



Analytic taxonomy and notes on marine, brackish-water and estuarine Gastrotricha

WILLIAM D. HUMMON¹ & M. ANTONIO TODARO^{2,3}

¹Department of Biological Sciences, Ohio University, Athens, Ohio 45701 USA. E-mail: hummon@ohio.edu

²Dipartimento di Biologia Animale, Università di Modena e Reggio Emilia, via Campi 213/d, I-41100 Modena, Italy. E-mail: antonio.todaro@unimore.it

³Corresponding author. E-mail: antonio.todaro@unimore.it

Abstract

Marine Gastrotricha, both Macrodasyida and Chaetonotida, are the subject of an analytic review, citing taxonomic status of names, authorships of taxa, and those responsible for changes, in accordance with the International Code of Zoological Nomenclature, 4th ed. (1999). Notes are included with regard to taxonomic usage so as to guide workers in the future. Among the proposed novelties are: within Macrodasyida, to restrict the family Lepidodasyidae Remane, 1927 to the genus *Lepidodasyis* Remane, 1926, and to establish a new family, Cephalodasyidae with *Cephalodasyis* Remane, 1926 as its type-species to house the remaining genera and species that have been contained in the polyphyletic family Lepidodasyidae. *Hemidasys agaso* Claparède, 1867 is considered extinct, and the new name *Tetranchyroderma antenniphorum* is proposed for *Tetranchyroderma antennatum* Luporini, Magagnini & Tongiorgi, 1973; in addition, five species are here considered to be *species inquirendae*: *Dactylopodola weilli* d'Hondt, 1965, *Paradasys nipponensis* Sudzuki, 1976, *Macrodasyis indicus* Kutty & Nair, 1969, *Tetranchyroderma forceps* d'Hondt & Balsamo, 2009 and *Turbanella plana* (Giard, 1904b). Among Chaetonotida: the *Xenotrichula velox*-species group Ruppert, 1979 and the *Xenotrichula intermedia*-species group Ruppert, 1979 were given each the rank of subgenus. *Chaetonotus pleuracanthus* Remane, 1926 is rejected as a synonym for *Chaetonotus marinus* Giard, 1904; *Chaetonotus somniculosus* Mock, 1979 is transferred to the genus *Halichaetonotus*, the new name *Halichaetonotus euromarinus* is proposed for *Halichaetonotus spinosus* Mock, 1979, and *Xenotrichula carolinensis* Ruppert, 1979 is re-established. *Heteroxenotrichula variocirrata* d'Hondt, 1966 is here considered to be *species inquirenda*.

Key words: Gastrotricha, Macrodasyida, Chaetonotida, new family, new subgenus, new species, taxonomy, marine, brackish-water, estuarine

Introduction

With the field of meiofauna research in a mode of rapid change and an exponential increase of electronically disseminated nominal lists of the world biota, we felt that it was time for an authoritative review of the taxonomic status of marine and brackishwater/estuarine Gastrotricha, along with the author that was responsible for changes, and reasons why changes have been made; our intent is not to provide a complete taxonomic history from the 18th century onward, but to establish correct 21st century taxonomic usage. Each of us has produced lists before (see Todaro 2008, Hummon 2009b), but with greater responsibility on us for our published stand, this list is probably more conservative than either of us would otherwise be, as it has been drafted using the International Code of Zoological Nomenclature (ICZN) recommendations as a guideline. With more than 550 taxa and over 110 papers to consider, several of which belong to the “grey” literature and some of uncertain publication date, absolute perfection would be difficult to reach. However, we strive for at least ninety-five percent accuracy. Where we have given a source or date, we welcome friendly changes and hope to incorporate them as we continue forward; we also welcome those who differ with us on facts or interpretation to correct or update us by use of print medium, which should meet the criteria of scientific literature (i.e., peer reviewed papers).

Recently, a work somewhat comparable to ours has been proposed for the freshwater taxa (Balsamo, d'Hondt, Pierboni & Grilli, 2009). We regard this as an important and useful taxonomic tool, though we have reservations on some points. We hold that new hypotheses for the re-systematization of well-established taxa should be based on new, unambiguous evidence (e.g. molecular data, additional morphological data acquired by novel techniques etc.) rather than on the rescoring of well-known traits. Consequently, for purposes of this paper the taxon *Hystrichochaetonous* will be considered as a valid subgenus within *Chaetonotus*, according to Schwank (1990) and Kisielewski (1997). Likewise, the recent paper of d'Hondt & Balsamo (2009) has been answered with respect to each of the cases on which well-established systematization has been challenged.

Our work will hopefully prove useful to a wide audience, including senior and especially junior researchers who work on gastrotrichs, but also to marine zoologists and ecologists who find these abundant metazoans in the course of research on interstitial meiobenthos and who want to refer to them correctly. Obviously, the paper may be used as a reference source to be checked against for validation by editors and keepers of electronically disseminated lists devoted to these animals.

