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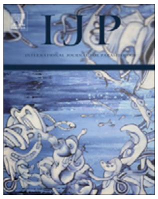

Evolution of the bomolochiform superfamily complex (Copepoda: Cyclopoida): New insights from ssrDNA and morphology, and origin of umazuracolids from polychaete-infesting ancestors rejected ☆

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ABSTRACT

Poecilostome cyclopoids are among the most morphologically diverse copepods, having established symbiotic relationships with teleosts, elasmobranchs and invertebrate hosts belonging to no fewer than 14 marine phyla. Many parasitic lineages display radically divergent body plans and on that basis have traditionally been placed at higher taxonomic rank than they deserve. The most recent example is the monotypic family Umazuracolidae, established for a derived fish parasite with bomolochiform affinities. Phylogenetic analysis of complete ssrDNA (18S) sequences of 44 species belonging to 21 families of cyclopoid copepods shows that there is no support for the familial distinctiveness of the Umazuracolidae. Both maximum parsimony tree reconstruction and Bayesian inference, operating under the GTR + I + Γ model of nucleotide substitution, unambiguously placed *Umazuracola elongatus* in the Taeniacanthidae within the predominantly fish parasitic bomolochiform complex, refuting the original suggestion of a shared most recent common ancestry with polychaete symbionts. The phylogenies also revealed that the bomolochiform families and the Clausidiidae (and allies) form a monophyletic group, the clausidiiform complex, with high nodal support under both methods. Bayesian inference suggested a diphyletic origin of the "Poecilostomatoida" with the clausidiiform family-group holding a basal position while the traditional cyclopoid families form a monophyletic group in apposition to a second poecilostomatoid clade; however, maximum parsimony results were equivocal, depending on outgroup selection. Scrutiny of the morphological characters diagnosing the monotypic families Tegobomolochidae and Tuccidae demonstrated that they merely represent derived lineages within more inclusive taxa, the former being related to a group of nostril-inhabiting genera within the Bomolochidae, the latter forming the sister-group of *Taeniacanthodes* within the Taeniacanthidae. The taeniacanthid genus *Makrostrotos* occupies a position at the base of the bomolochiform complex and is fixed as the type of a new family, Makrostrotidae. Although both morphological and molecular evidence hint that the Bomolochidae is nested within a paraphyletic Taeniacanthidae, the status quo of maintaining both families is favoured here pending additional molecular data. The bomolochiform complex, comprising the Bomolochidae, Taeniacanthidae, Telsidae and Makrostrotidae, is attributed superfamilial rank as the Bomolochoidea. A recent controversial phylogenetic analysis of the poecilostomatoid families is shown to be flawed, being based on a dataset containing imperfect or misleading information, and characters whose states were wrongly assessed.

1. Introduction

Monacanthidae (filefish or leatherjackets) is a small family of tropical to subtropical tetraodontiform marine fishes, comprising approximately 106 species assigned to 28 genera (Froese and Pauly, 2010). Found in the Atlantic, Pacific and Indian Oceans, filefish generally occur in shallow water, inhabiting depths of no more than approximately 30 m. Several species serve as hosts for ectoparasitic copepods belonging to the genus *Hatschekia* Poche, 1902 in the Hatschekiidae (Siphonostomatoida) and the genera *Cirracanthus* Dojiri & Cressey, 1987, *Nudisodalis* Dojiri & Cressey, 1987 and *Taeniacanthus* Sumpf, 1871 in the Taeniacanthidae (Cyclopoida) (Yamaguti, 1939; Heegaard, 1962; Dojiri and Cressey, 1987; Uyeno

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and Nagasawa, 2009, 2010). Recently, Ho et al. (2006) described a new genus and species, *Umazuracola elongatus*, from the body surface of the black scraper, *Thamnaconus modestus* (Günther, 1877), collected from the Seto Inland Sea of western Japan, and assigned it to a new monotypic family, Umazuracolidae, in the order "Poecilostomatoida" (= Cyclopoida). Although a comparison of *Umazuracola* with the fish-parasitising families of the bomolochiform complex (Dojiri and Cressey, 1987) showed a close similarity in the morphology of the antenna and mouthparts, the cladistic analysis of Ho et al. (2006) suggested that the Umazuracolidae originated within a clade of polychaete symbionts, containing the families Entobiidae and Nereicolidae.

