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RESEARCH PAPER

New early Jurassic decapod crustacean from Patagonia (Chubut province), Argentina

M. A. Pagani · S. E. Damborenea · M. O. Manceñido · S. M. Ferrrari

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Abstract A well-preserved decapod specimen was found in early Toarcian deposits cropping out on the western slope of Meseta Catreleo, central Chubut province, Argentina. It is a nearly complete exoskeleton preserved in lateral view, slightly crushed, in fine-grained sandstones. The skeleton is mostly articulated, though some pieces are disarticulated or missing. Taphonomic features indicate a relatively rapid burial after death, with little or no transport. This specimen is here described as a new species of the genus Mecochirus Germar (Decapoda: Glypheoidea). Mecochirus robbianoi n. sp. is characterized by a very long, achelate, first pair of pereiopods with a narrow, long, straight dactylus, a thin carapace ornamented by low tubercules, with a slightly oblique cervical groove and a short acute rostrum. The family Mecochiridae arose in the Triassic, but the group diversified during the Early Jurassic. Mecochirus had a wide geographical distribution and is

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M. O. Manceñido e-mail: mmanceni@fcnym.unlp.edu.ar known for sure from Lower Jurassic to Upper Cretaceous deposits. The new record from Chubut is one of the oldest for the genus, the oldest for South America, and the first for Argentina, thus considerably extending the known distribution of the genus during the Early Jurassic.

Keywords Decapoda · Glypheoidea · *Mecochirus* · Early Jurassic · Patagonia · Chubut · Argentina

Kurzfassung Ein gut erhaltener Decapode wurde in Ablagerungen des unteren Toarciums auf der Westseite der Meseta Catreleo im Zentrum der Provinz Chubut (Argentinien) gefunden. Es handelt sich um ein fast komplett erhaltenes Exoskelett, welches in einem feinkörnigem Sandstein leicht verdrück in Seitenlage eingebettet ist. Die taphonomische Analyse deutet auf eine rasche Einbettung nach dem Tod, mit nur geringem oder fehlendem Transport. Das hier beschriebene Exemplar wird als neue Art der Gattung Mecochirus Germar (Decapoda: Glypheoidea), M. robbianoi n. sp., beschrieben. Sie zeichnet sich durch ein sehr langes, achelates Paar der ersten Pereiopoden mit schmalen, langem, geradem Daktylus, einem mit flachen Tuberkeln verzierten Carpax mit leicht gerundeter Cervicalfurche und ein kurzes, spitzes Rostrum aus. Die Familie Mecochiridae erschien in der Trias; im Unterjura kam es zu einer Diversifikation. Mecochirus hatte eine weite paläogeographische Verbreitung und ist vom Unterjura bis in die Oberkreide mit Sicherheit bekannt. Die neue Art ist eine der ältesten der Gattung, die älteste aus Südamerika und zugleich der erstnachweis aus Argentinien. Dies weist auf eine viel größere Verbreitung im Unterjura hin als bisher angenommen.

Schlüsselwörter Decapoda · Glypheoidea · *Mecochirus* · Unter Jura · Patagonia · Chubut · Argentina

Introduction

Decapod crustaceans are largely underrepresented in the fossil record for a number of reasons (Förster 1985). As a consequence, every specimen discovered usually provides a wealth of new information, either on the biology of the group involved or about its geographical and stratigraphical distribution (or both). From the few available data, it is evident that the Decapoda underwent a first radiation during early Triassic times (Förster 1985; Schram and Dixon 2004), but were still somewhat poorly represented during the Early Jurassic.

