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The status of the Australian genus *Caridinides* Calman, 1926 (Crustacea: Decapoda: Atyidae) with reference to recent phylogenetic studies

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Traditionally four subfamilies have been recognised within Atyidae (Holthuis 1986) based on an expanded version of Bouvier's (1925) "série" concept, namely Atyinae De Haan, 1849, Caridellinae Holthuis, 1986, Paratyinae Holthuis, 1986, and Typhlatyinae Holthuis, 1986. The distinction between these subfamilies and the assignment of genera to them was based on the relative development of exopods on the pereopods, the branchial formulae, pigment presence and reduction of eyes, the number of spines on the uropodal diarsis, as well as the shape and proportions of the chelipeds. In recent years, this subfamily division has not been consistently used in primary taxonomic literature (see Richard *et al.* 2012) and a growing body of phylogenetic studies have cast considerable doubt on their relevance to common ancestry. This phylogenetic work recently culminated in the comprehensive study of von Rintelen *et al.* (2012), who included 32 genera (out of the 42 then known) in analyses of one mitochondrial (16S) and two nuclear genes (28S, H3). They found no molecular support to continue to recognise subfamilies as phylogenetic realities, and suggested using informal group names for the five deep clades they recovered.

On a more inclusive level, the study of von Rintelen *et al.* (2012) also highlighted considerable levels of non-monophyly in *Caridina* as currently defined, which had been alluded to before (Page *et al.* 2007a). Most importantly, from a traditional systematic point of view, was the fact that 13 genera were recovered as embedded within their *Caridina* sensu lato clade (their "*Caridella*-group"), including *Atyella* Calman, 1906, *Caridinides* Calman, 1926, *Caridinopsis* Bouvier, 1912, *Caridella* Calman, 1906, *Edoneus* Holthuis, 1978, *Limnocaridina* Calman, 1899, *Marosina* Cai & Ng, 2005, *Neocaridina* Kubo, 1938, *Paracaridina* Liang, Guo & Tang, 1999, *Parisia* Holthuis, 1956, *Pycneus* Holthuis, 1986, *Pycnisia* Bruce, 1992 and *Sinodina* Liang & Cai, 1999. *Lancararis* Cai & Bahir, 2005 is also closely related to this clade, and falls within it in some analyses. All of these genera are morphologically close to *Caridina* sensu stricto, and are either troglomorphic with considerable morphological adaptations (e.g., *Edoneus*, *Marosina*, *Pycneus*) or are considered different at generic level from *Caridina* on the basis of the same suite of characters used to delineate subfamilies (e.g., *Atyella*, *Caridinides*, *Paracaridina*). This raises important questions as to the delineation of the majority of genera in Atyidae, and suggests a revision of the morphological characters on which these taxa have been traditionally based.

The aim of the present contribution is to re-assess the unique, single morphological character that separates the monotypic, Australian genus *Caridinides* from *Caridina*.

Caridinides was erected by Calman (1926) for a single species, *C. wilkinsi* Calman, 1926, discovered in the Cape York Peninsula, Queensland, Australia. The generic diagnosis reads: "...resembling *Caridina*, but having a well-developed exopod on the first pair of chelipeds. No supra-orbital spine. Chelipeds of the *Caridina*-type, carpus of first pair slightly excavated. An arthrobranch at the base of first chelipeds (nine pairs of gills). A number of spines on exopod of uropods...". Calman himself already pointed out that, except for the presence of the exopod on the first pereopod, the species was a normal *Caridina*, which he thought to belong to the *Caridina nilotica* group. This is perhaps reflected in the etymology of the name he chose, which means "son of *Caridina*". He further states that he uses the generic name as a measure of practical convenience and not to indicate that the species may be phylogenetically more primitive than *Caridina*.

Johnson (1961) already raised some doubts whether the presence of an exopod on the first pereopod alone would be sufficient to maintain *Caridinides* as distinct, and suggested the species should perhaps be transferred to *Caridina*. Smith & Williams (1982) elegantly re-described and fully illustrated the species on the basis of extensive material from across

its northern Australian range in Queensland and the Northern Territory, and included the selection of a lectotype. Although they acknowledge the close, morphological, relationship between *Caridinides* and *Caridina*, they uphold the generic distinction. They further expanded the generic diagnosis by a single statement: "...and sometimes a reduced exopod on the second pair...". However, this additional character was only found in 5 out of the 12 specimens from the two Northern Territory locations combined, with none of the 23 specimens from the three Queensland locations therein examined, displaying this additional character. Furthermore, their Fig 4G–K shows considerable variation in the development of this exopod, from almost vestigial to well-developed. Given the rare occurrence of this character and its varied development, it is herein considered of no generic level significance, but merely a local population variant.

