

PODOCALLICHIRUS LAEPAENSIS, A NEW GHOST SHRIMP (CRUSTACEA, DECAPODA, CALLIANASSIDAE) FROM THE LATE MIOCENE OF SOUTHWEST SPAIN

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ABSTRACT—Callianassids are among the most commonly found decapod crustacean fossils but their generic assignment is often difficult. Numerous cheliped remains have been found in the upper Miocene deposits of southwest Spain allowing description of a new species of a ghost shrimp, *Podocallichirus laepaensis*. The assignment of the new form to the respective genus is based mainly on the morphology of the major cheliped merus and provides useful implications for paleontological studies. *Podocallichirus laepaensis* is the first fossil record of the genus known to date. Several specimens preserved in association with and within *Ophiomorpha* traces are interpreted as in situ preservation. Thus, the new ghost shrimp is identified as the producer of trace fossils.

INTRODUCTION

CALLIANASSIDAE DANA, 1852 is a distinct family of fossorial shrimps, classified within the superfamily Callianassoidea Dana, 1852. Members inhabit predominantly intertidal and subtidal marine environments of mainly tropics and subtropics (Dworschak, 2000, 2005) and exhibit sophisticated behavior involving digging complex burrow systems. They can rework huge amounts of substrate and are considered true ecosystem engineers (Tamaki, 2004).

Callianassoid shrimp remains are among the most commonly found decapod remains in the fossil record; however, because of the delicate structure of most cuticular surfaces, only chelipeds which are usually heavily calcified are likely to be preserved (Bishop and Williams, 2005). The biological classification of the Callianassidae is based mainly on soft part morphology with poor or no fossilization potential, thus the fossil material usually lacks the diagnostic characters of extant taxa. Manning and Felder (1991) turned attention to the characters on chelipeds, although they discussed extant American taxa only. The taxonomic importance of the chelipeds in systematics of callianassid genera was emphasized also by Ngoc-Ho (2003) when comparing genera within the subfamily Eucalliinae Manning and Felder, 1991. Such studies are thus considered of great importance for paleontologists working with incompletely preserved individuals.

Material representing a new callianassid shrimp shows characters present in several genera of the subfamily Callichirinae Manning and Felder, 1991, notably *Callichirus* Stimpson, 1866, *Neocallichirus* Sakai, 1988, *Sergio* Manning and Lemaitre, 1994, *Podocallichirus* Sakai, 1999 and *Glypturoides* Sakai, 2011. Based mostly on the morphology of the merus of the major cheliped, the new form is assigned to the genus *Podocallichirus*. It constitutes the first callianassid taxon identified to species level from the late Miocene strata of Spain.

GEOLOGIC SETTING AND STRATIGRAPHY

The studied section named “Valleforero” (Muñiz, 1998) located in the surroundings of the town of Lepe (Huelva province, SW Spain) lies in the western sector of the Guadalquivir Basin (Fig. 1). This Neogene foreland basin describes an ENE-WSW elongated triangle with remarkable asymmetry. Its southern limit corresponds to the External

Zone of the Betic Ranges, while the northern passive margin is bounded by the Paleozoic basement of the Iberian Massif.

The origin of this basin is linked to the collision of the African and Iberian plates during the Neogene. This caused asymmetrical uplift of the sediments filling the basin and, as a consequence, the deposits of the easternmost side are now exposed at an elevation of more than 800 m above sea level, whereas the western end of the basin (opening to the Atlantic Ocean) was much less affected by tectonics (Sanz de Galdeano, 1990; Braga et al., 2003). During the Miocene and Pliocene, the northern passive margin and the center of the basin were filled with autochthonous and parautochthonous terrigenous and biogenic deposits, whereas the active south and southeastern margins were filled with allochthonous materials of the olistostrome structural unit (Sierro et al., 1996).

In the Huelva province, Neogene marine autochthonous sediments have been divided into four formally-defined formations, which from bottom to top are: 1) the Niebla Formation (Baceta and Pendón, 1999), also known as Basal Transgressive Complex (Pendón et al., 2004; Abad et al., 2005), the occurrence of *Neogloboquadrina humerosa* suggests a late Tortonian (late Miocene) age (Sierro et al., 1990); 2) the Gibrleón Clays Formation (Civis et al., 1987) is interpreted as upper Miocene (upper Tortonian, *Turborotalia humerosa* biozone sensu Sierro, 1985) and lower Pliocene (*Globorotalia miotumida* and *G. margaritae* biozones sensu Sierro, 1985); 3) the Huelva Sands Formation consists of a condensed basal level of glauconitic sandstone, with siltstone and fine sandstone above. Based on the occurrence of *Globorotalia margaritae* and *G. puncticulata*, this formation is interpreted as lower Pliocene (Sierro, 1985); and 4) the Bonares Sands Formation occurs at the top of the Neogene succession. Sierro et al. (1996) suggested an upper lower Pliocene age for this unit, although no definitive biostratigraphic data are yet available.

The ‘Lepe White Silts’ in the Lepe-Ayamonte area.—In the Lepe-Ayamonte sector of the Guadalquivir Basin, the Neogene sediments are represented by an array of marginal marine siliciclastic facies informally known as the ‘Lepe White Silts’ (Muñiz et al., 2010). This unit unconformably lies upon Lower Carboniferous graywackes and shales and it is unconformably overlain by lower Pleistocene sands, gravels and conglomerates interpreted as fluvial terrace deposits

