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Source: Zoological Science, 19(10) : 1175-1180

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.19.1175>

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Comments on the Taxonomic Status of *Ikeda taenioides* (Ikeda, 1904) with Some Amendments in the Classification of the Phylum Echiura

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ABSTRACT—Examination of thin sections of trunk wall in an old specimen of *Ikeda taenioides* from Misaki, Sagami Bay revised previous false information about the wall musculature, actually consisting of outer circular, middle longitudinal, and inner-most oblique layers, like all other echiurans. This finding, together with the reexamination of relevant museum specimens, led to some taxonomic changes. These include that the definition of the genus *Ikeda* was amended to be a senior synonym of *Prashadus*; the family Ikedidae was regarded as a junior synonym of the family Echiuridae; and the order Heteromyota, erected virtually for *I. taenioides*, was abolished. Non-discovery of males and some other features in the amended genus *Ikeda* were noted with reference to its possible relationship with the family Bonelliidae.

Key words: Echiura, Taxonomic revision, *Ikeda taenioides*, *Prashadus*, Abolishment of order Heteromyota

INTRODUCTION

The phylum Echiura, if this taxonomic rank is accepted in spite of current influential objections (e.g., McHugh, 1997, Nielsen, 2001; but also see Rouse and Fauchald, 1998), is usually classified into the 3 orders, Echiuroinea Bock, 1942 (with the 2 families Echiuridae Quatregages, 1847 and Bonelliidae Lacaze-Duthiers, 1858 having many genera and species), Xenopneusta Fisher, 1946 (with one family Urechidae Monro, 1927 comprising only 4 species of the genus *Urechis*), and Heteromyota Fisher, 1946 (with one family Ikedidae Bock, 1942 with a single named species shown below) (see Stephen and Edmonds, 1972, Edmonds, 2000; for objections see DattaGupta, 1976, DattaGupta and Menon, 1976; and for family names and authorships see Nishikawa, 1998). Saxena (1983) established a new order Bonelloinea only for the family Bonelliidae, although this classification has not been subsequently followed.

The order Heteromyota was “based on the remarkable genus *Ikeda* Wharton, 1913 ...[with its] Type, *Thalassema taenioides* Ikeda, 1904”, because “the arrangement of muscle layers is different from that of all other echiuroids [=echiurans] and indicates a long separation from typical stock” (Fisher, 1946, p. 220). That is, in *Ikeda taenioides* (Ikeda, 1904) the “longitudinal [muscle] layer of body wall lying out-

side of both the circular layer and inner oblique layer, while in all the other echiuroids [=echiurans] the longitudinal layer lying between outer circular layer and inner oblique layer” (Fisher, 1946, p. 220). Nomenclatural problems and proposals regarding *I. taenioides* were presented elsewhere (Nishikawa, 2001).

This order has generally been recognized valid (see, e.g., Nishikawa, 1992, Pilger, 1993, McKenzie and Hughes, 1999, Edmonds, 2000; for silent objections see DattaGupta, 1976, DattaGupta and Menon, 1976). Soft-bodied worms such as nemerteans, annelids, sipunculans, and even echiurans usually have outer circular and inner longitudinal muscle layers below the epidermis (see, e.g., Fretter and Graham, 1976). Therefore, the mentioned peculiar arrangement, if actually present, might merit such a high taxonomic category as an order in the Phylum Echiura.

Current tendencies to claim the lowering of taxonomic rank of echiurans urged me to reexamine the actual nature of the peculiar arrangement. Although failing to examine the name-bearing types which appear to be lost and the newly collected specimens, I fortunately found the museum specimens referable to *I. taenioides* collected about 100 years ago from the type locality (Misaki, Sagami Bay). Here I give a result of detailed observations on trunk wall structure of these specimens, as well as the specimens of *Ikeda* sp. described by Edmonds (1987) without any references to the muscular arrangement, and *Prashadus pirotansis* (Menon and DattaGupta, 1962) of the family Echiuridae, similar to *I. taenioides* if putting the arrangement aside.

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In the present study, I am adopting the echiuran terminology given by DattaGupta and Singh (1976) and Saxena (1983), “gonoduct” and “gonostome”, instead of “nephridium” and “nephrostome”, respectively, because “an excretory function — has not been demonstrated” for the organ historically called nephridium (Pilger, 1993, p. 226). This organ works only for collecting ripe gametes (through the gonostome) from the coelomic fluid and storing them until spawning through the gonopore (see Pilger, 1993).

