THE SYSTEMATICS AND DISTRIBUTION OF ABYSSAL AND HADAL (ULTRA-ABYSSAL) ECHIUROIDEA

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INTRODUCTION

Material and methods

The Echiuroidea are a group of marine animals which are highly responsive to methods of fixation. In the greater number of cases they have exceedingly thin body walls and very fine walls in the intestine, which is usually packed with a great amount of heavy bottom material. However, notwithstanding the fact that the body walls are thin, fixative solutions penetrate poorly into the body.

Owing to these peculiar features the Echiuroidea demand rapid and special fixation, especially when they are collected in a hot climate. Immediately after a sample has been brought onto the deck, any echiuroids present ought to be fixed without delay. The fixation procedure should be carried out in two stages: first the animal should be submerged in the fixative, and secondly, after its submersion, a small amount of 10% formalin should be injected into the body cavity with the aid of a syringe.

Aboard the "Galathea" these precautions had not been observed, and hence, the greater part of the obtained echiuroid material has been impaired. In some samples the inner organs have been totally destroyed, as is the case with the most interesting new form *Bruunellia*. The intestines and the vascular system were totally destroyed in all the examined specimens and the anal glands were preserved in only a few cases. The interior of one of the *Bruunellia* specimens was completely decomposed, and even with a series of histological sections it has been impossible to reconstruct the inner organization of the animal. The nephridia proved to be best preserved.

The above-mentioned factors have considerably devalued this investigation of a most important deep-sea fauna material, and hence, the descriptions lack completeness, accuracy and detailed treatment. However, because so little is known about deep-sea echiuroids, this paper is presented in the hope that it may be useful to those working with deep-sea fauna.

The present material is comprised of 65 specimens (and many fragments) collected at 14 abyssal and hadal (ultra-abyssal) stations (Fig. 1). It is kept in the Zoological Museum, Copenhagen; some duplicate specimens are in the Institute of Oceanology, Moscow.

The "Galathea" material from sublittoral depths is dealt with elsewhere (ZENKEVITCH 1966).

Acknowledgments

It is with the feeling of profound respect and gratitude that I recollect the name of the late Dr. ANTON

BRUUN who so kindly loaned me the material collected by the famous Galathea Expedition. It is a great honour to participate in the treatment of the material collected by that renowned ship.

I wish to extend my thanks to Dr. TORBEN WOLFF for his friendly assistance and help showed in the preparation of this paper and to Dr. ANATOLY SAVILOV for making the drawings.

List of "Galathea" Stations with Echiuroidea

St.	Position	Depth (metres)	Echiuroids
52	1°42′N, 7°51′E	2550	*Alomasoma* sp.
66	4°00′S, 8°25′E	4020	*Choanostoma* sp.
194	34°09′S, 30°45′E	4360	*Choanostoma ?bruuni* Zenkevitch
232	9°03′S, 49°22′E	4930	*Choanostoma ?bruuni* Zenkevitch
419	10°19′N, 126°39′E	10.150-10.210	*Vitjazema* sp.
471	10°26′S, 114°15′E	2780	*Alomasoma* sp.
495	5°26′S, 130°58′E	7290-7250	*Bruunellia bandae* n. gen., n. sp.
574	39°45′S, 159°39′E	4670	*Alomasoma* sp.; *Bonellia achaeta* Zenkevitch
601	45°51′S, 164°32′E	4400	*Bonellia achaeta* Zenkevitch
649	35°16′S, 178°40′W	8210-8300	*Torbenwolffia galatheae* n. gen., n. sp.
651	32°10′S, 177°14′W	6960-7000	*Torbenwolffia galatheae* n. gen., n. sp.
654	32°10′S, 175°54′W	5850-5900	*Torbenwolffia galatheae* n. gen., n. sp.
658	35°51′S, 178°31′W	6660-6770	*Torbenwolffia galatheae* n. gen., n. sp.
664	36°34′S, 178°57′W	4540	*Jakobia sp.*
726	5°49′N, 78°52′W	3670-3270	*Jakobia* sp.; *Alomasoma belyaevi* Zenkevitch

SYSTEMATIC PART

It is known that some investigators regard Echiuroidea as a class and others as a phylum. The systematics of this group is inadequately developed and requires fundamental revision. The problem is most confused when one deals with generic and specific definitions.

The author regards Echiuroidea as a class with one order, Echiuroinea, and finds it proper to single out three families within this order: Echiuridae, Thalassematidae and Bonelliidae; in other words, I find it appropriate to follow the system suggested by SIXTEN BOCK (1942). The three families are easily told apart: Echiuridae are distinguished by the presence of anal setae; Thalassematidae by one to seven pairs of nephridia, with the extended edges of nephrostomes twisted in a spiral fashion; and finally, Bonelliidae by one pair or, more frequently, merely by a single nephridium with a simple nephrostome, as well as by sexual dimorphism.

