# The abyssal Bivalvia

# LIST BY STATION OF GALATHEA BIVALVIA

Abbreviation of gears used (cf. BRUUN 1959, p. 22): HOT: herring otter trawl; SOT: shrimp otter trawl; ST 300 and ST 600: sledge (Agassiz, Sigsbee) trawl, 3 m and 6 m wide: PGI, 0.2 m<sup>2</sup>: Petersen grab (bottom sampler) covering 0.2 sq.m.

- 24. Monrovia-Takoradi (3°54'N, 8°22'W), 3196 m, (2.7°C), 15 Nov. 1950, ST 300. Brevinucula verrilli (Dall) Ledella crassa n.sp. Yoldiella abyssorum n.sp. Yoldiella abyssorum n.sp. Neilonella guineensis (Thiele) Acar asperula (Dall) Arca orbiculata Dall Abra profundorum (Smith)
- 30. Monrovia-Takoradi (0°42'N, 5°59'W), 5160 m, (2.2°C), 18 Nov. 1950, ST 300. Ledella crassa n.sp. Ledella galatheae n.sp. Limopsis galatheae n.sp. Abra profundorum (Smith)
- 52. San Thomé-Cameroon (1°42'N, 7°51'E), 2550 m, (3.0°C), 30 Nov. 1950, SOT. Nuculana vestita (Locard) Acar asperula (Dall) Cyclopecten (H.) undatus (Verrill & Smith) Abra profundorum (Smith) Xylophaga africana Knudsen Xylophaga guineensis Knudsen Cuspidaria guineensis n.sp.
- 65. Off Gabon (2°17'S, 8°10'E), 2770 m, (3.0°C), 4 Dec. 1950, ST 300. Nuculana vestita (Locard) Neilonella guineensis (Thiele) Malletia estheriopsis Barnard Cyclopecten (H.) undatus (Verrill & Smith)
- 66. Off Gabon (4°00'S, 8°25'E), 4020 m, (2.3°C).
  5 Dec. 1950, ST 300 + D 45. Nuculana pallida (Smith) Yoldiella clarkei n.sp. Neilonella galatheae n.sp. Neilonella guineensis (Thiele) Limopsis pelagica pelagica Smith
- 99. Off Angola (8°40'S, 11°10'E), 2690 m, (2.8° C), 11 Dec. 1950, SOT.

Cyclopecten (H.) undatus (Verrill & Smith) Policordia lisbetae n.sp.

- 107. Loanda-Lobito (11°33'S, 11°51'E), 2370 m, (2.9°C), 18 Dec. 1950, PG 0.2.
  Arca orbiculata Dall
- 176. Cape Town-Durban (35°12'S, 27°35'E), 4350 m, (1.2°C), 21 Jan. 1951, ST 300. *Ledella crassa* n.sp.
- 180. Cape Town-Durban (34° 56' S, 36° 31' E), 5220 m, (0.7° C), 25 Jan. 1951, ST 300.
  Abra profundorum (Smith)
- 190. Off Durban (29°43'S, 32°19'E), 2640 m, (2.5°C), 3 Feb. 1951, ST 300. Cuspidaria natalensis n.sp.
- 192. Off Durban (32°00'S, 32°41'E), 3530 m, (1.1°C), 5 Feb. 1951, SOT.
  Malletia cuneata (Jeffreys)
  Poromya tornata (Jeffreys)
  Cuspidaria barnardi n.sp.
- 194. Off Durban (34°09'S, 30°45'E), 4360 m, (0.7°C), 7 Feb. 1951, SOT. *Myonera undata* (Verrill)
- 217. Mozambique Channel (14°20'S, 45°09'E),
  3390 m, (1.6°C), 27 Feb. 1951, HOT. *Propeamussium meridionale* (Smith)
- 231. Madagascar-Mombasa (8°52'S, 49°25'E), 5020 m, (1.3°C), 7 Mar. 1951, ST 300 + D 80. *Myonera undata* (Verrill)
- 233. Madagascar-Mombasa (7°24'S, 48°24'E), 4730 m, (1.4°C), 9 Mar. 1951, ST 300. Poromya tornata (Jeffreys) Myonera undata (Verrill)
- 234. Madagascar-Mombasa (5°25'S, 47°09'E), 4820 m, (1.3°C), 10 Mar. 1951, HOT. Portlandia abyssicola n.sp. Propeamussium meridionale (Smith) Abra profundorum (Smith) Galatheavalva holothuriae n.gen., n.sp. Laevicordia galatheae n.sp.
- 235. Madagascar-Mombasa (4°47'S, 46°19'E),
  4810 m, (1.3°C), 11 Mar. 1951, HOT.
  Abra profundorum (Smith)
  Galatheavalva holothuriae n. gen., n. sp.
- 279. Seychelles-Ceylon (1°00' N, 76°17' E), 4320 m, (1.3°C), 8 Apr. 1951, ST 300.
  Propeamussium meridionale (Smith)
  Poromya tornata (Jeffreys)
  Myonera undata (Verrill)

- 280. Seychelles-Ceylon (1°56' N, 77°05' E), 4350 m, (1.3°C), 9 Apr. 1951, SOT.
  Propeamussium meridionale (Smith) Kelliella indica n.sp.
  Poromya tornata (Jeffreys) Myonera undata (Verrill)
  281. Seychelles-Ceylon (3°38' N, 78°15' E), 3310 m, (1.7°C), 10 Apr. 1951, ST 300.
- Acar asperula (Dall) Limopsis pelagica pelagica Smith Cetoncha ceylonensis n.sp. Poromya tornata (Jeffreys)
- 282. Seychelles-Ceylon (5°32'N, 78°41'E), 4040 m, (1.4°C), 11 Apr. 1951, HOT. *Limopsis pelagica pelagica* Smith *Propeamussium meridionale* (Smith)
- 299. Bay of Bengal (17°10'N, 84°20'E), 2820 m, (1.8°C), 24 Apr. 1951, HOT.
  Spinula sp.
  Tindaria bengalensis n.sp.
  Acar asperula (Dall)
  Limopsis pelagica Smith
- 314. Bay of Bengal (15°54'N, 90°17'E), 2600 m, (1.9°C), 3 May 1951, HOT. *Acar asperula* (Dall)
  471. Sunda Trench (10°26'S, 114°15'E), 2780 m,
- 4/1. Sunda Trench (10°26 S, 114°15'E), 2780 m, (1.7°C), 9 Sep. 1951, PGI 0.2. *Tindaria sundaensis* n.sp.
- 474. Sunda Trench (9°49'S, 114°13'E), 3840-3810 m, (1.2°C), 11 Sep. 1951, ST 300. *Ledella ultima* (Smith) *Abra profundorum* (Smith)
- 550. Tasman Sea (31°27'S, 153°33'E), 4090 m, (1.2°C), 12 Nov. 1951, PGI 0.2, ST 200, D 45. Acar asperula (Dall) Abra profundorum (Smith) Xylophaga galatheae Knudsen
- 574. Tasman Sea (39°45′S, 159°39′E), 4670 m, (1.2°C), 18 Dec. 1951, ST 600.
  Nuculana pallida (Smith)
  Spinula oceanica Filatova
  Acar asperula (Dall)
  Arca orbiculata Dall
  Propeamussium meridionale (Smith)
  Cyclopecten (H.) sp.
  Abra profundorum (Smith)
- 599. Tasman Sea (45°47'S, 164°39'E), 4390 m, (1.2°C), 13 Jan. 1952, ST 300. Malletia cuneata (Jeffreys) Cuspidaria tasmanica n.sp.
- 601. Tasman Sea (45°51'S, 164°32'E), 4400 m, 1.2°C, 14 Jan. 1952, HOT.

Tindaria antarctica Thiele Kelliella tasmanensis n.sp. Cetoconcha galatheae n.sp. Cuspidaria delli n.sp. Cuspidaria tasmanica n.sp. 602. Tasman Sea (43° 58'S, 165° 24'E), 4510 m, (1.1°C), 15 Jan. 1952, ST 300. Malletia cuneata (Jeffreys) 607. Tasman Sea (44°18'S, 166°46'E), 3580 m, (1.2°C), 17 Jan. 1952, HOT. Spinula tasmanica n.sp. Malletia cuneata (Jeffreys) Malletia galatheae n.sp. 654. Kermadec Trench (32°10'S, 175°54'W), 5850-5900 m, (1.2°C), 18 Feb. 1952, HOT. Spinula kermadecensis n.sp. Nuculanidae sp. Kelliella bruuni (Filatova) 663. Kermadec Trench (36°31'S, 178°38'W), 4410 m, (1.2°C), 24 Feb. 1952, HOT. Acar asperula (Dall) Arca orbiculata Dall Abra profundorum (Smith) 664. Kermadec Trench (35° 34' S, 178° 57' W), 4540 m, (1.1°C), 24 Feb. 1952, HOT. Spinula calcar (Dall) Tindaria antarctica Thiele *Neilonella kermadecensis* n.sp. Malletia cuneata (Jeffreys) Acar asperula (Dall) Arca orbiculata Dall Abra profundorum (Smith) Kelliella sp. 665. Kermadec Trench (36°38'S, 178°21'E), 2470 m, (2.1°C), 25 Feb. 1952, HOT. Ledella kermadecensis n.sp. Propeamussium meridionale (Smith)

- 668. Kermadec Trench (36°23'S, 177°41'S), 2640 m, (2.0°C), 29 Feb. 1952, HOT. *Propeamussium meridionale* (Smith)
- 716. Acapulco-Panama (9°23'N, 89°32'W), 3570 m, (1.8°C), 6 May 1952, HOT. *Limopsis pelagica dalli* Lamy *Dacrydium panamensis* n.sp. *Kelliella galatheae* n.sp. *Policordia* cf. *alaskana* Dall *Cuspidaria haasi* n.sp.
- 724. Gulf of Panama (5°44'N, 79°20'W), 2950-3190 m, (2.0°C), 12 May 1952, ST 600. Malletia cuneata (Jeffreys) Limopsis pelagica dalli Lamy Kelliella galatheae n.sp.

726. Gulf of Panama (5°49'N, 78°52'W), 3670-3270 m, (2.0°C), 13 May 1952, HOT. Acharax johnsoni (Dall) Dacrydium panamensis n.sp. Modiolus abyssicola n.sp. Cyclopecten (H.) graui n.sp. Cyclopecten neoceanicus (Dall) Xylophaga concava Knudsen Lyrodus bipartita (Jeffreys)
759 Decete Dice Terrech (10°45/N) ((°27/M) 2840

758. Puerto Rico Trench (18°45' N, 66°27' W) 2840 m, (2.9°C), 30 May 1952, ST 600. Acar asperula (Dall) Cardiomya abyssicola Verrill & Bush

# LIST BY STATION OF ADDITIONAL SAMPLES

"Albatross":

3604. Bering Sea (54° 54' N, 168° 59' W), 2562 m, (1.8° C), 12 Aug. 1895, large beam trawl. *Tindaria brunnea* Dall *Dacrydium pacificum* Dall

# "Monaco":

2964. N.W.Atlantic (46°17'N, 30"N, 50°42'W), 4380 m, 2.8°C, 20 July 1910. *Cuspidaria testai* n.sp.

#### "Ingolf":

38. N. W. Atlantic (59°12'N, 51°05'W), 3521 m, (1.3°C), 30 July 1895.
Malletia cuneata (Jeffreys)

## "Vitiaz":

- 3156. N.W. Pacific (39°57'N, 165°08'E), 5535 m, (1.6°C), 28 May 1954, Sigsbee trawl. Spinula calcar Dall
- 3162. N.W.Pacific (43°15'N, 157°48'E), 5582 m, (1.6°C), 1 Oct. 1954, Sigsbee trawl. Spinula oceanica Filatova
- 3575. N.W.Pacific (38°02'N, 146°33.1'E), 5450-5475 m, (1.6°C), 8 May 1957. Spinula oceanica Filatova

## "Vema":

- 14. S.E.Atlantic (30°14.9'S, 13°03'E), 3114 m, (2.4°C), 30 Apr. 1957, L.G.O. biotrawl. Arca orbiculata Dall Limopsis pelagica pelagica Smith
- 51. S.E. Atlantic (45°34'S, 06°02'E), 4585 m, (0.9°C), 22 Mar. 1958, L.G.O. biotrawl. *Arca orbiculata* Dall

- SIO:
  - 41. Off the Gulf of California (22°32.2'N, 109° 43'W), 2790-2817 m, (1.5°C), 22 Mar. 1959, deep diving dredge. *Limopsis pelagica dalli* Lamy *Cuspidaria parkeri* n.sp.
  - 42. Off the Gulf of California (22°35.6'N, 110° 06.5'W), 2622-2715 m, (1.5°C), 26 Mar. 1959, deep diving dredge. Limopsis pelagica dalli Lamy
  - 86. Off the Gulf of California (22°38.5' N, 107° 08'W), 2030 m, (2.0°C), 9 May 1959, Petersen grab.
    Arca orbiculata Dall
  - 96. Off the Gulf of California (22°11.2'N, 107° 46.1'W), 3001-2988 m, (2.0°C), 15 May 1959, 40' otter trawl.
    Nuculana agapea (Dall) Limopsis pelagica dalli Lamy
- 128. Off Mexico (14°28'N, 95°09'W), 3529-3557 m, (1.5°C), 18 Nov. 1958, deep diving dredge. Acharax johnsoni (Dall) Limopsis pelagica dalli Lamy Myonera mexicana n.sp.
- 131. Off Guatamala (12°20'N, 91°51'W), 3596-3642 m, (1.5°C), 21 Nov. 1958, deep diving dredge. *Acharax johnsoni* (Dall)
- 139. Off California (29°40.2'N, 117°06.6'W), 2708-2763 m, (2.0°C), 15 Feb. 1960, 30' otter trawl. *Tindaria compressa* Dall *Arca orbiculata* Dall *Limopsis pelagica dalli* Lamy
- 145. Off California (33°40.5'N, 119°29.3'W), 1880-1936 m, (2.5°C), 11 Mar. 1960, 16' otter trawl.

Acharax johnsoni (Dall)

256. Off California (34° 56' N, 121° 49.5' W), 1669-2198 m, (2.5°C), 9 Nov. 1960, 16' otter trawl. *Poromya leonina* (Dall)

274. Off Baja California (30°52′N, 116°53′W),

 274. Off Baja California (30°52′ N, 116°53′ W), 1986-1975 m, (2.5°C), 28 Apr. 1961, 30' otter trawl.

Nucula panamina Dall

285. Off Baja California (23°59.5'N, 113°11.9' W), 3481-3518 m, (2.5°C), 3 May 1961, 10' beam trawl. Arca orbiculata Dall Abra californica n.sp. Poromya perla Dall 287. Off Baja California (27°20'N, 115°23.1'W), 4191-4163 m, (1.2°C), 6 May 1961, 10' beam trawl.
Acharax johnsoni (Dall) Limopsis pelagica dalli Lamy

# A SURVEY OF THE ABYSSAL BIVALVES

## Remarks to Table 1

A survey of all (1152) molluses recorded from depths greater than 1000 fathoms (i.e. 1829 m) was given by CLARKE (1962 a), and the principal points in which the present revised survey of the abyssal and hadal bivalves differs from that of CLARKE are:

1) The upper limit is generally put at a depth of 2000 m (with som exceptions mentioned below) and thereby a number of species listed by CLARKE are excluded.

2) Species recorded from the following seas only have been excluded: the Artic Ocean (southwards to the N. Atlantic Ridge), the Mediterranean, the Red Sea, and the Sulu Sea. The first has a maximum depth of about 4500 m and negative bottom temperatures (to  $-1.6^{\circ}$ C), the three last are characterized by having high temperatures at abyssal depths. Thus, the Red Sea attains a depth of 2100 m with bottom temperatures of about 22°C. The Sulu Sea has a maximum depth of about 5600 m and a bottom temperature of about 10°C, while the Mediterranean has a maximum depth of about 5000 m with a bottom temperature of about 13°C. The four areas mentioned thus exhibit temperatures widely different from that of the world ocean.

3) CLARKE (1962a) listed 41 species of sublittoral and bathyal bivalves which have been recorded from depths below 1000 fathoms, but which have been found only as valves or are obviously misidentifications, and accordingly should not be included in a list of abyssal species.

As a result of my examination of numerous samples of deep-sea bivalves I am able to increase the number of rejected records still further; a few species have been disregarded because they have obviously been listed by mistake or misidentification and no sample of the species in question could be found in the material examined. These rejected records are listed in Table 11 (p. 220). 4) Numerous taxa listed as separate species by CLARKE have been synonymized as a result of the the taxonomic revision I have undertaken.

Table 1 is based on a card index listing all abyssal stations at which bivalves have been obtained and the species in question. In a number of cases it may be difficult to decide whether a station should be considered as abyssal or not, for instance at about 2000 m depth and at 3.9°C containing species known only from that station. In such cases, however, the species have been listed as abyssal. Also, if such a station contains a number of species, these have all been listed as abyssal if at least one of them with certainty can be considered as abyssal. In some areas (E. Pacific) a temperature below 4°C is found at depths considerably less than 2000 m (between 1200 and 1500 m). A few species occurring at these stations could not be considered as bathyal (being known only from a single station), and are tentatively included in the present list.

Cases like these form, however, only a small fraction of the total number of stations dealt with. Usually the stations can easily be classified either as abyssal or as bathyal.

In Table 1 all previous records (with a few exceptions) of the individual species, not dealt with in the taxonomic part, have been listed. Under the heading "number of records", " $\pm$ " indicates that the number given is approximate only. The records of valves are in brackets and, for instance, 8, (3) means that the species in question has been recorded taken alive at eight stations, while valves only were recorded from the three additional stations. The heading "vertical distribution" gives the minimum and maximum records rounded off to the nearest 100 m. In cases where only one record is available, the depth is listed in the column between the minimum and maximum records. The temperature records are arranged in the same way. No temperature records have been listed for the species known from valves only. As far as possible the location of the type is given, and it is indicated whether I have seen the species (+) or not (-).

In the last column I have attempted to assign the individual species to one or several of the following categories: sublittoral, bathyal, abyssal and hadal. This has been done to examine whether it is possible to distinguish between an endemic abyssal fauna and faunal elements which are common to the abyssal zone and one or several of the other regions mentioned.

		No. of records	Horizontal	Verti	cal distrib	ution	Tem	perature i	ange	Type spe	cimen	Depth Zone
Species	Additional records	(a and h) <sup>1</sup> () valves only	distribution	min.	valves on	max.	min.	specimens	max.	Location	the author	O valves only
NUCULIDAE												
Nucula agujana Dall, 1908:370	Hertlein & Strong 1940:384	1	E. Pacific		1900			3.0		USNM	+	a
	Clarke 1962a:47											
- cancellata Jeffreys, 1881 b:951	JEFFREYS 1876a:429	$\pm 15$	N. Atlantic	700		3200	2.4		4.4	?		b+a
	Smith 1885:229					•						
	VERRILL & BUSH 1898:854											
	DAUTZENBERG 1927:288											
	Clarke 1962a:48											
- cardara Dall, 1916:394	Oldroyd 1924:12	(1)	E. Pacific		(2000)					USNM	+	(a)
	Hertlein & Strong 1940:383	•			•							~ /
	Clarke 1962a:48											
- notobenthalis Thiele, 1912:254	Clarke 1962a:48	1	Antartic		2700			0.8			_	a
- obliterata Dall, 1886:247	DALL 1889 b:42	1	W. Atlantic		2900			3.9		USNM	? —	а
	Clarke 1962a:48											
– panamina Dall, 1908; see p. 18		2	E. Pacific	2000		3100	2.4	•	2.5			а
- profundorum Smith, 1885:229	Clarke 1962a:48	(1)	N. Pacific		(3700)			_	•	BMNH	+	(a)
- turnerae Clarke, 1961 b:367	Clarke 1962a:49	1	S. Atlantic		5100			0.3		MCZ	+	a
Brevinucula verrilli (Dall, 1886), see p. 19		8, (3)	Atlantic	1600		3100	2.6		3.3		,	a
Pronucula benguelana Clarke, 1961 b:368	Clarke 1962a:49	3	S. Atlantic	2700-		3800	0.1		2.4	MCZ	+	a
0 ,				3200							1	u
<i>– chrysocoma</i> (Dall, 1908):370	Hertlein & Strong 1940:385	1	E. Pacific		4100			1.8		USNM	+	а
	Clarke 1962a:48				•	•						
NUCULANIDAE												
Pristigloma japonica (Smith, 1885):325	Clarke 1962a:51	1	W. Pacific	•	3400		•	1.8	•	BMNH		а
– <i>nitens</i> (Jeffreys, 1876a):433	Jeffreys 1879:573	$\pm 12$	N. Atlantic	1000?-	•	3500	1.3	•	4.2	USNM	+	а
	Smith 1885:248	•		2300	•	•						
	VERRILL & BUSH 1898:848	•		•	•	•						
~	Clarke 1962a:51	•		•	•	•						
Sarepta abyssicola Smith, 1885:243	Clarke 1962a:51	(2)?	C. & S. Pacific	(3700)	•	(4400)	•	-	•	BMNH	+	(a)
- hadalis n. sp., see p. 23			W. Pacific	•	10.200		•	1.5	•			h
– sp.	Barnard 1963:449	(1)	S. Atlantic	•	2700-		•	-	•			(a)
					3200							
Nuculana agapea (Dall, 1908), see p. 25		3	E. Atlantic	2900		3100	2.0		2.4			а
– extenuata (Dall, 1897):8	Dall 1921:12	1	N. Pacific	•	2900			1.6		USNM	+-	а
	Oldroyd 1924:22	•			•							
	Clarke 1962a:52	•										
- liogona (DALL, 1916):396	Dall 1921:11	1	N. Pacific		2600			1.8	•	USNM	+	а
	Oldroyd 1924:18	•										
	Clarke 1962a:52											
- loshka (Dall, 1908):376	Hertlein & Strong 1940:404	1	E. Pacific		2300			2.4		USNM	+	а

a 10/0 -

# Table 1. List of known abyssal and hadal bivalvia.

• • • • • •			S. W. Pacific	4000			1.2					
- oblonga Pelseneer, 1903:23	Powell 1960:170	1	Antarctic	500		2800	_			?		b+a
0 2	Clarke 1962a:53											
- parsimonia Barnard, 1963:448		1	S. Atlantic	•	2700- 3000		·	2.4	•	SAM		а
- peruviana (Dall, 1908):377	Hertlein & Strong 1940:405 Clarke 1962a:53	(1) ·	E. Pacific	•	1900		•	konst		USNM		(a)
- ramsayi (Smith, 1885):241		(1)	S.W. Pacific		(1700)					BMNH	+	(a)
- vestita (Locard, 1898); see p. 28		9, (2)	E. Atlantic	2300- 2700	•	3000	2.4	•	3.3			а
Ledella crassa n. sp., see p. 30		3	S.E. Atlantic	3200	•	5200	1.2		2.7			а
			S.W. Indian Ocea	n.								
- galatheae n.sp., see p. 32		1	S.E. Atlantic		5100			2.2				a
- inopinata (Smith, 1885):236	Prashad 1932:21	2, (2)	S.W. Pacific	(1200)-		2800	2.4	•	3.1	BMNH	+	а
	Clarke 1962a:53	•	S.E. Asian	1700		•						
- kermadecensis n.sp., see p. 33		1 .	C. Pacific	•	2500	•	•	2.1	•			а
- messanensis (Seguenza, 1877):15	VERRILL & BUSH 1898:856	1	N. Atlantic	1000?		2700	2.4	•	$\pm 9.0?$	?		b+a
	DAUTZENBERG 1927:292	•		•	•	•						
	Clarke 1962a: 52	•		•	•	•						
– <i>pusio</i> (Philippi, 1844):47	Jeffreys 1879:578	1?	N. Atlantic	500		2700	2.4	•	$\pm 10.0$	?		b+a
	Locard 1898:348	•		•	•	٠						
	CLARKE 1962a:53	•		•	•							
– pustulosa (Jeffreys, 1876a):430	Locard 1898:345	3, (3)	N. Atlantic	600?	•	2700	2.4	٠	$\pm 10.0$			b+a
	CLARKE 1962a:53				•		0.1					
- <i>ultima</i> (Smith, 1885), see p. 34		7, (1)	E. & S. Atlantic	2300	•	5100	0.1	·	3,3			а
	Was 10(0.112	1	Indian Antarctic	•		•		2.1				1
– <i>ultraabyssalis</i> (nomen nudum)	WOLFF 1960:113	1	N. Pacific	•	9000	•	•	2.1	•			n
	CLARKE 1902a.32	•		•	•	•						
Spinula hagarani Filataya 1958; saa p. 36	BELIAEV 1900.115	1	N Pacific	•	6800	•		1.8				h
adaar (Dall 1908) see p. 37		$\frac{1}{7(1)}$	Pacific		0800	6100	. 1 1	1.0	18			
- filatovae Knudsen 1967:257		<i>i</i> , (1)	Indian	4100	2300	0100	**1	27	1.0	BMNH		a 3
- kermadecensis n sp. see p. 39		1	C Pacific	•	5900	•	•	i 2	•	Divitvit	I	и Э
- oceanica (Filatova 1958) see p 39		19	W Pacific	4600	0700	6300	12	1,20	17			и Я
- prolata (Smith, 1885):320	CLARKE 1962a:53	1	N. Pacific		5400			1.8		BMNH	+	a
- subercisa (Dautzenberg &	DAUTZENBERG 1927:295	6?	Atlantic	1800?		5100	0.3?-		3.8?	9	, 	a
Fischer, 1897):205	CLARKE 1961 b:377			2800			2.6			•		u
* 1001101 + 105 () + 100	CLARKE 1962a:52						2.0		-			
- tasmanica n. sp., see p. 41		1	S.W. Pacific		3800			1.2				а
- vitvazi Filatova, 1964; see p. 42		7	N. Pacific	6500		8400	1.7		2.0		100 col 100	h
- sp., see p. 44		1	Indian		2800			1.8				а
Phaseolus faba n.sp., see p. 24		1	W. Pacific		7000			1.3				h
Silicula fragilis Jeffreys, 1879:574	Clarke 1962a:54	1	N. Atlantic	1500		2200	2.8		4.2	USNM	+-	b?+a
Yoldia hoylei Smith, 1885:320	Clarke 1962a:54	1	C. Pacific		5300			1.8		BMNH		a
- kermadecensis n. sp., see p. 46		1	W. Pacific		8300			1.5				h

.

