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Crustaceana 87 (10) 1258-1272

CRUSTACEANA

ON STABILISING THE NAMES OF THE INFRAORDERS OF THALASSINIDEAN SHRIMPS, AXIIDEA DE SAINT LAURENT, 1979 AND GEBIIDEA DE SAINT LAURENT, 1979 (DECAPODA)

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DOI:10.1163/15685403-00003354

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ABSTRACT

The names Gebiidea and Axiidea, erected by de Saint Laurent (1979), have priority over others for the two infraorders of shrimps previously included in Thalassinidea. Importantly, Thalassinidea are not monophyletic and the name should be replaced. Gebiidea and Axiidea, besides having priority and describing two monophyletic taxa, are now in common use (130 citations) and are more stable than alternative schemes proposed by Sakai (2005 and later). The history of the names of higher taxa applied to these groups is reviewed, and all family-group taxa listed.

RÉSUMÉ

Les noms Gebiidea et Axiidea, établis par de Saint-Laurent (1979), priment sur les autres pour les deux infraordres de crevettes préalablement inclus dans les Thalassinidea. Surtout, le groupe des Thalassinidea n'est pas monophylétique et le nom doit être remplacé. Gebiidea et Axiidea, en plus d'avoir la priorité et de décrire deux taxa monophylétiques, sont maintenant d'usage courant (130 citations) et sont plus stables que les systèmes alternatifs proposés par Sakai (2005 et ultérieurement). L'histoire des noms des taxa de rang plus élevé appliqués à ces groupes est revue, et tous les taxa de niveau famille sont listés.

INTRODUCTION

The names of higher taxa, those above family-group, are not governed by the conventions of the International Code of Zoological Nomenclature (ICZN, 1999: Article 1.2.2) but many of the same principles tacitly apply. Over the last decade new competing nomenclatures have been introduced for the higher taxa that for over 180 years have been known as thalassinidean shrimps belonging to the diverse crustacean order Decapoda. These new nomenclatures have been proposed to represent new insights into the phylogenetic relationships amongst the thalassinidean shrimps and a desire to have our taxonomy reflect evolutionary relationships. Here, we argue for a stable nomenclature based firstly, on the need to replace the name Thalassinidea (because it is not monophyletic), secondly on priority, and thirdly on prevailing usage, the last two being the most important principles of zoological nomenclature. We advocate the use of infraordinal names Gebiidea and Axiidea for the two remotely related monophyletic groups of thalassinidean shrimps, names erected by de Saint Laurent in 1979, as replacement names for Thalassinidea.

CHRONOLOGY

Latreille (1831) introduced the term 'Thalassinides' as the seventh tribe of the 'Macroures (Macrouri)' for four genera: *Gebia* Leach, 1815, *Thalassina* Latreille, 1805, *Callianassa* Leach, 1814 and *Axius* Leach, 1815. The name served as the basis for the Latinised infraordinal name Thalassinidea (Decapoda Pleocyemata) and the family name Thalassinidae, both first introduced by Dana (1852).

Dana (1852) recognised Thalassinidea as one of three 'sections' or 'subtribes' of 'Macroura'. Macroura or Macrura, is no longer used as it was in earlier literature as a suborder of Order Decapoda to include the long-tailed lobsters and shrimps, contrasting with the Brachyura and Anomura, short-tailed crabs and their relatives. Dana divided Macrura into two groups, Thalassinidea Eubranchiata and Thalassinidea Anomobranchiata. In the former he included three families: Gebiidae Haworth, 1825 (for genera now included in Upogebiidae Borradaile, 1903, Axiidae Huxley, 1879, and Laomediidae Borradaile, 1903), Callianassidae Dana, 1852, and Thalassinidae Latreille, 1831. *Callianidea* H. Milne Edwards, 1837 (now in Callianideidae Kossmann, 1880) is now the only representative of Thalassinidea Anomobranchiata. The name Thalassinidea became well established following the revision of Borradaile (1903).