As to the subdivision of representatives of the Bonelliidae into genera and species, one is confronted with considerable difficulties and obscurity, and new species have often been described on the basis of specimens with a poorly preserved proboscis, or ones with a proboscis lacking the anterior end or even on ones where the entire proboscis is missing. For example, in FISHER's (1946) description of the new genus *Prometor* he emphasized that the proboscis is characterized as short and straight, whereas in reality its anterior end was torn off. This fact served as a basis for the description of a new genus *Tatjanellia* (Zenkevitch 1957), which was considered related to the genus *Prometor,* as was also noted by HARTMAN & BARNARD (1960).

The vascular system, which appears to be a very convenient systematic feature, as a rule undergoes total destruction. Of the external characters which could be used for the description of genera and species it is worthwhile to mention first the shape of the proboscis, the presence of a bilobate or simple proboscis terminal, its taeniate or rounded shape in section, and the presence of a special cup or a whole collar at the proboscis base; the presence or absence of ventral setae; and finally, the presence of one or two nephridiopores. As to internal organs the following characters ought to be regarded of systematic significance: the number of nephridia (one, two or numerous), their shape and placement of nephrostomes in the nephridium (terminal or basal); the structure of anal glands, their shape and branching; and possibly, to a greater extent, the structure of the vascular system which, however, is almost never preserved.

The most reliable character is the structure of the

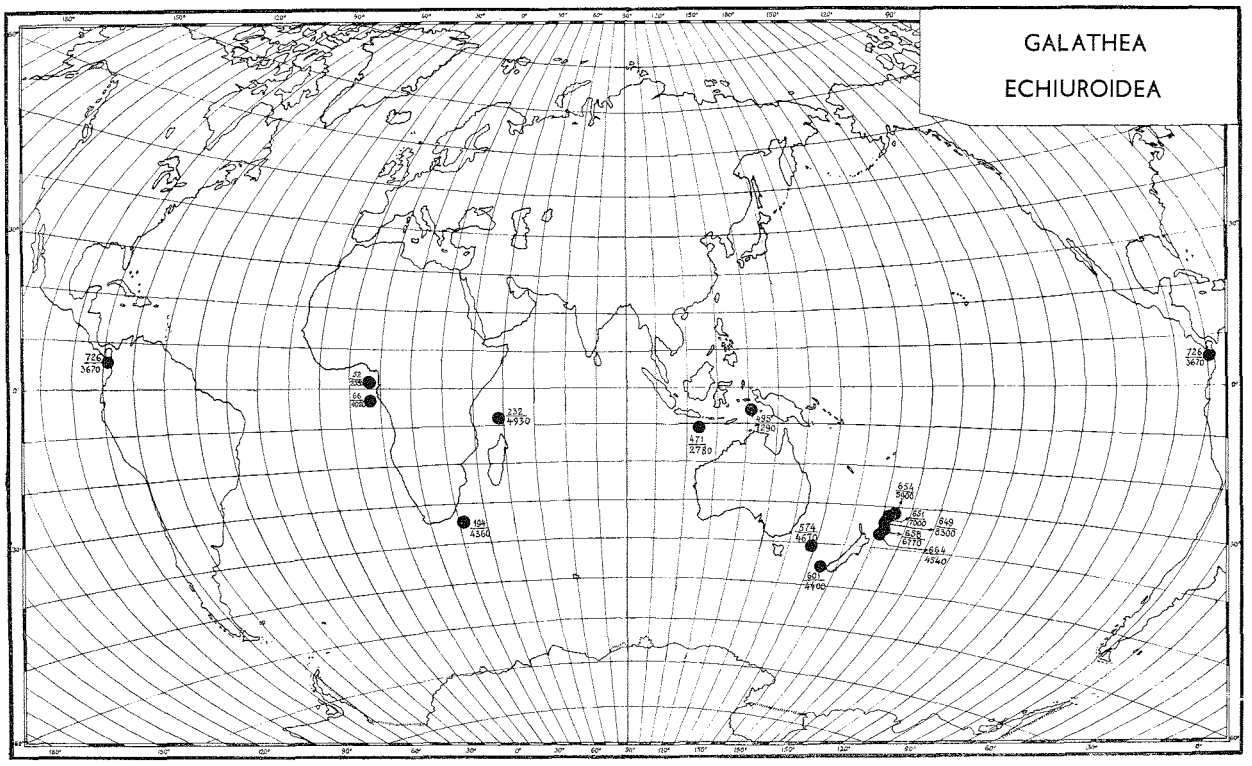

Fig. 1. Map of "Galathea" stations where echiuroid material was collected. Nominator: station number; denominator: depth.

proboscis, but, unfortunately, this is not usually completely preserved. As to the setae and nephridia, their variability fails to be of systematic importance. SLUITER (1902) emphasizes that in *Hamingia arctica* collected near Spitsbergen – and the author had an ample number of this species – equal numbers of specimens had two and one nephridia. Thus, the same species exhibits a variation in number of nephridia.