Page *et al.* (2007a) were the first to incorporate material of the genus in a molecular phylogenetic study, based on two populations from Queensland. Using two mitochondrial genes, they recover the genus embedded within their *Caridina* clade, with a firm sister relationship to the Australian "*indistincta*" clade, itself a species complex (see Page *et al.* 2005). Cook *et al.* (2011) included specimens of *Caridinides* from Queensland and Northern Territory, which also fell within a clade of Australian *Caridina*. This is mirrored by the placement of the genus in the more comprehensive, global analysis of von Rintelen *et al.* (2012), who recover the genus as part of a sub-clade containing both Australian and non-Australian *Caridina* (as well as the Australian *Pycneus morsitans* Holthuis, 1986 and *Parisia gracilis* Williams, 1964), with this sub-clade deeply embedded in the over-arching *Caridina* sensu lato clade (their "*Caridella*-group").

In light of this substantial, independent, phylogenetic evidence that *Caridinides* should not be maintained as a genus distinct from *Caridina*, how should the sole distinguishing morphological character be interpreted? Are there overlooked morphological characters that would lend more weight to morphological evidence? Are there other "*Caridina*" species with exopodites, perhaps vestigial ones, on the first pereopod? Should the molecular evidence be given more weight than the morphology (see Page & Hughes 2011) and the genus be synonymised?

An examination of two lots of specimens of *C. wilkinsi* in the Oxford University Museum of Natural History (OUMNH.ZC.2009-09-028, Three Quarter Mile Lake, McIlwraith Range, QLD, leg. S. Choy, 19/07/1995, comprising 5 males, 7 ovig. females, 3 females; OUMNH.ZC.2011-01-029, Lockhart, Three Quarter Mile Lake, McIlwraith Range, QLD, leg. S. Choy, 19/07/1995, comprising 2 males, 5 ovig. females, 2 females), as well as the description of the species in Smith & Williams (1982) suggests that all the characters, (branchial formula, first and second cheliped structure, carapace ornamentation, dactyls of ambulatory pereopods, first and second male pleopod) of *C. wilkinsi*, except one, fall within the morphological variation of *Caridina*, as presently defined. The only morphological difference with "*Caridina*" sensu stricto remains the presence of a well-developed exopod on the first pereopod in *C. wilkinsi*.

An examination of the original descriptions of all valid species of *Caridina* listed in De Grave & Fransen (2011), and subsequent new species, as well as the direct examination of 45 species in the collections of OUMNH, reveals that no species were described as having such an exopod, nor were any noted in the material examined. Additionally, none of the other 13 or 14 genera included in von Rintelen *et al.*'s (2012) *Caridina* sensu lato clade harbour an exopod on the first pereopod. Indeed, in none of these genera (including *Caridina* sensu stricto) are exopods present on any pereopods, although they are present in more basal clades in Atyidae. However, there is a one mention in literature, as Riek (1953) states that a single specimen of *Caridina thermophila* Riek, 1953, a somewhat distantly related species (see Page *et al.* 2007b), was provided with an exopod, although only on the left side. As Riek's sample of this species was from "...an artesian bore drain where they [*C. thermophila*] were simply swarming...", indicative of an extensive series of material examined, perhaps not too much importance should be accorded to this observation. Nevertheless Choy & Horwitz (1995) mention in their key to Australian species that "... vestigial exopods may be present in some specimens of *Caridina thermophila*..." It currently remains unclear how common this phenomenon may be in this species.

Curiously, Jalihal *et al.* (1988) rather casually mention the occurrence of *Caridinides* in Karnataka State (India) in their introduction to a *Macrobrachium* paper from that area. A description of this (these?) species has so far not appeared in the literature. Page *et al.* (2007a), however, recover *C. wilkinsi* as part of an endemic Australian radiation, refuting an earlier suggestion by Smith & Williams (1982) that the species migrated to Australia via New Guinea. Although speculative, the most parsimonious suggestion would thus be that there is indeed an as yet undescribed species of *Caridina* in India with an exopod on the first pereopod, or alternatively at least some specimens of either a described or undescribed *Caridina* species, as no other genera of the "*Caridella*-group" (sensu von Rintelen *et al.* 2012) occur in India.

The evolutionary scenario for the family described in von Rintelen *et al.* (2012), suggests that the exopods on the first two pereopods have been lost at a relatively early stage, with the only taxon in their sister groups, "*Caridella*-group" and "*Atya*-group", exhibiting this character state being *C. wilkinsi* (notwithstanding the unsubstantiated Indian record). This is here interpreted as an evolutionary reversal for a single species, and accordingly is not afforded generic significance. *Caridinides* Calman, 1926 is therefore formally synonymised with *Caridina* H. Milne Edwards, 1837, and

the species should now be referred to as *Caridina wilkinsi* (Calman, 1926) **comb. nov.** The presence of an exopod on the first pereopod amply serves to distinguish this species from all other known *Caridina*.

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