakly convex; orbits ovoid with narrow, beaded rims; anterolateral margin with finely beaded rim; carapace regions not strongly inflated, defined by distinctly wrinkled groove patterns; chelipeds with rows of tiny spines on upper and lower surfaces.

**Discussion.**—Placement of *Pharkidodes* within the Pinnotheridae is clearly indicated by the conformation of the male abdomen, in addition to the general conformation of the carapace. Comparison of the male abdomina of families containing species in which the carapace shape is similar, the Hexapodidae Miers, 1886, and the Chasmocarcinidae Serène, 1964, within the Goneplacoidea MacLeay, 1838, reveals that none, other than the Pinnotheridae, are generally straight-sided, and unfused. Within the Varunidae, *Asthenognathus* Stimpson, 1858, has fused abdominal somites 4–6 (Schweitzer and Feldmann 2001). It is fortunate that a single specimen of *Pharkidodes* exposes a nearly complete abdomen for study. Without it, the placement would be equivocal.

Pinnotherids are generally characterized by an overall absence of regional development, although some genera

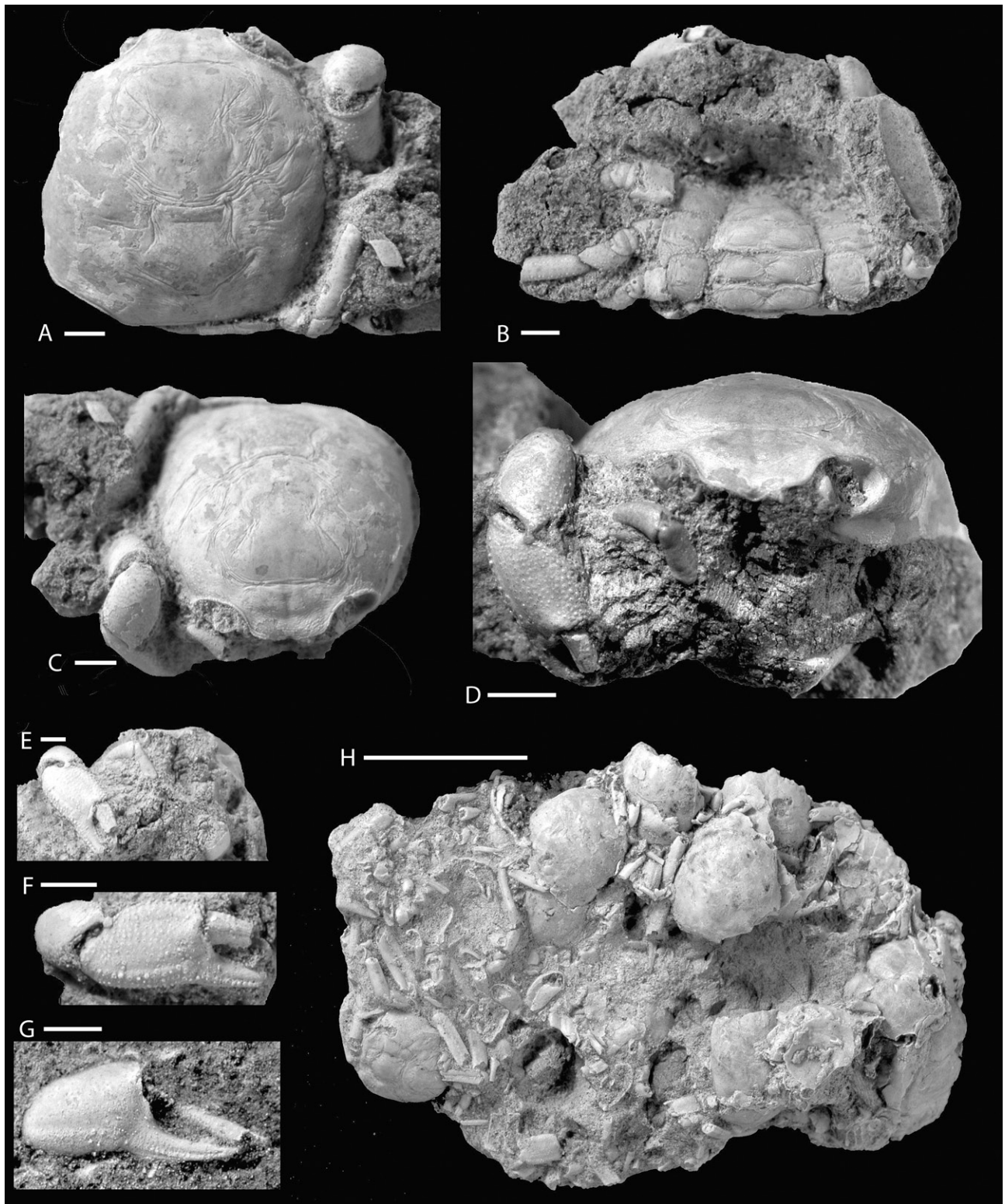


Fig. 12.—*Pharkidodes agele*, new genus and species. A–F, Holotype CADIC PI 148, dorsal carapace showing diagnostic wrinkles (A), sternum and abdomen (B), oblique frontal view (C), anterior view (D), and oblique anterior view (E) and outer surface of cheliped (F); G, inner surface of chela, CADIC PI 149; H, mass of imbricated individuals, CADIC PI 150. Scale bar = 1 mm.



are exceptional in this regard. They all are tiny, have thin carapaces, narrow fronts, and many have uniquely shaped chelipeds. The majority of species are adapted to a commensal lifestyle within a host of organisms, including mollusks, echinoderms, polychaete worms, ascidians (Davie 2002), and brachiopods (Sakai 1976; Feldmann et al. 1996). In many species the females live nearly all their life within the host, whereas the males may be free living (Davie 2002).

*Pharkidodes* conforms to the diagnosis of the family, but it cannot be placed within any of the previously-named genera. The conformation of the front; ratios of fronto-orbital width to width and posterior width to width; the beaded, angular anterolateral margin; and the wrinkled aspect of the carapace and the groove pattern are all features of the carapace that are not shared with other genera. In addition, the chelipeds differ in that they bear distinctive rows of tiny, distally-directed spines, whereas other pinnotherid taxa either have aberrant claws modified for commensal life or have smooth chelipeds. Thus, creation of a new genus is necessary.