De Saint Laurent (1973) recognised the differences of *Upogebia* from other Callianassidae and elevated the subfamily in which the genus was included to family rank. Later (1979a), she grouped the Callianassidae, Callianideidae and Axiidae together in a superfamily Axioidea which she diagnosed. In the same year, de Saint Laurent (1979b) divided the Reptantia (one of two groups of decapods, the other being Natantia) into ten groups that she believed resulted from a 'radiation Triassique'. She argued that the Thalassinidea were the only group of Reptantia impossible to define precisely and introduced the term ('vocable' in French) 'Thalassinacea'. The relationship between the epistome and the carapace that was used inter alia to define the other groups varied notably from one family to another, the number of chelate pereopods was sometimes one and sometimes two, an appendix interna was not always present, and larvae included what Gurney (1942) called both nephropoidean and anomuran forms. As a consequence, she separated the 'Thalassinacea' into two sections for which she introduced new names, Axiidea and Gebiidea. De Saint Laurent included Axiidae and Callianassidae in Axiidea, both families having chelate pereopods 1 and 2 as both adults and zoeae, and Upogebiidae, Laomediidae and Thalassinidae in Gebiidea, all having similar body shapes as a result of their digging behaviour. The forms of the zoeae of Gebiidea vary. She suggested affinities between the Axiidea (showing 'dichélie' or two pairs of chelate pereopods) and Glypheidea (without chelate pereopods). The Gebiidea, on the other hand, (showing monochélie or only pereopod 1 chelate) were said to be

more like Dromiacea (Dromiidae) and other Brachyura. Forest & de Saint Laurent (1981) examined the morphology of the glypheidean *Neoglyphea inopinata* Forest & de Saint Laurent, 1975 and elaborated on its relationship to Axiidea. Although de Saint Laurent's paper was mentioned, Felgenhauer & Abele (1983) did not discuss her proposed names in their historical review of classification of shrimp-like decapods.

The only later paper by de Saint Laurent to refer to Thalassinidea (Sakai & de Saint Laurent, 1989) was prepared largely by the first author but not approved by her (M. de Saint Laurent, pers. comm. to GCBP, 1990). This paper, on Axiidae, placed the family as a member of 'Decapoda, Crustacea, Thalassinidea, Anomula [sic]' but did not discuss higher classification.

The first cladistic analysis of the Thalassinidea was based on morphological characters (Poore, 1994). It found the group to be monophyletic and divided into three superfamilies, Callianassoidea, Axioidea and Thalassinoidea, contrary to de Saint Laurent's hypothesis. Though widely adopted (e.g., Martin & Davis, 2001), support from later studies is weak. In any case, these superfamily names are not germane to the present discussion.

Subsequent phylogenetic studies using morphological and molecular data, although not necessarily challenging overall thalassinidean monophyly, saw the group divided into two strongly supported clades corresponding to de Saint Laurent's Axiidea and Gebiidea. The first molecular phylogeny of Thalassinidea (Tudge & Cunningham, 2002), based on 14 species, found the monophyly of the infraorder to be only weakly supported by the 18S rRNA gene sequence data and unsupported by the 16S rRNA data. Tudge & Cunningham (2002) concluded that Callianassidae and Strahlaxiidae were sister taxa while Upogebiidae, Axianassidae, Thalassinidae and Laomediidae grouped in a second clade sister to an outgroup comprising six representatives from Astacidea, Brachyura, Anomura and Achelata. Tudge (1995) had concluded earlier that the sperm cells of *Trypaea australiensis* Dana, 1852 and *Neaxius glyptocercus* (von Martens, 1868) were more similar to each other than to those of *Thalassina squamifera* de Man, 1915. In the same year Morrison et al. (2002), using complete mitochondrial data of many representatives of Decapoda, questioned the monophyly of Thalassinidea. Ahyong & O'Meally (2004) concluded on the basis of a combined morphological-molecular analysis that Thalassinidea were monophyletic and comprised two clades similar to those of Tudge & Cunningham.

Sakai (2005a) compared the gastric mill in some representative species of the Thalassinidea and found the group 'diphyletic', comprising two superfamilies: Callianassoidea (Callianassidae, Axiidae, Callianideidae, Ctenochelidae Manning & Felder, 1991 and Gourretiidae Sakai, 1999); and Thalassinoidea (Thalassinidae, Upogebiidae and Laomediidae). He neither confirmed nor rejected thalassinidean

monophyly. These family groupings are the same as those proposed by de Saint Laurent (1979). The names for the infraorder Thalassinidea and superfamily Callianassoidea were used again by Sakai (2005b).

