

How to distinguish *Neocallichirus*, *Sergio*, *Podocallichirus* and *Grynaminna* (Decapoda: Callianassidae: Callichirinae) from each other in the fossil record?

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Abstract

This contribution discusses the generic assignment of several callianassid genera of the subfamily Callichirinae Manning and Felder, 1991 in the fossil record, namely *Neocallichirus* Sakai, 1988; *Sergio* Manning and Lemaitre, 1994; *Podocallichirus* Sakai, 1999; and *Grynaminna* Poore, 2000. We argue that generic assignment of fossil callianassid remains can be done successfully on the basis of chelipeds, but only if all cheliped elements (ischium, merus, carpus, propodus and dactylus) are at hand. Moreover, thorough comparisons between fossils and extant material should be always made before assignment of the fossil remains to the genus level. "*Neocallichirus*" *grandis* Karasawa and Goda, 1996 from the Middle Pleistocene of Japan is revised and assigned to the genus *Grynaminna*.

Key words: Decapoda, Callianassidae, *Neocallichirus*, *Sergio*, *Podocallichirus*, *Grynaminna*, fossil record, systematics

Introduction

One of the greatest challenges of modern decapod crustacean palaeontology is the interpretation, both systematic and ecological, of callianassid burrowing ghost shrimps (Decapoda: Axiidea: Callianassidae). Their fossil record is very robust and they are present in most associations of Cenozoic decapod crustaceans described so far. However, the generic assignment of the callianassid remains is very difficult, partly because there is great inconsistency also in the biological classification and taxonomy of this group.

This contribution aims to discuss the generic assignment of several callianassid genera of the subfamily Callichirinae Manning and Felder, 1991 in the fossil record when dealing with chelipeds only. In biological literature there is often little attention paid to the nature of chelipeds when defining genera (but see the discussion on differences between eucalliace genera in Ngoc-Ho, 2003), which are usually the only fossil remains of these animals. In this respect assigning fossil material to the genera *Neocallichirus* Sakai, 1988; *Sergio* Manning and Lemaitre, 1994; *Podocallichirus* Sakai, 1999; and *Grynaminna* Poore, 2000 is a very complex topic, as no general agreement about their systematic status is currently at hand.

Generic assignment of callianassid ghost shrimps

The biological classification of the Callianassidae Dana, 1852 is based mainly on soft part morphology, which include the dorsal carapace architecture, the nature of maxillipeds, form of the abdomen, pleopods, uropods and telson; for discussion on this issue with respect to the fossil record see e.g. Schweitzer and Feldmann (2002) and Schweitzer *et al.* (2006a). The classification itself is, however, not consistent throughout the biological literature and is in a need of comprehensive revision. Major monographs focused on this group recently published by Sakai (1999, 2005, 2011) met little agreement from the side of other workers (Tudge *et al.*, 2000; Poore, 2000, 2008; Dworschak, 2007; Felder and Robles, 2009). 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).

Many extant callianassid genera have been erected without taking detailed account on their chelipeds. No wonder, because chelipeds in general are very variable features. There are many species with proven polymorphism in their nature (e.g. Sakai, 1969); in several genera chelipeds are sexually dimorphic which is often connected with the allometric growth (e.g. Felder and Lovett, 1989; Dworschak, 2006). On the other hand there are characters present on chelipeds which can be considered of taxonomic importance. The work of Biffar (1971) can

be considered as first such step towards the systematic evaluation of such characters. He provided two separate keys to the Western Atlantic *Callianassa* species; one of them evaluates major chelipeds only. Later Manning and Felder (1991) emphasized the importance of some hard-part morphology characters for generic assignment, some of them present on merus of major cheliped. Following their work biologists usually add a presence or absence of a meral hook in the diagnoses of new genera or emendations of older ones. Unfortunately, it is of little help to palaeontologists, because there are many genera both with and without meral hook. Because chelipeds are most durable parts of ghost shrimps and are very frequent in the fossil record, palaeontologists can often rely solely on the characters present on them. Therefore an effort to identify diagnostic characters present not only on merus but also on other cheliped elements is needed.

In the world of palaeontology the work of Manning and Felder (1991) triggered several reassignments of fossil taxa previously referred to "*Callianassa sensu lato*". Since then there is always an attempt to classify fossil callianassids within biologically defined genera.

We discuss here basically two approaches of assignment of the fossil material to respective callianassid genera:

1) An approach refusing to identify the genus on the hard part morphology (chelipeds only), simply because of lack of soft part morphology characters on which the diagnoses of genera are usually based. This approach may use approximate generic assignment as "*Callianassa*" or *Callianassa sensu lato* as exemplified by works of Müller (1984) and Karasawa (1998, 2000), respectively. If the fossil material fails to be assigned more closely, it is recommended to classify fossil specimens within Callianassidae (or *Callianassa sensu lato* without reference to a subfamily or genus (Collins *et al.*,

1996). Sometimes the material may belong to a closely related family, Ctenochelidae *sensu* Manning and Felder (1991), not Sakai (2005, 2011).

