

A new Triassic decapod, *Platykotta akaina*, from the Arabian shelf of the northern United Arab Emirates: earliest occurrence of the Anomura

Jérôme Chablais · Rodney M. Feldmann ·
Carrie E. Schweitzer

Received: 10 May 2010 / Accepted: 27 July 2010 / Published online: 11 August 2010
© Springer-Verlag 2010

Abstract A Triassic decapod crustacean is described here for the first time from the Norian-Rhaetian Ghalilah Formation of the Musandam Peninsula, United Arab Emirates. The single specimen *Platykotta akaina* n. gen n. sp. is referred to a new family Platykottidae. The studied crustacean, initially with only the ventral exposure preserved, was collected from shallow-water, burrowed limestones. Using a chemical preparation, the dorsal view revealed a well-preserved, chitinous, granular carapace exhibiting characteristic carapace morphology and groove pattern of the Eocarcinoidea, the superfamily to which the new family is assigned. The dorsal view together with the ventral surface, rarely seen in the fossil record, provide new insight into the morphology of representatives of the Eocarcinoidea.

Keywords Triassic · Decapoda · Anomura · Eocarcinoidea · Tethys · United Arab Emirates

Kurzfassung In dieser Arbeit wird ein neuer triassischer Zehnfüßkrebis aus der Ghalilah-Formation (Norium-Rhaetium) der Musandam-Halbinsel (Vereinigte Arabische

Emirate) beschrieben. Das einzige Exemplar *Platykotta akaina* n. gen n. sp. wird der neuen Familie Platykottidae zugeordnet. Der hier untersuchte Krebs, der ursprünglich nur von der ventralen Seite sichtbar war, wurde in einem flachmarinen Kalkstein gefunden. Die dorsale Seite, die mit Hilfe chemischer Präparation freigelegt wurde, ergab einen gut erhaltenen, chitinenen, granulierten Carapax mit dem charakteristischen Furchenmuster der Eocarcinoidea, der Überfamilie, zu der die neue Familie Platykottidae gestellt wird. Die beschriebene dorsale und vor allem die ventrale Partie, die fossil nur selten überliefert ist, liefern neue Erkenntnisse über die Morphologie der Vertreter der Eocarcinoidea.

Schlüsselwörter Trias · Decapoda · Anomura · Eocarcinoidea · Tethys · Vereinigte Arabische Emirate

Introduction

Knowledge about Triassic decapod crustaceans is very limited, due to the paucity of Triassic fossils throughout the world. Around 65 species of Triassic shrimps and lobsters have been reported, mainly from Tethyan and Eurasian localities (i.e., Peri-Tethys area), as well as a few from North America (Schram 1971; Feldmann 1981; Zonneveld et al. 2002; Amati et al. 2004) and Madagascar (Garassino and Teruzzi 1995; Garassino and Pasini 2002). Feldmann and Schweitzer (2006) compiled the records of decapods and their paleobiogeographic patterns from the Southern Hemisphere spanning the Early Triassic to Pleistocene. Recently, Schweitzer et al. (2010) compiled all known species of fossil decapod crustaceans.

From a general point of view, the crustaceans rapidly diversified in the Mesozoic, taking advantage after the

J. Chablais (✉)
Department of Geology and Paleontology,
University of Geneva, 1205 Geneva, Switzerland
e-mail: jerome.chablais@unige.ch

R. M. Feldmann
Department of Geology,
Kent State University, Kent, OH 44242, USA
e-mail: rfeldman@kent.edu

C. E. Schweitzer
Department of Geology, Kent State University at Stark,
6000 Frank Ave. NW, North Canton, OH 44720, USA
e-mail: cschweit@kent.edu

Paleozoic of the demise of marine arthropods (e.g., trilobites) that would otherwise have occupied similar ecological niches (Zonneveld et al. 2002). The decapod fossil record has been particularly well recorded from Late Jurassic–Early Cretaceous rocks (Feldmann 1981; Feldmann and Schweitzer 2006), but decapod fossils remain rare in the fossil record in comparison with other marine organisms such as ammonites. One reason for the relatively small number of fossil decapod crustaceans is the susceptibility of the carapace to be consumed by many predators and scavengers (Tshudy et al. 1989; Feldmann 2003) and to the post mortem fragmentation of organisms by wave action (Feldmann 1981). These last two factors, together with the rate of sedimentation and microbial activity, are the main processes decreasing crustacean preservation potential. The completeness of a fossil crustacean is enhanced by the absence of scavengers and bottom-dwelling organisms, anaerobic conditions at the bottom, as well as sedimentation in low-energy environments (Förster 1985). As a result, the discovery of new fossil decapod crustaceans commonly marks a notable addition to the taxonomic and systematic knowledge of the group.

Thus, the present specimen, identified as a Triassic anomuran and collected from the Upper Triassic carbonates of the Ghalilah Formation (Musandam Peninsula, United Arab Emirates), brings new insight into crustacean origins, dispersal, and radiation along the carbonate shelf of the Tethys during the Triassic. Until now, Triassic crustaceans known from the Southern Hemisphere only have been reported from Madagascar (Garassino and Teruzzi 1995; Garassino and Pasini 2002; Feldmann and Schweitzer 2006). This is the first known occurrence of anomurans from this part of the world. Furthermore, the new species represents the oldest occurrence of the *Anomura* MacLeay (1838) known to date.

Geological setting

The investigated area is located in the Musandam Peninsula, which forms the northern extension of the Oman Mountains and separates the Persian Gulf from the Gulf of Oman (Fig. 1a). The Musandam Mountains are situated in two countries, the United Arab Emirates and Oman. They offer spectacular exposures of Permian to Cretaceous shallow-marine carbonates which were deposited on the passive margin of the Arabian Plate bordering the southern Tethys during that time (Glennie et al. 1974). Permian to Cretaceous rocks were thrust and uplifted due to the folding of the Zagros Mountains during the Cenozoic (Searle 1988). In comparison with the Zagros Mountains, the Musandam Mountains have undergone minor tectonic

overprinting, exhibiting well-preserved lateral and vertical facies relationships.

