THE FOSSIL RECORD OF *GLYPTURUS* STIMPSON, 1866 (CRUSTACEA, DECAPODA, AXIIDEA, CALLIANASSIDAE) REVISITED, WITH NOTES ON PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY

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Abstract: The fossil record of the callianassid genus *Glypturus* (Decapoda, Axiidea) is re-evaluated. Our systematic revision, both of extant and fossil taxa, is based on major cheliped morphology only, thus providing an important impetus for palaeontological studies. Both spination and tuberculation of chelipeds are herein considered of great taxonomic importance. Presence of spines on the upper margins of the merus and propodus and the lower margin of the carpus are significant for generic assignment, whereas the extent of tuberculation on lateral surfaces of the propodus is important for assignment at the species level. Altogether, four extant and six exclusively fossil species of *Glypturus* are recognized. Several extinct callianassid taxa are now transferred to the genus, namely *Callianassa berryi*, *Callianassa fraasi*, *Callianassa munieri*, *Callianassa pugnax* and *Callianassa spinosa*; *Callianassa pseudofraasi* is considered a junior synonym of *C. fraasi*. Based on a comparison of ecological preferences of extant representatives, the presence of *Glypturus* in the fossil record is considered to be linked with tropical to subtropical, nearshore carbonate environments of normal salinity. We argue that *Glypturus* is of Tethyan origin, with a stratigraphical range going as far back as the Eocene. Since then, the genus migrated both westwards and eastwards, establishing present-day communities in the western Atlantic and Indo-West Pacific which both comprise several distinct species. In the presumed area of origin, the genus does no longer occur today. The exlusively fossil (middle Eocene) genus *Eoglypturus* from Italy is considered closely related to *Glypturus* and is thus assigned to the subfamily Callichirinae as well.

Key words: Decapoda, Callianassidae, *Glypturus*, *Eoglypturus*, palaeoecology, palaeobiogeography.

THE family Callianassidae Dana, 1852, constitutes a distinct group of fossorial shrimps that inhabit predominantly shallow intertidal and subtidal marine environments, mainly in the tropics and subtropics (Dworschak 2000, 2005). Members of this family exhibit sophisticated behaviour that involves digging complex burrow systems. Callianassids often show pronounced heterochely and in some cases also sexual dimorphism in the nature of the major cheliped, which has a great impact on interpretations of fossil material.

De Grave *et al.* (2009) listed 41 callianassid genera, seven of which were known as fossils only. Following their classification, the family can be subdivided into 10 subfamilies, with the great majority of named species being members of the Callianassinae Dana, 1852 and the Callichirinae Manning and Felder, 1991. However, there still is disagreement over the generic and suprageneric arrangement within the family (compare Sakai 1999, 2005, 2011 and De Grave *et al.* 2009). Several phylogenetic analyses, based both on morphological and molecular evidence, have been carried out in an attempt to resolve the status of the various genera (Poore 1994; Tudge *et al.* 2000; Felder and Robles 2009; Robles *et al.* 2009).

In view of the delicate nature of most of the cuticular surfaces, extinct callianassids are represented mainly by isolated chelae. Thus, the fossil material usually lacks the diagnostic characters of extant taxa, which include dorsal carapace architecture, nature of maxillipeds, form of the abdomen, pleopods, uropods and telson (for a discussion, see Schweitzer and Feldmann 2002; Schweitzer *et al.* 2006*a*). In some cases, however, these criteria can also be applied with some certainty to the fossil record (e.g. Schweitzer-Hopkins and Feldmann 1997; Schweitzer and

Feldmann 2002), notably when the features essential for generic assignment occur on chelipeds (see Manning and Felder 1991). The genus *Glypturus* Stimpson, 1866 is such a case, and here we re-examine several fossil taxa with respect to extant ones.

MATERIAL

The material studied can be divided into two sets: specimens examined personally by at least one of us and material unseen but checked carefully according to pertinent items of literature (illustrations and descriptions) and/or additional photographs supplied to us. Details of all specimens studied are supplied under each taxon in the systematic section later. Parameters measured are the same as in the study of Hyžný and Schlögl (2011, text-fig. 3).

Institutional abbreviations. The repositories of specimens illustrated or referred to later are as follows: BMNPH PI IC, Department of Palaeontology, The Natural History Museum, London, UK; E, Hungarian Geological Survey (Magyar Állami Földtani Intézet), Budapest, Hungary; KGP-MH, Department of Geology and Paleontology, Comenius University, Bratislava, Slovakia; M (old acquisitions) or PAL (acquisitions since 2011), Hungarian Natural History Museum, Budapest, Hungary; MB.A, Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Humboldt-Universität, Berlin, Germany; MCZ, Museo Civico 'G. Zannato', Montecchio Maggiore, Vicenza, Italy; MNHN.F, Collection de Paléontologie, Muséum national d'Histoire naturelle, Paris, France; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NMCR, National Museum of the Philippines, Manila, the Philippines; USNM, United States National Museum (Smithsonian Institution), Washington DC, USA.

SYSTEMATIC PALAEONTOLOGY

Remarks. Higher-rank classification follows De Grave *et al.* (2009).

Order DECAPODA Latreille, 1802
Infraorder AXIIDEA de Saint Laurent, 1979

Family CALLIANASSIDAE Dana, 1852

Remarks. There is an extensive fossil record of Callianassidae from around the world, but most of the material has not yet been restudied with respect to modern classification. As a result of ongoing research of extinct callianassids using biological and palaeontological criteria for generic assignment, it is now possible to determine the placement of numerous fossil specimens, previously referred to as '*Callianassa*' (e.g. Müller 1984a), more precisely. As already noted, fossil remains of Callianassidae are often represented exclusively by isolated chelae, making generic assignment very difficult. Moreover, occasionally ctenochelid genera, notably *Gourretia* de Saint Laurent, 1973 and *Callianopsis* de Saint Laurent, 1973, can easily be misinterpreted as callianassids when dealing with cheliped fragments only. This actually happened in the case of *Gourretia aquilae* (Rathbun, 1935) and several species of *Callianopsis*; for a more detailed discussion of this issue, reference is made to Hyžný and Schlögl (2011, p. 325).

Subfamily CALLICHIRINAE Manning and Felder, 1991

Remarks. The original diagnosis (Manning and Felder 1991, p. 775) is rather short and based on characters which usually are absent in the fossil record: dorsal carapace, maxillipeds and pleopods. The definition proposed by Sakai (2005, p. 120) is more detailed, but mostly fails to assist palaeontologists in interpreting their material. For instance, with regard to chelipeds, his definition (Sakai 2005, p. 210) states, 'P1 chelate, unequal or subequal, and similar or dissimilar; larger cheliped with or without meral hook'. However, much the same can be said of the Callianassinae (see Sakai 2005, p. 11). Without having diagnostic characters of maxillipeds and pleopods, assignment of fossil species to subfamilies is virtually impossible. When dealing with fossils, the subfamilial assignment depends on the identification of specimens as members of extant genera. Therefore, several exclusively fossil callianassid genera cannot be assigned to any subfamily (see e.g. De Grave *et al.* 2009, p. 22).

The fossil record of the Callichirinae is fairly extensive, although the majority of species studied have been assigned to *Neocallichirus* Sakai, 1988. According to De Grave *et al.* (2009) and Schweitzer *et al.* (2010), some 39 species in nine genera of the Callichirinae have been described from the fossil record. Since then, three additional species have been erected, namely *Callichirus bertalani* Hyžný and Müller, 2010, *Neocallichirus hattai* Karasawa and Nakagawa, 2010 and *Neocallichirus agadirensis* Garassino, De Angeli and Pasini, 2011. It should be noted that a recent molecular study (Felder and Robles 2009) failed to resolve the subfamily Callichirinae in its present arrangement as a monophyletic grouping.

Hyžný and Müller (2010) have recently reviewed the fossil record of *Callichirus*, providing also a diagnosis of the genus based on hard-part morphology. Currently, the genus *Corallianassa* Manning, 1987 is known from three fossil taxa (De Angeli and Garassino 2006), while there is but a single fossil record of *Lepidophthalmus* Holmes, 1904 (see Collins *et al.* 2009) and of *Michaelcallianassa*

Sakai, 2002, no extinct taxa are known. Assignment of *Grynaminna* Poore, 2000, *Neocallichirus*, *Podocallichirus* Sakai, 1999 and *Sergio* Manning and Lemaitre, 1994 deserves special attention. These four genera are virtually indistinguishable from one another when considering only chelipeds. Unfortunately, numerous fossil species have been assigned to *Neocallichirus* (i.e. Schweitzer *et al.* 2010 list 18), whose diagnosis, based exclusively on hard parts, is rather wide (Manning 1993, p. 108; Sakai 2005, p. 160). Differences in hard-part morphology of taxonomic importance in *Grynaminna*, *Neocallichirus*, *Podocallichirus* and *Sergio* and implications for the fossil record have recently been outlined by Hyžný and Karasawa (2012). The present study focuses on the systematics and fossil record of the genus *Glypturus*.

Genus GLYPTURUS Stimpson, 1866

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

Included species. See Table 1.

Diagnosis. Reference is made to Manning (1987, p. 390) and Manning and Felder (1991, p. 778).

General remarks. The genus was erected by Stimpson (1866) and redefined by Manning (1987), who distinguished it definitively from *Callianassa* Leach, 1814 and provided a proper diagnosis. The primary features are a sharp, upturned rostral spine; anterolateral spines of the carapace are separated from the carapace by a noncalcified membrane, and claw ornament, with dorsal spines on both meri and propodi of chelipeds.

Manning (1987) synonymized *Callianassa armata* A. Milne-Edwards, 1870 with *G. acanthochirus* and listed several different species that were possibly attributable to *Glypturus*, although he hesitated to re-assign any of them without proper re-examination of the type material. Amongst those species, he mentioned also *Callichirus laurae* de Saint Laurent *in* de Vaugelas and de Saint Laurent, 1984 and noted that it shared with *G. acanthochirus* a tuberculate palm. Later, Poore and Suchanek (1988) disagreed with the synonymization of *C. armata* with *G. acanthochirus*, recognizing them as separate species of *Glypturus*, together with *C. laurae*, and adding a new one, *G. motupore* Poore and Suchanek, 1988. Manning and Felder (1991) concurred with Poore and Suchanek (1988) in accepting four species of *Glypturus*, all of them possessing a distinctly spiny merus, carpus and propodus. Sakai (1988) omitted spines on chelipeds as one of the diagnostic features of *Glypturus*. Instead, he presented a rather wide diagnosis of the genus and listed the following species for Australia: *Callianassa collaroy* Poore and Griffin, 1979, *C. martensi* Miers, 1884 (= *C. haswelli* Poore and Griffin, 1979), *C. mucronata* Strahl, 1861 and *C. karumba* Poore and Griffin, 1979. Later (Sakai 1999, 2005), he relegated *Corallianassa* Manning, 1987 and *Corallichirus* Manning, 1992 into the synonymy of *Glypturus*, an action criticized by several authors (Ngoc-Ho 2005; Dworschak 2007). Finally, he recognized some 15 species as members of *Glypturus* (Sakai 2005, p. 132) and also (Sakai 1999, 2005) transferred *G. motupore* to the genus *Neocallichirus* (!) and synonymized *C. laurae* with *C. armata*. The shape of the telson in larval stages of *C. laurae* and *C. armata*, however, speaks for their specific distinction (Seridji 1995). Sakai (2011) maintained the synonymy of *Corallianassa* with *Glypturus* and listed 13 species for this 'wider' genus, yet did recognize *Corallichirus* as valid with three species, based upon differences in male first and second pleopods.

Tudge *et al.* (2000) listed seven species of *Glypturus*, viz. *G. acanthochirus*, *G. armatus*, *G. karumba*, *G. laurae*,

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

Species with an exclusively recent record		
G. laurae		
G. sp. (= *G. rabalaisae sensu* Sakai, 2005, 2011; *nomen nudum*)		
Extant species known also from the fossil record		
G. armatus	Pliocene	Vanuatu
G. acanthochirus	Late Pleistocene	Jamaica
Exclusively fossil species		
G. fraasi comb. nov.	Middle–late Eocene	Egypt, Spain, Hungary, ?Namibia
G. spinosus comb. nov.	Late Eocene	Hungary
G. berryi comb. nov.	Oligocene	USA (Mississippi)
G. munieri comb. nov.	Middle–late Miocene	Hungary, Austria, Malta
G. toulai	Late Miocene	Panama
G. pugnax comb. nov.	Late Miocene	Java

Note: data on stratigraphical age and geographical distribution are supplied only for fossil taxa. Reference is made to the text for details of geographical distribution of exclusively extant forms.

G. martensi, *G. motupore* and *G. mucronata*. Interestingly, results presented by those authors favoured a paraphyletic or even polyphyletic nature for *Glypturus* in such an arrangement. This is not surprising, as *C. martensi*, *C. karumba* and *C. mucronata* lack distinct spines on chelipeds and are very different in other respects from species of *Glypturus* (*sensu* Manning 1987).

Herein, we follow the diagnosis provided by Manning (1987), in support of Manning and Felder (1991), Poore (1994) and Ngoc-Ho (2005). We agree that the spinulous character of the chelipeds is typical of *Glypturus*; usually, there are three spines on the upper margin of the propodus and spines on lower margins of the carpus, merus and ischium. As a conclusion, we argue that the genus can be distinguished from others on the basis of chelipeds only and accept as valid four extant species, viz. *Glypturus acanthochirus*, *G. armatus*, *G. laurae* and *G.* sp. (= *G. rabalaisae sensu* Sakai 2005, 2011; name unavailable). We consider *G. motupore* to be a junior synonym of *G. armatus*.

In several callianassid and ctenochelid genera and species, cheliped morphology is an expression of sexual dimorphism. Thus, this may be of use to palaeontologists who have no other means of determining sex in the fossil material. Unfortunately, no sexual dimorphism in chelipeds of *Glypturus* has been observed to date (e.g. Biffar 1971; Poore and Suchanek 1988).

Spination and tuberculation of chelipeds. The systematic value of cheliped characters, notably 'dentition and spination' was already mentioned by Biffar (1971, p. 642). This is very useful for palaeontologists when generally only chelipeds are available. As to tuberculation, this is a more variable feature which does not occur in all species. However, when present, it has taxonomic potential for specific identification. Here, we use the term 'tuberculation', rather than 'granulation', although there is no strict consensus in the usage of either term.