2) An approach trying to find unifying characters present on chelipeds of taxa classified within a certain genus concept based on soft part morphology. In this approach extant congeneric taxa are studied in detail to identify these common characters on chelipeds. It is needed to test different generic concepts to see whether presence of chosen characters is consistent throughout the supposedly congeneric taxa or not. This approach is basically about looking for a generic diagnosis based on chelipeds only which would not contradict the diagnosis based on soft part morphology.

Neocallichirus in the fossil record

The genus *Neocallichirus* is relatively widely defined and after *Callianassa* it is the most speciose extant callianassid genus (De Grave *et al.*, 2009). For generic assignment always a combination of characters has to be used, as also such important taxonomic character as 3rd maxilliped is not specific solely for *Neocallichirus* (Sakai, 1988). Manning and Felder (1991) reconsidered the diagnosis of *Neocallichirus* and added also the characters on the chelipeds, notably on the merus. The merus of *Neocallichirus* is variable in shape but is always serrated along the lower margin. According to Manning and Felder (1991) it lacks a meral spine or hook; according to Sakai (1999, 2005) it is with or without meral hook (mainly due to the synonymisation with the genus *Sergio*), whereas Sakai (2011) stated that merus is with or without ventral convexity. Schweitzer and Feldmann (2002) and Schweitzer *et al.* (2006a) discussed usage of the characters on major cheliped (not

Table 1. List of fossil taxa presently classified as *Neocallichirus* (after Schweitzer *et al.*, 2010; Karasawa and Nakagawa, 2010; Garassino *et al.*, 2011). Note that *N. rodfeldmanni* Hyžný, 2010 is a replacement name for *N. manningi* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg and Ross, 2003 (name preoccupied).

| Taxon | Age | Occurrence | Remarks |
|--|-----------------------|---------------------------|-----------------------------|
| <i>N. aetodes</i> Schweitzer <i>et al.</i> , 2006b | Early Oligocene | Puerto Rico | |
| <i>N. agadirensis</i> Garassino <i>et al.</i> , 2011 | Cenomanian | Morocco | generic assignment doubtful |
| <i>N. allegranzii</i> Beschin <i>et al.</i> , 2005 | Middle Eocene | Italy | generic assignment doubtful |
| <i>N. bona</i> (Imaizumi, 1959) | Early–Middle Miocene | Japan | generic assignment doubtful |
| <i>N. borensis</i> Beschin <i>et al.</i> , 2006 | Late Eocene | Italy | |
| <i>N. dijki</i> (Martin, 1883) | Late Miocene | Phillipines, Java | |
| <i>N. fortisi</i> Beschin <i>et al.</i> , 2002 | Middle Eocene | Italy | generic assignment doubtful |
| <i>N. hattai</i> Karasawa and Nakagawa, 2010 | Early–Middle Miocene | Japan | |
| <i>N. matsoni</i> (Rathbun, 1935) | Early Miocene | USA (Florida) | generic assignment doubtful |
| <i>N. maxima</i> (A. Milne-Edwards, 1870) | subfossil | Thailand, India (?) | |
| <i>N. nishikawai</i> (Karasawa, 1993) | Miocene | Japan | generic assignment doubtful |
| <i>N. okamotoi</i> (Karasawa, 1993) | Late Oligocene | Japan | generic assignment doubtful |
| <i>N. peraensis</i> Collins <i>et al.</i> , 1996 | Late Pleistocene | Jamaica | |
| <i>N. porterensis</i> (Rathbun, 1926) | Oligocene | USA (Washington, Oregon) | |
| <i>N. quisquellanus</i> Schweitzer <i>et al.</i> , 2006b | Middle Miocene | Dominican Republic | generic assignment doubtful |
| <i>N. rhinos</i> Schweitzer and Feldmann, 2002 | Middle Eocene | USA (California) | |
| <i>N. rodfeldmanni</i> Hyžný, 2010 | Campanian | Canada (British Columbia) | generic assignment doubtful |
| <i>N. sakiae</i> Karasawa and Fudouji, 2000 | Oligocene | Japan | generic assignment doubtful |
| <i>N. scotti</i> (Brown and Pilsbry, 1913) | Oligocene–Pleistocene | Caribbean | |
| <i>N. wellsi</i> Schweitzer <i>et al.</i> , 2004 | Late Eocene | Pakistan | |

only on merus, but also on carpus, propodus and dactylus) in the fossil record for assignment to the genus *Neocallichirus*.