The proposal of the Umazuracolidae by Ho et al. (2006) cannot help but attract controversy and invite criticism that it illustrates two problematic issues in current thinking of copepod evolutionary biology: the uncritical acceptance of similarities as supporting evidence for phylogenetic relatedness, and the proliferation of family-level rankings for parasites with highly derived body plans. The first issue relates to the enormous morphological plasticity of poecilostomatoids, making them the most diverse lineage of copepods in terms of gross body morphology (Huys and Boxshall, 1991). The phylogenetic analysis by Ho et al. (2006) of 61 poecilostomatoid families (the Bradophilidae was not considered) employed 138 adult-female morphological characters; however, not all of them are informative and some are implicitly wrong. In several cases the "apomorphic" character states used in reality refer to the plesiomorphic condition (e.g., antennule 8-segmented, maxillule bilobate, maxilliped with 2-segmented endopod, distal exopod segment of leg 4 with nine elements, leg 5 2-segmented with four elements on exopod). Other characters fail the test of positional homology. For example, their character 47 was scored as 'third exopod segment of leg 1 with 9 elements' for the Tegobomolochidae, which would make *Tegobomolochus nasicola* Izawa, 1976 the only extant copepod with this armature pattern because the maximum number of elements recorded in the Copepoda is eight. However, Izawa's (1976) description clearly shows that the exopod is 2-segmented and consequently at least one of the nine elements included in his count must be homologous with the outer spine of the ancestral middle segment. Similarly, the claim by Ho et al. (2006) that the Polyankyliidae have seven elements on the third endopod segment of leg 1 (character 56) is incorrect because the only two species included in this family (Ho and Kim, 1997; Karanovic, 2008) display a 2-segmented endopod with an armature formula [0–1; I,6]. Character 77 was coded for the Polyankyliidae, Paralubbockiidae and Tuccidae as 'third endopod segment of leg 2 with 7 elements', but this is incorrect because these families all have a 2-segmented endopod with the distal segment bearing elements that originated from two segments that failed to separate. Character 135, which was scored for the Philichthyidae and Serpulidicolidae as 'leg 6 represented by 4 setae on genital operculum', is not different from character 136 (leg 6 represented by two setae), the former being based on the total number of armature elements of the sixth pair of legs (left and right) while the latter refers to only one member of the same pair. Leg 6 is represented by an unarmed genital operculum in female Xarifiidae; however, both characters states 136 (leg 6 represented by two setae) and 138 (leg 6 absent) were coded for this family – a bald contradiction.

Lack of rigour in character analysis is a major source of error in phylogenetic inference (Wägele, 1999), and the problem is exacerbated when phylogenies are used to estimate historical ecological associations and life history traits. Sound morphological evidence indicates that cyclopoid copepods colonised fish hosts independently five times (Table 1); this estimate excludes single-species associations in families utilising predominantly invertebrate hosts (Avdeev, 1975; Avdeev and Kazatchenko, 1986). The bomolochiform complex, the Ergasilidae and the Lernaeidae –– i.e., groups I, IV and V in Table 1 –– have radically different morphologies from one another, strongly suggesting they represent three independent colonisation events. The Chondracanthidae (including the Lernaeosoleidae) and Philichthyidae are closely related (Boxshall and Halsey, 2004; Huys et al., 2006) and are treated here as the result of single colonisation of fishes as hosts (Group II in Table 1). The phylogenetic affinities of the Shiinoidae are uncertain (Group III in Table 1) (Huys et al., 2006; but see Boxshall and Halsey, 2004 for a dissenting opinion) and do not appear to lie with any of the other lineages. According to the analysis of Ho et al. (2006),