As Manning (1987) stated in his diagnosis of *Glypturus*, three spines on the upper margin of propodus are typical of the genus. They are arranged distally, which means that the position of the proximalmost spine is not beyond two-thirds of propodus length. Spines are usually oriented under a distally directed angle. Interestingly, some variability in spine arrangement and also number can be seen. Biffar (1971) noted in his diagnosis and description of *Callianassa acanthochirus* that there were two or three spines on the upper margin of the propodus. One specimen of *G. acanthochirus* examined for the present study (NHMW 24967) has five spines on the upper margin of the major cheliped (Fig. 2A–C) and four on the minor. Similarly, one specimen of *Glypturus* sp. (= *G. rabalaisae sensu* Sakai 2005, 2011), described and illustrated by Rabalais *et al.* (1981, text-fig. 3D, E) as *G. acanthochirus*, exhibits four spines. In the description of *Callianassa fraasi*, Noetling (1885) recorded variation between two and four spines. In this respect, it should be noted that the distalmost spine may occasionally be positioned more mesially (i.e. pointing inwards) than the other more proximal spines, which means that it can be overlooked when not fully

exposed. This may happen especially when working with poorly preserved fossil material. Notable examples include the case of *Callianassa pseudofraasi* and, possibly, Noetling's (1885, p. 492) description of *Callianassa fraasi*.

Spination of the carpus, merus and ischium also is a rather variable feature, although its presence is significant for generic assignment. In *Glypturus*, the number of spines on the lower margin of the carpus usually varies between six and 10. Spines typically point downwards and distally. It is worth mentioning that in some cases the spination on the lower margin of the carpus may be partially interrupted, as documented in a specimen of *G. laurae* (Fig. 3J). The upper margin of the carpus does not possess any spines.

On the merus, there are several ornament characters: spines on both lower and upper margins, presence of a longitudinal keel on the outer surface, dividing the merus into two halves (see Fig. 1A), and tuberculation in its lower half. On the upper margin, there usually are three spines; however, examples with two (e.g. *Glypturus armatus*, Fig. 1H; see also Rabalais *et al.* 1981, fig. 3E) and four spines (*G. armatus*, Fig. 1G) are also known. Rabalais *et al.* (1981, p.104) also recorded a single specimen of *G. acanthochirus* (= *G. rabalaisae sensu* Sakai 2005, 2011) with only one spine. Poore and Suchanek (1988) noted the presence of up to eight spines on the upper margin of the merus in *G. motupore*. In general, the most distally positioned upper meral spine may be situated slightly mesially. Spination of the meral lower margin usually is strongly developed; however, both the number of spines and spacing between individual spines vary both intra- and interspecifically. Most proximal spines usually are not aligned with the others; they originate above other spines on the lateral surface, at the position of the meral keel (Fig. 3G–J). Usually, only one spine is found in this position; however,
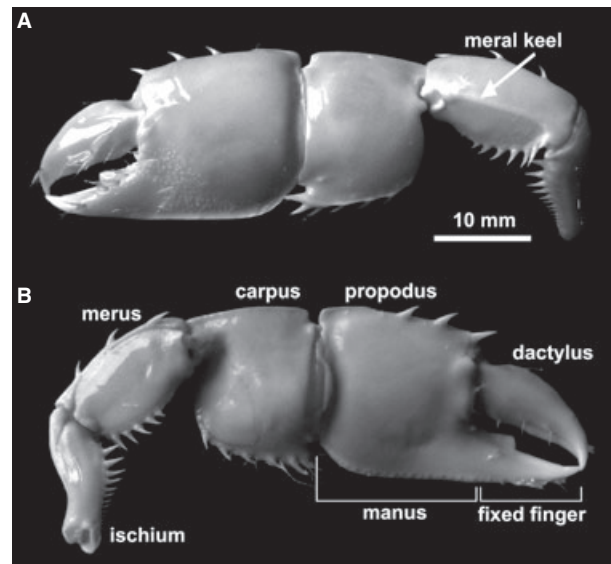

FIG. 1. Basic morphology of the major cheliped of *Glypturus acanthochirus* Stimpson, 1866 (NHMW 15342), with terminology used in the text, in outer (A) and inner (B) views. Note spination of the upper margins of the merus and propodus and of the lower margins of the ischium, merus and carpus.

two spines (Fig. 3J), or none at all, may also be observed (Fig. 3D).

The development of the meral longitudinal keel appears to be related to the development of tuberculation in the lower half of the meral lateral face. In species (or individuals) that lack tuberculation, the keel is very weakly developed and in strongly tuberculate species (or individuals) it is pronounced (Fig. 3D–J).

When dealing with chelipeds only, species of *Glypturus* can be distinguished from each other by the nature of the major chelae, especially with regard to tuberculation of the lateral surface of the propodus (Fig. 4). As demonstrated here, this criterion works for both extant and fossil material. It should be noted that tuberculation may also be subject to some variation depending upon the age and size of the animal. For instance, Poore and Suchanek (1988) examined 10 specimens of *G. motupore* with chelipeds, and all except one possessed lateral surfaces of the propodi without tubercles (Poore and Suchanek 1988, p. 202). Unfortunately, they did not mention whether the tuberculate specimen was exceptionally large or not, as it seems that larger specimens usually possess more prominent tubercles. More pronounced tuberculation in large specimens, as compared to smaller individuals, has also been observed in several callichirine species (P. C. Dworschak, pers. comm. 2010). Concerning the level of variation, it seems that tuberculation of the outer lateral surface is more consistent within the species and that on the inner is more variable (e.g. *G. munieri*). Occasionally, tuberculation is missing (e.g. *G. acanthochirus*; P. C. Dworschak, pers. comm. 2010).

It should be noted that cheliped spination also occurs in several other members of the Callianassidae. However, it never attains such arrangement and expression as in *Glypturus*. For instance, in *Lepidophthalmus grandidieri* (Coutière, 1899), spines are present distally both on upper and lower margins of the carpus, but confined only to the points of articulation with the propodus. A similar arrangement of spines was also recorded for *Eucalliax quadracuta* (Biffar, 1970) and *E. panglaoensis* Dworschak, 2006. *Eucalliax quadracuta* also possesses several tiny spines with larger ones positioned distally on the upper margin of the major propodus (Biffar 1970, p. 42; M. H., pers. obs.). It should be noted that in both *Lepidophthalmus* and *Eucalliax*, carpal spines do not occur in all species, and propodal spination has been noted for *E. quadracuta* only. Spination of the entire lower margin of the carpus occurs exclusively in species of *Glypturus*. In contrast, armature and tuberculation of the merus are quite common in many genera of the Callichirinae. However, the presence of several large spines along the entire lower margin is unique for *Glypturus*.

In addition to the fossil species that can clearly be assigned to *Glypturus*, there are several reports of Callianassidae which are worth mentioning here because of their broad resemblance to the genus studied.

Rathbun (1919) described a new species, *Callianassa anguillensis*, from the Miocene of Anguilla on the basis of several fragmentary specimens. The holotype (USNM MO 166941) is an incomplete propodus (Rathbun 1919, pl. 1, fig. 1); its tuberculation is much the same as the one seen in typical *Glypturus* as discussed earlier. The upper margin is insufficiently preserved to determine the number of expected spines; Rathbun (1919, p. 164), however, in the description of the holotype, stated that,

'… the surface thus exposed is blunt and transversely rugose, and on the inner side just below the (upper) margin and 3.7 mm from the distal end there is a curved tubercle, pointing forward; also in the same line a spine at the distal extremity'. Without re-examination of this material and lacking indications of the number of presumed propodal spines, we are at present hesitant to attribute this species to *Glypturus*.

Schweitzer *et al.* (2006*a*) noted the presence of several indeterminate callianassid species in the Bateque and Tepetate formations (Eocene) of Mexico. Their Callianassidae *sensu lato* species 2 (Schweitzer *et al.* 2006*a*, fig. 3.2) resembles *Glypturus* in several respects. The fixed finger has a large, oblong tooth on its occlusal surface. Most importantly, it possesses scattered tubercles on the lateral surface of the propodus near the base of the fixed finger arranged in a manner very similar to that of *Glypturus*. The upper margin of the propodus was described as very slightly convex and finely serrated; no spines, however, were noted.

Schweitzer *et al.* (2006*b*) described a new species, *Neocallichirus*? *quisquellanus*, from the Miocene of the Dominican Republic on the basis of a single specimen, a right major propodus with pronounced tuberculation on its outer surface resembling that of *Glypturus*. General propodus shape is also quite similar to *Glypturus*, but no spines on the upper margin were reported. The specimen was illustrated in matrix (Schweitzer *et al.* 2006*b*, fig. 3D), which means that the presence of still covered spines cannot be ruled out. Schweitzer *et al.* (2006*b*) noted that the specimen was unlike many species of *Neocallichirus*, which is why it was assigned to *Neocallichirus* with a query. Note, however, that in Schweitzer *et al.* (2010, p. 39), it is listed without a question mark.

Stratigraphic range. Middle Eocene to Holocene. Prior to the present study, the oldest fossil occurrence of the genus was Miocene (*Glypturus toulai*; see Todd and Collins 2005). Other occurrences included *Callianassa armata* from the Pliocene (Abrard 1947) and *G. acanthochirus* from the Pleistocene (Collins *et al.* 1996); both taxa also are extant.

EXTANT SPECIES

Glypturus acanthochirus Stimpson, 1866
Figures 1A–B, 2A–C, 3A–C, I, 4C

   *1866 *Glypturus acanthochirus* Stimpson, p. 46.
    1871 *Glypturus acanthochirus* Stimpson; Stimpson, p. 121.
    1899 *Glypturus acanthochirus* Stimpson; Kingsley, p. 821.
    1900 *Glypturus acanthochirus* Stimpson; Rathbun, p. 150.
    1901 *Glypturus acanthochirus* Stimpson; Rathbun, p. 93.
    1903 *Glypturus acanthochirus* Stimpson; Borradaile, p. 548.
    1928 *Glypturus acanthochirus* Stimpson; de Man, p. 19, 25, 180.
    1935 *Callianassa* (*Callichirus*) *acanthochirus* (Stimpson); Schmitt, p. 20, pl. 1, fig. 6; pl. 2, fig. 5; pl. 3, figs 4, 6.
    1943 *Callianassa acanthochirus* (Stimpson); Gurney, p. 84.
    1971 *Callianassa acanthochirus* (Stimpson); Biffar, p. 655, figs 3–4.
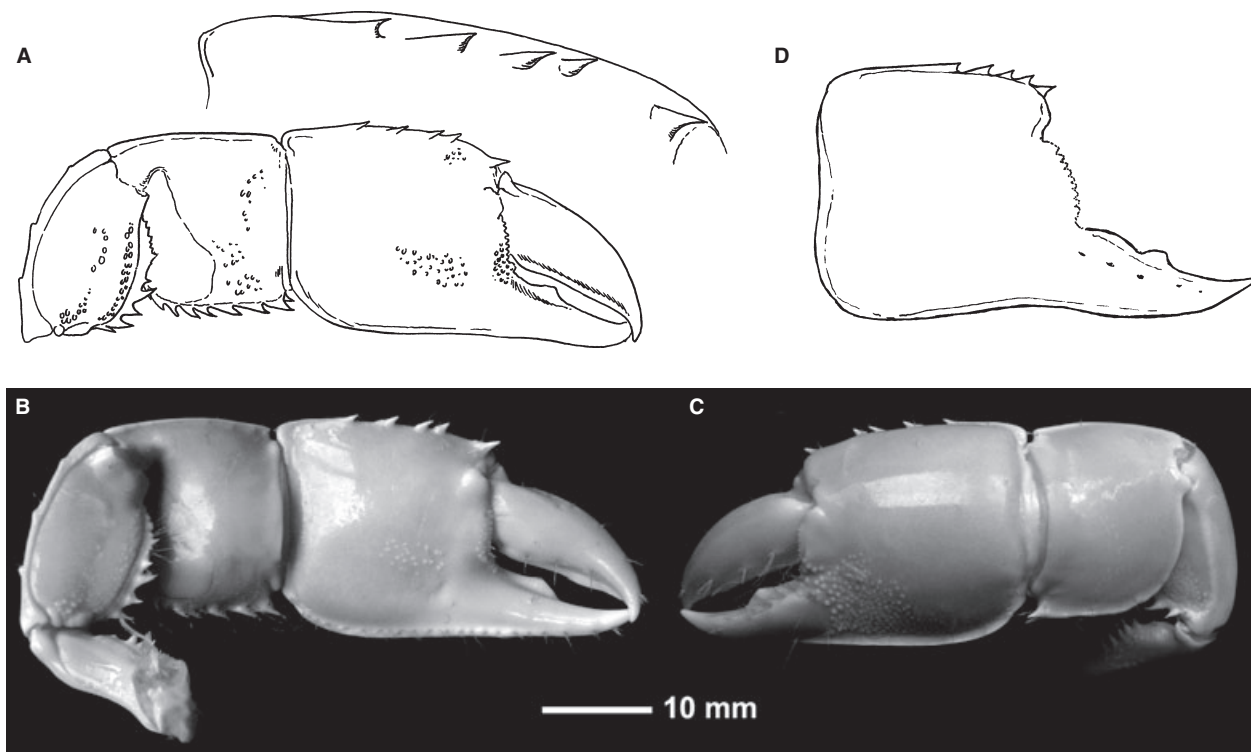   1979 *Callichirus acanthochirus* (Stimpson); de Saint Laurent and Le Loeuff, p. 96.

FIG. 2. Propodal spination in *Glypturus* and *Eoglypturus*. A–C, *Glypturus acanthochirus* Stimpson, 1866 (NHMW 24967), major cheliped in inner (A–B) and outer (C) views, with five propodal spines. D, Reconstructed appearance of the propodus of *Eoglypturus grolensis* Beschin, De Angeli, Checchi and Zarantonello, 2005 (after Beschin *et al.* 2005) with five spines (length of the element is approximately 2 cm). Spines are in a position that differs from that usually seen in *Glypturus*.

1987 *Glypturus acanthochirus* Stimpson; Manning, p. 390, fig. 3.

1988 *Glypturus acanthochirus* Stimpson; Poore and Suchanek, p. 201, fig. 4d.

1991 *Glypturus acanthochirus* Stimpson; Manning and Felder, p. 778.

1992 *Glypturus acanthochirus* Stimpson; Dworschak, p. 209.

1993 *Glypturus acanthochirus* Stimpson; Dworschak and Ott, p. 282.

1996 *Glypturus acanthochirus* Stimpson; Collins *et al.*, p. 54, pl. 12, fig. 1; pl. 15, figs 1, 3, 4.

1999 *Glypturus acanthochirus* Stimpson; Sakai, p. 73, fig. 14i.

2000 *Glypturus acanthochirus* Stimpson; Tudge *et al.*, p. 144.

2003 *Glypturus acanthochirus* Stimpson; Curran and Martin, pp. 230, 234, fig. 4B.

2004 *Glypturus acanthochirus* Stimpson; Dworschak, p. 20, fig. 4F.

2005 *Glypturus acanthochirus* Stimpson; Sakai, p. 133.

2005 *Glypturus acanthochirus* Stimpson; Abed-Navandi and Dworschak, p. 160.

2009 *Glypturus acanthochirus* Stimpson; Collins *et al.*, p. 70.

2009 *Glypturus acanthochirus* Stimpson; Felder *et al.*, p. 1062.

2011 *Glypturus acanthochirus* Stimpson; Sakai, p. 431, fig. 65A, B.