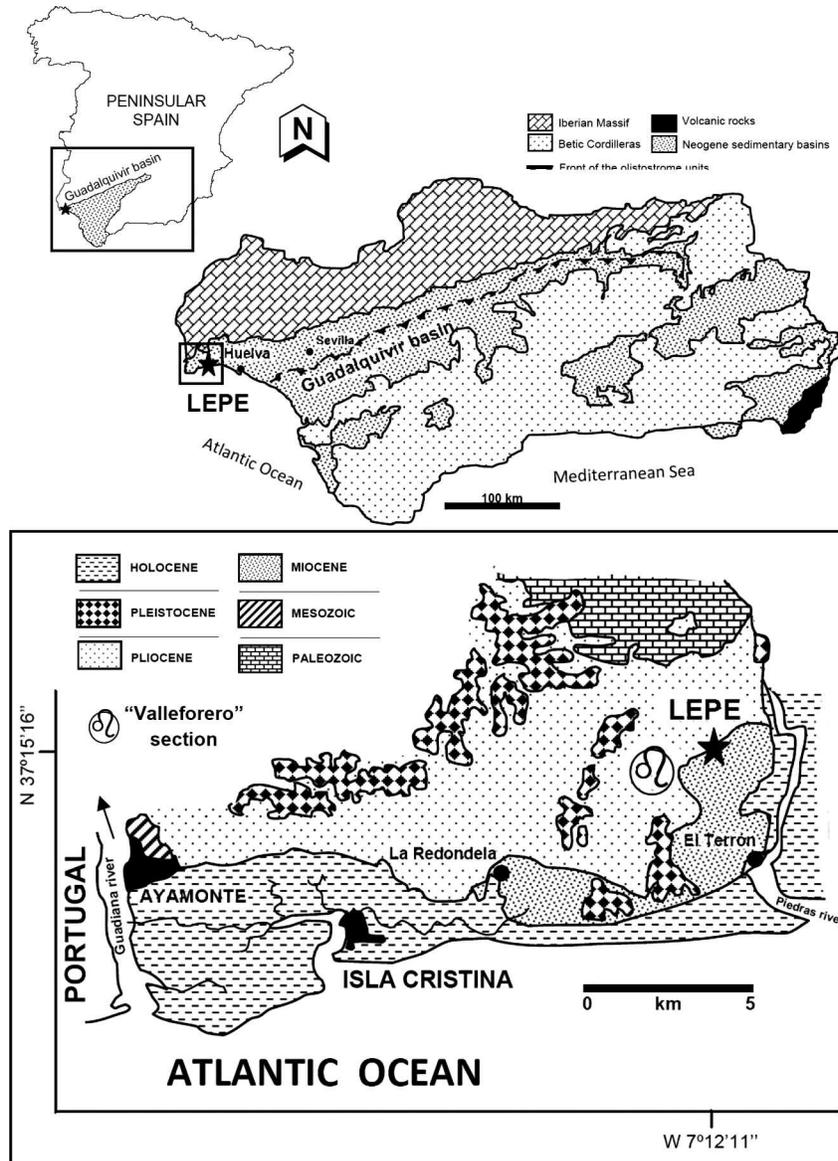


FIGURE 1—Geographic position of the Guadalquivir Basin and surroundings of the town of Lepe. *Podocallichirus laepaensis* n. sp. originates from the medium to coarse sands of the unit 5 (upper Miocene) of the “Valleforero” section.

(Cáceres Puro, 1995). The Neogene succession includes upper Miocene and Pliocene intervals, which are bounded by an erosive surface.

The upper Miocene succession (Fig. 2) consists of a coarsening upward sequence from blue mudstones (unit 1) to sandy silts (unit 2) and to sandy facies (units 3, 4, and 5). The sandier interval lies at different localities and includes fine-grained glauconitic sands (unit 3), medium- to coarse-grained sands with carbonate concretions (unit 4), and medium- to coarse-grained sands with abundant invertebrate shells (unit 5). The stratigraphic correlation between these units is not clear but it seems that at least 3 and 4 could be partly lateral equivalents. Available chronostratigraphic data for these units is restricted to the sandy units on the top. K/Ar radiometric dating of glauconite in unit 3 yielded ages of 6.6 ± 0.3 and 6.7 ± 0.3 Ma (Galán et al., 1993; Mayoral and Muñiz, 1994), which correspond to the Messinian (late Miocene) (Muñiz et al., 2001a, 2001b). Also, bivalves and gastropods in unit 4 seem to indicate a similar age, while calcareous

nannoplankton from the same unit corresponds to biozone CN9 sensu Okada and Burky (1980), which is upper Tortonian-Messinian (Muñiz et al., 2001b). The dating of unit 5, from which the material of *Podocallichirus laepaensis* new species comes, is more obscure. While calcareous nannoplankton correspond to the biozone CN11 sensu Okada and Burky (1980) (late Zanclean) (Muñiz et al., 2001b), the well-preserved malacofauna contains a number of species present in the Miocene Mediterranean and Atlantic basins but absent in the Pliocene sediments (Muñiz et al., 2010).

The Pliocene part of the Neogene succession (Fig. 2) crops out mainly in the interior part west of Lepe. Mapping revealed an erosional boundary between the Miocene and the Pliocene units (Muñiz et al., 2001a, b). The Pliocene succession begins with an erosive boundary on top of unit 5. This surface is covered by a unit consisting of medium- and coarse-grained sands and reddish gravels and conglomerates with intercalated lenses of white clay (unit 6). This is overlain by a sandy unit (unit 7), which grades into white sandy silts (unit 8). The

