

The biogeography of some abyssal Polychaetes

Jørgen B. KIRKEGAARD

Zoological Museum, Universitetsparken 15
K-2100 Copenhagen, Denmark

ABSTRACT

The Danish Galathea Expedition obtained polychaetes from 83 stations in the bathyal and abyssal zones of the South Atlantic, Indian, and southern Pacific Oceans; 104 species were identified. On the basis of the distribution of some of these species and results from earlier publications a biogeographical analysis is given. The species treated in detail were: *Laetmonice benthaliana* McIntosh, *Leanira quatrefagesi* Kinberg, *Aglaophamus elamellata* Eliason, *Bathyliasona kirkegaardi* (Uschakov), *B. nigra* (Hartman) and *Paradiopatra paucibranchis* (Ehlers). This analysis showed a worldwide distribution of many abyssal polychaetes. The abyssal and hadal polychaetes are derived from the polychaete fauna in the bathyal zone. Many of these species were eliminated during the glacial ages when temperatures in the deep sea dropped from 10 °C to 2 °C. The present deep-sea polychaete fauna consists of eurythermic and eurybathic species, relics of a preglacial fauna, and new invaders from the bathyal zone.

RÉSUMÉ

Biogéographie de quelques Polychètes abyssaux

L'expédition danoise de la "Galathea" a récolté des polychètes dans 83 stations, dans les zones bathyale et abyssale de l'Atlantique du Sud, de l'Océan Indien et du Pacifique du Sud. Cent quatre espèces ont été identifiées. Il est fourni, sur la base de la distribution de quelques unes de ces espèces et de résultats antérieurs, une analyse biogéographique. Les espèces suivantes ont été étudiées en détail : *Laetmonice benthaliana* McIntosh, *Leanira quatrefagesi* Kinberg, *Aglaophamus elamellata* Eliason, *Bathyliasona kirkegaardi* (Uschakov), *B. nigra* (Hartman) et *Paradiopatra paucibranchis* (Ehlers). Les polychètes abyssaux et hadaux dérivent de la faune de polychètes de la zone bathyale. Plusieurs de ces espèces ont disparu au cours des périodes glaciaires, quand les températures dans l'océan profond baissaient de 10 °C à 2 °C. Il en résulte que la faune actuelle de polychètes de l'océan profond se compose d'espèces eurythermes et eurybathes, des restes d'une faune pré-glaciaire, et de nouveaux envahisseurs de la zone bathyale.

INTRODUCTION

The polychaetes have long been considered to be a group with many cosmopolitan species. In recent years polychaete specialists have reexamined so-called cosmopolitan species resulting in revision of genera and species

in many families. This has shown that in many cases the purportedly cosmopolitan distribution in the oceans was due to inadequate descriptions or lack of comparison with type specimens. As a result many of the so-called cosmopolitan species have been split up into several species with a more restricted distribution. However, this is probably not true of polychaetes living in the deep sea.

DEEP-SEA POLYCHAETES

Before 1940 little was known about the deep-sea fauna. Our knowledge of the deep-sea polychaetes was based mostly on the investigation of the "Challenger" expedition (MCINTOSH, 1885). Since the late 1940s several expeditions have investigated deep-sea fauna with research vessels such as the Swedish "Albatross", the Danish "Galathea", the Soviet "Vityaz" and the American "Anton Bruun". Later, British, German, French, and Japanese research vessels sampled bathyal, abyssal and hadal bottoms. We now have more detailed knowledge of the polychaete fauna of the deep sea, however, since more than half of the world's oceans is occupied by the abyss, only a small part has been sampled.

The Danish "Galathea" expedition round the world in 1950-52 collected polychaetes from 97 deep-sea stations. These stations were situated in the Southeast Atlantic, the Indian Ocean and the South Pacific. Fourteen of the stations were located in trenches deeper than 6,000 m, the so-called hadal region, from which 15 species were obtained (KIRKEGAARD, 1956). The remaining 83 stations were from the abyssal (43) and bathyal (40) regions. The errant species from these 83 stations have been identified and comprise 104 species from 17 families (KIRKEGAARD, in prep.). These species were obtained using several different gears, including sledge trawls, commercial trawls, dredges, and Petersen grab. The material was washed through sieves of different mesh size, the smallest with a mesh of 1 mm. However, the results from this expedition and from other expeditions (LEVENSTEIN, 1962, 1971, 1975, 1978a, b, 1984, 1991; USCHAKOV, 1955) make it possible to draw some conclusions on the biogeography of deep-sea polychaetes.

