

**A MONOGRAPH OF THE FRESHWATER
BRYOZOA - PHYLACTOLAEMATA**

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ABSTRACT

1. This paper presents the taxonomy of the Bryozoa Phylactolaemata. The group is found to contain a number of series. The present classification reveals that a number of specific names are synonyms.

2. The evolution of the group is described on the basis of the development of the zoarium and the species-specific statoblasts.

3. The Phylactolaemata are to be considered as a group that have completed their evolution with the development of giant species with giant and specialized forms of statoblasts; this has been accompanied by a reduction in the number of tentacles.

4. The distribution of the species was assessed from the available data. The main concentration is found to occur in the southern hemisphere.

5. The distribution supports the conclusion that the continents were formerly connected; the present distributional pattern can be explained only on this basis.

6. The statoblasts were investigated with particular attention to various types of illumination and certain histochemical methods. The electron-microscopical study forming part of this investigation led to interesting results. The histochemical study also produced new information.

7. The statoblasts are illustrated with characteristic microphotographs.

8. The characters are given according to groups in the keys. Various data are presented in tables.

9. A short historical review is provided.

10. Wherever possible, relevant data on subjects other than the taxonomy of the various species have been added.

INTRODUCTION

The discovery of *Lophopus crystallinus* by Trembley in April 1741, in a pond on the country estate of Sorghvliet situated at the edge of The Hague in The Netherlands (Trembley, 1744), marked the beginning of the study of the freshwater Bryozoa, the Phylactolaemata. Trembley's pre-linnean publication was followed by a paper in which Pallas (1768) gave the species the name by which it is now known.

The Phylactolaemata are difficult to study because of their relative rarity and inaccessibility, and because they can be collected only during a brief period and not throughout the year. But in spite of these problems they have fascinated many investigators and are among the oldest objects of scientific study. At first, only an occasional study of a species appeared; Blumenbach (1779, 1780) discovered the most widely distributed species, *Fredericella sultana*; Pallas (1768) described *Plumatella fungosa*, also a frequent species; Cuvier (1798) recorded *Cristatella mucedo*, the most highly developed species. In the middle of the nineteenth century the study of this group began to acquire momentum. Allman (1856) devoted a monograph to the species then known, primarily those of western Europe, and introduced the name Phylactolaemata. Hancock (1850, 1860), Leidy (1851-1879), Ridley (1866), Davenport (1890-1904), Oka (1890-1912), Meissner (1893-1898), Rousselet (1904-1916), and Sollas (1908) made contributions from all the continents. Special mention should be made here of the publications by Wesenberg-Lund (1895-1939), Braem (1888-1913), and Kraepelin (1884-1914), describing the reproduction and histology. Kraepelin's „Monographie der deutschen Süßwasser-Bryozoen" (1887, 1892), in two volumes with exceedingly fine plates, is an unsurpassed achievement. The list of authors on this subject includes the most celebrated biologists: Linnaeus (1758, 1767), Cuvier (1798), Lamarck (1816), and De Vries (1887).

Among the more recent investigators are Abricossoff (1924-1959, Russia); Annandale (1907-1922, South Asia); Borg (1930-1941, Sweden, Germany, and outside Europe); Harmer (1901-1935, England); Hastings (1929-1938, England and elsewhere); Lacourt (1948-1959, The Netherlands, Belgium, Congo, Sumatra); Loppens (1905-1948, Belgium); Marcus (1926-1958, Denmark, Brazil). Prenant & Bobin (1956) treated the European species; Rogick (1934-1957) in a series of publications, those of North America, and Toriumi (1941-1963) those of Japan and its surrounding regions. Mention should be made of Marcus (1926-1958) for his biological investigations and of Cori (1941) for his magnificent paper in "Handbuch der Zoologie", the 240 pages of which contain the entire knowledge to that

date of the histology of the marine and freshwater Bryozoa. The taxonomy of the group, however, was not discussed by Cori.

The most prominent investigators of recent years are Brien and Toriumi. Brien (1934-1960) took up the work of Braem and Kraepelin, studied the structure and development of the zoarium and re-examined the histology and reproduction of a number of species. His paper (1960) in "Traité de Zoologie" contains a discussion of the Bryozoa comparable with Cori's above mentioned publication. Toriumi (1951-1956) treated the taxonomy of a number of species exhaustively in a series of publications. Wiebach (1958a), lastly, provided a superbly written summary of the biology of this group.