***Pharkidodes agele*, new species**  
(Figs. 12A–H)

**Diagnosis.**—As for genus

**Description.**—Carapace small, quadrate, maximum width ca. 89% maximum length, weakly vaulted longitudinally, weakly vaulted transversely on dorsal surface with steeply inclined flanks. Surface very finely granular laterally. Regions not strongly inflated, smooth, defined by narrow bands exhibiting wrinkled surfaces.

Front weakly convex, about 27% maximum width measured at posterolateral corner, prominent axial reentrant on downturned anterior margin of front. Lateral margin of front curves posterolaterally into inner orbital margin then curves laterally into straight element terminating at anterolateral corner; lower orbital margin smooth, sharply defined. Upper orbital rim narrow, elevated, with beaded edge, lacking fissures. Ocular peduncle short, arises adjacent to rostrum, diameter about one half length of orbit. Fronto-orbital width about 64% maximum width. Anterolateral margins weakly curved, diverging posteriorly, defined by well-defined beaded rim. Anterolateral flanks nearly vertical. Posterolateral margin not defined by rim, dorsal surface curves smoothly onto posterolateral flank. Posterior end of flank defines widest point on carapace. Posterolateral corner narrowly rimmed, curves axially defining 35° angle with posterior border. Posterior border narrow, 47% maximum width, narrowly rimmed, straight.

Frontal region with weakly transversely swollen, granular elevations separated by shallow axial depression. Epigastric regions smooth, weakly swollen transversely. Mesogastric region broadens uniformly posteriorly to mid-length terminating posteriorly as nearly circular field bearing one tiny axial node at level of broadening of region

and faint, relatively large gastric muscle scars. Metagastric and urogastric regions not differentiated, rectangular, 26% maximum width, about four times as wide as long, separated from cardiac region by single, narrow groove. Cardiac region pentagonal, about 32% maximum width, with two tiny nodes placed transversely at point of maximum width. Intestinal region indistinct.

Cervical groove extends as hemispherical arc of three narrowly spaced wrinkles around mesogastric region to point of maximum width of that region where it curves anterolaterally to terminate at the ovoid, finely granular hepatic region.

Protogastric region bilobed; axial part separated from lateral part by groove forming obovate outline around lateral part. Epibranchial region nearly circular, smooth, surrounded by wrinkled zone. Mesobranchial region an indistinct swelling at level of metagastric-urogastric region. Metabranchial region with undulose surface, transversely striated posteriorly.

Sternum of male with sternites 5–7 exposed, straight sided, broadening to sternite 6, narrowing slightly to sternite 7. Visible sternites rectilinear with smooth, weakly elevated surfaces; sternites and episternal projections with fine, beaded rim. Sternites 5 and 6 parallel to carapace surface; sternite 7 steeply inclined upward. Maximum sternal width 82% maximum carapace width.

Abdominal somites tapering uniformly anteriorly, straight sided. Somite 1 very short, poorly exposed, somites 2–6 each with lateral transverse swellings surrounded by wrinkled edge; somites 4 and 5 may be fused. Telson not exposed.

Manus of first pereiopod stout, broadening distally, height 64% length, elongate oval in outline with upper and lower carpus/propodus points of articulation forming about 55° angle with long axis of propodus; outer surface sparsely granular; upper and lower surfaces with rows of coarser, distally directed, small spines. One or more rows on lower surface extend onto lower margin of distally tapering fixed finger. Single row of punctae separate spine rows on finger from smooth outer surface; similar pattern exhibited on dactylus. Occlusal surfaces finely and uniformly dentate. Carpus longer than high, widening distally; upper and lower surfaces finely spinose, outer surface smooth. Merus with thick distal rim; exposed surface granular. First pereiopod carried vertically relative to carapace surface, with tips of fingers directed downward. Other pereiopods granular, circular in cross-section. Fifth pereiopod about one half diameter of fourth pereiopod, carried dorsally.

**Etymology.**—The trivial name is taken from the Greek *agele* = herd, in reference to the large number of specimens collected together. This suggests a gregarious habit.

**Types.**—The holotype is CADIC PI 148, and the paratypes are CADIC PI 149 and 150. Topotypes are CM 56128–56132.

**Occurrence.**—The types were collected in March 2008, from the San Julio section.

**Discussion.**—*Pharkidodes agele* was collected from a conglomeratic sequence with interbedded reddish brown medium sandstone. The conglomerates contain numerous dense grey concretions from which the specimens were taken. Although the species was collected in association with other decapods, no others occurred in such great numbers. At least 76 specimens of *P. agele* were collected. The specimens were often associated with large masses of disarticulated segments of pereopods and were so tightly packed that carapaces were often arrayed in imbricated fashion (Fig. 12H). Specimens were disarticulated, with the sole exception of the holotype, CADIC PI 148, which was nearly complete, and although the pereopods were displaced, they were preserved in close proximity to the carapace (Fig. 12E). The accumulations certainly suggest that the organisms associated in swarms and that, upon death, the fragile skeletons disarticulated readily but were not displaced any significant distance. The accumulation also strongly indicates that the animals were free living rather than being occupants of a host organism. As discussed above, within the Pinnotheridae it is common that the males do not regularly occupy the host animal, whereas the females spend most of their lives within the host. The sole nearly complete specimen, the holotype, was that of a male (Figs. 12A–F). Comparison of the carapace of that specimen with the dissociated specimens indicated that they were all morphologically very similar. Thus, it is likely that all of the specimens were males, which is consistent with the observation that only the males are free living.

The presence of a pinnotherid in Miocene rocks of Tierra del Fuego represents only the second occurrence of the family in the fossil record of southern South America. *Pinnixa navidadensis* Feldmann et al., 2005, is known from the Miocene Navidad Formation in central Chile. No pinnotherid fossils have been collected along the Atlantic coast in Patagonia, although in modern oceans pinnotherids are found all around the South American continent (Boschi 2000).

Superfamily Grapsoidea MacLeay, 1838  
Family Varunidae H. Milne-Edwards, 1853  
Subfamily Asthenognathinae Stimpson, 1858

**Discussion.**—The Asthenognathinae was originally placed within the Pinnotheridae de Haan, 1833, albeit with the caveat that they were free-living members of the family. Števcíć (2005) and Cuesta et al. (2005) originally suggested that the Asthenognathinae might be best associated with the Grapsoidea, and Ng et al. (2008) and Palacias-Theil et al. (2009) provided a lengthy discussion and justification for placing the subfamily within the Varunidae. We follow that placement here.

