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Opinion

Size polymorphism in *Oncaea venusta* Philippi, 1843 and the validity of *O. frosti* Heron, 2002: a commentary

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Abstract

The morphological characters used to describe *Oncaea frosti* Heron, 2002 (Copepoda, Poecilostomatoida), an Atlantic medium-sized form variant of *O. venusta* Philippi, 1843, appear to be inadequate in view of the great polymorphism known for this ubiquitous species. Comparative analysis of published and newly collected length data of *O. venusta* variants worldwide demonstrates that *O. frosti* cannot be unequivocally delineated in the Indo-West Pacific. The validity of *O. venella* Farran *sensu* Heron (2002) is questioned and comments are given on Heron's synonymization of *O. venusta* f.*venella sensu* Ferrari (1975) and *sensu* Böttger-Schnack (2001) with *O. frosti*. As long as the significance of the morphological characters used to separate *O. venusta* form variants is not substantiated by data emerging from alternative taxonomic methods, such as the analysis of gene sequences, the species names *O. frosti* and *O. venella* Farran *sensu* Heron (2002) are regarded as *species inquirendae* in the genus *Oncaea*.

The type species of the marine microcopepod family Oncaeidae, *Oncaea venusta* Philippi, 1843, is widely distributed in the Atlantic, Pacific and Indian Oceans at latitudes between 65° N and 45° S (Malt, 1983). The species is known for its great variability in total body length, ranging from 0.75 to 1.4 mm in the female and from 0.55 to 0.98 mm in the male. Within this size range up to three size groups have been reported in the literature (see Böttger-Schnack, 2001 for a review). Farran (1929) was the first to describe two size groups of *O. venusta* from the Atlantic and named the smaller size variant, forma *venella*, as opposed to the larger size variant, forma *typica*. In a subsequent report on *O. venusta* from the NW Pacific (Great Barrier Reef), however, Farran (1936) was unable to distinguish between the two size groups of *O. venusta* because specimens intermediate in size occurred in that area. In the following decades, the occurrence of different size groups among *O. venusta* populations has occasionally been reported from localities in the Indian Ocean and the Red Sea (Sewell, 1947; Tanaka, 1960; Böttger-Schnack et al., 1989), the Atlantic (Corral Estrada, 1970; Ferrari, 1975; Boxshall, 1977) and the NW Pacific (Itoh, 1997). In some populations of *O. venusta*, the length range between the (two) size groups did not overlap (e.g. Ferrari, 1975; Böttger-Schnack et al., 1989), and the consistent occurrence of the size groups over several years (Ferrari, 1975) as well as their different seasonality in abundance and/or vertical distribution (e.g. Böttger-Schnack, 1990) suggested a potential ecological separation of these morphs. In other populations, however, individuals intermediate in size were found (e.g. Boxshall, 1977; H. Itoh, pers. comm.), which could not confidently be assigned to either the *typica* or the *venella* size morph.

Morphological differences other than size, such as the shape of the prosome, the length to width ratio of the caudal rami and the genital double-somite, the relative lengths of the exopodal spines and/or the ornamentation of the exoskeleton (prosome and gen-

ital double-somite) reported by the authors mentioned above were all found to be highly variable and thus did not allow for an unequivocal differentiation of the size variants on a morphological basis. A new and quite distinct morphological character used for separating different *venusta* morphs is the presence of a dorsoposterior swelling on the P2-bearing somite, first noted for small-sized form variants of *O. venusta* in the Red Sea (Böttger-Schnack, 2001). However, the variability of this character in the Indo-west Pacific and other areas was not known at that time and thus it was not regarded as sufficient to warrant the recognition of the small Red Sea morph as a distinct species. Furthermore, the absence of such swelling in forma *venella* males implied that males of both morphs were virtually indistinguishable by morphology alone.