Species		No. of		Vert	ical distril	oution	Ten	perature	range	Type spo	ecimen	Depth
Species	Additional records	(a and h) <sup>1</sup> () valves only	distribution	min.	) valves or	nly max.	live min.	specimer	ns only max.	Location	Seen by the author	Zone () valves only
Yoldia leonilda Dall, 1908:382	Hertlein & Strong 1940:417	1	E. Pacific	•	3100	•	•	2.4	•	USNM	+	a
- profundorum Melvill & Standen, 1912:	CLARKE 1962a:55 Powell 1960:170	1	Antarctic	•	2600		•	-1.2		RSM	+	a
- vincula Dall, 1908:379	HERTLEIN & STRONG 1940:413	· 2?	E. Pacific	2700?	•	3100	2.4		2.6?	USNM	+	а
Portlandia abyssicola n. sp., see p. 45 – subcircularis Odhner, 1960:369	CLARKE 19024.55	1 1	Indian W. Atlantic	·	4800 5500-	•	•	1.3 2.1	•	NMG		a a
Yoldiella abyssorum n. sp., see p. 47		1	E. Atlantic		6000 3200			2.7	٠			a
- curta Verrill & Bush, 1898:868	Verrill 18855:576 Clarke 1962a:54	1	N. Atlantic	900	4000	2400	3.2	2.3	4.1	USNM	-+-	a b+a
- dissimilis Verrill & Bush, 1898:872	Soot-Ryen 1966:5 Clarke 1962a:54	3	W. Atlantic	. 2700	•	3100	2.7		3.6	USNM	+	а
- expansa (Jeffreys, 1876a): 431	Jeffreys 1879:580 Locard 1898:354	6? •	N. Atlantic	600?	•	3200?	1.2?	•	10.5	?		b+a
- hadalis n.sp., see p. 49	CLARKE 1962a:52	1 2	W. Pacific		10.000			1.6				h
- <i>lata</i> (Jeffreys, 1876a):431	Soot-Ryen 1966:4 Jefereys 1879:579	, , 2	N. Atlantic	. 300	•	2900	3.3	•	3.7	USNM		a?
	VERRILL & BUSH 1898:866 DAUTZENBERG 1927:294 CLARKE 1962:2:55	•	1.1.2.660.000		• •	5400	2.0	•	±10.0	:	Prosecut	0+a
- <i>lucida</i> (Lovén, 1846):34	Jeffreys 1879:579 Verrill & Bush 1898:861	3	N. Atlantic Arctic	<50	• • •	2500	0?		> 10	?	#1970.00	s+b+a
	Ockelmann 1958:29 Clarke 1962a:54 Soot-Ryen 1966:4		Mediterranean?	•								
- minuscula Verrill & Bush, 1898:870	Verrill 1884:229 Verrill 1885b:576	1	N. Atlantic	1300	• • •	2400	3.2		3.7	USNM	÷	а
- sootryeni n.sp., see p. 50 Nuculanidae sp., see p. 51	Clarke 1962a:55	1 1	E. Atlantic C. Pacific	• • •	3200 5900	•	•	2.7 1.2	•			a
MALLETIIDAE						-	-		·			u
<i>Tindaria acinula</i> (Dall, 1890a):253 - <i>antarctica</i> Thiele, 1931; see p. 52	Clarke 1962a:49	1 5	W. Atlantic Antarctic S. W. Pacific	3500	1600	4600 -	—0.5	3.3	1.3	USNM	+	a a
- atossa Dall, 1908:388	Hertlein & Strong 1940:426 Clarke 1962a:49	2	E. Pacific	1900	•	2300	2.4		2.7	USNM	+	а

	championi Clarke, 1961 b:372	Clarke 1962a:49	2	S. Atlantic	3100		5100	0.3		2.4	MCZ	+	а
_	compressa Dall. 1908: see p. 55		3	E. Pacific	2700		4100	2.0		2.4			а
-	dianhana Clarke, 1961 b:374	Clarke 1962a:50	1	S. Atlantic		5000			1.1		MCZ	-	а
	erebus Clarke, 1959:236	Clarke 1962a:49	1	W. Atlantic		5200			2.2		MCZ		а
-	martiniana Dall. 1916:401	Dall 1921:15	1	E. Pacific		2000			2.5		USNM	+	а
	······	Oldroyd 1924:39											
		Clarke 1962a:49											
	murrayi Knudsen, 1967:252		1	Indian		2300			2.7		BMNH	+	а
	panamensis Dall, 1908:388	Hertlein & Strong 1940:426	1	E. Pacific		2300			2.4		USNM	+	а
	<b>a</b> ,	Clarke 1962a:49											
	quadrangularis (Dall, 1881):387	Dall 1886:253	(1)	W. Atlantic		2600-		•	-		USNM	+	(a)
		Clarke 1962a:50				2900							
<u> </u>	salaria Dall, 1908:387	Hertlein & Strong 1940:427	(1)	C. Pacific		2100			_		USNM		(a)
	·	Clarke 1962a:49											
	similis Okutani, 1962:6	Okutani 1968a:24, 25	1	W. Pacific		3200-			1.6		TFL		a
	,					3500							
	smirna Dall, 1908:389	Hertlein & Strong 1940:427	1	E. Pacific		3100			2.4		USNM		a
		Clarke 1962a:49											
_	sundaensis n.sp., see p. 56		1	Indian		2800			1.7				а
-	thea Dall, 1908:390	Hertlein & Strong 1940:427	1	E. Pacific		2000	•	•	3.0		USNM	+	a
		Clarke 1962a:50	1										
	cf. virens Clarke, 1961:371	Clarke 1962a:50	1	S. Atlantic		3100			2.6		USNM		a
Neilone	ella brunnea (Dall, 1916); see p. 57		1	N. Pacific		2600			1.8		USNM	+	a
berret	galatheae n.sp., see p. 58		1	S. Atlantic		4000			2.3				a
-	guineensis (Thiele, 1931); see p. 59		6?	E. Atlantic	2300	•	4000	2.3		3.3			a
	hadalis n. sp., see p. 61		2	W. Pacific	6700		7000		1.3				h
	kermadecensis n. sp., see p. 63		1	C. Pacific		4500			1.1				a
	menziesi Clarke, 1959:235	Clarke 1962a:50	1	W. Atlantic		5200			2.2		MCZ		а
	sericea (Jeffreys, 1876a):432	Jeffreys 1879:579	4?	N. Atlantic	2400		2700?	2.4		3.0?	USNM?		а
		Clarke 1962a:54	•		•	•	•						
	subovata Verrill & Bush, 1897:57	Verrill & Bush 1898:878	5?	N. Atlantic	200		3200?	3.3		$\pm 10?$	USNM?		b + a
		Clarke 1962a:50				•	•						
Malleti	a abyssorum Verrill & Bush, 1898:875	Clarke 1962a:50	1	W. Atlantic	•	4800	•	•	2.4	•	USNM	+	a
	bermudensis Haas, 1949:5	Clarke 1962a:50	(1)	W. Atlantic	•	3100		•	****	•	FMNH	+	(a)
	concentrica Thiele, 1912:254	Clarke 1961 b:371	3?	S. Atlantic	2700-	•	3400?	0.1?		2.6	ZMHU		а
		Clarke 1962a:50	•	Antarctic	3000	•	•						
	cuneata (Jeffreys, 1876a); see p. 64		23?, (3)	World Ocean	2400	•	6200	1.4	•	3.0	BMNH		а
		_		Arctic									
_	»cuneata« Odhner 1960:368; see p. 66	)	1	W. Atlantic	•	5500-	•	•	•	•			а
		~				6000							
	dunkeri Smith, 1885:323	Clarke 1962a:51	1	N. W. Pacific		3400	•		1.8	•	BMNH	+	а
	estheriopsis Barnard, 1963; see p. 67		5	S. E. Atlantic	3200	•	3400	2.0		3.0	SAM		a
	galatheae n.sp., see p. 69		1	S. W. Pacific		3800			1.2				a

		No. of	TT a loss to 1	Vert	tical distri	bution	Tem	perature	range	Type sp		Depth
Species	Additional records	(a and h) <sup>1</sup> () valves only	distribution	min.	) valves o	nly max.	live min.	specime	ns only max.	Location	Seen by the author	O valves only
Malletia goniura Dall, 1890:251	Dall 1908:386	2	E. Pacific	1400		3100	2.4		3.6	USNM	-+-	а
	Hertlein & Strong 1940:422											
	Clarke 1962a:51											
- johnsoni Clarke, 1961 b:370	Clarke 1962a:51	2	S. Atlantic	1800		3100	2.6		2.9	MCZ	+	а
- obtusa G. O. Sars, 1878; see p. 69		14?	N. Atlantic	400		2900	2.7		8.0			b+a
- peruviana Dall, 1908:384	Hertlein & Strong 1940:424	1	E. Pacific		1900			3.0		USNM	+	a
•	Clarke 1962a:51											
- <i>polita</i> Verrill & Bush, 1898: 876	Clarke 1962a:51	(1)	W. Atlantic		(2900)			*****		USNM	+	(a)
– <i>talama</i> Dall, 1916:400	Dall 1921:14	1	N. Pacific		3200			1.7		USNM	+	a
· · · · · · · · · · · · · · · · · · ·	Oldroyd 1924:36											
	CLARKE 1962a:51											
- truncata Dall, 1908.384	HERTLEIN & STRONG 1940-424	4	E. Pacific	2700	•	3300	2.0		2.6	USNM	+	а
muneura san, 1900.501	CLARKE 1962a:51			_,		0000		•	2.0	ODITIN	1	u
	PARKER 1964.87	•			•	•						
	TARKER TOOLST	•		•	•	•						
SOLEMYIDAE												
Acharax grandis (Verrill & Bush, 1898):885	CLARKE 1962a:55	?	W. Atlantic	700?		2900?		?		USNM	+	(b+a)
<i>– johnsoni</i> (Dall, 1891); see p. 70		7?	E. Pacific	700	•	3600	1.5		5.3	USNM	+	a
ADCIDAE												
Acar asperula (Dall 1881): see p. 73		41-43	World Ocean	400		5000	11		11 7			0
neur asperata (Dan, 1881), see p. 15		(4)	World Occan	400	•	5000	1.1	•	11.7			a
Area orbioulata Dell 1881, and p. 76		24.25	World Ocean	2000		5200	0.2		26			_
Area oroiculata Dall, 1881, see p. 70		(2)	wond Ocean	2000	•	5500	0.3	•	5.0			а
nantungulaidan Sanaahi 1922:92	LOCARD 1808-318	(2)	N & C Atlantia	150.2		2200	27		1.1.2	0		1 ) 9
- pectunculoues Scacelli, 1855.82	Deurapuppa c. 1027-280	14	N. & C. Atlantic	150 :	•	3300	2.1	•	$\pm 12$	ſ		b+a?
	DAUTZENBERG 1927:280	•		•	•	•						
	OCKELMANN 1958:59			•	•	•						
	CLARKE 1962a:56	•		•	•	•						
	SOOT-RYEN 1966:6	•		•	•	•						
LIMOPSIDAE												
Limopsis galatheae n.sp., see p. 81		4	C. & E. Atlantic	4400		5100	2.2		3.0			а
– <i>juarezi</i> Dall, 1908:396	Clarke 1962a:57	2-4	E. Pacific	1700?-		3400-	2.1?		2.79	USNM	+	a
J J	······································			2300	•	4100?		•	<i>2</i>	CONTRA	'	a
- panamensis Dall. 1902:559	Dall 1903:951	1	E. Pacific		1900			27		USNM	-4	2
r mancelos zan, 19021005	DALL 1908:396	*		•	1700	•	•	4.1	·	ODIAM	.Т.	a
	CLARKE 1962 2:57	•		•	•	•						
- nolagies polagies Smith 1995, and	22		Atlantic	1000	•	5000	1 3		20			
- penagica penagica sinti, 1885; see p.	. 05	(2)	Indian	1900	•	5000		•	3.8			a
poloning dalli I 1010, and 00		(3)	E Dooiff-	2100		4000	1.0		~ ~			
- petagica datti Lamy, 1912; see p. 86		15	E. Pacific	2100	•	4200	1.2	•	2.7			а
U. T. C 1076 422	D 1001 110	(1)	NT 4/1. /*	1.000								
- tenella Jettreys, 18/6a:433	DALL 1881:118	5?	N. Atlantic	1600	•	3700	2.3	•	4.7	?		b?+a

	Clarke 1962a:57	1										
MYTILIDAE												
Dacrydium »albidum« Pelseneer, 1903:26	Clarke 1961 b:378	5	Antarctic	351	•	3000-	1.4?	•	2.6	IRSN	-	а
	Clarke 1962a:58	•	S. Atlantic	•	•	4200						
	Dell 1964:177	•		•	•							
<ul> <li>»modioliforme» Thiele, 1912:226</li> </ul>	Thiele in: Thiele & Jaeckel 1931:12	1	Antarctic	400?	•	4600	0.5	•	2.0?	ZMHU	+	a
	Clarke 1962a:58											
– pacificum Dall, 1916; see p. 89		1	N. Pacific		2600			1.8				а
- panamensis n sp., see p. 91		2	E. Pacific	3300		3700	1.8		2.0			а
– »vitreum«	Ockelmann 1958:48	?	N. & C. Atlantic	3800		4500	2.5		3.0			a
Idas argenteus Jeffreys, 1876a:428	Jeffreys 1879:570	1,	N. Atlantic	300		1800-	3.0		$\pm 10$	USNM?		b+a
	Jensen 1912:56	(1)				(2700)						
	DAUTZENBERG 1927:275											
	Clarke 1926a:58											
Modiolus abyssicola n.sp., see p. 92		1	E. Pacific		3500			2.0				a
Adipicola coppingeri (Smith, 1885): 281	Pelseneer 1888:13	1	W. Pacific		2600			2.2		BMNH	+	а
-	Clarke 1962a:58											
Crenella columbiana Dall, 1897: 4	Dall 1921:24	?	N. Pacific	100		4200	0.5		?	USNM?		s+b+a
	Scarlato 1960:66											
	Clarke 1962a:58			•								
PECTINIDAE												
Proneamussium and amanicum Smith 1894.172	KNUDSEN 1967-273	1	Indian	1200		2000	3 /		67	9		1. La
<i>cancellatum</i> Smith, 1885:315	DALL 1886:213	32	N Atlantic	252	•	2000	2.5	•	0.2 	; 9		b+a b⊥a
	CLARKE 1962a:59	5.	14. Milantie	3302	•	4500-	ل . بند	•	T 10	£		0+a
- meridionale Smith, 1885	Contract 1902 and 9	20	Indian	1900	•	4800	0.8		4.0			
see p. 94		20	Antarctic Pacific	1700	•	4000	0.8	•	4.0			a
- octodecim-liratum Melvill &	POWELL 1960-176	2	Antarctic	3700	•	4600	0.3		0.0	DCM		
Standen, 1907:147	CLARKE 1961 b: 378	ind .	marche	5700	•	4000		•	0.9	ROM	Ŧ	a
	CLARKE 1962a:60	•		•	•	•						
– <i>permirum</i> Dautzenberg.	DAUTZENBERG 1927:271	29	N Atlantic	4400	•	1900		28		MOM		0
1925:11	CLARKE 1962a.61	2.	i vi Mianne	4400	•	4900	•	2.0	•	MOM	+	a
- solitarium Smith	ALCOCK & ANDERSON 1897	1	Indian	•	. 3300	•		1 77 9		0		
1894.173	WINCKWORTH 1940.26	,	mulan	•	5500	٠	•	1.74	•	1		a
	CLARKE 1962a:61	•		•	•	•						
	K NHIDSEN 1967:332	•		·	•	•						
- watsoni Smith 1885:309	OKUTANI 1962-15	. 2	W Pacific	2000	•	. 2100	2.1		2.4	DANH		
<i>nation</i> billin, 1005.507	CLARKE 1962a-61	4	TT. I acific	2000	•	<i>4</i> 100	∠.1	•	∠.4	BMNH	+	а
Cyclonecten grauin sp. see n. 97	SEARCE 17020.01	• 1	E Pacific	•	3200	•		20				
eyelepeelen gruut map., 500 p. 27		I	E. Tacine	•	2700	•	٠	2.0	•			а
- hadalis n sn see n 98		2	W Pacific		5700			1.2				1
<i>nuuuus</i> n.sp., see p. 30		2	w. Facilie	0700	•	/000	•	1.3	•			h

		No. of		X7	ant distuit			maratura	******	Type spe	cimen	Depth
Species	Additional records	records (a and h) <sup>1</sup> () valves only	Horizontal distribution	min.	valves of	nly max.	live min.	specimer	max.	Location	Seen by the author	Zone O valves only
Cyclopecten hemiradiatus (de Folin, 1887):	Locard 1898:401	1	E. Atlantic	•	2300	•	•	3.0	•	CERS	+	a
210	Кізсн 1960:144	•		•	•	•			• •			
- neoceanicus (Dall, 1908); see p. 1	00	2	E. Pacific	3300- 3700	•	3800	1.7	•	2.0			a
- notalis (Thiele, 1912):251	Clarke 1962a:61	1	Antarctic		3400		•	0.1	•	ZMHU		а
– <i>liriope</i> (Dall, 1908):402	Grau 1959:27	1	E. Pacific	(1500)		2300	•	2.4	•	USNM	+	а
	Clarke 1962a:59			•		•						
murrayi (Smith, 1885):303	Clarke 1962a:60	1	W. Pacific	•	2600	•	•	2.2	•	BMNH	? —	а
- undatus (Verrill & Smith, 1885);		5, (14)	Atlantic	800		3300	2.0	•	8.0			а
see p. 101		•	Antarctic	•	•	•						
- vitreus (Chemnitz, 1784):335	VERRILL 1897:66	3	N. Atlantic	200	•	3100-	1.5	•	6.0			b+a
	Jensen 1912:27	•		•	•	4300?						
	Grau 1959:47	•		•	•	•						
	Clarke 1962a:60	•		•	•	•						
– sp., see p. 102		1	S.W. Pacific	•	4700	•	•	1.2				a
Delectopecten profundicola Okutani, 1962:16	Okutani 1968a: 24, 25, 68	1	W. Pacific	3200	•	3400	•	1.6	•	TFL		a
- randolphi (Dall, 1897):86	Grau 1959:44	2-5?	N. Pacific	600	•	6800?	0.2		3.4	USNM		b+a+h?
	Scarlato 1960:98	•	Indian?	•	•	•						
	Filatova 1961:133	•		•	•	•						
	Clarke 1962a:60	•		•	•	•						
	Belyaev 1966:115	•		•	•	•						
LIMIDAE												
Limatula confusa (Smith, 1885):292	Jeffreys 1876a:426 Dautzenberg & Fischer 1897:187	1	N. & C. Atlantic	800?	•	2700?	•		•	USNM		b+a
	DAUTZENBERG 1927:25				•							
	Clarke 1962a:62											
– gibba (Jeffreys, 1876a):428		3	N.W. Atlantic	2700?	•	3400?	1.2	•	2.6	USNM	?	а
- subovata (Jeffreys, 1876a):427	Jeffreys 1879:563	8	N. & C. Atlantic	800		3500	1.3	٠	6.1	USNM		b+a
	JENSEN 1912:44				•	•						
	Clarke 1962a:62			•	•	•						
	Soot-Ryen 1966:10	•			•	•						
THYASIRIDAE												
Thyasira brevis (Verrill & Bush, 1898):790	Clarke 1962a:65	?	N. Atlantic	1800?	•	3200	<4	•	$\pm$ 6?	USNM	+	b+a
- equalis (Verrill & Bush, 1898):788	Clarke 1962a:64	2	N. Atlantic	200	•	2800	2.7	•	$\pm 10?$	USNM		b+a
- ferruginea Winckworth, 1932:251	Forbes 1844:192	6, (1)	Atlantic	$<\!200$		3800	0.1	•	>10	?		s+b+a
	DAUTZENBERG 1927:313											
	Clarke 1961 b:379			•		•						
	Clarke 1962a: 65	•		•	•							
- incrassata (Jeffreys, 1876b):492	Jeffreys 1879:703	4	N Atlantic	?	•	3400	1.2	•	$\pm 10?$	?		b+a?
	Clarke 1962a:64											

MONTACUTIDAE												
Montacuta luzonica (Smith, 1885):192	Pelseneer 1888:15 CLARKE 1962a:64	1	S.E.Asian w.	•	1900	•	•	2.8	•	BMNH	+	а
- moseleyi (Smith, 1885):189	PELSENEER 1888:13	1	S. Atlantic	•	3500		•	1.9		BMNH	+	a
	Clarke 1962a:64	•		•	•	•						
- symmetros Jeffreys, 1876b:491	VERRILL & BUSH 1898:796	2	N. Atlantic	2700	•	3200	1.2	•	3.1	USNM	+	а
	CLARKE 1962a:65, 66		D. D	•		•		1.0		TICNING		_
Kelliopsis borniana (Dall, 1908):413	CLARKE 1962a:66	1	E. Pacific	•	3700	•	•	1.0	•	USINM	-1-	a
Tellimya japonica Okutani, 1962:26		1	N. Pacific	•	2300	•	•	2.0	•	IFL		а
SCROBICULARIIDAE												
Abra californica n. sp., see p. 103		1	E. Pacific		3500			2.5				а
- profundorum (Smith, 1885); see p. 104		33, (3)	Atlantic Indian W. & C. Pacific	2100		5300	1.1		3.9			а
VESICOMYIDAE												
Vesicomya angulata (Dall, 1896):19	Dall 1908:419	(2)	E. Pacific	(2300)	÷	(3100)	•			USNM	+	(a)?
	Odhner 1960:374											
	Clarke 1962a:63			•								
- chuni Thiele & Jaeckel, 1931:228	Odhner 1960:374	(1)	E. Atlantic		(2500)	•	•		•	ZMHU	+	(a)?
	Clarke 1962a:63			•	•	•						
– donacia Dall, 1908:417	Odhner 1960:374	(1)	E. Pacific	•	(2300)	•	•		•	USNM	+	(a)?
	Clarke 1962a:63			•	•	•						
- guineensis Thiele & Jaeckel,	Odhner 1960:374	(1)	E. Atlantic	•	(2500)	•	•		•	ZMHU	+	(a)?
1931:229	Clarke 1962a:63			•	•	•						
- longa Thiele & Jaeckel, 1931:229	Odhner 1960:374	(2)	E. Atlantic	•	(2500)	•	•			ZMHU	+	(a)?
	Clarke 1962a:63	•		•	•	•						
KELLIELLIDAE												
Kelliella adamsi (Smith, 1885):155	Odhner 1960:372	2	E. Atlantic	4500	•	5300	•	2.3	•	BMNH	+	а
	Clarke 1962a:63	•		•	•	•						
<ul> <li>atlantica (Smith, 1885):157</li> </ul>	Dall 1886:273	1	C. & W.	1800	•	2900	•	3.8	•	BMNH	+	a
	Smith 1900:82	•	Atlantic	•	•	•						
	DAUTZENBERG 1927:305	•		•	•	•						
	Odhner 1960:374	•		•	•	•						
	Clarke 1962a:63	•		•	•	•						
– bruuni (Filatova, 1969), see p. 107		6	W. Pacific	5900	•	8900- 9200	1.2		1.5			h
- galatheae n. sp. see p. 110		2	E. Pacific	3000- 3200	•	3600	1.8	•	2.0			а
- <i>indica</i> n. sp., see p. 111		1	Indian	•	4400	•		1.3				a

		No. of		Verti	cal distrib	ution	Tem	nerature rs	anoe	Type spe-	cimen	Depth
Species	Additional records	records (a and h) <sup>1</sup>	Horizontal distribution	0	valves or	ylı	live a	specimens	only	Location	Seen by the	Zone O valves
		U valves only		min.		max.	min.		max.		author	oury
Kelliella nitida Verrill, 1885:438	Verrill & Bush 1898:778	1, (1)	W. Atlantic	2800	•	(3700)	•	2.7		NSNM	+	ъ
	DALL 1927:15				•							
	CLARKE 1962a:63	•		•	•							
- pacifica (Smith, 1885):156	SMITH 1885:320	6	C. Pacific	5300	•	6800?	1.5	•	1.8	BMNH	+	a, h?
	ODHNER 1960:374		Indian?	•	•							
	Filatova 1961:133				•	•						
	CLARKE 1962a:63			•								
	Belyaev 1966:112											
- sundaensis n. sn., see n. 113		. <del></del>	Indian		7000			1.5				4
- tasmanensis n sn see n 115			S. W. Pacific	•	4400	•	<b>.</b> .	1.6	•			1 00
- sp., see p. 117		• ••	C. Pacific		4500			1.1				50
4 •												
PHOLADIDAE												
Xylophaga abyssorum Dall, 1886:317	TURNER 1955:156	5	W. Atlantic	250	·	2500	4	•	15?	MCZ	+	b+a
	KNUDSEN 1961:203	•		•	•	•						
- africana Knudsen, 1961:186		-	E. Atlantic	•	2600			3.0		ZMUC	+	a
- atlantica Richards, 1942:68	TURNER 1955:152		W. Atlantic	0	•	3200	ż	·	23	ANSP	1	s+b+a
	KNUDSEN 1961:203			•	•	•						
- concava Knudsen, 1961:167		1	E. Pacific	-006	•	3300-	2.0		5.0	ZMUC	+	b+a
				1000	•	3700						
- galatheae Knudsen, 1961:171			S. W. Pacific	•	4500		•	1.0	•	ZMUC	+	9
- grevei Knudsen, 1961:176		m	S.E. Asian w.	600	•	7300	3.6	•	11.7	ZMUC	+	b+(a) $\pm b$
– <i>vuineensis</i> Knudsen, 1961:195		Ξ	E. Atlantic		2600			3.0		ZMUC	4	- e
- hadalis Knudsen, 1961:173		) <del>-</del>	W. Pacific	•	6700			1.3		ZMUC	• +	h
a v chuide dati												
LENEDINIDAE Lynodus hinartita (Jeffreus 1860): see n 118			F Atlantic-	C		3700	00		20			0
			E. Pacific	,	•		i	•	ì			5
Bankia carinata (Gray, 1827); see p. 118		1	Atlantic, Indian,	0		7300	3.6	•	> 20			s
			S.E. Asian w.,	•	•	•						
			N. W. Pacific	•	•							
Uperotus clavus (Gmelin, 1791); see p. 118		1	Indian, S.E.	0	•	7300	3.6	•	> 20			s
			Asian w.	•	•	•						
			W. Pacific	•	•	٠						
PHOLADOMYIDAE												
Pholadomya africana P. Fischer, in:	CLARKE 1962a:68	1	E. Atlantic		2100-		3.4?- :	5.0?	•	MNHN		a
LOCARD 1898:165					2300	-						

THRACHDAE

$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	VERRILL 1884:221 Dall 1886:283 Dall 1889 a:447
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ODHNER 1960:38 CLARKE 1962a:68
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	~
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	DALL 1916:407
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ABBOTT 1951:33
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	CLARKE 1962a:70
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Pelseneer 1888:22
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	CLARKE 1962a:70
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ABBOTT 1951:55 Clarke 1962a:71
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	OLSSON 1961:467
14, (9)?       E. Pacific       2000       .       3500       .       2.5       .         14, (9)?       Atlantic       3100       .       5300       1.1       .       3.0         14, (9)?       Atlantic       3100       .       5300       1.1       .       3.0         1       E. Atlantic       3100       .       4800       .       1.9       .       USNM         1       C. Pacific       .       2100       .       4400       2.6       .       3.0       BMNH       +         2       C. Atlantic       3400       .       4400       2.6       .       3.0       BMNH       +         2       C. Atlantic       3400       .       4400       2.6       .       3.0       BMNH       +         1       C. Pacific       3400       .       4400       2.6       .       3.0       BMNH       +         3       E. Atlantic       .       .       .       .       .       .       .         3       E. Atlantic       .       .       .       .       .       .       .       .       .       .       .       .	
	CLARKE 1962a:70
1       E. Atlantic       4800       13       10         1       C. Pacific       19       19       10         2       C. Atlantic       3400       4400       2.6       3.0       BMNH       +         2       C. Atlantic       3400       4400       2.6       3.0       BMNH       +         2       C. Atlantic       3400       1400       2.6       3.0       BMNH       +         3       E. Pacific       600-       3600       1.6       .       3.0       BMNH       +         1, (1)       N. Atlantic       3300       .       2.7       .       WMN       +         1, (1)       S. Atlantic       .       2300-       .       .       .       WMN       +         (1)       S. Atlantic       .       2300-       .       .       .       WMN       +         (1)       S. Atlantic       .       .       .       .       .       WMN       +         .       .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       . <t< td=""><td></td></t<>	
1       E. Atlantic $\cdot$ 4800 $\cdot$ $\cdot$ $1.3$ $\cdot$ $USNM$ $+$ $\cdot$ C. Pacific $\cdot$ $2100$ $\cdot$ $1.9$ $\cdot$ $USNM$ $+$ $\cdot$ C. Atlantic $3400$ $\cdot$ $4400$ $2.6$ $\cdot$ $3.0$ $BMNH$ $+$ $\cdot$ $\cdot$ $ 4400$ $2.6$ $\cdot$ $3.0$ $BMNH$ $+$ $\cdot$ $  4400$ $2.6$ $\cdot$ $3.0$ $BMNH$ $+$ $\cdot$ $  4400$ $2.6$ $\cdot$ $3.0$ $BMNH$ $+$ $\cdot$ $  4400$ $2.6$ $\cdot$ $3.0$ $BMNH$ $+$ $\cdot$ $                            -$ <td></td>	
	Clarke 1962a:69 Soot-Ryen 1966:24
R <td< td=""><td>SMITH 1885:75 Der senteren 1889:17</td></td<>	SMITH 1885:75 Der senteren 1889:17
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	DAUTZENBERG & FISCHE 1897:228
.       E. Pacific       600-       .       3600       1.6       .       .         3       E. Pacific       600-       .       3600       1.6       .       .         1, (1)       N. Atlantic       .       3300       .       2.7       .       USNM         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       . <t< td=""><td>DAUTZENBERG 1927:348</td></t<>	DAUTZENBERG 1927:348
3       E. Pacific       600-       .       3600       1.6       .       .         1, (1)       N. Atlantic       .       3300       .       2.7       .       USNM         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       .       .         .       .       .       .       .       .       .       WNM       +         .       .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       .       MNHN         .	CLARKE 1962a:69
3       E. Pacific       600-       .       3600       1.6       .       .         1, (1)       N. Atlantic       .       3300       .       .       2.7       .       USNM       +         .       .       .       .       .       .       .       .       NMIN         .       .       .       .       .       .       .       NNIN       +         .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       .       MNHN         . </td <td>SOOT-RYEN 1966:24</td>	SOOT-RYEN 1966:24
1, (1)       N. Atlantic       .       3300       .       2.7       .       USNM       +         .       .       .       .       .       .       NHNN         .       1)       E. Atlantic       .       2300-       .       .       NHNN         .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       .       MNHN         .       .       .       .       .       .       .       .       .       .       .         . <td></td>	
(1)       E. Atlantic       :       2300-       :       -       MNHN         .       .       .       2500       :       -       .       MNH         (1)       S. Atlantic       .       (3500)       :       -       .       BMNH       +	CLARKE 1962a:69 Soot-R ven 1966.31
. 2500 . (1) S. Atlantic . (3500) . – BMNH +	CLARKE 1962a:69
(1) S. Atlantic . (3500) – . BMNH +	SOOT-RYEN 1966:21
	CLARKE 1962a:69 Soot-R ven 1966.20