*Asthenognathus* Stimpson, 1858

**Type Species.**—*Asthenognathus inaequipes* Stimpson, 1858, by monotypy.

**Other Species.**—*Asthenognathus atlanticus* Monod, 1933 (extant); *A. australensis* new species; *A. cornishorum* Schweitzer and Feldmann, 1999 (Oligocene–Miocene); *A. globosum* (Karasawa, 1990) (Miocene); *A. hexagonum* Rathbun, 1909 (extant); *A. microspinus* Casadío et al., 2004 (Oligocene); *A. urretae* Schweitzer and Feldmann, 2001 (Oligocene–Miocene).

**Diagnosis.**—Carapace trapezoidal to hexagonal, wider than long, length to width ranging from 0.60–0.90; front downturned, bilobed or straight, about 20% maximum carapace width; orbits rimmed, directed forward, fronto-orbital width 0.45–0.70 maximum carapace width, occupying almost entire anterior margin of carapace but short straight segments to either side of it; often a granular ridge along lateral margins; posterolateral reentrant well-defined, with granular rim; dorsal carapace often with oblique, weak ridge extending in approximately the epibranchial area; mesobranchial and cardiac regions moderately defined, remainder of carapace regions poorly defined; all male abdominal somites free, first and second somite short, telson much smaller than somite 6; first gonopod long, very weakly curved along entire length; male abdomen extending well beyond sternite 4.

**Discussion.**—The genus as currently construed is rather variable in terms of dorsal carapace morphology, the part that is most often preserved in fossils. A compounding factor in assigning fossils to the genus is that there are several brachyuran families and genera with rectangular to trapezoidal, rather unornamented, dorsal carapaces (see Schweitzer and Feldmann 2001, for example). This makes dealing with such fossils difficult in the absence of sterna and abdomina. Fortunately, most of the fossil species of *Asthenognathus* retain elements of the sternum and abdomen, making placement within the genus more definite.

Casadío et al. (2004: table 4) discussed the variability in some of the features of the dorsal carapace of the genus. One of the features they noted was the presence of a bilobed front in the extant species and a straight front in the fossil species. In the recently described male *A. hexagonum*, the front was described as straight with a slightly concave center (Yang and Tang 2008:596); thus, the front can be straight in extant species as well as fossil species. Casadío et al. (2004) discussed the variability of the oblique ridge seen on the dorsal carapace of some extant and fossil members of the genus; it is not present on all species, either recent or fossil. *Asthenognathus hexagonum* apparently lacks such as ridge, as does the new fossil species.

In light of this apparent variability, we reexamined specimens of both *A. microspinus* and *A. urretae* housed at Kent State University to confirm their placement in