Recently, Heron (2002) examined *venusta* size variants from different localities in the Atlantic and Pacific Oceans and distinguished three size-groups of extraordinary morphological closeness. The largest size group of *O. venusta* from the Atlantic (mainly from the Mediterranean, near the type locality) and both sides of the Pacific she regarded as representing the typical form of *O. venusta* Philippi, as redescribed in more detail by Giesbrecht (1892) [see also Heron & Bradford-Grieve, 1995]. A medium-sized form variant from the Atlantic, exhibiting a dorsal swelling on the P2-bearing somite, was described by Heron (2002) as a new species, *Oncaea frosti*. Finally, small-sized specimens from the Atlantic (1 individual only) and the NE Pacific Ocean, which lacked this dorsal prosomal swelling, were assumed by Heron to represent the *venella*-form *sensu* Farran (1929) and raised to full species level as *O. venella* Farran, 1929. The dorsal swelling on the P2-bearing somite was the only morphological character (other than size) separating *O. frosti* from its two sibling species, and it was regarded as the main character for species identification since some overlap in size was noted between the three size groups. On the basis of this character, Heron (2002) consequently synonymized the smaller size group of *O. venusta sensu* Ferrari (1975) from the Gulf of Mexico as well as *O. venusta* f. *venella sensu* Böttger-Schnack (2001) from the Red Sea with *O. frosti*.

The separation of size morphs in the Oncaeidae is an intricate problem faced by many plankton specialists, taxonomists and ecologists alike. Although Heron (2002) appears to present an elegant and easy-to-use solution to the specific problem surrounding the *O. venusta* complex, there are some flaws in her rationale behind the distinction of the three morphs (or species) in her study. In the present paper, we present a dissenting opinion, highlighting the problems in Heron's (2002) morphological description of *O. frosti*, and commenting on the limitations in applying her taxonomic criteria to the differentiation of form variants of *O. venusta* in different oceanic areas. By taking into consideration the available literature information of *O. venusta* size variants it will be demonstrated that Heron's characters are inadequate for an unequivocal identification of the various *venusta* form variants (species?) known so far. The validity of the species name *O. venella* Farran *sensu* Heron (2002) will be discussed and the supposed conspecificity of *O. frosti* and *O. venusta* f.*venella sensu* Böttger-Schnack (2001) questioned.

Descriptive problems

According to Heron (2002), *O. frosti* can be separated from its two congeners merely by size and by the dorsal swelling on the P2-bearing somite. She also listed other morphological characters found to differ between the three species, such as (1) flexing of the urosome and telescoping of urosomites, (2) shape of prosome, (3) ornamentation of the exoskeleton, and (4) colour of freshly collected specimens. The first three were recorded to be variable by Heron (2002) herself whereas the last one has the unfortunate characteristic that it cannot be observed or verified in preserved specimens. In addition, flexure and telescoping of somites are generally hard to quantify, not least because different preservation techniques may have differential effects on them. In the absence of standardized fixation and preservation methods, we regard such characters are inappropriate for taxonomic purposes.

Table 1 summarizes the length ranges of female *O. venusta* form variants recorded in the literature up to and including Heron's (2002) study. Additional length data obtained during a recent study investigating molecular lineages in *O. venusta* from the Red Sea and Indo-West Pacific regions (Elvers et al., in prep.) are also included. All length measurements were conducted using the methods described by Böttger-Schnack et al. (1989). Except for Heron's data and those of the present study, only references of populations containing more than one size group have been included in Table 1. Specimens exhibiting a dorsal swelling on the P2-bearing somite are marked in bold. In order

Table 1. Total body length (mm) of size variants of female Oncaea venusta in different areas of the Atlantic, Indian and Pacific Oceans. Size groups exhibiting a dorsal swelling on the P2-bearing somite are marked in bold. * = single specimen

ATLANTIC OCEAN			INDIAN OCEAN			PACIFIC OCEAN			Locality	Source
Small	Medium	Large	Small	Medium	Large	Small	Medium	Large		
	0.92–1.07	1.08–1.16					0.92–1.07	1.08–1.16	Trop. Atl.; SW Pacific	Farran (1929
						0.84—	—	—1.33	Great Barrier Reef	Farran (1936)
			0.85–0.91		1.18–1.25				Arabian Sea	Sewell (1947)
				0.90–1.0	1.13–1.39				South Indian Ocean	Tanaka (1960)
	0.87–0.95	1.05–1.25							NE Atl., Teneriffe	Corral Estrada (1970)
	0.92–0.99	1.1–1.2							NW Atl., Gulf of Mexico	Ferrari (1975)
	0.83—~1.05	~1.05–1.27							NE Atl., Cape Verde	Boxshall (1977)
	0.88—	1.04								"robust" form
			0.75–0.88		1.00–1.23				Red Sea	Böttger-Schnack et al. (1989)
						0.87–0.94		1.09–1.23	NW Pacific	Itoh (1997)
0.81*		1.09–1.22							Mediterranean Sea	Heron (2002)
	0.96–1.07								NE Atl., Liberia	-"-
	0.96–1.15								NW Atl., Gulf of Mexico	-"-
								1.04–1.29	SW Pac., New Zealand	-"-
						0.81–0.93			NE Pac., California	-"-
						0.81–0.93			NE Pac., Panama	-"-
			0.78–0.90						Red Sea	This study
			0.85–0.90		1.06–1.26				Arabian Sea	-"-
						0.84–1.02	0.98–1.14	1.1–1.36	NW Pac., off Japan	-"-
						0.76–0.78	0.80–1.04	1.1–1.2	NW Pac., subtropical	-"-
						0.84–0.88	0.95*		SW Pac., off Australia	-"-

