

## I. INTRODUCTION

The primary aim of the present paper is to present the results of a taxonomic study of the abyssal bivalves collected by the Galathea Expedition 1950-52. The collection has the advantage of having been collected throughout the greater part of the world ocean, thus in several cases providing samples of the same species from widely separated regions. Another advantage is that several species were obtained in rather large numbers, thus enabling a study of, among other things, the intraspecific variation.

The "Galathea" collection has, however, also its shortcomings. The collecting methods employed obviously favoured larger bivalves at the expense of the minute forms, which are known to be present in large numbers in the abyssal zone (HESSLER & SANDERS 1967). It will also be noticed throughout the present paper that, although several species are represented by numerous specimens, the majority of the species are represented by a single or very few specimens.

At an early stage of the work it was realized that to obtain a reasonably satisfactory solution of the innumerable taxonomic problems encountered it was necessary to examine as much material as possible from earlier deep-sea expeditions. In addition it was found that in the majority of the literature dealing with deep-sea bivalves it is not indicated whether specimens were alive at capture or only taken as empty valves. It turned out to be desirable to make a complete survey of all recorded abyssal bivalves. This was done by visiting a number of institutions containing collections of abyssal bivalves and by borrowing from a number of other institutions.

The following institutions were visited:

- British Museum (Nat. Hist.), London (1958, 1962)
- Institut Océanographique, Monaco (1964)
- Muséum National d'Histoire Naturelle, Paris (1964)
- Museum of comparative Zoology, Cambridge, Massachusetts (1965)
- United States National Museum, Washington, D.C. (1965)
- Naturhistoriska Museet, Gothenburg, Sweden (1966)

Samples of deep-sea bivalves were borrowed from the following institutions:

- Centre d'Études et de Recherches Scientifiques, Biarritz, France
- Field Museum of Natural History, Chicago, Illinois, U.S.A.
- The Royal Scottish Museum, Edinburgh, Great Britain
- South African Museum (Nat. Hist.), Cape Town, South Africa
- Zoölogisch Museum, Amsterdam, the Netherlands
- Zoologisk Museum, Bergen, Norway
- Institut f. Spezielle Zoologie u. Zoologisches Museum d. Humboldt-Universität, Berlin, Germany

Besides the above-mentioned institutions, several samples were also borrowed from the institutions visited.

The numerous samples from previous expeditions generally turned out to be in good condition, and were extremely useful in spite of the fact that many were collected between 50 and nearly 100 years ago.

During the present work great difficulties were frequently encountered when assigning species to genera. I agree with DELL, who in his comprehensive report (1964) on antarctic bivalves stated that "most of the families of marine mollusca require revision both at the generic and the specific level. ... the systematics of the group viewed on a world-wide basis are remarkably underworked, especially at the generic level". As will appear from the following many previous workers on abyssal bivalves tended to concentrate their study to restricted areas, paying too little attention to other regions. The result has frequently been that the same species has been described under different names.

One aspect has been completely neglected in the present paper, namely that of the quantitative occurrence of the group. A few grab samples have been obtained by various recent expeditions ("Vitiaz", "Galathea" and a few more). Very few conclusive data concerning the bivalves have, however, been obtained. In this respect reference is made to the stimulating paper of HEDGPETH (1953). It should be mentioned, however, that a comprehensive quantitative investigation of the abyssal fauna is in progress (see SANDERS *et al.* 1965).

## ABBREVIATIONS OF MUSEUM AND INSTITUTION NAMES

- ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.
- BMNH: British Museum (Nat. Hist), London, England
- CERS: Centre d'Études et de Recherches Scientifiques, Biarritz, France
- FMNH: Field Museum of Natural History, Chicago, Illinois, U.S.A.
- IOAN: Institute of Oceanology, Akademija Nauk, Moscow, USSR.
- IRSN: Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium
- MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
- MNHN: Muséum National d'Histoire Naturelle, Paris, France
- MOM: Musée Océanographique, Monaco
- NMG: Naturhistoriska Museet, Gothenburg, Sweden
- NSM: National Science Museum, Tokyo, Japan
- RSM: The Royal Scottish Museum, Edinburgh, Great Britain
- SAM: South African Museum (Nat. Hist.), Cape Town, South Africa
- SIO: Scripps Institution of Oceanography, La Jolla, California, U.S.A.
- TFL: Tokai Regional Fisheries Research Laboratory, Tokyo, Japan
- USNM: United States National Museum, Washington, D.C., U.S.A.
- WHOI: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, U.S.A.
- ZIA: Zoological Institute of the Academy of Sciences, Leningrad, USSR.
- ZMA: Zoölogisch Museum, Amsterdam, Netherlands
- ZMB: Zoologisk Museum, Bergen, Norway
- ZMHU: Institut f. Spezielle Zoologie u. Zoologisches Museum d. Humboldt-Universität, Berlin, Germany
- ZMUC: Zoological Museum, University of Copenhagen, Denmark
- ZSI: Zoological Survey of India, Calcutta, India