The whole sedimentary succession can exceed 1,500 m in thickness and can be stratigraphically grouped into the Bih (Upper Permian), Hagil (Lower Triassic), Ghail (Middle Triassic), Milaha (Norian), and Ghalilah (Norian–Rhaetian) Formations (Fig. 1b). Maurer et al. (2008, 2009) gave a detailed overview of the stratigraphy, facies, and evolution of the Arabian shelf in this region.

The fossil decapod (sample MHNG GEPI 78420) was found in Wadi Naqab close to Ras Al Khaimah City (United Arab Emirates). The studied section (Fig. 1c) starts with the Milaha Formation at the base and ends with the Ghalilah Formation at the top. The fossil decapod was collected in an extensively burrowed limestone level, at the top of the section, within the Ghalilah Formation (Norian–Rhaetian). Important fossiliferous carbonates surround the sampling area containing megalodontid and wallow-conchid bivalves, brachiopods, crinoids, and sponges (Senowbari-Daryan and Maurer 2008), as well as dendroid and phaceloid corals. This biotic association reflects warm water conditions in a tropical to subtropical, subtidal setting, with open marine connections (Maurer et al. 2008).

The great abundance and high biodiversity of decapod crustaceans in the shallow-water environment of the Arabian shelf during the Triassic is suggested by the large number and variety of burrows on the exposures (Fig. 2). The collected fossil came from a dismantled, burrowed limestone level and was associated with large *Spongeliomorpha* burrows (maximum 5 cm in diameter, similar to in Fig. 2a). Reptantian crustaceans with long cephalothorax and slightly curved abdomen are typically bottom-dwelling organisms, and they seem well adapted to such settings.

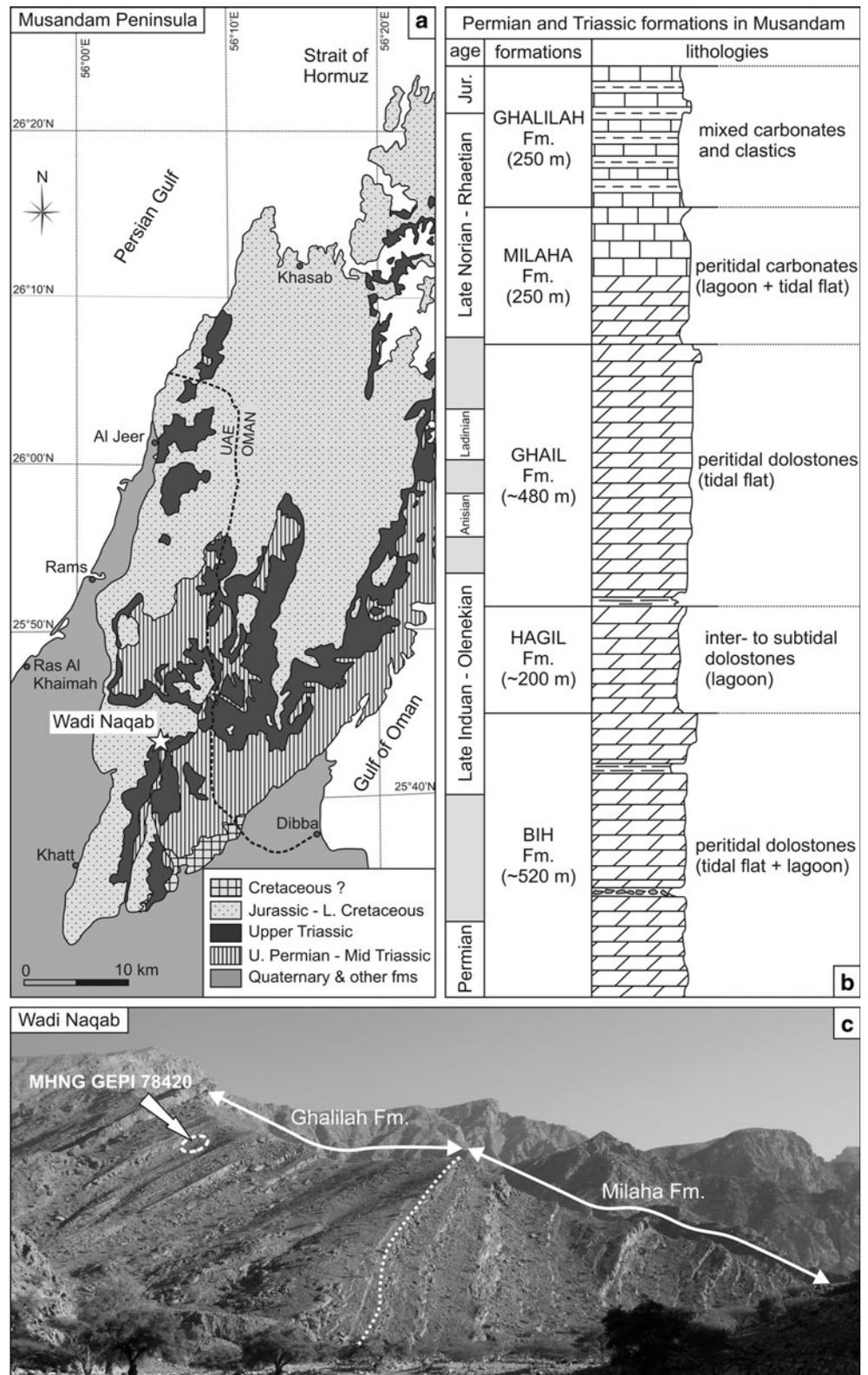
The Ghalilah Formation is assumed to have been deposited during the late Norian to Rhaetian, documented by the foraminiferal index marker *Triasina hantkeni* Majzou (1954), the hydrozoan *Heterastridium* Reuss (1865), and the ammonoid *Neotibetites* Krumbeck (1913) of Norian to possibly Rhaetian age (Maurer et al. 2008).