to avoid confusing the reader we refrained from using the terms f. *typica* and f. *venella* below, referring instead to the different size groups of *O. venusta* as 'small', 'medium' and 'large'. Table 1 shows that *O. venusta* specimens from all great oceanic basins fall into three size categories: small (<0.9 mm), medium (0.9 – ~1.0 mm) and large (>1.0 mm). A dorsal swelling on the P2-bearing somite is found in medium-sized specimens from the Atlantic ('*O. frosti*' Heron) and in small-sized specimens from the Indo-West Pacific, including the Red Sea. It is absent in medium-sized specimens from the NE Pacific (*'O. venella' sensu* Heron) and apparently also in small-sized specimens from the Atlantic, although this observation is thus far based only on a single specimen from the Mediterranean (Heron, 2002). Since both small and medium-sized groups comprise two different morphs, characterized by presence/absence of the dorsal prosomal swelling, there are possibly five different form variants of *O. venusta* worldwide, not just three as assumed by Heron (2002). Hence, there is no unique congruence between medium size and the presence of the swelling which could help delineating *O. frosti* from other *venusta*-like forms.

Limitations of Heron's (2002) criteria for identification

Application of Heronþs (2002) identification criteria to *O. venusta*-like specimens from the NW Pacific off Japan (Table 1) demonstrates that her division into three species is taxonomically untenable. For example, it cannot be confirmed whether the small-sized specimens from that area should be assigned to *O. frosti* Heron (based on the presence of the swelling) or to *O. venella* Farran *sensu* Heron (based on their size). Similarly, the NW Pacific medium-sized specimens fit the length range of *O. frosti*, but cannot be assigned to this species, because of the absence of the dorsal swelling.

Validity of *O. venella* Farran *sensu* Heron (2002)

Heron (2002) assumed that small-sized specimens (<0.9 mm) lacking a dorsal swelling on the P2-bearing somite were conspecific with the *venella* form variant described by Farran (1929). However, as can be seen from Table 1, the length range of Farran's f. *venella* corresponds with that of medium-sized

venusta specimens (∼0.9 – ∼1.0 mm), not with small ones. Heron (2002: 150) claimed that Farran had revised the length range of his *venella* form in a subsequent report from the Great Barrier Reef and stated that the ". . . smaller size reported by Farran (1936) is considered the most authentic, since it was based on additional material". However, her argument appears to be unsubstantiated for three reasons:

(1) Farran (1936) explicitly stated that he had **not** been able to distinguish between different size groups of *O. venusta* in the material from the Great Barrier Reef and just mentioned a different coloration for the smaller-sized specimens (0.84–0.91 mm) which displayed ". . . a distinct reddish tinge on the mouthparts and legs".

(2) Farran's (1929) original description, however brief, provides the sole objective standard of reference for the application of the name *O. venusta* var. *venella*. The only reliable diagnostic character given by Farran is female body size which ranged in his samples from 0.92 to 1.07 mm. Farran's (1936) smaller size range (0.84–0.91 mm) therefore refers to another size morph and there is nothing in his report indicating that he was dealing with genuine *venella*. Heron's (2002) argument that the size range for *venella* appears to be confirmed because specimens conforming to Farran's (1936) smaller size range have been reported from three different areas does not hold. Indeed, specimens fitting Farran's (1929) original medium size range have now also been recorded from all three oceans (Table 1) and are more likely to represent *venella*. In view of the amazing diversity of the Oncaeidae worldwide, it should be noted that medium size in itself is probably not sufficient to diagnose *venella* since several (as yet undescribed) cryptic species may fit this size range. However, as a discriminant, medium size can be safely used to rule out potential identity (or conspecificity) between *O. venella* sensu Heron (2002) and Farran's (1929) variety *venella*.