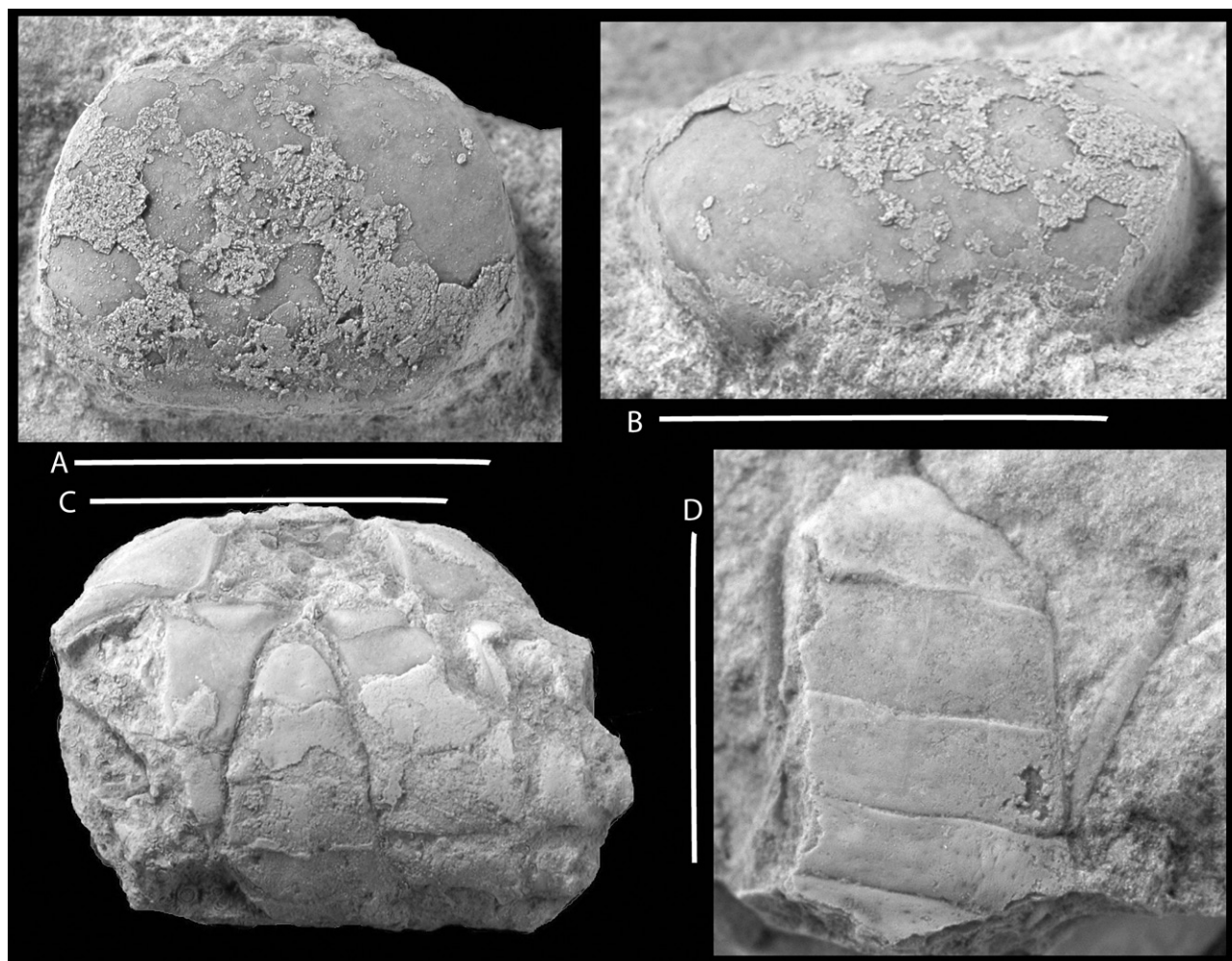


Fig. 13.—*Asthenognathus* spp. **A–B**, *Asthenognathus australensis*, new species, Holotype CADIC PI 151, dorsal (**A**) and anterior (**B**) view; **C**, *Asthenognathus urretae* Schweitzer and Feldmann, 2001, KSU D249a, showing male abdomen and sternum; **D**, *Asthenognathus urretae* Schweitzer and Feldmann, 2001, KSU D249b, showing male abdomen and gonopod 1 extending obliquely to the right of abdomen. Scale bars = 1 cm.

*Asthenognathus*. Examination of these specimens demonstrates that they are not members of the Rhizopinae of the Pilumnidae, which may have rectangular or trapezoidal carapaces. The abdomen of both males and females of *A. urretae* extends well beyond the 4<sup>th</sup> sternite (Fig. 13C), which is typically seen in thoracotremes and not in pilumnids. The dorsal carapace of *A. urretae* and *A. microspinus* lacks any sort of anterolateral spines or lobes, which typify members of the Rhizopinae, and each possess the oblique dorsal carapace ridge seen on some species of *Asthenognathus*. Members of the Pilumnidae, which includes the Rhizopinae, have sinuous first male gonopods which are often markedly recurved at their tips (Davie 2002; Poore 2004); that of *A. urretae* is gently curved along its entire length and is not sinuous (Fig. 13D). The two species are clearly not members of the Chasmocarcinidae, because they lack the accessory plate on the male sternum between sternites seven and eight. Hexapodidae Miers, 1886, cannot

embrace the specimens because they clearly possess eight sternites and five pereopods.

Unfortunately, until recently, there have been few illustrations and descriptions of male members of *Asthenognathus* (Yang and Tang 2008: figs. 1–2). When compared to the male specimen of *A. hexagonum*, male specimens of *A. urretae* are remarkably similar. The male abdomen is nearly the same shape in terms of the somites and telson. All of the male somites are free, as in *A. hexagonum*. In *A. hexagonum*, somites 1 and especially 2 are very short, and in *A. urretae*, these somites are not preserved, which might be expected for such small somites. In one specimen of *A. urretae*, male gonopods 1 are preserved. They are long, slender, and appear to have a blunt, simple termination (Fig. 13D). This is the same configuration as seen in *A. hexagonum* (Yang and Tang 2008: fig. 2E). Both *A. microspinus* and *A. urretae* are typified by the granular ornamentation and marked posterolateral flange and reentrant seen

on *A. hexagonum*. Thus, we are confident in the referral of both of these species to *Asthenognathus*.

The new species described below is represented by only one specimen, lacking any elements of the sternum or abdomen. However, its dorsal carapace possesses granular ornamentation on the orbits and posterolateral flange, an overall carapace shape, and carapace size ratios that are quite similar to those of *A. microspinus* and *A. urretae*. Thus, we place the species into *Asthenognathus*.

*Asthenognathus australensis*, new species

(Figs. 13A–B)

**Diagnosis.**—Carapace trapezoidal, with weak granular rims on lateral margins; granular ornamentation on anterior regions of carapace and lateral portions of posterior regions of carapace; oblique epibranchial ridge absent.

**Description.**—Carapace wider than long, length about 75% maximum carapace width measured just anterior to posterolateral reentrant, about 75% the distance posteriorly on carapace; carapace moderately vaulted longitudinally and weakly vaulted transversely; lateral flanks steep, perpendicular to dorsal carapace.

Front barely projecting beyond orbits, very weakly convex, rimmed, merging smoothly into orbits; frontal width about 17% maximum carapace width and about 40% fronto-orbital width. Orbits shallow, directed forward, with beaded rim, merging smoothly into remainder of anterior margin which is a short, convex segment; fronto-orbital width about 43% maximum carapace width. Lateral margins moderately convex, diverging posteriorly, appearing to have had a weak rim anteriorly. Flanks steep, lateral margin of flank beaded. Posterolateral reentrant large, rim beaded; with blunt, broad projection at mid-width. Posterior margin beaded, nearly straight, about 56% maximum carapace width.

Epigastric regions square, weakly inflated. Mesogastric region elongate triangular, widest posteriorly, grooves bounding posterior margin particularly deep. Protogastric and hepatic regions confluent, not well differentiated, ornamented with small granules anteriorly. Cardiac region a broad, circular swelling. Branchial regions not differentiated, ornamented with granules laterally, with wrinkles axially.

**Measurements.**—Measurements (in mm) taken on the dorsal carapace of *A. australensis*: maximum carapace length, 9.3; maximum carapace width, 12.6; fronto-orbital width, 5.4; frontal width, 2.1; posterior width, 7.0; length to position of maximum width, 6.9.

**Type.**—The holotype and sole specimen is CADIC PI 151. A cast of the holotype, CM 56118, is deposited in the Carnegie Museum of Natural History.

**Occurrence.**—The holotype was collected from the Cerro Águila section.

**Discussion.**—Some details of the dorsal carapace are better seen on the mold of the interior, including the granular ornamentation.

BIOGEOGRAPHY

**Decapod Biogeography.**—Boschi (2000) defined 16 zoogeographic provinces on the continental shelf areas of the Americas based upon distribution of 2472 extant decapod species. In southern South America, he recognized a warm temperate Argentinian Province that extended from about 44°S, just south of Trelew, Argentina, to Cabo Frio, Brazil, approximately on the Tropic of Capricorn; and a cold, subantarctic Magellanic Province, extending from north of Chiloe Island, Chile, at about 41°S, around Cape Horn to about 35°S in the South Atlantic. From 44°S to 35°S, the Magellanic Province lies on the outer continental shelf whereas the Argentinian Province occupies the inner continental shelf. The third province in the region, the cool to warm temperate Perú-Chilean Province, extends from north of Chiloe Island north to Bahía Sechura, Peru, at about 6°S. Diversity varies considerably between these provinces, with 330 species recorded from the Argentinian Province, of which 42 are endemic; 79 species from the Magellanic Province, of which 19 are endemic; and 212 species from the Perú-Chilean Province, with 77 endemic species.