Material. NHMW 6770 (Fig. 3A), NHMW 15338, NHMW 15342 (Fig. 3G), NHMW 24967 (Fig. 2A–C), NHMW 24968 (Fig. 3B–C).

Occurrence. To date, this species is known from the western Atlantic (Atlantic coast of Florida, Gulf of Mexico, entire Caribbean, plus Caribbean coast of Colombia and Venezuela; see Dworschak 1992; Sakai 2005; Felder *et al.* 2009). Fossil representatives have been recorded from the upper Pleistocene Port Morant Formation of Jamaica by Collins *et al.* (1996).

Diagnosis. See Biffar (1971, p. 655).

Remarks. Glypturus acanthochirus is a well-known species. With regard to hard-part morphology, it can be distinguished from congeners on the basis of tuberculation on the lateral surfaces of the propodus (Fig. 4). Propodal tuberculation as a relatively consistent distinguishing feature was previously mentioned by Biffar (1971, p. 660) and Manning (1987, p. 392); the former author compared 'tuberculated' *G. acanthochirus* to 'smooth' *G. armatus*.

Of all extant species, *G. acanthochirus* has the comparatively most robust chelipeds. Tuberculation on the propodus is rather coarse and prominent; the same goes for the carpus (in part), merus and ischium. The merus is deep
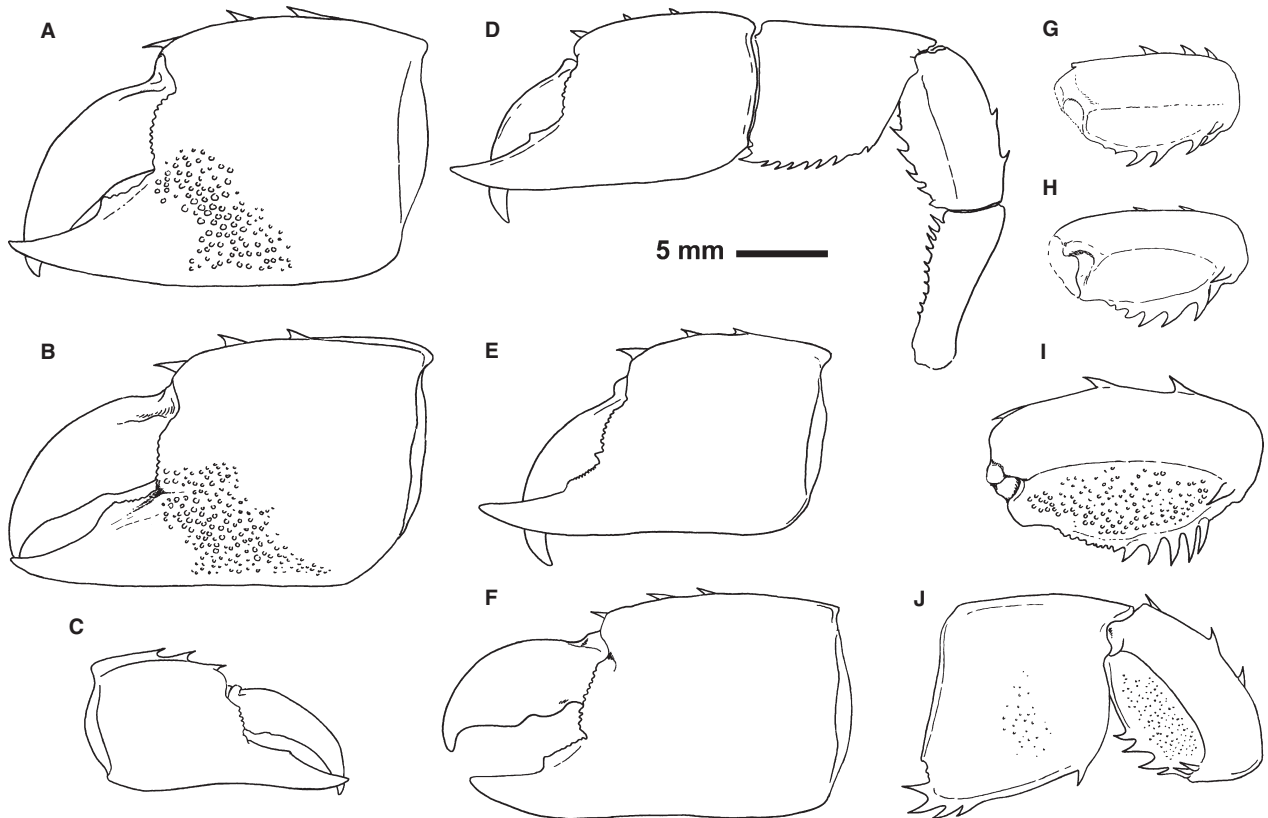
FIG. 3. Extant species of *Glypturus*. A, *G. acanthochirus* Stimpson, 1866, NHMW 6770 (major), left propodus and dactylus. B, *G. acanthochirus* Stimpson, 1866, NHMW 24968 (major), left propodus and dactylus. C, *G. acanthochirus* Stimpson, 1866, NHMW 24968 (minor), right propodus and dactylus; note pronounced keel on the upper margin of the propodus. D, *G. armatus* (A. Milne-Edwards, 1870), NHMW 23822 (major), left cheliped. E, *G. armatus* (A. Milne-Edwards, 1870), NHMW 21941 (major), left propodus and dactylus. F, *G. armatus* (A. Milne-Edwards, 1870), NMCR 39031 (major), left propodus and dactylus. G, *G. armatus* (A. Milne-Edwards, 1870), NHMW 21941 (major), left merus. H, *G. armatus* (A. Milne-Edwards, 1870), NMCR 39031 (major), left merus. I, *G. acanthochirus* Stimpson, 1866, NHMW 15342 (major), left merus. J, *G. laurae* (de Saint Laurent *in* de Vaugelas and de Saint Laurent, 1984), NHMW 6973 (major), left merus and carpus; note missing spines on the lower margin of the carpus. In all figures, setae are omitted. All figures to the same scale.

and bears a pronounced keel on the lateral surface (Figs 1A and 3J); tuberculation of the lower half usually is well developed (Fig. 3J).

The tuberculate area on the outer lateral surface of the propodus extends from the base of the fixed finger and extends diagonally to the lower margin (Fig. 4C); it does not extend to the proximal lower corner as in *Glypturus berryi* comb. nov. (Fig. 4E) and *G. fraasi* comb. nov. (Fig. 4F). Tuberculation on the inner lateral surface extends to a lesser extent, and tubercles are not as closely spaced as on the outer surface (Fig. 4C). Not all specimens possess tuberculation on the inner surface, because its extent and development depend more or less of size and/or age of the specimen (P. C. Dworschak, pers. comm. 2010). The general pattern of tuberculation on the outer surface is, however, quite consistent within the species.

Glypturus armatus (A. Milne-Edwards, 1870)
Figures 3D–H, 4A, 5A–D

*1870 *Callianassa armata* A. Milne-Edwards, pp. 90, 101, pl. 1.
1902 *Callianassa armata* A. Milne-Edwards; de Man, p. 754.
1903 *Callianassa (Callichirus) armata* A. Milne-Edwards; Borradaile, p. 547.
1928 *Callianassa (Callichirus) armata* A. Milne-Edwards; de Man, pp. 28, 93, 109.
1947 *Callianassa armata* A. Milne-Edwards; Abrard, p. 92, pl. 5, figs 42–43.
1975 *Callianassa armata* A. Milne-Edwards; Kensley, p. 48, fig. 1A–H.
1987 *Callianassa armata* A. Milne-Edwards; Manning, pp. 390, 392.
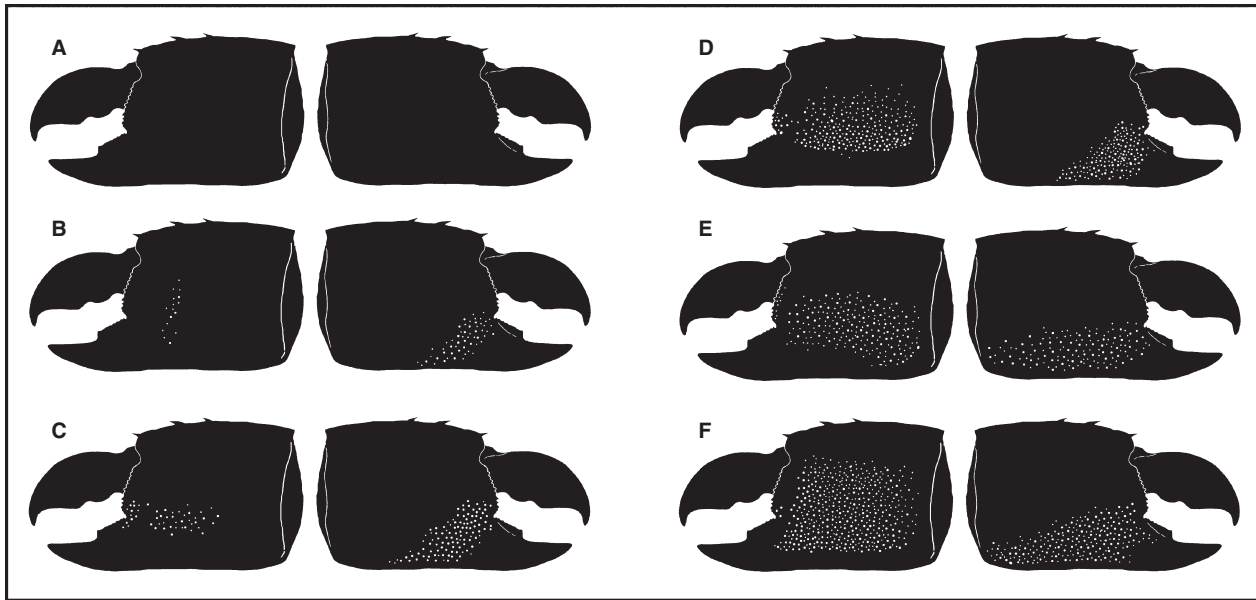1987 *Glypturus acanthochirus* Stimpson; Manning, p. 390, figs 4–5 (*partim*).

FIG. 4. Scheme of tuberculation on the major propodus in *Glypturus* (not to scale). A, *G. armatus* (A. Milne-Edwards, 1870) (based on NHMW 21941). B, *G. laurae* (de Saint Laurent *in* de Vaugelas and de Saint Laurent, 1984) (based on NHMW 6973). C, *G. acanthochirus* Stimpson, 1866 (based on NHMW 15338). D, *G. munieri* (Brocchi, 1883) comb. nov. (based on M.86.309, see also Fig. 8D–H). E, *G. berryi* (Rathbun, 1935) comb. nov. (based on USNM MO 495112, holotype). F, *G. fraasi* (Noetling, 1885) comb. nov. (based on Vía Boada 1969). Left column – inner surface; right column – outer surface.
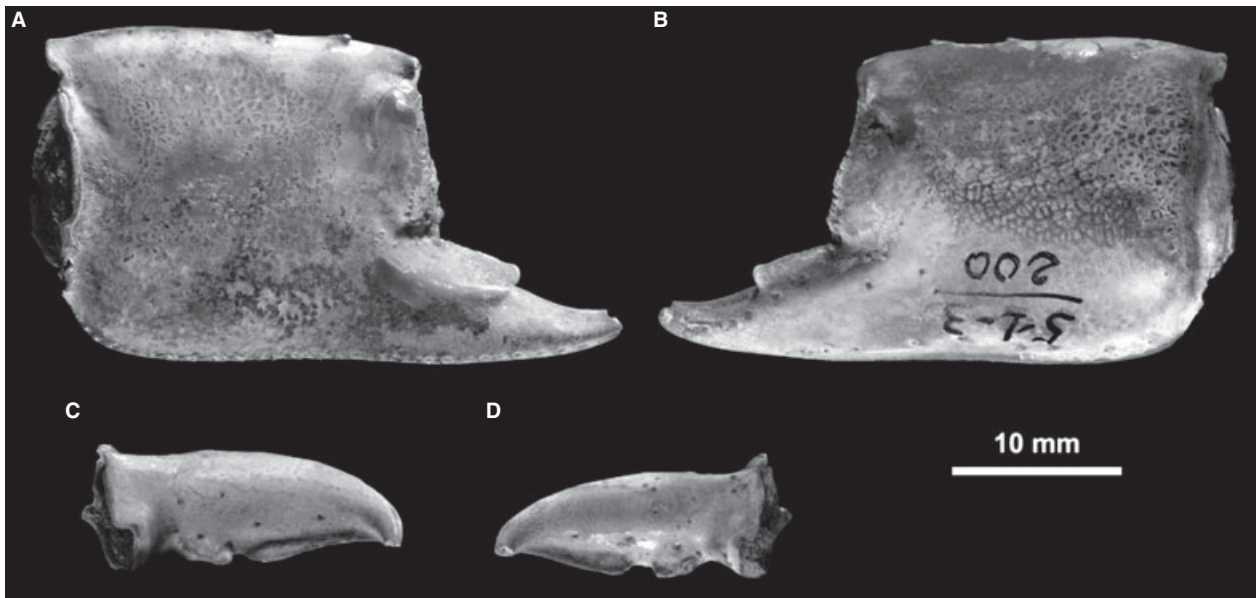

FIG. 5. *Glypturus armatus* (A. Milne-Edwards, 1870). A–B, left major propodus in inner and outer views, respectively. C, left major dactylus. D, right major dactylus. All materials (MNHN.F A27009, Aubert de la Rüe Collection) from the Pliocene of Vanuatu (Abrard 1947). All figures to the same scale.

1988 *Glypturus motupore* Poore and Suchanek, p. 198, figs 1–3, 4a.

1988 *Glypturus armatus* (A. Milne-Edwards); Poore and Suchanek, p. 201.

1991 *Glypturus armatus* (A. Milne-Edwards); Manning and Felder, p. 778.

1991 *Glypturus motupore* Poore and Suchanek; Manning and Felder, p. 778.

1999 *Glypturus armatus* (A. Milne-Edwards); Sakai, p. 76 (*partim*).

1999 *Neocallichirus motupore* (Poore and Suchanek); Sakai, p. 105.

2000 *Glypturus armatus* (A. Milne-Edwards); Tudge *et al.*, p. 144.

2000 *Glypturus motupore* Poore and Suchanek; Tudge *et al.*, p. 144.

2005 *Glypturus armatus* (A. Milne-Edwards); Sakai, p. 137 (*partim*).

2005 *Neocallichirus motupore* (Poore and Suchanek); Sakai, p. 182.

2007 *Glypturus armatus* (A. Milne-Edwards); Anker and Dworschak, p. 290.

2011 *Glypturus armatus* (A. Milne-Edwards); Sakai, p. 432 (*partim*).

Material. Extant examples include NHMW 21941 (Fig. 3E, G), NHMW 23822 (Fig. 3D) and NMCR 39031 (Fig. 3F, H). Fossil material comprises a left major propodus, one left major dactylus and one right major dactylus (Fig. 5A–D) from the Aubert de la Rüe Collection (MNHN.F A27009).

