

EOCENE DECAPOD CRUSTACEA (THALASSINIDEA AND BRACHYURA)
FROM PATAGONIA, ARGENTINA

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ABSTRACT

Rocks of the Río Turbio Formation, exposed in southern Patagonia, Argentina, represent one of very few occurrences of Eocene rocks in the region. Decapod crustaceans collected from the unit include one species of thalassinidean mud shrimp; *Turbiocheir minutospinata*, new genus, new species; and three species of brachyurans; *Raninoides rioturbiensis*, new species; *Megokkos patagoniensis*, new species; and *Nitotacarcinus antipodes*, new species. The three brachyuran genera are also known from species in the Northeast Pacific, suggesting an amphitropical distributional pattern.

KEY WORDS: Argentina, Brachyura, Decapoda, Eocene, paleobiogeography, Patagonia, Thalassinidea.

INTRODUCTION

The record of Eocene decapod faunas in the high southern latitudes of South America is sparse despite the presence of a rich and diverse Eocene fauna in the Antarctic Peninsula (e.g., Feldmann and Woodburne 1988). Paleogeographic reconstructions of South America during this time (Scotese 2006) suggest that the extent of marine conditions in the Eocene were limited. Exposures of marine Eocene rocks are known from limited areas in southern Patagonia, and several decapod crustaceans have been collected from them. Thus, it is the purpose of this paper to describe new species of thalassinoid and brachyuran decapods from southern South America and to consider the paleobiogeographic relationships of these organisms to congeneric forms elsewhere in the world.

GEOLOGIC SETTING

Modifications in the oceanic circulation patterns during the Paleogene had long-lasting effects on climate change and the distribution of marine faunas in the Southern Hemisphere. In Patagonia, these effects combined with tectonic and volcanic activity related to subduction along the Pacific margin of South America. At the same time,

relative sea level changes along the Atlantic margin were responsible for major transgressions. One such transgression took place in Patagonia at the end of the Maastrichtian and beginning of the Paleogene and covered more than 500,000 km² of present day emergent land (Malumián and Caramés 1995). It was an important paleogeographic feature that surely played a key role in climatic and evolutionary events at that time in this part of the continent. The onset of carbonate sedimentation in northern Patagonia during the late Maastrichtian–early Danian suggests a temperature increase in the sea water (Casadío et al. 2005; Aguirre-Urreta et al. 2008). These temperature conditions in the Danian extended southward to the southern tip of South America, where it is recorded in rocks included in the Cerro Dorotea Formation (Malumián et al. 1998).

The influence of warm water along the Atlantic seaboard extended southward to at least 45°S, as evidenced by the decapods described from the Salamanca Formation (Feldmann et al. 1997). This is consistent with the paleoenvironmental information provided by foraminifera (Malumián and Caramés 1995), plants (Petriella and Archangelsky 1975), and vertebrates (Volkheimer 1971). Manceñido and Griffin (1988) suggested that the warming influence may have extended even further south to latitudes approaching the Antarctic Peninsula. However, this

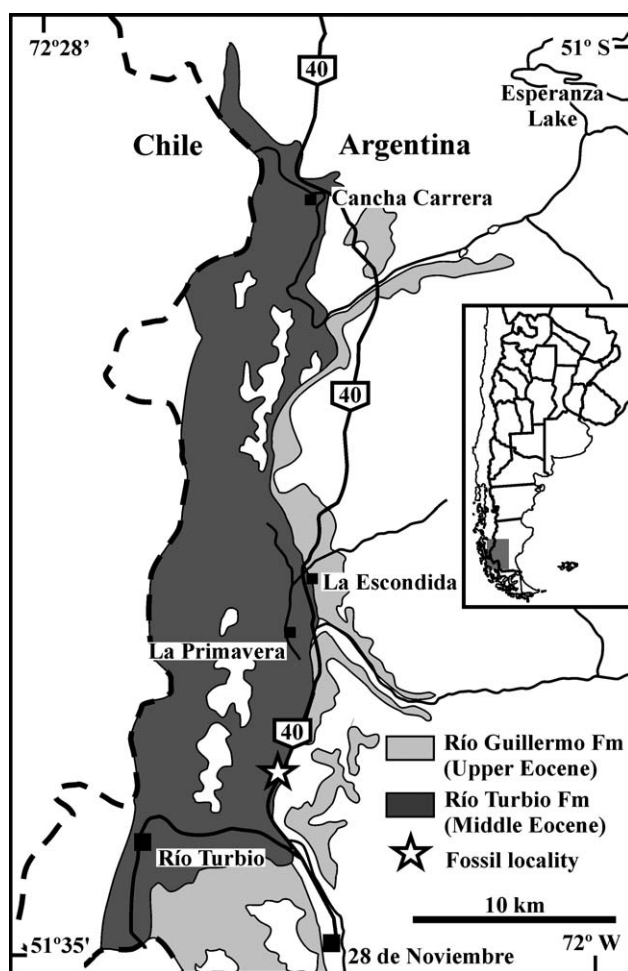


Fig. 1.—Location map showing outcrop area of Río Turbio Formation. Star indicates decapod fossil locality. Inset shows position of outcrop area in southern Argentina.

influence is only fully noticeable south of 50°S during the Eocene (Nocchi et al. 1991).

Panza et al. (1998) suggested paratropical conditions persisted in southern Patagonia up to the middle Eocene. This coincides with information from rocks of that age in other regions of the Southern Hemisphere, including Antarctica (Dutton et al. 2002; Buick and Ivany 2004). In the subantarctic area, paleotemperatures ranging from 10° to 17°C were obtained for samples of middle Eocene planktonic foraminifera (Kennett 1980; Kennett and Barker 1990). Stott et al. (1990) suggested a maximum summer surface-water temperatures of 12–13°C and winter temperatures of 7°–8°C for samples from the same region and age. Similar ranges were indicated for the southern Indian Ocean during the middle Eocene (Barrera and Huber 1991). Variable temperatures in the 12°–20° range for the South Atlantic during that time have been suggested (Hsü and Wright 1985; Oberhänsli and Toumarkine 1985; Zachos et al. 1994).

The existence of a latitudinal zonation accompanying the climate deterioration after the middle Eocene in the Antarctic Peninsula and Patagonia is supported by the flora (Gandolfo et al. 1998), the land mammals from the northern Antarctic Peninsula (Reguero et al. 1998), and also by the late Eocene vertebrates from Patagonia (Heizler et al. 1998). This is coincident with one of the sharpest global cooling events during the Paleogene. This event is currently dated at about 33.5 Ma (Berggren and Prothero 1991). A satisfactory appreciation of the impact that the paleoenvironmental and oceanographic changes had on the marine ecosystems of the southern tip of South America during the Eocene requires improvement of the available stratigraphic and paleontological knowledge on successions of this age in Patagonia.