Examination of the paleobiogeographic distributions of late Oligocene and Miocene decapod crustaceans suggests that the provinces defined by Boschi (2000) cannot be strictly applied to the ancient occurrences. When the Oligocene and Miocene taxa in southern South America are arrayed according to the modern provincial regions, there is virtually no difference between the decapod faunas in the Pacific part of the Magellanic Province and those in the Perú-Chilean Province (Feldmann et al. 2010). Note, however, that there are no known Oligocene or Miocene rocks that have yielded decapods on the Pacific coast south of Isla Guafo at about 43°30'S. Similarly, there are few differences between the fossil taxa in the Argentinian Province of Boschi (2000) and those in the Atlantic part of the Magellanic Province of Boschi (2000) to a latitude of 50°S. The only region that contains a distinctly different fauna in the high southern latitudes is that of Tierra del Fuego, the subject of this study. Thus, it appears that a more realistic provincial arrangement during the late Oligocene and Miocene is to recognize just two major provinces, the Argentinian Paleobiogeographic Province and the Chilean Paleobiogeographic Province, separated from one another by what may be a narrow ecotone (Table 3). Five genera, *Austromunida*, *Archaeogeryon*, *Chaceon*, *Hepatus*, and *Asthenognathus*, are found in both the Argentinian and Chilean paleobiogeographic provinces; however, of the eleven species within those genera, only one, *Austromunida casadioi*, is found in both oceanic masses. The Argentinian Paleobiogeographic Province has 12 species unique to it, and the Chilean Paleobiogeographic Province has 22



**TABLE 3.** Paleobiogeographic distribution of late Oligocene and Miocene decapods from Argentina and Chile  
(continued on next page).

The Argentinian Paleobiogeographic Province (A) extends along the Atlantic coast to Río Grande, Tierra del Fuego, and the Chilean Paleobiogeographic Province (C) extends as far northward on the Pacific coast to the latitude of Santiago, Chile. Genera known only from the Tierra del Fuego localities are denoted (F). Occurrences of the genera outside the study area and during the late Oligocene – Miocene are denoted by AN (Antarctica), NA (North Atlantic), NP (North Pacific), NZ (New Zealand), and TE (Tethyan). Asterisk (\*) denotes taxa that have been tentatively identified but that have not been verified.

#### ARGENTINIAN PALEOBIOGEOGRAPHIC PROVINCE

##### 1. Puerto Madryn Formation (late Miocene)

Puerto Pirámide, Argentina (Casadío et al. 2005), S 42°34' 45'', W 64° 16' 16''

<i>Osachila valdesensis</i> Casadío et al., 2005	A
<i>Rochinia boschii</i> Casadío et al., 2005	A
<i>Romaleon parspinosus</i> Casadío et al., 2005	A
<i>Archaeogeryon latus</i> Glaessner, 1933	AC
<i>Chaceon peruvianus</i> (d'Orbigny, 1842)	AC
<i>Panopeus piramidensis</i> Casadío et al., 2005	A
Xanthoidea sp. indeterminate	
<i>Ocypode vericoncava</i> Casadío et al., 2005	A

##### 2. Gaiman Formation (early Miocene)

Bajo del Gualicho, Argentina S 40° 20' 44'', W 65° 39' 52.7''

Callianassids*	
<i>Chaceon</i> sp.*	AC
Carpiliid?	

##### 3. Gaiman Formation (early Miocene)

Bryn Gwyn, Argentina, S 43° 21' 22'', W 65° 27' 49''

<i>Chaceon</i> sp.*	AC
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##### 4. Chenque Formation (early Miocene)

Comodoro Rivadavia, Argentina, S45° 57' 10'', W 67° 33' 4''

<i>Archaeogeryon latus</i> *	AC
<i>Archaeogeryon fuegianus</i> ?	AC

##### 5. San Julián Formation (late Oligocene–early Miocene)

San Julián, Argentina, S 49° 30' 57'', W 68° 14' 43''

<i>Notomithrax</i> sp.*	A
<i>Archaeogeryon latus</i> ?	AC

Cabo Curioso, S 49° 12' 4'', W 67° 39' 30''

Paguroidea*	
<i>Chaceon</i> sp.*	AC
Cancridae indet.*	

##### 6. Monte León Formation (early Miocene)

Monte León, Argentina (Crawford et al. 2008), S 50° 19' 21'', W 68° 51' 27''

<i>Archaeogeryon latus</i> Glaessner, 1933	AC
<i>Chaceon peruvianus</i> (d'Orbigny, 1842)	AC

##### 7. Centinela Formation (late Oligocene–early Miocene)

Veranada de Cárcamo, Argentina, S 47° 35' 76'', W 71° 56' 47''

<i>Chaceon</i> sp.	AC
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##### 8. Guadal Formation (late Oligocene–early Miocene)

Pampa Castillo, Chile (Frassinetti and Covacevich 1999), S 47°, W 72° 25'

<i>Archaeogeryon</i> sp.	AC
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**TABLE 3** (continued). Paleobiogeographic distribution of late Oligocene and Miocene decapods from Argentina and Chile, (continued on next page).