Knowledge about Jurassic Decapoda from South America is limited to very few records, from Pliensbachian to Tithonian age. Based on a well-preserved isolated carapace found in Toarcian deposits of southern Mendoza, Damborenea and Manceñido (1987) described the new species Glyphea eureka. A fragmentary astacidean molt was recently figured by Lanés et al. (2007, fig. 7.F) from early Pliensbachian beds in southern Mendoza. A few records referred to as "arthropod remains" were mentioned but never illustrated from Toarcian beds at Loncopán, Chubut (Malumián and Ploszkiewicz 1977: 280; Blasco et al. 1980: 191). The following species have been described from late Jurassic deposits of the Cordillera de Domeyko, Chile: Chilenophoberus atacamensis Chong and Förster (1976; another specimen illustrated by Schultze 1989, pl. 1, fig. 4) from Upper Oxfordian beds probably deposited in anaerobic environments (Vicente 2006: 411) and Mecochirus chilensis Förster (in Förster and von Hillebrandt 1984) from Kimmeridgian shallow marine deposits at Quebrada del Profeta, Cordillera de Domeyko. Arratia (1987, pl. 3, fig. 1) figured a crustacean from the same locality in beds referred to the Oxfordian. Rusconi (1948) described Jurassic material from Mendoza as two new species of the new genus Pehuenchia. He referred this material to the Palinura and to the Middle Jurassic. Nevertheless, it is almost certain that the bituminous schists that bear this material belong to the Vaca Muerta Formation of Tithonian to Berriasian age. The generic name Pehuenchia was overlooked by the Treatise (Glaessner 1969), and even by the Nomenclator Zoologicus (Neave 1939–1950). The actual affinities of this very poorly preserved material remained doubtful (Camacho 1966: 479), though they were later assigned to the genus Mecochirus by Förster and Hillebrandt (1984: 76) without further comments, but subsequently compared to callianassids by Aguirre-Urreta (1989, 1994) upon observation of the specimens, concluding that the genus Pehuenchia would be a junior synonym of Callianassa or Protocallianassa (Aguirre-Urreta and Scasso 1998). The material described by Rusconi is housed in the Museo de Historia Natural de Mendoza under catalogue numbers 3578-3584. Jurassic decapods from Antarctica are likewise scarce, limited to a *Cycleryon* sp. from probably Callovian beds in Ellsworth Land (Quilty 1988), and the palinurid *Antarcticheles antarcticus* Aguirre-Urreta et al. 1990, found in clasts of the Late Jurassic Ameghino Formation within conglomerates of the Cretaceous Kotick Point Formation in James Ross Island.

The purpose of this contribution is to describe and discuss an interesting new record of a mecochirid lobster from the Early Jurassic of Patagonia, Argentina. This represents a significant addition to the Jurassic decapod fauna known from South America, and it considerably extends the geographical range of Early Jurassic mecochirid crustaceans.

Geological and stratigraphical setting

The Lower Jurassic sedimentary rocks of central Chubut province are widespread (Fig. 1a), but rather poorly exposed and show frequent and sudden facies changes that involve volcaniclastic and siliciclastic sediments. This has considerably compounded the lithostratigraphic nomenclature of these deposits, and, more importantly, has led to different geological interpretations about their history and relationships. They lie unconformably over Upper Paleozoic marine sediments referred to the Tepuel Group. In the Cajón de Ginebra area (near Paso de Indios town, see Fig. 1), the Paleozoic substratum is not exposed, the Lower Jurassic marine sediments are known as Osta Arena Formation (Musacchio in Herbst 1966) or Lomas Chatas Formation (Robbiano 1971), and they overlie and are interdigitated with the andesitic conglomerates of the El Córdoba (=? Olte) Formation (Robbiano 1971; Musacchio and Riccardi 1971; Musacchio 1975, 1981; Nullo 1983; Riccardi and Damborenea 1993). The Osta Arena Formation is dominated by medium- to fine-grained sandstones and tuffs, with a diverse marine fauna including bivalves, ammonites, gastropods and brachiopods (Robbiano 1971; Musacchio and Riccardi 1971; Blasco et al. 1979; Nullo 1983; Damborenea 2002; Ferrari 2009).

The material described here was found on the western slope of Meseta de Catreleo, about 2 km north of Quebrada El Córdoba, and about 200 m northwest of Puesto Currumil (indicated as Acuña in the geological map by Nullo 1983 and as El Córdoba fossiliferous locality by Ferrari 2009), in fine- to medium-grained massive thin-bedded sandstones (Fig. 1d). These beds were deposited in a shoreface environment, and also contain ammonoids, bivalves, gastropods and plant fragments. They are partly equivalent to those beds logged by Robbiano (1971) at the nearby Quebrada El Córdoba, where the Osta Arena Formation is nearly 250 m thick (Fig. 1c). The total thickness exposed at Puesto Currumil is much less, only about 30 m,



Fig. 1 a Outcrop areas of Lower Jurassic marine sediments in central Chubut Province, Patagonia Argentina. b Location of Puesto Currumil and Quebrada El Córdoba in the Pampa de Agnia area, *fossiliferous locality. c Sketch of stratigraphical section measured

mostly covered, and the relationships of these sediments with the underlying unit are not seen there, as the small outcrop is limited by faults and intruded by dykes. South of Puesto Currumil these sediments are transitionally covered by fine-grained sandstones and mudstones with plant remains and volcaniclastic rocks.