		No. of	Horizontal	Vertica	al distrib	ution	Tem	perature 1	ange	Type spe	cimen	Depth Zone
Species	Additional records	(a and h) <sup>1</sup> () valves only	distribution	O v min.	alves on	ly max.	live min.	specimens	only max.	Location	Seen by the author	O valves only
Policordia insculpta (Jeffreys, 1881b):932	DAUTZENBERG 1889:88	2	E. & C. Atlantic	100-	•	3900	2.5	±10		USNM	+	s+b+a
	Locard 1898:206			200								
	DAUTZENBERG 1927:347	•		•	•	•						
	Clarke 1962a:69			•	•							
	SOOT-RYEN 1966:20											
- lisbetae n.sp., see p. 132		1	E. Atlantic	•	2700		•	2.8				а
<i>– papyracea</i> (Smith, 1885):73	Pelseneer 1888:18	1 + 1?	Antarctic	1800		3600	0.0		1.9	BMNH	+	а
	Sмітн 1906:263		Indian	•								
	WINCKWORTH 1940:28											
	Clarke 1962a:69											
	Soot-Ryen 1966:21											
	Knudsen 1967:335											
- triangularis (Locard, 1898):	Clarke 1962a:70	1	C. Atlantic		3000			3.4		MNHN	( +	a
Thracidora transversa (Locard, 1898):201	Clarke 1962a:70	1	C. Atlantic		4200			2.9		MNHN	· +	a
Verticordia granulifera (Verrill, 1885a):434	Verrill & Bush 1898:816	2, (1)	W. Atlantic	(2600)-		3400	2.3		2.9	USNM	-+-	a
	Clarke 1962a:69			3100						0.01111		
– guineensis Thiele & Jaeckel.		·		0.00		•						
1931:246	CLARKE 1962a:69	1	E. Atlantic		2300			3.3		ZMHU		а
Halicordia auadrata (Smith, 1885):169	CLARKE 1962a:69	1	E. Atlantic		2100	·	•	39	•	?	<u> </u>	a
	SOOT-RYEN 1966:25	•					·	5.5	·	·		u
CUSPIDARIIDAE												
Myonera garretti Dall, 1908:434		1	E. Pacific		1600			2.9		USNM		а
- gigantea (Verrill, 1884):223	VERRILL & BUSH 1898:811	(3)	W. Atlantic	(3300)		(3500)				USNM	+	(a)
	Clarke 1962a:71, 73			`.							•	()
– laticella Dall, 1886:305		1	W. Atlantic		3100			4.1	-	USNM	-+-	а
- mexicana n. sp., see p. 134		1	E. Pacific		3500			1.5				a
- murrayi (Smith, 1885):319	Clarke 1962a:72	1	C. Pacific		5300			1.8		BMNH	-+-	a
- ruginosa (Jeffreys, 1881b):942	Locard 1898:182	1	N. Atlantic	400 ?-		3300	2.7		+12	?		$b^{-}$
	Verrill & Bush 1898:811			1800						•		0.14
	DAUTZENBERG 1927:337											
	Clarke 1962a:73								•			
<i>– undata</i> (Verrill, 1884); see p. 136		11. (1)	Atlantic	4300	•	5300	0.7	•	28			9
		,(1)	Indian	1000	•	2200	0.17	•	2.0			u
Cardiomya abyssicola Verrill & Bush 1898		(2)	C Atlantic		(3000)							(a)
see n 138		(4)	Corthannie		(3000)	•	•		•			(a)
- sihagai (Preshed 1932).331		1	S E Asian w		2100			2.2		714		c
Cusnidaria anodama Dall 1916:407	DALL 1921-28	(1)	D. E. Asiali W.	•	2100	•	•	3.3	•	LINA	· •••••	a
Caspiaaria apoaema 19an, 1910.407	OLDBOYD 1924-98	(1)	iv. racine	. (	(2900)	•	•	*****	•	USINM		a
	CLARKE 10620-71	•		•	•	•	•	•				
harmardin on soon 120	CLARKE 1902a:/1	1	Indian	•		•	•					
- ournaria in sp., see p. 159		1	mulan S. W. D 10	•	3300	•	•	1.1	•			а
- <i>aeui</i> n. sp., see p. 141		1	S. W. Pacific		4400			1.2				а

	guineensis n. sp., see p. 145		1	Lo / Municiv	•	2000	•	•		•			
	haasi n.sp., see p. 145		1	E. Atlantic	•	3600			1.8				a
	hadalis n.sp., see p. 146		2	S.E.Asian w.	6600		7300	3.5		3.6			h
	lischkei Smith, 1891:438	Clarke 1962a:73	1	W. Pacific		3400			1.8		BMNH	-+-	а
-	cf. maxima Barnard 1963:451		(2)	S. Atlantic	(2700-		(2900)						(a)
					3200)								
-	meridionalis (Smith, 1885):43	Clarke 1962a:72	(1)	Antarctic	•	(3600)			_		BMNH	-+-	(a)
-	natalensis n. sp., see p. 148		1	Indian		2600			2.5				а
-	»panamensis« see p. 179		2	E. Pacific	2000		2800	1.5		2.5	USNM	+	а
_	parkeri n. sp., see p. 150		1	E. Pacific	•	2800			1.5				а
	parva Verrill & Bush, 1898:801	Clarke 1962a:72	1	N. Atlantic	900-		2400	3.2	•	4.3	USNM	+	b+a
					1300								
	cf. rostrata (Spengler, 1793)		2	E. Atlantic		3000			2.5		?		а
-	semirostrata Locard, 1898:177	Clarke 1962a:72	(2)	N. Atlantic	(2100)		(3200)	•			MNHN	+	(a)
-	subglacialis Dall, 1913:593	DALL 1921:28	1	E. Pacific		(2000)			•		USNM	+	а
		Oldroyd 1924:98			•		•						
-	tasmanica n. sp., see p. 152		2	S.W.Pacific		4400		•	1.2				а
	testai n. sp., see p. 154		1	N.W.Atlantic		4400			2.8				a
1	turgida Verrill & Bush, 1898:799	Clarke 1962a:73	1	W. Atlantic	•	3300		•	2.3	•	USNM	+	а
	ventricosa Verrill & Bush, 1898:802	Clarke 1962a:73	(2)	W. Atlantic	•	(3200)	•	•	•	•	USNM	+	а
GALAT	THEAVALVIDAE												
Galatheau	valva holothuriae n.sp., see p. 156		2	Indian	•	4800	•	•	1.3				a

Nucula cancellata JeffreysIdas argenteus JeffreysLedella messanensis (Seguenza)Propeamussium andama- pusio (Philippi)- cancellatum Smith- pusio (Philippi)- cancellatum Smith- pusulosa (Jeffreys)Delectopecten vitreus (ChaSilicula fragilis JeffreysDelectopecten vitreus (ChaYoldiella curta Verrill & BushLimatula confusa (Smith- expansa (Jeffreys)- subovata (Jeffreys)- lata (Jeffreys)Thyasira brevis Verrill- lucida (Lovén)- equalis (Verrill & BushMalletia obtusa G. O. Sars- incrassata (Jeffreys)Acharax grandis (Verrill & Bush)- subovata (Jeffreys)- subovata G. O. Sars- incrassata (Jeffreys)- subovata (Jeffreys)- subovata (Jeffreys)- incrassata (Jeffreys)- subovata (Jeffreys)	Vesicomya angulata (Dall)nicum Smith- chuni Thiele & Jaeckel- donacia Dallemnitz)- guineensis Thiele & Jaeckeli (Dall)- longa Thiele & Jaeckelch)Xylophaga abyssorum Dall- atlantica Richards& Bush- concava Knudsenish)- grevei KnudsenrthPolicordia insculpta (Jeffreys)Myonera ruginosa (Jeffreys)Cuspidaria parva Verrill & Bush
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A closer examination of the distribution of the species occurring both in the abyssal and in the overlying zones clearly shows that many species have their main distribution in the bathyal zone (a few in the lower part of the sublittoral zone), extending their vertical distribution more or less into the abyssal zone. They have been considered as "guests" in the abyssal zone.

The majority of the species, however, are confined in their vertical distribution to the abyssal zone and may be termed endemic abyssal species.

#### The "guest" species

The occurrence of "guests" in the abyssal zone is a well-known phenomenon and has been discussed by MADSEN (1961b) who gives examples from different phyla (Coelenterata, crustaceans, echinoderms, molluscs). He states that the presence of "guests" from the overlying region makes it possible to distinguish between several subregions of the abyssal zone, since the bathyal zones have rather restricted distributions. A population which has descended into the abyssal may be unable to reproduce (although, as far as I know, this has never actually been investigated), being dependent on the bathyal population for its replenishment. Other species, however, may be better adapted to the life in the abyss and be able to reproduce under favourable food conditions.

A total of 38 species of bivalves should probably be considered as "guests" in the abyssal zone (Table 2). It is possible, however, that the majority of the bathyal species may establish themselves, at least for some time, in the abyssal zone. One of the species listed in Table 2, *Delectopecten randolphi*, is found in the deepest part of the abyssal zone (and possibly also the hadal zone see p. 221), but otherwise the remaining species are recorded essentially from the upper part of the abyssal zone. This appears from the following survey of the lower limit of 35 of the species (in two species, *Amussium cancellatum* and *Cyclopecten vitreus*, the available indication of the greatest depth is such a wide depth range that it is useless).

Greatest depth	No. species
2000-2400 m	6
2500-2900 m	13
3000-3400 m	11
3500-3900 m	5
4000 +	0

It will be noted that from the depth interval 2500-2900 m and downwards there is a regular decrease of "guests" from the overlying zones. Only five species penetrate down to the 3500-3900 zone, and not a single bathyal species has been found deeper.

It should be mentioned that the following three species have been found both in the sublittoral, bathyal and the hadal zones, and no doubt the species occur also in the abyssal zone:

*Xylophaga grevei* Knudsen (1961, p.176), S.E. Asian waters, bathyal, 600-1500 m and hadal, 7300 m.

Bankia carinata (Gray), see p.118. Widely distributed. Littoral and hadal, 7300 m.

*Uperotus clavus* (Gmelin), see p. 118. Indian Ocean, N.E. Australia, Japan. Littoral, hadal, 7300 m.

However, it is not possible at present to make an absolutely clear distinction between the endemic abyssal species and the "guest" species. One main reason for this is the fact that there are too few records of the majority of the species.

#### Notes on some of the species listed in Table 1

The following abyssal species are figured here for the first time:

Nuculana liogona (Dall): Pl.1, Figs.6, 7. Tindaria martiniana Dall: Pl.3, Fig.10. Tindaria thea Dall: Pl.3, Fig.9. Malletia talama Dall: Pl.6, Fig.14.

Laevicordia pacifica (Dall): Pl.15, Figs. 3, 4.

Cetoconcha malespinae (Ridewood): Pl. 15, Figs. 6, 7.

Myonera laticella Dall: Pl. 16, Figs. 9, 10.

Cuspidaria apodema Dall: Pl. 16, Figs. 11, 12.

#### Nucula obliterata Dall, 1886.

DALL (1886, 1889b) referred a number of samples of *Nucula* from about 180 to 2909 m depth to *N. crenulata* Adams var. *obliterata*. I found that one sample (one specimen with dry soft parts) from "Blake" St. 236 at 2909 m depth, differed widely from the rest and evidently is specifically different, close to, and possibly conspecific, with *N. cancellata*. I propose that provisionally the specific name *obliterata* be used for the specimen.

#### Pronucula chrysocoma (Dall, 1908).

The species appears to be closely related to P. benguelana Clarke (Pl. 1, Fig. 5). However, the latter has about 65 radiating ribs, while 56-58 are present in P. chrysocoma.

#### Pristigloma nitens Jeffreys.

The species has been recorded by SMITH (1885) from "Challenger" St. 323, S.W. Atlantic, 3475 m. I have not seen the sample, which does not seem to be in the collection of the BMNH. The record should be considered doubtful.

#### Sarepta abyssicola Smith, 1885.

Both of the samples recorded by SMITH (1885), including the type, have been destroyed by shell disease.

# Ledella inopinata (Smith, 1885) (Pl.2, Figs. 6, 7).

Both the "Challenger" and the "Siboga" samples have been examined and found to be conspecific.

#### Yoldia leonilda Dall, 1908.

The type (the only specimen present) has dry soft parts. The shell is heavily corroded and fragmented. It has never been figured.

#### Yoldia vincula Dall, 1908.

DALL records the species from the type locality, "Albatross" St. 3360, (3058 m), from St. 3361, (2690 m), and from St. 3354, (589 m). The samples from the two latter stations could not be located at the USNM, and the records from St. 3354 is highly improbable and should be disregarded.

## Yoldiella inflata Verrill & Bush, 1898.

SOOT-RYEN (1966) recorded a live specimen from the Michael Sars Expedition St. 70, N.W. Atlantic, 1100 m.

#### Tindaria panamensis Dall, 1908.

Appears to be closely related to T. martiniana Dall, 1916. A comparison of the types of the two species showed differences in the sculpture and also in other characters.

## Tindaria quadrangularis (Dall, 1886).

The only material available consists of a worn valve without any trace of soft parts.

#### Tindaria salaria Dall, 1908.

The only material available consists of three valves in very poor condition and without any trace of the soft parts. The species has never been figured.

#### Tindaria sericea (Jeffreys, 1876).

It is doubtful whether the specimens assigned to T.sericea by DAUTZENBERG (1927) actually are conspecific with JEFFREYS' species.

#### Tindaria smirna Dall, 1908.

The species is closely related to T.atossa Dall and may be conspecific with it.

#### Tindaria cf. virens Clarke, 1961.

T. virens Dall, 1890a (p. 254, pl. 13, fig. 3) was obtained in the S.E. Pacific, off Chile, 223-821 m. By comparison with paratypes CLARKE (1961b) found differences in the hinge teeth between the "Vema" specimens and T. virens, concluding that the differences are too slight to be given taxonomic significance. I have not seen any specimens, but the identification seems unlikely and should be examined more closely.

#### Tindaria sp.

Listed as *Neilonella subovata* Verrill & Bush, 1897 by WOLFF (1960).

#### Neilonella subovata Verrill & Bush, 1897.

VERRILL (1884) originally had assigned the specimens to *N. sericea* var. *striolata*. I have not studied the samples. The figures of *N. sericea* and *subovata* indicate that the revised conclusion of VERRILL & BUSH (1897) is correct, but a detailed study of all available material is much needed. *Neilonella subovata*, listed by WOLFF (1960), is probably a *Tindaria* sp.

#### Acharax grandis Verrill & Bush, 1898.

VERRILL & BUSH (1898) recorded the species from "1600 fathoms" without giving, however, any station number. The sample was found neither at the MCZ, nor at the USNM. The only sample seen by the present author is from "Albatross" St. 2213, at a depth of 700 m. It consists of worn fragments only.

# Arca cf. pectunculoides Scacchi, 1833 Pl.8, Figs. 11-13.

OCKELMANN (1958) states *A.pectunculoides* to be rather polymorphus. The species was described from Miocene and Pliocene deposits in Europe (SORGEN-FREI 1958). The problem of whether the recent and the fossil "*pectunculoides*" are really conspecific should be carefully re-considered. I have examined *A.dakarensis* Locard, 1898 (p. 321, pl. 13, figs. 25-28). It is known from a single valve only, obtained from "Talisman" St. 105, from a depth of 3200 m. It is undoubtedly *A.pectunculoides*.

#### Limopsis juarezi Dall, 1908.

DALL (1908, p. 396) described *L. stimpsoni*, which appears never to have been figured, from "Albatross" St. 3392, 2323 m. I have examined the type specimen and compared it carefully with *L. juarezi*. DALL (1908) recorded *L. juarezi* both from "Albatross" St. 3360, 3058 m and from St. 3418, 1207 m. At the latter station, however, only a single 4 mm long specimen was found, which appeared to be different from *L. juarezi*.

#### Limopsis panamensis Dall, 1902.

The epidermal bristles are black, crescent-shaped in cross section, dorsally curved, and very pointed. No other species I have seen shows similar bristles.

#### Limopsis tenella Jeffreys, 1876.

The species appears not to be figured. I have not seen any specimen, and no information is available regarding the occurrence of live specimens.

#### Dacrydium "albidum" Pelseneer, 1903.

The species was described from the Antarctic Ocean (Pacific sector) at a depth of 400 m. CLARKE (1961 b) referred his specimens from the S. Atlantic from abyssal depths to *D. albidum*, expressing, however, some doubt as to the assignment. A more detailed study of the material is necessary, before *D. albidum* can be included in the abyssal species. CLARKE's specimens may be one or several new species.

#### Dacrydium modioliforme Thiele, 1912.

The species was described from the "Gauss" station in the Antarctic Ocean, at about 66° S and 90° E, 385 m. THELE (1931) identified a specimen from "Valdivia" St. 152, Antarctic Ocean, 4636 m, as *D.modioliforme*. I have seen the latter specimen, which has dry soft parts. In fact it differs widely from *D.modioliforme*, and should probably be considered as specifically different.

#### Amussium cancellatum Smith, 1885.

JEFFREYS (1879, p. 561) recorded a specimen from "Porcupine" St. 37 as *A. fenestratum* var. *cancellata*. DALL (1886) with some doubt considers it a synonym of *A. cancellata*, recorded by DALL (1886) from a number of bathyal stations, plus a single finding from about 25 m depth. I have not seen the material. Possibly several species are merged together.

Amussium octodecim-liratum Melvill & Standen, 1907 (Pl. 12, Figs. 10-12).

The species appears to be closely related to *A. permirum* Dautzenberg, 1925. In the latter the number of costae is 13, and the concentric sculpture of the right valve is much less developed, and not cancellate as in *A.octodecim-liratum*. In addition, there are differences in the size and shape of the auricles, and in the shape of the posterior part of the shell.

#### Amussium solitarium Smith, 1894.

There is nothing to indicate whether live material was obtained.

#### Amussium watsoni Smith, 1885.

OKUTANI (1962) assigned his specimens to a new subspecies *bayonnaisense*, distinguished from the nominate subspecies by lacking serration of the dorsal edge. The validity of the subspecies was refuted by KNUDSEN (1967).

Cyclopecten hemiradiatus (de Folin 1887) (Pl.14, Fig.5).

The type (the only specimen known) is a wellpreserved specimen with remnants of the soft parts. REHDER (1946) states the year of publication to be 1887 and not 1884 as given by LOCARD (1898).

#### Cyclopecten liriope (Dall, 1908).

GRAU (1959) referred two valves from "Albatross" St. 2807, 1485 m, to *C.liriope*.

#### Cyclopecten vitreus (Chemnitz, 1784).

SMITH (1885, p. 303) recorded *Pecten vitreus* from the S.E. Pacific, off Japan and the Philippines, at a total of eight stations, 183-1280 m. GRAU (1959, p. 47) accepts the identification. The samples should, however, be thoroughly studied and compared to samples from the N.Atlantic before the conspecificy is accepted. JENSEN (1912) found that the species was widely distributed in the North Atlantic, most of the records being from bathyal depths. It was found that the species does not enter into the "cold" area north of the N.Atlantic ridge. CLARKE (1962a) states that this is the only abyssal noncephalopod mollusc now thought to be cosmopolitan.

I have not made a thorough examination of the samples from outside the N. Atlantic, but find it unlikely that the species should have such a wide horizontal and vertical distribution as stated by CLARKE (1962a).

#### Limatula gibba (Jeffreys, 1876).

The species has never been figured, and I have not seen JEFFREYS' samples. J.STUARDO, revising the family Limidae, states (personal communication) that *L.gibba* seems a good species, but closely related to both *L.confusa* (Smith) and *L.subovata* (Jeffreys).

#### Thyasira tricarinata Dall, 1916.

The species was not figured by DALL, and is only known from a single locality, "Albatross" St. 4425, off California. I have compared the type to *T. excavata* Dall (1901, p. 818, pl. 39, figs. 12, 15). The latter species is known from the Gulf of California and off Oregon, 1437 and 1840 m. It appears to be known from valves only. The comparison strongly indicates that *T. tricarinata* might be a synonym of *T. excavata*. OLDROYD (1924) considered them separate species.

Montacuta luzonica (Smith, 1885).

Assigned to *Cryptodon* (Thyasiridae) by SMITH (1885) and PELSENEER (1888).

#### Montacuta moselevi (Smith, 1885).

Assigned to *Cryptodon* (Thyasiridae) by SMITH (1885) and PELSENEER (1888).

#### Montacuta symmetros (Jeffreys, 1876).

OCKELMANN (personal communication) considers *Axinodon ellipticus* Verrill & Bush (1898) to be a synonym of *M.symmetros*.

#### Asthenothaerus sp.

PELSENEER (1888) gave a brief description and a figure of the soft parts. The species was not included in PRASHAD's report (1932), and the shell seems never to have been figured.

## Cetoconcha bulla (Dall, 1878).

The sample reported on by ODHNER (1960) consists of two specimens without shells. The identification remains somewhat uncertain. CLARKE (1962a) listed the species both under *Lyonsia* (p. 68) and *Cetoconcha* (p. 70).

#### Cuspidaria filocarinata Smith, 1885.

LOCARD (1898, p.177) recorded the species from two bathyal stations in the E.Atlantic, 1213 and 1353 m. I have not seen the samples, but the identification is possibly incorrect.

# Cuspidaria panamensis Dall, 1908 (Pl. 16, Figs. 6, 7).

PARKER (1964) referred two samples of *Cuspida*ria from the E. Pacific (SIO St. 41, 2800 m depth, and St. 274, 2000 m depth) to *C.panamensis* Dall. This species is known from the E. Pacific at about 1000 m depth ("Albatross" St. 3394). I have compared PARKER's material with the type, a specimen with dry soft parts. There are marked differences between PARKER's specimens and *C.panamensis*, and they are not conspecific. Differences are found in the sculpture, the shape of the posterior adductor scar and the hinge tooth of the right valve.

#### Cardiomya pseustes (Dall, 1908) (Pl. 16, Figs. 2, 3).

The species has never been figured. It was described by DALL (1908, p.432) from the Gulf of Panama ("Albatross" St. 3392, 2323 m). I have examined the type which consists of a pair of valves without soft parts. By comparison with the type of *C.planetica* Dall I found that they were certainly

conspecific. The latter species has been recorded from the N. Pacific (Aleutian Is.) to the Galapagos region at depths between 150 and 2500 m. The type is from "Albatross" St. 2925, about 620 m. I have not seen any material from 2500 m depth.

#### Cuspidaria cf. rostrata (Spengler, 1793).

I have seen JEFFREYS' samples. One sample from "Porcupine" St. 11 consists of a small, well preserved specimen. It is completely covered with mud and it is unlikely that JEFFREYS could actually identify the specimen. The other sample comes from "Porcupine" St. 55 and comprises several valves and at least one specimen with dry soft parts. It may be *C. rostrata* or a closely related species.

#### Cuspidaria ventricosa Verrill & Bush, 1898.

VERRILL & BUSH (1898) recorded the species from three "Albatross" stations. I have examined all three samples at USNM, consisting of valves without the soft parts. Two samples, from Sts. 2572 and 2715, 3235 and 3206 m, were conspecific while the third sample from St. 1093, 638 m, obviously should be referred to a different species. The type is a somewhat worn left valve labelled "Type" no.78783.

# THE ENDEMIC ABYSSAL BIVALVE FAUNA

#### The families

The composition of the endemic abyssal bivalve fauna appears from Table 3 which gives the number of known endemic abyssal species within each family and their percentage of the total fauna. It appears that until now 20 families have been recorded, including the monotypic Galatheavalvidae and the Pholadomyidae and Thraciidae, each represented only by a single species recorded once from the uppermost part of the abyssal zone. Possibly the two last-mentioned families should not be considered as abyssal. VOKES (1967) recognizes 80 families of recent marine bivalves, and thus only one fourth (or a little less) is represented in the abyssal fauna. Apart from the Galatheavalvidae, all the families are also well known from more shallow water. In fact, most families occur in the upper part of the sublittoral zone.

It is of some interest to make a comparison with the two other major cold water faunas of the world, viz., the antarctic and the arctic shallow water faunas.

Regarding the antarctic fauna, EKMAN (1953) and many earlier workers distinguished between an antiboreal (= subantarctic) fauna and an antarctic fauna. The former is delimited towards the north by the antiboreal convergence, and the latter, i.e., the antarctic region, is delimited towards the north by the antarctic convergence. DELL (1964), however, states that recent workers have begun to treat the antarctic and the subantarctic fauna as a whole. The antarctic shallow water bivalve fauna is assigned to some 30 families (DELL 1964), while the arctic bivalve fauna comprises about 19 families (OCKELMANN 1958). Twelve families are common to the antarctic and the abyssal faunas. Among the 18 families found in the Antarctic, but not in the abyssal, the following should be mentioned: Philobryidae (confined to antarctic sublittoral waters, a few species are bathyal in the regions adjacent to the Antarctic), Carditidae (widely distributed in sublittoral waters, numerous species in tropical shallow water regions), Condylocardiidae (mainly antarctic, exclusively sublittoral), Cyamiidae (antarctic and warm temperate regions, mainly sublittoral), and Gaimardiidae (antarctic and warm temperate regions of the southern hemisphere). The remaining families found in the antarctic but not in the abyssal zone are widely distributed and represented only by one or a few species.

The arctic region has 11 families of bivalves in common with the abyssal zone. Among the families found in the arctic but not in the abyssal zone special mention should be made of the Astartidae which comprises several arctic species and one antarctic. In addition, a number of species occur in the northernmost part of the Pacific (FILATOVA 1957; DALL 1903). Most of the known species are sublittoral, while a few are bathyal. The remaining families found in the arctic but not in the abyssal zone are represented by one or two species (except the Cardiidae and the Tellinidae with three and four species, respectively). These families are otherwise distributed in the sublittoral zone of the temperate and tropical zones.

Turning now to the bathyal zone of the world ocean, it appears that about 35 families of bivalves are present (data compiled from: DALL 1908; DELL 1956; KNUDSEN 1967; OKUTANI 1962, 1966). The bivalve fauna of the bathyal zone may be subdivided into several regions (KNUDSEN 1967), which at least to some extent correspond to the subdivisions of the sublittoral-littoral, and some families are confined to certain regions. Most of the families,

Order	Family	No. of species	%
Nuculoidea	Nuculidae	10	5.2
	Nuculanidae	40	20.7
	Malletiidae	39	20.2
Solemyoida	Solemyidae	1	0.5
Arcoida	Arcidae	2	1.0
	Limopsidae	6	3.1
Mytiloida	Mytilidae	7	3.6
Pterioida	Pectinidae	14	7.3
	Limidae	1	0.5
Veneroida	Thyasiridae	1	0.5
	Montacutidae	5	2.6
	Scrobiculariidae	2	1.0
	Kelliellidae	8	4.1
Myoida	Pholadidae	3	1.6
Pholadomyoida	Pholadomyidae	1	0.5
	Thraciidae	1	0.5
Septibranchoidea	Poromyidae	10	5.2
	Verticordiidae	14	7.3
	Cuspidariidae	27	14.0
Not classified	Galatheavalvidae	1	0.5
	Total no. of species	193	99.9

Table 3.	The com	position	of the	endemic
	abyssal	bivalve f	launa.	

however, occur in the sublittoral as well and are very widespread. With the exception of the Galatheavalvidae, all the families represented in the abyssal zone are also bathyal. The following families are essentially confined to the bathyal and abyssal zones: Limopsidae, Kelliellidae, Poromyidae, Verticordiidae and Cuspidariidae, and are represented in the sublittoral zone (particularly its deeper part) by a few species only.

The Nuculanidae and Malletiidae are by far the dominating (Table 3), followed by the Cuspidariidae, Pectinidae, Verticordiidae, Nuculidae and Poromyidae, and these seven families form nearly 80 % of the total number of species. The families belonging to the order Nuculoidea form about 46 % of the fauna, followed by those belonging to the Septibranchoidea, which form about 27 %. The order Veneroida, which, *inter alia*, comprises such large shallow-water families as the Cardiidae, Veneridae, Mactridae and Donacidae, is represented in the abyssal zone by four families only, forming about 8 % of the abyssal fauna.

The composition of the bivalve fauna concerns, however, more than the presence or absence of certain families in certain zones or regions. There are also conspicuous differences in the relative importance of different families within the regions compared. This appears from Fig. 116 which shows the composition of the bivalve faunas of some selected regions. All the families represented in the endemic abyssal fauna have been considered, as well as all those families from the other areas which were found to constitute 3 % or more within at least one of the areas. The remaining families have been merged under "miscellaneous groups".