MATERIALS

Ikeda taenioides Among the echiuran collection of 17 bottles in UMUT (=The University Museum, University of Tokyo), the 4 bottles, UMUTZ-Ecur-1, -8, -9, -12 were referable to *Ikeda taenioides*; of these, only the UMUTZ-Ecur-1 was good for detailed examination of internal structure. This material, labeled “*Thalassema halotan.*, Dec. 24th, 1901, Moroiso”, consisted of 3 fragments (#1–#3), with #1 and #2 coming probably from an individual; a small piece of posterior-most part of the fragment #2 was cut off with permission of UMUT for serial thin sections so as to include relevant part of ventral nerve cord.

According to Ikeda (1907, p. 18), *T. taenioides* Ikeda, 1904 was established for “six specimens” collected “during October and November 1901” in the inlet of Moroiso, Misaki, Sagami Bay. Although collected from Moroiso, the UMUTZ-Ecur-1 material cannot be allotted to any of the 6 syntypes, because the former was collected in December (see above). The second part of the label name “*Thalassema halotan.*” of Echiura-1 obviously represents the abbreviation of *halota[n]ia* which is an earlier unused name proposed by Ikeda (1901) and is to be suppressed for conservation of currently used binomen *I. taenioides* (see Nishikawa 2001). Therefore, the material was probably identified by Iwaji Ikeda himself just after its collection in December, 1901.

Ikeda. sp. SAM (=South Australian Museum) E-1509, “*Ikeda sp.*”, St. Vincent Gulf, South Australia, 9–10 m deep, described as *Ikeda sp.* by Edmonds (1987, pp. 135–136), an incomplete individual having 10 mm basal part of proboscis and 330 mm incomplete trunk (posterior part missing). With permission of SAM, a small piece of trunk wall was cut off for serial thin sections so as to include relevant part of ventral nerve cord.

Prashadus pirotansis NMS (=National Museums of Scotland) 1967.32, labeled as “*Ikedosoma pirotansis* Menon and DattaGupta 1962, Pirotan Island (Gulf of Kutch), Oct. 1965, coll. by P. K. B. Menon, Topotype”, 2 inds; only the larger ca. 150 mm one was examined. (Another specimen registered as NMS 1974.48.1, collected from Pirotan Island, was too damaged to examine.); these two materials were referred to, though not described, by Hughes and Crisp (1976). “The holotype is deposited in the Museum of the Zoology Department of Birla College” (Menon and DattaGupta, 1962, p. 307) until 1973 (K. R. Chandhoke, person. comm.), but since then the whereabouts remained unknown.

RESULTS

Ikeda taenioides

In the specimen composed of the fragments #1 and #2 of UMUTZ-Ecur-1, the incomplete proboscis is 140 mm long and the incomplete trunk is 650 mm long; interbasal muscle is present between a pair of ventral setae; ca. 45 mm long region of anterior part of trunk is furnished with a great number of gonoducts (containing eggs) arranged very crowd-

edly, their exact number is uncountable due to injury; undamaged gonoducts are tubular in shape, each with a gonostome situated distally. The large body size and a great number of gonoducts with distally situated gonostomes are consistent with the original and supplementary descriptions of *Ikeda taenioides* given by Ikeda (1904, 1907) which show that the trunk reaches 40 cm long with up to 150 cm long proboscis and that the number of gonoducts is ca. 200–400 in total. Trunk musculature consists of outer circular, middle longitudinal, and inner-most thin oblique layers (Fig. 1A–C), unlike the detailed description of name-bearing types given by Ikeda (1907) as shown below. Ikeda (1904, 1907) noted the five narrow externally visible longitudinal lines due to the special thickenings of the continuous, non-fasciculate sheet of longitudinal muscle. This was confirmed by my observation of thin sections (Fig. 1B–C).