(3) The middorsal swelling is not conspicuous and is discernible only when the body is viewed in lateral aspect. Since Farran (1929) only presented a dorsal habitus drawing it remains unconfirmed whether his *venella* specimens displayed the prosomal dilation or not. If they did, it is conceivable that *O. frosti* is a synonym of Farran's variety *venella*.

Synonyms of *O. frosti*

Heron (2002) listed *O. venusta sensu* Ferrari (1975) from the Gulf of Mexico as a synonym of *O. frosti*. Ferrari (1975) reported two size groups which he equated with the formae *typica* (♀ ♀: 1.10–1.20 mm; ♂ ♂ 0.76–0.86 mm) and *venella* (♀ ♀: 0.92–0.99 mm; ♂ ♂: 0.57–0.63 mm). Heron did not specify which forma she regarded as conspecific with *O. frosti* but it is likely that she alluded to *venella* since it is excluded from her synonymy of *O. venella* and its size falls into the range of *O. frosti* (cf. Table 1). As part of the latter's synonymy, Heron also referred to Ferrari's (1975) Figure 5I which illustrates a female in lateral view, showing a small insignificant dorsal swelling on the P2-bearing somite. This could have been an additional piece of circumstantial evidence in favour of Heron's course of action, were it not that Ferrari only illustrated the larger forma *typica* and not the smaller one. The conspecificity of *O. frosti* and Ferrari's forma *venella* remains therefore unsettled since it is based on size only.

Heron also synonymized *O. venusta* f. *venella sensu* Böttger-Schnack (2001) from the Red Sea with *O. frosti*, based on the presence of the dorsal swelling on the P2-bearing somite in both species. In doing so, she disregarded the size of the Red Sea specimens, which are distinctly smaller than *O. frosti* and correspond much better with the small-sized specimens from the Atlantic and Pacific described by Heron (Table 1). It is puzzling why Heron attached more importance to the dorsal swelling in the Red Sea specimens, and regarded size more significant in the case of Ferrari's (1975) forma *venella*. As long as the taxonomic significance of the prosomal swelling within the small and medium size groups of *O. venusta* is not elucidated, we regard it premature to synonymize Ferrari's (1975) and Böttger-Schnack's (2001) forma *venella* with *O. frosti*.

Although body size in copepods may vary on a seasonal or regional basis, it has been demonstrated that Oncaeidae show virtually no seasonal variation in body length compared to other planktonic taxa such as *Oithona* and calanoids (Riccardi & Mariotto, 2000). Size may therefore be an important discriminant in the *O. venusta* complex, suggesting that the small swelling-bearing Red Sea form is probably not conspecific with either Farran's *venella* or *O. frosti* but represents a distinct form (or species). Small-sized *O. venusta* specimens exhibiting a dorsal swelling on the P2-bearing somite have been found in various localit-

ies in the Indo-West Pacific during the present study (Table 1) and are not a local phenomenon in the extreme environment of the Red Sea, as assumed earlier by Böttger-Schnack et al. (1989).

In conclusion, the morphological characters applied by Heron are not adequate for unequivocal species identification and consequently her designation of two *venusta* form variants as new species appears to be premature. At present, it cannot be decided whether the small- and medium-sized *O. venusta* forms from the Atlantic and Indo-Pacific are conspecific or not and whether the character 'swelling' is appropriate for separating additional species within each size group. These taxonomic issues cannot be elucidated by traditional microscopical examination of the body morphology, but require alternative taxonomic methods, such as the analysis of gene sequences. Preliminary results of a forthcoming molecular study using two mitochondrial genes (ITS-1 and cyt b) indicate that the Indo-West Pacific size variants of *O. venusta* are very closely related, yet genetically distinct (D. Elvers, unpublished data). The results provide further evidence that small-sized specimens from the Red Sea and the NW Pacific belong to the same group. Whether or not these *venusta* forms will have to be regarded as separate species in the future presently remains a matter of debate and has to await the results of DNA analysis. Meanwhile, as long as the significance of the morphological characters used to separate *O. venusta* form variants is not substantiated by alternative taxonomic methods, the species names *O. frosti* and *O. venella* Farran *sensu* Heron (2002) have to be relegated to *species inquirenda* in the genus *Oncaea*.

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