Within this general framework, the Eocene rocks from Patagonia, both marine and continental, offer an excellent opportunity to understand the relationships between the terrestrial and marine ecosystems on the continent. Marine Eocene rocks and faunas were first recorded in southern Argentina in the early Twentieth Century (Malumián et al. 2000), and interest in their study has been recently renewed (Camacho et al. 2000, 2001; Casadío et al. 2009). These rocks are widely distributed in the Austral or Magallanes Basin (Calegari et al. 1993), and they are exposed along the southwest corner of Santa Cruz Province and along the Atlantic coast of Tierra del Fuego.

Marine Eocene rocks encompass the Man Aike and Río Turbio formations exposed along the western margin of the Austral Basin. In the Lago Argentino area, Santa Cruz Province, the Man Aike Formation unconformably overlies the Upper Cretaceous rocks of the Calafate Formation (Casadío et al. 2009). According to Casadío et al. (2009), south of the town of El Calafate the Man Aike Formation represents the infilling of an incised valley excavated during the middle Eocene phase of the Patagonian Cordillera uplift, while sedimentation in subtidal environments began during a transgressive period during the late middle Eocene (Malumián 2002). A glauconitic bed representing this transgressive event is widely distributed within the Austral Basin (Calegari and Baldi 1993) and is found in the Río Turbio, Man Aike, “Glauconítico B,” and Leticia formations.

In the southwestern corner of Santa Cruz Province, the Río Turbio Formation unconformably overlies the Paleocene rocks of the Cerro Dorotea Formation. Deposits of the Río Turbio Formation were interpreted as forming in an estuary subjected to the action of both tidal and wave processes (Azcuy and Amigo 1991) or in a shallow marine environment with periodical hyperpycnal discharges (Rodríguez Raising 2010). The fossils studied herein were collected from the Upper Member (late middle Eocene–early late Eocene) of the Río Turbio Formation (Sequence VI of Rodríguez Raising 2010).

The section that contains the rocks bearing the decapods is located along National Highway 40 about 15 km north of the town of Río Turbio (lat. 51°30′35.2″S, long.

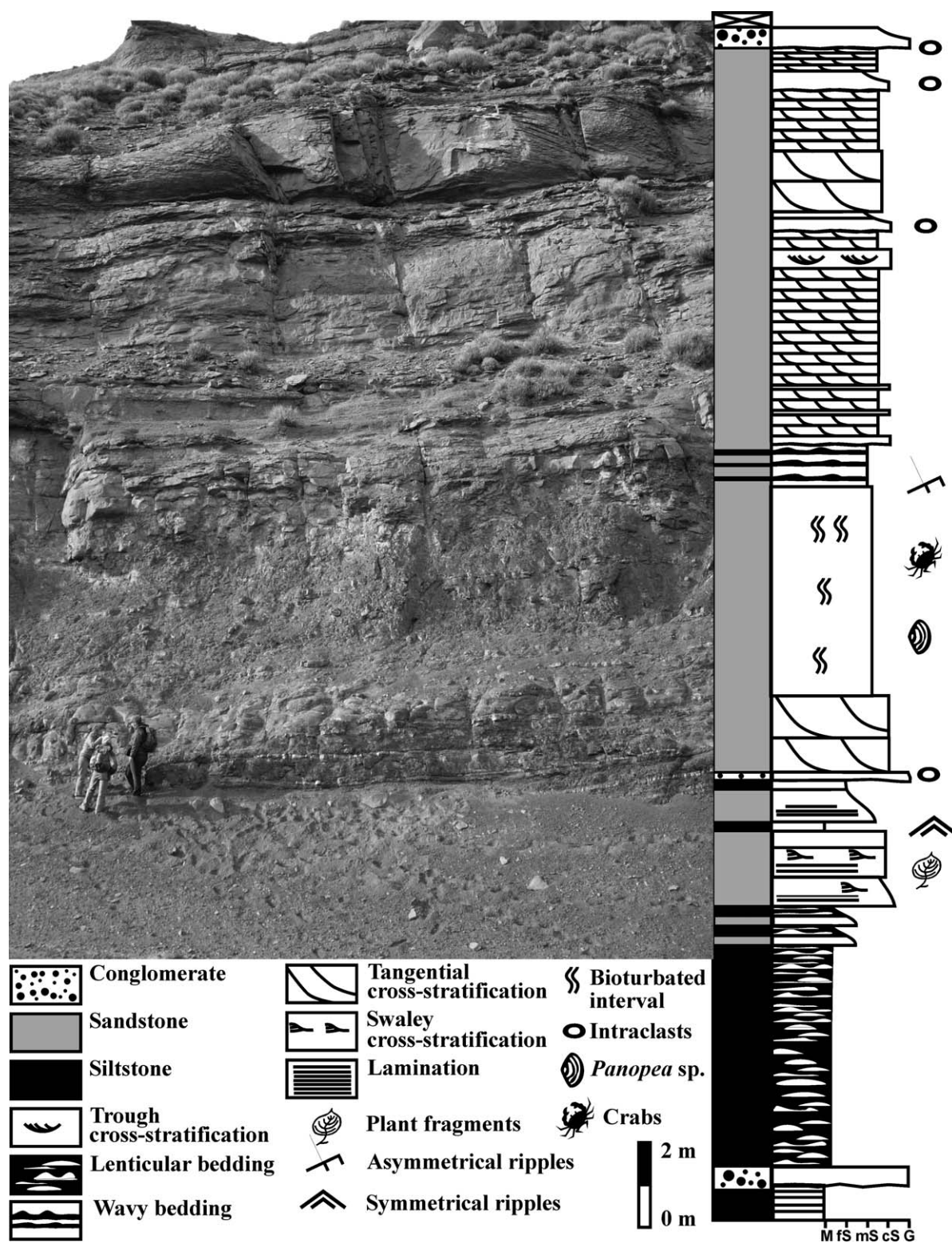


Fig. 2.—Stratigraphic section measured at decapod collecting locality, lat. 51°30'35.2"S, long. 72°15'31.1"W, our Waypoint 20. M, mudstone; fs, fine sandstone; mS, medium sandstone; cS, coarse sandstone; G, gravel.

72°15'31.1"W, our Waypoint 20) (Fig. 1). The exposed section is 30 m thick (Fig. 2), the lower part consisting of alternating medium-grained sandstone and siltstone with lenticular bedding. Sandstones have climbing ripple laminations. These beds are followed by sandstones, minor clasts, and matrix-supported conglomerate lenses containing fragments of mollusk shells. Heterolithic beds were interpreted as the deposits generated by dilution of non-cohesive sediment-gravity flow after deposition of the coarser fraction. The conglomerate lenses record major flow events that probably originated during exceptional fluvial discharges (Rodríguez Raising 2010). Deposits forming the upper part of the section consist mainly of sandstones showing tangential cross-stratification, trough cross-stratified sandstone, and subordinated conglomerates with intraclasts. They were interpreted as tidal sandbars, dune topsets, and foresets originating as a migration of subaqueous dunes with lateral accretion (Rodríguez Raising 2010). The bed with decapods is a massive bioturbated sandstone that is interpreted as a relatively condensed interval generated during a period of stability.

Depository.—The specimens in this study are deposited in the Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina (MPEF-PI). Casts of the specimens are deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA (CM).