The abyssal material of Bonelliidae collected by "Galathea" and later by "Vityaz" does not permit the revision of the family system and the author is thus forced to restrict this paper to a mere description of new forms.

Family BONELLIIDAE (Baird, 1868)

Genus *Alomasoma* Zenkevitch, 1958

Alomasoma belyaevi Zenkevitch, 1964

Material:

St. 726, Gulf of Panama (5°49′N, 78°52′W), 3670-3270 m, 13.5.1952. Bottom: clay. Bottom temp.: *c.* 2.0°C. – 1 specimen.

According to all of its characters this worm coincides with the form described by me (ZENKEVITCH 1964a) from material collected by "Vityaz" in the area of 44°53.8′N and 128°32.1′W, and also in the eastern Pacific, close to Northern America, and further north than the "Galathea" record.

Alomasoma sp. No. 1

(Fig. 2).

Material:

St. 52, San Tomé – Cameroon (1°42′N, 7°51′E), 2550 m, 30.11.1950. Bottom: muddy clay. Bottom temp.: *c.* 3.0°C. – 2 specimens.

The lengths of the two specimens are 25 and 46 mm. In both, the proboscis is missing. The specimens have ventral setae. All the internal organs are de-

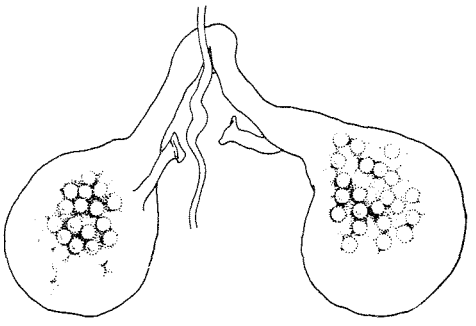

Fig. 2. *Alomasoma* sp. from St. 52. Nephridia (×8.5).

stroyed, except that one specimen has preserved nephridia packed with mature eggs. The single pair of nephridia (Fig. 2) is small and rounded, with basal nephrostomes situated on elongated necks and independently opening outward.

Alomasoma sp. No. 2

Material:

St. 471, Java (Sunda) Trench (10°26′S, 114°15′ E), 2780 m, 9.9.1951. Bottom: clay. – 1 specimen.

Alomasoma sp. No. 3

Material:

St. 574, Tasman Sea (39°45′S, 159°39′E), 4670 m, 18.12.1951. Bottom: temp. *c.* 1.1°C. – 1 specimen.

The specimens from Sts. 471 and 574 can only provisionally be referred to the genus *Alomasoma*.

Genus *Choanostoma* Zenkevitch, 1964

Choanostoma ? bruuni Zenkevitch, 1964

Material:

St. 194, off Durban (34°09′S, 30°45′E), 4360 m, 7.2.1951. Bottom: Globigerina ooze. – 3 specimens.

St. 232, Madagascar – Mombasa (9°03′S, 49° 22′E), 4930 m, 8.3.1951. Bottom temp.: *c.* 1.3°C. – 1 specimen.

The lengths of the specimens from St. 194 are 34, 48 and 62 mm, respectively. All specimens are in a very bad condition; they are provisionally ascribed to *C. bruuni*. This species was previously recorded by the author from the northern part of the Arabian Sea at 3676 m depth.

Choanostoma sp.

(Fig. 3).

Material:

St. 66, off Gabon (4°00′S, 8°25′E), 4020 m, 5.12.1950. Bottom: greenish-grey mud. – 2 specimens.

Only the basal part of two probosces (17 and 25 mm long and 6 and 7 mm wide) have been preserved. The proboscis base is surrounded by a collar tightly pressed to it and free at the peripheral part. The collar has a deep cut on its ventral side (Fig. 3a). The edge of the collar is cut aslant and is half as wide on the dorsal side as on the ventral one (Fig. 3b, c). Within the proboscis base there is a muscular pharynx (Fig. 3d). A similar type of collar was described by me in *Choanostoma bruuni* (ZENKEVITCH 1964a), found in the "Vityaz" collections from the northern part of the Indian Ocean; this type of collar is also encountered in another species of *Choanostoma (C. filatovae)* discovered by "Vityaz" in the Pacific Ocean (ZENKEVITCH 1964b). For this reason these fragments have been referred to the genus *Choanostoma*.