The Netherlands thus saw the first discovery and the first publication in this field. And from The Netherlands is now offered a monograph on the species of *Phylactolaemata*, their taxonomy, and their distribution. This is not meant to imply that the present publication contains the last word on the subject. Quite to the contrary, it is my hope that it will serve especially to encourage further study, at least if monographs such as the present one do not prove to be the epitaphs of these groups, considering the current rate of destruction of Nature. One sometimes has the feeling that one is describing things as they were, as in the case of Lake Erie to cite one example, and should use the past tense.

My work has taken the form of collecting data from the literature and of material supplied on request by many of the larger museums throughout the world; it has been compiled over a period of many years. With sincere gratitude I wish to express my indebtedness to all those who gave me their cooperation and put material and literature at my disposal. For the English translation of the text I am most grateful to Mrs. I. Seeger-Wolf, Leiden. Under the heading "Material", all the material at the author's disposal is recorded. From the multiplicity of data, critically arranged, the species have been, as it were, crystalized out and the areas of distribution determined. Reference is made in the list of publications to other investigations (biological, histological, etc.). In the treatment of the synonyms the very old names are not referred to in detail; if the old literature still conceals a description of a species, the type material has in all likelihood been lost and the species would no longer be recognizable. The work is provided with a collection of microphotographs of statoblasts most of them taken by the author, and the most complete bibliography it was possible to assemble. An attempt has been made to indicate the characteristics of the species according to groups and comparatively. For identification, the microphotographs of the statoblasts are indispensable. At present, 29 species are known.

The histology and the more finely detailed anatomical aspects are not

discussed here; they are not, in this group, necessary or even usable for the taxonomy of the various species concerned, at least not at the present level of our knowledge; furthermore, the subject has already been treated by others better than I could have done. But until now the elementary basis, the identification of the species, has been lacking, and this will be given in the present monograph.

The technique used for preparing the statoblasts is simple; the zoaria are opened under the microscope with needles, the statoblasts detached and brought with a fine brush on a glass slide provided with a drop of alcohol. Glycerin is then very gradually added because this liquid does not easily penetrate the chambers of the annulus. For permanent storage in glycerin,

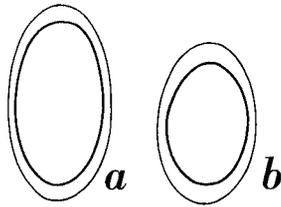


Fig. 1. Outlines of F statoblasts of *Plumatella philippinensis* Kraepelin.

strips of thin paper should be inserted under the edges of the cover glass for support, before sealing with canada balsam or some other substance. A sealing material in aqueous solution may also be used. Reference on this point may be made to the handbooks on microscopical techniques.

Many authors combine the Bryozoa with a few smaller groups in a separate phylum: Tentaculata; others include them with larger groups in the phylum Oligomeria (Hadži, 1958). In this study only the Ectoprocta are assigned to the Bryozoa, a conclusion arrived at by many authors, e.g. Brien & Papijn (1955, on the basis of comparative studies), Hadži (1958), and Kaestner (1954: 176). Brown (1958) stated that under the name

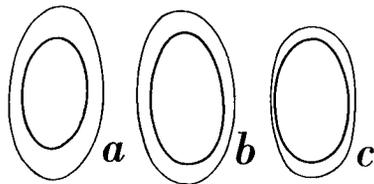


Fig. 2. Outlines of F statoblasts of *Plumatella agilis* (Marcus).

Bryozoa are combined large, mutually differing groups which later had to be split off, but this surely does not apply only to the Bryozoa. Has it not also been done for many other groups, with retention of the original name? He also argued that many prominent investigators have used the name "Polyzoa". But these were exclusively English-speaking authors. Others, equally prominent authors, and all of them from the European continent, have consistently used the term Bryozoa.