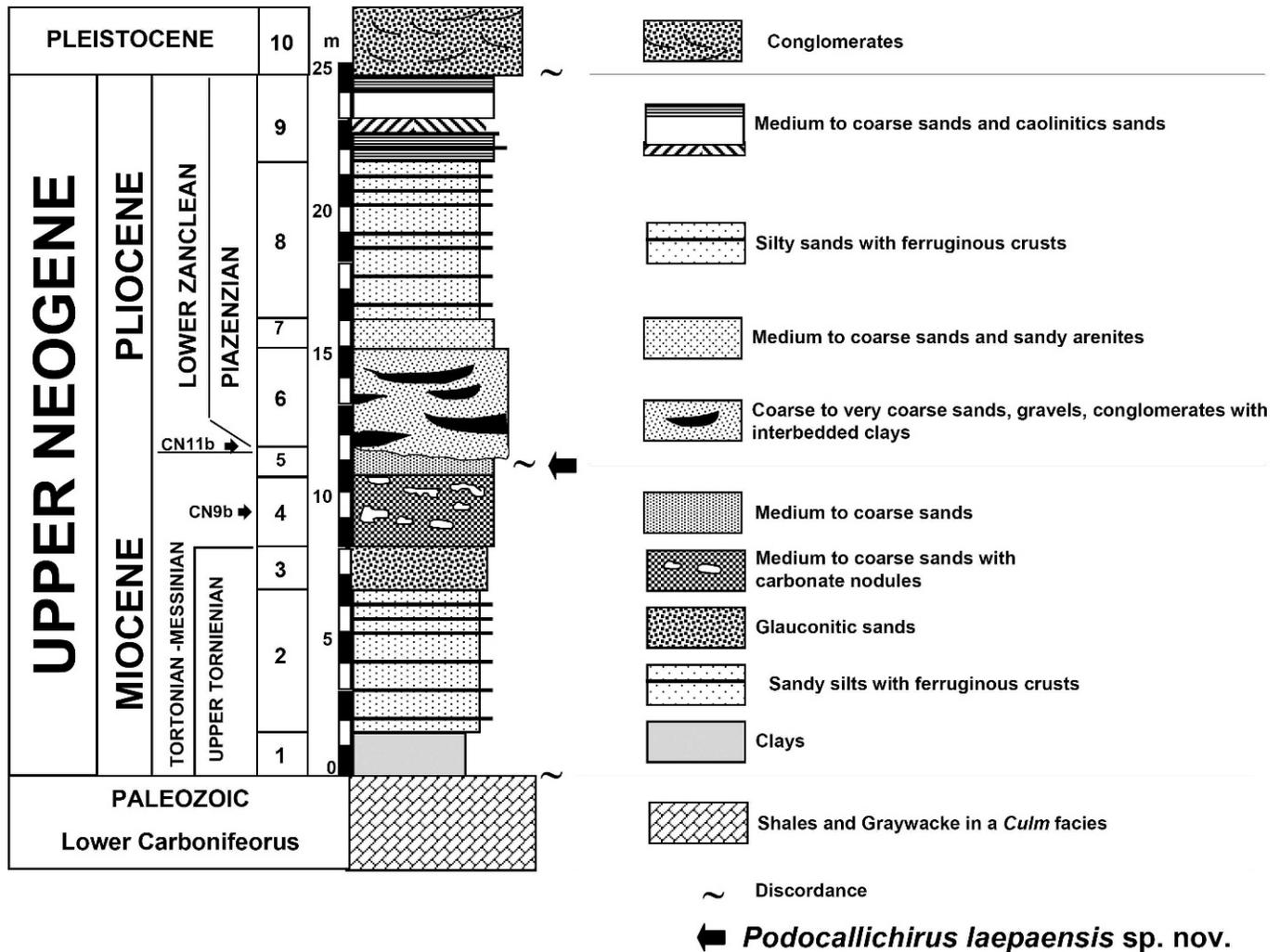


FIGURE 2—The Neogene succession of the ‘Lepe White Silts’. *Podocallichirus laepaensis* n. sp. originates from the unit 5 (black arrow).

Pliocene succession culminates with unit 9, medium- to coarse-grained sands, silts and kaolinitic sands (Galan et al., 1993). The Pliocene age of these units is constrained by the presence of late Zanclean nannoplankton in the underlying unit 5 and by the early Pleistocene age of the overlying fluvial gravels. Thus, a middle-late Pliocene age seems the most reasonable for this succession (Muñiz et al., 2010).

Paleoenvironmental and depositional evolution of the Lepe-Ayamonte sector in Neogene.—The Neogene deposits of the Lepe-Ayamonte area indicate the persistence of marginal marine conditions (Muñiz, 1998). The Miocene succession began after a generalized transgression during the Tortonian (Muñiz et al., 2001a). During this interval sedimentation was dominantly silty (unit 2) in a marine infralittoral setting, probably partly restricted, such as a confined bay, affected by periodic small eustatic pulses, which may have even resulted in exposure in an intertidal setting. Glauconitic sands at the top of the sequence could correspond to the maximum transgression (Mayoral and Muñiz, 1996a; Muñiz, 1998; Muñiz et al., 1998; Muñiz and Mayoral, 2001).

Following these deposits, there is a significant stratigraphic hiatus including at least part of the Messinian and the Zanclean (Muñiz, 1998; Muñiz et al., 1998). The overlying unit, probably Piazanian in age, overlies an erosional surface. This resulted in paleorelief with the Miocene units forming a

SW-NE paleohigh, which confined the sector where Pliocene sedimentation took place. The units of Pliocene age consist of an array of facies that suggest an estuarine system (Muñiz and Mayoral, 1998) with tidal and fluvial influence under subtropical climate conditions (Mayoral and Muñiz, 1996b; Barrón et al., 2003).

Neogene decapod faunas of Spain.—Miocene and Pliocene decapod crustacean associations of Spain have been reported by several authors. For summarizing works of the Miocene decapods of Catalonia references are made to works of Solé and Via Boada (1989) and Müller (1993). Recently, Artal (2008) reported the presence of the ocypodid *Uca* Leach, 1814 from the middle Miocene of the same area.

The Miocene and Pliocene decapods of the Guadalquivir Basin are poorly known. Mayoral et al. (1998) described decapod associations from the lower Pliocene of the Guadalquivir Basin. This paper is the first report of an upper Miocene decapod crustacean from the respective area.