9. Centinela Formation (late Oligocene–early Miocene)		
Calafate, Argentina (Schweitzer and Feldmann 2000a, 2000b, 2001), S 50° 30.716', W 72° 15.303'		
<i>Austromunida casadioi</i> (Schweitzer and Feldmann 2000c)	AC	
<i>Raninoides</i> sp.*	A	NA, NP
<i>Archaeogeryon latus</i> (Glaessner, 1933)*	AC	
<i>Chaceon peruvianus</i> (d'Orbigny, 1842)	AC	
<i>Notocarcinus sulcatus</i> Schweitzer and Feldmann, 2000d	A	
<i>Rochinia</i> cf. <i>R. hystrix</i> (Stimpson, 1871a)*	A	
<i>Notomithrax</i> sp.*	A	NZ
<i>Hepatus</i> sp.*	AC	TE
<i>Asthenognathus urretae</i> Schweitzer and Feldmann, 2001	AC	NP
9a. Santa Cruz Formation (Miocene)		
Calafate, Argentina, S 50° 30' 3". W 72° 12' 23"		
Geryonidae, not <i>Chaceon</i> *		
<i>Asthenognathus</i> sp.*	AC	NP
10. Carmen Silva Formation (middle Miocene)		
Estancia San Julio, Tierra del Fuego, Argentina (Herein), 53° 39' 47.7"S, 68° 26' 49.3"W		
<i>Archaeogeryon fuegianus</i> Colosi, 1924	AC	
<i>Tierrapilumnus edseli</i> n. sp.	F	
<i>Pharkidodes agele</i> n. sp.	F	
<i>Asthenognathus australensis</i> n. sp.	AC	NP
11. Carmen Silva Formation (middle Miocene)		
El Cachimbo, Tierra del Fuego, Argentina (Herein), 53° 29' 41.9S"; 68° 31' 45.6"W		
<i>Archaeogeryon fuegianus</i> Colosi, 1924	AC	
<i>Tierrapilumnus edseli</i> n. sp.	F	
12. Cerro Águila Conglomerate, Cabo Domingo Group (early? Miocene)		
Tierra del Fuego, Argentina (Herein), 53° 50' 14.3"S, 67° 47' 35.4"W		
Callianassoidea, genus and species indet.		
Lithodidae, genus and species indet.		
<i>Miotymolus quadratus</i> n. sp.	F	
<i>Mursia fuegiana</i> n. sp.	F	
<i>Archaeogeryon fuegianus</i> Colosi, 1924	AC	
<i>Chaceon peruvianus</i> (d'Orbigny, 1842)	AC	
<i>Tierrapilumnus edseli</i> n. sp.	F	
CHILEAN PALEOBIOGEOGRAPHIC PROVINCE		
13. Sandstone and siltstone (late Pliocene)		
Guafo Island, Chile (Feldmann et al. 2010), S43° 37', W 74° 36'		
<i>Trichopeltarion frassinetti</i> Feldmann et al. 2010	C	NP, NZ
14. Miocene – early Pliocene siltstone		
Ancud, Chiloé Island, Chile (Feldmann et al. 2010), S 43° 41' 08", W 74° 06' 16"		
<i>Ctenocheles notialis</i> Feldmann et al., 2010	C	NP, TE
<i>Axianassa? chilensis</i> Feldmann et al., 2010	C	
<i>Pirulella antipodea</i> Feldmann et al., 2010	C	
<i>Geryon manningi</i> Feldmann et al., 2010	C	
<i>Archaeogeryon navidad</i> Feldmann et al., 2005	AC	
<i>Pilumnus cucaoensis</i> Feldmann et al. 2005	C	TE
<i>Chasmocarcinus chiloensis</i> Feldmann et al., 2010	C	AN
<i>Pinnixa navidadensis</i> Feldmann et al., 2005	C	NP, TE



**TABLE 3** (continued). Paleobiogeographic distribution of late Oligocene and Miocene decapods from Argentina and Chile.

15. Río Foyel Formation (middle Oligocene)		
Bariloche, Argentina (Casadio et al. 2005; Crawford 2008), S 41° 42' 02", W. 71° 26' 06"		
<i>Austromunida casadioi</i> (Schweitzer and Feldmann, 2000c)	AC	
<i>Callianopsis australis</i> Casadio et al., 2004	C	NP
<i>Paromola vetula</i> Crawford, 2008	A	
<i>Archaeogeryon corsolini</i> (Casadio et al., 2004)	AC	
<i>Trichopeltarion levis</i> Casadio et al., 2004	C	NP, NZ
<i>Baricarcinus mariae</i> Casadio et al., 2004	C	
<i>Asthenognathus microspinus</i> Casadio et al., 2004	AC	NP
16. Santo Domingo Formation (early–middle Miocene)		
Valdivia, Chile (Feldmann et al. 2010), S 39° 23' 33", W 73° 12' 43"		
<i>Trichopeltarion levis</i> Casadio et al., 2004	C	NP, NZ
<i>Trichopeltarion frassinetti</i> Feldmann et al., 2010	C	NP, NZ
<i>Chaceon quadrata</i> Feldmann et al., 2010	AC	
<i>Archaeogeryon navidad</i> Feldmann et al., 2005	AC	
<i>Pilumnus cucaoensis</i> Feldmann et al., 2005	C	TE
<i>Chasmocarcinus chiloensis</i> Feldmann et al., 2010	C	AN
17. Ranquil Formation (Miocene)		
Lebu, Chile (Feldmann et al. 2010), S 37° 33' 17", W 73° 36' 15"		
and		
Isla Mocha (Feldmann et al. 2010), S 38° 20', W 73° 55'		
<i>Phenopthalmus mochaensis</i> Feldmann et al., 2010	C	
<i>Minohellenus araucana</i> (Philippi, 1887)	C	NP
18. Navidad Formation (Miocene)		
Navidad, Chile (Feldmann et al. 2005), S 33° 58' 28", W 71° 50' 56"		
<i>Callichirus?</i> sp.	C	
<i>Ctenocheles</i> sp.	C	NP, TE
Callianassoidea – 3 species		
<i>Calappilia? chilensis</i> Feldmann et al., 2005	C	TE
<i>Hepatus spinimarginatus</i> Feldmann et al., 2005	AC	TE
<i>Archaeogeryon navidad</i> (Feldmann et al., 2005)	AC	
<i>Trichopeltarion levis</i> Casadio et al., 2004	C	NP, NZ
<i>Pilumnus cucaoensis</i> Feldmann et al., 2005	C	TE
Rhizopinae sp.		
<i>Pinnixa navidadensis</i> Feldmann et al., 2005	C	NP, TE

species not known from the Atlantic region. The separation of the Argentinian and Chilean paleobiogeographic provinces, based upon the distribution of the fossil decapods, seems clear. The Tierra del Fuego region has seven endemic species.