In a paper reorganising the infraorders of the Decapoda Pleocyemata, Sakai & Sawada (2006) introduced the new infraordinal name 'Callianassidea Dana, 1852 new status' for the superfamily Callianassoidea and retained 'Infraorder Thalassinidea Latreille, 1831 [sensu stricto]' for superfamily Thalassinoidea alone. As before, these and other pleocyemate decapod infraorders were justified on the structure of the prepyloric gastric ossicle. Relationships among the infraorders were not discussed, nor was the choice of names.

In two papers, Tsang et al. (2008a, b) inferred from mitochondrial and nuclear rDNA sequences that Thalassinidea are polyphyletic and comprise two superfamilies that aligned with the groups proposed by de Saint Laurent (1979a, b) and Sakai (2005a, b) and Sakai & Sawada (2006). Further, they concluded that the two groups were not sister to each other.

Robles et al. (2009) undertook a molecular phylogeny of the thalassinideans and discovered the same two groups as did de Saint Laurent (1979a, b), Tudge & Cunningham (2002), Ahyong & O'Meally (2004) and Tsang et al. (2008a, b). They discussed these and other studies based on molecular and morphological data in support, or otherwise, of these groups and concluded that the consensus supported de Saint Laurent's proposition. These results were later corroborated by Chu et al. (2009), Bracken et al. (2009), Lin et al. (2012) and Bracken-Grissom et al. (2014). Robles et al. (2009) revived de Saint Laurent's names as infraorders, Axiidea (for a clade sister to a larger one that also included Achelata, Brachyura and Anomura) and Gebiidea (sister to these four). They used this finding to justify abandoning the name Thalassinidea, it being no longer monophyletic.

In his major revision of the Axioidea, Sakai (2011a) reverted to treating all taxa within a single infraorder Thalassinidea which he divided into two: 'Section Callianassida Dana, 1852 [sectio nov.]' and 'Section Thalassinida Latreille, 1831 [sectio nov.]'. This scheme was retained by Sakai (2012a).

In their major review of the biology of thalassinidean shrimps Dworschak et al. (2012) justified the use of Axiidea and Gebiidea in place of Thalassinidea, diagnosed both infraorders and listed the families in each accepted by them (see table I).

Sakai & Türkay (2014) abandoned the classification used by Sakai in 2011 and 2012 and revived the scheme introduced by Sakai & Sawada (2006), infraorders Thalassinidea s.s. and Callianassidea. They argued in some detail that de Saint Laurent's (1979) name Gebiidea is 'nomenclaturally inappropriate' because it 'seems to have been derived from the earlier rejected family name Gebiidae'. They also

TABLE I
Lists of available family-group names in infraorders Axiidea and Gebiidea

AXIIDEA de Saint Laurent, 1979
Axiidae Huxley, 1879
Calocarididae Ortmann, 1891
Coralaxiinae Sakai & de Saint Laurent, 1989
Eiconaxiidae Sakai & Ohta, 2005
Eiconaxiopsididae Sakai, 2011
Callianassidae Dana, 1852
Anacalliacinae Manning & Felder, 1991
Bathycalliacinae Sakai & Türkay, 1999
Callichirinae Manning & Felder, 1991
Callianideidae Kossman, 1880
Callianopsinae Manning & Felder, 1991
Calliapaguropinae Sakai, 1999b
Cheraminae Manning & Felder, 1991
Eucalliacinae Manning & Felder, 1991 (erected as Eucalliinae)
Lipkecallianassinae Sakai, 2005b
Neocallianopsinae Sakai, 2011
Paracalliacinae Sakai, 2005b
Thomassiniinae de Saint Laurent, 1979a
Vulcanocalliacinae Dworschak & Cunha, 2007
Ctenochelidae Manning & Felder, 1991 (erected as subfamily)
Ctenocheloididae Sakai, 2011 (erected as Ctenocheloidae)
Dawsoniinae Sakai, 2006a
Gourretiinae Sakai, 1999a
Pseudogourretiinae Sakai, 2005b
Micheleidae Sakai, 1992
Meticonaxiinae Sakai, 1993
Strahlaxiidae Poore, 1994