MATERIAL AND METHODS

Material comes from unit 5 of the section “Valleforero” (Muñiz, 1998). It is composed mostly of isolated dactyli and fragmented fixed fingers of major chelae. A limited number of carpi, meri, and propodi have also been found (see Fig. 3 for terms describing the cheliped elements). Material comes from

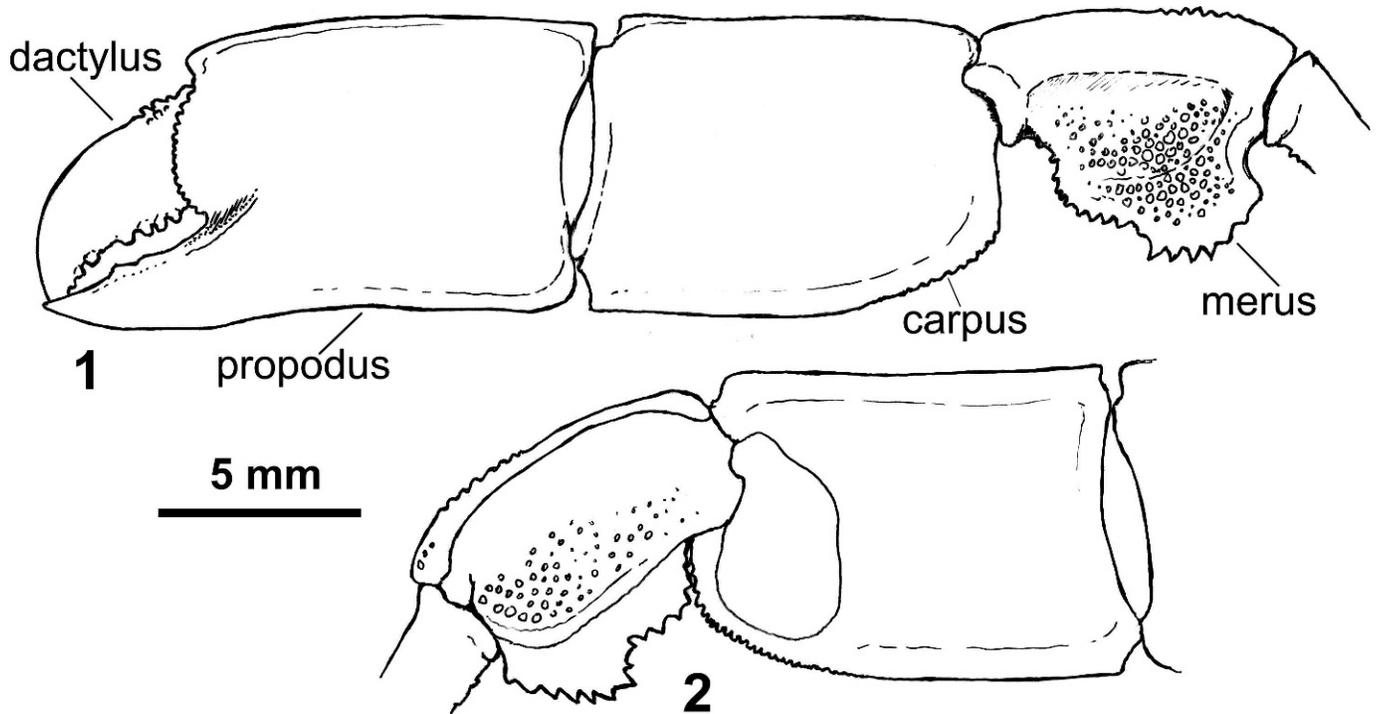


FIGURE 3—*Podocallichirus masoomi* (Tirmizi, 1970), Qeshm Island, Persian Gulf, Iran, deposited under number NHMW 24990. 1, major left cheliped from lateral view; 2, major left cheliped (merus and carpus) from mesial view. Note the shape of meral blade and tuberculation on both, lateral and mesial, surfaces.

unconsolidated sandstone and tends to disintegrate. Before study it was impregnated with the adhesive solution Herkules. Specimens were studied with a Leica EZ4 binocular microscope. To enhance contrast the material was coated with ammonium chloride prior the photography.

Comparisons with the extant members of the genera *Neocallichirus*, *Sergio*, and *Podocallichirus* were based mostly upon published figures and descriptions as discussed in the systematic paleontology section of the paper. Additionally, extant specimens of *Neocallichirus calmani* (Nobili, 1904) (NHMW 6780), *N. grandimanus* (Gibbes, 1850) (NHMW 19826), *N. karumba* (Poore and Griffin, 1979) (NHMW 21937), *Podocallichirus masoomi* (Tirmizi, 1970) (NHMW 24990) (Fig. 3) and *Sergio mirim* (Rodrigues, 1971) (NHMW 6753) deposited in NHMW were also examined for comparative purposes.

Institutional abbreviations.—CBG/CD=Centro para la difusión e investigación de la Biodiversidad y geodiversidad, Ciudad de Lepe (Center for diffusion and research of biodiversity and geodiversity, City of Lepe), Spain; KGP-MH=Department of Geology and Paleontology, Comenius University, Bratislava, Slovakia; NHMW=Department of Zoology, Naturhistorisches Museum in Wien, Austria.

SYSTEMATIC PALEONTOLOGY

Currently, the biological classification of ghost shrimps is in flux. In general, there are several different views on the evaluation of taxonomically important characters as exemplified by works of Biffar (1971), Manning and Felder (1991), Poore (1994, 2008), and Sakai (1999, 2005, 2011). Paleontological literature usually emphasizes the contribution of Manning and Felder (1991). In this context the discussion on the assignment of the callianassoid fossil remains to respective genera in recently published papers (Schweitzer-Hopkins and Feldmann, 1997; Schweitzer and Feldmann, 2002; Schweitzer et al., 2006a, 2006b; Vega et al., 2007; Hyžný and Schlägl, 2011;

Hyžný and Karasawa, 2012; Hyžný and Hudáčková, 2012) further develops the ideas of Manning and Felder (1991). The higher classification 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
PODOCALLICHIRUS Sakai, 1999

Type species.—*Callianassa madagassa* Lenz and Richters, 1881.