The beds with *Mecochirus* also contain *Dactylioceras* (*Orthodactylites*) *hoelderi* von Hillebrandt and Schmidt-Effing 1981, and some Hildoceratidae. The gastropods are Cryptaulax damboreneae Ferrari, *Procerithium nulloi* (Ferrari), *Calliotropis espinosa* (Ferrari), *Colpomphalus*? sp. and *Striatoconulus* sp. (Ferrari 2009). The associated bivalves include Ostreoidea and Nuculoidea, but the same

by Robbiano (1971) at Quebrada El Córdoba. **d** Detail of stratigraphical section measured at Puesto Currumil (equivalent position in (c) marked by *), indicating bed with decapod remains (PA6)

unit bears *Kolymonectes weaveri* Damborenea 1998, *Grammatodon costulatus* (Leanza 1942) elsewhere.

The beds that bear the material here described are dated as Early Jurassic (early Toarcian, *Dactylioceras hoelderi* Assemblage Zone, according to current biostratigraphic zonation in Argentina (Riccardi 2008a, b).

Materials and methods

The material was collected during a field trip to early Jurassic outcrops in central Chubut organized by the Museo Paleontológico Egidio Feruglio (MEF) and was prepared by MEF technicians in Trelew. The section was logged and the fossiliferous levels were thoroughly sampled. The decapod specimen and the associated fauna are deposited in the paleontological collection of MEF under the prefix MPEF-PI.

The specimen was photographed using a Nikon camera with a macro lens, and some details were also photographed with a scanning electronic microscope, in low vacuum and backscattered electron signal (BES) conditions, in ALUAR S.A., Puerto Madryn, Chubut.

Systematic description

We follow the systematic arrangement proposed by Martin and Davis (2001) and Feldmann et al. (2002), updated by De Grave et al. (2009), who placed Mecochiridae and Glypheidae in the infraorder Glypheoidea near the Astacidea and not within the Palinura, as formerly done (Glaessner 1969). These changes were prompted by the discovery of living glypheoids (Forest and de Saint-Laurent 1975; Feldmann and de Saint-Laurent 2002; Forest 2006 and references therein) and were recently confirmed by an analysis of both morphological and molecular characters (Ahyong and O'Meally 2004).

Order Decapoda Latreille 1802 Suborder Pleocyemata Burkenroad 1963 Infraorder Glypheoidea Winckler 1883 Family Mecochiridae van Straelen 1924

Remarks. The Glypheoidea most probably appeared in the Permian-Triassic and throve in the Jurassic, when several genera lived worldwide. For many years the superfamily was believed to be extinct since the Eocene. Yet, it is a good example of a Lazarus group, represented by only two known living species (Forest 2006).

The extinct family Mecochiridae was revised by Förster (1971), who provided a detailed diagnosis of the main genera and discussed their distribution and relationships. According to De Grave et al. (2009) and Schweitzer et al. (2010), the family includes 48 species of the following genera: *Pseudoglyphea* Oppel 1861, *Mecochirus* Germar 1827, *Meyeria* M'Coy 1849, *Huhatanka* Feldmann and West 1978. *Jabaloya* Garassino et al. 2009, *Selenisca* von Meyer 1847 and *Praeatya* Woodward 1869.

The generic name *Meyerella* was proposed in an unpublished thesis by Simpson and first mentioned in Simpson and Middleton (1985) without fulfilling the ICZN requirements for valid publication; furthermore, the intended proper description and proposal never materialized. Besides, the name has several homonyms (fide Neave, 1939–1950) and is preoccupied. This name was used by Aguirre-Urreta (1989: 534), Garassino (1996: 352–354)

and Garassino and Schweigert (2006: 20), and, if regarded as a separate taxon, it should be replaced (see discussion in Feldmann and Schweitzer 2006).