Areas covered by recent summarizing papers and believed to elucidate some of the characteristics of the abyssal fauna have been selected for comparison. The information has been derived from the following sources:

Area		Author	No. of spp.
N.E.Atlantic	challow	Tebble 1966	166
Antarctic	shanow	Dell 1964	123
Arctic	water	Ockelmann 1958	73
New Zealand	bathyal	Dell 1956	86
Indian Ocean	**	Knudsen 1967	53
World Ocean	abyssal	present paper	193

The Nuculidae constitute between 3 and 4-5 % of the bivalve fauna in the arctic and antarctic region and in the abyssal zone (Fig. 116), and attain their largest percentage (6-8) in the bathyal zone. The Nuculanidae and Malletiidae (which, as mentioned p. 21, possibly should be considered as one family) are insignificant in the N.E. Atlantic, while in the arctic and antarctic the two families together constitute about 10 and about 15 %, respectively. In the New Zealand bathyal zone they constitute 15 % of the fauna, and about 8 % in the Indian Ocean bathyal. In the abyssal zone the two families together constitute more than 40 % of the total fauna, the two families being about equal in number. The Arcidae are only of importance in the arctic fauna (about 6 %), but otherwise the number of species is low in all areas considered. The Limopsidae constitute 3-4 % of the fauna in the Antarctic, the Indian Ocean bathyal and the abyssal zones, but in the three other regions the family is of little importance. The Mytilidae are of importance in the N.E. Atlantic, Arctic and Antarctic (the three shallow water areas), but of much less importance in deep water, although it will be noted that in the abyssal zone the family constitutes 3.6 %, i.e., roughly two-three times the percentage found in the bathyal zones (1.9 and 1.2 %). The Pectinidae appear to be rather important in all areas considered, but it will be noted that they are



Fig. 116. Percentage composition of families of Bivalvia within the areas indicated.

particularly important in the two bathyal areas (about 9 % in New Zealand and 17 % in the Indian Ocean) and that the family constitutes a somewhat higher percentage (about 7 %) of the abyssal fauna than it does in any of the shallow water areas considered (4-5.5 %). The Kelliellidae form about 4 % of the abyssal fauna, but do not show up in the other areas considered. However, a few species of the family are known from the bathyal zones of other regions and from the lower part of the sublittoral. The Myochamidae are an example of a family largely confined to the bathyal zone, being represented by some sublittoral species in the Indo W. Pacific area. While the Poromyidae are poorly represented in the shallow water and bathyal areas considered, constituting less than 2 % of the fauna,

this family constitutes more than 5 % of the abyssal fauna. The Vertic ordiidae are well represented in both bathyal zones considered, with 3.5 % of the New Zealand bathyal fauna and 7.6 % of the Indian Ocean bathyal fauna; they are equally well represented in the abyssal zone (7.3 %). Finally, the Cuspidariidae are important in the bathyal zones; the two areas considered have roughly 9 and 13 %, while in the abyssal fauna this family constitutes some 14 %.

Table 4 shows the greatest depth in which the families represented in the endemic abyssal bivalve fauna have been found.

It appears that nine of the 18 (20?) abyssal families are found at depths exceeding 5000 m, and five families are not found deeper than between

Table 4. The gre	atest depth	occurrence
of the ab	oyssal famil	ies.

	Depth in meters				
Family	2000- 3000	3000- 4000	4000- 5000	5000- 6000	
Nuculidae				×	
Nuculanidae	•			×	
Malletiidae		•	•	×	
Solemyidae		×	•	•	
Arcidae	•	•	•	×	
Limopsidae		•		×	
Mytilidae			×		
Pectinidae			×		
Limidae		×		•	
Thyasiridae	•	×	•	•	
Montacutidae		×	•		
Scrobiculariidae				×	
Kelliellidae				×	
Pholadidae		•	×	•	
Pholadomyidae	×	•	•	•	
Thraciidae	×			•	
Poromyidae			•	×	
Verticordiidae	•		×	•	
Cuspidariidae	•		•	×	
Galatheavalvidae	•	•	×		

4000 and 5000 m. Four families are not found deeper than between 3000 and 4000 m. It should be noted that two of these families, the Limidae and the Thyasiridae have been recorded from the hadal zone (see Table 13, p. 222), and it is therefore to be expected that representatives of the families are to be found also in the deepest part of the abyssal zone. Two families, the Pholadomyidae and the Thraciidae are restricted to the uppermost part of the abyssal zone, and it is possible that they should not be considered as abyssal at all.

From this it would appear that ten out of the 18 (20?) abyssal families extend to the deepest part of the abyssal zone and five more families extend at least to between 4000 and 5000 m.

Future investigations may well demonstrate that some of the families at present known only from the upper part of the abyssal zone are also found in the deep abyssal. This, for instance, could be the case with the Montacutidae, a family consisting of small species and therefore likely to escape the generally coarse nets which have been used by most deepsea expeditions.

## The genera

The endemic abyssal species are referred to 45 genera, which are only 3.5 % of a total of about 1330 Recent marine genera recognized by VOKES (1967). However, within many families of bivalves the limitation of numerous genera (for instance, in the Nuculoidea, Arcoida and many of the large shallow water families) is very uncertain. Accordingly, the assignment of many species to genus becomes difficult, and in many cases provisional.

A careful survey has been made concerning the extent to which the abyssal genera are endemic or may occur also in the overlying zones. In order to find reliable records from the bathyal and shallow water zones of representatives of the less common genera, the following comprehensive papers were consulted: BARNARD (1964), BOWDEN & HEP-PEL (1966, 1968), COTTON (1961), DAUTZENBERG (1927), HABE (1958a, 1958b), OKUTANI (1962, 1966), SOOT-RYEN (1955, 1966), VERRILL & BUSH (1898). In each case an attempt was made to trace records of living specimens of the genera in question, but whether the assignment to genus was correctly made by the authors was not always examined.

The survey demonstrates that with the exception of *Galatheavalva* all the genera are represented in the bathyal zone and many also in shallower depths.

NICOL (1967) compared the arctic and the antarctic bivalve faunas and to a lesser extent included the abyssal fauna in his considerations. It was concluded that the deep-water fauna, even at the generic level, shares biological characteristics with the faunas of either or both polar regions. A few genera present in the deep-sea are not found in the two other regions. Among the seven examples mentioned are the following, which, however, are only found as displaced valves from shallow water: Anomia, Hinnites and Pycnodonte. Other examples mentioned are Mytilimeria and Periploma, which are probably bathyal rather than abyssal. Attention was called to the dominance in the abyssal zone of the Nuculanidae and the Cuspidariidae and it was noted that some of the families which are represented by numerous species in shallow warm water are represented by few species only in the abyssal zone. However, NICOL's analysis is based on CLARKE's list (1962a), which, as mentioned on p. 163, has been compiled in a way differing considerably from the present one. It is therefore difficult to directly compare NICOL's results with the present investigation.

Table 5 shows that 18 genera are known from

Table 5. The depth distribution of the abyssal
genera and their occurrence in the Antarctic
and Arctic.

	Depth in meters				ctic	
Genus	2000- 3000	3000- 4000	4000- 5000	5000- 6000	Antar	Arctic
Nucula				×	+	+
Brevinucula		×				
Pronucula			×		+	
Pristigloma		Х				
Sarepta			$(\times)$			_
Nuculana			•	×	+	+
Ledella				×	—	_
Spinula			•	×		-
Yoldia				×	-+-	+-
Portlandia				$\times$		+
Yoldiella			×		+-	
Tindaria				×		
Neilonella				×	—	
Malletia				×	+	_
Acharax		Х			—	
Acar				×		_
Arca				$\times$		+
Limopsis				$\times$	+	
Dacrydium			×		+	
Modiolus		×			_	
Adipicola	×					_
Propeamussium			×			
Cyclopecten		×			+	+
Delectopecten		Х		•		—
Limatula		×			+	+
Thyasira	×		•		+	+
Montacuta		×				.—
Kelliopsis		×				
Tellimya	Х			•	+	—
Abra	•	•		$\times$	—	
Kelliella	•	•	•	$\times$		
Xylophaga	•	·	•	$\times$		—
Pholadomya	×	•		•	+	
Asthenothaerus	Х	٠		•		—
Cetoconcha	٠	٠	•	$\times$	—	
Poromya	·	•	٠	$\times$		+
Laevicordia	•	•	×	•	—	—
Policordia	·	×	·	•		
Thracidora	·	•	X	•		
Verticordia	•	•	×	·	•	
Halicordia	×	•	·	·		
<i>Myonera</i>	•	•	•	Х		
Cardiomya	٠	(×)	•	·		 ,
Cuspidaria	•	·	×	•	+	+
Galatheavalva	·	·	×	•		—

the deepest part of the abyssal zone below 5000 m. Since *Cuspidaria* has been recorded from the hadal zone the genus will occur also in the deepest part of the abyssal zone as is also the case with at least one genus within the Thyasiridae (see Table 13). Thus altogether 20 genera would appear to be known from below 5000 m depth. Another nine genera are known as far down as between 4000 and 5000 m, while 12 genera are known from between 3000 and 4000 m, and finally six genera only between 2000 and 3000 m. Most of the genera recorded only from the two last-mentioned depth zones are represented by single species recorded only once, viz. *Modiolus, Adipicola, Tellimya, Pholadomya, Asthenothaerus, Halicordia.* No doubt further investigations will also demonstrate the occurrence of most of the genera mentioned in the deepest part of the abyssal zone.

Table 5 also shows that only 14 of the 45 genera found in the abyssal zone are found also in the antarctic. Several of the genera within the Nuculoidea which are found in the abyssal zone are not known from the Antarctic, but to some extent this may be due to the uncertain conception of these genera, which has resulted in some diverging opinions of the different authors. In several cases, however, the difference between the faunas may be real. For instance, the following abyssal genera do not seem to occur in the antarctic or arctic regions: Ledella, Spinula, Tindaria and Neilonella. It will also be seen that the genera Abra and Kelliella are lacking in the two areas mentioned and that Cuspidaria is the only genus of the Septibranchoidea found in all three areas. No genus within the Arcidae appears to be known from the Antarctic.

Only 11 genera are common to the abyssal zone and the Arctic. Again, many of the genera of Nuculoidea present in the abyssal zone are lacking in the Arctic, but on the other hand *Arca* (absent from the Antarctic) is represented. *Limopsis* which is found in the Antarctic is absent from the Arctic. A number of genera within the order Veneroida are also lacking in the Arctic, and only two of the abyssal genera of the Septibranchoidea, *Poromya* and *Cuspidaria*, are found also in the Arctic.

The following eight genera are found in all three areas (Arctic, Antarctic, Abyssal): Nucula, Nuculana, Yoldia, Dacrydium, Cyclopecten, Limatula, Thyasira and Cuspidaria.

Conclusion: The above survey thus indicates that the abyssal bivalve fauna has relatively little in common with the antarctic or the arctic fauna both at the family and the generic level.

Many earlier workers held the opinion that the abyssal fauna was derived from the cold regions of the shelf. EKMAN (1953) discussed this problem, mentioning a number of these authors, but concluded that the shelves of the warmer coasts have obviously played a more important part than the colder shelf regions. DAHL (1954), in discussing the deep-sea crustaceans, stated that most of the Decapoda present in the deep sea probably invaded it from the continental shelf or the pelagic region of warm areas. BRUUN (1956) found that the true abyssal fauna is derived from the bathyal fauna, without, however, giving examples. MADSEN (1961b) stated that the family Porcellanasteridae (Asteroidea) has arisen from astropectinid-like forms having their chief development in the tropical sublittoral and bathyal regions. The Porcellanasteridae, comprising 25 species, is essentially abyssal; most species are confined to depths below 2500 m and only three monotypic genera are bathyal, being found at depths between 900 and 2300 m. CLARKE (1962b) came to the conclusion that the abyssal mollusc fauna was probably derived from invasions from shallow water regions all over the world, and not primarily from high latitudes. The Holothurians obviously differ from this pattern of development. HANSEN (1967) found that not only species but also higher taxa evolved wholly within the deepsea. Thus the order Elasipoda, forming about half of the about 180 deep-sea holothurians, is exclusively confined to the deep-sea. Several families are exclusively abyssal or with few species occurring in the deeper part of the bathyal zone. Relationships were also observed to be closest between species from the same bathymetrical zone.

In the bivalves, however, it seems reasonable to assume a rather direct derivation from the warm water sublittoral and the bathyal zones and the differences between the abyssal zone and the bathyal and shallow water zones is restricted to the specific level.

#### The species

As previously mentioned, the survey of the abyssal bivalves (Table 1) differs in many respects from that of CLARKE (1962a), particularly by containing a smaller number of species. CLARKE listed 402 species, while the present list contains 245 species, including the 50 new species I have described here and in the paper of 1961. In addition, 38 species should probably be considered as "guests", having their main distribution in the bathyal zone.

The number of finds within the individual species differs considerably, as will be seen from the following survey:

No. of records	No of species	% of known abyssal species	No. of spp. known as valves only
1	122	65.0	14
2	28	14.7	4
3	11	5.8	1
4	5	2.1	0
5	6	3.1	0
6	2	1.0	0
7	3	1.5	0
8	1	0.5	0
9	1	0.5	0
10-19	5	2.6	0
20 +	6	3.1	0
Total	191	99.9	19

No less than 65 % of the endemic abyssal species have been recorded only once, 86 % have been recorded three times or less and less than 6 % have been recorded ten times or more; 10 % of the species are known as valves only.

The present investigation has increased the known number of abyssal bivalve species by some 18 %. A rather high proportion of new species has also been added by other recent deep-sea expeditions. This would indicate that our knowledge of the abyssal bivalve fauna is still far from complete (cf. HESSLER & SANDERS 1966, 1967 who found an abundance of minute species at abyssal depths). Some of these small forms may be juveniles of shallow water species which have been carried astray during the pelagic phase and may be able to subsist as "guests" in the abyssal zone. There is little doubt, however, that the abyssal zone harbors numerous minute species which, owing to too crude sampling methods, have remained unknown. SANDERS & HESSLER (1969) emphasized the abyssal faunal diversity and suggested it to be due to the constancy of the physical conditions and the long past history of physical stability. They state that similar diverse communities are tropical shallow-water environments and tropical rain forests which have also evolved under physical conditions which have remained constant and uniform for long periods.

It is apparent that the abyssal bivalve fauna contains a large number of species as compared to the two other large cold-water areas of the world, i.e., the Antarctic and the Arctic. Both areas are reasonably well explored, at least when compared to the abyssal zone. Although there are probably still some undiscovered species to be added to the antarctic fauna, this is probably not the case with the arctic fauna. The total number of antarctic bivalves may be put at about 125, while the total arctic bivalve fauna may be at most 100 species. Already at this stage of our knowledge the abyssal fauna contains roughly twice the number of species known from either of the two regions mentioned.

genera with few species. It is added that families which are confined to the deep-sea do not seem to exist.

The composition of the abyssal bivalve fauna has only been briefly referred to by previous workers. EKMAN (1953) states that although no compilation allowing a survey exists, it seems justified to assume that in the shell-bearing molluscs the species are in general members of eurybathic genera or otherwise of CLARKE (1962 b) made a brief survey of the composition of the abyssal molluse fauna (as defined p. 312) as to orders. The percentage of abyssal species in the individual order was calculated on the basis of all the abyssal molluse species recorded (1152 spp.). The result is compared to the present investigation in the following survey:

CLA	Present survey				
Order	No. of abyssal spp.	% of known molluscs (1152 spp.)	% recal- culated (402 bivalve spp.)	% of known species	Order
Protobranchiata	138	12.0	35	47 {	Nuculoidea Solemyoida
Filibranchiata	33	2.9	8	4	Arcoida
Anisomyaria	62	5.4	16	11 {	Mytiloida Pterioida
Eulamellibranchiata	84	7.3	21	11 {	Veneroida Myoida Pholadomyoida
Septibranchiata	85	7.4	21	27	Septibranchoidea
 Total	402		101	100	

In the third column CLARKE's figures from the left column have been re-calculated on the base of the 402 spp. of bivalves which he listed. The corresponding percentages based on the 193 species recognized in the present survey are found in the fourth column. The dominance of the Nuculoidea (and Solemyoidea), followed by the Septibranchoidea, is even more pronounced than observed by CLARKE.

#### THE HORIZONTAL DISTRIBUTION

#### The distribution of the species

*Malletia cuneata* (Jeffreys) (Fig. 117) is the most widely distributed abyssal bivalve known. It is recorded from all areas of the world ocean, including the Antarctic and both the W. and E. Pacific. In addition, the species has been recorded several times from the Arctic Ocean, at depths ranging from 2400 to 3700 m. It is the only known species common to the world ocean and the abyssal depths of the Arctic Ocean.

Arca orbiculata Dall (Fig.118) is very widely distributed. It is found in the N.W.Atlantic at about  $40^{\circ}$ N and in several localities in the S.E. Atlantic, as well as in the Atlantic sector of the

Antarctic Ocean. There are several records in the S.W.Pacific (Tasman Sea, Kermadec area) and in the C.Pacific. Finally, a number of records are at hand from the E.Pacific between  $40^{\circ}N$  and  $40^{\circ}S$ . Its absence from the Indian Ocean is probably due to lack of investigation.

Acar asperula (Dall) (Fig. 119) is likewise widely distributed. In the Atlantic there are numerous records from between about 40 °N to the equator, while there are no records from the S. Atlantic and the Antarctic. Numerous records are at hand from the northern part of the Indian ocean and the S.E. Asian waters. In the Pacific the species has been found in the northwestern part up to about 45 °N. In the S.W. Pacific it has been recorded from the Tasman sea and the Kermadec area. There are no records from the C. Pacific, but there are two records from the S.E. Pacific and probably the species is found also in the E. Pacific (see p. 88).

Limopsis pelagica Smith (Fig. 120) appears to comprise two allopatric subspecies. The nominal subspecies, *L. pelagica pelagica*, is found throughout the N. Atlantic, all records with the exception of one being south of 40  $^{\circ}$ N. It is also found in the S. Atlantic and one record from the Antarctic is possibly this subspecies also. In addition the subspecies



Fig. 117. Records of Malletia cuneata (Jeffreys): 
Galathea", 
other expeditions; 
valves. 
Tindaria antarctica Thiele.



Fig. 118. Records of Arca orbiculata Dall. 
Galathea", 
other expeditions; 
valves.

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Fig. 119. Records of Acar asperula (Dall): • "Galathea", other expeditions; open signatures: valves.

is found in the northern part of the Indian Ocean, all finds except one from north of the equator. There are no records from the S.E. Asian waters or the Pacific. The subspecies *L.pelagica dalli* is found in the easternmost Pacific between about 30 °N and the equator. The two subspecies thus are separated by an enormous geographical gap.

Abra profundorum (Smith) (Fig. 121) has been recorded frequently from the N.Atlantic up to about  $45^{\circ}$ N and from the S.E.Atlantic. There are several records from the western Indian Ocean, while only a single record comes from the eastern

part of the Indian Ocean. There are no records so far from the S.E.Asian waters, but it probably occurs there also. In the Pacific it has been recorded once in the northwestern part and several times in the S.W.Pacific (Tasman Sea and Kermadec area), as far east as the 180th meridian. Apparently it is absent from the Antarctic Ocean. *A. californica* n.sp., known only from a single specimen from the E.Pacific, and *A. profundorum* are possibly another example of allopatric species.

Poromya tornata (Jeffreys) (Fig. 122) is known from the N.Atlantic south of about 40°N. Most



Fig. 120. Records of *Limopsis pelagica pelagica* Smith (), and *L.p. dalli* Lamy () valves.



Fig. 121. Records of *Abra profundorum* (Smith) ● (a few records from the N.W.Atlantic have been omitted), and of *A. californica* n.sp. ■.

records and e.g. the two only records in the region north of about 40 °N, refer to valves only. Three records are at hand from the C. Atlantic, round the equator, and a number of records from the western and northern Indian Ocean. It has not been found in the Antarctic, the S.E. Asian waters and the Pacific. In the easternmost Pacific occurs an allopatric species, *P. perla* Dall, which is recorded from about 32 °N to the equator.

Two Pectinidae, *Propeamussium meridionale* (Smith) and *Cyclopecten undatus* (Verrill & Smith) (Fig. 123) appear to have entirely different distribution patterns. *P.meridionale* has been recorded from the Indian Ocean (the northwestern parts) and the Antarctic (Indian Ocean sector). It is apparently absent from the S. E. Asian waters, but has been recorded from the S. W. Pacific (Tasman Sea and Kermadec area), the C. Pacific (one record), the E. Pacific (several records from the Gulf of Panama region) and the S. E. Pacific (one record from about  $40^{\circ}$ S). *Cyclopecten undatus* has been recorded repeatedly in the N. Atlantic up ot about  $60^{\circ}$ N and



Fig. 122. Records of Poromya tornata (Jeffreys) • and P. perla Dall : O valves (a few findings of valves have been omitted).



Fig. 123. Records of *Propeamussium meridionale* (Smith): ■ "Galathea", ● other expeditions, and of *Cyclopecten undatus* (Verrill & Smith) ▲; open signatures: valves (a few findings of valves have been omitted).



Fig. 124. Records of Ledella ultima (Smith).



Fig. 125. Records of Myonera undata (Verrill).



Fig. 126. Records of Nuculana agapea (Dall) , N. pallida (Smith) , and N. vestita (Locard) A.

also from the S.E. Atlantic (off the coast of W. Africa), and one from the Antarctic Ocean (Indian Ocean sector), but unfortunately only four of the records out of a total of 21 refer to live specimens. The species has not been recorded from either the Indian Ocean or the Pacific. Possibly the two species *P. meridionale* and *C. undatus* replace one another, though in the Antarctic they have been recorded alive from the same locality, viz., "Challenger" St. 146.

The following species have apparently a more

restricted distribution: Ledella ultima (Smith) (Fig. 124) is known from the C. and S. Atlantic, from the Antarctic (Atlantic sector) and from a single record from the eastern part of the Indian Ocean. Tindaria antarctica Thiele (Fig. 117) is likewise known from the Antarctic and also from the S. W. Pacific (Kermadec area). A similar distribution is known for Nuculana pallida (Smith) (Fig. 126), which has been recorded from the S. E. Atlantic, the Antarctic and the Tasman Sea. Nuculana vestita (Locard) (Fig. 126) is known only from the E. Atlantic, off the



Fig. 127. Records of *Nucula cancellata* Jeffreys, left (a few findings in the N.W. Atlantic have been omitted), and of *Pristigloma nitens* (Jeffreys), right (a few findings W of Ireland have been omitted).



Fig. 128. Records of Spinula calcar (Dall) •, and S. oceanica Filatova •, left. Abyssal records of Malletia obtusa G.O. Sars, right. (Some records from the N.W. Atlantic of live specimens and nearly all records of valves have been omitted);

W.coast of Africa, between about  $20^{\circ}$ N and  $35^{\circ}$ S. Nuculana agapea (Dall) (Fig. 126) is recorded only from the E. Pacific where its distribution is similar to that of Limopsis pelagica dalli, Abra californica and Poromya perla (see above).

The distribution of *Myonera undata* (Verrill) (Fig. 125) is similar to that of *Limopsis pelagica pelagica* and *Poromya tornata*. *M.undata* has been recorded in the N.Atlantic up to about  $45^{\circ}$ N, and in addition there are a couple of records from the C. and S. Atlantic. In the Indian Ocean it has been recorded both from the western and northern parts, but it is not known east of  $80^{\circ}$ E, and is absent from the Antarctic, where *L.p.pelagica* may possibly be present.

The distribution of *Spinula calcar* Dall (Fig. 128) is an instructive example of how, in the light of extended investigations, a species originally known only from a very restricted area actually has turned out to be very widely distributed. Originally described from off Peru, it might be considered a typical member of the E. Pacific abyssal fauna (see p. 196). The "Vitiaz" demonstrated the presence of the species in the N. Pacific, and the "Galathea" obtained *S. calcar* in the Kermadec region. *Spinula oceanica* Filatova (Fig. 128) is, so far, only known from the W. Pacific from about 50° N to about 40° S.

Three species are until now only known from the N. Atlantic: *Nucula cancellata* (Jeffreys) (Fig. 127), recorded in the W. Atlantic at about 40°N, in the

N. W. Atlantic at about 62 °N., and the E. Atlantic at about 55 °N. *Pristigloma nitens* (Jeffreys) shows similar distribution (Fig. 127), except that there is also a doubtful record from the S. W. Atlantic. *Malletia obtusa* G. O. Sars (Fig. 128) has approximately the same distribution, except that there is one record from the Gulf of Mexico, and two doubtful records of valves from off W. Africa. Both *Nucula cancellata* and *Malletia obtusa* have been frequently recorded from bathyal depths and have been classified as abyssal guests, while all the remaining species mentioned belong to the endemic abyssal fauna.

However, as pointed out (p. 185), no less than 122 out of the 193 species referred to the endemic abyssal fauna have been recorded only once, and only 11 species have been recorded ten times or more. Only about 280 abyssal samples contained bivalves and only 80 of these were taken below a depth of 4000 meters, the approximate average depth of the world ocean. Our knowledge of the distribution of abyssal bivalves is still very fragmentary.

# The cosmopolitan distribution of benthic abyssal organisms

In the previous section three species of abyssal bivalves were shown to have a cosmopolitan distribution. This type of distribution has been much dis-

cussed since the early days of deep-sea exploration. MADSEN (1961b) gave a review of the discussion. On the basis of a taxonomic revision of the Porcellanasteridae and a survey of the literature MADSEN concluded that the cosmopolitan pattern of distribution is the general rule as regards the true abyssal species, i.e., those which are endemic in the region. A number of examples are mentioned. The term "cosmopolitan" designates species for which records are at hand from the Atlantic, Indian and the Pacific without considering whether the species in question were recorded from the E. Pacific or not. This would mean that, e.g., Nuculana pallida (Fig. 126) should be regarded as cosmopolitan. MADSEN (1961a) mentioned the following Porcellanasteridae, both unknown from the E.Pacific, as cosmopolitan: Styracaster horridus and S. chuni. For the present discussion I suggest that a cosmopolitan species should be expressly understood as a taxon distributed throughout the world ocean with the E.Pacific included.

Besides the three bivalves mentioned above (*Malletia cuneata, Acar asperula* and *Arca orbiculata*), the following abyssal species (both endemic and "guests") have a cosmopolitan distribution:

#### Pennatularia:

Umbellula lindahli Kölliker. Known from the Atlantic, Antarctic, Indian and both the W. and the E.Pacific (Broch 1959). The accessible data do not yet indicate geographical races or varieties.

Umbellula thomsoni Kölliker. Distributed in the Atlantic and the Indian Oceans (Broch 1959). In addition there were two records from the W. Pacific. The species was obtained by the "Galathea" in the Gulf of Panama (Madsen 1961b).

Distichoptilum gracile Verrill. Occurring in the N.Atlantic, the Indian Ocean and the E.Pacific (KÜKENTHAL & BROCH 1911). In the latter region it is distributed from about  $24^{\circ}N$  to the equator.

Anthoptilum grandiflorum Kölliker. Distributed throughout the Atlantic, the Indian Ocean and the Pacific, including the E.Pacific at about 32°N (KÜKENTHAL & BROCH 1911).

## Scyphozoa:

Stephanoscyphus simplex Kirkpatrick. Previously recorded from the Atlantic and Indian Oceans; the findings of the Galathea Expedition extended the distribution also to the W. and E. Pacific (KRAMP 1959). There appears to be no taxonomic subdivision.

#### Echinodermata:

Thoracaster cylindratus Sladen and Porcellanaster coeruleus Wyville Thomson. (Asteroidea) Found in the Atlantic, Indian and Pacific Oceans (MADSEN 1961a). In the E. Pacific they have been recorded in a restricted area off the Gulf of Panama.

MADSEN (1951) mentions the following abyssal Ophiuroidea as having a cosmopolitan distribution (including also the E. Pacific):

Ophiacantha cosmica Lyman Amphichilus dalea (Lyman) Ophimusium lymani Wyville Thomson Ophiosphalma serratum (Lyman) Ophiernus vallincola Lyman

# Tunicata:

Dicarpa simplex Millar. Recorded from the following regions: the C.Atlantic, the S.W.Pacific (Kermadec area) and the E.Pacific (MILLAR 1959).

# The Atlanto-W. Pacific distribution of abyssal organisms

A number of abyssal species appear to have a distribution which comprises the Atlantic, the Indian and the Antarctic Oceans, having their eastern limit in the region between the eastern part of the Indian Ocean and the C. Pacific. In the E. Pacific they may in some cases be represented by allopatric species or subspecies. The following bivalves are believed to have this distributional pattern:

Atlanto-W. Pacific	E. Pacific
Limopsis pelagica pelagica	L. p. dalli
Abra profundorum	A. californica
Poromya tornata	P. perla

In addition the following examples from other invertebrates can be mentioned:

Atlanto-W. Pacific	E. Pacific	Reference
HOLO-		
THURIOIDEA:		
Oneirophanta mutabilis		HANSEN (1967)
mutabilis	O.m.affinis	
Deima validum validum	D.v.pacificum	Hansen (1967)
Scotoplanes globosa	Scotoplanes n.sp.	Hansen (1967)
ASTEROIDEA:		
Styracaster chuni	S. paucispinus	Madsen (1961 a)
TUNICATA:		
Culeolus suhmi	C. pyramidalis	Millar (1959, 1964)

# The restricted distributions in abyssal organisms

Some species of bivalves appear to have a restricted distribution within the world ocean, although this may be due only to lack of sufficient investigation. One type of restricted distribution comprising the easternmost part of the Pacific between about  $30^{\circ}$ N and  $10^{\circ}$ S has been briefly referred to above. There is some indication that the Antarctic Ocean, including the adjacent parts of the other oceans, has some endemic species, viz. Tindaria antarctica, Nuculana pallida and Ledella ultima. MADSEN (1961a) mentioned three species of Porcellanasteridae which have been recorded only from the Antarctic: Hyphalaster scotiae Koehler, Styracaster robustus Koehler and Abyssaster planus (Sladen) which are, however, known only from the type localities. On the whole, the antarctic abyssal fauna is very poorly known and much more collecting is needed before its zoogeography can be properly discussed. The distribution maps (Figs. 117-128) also indicate endemism in the N.Atlantic, north of about 40°N and in the N.W.Pacific. Attention should also be called to the apparent northern limit at 40-45°N in the N.Atlantic of several widely distributed species (Acar asperula, Limopsis pelagica pelagica and several others). Does this really indicate a northern limit of distribution for these species, or does it merely reflect the fact that the Atlantic south of 40-45°N was the main working ground for some of the major deep-sea expeditions such as "Albatross", "Travailleur", "Talisman" and "Monaco", while the northernmost part of the N.Atlantic has been much less explored?