There are several genera different from *Neocallichirus*, namely *Sergio*, *Podocallichirus*, and *Grynaminna*, which share very similar chelipeds. Much confusion has been created by Sakai (2005) when he synonymized *Sergio* with *Neocallichirus* and *Grynaminna* with *Podocallichirus*. Recently, Sakai (2011) redefined all these genera. The taxonomic history of all four of them is very complex and until now no general agreement has been achieved.

Cheliped morphology seen in the genera mentioned above is in palaeontological literature connected virtually with *Neocallichirus* only. According to De Grave *et al.* (2009) and Schweitzer *et al.* (2010) there are 18 fossil species identified as *Neocallichirus*, one fossil species as *Podocallichirus*, one extant species of *Sergio* is also known from the fossil state and no fossil *Grynaminna* is known. Since then two more *Neocallichirus* species have been described (Karasawa and Nakagawa, 2010; Garassino *et al.*, 2011) (see Table 1).

The morphology of fossil taxa assigned to *Neocallichirus* is just as variable (and maybe even more) as that of the extant species of the genus. In this context it should be noted that the characteristics of the chelipeds typical for the genus *Neocallichirus* were summarized only in several papers dedicated to fossil taxa (Schweitzer and Feldmann, 2002; Schweitzer *et al.*, 2006a; see also Hyžný and Hudáčková, submitted) and according to published figures only. No exhaustive study has been made to make attempt to evaluate chelipeds within this speciose genus. According to Schweitzer *et al.* (2006a: 278): “assignment of fossils to *Neocallichirus* must be based on the highly variable morphology of the major cheliped of extant species, and truly confident assignment of fossils to the genus will probably only occur when other aspects of the body of the animal are recovered”. Many fossil taxa were assigned to *Neocallichirus* on the basis of very few characters (mainly on propodus only); thus, revision of all fossil *Neocallichirus* species referred at some time to this genus is needed to specify precisely the morphological variability of the taxonomically important species and compare it to the variability seen in the extant taxa. As in neontological studies the genus *Neocallichirus* is usually recognized on soft part morphology only, the genus concept as used in palaeontological practice, and thus as discussed herein, should be regarded as preliminary one until more

Table 2. List of extant taxa classified at some time within the genus *Sergio* Manning and Lemaitre, 1994.

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| <i>Neocallichirus cacahuete</i> Felder and Manning, 1995 |
| <i>Sergio guaiqueri</i> Blanco Rambla, Liñero Arana and Beltán Lares, 1995 |
| <i>Callianassa (Callichirus) guara</i> Rodrigues, 1971 |
| <i>Callianassa (Callichirus) guassutunga</i> Rodrigues, 1971 |
| <i>Neocallichirus lemairei</i> Manning, 1993 |
| <i>Sergio mericeae</i> Manning and Felder, 1995 |
| <i>Callianassa (Callichirus) mirim</i> Rodrigues, 1971 |
| <i>Callichirus monodi</i> de Saint Laurent and Le Loeuff, 1979 |
| <i>Callianassa pachydactyla</i> A. Milne-Edwards, 1870 |
| <i>Sergio sulfureus</i> Lemaitre and Felder, 1996 |
| <i>Callianassa trilobata</i> Biffar, 1970 |

comprehensive study is provided.

Considering the difficulties with assigning fossil material to extant callianassid taxa and different approaches applied when erecting fossil taxa, it is fairly possible that the genus *Neocallichirus* as usually recognized in the fossil record is a mixture of different genera as the personal re-examination of some of them by one of the authors (MH) might show.

Neocallichirus vs. *Sergio*

Originally, the genus *Sergio* was erected to accommodate four species previously referred to *Neocallichirus*, based upon the characters of the telson and uropods (Manning and Lemaitre, 1994). The diagnosis was based on four species firstly described by Biffar (1970): *Callianassa trilobata*; and Rodrigues (1971): *C. guara*, *C. guassutunga*, and *C. mirim*. Later, another three species were described under this genus: Blanco Rambla *et al.* (1995) introduced *Sergio guaiqueri*; Manning and Felder (1995) described *Sergio mericeae* and reexamined *S. guassutunga*; and the last systematic study devoted to the genus *Sergio* was that by Lemaitre and Felder (1996) who described *S. sulfureus*. It is worth mentioning that the generic diagnosis was not amended in these studies. *Sergio* was then synonymised with *Neocallichirus* by Sakai (1999), however, many workers did not accept this synonymisation (Poore, 2000; Schweitzer *et al.*, 2006a; Dworschak, 2007; Poore, 2008; De Grave *et al.*, 2009; Felder and Robles, 2009). Sakai (1999, 2005) argued with the presence of intermediate forms between *Neocallichirus* and *Sergio* concerning the nature of telson and uropods. He stated (Sakai, 2005: 125) that within “the species assigned to *Sergio*, the character of the tail fan should be defined as a specific character within the genus *Neocallichirus*”. He (Sakai, 1999: 85) also pointed out on the presence of the meral hook in *Sergio* contrary to the diagnosis of the genus (Manning and Lemaitre, 1994: 40). Schweitzer *et al.* (2006a) suggested that palaeontologists should use the presence or absence of a proximal meral hook to distinguish between *Sergio* and *Neocallichirus*. This issue deserves more discussion.

