

# The fossil record of *Glypturus* (Decapoda: Axiidea: Callianassidae) revisited with additional observations and description of a new species

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**Abstract** The extent of propodal tuberculation is considered taxonomically important for species of the callianassid genus *Glypturus* (Decapoda: Axiidea). Based on cheliped material from the Middle-Late Miocene of Iran, *Glypturus persicus* n. sp. is described here. It possesses no tuberculation on the outer surface of the major propodus, whereas its inner surface is moderately to heavily tuberculated in terms of its extent. It resembles extant *Glypturus armatus*, but this species is completely smooth on both propodal surfaces. A reappraisal of *Glypturus toulai* from the Early and Late Miocene of Panama is presented.

Additionally, the type material of *Glypturus fraasi* from the Late Eocene of Egypt is figured. In the nature of tuberculation, an evolutionary trend is observable in *Glypturus* with the most tuberculated forms from the Palaeogene and less tuberculated forms from the Neogene. This trend is clearly seen in the possible West Atlantic lineage of the genus.

**Keywords** Decapoda · Axiidea · Callianassidae · *Glypturus* · Eocene · Miocene · New species

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## Introduction

Callianassid ghost shrimp remains are among the most commonly found decapod crustacean fossils, and, as Glaessner (1969: R435) noted, their “chelae are almost ubiquitous in Tertiary sediments”. Yet, our understanding of the fossil record of ghost shrimps is comparatively poor because most extinct taxa have not been re-examined with respect to modern classifications and much material remains to be discovered and described. Recently, in several contributions, fossil callianassid taxa attributable to the subfamilies Eucalliinae Manning and Felder, 1991 (Hyžný 2012; Hyžný and Hudáčková 2012) and Callichirinae Manning and Felder, 1991 (Schweitzer and Feldmann 2002; Hyžný and Müller 2010, 2012; Hyžný and Karasawa 2012; Hyžný and Muñiz 2012) were revised and discussed in detail. Much of this work was stimulated by the pioneering work of Manning and Felder (1991).

The genus *Glypturus* Stimpson, 1866 (subfamily Callichirinae) was documented at length by Hyžný and Müller (2012). Since then, however, additional material has been collected from the Miocene of Iran allowing description of a new species. Moreover, because of a lack

of material, *G. toulai* (Rathbun, 1919) was discussed only cursorily by Hyžný and Müller (2012). Recently, part of the original material of Toulai (1911) was rediscovered at the Naturhistorisches Museum Vienna, Austria, which, together with additional comparative material from the Miocene of Panama, allows a reappraisal of *G. toulai*. Additionally, the type material of *G. fraasi* (Noetling, 1885) is figured. Thus, this work provides a more complete understanding of the fossil record of *Glypturus*.

## Material

Details of all specimens studied are supplied under each taxon in the systematic palaeontology section.

**Repositories.** Geological Museum of the Department of Geology, University of Isfahan, Iran (EUIC); Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Humboldt-Universität, Berlin, Germany (MB.A); Naturhistorisches Museum Wien, Austria (NHMW); Florida Museum of Natural History at the University of Florida, Gainesville, Florida, USA (UF).

## Systematic palaeontology

Higher classification of decapods follows De Grave et al. (2009).

Order Decapoda Latreille, 1802

Infraorder Axiidea de Saint Laurent, 1979

Family Callianassidae Dana, 1852

Subfamily Callichirinae Manning and Felder, 1991

Genus *Glypturus* Stimpson, 1866

**Type species.** *Glypturus acanthochirus* Stimpson, 1866, by monotypy.

**Included species.** See Table 1.

**Diagnosis.** See Manning (1987: p. 390) and Manning and Felder (1991: p. 778).

**Remarks.** The propodal spination with usually three distinct spines positioned on the upper margin and directed distally immediately identifies specimens of the genus (Manning 1987; Manning and Felder 1991).

Hyžný and Müller (2012) provided a systematic revision of extant and fossil species of *Glypturus*. They based their revision on the morphology of the major cheliped, with emphasis on spination and tuberculation. They considered the extent of tuberculation on both lateral surfaces of the major propodus to be important in species assignment.

Recently, Beschin et al. (2012) re-assigned *Callianopsis microspineus* Beschin, De Angeli, Checchi and Zarantonello, 2005, to *Glypturus*. Hyžný and Schlögl (2011) already cast doubt on the generic assignment of *C. microspineus*. Generic re-assignment of this taxon to *Glypturus* looks similarly unwarranted. Beschin et al. (2005) based a new species on two fragmentary propodi. The authors mentioned the presence of one small spine distally on the upper propodal margin. However, Beschin et al. (2012) indicated the presence of two spines and noted that the dorsal margin is broken distally, which implies that a third spine could be present. Indeed, a line drawing in Beschin et al. (2012: fig. 13) showed a broken distalmost portion of the upper margin. However, in the original figure this portion appears complete in both the line drawing (Beschin et al. 2005: fig. 7) and the photograph of the holotype (Beschin et al. 2005: pl. 2, fig. 1). Moreover, even in the case of three propodal spines in *C. microspineus*, their position would be very strange for *Glypturus*. All members of the genus exhibit a proximalmost spine positioned approximately at the mid-length of the upper margin of the propodus, which is not the case in *C. microspineus*. Because of the fragmentary nature of the material and until new material is discovered, we refrain from referring *C. microspineus* to *Glypturus*.