Genus Mecochirus Germar 1827

Type species. Macrourites longimanatus von Schlotheim 1822, from the Late Jurassic of Solnhofen, Germany, subsequent designation by Woods 1927: 64 (synon. *Mecochirus locusta* Germar 1827).

Synonyms. See van Straelen 1924; Woods 1927 and Glaessner 1929).

Discussion. The genus *Mecochirus* had a wide geographical distribution from the Early Jurassic (Sinemurian) to the Late Cretaceous (Maastrichtian) (Förster 1971; Schweitzer et al. 2010), but in South America it was previously recorded only from the Upper Jurassic of Chile (Förster and von Hillebrandt 1984). The new record described here extends its range in South America back to the early Toarcian, and it is the first known occurrence in Argentina.

Mecochirus is distinguished from other Mecochiridae by the cervical groove positioned oblique to the dorsal line, the lack of a gastroorbital groove, a nearly straight groove in the antennal region, a short rostrum, the hepatic groove not reaching the cervical groove, postcervical and branchiocardic grooves not reaching the dorsal midline, first abdominal pleura expanded anteriorly, and extremely long propodus of the first pereiopod ending in a terminal dactylus (see van Straelen 1924; Förster 1971; Garassino and Schweigert 2006).

Mecochirus robbianoi n. sp. Figs. 2a–d, 3, 4a–f.

Derivation of name. The specific name refers to J.A. Robbiano, who contributed substantially to the geological knowledge of the Jurassic of central Chubut.

Holotype. MPEF-PI 1261a and b. The specimen is an almost complete exoskeleton, preserved mostly articulated but crushed; however, some pieces are disarticulated and slightly out of place, and most appendices are missing (Fig. 3). Both part and counterpart are preserved (Fig. 2a–b).

Type locality. Near Puesto Currumil, southwest of Meseta Catreleo, central Chubut, Argentina (Fig. 1b).

Type horizon and age. Fine-grained sandstones in the Osta Arena (=Lomas Chatas) Formation, *Dactylioceras hoelderi* Assemblage Zone, early Toarcian.

Diagnosis. Mecochirus with a pustulose carapace, bearing a slightly oblique cervical groove, an acute but short rostrum, and two tuberculated cephalic anterior ridges. Abdomen and cephalotorax almost equally long. First pair of pereiopods achelate, having a very narrow, straight and long dactylus with a pointed end and a short posterodorsal hook-like outgrowth.

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Fig. 2 *Mecochirus robbianoi* n. sp. MPEF-PI 1261. **a-b** Photographs of part and counterpart of slab with the whole specimen. Inset in **a**: enlarged detail showing possible mouthpart. **c** Drawing of part of the specimen pointing to the different parts of the skeleton that were

Description. The carapace is thin; the cephalothorax is roughly oval in outline, with deep flanks, dorsal surface somewhat convex and with a moderate notch where cervical groove crosses the carapace. The anterior region is small in comparison with the branchiocardic region. The cervical groove is moderately defined and oblique, forming an angle of about 56° with the dorsal midline and merging with the antennal groove, which has a straight anterior portion. Branchiocardic and postcervical grooves badly defined because that part of the carapace is crushed, but anterior portion of branchiocardic groove appears to be directed backwards at a low oblique angle. Hepatic groove not reaching the cervical groove. The carapace is densely ornamented by low pustules, which decrease toward the dorso-posterior region (Fig. 4a). The rostrum is acute but short (Fig. 4b). At least two tuberculated longitudinal ridges are present on each side of the anterior part of the carapace. One of them, the subdorsal carina (Holthuis 1974), is close to the dorsal midline of the cephalothorax



recognized. **d** Detail of the tip of the first pair of pereiopods, showing the distal end of the propodus and the long, narrow and nearly straight dactylus; *white arrows* point to hook-like outgrowth at the base of each dactylus. Scale bars = 10 mm