Phylogenetically, the Phylactolaemata must be very old. If the use of calcium for the construction of an internal or external skeleton is characteristic of more advanced evolution, the Phylactolaemata must have already been in existence in a very early period. Fossils of marine Bryozoa with calcified cuticula have been dated in the Cambrium. The Phylactolaemata are

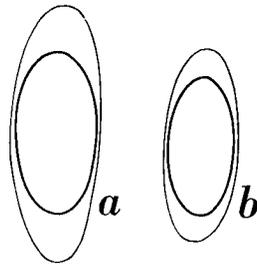


Fig. 3. Outlines of F statoblasts of *Plumatella fruticosa* Allman.

therefore older; their non-calcified body wall and their consequently still very simple anatomy are primitive characteristics. The structure of the marine Bryozoa is more complex, as is the manner of their reproduction. The one-year life cycle of the Phylactolaemata (the zoaria usually die off annually) is related to, as well as being the cause of, the formation of statoblasts, the encapsuled "initial stage" of new zoaria. Brien (1960a) summed up the situation as follows: „Les Phylactolèmes apparaissent aujourd'hui comme les survivants d'une branche très ancienne des Bryozoaires, à la fois primitive et spécialisée, issue de la base même de la souche ancestrale. Ils se distinguent très nettement des Gymnolèmes par la taille, la structure de leurs zoécies, la croissance et l'aspect de leurs colonies, les particularités de la reproduction sexuée, la viviparité, la nature de leurs larves, les modalités de leur métamorphose, la production des statoblastes". Palaeontology shows that every group exhibits a regression after having reached the apex of its development. In the Phylactolaemata the regression consists of a reduction in the number of tentacles of the latest species, *Cristatella mucedo*, which

suggests the conclusion that the Phylactolaemata have completed their evolution. But *Cristatella mucedo*, as far as is known also possesses the most highly developed statoblast. There are no indications that the group is becoming extinct, although water pollution is just as fatal to them as it is to man.

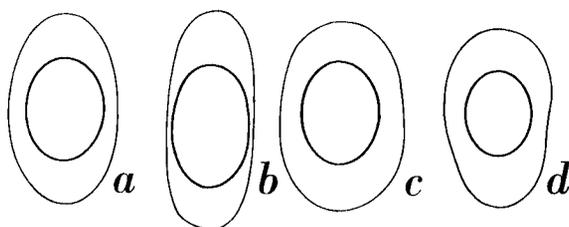


Fig. 4. Outlines of F statoblasts of *Plumatella longigemmis* (Annandale).

The nature of the zoaria virtually excludes fossilization; fossil statoblasts are unknown and because of their small size they would be exceedingly difficult to find, at least in solid rock. However, L. R. Wilson (in Shrock & Twenhofel, 1953: 217) was of the opinion that some chitinous cysts in rocks from Ordovician to Pleistocene age may be bryozoan statoblasts. Subfossil statoblasts of recent species, however, have been found by pollen-analysis of samples collected from Quaternary peat layers in Scandinavia, Lapland, Finland, Denmark, northern Germany, The Netherlands, and Switzerland.

Frey (1964) summarized the information on fossil remains of animals in quarternary lake and bog sediments. He mentioned finds of fossil bryozoan statoblasts in Europe (England, Ireland, Denmark, Finland, northern Germany, southern Bavaria, Austria and Russia) and North America (Indiana, Connecticut). These statoblasts belong to the species *Plumatella*

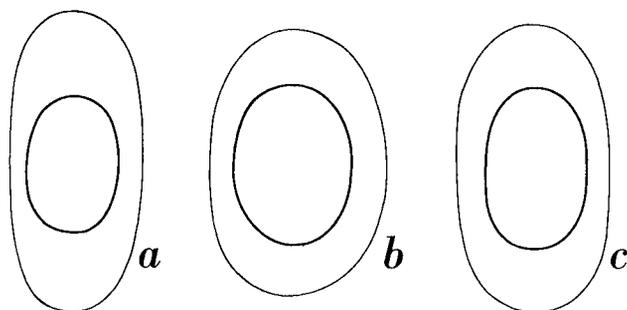


Fig. 5. Outlines of F statoblasts of *Plumatella toanensis* (Hozawa & Toriumi).

repens, *P. fungosa*, *P. fruticosa*, *Pectinatella magnifica* and *Cristatella mucedo*, the latter species being more common than any of the others.