**Table 1** Synopsis of species of *Glypturus* known to date.

*G. sp.* = *G. rabalaisae* sensu Sakai (2005, 2011); *nomen nudum*. For map of areal extent of Recent species see Hyžný and Müller (2012: fig. 11)

Taxon	Age	Occurrence
<i>G. fraasi</i>	Middle–Late Eocene	Egypt, Spain, Hungary, Italy, ?Namibia
<i>G. spinosus</i>	Late Eocene	Hungary
<i>G. berryi</i>	Oligocene	USA (Mississippi)
<i>G. pugnax</i>	Early Miocene	Java
<i>G. munieri</i>	Middle–Late Miocene	Hungary, Austria, Malta
<i>G. persicus</i> n. sp.	Middle–Late Miocene	Iran
<i>G. toulai</i>	Late Miocene	Panama
<i>G. armatus</i> (= <i>G. motupore</i> )	Pliocene–Recent	Vanuatu (fossil); Indian Ocean + West Pacific
<i>G. acanthochirus</i>	Late Pleistocene–Recent	Jamaica (fossil); Caribbean (Recent)
<i>G. laurae</i>	Recent	Red Sea
<i>G. sp.</i>	Recent	Gulf of Mexico

*Glypturus fraasi* (Noetling, 1885)

\*1885 *Callianassa Fraasi* Noetling, p. 492, pl. 4, figs 4–6.

1929 *Calianassa* [sic] *pseudo-Fraasi* Lörenthey in Lörenthey and Beurlen, p. 55, pl. 1, fig. 12.

1969 *Calianassa fraasi* (Noetling); Vía Boada, p. 34, text-fig. 1; pl. 1, figs 1–8.

2012 *Glypturus fraasi* (Noetling); Hyžný and Müller, p. 976, figs 4F, 7A–C.

2012 *Glypturus fraasi* (Noetling); Beschin, De Angeli, Checchi, and Zarantonello, p. 17, fig. 12, pl. 2, figs 1–3.

See Hyžný and Müller (2012) for full synonymy list.

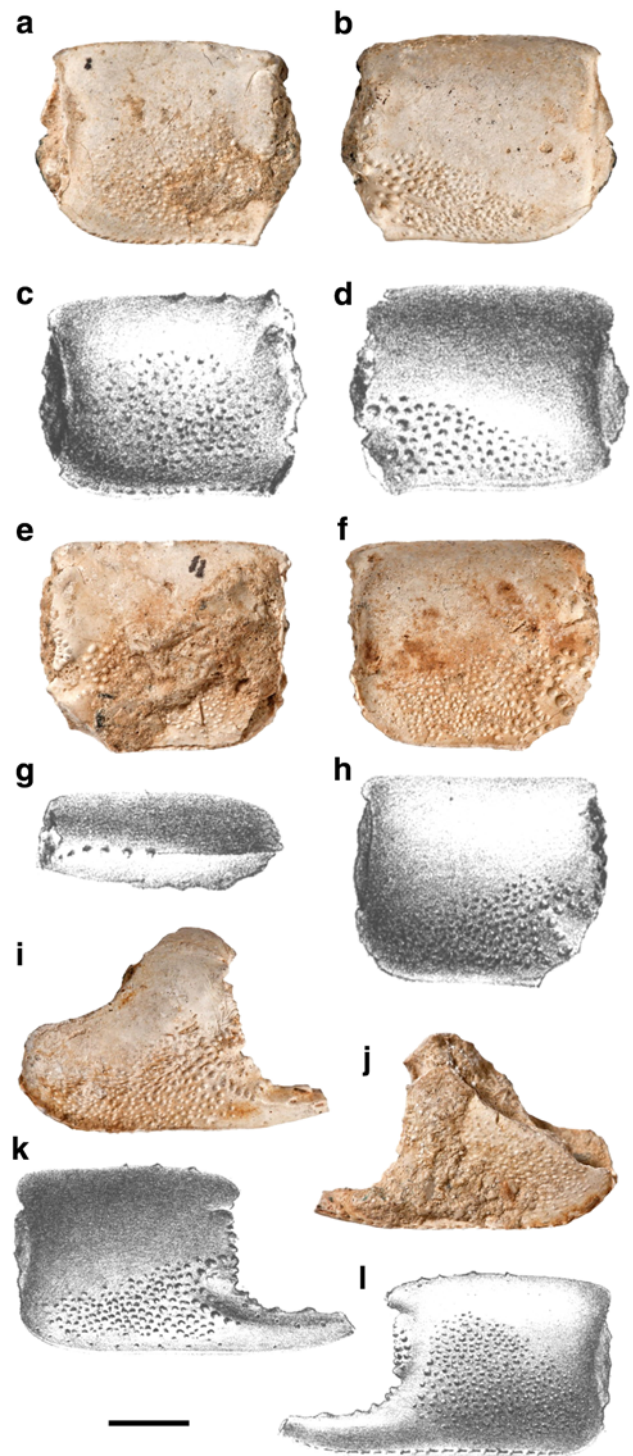
**Material.** The type material of *Glypturus fraasi* consists of three fragmentary propodi deposited under numbers MB.A 1571–1573. Noetling (1885) did not designate a holotype; instead the type collection represents three syntypes. Specimen MB.A 1571 is designated herein as the lectotype; the two paralectotypes are MB.A 1572 and 1573. Noetling (1885), as shown in Fig. 1, accurately depicted the specimens, instead of figuring idealised reconstructions. Nevertheless, the paralectotype MB.A 1573 does not really fit the original figure (Noetling 1885: pl. 4, fig. 6; refigured herein as Fig. 1k–l). We assume that the specimen was damaged sometime after the publication of Noetling's report.