The abyssal plains stretch from south of Greenland southwards through the Atlantic, south of Africa to the Indian Ocean, south of Australia and into the Pacific. These plains occupy the bottom of nearly all of the large oceans, 273 million km². The conditions for life are similar throughout these large areas: 2-4 °C, 35 P.S.U. salinity, oxygen: 4 ml. l⁻¹ pressure: 200-600 atm., and darkness (BRUUN, 1956). It is on these large areas with similar conditions for life from one ocean to another that cosmopolitan species, if they exist, might be expected to occur.

RESULTS

Laetmonice benthaliana McIntosh, 1885

(DAY, 1967, fig. 1.1 f-l) Fig. 1.

RECORDS. — *Laetmonice producta* var. *benthaliana* McIntosh, 1885 p. 45 pl. 8, figs 4-5, pl. 4A, fig. 12, pl. 5A figs 1-2. — *Laetmonice producta benthaliana* HARTMAN, 1964 p. 12, pl. I figs 4-5. — *Laetmonice benthaliana* USCHAKOV, 1962 p. 147; DAY, 1963 p. 356, 1967 p. 33.

MATERIAL EXAMINED. — St. 186, SE of Natal, 32°33'S, 32°01'E, 3620 m, SOT, two specimens: 50 x 20 mm (complete, 34 setigers), 50 x 20 mm (bad condition). St. 192, off Durban, 32°00'S, 32°41'E, 3,530 m, SOT, five complete specimens, 34 setigers: 20 x 5, 35 x 15, 40 x 15, 45 x 15, 45 x 20 mm; one destroyed specimen. St. 198, off Durban, 30°32'S, 34°27'E, 2,700 m, ST100, one complete specimen, 34 setigers: 34 x 12 mm. St. 217, Mozambique Channel, 14°20'S, 45°09'E, 3,390 m, HOT, one complete specimen, 34 setigers: 40 x 15 mm. St. 233, N of Madagascar, 7°24'S, 48°24'E, 4,720 m, ST300, one specimen, 34 setigers: 55 x 20 mm. St. 235, E of Mombasa, 4°47'S 46°19'E, 4,810 m, HOT, 1 specimen, 34 setigers: 60x15 mm. St. 238, off Kenya, 3°23'S, 44°04'E, 3,960 m, 43 specimens: 50 x 20 mm. St. 241, off Kenya, 4°00'S, 41°27'E, 1,510 m, HOT, one specimen: 10 x 5 mm (smashed). St. 601, SW of New Zealand, 45°51'S, 164°32'E, 4,400 m, HOT, seven complete specimens, 34 setigers: 35 x 10-45 x 15 mm, three fragments: 20 x 8-40 x 15 mm. St. 607, SW of New Zealand, 44°18'S, 166°46'E, 3,580 m, HOT, 10 specimens, 34 setigers: 10 x 5-33 x 15 mm. St. 661, Kermadec Trench, 36°07'S, 178°32'W, 5340 m, ST600, three complete specimens: 23 x 10, 30 x 12, 35 x 12 mm. St. 663, Kermadec Trench, 36°31'S, 178°38'W, 4,410 m, HOT, 181 specimens 33-34 setigers: 35 x 10-15 x 5 mm. St. 664,

Kermadec Trench, 36°34'S, 178°57'W, 4,540 m, HOT, 76 specimens, many destroyed: 35 x 12 mm. St. 665, Kermadec Trench, 36°38'S, 178°21'E, 2,470 m, HOT, three complete specimens: 20 x 10, 20 x 10, 25 x 12 mm; one fragment. St. 716, Gulf of Panama, 9°23'N, 89°32'W, 3,570 m, HOT, one specimen: 30 x 10 mm.