When we first regard the Phylactolaemata we are struck by the fact that

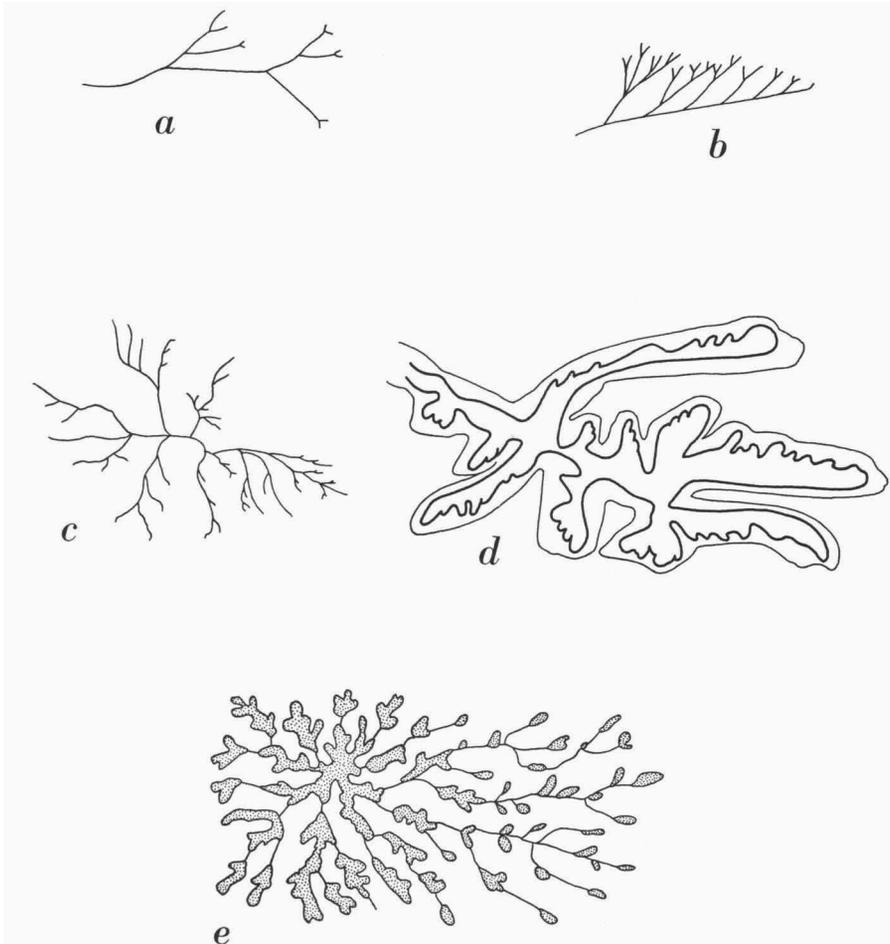


Fig. 6. Zoarial growth in: a, *Fredericella sultana* (Blumenbach) (after Wesenberg-Lund, 1937); b, *Plumatella fruticosa* Allman (after Wesenberg-Lund, 1937); c, *Plumatella repens* (Linnaeus); d, *Hyalinella lendenfeldi* (Ridley) (after Hastings, 1929); e, *Stephanella hina* Oka (after Oka, 1908).

the colonies, the zoaria, ordinarily form an irregular mass. This phenomenon gave rise to a confusing synonymy in the nomenclature because specific value was repeatedly assigned to the external shape. We now know that this is incorrect. Toriumi (1951-1956) demonstrated in a number of highly detailed and precise studies that the variation in the shape of the zoarium is not of specific value. Brien & Mordant (1956) came to the conclusion that

the shape of the zoarium is influenced by such factors as age and derivation: differences are determined according to sexual or asexual origin. Ecological circumstances also exert a strong influence: copious or scanty food supply,