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providing photographs of specimens, sending me reprints, identifying organisms from stomach contents, or providing information of various kinds. In particular I want to extend my thanks to the following: J. L. BARNARD (USNM), C. BARRIETY (CERS), W. J. CLENCH (MCZ), S. P. DANCE (then at BMNH), T. V. D. FEEN (ZMA), Z. FILATOVA (IOAN) E. FISCHER-PIETTE (MNHN), J. R. GRINDLEY (SAM), the late F. HAAS (FMNH), M. HORIKOSHI (The University, Tokyo), B. HUBENDICK (NMG), N. C. HULINGS (USNM), R. KILIAS (ZMHU), J. KJENNERUD (ZMB), T. OKUTANI (TFL), R. H. PARKER (then at SIO), A. S. RAJAGOPAL (ZSI), the late W. J. REES (BMNH), H. A. REHDER (USNM), J. ROSEWATER (USNM), A. SOLEM (FMNH), T. SOOTRYEN (Zool. Mus., Oslo), J. STUARDO (then at MCZ), N. TEBBLE (then at BMNH), G. TESTA (MOM), R. D. TURNER (MCZ), A. R. WATERSTON (RSM), W. VERVOORT (Rijksmuseum v. natuurlijke Historie, Leiden), World Data Center A, Washington, D.C.

Although unforeseen circumstances prevented my planned participation in the Galathea Expedition this has to a great extent been compensated for by frequent discussions with more fortunate colleagues at ZMUC. The following should be particularly mentioned: BENT HANSEN, J. B. KIRKEGAARD, F. J. MADSEN, T. WOLFF. Their wide knowledge of deep-sea biology has been a great help to me, and they have assisted me in many ways, such as calling my attention to relevant literature, identifying specimens, etc. I wish to thank the above-mentioned colleagues as well as the following, who, although not members of the Galathea Expedition, have assisted me in various ways: Mrs. E. ASMUSSEN, O. MUNK, J. G. NIELSEN, the late A. NØRVANG, K. W. OCKELMANN, K. W. PETERSEN, O. TENDAL. I particularly want to thank T. WOLFF for carefully reading the manuscript and commenting on it.

I wish to acknowledge the indispensable assistance of the two artists, the late POUL H. WINTHER (with whom I had many years of fruitful cooperation), and KAI OLSEN. Without their talent and cooperation it would not have been possible to have the numerous species figured in such a correct, but still artistic way. I am likewise greatly indebted to E. LEENDERS, who executed the diagrams and to H. V. CHRISTENSEN, who executed most of the photographs for the plates.

I also wish to thank Mrs. MARY E. PETERSEN for correcting the English, Mrs. KATE PETERSEN for typing the manuscript and Mrs. L. WOLFF for reading the proofs.

I wish here to express my gratitude to the late Professor R. SPÄRCK, who by his most inspiring teaching turned my interest to marine biology, and to the leader of the Galathea Expedition, the late A. F. BRUUN, with whom I worked for about 20 years until his untimely death in 1961. BRUUN was the inspiring leader of the Atlantide Expedition in 1945-46, of which I was fortunate enough to be a member, and on this occasion he introduced me to the scientific work at sea. The initial phases of the present work were followed by BRUUN with the enthusiasm and interest which was so characteristic of him.

I also want to thank the head of the Mollusc Department of ZMUC, H. LEMCHE, not only for handing the "Galathea" bivalve collection over to me, but also for the great interest he has taken in the work and for the numerous suggestions and many pieces of good advice he has given.

Finally it is a great pleasure to extend my thanks to the Rask-Ørsted Foundation for the generous grants which have enabled me to visit the institutions mentioned above.

## ACCOUNT OF PREVIOUS EXPEDITIONS

The following account is arranged chronologically from the start of each expedition. The number of stations indicate the stations at which abyssal bivalvia (both live specimens and shells) were obtained.

### 1) The Porcupine Expedition, 1869, 1870.

Area: N. E. Atlantic. 10 stations.

