

ZUZALPHEUS RÍOS AND DUFFY, 2007: A JUNIOR SYNONYM OF SYNALPHEUS BATE, 1888 (DECAPODA: ALPHEIDAE)

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ABSTRACT

The genus *Zuzalpheus* Ríos and Duffy, 2007 was established for species of the presumably monophyletic *Synalpheus gambarelloides* species group of the second-most speciose alpheid genus, *Synalpheus* Bate, 1888. However, the validity of *Zuzalpheus* as a distinct genus is questionable. First, *Zuzalpheus* is embedded within *Synalpheus* in a previously published phylogeny of *Synalpheus* based on molecular and morphological data, making *Synalpheus* paraphyletic. Secondly, the three morphological characters used by Ríos and Duffy (2007) to distinguish these two genera are minor compared to distinctions among other alpheid genera; only two of these characters can be considered valid, and only tentatively so. Therefore, *Zuzalpheus* is synonymized with *Synalpheus*. However, *Zuzalpheus* does remain an available name, which could be used in a future subgeneric classification based on a comprehensive phylogenetic assessment of *Synalpheus*.

KEY WORDS: Caridea, taxonomy, *Synalpheus*, *Zuzalpheus*

INTRODUCTION

After *Alpheus* Fabricius, 1798, *Synalpheus* Bate, 1888 is the second-most speciose genus in the caridean shrimp family Alpheidae with around 150 species worldwide (Banner and Banner, 1975; Chace, 1988; Anker et al., 2006; Ríos and Duffy, 2007). The actual number of species is probably much higher as indicated by a great number of cryptic species (Ríos and Duffy, 2007; A. Anker, personal observation).

Synalpheus is a morphologically homogeneous genus, especially when compared to *Alpheus*. However, the intrageneric structure of *Synalpheus* is still poorly known. Coutière (1909) subdivided the genus into six species groups, without giving them a formal, subgeneric status. In a review of the Australian species of *Synalpheus*, Banner and Banner (1975) suggested that only three of Coutière's six groups were coherent enough to continue to be recognized, but again refrained from assigning them a subgeneric rank. These species groups are the exclusively Indo-West Pacific *S. comatularum* (Haswell, 1882) group, which near-exclusively is comprised of crinoid-associated species; the exclusively eastern Pacific/western Atlantic *S. brevicarpus* (Herrick, 1891) group, which includes both free-living and sponge-associated species; and the worldwide *S. gambarelloides* (Nardo, 1847) group, which comprises exclusively sponge-dwelling species. Chace (1988) expressed little doubt that the genus *Synalpheus* would need to be restricted to the *S. comatularum* group, but refrained from such action in view of the considerable taxonomic confusion this would temporarily cause. These three groups combined, however, include less than half of all presently known species of *Synalpheus*. The rest of the genus can be best described as being in a phylogenetic and in many cases also taxonomic chaos, making it one of the taxonomically most challenging caridean genera.

SYSTEMATICS

The type species of *Synalpheus* is *S. falcatus* Bate, 1888 (by monotypy, Bate, 1888). However, Coutière (1899) subsequently placed *S. falcatus* in synonymy of *S. comatularum* (originally described as *Alpheus Comatularum* Haswell, 1882). According to the ICZN (1999, p. 66, Article 67.1.2) "The name of a type species remains unchanged even when it is a junior synonym or homonym, or a suppressed name". Therefore, *S. comatularum*, which is also the nominal taxon of the *S. comatularum* group, is the currently valid senior synonym of the type species of *Synalpheus*. In addition, two nominal genera were placed in synonymy of *Synalpheus*: *Homaralpheus* Bate, 1888, with *Alpheus minus* Say, 1818 as its type species by subsequent monotypy and subsequent selection by Holthuis (1955), and based on a larval form (Chace, 1988); and *Alpheinus* Borradaile, 1899, with *Alpheinus tridens* Borradaile, 1899 as type species (by monotypy) currently considered a junior homonym of *S. stimpsoni* (De Man, 1888), a species unequivocally included in the *S. comatularum* group (Banner and Banner, 1975).