Material and methods

Only one decapod specimen (sample MHNG GEPI 78420) has been discovered. Nevertheless, several small fragments of crustacean carapaces and especially very small remains of ventral parts (Fig. 3a) have been observed along the different Upper Triassic sections investigated during the study of the Musandam Peninsula.

Originally, only the ventral surface of the specimen was exposed, making identification difficult because there are few specimens preserved in this orientation with which it could be compared. The ventral surface is preserved in a

Fig. 1 **a** Distribution of the Permian to Cretaceous shallow-marine carbonates across the Musandam Peninsula, including the location of the studied area in Wadi Naqab (*white star*, modified from Senowbari-Daryan and Maurer 2008). **b** Composite stratigraphic log of the Upper Permian to Triassic formations occurring in Musandam (modified from Maurer et al. 2008). **c** Outcrop photograph of the Wadi Naqab section (25°43'28.6"N, 56°05'51.6"E) where the studied fossil (sample MHNG GEPI 78420) was collected



fine-grained, bioclastic mudstone-wackestone, whereas the dorsal part, originally obscured, was covered by coarse-grained bioclastic packstone.

Due to the weakness of the carapace, the dorsal part was exposed using a chemical preparation method, more common for fish fossil extraction and which is more delicate

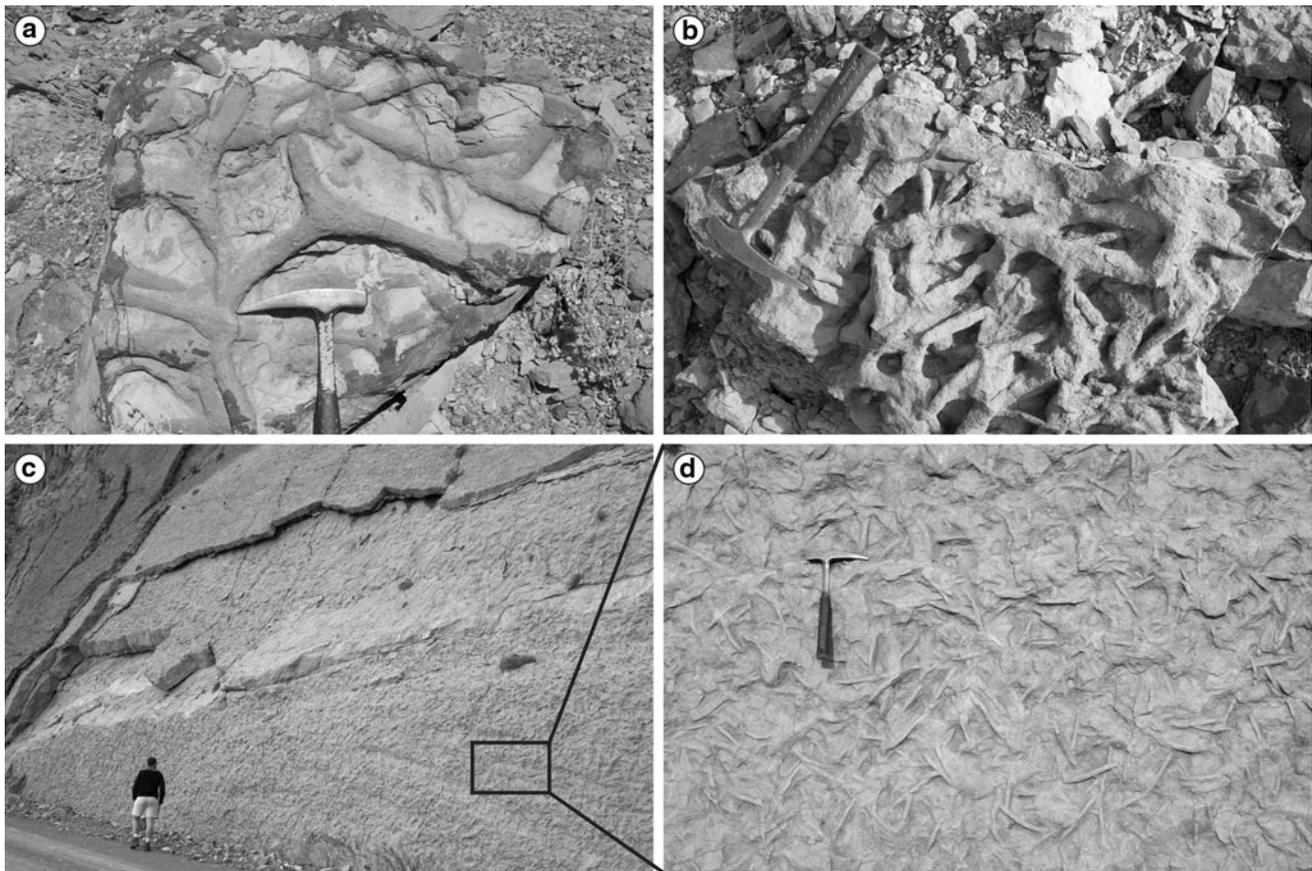


Fig. 2 Different types of burrows cropping out in the Upper Triassic limestones of the Milaha and Ghalilah Formations, Musandam Peninsula. **a, b** Wadi Milaha, southeast of Ras Al Khaimah

(25°45′37.5″N, 56°03′05.0″E). **c, d** Amazing vertical level completely burrowed, observed along the track between Khasab and Dibba (25°57′55.50″N, 56°13′34.58″E)

than mechanical techniques. Excellent results are generally obtained quite quickly, and much more fragile structures, essential for anatomical description, may be revealed than by mechanical means.