It is clear that the decapod fauna of the Tierra del Fuego region differs markedly from both the Argentinian and Chilean provinces; however, the limited areal extent of the Miocene rocks in the area introduces the possibility that it is not a discrete province but that the faunal difference arises as a result of ecologic, rather than biogeographic, factors. The seven taxa unique to the region of Tierra del Fuego may provide some insight into its faunal affinities. *Archaeogeryon fuegianus* and *A. australis* are known only from the region but are congeneric with species

in both the Argentinian and Chilean paleobiogeographic provinces. Thus, they may document some faunal interchange around the southern tip of the continent from the Chilean to the Argentinian Paleobiogeographic Province. *Mursia*, represented in Tierra del Fuego by *M. fuegiana*, is not known from anywhere else in the fossil record of the Southern Hemisphere, but extant representatives are well represented in Panama (Rathbun 1918), the Caribbean (Collins and Donovan 2002, 2004), the circum-North Pacific, and the North Atlantic (Schweitzer and Feldmann 2000a; Schweitzer et al. 2002; Feldmann and Schweitzer 2006, for summaries). The presence of the genus in the high southern latitudes suggests global distribution of the taxon during the late Oligocene and Miocene. The other taxa from Tierra del Fuego, *Tierrapilumnus edseli*,

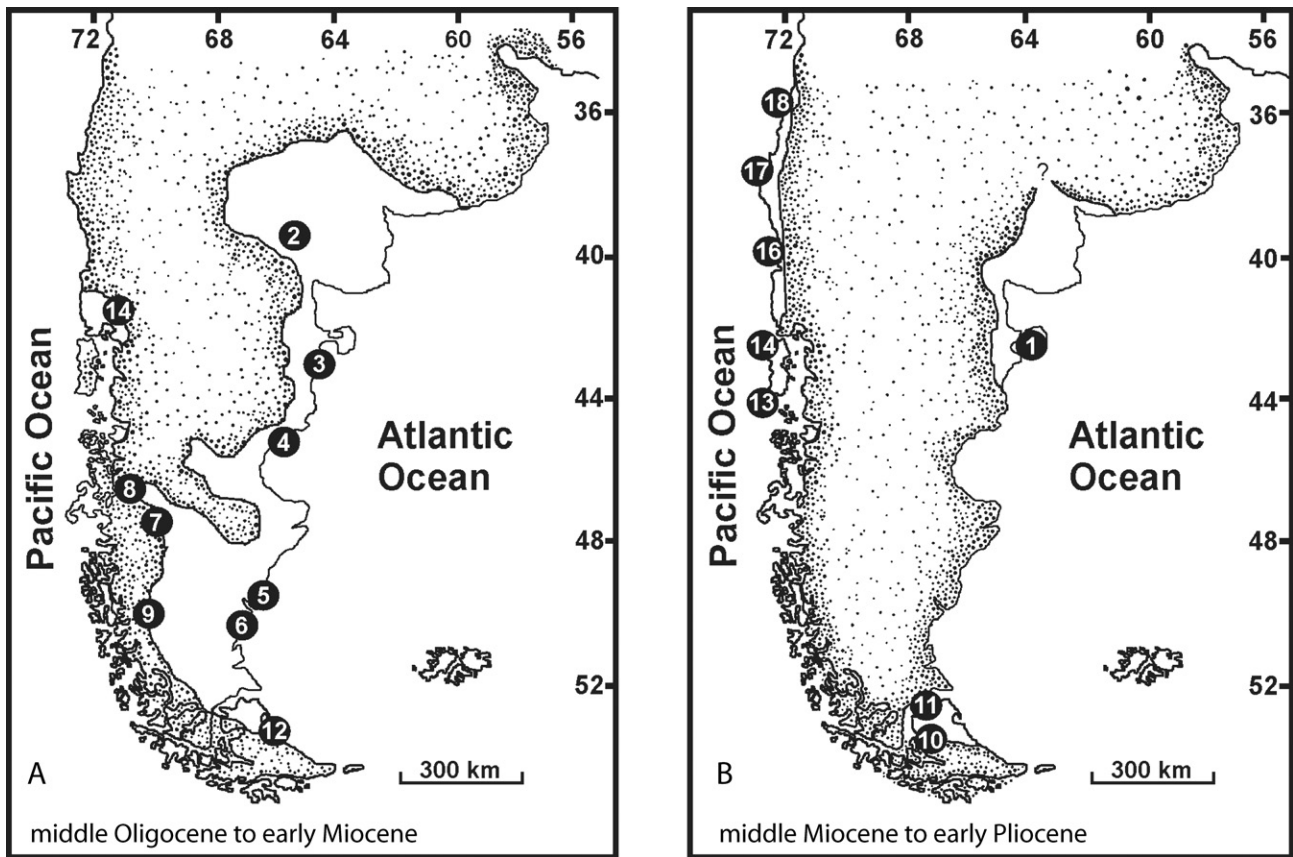


Fig. 14.—Paleogeographic maps of southern South America during **A**, the middle Oligocene–early Miocene, and **B**, the middle Miocene–Pliocene, showing the sites from which decapod collections referred to in the paper have been made. The locality numbers correspond to those in Table 3. Paleogeographic reconstructions after Malumián (1999).

*Pharkidodes agele*, *Miotymolus quadratus*, and the indeterminate lithodid have no generic counterparts in either the Argentinian or Chilean provinces, so that they provide no insight into provincial affinities. As discussed above, the families to which these taxa are assigned have global distributions in modern oceans. Coupled with the observation that the molluscan fauna of Tierra del Fuego, discussed below, favors inclusion of the region in the Argentinian Paleobiogeographic Province, the most prudent interpretation is that the Fuegian fauna is ecologically, rather than geographically, unique. Cyclodorippids and lithodids typically inhabit deep or cold water regions which is consistent with their presence in the Tierra del Fuego assemblage, the southernmost exposures of late Oligocene and Miocene rocks in South America. *Mursia* frequents cool temperate and deep water environments in modern seas. It would seem reasonable to postulate that the rocks in Tierra del Fuego were deposited in cooler and perhaps deeper water than those of the other regions of the Argentinian Paleobiogeographic Province.