Station list: THOMSON (1873).

Publications: JEFFREYS (1879, 1881 a, 1881 b).

Location of collection: USNM.

### 2) The Challenger Expedition, 1873-76.

Circumnavigation. 32 stations.

Station list: THOMSON & MURRAY (1895).

Publications: SMITH (1885, 1891), PELSENEER (1888), the latter describing the gross anatomy of a few species.

Location of collection: BMNH, several samples are at USNM. A few samples have not been located.

### 3) The Valorous Expedition, 1875.

Area: N. Atlantic. 8 stations.

Station list: JEFFREYS & CARPENTER (1876).

Publications: JEFFREYS in: JEFFREYS & CARPENTER (1876), JEFFREYS (1876 a, 1876 b).

Location of collection: USNM.

*Remarks:* Some uncertainty prevails regarding both the material from the Porcupine and the Valorous Expeditions: the labels of some samples appear to be inconsistent with the station numbers given in JEFFREYS' papers, and in some cases samples have been merged. In other cases a sample appears to contain several species, but only one specific name is written on the label. The two collections should be thoroughly revised, and good detailed figures should be published of many of the species. Obviously many misidentifications occur.

### 4) The Blake Expedition, 1877-78 and 1879-80.

Area: W. Atlantic: Gulf of Mexico and Caribbean Sea. 3 stations.

Station list: PEIRCE & PATTERSON (1881).

Publications: DALL (1878, 1881, 1886, 1889a, 1889b).

Location of collection: USNM, MCZ.

### 5) The Travailleur & Talisman Expeditions, 1880-1883.

Area: E. Atlantic from the Bay of Biscay to Senegal; C. Atlantic: Sargasso Sea, Azores region. 19 stations.

Station lists: Miméographed list, Annales Hydrographiques, S. SMITH (1889).

Publications: JEFFREYS (1880), LOCARD (1898).

Location of collection: MNHN.

*Remarks:* The expeditions adhered to a somewhat complicated system of numbering of the stations. Each of the years started with "dragage" no. 1, but in 1881 the station numbers were in two series, each beginning with no. 1. During the 1882 cruise the individual stations had, besides the station number, a "sounding" number differing from the former. The Annales Hydrographiques lists only the sounding number for the 1882 cruise, while for the 1883 cruise the station numbers of the miméographed list are given as "sounding" numbers. Most of the samples are labelled with station number and depth only, and in some cases the year is also indicated. By means of the depth indicated it is in most cases possible to refer a sample to the correct station. In some cases samples of the same species from several stations, often of widely different depths, have been pooled. For the reasons mentioned the records contain a number of errors and dubious records.

JEFFREYS (1880) gives only a brief list of the species obtained in the Bay of Biscay, without giving any information on exact locality or depth.

6) The Albatross Expeditions, 1883-87.

Area: W. Atlantic, off the coast of N. and C. America. Most abyssal stations were located between 35° and 41° N, but a few were run in the Gulf of Mexico and the Caribbean Sea. 37 stations.

Station list: TOWNSEND (1901).

Publications: DALL (1889b, 1901); VERRILL (1884, 1885a, 1885b, 1897); VERRILL & BUSH (1897, 1898).

Location of collection: USNM, MCZ.

7) The Albatross Expeditions, 1888-1911.

Area: E. Pacific, off the coast of the Americas from the Bering Sea to S. Chile, most abyssal stations being located between 8° S and 14° N. 36 stations.

Station list: TOWNSEND (1901); "Albatross" (1906, 1907, 1921).

Publications: DALL (1891, 1895, 1896, 1897, 1901, 1902, 1908, 1913, 1916, 1921).

Location of collection: USNM, MCZ.

8) The Hironnelle & Princesse-Alice Expeditions, 1886-1913.

Area: E. Atlantic from the Bay of Biscay to the region of the Cape Verde Isl.; C. Atlantic: Azores region; a couple of stations in the NW. Atlantic. 16 stations.

Station list: DAUTZENBERG (1927); Temperature data: ROUCH (1948).

Publications: DAUTZENBERG & FISCHER (1897); DAUTZENBERG (1925, 1927).

Location of collection: MOM.

*Remarks:* DAUTZENBERG (1889) records previous abyssal records (Porcupine, Challenger, Travailleur & Talisman Expeditions) from the Azores region without adding anything new. In the present paper the expeditions have been referred to as the "Monaco Expeditions".