The chemical technique employed here, requiring a well-ventilated area, is an acid preparation, using dilute organic (acetic) acid to dissolve limestone but leaving the carapace (chitin) intact. This technique is well established (see Maisey 1991, pp. 98–103) and involves dissolving away the calcareous limestone matrix to expose the chitinous carapace of the crustacean, after embedding the fossil in a frame of transparent epoxy resin. This technique is also called the “transfer method” (Maisey 1991), because the fossilized remains are transferred from the limestone matrix to the resin, making the previously entombed carapace visible.

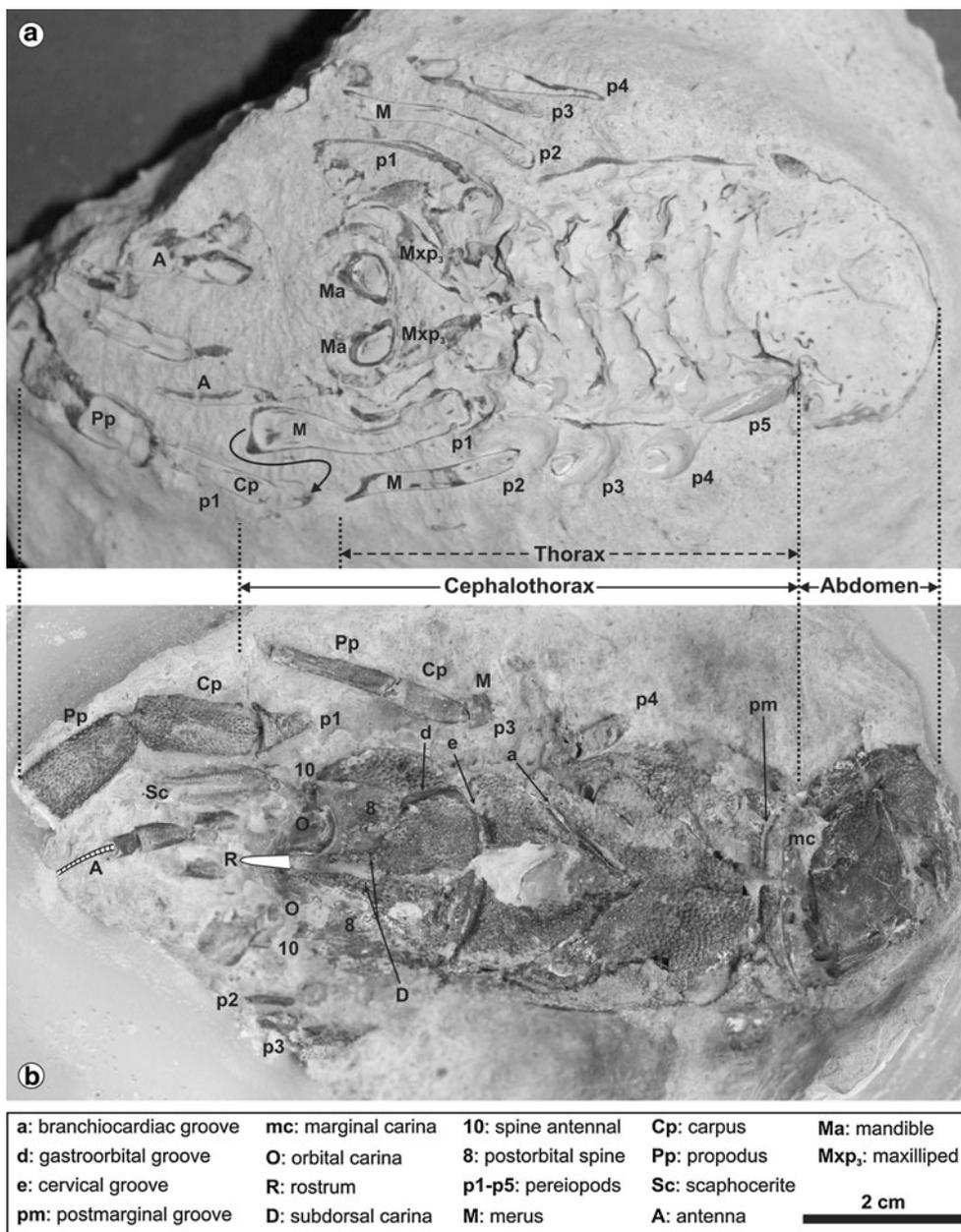
The initial step is to trim away as much excess matrix as possible, using a diamond saw. A mold (dam) to contain the embedding resin and the trimmed sample is then constructed using silver foil. A cement paste is applied along the outer base (perimeter) of the silver foil, forming a watertight bulkhead. A paraffin solution is

poured into the silver-foil mold up to the top of the sample to maintain this latter within the mold. The second solution poured into the mold is the transparent epoxy resin (type Tanslux D150 from Axson), embedding the specimen and covering the area to protect it (maximum 2 cm thick). The epoxy resin used here is characterized by low viscosity, preventing bubble formation, and ensuring high transparency.

When completely set, the silver-foil mold and the excess paraffin are peeled away.