Systematic account

Phylum GASTROTRICHA Metschnikoff, 1865:458

Class

There are no classes within the Gastrotricha, as it was itself at one time considered a class within the phylum Aschelminthes!

Order Macrodasyida Remane, 1925:125. —Includes 32 genera and 297 species, of which 30 genera and 295 species are marine or brackish

[The name as given by Remane had an -oidea ending, that of a superfamily (ICZN 29.2), which was first altered to a preferred ordinal -ida ending by Brunson (1950:328) and later to be formally so designated by Rao, 1970: 109 and Rao & Clausen, 1970:80, and has almost universally been accepted as emended]

Family Cephalodasyidae —**new family**—Includes 6 genera and 31 species [Established in this publication to include *Cephalodasy*, *Dolichodasy*, *Megadasy*, *Mesodasy* and *Paradasy*, previously affiliated with the family Lepidodasyidae. The rationale for our choice rests on the growing body of evidence that concurs in showing the unnatural grouping of the traditional Lepidodasyidae (e.g. Ruppert 1978; Hochberg & Litvaitis 2000; Guidi *et al.*, 2004; Todaro *et al.* 2006) and on the vast consensus among workers in indicating that the major source of polyphyly in the family lies in the difference between *Lepidodasy* and the remaining constituents of the former family. The name derives from *Cephalodasy*, the first genus in the group to be named, while the data for the family diagnosis have been gathered from published work. Note that a split of the former Lepidodasyidae somewhat comparable to ours had been proposed by d'Hondt (1975:657) at the tribal level. However, that division was based only on the presence or absence of scales, which in our judgment was not of sufficient importance to warrant such a high-ranking division, but most of all it did not address the evident polyphyly of the former taxon]

Cephalodasyidae diagnosis [In this publication]

Elongate Macrodasyida, flattened ventrally and vaulted dorsally in transverse section with small to medium terminal or slightly subterminal mouth opening and little to marked head delimitation. Cuticle naked. Monociliated or multiciliated epidermal cells; ventral cilia in two longitudinal rows, often united fore and aft. Epidermal glands vary in size and number. Anterior adhesive tubes (TbA) in two groups behind the mouth, either inserting directly on the cuticle (*Dolichodasy*, *Megadasy*, *Mesodasy* and *Paradasy*) or inserting on fleshy hands (*Cephalodasy* and *Pleurodasy*); lateral, dorsolateral and ventrolateral adhesive tubes (TbL/TbDL/TbVL) arranged in columns along the body, occasionally absent (*Paradasy*) or in form

of adhesive papillae (*Dolichodasys*); posterior adhesive tubes (TbP) arranged marginally around the blunt to pointed posterior end. Sphincter muscle developed around mouth opening; well-developed striated radial pharyngeal musculature; pharyngeal pores basal. Circular muscles present in lateral regions of the body. Y-cells absent. Gonads paired; male anterior, female posterior; male gametes mature posterior to anterior, female gametes posterior to anterior (*Megadasys*, *Mesodasys*, *Paradasys*, *Pleurodasys*) or anterior to posterior (*Cephalodasys*, *Dolichodasys*); male pores, when present, single (*Cephalodasys*, *Megadasys*, *Mesodasys*), or paired (*Dolichodasys*, *Pleurodasys*); frontal and/or caudal organ usually present. Intertidal or subtidal in distribution; fine to coarse sand.

Type-Genus *Cephalodasys* Remane, 1926b:681 [Includes =*Psammodasys* d'Hondt, 1974b:675]