9) The Investigator Expeditions, 1884-1913 (abyssal stations only between 1890-1903).

Area: N. part of the Indian Ocean, both the Bay of Bengal and the Arabian Sea. 8 stations.

Station list: "Investigator", List of stations (1914).

Publications: WOOD-MASON & ALCOCK (1891), E. A. SMITH (1894, 1895, 1904, 1906); ALCOCK & ANDERSON (1897); WINCKWORTH (1940); KNUDSEN (1967).

Location of collection: ZSI.

*Remarks:* WINCKWORTH (1940) compiled a list of the species with references to the papers in which they were mentioned and references to figures. KNUDSEN (1967) made a survey of the "Investigator" bathyal and abyssal bivalves arranged according to stations, designating the type localities for nearly all the new species described. He also listed all the bathyal and abyssal species with their known horizontal and vertical ranges. The temperatures range for each species was given and an attempt was made to determine, which species were bathyal and which should be regarded as abyssal. Four species were found to be decidedly abyssal, another four only with some doubt could be considered as abyssal, and the remaining 46 were found to be bathyal.

10) The Ingolf Expeditions, 1895 & 1896.

Area: N. Atlantic. 7 stations.

Station list: JENSEN (1912).

Publications: JENSEN (1904, 1912).

Location of collection: ZMUC.

*Remarks:* JENSEN (1912) studied only the following abyssal groups: Pectinidae, Limidae, Mytilidae. The remaining groups have never been worked up, but a few samples have been identified (but not published) by K. W. OCKELMANN.

11) Expédition Antarctique Belge, 1897, 1898, 1899. S. Y. "Belgica".

Area: Antarctic Ocean. 1 station.

Station list: -

Publication: PELSENEER (1903).

Location of collection: -.

12) Deutsche Tiefsee-Expedition, 1898-99. "Valdivia".

Area: E. Atlantic, off W. Africa, Antarctic and Indian Oceans (W. of Sumatra, off E. Africa). 5 stations.

Station list: SCHOTT (1902).

Publication: THIELE & JAECKEL (1931).

Location of collection: ZMHU.

*Remarks:* THIELE is responsible for the study of the Nuculoidea, Pectinidae, Limidae and the Mytilidae. The remaining groups were studied jointly. In the present paper the expedition has been referred to as the Valdivia Expedition.

13) The Siboga Expedition, 1899-1900.

Area: SE. Asian waters. 2 stations.

- Station list: WEBER (1902).  
 Publications: PELSENEER (1911); PRASHAD (1932).  
 Location of collection: ZMA.
- 14) The "Deutsche Südpolar-Expedition", 1901-1903. "Gauss".  
 Area: Antarctic Ocean, Indian Ocean sector. 3 stations.  
 Station list: not available, relevant data compiled from several papers of the expedition's report.  
 Publication: THIELE (1912).  
 Location of collection: ZMHU.
- 15) The "Scottish National Antarctic Expedition", 1902-1904.  
 Area: Antarctic Ocean, Atlantic sector; S. Atlantic. 5 stations.  
 Station list: not available, relevant data compiled from several papers of the expedition's report.  
 Publications: MELVILL & STANDEN (1907, 1912).  
 Location of collection: RSM.
- 16) The Michael Sars North Atlantic Deep-sea Expedition, 1910.  
 Area: N. Atlantic. 3 stations.  
 Station list: "Michael Sars" -, List of observing stations (1910).  
 Publications: GRIEG (1920, 1931); SOOT-RYEN (1966).  
 Location of collection: ZMB.  
*Remarks:* SOOT-RYEN (1966) undertook a complete revision of the collection, correcting several erroneous identifications and including several samples not mentioned by GRIEG.
- 17) The John Murray Expedition, 1933-34.  
 Area: N. W. part of the Indian Ocean. 6 stations.  
 Station list: SEWELL (1935).  
 Publication: KNUDSEN (1967).  
 Location of collection: BMNH.
- 18) WHOI vessel "Atlantis" cruise, 1947.  
 Area: Azores region. 1 station.  
 Station list: data from specimen labels.  
 Location of collection: MCZ.
- 19) The Swedish Deep-sea Expedition, 1947-48.  
 Area: C. & W. Atlantic. 4 stations.  
 Station list: NYBELIN (1951).  
 Publication: ODHNER (1960).  
 Location of collection: NMG.
- 20) Chicago Natural History Museum Bermuda Deep-sea Expedition, 1948.  
 Area: W. Atlantic. 1 station.  
 Station list: HAAS (1949).  
 Publication: HAAS (1949).  
 Location of collection: FMNH.
- 21) The Vitiaz Expeditions, 1949-1959.  
 Area: N. W. & W. Pacific, Indian Ocean. 25 abyssal and 22 hadal stations.  
 Station list: data compiled from FILATOVA (1958), BELYAEV (1966) and ZENKEVITCH (1958). Temperature data mostly from "World Data Center A".  
 Publications: FILATOVA (1958, 1961, 1964, 1969); BELYAEV (1966).  
 Location of collection: ZIAL.  
*Remarks:* The very extensive collections of the "Vitiaz" cruises have only partly been studied and identified. Most work has been done on some species of *Spinula* (FILATOVA 1958, 1964). BELYAEV (1966) listed a number of hadal forms, of which, however, several are assigned to genus only, and in some cases the assignment is obviously provisional. A few of the bivalves listed in the present paper were seen by the present author at an exhibition at the XVth International Congress of Zoology, London 1958.
- 22) The Danish Deep-Sea Expedition Round the World, 1950-52. "Galathea".  
 See p. 16.
- 23) The Theta Expedition, 1956.  
 Area: C. Atlantic. 2 stations.  
 Station list: CLARKE (1959).  
 Publication: CLARKE (1959).  
 Location of collection: MCZ.
- 24) The Vema Expedition, 1957.  
 Area: S. Atlantic. 16 stations.  
 Station list: data compiled from CLARKE (1961b) and BARNARD (1962).  
 Location of collection: MCZ.  
*Remarks:* some samples were not included in CLARKE's paper (1961b) and a few were presented to ZMUC. Most of the latter specimens have been included in the present study.
- 25) The Africana II Expedition, 1959.  
 Area: S. Atlantic, off SW. Africa. 9 stations.  
 Station list: BARNARD (1963).  
 Publication: BARNARD (1963).  
 Location of collection: SAM.