Although Manning and Lemaitre (1994) stated that *Sergio* does not possess a meral hook, Rodrigues (1971: 206) in the description of *C. guassutunga* (type species of *Sergio*) noted, that “there are two or three moderately long spines followed by five short irregular spines and about eight rounded granules” on the lower margin of merus in males and “two large proximal spines followed by five to eight smaller ones” in females. Similarly in *C. guara*, “the merus has a strong serrated tooth near the proximal extremity of the lower margin which is denticulated (Rodrigues, 1971: 211).” *Callianassa trilobata* and *C. mirim* are in their original descriptions characterized also by “triangular ventral keel on merus (Biffar, 1970: 36)” in *C. trilobata* and “the lower edge produced into a laminar serrated tooth (Rodrigues, 1971: 216)” on merus in *C. mirim*. *Sergio mericeae* has major cheliped “with inferior margin of merus armed proximally by elongate process of 2–3 fused spines, beyond which is short gap in marginal dentition (Manning and Felder, 1995: 268).” *Sergio sulfureus* has lower margin of merus “armed with small spines and strong bifid process proximally (Lemaitre and Felder,

1996: 458”).

The only exception is *S. guaiqueri* which clearly lacks any proximal meral hook, spine or tooth (Blanco Rambla *et al.*, 1995). However, this species was based on only four rather small specimens. Thus, when assuming that degree of spinosity of chelipeds depends on age of the animal, we can conclude that those specimens represent immature stages. This view can be supported with described and figured major chelipeds of immature specimens of *S. sulfureus* (Lemaitre and Felder, 1996: figs. 4a, b) and *S. mericeae* (Manning and Felder, 1995: fig. 5f) which do not have any proximal tooth or spine either, but only a serrated lower margin. It should also be noted that the figured male of *S. guaiqueri* does not possess strongly armed dactylus and fixed finger, which are otherwise quite typical for mature specimens of the genus as described and figured in literature (Rodrigues, 1971; Manning and Felder, 1995; Lemaitre and Felder, 1996). Increased spinosity with size (or age) of the specimens was documented also in *Neocallichirus karumba* Poore and Griffin, 1979 (= *Neocallichirus kemp* Sakai, 1999) by Dworschak (2008). Major chelipeds of larger specimens in this species interestingly possess a similar bi- or trifold proximal projection on lower margin of merus. The same conclusion concerning the immaturity of the type material of *S. guaiqueri* was reached also by Sakai (1999: 90): “It seems that the male holotype is immature because the carapace is only 4.2 mm long, and the male Plp1–2 are undeveloped (Blanco Rambla *et al.*, 1995: figs. 3a, b).”

Finally, recent molecular studies (Tudge *et al.*, 2000; Felder and Robles, 2009) resolved *Sergio* as of paraphyletic nature in the arrangement presented above (see also Table 3). In Felder and Robles (2009: fig. 1) two tested taxa, *S. mericeae* and *S. trilobata* were positioned in distinctly different branches. *Sergio mericeae* (considered to be a close relative of the type species of *Sergio*) was allied with otherwise monophyletic *Neocallichirus*, *S. trilobata* was, however, positioned basally to the grouping of genera *Corallianassa* Manning, 1987, *Glypturus* Stimpson, 1866, *Grynaminna* and *Neocallichirus*. Felder and Robles (2009: 334) noted that such arrangement “raises a question as to the validity of the genus and, regardless of that issue, argues for generic reassignment of *S. trilobata*”. Sakai (2011) erected a new genus, *Glypturoides*, for this taxon. We agree with this generic

reassignment.

Reassessment of the genus *Sergio* by Sakai (2011) (in fact, its resurrection when considering the previous synonymisation) does not really help to resolve the relationship between the taxa discussed above, as it is based on variable characters which may change during ontogeny, i.e. first two pairs of male pleopods. Already Biffar (1971: 643) mentioned that callianassid juveniles lack the characteristic shape of the adult appendages. Similarly Felder and Manning (1995) reported the same for *Neocallichirus cacahuete* Felder and Manning, 1995 and pointed on differences in male pleopod shape between *N. cacahuete* and *N. lemaitrei* Manning, 1993; Sakai (2011) treats both species as *Sergio*. Dworschak (2008, 2011a, 2011b) reported the variability in the shape of the first two male pleopods in *N. karumba*, *N. jousseaumei* (Nobili, 1904) (= *Callianassa indica* de Man, 1905; *Neocallichirus taiaro* Ngoc-Ho, 1995) and *N. vigilax* (de Man, 1916) (= *N. denticulatus* Ngoc-Ho, 1994), respectively.