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802

Infraorder Thalassinidea Latreille, 1831

Superfamily Callianassoidea Dana, 1852

Family Callianassidae Dana, 1852

Turbiocheir, new genus

Type species.—*Turbiocheir minutospinata*, new species, by monotypy and original designation.

Diagnosis.—Weakly heterochelous, merus, carpus, and propodus with very finely serrated lower surfaces; merus of left cheliped short, equidimensional, with keel on outer surface; carpus 1.5 times as high as long; hand higher than long, quadrate; fingers long for callianassids, apparently edentulous, outer surface of fixed finger and dactylus keeled. Pleopod 3(?) large.

Etymology.—The generic name is derived from a part of the name of the city near the locality, Río Turbio, and the Greek word *cheir*, meaning hand. The gender is feminine.

Discussion.—The diagnostic features above refer solely to features commonly seen in fossil callianassids. Identification of genera and species, for that matter, of callianassids in the fossil record is fraught with difficulties because fossils are typically limited to the well calcified claws. Work is currently under way to clarify our understanding of the

fossil record of the group (M. Hyžný, personal communication). To avoid needless confusion and additional biogeographic chaos, it seems most prudent to erect a new genus for the new material from Río Turbio, instead of referring the material to an extant genus. Indeed, the new material is sufficiently morphologically unique to warrant a new genus.

The new genus exhibits a plexus of characters distinguishing it from other genera within the family. The merus exhibits a very finely serrated lower margin, and a well-developed keel extends obliquely across the outer surface of the merus. The merus also exhibits a shape unlike that of other callianassids in having an upper margin composed of two segments, yielding an unusually angular merus. General proportions of the carpus and propodus in addition to the development of serrations along the lower surface of the merus, carpus, and propodus are reminiscent of species of *Neocallichirus* Sakai, 1988. However, the most striking difference between *Turbiocheir* and *Neocallichirus* is that the fingers of the former are as long as, or longer than, the hand, and they are straight and slender, rather than stout and terminally hooked as they are in *Neocallichirus*. The degree of heterochely in the Río Turbio specimen is difficult to determine because the right cheliped is situated beneath the left one in the concretion. Examination of the lower margin of the propodus of the right cheliped suggests that it is very slightly longer than that of the left so that at least some degree of heterochely exists.

The only other morphological feature exposed on the fossil specimen is a single pleopod, interpreted to be the third pleopod based upon general similarity with those of *Callianassa subterranea* (Montague, 1808) (Manning and Felder 1991:fig. 8j) and *Dawsonius latispinus* (Dawson, 1967) (Manning and Felder 1991:fig. 16j). The pleopod on *T. minutospinata* is, however, very large by comparison with the chelipeds.

Turbiocheir minutospinata, new species

(Fig. 3)

Diagnosis.—Lower margin of merus, carpus, and manus bearing fine, triangular spines; fixed finger and dactylus long, longitudinally keeled, apparently without denticles on occlusal surfaces.

Description.—Merus of right cheliped about as long as high, short; proximal margin approximately straight; upper margin composed of two straight segments, proximal one shorter than distal one, so that it is highest medially; lower margin convex; distal margin apparently short, convex; outer surface with concave upper distal area and lower distal keel. Carpus of right cheliped crushed, higher than long; proximal margin with upper projection articulating with merus, overall sinuous; lower margin with tiny triangular spines; upper margin weakly convex; distal margin straight. Manus of right cheliped short, about as high as long; proximal margin straight; upper margin weakly

convex; lower margin with tiny triangular spines; distal margin oriented at about 100° angle to upper margin; outer surface weakly convex. Fingers with blunt keels parallel to occlusal surfaces and row of setal pits parallel to keel. Lower margin of manus of left cheliped and proximal portion of fixed finger with tiny triangular spines. Left cheliped appears to be slightly longer than right, based upon small exposed segment.

Exopod of pleopod 3(?) twice as long as high; outer margin nearly straight; inner margin weakly convex proximally to a distance of about 2/3 length, then curves abruptly to become slightly concave; distal margin bluntly rounded; endopod shorter, strongly arcuate outer margin, inner margin weakly concave.

Etymology.—The trivial name is derived from the Latin words *spina*, meaning thorn, and *minutus*, meaning small, in reference to the small spines on the margins of the carpus and the manus.

Type.—The holotype, MPEF-PI 5401, is deposited in Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina. A cast of the holotype, CM 56702, is deposited in the Carnegie Museum of Natural History.

Remarks.—*Turbiocheir minutospinatus* exhibits the combination of characters described above that serve to distinguish it from other callianassids. The outlines of the carpus and propodus coupled with the serrate lower surface of the chelipeds are much like those of species of *Neocallichirus*, however, the extremely long, straight, keeled fingers along with the overall proportions of the hand and the shape of the merus are distinctive features of the new genus and species.

Because only a single species of *Turbiocheir* has been recognized, it is not possible to make broad statements about its biogeographic distribution. However, presence of the new taxon in the high southern latitudes of Patagonia separates it from species of *Neocallichirus*, all of which occur in the Northern Hemisphere.

Infraorder Brachyura Linnaeus, 1758
Section Raninoidea De Haan, 1839
Superfamily Raninoidea De Haan, 1839
Family Raninidae De Haan, 1839

Subfamily Raninoidinae Lörenthey in Lörenthey and Beurlen, 1929

Diagnosis.—Carapace elongate; frontal margin generally wide, rostrum and orbital spines well-developed, generally long, orbit often with long orbital fissures; anterolateral margin with spine; sternites 1–4 fused, 1–3 forming cap-like structure, sternite four with lateral projections anteriorly and posteriorly; sternite five reduced; sternite six very long; sternites 7 and 8 narrow, long; spermatheca very closely spaced; sternum often with longitudinal groove on sternites 5–8.

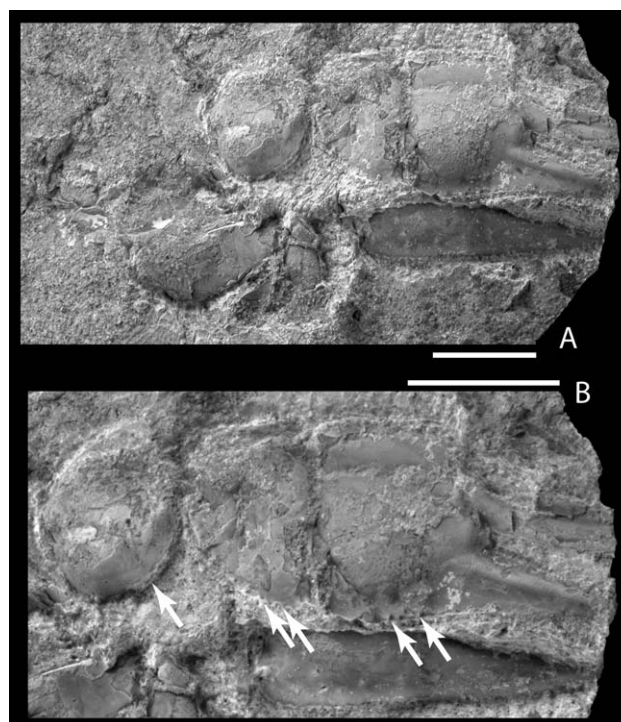


Fig. 3.—Callianassidae, *Turbiocheir minutospinata*, new species, holotype, MPEF-PI 5401. **A**, Outer surface of left cheliped, inner surface of right chela below it, and pleopod 3? below merus of left chela; **B**, enlargement of left chelipeds, arrows indicate tiny spines on lower margins of merus, carpus, and manus. Scale bars = 1 cm.