- 26) The SIO cruises, 1959-1961.  
 Area: E. Pacific, off the coast of N. & C. America between 12 and 34 N. 10 stations.  
 Station list: PARKER (1964).  
 Publication: PARKER (1964).  
 Location of collection: ZMUC, MCZ.  
*Remarks:* Most of the abyssal samples have been re-studied and included in the present paper. The samples in question are all in the ZMUC.
- 27) The "Soyo-Maru" cruises, 1959-60, & the "JEDS-4" cruise, 1961.  
 Area: N.W. Pacific, off Japan. 4 abyssal and 1 hadal stations.  
 Station lists: "Soyo-Maru": OKUTANI (1962, 1968a).  
 "JEDS-4": SUYEHIRO, OKADA *et al.* (1962).  
 Publications: OKUTANI (1968a); SUYEHIRO, OKADA *et al.*, (1962); FILATOVA (1964).  
 Location of collections: TFL.
- 28) The WHOI cruises, 1960-65.  
 Area: W. Atlantic. 9 stations.  
 Station list: ALLEN & SANDERS (1966).  
 Publication: ALLEN & SANDERS (1966).  
 Location of collection: WHOI.  
*Remarks:* A detailed investigation of a transect Gay Head-Bermuda covering shallow water (about 100 m) to a depth of about 5000 m. The transect was run regularly with a modified anchor dredge allowing quantitative sampling. For details see SANDERS, HESSLER and HAMPSON (1965). The bivalve material has not yet been worked up except for a single species, *Abra profundorum*. HESSLER & SANDERS (1968) recorded a large number of both species and specimens.

In general the works dealing with abyssal bivalves are purely taxonomic and descriptive, and only in exceptional cases do the authors give some general conclusions of their work. This is, for instance, the case with DALL who (1889a, 1890b) commented on the life conditions of the deep-sea molluscs based on observations of the Blake and Albatross Expeditions. LOCARD (1898) gave a survey of the molluscs of the N. Atlantic, including the abyssal species found by the Travailleur and Talisman Expeditions. In his survey he did not distinguish between live specimens and valves, and on the whole his conception of zoogeographical problem is now only of historical interest.

CLARKE (1962a) undertook the hitherto only com-

pilation of a list of all recorded abyssal molluscs, 1152 species, based on a survey of the literature. Although, as will appear, I have considerably changed the list as far as bivalves are concerned, CLARKE's work is an excellent base for a further development of the knowledge of the abyssal Mollusca.