Ikeda species from Australia

Additional notes to the description given by Edmonds (1987) are as follows. The trunk wall musculature consists of outer-most circular, middle longitudinal, and inner-most thin oblique layers (Fig. 1D–E); interbasal muscle is indiscernible due to heavy damage to setal region; a certain number of gonoducts missing due to injury, and the number of remaining ones is ca. 50 on the left side and ca. 40 on the right, crowdedly arranged roughly in a row along each side of ventral nerve cord; the gonostome is situated distally at the top of distal elongation of each gonoduct. According to Edmonds’ (1987) description, the “longitudinal musculature grouped in 5 bands prominent externally” (p. 136). My reexamination also recognized the 6 (instead of 5) longitudinal lines recognizable externally in the trunk wall, irrelevant to the presence or absence of epidermal papillae. These “lines” are represented by very obscure thickenings of longitudinal muscle layers (Fig. 1D, arrows). Longitudinal musculature comprises a continuous sheet of nearly the same thickness throughout trunk’s contour, instead of being fasciculated. Anal vesicles are unknown due to lack of posterior end of trunk.

Prashadus pirotansis

The examined specimen with 30 mm long proboscis and 120 mm long trunk, was compared well with the original description of this species given by Menon and DattaGupta (1962) and the subsequent one by Hughes and Crisp (1976). Trunk wall musculature is composed of outer circular, middle longitudinal, and inner-most thin oblique layers; the longitudinal muscle layer is much thicker than the circular one. Each of the 3 layers is continuous, without any thickenings. The interbasal muscle is present as described by DattaGupta and Menon (1976) and Hughes and Crisp (1976). Gonoducts are at least 20 in total number (probably lacking posterior ones due to injury), arranged roughly in pairs on each side of ventral nerve cord, and full of eggs; wall of gonoducts is very thin and fragile. The gonostome is situated at the top of distal elongation of each gonoduct. A