Fig. 3 *Mecochirus robbianoi* n. sp. Restoration sketch of the whole skeleton (S.D.). Parts in *grey* are those easily recognizable in the preserved specimen; parts in crossed pattern are those possibly present. Morphology of parts not recognized or missing (in *white*) is conjectural. Pleopods omitted

and extends into the rostrum (Fig. 4a–b); the other is below it and corresponds to the supraorbital carina. Tubercles along the supraorbital carina are aligned in one single row, while those of the subdorsal carina are arranged in a rather irregular zig-zag pattern. Below the supraorbital carina the pustule density decreases, and there is no proper antennal Fig. 4 Mecochirus robbianoi n. sp. MPEF-PI 1261a. MEB photographs. a Anterior part of carapace, showing subdorsal and supraorbital carinae, scale bar = 500 μ m. **b** Detail of rostrum, scale bar = $100 \ \mu m$. c Part of merus of second(?) pereiopod showing dorsal row of tubercles, scale bar = 100 μ m. **d** Proximal end of carpus of first pereiopod, showing ornamentation pattern, scale bar = 200 μ m. e Rounded process below orbit, scale bar 100 μm. f Pleural surface of fifth somite, scale $bar = 500 \ \mu m$



ridge, though there are a few large tubercles not arranged in a row in this region of the carapace. An elongated, rounded process is present below the orbit; this has a convex outer surface covered with small tubercles (Fig. 4e). The inferred position of the "adductor testis" muscle is represented by a rounded protuberance surrounded by the hepatic groove. One very poorly preserved fragment could doubtfully be part of a cephalic appendage (mouthpart?, Fig. 2a inset). Other cephalic appendages and antennae are unknown.

The abdomen is slightly shorter than the cephalotorax. Five somites are preserved, the second one wider than the others. The dorsal tergum of each somite has a rounded keel; terga appear to be transversely ridged and pleura nearly smooth, without tubercles or spines on their surface. The pleural surface is irregular and bears a micro-ornamentation of short faint ridges (Fig. 4f). The second pleuron is almost twice as long as the third and the fourth pleura, and is anteriorly expanded. Pleura have a rounded ventral margin anteriorly, with an angular postero-ventral corner.

Only podomeres of the first three pairs of pereiopods are preserved (Fig. 3). Some pereiopod segments from both sides are fragmentary, and occur overlapping each other and the cephalothorax. Especially the first pair is strongly elongated, ischium longer than high, merus very long with a longitudinal line of tubercles in the middle region, carpus laterally flat and densely covered by pustules (Fig. 4d) and a median row of tubercles (Fig. 4c). The propodus is only partially preserved, distally bears traces of two parallel rows of pustules and ends in a widened crenulated margin (Fig. 2d). This first pereiopod is achelate, ending in a long and narrow dactylus, which is nearly straight and has a pointed sharp end. The stiletto-like dactylus is carinated: a low oblique ridge extends from its postero-ventral corner to its tip. A short postero-dorsal hook-like outgrowth is conspicuously present at the base of both dactyli (Fig. 2d).

Carpus nearly as long, propodus 60% longer and merus 30% longer, relative to the dactylus.

Other pereiopods are only preserved as disarticulated fragments. Shape of pleopods, uropods and telson are unknown. Possibly part of the uropods are preserved as disarticulated fragments near the posterior part of abdomen.

Although a single specimen from Chubut is available thus far, it is likely that it may represent a female, as suggested by the anteriorly expanded and overlapping epimere of the second pleuron (cf. Taylor 1979: 19–20, figs. 7–8) which lacks a postero-ventral spine (cf. Feldmann et al. 2002: 30), and by the remarkably long first pereiopod, with the propodus not shorter than carapace (cf. Garassino and Schweigert 2006: 20).

Measurements. Carapace length: 17.5 mm. Carapace height: 11.2 mm. Abdomen length: 13.8 mm. Distance, along dorsal midline, from cervical groove to anterior end of rostrum: 6.5 mm. Pereiopod 1: length: 46.2 mm.

Remarks and comparison. All the available characters allow reference of this species to *Mecochirus*. The specimen has all the distinctive features that Förster (1971) listed as typical of this genus, such as the shape and size of the first pereiopod and its dactylus, and the pattern of carapace grooves.

Our material is distinguished from species referred to *Pseudoglyphea*, including Early Jurassic German material illustrated by Quenstedt (1856), pl. 11, figs. 15–16) as *Mecochirus grandis* (regarded as a *Pseudoglyphea* by van Straelen 1924: 197), since the latter have a strongly spinose median dorsal carina and rostrum, as well as a distally wide propodus and a robust dactylus.