The fossil record of the genus *Sergio* is obscure. Interestingly, Todd and Collins (2005) recognized *Callianassa scotti* Brown and Pilsbry, 1913 (= *Callianassa vauhani* Rathbun, 1918; *C. crassimana* Rathbun, 1918; *C. miocenica* Rathbun, 1919; *C. rathbunae* Glaessner, 1929) from the Oligocene to Pleistocene of the Caribbean as a member of the genus *Sergio*. However, under influence of Sakai's (2005) synonymisation of the genus with *Neocallichirus*, they treated the taxon as *Neocallichirus scotti*. As such it appeared also in the fossil decapod species list by Schweitzer *et al.* (2010). Another fossil occurrence coming from the Pliocene–Pleistocene strata of Florida (Portell and Agnew, 2004) has been identified as extant *Sergio trilobatus* (Biffar, 1970).

As shown above, the problem of distinguishing *Neocallichirus* and *Sergio* from one another in the fossil record is more-less a matter of their definition as biologically defined taxa. In this respect, the fossil record can tell only little to solve this issue.

Neocallichirus vs. *Podocallichirus*

The present status of the genus *Podocallichirus* is rather confusing. It was erected by Sakai (1999) to accommodate seven species previously mostly treated as *Callichirus sensu* Le Loeuf and Intès (1974) (see

Table 3. Taxonomic history of generic assignment of extant taxa treated as *Sergio* Manning and Lemaitre, 1994.

| Taxon | Sakai (1999) | Tudge <i>et al.</i> (2000) | Sakai (2005) | Poore (2010) | Sakai (2011) |
|------------------------|-----------------------|----------------------------|-----------------------|-----------------------|-----------------------|
| <i>N. cacahuete</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Sergio</i> |
| <i>S. guaiqueri</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> |
| <i>C. guara</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> |
| <i>C. guassutinga</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Sergio</i> |
| <i>N. lemaitrei</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Sergio</i> |
| <i>S. mericeae</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Sergio</i> |
| <i>C. mirim</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> |
| <i>C. monodi</i> | <i>Neocallichirus</i> | <i>Callichirus</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Sergio</i> |
| <i>C. pachydactyla</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Neocallichirus</i> | <i>Sergio</i> |
| <i>S. sulfureus</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Sergio</i> |
| <i>C. trilobata</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Neocallichirus</i> | <i>Sergio</i> | <i>Glypturoides</i> |

Tables 4 and 5). *Podocallichirus* as understood in the classification of De Grave *et al.* (2009) apparently comprises these seven taxa. Poore (2000) erected the genus *Grynaminna* to accommodate the new species *G. tamakii*. This genus was considered as a junior synonym of *Podocallichirus* by Sakai (2005). Later he (Sakai, 2011) recognized *Grynaminna* as a separate genus and divided *Podocallichirus* in five(!) independent genera; *Podocallichirus* remained monotypic containing only its type species (*Callianassa madagassa* Lenz and Richters, 1881). The remaining species are accommodated within the newly established genera *Balsscallichirus*, *Barnardcallichirus*, *Forestcallichirus* and *Tirmizicallichirus*. Their recognition as separate genera is obscure, as they are based on characters changing during ontogeny (see above), and thus conclusions based on their nature can be misleading. It is worth mentioning that restriction of *Podocallichirus* to *C. madagassa* only is supported also by Poore (2010). He classifies the rest of *Podocallichirus* species *sensu* Sakai (1999) as members of broadly defined *Callichirus* (Table 5).

As a result we can talk about two distinctly different concepts of the genus *Podocallichirus* 1) original concept given by Sakai (1999) comprising type species plus six other species, here referred as *Podocallichirus sensu lato*; and 2) concept of the monotypic genus *Podocallichirus* comprising the type species, *Callianassa madagassa*, only, thus *Podocallichirus sensu stricto* (supported by Poore, 2010 and Sakai, 2011). When comparing chelipeds of these two concepts, one can have difficulties to find a suite of common characters which are not present also in *Neocallichirus*. *Podocallichirus sensu lato* possesses several characters which are not very common in *Neocallichirus*, such

as proximally positioned serrated meral blade, however, in general, the states of these characters overlap in many cases with typical *Neocallichirus* species. Contrary to that, *Podocallichirus sensu stricto* comprises very unusual species, whose minor cheliped and also some characters of the major one, is different than majority of callianassid taxa (see Lenz and Richters, 1881: figs. 20, 21; virtually the only species with broadly similar minor chela has been described as *Lepidophthalmus socotrensis* Sakai and Apel, 2002). Nothing similar has been found in the fossil record so far. As a consequence, when dealing with fragmentary material, *Podocallichirus sensu lato* would be identifiable in the fossil record as a member of broadly defined *Neocallichirus*.