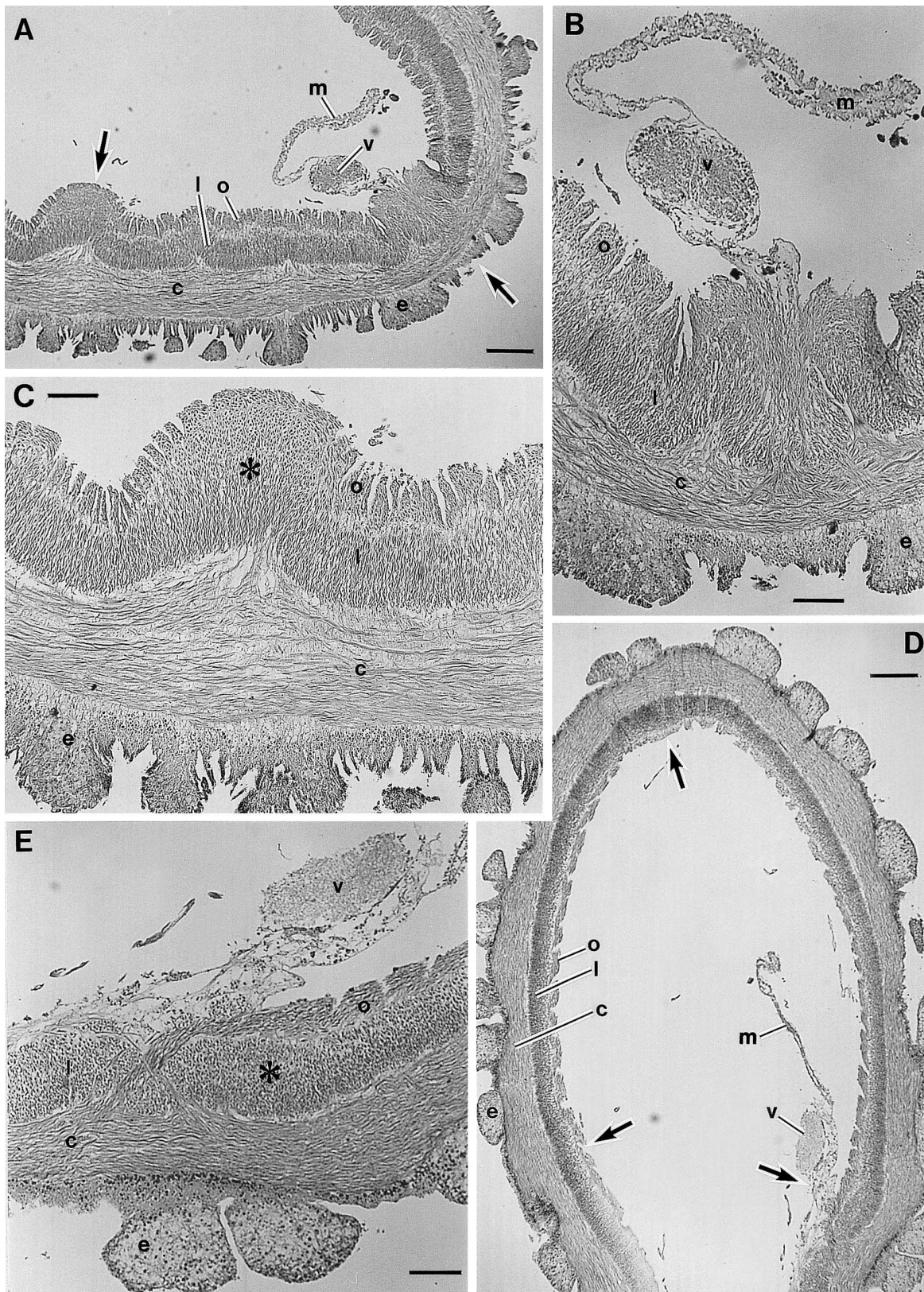


Fig. 1. Transverse section of trunk wall. A–C: *Ikeda taenioides* from Misaki, Sagami Bay (UMUTZ-Ecur-1). D–E: *Ikeda* species sensu Edmonds (1987) from South Australia (SAM E-1509). B and E, enlargement of mid-ventral part in A and D, respectively; C, enlargement of a thickened part of the wall situated ventro-laterally in A. c, circular muscle layer; e, epidermal papilla; l, longitudinal muscle layer; m, mesentery and ventral vessel; o, oblique muscle layer; v, ventral nerve cord. Arrows indicate longitudinal lines seen from the trunk surface, probably corresponding to the thickenings (*) of longitudinal muscle layers. Scales for A and D indicating 250 μ m, for B, C, and E 100 μ m

pair of anal vesicles are densely furnished over the surface with much elongated tubules as shown by Menon and DattaGupta (1962, fig. 3).

DISCUSSION

Trunk wall musculature in *Ikeda taenioides*

Ikeda's (1904) original description lacks information about the arrangement of circular, longitudinal, and oblique muscle layers. However, according to Ikeda's (1907) supplementary descriptions of name-bearing types, "the strongly developed muscular layer is of the usual composition, consisting, as it does, of the longitudinal (fig. 26, l. m.), the circular (c. m.) and the oblique systems." (p. 24). The mentioned figure 26 of plate 3, representing "a transverse section" according to his explanation of the figure, clearly shows the peripheral position of longitudinal layer in relation to the circular one. The present reexamination of the specimen from the type locality and identified as "*Thalassema halotan*." (= *I. taenioides*) by its author Ikeda himself shows that the trunk musculature is really "of the usual composition", comprised of outer circular, middle longitudinal, and inner-most oblique layers. His figure 26 may well have come from a longitudinal, not transverse section. Thus, *Ikeda taenioides* is the same as the remaining echiurans with regards to the trunk wall musculature.

Then, *I. taenioides* can be compared with echiurans having many gonoducts with gonostomes situated distally, that is, *Ikeda* species sensu Edmonds (1987) and *Prashadus pirotansis*, the latter belonging to the family Echiuridae of the order Echiuroinea. Judging from previous relevant descriptions and my actual examinations of specimens, the former (*Ikeda* species) is similar to *I. taenioides* in the giant body size, the existence of interbasal muscles and the narrow longitudinal lines (due to thickenings of continuous, non-fasciculate longitudinal muscle layers), the trunk musculature, and the great number of gonoducts. The latter species is referred to below.