The peculiar dorsal hook-like outgrowth at the base of the dactylus in the first pereiopod is seen in M. *robbianoi* n. sp. because the dactyli are disarticulated; in most other species the dactyli are usually preserved articulated, in a position that prevents observation of such feature. This hook most likely was a lever-like muscular attachment structure, allowing the movements of the dactylus.

According to Förster (1971) there are about 30 species reported from the Mesozoic around the world, yet some of the names are probably synonyms. As *Meyeria* is now regarded as a separate taxon, the species within *Mecochirus* s.s. are fewer than 20 (De Grave et al. 2009; Schweitzer et al. 2010).

The best known species is the type, *M. longimanatus* (v. Schlotheim), from the Tithonian Solnhofen limestones in southern Germany. It has a more elongated carapace than *M. robbianoi*, with three keels on its anterior portion in lateral view (Förster 1969, pl. 2, fig. 1; 1971, figs. 5, 6B, 7B; Wang 1981, fig. 1; Garassino and Schweigert 2006, text-fig. 9, pl. 5, fig. 1, pl. 13, fig. 6, pl. 14, fig. 1; Schweitzer et al. 2009: 2). The first pair of pereiopods is subchelate and longer in adult specimens of the type

species than in the material from Chubut. In *M. longi*manatus the length of the first pereiopod relative to carapace length is allometric and changes considerably during ontogeny, making comparison based on this feature meaningless if the ontogenetic stage of the specimens compared is not known.

The Early Jurassic species *M. olifex* Quenstedt (1856: 89, pl. 11, fig. 17; Oppel 1862: 81, pl. 22, fig. 1; van Straelen 1924: 214; Beurlen 1928: 142), from the early Sinemurian of southern Germany, is not well known and is included in *Mecochirus* on the basis of the first pereiopods size and shape. It can be distinguished from the species here described because the first pereiopods are relatively shorter than the body, the carpus is almost as long as the propodus, and the pleon somites are carinated.

Mecochirus germari Garassino (1996: 346, figs. 9, 10, 26–29), from the early Sinemurian of Lombardy (Italy), differs from *M. robbianoi* by its coarsely tuberculated carapace, without cephalic anterior carinae, by its sub-chelate first pereiopod bearing two strong longitudinal carinae along all segments, and the carpus half as long as the propodus.

The original material described as *Mecochirus eckerti* Frentzen (1937, fig. 2), from the early Toarcian of Germany, is not complete, but the proportions among the various podomeres of the first pereiopods are different from those in *M. robbianoi* n. sp. although both specimens are approximately of similar overall size. Besides, the very long dactylus of the German species is somewhat curved, and being disarticulated, it apparently lacks the hook-like projection present in the Patagonian species. Instead, the first pereiopod of *M. eckerti* is subchelate, with a long, curved, pointed thorn at the inner distal end of each propodus.

Mecochirus pearcei McCoy, from the Oxfordian of southern England (Carter 1886, pl. 16, figs. 13, 13a), has a merus and carpus of approximately the same length. *Mecochirus peytoni* Woodward (1876: 48, pl. 6, figs. 3–4) from the Kimmeridge Clay in southern England and Belgium, and *M*. cf. *eckerti* Frentzen in Etter 2004, from the Middle Jurassic of Switzerland, have unusually long rostra.

The species previously known from the Late Jurassic of the southern Hemisphere can also be easily distinguished from *M. robbianoi*. *Mecochirus chilensis* Förster, from the Kimmeridgian of northern Chile, is known from several carapaces (Förster and von Hillebrandt 1984, pl. 2, figs. 1–8; pl. 3, figs. 1–2; text figs. 3–7), which are characterized by a strong longitudinal ridge in the branchial region that is a continuation of the antennal ridge. This feature is missing in the species here described, but the size and shape of the rostrum are comparable, as are also the proportions between anterior and branchiocardiac regions of the carapace. *Mecochirus marwicki* Glaessner (1960, pl. 2, figs. 2–3, text-fig. 1), from the Heterian (Late Jurassic) of New Zealand, has a styliform, long rostrum, and is clearly distinguishable because all segments of the first pereiopod are strongly spinose.

An undescribed specimen of *Mecochirus* sp. from Norian (Warepan) deposits of Taringatura Hills, New Zealand (Feldmann and Keyes 1992, pp. 12, 15, 67, 68) consists of a single pustulose carapace, which is longer than high, apparently with an inferior groove and without any cephalic anterior carinae, but has only few proximal fragments of the pereiopods preserved. If this material is indeed a *Mecochirus*, it would be the oldest (Triassic) record for the genus, yet it is clearly distinguishable from *M. robbianoi*.