Remarks.—The present status of the genus *Podocallichirus* is rather confusing. It was erected by Sakai (1999) to accommodate several species previously mostly treated as *Callichirus* sensu Le Loeuf and Intés (1974). Poore (2000) erected the genus *Grynaminna* to accommodate the new species *G. tamakii*. *Grynaminna* is similar to *Neocallichirus* and *Sergio*, but it differs in the nature of antennae, uropods, and pleopods (Poore, 2000, p. 151). *Grynaminna* lacks the meral hook on the major cheliped and possesses non-tapering chelipeds. It was considered a junior synonym of *Podocallichirus* by Sakai (2005). Later Sakai (2011) recognized *Grynaminna* as a separate genus and divided *Podocallichirus* into four new additional genera: *Balsscallichirus*, *Barnardcallichirus*, *Forestcallichirus* and *Tirmizicallichirus*. *Podocallichirus* remained monotypic containing only its type species, *Callianassa madagassa* Lenz and Richters, 1881. The recognition of the above mentioned genera can be considered as obscure, as they are based on variable characters which may change during ontogeny, i.e., first two pairs of male pleopods. Biffar (1971, p. 643) previously mentioned that callianassid juveniles lack the characteristic shape of the adult appendages. Intraspecific variability in the shape of the first two male pleopods in the genus *Neocallichirus* was reported by several

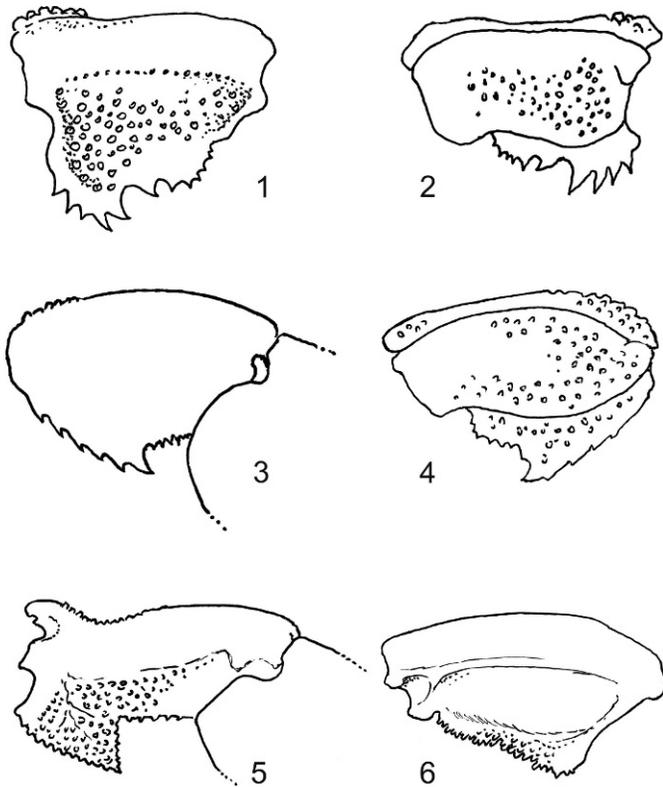


FIGURE 4—Major cheliped merus in selected extant callichirine taxa. 1, *Podocallichirus masoomi* (Tirmizi, 1970), in lateral and dorsomesial view, respectively; after Sankolli (1971, figs. 7b, d); 3, *Podocallichirus gilchristi* (Barnard, 1947), lateral view; after Sakai (1999, fig. 9c); 4, *Podocallichirus gilchristi* (Barnard, 1947), lateral view; after Barnard (1950, fig. 95b); 5, *Callichirus major* (Say, 1818), lateral view; after de Man (1928, fig. 14a); 6, *Glypturoides trilobatus* (Biffar, 1970), lateral view; after Portell and Agnew (2004, pl. 2, fig. F).

authors (Felder and Manning, 1995; Dworschak, 2008, 2011a, 2011b).

For the aims of this contribution, the classification of Sakai (1999) is followed in recognizing seven species of the genus *Podocallichirus*, although the nature of the genus itself is far from being resolved. We agree with recognizing *Grynaminna* as a separate genus. The issue on recognizing *Podocallichirus* sensu Sakai, 1999 in the fossil record was recently discussed by Hyžný and Karasawa (2012).

The best generic assignment of the studied material seems to be identifying it as a member of *Podocallichirus* based on major similarities between the studied material and two extant *Podocallichirus* species: *P. masoomi* (= *Callianassa kewalramanii* Sankolli, 1971) and *P. gilchristi* (Barnard, 1947). Sakai (2011) classified the species within *Tirmizicallichirus* and *Barnardcallichirus*, respectively. Studied material shares with these species similarly shaped meri (Fig. 5.5–5.7) with distinct triangular hooks; pronounced tuberculation present on both, lateral and mesial surfaces of merus; fixed finger distinctly shorter than palm; and armature of dactylus (Barnard, 1950; Tirmizi, 1970; Sankolli, 1971; Sakai, 1999).

A similarly shaped merus with distinctly broad meral hook is present also in *Callichirus*, notably in *Callichirus major* (Say, 1818) as figured by several authors (de Man 1928, fig. 14; Rodrigues, 1971, fig. 11; Manning and Felder, 1986, fig. 1c; Portell and Agnew, 2004, pl. 1, fig. E). In this taxon, however, the merus is distinctly longer than high (Fig. 4.5) and not ovoid as it is in the studied material. Moreover, the morphology of the propodus in *C. major* is also different.

In other respects *Podocallichirus laepaensis* n. sp. is close to *Neocallichirus* (notably to *N. audax* de Man, 1911; *Neocallichirus frouini* Ngoc-Ho, 2005; and *N. mauritanus* Miers, 1882) and *Glypturoides* Sakai, 2011. *Neocallichirus audax* (de Man, 1928, fig. 31c, 31d; Rao and Kartha, 1967, fig. 2A) and *Glypturoides trilobatus* (Biffar, 1970) (Portell and Agnew, 2004, pl. 2, figs. D, E) have fixed finger with rows of tubercles not dissimilar from studied material. *Neocallichirus frouini*