**Occurrence.** Middle Eocene of Spain (Vía Boada 1959, 1969), Late Eocene of Egypt (Noetling 1885) and Hungary (Lörenthey 1897, 1898; Hyžný and Müller 2012) and, possibly, Eocene of Namibia (Böhm 1926).

**Diagnosis.** Strongly tuberculated *Glypturus*; lateral tuberculation on propodus confined to lower two-fifths of outer surface and nearly entire inner surface (after Hyžný and Müller 2012: 978).

**Remarks.** Hyžný and Müller (2012) revised the species. They also synonymised *Callianassa pseudofraasi* Lörenthey in Lörenthey and Beurlen, 1929, from the Eocene of Hungary to *C. fraasi*. Numerous specimens have been recovered from the Middle Eocene strata of Spain (Vía Boada 1969; see also Hyžný and Müller 2012 and references therein).

Interestingly, in paralectotype MB.A 1572 (Fig. 1e, g) the number of spines on the upper propodal margin exceeds three and in this respect it is reminiscent of a specimen of *G. acanthochirus* depicted by Hyžný and Müller (2012: fig. 2A–C). Similarly, *Eoglypturus* Beschin, De Angeli, Checchi and Zarantonello, 2005, from the Middle Eocene of Italy, possesses five spines (Beschin et al. 2005, 2012). In this respect, it is worth noting the presence of *G. fraasi* at the same locality as *E. grolensis* Beschin, De Angeli,



**Fig. 1** *Glypturus fraasi* (Noetling, 1885) from the Late Eocene of Egypt. **a–d** major left propodus (lectotype MB.A 1571), inner lateral surface (**a**, **c**), outer lateral surface (**b**, **d**), **e–h** major right propodus (paralectotype MB.A 1572), inner surface (**e**), outer surface (**f**, **h**), upper view (**g**), **i–l** major right propodus (paralectotype MB.A 1573), inner surface (**j**, **l**), outer surface (**i**, **k**). Scale bar 5 mm

Checchi and Zarantonello, 2005. Taking into account the variability in the number of propodal spines as discussed by Hyžný and Müller (2012: p. 970), *Eoglypturus* may be found synonymous to *Glypturus* in the future when more complete material is recovered.

*Glypturus persicus* new species

Figures 3, 7

**Material.** Major left propodus (holotype EUIC 101825), major right propodus (paratype EUIC 101826), major left propodus (paratype EUIC 101827), major right dactylus (EUIC 101828). Numerous fragmentary chelae (propodi) deposited under collective numbers EUIC 101829–101831.

**Occurrence.** Middle-Upper Miocene of the Mishan Formation, Iran. The Mishan Formation consists of alternating marls and sandy limestones (James and Wynd 1965). Ghost shrimp remains originate from two sandy limestone horizons above the Guri Member (Kashfi 1982) in the upper part of the Mishan Formation exposed at the Konar-Takhteh and Ahram sections (Fig. 2). Both sections are situated in the folded zone of the oil field of the Zagros Basin, southwestern Iran. The Konar-Takhteh section is located approximately 45 km east from Konar-Takhteh city (co-ordinates 29.3317°N/51.2845°E); the Ahram section is located approximately 20 km east from Ahram city (co-ordinates 28.4739°N/51.2053°E). Details on the geology and sedimentology of the Mishan Formation were provided by Vega et al. (2010) and Heidari et al. (2012).

**Diagnosis.** *Glypturus* with lateral tuberculation on inner surface of propodus covering central portion of manus and also extending distally; outer surface of propodus smooth.

**Etymology.** The specific epithet refers to Persia, which is a former name for Iran, the country where the type material comes from.

**Description.** Manus as long as high, or slightly longer (length/height ratio ~ 1.0–1.1); upper margin converging distally, proximally keeled, bearing three spines distally, keel terminating in blunt corner proximally; lower margin sharp with rows of setal pits on inner lateral surface; outer lateral surface completely smooth, unornamented; inner lateral surface covered with tubercles, the extent of tuberculation variable but usually covering the central portion of the manus and also extending distally. Fixed finger with distinct blunt tooth on occlusal margin (visible in Fig. 3b); tip of fixed finger not preserved. Dactylus stout; occlusal margin with large blunt tooth positioned proximally and smaller one distally.

**Remarks.** *Glypturus persicus* n. sp. possesses no tuberculation on the outer surface of the major propodus whereas its inner surface is moderately to heavily tuberculated in

terms of its extent. Such combination is unknown in previously described *Glypturus* species. *Glypturus armatus* (Milne Edwards, 1870) is the only species without tuberculation on the outer surface of the major propodus, but its inner surface also lacks tuberculation. Thus, erecting a new species is warranted.

*Glypturus toulai* (Rathbun, 1919)

Figures 4, 5, 6, 7b

1911 “Krabbenschere” Toulai, p. 512 (26), pl. 30(1), fig. 14.

\*1919 *Callianassa toulai* Rathbun, p. 146.

2005 *Glypturus toulai* (Rathbun); Todd and Collins, p. 63, pl. 1, fig. 1.

2009 *Glypturus toulai* (Rathbun); Collins et al., pp. 70–71.

2012 *Glypturus toulai* (Rathbun); Hyžný and Müller, p. 983, text-fig. 10A–D.