Raninoides H. Milne Edwards,
1837 [in 1834–1840]

Type species.—*Ranina laevis* Latreille, 1825, by monotypy.

Included fossil species.—See Schweitzer et al. (2010).

Diagnosis.—Carapace longer than wide, length about 70% maximum carapace width but may be as low as 60% and as high as 90%; rostrum with triangular central spine and triangular lateral spines which also form inner-orbital spines; rostral width about 30–40% maximum carapace width; upper orbital margin with open grooves, narrow grooves, or fissures; intra-orbital spine well-developed; outer-orbital spine bifid; one-anterolateral spine; carapace with or without post-frontal ridge; sternites 1–3 fused; sternite 4 long, with anterior and posterior lateral projections, concave between projections; sternite 5 very short and narrow; sternite 6 widening posteriorly, with arcuate, biconcave posterior margin; posterior portion of sternite 4 and sternites 5 and 6 with longitudinal groove.

Discussion.—*Raninoides* and *Laeviranina* have been thoroughly discussed in recent years (Tucker 1998; Schweitzer et al. 2000, 2003, 2006). The similarities between species of *Raninoides* and *Macroacaena* Tucker, 1998, a mem-

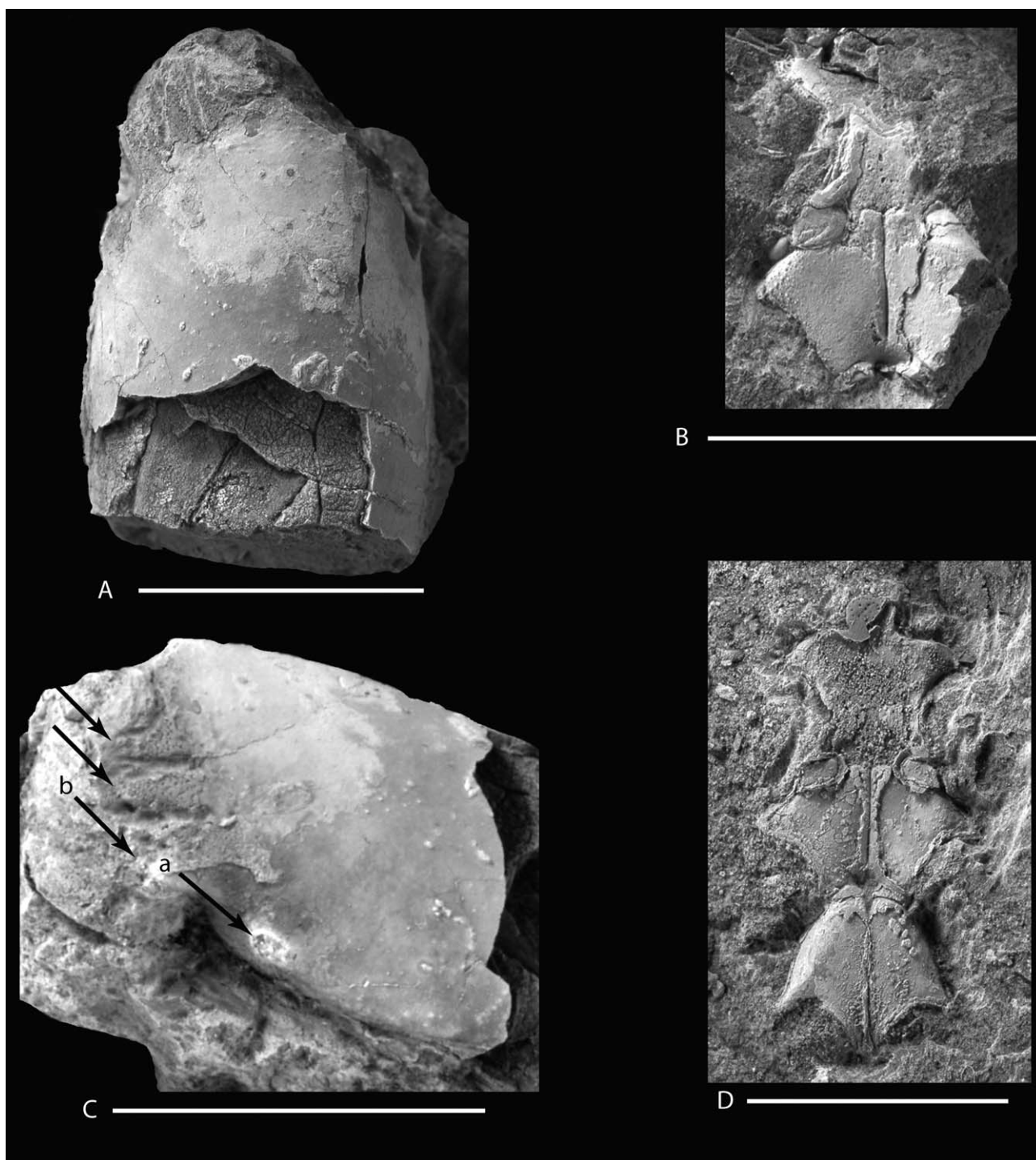


Fig. 4.—Raninidae, *Raninoides rioturbiensis*, new species. **A**, dorsal carapace of holotype, MPEF-PI 5402, note lack of postfrontal ridge; **B**, paratype, MPEF-PI 5403, partial sternum with axial groove on sternite 5; **C**, oblique lateral view of holotype, MPEF-PI 5402, arrow a indicate base of anterolateral spine, arrow b indicates bifid outer-orbital spine, uppermost unlabeled arrow indicates lateral spine of trifold rostrum, lowermost unlabeled arrow indicates intra-orbital spine; **D**, paratype, MPEF-PI 5404, nearly entire sternum showing tiny, caplike sternites 1-3, and deep groove on sternites 5-6. Scale bars = 1 cm.

ber of the Lyreidinae Guinot, 1993, have also been discussed and means by which to discriminate the two genera were detailed (Schweitzer et al. 2003). The new species is

referable to *Raninoides* based upon its broad fronto-orbital and frontal widths, and its sternal architecture, which includes a very long sternite 4 and grooves in sternites 4-6,

which occur in the Raninoidinae but not the Lyreidinae (Guinot 1993; Schweitzer et al. 2003).

***Raninoides rioturbiensis*, new species**
(Fig. 4)

Diagnosis.—Intra-orbital spine longer than frontal spine and outer-orbital spine; outer-orbital spine appearing to be weakly bifid; carapace lacking post-frontal ridge.