Occurrence. To date, this species is known from the Indo-West Pacific (Mataiva, Tuamotu Archipelago; Mauritius; Ternate, Indonesia; Fiji; Djibouti, Gulf of Aden; see Sakai 2005). *Glypturus motupore*, here considered a junior synonym of *G. armatus*, was recorded from Papua New Guinea (Poore and Suchanek 1988). The species is also known from the fossil record. Abrard (1947) recorded an isolated propodus and two dactyli (Fig. 5) from the Pliocene of Vanuatu.

Diagnosis. See Sakai (2005, p. 137).

Remarks. Chelipeds virtually lack tuberculation; however, larger-sized specimens usually have some tubercles at least on the merus and ischium. The lateral surfaces of the propodus usually are smooth (Fig. 4A). The merus is comparatively longer than in other extant species; therefore, it appears to be relatively slender. The meral keel usually is very weakly developed (Fig. 3D, G–H).

In their description of *G. motupore*, Poore and Suchanek (1988) stated that their new species lacked tuberculation on the chelipeds, thus being closely similar to *G. armatus*. When strictly applying criteria for the distinction of species of *Glypturus*, as presented here, the two can be considered synonymous. Actually, Sakai (2011) has recently synonymized *G. motupore* with *G. armatus* on the basis of soft-part morphology. However, contrary to Sakai (1999, 2005, 2011), we treat *G. laurae* as a distinct species.

Glypturus laurae (de Saint Laurent *in* de Vaugelas and de Saint Laurent, 1984)
Figures 3J, 4B

*1984 *Callichirus laurae* de Saint Laurent *in* de Vaugelas and de Saint Laurent, p. 147, pl. 1, fig. A–D.

1988 *Callichirus laurae* de Saint Laurent *in* de Vaugelas and de Saint Laurent; Abu-Hilal *et al.*, p. 234.

1988 *Glypturus laurae* (de Saint Laurent *in* de Vaugelas and de Saint Laurent); Poore and Suchanek, p. 201, fig. 4c.

1991 *Glypturus laurae* (de Saint Laurent *in* de Vaugelas and de Saint Laurent); Manning and Felder, p. 778.

1999 *Glypturus armatus* (A. Milne-Edwards); Sakai, p. 76 (*partim*).

2000 *Glypturus laurae* (de Saint Laurent *in* de Vaugelas and de Saint Laurent); Tudge *et al.*, p. 144.

2005 *Glypturus armatus* (A. Milne-Edwards); Sakai, p. 137 (*partim*).

2011 *Glypturus armatus* (A. Milne-Edwards); Sakai, p. 432 (*partim*).

Material. NHMW 6973 (Fig. 3J).

Occurrence. This species is known from the Red Sea (Gulf of Aqaba) (Dworschak 1992). Farrow (1971) and Braithwaite and Talbot (1972) described burrows attributed to *Callianassa* sp. from Aldabra and the Seychelles, respectively. Dworschak and Ott (1993, p. 287) stated that these were most probably made by *G. laurae*. No fossil material of *G. laurae* has been recorded so far.

Diagnosis. See de Vaugelas and de Saint Laurent (1984, p. 147).

Remarks. According to Dworschak (1992), this species is very close to *G. acanthochirus*. However, it can be distinguished by the faint tuberculation of the outer lateral surface of the propodus (Fig. 4B), as opposed to the prominent tubercules in *G. acanthochirus* (Fig. 4C). The sole specimen that we have examined ourselves (NHMW 6973) has few tubercles on the inner surface of the propodus extending almost vertically (Fig. 4B).

Glypturus sp.

1979 *Callianassa* (*Callichirus*) *acanthochirus* (Stimpson); Heard and Reames, p. 52.

1981 *Callianassa acanthochirus* (Stimpson); Rabalais *et al.*, p. 103, fig. 3.

2005 *Glypturus rabalaisae* Sakai, p. 135 (name unavailable).

2007 *Glypturus rabalaisae* Sakai; Dworschak, p. 159 (*nomen nudum*).

2009 *Glypturus* sp. Felder *et al.*, pp. 1062, 1093.

2011 *Glypturus rabalaisae* Sakai; Sakai, p. 438 (name unavailable).

Material. None.

Occurrence. This form is known solely from the northern part of the Gulf of Mexico (Felder *et al.* 2009).

Remarks. Rabalais *et al.* (1981) described several specimens as *Glypturus acanthochirus*. Sakai (2005) recognized them as members of a separate taxon which he named

G. rabalaisae. However, he failed to designate a type specimen, which is why the name is unavailable, as pointed out by Dworschak (2007). Later, Sakai (2011) did select a holotype for the species, but failed to indicate its repository. As such, the specific epithet still is unavailable. Felder *et al.* (2009) listed this species as '*Glypturus* sp'.

Rabalais *et al.* (1981, p. 103) did not describe the tuberculation on the lateral surfaces of the propodus in detail, but did mention the presence of 'two reduced spines on the submedian mesial surface of the merus of the major cheliped rather than with three large spines on the dorsal margin'.

FOSSIL SPECIES

Glypturus berryi (Rathbun, 1935) comb. nov.
Figures 4E, 6A–E

*1935 *Callianassa berryi* Rathbun, p. 96, pl. 21, figs 12–14.
1969 *Callianassa berryi* Rathbun; Vía Boada, p. 40.
2010 *Callianassa berryi* Rathbun; Schweitzer *et al.*, p. 34.

Material. KGP-MH HC001, a cast of the holotype (USNM MO 495112), a fragmentary left propodus of the major cheliped (Fig. 6A–E). For measurements, see Rathbun (1935, p. 97).

Occurrence. The holotype, and sole specimen known, comes from the Glendon Limestone (Vicksburg Group) of Oligocene age at Vicksburg (Warren County), Mississippi (Rathbun 1935).

Diagnosis. Strongly tuberculate *Glypturus*; lateral tuberculation on the propodus limited to the lower two-fifths of the outer surface and lower two-thirds of the inner surface.

Description. A detailed description of the type was provided by Rathbun (1935, p. 96), to whom reference is made.

Remarks. Rathbun (1935) pointed out that the great roughness of both inner and outer surfaces, the presence of two strong spines on the upper margin and a row of obliquely placed sockets along the inner surface of the lower margin distinguished this species from similarly shaped forms. In view of the fact that the distal margin of the specimen is damaged (Fig. 6A, C), it is feasible that there originally was a third spine at the very distal end of the upper margin of the propodus. All these characters clearly indicate this species to be a member of *Glypturus*, to which it is here transferred.

The nature of the tuberculation in the present species (Fig. 4E) was indicated by Rathbun (1935, p. 96) to be, 'outer surface much more convex than the inner, its lower two-fifths covered with large, separated granules or round sockets. (...) The inner surface has a depression on

its lower distal portion. The lower two-thirds of this surface is covered with coarse granules like those on the outer surface.' Such tubercle arrangement is similar to that in *G. munieri* comb. nov. (Fig. 4D) from the Miocene of the Central Paratethys and Mediterranean and in *G. fraasi* comb. nov. (Fig. 4F) from the Eocene of Europe and Africa. Unfortunately, Rathbun (1935) had only a single fragmentary right propodus at her disposal, precluding determination of intraspecific variation.

Glypturus fraasi (Noetling, 1885) comb. nov.
Figures 4F, 7A–C

*1885 *Callianassa Fraasi* Noetling, p. 492, pl. 4, figs 4–6.
1897 *Calianassa* [*sic*] cf. *Fraasi* Noetling; Lőrenthey, pp. 102, 114.
1898c *Calianassa* [*sic*] cf. *Fraasi* Noetling; Lőrenthey, p. 74, pl. 5, fig. 4.
?1926 *Callianassa* cfr. *Fraasi* Noetling; Böhm, p. 74.
1929 *Calianassa* [*sic*] *pseudo-Fraasi* Lőrenthey *in* Lőrenthey and Beurlen, p. 55, pl. 1, fig. 12.
1929 *Calianassa* [*sic*] *Fraasi* Noetling; Lőrenthey *in* Lőrenthey and Beurlen, p. 55.
?1929 *Callianassa* cf. *Fraasi* Noetling; Glaessner: 81.
1929 *Callianassa Fraasi* Noetling; Glaessner: 81.
1929 *Callianassa pseudofraasi* Lőrenthey *in* Lőrenthey and Beurlen; Glaessner, p. 88.
1930 *Callianassa Fraasi* Noetling; Cuvillier, p. 276.
1959 *Callianassa fraasi* Noetling; Vía Boada, p. 356.
1961 *Callianassa Fraasi* Noetling; Farrés Mallian, p. 62.
1969 *Callianassa fraasi* Noetling; Vía Boada, p. 34, text-fig. 1; pl. 1, figs 1–8.
1969 *Callianassa pseudo-fraasi* Lőrenthey *in* Lőrenthey and Beurlen; Vía Boada, p. 40.
1970 *Callianassa fraasi* Noetling; Vía Boada, p. 12.
?1981 *Callianassa* cf. *fraasi* Noetling; Kensley, p. 14.
1991 *Callianassa pseudofraasi* Lőrenthey *in* Lőrenthey and Beurlen; Müller and Collins, p. 49.
2003 *Callianassa fraasi* Noetling; Serra Kiel *et al.*, p. 211.
2010 *Callianassa fraasi* Noetling; Schweitzer *et al.*, p. 35.
2010 *Callianassa pseudofraasi* Lőrenthey *in* Lőrenthey and Beurlen; Schweitzer *et al.*, p. 36.

Material. The holotype of *Callianassa pseudofraasi* Lőrenthey *in* Lőrenthey and Beurlen, 1929 is E 9257; this is the left propodus of the major cheliped (Fig. 7A–C), the manus of which measures 21.7 and 20 mm, in maximum length and height, respectively.

The type material of *Callianassa fraasi* comprises several propodi of fragmentary nature deposited under numbers MB.A 1571–1573 corresponding to published figures in Noetling (1885, pl. 4, figs 7, 5, and 6, respectively). This material was studied only through photographs provided by Christian Neumann.

Occurrence. As understood here, this species has been recorded from the Eocene of Egypt, Spain, Hungary and, possibly,
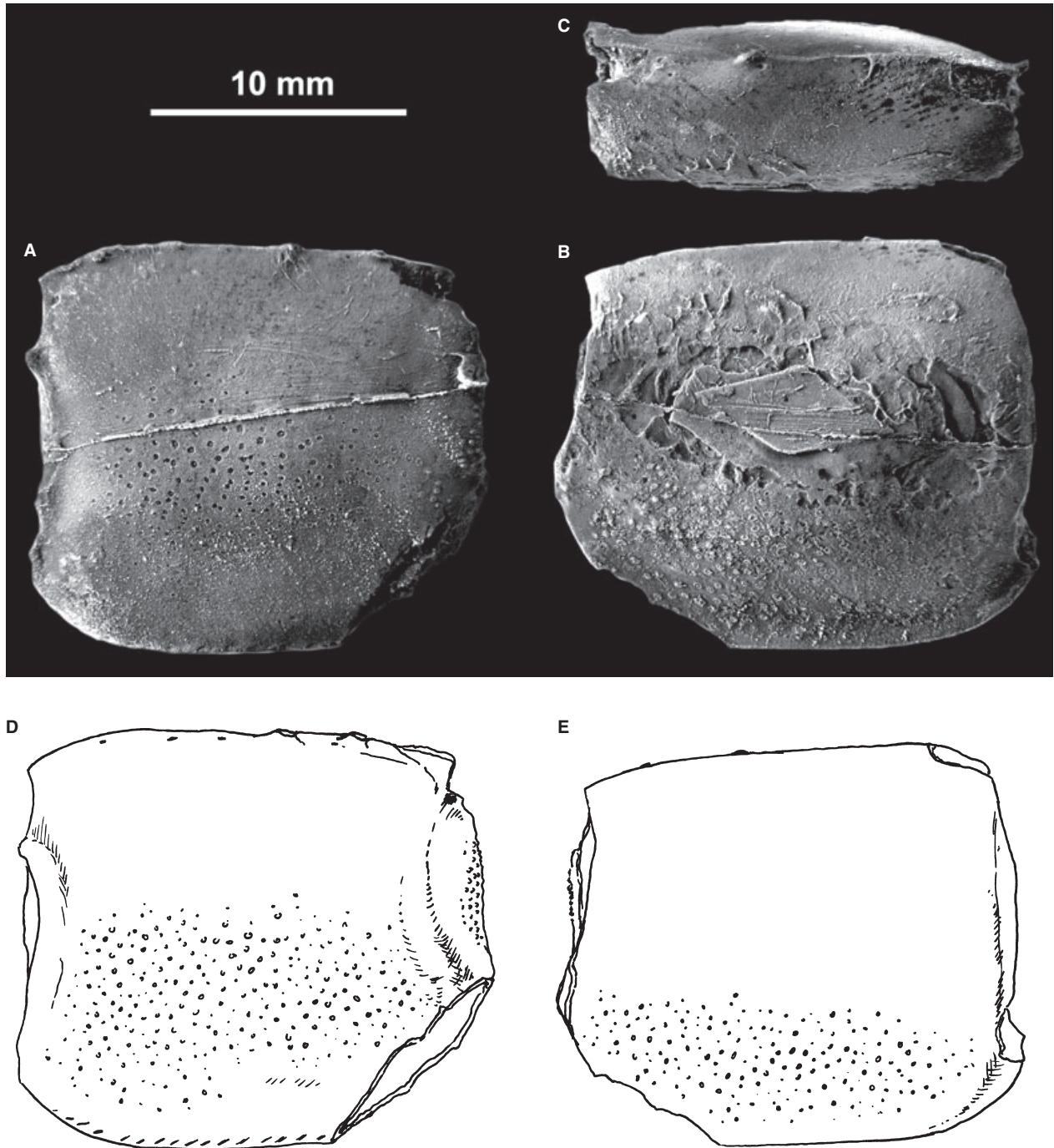
FIG. 6. *Glypturus berryi* (Rathbun, 1935) comb. nov. A–C, Left major propodus in inner, outer and upper views, respectively, Oligocene, Mississippi, USA (KGP-MH HC001, a cast of the holotype USNM MO 495112). D–E, interpretive drawings of A and B, respectively; note the broken propodal spines.

Namibia. The original record is from the upper Eocene of Egypt (Noetling 1885; see also Cuvillier 1930). Lőrenthey (1897, 1898c) described a single specimen, as *Callianassa pseudofraasi*, from the upper Eocene of Hungary. Vía Boada (1959, 1969, 1970), Farrés Mallian (1961) and Serra Kiel *et al.* (2003) have subsequently noted this species from the middle Eocene of Spain.