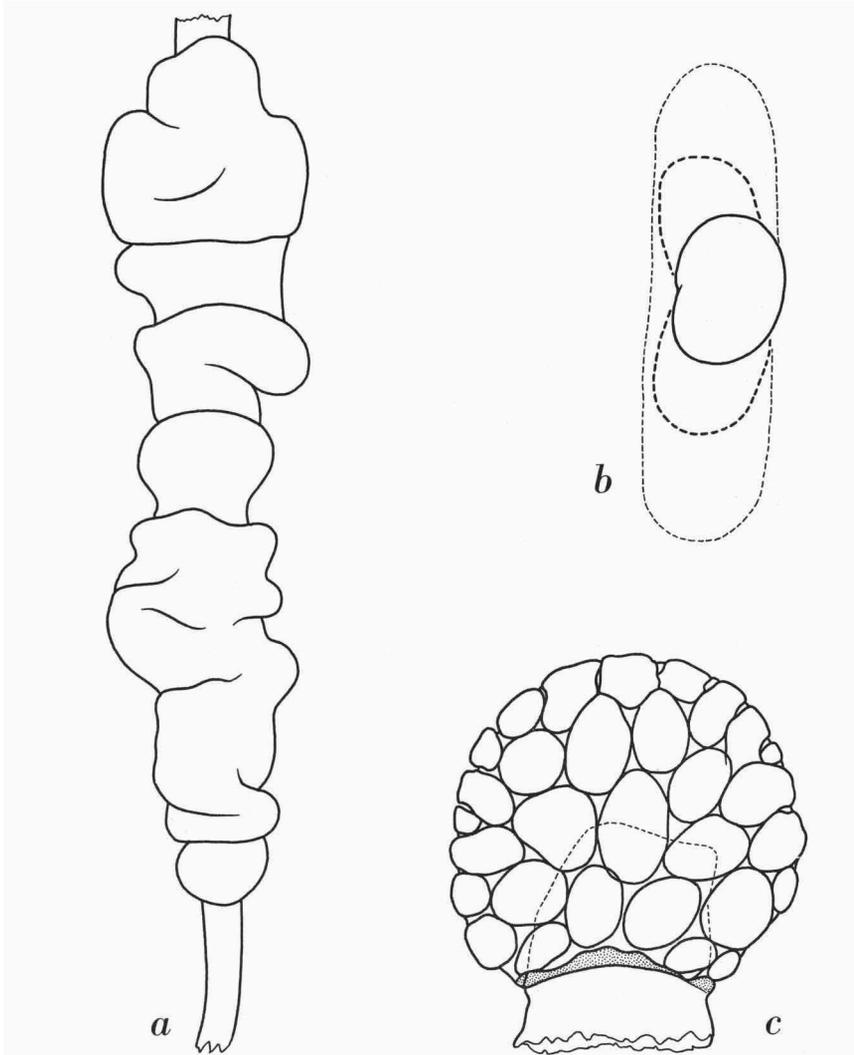


Fig. 7. Shape of the zoarium in: a, *Plumatella fungosa* (Pallas); b, *Cristatella mucedo* Cuvier (after Braem, 1890); c, *Pectinatella magnifica* (Leidy) (after Hyatt, 1866).

temperature, and the chemical composition of the milieu all contribute to the degree of development achieved. The mode of ramification, i.e. the scheme according to which bud formation takes place, differs among many species, however.

The outermost layer of each zoarium consists of chitin and should be called the cuticula. The cuticula is secreted by the outer cellular layer, the ectocyst. Very often, and very incorrectly, the ectocyst is indicated as the outermost layer, especially by English-speaking authors. What is valid for the zoaria in their entirety also holds for the single individual, the zooid. The individual specimen consists of two parts: (1) a body wall, or zoecium and (2) the internal organs, as entity called the polypide. The polypide can be protruded by evagination (fig. 8; pl. 11 fig. a).

For the anatomical details, the reader is referred to Cori (1941) and Brien (1960). This subject is treated more simply by Borg (1930: 109) and by

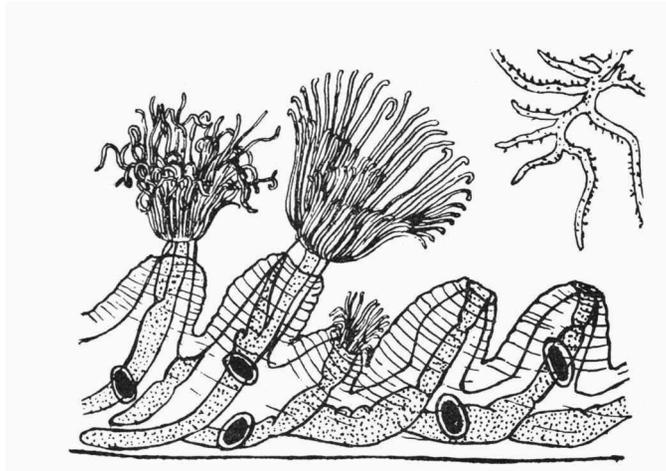


Fig. 8. Zoarium and polypide of *Hyalinella punctata* (Hancock) (after Prenant & Bobin, 1956).