Description.—Carapace longer than wide, elongate-ovate; strongly vaulted transversely, weakly vaulted longitudinally, widest posterior to anterolateral spine.

Rostrum with triangular lateral spine directed anterolaterally, remainder of rostrum broken, rostral width about 40% maximum carapace width. Orbital margin with two long, broad, open fissures, directed anterolaterally; intra-orbital spine bounded by fissures, extending slightly beyond frontal spine; outer-orbital spine bifid, shorter than intra-orbital spine; intra-orbital and outer-orbital spines subparallel to lateral rostral spine and fissures; fronto-orbital width about 85% maximum carapace width. Anterolateral spine separated from outer-orbital spine by short distance, with ovate cross-section at base, directed more strongly anterolaterally than orbital spines. Remainder of known lateral margin weakly convex. Frontal region granular but lacking post-frontal ridge, at least on mold of interior of carapace.

Sternites 1–3 fused, small; sternite 4 long, with anterior and posterior lateral projections, concave between projections; sternite 5 very short and narrow; sternite 6 widening posteriorly, with arcuate, biconcave posterior margin; posterior portion of sternite 4 and sternites 5 and 6 with longitudinal groove; sternites 7 and 8 not preserved.

Measurements.—Measurements (in mm) taken on dorsal carapace of holotype of *R. rioturbiensis*, new species: maximum width, 12.7; frontal width, 5.4; fronto-orbital width, 11.2.

Etymology.—The trivial name is derived from Río Turbio, the name of the formation from which, and the town near which, the specimens were collected.

Types.—The holotype MPEF-PI 5402, and paratypes, MPEF-PI 5403 and 5404, are deposited in Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina. A cast of the holotype, CM 56703, and a cast of paratype MPEF-PI 5403, numbered CM 56704, is deposited in the Carnegie Museum of Natural History.

Remarks.—One other species of *Raninoides* has been reported from southern South America, *R. araucana* (Philippi, 1887). *Raninoides rioturbiensis* differs from *R. araucana* in lacking a post-frontal ridge; Philippi's (1887) illustration shows a well-developed post-frontal ridge on the carapace. One species has been reported from the Eocene of New Zealand (Glaessner 1960). Members of a

related genus, *Quasilaeviranina* Tucker, 1998, are known from New Zealand but differ from *R. rioturbiensis* in being markedly wider than long and in having post-frontal ridges. *Raninoides* was widespread in the Eocene of the Northern Hemisphere, with occurrences in Denmark, Hungary, Italy, Japan, Mexico, Pakistan, UK, and Pacific coastal USA (summarized in Schweitzer et al. 2006). Two specimens of *R. rioturbiensis* are preserved only as isolated sterna, an unusual preservation type within the family, suggesting conditions favoring gentle disarticulation yet rapid burial.

Section Eubrachyura de Saint Laurent, 1980
Superfamily Portunoidea Rafinesque, 1815

Family Macropipidae Stephenson and Campbell, 1960

Diagnosis.—Carapace moderately broad, length about 65–80% maximum carapace width, widest between 50 and 60% the distance posteriorly, usually with longitudinal branchial ridges parallel to axis, often with large granules or tubercles ornamenting carapace; orbits usually moderate sized, with two fissures, fronto-orbital width usually 50–60% maximum carapace width, rarely approaching 90% (*Coenophthalmus* A. Milne-Edwards, 1879, and some *Archaeogeryon* Colosi, 1925); front spined, number and size of spines variable, usually with an axial notch but sometimes with an axial spine (*Macropipus* Roux, 1830); front ranging from 20–40% maximum carapace width but rarely reaching 60% (*Coenophthalmus*); anterolateral margins with three to five spines including outer-orbital spine, last anterolateral spine often long and directed laterally; epibranchial ridge arcuate, extending from last anterolateral spine to axial regions; large posterolateral reentrant for insertion of last pereopods; male pleonal somites 3–5 fused and usually with clear evidence of sutures or indentations in the margins marking the position of somites or all male somites free; somite three and sometimes others with transverse keels, somite three generally markedly wider than other somites; telson extending to middle or anterior of sternite 4; median groove present on male sternite 3; portion of male sternite 8 usually visible in ventral view but sometimes completely obscured by pleon; sternal sutures appearing to be incomplete with occasional exception of 6/7 and 7/8 (*Nectocarcinus* A. Milne-Edwards, 1860); portunid lobe usually present; basal antennal article fixed or free, usually lacking laterodistal spines; chelae usually keeled; some pereopods as long as chelipeds; dactylus of fifth pereopod oblongate or obovate, very rarely ovate and paddle-like in traditional sense (*Parathranites* Miers, 1886; after Karasawa et al. 2008).

Megokkos Schweitzer and Feldmann, 2000

Type species.—*Portunites alaskensis* Rathbun, 1926, by original designation.

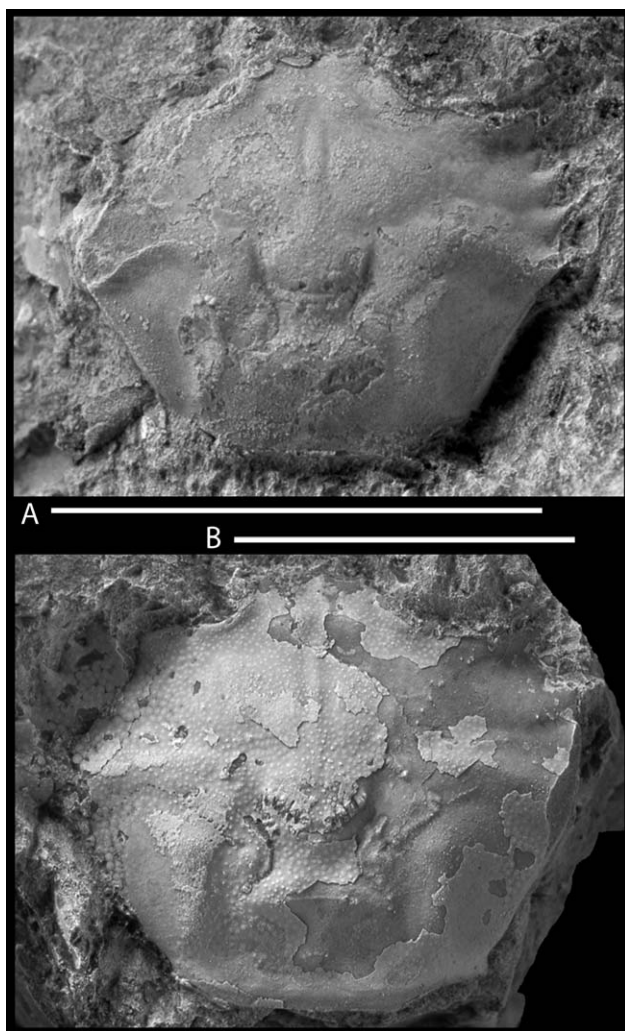


Fig. 5—Macropipidae, *Megokkos patagoniensis*, new species. **A**, dorsal carapace of holotype, MPEF-PI 5405, showing wide orbits and five anterolateral spines including outer-orbital spine; **B**, paratype, MPEF-PI 5406, with well-defined axial and branchial ornamentation. Scale bars = 1 cm.