Preservation and taphonomy

As is frequent among fossil glypheoids and astacoids (Feldmann et al. 2002), the specimen is preserved in lateral view (Fig. 2), since this is the stable resting position after death. Although the abdomen is slightly displaced from the carapace, the preserved relative position of the pereiopods and carapace indicates that the specimen was a corpse rather than a molt (cf. Simpson and Middleton 1985, fig. 5; Feldmann 2003, fig. 1 for good examples of fossil molts).

The material is a nearly complete exoskeleton, preserved in a fine-grained sandstone bed, and both part and counterpart are available. The specimen is fairly well preserved, but it is not intact: in parts it is still articulated, but somewhat dismembered and slightly disturbed, and some parts are missing, all probably due to activities by scavenger organisms. This is also suggested by the presence of a large amount of very small, comminuted, cuticle fragments around the specimen, partly concentrated near the abdomen and arranged as a trail that extends away from the dorsal part of the carapace-abdomen junction (see Fig. 2a, cf. Seilacher 2007, pl. 75). There is no indication as to the identity of the scavengers, but it is obvious that they were organisms that could not gulp the whole carcass or bite off large parts of it. The role of scavenging as a taphonomic process in the preservation of decapods has only been examined superficially (Feldmann 2003: 1033), but it is believed to be a major factor in the destruction of burrowed arthropod remains (Plotnick 1986).

Missing telson, uropods, terminal abdominal somite and pleopods appear compatible with a cephalopod scavenger, inasmuch as certain selective scavenging behavioral patterns recorded in extant *Nautilus* (Tshudy et al. 1989) might have been widespread since Jurassic times. Living nautiloids are known to consume dead decapod crustaceans as well as their molts, which appear highly fragmented in their gut contents (e.g., Saunders et al. 1978; Tshudy et al. 1989). More conclusive evidence is needed in this case, since participation by other necrophagous animals (including crustaceans) cannot be dismissed.

The slab containing the specimen also shows clear evidence of the activity of small burrowing organisms, which probably contributed to physically disturb the carcass. These left very small, slender galleries less than 1 mm in cross section, which may form flexuous loops with parallel arms (Fig. 2a, b).

As Etter 2004: 389 clearly summarized, "the non-mineralized parts of the cuticle and the other soft-parts decay within a few days ... and within a few weeks, the sclerotized parts of the cuticle become decalcified and hence softer". He concludes that transport without destroying the remains is possible only within the first few days after death, and during that time such destruction is mainly due to scavenging and/or the activity of burrowing infauna.

The articulation and position of the skeleton pieces of the material here described point to absence of transport prior to burial, and to a relatively rapid and definitive burial after death (see Schäfer 1972, p. 127). The action of scavengers could have taken place before or, more probably, just after burial. Nevertheless, this action was limited and probably lasted only from some hours to a few days, according to Plotnick's (1986) burial experiments of shrimp carcasses. He concluded that the degrees of sediment and exoskeleton disruption depend directly on the size and density of scavengers and bioturbators.

Palaeoecology

Förster (1971) suggested that Mecochirus species fed on small invertebrates and were endobenthic, either as shallow burrowers or hidden in holes to ambush prey. He compared their mode of life to the extant Nephrops species and stressed that the former could not build Thalassinoides-like burrows because the very long first pereiopod would have made it impossible for the organism to turn around within such burrows. Due to the weakly calcified carapace of Mecochirus cf. eckerti Frentzen, Etter (2004: 387) assumed a mainly endobenthic mode of life for it, yet he further indicated that Mecochirus and Thalassinoides never occur in the same or adjacent horizons. However, a population of an Early Cretaceous species referred to Mecochirus was found within Thalassinoides burrows in Portugal (Neto de Carvalho et al. 2007), indicating that they were the producers of the burrows and at least that species had an infaunal mode of life.