Although a wide, and in some cases cosmopolitan, distribution may be found in the majority of endemic abyssal bivalves, some species may be quite restricted in their distribution. KNUDSEN (1961) suggested this for species of the wood-boring genus *Xylophaga*, due to the restricted and patchy distribution of plant debris in the deep sea. Future investigation may demonstrate that certain genera of bivalves, such as *Dacrydium* and *Kelliella*, have restricted distributions.

#### Discussion of the horizontal distribution

MADSEN (1961 b) discussed the problems of the horizontal distribution of the abyssal fauna. He gave a thorough review of the different opinions held by previous workers and concluded that a cosmopolitan distribution is probably the general rule in the abyssal species. The present section discusses some papers dealing with this problem, most of which have appeared since MADSEN'S paper.

EKMAN (1953) suggested that the abyssal species have generally a wider distribution than the archibenthal (= bathyal) species, and that there are many cosmopolitan species. VINOGRADOVA (1959a, 1962b) and ZENKEVITCH (1963) found that those abyssal species which actually had a cosmopolitan distribution were eurybathic, and that there was an increasing isolation of deep-water faunas with increasing depth. VINOGRADOVA (1962b) stated that the phenomenon could not be explained solely by the unequal extent of our knowledge of various regions, and that it could easily be traced in regions "equally and adequately investigated" (see p. 185).

While the suggestion of a considerable vertical range in cosmopolitan species is consistent with the present investigation (see p. 198), the suggestion of an increasing isolation of the abyssal fauna with increasing depth is untenable. Besides the present investigation, several papers on collections of the Galathea Expedition have demonstrated an increasing number of widely distributed species (KRAMP 1959; MILLAR 1959; HANSEN 1967). HAN-SEN states that in abyssal species a world-wide distribution may prove to be the rule.

Contrary to VINOGRADOVA's opinion (1962b) that some abyssal regions have been adequately investigated, I believe that this is far from being the case. This will, for instance, appear from the numerous recent records of abyssal Pogonophora (SOUTHWARD & SOUTHWARD, 1967), the recent findings of additional specimens of Neopilina (TEBBLE 1967; FILATOVA et al. 1968) and from the diversity of organisms obtained by the current investigation by SANDERS and co-workers (see p. 185). To this could be added the above-mentioned fact that 65 % of the abyssal bivalves have been recorded only once. I think that no abyssal region can be said to have been adequately investigated and that the apparent restricted distribution of many abyssal organisms is simply due to lack of thorough investigation and, what is probably of great importance and is not mentioned by VINOGRADOVA (1959a), due to lack of proper taxonomic investigation. VINOGRADOVA suggested that the distribution of deep-water species is apparently restricted to certain areas by the relief of the bottom, especially by the features of the macro-relief. Hence the boundaries of the zoogeographical areas for deep-

water bottom fauna correspond with submarine mountain chains. If so, the distribution of many species should be delimited by the major topographical features of the ocean bottom such as the Mid-Atlantic Ridge and the Mid-Indian Ridge, probably two of the most conspicuous formations of the world ocean. However, by inspection of the distribution maps (Figs. 117-128) it will be seen that no species seems to be delimited by any of the structures mentioned, or by any other similar structure. Three species have their easternmost known occurrence just east of the Mid-Indian Ridge: Limopsis p.pelagica, Poromya tornata and Myonera undata. With the exception of two species, all those which have been recorded from the Atlantic Ocean are known from both sides of the Mid-Atlantic Ridge. KNUDSEN (1967) dealt with 44 species of bathyal and abyssal bivalves collected in the northern part of the Indian Ocean by the John Murray Expedition, and in addition a compilation was made of the 54 bathyal and abyssal bivalves obtained by the Investigator Expeditions (see p. 12). Some of the species, it is true, were found on only one side of the Mid-Indian Ridge, but in most cases species known from several localities turned out to occur on both sides of the ridge. In 44 species of the "John Murray" material, four were widely distributed and abyssal, four appeared to occur in the Red Sea only, and two were abyssal and only recorded once (Tindaria murrayi and Spinula filatovae). Of the 34 remaining bathyal species 22 were found on both sides of the Mid-Indian Ridge, 12 of these extending from off E. Africa to off S. Japan. It can thus be concluded that as far as bivalves are concerned, neither the bathyal nor the abyssal species are influenced by the presence of the Mid-Indian Ridge. The same has been found in other groups also. MADSEN (1961a) mapped the distribution of 26 species of Porcellanasteridae; ten species have been recorded from the Indian Ocean, and nine of these are found on both sides of the ridge. CLARKE (1959, 1962b) stated that in the abyssal Mollusca there is a significant degree of endemism in the major ocean basins. He found (1962b) that the mean geographic spread of an abyssal species was only 2.0 ocean basins and that when a species was found in several basins, these are contiguous. This is supported by a comparison of the mollusc faunas of two basins in the N.Atlantic (viz., the N.American Basin and the Canary Basin) with the other N.Atlantic basins. The proportion of species from the two basins mentioned decreases with increasing distance from the basin in question. This has not been confirmed by the present investigation, which, however, did not take the other mollusc groups into account. To a large extent CLARKE's result may be due to the uncertain taxonomy in abyssal molluscs.

CLARKE (1962a) listed *Cyclopecten vitreus* (Gmelin) as the only abyssal non-cephalopod mollusc thought to be cosmopolitan. As mentioned p. 179, the records outside the Atlantic should be confirmed.

MENZIES (1965) agrees with VINOGRADOVA'S conception of a restricted distribution of abyssal species. Disregarding the paper of MADSEN (1961 b), he states that this opinion contrasts boldly with the "old view", held by BRUUN (1957), of wide distribution among abyssal species, and that it is very likely that the broad concepts of abyssal zoogeography outlined by VINOGRADOVA (1959) will prove valid.

Although many abyssal animal groups are dominated by widely distributed species, species having restricted distributions do occur in these groups. Reference was made above to the boring bivalves of the genus Xylophaga. Similar examples might be found in organisms occupying special, restricted ecological niches. In addition it appears that several groups are actually dominated by species having very restricted distributions, often confined to single basins. This appears to be the case in Amphipoda (BARNARD 1961), Isopoda (WOLFF 1962), Cumacea (JONES 1969) and Pogonophora (IVANOV 1963; SOUTHWARD 1963; SOUTHWARD & SOUTHWARD 1967). The problem is, however, difficult, because in a region as poorly investigated as the abyssal zone, negative evidence is of very little value. Therefore it is at present impossible to decide with any certainty whether the absence of a species from a region is really because of non-occurrence or because the area has been sampled inadequately.

BARNARD (1961) found that in the Amphipoda there is a strong tendency towards basin endemism, each basin containing about 12 endemic species (only benthic forms are considered). He further suggested that the same six to seven families are represented in each basin by about two species each, concluding that if isolation occurs in trenches (see p. 221), then it should occur also in the abyssal basins, and that the cases of interbasin pandeism appear to concern eurybathic and possibly pelagic species.

It thus appears that in certain animal groups there are a number of species having a cosmopolitan

distribution, while for other species in these groups the central Pacific may act as a barrier separating an E. Pacific abyssal element (MADSEN 1961b). The reason for this may be the poor food conditions which supposedly prevail over large areas of the C. Pacific, because so little terrestrial organic material is deposited. In addition, the circulation of water is such that bottom water from the deep Indian Ocean is introduced at high southern latitudes. It is then circulated so that the deep water of the N.E. Pacific is presumably the "oldest" water (WOOSTER & VOLKMANN 1960; REID 1969), which might have an adverse effect on the development and settlement of the juveniles, as has been shown to be the case for polychaete larvae (WILSON 1951). That the barrier does not cause a complete isolation of the abyssal fauna of the E.Pacific is obvious from the several examples of cosmopolitan abyssal species already known. The distribution of Spinula calcar is another example. It should finally be mentioned that TEBBLE (1967) recorded Neopilina adenensis from the Indian Ocean (Gulf of Aden) at 3000-3900 m depth. LEMCHE (personal communication) is of the opinion that TEBBLE's species is synonymous with N.galatheae Lemche from the E. Pacific ("Galathea" St. 716, 3570 m depth).

In the groups with pronounced basin endemism the bottom configuration probably acts as a barrier.

#### Remarks on bipolarity in abyssal organisms

Екман (1953) defined bipolarity as "a distribution spread over a region in the northern and one in the southern hemisphere with a gap in distribution between the two". He added that a more accurate knowledge of the abyssal fauna had shown that some of the species contained in the older lists of bipolarity had to be deleted because they were found to be "fairly cosmopolitan" and further stated that because of our incomplete knowledge of the abyssal fauna it was premature to ask whether bipolarity exists in purely abyssal animals. Although the phenomenon will not be discussed here in detail, I have found that in the abyssal Bivalvia it is not possible to find a single case of bipolar distribution. It is also impossible to point out any ecological factor which might be considered as responsible for such a distribution. ZENKEVITCH (1963), however, states that the deep-water fauna is to a great extent bipolar and amphiboreal in its distribution. A map (fig. 362) shows the distribution of ten supposedly bipolar abyssal organisms. The ten examples mentioned call for some comments:

1) Scina wegleri var. abyssalis (Amphipoda). All species of Scina are pelagic forms as are all members of the suborder Hyperidea. The species in question is recorded from three localities in the W.Pacific. One locality is from south of Kamchatka, the two other records are from about  $28 \,^{\circ}$ N and  $25 \,^{\circ}$ S. The species can not be listed as benthic and bipolar (J.JUST, personal communication).

2) Hymenaster anomalus (Asteroidea). The species appears to be known only from the S. Atlantic, off Tristan da Cunha, one locality at about 2700 m depth ("Challenger" St. 335) ZENKEVITCH's record of this species from the E. Atlantic, at about 30 °N may be a mistake, arising from the fact that PER-RIER (1894), in his treatment of the echinoderms of the "Travailleur" and "Talisman", gives a list of the then-known species of Hymenaster, including H. anomalus. The species was not obtained by these expeditions, and there is no evidence that it has ever been recorded outside the type locality (F. J. MADSEN, personal communication).

3) Kolga nana (Holothurioidea). This has been recorded from the W. Atlantic and the Antarctic (Indian Ocean sector). According to B. HANSEN (personal communication), the finds from the Atlantic are to be referred to Kolga hyalina, which is known from abyssal depths in the N. Atlantic and the Arctic Ocean (Norwegian and Greenland seas). The single sample from the Antarctic (Challenger Expedition) is in such a poor state of preservation that it can not be identified.

4) Culeolus suhmi (Tunicata). MILLAR (1959) recorded the species from the Indian Ocean and the Tasman Sea. Both these finds are intermediate between the previous records, filling out the gap in the apparently bipolar distribution: the N.Atlantic and the Antarctic.

5) Culeolus murrayi (Tunicata). The species was recorded by ZENKEVITCH (1963) from the W.Pacific at 30 °N and from two localities in the Antarctic, which are apparently the only records. However, MILLAR (1959) states that in the genus Culeolus the conception of the species is insatisfactory and that C.murrayi and C.gigas may be synonyms. It is therefore obvious that the taxonomy of the genus Fig. 129. Vertical range of abyssal Bivalvia known from 2-3 records.



should be reconsidered before zoogeographical conclusions are drawn.

6) Nymphon procerum (Pantopoda). First caught by the "Challenger" in the S.E. Pacific at about 33 °S. The second record came from the N.W. Atlantic (FAGE, 1951). Two additional records shown on the map given by ZENKEVITCH (1963) may be from the Vitiaz Expeditions. FAGE (1951) discusses the distribution of some abyssal Pantopoda, including *N.procerum*, known from a few, widely separated finds, but from two oceans. He believes that they are probably cosmopolitan species; I think this latter viewpoint is the correct one.

7) Munidopsis antoni and Clyphocrangon rimapes (Crustacea Decapoda). T. WOLFF (personal communication) informed me that the taxonomy of the deep-sea decapod crustaceans is in such a confused state that it is not advisable to classify the two species mentioned as bipolar.

8) *Phascolion eutense* (Sipunculoidea) and *Tatianella grandis* (Echiuroidea). Both of these are known both from the N.W. Pacific and the Antarctic (South of Australia). The intermediate region has been poorly investigated and the possibility cannot be ruled out that the two species may occur there. In addition, many species of the two groups appear to have a wide distribution.

From the above I think it can be definitely concluded that bipolarity in abyssal, benthic invertebrates is non-existent and that apparent examples are due to too few available records, deficient taxonomy, or misunderstandings.

# THE VERTICAL DISTRIBUTION

The known vertical distribution of 34 of the endemic abyssal bivalves recorded from two and three findings only is shown in Fig. 129, and that of 28 species known from four records and more in Fig. 130. It is conspicuous that a greater vertical range is found in the latter group as compared to the former. The majority of the species have their upper limit between 2000 and 3000 m, but there is a great variation in both the upper and the lower limit, which to a large extent is due to the small number of records. It is furthermore evident that in the bivalves there is no obvious indication of a subdi-



Fig. 130. Vertical range of abyssal Bivalvia known from 4 or more records.

vision of the abyssal zone. This was suggested by VINOGRADOVA (1959a, b, 1962a, b) and discussed in detail by MADSEN (1961b), who came to the conclusion that in the Porcellanasteridae there appeared to be a change in the species composition at 4000-5000 m depth, supporting the distinction of an upper and a lower abyssal zone. It may be significant, however, that three bivalves shown in Fig. 130 have their upper limit at about 4500 m depth: Spinula calcar, Limopsis galatheae and Myonera undata. As will be dealt with below, the number of samples containing bivalves from below 4000 m is very low, so the possibility still exists that there may be a faunal element of bivalves confined to depths between 4500 and 6000 m. Some species have been recorded from rather shallow water outside the abyssal zone and this "extraabyssal" occurrence will be briefly discussed below (p. 202).

VINOGRADOVA (1962a, 1962b) undertook a comprehensive survey of abyssal benthic invertebrates of different groups: Porifera, Coelenterata, Isopoda, Decapoda, Pantopoda, Echinodermata (without the Ophiuroidea) and Pogonophora, altogether 1031 species from depths greater than 2000 m. The Bivalvia were not included. It was found that in general the horizontal distribution was rather restricted, and only 4 % of the species were found in all three oceans, while 15 % were found in more than one ocean. It was also stated that the Pacific has 73 %, the Atlantic 76 %, and the Indian Ocean only slightly over 50 % endemic species. On comparing the fauna of the Antarctic Ocean with the faunas of the Atlantic and the Pacific Oceans and in the same way the abyssal fauna of the W. and E.Atlantic with that of the W. and E. Pacific, it was found that among the species known from 2000 m depth the degree of endemism is rather small, but with increasing depth there is an increasing percentage of endemism. Thus in the N.Atlantic 49% of the species ascending above 2000 m are common to both the western and eastern part, but below 3000 m only 7.2 % of the species are common and none are common below 4000 m. Corresponding figures were found on comparing the western and eastern part of the N.Pacific and the Indian Ocean. In other words, species occurring in the deeper part of the abyssal zone have a more restricted distribution than species from the upper abyssal zone. This does not appear to be the case in the Bivalvia. There are several species occurring in the deepest part of the abyssal zone which have an extremely wide horizontal distribution and at the same time are found also in the upper part of the abyssal zone (Fig. 130). This applies to the following cosmopolitan species: Malletia cuneata, Acar asperula and Arca orbiculata, all of which also ascend to about 2000 m depth. Limopsis pelagica pelagica and Abra profundorum are wide-ranging, both horizontally and vertically. Myonera undata is an example of a species with a rather restricted vertical distribution in the lower part of the abyssal zone, and might therefore be expected to be endemic. Nevertheless, the 11 records of live specimens have shown the species to have a considerable distribution (see p. 190), covering seven ocean basins. The theory of extensive endemism in the lower abyssal zone was corroborated by ZENKEVITCH (1963), who stated, however, that to a certain extent the endemism was accounted for by the deepwater fauna not having been sufficiently studied. I think that such considerations are irrelevant for at least two obvious reasons:

1) VINOGRADOVA's survey includes animal groups which fundamentally have a restricted distribution (Isopoda, Pogonophora). But some of the other groups mentioned by VINOGRADOVA (1959a) have in fact been shown to have generally wide distributions. The revision of the Porcellanasteridae by MADSEN (1961a) should be consulted; and also the thorough revision of the abyssal Holothurioidea by HANSEN (1967) is an example of this. To this should be added that the Decapoda are badly in need of a revision and until that has been done little can be stated with any degree of certainty about the distribution of the individual species (T. WOLFF, personal communication).

2) ZENKEVITCH's statement that the results to a certain extent are influenced by the insufficient investigation of the abyssal zone is hardly exaggerated.

The small number of hauls made, for instance below 4000 m depth, makes it likely that this factor exerts a profound influence on the results. The considerable extension of the known distribution of numerous animals as a result of the work of the Galathea Expedition is a strong indication that this is so.

The known number of species of endemic abyssal bivalves varies considerably with depth, as appears from Fig. 131, curve A showing the number of species known from the depth intervals indicated. All endemic abyssal species are included with the exception of species which are known from valves only, since - although probably abyssal - they might have been displaced, and thus make the curve less reliable. No bathyal species have been included, even if occurring also in the abyssal zone. The greatest number of species, 64, has been found in the interval 3000-3500 m, and a slightly smaller number of species, 61, in the nearest overlying interval, 2500-3000 m. In the interval 2000-2500 m there are 46 species, this number decreasing rapidly towards shallower water. As already pointed out (p. 163), it is in some cases difficult or impossible with certainty to decide whether a given species is bathyal or abyssal if it is known from one or a few finds at 2000-2500 m depth. If some of these now assigned to the abyssal fauna should turn out to be bathyal when we later obtain additional records, this would mean a steeper decline of the upper part of the curve A towards shallower depth, i.e., a sharper demarcation of the border zone between the bathyal and abyssal zone. The lower part of the curve clearly shows the decline in the number of known species with increasing depth. It will be seen that in the 4500-5000 m interval the number has decreased to half the maximum number of species in the 3000-3500 m interval.

Curve B shows the number of species known from two and three records only. The maximum number of species is found at the 3000-3500 m interval, as in curve A, and from this interval there is a steady decrease in the number of species with increasing depth. Already in the interval 3500-4000 m the number of species known decreases to half the maximum number. Curve C shows the species from four records or more. The maximum number of species, 21, is again found in the 3000-3500 m interval and below that a moderate decrease from 17 to 13 species is found from the 3500-4000 m interval down to the 5000-5500 m interval. The maximum in curve A at the intervals 2500-3000





Fig. 131. Number of species of abyssal Bivalvia occurring at depth intervals of 1000 m. A, total number of species known from living specimens, B, number of species known from 2-3 records, C, number of species known from 4 or more records.

Fig. 132. Left side: number of hauls containing bivalves carried out at the depth zones indicated. Right side: percentage distribution of the hauls.

and 3000-3500 m is more pronounced than the maxima seen in curves B and C. This is due to the relatively very large number of species found only once at these depths.

The decrease in the number of species of abyssal animals with increasing depth has frequently been referred to. This was first noted by the Challenger Expedition (THOMSON & MURRAY, 1895), and discussed later by EKMAN (1953), who reproduced a table from THOMSON & MURRAY which shows this very convincingly. EKMAN added that it is not very probable that depth alone is the decisive factor, but that distance from the shore also plays an important part, as well as the nature of the bottom sediment.

To some extent the decrease of the number of species with increasing depth is correlated with the distance from larger land masses, since a large proportion of the deepest hauls actually have been made far from land and in places where there is only little addition of terrigenous organic matter. Another possibility is that the low number of species is due to too little collecting activity.

To obtain some impression of the latter problem a survey has been made of all abyssal hauls and their distribution as to depth. Only hauls in which abyssal bivalves have been obtained (about 280) have been included, and the hauls of the Vitiaz and WHOI Expeditions have been excluded because only a few species of the bivalves obtained have been worked up. It should be noted that the actual number of hauls made at depths less than 2500 m is in fact much higher than indicated, but numerous hauls containing decidedly bathyal species have been omitted. There is a rapid decrease in the number of hauls with increasing depth (Fig.132). Of the hauls considered, 38 % have been made between 2500 and 3500 m depth and only 81 hauls, 29 %, have been made below 4000 m, which is the average depth of the world ocean. It is seen that the curve on the left in Fig.132 has a shape which is very similar to curve A (Fig. 131), this gives some indication that the decrease in the number of species with increasing depth is dependant on the number of hauls made.

The above survey is admittedly a very crude one,

lumping together samples with widely different gears taken by many different ships of presumably widely different fishing efficiency. It is, of course, completely unsuitable for any quantitative purpose. In this respect the investigations of SANDERS et al. (1965) and HESSLER & SANDERS (1967), already referred to, are of great interest. The investigations are based upon series of hauls with a quantitative dredge, taken along a section in the N.W.Atlantic from the sublittoral zone down to about 5000 m depth. The content of the dredge is sieved through a screen with 0.42 mm mesh. The results show much greater densities than those reported from previous studies, probably a result from using fine-meshed sieves. Generally a decrease in the density of organisms with increasing depth and distance from land was observed. The following numbers from HESSLER & SANDERS (1967) show the diversity of the bivalves in some of their abyssal stations:

	Bivalvia					
St. no.	Depth in m	no. spp.	no. specimens			
62	2496	21	430			
64	2886	29	512			
70	4680	21	1746			
72	2864	26	567			

It will be seen that the number of species is much higher than in any of the "Galathea" stations, and with a single exception, the same is the case with the number of individuals. It will also be seen that in the examples shown the largest number of specimens is found in the deepest sample.

SANDERS et al. (1965) reviewed the earlier scanty data on the quantitative investigations of the abyssal zone carried out with various kinds of grabs. It was found that these investigations - including those of the "Galathea", published by SPÄRCK (1951), and of "Vitiaz", summarized by VINOGRA-DOVA (1962b) - yielded a smaller number of abyssal species than those obtained by SANDERS et al. On examining successful hauls from earlier expeditions, SANDERS et al. (1965) found that only one station from the "Challenger" (at a depth of about 1100 m) and one from the "Galathea" (St. 716, 3570 m depth, summarized by WOLFF 1961b), both non-quantitative, had a number of species approaching the diversity found in their hauls. Finally, the authors carried out hauls with the quantitative dredge on various types of shallow water bottoms. On comparing the results with those obtained from abyssal depths, the authors conclude that the diversity of benthic invertebrates in the deep-sea well exceeds that of temperate shallow benthic communities and is actually comparable to that found in tropical shallow water communities. These data clearly refute the classically held notion of a depauperate deep-sea fauna. However, it remains to be seen whether some parts of the ocean, such as, for instance, the central Indian Ocean and the central Pacific, are not rather poor in numbers of both species and specimens, as indicated by the scanty investigations carried out in the two regions mentioned.

SANDERS & HESSLER (1969) state that the deepsea benthos shows a decrease in animal life with increasing depth and distance from land probably determined by the amount of food present.

THIEL (1966) studied the meiofauna in abyssal samples, down to a depth of about 5000 m, from the northwestern part of the Indian Ocean. His results can not be directly compared to those of SANDERS *et al.*, but some of the samples had a quite high number of specimens, particularly of Nematoda. By comparison with other investigations of meiofauna from various shallow water localities, THIEL concluded that the number of individuals in the abyssal meiofauna is of the same magnitude as that of some poorer shallow-water localities. As the investigation is still in its preliminary stages, nothing has yet been mentioned about the number of species.

VINOGRADOVA (1959, 1962a, 1962b) demonstrated that the decrease in the number of species with increasing depth and changes in the composition of the bottom fauna are not uniform, but occur in certain depths more rapidly and abruptly than in others. The most marked changes occur at 3000, 4500 and 6000 m. According to this the abyssal zone may be divided into an upper and a lower subzone above and below about 4500 m. The depths at which the changes occur are identical in all oceans. They vary, however, in different systematic groups but as a rule there is a certain increase in the total number of species around the depths mentioned. The most pronounced deep-sea maxima are found in ancient groups of invertebrates such as Porifera (incl. Triaxonida), Porcellanasteridae, Asellota (Isopoda) and others. From this it is concluded that the vertical distribution existing today may have been determined by the conditions existing in past geological times. ZEN-KEVITCH (1963) holds the same opinion.

This problem has been discussed by WOLFF (1962) with respect to the asellote isopods. WOLFF

found that a double maximum actually does exist when all recorded species are considered. However, when correctly excluding the species known from one find only, he found that the maximum is considerably reduced, and if only species known from more than four finds are considered, the maximum between 4500 and 500 m disappears. WOLFF concluded that as far as the Asellota are concerned there is nothing to indicate a lower abyssal zone. HANSEN (personal communication) is of the opinion that in the abyssal Holothurioidea there is no real double maximum, but rather a regular decrease of the known number of species with increasing depth. TENDAL (personal communication), in a survey of abyssal Porifera, made the same observation. Both authors hold the opinion that the apparent maxima to some extent at least are due to unsatisfactory taxonomy prevailing in the two groups mentioned.

VINOGRADOVA's suggestion that the maxima are particularly distinct in ancient groups is contradicted by the opinion of MADSEN (1961b) that the Porcellanasteridae are not primitive, as previously supposed, but rather of comparatively young phylogenetic origin. The same is the case with the Elasipoda (MADSEN, 1961b; HANSEN, 1967), which form about half of the deep-sea holothurians and which were also found to have distinct maxima.

MENZIES & GEORGE (1967) published a diagram showing the vertical distribution of "numbers of animals by groups" in the Milne-Edwards Trench (part of the Peru-Chile Trench). According to this the bivalves show a slight constant decrease from about 2000 m to about 4500 m, a maximum at about 5000 m, and a subsequent decrease towards 6000 m. The diagram is difficult to discuss, since there is no information about the number of species involved, and it is not clear whether the diagram deals with the number of species or with the number of specimens.

SANDERS & HESSLER (1969) did not find such abrupt changes of the fauna as postulated by VINOGRADOVA.

As appears from Fig. 131, there is nothing to indicate the presence of depth zones with a maximum of species in the bivalves. Even if the Nuculoidea, generally considered the most primitive bivalves, are considered separately, such a maximum can not be found. Nor has it been possible to suggest any environmental factor causing concentrations of numbers of species in certain depth zones.

# ON THE EXTRA-ABYSSAL DISTRIBUTION OF ABYSSAL SPECIES

In the foregoing sections the term "endemic" abyssal species has been used to designate a species whose vertical distribution is confined to the abyssal zone, in contrast to the abyssal "guest" which has its normal habitat in the bathyal zone, but penetrates into the upper part of the abyssal zone. However, the abyssal endemism is not complete, as will appear from Table 1, since several species formerly considered to be endemic abyssal are under certain circumstances able to live in much more shallow water than they are usually found. A few examples are shown in Fig. 130. Of these Acar asperula is of particular interest. As mentioned before (p. 75), it has been found in the W. Indies at a depth of about 570 m ("Blake" St. 19) and a temperature of about 11.3 °C. In addition it has been found in the Banda Sea at a depth of only 430 m and at a temperature of 7.8 °C. (Mortensen St. 29) and in the Sulu Sea, 1500 m,  $11.7 \degree$ C.

The record from the Banda Sea is of particular interest. MORTENSEN (1923) called attention to the surprising fact that in the Banda Sea numbers of truly abyssal forms occurred here in relatively shallow water. This assumption was based partly on examination of the findings of the "Challenger" and "Siboga" and partly on his own research. It was shown that here the abyssal fauna was actually found at depths of 200-300 m. Acar asperula constitutes a typical example of the correstness of MORTENSEN's statement. The reason for this ascent of the abyssal fauna is probably due to the fact that in this region, under the influence of the southeast monsoon, there is an upwelling of deep water from May to August (WYRTKI 1961). Such an upwelling could at times, at least, carry eggs of A. asperula upwards, and under favorable circumstances they may develop into adults. A similar case may be the above-mentioned finding of the species at 570 m in the W. Indies, although I have not found any mention of upwelling. The record of A. asperula in the Sulu Sea at 1500 m is noteworthy. This basin has a sill depth of 420 m, a maximum depth of about 5600 m, and a minimum temperature of about 10.1 °C (WYRTKI 1961). It is unfortunately not known whether the great depth of the Sulu Sea harbours an endemic population of Acar asperula or whether the population is dependant on an inflow of eggs and larvae from the outside. In the latter case they must ascend to a depth less than the sill depth of 420 m.

Similar irregular vertical distributions may occur in several abyssal species, in particular those having pelagic eggs and larvae. It may also occur in other upwelling regions, such as those off the northwest coast of Australia, off W. Africa, and off Peru (SMITH 1969).

No abyssal bivalve species seems to ascend to the sublittoral zone, not even in areas where the temperature conditions are such that one might expect this to occur, e.g. the well explored arctic and boreal zones of the N.Atlantic and the Arctic Ocean (see p. 204).

Like the occurrence of abyssal guests from the bathyal zone, the extra-abyssal distribution of endemic abyssal species makes the limit (or rather border zone) between the bathyal and abyssal zones less clear cut.