Prenant & Bobin (1956: 125). In addition to the photograph of an evaginated polypide (pl. 11 fig. a), the illustrations include a photograph of the mouth or orifice, shown closed, i.e. retracted, slightly twisted, and pleated (pl. 12 fig. a), and one of an invaginated polypide, contracted and twisted (pl. 11 fig. b).

For biological, physiological, and other data, reference is made to the already-mentioned work of Wiebach (1958a) and the literature references for the various species.

PRESENT STUDY

Because of the lattice structure of the annulus, the statoblasts can be satisfactorily observed with light-field illumination; dark-field observations

are impossible. Photography done with partial dark-field illumination gives a picture with a sunset effect, however (pl. 11 fig. d). In polarized light the statoblasts show the cross of polarization in the following species: *Plumatella fruticosa* (pl. 11 fig. e), *P. emarginata*, *P. fungosa*, *Lophopodella carteri*, *Pectinatella magnifica* and in the sessile statoblast of *Hyalinella punctata*. It may be assumed that this is the case for all species. All species do not show the same picture. It is especially the capsule which is luminous. This phenomenon is an indication of a crystalline structure of the chitinized valves of the capsule. It is impossible to say whether the contents of the capsule also contribute to the effect. In the sessile statoblast of *Hyalinella*

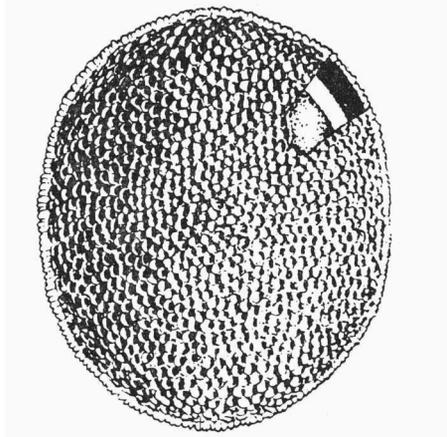


Fig. 9. S statoblast of *Fredericella sultana crenulata* du Bois Reymond-Marcus (after du Bois Reymond-Marcus, 1946).

punctata it is not the capsule that is luminous but the annulus, which is very narrow (pl. 11 fig. f).

Polarized light reveals the structure of the statoblast better. The zones of the annulus outside the capsule, the zone that extends over the capsule and often differs dorsally and ventrally, and the uncovered part of the capsule then show different colours.

Observations with the fluorescence microscope with ultra-violet illumination have demonstrated a pale blue autofluorescence of the statoblast. Remnants of the gelatinous mass in which the statoblasts are embedded during growth showed this phenomenon somewhat more strongly. A light-field photograph of the gelatinous mass is given in pl. 12 fig. d.

Electron-microscopy has provided new information. The evaluation of the electron-microscopical photographs is based on a cross-section through

a statoblast of *Plumatella* spec. (text-fig. 11) and the description by Kaestner (1963: 1087, fig. 938). He gave the following picture of the development of the statoblast: "Die Statoblasten bilden sich vom Frühsommer ab am Funiculus, bei manchen Arten in jedem Zoid in der Einzahl, bei anderen in ganzen Reihen. Für *Plumatella* ist nachgewiesen, daß ihre Bildungszone lediglich den im Jugendstadium des Zoids wandnahen Abschnitt des Funi-