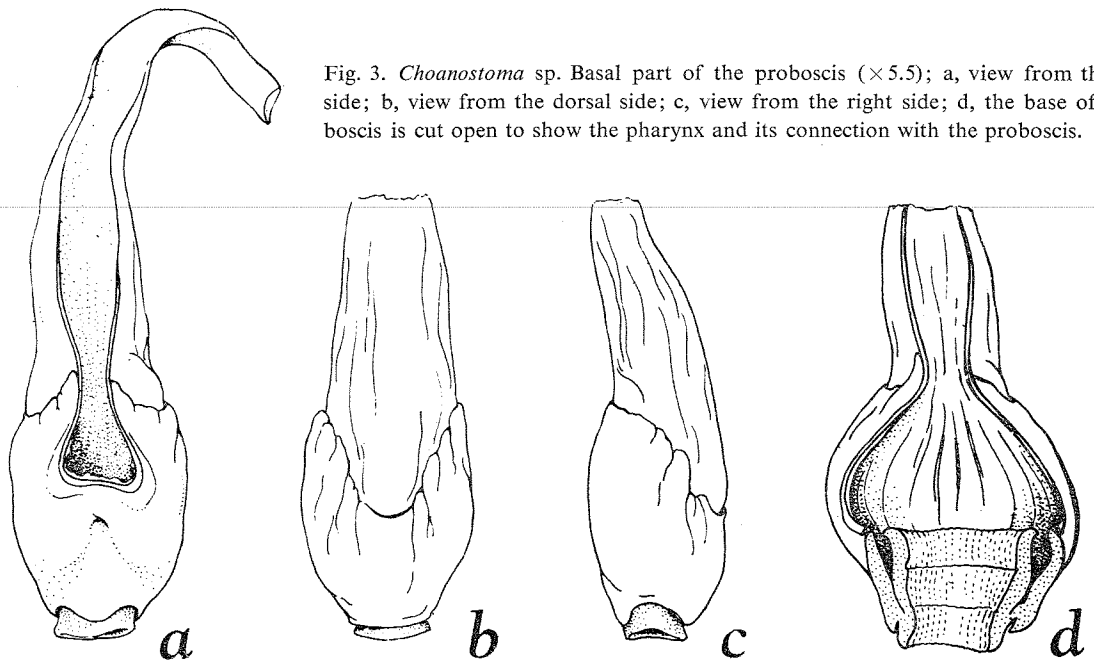

Fig. 3. *Choanostoma* sp. Basal part of the proboscis (×5.5); a, view from the ventral side; b, view from the dorsal side; c, view from the right side; d, the base of the proboscis is cut open to show the pharynx and its connection with the proboscis.

Genus ***Bruunellia*** n. gen.

Diagnosis:

The proboscis is of oval shape and fixed form. Ventral setae are absent. There is a peculiar rosette around the anal opening.

Type species: *Bruunellia bandae* n. sp.

The genus is named after Dr. ANTON BRUUN, the late leader of the Galathea Expedition.

Bruunellia bandae n. sp.
(Fig. 4 and Pl. XVII)

Material:

St. 495, Banda Trench (5°26′S, 130°58′E), 7290-7250 m, 22.9.1951. Bottom: clay. Bottom temp.: 3.6°C. – 6 specimens.

The body length of these peculiar minute echiuroids varies from 12 to 22 mm and the proboscis length ranges between 13 and 18 mm. In section the proboscis is of uniform width throughout its length; it is of oval shape and not of the grooved type. It is similar to the proboscis of *Jakobia birsteini* Zenkevitch which was found in the Kurile-Kamchatka Trench. Apart from in *Bruunellia* and *Jakobia,* rounded probosces have not been observed in the Echiuroidea. Sexual setae are absent. The cutis is thick, nontransparent and entirely covered with papillae.

The anal rosette which permits great expansion of the anal aperture is of a peculiar design (Fig. 4e).

The internal organs are totally destroyed. One specimen was sectioned, but even by this method it was impossible to reconstruct the internal organization of the body.

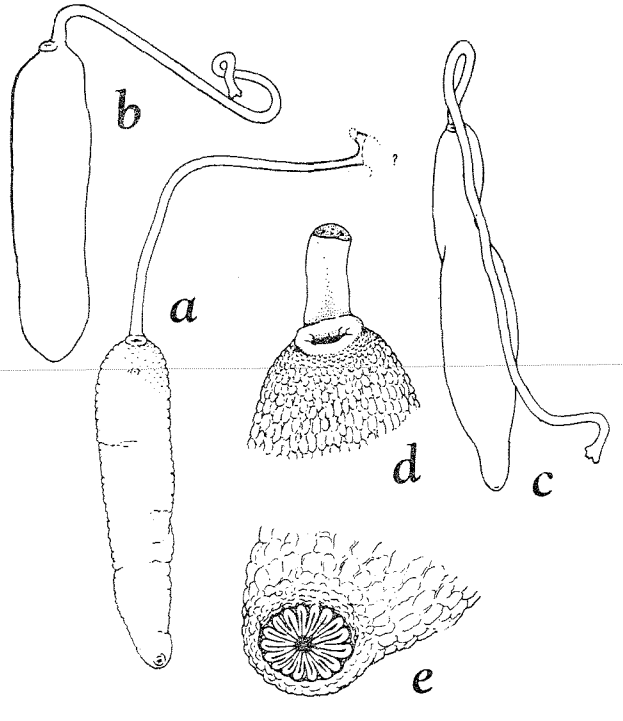

Fig. 4. *Bruunellia bandae* n. gen., n. sp.; a, holotype; b-c, general view of two other specimens; d, view of anterior end with the base of the proboscis; e, the rear end of the body and the anal rosette. (a-d, ×4-5; e, ×10).