On the other hand, Simpson and Middleton (1985) discussed the possible mode of life of the Early Cretaceous mecochirids *Meyeria magna* (McCoy) and *Meyeria ornata* (Phillips), and concluded that they were active members of

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the epifauna and probably scavengers rather than carnivores. The type species of *Mecochirus* was sometimes found at the end of its crawling tracks in Solnhofen (e.g., Glaessner 1969, fig. 243A; Viohl 1990; Seilacher 2007, pl. 75), revealing that they were able to crawl either forward or backward.

It is clear from their morphology that the first and second pereiopods were not used for walking. The function of the extremely long first pereiopods is still debatable. Förster (1971) proposed that they were grasping appendages, which is very unlikely from a functional point of view, due to difficulties in transferring any prey to the mouth; thus, he later agreed that the main function of these limbs could have been sensory (Taylor 1979). Feldmann and West (1978) argued that the dactylus could be used to probe the sediment, and Simpson and Middleton (1985) favored this view. Förster (1971) also stated the additional advantage of a possible defensive function for the long first pereiopods.

The function of the second pereiopods of *Meyeria* and other mecochirids was also discussed by Simpson and Middleton (1985), who compared their shape with similar appendages of living forms, and concluded that they were probably involved in feeding, passing food to the mouth, and/or in burrowing or digging for food.

Mecochirus robbianoi n. sp. was found (and apparently lived) on a fine-grained substrate in a fully marine, nearshore, storm-dominated environment, as indicated by the accompanying fauna with free epifaunal (probably swimming) bivalves, small gastropods and a few shallow burrowing bivalves. The presence of detritivorous palaeotaxodonts suggests that the sediments had a rich organic content.

Palaeobiogeography

The genus Mecochirus is known with certainty from Sinemurian to Maastrichtian times, but only between the Oxfordian and Albian the genus attained a wide geographical distribution (Europe, North America, South America, New Zealand, Antarctica and Africa, see Fig. 5). By contrast, very little is known of the geographic distribution of the genus during the Early and Middle Jurassic, when up to now it was only known from Europe (Quenstedt 1854, 1856–1857, Oppel 1862; Carter 1886; Krause 1891; van Straelen 1924; Beurlen 1928; Glaessner 1929; Frentzen 1937; Förster 1971; Etter 2004; Garassino 1996). Nevertheless, Feldmann and Schweitzer (2006) indicated that Mecochirus "had its earliest occurrence in the North Atlantic in Sinemurian time but radiated into the Southern Hemisphere by the Toarcian," but they did not provide any evidence to back this statement. This new record is thus



Fig. 5 Palaeobiogeographical distribution of *Mecochirus*. Base map modified from various sources, corresponding to Late Jurassic palaeogeography (S.D.). Further discussion in text. Data from: Beurlen 1928; Carter 1886, 1898; Collins and Rasmussen 1992; Etter 2004; Feldmann and Keyes 1992; Feldmann et al. 2007; Förster 1971; Förster and von Hillebrandt 1984; Frentzen 1937; Garassino 1996; Garassino and Schweigert 2006; Glaessner 1929, 1960; Hée 1924; Herrick and Schram 1978; Krause 1891; Oppel 1862; Quenstedt 1854, 1856–1857; Secretan 1964, 1968; van Straelen 1924, 1936; Taylor 1979; da Veiga Ferreira 1955; Woodward 1876

highly significant because it clearly shows that by that time the group was already well distributed around the world.

It is becoming more evident that several groups of decapod Crustacea inhabited southern South America by the beginning of the Jurassic and that the reduced fossil record of the group in the Southern Hemisphere by that time may be mostly the result of insufficient knowledge of the faunas. There is a late Triassic record from southern New Zealand (Feldmann and Keyes 1992; see above), which, even if eventually not confirmed as a *Mecochirus* s.s., still adds an interesting perspective to understand the origin and early distribution of the Mecochiridae.

Conclusions

The early representative of the genus *Mecochirus* here described already shows the main diagnostic features of the genus. This is the oldest record of a mecochirid from South America, and the first one for Argentina, and considerably extends the palaeogeographic distribution of the genus

during the Early Jurassic, previously known only from Europe by that time.

Mecochirus robbianoi n. sp. lived in a fully marine, near-shore, storm-dominated environment, probably on a fine-grained sandy substrate. The specimen appears to be a corpse slightly disarticulated by the action of scavengers. Taphonomic conditions suggest that there was no significant transport prior to a relatively rapid and deep burial after death.

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