REMARKS. — This species was originally described as a subspecies of *Laetmonice producta* by McINTOSH (1885). USCHAKOV (1962) raised it to species level and DAY (1963) agreed. It differs from the stem species by its smooth venter and by always having 15 pairs of elytra compared to 18–20 pairs in *L. producta*. The number of setigers is also smaller, 33–34 in *L. benthaliana*, 45–47 in *L. producta*.

DISTRIBUTION. — Antarctic; Indian Ocean, E and S of Africa, Arabian Sea, S of Ceylon; Pacific, W of New Zealand, Kermadec Trench, Japan, Central Pacific, Gulf of Panama. 50–6,875 m.

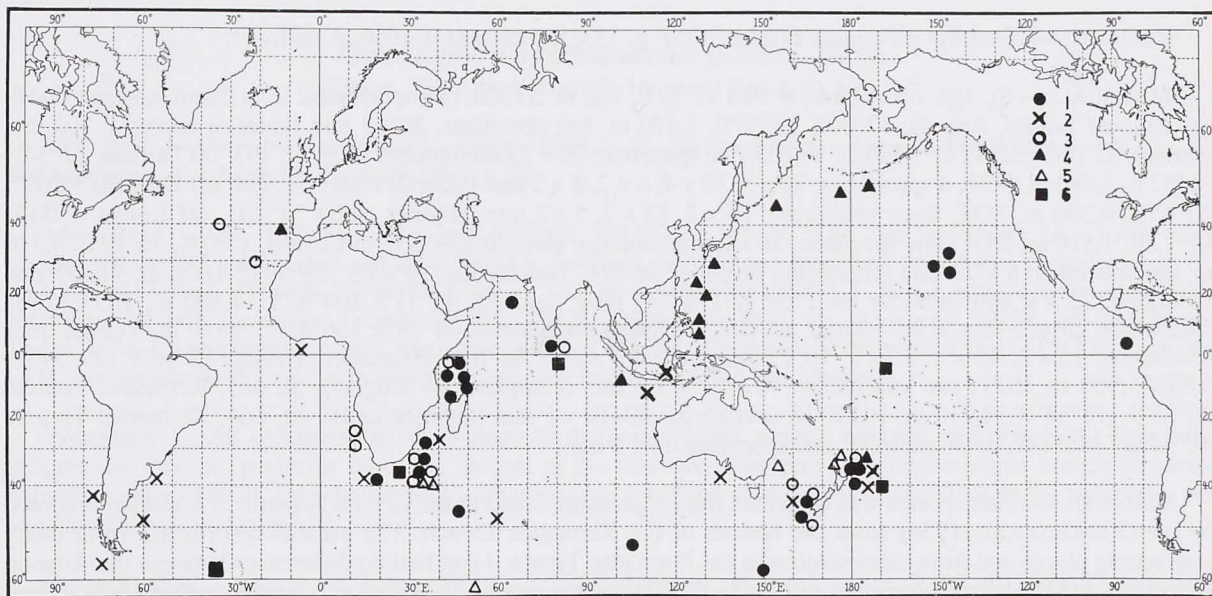


FIG. 1.— Distribution of *Laetmonice benthaliana* (1), *Leanira quatrefagesi* (2), *Aglaophamus elamellata* (3), *Bathyliaisona kirkegaardii* (4), *Paradiopatra paucibranchis* (5), and *Bathyliaisona nigra* (6).

Leanira quatrefagesi Kinberg, 1855

(PETTIBONE, 1970, figs 1–3), Fig. 1.

RECORDS. — PETTIBONE, 1970 p. 4; WESENBERG-LUND, 1962, p. 27. *Leanira hystrix* DAY, 1963, p. 360.