Böhm (1926) described, under the name of *Callianassa* cf. *fraasi*, callianassid remains from the Eocene of Bogenfels (south-west Africa, nowadays Namibia), but failed to illustrate these. In view of the great distance separating this record from the European–North African occurrences, we hesitate to consider this conspecific with *G. fraasi* comb. nov.
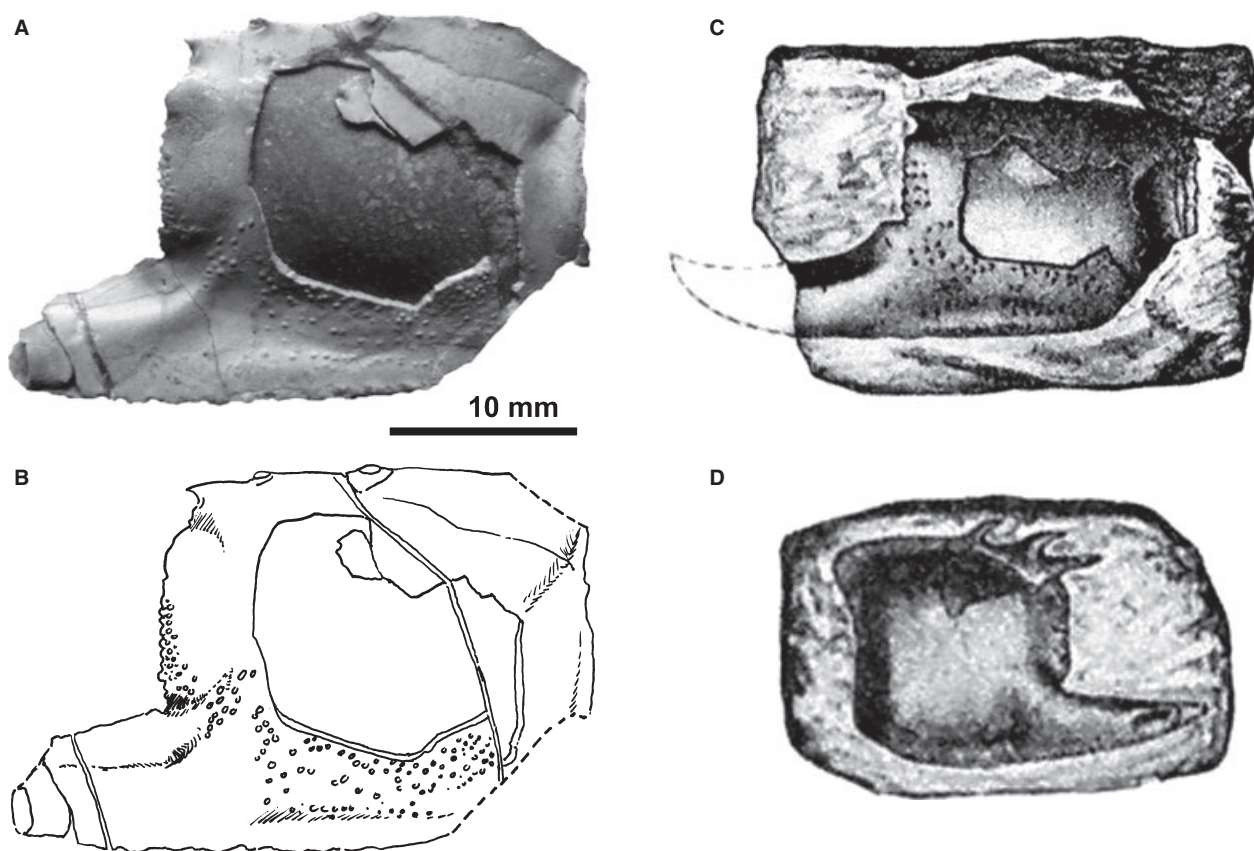
FIG. 7. Species of *Glypturus* from the Eocene of Hungary. A–B, Right major propodus (inner view) of *Glypturus fraasi* (Noetling, 1885) comb. nov., the holotype (E 9257) of *Calianassa* [*sic*] *pseudofraasi* Lőrenthey *in* Lőrenthey and Beurlen, 1929. C, *Calianassa* [*sic*] *pseudofraasi*, digital copy of Lőrenthey and Beurlen (1929, pl. 1, fig. 12). D, *Glypturus spinosus* (Lőrenthey, 1897) comb. nov., digital copy of Lőrenthey & Beurlen (1929, pl. 1, fig. 14).

Diagnosis. Strongly tuberculate *Glypturus*; lateral tuberculation on the propodus confined to the lower two-fifths of the outer surface and nearly the entire inner surface.

Description. A detailed description of this species was provided by Vía Boada (1969, p. 37), to whom reference is made.

Remarks. Lőrenthey (1897, 1898c) described a single specimen as *Calianassa* [*sic*] cf. *Fraasi* from the upper Eocene near Budapest, Hungary. Later, he (Lőrenthey *in* Lőrenthey and Beurlen 1929) reassigned this to a new species, *Calianassa* [*sic*] *pseudo-Fraasi*, on the basis of cheliped size, arguing also that that form had two spines on the upper margin of the propodus, rather than three in *C. fraasi*. However, our re-examination of the holotype has revealed that in fact there are three spines. The extent of tuberculation, although poorly preserved, seems to correspond that of *C. fraasi*. Therefore, we consider *C. pseudofraasi* to be as junior synonym of *C. fraasi*. The stratigraphical distribution of the latter supports such a conclusion.

Spination and tuberculation, together with overall propodus morphology, clearly favour assignment to *Glypturus*. Propodal tuberculation on the propodus has the widest extension of all species discussed herein (Fig. 4F). Tubercles cover nearly the lower two-fifths of the outer surface and extend also to the lower distal corner, as they do in *G. berryi* comb. nov (Fig. 4E). The inner surface is nearly completely covered with tubercles, while the lower and upper margins are bare.

It may be worth mentioning that the only published figure of *C. pseudofraasi* (reillustrated here as Fig. 7C) does not really fit the ratios of the actual specimen. The inaccurate nature of some of the illustrations published by Lőrenthey and Beurlen (1929) has previously been noted by Müller (1984a, p. 32).

Glypturus munieri (Brocchi, 1883) comb. nov.
Figures 4D, 8A–J, 9A–M

*1883   *Callianassa munieri* Brocchi, p. 5, pl. 5, figs 5–6.

1893   *Calianassa* [*sic*] *Munieri* Brocchi; Bittner, p. 10.
1897   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey, pp. 150, 160.
1898a   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey, pp. 93, 105, 114.
1898b   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey, pp. 105, 132, 155.
1898c   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey, p. 104.
1904a   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey, p. 161.
1904b   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey, p. 30.
1911   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey, p. 522.
1913   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey, p. 322.
1929   *Callianassa Munieri* Brocchi; Glaessner, p. 86.
1929   *Calianassa* [*sic*] *Munieri* Brocchi; Lőrenthey *in* Lőrenthey and Beurlen, pp. 33, 62–64, pl. 2, figs 19–23 (*non* fig. 24).
1929   *Portunus rákosensis* Lőrenthey (*partim*) *in* Lőrenthey and Beurlen, p. 173, pl. 12, figs 22–23.
?1953   *Callianassa* spec. ind.; Bachmayer, p. 242.
1969   *Callianassa munieri* Brocchi; Vía Boada, p. 40.
1975   *Callianassa munieri* Brocchi; Müller, p. 507.
1979   *Callianassa munieri* Brocchi; Müller, p. 274.
1984a   *Callianassa munieri* Brocchi; Müller, p. 50, pl. 1, figs 1–7; pl. 2, figs 1–2.
1984b   *Callianassa munieri* Brocchi; Müller, pl. 2, fig. 6.
1990   *Callianassa munieri* Brocchi; Moissette and Müller, p. 739.
1993   *Callianassa munieri* Brocchi; Kókay and Müller, p. 43.
2010   *Callianassa munieri* Brocchi; Schweitzer *et al.*, p. 36.
2010   *Callianassa munieri* Brocchi; Gatt and De Angeli, p. 1324, pl. 2, figs 1–2.

Material. All materials studied represent elements (often fragmentary) of major chelipeds and are from the following localities in Austria: Baden-Sooss (NHMW 2012/0010/0001; one right propodus, Fig. 8I); Wagna bei Aflenz (NHMW 2012/0008/0001, one right propodus, Fig. 8A–B) and Pöls (NHMW 1861/0001/0325, one left merus articulated with carpus; NHMW 2012/0009/0001, one right propodus, Fig. 8C). Material from
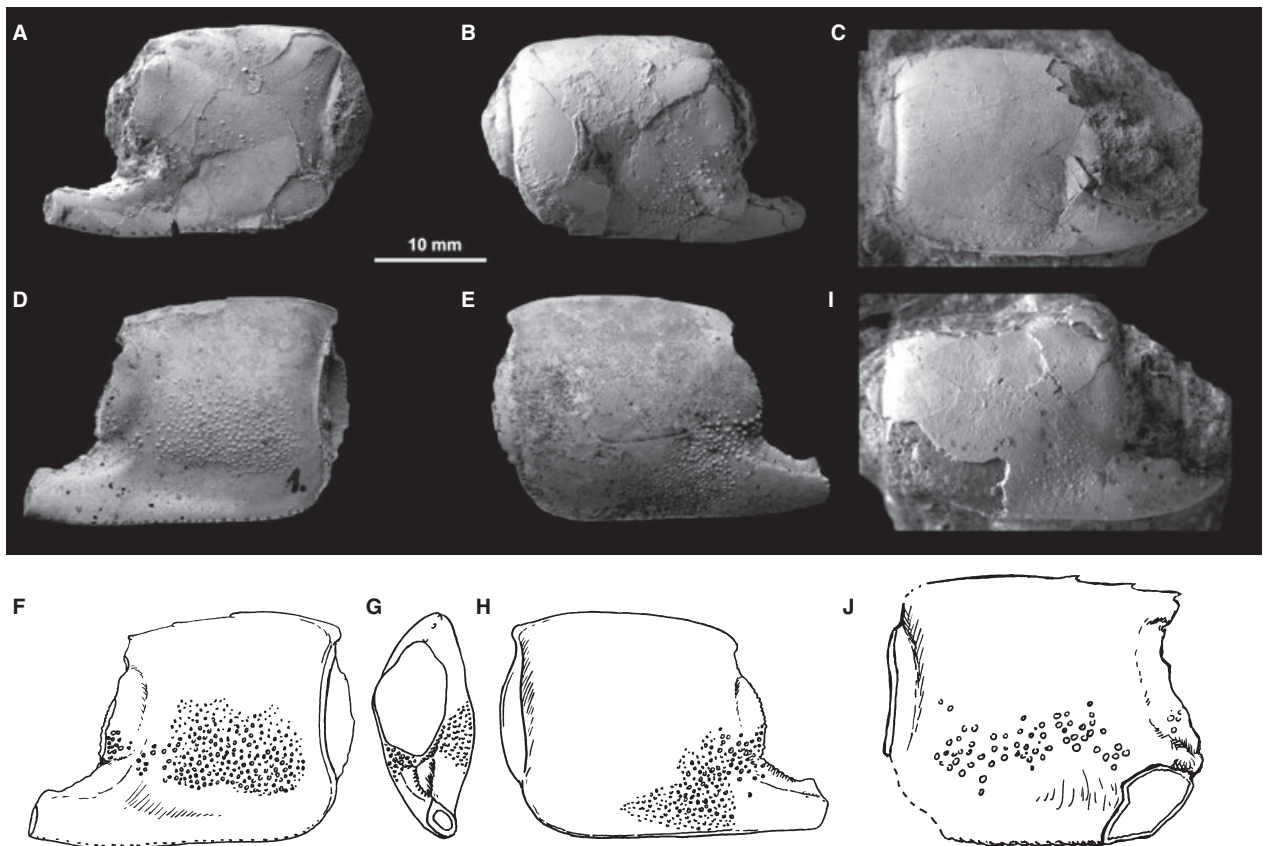

FIG. 8. *Glypturus munieri* (Brocchi, 1883) comb. nov. A–B, Right major propodus in inner and outer views, respectively (NHMW 2012/0008/0001), Wagna bei Aflenz, Austria. C, Right major propodus in outer view (NHMW 2012/0009/0001), Pöls, Austria. D–E, Right major propodus in inner and outer views, respectively (M.86.309), Budapest-Rákos, Hungary. F, H, Interpretive drawings of D and E, respectively. G, The same specimen in distal view. I, Right major propodus in outer view (NHMW 2012/0010/0001), Baden-Sooss, Austria. J, Fragmentary left major propodus in inner view (M.86.273), Budapest-Rákos, Hungary; compare extent of tuberculation with Figure 8F. At all localities, strata outcropping are of middle Miocene age. All figures to the same scale. Specimens in A–C, I were coated with ammonium chloride prior to photography.
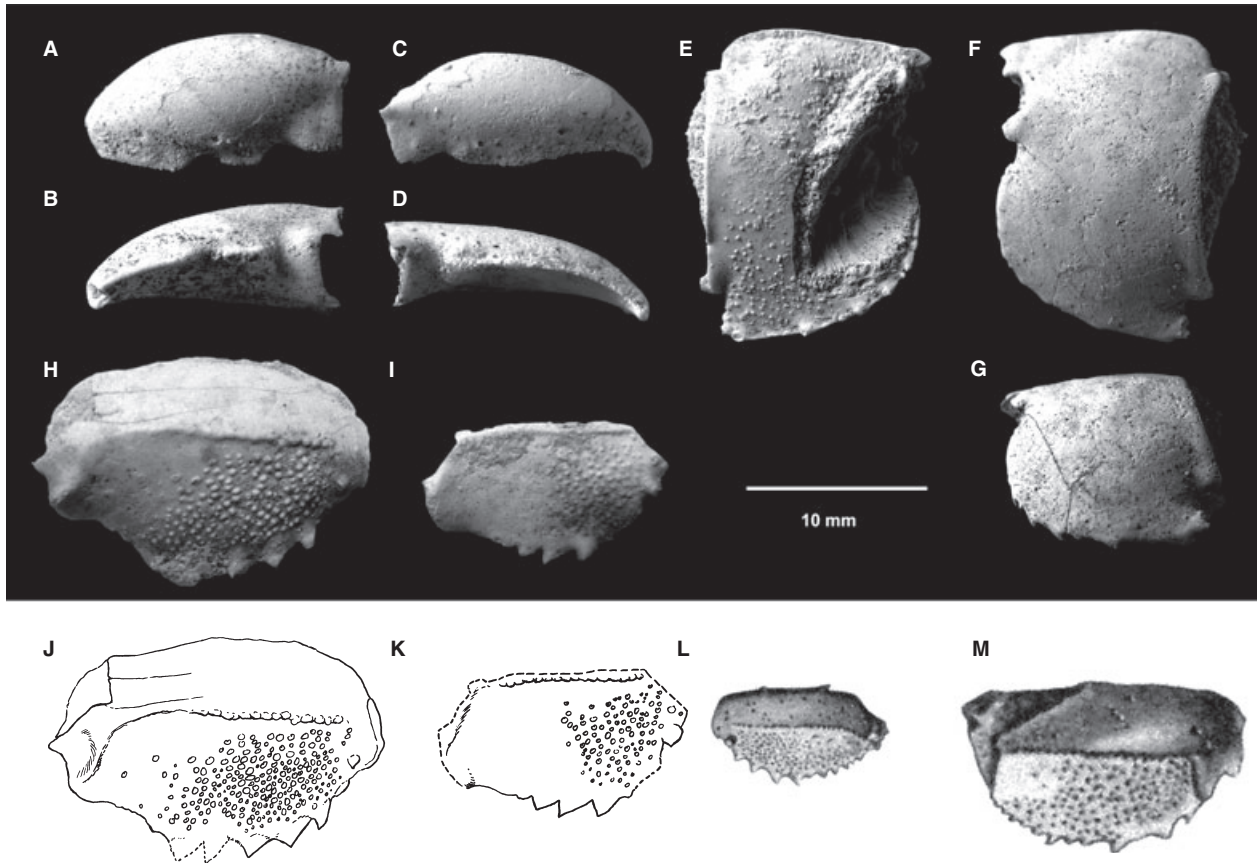
FIG. 9. *Glypturus munieri* (Brocchi, 1883) comb. nov. A–B, Left major dactylus in outer and occlusal views, respectively (PAL 2011.40); note broken tip. C–D, Right major dactylus in outer and occlusal views, respectively (PAL 2011.39). E–G, Right major carpus in inner, outer and oblique views, respectively (PAL 2011.38); note tuberculation on inner surface and spines on lower margin. H, Left major merus in outer view (M.86.273). I, Fragmentary left major merus in outer view (M.86.273). J–K, interpretive drawings of H and I, respectively. L–M, Right and left major merus in outer view, digital copies of Lőrenthey and Beurlen (1929, pl. 12, figs 22, 23). All materials are from Budapest-Rákos (Hungary) and are of middle Miocene age. All figures to the same scale. Specimens in A–G were coated with ammonium chloride prior to photography.