Diluted acetic acid solution (5–10%) is used to dissolve the calcareous matrix, but formic acid can be substituted. A trial test should be conducted to determine which acids cause the least damage to the carapace. The diluted acid is then mixed in a suitably sized rubber or durable plastic container, and the embedded specimen is then immersed. The immersion can vary in duration, depending on the solution strength and matrix content, but the degree of reaction has to be constantly monitored. A 24-h immersion is normal during the first weeks. Once an area of carapace is visible, the sample is delicately removed from the acid bath and washed in running water (very low energy) for at

Fig. 3 Ventral (a) and dorsal (b) views of *Platykotta akaina* n. gen. n. sp. with codification of the groove patterns and other morphological criteria



least 24 h to remove any residual acid and soluble byproducts, and then allowed to dry for several hours. The next step is the conservation treatment of the fossil before being returned to a fresh acid bath. This treatment is necessary each time the specimen is treated in acid, in order to harden and strengthen the exposed carapace. We used a cyanoacrylate solution (“super glue”) applied to the exposed carapace by a glass pipette to consolidate the fossil. Cyanoacrylate solution is desirable because it can be easily removed if needed when thinned in acetone.

Many cycles of acid immersion and strengthening of the specimen are required (about 3 months) to obtain the present result of exposure of the dorsal surface. At the end, the embedded specimen is completely immersed in an

acetone bath (15 min or more) to remove all the cyanoacrylate layers to obtain a clean carapace (here, dorsal face) for photography. Cyanoacrylate layers are thus completely dissolved in the bath, obviating use of brushes to remove excess acetone which could cause irreversible damage. After photographic treatment, additional applications of cyanoacrylate are necessary to protect the exposed carapace from possible damage.

Systematic paleontology

- Order Decapoda Latreille, 1802
- Suborder Pleocyemata Burkenroad, 1963
- Infraorder Anomura MacLeay, 1838

Discussion The new decapod taxon is placed within the Anomura based upon characters judged to be apomorphic for the infraorder (Dixon et al. 2003; McLaughlin et al. 2007). These include a carapace that is not fused to the epistome, possession of a large antennal peduncle and a notch on the carapace defining the position of the antenna, possession of at least two chelate pereopods with first cheliped lying in a plane parallel to the long axis of the carapace, and reduced or absent uropods. This combination of characters separates the anomurans from shrimp, lobsters, and crabs. In addition to these characters, the new decapod taxon possesses stout mandibles and long, foliaceous third maxillipeds. These same features are seen in members of the Chirostylidae and Galatheidae, in which the configuration is nearly identical to that seen in the new taxon. This strongly supports an alliance with the Anomura. Finally, the new taxon has a large first pereopod and appears to have a much reduced fifth pereopod based upon the comparative size of the coxae. Pereopods 2–4 are moderate in size. This configuration is seen in anomurans, but not in lobsters.

Superfamily Eocarcinoidea Withers, 1932

Discussion Until now, the Eocarcinoidea has been restricted to a single species, *Eocarcinus praecursor* Withers (1932). Originally placed within the Brachyura and considered to be the most primitive representative of the infraorder (Withers 1932; Förster 1979), *E. praecursor* Withers has recently been reconsidered and placed within a unique superfamily of the Anomura (Feldmann and Schweitzer 2010). The basis for the reassignment included the observation that the species does not reflect a degree of carcinization warranting placement within the Brachyura, in addition to many other features. Specifically, *E. praecursor* Withers has an elongate, cylindrical carapace lacking true orbits in which the epistome is not fused to the carapace, an abdomen with well-developed articulating rings and pleurae that extend posteriorly rather than being carried ventrally, first pereopods that are carried more or less parallel to the long axis of the animal rather than transverse to it, and chelipeds on at least one other pair of pereopods besides the first. Within the limits of the material upon which the new taxon is defined, these same generalizations apply as well. Thus, it is assigned to the Eocarcinoidea.

In addition to these similarities, the architecture of the cephalic regions in *Eocarcinus* Withers and the new taxon exhibits enough similarities to ally these two taxa in the same superfamily. Similarities include well-defined cervical and antennal grooves, a well-developed, axially sulcate rostrum, and similar orbital structures. Possession of two

transverse grooves is a feature that is observed in *Eocarcinus praecursor* Withers and the new taxon, but is rarely observed in clawed or achelate lobsters. In contrast, possession of two grooves is not typical of astacideans, glypheoids, and palinurids.

Family Platykottidae n. fam.

Included genus *Platykotta* n. gen.

Diagnosis Eocarcinoid with cephalic region bearing prominent spines; epigastric region elevated slightly above remainder of cephalic region, flattened, and defined by finely spinose rim. Carapace granular. Abdominal somites with smooth, axially keeled tergum and granular pleura. Sternum triangular, sternites increasingly wide posteriorly; coxae of pereopods decreasing in size posteriorly; mandibles stout, heavily calcified; third maxillipeds long, pediform.

Discussion An important character that is exhibited in the new taxon and that serves as a distinguishing feature of Platykottidae n. fam. is the presence of a triangular sternum that widens posteriorly and places the coxal elements of the pereopods away from the midline. This form is in marked contrast to the glypheoid and astacid lobsters, in which the sternum is extremely narrow and the coxae nearly meet at the midline. The triangular form of the sternum is exhibited in palinurid lobsters, a group that is excluded from consideration because of the development of carapace grooves discussed above. The sternum is not known in *Eocarcinus* Withers, and it only may be inferred from the outline of the carapace and the orientation of the preserved specimens. Many other members of the Anomura possess a triangular sternum. These include the Galatheidae, Chirostylidae, and Aeglidae. Thus, the architecture of the sternum of the new taxon clearly allies it with other Anomura.

The configuration of the sternum commonly dictates the resting position of corpses. Because astacideans and glypheoids have a very narrow sternum, resulting in a laterally compressed carapace, they are most commonly preserved in lateral aspect. The palinurids, by contrast, possess a broad, triangular sternum, and the carapace tends to be broad and dorsoventrally compressed. As a result, they are generally preserved in dorsal aspect. The present specimen, as with the specimens of *E. praecursor* Withers, is also preserved with the dorsal surface parallel to the bedding surfaces. Although a sternum has not been observed in *E. praecursor* Withers, its relatively broad carapace and burial posture supports the supposition that the sternum was broad.