MATERIAL. — St. 214, off Beira, 20°12'S, 35°15'E, 380 m, PG 0,2, one specimen: 25 x 5 mm (anterior end). St. 443, Mindanao Sea, 8°48'N, 124°09'E, 1,500 m, ST300, three specimens: 32 x 7, 30 x 8, 22 x 6 mm (anterior end). St. 453, Makassar Strait, 3°56'S, 118°26'E, 2,000 m, ST300, one specimen: 45 x 4 mm. St. 480, S of Bali, 8°49'S 115°00'E, 440 m, PG 0,2, one specimen: 8 x 0.5 mm (anterior end). St. 491, Makassar Strait, 4°56'S, 117°39'E, 1,560 m, ST300, one specimen: 22 x 4 mm (anterior end), one fragment. St. 554, Great Australian Bight, 37°28'S, 138°55'E, 1,340–1,320 m, ST300, 16 specimens: 33 x 1–9 x 0.5 mm (anterior ends). St. 626, W of New Zealand, 42°10'S, 170°10'E, 610 m, HOT, 10 specimens: 22 x 1–5 x 1 mm (anterior ends), two posterior

ends, three fragments. St. 665, Kermadec Trench, 36°38'S, 178°21'E, 2,470 m, HOT, 13 specimens: 32 x 6–12 x 1 mm (anterior ends), eight fragments. ? St. 668, Kermadec Trench, 36°23'S, 177°41'E, 2640 m, HOT, one fragment (only parapodia with setae).

REMARKS. — This fairly large number of specimens from different parts of the world agrees with Pettibone's description and figures.

DISTRIBUTION. — South Atlantic off Argentina, West and South Africa, Indian Ocean off Mozambique, Malaya Archipelago, Pacific off Chile, W of New Zealand, Kermadec Trench, Magellan area, Falkland Islands, Antarctic. 0–6,150 m.

Aglaophamus elamellata (Eliason, 1951)

(ELIASON, 1951, fig. 2), Fig. 1.

RECORDS. — *Nephtys elamellata* Eliason, 1951, p. 133; KIRKEGAARD, 1956, p. 68 fig. 7.

MATERIAL. — St. 101, off Angola, 8°50'S 12°32'E, 990 m, ST300, two specimens: 20 x 2 mm (anterior ends). St. 108, off Lobito, Angola, 12°00'S 13°00'E, 1,470 m, one specimen: 20 x 2 mm (anterior end). St. 192, off Durban, 32°00'S, 32°41'E, 3,430 m, ST100, one specimen: 20 x 3 mm (anterior end). St. 193, off Durban, 32°34'S 31°52'E, 3,680 m, SOT, 4 specimens: 22 x 3, 10 x 4, 6 x 2, 3 x 2 mm (anterior ends). St. 194, off Durban, 34°09'S 30°45'E, 4,360 m, SOT, three specimens: 25 x 2, 18 x 2, 5 x 2 mm (anterior ends). St. 241, off Kenya, 4°00'S, 41°27'E, 1,510 m, HOT, one specimen: 10 x 2 mm (anterior end). St. 279, SW of Ceylon, 1°00'N, 76°17'E, 4,320 m, one specimen: 5 x 0.5 mm (complete), juvenile? St. 574, Tasman Sea, 39°45'S 159°39'E, 4,670 m, ST600, one specimen: 22 x 4 mm (anterior end). St. 601, W of New Zealand, 45°51'S 164°32'E, 4,400 m, HOT, three specimens: 25 x 5, 16 x 5, 20 x 5 mm. St. 607, off SW New Zealand, 44°18'S; 166°46'E, 3,830 m, VG 0.2, four specimens: 15 x 3, 15 x 3, 15 x 3, 10 x 2 mm (anterior ends). St. 654, Kermadec Trench, 32°10'S 175°54'W, 5,850–5,900 m, HOT, two specimens: 40 x 5, 38 x 5 mm (complete, 54 setigers). St. 663, Kermadec Trench, 36°31'S 178°38'W, 4,410 m, HOT, 18 specimens: 40–10 x 5 mm (anterior ends). St. 664, Kermadec Trench, 36°34'S, 178°57'W, 4,540 m, HOT, one specimen: 15 x 3 mm.

REMARKS. — This species was described from specimens found in the Central Atlantic. It was later recorded by me (KIRKEGAARD, 1956) from the bottom of the Kermadec Trench. The present records are from many intervening places and from other stations in the Kermadec Trench. I can find no differences between the Atlantic specimens and those from deep water in the Indian Ocean and around New Zealand. It appears that this is a deep water species with a cosmopolitan distribution.

DISTRIBUTION. — Atlantic (Azores, Canary Islands, off West Africa). 990–4,600 m. Indian Ocean (off East Africa, Ceylon). 1,510–4,360 m. Pacific (Tasman Sea, Kermadec Trench). 3,830–7,000 m.