Neocallichirus vs. *Grynaminna*

The monotypic genus *Grynaminna* was erected for a distinct species from Kyushu, Japan. As defined by Poore (2000) it is very similar to *Neocallichirus*, however, it differs in the nature of antennae, uropods and pleopods (Poore, 2000: 151). It lacks the meral hook on major cheliped, and possesses non-tapering chelae which are otherwise quite typical for *Neocallichirus* and *Sergio*.

It seems that chelipeds of *Grynaminna tamakii* Poore, 2000 (type species of *Grynaminna*) are sexually dimorphic. In males there is a notch at the base of the fixed finger of major chela which is not present in females. In males the dactylus is armed with several teeth, whereas in females it is straight (Poore, 2000: fig. 3).

Sakai (2005) synonymised *Grynaminna* with *Podocallichirus* Sakai, 1999, however, in his later work (Sakai, 2011) he recognized it as a distinct genus (see Table 5). We concur.

The fossil record of *Grynaminna* is obscure, however, we argue that “*Neocallichirus*” *grandis* Karasawa and Goda, 1996 from the Middle Pleistocene of Japan (Aichi Prefecture) can be accommodated within the genus. Although very well preserved, the material comprises chelipeds only. Based on cheliped morphology Obata and Hayashi (2001) removed “*N.*” *grandis* to *Grynaminna*. Later, Karasawa *et al.* (2006), following the work of Sakai (2005), removed the species to *Podocallichirus* and as such the species appeared in a list of fossil decapod crustaceans by Schweitzer *et al.* (2010). Now, after the publication of Sakai's (2011) systematic reconsideration of callianassoid ghost shrimps one has difficulties to judge how to classify “*Neocallichirus*” *grandis*. Virtually

Table 4. List of extant taxa classified at some time within the genus *Podocallichirus* Sakai, 1999.

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| <i>Callianassa</i> (<i>Callichirus</i>) <i>balssi</i> Monod, 1933 |
| <i>Callichirus foresti</i> Le Loeuff and Intès, 1974 |
| <i>Callianassa gilchristi</i> Barnard, 1947 |
| <i>Callianassa</i> (<i>Callichirus</i>) <i>guineensis</i> de Man, 1928 |
| <i>Callianassa madagassa</i> Lenz and Richters, 1881 |
| <i>Callianassa</i> (<i>Callichirus</i>) <i>masoomi</i> Tirmizi, 1970 |
| <i>Grynaminna tamakii</i> Poore, 2000 |
| <i>Callichirus tenuimanus</i> de Saint Laurent and Le Loeuff, 1979 |

Table 5. Taxonomic history of generic assignment of extant taxa treated as *Podocallichirus* Sakai, 1999.

| Taxon | Sakai (1999) | Tudge <i>et al.</i> (2000) | Sakai (2005) | Poore (2010) | Sakai (2011) |
|----------------------|------------------------|----------------------------|------------------------|------------------------|---------------------------|
| <i>C. balsii</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Balsscallichirus</i> |
| <i>C. foresti</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Forestcallichirus</i> |
| <i>C. gilchristi</i> | <i>Podocallichirus</i> | <i>Callianassa</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Barnardcallichirus</i> |
| <i>C. guineensis</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Balsscallichirus</i> |
| <i>C. madagassa</i> | <i>Podocallichirus</i> | <i>Callianassa</i> | <i>Podocallichirus</i> | <i>Podocallichirus</i> | <i>Podocallichirus</i> |
| <i>C. masoomi</i> | <i>Podocallichirus</i> | <i>Callianassa</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Tirmizicallichirus</i> |
| <i>G. tamakii</i> | - | <i>Grynaminna</i> | <i>Podocallichirus</i> | <i>Grynaminna</i> | <i>Grynaminna</i> |
| <i>C. tenuimanus</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Podocallichirus</i> | <i>Callichirus</i> | <i>Barnardcallichirus</i> |

two options are available: 1) if following Poore (2000) and Sakai (2011) in recognition of *Grynaminna* as a distinct genus, and considering the similarity between *N. grandis* and *G. tamakii* as of taxonomic importance, then “*N.*” *grandis* should be classified within the genus *Grynaminna* as recognized by Obata and Hayashi (2001; 2) another option is to consider *Neocallichirus*, *Grynaminna* and *Podocallichirus*

as undistinguishable when dealing with chelipeds only. In that case it should be classified within the genus *Neocallichirus* (as originally proposed) in the broadest sense, thus as defined by Manning and Felder (1991). We assume that at the present state of knowledge the classification of “*N.*” *grandis* within the genus *Podocallichirus* seems to be misleading.