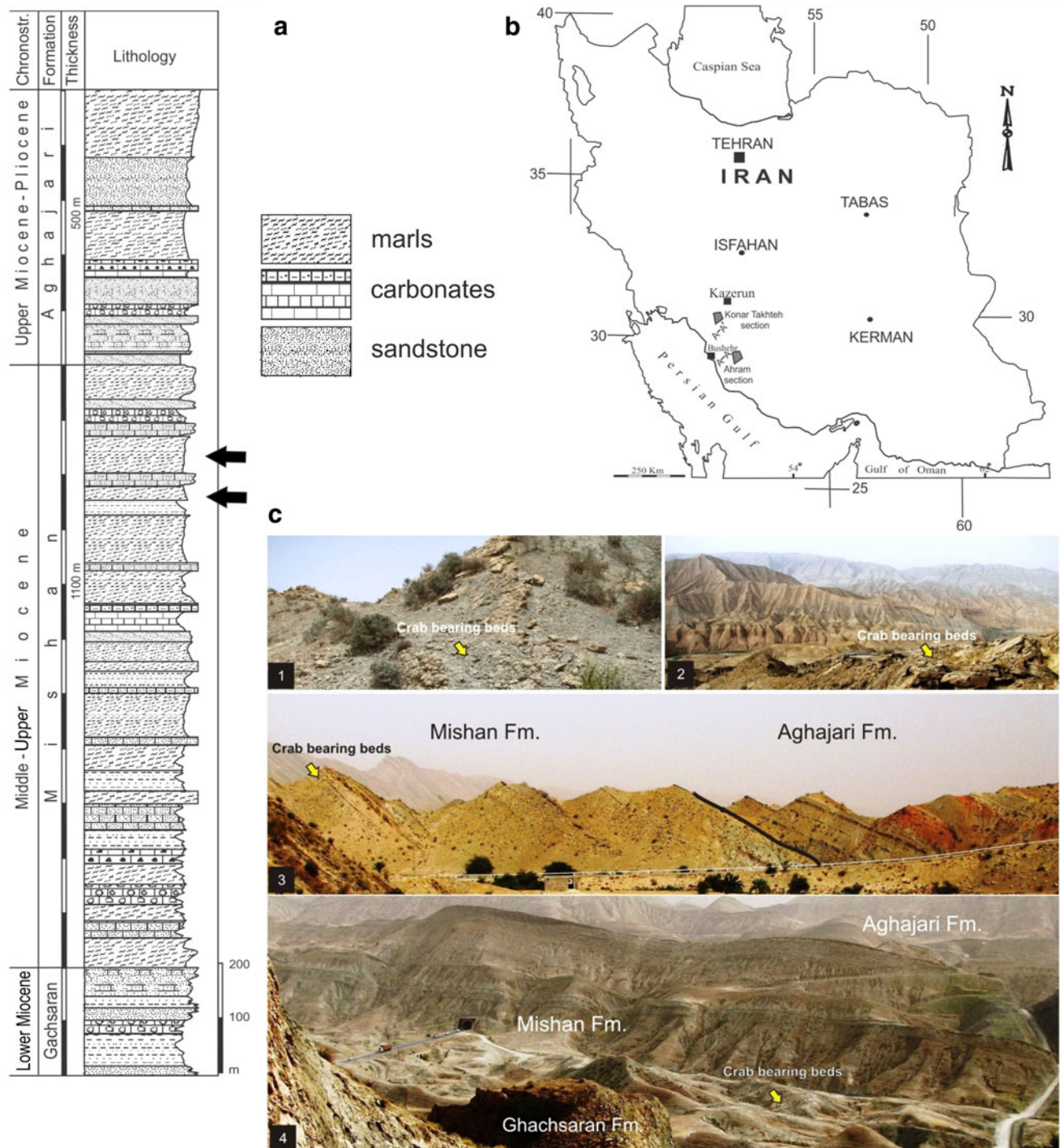
**Type material.** Toulai (1911) described two chelae from the Late Miocene of Panama merely as “Krabbenschere”, illustrating one left major propodus and the dactylus. To accommodate this, Rathbun (1919) erected a new ghost shrimp species, *Callianassa toulai*, but did not select a type specimen. Later, Todd and Collins (2005), without re-examination of the actual specimen, designated the chela illustrated by Toulai (1911, pl. 30(1), fig. 14) as a lectotype. The lectotype is, however, missing among the rediscovered Toulai material. For the time being, it is considered lost. Rediscovered Toulai material as presented herein (Fig. 4) is considered to represent paralectotypes and consists of one complete right major propodus (Fig. 4a–c) and three fragmentary fixed fingers (Fig. 4d–f), bearing the collective number NHMW 1933/0018/0160.

**Additional material.** One propodus and accompanying dactylus found at Sabanitas behind Las Lomas Suites, lower Gatun Formation, Colon Province, Panama (co-ordinates 9.35711°N/-79.8387°W, UF 203348) (Fig. 5); 13 propodi found at Lirio Norte West 01, Paraiso area, Culebra Formation, Panama Province, Panama, co-ordinates 9.05814°N/-79.66479°W, UF 233762–233767 (Fig. 6a–d, i); and 3 specimens from Lirio East 01, Paraiso area, Culebra Formation, Panama Province, Panama, co-ordinates 9.0509°N/-79.6506°W, UF 233792–233794 (Fig. 6e–h, j–k).

**Occurrence.** Lower Miocene, Culebra Formation, Panama (herein); Upper Miocene, Gatun Formation, Panama (see Todd and Collins 2005; herein).