One aspect of the new taxon as well as *Eocarcinus* Withers that differs from some other anomurans is that the carapace is much longer than wide. Most anomurans bear

carapaces that are quite variable in dimensions, but they are typically only slightly longer than wide.

Genus *Platykotta* n. gen.

Type species *Platykotta akaina* n. sp., by original designation.

Included species *Platykotta akaina* n. sp.

Etymology The generic name is derived from the Greek *platys* = flat, and *kotta* = head, in reference to the flattened surface of the metagastric region. The gender is feminine.

Diagnosis Carapace in dorsal view, bearing two deep transverse grooves; anterior with prominent rostrum and several strong spines; metagastric region elevated, flattened, rimmed by small spines; entire surface granular. Abdominal somites 1 and 2 smooth axially, granular laterally. Pereiopods generally slender and granular. Sternum triangular, broad posteriorly, with paired pits on each sternite. Coxae of pereiopods decreasing in size posteriorly; mandibles stout, heavily calcified; third maxillipeds long, pediform.

Platykotta akaina n. sp. (Figs. 3, 4).

Etymology The trivial name is derived from the Greek *akaina* = thorn or spine, in reference to the spinose nature of the cephalic region.

Diagnosis As for genus.

Description Terminology and notations for grooves, spines, and carinae follow the definitions of Holthuis (1974). Carapace large, 50.2 mm long measured from base of deep, smoothly concave, orbital carina to posterior midline. Carapace from cervical groove to base of orbital concavity 16.6 mm, complexly sculptured. Rostrum long, extending 7.0 mm from base of orbital concavity to broken tip, axially sulcate, granular laterally, sharply rimmed, and bearing anteriorly directed spines increasing in size posteriorly. Rostral rim continues onto carapace about 1/3 distance to cervical groove as subdorsal carina (D). Rostral sulcus continues onto carapace to cervical groove. Cervical groove (e) smooth and deeply impressed, smoothly concave forward, continuous across midline. Gastroorbital groove (d) smooth, relatively broad, extends from cervical groove anteriorly about 1/2 distance to base of orbit, at which point it bifurcates with dorsal limb extending just posterior to strong, forward-directed postorbital spine (8) becoming obscure as it approaches subdorsal carina; ventral limb extends to base of very strong, sharply pointed antennal spine (10). Metagastric region defined laterally by gastroorbital groove, surface slightly elevated, flattened, bounded by well-defined, finely spinose rim. Postorbital

and hepatic (?) regions flare out ventrally, less coarsely granular than axial area.

Carapace region bounded by cervical groove and branchiocardiac groove (a) uniformly granular. Posterior groove (postcervical?) intersects midline at about 45° angle. Abdominal somites poorly preserved. Antermost preserved somite (2?) with axially keeled tergum. Tergum smooth medially and separated from granular lateral area by shallow, concave-forward depression. Pleura granular, margins not exposed.

Thoracic sternum prominent, broadly triangular. Sternites 1–3 obscured, apparently small, narrow. Sternites 4–7 broadening posteriorly, axially keeled, laterally with transversely ovoid depressions. Sternite 8 slightly narrower, not axially keeled.

Antennae (A) with at least two segments before flagellum; proximal one with strong anteriorly directed spine. Scaphocerite (Sc) prominent, flattened, bearing sharp terminal spine. Mandibles (Ma) poorly preserved, strong, ovoid in outline. Third maxillipeds (Mxp₃) long, slender, arising on sternite 3 very near midline.

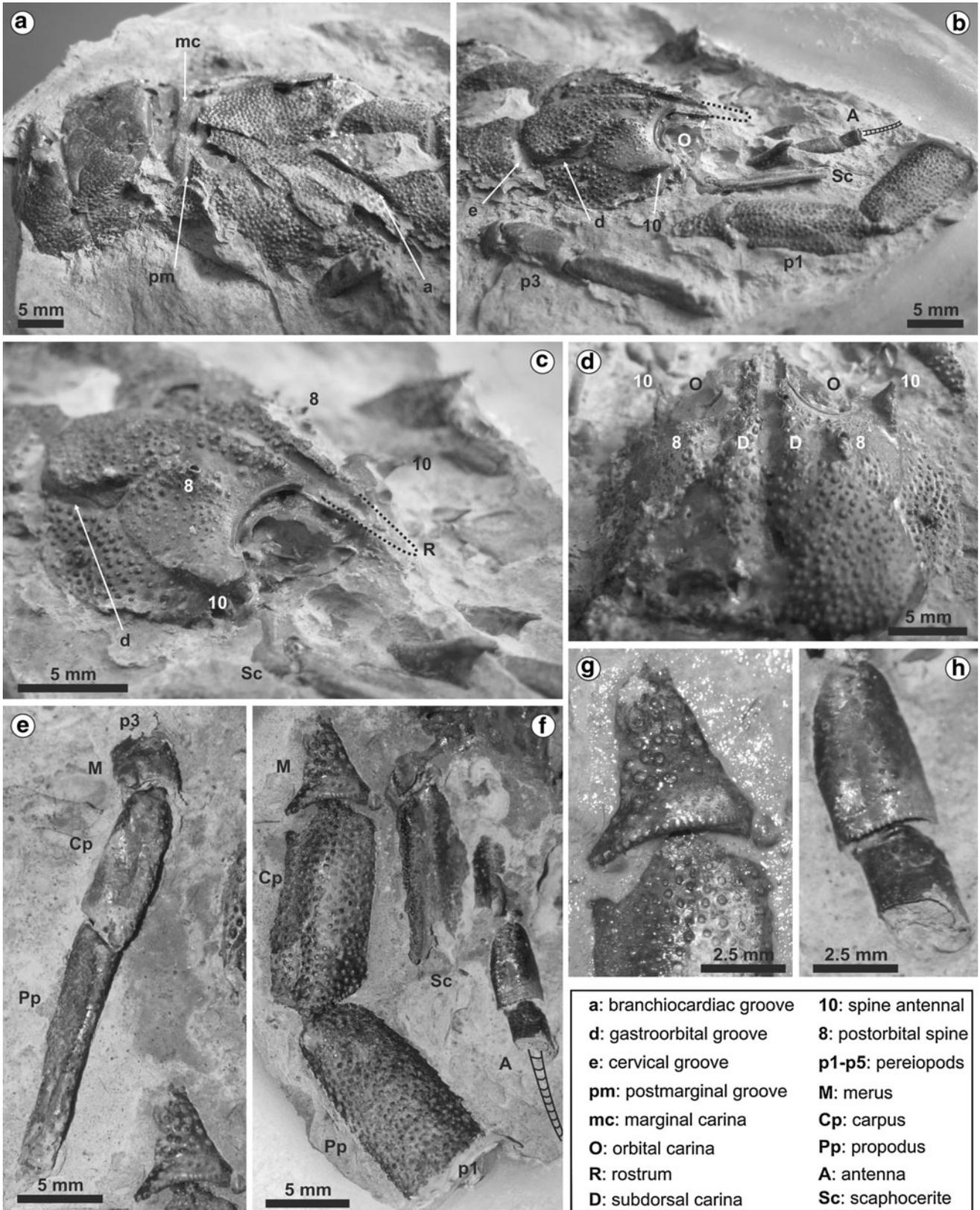
Pereopod 1 (p1) stronger than pereopods 2–5, apparently nearly circular in outline, granular; terminal segments not preserved. Pereopod 2 (?) flattened with keel on upper surface; propodus long, keeled, flattened laterally.