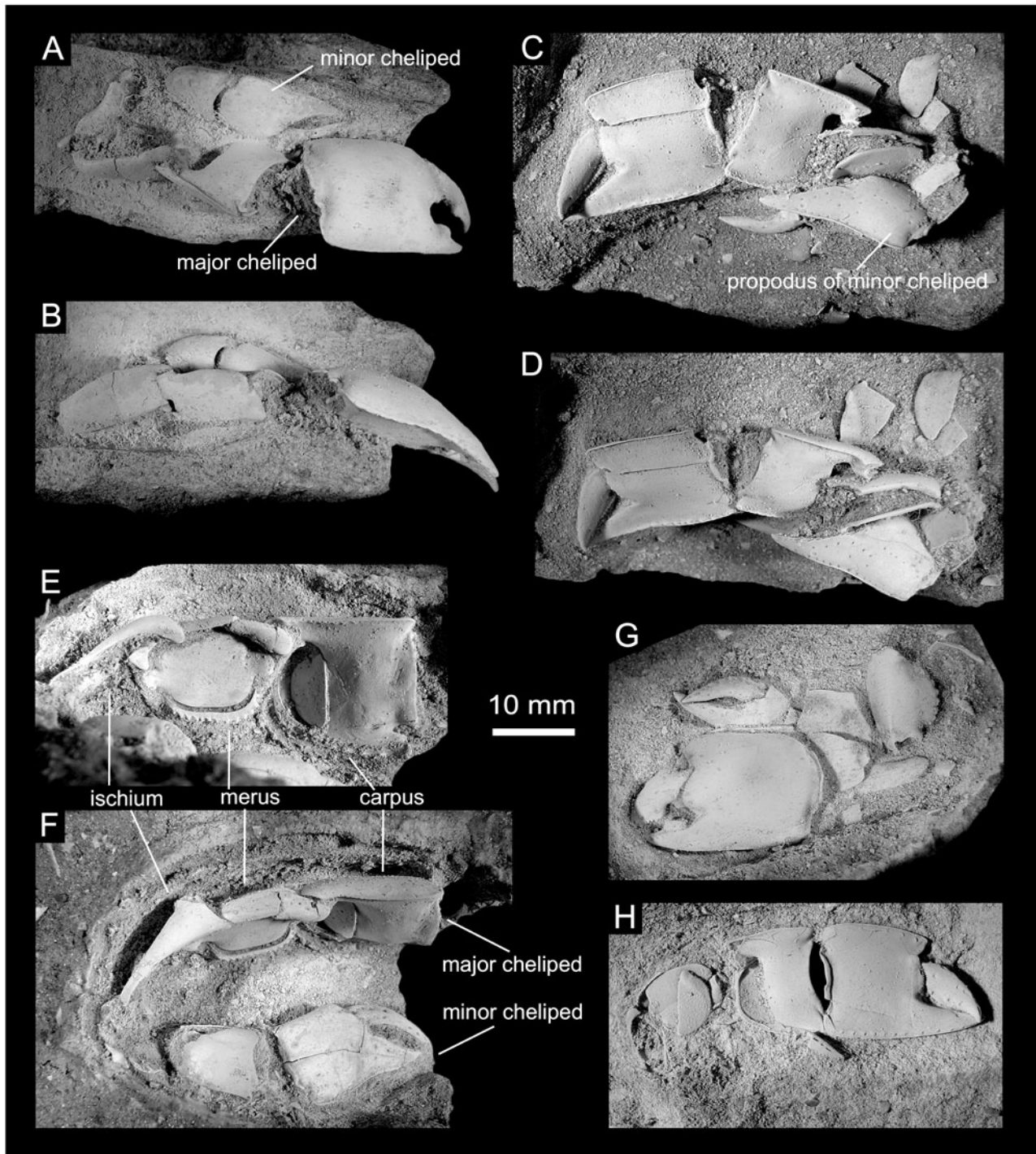


Fig. 1. *Grynaminna grandis* (Karasawa and Goda, 1996) from the Middle Pleistocene, Atsumi Group (Japan). A–B, both chelipeds of a presumed male specimen in lateral (A) and dorsal view (B) (MFM142381), note serrated lower margin of propodus (B), which is preserved turned over in contrast to the rest of the cheliped; C–D, both chelipeds of a presumed female specimen in mesial (major chela) and lateral view (minor chela) (MFM142497), note keeled upper and lower margins of propodus and carpus; E, ischium, merus and carpus from mesial view (MFM142500), note serrated lower margin of the merus; F, remains of both chelipeds of the same specimen (MFM142500); G, both chelipeds of a presumed male specimen (MFM142499), major cheliped in lateral view and minor cheliped in mesial view; H, major cheliped of a presumed female specimen in mesial view (MFM142498). All specimens were covered with ammonium chloride prior the photography. All specimens are preserved within the burrows.