Considerations on *Prashadus pirotansis*

Ikedosoma pirotansis Menon and DattaGupta, 1962 was established for the holotype and 2 paratypes of a large echiuran (74 cm or longer in preserved state, including proboscis) with long proboscis in living and 20 pairs of gonoducts, collected from the intertidal muddy flat in Pirotan Island, Gulf of Kutch, India. The large body size with elongated proboscis and the distal position of gonostomes in *I. pirotansis* are highly reminiscent of *Ikeda taenioides*; however, the original description lacked any information about the trunk wall musculature. Stephen and Edmonds (1972) erected a new genus *Prashadus* for *Ikedosoma pirotansis* on the ground that "this genus is unique in the family Echiuridae on account of the distal position of its nephrostome [=gonostome]" (Stephen and Edmonds, 1972, p. 463). Another genus *Rubricelatus* was erected also for *Ikedosoma pirotansis* by DattaGupta and Menon (1976). This genus can

clearly be regarded as a junior objective synonym of the genus *Prashadus*.

Based on thin sections of their material of *Rubricelatus pirotansis* [= *Prashadus pirotansis*], DattaGupta and Menon (1976) claimed the normal arrangement of body wall musculature (consisting of outer circular, middle longitudinal, and inner-most oblique layers) and the continuous texture of longitudinal muscle layer. Further, Hughes and Crisp (1976) gave a detailed description of *P. pirotansis* for newly collected specimens from the Arabian Gulf, which revealed also the normal arrangement of body wall musculature, the continuous texture of each layer, and the occurrence of "15 to 30 nephridia [=gonoducts] on each side; (p. 237) arranged almost always in pairs. In the present study the type series was unavailable, but I could examine a specimen identified as *I. pirotansis* by Menon, one of the authors, and confirmed the normal arrangement of the musculature, the continuous texture in each muscle layer, and the presence of at least 20 gonoducts in total.

Amalgamation of the genera *Ikeda* and *Prashadus*

As shown above, *Ikeda taenioides* and *Prashadus pirotansis* are distinguishable from each other only by the differences in the number of gonoducts (200–400 in total in the former, instead of up to 30 on either side in the latter) and in the thickenings of non-fasciculate longitudinal muscle layer recognizable as longitudinal lines on the outer surface of the trunk (present in the former, absent in the latter). These differences don't seem to merit a generic distinction, if taking all the genera of the family Echiuridae into account. The genus *Prashadus* is regarded here as a junior synonym of the genus *Ikeda* with its amended description as follows:

Genus *Ikeda* Wharton, 1913

Ikeda Wharton, 1913, p. 261 (type species by monotypy: *Thalassema taenioides* Ikeda, 1904)

Prashadus Stephen and Edmonds, 1972, pp. 462–463 (type species by original designation: *Ikedosoma pirotansis* Menon and DattaGupta, 1962)

Rubricelatus DattaGupta and Menon, 1976, pp. 137–138 (type species by original designation: *Ikedosoma pirotansis* Menon and DattaGupta, 1962)

Diagnosis (amended in the present study): Echiurans of the family Echiuridae, having the elongated, simple proboscis; the trunk musculature of normal composition (consisting of outer circular, middle longitudinal, and inner-most oblique layers); all the 3 layers as continuous, non-fasciculate sheets; a few longitudinal thickenings of longitudinal muscle layer present or absent; the interbasal muscle present; many (up to 200–400 in total) gonoducts along ventral nerve cord; and the gonostome located distally.

Remarks: This genus is unique among the echiurans of the family Echiuridae in the distal position of gonostomes. A large number of gonoducts may be reminiscent of other echiurid genera *Ochetostoma* (up to 7 pairs) and *Ikedosoma* (3–8 groups each of 1–4 gonoducts on each side), but the

gonostomes in these genera are situated basally. *Ikeda* species sensu Edmonds (1987) obviously fits well with the amended definition of the genus *Ikeda*, having an intermediate number of gonoducts (at least ca. 90 in total) between *I. pirotansis* (30 or more) and *I. taenioides* (200–400). An antarctic specimen referred to as *Prashadus* species by Saiz-Salinas (1996) can also be included in *Ikeda*; the specimen is distinguishable from the congeners by its smaller number of gonoducts (10 in total).

Species included: *Ikeda taenioides* (Ikeda, 1904) so far recorded from Japanese coasts, intertidal to ca. 10 m (Ikeda, 1904, 1907, Sato, 1931); *Ikeda pirotansis* (Menon and DattaGupta, 1962) from Indian coasts, intertidal (Menon and DattaGupta, 1962, DattaGupta *et al.*, 1963, DattaGupta and Menon, 1976, Halder, 1981) and Arabian Gulf, intertidal (Hughes and Crisp, 1976); *Ikeda* species from South Australia, 9–10 m (Edmonds, 1987); *Ikeda* species from the Antarctic, 99 m deep (as *Prashadus* sp., Saiz-Salinas, 1996).