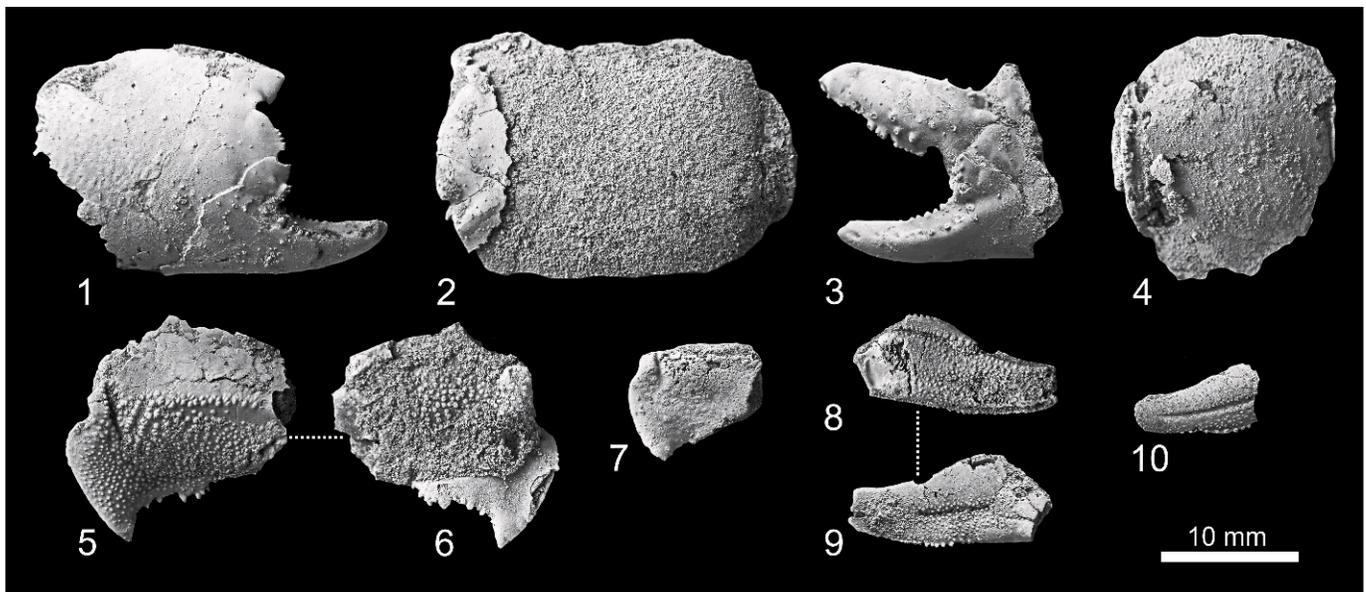


FIGURE 5—*Podocallichirus laepaensis* n. sp., isolated major cheliped elements. 1, right propodus, paratype CBG/CD/002; 2, left propodus with the broken fixed finger, paratype CBG/CD/004; 3, right fragmentary propodus articulated with dactylus, paratype CBG/CD/003; 4, left carpus, paratype CBG/CD/006; 5, 6, right merus, holotype CBG/CD/001; 7, right fragmentary merus, KGP-MH LE-001; 8, 9, right ischium, in mesial and lateral views, respectively, paratype CBG/CD/005; 10, right fragmentary ischium, lateral view, CBG/CD/074. All specimens were coated with ammonium chloride prior to photography.

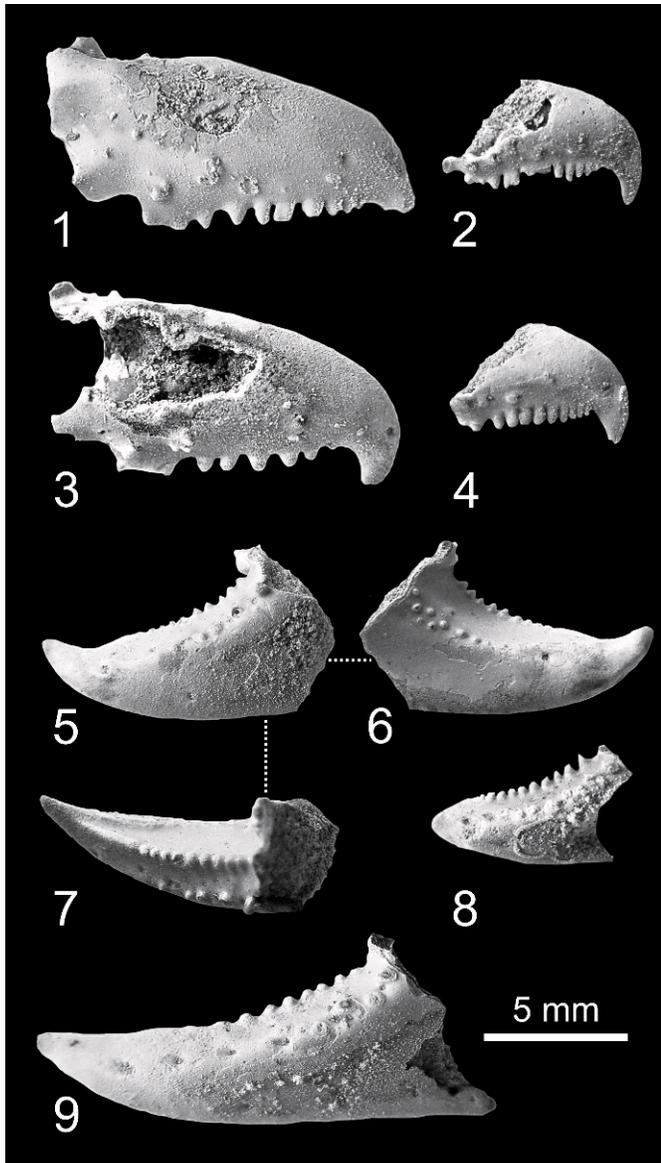


FIGURE 6—*Podocallichirus laepaensis* n. sp., isolated fingers. 1, right dactylus, paratype CBG/CD/010; 2, right dactylus, paratype CBG/CD/037; 3, right dactylus, paratype CBG/CD/029; 4, right dactylus, paratype CBG/CD/038; 5–7, left fixed finger, in outer view, mesial view, occlusal margin view, respectively, paratype CBG/CD/064; 8, left fixed finger, paratype CBG/CD/067; 9, left fixed finger, paratype CBG/CD/041. All specimens were coated with ammonium chloride prior the photography.

(Ngoc-Ho, 2005, fig. 14C), *N. mauritanus* (de Man, 1928, fig. 4b) and *G. trilobatus* (Biffar, 1970, fig. 1h; Portell and Agnew, 2004, pl. 2, fig. F; see also Fig. 4.6) have also similarly shaped meri, but none of them is morphologically close to the above mentioned *Podocallichirus* species.