Syn. *Psammodasys* d'Hondt, 1974b:675 [Hummon, 2008b:121. d'Hondt and Balsamo (2009:273) reject the synonymy, considering *Psammodasys* to be a valid genus based on hypothetical differences on the arrangement of the accessory sexual organs; according to them *Psammodasys* species have bursa copulatrix (=bourse copulatrice) and seminal receptacle (=réceptacle séminal) topographically separated (bursa being much posterior) whereas *Cephalodasys* species have the seminal receptacle that immediately precedes the bursa. In our opinion these apparent differences are due to the nomenclatural misuse of the gastrotrichs' accessory sexual organs, which in the past has plagued the descriptions of several taxa, and derived from early misunderstanding about the function of these organs. As later pointed out (e.g. Ruppert 1978, 1991), bursa and seminal receptacle are synonymous and constitute the frontal organ, which is part of the female sexual apparatus, in that it receives and stores allosperm from cross fertilization. Where present, shape and size of the frontal organ vary across the taxonomic spectrum and may be species specific. In some cases, the functional regions of the frontal organ may be clearly discernable morphologically (e.g., in *Macrodasys*, see Ruppert 1978); in others the frontal organ is visible only in specimens that have copulated (i.e. containing allosperm, e.g. *Turbanella*). In Gastrotricha, the male counterpart of the frontal organ is the caudal organ. Physiologically, it functions as a penis. However, because of the anatomical discontinuity between testis and the caudal organ, which characterize the phylum, this peculiar penis must first be charged with autosperm before its copulatory function can be performed (e.g. Ruppert 1991). Presence/absence of the caudal organ varies across the taxonomic spectrum, whereas the shape and size may be species specific. In general, where both frontal organ and caudal organ are present, they appear to be topographically separated, or next to each other but always without luminal continuity; a notable exception are, perhaps, the gastrotrichs Thaumastodermatinae (Ruppert 1978). With these premises it appears clear that in *Cephalodasys*/*Psammodasys* what is called a seminal receptacle actually is the frontal organ, a structure female in function, whereas the "bourse copulatrice" corresponds to the caudal organ (penis). Although in all the species in which a bursa has been reported it has been considered part of the female sexual apparatus, and in *C. caudatus* Rao, 1981 the author clearly stated that the species lacks a penis (see Rao, 1981, not 1961, as mistakenly reported in d'Hondt & Balsamo, 2009). That said, it is obvious that the two organs (frontal and caudal organs =seminal receptacle and "bourse copulatrice"), even when they appear to be next to each other, cannot have their lumina in anatomical continuity; consequently, it is functionally irrelevant whether these organs are topographically separated or adjacent to each other. Therefore, in our opinion the establishment of a genus (i.e. *Psammodasys*) to allocate species with characteristics of *Cephalodasys* but having caudal and frontal organ topographically separated appears not to be justified. Our position is strengthened by knowing that, within the genus, several species for which only the frontal organ is reported (e.g. *C. pacificus* and *C. palavensis*) and species which seem to be parthenogenetic (e.g., *C. hadrosomus*) provide a complex situation, which is matched within the Macrodasysida by the genus *Urodasys*]

Type-species *Cephalodasys maximus* Remane, 1926b:681

Cephalodasys cambriensis (Boaden, 1963a):404

is a subadult of about 190 µm in length of the body, or mid-way between the adult and the subadult of the Hummon (2009b) figure, with cephalic appendages midway between those of the two specimens; we thus consider 'brevis' to be a developmental stage of *D. cornuta* and reject 'brevis' as referring to any distinct infraspecific category or species taxon]

Dactylopodola indica (Rao & Ganapati, 1968):45

Syn. *Dactylopodalia indica* Rao & Ganapati, 1968:45 [d'Hondt, 1971b:164]

Dactylopodola mesotyphle Hummon, Todaro, Tongiorgi & Balsamo, 1998:109

Dactylopodola roscovita (Swedmark, 1967):325

Syn. *Dactylopodalia roscovita* Swedmark, 1967:325 [d'Hondt, 1971b:164]

Dactylopodola typhle (Remane, 1927):213 [Strand, 1929:5]

Syn. *Dactylopodella typhle* Remane, 1927:213 [Strand, 1929:5]

Syn. *Dactylopodalia typhle* (Remane, 1927):213 [Blake, 1933:606]

Dactylopodola weilli (d'Hondt, 1965:6) [Luporini, Magagnini & Tongiorgi, 1970:15 considered this species to be a junior synonym of *D. typhle*; the synonym was rejected by Kisielewski 1987:847, the species listed as *Dactylopodola weilli* (d'Hondt, 1965):6; the synonym was then reinstated by Todaro, Balsamo & Tongiorgi, 1992:473. Recently the synonym has been rejected once again by d'Hondt & Balsamo 2009:271, and though the latter authors do not bring any new evidence to sustain their statement, they reiterate as discriminatory traits between the two species features whose taxonomic unreliability has already been discussed by authors favorable to the synonymy. Recent DIC micrographs and drawings by Kinieke *et al.* (2008: Figs. 1, 4) of *D. typhle*, collected near the type locality, show a different arrangement of the anterior and lateral adhesive tubes than those shown by Remane, 1927: Fig. 6; indeed, the head shape and anterior adhesive tubes of putative *D. weilli* specimens studied by Kisielewski (1987) differ from those reported for the typical *D. weilli* studied by d'Hondt (1965), both from Bassin d'Arcachon. Neither d'Hondt or Kisielewski have reported seeing *D. typhle*; nor has any other worker ever reported seeing the presumptive *D. weilli*, suggesting that further work needs to be carried out before the status of *D. weilli* can be ascertained. This would include investigation of both type locales, and inclusion of other traits such as anatomy of the reproductive system. In the meantime, it is preferable to treat *D. weilli* as a *species inquirenda*]

Genus *Dendrodasys* Wilke, 1954:507

Type-species *Dendrodasys gracilis* Wilke, 1954:507

Dendrodasys affinis Wilke, 1954:511 *sensu* Hummon, Todaro, Tongiorgi & Balsamo, 1998:112