**Emended diagnosis.** Moderately tuberculated *Glypturus*; lateral tuberculation on outer surface of propodus extending from near base of fixed finger diagonally to lower margin and reaching proximal lower corner; lateral



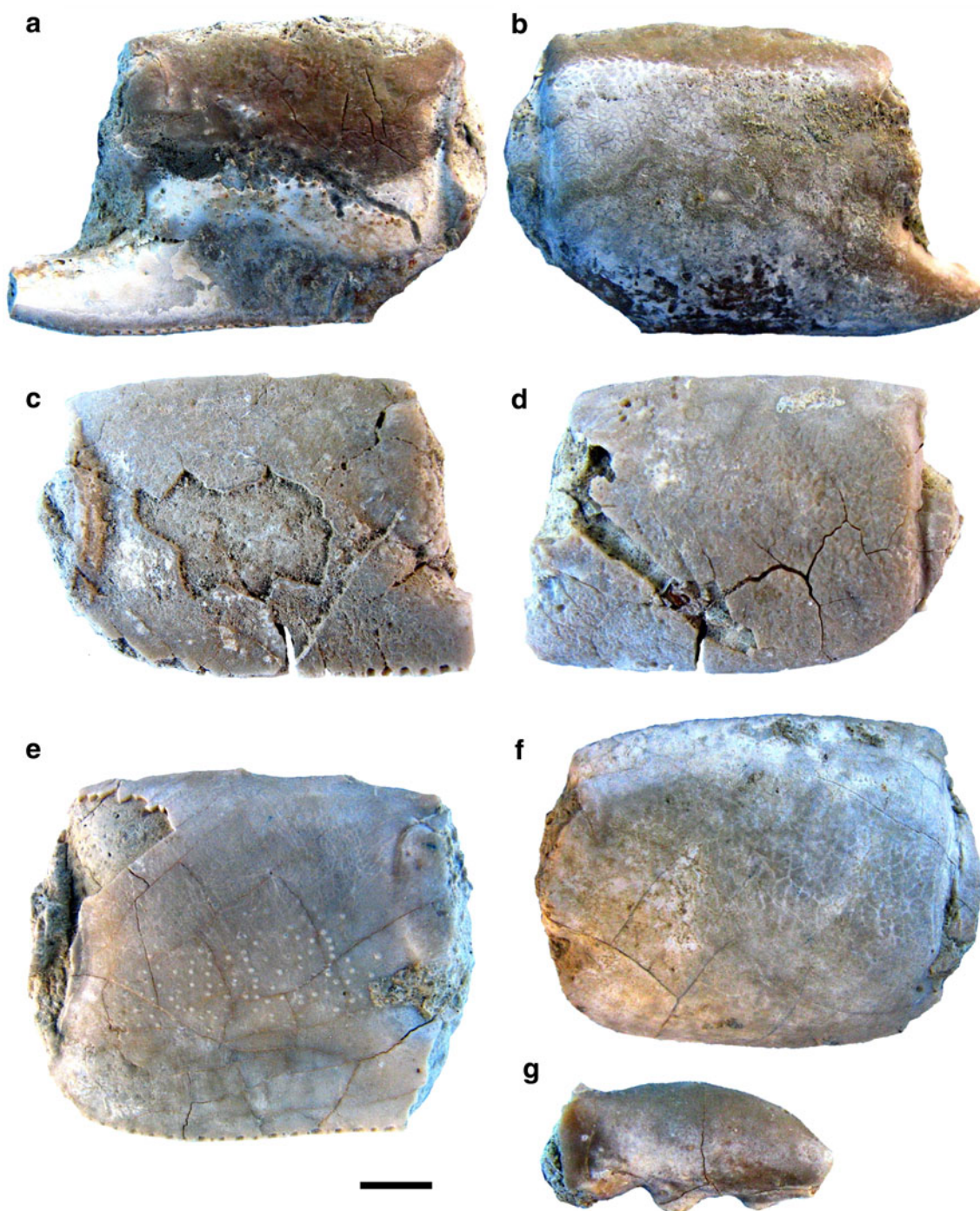


**Fig. 2** Stratigraphy and locality of Miocene strata in Iran in which *Glypturus persicus* n. sp. was found. **a** Lithostratigraphic scheme of the Mishan Formation at the Konar-Takhteh section. Arrows indicate crab bearing beds with remains of *Glypturus persicus* n. sp.; **b** Generalised map of Iran with locations of the Konar-Takhteh and the Ahram sections; **c**: photographic documentation; (1) intercalated

limestone horizons in green marls of the Mishan Formation at the Konar-Takhteh section; (2) panoramic view at the exposed parts of the Mishan and Aghajari formations at the Konar-Takhteh section; (3) panoramic view of the Ahram section; (4) a different view of the Konar-Takhteh section with indication of crab bearing beds. Photos by Mehdi Yazdi

tuberculation on inner surface of the propodus restricted mainly to area of articulation with dactylus in small specimens, but covering large lower part of manus in large

specimens with lower margin of tuberculated area diagonally crossing from area of articulation of dactylus toward proximal lower corner.