Considering all these similarities and assuming that the morphology of the merus is usually consistent with the genus concept based on the soft part morphology, as shown by Manning and Felder (1991), we classify studied material within *Podocallichirus* sensu Sakai (1999). This assignment should be considered preliminary until more complete material is recovered and the generic assignment of the morphologically closest extant taxa (*P. masoomi*, *P. gilchristi*) is resolved.

The only fossil representative of *Podocallichirus* listed by Schweitzer et al. (2010) as *Podocallichirus grandis* (Karasawa

and Goda, 1996) was recently reconsidered to be a member of *Grynaminna* (Hyžný and Karasawa, 2012). The latter authors gave details about the taxonomic history of this taxon. Following their work the present material can be considered to represent the only known fossil representative of *Podocallichirus*.

PODOCALLICHIRUS LAEPAENSIS new species

Figures 5.1–5.10, 6.1–6.9

Diagnosis.—Callichirine ghost shrimp with robust major cheliped; merus ovoid with distinct keel on the lateral surface, lower part strongly tuberculated; lower margin of merus denticulated with well developed meral hook, meral hook denticulated distally; propodus longer than high, lower margin of propodus slightly concave at the base of fixed finger; fixed finger shorter than palm with three rows of tubercles on its occlusal margin, mesial row longest; dactylus with distinctly hooked tip, occlusal margin with molariform tooth followed with numerous peg-shaped teeth.

Description.—Major cheliped robust with strongly tuberculated proximal elements.

Ischium longer than high, highest near the articulation with merus, slightly sinuous; lateral surface with longitudinal furrow extending along midline and dividing the element into two parts, the lower half tuberculated; mesial surface strongly tuberculated virtually over its entire extent, tubercles fading away distally; the proximal half of the lower margin serrated with tiny denticles, larger denticles positioned more distally; upper margin rather smooth, not well preserved. Merus ovoid with well developed meral blade (or lobe) and distinct proximal hook; lateral surface with longitudinal keel dividing the element into two parts; lower part strongly tuberculated; mesial surface strongly tuberculated, mesial surface of the hook smooth; lower margin denticulated with uneven spines; meral hook strongly convex and smooth proximally, denticulated distally; upper margin not well preserved. Carpus not well preserved, seems to be slightly higher than long, with rounded lower margin; lateral surface smooth. Propodus longer than high, slightly converging distally; lateral surface of palm (manus) smooth; distal margin rounded and serrated; lower margin slightly concave at the base of the fixed finger. Fixed finger shorter than palm, triangular in shape, distinctly longer than high, the tip pointing slightly upward; three rows of tubercles present on the occlusal margin, one of them positioned medially, two of them positioned laterally at the mesial and lateral edges of the occlusal margin, median row with 10 to 20 denticles, lateral row extending to the articulation with dactylus. Dactylus longer than high, usually with distinct hook at its tip; upper surface with several tubercles proximally near the articulation with propodus; lateral surface smooth or with few tubercles proximally; occlusal margin with long bilobed molariform tooth followed with usually up to 10 peg-shaped teeth, teeth becoming smaller distally.

Minor cheliped unknown.

Variations.—The material shows variation in the nature of cheliped fingers. On the fixed finger the variation comprises mainly the differences in number of tubercles in the lateral, medial, and mesial rows (Fig. 6.7). Interestingly, distinctly shorter (and usually smaller) fixed fingers in general have more tubercles (up to 20 in the medial row) which are more peg-shaped (Fig. 6.8), whereas in longer (and usually larger) fixed fingers these are less numerous (around 10 in the medial row) and are more rounded (Fig. 6.9). This variation seems to

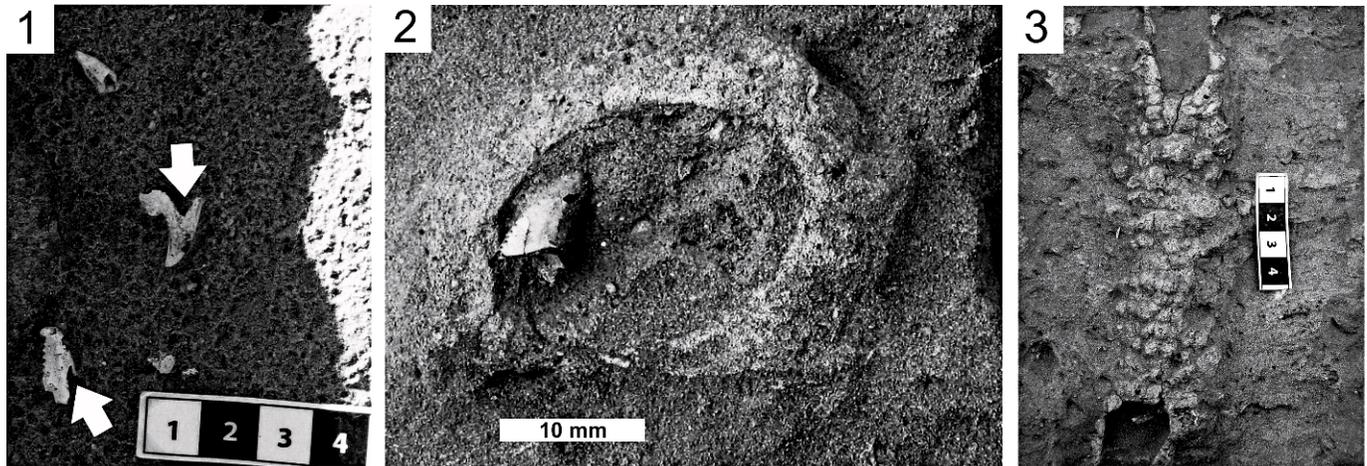


FIGURE 7—Field photographs from the “Valleforero” section. 1, isolated fingers of *Podocallichirus laepaensis* n. sp., note V-shaped reentrants on the proximal region of the fingers; 2, horizontal cross-section of *Ophiomorpha nodosa* Lundgren, 1891 with fixed finger of *P. laepaensis* in the internal filling; 3, *Ophiomorpha nodosa* exhibiting a strongly developed pelletal lining.

be associated with growth: in larger individuals the tubercles fade away distally.