#### TEMPERATURE

In general temperature is one of the important factors governing the distribution of marine organisms. However, very little is known about temperature relationships of abyssal organisms, and the matter was only briefly referred to by EKMAN (1953). In his provisional division of the deep-sea fauna, BRUUN (1955a, 1956, 1957) used the upper temperature limit of 4 °C for the abyssal fauna and stated that this temperature is found at different depths in different areas. Thus, in the Atlantic this temperature is not reached until about 2000 m depth, whereas in the Indian and Pacific Oceans it occurs already at 1500 or even 1000 m. BRUUN mentioned that much of the discussion about the vertical range of the bathyal and abyssal zones is undoubtedly due to these differences in the position of the 4°C isotherm in the various regions.

KRAMP (1959) found that the essentially abyssal scyphozoan *Stephanoscyphus simplex* has its principal occurrence at temperatures below  $4^{\circ}$ C, but under certain conditions it ascends into the bathyal region where it tolerates temperatures up to  $10^{\circ}$ - $11^{\circ}$ C (perhaps even to  $13^{\circ}$ C). However, by far most of the catches are from depths below 2000 m and temperatures below  $4^{\circ}$ C, and KRAMP suggested that the occurrences in the bathyal zone at temperatures above  $4^{\circ}$ C were due to favorable food conditions.

MADSEN (1961a) stated that the distribution of the Porcellanasteridae may to a great extent be controlled by the temperature, but no member of the family has hitherto been found in shallower depths in the polar seas, areas to which some other deep-sea groups of echinoderms have expanded their range.

MENZIES (1965) coined the term hypopsychral for the fauna inhabiting water of temperatures less than 0 °C. We do not know, however, whether the abyssal zone of the world ocean harbours a specific faunal element confined to areas with negative bottom temperatures; such a fauna is found in the Arctic Ocean (see, for instance, EKMAN, 1953 and OCKELMANN, 1958). MENZIES suggested that the low temperature causes the gigantism stated to occur in abyssal representatives of some animal groups.

HANSEN (1967) believes that the temperature is apparently the decisive factor in the bathymetrical distribution of the species of holothurians (*Elpidia* glacialis, Scotoplanes globosa) which ascend into shallower depths in colder regions. However, by far most of the deep-sea holothurians stick to their depth even in regions where the temperature would permit them to live in shallower water. For most of the deep-sea species temperature is apparently not the crucial limiting factor.

In the preceding sections on the distribution of the individual species the total known temperature range is given. For most species the number of records is small and it is therefore to be expected that the total range will turn out to be greater than is known at present. It is, however, of greater ecological interest to know the temperature conditions under which the majority of the individuals of a species lives. Unfortunately it has not been possible to study this in abyssal organisms. However, in a few species of bivalves the temperature data may give some indication of this. In Malletia cuneata (p. 67) there is only a single record at 3°C, all the remaining records being from water of less than 2.5°C. In Acar asperula there are some extraabyssal records with temperatures up to 11.7°C (p. 75), but 75 % of the records are from temperatures below  $4^{\circ}C$ , and more than 50 % are from below 3°C. In Arca orbiculata more than 80 % of the records are from below 2.5°C. In Limopsis pelagica (p. 86) about half of the records are from below 2.5°C, and in *Abra profundorum* more than 60% of the records come from less than  $2.5^{\circ}$ C. In the species mentioned here, and also in many other species of abyssal bivalves, the majority of the records are from temperatures below the maximum temperatures. It should be emphasized, however,

that owing to the small number of hauls made in the deepest part of the abyssal zone, the lower temperature range of the species is poorly known, and from the present data we cannot draw any conclusions about the temperature preference of the individual species.

The known upper temperature limit of the abyssal bivalves appears from the following survey comprising species with four records or more:

Temperature range °C	No. of species
below 1.9	3
2.0-2.4	1
2.5 - 2.9	3
3.0-3.4	8
3.5-3.9	4
4.0-4.4	3
4.5-4.9	0
5.0- +	3

It will be seen that although the data are scanty, nearly half of the species considered have their upper limit at temperatures between  $3^{\circ}$ C and  $4^{\circ}$ C. There may, however, be species which have their upper limit at a considerably lower temperature. This is the case with *Spinula oceanica* of which 19 records of live specimens are at hand, but in no case does the recorded temperature exceed  $1.7^{\circ}$ C. The three species listed having their upper temperature limit above  $5^{\circ}$ C are: *Acar asperula* (see above), *Acharax johnsoni* and *Cyclopecten undatus*.

Unfortunately, the available samples can not be used for a study of the different positions of the upper limit of the abyssal zone as suggested by BRUUN (1957).

Although the temperature is an important factor in determining the distribution also of the abyssal bivalves, other factors as yet unknown exert a profound influence. One of these factors may be the hydrostatic pressure.

If temperature was the dominating factor, we should, as mentioned above, expect that arctic shallow water areas would harbour at least some abyssal species. OCKELMANN (1958), in dealing with the bivalves of E. Greenland, found that different water masses had different species of bivalves. One of the water masses distinguished is the "Atlantic undercurrent water", which occurs along the outer shelf of E. Greenland at 50-400 m depth and fills up most of the large fjords, from the lower part of the overlying Polar current to the bottom. The "Atlantic undercurrent water" is a mixture of Polar current water and varying portions of the Atlantic water mass. It has a temperature of  $0-3^{\circ}$ C, i.e.,

within the temperature range of the abyssal zone. Among the species mentioned by OCKELMANN (1958) as associated with this water mass there is not a single species belonging to the endemic abyssal fauna, and on the whole I have been unable to find any records of endemic abyssal bivalves from the arctic shallow water. This strongly indicates that an efficient ecological barrier other than temperature must exist which separates the abyssal bivalve fauna of the world ocean from the arctic shallow water fauna living under the same temperature conditions.

# THE HYDROSTATIC PRESSURE

The hydrostatic pressure has been assumed to be of great importance to deep-sea organisms, although very few relevant facts on the topic seem to exist. BRUUN (1957) discussed the problem reviewing some of the results obtained by applying high pressure to shallow water organisms. MADSEN (1961b) stated that temperature, although it is extremely important, evidently is not the sole factor determining the vertical distribution of the Porcellanasteridae (Echinodermata), but that pressure may be significant, although its influence on abyssal organisms is actually unknown. The apparent absence of the Porcellanasteridae in more moderate depths in polar regions might lead to the assumption that they are dependant on the hydrostatic pressure. MADSEN, however, was of the opinion that the upper limit of the occurrence of the Porcellanasteridae should rather be explained by their relations to other animals in the habitat, competitors for food and predators.

As mentioned above, no abyssal bivalve has yet been found in the arctic shallow water, which may or may not indicate a dependence on pressure. WOLFF (1962) suggested that the gigantism he observed in abyssal crustaceans might be due to the hydrostatic pressure. HANSEN (1967) found that many deep-sea groups of holothurians have narrow vertical ranges and suggested that these groups were physiologically adapted to the high pressures under which they live.

Although the apparent absence of endemic abyssal bivalves from arctic shallow water may be correlated with the pressure, the wide vertical range of several species proves that a wide range of pressure is tolerated. As will be mentioned below (p. 211), there appears to be no variation in the external shell morphology between populations from the upper and the lower parts of the abyssal zone.

#### SEDIMENT

The present survey has not demonstrated any relation between bottom sediment and the distribution of bivalves. This does not mean, however, that such a relation is non-existent. The information on the bottom sediments collected by biological deep-sea expeditions has until now been both fragmentary and subjective, the diagnosis of any given sediment type obviously differing widely from one expedition to another. In the future a rational analysis of bottom sediments may demonstrate that many bivalve species are in fact confined to particular sediment types.

The effect of burrowing animals was discussed by BRUUN & WOLFF (1961). Where large numbers of burrowing bivalves are present they may contribute considerably to the re-working of sediments.

GRIGGS et al. (1969) thus found that in sediments from 2800-2900 m depth in the N.E. Pacific (Cascadia Plain and Channel) a considerable re-working has taken place. Burrows of different sizes are mentioned and figured together with specimens of corresponding sizes which might have caused them, e.g. fig. 8 showing three bivalves, which apparently are Arca orbiculata. GRIGGS et al. found that the Cascadia Channel axis and the region at the base of the continental slope had about four times as many animals per square meter as was found on the plain proper. At the same time they found that the areas rich in benthic life had a higher organic carbon content in the sediment, and in these localities more burrows were present. A closer examination of the sediment samples showed that during the Pleistocene, turbidity currents have occurred repeatedly and that sediments from these are separated by thin, less rich hemipelagic clays. The time interval between the turbidity currents can not be evaluated. The authors suggest that besides acting as a conveyer of nutrient organic material, the turbidity currents are destructive to the benthic fauna, which becomes completely sealed off.

# THE GEOLOGICAL AGE OF THE ABYSSAL BIVALVE FAUNA

#### A survey of the literature

An important aspect of the problem concerning the abyssal fauna is that of the existence of elements of an archaic relic fauna in the abyss. An "archaic relic fauna" is here understood as a fauna of Palaeozoic organisms from shallow (littoral or sublittoral) water which has penetrated into the abyssal zone and, while still surviving in the abyss, has become extinct in shallow water.

Based on the results of the Challenger Expedition, the idea earlier held by many 19th century biologists that the deep-sea should be inhabited by an archaic fauna was convincingly refuted by MOSELEY (1880). This viewpoint was also agreed with by e.g. SPÄRCK (1954).

EKMAN (1953) stated that the archaic deep-sea forms are "by no means few in number", although he was aware of the fact that specialized forms also occur. He concluded that the deep-sea fauna is relatively richer in archaic forms and that the deep sea has become a refuge for more conservative types which have elsewhere become extinct. In any case it can be regarded as established that a deepsea fauna has existed for a very long time.

DAHL (1954), in reviewing the distribution of the deep-sea crustaceans, concluded that there is every reason to believe that the invasion of the deep-sea by species from the continental shelf is still in progress. The concept of the deep-sea as a habitat inhabited on the one hand by archaic types and on the other hand by comparatively advanced representatives of modern groups is much too static. The deep-sea is simply more likely to preserve a species or a type comparatively unchanged for a longer time than the shallower areas with their much greater fluctuations of environmental factors. Several of the oldest crustacean groups are scarce or absent in the deep-sea.

GISLÉN (1951) concluded that the more specialized forms of Crinoidea occur mainly at great depth.

BRUUN (1956, 1957) found it probable that in the Tertiary and earlier the abyssal zone had a temperature of between  $4^{\circ}$  and  $10^{\circ}$ C, an assumption based on the data obtained by EMILIANI *et al.*, from examination of oxygen isotopes of fossil benthic foraminiferans. BRUUN suggested that the onset of the glacial age might have caused a catastrophic cooling of the abyssal water to below  $4^{\circ}$ C. The cooling possibly resulted in a large scale elimination of a large part of the abyssal fauna. Only the relatively eurythermic and eurybathic species could survive. The abyssal fauna is thus of fairly recent geological age.

MENZIES & IMBRIE (1958) stated that part of the controversy was due to different meanings of the words "ancient" and "deep". After having examined the condition in six major groups of invertebrates (the Mollusca were not included) they came to the following conclusions:

1) The abyss has preserved fewer ancient forms of life than shallower depths.

2) The relative age of the genera of the marine fauna decreases with increasing depth. The Tertiary component of all groups studied is higher in the abyss than in the intertidal.

3) Percentage-wise, the abyssal fauna having a known geological age consists mostly of Tertiary types.

4) The concept that the abyssal fauna is an ancient one must be discarded in favour of the concept maintaining that it is a relatively recent one in the geological sense.

ZENKEVITCH & BIRSTEIN (1960) postulated that the colonization of the abyssal zone has extended over a very long geological time. The recent deepsea fauna contains species which immigrated into the abyssal zone at different periods. At the same time they are of the opinion that many undoubtedly ancient elements exist in the abyssal zone. The percentage of primitive archaic forms in the abyssal fauna is far higher than in the fauna of the shelf, thus providing evidence of the greater antiquity of the abyssal fauna. The authors mention a series of examples of ancient elements in the abyssal zone. Among these are the Porcellanasteridae. This group has, however, been shown by MADSEN (1961b) to be specialized forms. The Pogonophora are also considered an archaic group. Judging from their aberrant anatomy and their peculiar mode of feeding, they should rather be considered as highly specialized forms. POULSEN (1963) demonstrated, however, that the group appears to have existed already in the Middle Cambrian, so that the Pogonophora may be among the oldest known invertebrates, together with brachiopods and trilobites. Although there are numerous records of Pogonophora from abyssal depths, there are many records also from more shallow waters. More than half of the existing records are from bathyal depths, and there are several records from the lower part of the sublittoral zone (SOUTHWARD 1963, SOUTHWARD & SOUTHWARD 1967). WEBB (1965) mentions several records from the lower part of the sublittoral zone off the Norwegian coast and even a single record from only 25 m. Thus, there is no reason to consider

the Pogonophora as confined to the abyssal zone. SOUTHWARD & SOUTHWARD (1967) state that the group lives rather on the slopes than on the abyssal plains, and that they appear to tolerate an annual temperature range of as much as  $5^{\circ}$ C and a summer maximum of up to  $12^{\circ}$ C. POULSEN (1963) considers the Cambrian Pogonophora, *Hyolithellus*, to have lived in shallow water. This assumption, together with the abundant occurrence in both sublittoral and bathyal depths, would rather suggest that the group originated in shallow water, and that during the time representatives of the group have penetrated into the abyssal zone, where for nutritional reason they have largely remained on the slopes or the trenches adjacent to land.

As far as the Mollusca are concerned, ZENKE-VITCH & BIRSTEIN (1960) mention *Neopilina*. The group seems not to be represented in depths less than 2000 m, at which depth a species of *Neopilina* was recorded by FILATOVA *et al.* (1968). The remaining known species are from between 2800 and 6300 m. PARKER (1961) recorded a shell fragment from about 1800 m depth. Thus *Neopilina* might well be considered the only known example of a Palaeozoic organism originally living in shallow water and having its recent occurrence confined to the abyssal zone.

ZENKEVITCH & BIRSTEIN (1960) also mention the following bivalve genera as ancient elements in the deep-sea fauna: Spinula, Tindaria, Malletia, Neilonella, Neilo, Leda, Yoldia, Yoldiella, Nucula. This problem will be discussed below (p. 208). The two authors state that the genus Spinula should be closely related to the Silurian genera Silura (=? Silurina) and Hercynella. VOKES (1967) assigns the two latter genera to the exclusively fossil family Antipleuridae, Order Praecardioida, while Spinula is assigned to the Nuculanidae, Order Nuculoidea. Comparison of figures of Hercynella with Spinula has also convinced me that they are not at all closely related.

ZENKEVITCH & BIRSTEIN (1960) criticize the views of MENZIES & IMBRIE (1958) and BRUUN (1956, 1957). BRUUN'S suggestion of a Tertiary cooling of the deep sea is refuted on the statement that the investigation of the palaeotemperatures was made on shallow water foraminiferans deposited in abyssal sediments. Young elements of the deep-sea fauna are also dealt with by ZENKEVITCH & BIRSTEIN (1960). They state that the process of colonization of the abyssal zone by the different elements of its fauna was not continuous and that along with

the specific ancient deep-water forms there exist many groups of relatively young deep-water animals closely related to shallow-water forms. There are classes, genera and species of recent settlers whose stay in the abyssal zone has not been long enough for a marked morphological differentiation from their shallow-water ancestors, and who have no primitive archaic features. The sipunculoidea are mentioned as an example. ZENKEVITCH & BIRSTEIN (1960) then distinguish between the ancient and the secondary deep-water forms. It is stated that they have different patterns of distribution: "In most secondary deep-water animals the number of species regularly and rapidly decreases with increasing depth, whereas in the ancient deep-sea animals the number of species tends to increase with depth and begins to diminish only with the passage to the lower abyssal and the ultraabyssal water." This is illustrated on a diagram giving the vertical distribution of Sipunculoidea, representing the secondary element and the Pogonophora, representing the ancient element. In the former the largest number of species is found in more shallow water, below 200 m depth, and there is a rather regular decrease towards the hadal zone. The Pogonophora show a relatively small number of species in shallow water and a maximum number of species round 4000 m. From this depth the number of species decreases rapidly towards 5000 m, and from the latter depth down to 11,000 m only a rather small number of species is found. However, this shape of the configuration may well be an artefact caused by too little investigaion. In recent years there have been numerous records of Pogonophora from many regions of the world ocean and from fairly shallow water (see above). In summarizing Southward & Southward's (1967) data on the distribution of the Pogonophora in the Atlantic in the same way as done by ZENKEVITCH & BIRSTEIN, we obtain a configuration showing a maximum number of species between 400 and 900 meters, with a regular decrease towards greater depths, i.e., a configuration having the same shape as that of Sipunculoidea, except that the maximum number of species occurs a little deeper. The conclusion is that a distinction such as that proposed by ZENKEVITCH & BIRSTEIN cannot be made. They further stated that secondary deep-water species of fish appear to have very narrow ranges of distribution and are confined mainly to the continental slope and adjoining parts of the abyssal zone. The ancient fishes, on the other hand, are characterized by very wide, sometimes panoceanic ranges. ZENKEVITCH & BIRSTEIN doubt whether this statement can be applied to all invertebrates without reservation, but still advocate the idea that it is possible to distinguish the relatively ancient and the relatively young inhabitants of the abyssal zone without recourse to palaeontological data.

The problem of the antiquity of the abyssal fauna was discussed in detail by MADSEN (1961 b) who held the opinion that the recent deep-sea fauna is of no great age and that at least the concept of its being essentially archaic is erroneous. He suggested that a large part of the present day abyssal fauna dates back to the Tertiary only, and that from a geological point of view, on the whole it would seem that the greater the depth the younger the inhabitants. MADSEN mentioned the bivalve families Nuculidae and Ledidae (= Nuculanidae) as examples of Palaeozoic groups which may not have extended their distribution into the abyssal zone until a comparatively late geological period.

MADSEN (1961b) also discussed the possible decrease of temperature in the abyssal zone during the Tertiary. He calculated that the annual decrease during the period was of the magnitude  $0.23 \times 10^{-6^{\circ}}$ C and concluded that the extinction of the greater part of the possibly Palaeozoic and Early Mesozoic abyssal fauna would have been a gradual phenomenon proceeding during the whole of the Tertiary rather than a relatively sudden mass-mortality at the initiation of the Glacial Epoch as suggested by BRUUN (1956, 1957).

The problem of temperature decrease of the abyssal and hadal waters prior to the Cenozoic was discussed by EMILIANI (1960), who took into consideration the statement of ZENKEVITCH & BIRSTEIN (1960) concerning the validity of the measurements of palaeotemperatures. There is no reason to doubt the validity of the isotopic investigations, and evidence is given to support the idea that a temperature decrease has taken place both in the high latitudes and in the abyssal and hadal regions. The decrease is of the magnitude of 12°C in both areas. It is suggested that if constant temperature is more important for the survival of archaic forms than other factors, the equatorial pelagic fauna should show more archaic affinities than other marine faunas.

In a discussion of the age of the abyssal fauna J. L. BARNARD (1961) stated that highly specialized forms occur among the Amphipoda and that there is no endemic abyssal family among the benthic forms. Concerning the idea of ZENKEVITCH & BIR-STEIN (1960) of an increased diversity in archaic deep-sea animals, he found that one family of amphipods, the Pardaliscidae, shows an increased number of species with increasing depths, but may not necessarily be primitive; on the contrary, the mandibles are highly specialized. BARNARD believes that the amphipod fauna is a recent one. Markedly primitive forms are absent and there are few endemic genera. Most of the abyssal species are closely related to nearby shallow-water forms, and the occurrence of regional endemism indicates either a recently evolved abyssal fauna or a very strong restriction by undersea topographic barriers.

HESSLER & SANDERS (1967), in studying the diversity of the abyssal fauna, found it difficult to conceive that such a diverse fauna could be as young as suggested by some workers. They suggested a long-term physiological adaptation. They do not consider MADSEN's above mentioned calculation of the annual decrease of the temperature, but by inspecting EMILIANI's graphs on changes in abyssal temperatures, they concluded that there has been an almost constant rate of change from Oligocene to the Upper Pliocene. They further concluded that the short term temperature fluctuation occurring in the deep-sea was probably no greater before or during the Pleistocene than it is today, and that the organisms would have gradually adapted themselves to the changing physical conditions. Therefore it is not necessary to postulate large scale Quarternary extinctions and invasions to account for the present conditions. A re-invading bathyal fauna would meet the same adaptive problems when adapting itself to the low temperature, the high pressure and perhaps other physiological factors as would a persistent abyssal fauna.

In discussing the age of the abyssal bivalve fauna the following quotation of N. D. NEWELL (1965) is worth considering: "It is evident that many of the family-group taxa have been astonishingly conservative, with long and continuous records that extend far back into the Palaeozoic-. Where the fossil record is good, there is abundant evidence that general shell characters in many groups have been quite stable, through hundreds of millions of years-."

MADSEN (1961 b) stated that "in theory, a taxon of e.g. family rank could have evolved in the abyssal deep-sea, and thereafter extended its range of distribution upwards, in competition with the bathyal and sublittoral faunas. But this course of events, if ever having taken place at all, will be the exception rather than the rule." This assumption is probably correct. If this actually was the normal sequence of events then we might also today expect in the abyssal zone endemic genera and families of bivalves which are either relic groups which have become extinct in shallow water or groups which have originated in the abyssal zone and have not yet migrated upwards. As has been shown, such endemic bivalve groups do not exist in the abyssal zone.

## **Present survey**

The geological age of the 20 families represented in the abyssal fauna is summarized in Table 6. The geological ages mentioned are from MÜLLER (1963) and CLARKE (1962b). In inspecting different palaeontological works, the information on the geological age of some groups is somewhat inconsistent. This is to some extent due to differences of opinion of delimiting the taxa, but the discrepancies are not large enough to change the overall picture. It will be seen that eight of the 20 families originated in the Palaeozoic, seven in the Mesozoic, and five in the Cenozoic. From this one might infer that the abyssal fauna is to a great extent an archaic one. However, returning to the statement of N. D. NEWELL (1965) about the great stability of many groups throughout their geological history, I think it is reasonable to assume that during the whole history of a given group abyssal species could split off, but at the same time the main stock of the taxon in question remained in shallow water. It is therefore hardly justifiable to consider these groups as relics in the abyssal zone. Table 7 shows the geological age of the abyssal genera. Of the 44 genera, no information could be obtained on 13 genera and six genera are classified as "Recent", which means that there is no geological record of the genus in question. Of remaining 25 genera, more than half (13) are Cenozoic (Tertiary). Since both the Palaeozoic and the Mesozoic genera are well represented in recent shallow water there is nothing to indicate that the abyssal species originated in Palaeozoic or Mesozoic, but the descent could have taken place at any later time. The majority of the genera, however, being Tertiary indicates a recent origin of a great part of the abyssal bivalve fauna. In the Nuculanidae, a family which dates back to the Silurian, two genera, Ledella and Spinula, date back only to the Tertiary. Besides the two just mentioned, many of the more important genera are of Tertiary origin: Tindaria, Neilonella, Kelliella, Abra, Poromya.

Possibly there has been a more or less continuous

PALAEO	ZOIC	Mesozoic	Cenozoic
Cambrian	Devonian	Triassic	Tertiary
-	Solemyidae	Limopsidae	Montacutidae
Ordovician	Mytilidae	Cuspidariidae	Scrobiculariidae
Nuculidae	Carboniferous	Jurassic	Kelliellidae
Silurian	Pectinidae	Pholadomyidae	Verticordiidae
Nuculanidae	Limidae	Thraciidae	Quaternary
	Pholadidae	Cretaceous	(Vesicomyidae)
	Permian	Malletiidae	
	Arcidae	Thyasiridae	
		Poromyidae	

Table 6. The geological age of the abyssal families.

descent of shallow-water organisms into the abyssal zone throughout the geological history. It could very well be that at certain times the descent was more intensive than at others. Simultaneously an extinction of abyssal animals has taken place, and, perhaps on a modest scale, also speciation. The relative importance of these three processes has undoubtedly changed during time in accordance with changes in the ecological conditions, such as the cooling off of the world ocean, suggested by BRUUN (1956) and MADSEN (1961b) to have taken place during the Tertiary. I am inclined to assume that the present composition of the abyssal bivalve fauna reflects the ecological conditions of the present time rather than the geological history of the world ocean. Unfortunately, deposits of ancient abyssal faunas are unknown, so for the moment the development of the abyssal fauna cannot be traced.

It has been suggested that many of the abyssal forms are organisms which compete less favorably, and hence have been "forced" down into the abyssal zone by competition from more efficient competitors. This view was held by ZENKEVITCH & BIRSTEIN (1960). However, MADSEN (1961b) held the opinion that those groups which during evolution became adapted to the life on a soft bottom, such as the Porcellanasteridae and the Elasipoda, and are now abundantly represented in the abyssal deep-sea, are conquerors of this habitat rather than refugees in it.

A somewhat similar point of view to that of ZENKEVITCH & BIRSTEIN was advanced by YONGE (1928) in dealing with the Septibranchoidea. They were found to be highly modified carnivores (p. 214). Still YONGE considers their feeding mechanism and their method of digestion a comparative failure; this may account for the small number of species. They have spread downwards into the abyssal regions where the sparseness of the animal population and the consequent lack of serious competition allowed them to survive in spite of the inadequate nature of their organs of feeding and digestion. He further suggested that as they became more specialized and so more capable of surviving the keen competition for food which exists in the shallower seas, they worked their way back into shallow water.

PALAEOZOIC	Mesozoic	Cenozoic	Quaternary	Unknown
Cambrian	Triassic	Tertiary	Pristigloma	Brevinucula
_	Arca?	Pronucula	Sarepta	Portlandia
Ordovician	Limopsis	Ledella	Dacrydium	Yoldiella
-	Cuspidaria	Spinula	Cyclopecten	Adipicola
Silurian	Jurassic	Tindaria	Cetoconcha	Delectopecten
Nuculana	Limatula	Neilonella	Myonera	Kelliopsis
Devonian	Xylophaga	Malletia		Tellimya
Nucula	Pholadomya	Acar?		Astenothaerus
Modiolus	Cretacean	Propeamussium		Laevicordia
Carboniferous	Yoldia	Montacuta		Policordia
·	Acharax	Abra		Thracidora
Permian	Thyasira	Kelliella		Halicordia
-		Poromya		Cardiomya
		Verticordia		

Table 7. The geological age of the abyssal genera.

It seems, however, that several investigations of later years have demonstrated that organic life in the abyss is both more abundant and diverse than believed when YONGE's paper was written. The competition is probably as high in the abyssal zone as in any other area. It is therefore unlikely that organisms having developed less efficient morphological and physiological structures should be able to escape extinction by a downwards migration and subsequently re-conquer niches in shallow-water areas. On the contrary, I think that the Septibranchoidea should be considered as highly successful forms which by their uniquely modified feeding have been able to conquer ecological niches in the abyssal zone.

The position of the Septibranchoidea among the bivalves has been dealt with by PURCHON (1959, 1963). He states that it has been traditional to treat the order as "the climax of the evolution of the Eulamellibranchia". But they appear to have certain similarities to the Protobranchia (= Nuculoidea), for instance in the anatomy of the stomach and the digestive diverticula. The matter is further complicated by YONGE's suggestion (1928, 1959) of a polyphyletic origin of the Septibranchioidea.

The establishment of specialized forms among the groups characterizing the bivalve fauna is, however, difficult at the present stage of our knowledge. N.D. NEWELL (1965), in discussing the classification of the bivalves, states that the morphological clues to genetic affinity are few. Consequently, parallel trends are rife, and it is difficult to arrange the class taxonomically in a consistent and logical way that takes known history into account.

The main conclusion from this is that at the present time the knowledge of the phylogeny of the bivalves does not permit us to draw far-reaching conclusions about the presence of specialized forms in the abyssal zone. However, we might perhaps consider the Septibranchoidea as specialized Nuculoidea, although it should be noted that the former group, although playing a major rôle in the abyss, by no means is confined to this zone.

In the bivalves there is at present no evidence of a family or genus which has been preserved in the abyssal zone and which is known only as extinct in the recent shallow water. However, even if the known abyssal bivalve fauna presumably in general is of a recent origin, the finding of *Neopilina* makes it reasonable to assume that some time representatives of Silurian forms, for instance of the Orders Nuculoidea (Ctenodontidae), Arcoida (Cyrtodontidae) and Trigonioida, may turn out to be present in the abyssal zone. Such findings are, however, no argument for considering the abyssal fauna as a whole as an archaic fauna.

# SOME SPECIALIZED ABYSSAL INVERTEBRATES

In the following a few examples of specialized forms from the abyssal zone will be briefly mentioned as a supplement of the cases referred to in the previous section.