Genus ***Bonellia*** Rolando, 1822

Bonellia achaeta Zenkevitch, 1958
(Fig. 5).

Material:

St. 574, Tasman Sea (39°45′S, 159°39′E), 4670 m, 18.12.1951. Bottom temp. *c.* 1.1°C. – 2 specimens.
St. 601, Tasman Sea (45°51′S, 164°32′E), 4400 m, 14.1.1962. Bottom: Globigerina ooze. Bottom temp.: *c.* 1.1°C. – 2 specimens.

The two specimens from St. 601 are each 44 mm long and 16 mm wide. The proboscis is torn off, with only its base remaining preserved. No sexual setae can be observed. There is one large nephridium. The nephrostome is spaced terminally. The anal glands are elongate in shape and amount to half of the body length.

In the two specimens from St. 574 the ventral setae are lacking. One nephridium is with a terminal funnel. The rest of the internal organs are de-

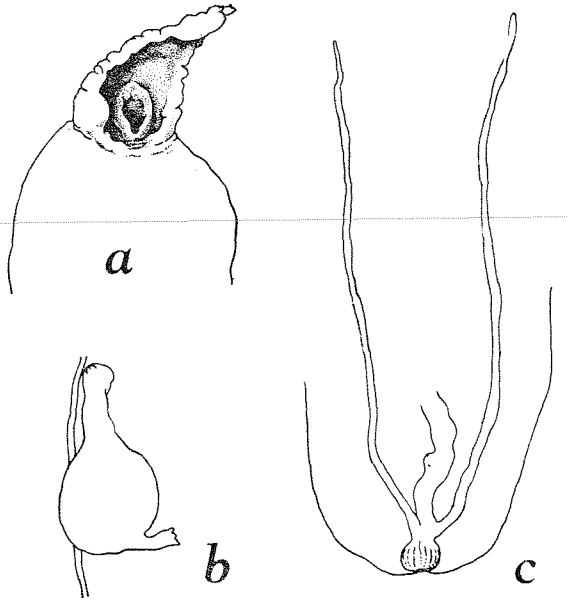

Fig. 5. *Bonellia achaeta* Zenkevitch; a, basal part of proboscis and pharynx from the ventral side (×4); b, nephridium (×5); c, anal glands (×7.5).

stroyed, so these two specimens can only tentatively be referred to *Bonellia achaeta.*

B. achaeta was described by me from the collections obtained by "Vityaz" in the north-western part of the Pacific; it was collected at depths of 3500 and 5540 m.

Genus ***Torbenwolffia*** n. gen.

Diagnosis:

A large, big proboscis with a bilobed end. In living specimens the proboscis exceeds the length of the body by several times. Ventral setae are absent. One nephridium, situated in the right side. Anal glands are short and unbranched, with a few funnels spaced along extended necks.

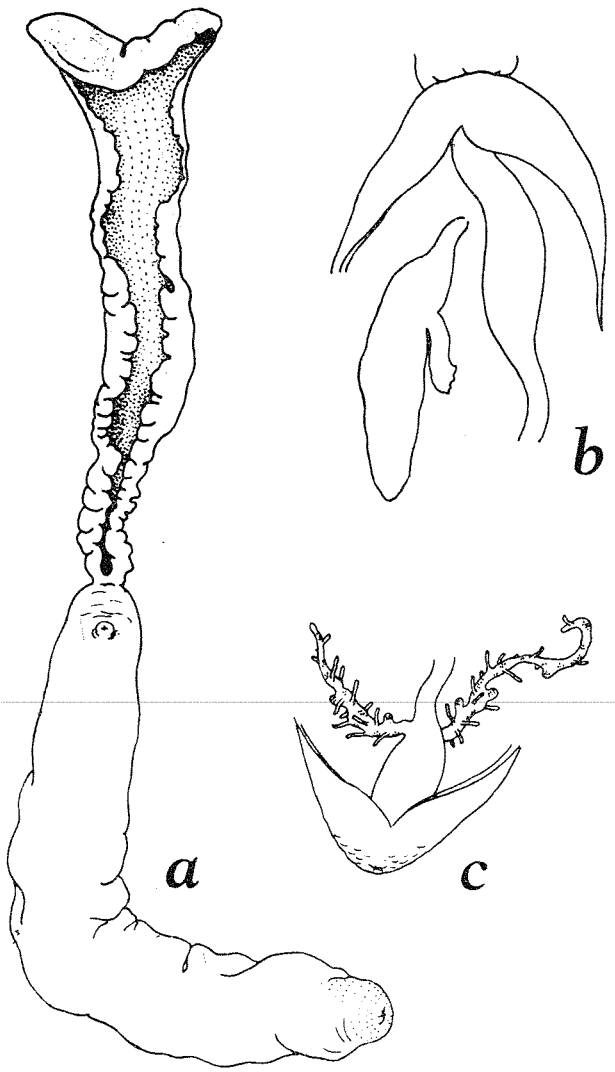

Fig. 6. *Torbenwolffia galatheae* n. gen., n. sp., holotype (St. 649); a, general view from the ventral side (×2); b, nephridium (×5); c, anal glands (×5).