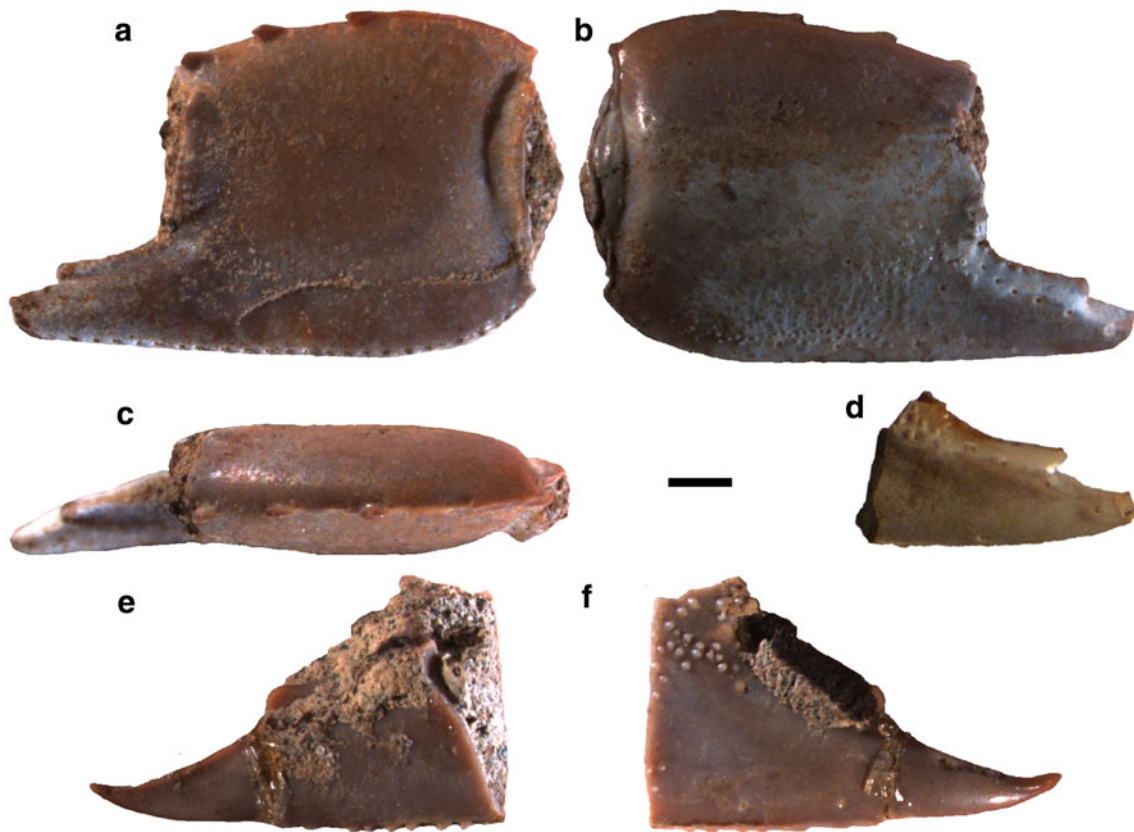
**Fig. 3** *Glypturus persicus* n. sp. from the Middle-Late Miocene of Iran. Major right propodus (paratype EUIC 101826), inner lateral surface (a), outer lateral surface (b). Major left propodus (paratype

EUIC 101827), inner surface (c), outer surface (d). Major left propodus (holotype EUIC 101825), inner surface (e), outer surface (f), major right dactylus (paratype EUIC 101828) (g). Scale bar 5 mm

*Emended description.* Manus length exceeding height (length/height ratio  $\sim 1.1$ – $1.2$ ); upper margin converging distally, proximally keeled, bearing three prominent spines pointing distally, proximalmost spine around mid-margin, keel terminating in blunt corner; lower margin sharp and keeled, in larger specimens denticulate, lined

with a row of setal pits on inner lateral surface; proximal margin convex on outer face, concave on inner; distal margin weakly convex; lateral tuberculation on outer surface from base of fixed finger diagonally to lower margin and proximal lower corner; lateral tuberculation on inner surface of propodus restricted mainly to area of



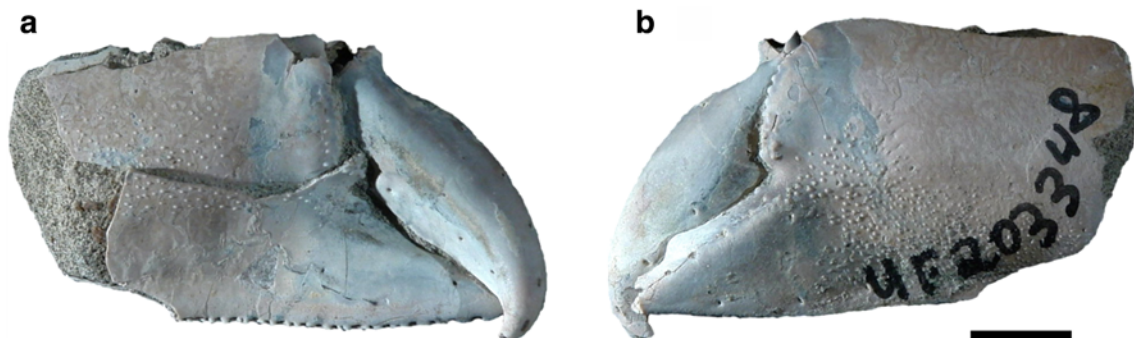


**Fig. 4** *Glypturus toulai* (Rathbun, 1919) from the Upper Miocene Gatun Formation of Panama (paralectotypes). Major right propodus, inner lateral surface (a), outer lateral surface (b), view from above (c); broken major right fixed finger (d); broken major right fixed finger,