localities in the Budapest area, Hungary, includes KGP-MH RA009 (one right dactylus); M.86.225 (one fragmentary left propodus); M.86.273 (two left meri, Fig. 9H–K; three right carpi, one right propodus, 1 left propodus, Fig. 8J; four left dactyli); M.86.309 (two right meri, two left carpi, one right carpus, one left propodus, seven right propodi, Fig. 8D–H; one right dactylus); M.86.393 (one left merus, one left carpus, one left propodus, one left dactylus); PAL 2011.38 (one right carpus, Fig. 9E–G); PAL 2011.39 (one right dactylus, Fig. 9C–D); PAL 2011.40 (one left dactylus, Fig. 9A–B). Specimens from Bia, Hungary, comprise M.86.460, M.86.461 and M.86.463 (all fragments of propodi).

Measurements of material are shown in Table 2.

Occurrence. This species has been recorded from the middle Miocene ('Badenian') of Hungary (Lőrenthey 1897; Lőrenthey and Beurlen 1929; Müller 1984a) and Austria (herein), as well as the upper Miocene (Messinian) of Malta (Gatt and De Angeli 2010).

Müller (1984a) mentioned it mainly from the upper 'Badenian' in Hungary (Budapest, Bia, Balatonakali), with but a single occurrence from lower 'Badenian' strata at Zebegény. Lőrenthey

(1898c) had previously noted that at Budapest-Rákos, the species was the commonest form; he had collected hundreds of specimens. All Austrian occurrences known to us are limited to deposits of early 'Badenian' age, at Pöls and Wagna bei Aflenz in the Styrian Basin and at Baden-Sooss in the Vienna Basin. Bachmayer (1953) described a single fragmentary chela from the Leitha Limestone of Deutsch-Altenburg (Austria) as *Callianassa* spec. ind., mentioned the presence of tubercles ('Höckerchen') and considered the specimen to be similar to *C. munieri*. However, he failed to provide an illustration, nor did he indicate the repository number, which is why its true nature remains unresolved.

Müller (1984a) presented details of palaeosettings and stratigraphy for localities in Hungary, while Handler *et al.* (2006) are referred to for a discussion of the sedimentology and stratigraphy of the section at Pöls, and Hohenegger *et al.* (2009) for that at Wagna bei Aflenz.

Diagnosis. Moderately tuberculate *Glypturus*; lateral tuberculation on the outer surface of the propodus extend-

TABLE 2. Measurements (in mm) of major cheliped elements of the best-preserved specimens of *Glypturus munieri* (Brocchi, 1883) comb. nov.

Specimen	Element	Handedness	Max. length	Max. height
M.86.273	Merus	L	17.2	12.0
M.86.273	Merus	L	13.6	>7.6
M.86.309	Merus	R	16.3	>9.0
M.86.309	Merus	R	13.0	>6.0
M.86.393	Merus	L	14.0	7.5
M.86.273	Carpus	R	15.2	20.7
M.86.273	Carpus	R	14.6	18.3
M.86.273	Carpus	R	11.0	15.0
M.86.309	Carpus	L	>10.4	16.4
M.86.309	Carpus	L	12.0	17.4
M.86.309	Carpus	R	7.6	11.7
M.86.393	Carpus	L	12.0	15.3
PAL 2011.38	Carpus	R	13.1	17.8
PM Rákos MN 10	Carpus	R	~14	18.4
PM Rákos MN 10	Carpus	R	10.6	13.4
NHMW 2012/0010/0001	Propodus	R	19.4	17.0
NHMW 2012/0009/0001	Propodus	R	15.0	15.6
NHMW 2012/0008/0001	Propodus	R	16.5	17.3
M.86.273	Propodus	L	24.0	22.4
M.86.273	Propodus	R	13.8	13.6
M.86.309	Propodus	R	15.5	15.0
M.86.309	Propodus	L	15.7	15.1
M.86.309	Propodus	R	21.6	20.5
M.86.309	Propodus	R	19.7	20.4
M.86.309	Propodus	R	18.3	18.6
M.86.309	Propodus	R	11.7	12.3
M.86.309	Propodus	R	10.0	10.7
M.86.309	Propodus	R	19.1	19.5
M.86.393	Propodus	L	15.6	15.2
PM MDSZ 1	Propodus	R	17.5	15.3
PM MKC-5.2	Propodus	L	17.0	14.7
PM MRW-2	Propodus	L	18.7	18.0
KGP-MH RA009	Dactylus	L	12.4	5.4
M.86.273	Dactylus	L	16.7	7.2
M.86.273	Dactylus	L	11.3	5.1
M.86.273	Dactylus	L	15.0	5.8
M.86.273	Dactylus	L	10.0	3.7
M.86.309	Dactylus	R	16.0	9.2
PAL 2011.39	Dactylus	R	15.0	6.4
PAL 2011.40	Dactylus	L	>15.3	7.0

Note that many specimens are deposited under collective numbers.

ing from the base of the fixed finger diagonally to the lower margin, but not to the proximal lower corner; lateral tuberculation on the inner surface of the propodus variable, usually covering the central portion of the manus and also extending proximally.

Emended description. Length of merus about two times height, narrowest at articulation with carpus, with keel extending longitudinally and dividing merus into two equal portions; lower portion covered densely with tubercles; lower margin convex with up to eight spines, upper margin straight, generally with three spines. Carpus broad, 1.5 times taller than long, shorter than merus; upper margin keeled, slightly convex, terminating distally in blunt corner; proximal margin with projection at articulation with merus; lower and proximal margins forming rounded edge with seven to 10 distinct spines pointing downwards; distal margin weakly concave, rimmed at articulation with manus. Propodus nearly square, slightly longer than high, converging distally; upper margin proximally keeled, bearing three small spines distally, keel terminating in blunt corner; lower margin sharp, inner lateral surface with row of setal pits; proximal margin convex on outer face, concave on inner; distal margin weakly convex; outer lateral surface covered with tubercles extending from base of fixed finger and continuing diagonally to lower margin, but not to proximal lower corner; tuberculation on inner surface variable, often covering central portion of manus. Fixed finger triangular with distinct blunt tooth on occlusal margin; dactylus with rounded upper margin, lower margin keeled with tooth-like elevation; occasionally high and stout.

Remarks. The similarity between *Callianassa munieri* and extant *C. armata*, that is, the spiny propodus, was already noted by Brocchi (1883, p. 6) and Lőrenthey and Beurlen (1929, p. 64). *Callianassa munieri* is closely similar to extant species of *Glypturus*, being morphologically closest to *G. acanthochirus*.

As to published illustrations of *Glypturus munieri* comb. nov., we wish to make the following remarks. In the original description by Brocchi (1883, p. 5), an account of the morphology of the dactylus is lacking, although the illustrated specimens did retain this. The carpus and merus in Müller's monograph (1984a, pl. 1, figs 6–7) are figured upside down, and in the description of the carpus, the phrase 'carpus is decorated with a row of teeth on upper edge' in actual fact refers to the lower margin. The illustrations of meri of *Portunus rakosensis* by Lőrenthey and Beurlen (1929, pl. 12, figs 22–23; reillustrated here as Fig. 9L–M) actually represent meri of *G. munieri* comb. nov., as already hinted at by Müller (1984a).

In *Glypturus munieri* comb. nov., the tuberculation on the outer lateral surface of the propodus is very similar to that of *G. acanthochirus*; the inner surface of the former is often densely tuberculate, in contrast to that in the latter. The area of tuberculation on the inner surface is occasionally defined along its lower margin (Figs 8D, F and 4D); its extent is similar to that in *G. berryi* comb. nov. (Fig. 4E). It should be mentioned also that specimens of *G. munieri* comb. nov. with only few tubercles on the inner surface are known to us (Fig. 8A, J). Such individuals usually have a fainter tuberculation on the outer propodal surface. Interestingly, one specimen of *Glypturus munieri* comb. nov. with four propodal spines

has been noted (M.86.309). Such variation is present also in other species of *Glypturus*.

Glypturus pugnax (Böhm, 1922) comb. nov.

   *1922 *Callianassa pugnax* Böhm, p. 524, pl. 63, figs 17, 22, 24, 25.
   1929 *Callianassa pugnax* Böhm; Glaessner, p. 88.
   1969 *Callianassa pugnax* Böhm; Vía Boada, p. 40.
   2010 *Callianassa pugnax* Böhm; Schweitzer *et al.*, p. 36.

Material. None.

Occurrence. Upper Miocene of Kembang Sokkóh and Goenoeng Spolóng in the West-Progo Mountains, Java, Indonesia (Böhm 1922).

Description. Reference is made to Böhm (1922, p. 524).

Remarks. Unfortunately, the material originally described by Böhm (1922) could not be restudied by us, which is why a detailed comparison with other species recorded herein cannot be made. However, the presence of spines on the upper margin of the propodus and the tuberculate area on its lateral surface, both mentioned in the description and shown in the illustrations, strongly suggests reassignment to *Glypturus*.

Glypturus spinosus (Lőrenthey, 1897) comb. nov.
Figure 7D

  non 1876 *Callianassa spinosa* de Tribolet, p. 294, pl. 1, fig. 1.
   *1897 *Calianassa* [*sic*] *spinosa* Lőrenthey, p. 158.
   1898 *Calianassa* [*sic*] *spinosa* Lőrenthey; Lőrenthey, p. 76, pl. 5, fig. 6.
   1929 *Calianassa* [*sic*] *spinosa* Lőrenthey; Lőrenthey *in* Lőrenthey and Beurlen, p. 57, pl. 1, fig. 14.
  non 1929 *Callianassa spinosa* de Tribolet; Glaessner, p. 90.
   1929 *Callianassa subspinosa* Glaessner, p. 91.
   2010 *Callianassa subspinosa* Glaessner; Schweitzer *et al.*, p. 37.

Material. None. The holotype, and sole specimen known, may be presumed lost.

Occurrence. Upper Eocene of Hungary. *Calianassa* [*sic*] *spinosa* Lőrenthey, 1897 came from the same horizon as *C. pseudofraasi*.

Description. For detailed description, reference is made to Lőrenthey (1898*c*, p. 76) and Lőrenthey *in* Lőrenthey and Beurlen (1929, p. 57).

Remarks. Lőrenthey (1897) described *Calianassa* [*sic*] *spinosa* on the basis of a single left propodus from the

upper Eocene of Kis-Svábhegy near Budapest. Later, he (Lőrenthey 1898*c*) provided an illustration of the specimen, and the same figure also appeared in the monograph by Lőrenthey and Beurlen (1929) (reillustrated herein as Fig. 7D). The name was preoccupied by *Callianassa spinosa* de Tribolet, 1876 from the Lower Cretaceous of Switzerland, which is why Glaesssner (1929) renamed it as *C. subspinosa*. As such, it also appeared in the most recent compilation by Schweitzer *et al.* (2010). On the basis of the original figure (de Tribolet 1876, pl. 1, fig. 1), *C. spinosa* would appear to be utterly different from any species of *Glypturus* known to date. In fact, it might not even represent a callianassid at all.

The possible assignment of *C. subspinosa* to *Glypturus* has recently also been addressed by Beschin *et al.* (2005, p. 10). We follow suite and propose a new combination, *Glypturus spinosus*, herein. This also makes the replacement name *Callianassa subspinosa* Glaessner, 1929 redundant.

According to Lőrenthey *in* Lőrenthey and Beurlen (1929), there were several features that differentiated *C. subspinosa* (i.e. *C. spinosa*) from *C. pseudofraasi*. The most obvious was the size of the spines on the upper margin of the propodus, which were larger in *C. spinosa*. However, as shown earlier, spination on the upper margin of the propodus may be relatively variable. Other differences noted by Lőrenthey *in* Lőrenthey and Beurlen (1929) concern the shape of the propodus, which is actually not a very reliable character upon which to distinguish species. Lőrenthey (1898*c*) mentioned that *C. pseudofraasi* had a tuberculate propodus, whereas Lőrenthey *in* Lőrenthey and Beurlen (1929, p. 57) stated that the lateral surface of *C. subspinosa* (i.e. *spinosa*) was completely smooth. This may be related to the fact that the size of the specimen as *C. subspinosa* (i.e. *spinosa*) is much smaller than that of *C. pseudofraasi*. The former may represent a minor chela which usually lacks tuberculation (Fig. 3C); the shape of the proximal part of the keel on the upper margin would argue for that (compare Fig. 3C). The fact that both species come from the same stratigraphical horizon at the same locality also favours their synonymization. Despite repeated searches, the holotype of *Calianassa* [*sic*] *spinosa* Lőrenthey, 1897 in the Hungarian Geological Survey (Budapest), which houses the Lőrenthey Collection, has not been traced so far; we assume it to be lost. We also hesitate to synonymize *C. subspinosa* with *C. pseudofraasi* (resulting in the combination *G. fraasi* comb. nov.), because a comparison would have to rely solely on a published figure (Lőrenthey 1898*c*, pl. 5, fig. 6; see also Lőrenthey and Beurlen 1929, pl. 1, fig. 14; reillustrated herein as Fig. 7D) which may not be a correct rendition of the actual specimen (see e.g. *C. pseudofraasi*). We must await the discovery of new material to determine the relationship between these two species.