Bathyeliasona kirkegaardii (Uschakov, 1971)

(PETTIBONE, 1976, figs 15–17), Fig. 1.

RECORDS. — USCHAKOV, 1971, p. 37; PETTIBONE, 1976, p. 27; HARTMANN-SCHRÖDER, 1975, p. 53. *Macellicephala abyssicola* KIRKEGAARD, 1956, p. 64.

MATERIAL. — St. 654, Kermadec Trench, 32°10'S, 175°54'W, 5,850–5,900 m, HOT, two fragments, two proboscises.

REMARKS. — The species was identified by the setae on an anterior and a posterior end

DISTRIBUTION. — Aleutian Trench, Kermadec Trench, Sunda Trench, off Portugal. 5275–7880 m.

Bathyliasona nigra (Hartman, 1967)

(PETTIBONE, 1976, figs 18–19), Fig. 1.

RECORDS. — PETTIBONE, 1976, p. 30. *Herdmanella nigra* Hartman, 1967, p. 25.

MATERIAL. — St. 194, off Durban, 34°09'S, 30°45'E, 4,360 m, SOT, one specimen: 40 x 20 mm. St. 281, SW of Ceylon, 3°38'N, 78°15'E, 3,310 m, ST300, one specimen: 35 x 10 mm.

REMARKS. — The specimen from St. 281 is in bad condition, but the shape of the setae and the black pigment together with the number of segments and the prostomium agree with Pettibone's description and figures. However, the specimen from St. 194 lacked setae on segment 1.

DISTRIBUTION. — Antarctic (South Sandwich Isl.), Indian Ocean (E of South Africa and S of Ceylon). 2,553–4,360 m.

Paradiopatra paucibranchis (Ehlers, 1908)

(Ehlers, 1908, pl. 10 figs 12–16, pl. 11 figs 1–6), Fig. 1.

RECORDS. — *Diopatra paucibranchis* Ehlers, 1908, p. 81. *Sarsonuphis paucibranchis* FAUCHALD, 1982, p. 77. *Paradiopatra paucibranchis* PAXTON, 1986, p. 38.

MATERIAL. — St. 182, SE of Durban, 33°28'S, 38°32'E, 5,110 m, SOT, one specimen: 18 x 1 mm (bad condition). St. 192, off Durban, 32°00'S, 32°41'E, 3,430 m, ST100, one specimen: 26 x 1 mm (anterior end). St. 550, NE of Sydney, 31°27'S, 153°33'E, 4,530 m, ST200, two specimens: 20 x 1, 10 x 1 mm (anterior ends), four fragments. St. 665, Kermadec Trench, 36°38'S, 178°21'E, 2,470 m, HOT, six specimens: 32, 32, 28, 20 x 3 mm, 18 x 1, 20 x 1 mm (anterior ends), fragments, tubes. ? St. 668, Kermadec Trench, 36°23'S, 177°41'E, 2,640 m, HOT, one specimen: 10 x 0.5 mm (anterior part), one fragment. All in bad condition.

REMARKS. — All specimens have six rings on the ceratophores, ventral cirri are cirriform in the first three setigers and digitate posterior lobes are present in the first seven setigers. The beginning of branchiae varies between setigers 16–20, subacicular hooks are present in some specimens from setiger 9 (as in the holotype), but in some others from setiger 10.

DISTRIBUTION. — Antarctic Ocean, 63°16'S 57°51'E, 4,636 m, off South Africa, 3,430–5,110 m, Tasman Sea, 4,530 m, Kermadec Trench, 2,470 m.

ORIGIN OF THE ABYSSAL POLYCHAETES

The abyssal fauna is probably derived from the bathyal fauna, from which species that can live under the high pressure and at low temperatures have spread downwards. LEVENSTEIN (1984) pointed out, on the basis of her analyses of the distribution of the deep-sea polynoids (especially the Macellicephalinae), that these polychaetes must have had two distribution centers, i.e., the eastern Atlantic Ocean and the western Pacific, which are the margins of the ancient Tethys Sea. However, during Oligocene (30–20 MY B.C.) the temperatures in abyssal depths decreased from around 10 °C to about 2 °C. This was shown by EMILIANI & EDWARDS (1953), who examined the oxygen isotopes of benthic Foraminifera of probably Oligocene age (30 MY) from the eastern part of the Central Pacific. This temperature change must have been catastrophic for abyssal and hadal faunas since only the eurythermic species survived.