The *Synalpheus gambarelloides* group is morphologically well defined (Coutière, 1909; Dardeau, 1984) and its monophyly was relatively well supported in a combined morphological/molecular analysis of the western Atlantic species of *Synalpheus* (Morrison et al., 2004; but see below). The *S. gambarelloides* group is also ecologically relatively homogeneous, as the majority of the constituent species are obligate associates of sponges, at least in the western Atlantic (Dardeau, 1984). However, sponge-dwelling is not restricted to this group and is relatively widespread in non-*gambarelloides* group species. From a biogeographical perspective, the group has explosively radiated in the western Atlantic (>30 species) and has only a few representatives in the eastern Atlantic (2 species,

including the nominal species), and the eastern Pacific (4 species, including 2 undescribed, A. Anker, personal observation), whilst the inclusion of the Indo-West Pacific species varies according to authors (e.g., Banner and Banner, 1975; Ríos and Duffy, 2007), but is certainly less than 10.

The genus *Zuzalpheus* Ríos and Duffy, 2007 was separated from *Synalpheus* to include all species of the *S. gambarelloides* group: "Examination of this material, together with molecular phylogenetic analyses (Morrison et al., 2004), led us to the conclusion, foreseen by previous workers (Banner and Banner 1975; Chace 1988), that it is necessary to separate the previously known *Gambarelloides* group of species as a distinct genus. Thus, we here erect *Zuzalpheus* n. gen., for this group of species, on the basis of morphological, ecological, and molecular evidence." (Ríos and Duffy, 2007). Of course, previous alpheid workers, including Coutière (1909), Banner and Banner (1975), Chace (1988) and for that matter Dardeau (1984), did not indicate a need of a generic rank for the *S. gambarelloides* group, an important fact not considered by Ríos and Duffy (2007), even though Banner and Banner (1975) and Chace (1988) did see merit in reviewing the taxonomic rank of some of Coutière's species groups. Curiously perhaps, the describers of *Zuzalpheus* did not try or even suggest to separate the *S. gambarelloides* group as a distinct genus in their previous taxonomic and phylogenetic studies (Duffy, 1996, 1998; Ríos and Duffy, 1999; Morrison et al., 2004; Macdonald and Duffy, 2006), beyond the following statement in an unpublished thesis: "it is recommended that the *Gambarelloides* group of species should be recognized as a distinct subgenus within *Synalpheus*" (Ríos, 2003).

There are other peculiarities in the description of *Zuzalpheus*, including the type species selection, the lack of a formal comparison with *Synalpheus*, the lack of comments on other *Synalpheus* species groups, and the relatively vague inclusion of several Indo-Pacific species. Ríos and Duffy (2007) explicitly state that *Zuzalpheus* is erected for Coutière's *Synalpheus gambarelloides* group, a name used by all prominent alpheid workers since Coutière (1909). However, Ríos and Duffy (2007) selected *Zuzalpheus kensleyi* Ríos and Duffy, 2007 as the type species of the genus. Although authors are free to select a type species of their choosing, this action raises several taxonomic and historical questions. Although Ríos and Duffy (2007) do provide a generic diagnosis for *Zuzalpheus*, a detailed comparison with related genera, as is the norm in taxonomic papers erecting new genera, is lacking. Equally, no mention is made of the other *Synalpheus* species groups. In order for the stability within *Synalpheus* and the correct generic placement of other taxa, not discussed by the authors, to be ascertained, such a comparison is strangely lacking and should have been requested by the responsible editor. As highlighted above, the true taxonomic position of many *Synalpheus* species is difficult to assess, given their variability, and lack of thorough descriptions. It is therefore somewhat surprising that the extralimital species which potentially belong to the *S. gambarelloides* group are merely indicated by a question mark, and their true status not properly assessed. This is further confounded by the definite

inclusion of *Synalpheus mulegensis* Ríos, 1992, a species not recorded since the original description, in which it is stated that the minor first pereopod is lacking in the holotype and single known specimen; in addition, Ríos' drawing does not show the coxa of the third pereopod (see below) (Ríos, 1992). Although these omissions/peculiarities do not by themselves invalidate the genus *Zuzalpheus*, they do raise the possibility the erection of the genus may have been premature. This aside, here we intend to show that the erection of genus *Zuzalpheus* was unwarranted on the basis of other available evidence, and that *Zuzalpheus* Ríos and Duffy, 2007 should be regarded as a junior synonym of *Synalpheus* Bate, 1888.