Hojnos (1923, 1933) described *Callianassa* [*sic*] *spinosa* var. *cserhática* from 'Badenian' (middle Miocene) strata

between the northern parts of the Cserhát and the Mátra Mountains. Unfortunately, the exact position of the locality is unknown although, as noted by Müller (1984*a*), it could actually refer to a small quarry in the valley of the Kis-Zagyva Creek near Mátraverebély-Szentkút. According to Müller (1984*a*), the material was lost, and the short description (without any figure) does not allow further conclusions. Interestingly, *C. spinosa* was originally described from upper Eocene strata, and it is therefore not very likely that Hojnos's material could be conspecific. More plausibly, it might represent *G. munieri* comb. nov., a common species at numerous localities with middle Miocene strata in Hungary and Austria.

Glypturus toulai (Rathbun, 1919)
Figure 10A–D

  1911 'Krabbenscheren' Toula, p. 512 (26), pl. 30(1), fig. 14.
  *1919 *Callianassa toulai* Rathbun, p. 146.
  1929 *Callianassa toulai* Rathbun; Glaessner, p. 92.
  2005 *Glypturus toulai* (Rathbun); Collins and Todd *in* Todd and Collins, p. 63, pl. 1, fig. 1.
  2009 *Glypturus toulai* (Rathbun); Collins *et al.*, pp. 70–71.

  2010 *Glypturus toulai* (Rathbun); Schweitzer *et al.*, p. 38.

Material. None.

Occurrence. Upper Miocene (Gatun Formation) of the Panama Canal (see Todd and Collins 2005).

Description. For a description, reference is made to Todd and Collins (2005, p. 63).

Remarks. Toula (1911) described two chelae from the Miocene of Panama merely as 'Krabbenscheren', illustrating one left major propodus, articulated with a dactylus. Later, Rathbun (1919) erected a new species to accommodate this, *Callianassa toulai*. However, in view of the fact that she failed to select a holotype, Todd and Collins (2005) designated the chela illustrated by Toula (1911, pl. 30(1), fig. 14), lectotype, although they did not re-examine the actual specimen (J. A. Todd, pers. comm. 2010). Todd and Collins (2005) also transferred the species to *Glypturus* on the basis of the presence of three spines on the upper margin of the propodus. In addition, they illustrated one recently collected specimen from both sides (pl. 1, fig. 1; reillustrated herein as Fig. 10).
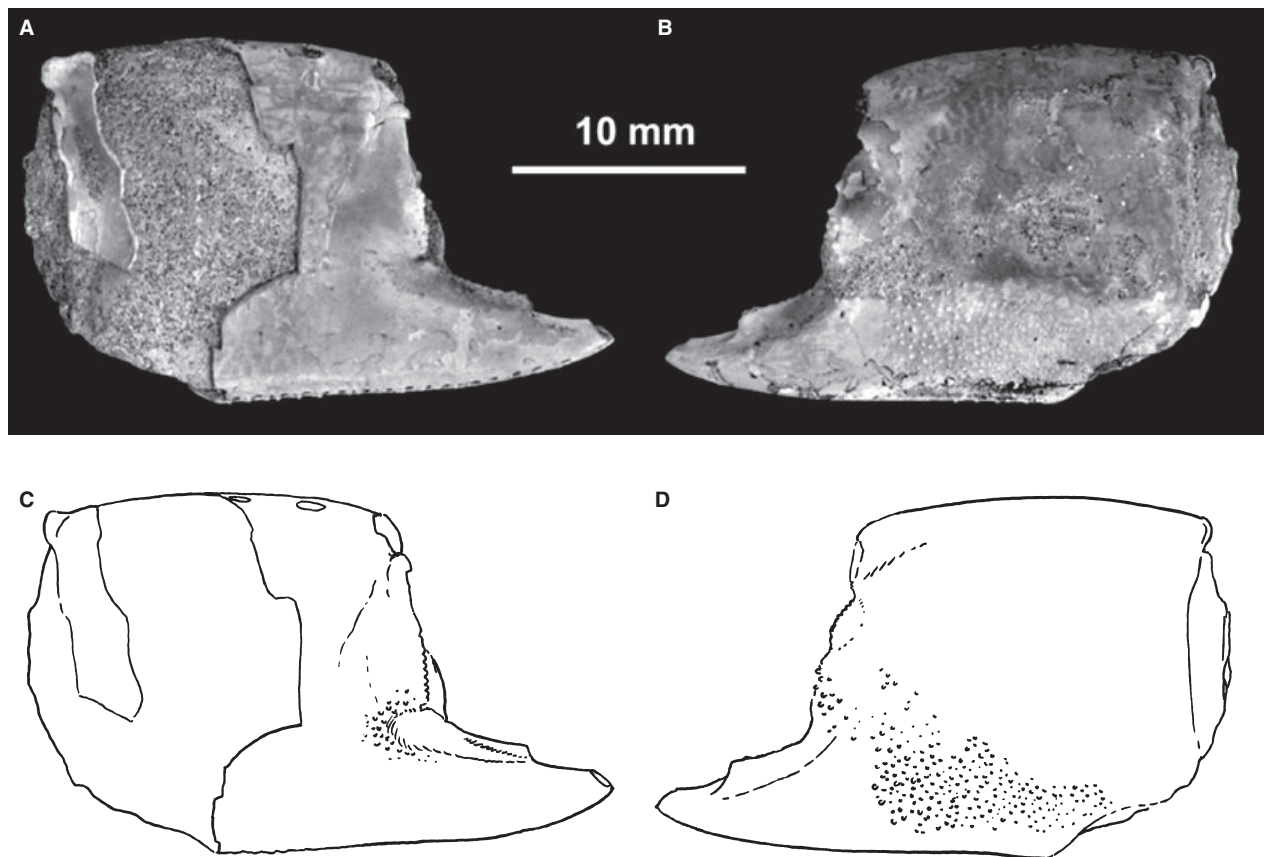

FIG. 10. *Glypturus toulai* (Rathbun, 1919) comb. nov. A–B, Left major propodus in inner and outer views, respectively (BMNPH PI IC 395), upper Miocene, Panama (reillustrated from Todd and Collins 2005, pl. 1, fig. 1a–b).

According to Todd and Collins (2005), there are fewer but coarser tubercles on the lateral surface of the propodus in *G. toulai* than in *G. acanthochirus*. They argued that the extent of tubercles on the latter is a variable feature and pointed out that *G. toulai* may in future be found to be synonymous with *G. acanthochirus*. Indeed, the tuberculation on the outer surface is very similar in both species. However, it seems that tubercles on the inner surface of the propodus in *G. toulai* are rather different from those usually present in *G. acanthochirus* (but see Fig. 1B), being limited to a small area at the base of the fixed finger (Fig. 10C). To determine the intraspecific variation of *G. toulai*, more material is needed.

Genus EOGLYPTURUS Beschin, De Angeli, Checchi and Zarantonello, 2005

Type species. Eoglypturus grolensis Beschin, De Angeli, Checchi and Zarantonello, 2005, by monotypy (Fig. 2D).

Diagnosis. Manus taller than long, robust, outer surface vaulted, upper margin with five spines; fixed finger as long as manus, occlusal margin with a tooth (after Beschin *et al.* 2005, p. 10).

Remarks. Here, we assign this genus to the Callichirinae on account of the presence of spines on the upper margin of the propodus and the overall shape of the propodus which is close to *Glypturus*. No other extant callianassid genus exhibits such spination of the propodus, consistent in all its species (*Eucalliax quadracuta*). As the taxonomic importance of spines has already been emphasized, we argue for a close link with *Glypturus*, and the subfamily Callichirinae at that (contrary to De Grave *et al.* 2009). The holotype, and sole known specimen, of *Eoglypturus grolensis* (MCZ 2381) does not preserve much of the original cuticular surface, precluding observation of any tuberculate area (Beschin *et al.* 2005; M. H., pers. obs. 2011).

As shown above, the number of propodal spines in *Glypturus* is a rather variable feature and it is questionable whether the arrangement of spines in *Eoglypturus grolensis* is distinct enough to constitute a sound basis for the erection of a distinct genus. So long as no other material is forthcoming, we keep *Eoglypturus* with *Glypturus* separate.

Stratigraphic range. The genus appears restricted to the middle Eocene of north-east Italy (Beschin *et al.* 2005).

PALAEOECOLOGICAL IMPLICATIONS

The distribution of many callianassids (and *Glypturus* is no exception) depends on sediment characteristics, depth, vegetation and water quality. Characteristic burrow architectures are diagnostic of species as well as suggestive of ecological adaptations (Griffis and Suchanek 1991; Dworschak and Ott 1993; Abed-Navandi and Dworschak 2005; Dworschak *et al.* 2006).

Members of the genus *Glypturus* prefer carbonate substrates of lagoons and leeward sand flats adjacent to coral reefs from the shore to depths of about 30 m (Manning and Felder 1991). However, Rabalais *et al.* (1981) also recorded this genus from much deeper settings in the Gulf of Mexico, down to depths of 91 m, although the majority of the material collected came from shallow-water settings. Rabalais *et al.* (1981) considered *Glypturus* to be an inhabitant primarily of shallow depths (10–25 m) in sandy, poorly sorted sediments.

The fossil record of *Glypturus* suggests similar ecological preferences during its stratigraphic range over at least 40 myr. Although records of *G. fraasi* comb. nov. and *G. spinosus* comb. nov. from the Eocene of Europe do not originate exclusively from carbonate facies (see e.g. Müller and Collins 1991; Serra Kiel *et al.* 2003), the Miocene occurrences appear to be typically connected with carbonate sedimentation.

Glypturus munieri comb. nov. from the middle Miocene of Hungary is found in fine homogeneous sands and is rather rare in or absent from medium- to coarse-grained calcarenites (Müller 1984*a*). Lőrenthey (1898*b*) noted that this species was very abundant at Budapest-Rákos, occurring both in the coarse limestone and in the calcareous sandstone rich in the benthic foraminifer, *Alveolina*. The Rákos palaeoenvironment was interpreted as a coral patch reef on a carbonate platform (Moissette *et al.* 2007, fig. 7). At Baden-Sooss (Austria), *G. munieri* comb. nov. occurs in limestone facies as well. During the middle Miocene, the climate in the Central Paratethys Sea was subtropical to warm-temperate, as documented by numerous groups of plants and animals (e.g. Moissette *et al.* 2006, 2007 and references therein). The sole late Miocene (Messinian) record of the species is from coralline limestones of Malta (Gatt and De Angeli 2010).

In conclusion, it follows that extinct species *Glypturus* are found in settings that are typical for modern relatives, that is, tropical to subtropical, nearshore carbonates of normal salinity.

Burrows and feeding strategy

Burrow morphology of *Glypturus* is fairly well known, having been the subject of several studies (e.g. de Vaugelas 1984; Poore and Suchanek 1988; Dworschak and Ott 1993). At the sediment/water interface, these burrows are characterized by large mounds and funnels; avalanches of sediment can often be seen sliding from the mounds into

the funnels. The burrows consist of a central spiralling shaft with several radiating tunnels branching off from the upper level, one of them leading to a funnel, the other to a mound; the others are blocked. Deeper side branches are often filled with coarse shell material (Dworschak and Ott 1993; Dworschak 2004).

The burrow morphology of *Glypturus acanthochirus* was described in detail and compared with burrows of congeners by Dworschak and Ott (1993). Curran and Martin (2003) reviewed this in the context of the fossil record. Burrows of *G. laurae* and *G. motupore* (= *G. armatus*) were described by de Vaugelas and de Saint-Laurent (1984) and Poore and Suchanek (1988), respectively. Abu-Hilal *et al.* (1988) studied the distribution of trace elements in burrows made by *G. laurae*. Curran and Martin (2003) noted that the ichnogenus *Ophiomorpha* Lundgren, 1891 may, at least in part, comprise burrows made by *Glypturus*. Although burrows of *Glypturus* have a highly distinct morphology, no undoubted fossil equivalents have yet been recovered.

There are several reports of presumed commensal decapod crustaceans inhabiting burrows produced by *Glypturus*. Dworschak *et al.* (2006) and Anker and Dworschak (2007) noted the laomediid shrimp *Naushonia* Kingsley, 1897 and the alpheid shrimp *Jengalpheops* Anker and Dworschak, 2007 in burrows made by *G. armatus* from Vietnam and the Philippines, respectively. To date, there are no records of fossil members of either family associated with *Glypturus*. However, this is hardly surprising, in view of the fact that such usually are of small size and only weakly calcified.

At Budapest-Rákos, portions of presumed callianassid burrows have been collected (compare Hyžný 2010, fig. 1D–F). Kókay and Müller (1993, p. 43) noted also the presence of large burrows, 'sometimes with callianassid chelae preserved within, probably belonging to their inhabitants. One of these, *Callianassa munieri*, was of remarkably big size.' In general, the *in situ* preservation of callianassid remains within burrow structures is very rare (see Hyžný 2011a for a review).

Glypturus acanthochirus has been interpreted to be a deposit feeder primarily, potentially able to exploit organic matter in surface or subsurface sediments (Griffis and Suchanek 1991; Dworschak and Ott 1993; Abed-Navandi and Dworschak 2005). There are also records of *G. acanthochirus* and *G. laurae* constructing burrow chambers filled with sediment and organic fragments of varying sizes and at various stages of decomposition (Suchanek 1985; Griffis and Suchanek 1991). When feeding, species of *Glypturus* are able to process large volumes of sediment (e.g. de Vaugelas 1985; Poore and Suchanek 1988; Dworschak and Ott 1993; Rowden and Jones 1993). Anker and Dworschak (2007, p. 298) noted that, '*Glypturus* feed on organic material that enters the funnel. Coarse

particles are sorted out and stored in blind tunnels. Fine material is pumped out of the burrow by vigorous beating of the pleopods, and accumulates in the form of mounds at the surface'.

GEOGRAPHICAL DISTRIBUTION OF FOSSIL AND EXTANT *GLYPTURUS*

Extant species of *Glypturus* are restricted to shallow-water marine settings (mainly carbonate shores) in the tropics and subtropics, below latitudes of 30 degrees. Biogeographically, two distinct groups have been recognized. In the western Atlantic occur *G. acanthochirus* and *G.* sp. (= *G. rabalaisae sensu* Sakai, 2005), while *G. armatus* and *G. laurae* inhabit the Indo-West Pacific (Fig. 11). It should be noted that *G. laurae* has been recorded solely from the Gulf of Aqaba (Red Sea); this species represents the most westerly occurrence of the genus in the Indo-West Pacific. In this respect, it is worth mentioning that the Red Sea is often considered to be a distinct province on account of the great percentage of endemics (Briggs 1995).

At present, there are no species of *Glypturus* in the Mediterranean Sea. However, the fossil record documents that the genus had much a wider distribution in the geological past (Fig. 12), both more to the south and north of its current range. This is likely to be attributable mainly to climatic changes during the Cenozoic. In consideration of the palaeobiogeography of *Glypturus*, the Tethys Realm as defined and discussed by Popov (1993) and Harzhauser *et al.* (2002, 2007) turns out to be a key area. Below, we adopt the palaeobiogeographical terms proposed by Harzhauser *et al.* (2002, 2007, 2008) and Harzhauser and Piller (2007).