### Corals:

SQUIRES (1967) studied the evolution of solitary, free-living corals belonging to the family Micrabaciidae, of which most species are found in the littoral zone. Three genera are found in the abyssal zone, one of them at depths exceeding 5000 m. The family first appears in lower Cretaceous and is assumed to be neritic. All the Cretaceous forms are small, about 10 mm or less in diameter, and are compact and massive. The number of trabeculae is from 20-30. They are still found in the lower Tertiary, and after a considerable gap the family reappears in Miocene, apparently living now in somewhat deeper water, not exceeding 200-300 m. Some forms tend to increase in size. It is suggested that the migration into deeper water has taken place at the conclusion of the Cretaceous. The adaptation to life in the abyssal zone shows the following morphological modifications:

- 1) Increasing size of animal
- 2) Decreasing weight of skeleton
- 3) Reduction of the number of septal trabeculae
- 4) Reduction in the thickness and the massiveness of the basal plate

The present case is particularly interesting since it possibly constitutes the only well-documented case where a taxon can be followed from its appearance in shallow water to its transformation to a deep-water organism.

#### Crustacea:

In studying the bathyal-abyssal *Probeebei mirabilis* Boone (Paguridea) WOLFF (1961 a) came to the conclusion that in one line of development there is a gradual increase in the calcification of the carapace and the abdomen, and that *Probeebei mirabilis*, which is the only representative of the genus, is the most advanced form within this line. It is also mentioned that the deepest recorded hermit crab, Tylapsis anomala Henderson, known from 4343 m depth (one location only), has a somewhat reduced abdomen which is possibly unprotected. In both forms the abdomen has become secondarily symmetrical. WOLFF (1961a) states that forms with a secondarily symmetrical abdomen are mainly found at bathyal and abyssal depths.

## Tunicata:

Octacnemus, which is represented in the abyssal zone by at least three species: O.bythius, O.herdmanni and O.ingolfi, was first described by Mose-LEY (1880), who termed it "the most important new animal, zoologically speaking, obtained from the deep water by the Challenger Expedition".

The genus has been studied by MILLAR (1956, 1959, 1966), who found that it contains species highly adapted to abyssal conditions. The adaptations seem to be related to a changed method of feeding, from filter feeding (as the basic type of feeding in Ascidia) to carnivore.

Gasterascidia sandersi Monniot & Monniot (1968) which is known from the N.W.Atlantic at a depth of 4680 m is highly modified, with a long inhalant siphon and completely reduced gill and mantle cavity. The stomach occupies most of the body. The authors suggest that it moves on the bottom. The anatomical modifications are adaptation to a predatory life. The authors consider that *G. sandersi* has the most peculiar shape and is the most specialized of all Tunicata.

#### VARIATION

#### Intraspecific variation

Very little is known about the intraspecific variation in abyssal animals. This is not only due to the fact that the subject has been neglected but also because in general few specimens have been available.

MADSEN (1961 a) stated that in the Porcellanasteridae polymorphism proved to be a pronounced feature in some forms, adding that "actually it is a quite remarkable intraspecific variation which has been found in some of the larger samples of single populations". HANSEN (1967) figured two specimens of the holothurian *Oneirophanta mutabilis affinis* from the same station, showing a great variation in the number of dorsal papillae. He found a geographical variation as well, and at no single locality is the whole variation represented. In abyssal bivalves intraspecific variation is only briefly mentioned by some authors. KNUDSEN (1967) studied the variation of shell characters in *Acar asperula*, based on a sample of 110 specimens from the Indian Ocean ("John Murray" St. 26) at a depth of 2312 m. A considerable variation in the shape of the shell, the sculpture and the position and number of hinge teeth was observed. In the present paper a similar observation has been made (see p. 73 and Pls. 7, 8). In both the "John Murray" sample just referred to and the sample from "Galathea" St. 299 the whole range of intraspecific variation is found. Even in some of the small samples, for instance those from Sts. 443 and 758, a very wide range of variation could be observed.

As mentioned by KNUDSEN (1967 and p. 87), a very wide intraspecific variation within both subspecies of *Limopsis pelagica* has been observed in the present samples, and the whole range of variation could be observed in larger samples. The variation concerns the shape ("obliqueness") of the shell, and the number, shape and position of the hinge teeth, as well as the size and shape of the fossette.

In other species the intraspecific variation seems to be less; this is for instance the case in *Arca orbiculata* where the variation in shape appears to be small, and the same appears to be the case with *Kelliella bruuni*. *Abra profundorum* and *Propeamussium meridionale* seem to show a very small intraspecific variation.

#### Geographical variation

There is a number of abyssal species which have an Atlanto-W. Pacific distribution, while an allopatric species is found in the E. Pacific (p. 193). In other cases one subspecies is Atlanto-W. Pacific, while another one is E. Pacific.

When the material permitted, bivalves from different localities were carefully compared with the view of examining whether geographical variation was present; however, no obvious instances were found. In some cases populations appeared to differ, but these cases occurred always in small samples only. It was observed that whenever larger samples were present, the whole range of shell morphology could be observed within a single population. This apparent lack of geographical variation within the area of distribution of a taxon was found not only in the horizontal direction but also in a vertical direction: Comparing specimens from the upper range of the vertical distribution with samples from the lower range did not reveal any differences between the two. This means that differences in hydrostatic pressure do not seem to affect the shell morphology.

#### Speciation

CARTER (1961) suggested that a low rate of speciation occurred in the deep-sea because of less separation between populations caused by the homogeneity of the environment. FRIEDRICH (1963) suggested that the presence of weakly developed isolating mechanisms, the uniform environment as compared to the shallow water, and a slow sequence of generations all result in a low rate of speciation in abyssal animals. He found that the fauna presumably consists of migrating forms which may possess some sort of preadaptation, and that both old and recent forms migrate into the abyss. MADSEN (1961b) suggested that the Porcellanasteridae may not be very exacting in their demands on the substratum, and this may be one reason accounting for the fact that these animals are apparently less less apt to speciation than some other deep-sea animals (for instance the smaller crustaceans previously discussed).

MENZIES (1965) held the opposite opinion, suggesting that speciation in the abyss may occur at a significantly higher rate than elsewhere in the sea, owing to accelerated mutation rate because of natural radioactivity.

KNUDSEN (1961) believed that in the genus Xylophaga the habitats (plant material) were restricted and at the same time the dispersal efficiency in the young was probably low. Both factors would seem to promote speciation within this group. Similar conditions may prevail in other abyssal organisms which are confined to restricted habitats.

In general the number of species per genus is low in the abyssal bivalves. There are, however, exceptions, such as for instance *Tindaria*, *Neilonella*, *Malletia* and other genera within the Nuculoidea, as well as *Kelliella* and *Cuspidaria*. The groups are preferably bathyal, and it seems likely that the speciation has taken place in these regions. Many genera contain few species, indicating a low rate of speciation, although the recent origin of the abyssal bivalve fauna should also be taken into consideration.

With an increased knowledge of the taxonomy and distribution of deep-sea organisms it seems likely that the same viewpoints can be employed as MAYR (1954) set forth in his paper on the speciation in tropical shallow-water Echinoidea. The possible existence of polytypic species of deep-sea bivalves may turn out to be a useful viewpoint. Thus within the abyssal Nuculidae, *Nucula chrysocoma*, *N.notobenthalis* and *N.(Pronucula) benguelana* may actually represent subspecies of a polytypic species. We may perhaps also consider *Abra longicallis* (Scacchi) and *A.maxima* Sowerby as bathyal subspecies (in the N.Atlantic and the Indian Ocean respectively) and *A.profundorum* and *A.californica* as abyssal subspecies of one polytypic species. Other examples of this may be found in the genera *Malletia* and *Nuculana*.

#### FEEDING

Feeding in abyssal bivalves was summarized by CLARKE (1962b). He compared the feeding types by referring a species to one of the following categories: deposit feeders, carnivores and suspension feeders, the assignment being based on information in the literature on shallow-water members of the same families. About 35 % of the species are stated to be deposit feeders, while about 41 % are suspension feeders and some 22 % are carnivores. The survey is based on the list in CLARKE (1962a). A similar survey based on the somewhat different list from the present paper (see p. 163) shows the following percentages: 47 % deposit feeders, 24 % suspension feeders and 25 % carnivores. The remaining 4 % is constituted by Xylophaga and a few species with an unknown mode of feeding.

SANDERS & HESSLER (1969) also found that deposit feeders dominated their samples of abyssal benthos. In the bivalves sampled 45 % were deposit feeders. SOKOLOVA (1958) gave a survey of the food of the invertebrates on the deep-sea bottom, but nothing is stated about the bivalves.

The deposit feeders comprise all species within the orders Nuculoidea and Solemyoida. However, in *Yoldia ensifera* and probably other species of the Nuculanidae suspension feeding also takes place (STASEK 1965). This problem was discussed in some detail by JØRGENSEN (1966). STASEK (1965) concluded that ctenidial ciliation was employed in the collection of potential food from particles taken from the overlying water and temporarily suspended within the mantle chamber. The relative importance of the two feeding methods is, however, unknown.

There is no reason to assume that the abyssal Nuculoidea should not possess the same lability in their food collecting. In an environment in which the food supply may be marginal over vast areas, the possibility of being able to switch over from one feeding method to another may be of great survival value to many populations.

ALLEN & SANDERS (1966) studied some aspects of the food uptake of the deposit feeder Abra profundorum. They measured the area of the various ciliated surfaces in the mantle cavity of six species of Abra, including A. profundorum, and found a marked correlation between the extent of the various ciliated surfaces and the depth at which the animals occur. A. profundorum had the smallest gills and the largest palps of the species considered, and is also the deepest-living species. The examination comprised also shallow-water species, including A. alba and A.nitida. However, the data on the vertical distribution are taken from the literature which frequently does not discriminate between valves and specimens alive at the time of capture, and according to my experience numerous misidentifications occur in older collections of Abra. ALLEN & SANDERS suggest that the reduction of the gills is clearly correlated with life on muddy substrates, the sorting function of the gill being reduced to a minimum and its function being simply to act as a conveyer belt, transferring particles from the proximal part of the siphon to the labial palps. This reduction is then counteracted by the increase in size of the palps. However, the differences found in the sizes of the gills and palps in the different species may not be directly correlated with depth, but could be adaptations of the individual species to deal with different types of soft sediments. ALLEN & SANDERS also state that the conveyer function becomes a critical factor in an abyssal species, where the sediment dealt with contains less nutrient material than shallow-water sediments. This is, however, not necessarily the case, the abyssal fauna being considerably richer than hitherto supposed (see p. 201), and as far as nutritional value is concerned, at least in some places the sediments may compare favourably with those of shallow water.

The question is, however, important, and the problem should be subjected to further research and extended also to other genera.

ALLEN & SANDERS (1966) also observed that the gut of the species of *Abra* undergoes modifications with increasing depth range. The relative length of the gut increases, as does the diameter of the lumen, and in addition several other modifications occur. In *Abra profundorum* much of the posterior half of

the body becomes a sac containing the faecal pellets, which are found in large quantities. They state that the significance of the sac cannot be determined, but suggest the possibility that nutrition may be extracted from the pellets, and thus its presence may be an adaptation to life in sediments poor in nutritive matter.

The structure of the hind gut in *A.profundorum* has also been observed in the present samples, but no other explanation can be suggested. In bivalves, however, it seems to be the only anatomical feature observed correlated with life in the abyssal zone.

The suspension feeders comprise the Arcidae, the Limopsidae, the Mytilidae, some Pectinidae and probably most of the families in the Order Veneroida. Filter feeding in the deep-sea was reviewed in detail by Jørgensen (1966). He mentioned the presence of particulate matter in the deep-sea, adding that the conditions for life deteriorate more rapidly with depth for suspension feeders than for other feeding types. The fact remains, however, that suspension feeders are able to live at great depths. Jørgensen states that the available evidence indicates that the concentration of bacterial food in the deep-sea is only about 1/10,000 of the amount needed to cover the food requirements in a suspension feeder clearing about 151 of water for each ml of oxygen consumed. Even when we do not know the lowest concentrations for particulate food to which the various types of suspension feeders are capable of adapting, the concentrations of heterotrophs recorded in the deep-sea would seem to be below the limiting level for suspension feeders. It is therefore suggested that where suspension feeders are present in the deep-sea their food must either be derived from other sources, i.e., organic detritus, or the concentrations of heterotrophic microorganisms must be much higher than indicated by the available data. However, close to the bottom the concentrations presumably often increase, especially in areas where currents may resuspend bottom sediments.

The presence of such relatively large suspension feeders as *Limopsis pelagica* and *Arca orbiculata* at a depth of 5000 m or more corroborates JØRGENSEN's statement concerning the possibility for suspension feeding at very great depths.

As suggested by JØRGENSEN (1966), the detritus particles themselves may not be the main source of nutrition for the suspension feeders, but rather the bacteria adhering to the particles. A similar viewpoint was advocated by R.NEWELL (1965) as regards shallow-water suspension-feeding molluscs (Macoma balthica and Hydrobia ulvae). It should also be mentioned that HAMILTON et. al. (1968) found unicellular, possibly heterotrophic organisms,  $1.4\mu$  diameter, down to a depth of 3400 m (no deeper samples were made) off California. They hold the opinion that the organisms live mainly attached to particulate detritus. They add a survey of previous observations of similar organisms. Although the authors do not mention it, it seems reasonable to assume that the organisms found may serve as food for abyssal suspension-feeding organisms.

The carnivores consist of some of the Pectinidae and the Septibranchoidea and altogether they form more than 25 % of the known species. As consumers of meiobenthos they may be of considerable ecological importance, since carnivorous bivalves have been obtained from roughly 50 % of all abyssal stations yielding bivalves. The carnivores are generally found in small numbers only, although at "Galathea" St. 282 no less than 42 specimens of *Propeamussium meridionale* were taken. Some species of abyssal *Cuspidaria* are among the largest species within their family, and also among the largest abyssal bivalves known.

KNUDSEN (1967) found that carnivores constitute about 50 % of the bathyal species in the Indian Ocean, but the sampling technique used probably favours larger carnivorous species, while the generally smaller deposit feeders are under-represented. The area considered had a much larger proportion of carnivores than had the corresponding depths of the N. Atlantic.

The food uptake of the Septibranchoidea has been studied by YONGE (1928) who gives a detailed account on the function of the septum and its role in capturing prey. It was found that water and food (small crustaceans and annelids) are drawn into the mantle cavity as a result of regular movements of the septum, the food items being pushed into the mouth by the muscular labial palps. KNUDSEN (1967) made some comments on the feeding of the carnivorous pectinids although no actual observations on live specimens were made. He suggested that a pumping function like the one described in the Septibranchoidea by YONGE (1928) may exist, the pumping being produced by vigorous movements of the shells ("swimming movements") in connection with a closing of the mantle cavity by means of the very well developed velum. The quick part of the adductor muscles is also very large and the efficiency of this muscle may be further increased

by its oblique position (the right insertion being located much more dorsally than the left one). YONGE (1936) suggested that the swimming habit in the Pectinidae evolved from the cleansing mechanism, i.e., movements of the shells with the purpose of cleaning the mantle cavity and its organs of bottom sediment. If the carnivorous Pectinidae capture food in this way this means a further development of the swimming habit into a feeding habit.

The food uptake and sorting of the carnivorous pectinids must be a very efficient one, since generally the stomach content was completely free from bottom sediments, apart from the occasional occurrence of a few sand grains. Such were also observed in the Septibranchoidea by YONGE (1928) who suggested that they may assist in the mechanical breaking up of the food items. Whether the food items of carnivorous pectinids consist of bottom-living or pelagic forms is of some interest. Most of the crustaceans found were benthic, some probably able to swim for short distances, but a few are to be considered as strictly swimming organisms (HU-LINGS, WOLFF, personal communication).

Tabel 8 summarizes the results of examinations of stomach contents of some of the carnivorous species, and it will be seen that small crustaceans dominate. There is little doubt that the carnivorous bivalves must exert a profound influence as consumers of the crustacean meiofauna. THIEL (1966) studied the meiofauna at eight localities (12 samples) from off Somali, E. Africa, at depths ranging from about 1000 to 5000 m and found the number of organisms to vary between 16 and 170 per 10 ml bottom sediment. Nematoda constituted between 63 and 79 % of the total number of specimens, but Crustacea (particularly Harpacticoida, Nauplia and Ostracoda) were quite frequent also. The total number of animals found appeared to be equal to that found in many shallow-water localities (although considerably higher numbers have been found in some of the latter). THIEL concluded that the nutritional condition of the deep-sea macrofauna seems to be more favourable than hitherto assumed. HESSLER & SANDERS (1966) observed a considerable diversity of the benthic fauna of the N.W. Atlantic deep-sea (see p. 201). A large proportion of the organisms obtained should be classified as meiobenthos, and in certain of their localities as many as about 25.000 organisms were obtained. HESSLER & SANDERS concluded that "the deep sea is not the harsh environment that it has generally been assumed to be".

Cetoconcha cevlonensis

Jun 202		St. 281, one specimen examined:
Specimen n	10.	About 25 specimens of foraminiferans, 0.1-0.8 mm,
1 One	harpacticoid (Diosaccidae?), 0.5 mm long	numerous fragments. The following species could
2 Rem	nains of crustacean integument	be recognized: Globigerina sp., Globorotalia menardii
3 Two	harpacticoids (Cletodidae), both 0.4 mm long	(D'Orbigny) and Pulleniatrina obliquiloculata (Parker
4 Rem	nains of crustacean integument	& Jones).
5 Two	plus (one?) harpacticoid, 0.3-0.4 mm long	
6 Two	harpacticoids, 0.4-0.6 mm long	Poromya tornata
7 Frag	gment of a harpacticoid, 0.4 mm long	St. 192, one specimen examined:
		One Eurycope (Isopoda), 5.7 mm long
St. 234		St. 235, one specimen examined:
13 Thre	ee Ostracoda, 0.1-0.2 mm long	Two harpacticoids, 0.5-0.8 mm long
Thre	ee harpacticoids (Cletodidae), 0.5-1.0 mm long	St. 279, one specimen examined:
14 One	harpacticoid, 0.5 mm long	One? isopod, about 1 mm; Two ostracods (Polycope),
15 Eigh	nt harpacticoids, two species, 0.4-0.8 mm long	0.2 mm long
		St. 280, one specimen examined:
Cetoconc	ha galatheae	One copepod (Ectinosomidae), about 1.4 mm long; One
St. 601,	one specimen examined:	harpacticoid, 0.5 mm long
One	copepod (Pseudobradya sp.), 1.3 mm long	St. 281, three specimens examined:
Two	o operculae of prosobranch, 1.2 mm diameter	1 One harpacticoid (Diosaccidae), 0.4 mm long
Eggs	s ?	2 Two copepods (Thalestridae) 1.5 mm long
Oesc	ophagus, jaws and bristles of a polynoid worm (Poly-	3 Remains of larger crustacean (?amphipod); two radio-
ch	naeta), probably Lagisca sp. The oesophagus is 2.5 mm	larians
10	ng, indicating that the worm was 8.5-9.0 mm long	
		Myonera undata
Laevicord	dia galatheae	St. 231, one specimen examined:
St. 234,	two specimens examined:	One benthic foraminiferan, Alveolophragmium subglo-
Each	h contained one ostracod (Polycope sp.), 0.3 and	bosum (G.O. Sars), 1.5 mm; one unidentified, oblong
1.	2 mm long	body, 5.3 $ imes$ 0.4 mm.
		St. 280, one specimen examined:
Policordi	a cf. alaskana	Legs of harpacticoid; a few unidentifiable remains.
St. 716,	one specimen examined:	St. 194, one specimen examined:
One	amphipod (Harpinia sp.), about 5.5 mm long	One isopod (Ilyarachna sp.), 2.5 mm long.

It is thus evident that some abyssal localities harbour a fairly rich meiofauna. The quantity of meiofauna probably differs from one locality to another, and these differences may influence the distribution of the carnivorous bivalves.

Propeamussium meridionale

The reason for the increased number of bivalve carnivores in the deep-sea may be the scarcity or even absence of such competitors as, for instance, young benthic fish, which feed on the meiobenthos in the shallow-water habitats. It may in this connection be noted that a carnivorous feeding habit has been adopted also by some abyssal tunicates (see p. 211).

The intestine of *Galatheavalva* (Pl. 20) appears to contain unsorted bottom sediment, including the meiobenthos, but it is not known which fraction is actually digested.

# REPRODUCTION

THORSON (1950) reviewed the reproduction and larval ecology of marine bottom invertebrates, including also the deep-sea fauna. He stated that the deep-sea species always have a small number of of very large eggs, the pelagic development being nearly or totally suspended, in which respect the deep-sea resembles the conditions in the Arctic and Antarctic.

OCKELMANN (1965) gave a survey of the developmental types within the shallow-water bivalves of the N.E. Atlantic, based on examination of egg size and prodissoconchs of more than 200 species. The type of development could be determined if either ripe eggs or the prodissoconch could be studied, and the following three types of development, which are probably of wide applicability, were found:

1) Planktotrophic larval development: The diameter of the ripe egg varies between 40 and  $85\mu$  (with very little intraspecific variation). From the egg a pelagic larva is developed, which in the beginning subsists exclusively on the yolk. The larval shell formed during this period is termed prodissoconch I. At a certain stage feeding on phytoplankton begins, at which time another larval shell, prodissoconch II, is formed. The two larval shells are generally easily distinguished. The size of prodissoconch I ranges between 70 and 150 $\mu$  in diameter, again with very little intraspecific variation, while the size of prodissoconch II may vary between 200 and 600 $\mu$ .

2) Lecithotrophic development with a short pelagic larval stage: In this category the diameter of the ripe egg ranges from 90 to  $140\mu$  and that of the prodissoconch ranges from 135 to  $230\mu$ , both stages with a narrow intraspecific variation. The pelagic life is short, lasting from a few hours to a few days. No (or very little) feeding takes place during the pelagic life. The prodissoconch II is confined to a narrow zone along the edge of prodissoconch I or it is completely absent.

3) Direct development: The diameter of the ripe egg varies between 150 and  $200\mu$ , the embryonic shell measures 230 to  $500\mu$  (sometimes even larger), both characters showing a rather large intraspecific variation. In the embryonic shell both prodissoconch I and II are well developed and easily distinguished from one another.

OCKELMANN (1965) stated that the lecithotrophic development predominates among bivalves of the deep-sea, e.g. the Nuculoidea, which as already mentioned constitute about 47 % of the endemic abyssal fauna. He found not a single case recorded of direct development in the Pectinidae and Cuspidariidae. Together these two families constitute more than 20 % of the endemic abyssal fauna (Table 3, p. 181. Finally he stated that unpublished data show that both direct development and brood protection are rare in abyssal bivalves.

This dominance of lecithotrophic development in deep-sea bivalves was corroborated by my study of the bathyal bivalves from the Indian Ocean (KNUDSEN, 1967). In the 26 species examined I found a lecithotrophic development in 15 species (58 %).

The type of development has been examined in a few species of the present material. The results, summarized in Table 9, are in accordance with OCKEL-MANN's findings.

Brood protection was found during the present study only in the following abyssal species: *Xylo*-

Tabel 9.	Size	of egg	and	prodisse	oconch	in	some
		abys	sal b	vivalves.			

Species	Diameter of egg (µ)	Length of prodisso- conch	Main type of develop- ment
Acar asperula	150	250-310	L
Arca orbiculata	190-210	310-330	D
Limopsis pel. p	140	230-270	L
– pel. dalli	125-140	230-260	L
Dacrydium panamensis	67-74	150-160	Р
Propeamussium meridionale .	110-130	230-250	L
Abra profundorum	-	270-290	Р
Kelliella galathea	-	190-210	L
– indica	110-115	-	L
- bruuni	-	220-250	L
- sundaensis	-	200-210	L
– tasmanensis	100-110	150-175	L
Laevicordia galatheae	170-180	230	L
Policordia lisbetae	150-170	-	L
– cf. alaskana	∫130-150 160-170	220-240	L
Cetoconcha ceylonensis	150-160	_	D
Poromya tornata	∫140-170 150-190	260	L
– perla	) 110-140 100-110	-	L
Myonera undata	165-180	-	L
Cuspidaria delli	170-180	-	L
– haasi	160-175	-	L
<i>– tasmanica</i>	150-160	-	L
Galatheavalva holothuriae	45-60	(750)	D

L: leicithotrophic; D: direct; P: pelagic.

phaga concava, X. africana and Galatheavalva holothuriae, although several hundred specimens have been opened and inspected.

In his comprehensive (but still somewhat incomplete) survey of brood protection in bivalves (Sellmer 1967), there is not a single of the abyssal species listed here in Table 1. He states that brood protection has arisen repeatedly and independently among bivalves of different groups and that it has developed in some animals as a mean of restricting them to environmental regions most suitable to their physiological requirements, the brood protection acting as a deterrent to dispersal. The three abyssal brood-protecting species I have found seem to be such cases, the *Xylophaga* spp. having to restrict themselves to the limited areas where plant material is available and *Galatheavalva* to the populations of the *Psychropotes* in which they live.

The short pelagic life prevailing in the majority of the abyssal bivalves is ecologically very important in securing the dispersal of the species over vast areas. Thus, as also indicated by OCKELMANN (1965), the mode of reproduction does not pose a hindrance for a wide distribution of the abyssal bivalves.

SANDERS & HESSLER (1969) summarized the scanty observations on the breeding patterns of abyssal benthic organisms. There is convincing evidence for reproductive periodicity in two species of ophiuroids studied by a previous worker. Observations on their own material failed to demonstrate any periodicity in an isopod and in *Nucula cancellata*. The scanty evidence indicates that no breeding pattern is universal to abyssal organisms.

### SHELL MORPHOLOGY

In general the abyssal bivalves have rather delicate and smooth shells, with weakly developed sculpture. NICOL (1965) stated that in the Nuculoidea no spinose species are found, and that the Septibranchoidea are essentially non-spinose. Spines are absent in arctic and antarctic bivalves and if spines occur in deep-water bivalves they are always short. The present investigation shows that only few species do have spines and that they are invariably very short (Pectinidae, *Poromya*, and others). The colour of the shell is generally dull, white or greyish white.

#### **GIGANTISM**

There is no general tendency towards gigantism in abyssal bivalves such as has been stated to occur in Isopoda (WOLFF 1962) and Cumacea (Jones 1969). This was later discussed by MENZIES & GEORGE (1967) and WOLFF (in press). However, some of the abyssal species of Cuspidariidae are among the largest and most thick-shelled within the family, and the same applies to *Limopsis pelagica* and *Abra profundorum* although in general the abyssal bivalves are not particularly large.

## ATTACHMENT

A few abyssal species are attached by a byssus. KNUDSEN (1967) studied the attachment of *Acar* asperula, giving some details of the substratum used. Additional observations have been made on the present collection, showing that a wide range of different substrata may be used for attachment (p. 74).

Contrary to what might be expected from a filter-feeding species taking advantage of a current, the individuals of a cluster of A. asperula are not orientated in the same direction on the bottom (Pls. 7 and 8).

A fine byssus was observed in Arca orbiculata, and this may anchor the individuals in the bottom by attachment to hard bodies, though none were actually observed. A byssus is also present in abyssal mytilids and in some pectinids. In the specimens of *Dacrydium* no byssus could be seen, but SUTER (1913) stated that *Dacrydium* lives in an elongated tubular nest woven of byssus and covered by Foraminifera and spicules of sponges, etc.; also *Dacrydium vitreum* is nest building (OCKELMANN 1958). This could not be observed in the present material. *Galatheavalva* anchors its byssus in the tissue of the holothurian in which it lives.

NICOL (1964) stated that the shell-attached bivalves are rare in deep water, and only three species listed by CLARKE (1962a) have this habit. One of these is an *Anomia* which is attached by a calcified byssus and the other two species are *Pycnodonte cochlear* and *Hinnites pusio* which attach by cementating one of the valves. However, the three species mentioned are shallow-water species known from the abyssal zone only by displaced valves. Shell cementation thus seems unknown in the abyssal zone. A reason for this may be the probable difficulty in producing the thick and heavily calcified shells which are invariably found in shell-attached bivalves.

# THE EPIFAUNA OF ABYSSAL BIVALVIA

The abyssal bivalves form a microhabitat for an epifauna, forming hard-bottom areas in the middle of very extensive soft-bottom habitats. There seems to be no previous study of this deep-water habitat. During the present investigation records were kept of the organisms found attached to the shells of the bivalves examined. The attached organisms were referred to group, and in several cases identified as far as possible. Since the majority of the known abyssal bivalves are burrowing, only a rather poor epifauna can be expected, but it was found that eleven species actually had epifauna, and altogether 15-20 different taxa were found. In most cases the organisms are small and occur in small numbers. Details of the observations made are mentioned in the biology section under each species of bivalve and summarized here (Table 10).

It is quite obvious that the majority of the epifauna is found living on a rather small number of speTable 10. Epifauna of abyssal bivalves.