A recent publication, V. G. KORT ed. (in Russian, 1969), deals with the deep sea of the Pacific Ocean. A chapter by FILATOVA (p. 46-52) is devoted to the abyssal bivalves. In addition there are general chapters on the distribution, origin and antiquity of the abyssal and ultraabyssal (= hadal) fauna. The publication came too late to be discussed in the present paper.

## METHODS

At an early stage of the present study it became necessary to obtain a survey of, as far as possible, all abyssal bivalves obtained by previous expeditions. To this end a card index comprising all abyssal stations at which bivalves have been taken, was made from the literature. The index contained all available information on position, depth, bottom, sediments, etc. The species obtained at each station were listed and eventually also whether a given sample contained valves only or specimens alive at time of capture. In addition was noted whether I had seen the sample or not.

To aid in studying the vertical zonation and in distinguishing between the abyssal and bathyal species, not only abyssal stations, but also numerous stations from the deeper part of the bathyal zone were included in the card index.

Information on position, depth and bottom sediments was nearly always available, either in the papers dealing with the bivalves in question or in the station lists, which have been published for nearly all the larger expeditions. In a number of cases, however, no temperature data were available. Often temperature measurements from nearby stations at the same depth from the same expedition were available, but otherwise data from the following sources were used: BRUNEAU, JERLOV & KOCZY (1953); Discovery Rep. (1942, 1944, 1947, 1957); FUGLISTER (1960); Japan Met. Agency (1959); van RIEL (1956) and THOMSEN (1937).

Finally, a number of bottom temperatures have been obtained from the World Data Center A, Washington, D. C. and from T. OKUTANI (personal communication). All the temperatures obtained

from the above-mentioned sources are in brackets. The hydrographical data of the Galathea Expedition have been published by KIILERICH (1964).

In the literature dealing with the abyssal bivalves it is sometimes indicated whether live specimens or valves only were obtained. This is of course very important when evaluating the distribution of a species, but information on this point is in most cases not given. It was therefore important to personally inspect as much material as possible. In most instances the older samples were dry but sometimes the soft parts were still inside. Frequently the interior of the valves had been cleaned, but even in these cases it is nearly always easy to detect remnants of the soft parts under a binocular microscope. United valves have been listed as "live specimens" if they were well preserved, indicating that they had probably not been transported very far.

Abyssal bivalves have been dredged from about 280 stations, yielding 650-700 samples. Altogether I have seen about 80 % of these (the "Vitiáz" and WHOI collections are not included, see p. 13, 14). In addition, a similar number of bathyal bivalves have been examined. This was done with the purpose of studying the border region between the bathyal and abyssal zones, but considerable attention was also paid to the problem of the occurrence of essentially abyssal species in the bathyal zone and on the taxonomic relationships between the bivalves of the two regions. The collections of the Zoological Museum, Copenhagen, have been extensively used for comparison, particularly the large collection of arctic littoral bivalves. During the study of deep-sea bivalves from foreign institutions, a few species were found which have either never been figured or have been figured only in papers not easily accessible. A number of these species have been illustrated in the present paper.

In many groups of bivalves, for instance the Nuculoidea, shell proportions are important in separating species. In the present study measurements of shell dimensions have been made in a number of species and proportions believed to be useful have been calculated. The measurements taken are shown in Fig. 4. In some cases measurements have been made with a pair of callipers, but in most cases they were made on enlarged outline drawings of the shells in question, which had been drawn with the aid of a camera lucida. All shell measurements are given in millimeters. Measurements of eggs and prodissoconchs, also made on enlarged drawings, are given in  $\mu$ . In the Nuculoidea

attention has been paid to the number of hinge teeth.

In most species some attention has been paid to the gross anatomy, which in many cases turned out to yield very useful taxonomic characters. This seems to be particularly useful in the study of abyssal bivalves, where the number of specimens of the individual species is frequently so small that taxonomic characters on shell proportions are not easily obtainable. I have not attempted to give a complete anatomical description for every species examined, but only to find easily observed structures, such as the siphon, mantle and foot and sometimes other structures, which seem to be useful in separating the species. In addition, the gonads of numerous specimens have been examined in order to obtain information on certain aspects of the reproduction, and in some species the stomach contents were examined. Attention has been paid to the intraspecific variation, and a record has been kept of the epifauna on the shells.

When examining many of the smaller specimens under the binocular microscope it was found to be convenient to place them in a dish containing black volcanic sand. By doing so the bivalve could easily be placed exactly in the position wanted and subsequent turning of the specimen was greatly facilitated.