On dactyli, a similar phenomenon can be observed: smaller specimens have numerous teeth on the occlusal margin (up to 20) (Fig. 6.2, 6.4). Their average number is around 10; the spaces between them are larger if the tooth number is lower (Fig. 6.1, 6.3). The shape of teeth is generally rounded, sometimes there are also bifid teeth positioned proximally. The proximal molariform tooth may be subdivided into two blunt teeth (Fig. 6.1).

Variation also can be observed in the way the hooked tip of the dactylus is developed. In some specimens (usually with lower number of teeth on the occlusal margin) the tip is moderately hooked (Fig. 6.1). In other specimens the tip is hooked at a right angle and is distinctly longer than the teeth on the occlusal margin (Fig. 6.2, 6.4). Transitional forms between both morphotypes are also present; thus, we do not interpret the variations in terms of sexual dimorphism.

Etymology.—From the Latin *Laepa* referring to the town of Lepe.

Types.—The holotype is a nearly complete right merus of major cheliped (CBG/CD/001) (Fig. 5.5, 5.6). The paratype collection consists of a nearly complete right propodus (CBG/CD/002), a fragmentary left propodus with articulated dactylus (CBG/CD/003), a nearly complete fragmentary left propodus (CBG/CD/004), a complete right ischium (CBG/CD/005), a nearly complete left carpus (CBG/CD/006), four complete or nearly complete right dactyli (CBG/CD/010, CBG/CD/029, CBG/CD/037, CBG/CD/038), and three fragmented left fixed fingers (CBG/CD/041, CBG/CD/064, CBG/CD/067) (Figs. 5, 6).

Other material.—Numerous (several hundred) additional cheliped elements of fragmentary nature deposited under numbers CBG/CD/007–009, CBG/CD/011–028, CBG/CD/030–36, CBG/CD/039–040, CBG/CD/042–063, CBG/CD/065–066, CBG/CD/068–075, CBG/CD/076 (collective number), KGP-MH LE-001–007 and KGP-MH LE-009–010 have been examined. The overwhelming majority of the material represents major cheliped fingers (isolated dactyli and fixed fingers).

Occurrence.—Medium- to coarse-grained sands (unit 5), Valleforero section (Muñiz, 1998), Lepe (Huelva, SW Spain). *Podocallichirus laepaensis* n. sp. is known from the type locality only.

Remarks.—*Podocallichirus laepaensis* has direct morphological affinities to its supposed congeners, *Podocallichirus*

masoomi and *P. gilchristi*. No fossil callianassid shrimp identified so far shares the shape of the major cheliped merus with *P. laepaensis*. The character combination, specifically tubercle rows on the fixed finger, peg-shaped teeth on the occlusal margin of dactylus and the shape and ornamentation of merus, readily distinguishes *P. laepaensis* from all fossil callianassids described to date.

Mayoral et al. (1998) reported several cheliped fragments classified as *Callianassa* sp. from the lower Pliocene of Guadalquivir Basin. They figured one fragmented propodus articulated with a dactylus (Mayoral et al., 1998, fig. 2.1). The overall morphology of this specimen clearly points to its identity as a laomediid, *Jaxea* Nardo, 1847. Indeed, at the same place remains of *Jaxea nocturna* Nardo, 1847 were also found (Mayoral et al., 1998; Hyžný, 2011b).

NOTES ON TAPHONOMY

Taphonomy and preservation of burrowing shrimps were discussed at length by Bishop and Williams (2005). They distinguished several types of resulting fossils in accordance of their preservation (Bishop and Williams, 2005, fig. 2). In this respect the material of *Podocallichirus laepaensis* n. sp., which is virtually entirely of an isolated and fragmented nature, can be classified as cheliped elements. No disassociation unit sensu Bishop and Williams (2005), a natural aggregation of exoskeleton elements preserved together, has been found. In decapod crustacean disarticulation, fragmentation, and decay are generally rapid (Schäfer, 1972; Plotnick 1986; Plotnick et al., 1988; Stempien, 2005; Krause et al., 2011), and this is highlighted in callianassid shrimp possessing a weakly calcified exoskeleton (except chelipeds). The strength of the cuticle in brachyurous crabs varies within the exoskeleton parts and throughout the growth cycle of the animal (Mutel et al., 2008; Waugh et al., 2009). The same can be postulated for burrowing shrimps.

Interestingly, the studied material shows a mode of preservation similar to that discussed by Mutel et al. (2008). Their experiments with deploying crabs on the sea bottom can be compared with the fossil record where the preservation of isolated fingers is much the same, thus, exhibiting a specific pattern of degradation. Remains of *P. laepaensis* show V-shaped reentrants on the proximal region of the fingers (Figs. 6.3, 6.8, 6.9, 7.1), which are virtually identical with

those in deployed crabs reported by Mutel et al. (2008, figs. 3B, 3D, 5B, 7A, 7B) and Krause et al. (2011, fig. 4C).

The fragmentary nature of *P. laepaensis* at the studied section can be attributed to a high bioturbation rate in the area. The cheliped fragments of *P. laepaensis* have been found in association with the trace fossil *Ophiomorpha nodosa* Lundgren, 1891 (Fig. 7.3). *Podocallichirus laepaensis* is suspected to be the potential tracemaker of these traces. Cheliped fragments can be found all around the trace fossils, some of them have been found within a burrow (Fig. 7.2). Direct connection between *Ophiomorpha* traces and callianassid shrimps was previously demonstrated by Weimer and Hoyt (1964) and discussed by Frey et al. (1978). Bishop and Williams (2005, p. 225) stated that “the direct occurrence of fossil thalassinoids within trace fossil burrows is unusual but occasionally has been reported or figured.” More recent discussion on this issue can be found in Neto de Carvalho et al. (2007), Buatois and Mángano (2011) and Hyžný (2011a).

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