Systematic palaeontology

Order Decapoda Latreille, 1802

Infraorder Axiidea de Saint Laurent, 1979

Family Callianassidae Dana, 1852

Subfamily Callichirinae Manning and Felder, 1991

Genus *Grynaminna* Poore, 2000

Type species: Grynaminna tamakii Poore, 2000, by original designation and monotypy.

Included fossil species: Grynaminna grandis (Karasawa and Goda, 1996).

Diagnosis: See Poore (2000: 150). We argue that the genus concept as presented by Sakai (2011: 438), i.e. based on the first two pairs of male pleopods is not enable (see above).

Grynaminna grandis (Karasawa and Goda, 1996)

(Fig. 1A–H)

Callianassa sp. Kato and Koizumi, 1992, p. 49, fig. 3–3.

Calliax sp. Karasawa and Tanaka, 1994, p. 12, fig. 2-1–12.

Neocallichirus sp. Karasawa, Nohara and Shimoji, 1995, p. 128, fig. 2.

“Neocallichirus” grandis Karasawa and Goda, 1996, p. 1, fig. 1; Karasawa, 1997, p. 33, pl. 5, figs. 1–4 (refigured from Karasawa and Goda, 1996).

Neocallichirus grandis Karasawa and Goda; Kato and Karasawa, 1998, p. 5, pl. 2, figs. 7–16; Schweitzer *et al.*, 2006b, p. 115 (in a list).

Grynaminna grandis (Karasawa and Goda); Obata and Hayashi, 2001, p. 46, fig. 3.1–12.

Podocallichirus grandis (Karasawa and Goda); Karasawa *et al.*, 2006, p. 127, pl. 2, figs. 1–6; Schweitzer *et al.*, 2010 p. 39 (in a list).

Material examined: MFM142381, MFM142497–142500 deposited at the Mizunami Fossil Museum, Gifu, Japan.

Remarks: The morphology of major and minor chelipeds of *“Neocallichirus” grandis* has been sufficiently described by Karasawa and Goda (1996). The species has major morphological similarities to *Grynaminna tamakii* Poore, 2000, as was already pointed out by Obata and Hayashi (2001). The similarities include characters on the major cheliped: the ovoid-shaped merus with serrated lower margin and without a pronounced meral blade or hook; nearly quadrate carpus; short, triangular fixed finger; and the dactylus armature in supposed male specimens (see below). *Grynaminna grandis* bears a large, blunt triangular tooth on the fixed finger, which *G. tamakii* lacks. In this case the characters on the fixed finger can be considered of taxonomic importance on the species level. Otherwise, the overall cheliped dimensions and ratios are virtually the same in both species. Thus, *“Neocallichirus” grandis* can be best accommodated within the genus *Grynaminna*.

The material of *Grynaminna grandis* comprises two morphotypes which seem to mirror sexual dimorphism and can be compared with sexually dimorphic chelipeds of *G. tamakii* (i.e., Kato and Karasawa, 2009; Kato, in preparation). The major propodus of *G. grandis* supposedly attributed to male has a distinct notch at the base of the fixed finger and armed both fixed finger and dactylus (Fig. 1G), whereas

specimens supposedly attributed to females do not possess a distinct notch and the armature of fingers is not well pronounced (Figs. 1C, H).

It seems that the genus *Grynaminna* is biogeographically restricted to Japan (Poore, 2000; Sakai, 2011). So far there is only one reported occurrence of extant *Neocallichirus* from Japan. Sakai (1999, 2005, 2011) reported *N. indicus* (= *N. jousseaumei*) from the Ryukyus; Dworschak (2011a) did not list this occurrence because of its unresolved species identity (P. C. Dworschak, pers. comm. 2011). The fossil record of the genus *Neocallichirus* in Japan extends back to the Miocene (Karasawa and Nakagawa, 2010). The extant and extinct *Podocallichirus sensu lato* and *Sergio* has not yet been reported from Japan.

Conclusions

From the present contribution several conclusions can be made:

1) Generic assignment of fossil callianassid remains can be done successfully on the basis of chelipeds only, but only if all cheliped elements (ischium, merus, carpus, propodus and dactylus) are at hand. Thorough comparisons between fossils and extant material should be always made before assigning the fossil remains to the genus level.

2) More comparative studies among the extant callianassids using the chelipeds is needed to recognize important characters which are consistent throughout all the members of the genus. In this respect a paper by Sakai (1969) on the major cheliped variations in some Japanese callianassids is very useful for palaeontological practice. Manning and Felder (1991) pointed out that some characters occurring on the merus (usually in the combination of other features of hard part morphology) can be used for generic assignment; since then, however, nearly twenty(!) new extant callianassid genera were designated, in many cases without any or little attention paid to the nature of the chelipeds.

3) Revision of all fossil species referred to *Neocallichirus* is needed to specify precisely the morphological variability of taxonomically important characters and compare it to the variability seen in extant *Neocallichirus* species.

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