For anatomical investigations a few of the smaller specimens were stained with borax carmine.

VOKES (1967) has been followed for genus and family names. The technical terms used in describing the shells are those listed in KEEN (1963). A few rarely used terms are explained in the text.

The drawings marked PHW were executed by the late artist POUL H. WINTHER, those marked K. O. by the artist KAI OLSEN. The diagrams were executed by Mr. E. LEENDERS. I am myself responsible for the remaining figures, which have been based on outline sketches made by means of a drawing tube. In many of the specimens photographed the outlines of the adductor scars and the pallial sinus have been accentuated by pencil.

The purely artificial, but practical subdivisions of the world ocean: the Atlantic, the Antarctic, the Indian and the Pacific Oceans have been delimited in accordance with SVERDRUP, JOHNSON & FLEMING (1946).

The Atlantic Ocean is separated from the Indian Ocean by the meridian of the Cape of Good Hope (20° E); the eastern border of the Indian Ocean is from Burma-Sumatra-Java-Timor to W. Australia

at Cape Londonderry (at about 127°E), and from Tasmania (at 147°E) southwards. Following the suggestion of WYRTKI (1961), the term S.E. Asian waters has been used for the sea extending (and including) the Philippine waters, the China Sea and the Indonesian waters, as well as the Andaman Sea. The border of the Antarctic Ocean is put at the subtropical convergence, at about 40°S.

The topographical names of basins, trenches, ridges and other structures are in accordance with the charts of SHEPARD (1963) and DIETRICH & ULRICH (1968). All depths are given in meters, and those originally given in fathoms have been recalculated. The vertical division of the sea follows BRUUN (1957, 1959) and WOLFF (1962):

Eulittoral: the tidal zone and down to 3-4 m depth.

Sublittoral: from 3-4 m depth to 200-400 m.

Bathyal: from 400 m to about 2000 m, temperature range 4-10°C.

Abyssal: from 2000 to about 6000 m, temperature below 4°C.

Hadal: below about 6000 m.

The term "shallow water" has been used to designate the two first-mentioned zones, while the term "deep-sea" has been used for the three last-mentioned zones.

The above subdivision is highly schematic and, as will be seen, it does not fit exactly the conditions actually observed in the deep-sea. This was already pointed out by BRUUN (1959), who predicted that when the collections from the Galathea Expedition had finally been worked up and results from other expeditions had been published, a revision of the general picture would most certainly be needed. WOLFF (1960), at having summarized the knowledge of the hadal fauna, suggested that the lower limit of the abyssal zone should rather be put at about 6500 m. However, the present material gives no evidence that this limit is preferable. For the sake of convenience the 6000 m depth limit has been used throughout the present paper.

The collections of the Galathea Expedition are preserved in 70 % alcohol and most specimens are in good condition. Valves are stored dry, but these were found in small numbers only and have generally not been included in the present study except when they were found useful for the study of variation or could provide information otherwise unobtainable.

## A SURVEY OF THE MATERIAL

The present study is based mainly on the collection of bivalves obtained from depths greater than 2000 meters by the "Galathea". Altogether 127 samples are present, originating from 50 stations. Of these, 19 samples from 10 stations are hadal. The collection contains about 1500 specimens, of which slightly more than 100 are hadal. Of the 76 species obtained, 46 (of which 10 are hadal) have been described as new. However, included in this number are six new species of *Xylophaga*, which were described by KNUDSEN in 1961. No specific name could be attached to four taxa. Three species (including one n.sp.) are represented by valves only.

Besides the four unidentifiable taxa and the three species represented only by valves the 69 species taken were distributed as follows:

No. of species	No. of specimens per species
27	1
23	2-9
7	10-19
7	20-49
2	50-99
2	100-499
1	500 +

The three most abundant species comprised about 840 specimens, i.e., well over half the total number of specimens obtained.