Glypturus in space and time

The oldest unequivocal member of the genus is *G. fraasi* comb. nov. from the middle Eocene of Spain (Vía Boada 1969) and the upper Eocene of Hungary (Lőrenthey and Beurlen 1929) and Egypt (Noetling 1885). It appears that *Glypturus* was a common and abundant faunal element in the Tethys Realm during the Eocene. Interestingly, the genus *Eoglypturus* from the middle Eocene of Italy (Beschin *et al.* 2005) is coeval with *Glypturus fraasi* comb. nov. (Fig. 13). Thus the question arises whether they represent sister taxa, or whether *Eoglypturus* is ancestral to *Glypturus*, or *vice versa*. In any case, the conclusion can be that *Glypturus* is of Tethyan origin (Fig. 13). Apparently, during the Eocene, the genus migrated to North America as documented by *G. berryi* comb. nov. from the Oligocene of Misssissippi (Rathbun 1935). It has been
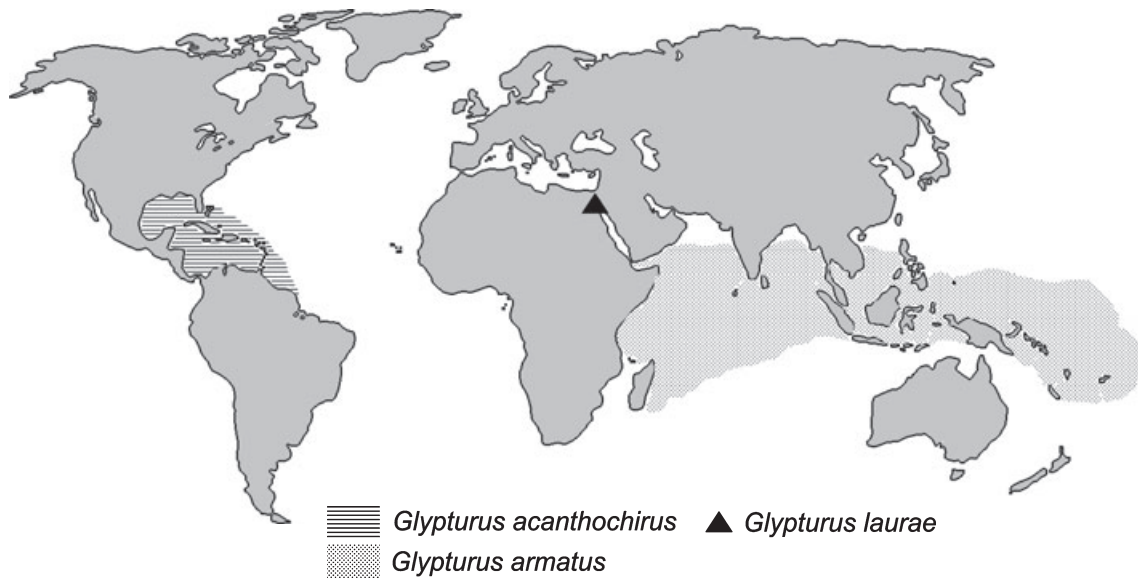
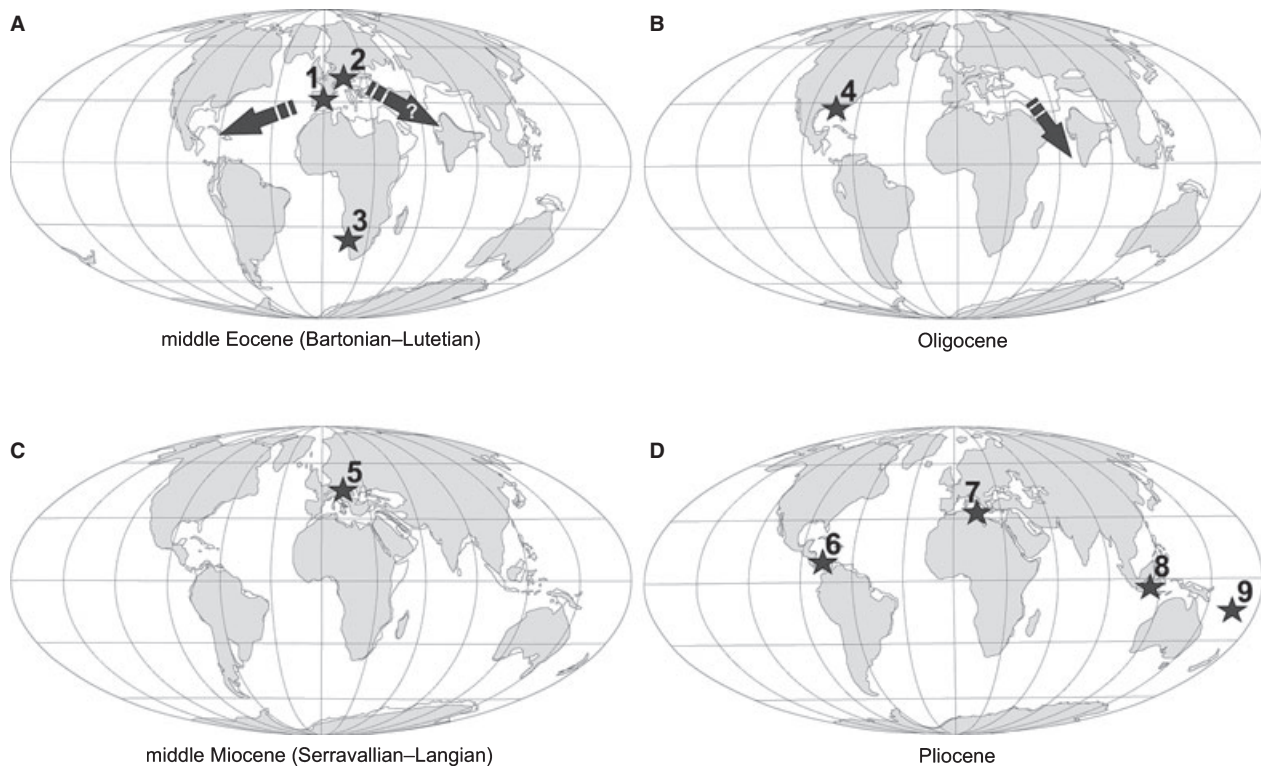**FIG. 11.** Geographic distribution of extant species of *Glypturus*. For details, see text.

FIG. 12. Palaeobiogeography of *Glypturus*. A, middle Eocene (Lutetian–Bartonian). B, Oligocene. C, middle Miocene (Langhian–Serravallian). D, Pliocene. 1, *G. fraasi*, Spain. 2, *G. fraasi* and *G. spinosus*, Hungary. 3, *Callianassa* cf. *fraasi*, Namibia. 4, *G. berryi*, Mississippi. 5, *G. munieri*, central Europe. 6, *G. toulai*, Panama. 7, *G. munieri*, Malta. 8, *G. pugnax*, Java. 9, *G. armatus*, Vanuatu. *Glypturus* occurrences are plotted on base maps from Smith *et al.* (1994). For details, see text.

shown on numerous occasions that many central American Eocene decapod crustacean taxa originated in the Tethys Realm and that migration from the Tethys to the central American bioprovinces took place during this interval (Feldmann *et al.* 1998; Schweitzer 2001; Schweitzer *et al.* 2002).

FIG. 13. Biogeographical evolution of *Glypturus*. E. = *Eoglypturus*; G. = *Glypturus*. Chronostratigraphical dates are adopted from Gradstein *et al.* (2004). For details, see text.
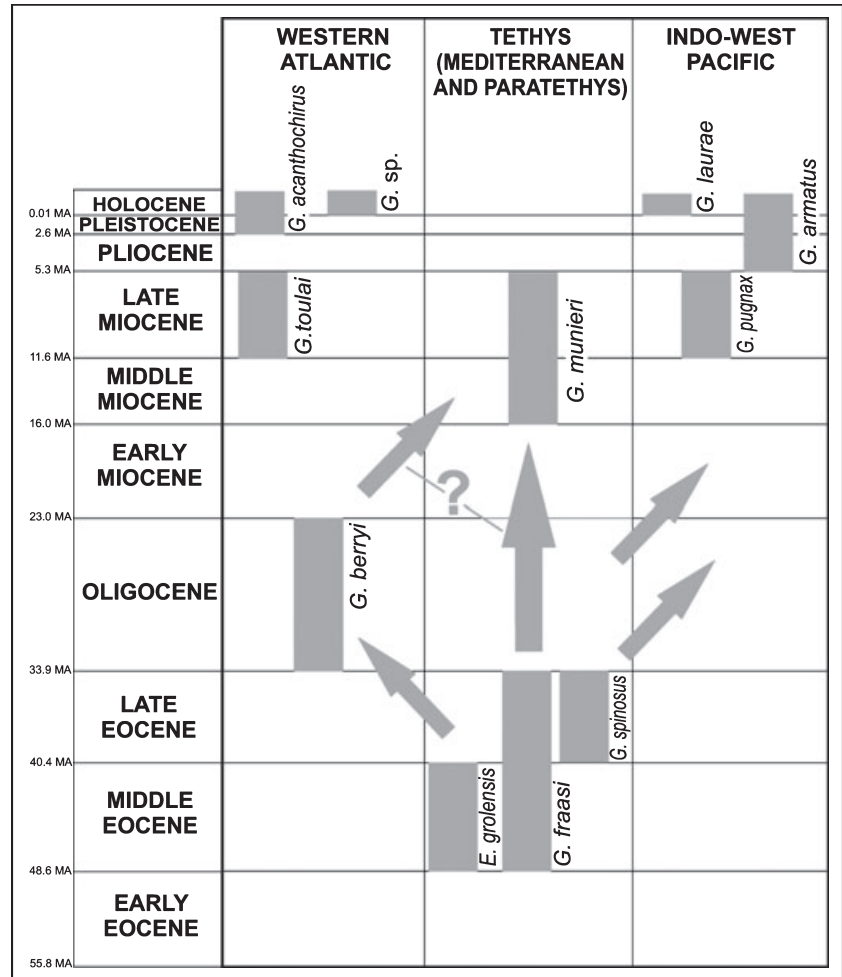
During the Oligocene, *Glypturus* is known only from North America (Mississippi); the absence of the genus from Europe may be explained by a global cooling event at the onset of the Oligocene (Zachos *et al.* 2001). However, as Feldmann (1986) observed, conclusions on decapod crustacean biogeography must be drawn on positive evidence; that is, the absence of fossils in a particular area does not necessarily mean that the taxon did not occur in that area. The presence of *Glypturus* (*G. munieri* comb. nov.) in the Miocene of the Mediterranean and central Paratethys documents either the persistence of the genus during the Oligocene or its subsequent re-introduction (Fig. 13) from North America. For gastropods (Harzhauser *et al.* 2002), such trans-Atlantic migrations during the early Miocene have been documented.

In the present-day Gulf of Mexico and the Caribbean Sea, the genus *Glypturus* occurred since its presumed immigration during the Eocene (Figs 12 and 13), with *G. toulai* comb. nov. in the upper Miocene of Panama (Todd and Collins 2005; Collins *et al.* 2009) and *G. acanthochirus* in the upper Pleistocene of Jamaica (Collins *et al.* 1996, 2009).

The presence of *Glypturus munieri* comb. nov. in the middle Miocene of the central Paratethys (Lőrenthey and Beurlen 1929; Müller 1984a) can be linked with the middle Miocene Climate Optimum during the Langhian stage (Zachos *et al.* 2001; Harzhauser *et al.* 2007). During that interval, the central Paratethys formed a distinct Danubian province within the Proto-Mediterranean–Atlantic Region (Harzhauser *et al.* 2002; Harzhauser and Piller 2007). Moissette *et al.* (2006) argued that exchange of faunas between the Mediterranean and the Paratethys was probably regulated by an anti-estuarine circulation permitting easier incursions of Proto-Mediterranean species into the Paratethys, but hindering Paratethys endemics from entering the Proto-Mediterranean. Seen in this light, *G. munieri* comb. nov. might be considered a Proto-Mediterranean immigrant, because it is also known from the upper Miocene of Malta. The final marine connection between the central Paratethys and Proto-Mediterranean seas was closed at the end of the middle Miocene (Serravallian). Subsequently, the central Paratethys Sea transformed into Lake Pannon, which gradually disappeared (Rögl 1998, 1999; Harzhauser and Piller 2007), which means that *Glypturus* must have

gone extinct in this area. The youngest European (Tethyan) record is *G. munieri* comb. nov. from the upper Miocene of Malta (Gatt and De Angeli 2011). Its final disappearance from the Proto-Mediterranean–Atlantic Region at the end of the Miocene can be correlated with the Messinian Salinity Crisis, which left marine faunas of the Mediterranean basins severely impoverished (Hsü *et al.* 1978; Harzhauser *et al.* 2002; Krijgsman *et al.* 2010). The Messinian Salinity Crisis triggered a turnover in nearshore faunas, and although shallow-marine molluscs did recolonize the Mediterranean basins from the Atlantic (Harzhauser *et al.* 2002), the same cannot be postulated for *Glypturus*. Final transformation from the Proto-Mediterranean–Atlantic Region to the modern Mediterranean–Atlantic Region occurred during the late Pliocene and Pleistocene, influenced by distinct cooling events (Rögl and Steininger 1983). As a consequence, tropical and subtropical gastropod taxa that were present in the assemblages of the Proto-Mediterranean–Atlantic Region are absent from modern-day communities (Harzhauser *et al.* 2002), a pattern similar to the disappearance of *Glypturus*.

Prior to the extinction of *Glypturus* in the area of the modern-day Mediterranean Sea, one more dispersal event can be documented for the genus. Apart from colonization of the western Atlantic during the Paleogene, the genus apparently migrated into the Indo-West Pacific (Figs 12 and 13). *Glypturus pugnax* comb. nov. from Java (Böhm 1922) is of late Miocene age and its presence can be linked with the open Tethyan seaway between the Proto-Mediterranean–Atlantic and Indo-West Pacific regions during the Oligocene and early Miocene (Reuter *et al.* 2007). This seaway was closed at the end of the middle Miocene (Rögl 1998, 1999; Harzhauser *et al.* 2002, 2007; Harzhauser and Piller 2007). The fossil record suggests migration of Tethyan marine faunas in an easterly direction during the Oligo-Miocene; this led to a major shift towards the West Pacific as a centre of diversity. Such has been documented by molluscs and ophiuroids (Harzhauser *et al.* 2007, 2008; see also Renema *et al.* 2008). Apparently, decapod crustaceans of Tethyan stock took the same migratory routes (Schweitzer 2001; Hyžný 2011*b*). At present, species of *Glypturus* occur all over the Indo-West Pacific (Fig. 11).

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