Included species.—*Megokkos alaskensis* (Rathbun, 1926); *M. hexagonalis* (Nagao, 1932); *M. macrospinus* (Schweitzer et al., 2000); *M. patagoniensis*, new species.

Diagnosis.—Carapace rounded-hexagonal, wider than long, length about 65–80% width; front straight with four projections; orbits very broad, with two fissures and possibly a small spine; fronto-orbital width 70–80% maximum carapace width; anterolateral margin with 4–5 spines including outer-orbital spine, last spine usually longest; hepatic region with transverse ridge extending from anterolateral spine; epibranchial region arcuate, extending axially from last anterolateral spine; posterolateral reentrant well-developed; branchial regions with ridge subparallel with axis; chelipeds heterochelous, chelae with large blunt denticles on occlusal surface; dactyl of fifth pereopod paddle-like (after Schweitzer and Feldmann 2000).

Remarks.—The new species is referable to *Megokkos* based upon its broad orbits with two fissures, keels on the hepatic and epibranchial regions, and longitudinal keel on the branchial region. Of the members of the Macropipidae, only *Megokkos* possesses this combination of characters. *Maeandricampus* Schweitzer and Feldmann, 2002; *Minohellenus* Karasawa, 1990; and *Portunites* Bell, 1858, all have much narrower orbits and fronto-orbital width to width ratios than do *Megokkos* spp. and the new specimens. *Minohellenus* spp. lack the longitudinal keel on the branchial regions of the carapace.

All other species of *Megokkos* are known from the Eocene and Oligocene temperate latitudes of the northern Pacific Ocean: Japan (*M. hexagonalis*), Alaska, British Columbia (*M. alaskensis*), and Washington (*M. macrospinus*) (Schweitzer 2001; Schweitzer et al. 2003). *Megokkos* is not the only genus within the Macropipidae to exhibit an antitropical distribution. *Maeandricampus* is reported from the Oligocene of the Pacific Northwest and the Eocene of New Zealand, and *Minohellenus* is known from the Oligocene–Miocene of the North Pacific and the Cenozoic of Chile (Schweitzer and Feldmann 2002).

Megokkos patagoniensis, new species
(Fig. 5)

Diagnosis.—Fronto-orbital width about 85% maximum carapace width, orbit with two fissures, lacking intra-orbital spine; anterolateral margins with 4 spines excluding outer orbital spines, anterolateral spines 2–4 about equal in size, hepatic keel weak.

Description.—Carapace wider than long, length about 80% maximum width measured between bases of last anterolateral spines, moderately vaulted longitudinally and transversely.

Front poorly known, about one-quarter to one-third maximum carapace width. Orbits very wide, directed forward; upper orbital margin sinuous, with weakly upturned rim, with two fissures spaced at one-third and two-thirds the distance to outer-orbital spine respectively; outer-orbital spine triangular, with arcuate, convex lower margin, directed forward; fronto-orbital width about 85% maximum carapace width.

Anterolateral margin with four spines excluding outer-orbital spine; first spine smallest; second through fourth spines appearing to be about same size, with sharp tips, directed anterolaterally. Posterolateral margin straight, keeled; posterolateral reentrant shallow, rimmed; posterior margin nearly straight, rimmed.

Epigastric regions weakly inflated. Protogastric regions broad, weakly inflated. Hepatic regions with weak transverse keel extending from third anterolateral spine. Mesogastric region weakly inflated, with pentagonal posterior portion with strong muscle scars; long, narrow anterior process terminating between epigastric regions. Urogastric region short, with concave lateral margins, depressed

below cardiac region. Cardiac region bulbous, with two large spherical inflations anteriorly and weaker posteriorly-directed inflation. Intestinal region small, weakly defined. Epibranchial region arcuate, extending in convex forward arc from fourth anterolateral spine to urogastric region. Remainder of branchial region undifferentiated, with longitudinal keel subparallel to axis and terminating at midwidth of posterolateral reentrant.

Measurements.—Measurements (in mm) taken on the dorsal carapace of the holotype (MPEF-PI 5405) and paratype (MPEF-PI 5406), respectively, of *Megokkos patagoniensis*: maximum carapace width: 9.4, 12.8; maximum carapace length: 8.1, 9.9; fronto-orbital width: 8.0, 10.8; frontal-width: 3.0, 2.8.

Etymology.—The trivial name denotes the occurrence of the species in Patagonia, the first occurrence of the genus in the Southern Hemisphere.

Types.—The holotype, MPEF-PI 5405, and four paratypes, MPEF-PI 5406–5409, are deposited in Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina. A cast of the holotype, CM 56705, and casts of the paratypes: MPEF-PI 5406, numbered CM 56706; MPEF-PI 5407, numbered CM 56707; and MPEF-PI 5408, numbered CM 56708; are deposited in the Carnegie Museum of Natural History.

Remarks.—*Megokkos patagoniensis* differs from the other species within the genus in having anterolateral spines of more or less the same size and in having a somewhat broader fronto-orbital width to width ratio. The hepatic ridge is somewhat weaker in *M. patagoniensis* than in other species. In general, this species is much smaller than the other species of the genus. All four specimens of *M. patagoniensis* are similarly small, so it does not appear that they are juveniles.

Superfamily Carpilioidea Ortmann, 1893

Family Tumidocarcinidae Schweitzer, 2005

Diagnosis.—Carapace wider than long, length about 80–90% maximum width, widest at position of last or penultimate anterolateral spine, about half the distance posteriorly on carapace; carapace markedly vaulted longitudinally, especially in anterior third; front four-lobed including inner-orbital spines, frontal width about one-quarter maximum carapace width; fronto-orbital width a little less than half to two-thirds maximum carapace width; orbits rimmed, sometimes with one or two very faint, completely fused fissures, circular, directed forward; antenna situated outside supraorbital angle; carapace regions well defined to poorly defined; anterolateral margins with three or four small, blunt spines excluding outer orbital spine or entire and granular; epibranchial regions usually arcuate. Male sternites 1 and 2 fused with no evidence of suture; very

clear, deep, continuous suture between sternites 2 and 3; sternites 3 and 4 with notch in lateral margins where suture intersects it, suture becoming increasingly shallow, becoming a shallow groove at midlength, completely interrupted axially; left and right sternal sutures between sternites 3 and 4 merge with deep groove extending anteriorly from sterno-pleonal cavity, forming prominent, Y-shaped groove pattern; suture between sternites 3 and 4 oriented at high angle; sternite 4 with very clear, longitudinal grooves near lateral margins, which appear to be episternal projections from sternite 3 fused with and prominent on sternite 4; sternal sutures not parallel; sternite 8 not visible in ventral view. Male pleon barely reaching or not quite reaching posterior margin of coxae of first pereopods; all male pleonal somites free; male pleon completely occupying space between coxae of fifth pereopods. Chelae subequal to very unequal; mani stout; fingers with black tips; coxae of first pereopods articulating with basis-ischium, basis-ischium not fused to merus; other pereopods slender (after Schweitzer 2005:282).