Holotype MHNG GEPI 78420, deposited in the Natural History Museum, Geneva, Switzerland.

Occurrence Late Norian to Rhaetian from the Ghalilah Formation on the Musandam Peninsula, United Arab Emirates, at approximately 25°44'N, 56°5'E.

Discussion Comparison of the two species, in separate families of the Eocarcinoidea, suggests some morphological trends that render *Platykotta* n. gen. somewhat more “lobster-like” than *Eocarcinus* Withers. The latter genus has a narrower, less strongly ornamented and regionalized cephalic area while retaining the broad branchial region, and it possesses a well-defined cardiac region in contrast to those features seen in *Platykotta* n. gen.

Placement of *Platykotta akaina* n. gen. n. sp. within the Anomura extends the range of the infraorder back to the Late Triassic. Previously, the earliest record of the group was that of *Eocarcinus praecursor* Withers from the Early Jurassic (Pliensbachian) of Yorkshire, England (Förster 1979). Recently, Senowbari-Daryan et al. (2010), using coprolite microfossils, emphasized an exceptional worldwide biogeographic distribution of decapod crustaceans over the Tethyan and Panthalassan Oceans during the Triassic. Thus, although the fossil record of body fossils of decapods remains limited in the Triassic, one can certainly anticipate additional discoveries in the future. It is possible



◀ **Fig. 4** Detailed photographs of *Platykotta akaina* n. gen. n. sp. with codification of the groove pattern and other morphological criteria. **a** Abdomen and posterior part of the carapace. **b** Anterior part of the carapace. **c, d** Anterior part exhibiting the rostrum, orbit, grooves, and spines. **e** Pereiopods p3 with merus carpus and propodus segments. **f** Pereiopods p1, scaphocerite, and antenna with reconstructed broken part. **g, h** Finely ornamented articulations of the pereiopod p1 and of the antennal peduncle

that fragmentary preservation or preservation in odd orientations may make discovery difficult. For example, the ventral exposure (Fig. 3a) of *Platykotta* n. gen. offers an unfamiliar view, making recognition of it as a crustacean fossil unlikely. Indeed, relatively few examples of venters exist in the fossil record, and it would be easy to miss this type of fossil in the field, especially if the pereiopods are not preserved.

Acknowledgments We sincerely thank P.-A. Proz and the Natural History Museum of Geneva, Switzerland, for help and assistance in the technical preparation of the fossil. We thank R. Martini and S. Rigaud for their invaluable help during field trips in the Musandam Peninsula, and F. Maurer for giving the precise coordinates and geological setting of the studied section. We also thank the reviewers A. Pagani and G. Schweigert for their constructive criticisms during the review process. We also thank K. Kremer for scientific advice. C. Melish and M. Munt facilitated our study of *Eocarcinus praecursor* at the Natural History Museum, London, UK. Fieldwork was supported by the Swiss National Science Foundation (grant #200021-113816 of R. Martini to J. Chablais). Museum work was supported by National Science Foundation grant EF0531670 to Feldmann and Schweitzer.