Dendrodasys pacificus Schmidt, 1974:31

Dendrodasys ponticus Valkanov, 1957:385

Genus *Dendropodola* Hummon, Todaro & Tongiorgi, 1993:111

Type-species *Dendropodola transitionalis* Hummon, Todaro & Tongiorgi, 1993:111

Family Lepidodasyidae Remane, 1927d:41—**Emended family**—Includes 1 genus and 5 species [Emended in this publication; the data have already been published and there is a consensus among workers that a major source of polyphyly in the family lies in the difference between *Lepidodasys* and the remaining constituents of the former family Lepidodasyidae; thus it only remains to make the formal taxonomic separation. The reasons for separating *Lepidodasys* from the others are contained in the respective diagnoses.

Lepidodasyidae emended diagnosis, modified from Ruppert, 1978a

Elongate Macrodasysida, most nearly circular in transverse section, with small, nearly terminal mouth opening and no head delimitation. Cuticle elaborated as flat-scales, ribbed-scales or hat-shaped scales, often organized in crossed helical patterns. Multiciliated epidermal cells; ventral cilia in two longitudinal rows, often partially reduced. Epidermal glands with granular or fibrous inclusions, sometimes extremely

well developed. Anterior adhesive tubes (TbA) in two groups or a semicircle behind the mouth; lateral, dorsolateral and ventrolateral adhesive tubes (TbL/TbDL/TbVL) arranged in columns along the body; posterior adhesive tubes (TbP) arranged marginally around the blunt posterior end. Sphincter muscle developed around mouth opening; powerfully developed radial pharyngeal musculature; lacking striations; pharyngeal pores absent. Circular muscles absent from lateral regions of the body. Y-cells contain myofilaments. Gonads paired; male anterior, female posterior; male gametes mature posterior to anterior, female gametes posterior to anterior; ova enter the central body region, dorsal to the gut, immediately anterior to the seminal receptacle. Male pores paired or single, located anterior to the caudal organ, where present; caudal organ with two canals sharing common ventral opening in front of the anus; one weakly developed canal leads into the seminal receptacle; the other is a blind, glandulomuscular sac. An oviduct is present. Mostly subtidal in distribution; fine to coarse sand.

Type-Genus *Lepidodasys* Remane, 1926b:684

Type-species *Lepidodasys martini* Remane, 1926b:684

Lepidodasys arcolepis Clausen, 2004b:428

Lepidodasys castoroides Clausen, 2004b:431

Lepidodasys platyurus Remane, 1927c:209

Lepidodasys unicarenotus Balsamo, Fregni & Tongiorgi, 1994:218

Family Macrodasysidae Remane, 1926b:723—Includes 2 genera and 43 species

Type-Genus *Macrodasys* Remane, 1924:290

Type-species *Macrodasys buddenbrocki* Remane, 1924:290

Macrodasys achradocytalis Evans, 1994:243

Macrodasys acrosorus Hummon & Todaro, 2009:50

Macrodasys affinis Remane, 1936:169

Macrodasys africanus Remane, 1950:35

Macrodasys africanus ssp. *ponticus* Valkanov, 1957:389 [In this publication. The trinomial was described as a variety (*Macrodasys africanus* var. *ponticus*), but with the date coming before 1960, and not being proposed as an infrasubspecific category, it must be treated as a subspecies (ICZN 45.6.4)]

Macrodasys ancocytalis Evans, 1994:240

Macrodasys andamanensis Rao, 1993:26

Macrodasys balticus Roszczak, 1939:6 [This species thus far has been found only in brackish-waters]

Macrodasys blysocytalis Evans, 1994:250

Macrodasys caudatus Remane, 1927:204

Macrodasys celticus Hummon, 2008b:128

Macrodasys cephalatus Remane, 1927c:206

Macrodasys cunctatus Wieser, 1957:374

Macrodasys deltocytalis Evans, 1994:245

Macrodasys digronus Hummon & Todaro, 2009:51

Macrodasys dolichocytalis Evans, 1994:248

Macrodasys fornerisae Todaro & Rocha, 2004:1619 [Change of gender ending from *M. fornerise* to *M. fornerisae*, in this publication (ICZN 34.2)]

Macrodasys gerlachi Papi, 1957:179

Macrodasys hexadactylis Rao, 1970:109

Macrodasys indicus Kutty & Nair, 1969:632 [The proper name is *M. indicus*, as in the text, and not *M. idicus*, as occurs in Fig. 7; this is as determined by the first reviser, Hummon, 2008b:127 (ICZN 24.2.2), where its morphological relationships were discussed; however, the information available is insufficient for reliable identification of the species; therefore we consider the taxon to be a *species inquirenda*]