Type species: *Torbenwolffia galatheae* n. sp.

The genus is named after Dr. TORBEN WOLFF, deputy leader of the Galathea Expedition.

Torbenwolffia galatheae n. sp.

(Figs. 6-8)

Material:

St. 649, Kermadec Trench (35°16′S, 178°40′W), 8210-8300 m, 14.2.1952. Bottom: grey clay with pumice. Bottom temp.: 1.5°C. – Holotype and 13 additional specimens.

St. 651, Kermadec Trench (32°10′S, 177°14′W), 6960-7000 m, 16,2.1952. Bottom: brown clay with pumice. Bottom temp.: 1.3°C. – 9 specimens.

St. 654, Kermadec Trench (32°10′S, 175°54′W), 5850-5900 m, 18.2.1952. Bottom: brown clay with pumice. Bottom temp.: 1.2°C. – 5 specimens.

St. 658, Kermadec Trench (35°51′S, 178°31′W), 6660-6770 m, 20.2.1952. Bottom: brown sand with clay stones. Bottom temp.: 1.3°C. – 6 specimens.

A large echiuroid with a large grooved proboscis which terminates with a bifurcated lobe. In fixed material the length of the body is 90-100 mm and that of the proboscis is 70-80 mm. In fixed material the terminal lobe of the proboscis may acquire various forms depending upon the rate of contraction (Fig. 7). The most common form is observed in Fig. 6. Fig. 7 shows one of the variants.

Among the specimens with a normal proboscis, one comes across specimens with abnormally thin probosces. However, in all other characters these

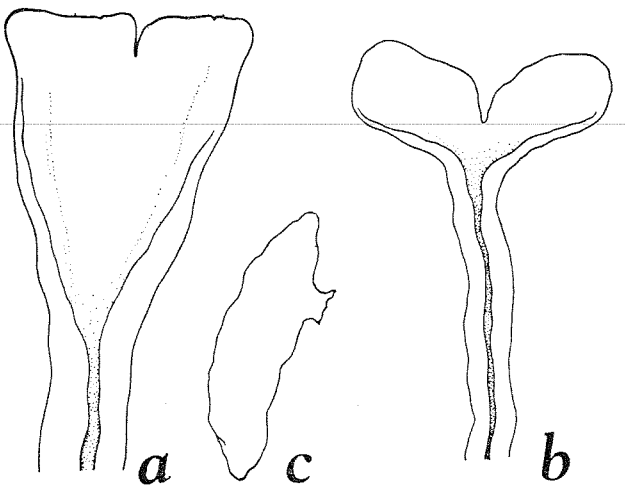

Fig. 7. *Torbenwolffia galatheae* n. gen., n. sp.; a-b, different forms of the anterior end of the proboscis in fixed material (×3); c, nephridium (×6).

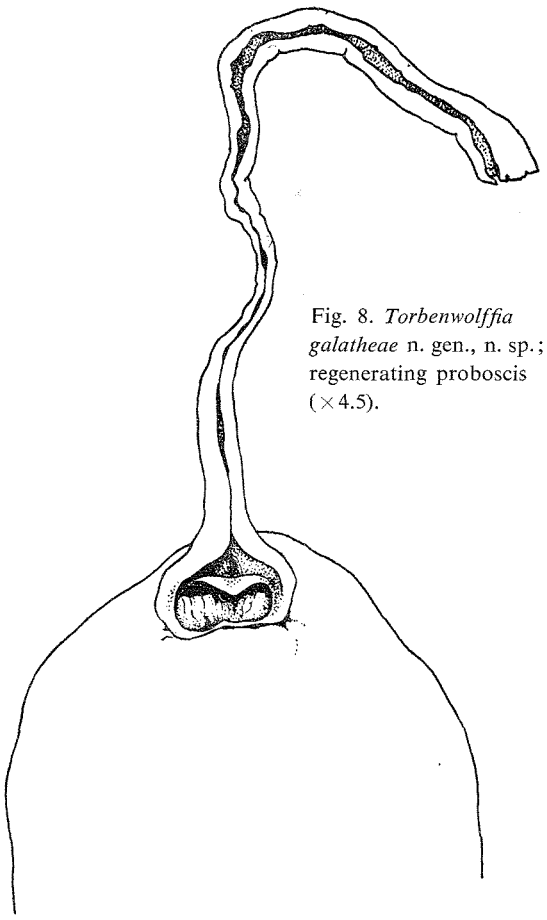

Fig. 8. *Torbenwolffia galatheae* n. gen., n. sp.; regenerating proboscis (×4.5).

specimens fail to differ from the typical forms from St. 649 (Fig. 8). It is possible to assume that in these particular cases one is observing the regeneration of a proboscis; it appears that in some Echiuroidea regeneration is quite a common phenomenon. A partial or total loss of the proboscis in some Echiuroidea may lead to confusion in descriptions of new species, as has been the case in describing the first species of the genus *Prometor* Fisher.