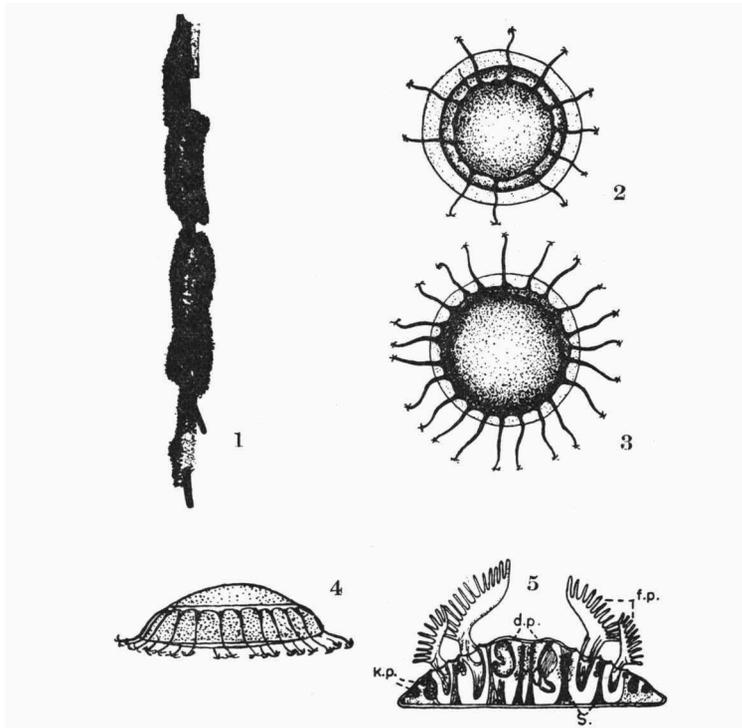


Fig. 10. *Cristatella mucedo* Cuvier. 1, zoarium; 2, dorsal view of F statoblast; 3, ventral view of F statoblast; 4, lateral view of F statoblast; 5, transversal section through zoarium; d.p. = degenerated polypides; f.p. = fertile polypides; k.p. = buds; s. = remnants of septa. (1, after Wesenberg-Lund, 1896; 2-4 after Kraepelin, 1887; 5, after Braem, 1890).

culus einnimmt, der sich nicht an der Spermaerzeugung beteiligt hat und sich erst nach der Geschlechtsperiode während des allgemeinen starken Wachstums des Zoids sehr verlängert. In ihn schiebt sich von der Knospungszone der Cystidwand aus ein Strang von Epidermiszellen ein, die einen Klumpen und schließlich eine einschichtige Hohlkugel bilden. Unter dieser entsteht eine Wucherung von Funiculuszellen, die sich mit dotterartigen Reservestoffen anfüllen. Dann umwächst — immer noch unter der Funiculus-

hülle — der zusammengedrückte Epidermissack diese mesodermalen Zellen. Wir haben nun eine doppelwandige Epidermisblase, die mit Mesodermzellen gefüllt ist — also eine Art solides Cystid vor uns. Ihre äußere Epidermisschicht sondert dann gegen die darunterliegende innere Epidermislage eine dicke, dunkle Chitinkutikula ab. Dabei bildet sich rings um den Äquator eine Furche, so daß die entstehende Chitinkapsel zweiteilig ist. Wenn dann die äußere Epidermis abstirbt, ist der sitzende Statoblast fertig ausgebildet. Zur Bildung des Schwimmringes erheben sich die Epidermiszellen längs des Äquators der Linse zu einem hohen ringförmigen Kiel. Diese langen Zellen sondern bald eine Kutikula an allen Wänden ab, worauf ihr Plasma abstirbt und ihr Lumen sich mit Luft füllt”.

It follows from this that the uppermost layer of the chitinized epidermal

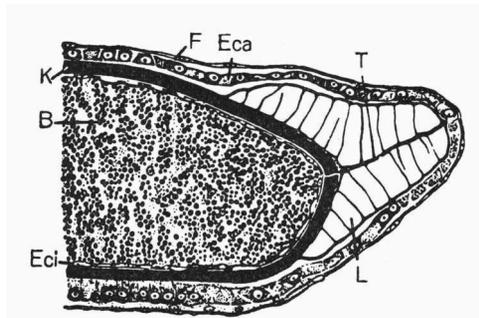


Fig. 11. Section through the right half of a nearly completely developed F statoblast of *Plumatella* spec. B = groups of mesodermal cells, forming a depot of nutrients for the coelomal epithelial cells of the future; Eca = outermost ectoderm, secreting the capsule of the statoblast; Eci = innermost ectoderm, later on developing into the wall of the cystide; F = epithelial covering of the funiculus; K = capsule of the statoblast; L = chambers of the swimming, developed from ectodermal cells that have lost their content; T = line along which the statoblast will split when development starts (after Kaestner, 1963).

cells (T) becomes the basal layer of the chambers in the mature statoblast, and what was originally the basal layer becomes the upper layer, i.e. the roof of the chambers. It is not certain, however, that the chambers contain air, since it is not clear how air could penetrate through the roof.

It must be kept in mind that this electron-microscopical investigation has not yet been concluded, with the result that in some cases the explanations are still provisional, but the chosen species are nevertheless representative for the *Phylactolaemata* series. One complicating factor here is that the material used was preserved, whereas electron-microscopical techniques demand fresh material; however, this can have had little influence on the chitinized structures. All the statoblasts were taken from zoaria; although

they were completely formed, it cannot be said with certainty whether the internal development had been completed in all cases when the material was collected and killed. The material was also collected at different times. For a comparative study of all the species the material should actually be collected at the same time, which is virtually impossible. In addition the exact age of zoaria and statoblasts is never known.