Accompanying taxonomic changes

The following taxonomic amendments are proposed here: the family Ikedidae Bock, 1942 (the type genus by monotypy: *Ikeda* Wharton, 1913) is regarded as a junior synonym of the family Echiuridae Quatrefages, 1847 (the type genus: *Echiurus* Guérin-Méneville, 1831) of the order Echiuroinea Bock, 1942; and the order Heteromyota Fisher, 1946 is abolished.

Thus, the phylum Echiura consists of the two orders, Echiuroinea Bock, 1942 (with the 2 families Echiuridae and Bonelliidae) and Xenopneusta Fisher, 1946 (with one family Urechidae).

Suggestions on phylogenetic position of *Ikeda*

All the informative specimens of the genus *Ikeda* were females, with eggs included in the gonoducts: i.e., in *I. taenioides*, Ikeda's (1904, 1907) 6 specimens, as well as another specimen in the present material; in *I. pirotansis*, Menon and DattaGupta's (1962) 3 specimens and Hughes and Crisp's (1976) 8 specimens; in *Ikeda* species sensu Edmonds (1987), one specimen; and in *Ikeda* species sensu Saiz-Salinas (1996), one specimen. Non-discovery of males in the genus *Ikeda* may naturally give rise to such a question that the genus be a member of the family Bonelliidae with a remarkable sexual dimorphism represented by the dwarf males.

Another similarity between *Ikeda* and bonelliids concerns the position of gonostomes. Actually, many bonelliid genera (such as *Vitjazema*, *Biporus*, *Pseudobonellia*, *Bonelliopsis*, *Metabonellia*, *Eubonellia*, *Ikedella*, *Dattaguptus*, and *Charcotus*) have distally-situated gonostomes, while the only genus showing this attribute in the echiurids is *Ikeda*. Furthermore, in *I. taenioides*, according to Ikeda (1907, p. 35), the tubules over anal vesicles are "either simple or are divided into 2–5 branches". Also in *Ikeda* species sensu Saiz-Salinas (1996), the anal vesicles bear "several primary branches at irregular intervals" (p. 367). These are highly

reminiscent of "usually branching, dendritic or arborescent" anal vesicles in bonelliid females (Stephen and Edmonds, 1972, p. 354).

On the other hand, bonelliid females have only "one or two (rarely three)" gonoducts (loc. cit.), in which the genus *Ikeda* (with 10 or far more gonoducts) is markedly different from the bonelliids. Eventually, comprehensive molecular and morphological analyses of a broad range of echiurans including *Ikeda* and some bonelliid specimens (together with relevant annelids) will give us a new perspective on the evolution and phylogenetic significance of such reproductive attributes as the sexual dimorphism with dwarf males and the existence of many gonoducts with distally-situated gonostomes.

ACKNOWLEDGEMENTS

I would like to express my cordial gratitude to Prof. E. B. Cutler of Harvard University for critical reading of the manuscript, and to Drs. G. Murina of the Ukrainian Academy of Science, R. Biseswar of the University of Durban-Westville, J. I. Saiz-Salinas of the Universidad del Pais Vasco, J. Staton of the University of South Carolina, and an anonymous referee for improving the manuscript, and to Ms. M. Nozaki and Ms. M. Iritani of Nagoya University for thin sections. Sincere thanks are also due to Dr. R. Ueshima of the University of Tokyo, Dr. F. Ware of National Museums of Scotland, Dr. T. Laperousaz of South Australian Museum, for the loan of specimens with the permission to dissect and/or make thin sections, to Dr. T. Sato of the University of Tokyo and Dr. K. Torigoe of Hiroshima University for information about the name-bearing types of *Ikeda taenioides*, and to Dr. K. R. Chandhoke of Birla Institute of Technology and Science for information about the holotype of *Prashadus pirotansis*. The present study was supported partly by a Grant-in-Aid for University and Society Collaboration of MEXT (No. 12794018; headed by Dr. M. Morisawa).

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(Received December 28, 2001 / Accepted August 9, 2002)