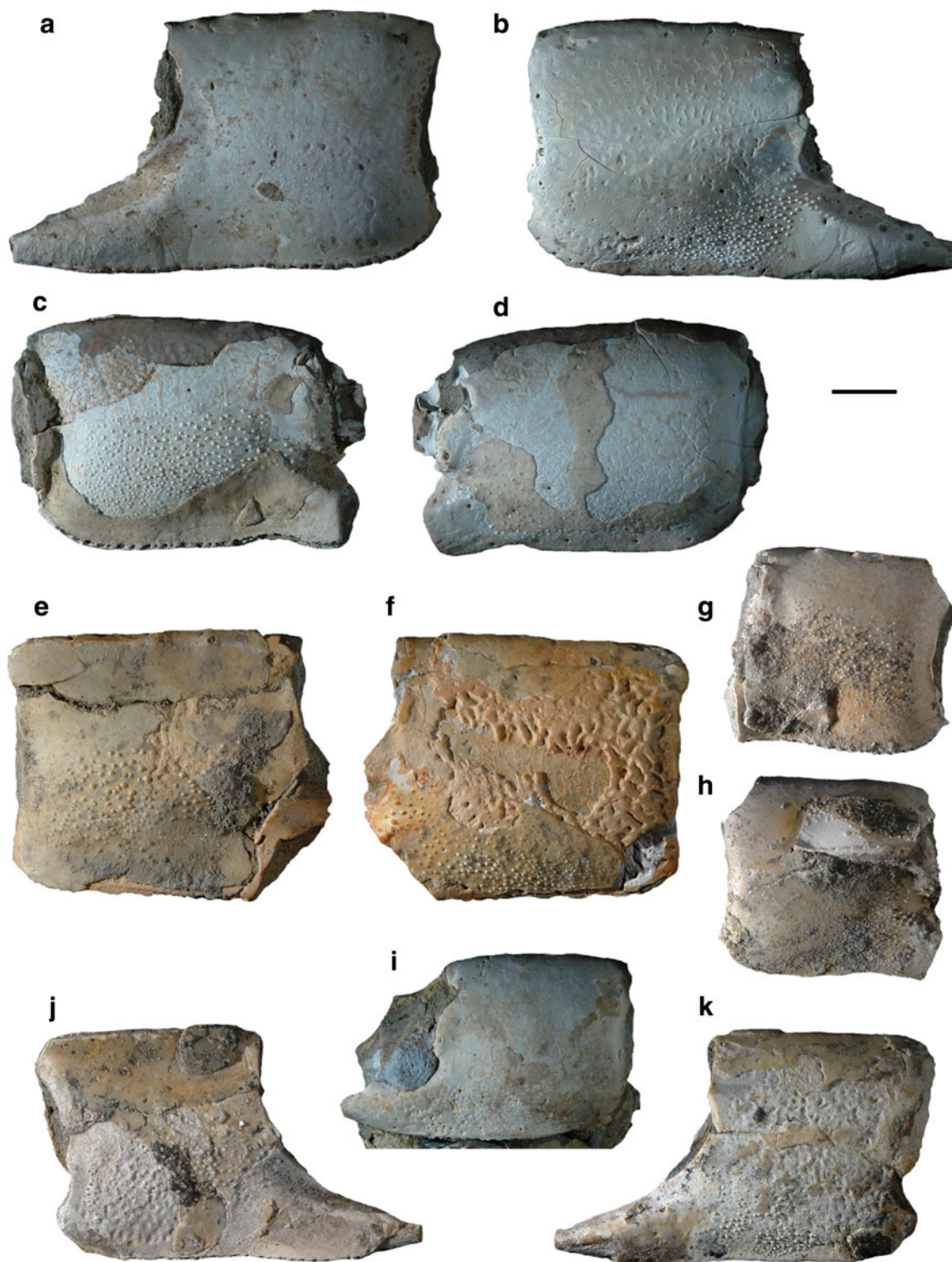
inner lateral surface (e), outer lateral surface (f). All specimens are deposited under collective number NHMW 1933/0018/0160. Scale bar 1 mm

articulation with dactylus in small specimens, but covering large lower part of manus in larger specimens with lower margin of tuberculated area diagonally crossing from area of articulation of dactylus toward (but not reaching) proximal lower corner; fixed finger triangular, sharply pointed, with distinct blunt tooth on occlusal margin around mid-length, tooth pointing distally. Dactylus stout, occlusal margin without evident tooth, tip hooked.

**Remarks.** Toulou (1911) noted possible affinities with the brachyuran family Trapeziidae Miers, 1886. The affinities of the material with Callianassidae were recognised by Rathbun (1919). On the basis of the presence of three spines on the upper margin of the propodus, Todd and Collins (2005) transferred the species to *Glypturus*. They argued that *Glypturus toulai* exhibited close similarities to extant *G. acanthochirus* and pointed out that *G. toulai* might be found to be synonymous to the former in the



**Fig. 5** *Glypturus toulai* (Rathbun, 1919) from the Upper Miocene Gatun Formation of Panama. Major left propodus (UF 203348), inner lateral surface (a), outer lateral surface (b). Scale bar 5 mm