Nitotacarcinus Schweitzer, Artal, van Bakel, Jagt, and Karasawa, 2007

Type species.—*Glyphithyreus bituberculatus* Collins and Jakobsen, 2003, by original designation.

Other species.—*Nitotacarcinus antipodes*, new species; *N. canadensis* Schweitzer et al., 2009; *N. lutarius* Schweitzer and Feldmann, 2011.

Diagnosis.—Carapace not much wider than long, regions well-defined; front axially notched, about 33% maximum carapace width; orbits with two fissures or with blunt intra-orbital spine, fronto-orbital width about 65% maximum carapace width; anterolateral margins with three or four spines or blunt projections excluding outer-orbital spines (Schweitzer and Feldmann 2011:8).

Nitotacarcinus antipodes, new species
(Fig. 6)

Diagnosis.—*Nitotacarcinus* with large anterolateral spines, including fourth and last spine, and well-defined carapace regions.

Description.—Carapace rectangular, wider than long, length about 84% maximum width measured at position of last anterolateral spine, about half the distance posteriorly on carapace; strongly vaulted longitudinally, flattened transversely; regions very well-defined by deep grooves.

Front and orbits broken. Anterolateral margin with four spines excluding outer-orbital spine; first two spines triangular, directed anterolaterally; third spine largest and longest, directed anterolaterally; last spine stout but apparently not long, broken. Posterolateral margin strongly convex, sinuous; posterior margin rimmed, weakly concave.

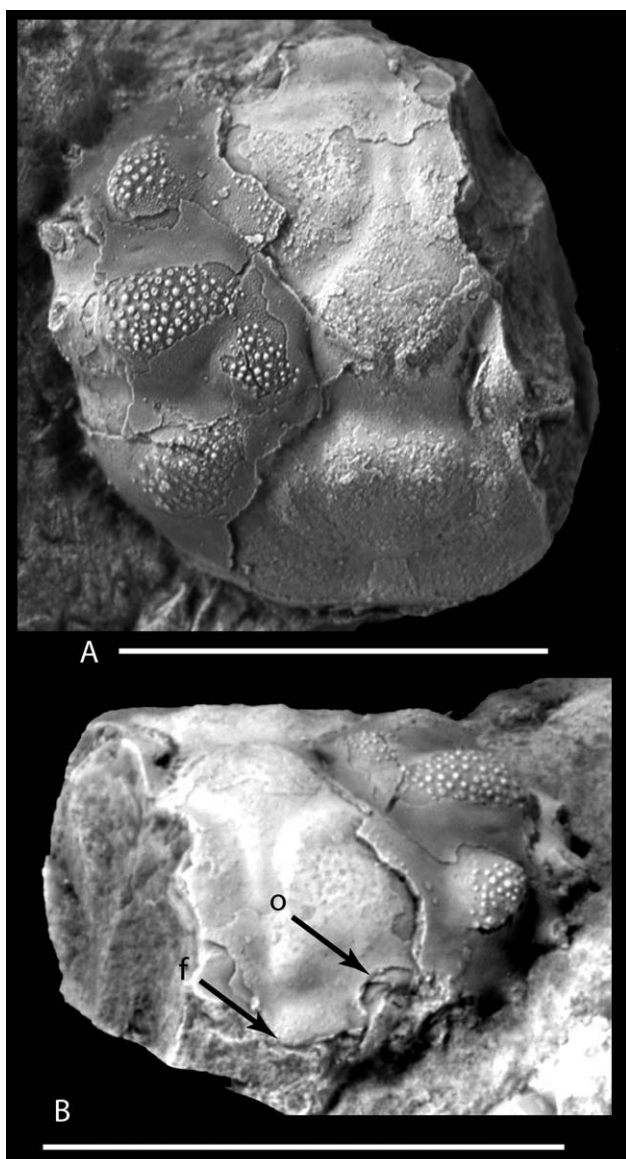


Fig. 6.—Tumidocarcinidae, *Nitotacarcinus antipodes*, new species, holotype, MPEF-PI 5410. **A**, dorsal carapace; **B**, anterior view showing front (f) and orbit (o). Scale bars = 1 cm.

Epigastric regions circular, moderately inflated. Proto-gastric regions quadrate, granular, with weak longitudinal depression. Mesogastric region inflated posteriorly with long, slender, anterior process which becomes progressively more weakly developed anteriorly; strong muscle scars on posterior portion of region. Urogastric and metagastric regions confluent; metagastric region slightly elevated above urogastric region, very short and with two small nodes. Cardiac region inflated, triangular with blunt apices, two swellings anteriorly and one posteriorly. Intestinal region depressed, smooth. Hepatic region strongly inflated centrally, with granules on apex of swelling. Epibranchial region composed of two swellings forming

a convex-forward arc extending from last anterolateral spine to urogastric region, granules on apices of swellings. Mesobranchial region inflated, granular. Metabranchial region depressed to level of intestinal region, smooth.

Remainder of carapace and appendages unknown.

Type.—The holotype, MPEF-PI 5410, is deposited in Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina. A cast of the holotype, numbered CM 56709, is deposited in the Carnegie Museum of Natural History.

Etymology.—The trivial name, *antipodes*, alludes to the high southern latitude occurrence of the species, the first occurrence of the genus in the Southern Hemisphere.

Remarks.—The new species fits all of the diagnostic characteristics of the genus, with the possible exception that the last anterolateral spine is somewhat larger than that seen in the other species. However, we consider that this may be accounted for by intrageneric variation. In possessing a rectangular carapace, four anterolateral spines, inflated carapace regions, what appears to be a straight front, and typical carapace regions, *N. antipodes* is very similar to the other species of the genus and other species within the Tumidocarcinidae.

The other known species of this genus are known from Eocene cool temperate northern latitudes: Denmark (*N. bituberculatus*); British Columbia, Canada (*N. canadensis*); and the UK (*N. lutarius*) (Schweitzer et al. 2009; Schweitzer and Feldmann 2011). Other genera and species within the family have previously been reported from South America, including *Baricarcinus* Casadio et al., 2004, and *Paratumidocarcinus* Martins-Neto, 2001. *Tumidocarcinus* Glaessner, 1960, is well-known from New Zealand. Other taxa within the Tumidocarcinidae, including *Nitotacarcinus* up until now, are reported from temperate Northern Hemisphere localities, strongly indicating an antitropical distribution for this family.