The only presently available molecular and morphological analysis of *Synalpheus* (Morrison et al., 2004) indicates that *Zuzalpheus* is embedded within *Synalpheus*. Thus by creating *Zuzalpheus*, Ríos and Duffy (2007) made *Synalpheus sensu stricto* (a grouping of over 120 species) a paraphyletic genus. Paraphyletic groupings are generally not encouraged in modern taxonomy (Wiley, 1981; de Quieroz and Gauthier, 1990; but see Brummitt, 2003 for defence of parphyly). It is far beyond the scope of this paper to discuss strict cladism (where only monophyletic groupings are accepted), versus evolutionary cladism (where some parphyly is allowed, especially in cases of highly derived lineages). However, it is our position that as far as possible strict cladism should be generally used in taxonomy to avoid ambiguity, but nevertheless allowance needs to be made for the fluid nature of the taxonomic process and each case should be judged on its merit. For instance, Anker et al. (2006) in a morphological cladistic analysis of alpheid genera found several minor, currently recognized genera, embedded within *Alpheus*. As these are highly derived lineages related to specific ecological associations (such as *Racilius* Paulson, 1875), and in view of the coding used (which the authors admit is not ideal to solve intra-*Alpheus* relationships), no formal action was taken. Nevertheless, as this is the only available generic level phylogenetic analysis within the Alpheidae, some taxonomists could consider *Alpheus* to be currently paraphyletic. Of course, the fluid nature of taxonomy and its time consuming progress can be responsible for paraphyletic or even polyphyletic taxa. For instance, *Periclimenes* Costa, 1844 (Palaemonidae) has long been suggested to be a polyphyletic assemblage and is now gradually being subdivided into several smaller genera (Bruce, 2004, 2007; Marin, 2006; Okuno and Fujita, 2007), but whilst work progresses, *Periclimenes sensu stricto* remains paraphyletic or even polyphyletic.

As *Zuzalpheus* does not represent a morphologically highly derived lineage, making *Synalpheus* paraphyletic is unwarranted. Strict cladists should reject *Zuzalpheus* straight off, but we here show that even under evolutionary cladism this change in taxonomic status of the *S. gambarelloides* group is equally unwarranted.

DISCUSSION

In recent years, there has been a score of new genera erected within Alpheidae, e.g., *Orygmalpheus* De Grave and Anker, 2000, *Jengalpheops* Anker and Dworschak, 2007; *Harper-*

alpheus Felder and Anker, 2007; and *Pseudalpheopsis* Anker, 2007. All these genera represented distinct, previously unknown lineages and were separated from other alpheid genera on the basis of several differential characters. Only one genus, viz., *Rugathanas* Anker and Jeng, 2007, was a result of a necessary generic rearrangement (Anker and Jeng, 2007), an action foreseen earlier (Banner and Banner, 1982). As a result of this comparative work, alpheid taxonomy at the generic level is now more uniform than in many other caridean families. Whilst we do not necessarily advocate the view point that all genera within a family should be defined on the basis of a fixed set of characters, a certain level of parity is desirable for the sake of systematic stability. In addition, splitting *Synalpheus* into several genera would result in loss of an important evolutionary entity within the Alpheidae.

The generic diagnosis of *Zuzalpheus* highlights only three relatively minor morphological differences, one of which is meristic, with none of the character/character states having been previously used in alpheid generic level systematics. These characters are: 1) the presence (*Zuzalpheus*) vs. absence (*Synalpheus*) of a dense brush of thick setae, arranged in parallel rows on the dactylus of the minor chela; 2) the stylocerite not reaching (*Zuzalpheus*) vs. reaching or overreaching (*Synalpheus*) the distal margin of the first antennular peduncle; and 3) the presence (*Zuzalpheus*) vs. absence (*Synalpheus*) of mesial lamellae on coxae of third pereiopods. However, the *S. paraneptunus* Coutière, 1909 species complex, included in *Zuzalpheus* by Ríos and Duffy (2007), represents an exception to the first and second proposed characters: species of this complex have only a sparse row of setae on the dactylus of the minor chela, and the stylocerite reaches (or even distinctly surpasses in one species) the distal margin of the first antennular peduncle. It should also be noted that the length of the stylocerite is extremely variable within *Alpheus* and some other alpheid genera (Banner and Banner, 1982; A. Anker, personal observation), showing its mediocre value as a character of generic importance. Morrison et al. (2004) found strong support for a sister-taxon relationship between *S. paraneptunus* and *S. kensleyi* (Ríos and Duffy, 2007), a typical member of the *S. gambarelloides* group. This warrants the inclusion of *S. paraneptunus* in the *S. gambarelloides* group. On the other hand, it suggests that in *S. paraneptunus*, the stylocerite became secondarily longer and setal rows were reduced to a single sparse row indicating a certain plasticity of these features within the genus.