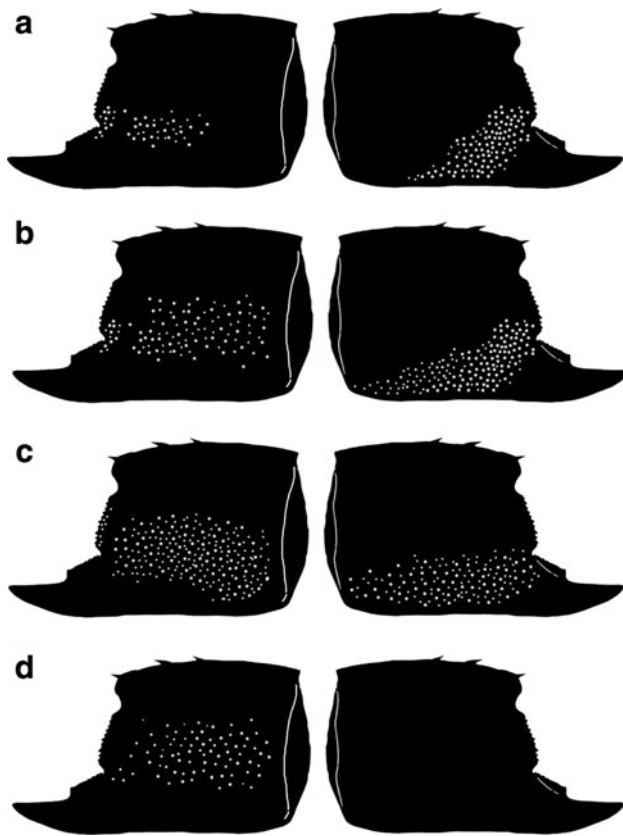
**Fig. 6** *Glypturus toulai* (Rathbun, 1919) from the Lower Miocene Culebra Formation of Panama. Major right propodus (UF 233767), inner lateral surface (a), outer lateral surface (b). Major left propodus (UF 233764), inner surface (c), outer surface (d). Major left propodus

(UF 233793), inner surface (e), outer surface (f). Major right propodus (UF 233794), inner surface (g), outer surface (h). Major left propodus (UF 233765). Major left propodus (UF 233792) (i), inner surface (j), outer surface (k). Scale bar 5 mm

future. The tuberculation on the outer surface of the propodus, considered of taxonomic importance (Biffar 1971; Manning 1987; Hyžný and Müller 2012), is not seen

in the figure supplied by Toulou (1911: pl. 15, fig. 14), but he described pustules on the lower side, apparently referring to tubercles. An illustration in Todd and Collins (2005:





**Fig. 7** Scheme of tuberculation on the major propodus of selected *Glypturus* species plotted on a standardised outline. Western Atlantic region – *G. acanthochirus* Stimpson, 1866, Pleistocene–Holocene (**a**); *G. toulai* (Rathbun, 1919), Miocene (**b**); *G. berryi* (Rathbun, 1935), Oligocene (**c**); **d** *Glypturus persicus* n. sp., Miocene of Iran. Left column inner lateral surface, right column outer lateral surface

pl. 1, fig. 1) is more informative, but lacks the lower proximalmost margin. The original material of Toulai (1911), recently retraced, enables a comparison with that of Todd and Collins (2005). The nature of the outer surface tuberculation is similar in both specimens. The additional specimen from the Upper Miocene Gatun Formation of Panama and the new material from Lower Miocene Culebra Formation of Panama provide new insight for larger specimens and confirm the extent of tuberculation on the outer lateral side.

The extent of the major propodal tuberculation on the outer lateral surface is close to that of *G. berryi* (Rathbun, 1935) (Oligocene, Mississippi, USA) and *G. fraasi* (Noetling, 1885) (Eocene, Europe), but the extent of the tubercles appears more pronounced at the proximalmost part in the latter two. Interestingly, the extent of tuberculation on the outer lateral surface in *G. toulai* seems to be intermediate (Fig. 7b) between *G. berryi* (Fig. 7c) and *G. acanthochirus* (Fig. 7a) from the Late Pleistocene of Jamaica (Collins et al. 1996, 2009) and the Holocene of the Gulf of Mexico and the Caribbean (Sakai 2011), suggesting

it may represent a single lineage. Future research will investigate this further.

## Discussion

The presence of propodal spination is critical in assigning fossil material to *Glypturus*. Although taxonomically important characters on the genus level are present also on the major carpus and merus (Hyžný and Müller 2012), these cheliped elements are generally rarely found in the fossil record. On the other hand, isolated propodi are the most common fossil remains of ghost shrimps in general. The extent of tuberculation on propodi has been considered taxonomically important on the species level for *Glypturus* (Hyžný and Müller 2012). In this respect, it is important to note that the preservation of material may prevent the identification of the fossil material to respective species. Taphonomic processes may obliterate the tuberculation patterns, especially in smaller specimens where the tubercles are not as strongly developed as in larger individuals.

An evolutionary trend is observable in *Glypturus* with the most tuberculated forms dating from the Eocene (*G. fraasi*) and Oligocene (*G. berryi*) and less tuberculated forms today (e.g., *G. armatus* and *G. laurae* (de Saint Laurent in de Vaugelas and de Saint Laurent, 1984)). This trend is clearly seen in the possible West Atlantic lineage *G. berryi*–*G. toulai*–*G. acanthochirus*. Similarly, in the Tethyan region, the stratigraphically older *G. fraasi* is distinctly more tuberculated than the younger *G. munieri* (Brocchi, 1883) from the Miocene (Hyžný and Müller 2012). In the Indo-West Pacific region the situation is less clear as the data on *G. pugnax* (Böhm, 1922) from the Early Miocene of Indonesia are limited (Hyžný and Müller 2012 erroneously stated its age as Late Miocene). Böhm (1922) mentioned the presence of a tuberculated area on both propodal surfaces; nevertheless its extent is difficult to determine from the figures only (Böhm 1922: pl. 63, figs 22, 24, 25). *Glypturus armatus* is completely smooth and *Glypturus persicus* n. sp. from the Middle-Late Miocene of Iran is tuberculated on the inner propodal surface only.

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