DISCUSSION

The Eocene fauna of southernmost Argentina described here clearly illustrates an antitropical distributional pattern (Fig. 7). The antitropical nature of the Pacific decapod fauna beginning by the Cretaceous was already known (Schweitzer 2001; Casadio et al. 2004). The brachyuran genera reported here from Eocene localities in southern Argentina are known from Eocene localities in the Pacific northwest of North America (Fig. 7), and some lingered into the Oligocene there (Schweitzer 2001; Schweitzer et al. 2003, 2007). Examination of the occurrences of the brachyuran genera suggests that at least *Raniniodes* (R) was already present in the Paleocene and even the Cretaceous of the Atlantic Basin (Collins and Rasmussen, 1992), and its range subsequently expanded during the Eocene. The other two genera (*Nitotacarcinus* [N] and *Megokkos* [M]) first appeared during the Eocene in both hemispheres; the fossil

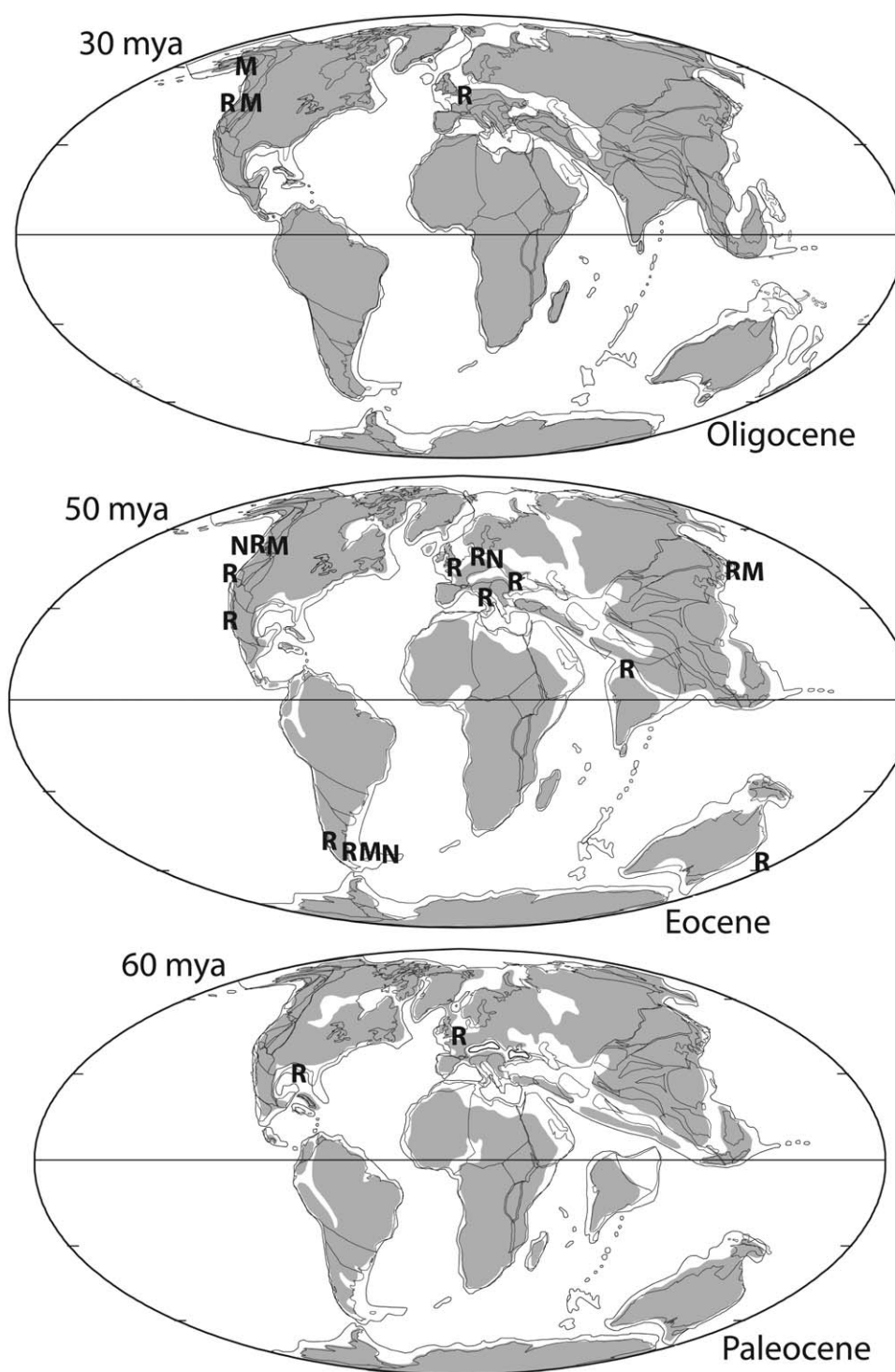


Fig. 7.—Paleocene, Eocene, and Oligocene occurrences of species of *Raninoides* (R), *Megokkos* (M), and *Nitotacarcinus* (N) plotted on their respective paleogeographic maps. Note that *Raninoides* is an extant genus whereas the other two are extinct. Maps from Scotese (2006).

record is not sufficiently constrained to determine which generic appearances were the earliest.

Lindberg (1991) and BurrIDGE (2002) summarized various hypotheses, both vicariant and dispersal, to account for antitropical distributions. Of all of them, descent into cooler, deeper water seems to be the best hypothesis for explaining this phenomenon within the Decapoda. Crame (1993) suggested that many antitropical organisms were adapted to shallow-water and thus might have exhibited such a dispersal pattern. Thus, organisms living in temperate climes, adapted to cooler sea temperatures, in either the Northern or Southern Hemisphere, would descend into deeper waters to maintain a preferred temperature regime in order to cross the tropics. Upwelling of cooler water along eastern Pacific coastal regions, even in the tropics, could also account for movement of the animals through the tropics (Lindberg 1991). Both the North American and South American faunas are documented to have inhabited at least offshore conditions (Zinsmeister and Feldmann 1984). Thus, they may already have been tolerant of cooler, deeper water and could have maintained their depth through the tropics.

Vicariance events could explain the Cretaceous and later Paleocene speciation events, as the Atlantic was narrow during the Cretaceous and expanded by the Paleocene. Vicariance based upon ancestral tropical populations that dispersed to the temperate zones has not been found to be an adequate mechanism for Pacific antitropical distributions based upon the fossil record of the animals occurring almost exclusively in higher latitudes to the exclusion of low latitudes (Lindberg 1991). This certainly is the case with the Decapoda, which do in fact have good Cretaceous and Cenozoic fossil records known from the Caribbean, Mexico, and Gulf Coastal USA (i.e., Rathbun 1935; Schweitzer et al. 2002; Feldmann and Schweitzer 2006; Collins et al. 2009; Vega et al. 2010); thus, lack of exposures is not the explanation.

Lindberg (1991:315) noted that for pelagic organisms or those with pelagic larvae, dispersal in geologic time would “appear instantaneous” because it occurs on such rapid timescales, tens of thousands of years. Thus, animals could disperse via ocean currents, or even by colonizing the continental shelf, very rapidly. During times of global cooling or warming, i.e., global homogeneity, dispersal could be accomplished rapidly. Then during times of climate change, the populations could be fragmented. The Eocene was a time of high sea-level and warmer temperatures, at least during the middle Eocene, and this may have made it possible for the animals to disperse globally, resulting in subsequent antitropical distributions. Oligocene occurrences are much more limited, probably at least in part due to more limited exposures of Oligocene rocks, and the antitropical pattern is not nearly as pronounced at that time.

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