The presence of mesial coxal lamellae on the third pereiopods may indeed be a synapomorphy of the *S. gambarelloides* group. However, its presence or absence in many Indo-West Pacific taxa remains to be confirmed, both within species tentatively included in *Zuzalpheus* by Ríos and Duffy (2006), and in *Synalpheus*. Additionally, these lamellae were not drawn or mentioned in the type description of *S. mulegensis*. As stated above, the true taxonomic status of some species is not unambiguously clear, and the same holds for many characters, many of which were not illustrated or discussed by earlier taxonomists, especially those previously not considered of taxonomic value. Although it can be argued that not all

species included in a given genus need to fully comply with a current generic diagnosis, such a debate clearly centres on the strength of the character differences. On the basis of the available evidence, the relative length of the stylocerite and the presence of a well-developed setal brush cannot be considered unambiguous character states for *Zuzalpheus*. This leaves the presence of mesial lamellae on the third pereiopod, as the potential single character state to differentiate *Zuzalpheus* from *Synalpheus*. Besides from the lack of knowledge on this character state in many *Synalpheus* species, the distinction between two closely related genera on the basis of a single present-absence character state in untenable. A classic example of this are the genera *Palaemon* Weber, 1795 and *Palaemonetes* Heller, 1869 (Palaemonidae), distinguished by the presence (*Palaemon*) or absence (*Palaemonetes*) of a mandibular palp. However, considerable variation in the development of the mandibular palp (including its absence) has been reported in *Palaemon* (see Fujino and Miyake, 1968; Chace, 1972), whilst at least one species has been described in *Palaemonetes* as harbouring a mandibular palp (Carvacho, 1979).

Contrary to Ríos and Duffy's (2007) statement on the unique ecology of *Zuzalpheus* species, there is no clear-cut ecological separation between *Zuzalpheus* and *Synalpheus*. Many *Synalpheus* species (not belonging to *Zuzalpheus*) also live in sponges, and at least some of them may even be eusocial (Banner and Banner, 1975; Didderen et al., 2006). Generally, ecology and biogeography are only additional attributes in generic diagnoses traditionally based on a unique combination of multiple morphological characters, and should not be used to justify generic status.

The monophyly of the *S. gambarelloides* group needs confirmation. The study by Morrison et al. (2004) targeted the western Atlantic members of the *S. gambarelloides* group, with the only extra-limital species being *S. gambarelloides*. Further, only six species outside of the *S. gambarelloides* group (out of a potential 100+) were included, and none from the homogeneous *S. comatularum* group (the true *Synalpheus* if restricted, as suggested by Chace, 1998). Notwithstanding the high quality of the research, monophyly of the *S. gambarelloides* groups is hard to demonstrate under such circumstances. In fact, as only one non-*Synalpheus* was included, even the putative monophyly or paraphyly of *Synalpheus* sensu lato would be hard to demonstrate. Nevertheless, this remains to date the only phylogenetic study of *Synalpheus*, and the morphological data do support the monophyly of the *S. gambarelloides* group with three synapomorphic characters [those listed above under 1), 2) and 3), and the sole characters used in the generic diagnosis of *Zuzalpheus*]. The monophyletic status of the *S. gambarelloides* group was not supported by the COI data, although it was supported by the 16S data and the combined 16S/COI + morphological data (Morrison et al., 2004). The morphological tree was particularly poorly resolved, and the combined 16S/COI + morphological consensus tree was obtained with use of weighted parsimony. Clearly alpheid (and indeed caridean) phylogeny is still in its infancy and more taxa, more genes, and more objective methods need to be employed before the proposed phylogeny can be accepted. The phylogeny of Morrison et

al. (2004) does indeed provide some support for the monophyly of the *S. gambarelloides* group, and it could be argued (primarily perhaps by non morphological systematics) that this provides unequivocal evidence for its status as a separate genus, i.e., *Zuzalpheus*. This raises the question if intermediate level taxonomic categories should be congruent with and supported by molecular and/or morphological phylogenies or whether morphological differences (or lack of in the case of *Zuzalpheus*) are of over-riding importance. Within Decapoda, there has been relatively little congruence between traditionally erected genera/subgenera and phylogenetic studies, although in some cases there is a move towards stability. For instance, in *Penaeus* Fabricius, 1798, several subgenera had been proposed a few decades ago and were finally raised to generic rank by Pérez-Farfante and Kensley (1997). Some of these genera have been supported by subsequent molecular (COI/16S) studies, while others have been recognized as para- or polyphyletic (Baldwin et al., 1998; Gusmão et al., 2000; Maggioni et al., 2001; Lavery et al., 2004; Voloch et al., 2005; reviewed by Dall, 2007). Similarly, *Uca* Leach, 1814 had been subdivided into several subgenera based on morphological (Bott, 1973; Rosenberg, 2001) or molecular data (Sturmbauer et al., 1996; Landstorfer et al., 2007), although the analysis by Landstorfer et al. (2007) puts some of the previous subgeneric classifications of *Uca* into question. This shows that a consensus for a generic or intrageneric classification of *Penaeus* and *Uca* has yet to be reached despite considerable taxonomic and phylogenetic efforts.