Torbenwolffia galatheae was collected by "Galathea" at four stations within the Kermadec Trench at depths of 5850-8300 m; this permits one to regard this form as a hadal (ultra-abyssal) species. The material was in such a severely distorted shape that one could barely count 34 complete specimens which were in a more or less destroyed state. In addition, there are a great number of body and proboscis fragments.

Genus ***Jakobia*** Zenkevitch, 1958

***Jakobia* sp.**

(Fig. 9)

Material:

St. 664, Kermadec Trench (36°34′S, 178°57′W), 4540 m, 24.2.1952. Bottom: brown sandy clay with pumice. Bottom temp.: 1.1°C. – 1 specimen.
St. 726, Gulf of Panama (5°49′N, 78°52′W), 3670-3270 m, 13.5.1952. Bottom: clay. Bottom temp.: *c.* 2.0° C. – 12 specimens.

The poor state of preservation, especially of the internal organs, and the absence of proboscis enables one to ascribe these forms only tentatively to

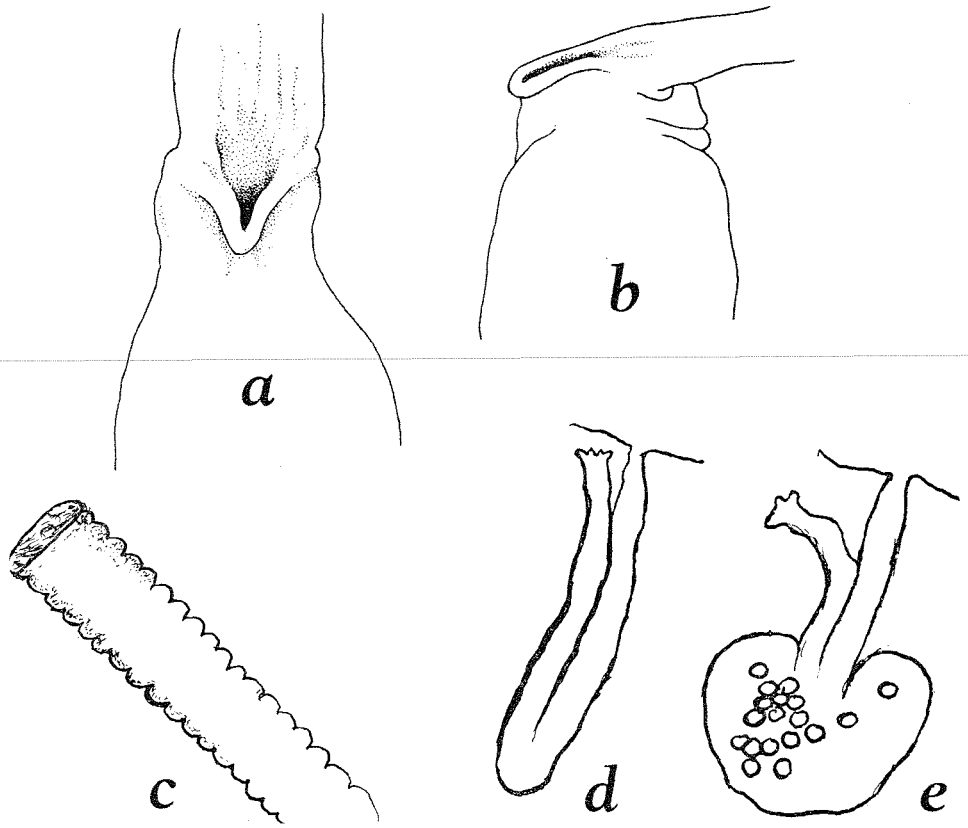

Fig. 9. *Jakobia* sp.; a, view from the ventral side (×5); b, view from the left side (×5); c, part of the proboscis (×4); d-e, different forms of nephridia (×6).

Jakobia but not to refer them to its only species, *J. birsteini.*

The characters of *Jakobia* are represented by a most characteristic form of pharynx (Fig. 9) not observed in any other echiuroid.

The jar with the specimen from St. 664 also contained a proboscis which lacks the anterior end. This proboscis is not grooved and is oval in transverse section, thus being similar to the pharynx form observed only in *Jakobia* and in the transverse section of the proboscis of *Bruunellia* described in this paper.