GEBIIDEA de Saint Laurent, 1979
Axianassidae Schmitt, 1924
Laomediidae Borradaile, 1903
Naushoniinae Chace, 1939
Thalassinidae Latreille, 1831
Upogebiidae Borradaile, 1903 (erected as subfamily)
Neogebiculinae Sakai, 2006b

Names are listed at the taxonomic level at which they were erected (with two exceptions) under the valid names (in bold) accepted by Dworschak et al. (2012). Nominal subfamily names are not repeated.

argued that Axiidea de Saint Laurent, 1979 is 'not nomenclaturally desirable' because it 'seems derived from the family name Axiidae', a name introduced later by Huxley (1879) than Callianassidae Dana, 1852. Sakai & Türkay (2014) included one superfamily, Thalassinoidea, to encompass all families of their restricted Tha-

lassinidea and two superfamilies, Axioidea and Callianassoidea, within Callianassidea. Incidentally, their list of infraorders of Pleocyemata included Palinura and Nephropidea (sic) Dana, 1852. Neither is now valid (see below) and Nephropsidea, so spelled, appeared in the literature only well after Dana's publication.

DISCUSSION AND CONCLUSION

The most recent molecular and morphological research indicates that the infraorder Thalassinidea s.l. is difficult to diagnose and is not monophyletic but instead comprises two distantly related groups at infraordinal rank. While Sakai (citations below) also agrees on there being two groups he is unclear on their relationship. Unlike names covered by the ICZN, higher taxon names are not governed by typological principles. For this reason the name Thalassinidea need not be retained for either group and should be abandoned to allow the two new taxa to be defined without being confused with the one they replace. Therefore, to invoke a natural classification scheme (i.e., one that reflects evolutionary relationships) for the decapod crustaceans, the usage of Axiidea and Gebiidea is preferred with the clear implication that the mud shrimps/lobsters are polyphyletic. Precedents for this can be found elsewhere in the Decapoda. Former division of Decapoda into Reptantia and Natantia has long been forgotten along with these names. The former Palinura is now treated as Achelata (spiny lobsters or rock lobsters) and Polychelida (deep-sea lobsters) (Scholtz & Richter, 1995), two groups with different evolutionary histories (Bracken-Grissom et al., 2014).

Names for the infraorders, Axiidea and Gebiidea, were first proposed by de Saint Laurent (1979) and it is sensible to allow precedence to fix these names in the literature, 35 years later.

Since their revival in 2009, Axiidea and Gebiidea, separately or together, have been used in at least 130 publications by numerous authors in many journals (citations available from the first author on request). The names have been adopted in studies on higher systematics (e.g., Bracken et al., 2010; Ahyong et al., 2011; Lin et al., 2012; Shen et al., 2013; Bracken-Grissom et al., 2014), taxonomy (Komai & Anker, 2010; Komai et al., 2010; Liu & Liu, 2010; Dworschak et al., 2012; Dworschak, 2013; and many others), fossils (e.g., Hyžný & Müller, 2010, 2012; Hyžný & Hudáčková, 2012; Hyžný & Karasawa, 2012; Schweitzer & Feldmann, 2012; Feldmann et al., 2013; Hyžný et al., 2013; Karasawa & Kinugawa, 2013), larval studies (e.g., Pohle et al., 2011; Kornienko et al., 2013, 2014; Pohle & Santana, 2014; Somiya et al., 2014), ecology (e.g., Hernáez et al., 2012; Kneer et al., 2013; Selin, 2013; Takeuchi et al., 2013), parasitology (Boyko et al., 2013) and in faunal lists (e.g., Baldwin, 2010; De Grave et al., 2009; Appeltans et al.,

2012; Moscoso, 2012). Axiidea and Gebiidea are fundamental to the classification used by the World Register of Marine Species (WoRMS Editorial Board, 2014) and the Paleobiology Database (2014). Sakai's scheme has appeared only in 18 papers by him and coauthors in three journals, *Crustaceana*, *Crustaceana Monographs* and *Marine Biodiversity* (Sakai, 2005a, b, 2006a, b, 2010a, b, 2011a, b, c, 2013; Sakai & Türkay, 2005, 2012a, b, 2014; Sakai & Sawada, 2006; Sakai & Lheknim, 2014; Sakai et al., 2014a, b), and has not been adopted by other authors.