A good example of taxonomy working synergistically with phylogeny is the revision of *Pontonia* Latreille, 1829 (Palaemonidae) by Fransen (2002), in which five new genera were erected for morphologically well defined clades. These six genera (including *Pontonia sensu stricto*) represent distinct lineages, each defined by a series of morphological characters, and in most cases also by their ecology (host group) and a particular type of colour pattern (Fransen, 2002; A. Anker, personal observation). Nevertheless, Bruce (2005) erected a further new genus, *Cainonia* Bruce, 2005 for an aberrant species of the *Dactyлонia* Fransen, 2002 lineage, a species included in the analysis by Fransen (2002), but not considered as a separate clade. This further highlights an ongoing discrepancy between traditional morphological taxonomy and the interplay between taxonomy and phylogenetic systematics.

Subdivision (splitting) of genera is indeed a common practice in taxonomy and is particularly prevalent in larger heterogeneous genera which are presumed to be non-monophyletic (either paraphyletic or polyphyletic), which is not the case in *Synalpheus*. Although we unequivocally regard *Zuzalpheus* as currently of no taxonomic value and consider it a synonym of *Synalpheus*, it could perhaps be argued (analogous to the *Penaeus* example) that *Zuzalpheus* should be relegated to subgeneric status. Subgeneric classifications based on morphological characters are currently used in some larger genera of crayfish, e.g., *Cambarus* Erichson, 1846 and *Orconectes* Cope, 1872 (Cambaridae) (see Hobbs, 1969, 1989; Fitzpatrick, 1987), although recent molecular data supported only some of them

(Sinclair et al., 2004), showing once more a strong need of a synergistic effort between morphological taxonomy and molecular systematics.

Synalpheus is a well defined, presumably monophyletic, speciose, yet morphologically homogeneous lineage, and a subgeneric subdivision of *Synalpheus* could appeal to some colleagues. However, it should not be attempted by creating a name for a particular clade (species group, species complex etc.) and leaving all other clades "unsorted and unnamed". Only a comprehensive phylogenetic analysis of *Synalpheus* would enable a solid subgeneric classification of this genus. It should include representatives of all three currently recognized species groups, such as the morphologically and ecologically distinct *S. comatularum* group (which contains the type species of *Synalpheus*), as well as numerous other taxa of the rather disparate *Synalpheus sensu lato*, across all biogeographical realms and ecological/morphological specializations. The importance of such an analysis has also been recognized by Ríos and Duffy (2007): "Nonetheless, as suggested by Dardeau (1984), the membership and geographic distribution of the new genus will remain somewhat uncertain until a careful phylogenetic comparison can be made with some of the Indo-Pacific species in the Coutièrei (previously Biunguiculatus) group, which share some morphological characteristics with *Z. paranepuntus* (Banner and Banner 1975)." As no subgeneric names exist for the other two well defined clades within *Synalpheus*, accepting *Zuzalpheus* at a subgeneric level does not remove the paraphyletic argument put forward previously, and we therefore do not advocate its use.

In summary, Ríos and Duffy (2007) created the genus *Zuzalpheus*, partially supported by an earlier preliminary phylogeny by Morrison et al. (2004) based on minor morphological characters. On the basis of the resulting paraphyly of *Synalpheus sensu stricto*, the minor morphological differences with *Synalpheus*, non-parity with other alpheid generic level differences, and the non-compliance with the generic diagnosis of several included species, we place *Zuzalpheus* in synonymy with *Synalpheus*. However, *Zuzalpheus* would obviously remain an available name for the *S. gambarelloides* group, as would indeed *Homaralpheus* if required for another clade, which could be used in the formal establishment of subgenera (based on morphologically well defined clades), after performing a more comprehensive and global phylogenetic assessment of *Synalpheus*.

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