The present polychaete fauna of the abyssal and hadal zones must be relics of a preglacial abyssal and hadal fauna, but besides these old components there must have been a new and still ongoing invasion of species from the bathyal zone to the abyss and to the hadal zone. LEVENSTEIN (1984) suggested that additional centers of distribution could be the eastern Pacific, the Arctic and the Antarctic.

The invasion to the hadal zone must have been from the abyss. LEVENSTEIN (1991) showed that of 80 identified species of polychaetes from this zone, 26 (32.5 %) were endemic to the trenches. Seventeen of these species were found to be endemic to only one trench, whereas the remaining nine were known from two-six

different trenches, some of them from neighbouring trenches, but also from trenches isolated by great distances in the Pacific Ocean. *Bathykermadeca hadalis* (KIRKEGAARD, 1956) (Polynoidae) is recorded from the Japan, Philippine, Yap, Kermadec, Bougainville and Banda trenches. This species is possibly a relict of an old preglacial polychaete fauna.

DISCUSSION

As appears from this investigation, there is very little variation in morphology and size over large geographical distances. *Laetmonice benthaliana*, which is represented by a fairly large collection, showed no difference from East Africa to New Zealand and the Gulf of Panama and agreed with descriptions from the Antarctic and Central Pacific. Other species, i.e., *Leanira quatrefagesi*, *Bathyliaosona kirkegaardi* and *Bathyliaosona nigra* are represented in the material by fewer specimens, but all three species have been revised by PETTIBONE (1970, 1976) and no differences were found between specimens from localities separated by long distances, i.e., South America–Africa (*L. quatrefagesi*), Kermadec Trench, Aleutian Trench, and Portugal (*B. kirkegaardi*). PETTIBONE (1976) examined a small collection of *B. nigra* from the Antarctic, but her description and figures agree well with the present material from off South Africa and south of Ceylon. Similar to this, *Paradiopatra paucibranchis* was revised by FAUCHALD (1982) on a small collection from Antarctic. His redescription of the holotype agrees well with the "Galathea" material from south of Africa and east of Australia. A few characters varied from the holotype, i.e., the place where branchiae (setigers 17–36 compared to 16–20) and subacicular hooks begin (9 compared to 10), but this is also known for other species of the genus. *Aglaophamus elamellata* (Eliason, 1951) is a species which has only been recorded by me since the original description. However, I have a fairly large collection from Africa, Ceylon and Australia-New Zealand and compared them with the type and found no morphological differences.

Some of the material from the "Galathea" was badly damaged, but in many cases the setae of these damaged specimens were so characteristic that identification was possible. Many different sampling devices were used, but there were no connection between the number, the size or the condition of the specimens with the type of gear used. However, all material of the "Galathea" was washed through a 1.0 mm sieve. As mentioned before, many small polychaetes must have passed through these sieves. Later, I (1980) showed that when a 0.5 mm sieve is used, small polychaetes are retained on the screen. These species have a wide geographical distribution. Thus 78 % of the 23 species found in the northeastern abyssal part of the Atlantic, were common to the polychaetes in the abyssal area between New England and Bermuda.

CONCLUSIONS

The present investigation shows that of the six named species from the "Galathea" expedition, four are distributed throughout the World, viz. *Leanira quatrefagesi*, *Aglaophamus elamellata*, *Bathyliaosona kirkegaardi* and *B. nigra*. The remaining two species: *Laetmonice benthaliana* and *Paradiopatra paucibranchis*, are recorded from the Indian Ocean and the Pacific and will probably be found in the Atlantic with additional studies.

Several abyssal species are shown to have a cosmopolitan distribution and several more probably occur. However, endemism in the deep sea does exist as was shown by LEVENSTEIN (1991) in her paper on the polychaetes in deep-sea trenches, in which 16 of the 26 hadal species in the trenches were endemic to one trench.

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