The available samples of *Jakobia* exhibit a large body, 100 mm long, and the proboscis from St. 664 has a length of 76 mm. The cutis of this particular form is firm and non-transparent, covered entirely with papillae. The internal organs are entirely destroyed, except that in some specimens the nephridia are preserved; these are situated on the right side. All the available specimens were preadolescent, and the nephridia lacked eggs and had a y-shaped folded canal (Fig. 9d). In adolescent *J. birsteini* specimens in the material from the Kurile-Kamchatka Trench, the nephridia were packed with eggs, and owing to this fact their terminal ends had a spherical bulge; possibly, empty nephridia in *J. birsteini* would also exhibit a folded canal.

No ventral setae were observed in any of the 13 "Galathea" specimens.

Genus ***Vitjazema*** Zenkevitch, 1958

***Vitjazema* sp.**

The collections from St. 419 in the Philippine Trench (10.150-10.210 m) contained a fragmentary specimen of a small green echiuroid with long chaetes. According to the drawing published by BRUUN *et al.* and reproduced here (Fig. 10) this is a specimen related to the genus *Vitjazema*. Unfortunately, the fragment is no more available.

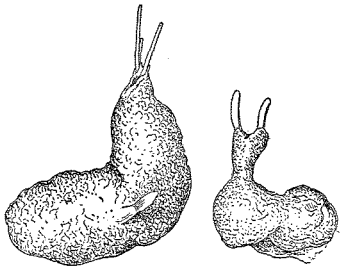

Fig. 10. *Vitjazema* sp.; fragment from St. 419. (After BRUUN *et al.*).

SOME DATA ON THE HORIZONTAL AND VERTICAL DISTRIBUTION AND SOME BIOLOGICAL PECULIARITIES OF THE ECHIUROIDEA

Of the three families comprising the echiuroids, two basic families – the Thalassematidae and the Bonelliidae – differ sharply in their vertical distribution. The former group populates the shallow areas of the sea, whereas the latter group represents a characteristic community of the abyssal and ultra-abyssal (hadal) fauna and reaches the greatest depths of the ocean.

Such genera as *Jakobia, Vitjazema* and *Alomasoma,* as well as *Bruunellia* and *Torbenwolffia* described in this paper, may be regarded as representatives of the ultra-abyssal zone. The inhabitants of the mean abyssal horizons (four species of *Prometor,* numerous species of *Bonellia* and *Hamingia,* as well as some others) may be added to this group. The occurrence of *Bonellia* and *Hamingia* at shallower depths in the cold regions of the ocean may be regarded as an example of a rather common ascent of abyssal forms to the shallower bathyal horizons and even into the sublittoral horizons in the polar regions. This phenomenon may also be observed in *Umbellula, Pourtalesia,* and *Brizaster,* in some species of Pogonophora, and in several others.

As far as the vertical distribution of Bonelliidae is concerned it is like that of the Pogonophora. They also resemble the Pogonophora, I dare to believe, in their immense antiquity and their morphological and taxonomical seclusion.

It is possible to assume that the acutely pronounced sexual dimorphism and the male parasitism in Bonelliidae developed as a reaction to life at great depths similar to the conditions observed in angler-fishes of the order Lophiiformes.

At the moment, owing to the inadequacy of our knowledge, it is believed that the distribution of the Bonnelliidae is characterized by rather strongly pronounced endemic features. However, forms inhabiting the upper horizons of the abyssal and bathyal zones are characterized by a greater geographical distribution. For example, the genus *Prometor* has both a bipolar distribution (*P. grandis)* and an amphi-pacific distribution *(P. benthophila* and *P. oculum* in the east, *P. grandis* and *P. gracilis* in the west). Possibly, an amphi-pacific distribution is characteristic also for *Alomasoma belyaevi* (ZENKEVITCH 1964b).

SUMMARY

The echiuroid material was collected during the Galathea Expedition and amounts to 65 specimens, obtained from 14 stations. Owing to the poor preservation of the material, especially of the internal organs, the description of the examined samples cannot be regarded as exhaustive. In most cases the probosces have proved to be partially or fully absent and the vascular system and the anal glands have not been preserved; this frequently refers also to the nephridial system.

However, some of the preserved features have permitted the establishment of 2 new genera and species *(Bruunellia bandae* and *Torbenwolffia galatheae)* and the refinding of 3 previously described species. In addition, 4 specimens are provisionally referred to the genus *Alomasoma*, 13 specimens to the genus *Jakobia*, and 1 specimen to the genus *Vitjazema*. The two latter genera were described by the author from the ultra-abyssal (hadal) part of the Kurile-Kamchatka Trench.

Thus far our knowledge on the abyssal Echiuroidea is inadequate for systematic and zoogeographic generalizations.

Male parasitism in the family Bonelliidae may be regarded as a result of adaptative adjustment to life in the oceanic depths and the entire family may be regarded as one of the most typical groups of the abyssal and hadal (ultra-abyssal) faunas.

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PLATE XVII

Bruunellia bandae n. gen., n. sp.

A. Transverse section of the proboscis (×60).
B. Transverse section of the body (×20).
C. Part of body wall. Exterior surface with cuticula (on the left). On the right is seen a layer of ring and longitudinal muscles (×80).