If the need for two new names, priority, and prevailing usage were not three sufficient justifications for the use of Axiidea and Gebiidea, the alternatives are too confusing, and sometimes even misleading in phylogenetic relationships, to be adopted. Sakai & Sawada (2006) introduced the new infraordinal name Callianassidea and retained Thalassinidea in a restricted sense; these were revived by Sakai & Türkay (2014). In the interim, Sakai (2011a) reverted to Thalassinidea sensu lato with two sections, Callianassida and Thalassinida, names spelled differently from those in the earlier paper.

Firstly, Sakai's scheme is unstable with varying names and ranks. Thalassinidea was used to include only some taxa at one time and for all taxa later. Also, introducing sectional ranks unnecessarily complicates the classification.

Secondly, whereas Callianassidae was introduced as a family name by Dana (1852), higher taxon names derived from the same root are not attributable to this author as Sakai seems to believe. This is the case for many names of crustacean orders and suborders (see catalogue of Martin & Davis, 2001). Even within taxa covered by the Code this is not a requirement — family names are derived from their type genus but their authorships are independent. So, Callianassidea and Callianassida are names erected by Sakai & Sawada (2006) and Sakai (2011a) respectively, not Dana who erected Callianassidae and, moreover, recognised the higher taxon Thalassinidea.

Thirdly, Sakai & Türkay (2014) attempted to justify their use of Callianassidea and Thalassinidea in rather convoluted ways. Callianassidea was advocated over Axiidea because Callianassidae, from which it was said to be derived, is an older family name than Axiidae; and Thalassinidea was chosen over Gebiidea because the latter was said to be based on an obsolete family name. In fact, as pointed out already there is no ICZN requirement for ordinal, subordinal or infraordinal names to be based on family or genus names at all. Many in zoology are not (e.g., Carnivora, Ephemeroptera) and examples from Crustacea include Decapoda, Dendrobranchiata, Pleocyemata, Brachyura, Anomura and Achelata.

Modern diagnoses of the infraorders Axiidea and Gebiidea and of some families and subfamilies can be found in Dworschak et al. (2012). Their listing of families is expanded here to include all available family-group names (table I) but the validity of several remains contentious; compare for example Felder & Robles (2009) and

Dworschak et al. (2012) on the one hand with Sakai (2011a) and Sakai & Türkay (2014) on the other.

Irrespective of names, all current evidence corroborates the reality of two distantly related major clades of what was formerly called Thalassinidea. The most widely accepted and consistently used nomenclature for these clades recognises them as the infraorders, Axiidea de Saint Laurent, 1979 and Gebiidea de Saint Laurent, 1979. In the interest of stability and consistency, all authors, journal editors and reviewers are urged to use these names over others until contradictory evidence shows otherwise.

ACKNOWLEDGEMENTS

This study was supported under funding from the U.S. National Science Foundation to D. Felder (BS&I grant no. DEB-0315995 and DEB/AToL grant no. EF-0531603). Extensive work on diversity and classification of fossil Axiidea and Gebiidea has been conducted under NSF grants DEB/AToL 0531670 to Feldmann and Schweitzer and EAR-1223206 to Schweitzer and Feldmann. Studies on fossil ghost shrimps of the families Callianassidae and Ctenochelidae were supported by the Slovak Research and Development Agency under the contract no. APVV-0436-12 to M. Hyžný. Rafael Robles and Fernando Mantelatto received support (Postdoctoral fellowship 2013/05663-8 and Grant no. 2010/50188-8) from a multidisciplinary research project Temático BIOTA–FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo, Brazil), which aims to produce a fine-scale assessment of the marine decapod biodiversity.

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In regard to the above article, the Editors of Crustaceana would like to make clear that:

1. Allowing 22 authors for this paper is an exception and in no way changes the regular rules of Crustaceana, which state that unless dictated by exceptional circumstances, the number of authors for any contribution remains restricted to 3 (three) for taxonomic papers in which new scientific names are published; 7 (seven) for other regular papers; and 9 (nine) for papers with a primarily biochemical or genetic content.
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On behalf of the Board of Editors,
J.C. VON VAUPEL KLEIN
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First received 29 May 2014.
Final version accepted 10 July 2014.