Group	Host	Expedition	St.
Foraminifera			
Unidentified spp.	Acar asperula	Galathea	299
	Arca orbiculata	_	663
	Limopsis p. pelagica	_	282
<u> </u>		Vema	14
	– – dalli	SIO	96
Placopsilina bradyi			
Cushm. & McClch.	Kelliella galatheae	Galathea	724
Porifera	-		
r official com	A age generula		200
Ondentined spp.	Acar asperada Anon orbioulata		299
	Limonsis nol dolli	_	716
Kana maa	Limopsis pei. uatti	80m	/10
Coelenterata			
Stephanoscyphus simplex			
Krkp.	Acar asperula		443
<u> </u>		-	758
	Arca orbiculata		663
Anaz -	Limopsis p. pelagica		281
	– – dalli	-	716
		SIO	96
been	Policordia lisbetae	Galathea	99
Pandeidae sp.	Ledella crassa	-	30
_	Yoldiella abyssorum	-	24
Perigonimus sp.	Neilonella kermadecensis	_	664
Rica	Malletia cuneata	-	664
Polychaeta			
2Notoproctus pacificus			
Moore	Limonsis nel dalli	Galathea	716
Protis sn	Acar asperula		443
<i>Trous</i> sp.	mean asper and		-115
Crustacea			
Lepadidae sp.	Acar asperula	Galathea	299
_	Limopsis dalli	\$IO	96
Mollusca			
Acar asperula	Limopsis p. pelagica	Galathea	281
		_	299
– – (byssus only)	— — dalli	*	716
Pterobranchia			
Cephalodiscus sp.	Acharax johnsoni	SIO	131
Tunicata			
Sp. indet.	Acar asperula	Galathea	443
	Limopsis pel. dalli	_	716
		SIO	. 96

cies of bivalves: Acar asperula, Arca orbiculata, Limopsis p. pelagica and L. p. dalli which all have coarse shells more or less covered with bristles offering good shelter for the settling young epifauna organisms. The heaviest infestation found was the population of Limopsis p.dalli from SI0 St. 96 in which about 60 % of the specimens had epifauna, but otherwise the degree of infestation is considerably lower. It was observed that in general the larger specimens within a population had the most abundant epifauna. Most of the epifauna seems to prefer the hinge area and the postero-dorsal edge, but frequently the posterior end is used. Less frequently the epifauna is attached to the anterior or ventral edge or the central part. It is worth noting that no epifauna has been found on the abyssal species of Pectinidae, a family which forms a favorite substratum for sessile organisms in shallow water (ALLEN 1953).

It is not known to which extent the sessile or-

ganisms listed here are specifically attached to bivalve shells. Several of the organisms can probably settle on any hard substratum. *Stephanoscyphus simplex* has been found also on dead valves of bivalves, both dead and live gastropods, corals, calcareous tubes (of polychaetes?), pumice, pebbles and cokes (KRAMP 1959).

A number of animal groups living on bivalve shells in shallow water have not yet been observed living on abyssal bivalves, although they do occur in the abyssal zone. This applies to the following groups: Actiniaria, Bryozoa, Entoprocta, Cirripedia, and Loricata.

The present observations take only the sessile organisms into account. A non-sedentary epifauna of Ciliata, Ostracoda, Harpacticoida and other organisms may take advantage of the shelter offered by the coarse shells.

There appear to be very few studies of the epifauna of shallow-water bivalves: KORRINGA (1951) studied the fauna of oyster shells at the Dutch coast inclusive of the non-sedentary organisms. It should be noted that the habitat to some extent is influenced by man, the oysters being regularly cleaned and relaid. Altogether about 125 species were present and the importance of the oyster shell to the sessile organisms is mainly by offering shelter. Several species appeared to live by preference in this habitat, and in general the epifauna consists of permanent residents.

ALLEN (1953) studied the epifauna of *Chlamys* septemradiata (Pectinidae) living on soft bottom in the Clyde area (Scotland) at about 70 m depth; fourteen epifauna species occurred on all or the majority of the host specimens.

About 120 spp. of animals and 25 spp. of algae were present on living *Aequipecten irradians* Say from shallow water shell bottom (ca. 2-3 m) in North Carolina (MARY E. PETERSEN, unpublished M.A. thesis 1964, Duke Univ.).

Although these three investigations cannot be directly compared with the present observations, there is no doubt that the epifauna of abyssal bivalves is both quantitatively and qualitatively much poorer than that of the shallow-water habitats.

# PREDATION

DALL (1890b) found that a singularly small number of valves of deep-sea molluscs showed signs of having been drilled or attacked by other molluscs. The valves of abyssal bivalves from the "Galathea" were examined for bore-holes of predators. The collection is rather small, comprising some 50 valves only. DALL's observation was confirmed since only two valves of an unidentified species of *Cuspidaria*, from St. 99, off W. Africa, at 2700 m depth, were found to have such perforations. In addition, the collection of the ZMUC contains a drilled valve of *Pecten frigidus* Jensen, from the Norwegian Sea, at a depth of 1800 m ("Ingolf" St. 117).

# SHELL DESTRUCTION

Damages of living specimens were found largely to fall into two categories, viz., corrosion of the external shell surface, and fractures.

Corrosion was found to occur in the following species: Spinula tasmanica, Portlandia abyssicola, Tindaria bengalensis, Limopsis pelagica dalli, Propeamussium meridionale, Abra profundorum, Policordia cf. alaskana, P.lisbetae, Poromya perla, Cuspidaria barnardi, C.haasi, C.natalensis.

The corrosions were either large irregular areas or small rounded, sharply delimited pits, both types frequently being concentrated around the umbonal part, although other areas of the shell may be attacked as well. The corrosions do not seem to be caused by gastropods, nor by organisms like algae, lichens, sponges and polychaetes, as is frequently the case in the shallow-water bivalves (see, for instance, BOEKSCHOTEN, 1966). It would rather seem as if the corrosion is due to some chemical process in the bottom sediment.

Shell repairs after fragmentation have been observed in *Propeamussium meridionale*; the fragmentation may be caused by too violent swimming movements (see p. 96).

# REMARKS ON THE OCCURRENCE OF VALVES OF SHALLOW-WATER BIVALVES IN THE ABYSSAL ZONE

Since the early days of deep-sea collecting the occurrence of valves of shallow-water bivalves in the deep-sea has been known. Thus DALL (1890b) stated that most of the species of any collection of the deep-sea fauna are represented by the shells alone, which may have been – as millions are daily – disgorged by fishes, and never have lived at the depth from which they were dredged. However, this observation has in general not been noticed by subsequent workers, and numerous shallow-water

Nucula corbuloides Seguenza	Astarte smithi Dall	Poromya granulata (Nyst &
– cymella Dall	– sulcata (da Costa) <sup>5</sup>	Westendorp)
Tindaria perrieri Dautzenberg & Fischer	Diplodonta orbiculata Locard	– neaeroides (Seguenza)
Malletia conspicua Smith	Lucina appendiculata Locard	- rotundata Jeffreys
Limopsis aurita Brocchi	Cardium minimum Philippi	Lyonsiella abyssicola Sars
Crenella decussata (Montagu)	Liocyma fluctuosa (Gould) <sup>6</sup>	– acuticostata (Philippi)
Musculus discors L. <sup>1</sup>	Ervilia castanea (Montagu)	- subquadrata Jeffreys
Amussium dalli Smith <sup>2</sup>	Abra longicallis (Scacchi)	Policordia gemma Verrill <sup>8</sup>
Propeamussium lucidum (Jeffreys)	- maxima (Sowerby)	Cardiomya planetica Dall
– propinquum Smith	– nitida (Müller)	- striata (Jeffreys)
- hoskynsi (Forbes) <sup>2</sup>	Macoma calcarea (Chemnitz) <sup>7</sup>	Cuspidaria depressa (Jeffreys)
- hypomeces Dautzenberg & Fischer	Xylophaga dorsalis (Turton)	- nitens Locard
Cyclopecten groenlandicum (Sowerby) <sup>3</sup>	Lyonsia formosa Jeffreys	– obesa (Lovén)
Lima excavata (Fabricius)	Mytilimeria compressa Locard	– pseustes Dall <sup>9</sup>
Anomia squamula L.	– <i>fischeri</i> Locard	- rostrata (Spengler)
Pycnodonte cochlear (Poli)	– flexuosa Verrill & Smith	- striolata Locard
Astarte borealis (Schumacher) <sup>4</sup>	Pholadomya loveni Jeffreys	- truncata (Jeffreys)
- compressa (Montagu)	Periploma papyracea (Say)	- wollastoni (Smith)
1. See Ockelmann 1958, p. 58	4. See Ockelmann 1958, p. 79	7. See Ockelmann 1958, p. 128
2. No abyssal sample could be located	5 p. 99	8. – VERRILL 1884, p. 278
3. See Ockelmann 1958, p. 72	6. – – – p. 125	9. – p. 179

Table 11. Rejected records of abyssal bivalves, based on dead valves only.

bivalves have been attributed a much too wide vertical range.

A few authors have, however, dealt with the problem, e.g. JENSEN (1900) and JOHANSEN (1901) who discussed the reason for the occurrence of shallowwater mollusc remains in the deep part of the Norwegian Sea. The former held the opinion that the shells represented an autochthonous fauna from a period when the sea bottom was at a higher level than at present, while the latter thought that the valves had been transported out from the shelf by means of ice.

The research of recent years suggests that shallowwater bivalves, both live specimens and valves, may be transported from the shelf region to the abyssal zone by means of turbidity currents, bringing about large scale transport of the sediment and the organisms contained. Turbidity currents have been dealt with by SHEPARD (1963, 1965) who notes the occurrence of shallow-water organisms in the abyssal sediments, although molluscs are not especially mentioned. The turbidity currents may extend far offshore and into rather deep water. NAYUDU (1962) recorded supposedly continental sediments in the N.E.Pacific as far as about 1000 km offshore and at nearly 4000 m depth.

CLARKE (1962a) gave a list of rejected records of abyssal molluses, containing 41 species of bivalves, six of which are known from the Mediterranean or the Arctic Ocean. The list is based on literature records, and most of them he has discarded because they are shallow-water species, recorded only from the abyssal zone as valves. I am able to confirm most of CLARKE's rejections and to a considerable degree increase the number of rejected records as a result of inspection of the material in question (Table 11). The "Galathea" collection contains a small number of shallow water bivalves from abyssal stations. A fragment of Amussium pleuronectes (L.), a common sublittoral bivalve in the Indo-W.Pacific region, was dredged at St. 453 (S. E. Asia) at 2030 m depth.

# LIST BY STATION OF HADAL BIVALVIA

Abbreviations: see p. 160.

"Galathea"

- 418. Philippine Trench (10° 13' N, 126° 43' E), 10190-10150 m, (2.5° C). 21 Jul. 1951, ST 300. Sarepta hadalis n.sp.
- 435. Philippine Trench (10° 20' N, 126° 41' E), 9984 m, (1.6° C). 7 Aug. 1951, ST 300. *Yoldiella hadalis* n.sp.
- 465. Sunda Trench (10° 20'S, 109° 55'E), 7000-6900 m, (1.5°C). 5 Sep. 1951. ST 300. *Kelliella sundaensis* n.sp.
- 495. Banda Trench (5° 26'S, 130° 58'E), 7290-7250 m, (3.6°C). 22 Sep. 1951. HOT. *Xylophaga grevei* Knudsen *Bankia carinata* (Gray) *Uperotus clavus* (Gmelin)
- 496. Banda Trench (5° 36' S, 131° 06' E), 7270 m, (3.6° C). 23 Sep. 1951, PGI 0.2. Cuspidaria hadalis n.sp.
- 499. Banda Trench (5° 21'S, 131° 17'E), 6880 m, (3.5°C). 24 Sep. 1951, PGI 0.2. *Cuspidaria hadalis* n.sp.
- 649. Kermadec Trench (35° 16'S, 178° 40'W), 8210-8300 m, (1.5°C). 14 Feb. 1952, ST 600. Yoldia kermadecensis n.sp. Kelliella bruuni Filatova
- 650. Kermadec Trench (32° 20'S, 176° 54'W),
  6620-6730 m, (1.3°C). 15 Feb. 1952, ST 600. *Cyclopecten (H.) hadalis* n.sp. *Kelliella bruuni* Filatova
- 651. Kermadec Trench (32° 10'S, 177° 14'W),
  6960-7000 m, (1.3°C). 16 Feb. 1952, HOT.
  Phaseolus faba n.sp.
  Neilonella hadalis n.sp.
  Cyclopecten (H.) hadalis n.sp.
  Kelliella bruuni Filatova
- 658. Kermadec Trench (35° 51'S, 178° 31'W),
  6660-6770 m, (1.3°C). 20 Feb. 1952, ST 600.
  Neilonella hadalis n.sp.
  Kelliella bruuni Filatova
  Xylophaga hadalis Knudsen

"Vitiaz"

2208. Kuril-Kamchatka Trench (49° 29'N, 158° 41'E), 7210-7230 m, (1.8°C). 22 Jun. 1953. Trawl. Spinula vityazi Filatova 3528. Ryuku Trench (27° 58'N, 130° 28'E), 6810 m, (1.8°C). 27 Oct. 1955. Sigsbee-Gorbunova trawl. *Spinula bogorovi* Filatova

# A SURVEY OF HADAL BIVALVES

The 18 hadal species of bivalves are listed in Table 12.<sup>1</sup> Among these are no less than four boring forms, three of which undoubtedly are "guest" species carried down with the plant material in which they live (see p. 118). The following also call for some remarks:

1) Ledella ultraabyssalis has apparently never been described or figured. Specimens labelled with the specific name were seen by me on an exhibit during the XVth international Congress of Zoology, London, 1958 and were listed by Belyaev (1966).

2) Delectopecten (= Cyclopecten) randolphi. The assignment appears doubtful, *D. randolphi* being known hitherto only from the N.Pacific, where it is primarily bathyal, although some records from abyssal depths, down to 6200 m, are at hand (see Table 1).

3) Kelliella pacifica. The assignment seems doubtful.

4) *Xylophaga hadalis* is known only as hadal, but might also occur in the abyssal and bathyal zones.

This leaves 11 hadal species, eight of which are described as new in the present paper. They have been recorded from seven different trenches; one species has been found in two neighbouring trenches, the remaining in one trench only. The deepest known species is *Sarepta hadalis* from about 10.200 m depth in the Philippine Trench.

The Sovjet expeditions of later years have, however, obtained many hadal bivalves which have only provisionally been referred to genus. BELYAEV (1966) recorded all hadal bivalves; those not included in Table 12 are listed in Table 13. This list contains many additional genera, but it should be noted that several generic names may have to change when the samples are studied more closely.

From the two tables it appears that the following 11 families, all known also from the abyssal zone, are represented in the hadal fauna: Nuculanidae,

<sup>1.</sup> The following three species listed as hadal by BELYAEV (1966) should not be considered hadal: Spinula calcar, S. oceanica and Malletia fiora (= M. cuneata).

Table 12. Hadal bivalves assigned to species.

Table 13. Hadal bivalves not assigned to species.

Nuculanidae	Trench
Nuculanidae	
Sarepta hadalis	Philippine
Ledella ultraabyssalis	Kuril-Kamchatka
Spinula bogorovi	Ryuku
– vityazi	Kuril-Kamchatka, Japan
Phaseolus faba	Kermadec
Yoldia kermadecensis	
Yoldiella hadalis	Philippine
Malletiidae	
Neilonella hadalis	Kermadec
Pectinidae	
Cyclopecten hadalis	_
– cf. randolphi	Java
Kelliellidae	
Kelliella bruuni	Kermadec
– pacifica?	Java
– sundaensis	_
Pholadidae	
Xylophaga hadalis	Kermadec
– grevei	Banda
Teredinidae	_
Bankia carinata	_
Uperotus clava	_
Cuspidariidae	
Cuspidaria hadalis	_

Malletiidae, Pectinidae, Limidae, Kelliellidae, Thyasiridae, Pholadidae, Teredinidae, Poromyidae, Verticordiidae, Cuspidariidae.

Apart from the boring forms, the hadal bivalves have been assigned to 21 genera, some of which, as mentioned, may be provisional assignments. Until now not a single endemic genus has been described among the hadal bivalves. The genus Phaseolus has so far not been recorded from the abyssal zone, being essentially bathyal. With the exception of the "guest" species just referred to, all the taxa assigned to species appear to be endemic. It should be emphasized, however, that the deepest part of the abyssal zone has been poorly investigated. It may be significant that at five abyssal stations ("Galathea" St. 654, 663, 664, 665 and 668) in the Kermadec area, at depths between 2500 and 5900 m, 13 species of bivalves were obtained and not a single of these has been found below 6000 m. Out of the 13 species mentioned five are widely distributed both horizontally and vertically: Acar asperula, Arca orbiculata, Abra profundorum, Malletia cuneata and Propeamussium meridionale. On the other hand, not a single of the six species found in the trench proper could be found in the five abyssal stations just mentioned. This indicates a distinct separation between the abyssal and the hadal bivalves of the region.

Taxon	Trench	Depth (m)
Phaseolus sp.	Kermadec	8900-9200
	Tonga	10400-10700
Spinula sp.	Kuril-Kamchatka	6900- 7200
_	Chinuk (N.E. Pacific)	6100
<i>Yoldiella</i> sp.		_
<i>Tindaria</i> sp.	Aleutian	6300-7300
	Kuril-Kamchatka	7200
_	Chinuk (N. E. Pacific)	6100-6300
<i>Neilonella</i> sp.	Aleutian	7200
-	Kuril-Kamchatka	6500-8400
<i>Malletia</i> sp.		6900-7200
_	N.W. Pacific	6100-6300
_	Japan	7600
Propeamussium sp.	Aleutian	6400-7200
	Kuril-Kamchatka	7200
-	New Britain	8000
-	New Hebrides	6700-6800
Delectopecten sp.	Kuril-Kamchatka	6900-8100
<i>Lima</i> sp.		9000-9100
-	Japan	6200
-	Idzu-Bonin	9700
	Vitiaz	6100
<i>Thyasira</i> sp.	Aleutian	6500-7300
-	Kuril-Kamchatka	9000-9100
-		6200
-	Japan	7600
-	New Britain	8000
-	Kermadec	10000
Axinopsis sp. Axinulus aff.	Japan	6200
pygmaeus Dall	Java	6800-6900
Axinulus sp.	Java	6800-7100
_	Tonga	10400-10700
-	Kermadec	8900-10000
_	New Britain	9000
<i>Kelliella</i> sp.	Kuril-Kamchatka	7200-9100
	Japan	6200-7600
_	Chinuk (N. E. Pacific)	6100
<i>Xylophaga</i> sp.	N. E. Pacific	6300
Poromya sp.		_
Lyonsiella sp.	Kuril-Kamchatka	8200-8800
-	N.W.Pacific	6300
<i>Myonera</i> sp.	Chinuk (N. E. Pacific)	6100
Gen. et sp. nov.	Java	6800-6900
Cuspidaria sp.	Japan	7600
_	New Britain	8000

BELYAEV's survey (1966) shows that bivalves have been obtained from an additional eight trenches and basins, and MENZIES & GEORGE (1967) indicate the presence of bivalves in the Peru-Chile Trench, so that bivalves are now known from 16 of the approximately 25 known trenches. There is no doubt that bivalves will also prove to be present in the remaining trenches as collecting is extended to these. The deepest bivalve recorded is *Phaseolus* sp. from the Tonga Trench, at a depth of 10,400-10,700 m.

There is a decrease in the number of known taxa of bivalves with increasing depth, as will appear from the following survey:

Species liste	ed in:		Depth in meters		
	6000-6900	7000-7900	8000-8900	9000-9900	10,000+
Table 12	6	6	3	1	2
Table 13	19	13	3	7	4

The decrease in the number of species with increasing depth is presumably due to less intensive collecting and increasing technical difficulties in obtaining representative samples from these depths. The data on the vertical distribution of the species are scanty indeed, but it will be noted from Table 1 that the only two species known from more than two finds *(Spinula vityazi* and *Kelliella bruuni)* have considerable vertical ranges.

As is the case in the abyssal zone, the Nuculoidea appear to play an important rôle also in the hadal fauna, since eight species out of the 17 listed in Table 12 belong to that group. This means that the deposit feeders dominate, while presumably the Kelliellidae, Thyasiridae, Limidae and possibly the Pectinidae are filter feeders. The scavengers are represented by *Cuspidaria hadalis* and by the Septibranchoidea listed in Table 13.

There appear to be no morphological structures in the bivalves which may be attributed to life in the trenches. In general the shells are delicate, a feature also commonly found in abyssal and shallow-water forms. Nearly all the known hadal species are small, less than 10 mm long. However, species like *Cyclopecten hadalis* and *Kelliella bruuni* appear to be no smaller than their abyssal congeners. On the other hand, *Cuspidaria hadalis* appears to be among the smallest species known in the genus.

A few observations have been made on the size of the prodissoconch. The results have been summarized below:

Length (in $\mu$ ) of prodissoconch		
190		
230		
230		
230		
220-250		
210		

This would indicate that the lecithotrophic development is of common occurrence as is the case in the abyssal zone.

BRUUN (1957) gave the first survey of the hadal fauna. He listed all the taxa known, the bivalves dealt with in the present paper being listed under provisional generic names. BELYAEV et al. (1958) described the results of trawlings made at about 10,500 m depth in the Tonga Trench; 21 specimens of bivalves and 75 valves of minute forms with soft and transparent shells were obtained. WOLFF (1960) made a comprehensive survey of the hadal fauna, based not only on the results of the Galathea Expedition, but also on the specimens obtained by the Sovjet expeditions, some of which were exhibited on the deep-sea exhibition shown at the XVth International Congress of Zoology, London, 1958. WOLFF gives a complete list of known taxa and a table of all hadal stations worked until then. In addition, he discussed the distribution and morphological characteristics of the hadal fauna. At that time 250-310 taxa were known, although only 127 were properly named species. From a re-consideration of the vertical distribution of the species, he suggested that the upper limit of the hadal fauna be put at 6800-7000 m, instead of 6000 m as previously suggested by BRUUN (1957). Fourteen genera and two families (one of which is actually hado-pelagic) seem to be endemic to the hadal fauna. He found that 58 % of the named species were endemic and that most species occur in one trench only, although nine species have been found in more than one trench. He suggested that the hadal fauna has been derived from the abyssal fauna, stating that morphologically the hadal species show the same adaptations to life in eternal darkness as many abyssal and even bathyal species. He also mentioned that gigantism, found in hadal crustaceans and possibly caused by the hydrostatic pressure, has not yet been reported among the hadal representatives of any other animal group.

FILATOVA (1961) reported on bivalves from the Sunda (= Java) Trench from depths of about 6800-7000 m. She found that bivalves play an important role in the bottom fauna of the Java Trench and a total of 1033 specimens belonging to five species were obtained. At one station, 483 specimens of *Thyasira* were obtained and at another station 431 specimens of a *Kelliella* were found. The remaining species were present in smaller numbers. That these numbers are much higher than those obtained by the "Galathea" may be due to differences in sampling technique. The reason for the high number of bivalves obtained is ascribed to the favorable nutritive conditions, owing to the proximity of the

Java Trench to substantial land masses from where organic matter is transferred.

WOLFF (1966) gave a brief survey of the hadal fauna. Since the 1960 paper the total number of named species has now increased to 171 and an additional 185-240 unidentified taxa have been recognized. The number of endemic genera has increased to 17, and an additional four seem to be mainly hadal. Only one family is endemic to the hadal fauna. Only 15 species are known to occur in more than one trench. The same year BELYAEV (1966) published a very comprehensive survey of the hadal fauna. All known taxa are mentioned, all hadal stations are recorded, and the main features of the zoogeography and ecology are discussed. The number of identified species has increased to about 300, and the author expects this number to increase to 700 after all the material has been properly studied. A total of 140 families and 200 genera are found to be hadal, and hadal endemism has been found in 68 % of the species, 10 % of the genera and in a single family. There appears to be very little overlapping between the abyssal and the hadal faunas, and the number of species decreases with increasing depth, the greatest diversity being found in the upper subzone. The different trenches have their own characteristic faunas. BELYAEV suggested that the hydrostatic pressure limits the diversity of the hadal fauna, while favorable feeding conditions prevail because of intensive sedimentation. The fauna appears to be dominated by younger derivates of the ancient abyssal fauna. The endemism is due to the geographical and ecological isolation of the trenches. Thirty-nine taxa, many referred to genus only, are listed (see Table 13).

The paper of MENZIES & GEORGE (1967) is essentially a criticism of the criteria supposedly suggested by WOLFF (1960, 1962) as distinctive of the hadal fauna. A main point in the conception of MENZIES & GEORGE is that there are no reliable characters separating hadal isopods from abyssal isopods, and consequently the authors can see no need for the term hadal other than as a convenience. The two authors discuss the criteria (such as

a decrease in the number of species with increasing depth, dominance of some groups and absence of others, a high percentage of endemism, morphological characters, gigantism) on the incorrect assumption that WOLFF believed them to be distinguishing characteristics of hadal (vs. abyssal) fauna. In actual fact, WOLFF (1962) was fully aware that decrease in number of species, blindness and gigantism occurred both in abyssal and hadal isopods. MENZIES & GEORGE (1967) state that percentages of hadal endemism given by WOLFF (58 %) and by BELYAEV (68 %) do not prove a high percentage of endemism, since other regions of the abyssal zone show comparable or higher percentages. This problem has been discussed above (p. 195), stating that in some groups (small crustaceans) there is a high degree of endemism, while in other groups endemism is low, many species having a wide distribution. A more detailed discussion of MENZIES & GEOR-GE's paper is given by WOLFF (in press).

HANSEN (1967) found that in holothurians the prevailing species in the Kermadec Trench have a remarkably wide bathymetrical distribution, quite apart from their occurrence at hadal depths. He also found that in two species there are morphological differences between the abyssal and hadal populations. This indicates at least a partial separation of populations, presumably due to topographical features. The holothurians thus show a distributional pattern widely different from that found in the bivalves.

More than half of the bivalve genera of the hadal fauna (Tables 12 and 13) are of Tertiary origin, i.e., the hadal bivalve fauna is generally of a rather recent origin and not a single known genus dates back to the Palaeozoic. Also the Spatangoidea, the only order of echinoids which descends into the hadal zone, is a young group dating back only to Cretaceous (MADSEN 1961b), KNUDSEN (1964) described a hadal gastropod, *Admete bruuni*, from the Kermadec Trench. The genus is known from the Pliocene, and may in some respects be considered as a specialized form, since it is a carnivore, but devoid of a radula.

# **Concluding remarks**

The rapidly increasing exploration of the deep-sea which has been conducted during the last few decades has resulted in a much more varied picture of the zone and its animal life. This applies to many fields of research. Thus studies of bottom topography has shown that the abyssal zone does not, as formerly assumed, consist largely of extensive, uniform plains covered with soft sediment It is now known that areas of hard bottom such as lava and manganese nodules occur. There are also topographical structures, such as ridges, guyots and seascarps, which are as conspicuous as the corresponding structures on land (SHEPARD 1963). Although the abyssal hard bottom is known to exist, it remains largely unexplored, and the fauna of these regions is known largely from photographs. The tremendous increase of the knowledge of abyssal bottom topography is illustrated very clearly by comparing the chart of bottom topography in SVERDRUP et al. (1946), based on data obtained prior to 1940, with the charts of DIETRICH & ULRICH (1968), the latter incorporating very recent data.

The movements of abyssal water masses have until now only been comparativley little studied, but may be of considerable biological importance in carrying food particles to and in dispersing eggs and larvae of benthic organisms, as well as in supplying oxygen. KNAUSS (1968) reviewed previous investigations on the subject, based largely on photographs, and reported on new data obtained by direct measurements and sea-bed drifters. The studies were made in the N.W.Atlantic and the E. Pacific at depths ranging from 3000 to well over 5000 m. The main conclusion from these studies was that the currents along the bottom of the deep ocean are probably not very much simpler than those at the surface of the ocean.

The diversity and complexity of the abyssal fauna has been repeatedly stressed by me. I think it can be safely concluded that the descriptive phase in the taxonomy of abyssal organisms will continue for some time in the future. It has also been stressed that as far as distributional patterns are concerned, rules generally applicable to all animal groups do not exist, a viewpoint also held by WOLFF (1962). In some groups a wide horizontal and vertical distribution may be the rule, and some well-established cases of cosmopolitanism and of allopatric species seem to occur. This pattern seems to exist in the bivalves and in some groups of coelenterates and echinoderms. In other groups, holothurians for instance, there is generally a wide horizontal distribution (including several cases of cosmopolitanism), but larger systematic units are confined to definite depth zones, and have possibly developed in situ. Finally, some groups of smaller crustaceans seem to have a very restricted distribution, often confined to single basins. Examples are found among the Isopoda, Amphipoda and Cumacea.

The present investigation is a crude overall survey of some of the problems of the deep-sea fauna. It supports the suggestion made by SANDERS *et al.* (1965) and SANDERS (1968) that the abyssal fauna is greatly diverse and neither so poor in species nor so uniform as previously assumed.

However, many important problems have been left untouched in the present study. Among these are growth, egg number, reproductive cycle, life span, mortality and quantitative distribution. Detailed investigations of restricted areas will therefore be necessary to solve many problems relating to the autecology and functional morphology of the individual species.

# **IV. SUMMARY**

The present paper deals primarily with the abyssal and hadal bivalves obtained by the Galathea Expedition, but in addition a number of samples from other sources have been included. The collection studied consists of 159 samples with about 1700 specimens and 91 species, of which 44 are considered as new. It appears to be the largest collection of deep-sea bivalves included in a single study.

At an early stage of the study it was considered necessary to examine as many samples from earlier

expeditions as could be located. The reasons for this were:

1) To solve at least some of the innumerable taxonomic problems arising during the work.

2) To decide whether a species was represented by specimens alive at capture or taken only as empty valves. This is not indicated by many of the previous authors. However, even though most samples are preserved dry, in the majority of the cases it was