Table 1

List of cyclopoid lineages (I–V) utilising fish hosts almost exclusively, including number of valid genera (G), valid species (S), habitat (H) (E = estuarine, FW = freshwater, M = marine) and primary host taxa. Numbers of valid genera and species are based on Walter and Boxshall (2008) – last accessed 22 October 2011). New genera proposed since Boxshall and Halsey (2004) have been included for the Bomolochidae (*Cresseyus* Ho & Lin, 2006; *Hamaticolax* Ho & Lin, 2006), the Taeniacanthidae (*Biacanthus* Tang & Izawa, 2005; *Caudacanthus* Tang & Johnston, 2005; but not *Makrostrotos* Ho & Lin, 2006), the Chondracanthidae (*Argentinochondria* Etchegin, Timi & Sardella, 2003; *Pseudolernentoma* Luque & Alves, 2003; *Brasilochondria* Thatcher & Pereira Júnior, 2004), the Ergasilidae (*Majalincola* Tang & Kalman, 2008) and the Lernaeidae (*Minilernaea* Thatcher & Huergo, 2005).

Family	G	S	H	Host group
I. Bomolochiform complex:				
Bomolochidae	19	146	M	Actinopterygii
Taeniacanthidae[a]	16	105	M	Actinopterygii + Elasmobranchii + Echinoidea
Tegobomolochidae	1	1	M	Actinopterygii
Telsidae	1	2	M	Actinopterygii
Tuccidae	1	1	M	Actinopterygii
Umazuracolidae	1	1	M	Actinopterygii
II. Chondracanthidae[b]	47	188	E/M	Actinopterygii (+ Elasmobranchii + Holocephali)
Philichthyidae[c]	9	78	M	Actinopterygii (+ Elasmobranchii)
III. Shiinoidae	2	12	M	Actinopterygii
IV. Ergasilidae[d]	26	252	FW/E/M	Actinopterygii (+ Elasmobranchii + Bivalvia)
V. Lernaeidae	17	143	FW	Actinopterygii

[a] Selected species of only three genera (*Taeniacanthus*; *Taeniacanthodes*; *Irodes* Wilson, 1911) utilise sharks or rays as hosts. An additional 14 species in three genera (*Echinirus*, *Echinosocius*, *Clavisodalis*) are associated with sea urchins. The genus *Makrostrotos* Ho & Lin, 2006 and its two species are not included in the count (see Section 4).

[b] Includes the two monotypic genera, *Lernaeosolea* Wilson, 1944 and *Bobkabata* Hogans & Benz, 1990, previously placed in the Lernaeosoleidae, a junior synonym of the Chondracanthidae (Huys et al., 2006). *Bereacanthus* Huys, 2009 was proposed as a new replacement name for *Berea* Yamaguti, 1963 (Huys, 2009). *Acanthocanthopsis* Heegaard, 1945 was resurrected by Tang and Ho (2005) while *Pterochondria* Ho, 1973 was recently recognised as a junior synonym of *Acanthochondria* Oakley in Leigh-Sharpe & Oakley, 1927 (Tang et al., 2010). A single species of *Acanthochondria* occurs on holocephalan hosts. The monotypic genus *Acanthochondrites* Oakley, 1930 utilises rajids.

[c] A single species, *Colobomatus lamnae* Hesse, 1873, parasitises the porbeagle *Lamna nasus* (Bonnaterre, 1788).

[d] The monotypic genus *Teredophilus* Rancurel, 1954 and one species of *Paraergasilus* Markevich, 1937 are associated with brackish-water or freshwater bivalves. Only one species has been reported from elasmobranch hosts (Ogawa, 1991; Kabata, 1992b).