References

- Amati, L., R.M. Feldmann, and J.-P. Zonneveld. 2004. A new family of Triassic lobsters (Decapoda: Astacidea) from British Columbia and its phylogenetic context. *Journal of Paleontology* 78: 150–168.
- Burkenroad, M.D. 1963. The evolution of the Eucarida (Crustacea, Eumalacostraca) in relation to the fossil record. *Tulane Studies in Geology* 2: 3–16.
- Dixon, C.J., S. Ahyong, and F.R. Schram. 2003. A new hypothesis of decapod phylogeny. *Crustaceana* 76: 935–975.
- Feldmann, R.M. 1981. Paleobiogeography of North American lobsters and shrimps (Crustacea, Decapoda). *Géobios* 14: 449–468.
- Feldmann, R.M. 2003. The Decapoda: New initiatives and novel approaches. *Journal of Paleontology* 77: 1021–1039.
- Feldmann, R.M., and C.E. Schweitzer. 2006. Paleobiogeography of Southern Hemisphere decapod Crustacea. *Journal of Paleontology* 80: 83–103.
- Feldmann, R.M., and C.E. Schweitzer. 2010. Is *Eocarcinus* Withers, 1932, a basal brachyuran? *Journal of Crustacean Biology* 30: 241–250.
- Förster, R. 1979. *Eocarcinus praecursor* WITHERS (Decapoda, Brachyura) from the Lower Pliensbachian of Yorkshire and the early crabs. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1979: 15–27.
- Förster, R. 1985. Evolutionary trends and ecology of Mesozoic decapod crustaceans. *Transactions of the Royal Society of Edinburgh* 76: 299–304.
- Garassino, A., and G. Pasini. 2002. Studies on Permo-Trias of Madagascar. 5. *Ambilogeia karojo* n. gen., n. sp. (Crustacea, Decapoda) from the Lower Triassic (Olenekian) of Ambilobé region (NW Madagascar). *Atti della Società italiana di Scienze naturali e del Museo Civico di Storia naturale in Milano* 143: 95–104.
- Garassino, A., and G. Teruzzi. 1995. Studies on Permo-Trias of Madagascar. 3. The decapod crustaceans of the Ambilobé region (NW Madagascar). *Atti della Società italiana di Scienze naturali e del Museo Civico di Storia naturale in Milano* 134: 85–113.
- Glennie, K.W., M.G.A. Boeuf, M.W. Hughes-Clarke, M. Moody-Stuart, W.F.H. Pilaar, and B.M. Reinhardt. 1974. Geology of the Oman Mountains. *Verhandelingen van het Koninklijk Nederlands Geologisch Mijnbouwkundig Genootschap* 31: 1–423.
- Holthuis, L.B. 1974. The lobsters of the superfamily Nephropidea of the Atlantic Ocean (Crustacea: Decapoda). *Bulletin of Marine Science* 24: 723–884.
- Krumbeck, L. 1913. Obere Trias von Buru und Misól (Die Fogi-Schichten und Asphaltschiefer West-Burus und der Athyridenkalk des Misól-Archipels). *Stuttgart E. Schweizerbart'sche Verlagsbuchhandlung*, 161 p.
- Latreille, P.A. 1802. Histoire naturelle, générale et particulière des Crustacés et des Insectes. *Familles naturelles des genres* 3, 467 p. F. DuFart, Paris
- MacLeay, W.S. 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In *Illustrations of the Annulosa of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836*, ed. A. Smith, 53–71. Fitted out by “The Cape of Good Hope Association for Exploring Central Africa”.
- Maisey, J.G. 1991. *Santana fossils. An illustrated atlas*, 459. Neptune City, NJ: TFH.
- Majzon, L. 1954. Contributions to the stratigraphy of the Dachstein Limestone. *Acta Geologica Academiae Scientiarum Hungaricae* 2: 243–249.
- Maurer, F., R. Martini, R. Rettori, H. Hillgärtner, and S. Cirilli. 2009. The geology of Khuff outcrop analogues in the Musandam Peninsula, United Arab Emirates and Oman. *GeoArabia* 14: 125–158.
- Maurer, F., R. Rettori, and R. Martini. 2008. Triassic stratigraphy, facies and evolution of the Arabian shelf in the northern United Arab Emirates. *International Journal of Earth Sciences* 97: 765–784.
- McLaughlin, P.A., R. Lemaitre, and U. Sorhannus. 2007. Hermit crab phylogeny: A reappraisal and its “fall-out”. *Journal of Crustacean Biology* 27: 97–115.
- Reuss, A.E. 1865. Zwei neue Anthozoen aus den Hallstädter Schichten. *Sitzungsberichte der Königlich-Preussischen Akademie der Wissenschaften* 51: 381–395.
- Schram, F.R. 1971. *Litogaster turnbullensis* (sp. nov.): a Lower Triassic glypheid decapod crustacean from Idaho. *Journal of Paleontology* 45: 534–537.
- Schweitzer, C.E., R.M. Feldmann, A. Garassino, H. Karasawa, and G. Schweigert. 2010. Systematic list of fossil decapod crustacean species. *Crustaceana Monographs* 10: 230 p.
- Searle, M.P. 1988. Thrust tectonics of the Dibba zone and the structural evolution of the Arabian continental margin along the Musandam Mountains (Oman and United Arab Emirates). *Journal of the Geological Society of London* 145: 45–53.
- Senowbari-Daryan, B., and F. Maurer. 2008. Upper Triassic (Norian) hypercalicified sponges from the Musandam Peninsula (United Arab Emirates and Oman). *Facies* 54: 433–460.
- Senowbari-Daryan, B., J. Chablais, and R. Martini. 2010. New crustacean microcoprolites of the Upper Triassic limestones of

- the Sambosan Accretionary Complex, Japan. *Journal of Paleontology* 84: 98–108.
- Tshudy, D.M., R.M. Feldmann, and P.D. Ward. 1989. Cephalopods: Biasing agents in the preservation of lobsters. *Journal of Paleontology* 63: 621–626.
- Withers, T.H. 1932. A Liassic crab, and the origin of the Brachyura. *Annals and Magazine of Natural History* 9: 313–323.
- Zonneveld, J.-P., S.G. Pemberton, T.D.A. Saunders, and R.K. Pickerill. 2002. Large, robust *Cruziana* from the Middle Triassic of Northeastern British Columbia: ethologic, biostratigraphic, and paleobiologic significance. *Palaios* 17: 435–448.