The horizontal distribution of the "Galathea" stations at which bivalves were obtained is shown on the chart Fig. 1. Organisms were obtained at 56 abyssal stations and at 15 hadal stations. The vertical distribution of the 50 stations at which bivalves were obtained, can be summarized as follows:

Depth range in meters	No. of stations
2000-2900	11
3000-3900	9
4000-4900	16
5000-5900	4
6000-6900	5
7000-7900	2
8000-8900	1
9000-9900	1
10000-+	1
	50

The number of species per station can be seen from the following survey:



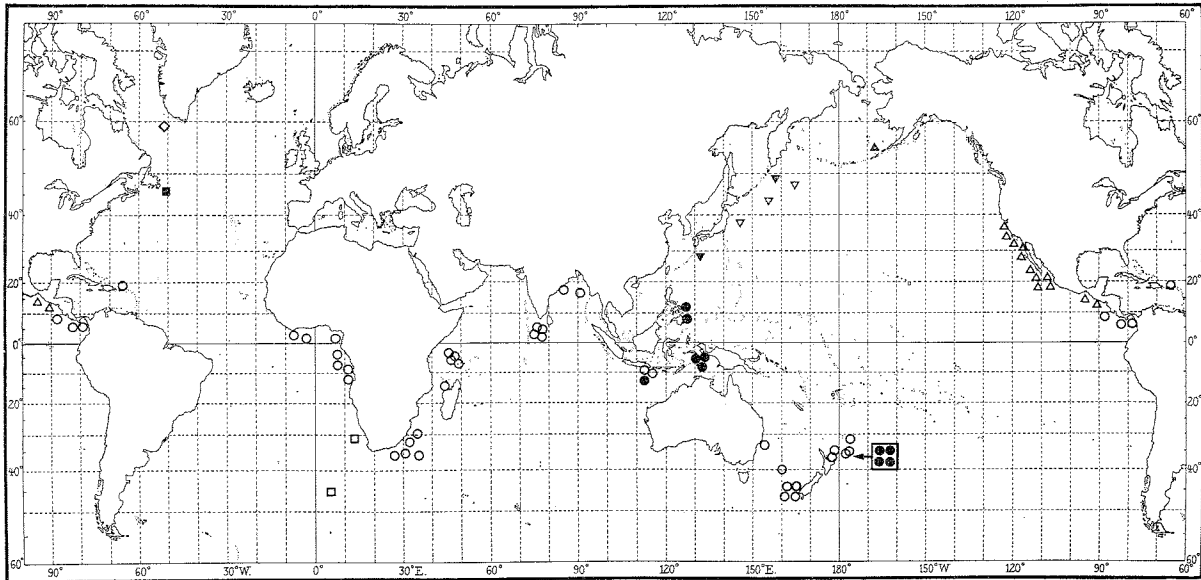


Fig. 1. Map showing the collecting stations of the present material. ○ "Galathea", abyssal sts.; ● "Galathea", hadal sts.; △ SIO; ▲ "Albatross"; ▽ "Vitiaz", abyssal sts.; ▼ "Vitiaz", hadal sts.; □ "Vema"; ◇ "Ingolf"; ■ Monaco.

#### Abyssal stations:

No. of species:	1	2	3	4	5	6	7	8
No. of stations:	11	7	8	5	4	0	3	2 = 40

#### Hadal stations:

No. of species:	1	2	3	4
No. of stations:	5	2	2	1 = 10

Besides the collections of the Galathea Expedition a number of additional samples of abyssal and hadal bivalves originating from various sources have been included in the present study:

- 1) Cruises of various research vessels from Scripps Institution of Oceanography provided 18 samples from 12 stations in E. Pacific, at depths between 2000 and 4200 m. The collection comprises about 100 specimens, referred to 11 species, of which three are described as new in the present report. The collection was included in PARKER's paper (1964).
- 2) Cruises of the USSR vessel "Vitiaz". Five samples, nine specimens, four species of *Spinula* spp. from the N.W. Pacific. The samples were included in the two papers of FILATOVA (1958, 1964).
- 3) Two samples from "Albatross" St. 3604, N.

Pacific. Thirty-five specimens, two species. From the USNM collections. The samples were included in DALL's report (1916).

- 4) Three samples from the 12th cruise of the "Vema" (Lamont Geological Observatory). There are 19 specimens, two species; these were not included in CLARKE's report on the mollusks of the expedition (1961 b).
- 5) The Ingolf Expedition 1895-96. One sample of two specimens. Never published.
- 6) Monaco Expeditions, St. 2964. One specimen. Described as a new species in the present report.

Besides the abyssal specimens listed above, a few bathyal samples of otherwise abyssal species have been included; one of these samples is from "Galathea" St. 443.

Altogether the present study comprises 159 samples with some 1700 specimens distributed over 91 taxa (including *Xylophaga* and *Teredo*, the two groups being only briefly referred to, see p. 118). It appears to be the largest collection of deep-sea bivalves included in a single study.

The whole collection studied, with the exception of the specimen listed under 6), is kept at the Zoological Museum of the University of Copenhagen.