The migration in provincial boundaries from the Miocene to the Holocene can probably be attributed to changes in oceanic circulation driven by a change in surface ocean temperature patterns (Kennett 1982). Warmer equatorial

waters in the Miocene and late Oligocene caused by a greater residence time of the water in low latitudes may have resulted in the extension of the South Atlantic Current farther south along the Argentinian coastline than at present. Concomitant with that would have been a reduction of influence of the Circumantarctic Current on the coastline of Tierra del Fuego. This combination of conditions would have resulted in a more pronounced temperature gradient near Cape Horn, effectively forming a thermal barrier between warm South Atlantic and cold South Pacific waters. Although a similar boundary exists today, colder water under the influence of the Circumantarctic Current results in a sort of ecotone in which species from the two water masses can mix with the resultant Magellanic Biogeographic Province.

Although the occurrences of decapod fossils within the Chilean Paleobiogeographic Province are largely confined to sites in Chile, the Río Foyel Formation which is a component of that province crops out in Argentina. That particular occurrence is placed with the Chilean Paleobiogeographic Province because of the close correspondence between the Río Foyel fauna and that of the Navidad Formation in Chile. This similarity with Pacific assemblages is perhaps not remarkable because the locality lies



on the western boundary of Argentina in the Andes Mountains. The occurrence supports at least some connection of the central Andean region of Argentina with the Pacific during the late Oligocene and possibly into the Miocene as suggested previously by Ramos (1982) and Casadío et al. (2004).

Several of the genera known from the high southern latitude paleobiogeographic provinces are also known from occurrences elsewhere in the world during the late Oligocene and Miocene (Table 3). Those genera recorded from the North Pacific or North Atlantic are considered to have amphitropical distributions. The North Pacific occurrences are noteworthy, because the Chilean Paleobiographic Province records substantially more such records (five genera) than does the Argentinian Paleobiographic Province (two genera). One of the Argentinian occurrences, *Asthenognathus*, is known to occur in the Chilean Paleobiographic Province which may have implications for a connection at this time between the eastern and western regions through the Andean Mountain chain.

Some of the genera noted from southern South America are also known to occur in Tethyan regions during the late Oligocene-Miocene. This suggests that species within those genera were eurythermal. Several other genera known from temperate regions in the Oligocene-Miocene have extant descendants in lower latitudes as well.

**Molluscan Biogeography.**—The fauna of invertebrates (other than crabs) contained in the Carmen Silva Formation includes mainly mollusks. These are quite common throughout the unit, although the composition of the faunas varies slightly among localities. The overall composition of the faunas closely resembles those of the Monte León and Centinela formations exposed in southern Santa Cruz Province—the two of them deposited during the same late Oligocene-early Miocene Atlantic transgression. All the genera present in the unit from Tierra del Fuego are also known from Santa Cruz, and in many instances are represented by the same or similar species. Outstanding examples of this are species in the following genera: *Neilo* Adams, 1854; *Cucullaea* Lamarck, 1801; *Glycymeris* Da Costa, 1778; *Zygochlamys* Ihering, 1907; *Swiftopecten*; *Pteromyrtea*, Finlay, 1926; *Fasciculicardia* Maxwell, 1969; *Retrotapes* del Río, 1997; *Dosinia* Scopoli, 1777; *Offadesma* Iredale, 1930; *Valdesia* del Río, 1985; *Turritella* Lamarck, 1799; *Calyptreaea*; *Perissodonta* Marten, 1878; *Polinices*; *Austrocominella* Ihering, 1907; *Ocenebra*? Leach, 1847; and *Adelomelon* Dall, 1906. All of them are represented in the Monte León and Carmen Silva formations either by the same or very closely allied species.

Fossil molluscan faunas along the Pacific coast of Chile show some remarkable differences, as is also shown in the modern faunas, probably reflecting different paleoceanographic conditions. Exposures of Miocene marine rocks in southern Chile are few, except for the isolated outcrops near Punta Arenas and at Cerro Guadal, just south of Lago General Carreras (i.e., Lago Buenos Aires). These faunas

are in need of revision, but the genera contained in the Carmen Silva, Monte León, and Centinela formations in Argentina are mostly present in them too. Mollusks contained in the Guadal Formation were described basically by Ortmann (1902) based on a fauna from the nearby “Patagonian” Formation exposed only a few kilometers across the international border with Argentina (= Centinela Formation = El Chacay Formation of Chiesa and Camacho, 1995). The faunas—whether from the Guadal or the Centinela Formation—are rather poorly preserved, but include mostly species within genera present in the Monte León Formation, as for instance the following: *Zygochlamys*; *Jorgechlamys* del Río, 2004; *Gregariella* Monterosato, 1883; *Lahillia* Cossman, 1899; *Valdesia*; *Perissodonta*; *Ficus* Röding, 1798; and *Sconsia* Gray, 1847. However, some discrepancies are noteworthy. *Neoinoceramus* Ihering, 1902, appears in the Centinela Formation but is absent in the Guadal and the Monte León Formations, as well as in the other Neogene units from Chile. However, this genus also appears in the Chenque Formation exposed along the coast of southern Chubut and northern Santa Cruz.

A large majority of the genera contained in the Miocene Navidad Formation in central Chile are not known from the more southern Chilean units or those exposed along the Atlantic coast of Argentina. Some genera (e.g., *Distorsio* Röding, 1798) appear to suggest slightly warmer conditions in the water.

Among material recovered from drillings in the Santo Domingo Formation near Valdivia (Chile) is *Perissodonta ameghinoi* (Ihering, 1897), a gastropod known from the Monte León and Carmen Silva formations. Although this variable genus is known from many localities of different ages in southern South America, these are all generally referable to different species. The specific identity of the material from the Monte León, Carmen Silva, and Guadal formations suggests some kind of connection between these areas at the time the respective rocks were deposited.

Generally speaking, the mollusk faunas from the Carmen Silva Formation show strongest similarities to the Monte León, Centinela and Guadal formations from further north on the Atlantic coast. Although many of the genera known to occur in it are also extant along the coast of Tierra del Fuego and Patagonia, there are others that are not known to occur in rocks younger than Miocene. Many of these genera appear to share a common southern origin and may well have arrived in southern South America from other continental areas along the Southern Ocean, i.e., New Zealand and Antarctica.

The relatively distinct difference between Atlantic and Pacific molluscan faunas in the Miocene and the absence of a discrete Magellanic Province at that time supports the supposition that there was a marked thermal barrier between the South Atlantic and South Pacific circulation. This provides external evidence that the decapod fauna of Tierra del Fuego is best considered a part of the Argentinian Paleobiogeographic Province.

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