Fredericella sultana has been taken as the starting point in this series, too. In this species the capsule is almost entirely smooth outside and somewhat rough inside (pl. 1 fig. a). This is the only statoblast in the series studied in which the innermost ectoderm was present. This ectoderm is composed of a single layer of cells (pl. 1 fig. b and pl. 3 fig. a); in the latter case it is detached from the capsule, probably as a result of handling. The mesodermal content is compact and contains many dark spots representing lipoid droplets, which were also encountered in a histochemical study of the statoblast. The thickness of the valves of the capsule could not be calculated because the specimen was cut obliquely.

In cross-section the valves of the capsule of the S statoblast of *Hyalinella punctata* show a virtually smooth outer surface; the inner surface is rough. On its outer surface the capsule is covered with a crust showing a foamy structure (pl. 2 fig. a). The narrow space separating the crust from the capsule may be an artefact. The crust contains a number of dark spots (indicated by arrows), that may represent cellular debris; its surface is uneven. In a number of cases the S statoblasts show a network of chitinized ridges, which may give rise to a continuous or discontinuous layer. This crust is also probably formed by the outermost ectoderm. The mesodermal content of the statoblast seems to show a certain degree of arrangement and some cracks are present. These cracks may be the result of the disappearance of cell-walls, since the contents of the statoblast are formed by fusion of a number of cells, during which process the walls disappear and the cytoplasm fuse (Gasser, 1962a, fig. 2, i-v). In pl. 2 fig. b this is just visible. The arrangement referred to above could also be an artifact caused by shrivelling as a result of the technique used. The dark spots are lipoid droplets.

The next species is *Plumatella emarginata*, of which the free statoblast was studied. A new important finding here is the presence of pores in the walls of the chambers of the annules (pl. 3 fig. b). These pores are closed by a membrane and the wall surrounding them shows a marked thickening. There is thus a system of communication between the chambers, and this was actually not to be expected in the "dead", rigid spaces of which the annulus is composed. It is not yet known whether there are also pores communicating with the external environment in the roof of the chambers. To investigate

this the statoblasts would have to be cut in serial sections. In this species the annulus appears to be fused with the capsule (pl. 4 fig. a). The basal layer of the annulus shows two zones, one light and one somewhat darker. The roof is much thicker than the walls and is homogeneous (pl. 5 fig. a). The capsule, roof, and basal layer all show a cloudy appearance due to the secretion of chitin by the epidermal cells.

In the annulus of this statoblast a group of aberrant chambers can be seen (pl. 5 fig. b). These chambers are separated by an exceedingly narrow cleft from the normal, much larger chambers with thinner walls: this situation is reminiscent of the reticulation of the sessile statoblasts. In this aberrant group and in *Cristatella mucedo* as well, the separation between the chitinized walls of the chambers is still visible. On the other photographs the walls have already become completely fused.

In plate 4 figure b the plasma in the chambers can be seen to have become detached from the walls and it appears to have undergone shrinking (see Kaestner, 1963). This may be indicative of the mechanism by which the statoblast at first — with filled chambers and thus heavier — lies deeper in the water and later — having become lighter — floats on the surface. The shrinkage could also result from the technical treatment, but this picture — in any case electron-microscopically — demonstrates the existence of material in the chambers. On the inner surface of the capsule a layer can be seen (pl. 6 fig. a, pl. 4 fig. a) which, judging from the photograph, cannot belong to the innermost ectoderm, even though the presence of cellular components would seem to be confirmed. This layer is conceivably identical to the layer found in the same position in *Lophopus crystallinus*, to be described below. A certain degree of longitudinal striation is present. Lastly, a highly magnified picture of the mesodermal contents of the capsule, showing remnants of cytoplasm, is given in plate 6 figure b.

In *Lophopus crystallinus* the chambers in cross-section form a very regular network of straight lines. Pores are present here too, but without local thickening of the walls; the membrane, however, is thicker than in *Plumatella emarginata*. Remnants of shrunken cytoplasm are seen in the chambers (pl. 7 fig. a). The roof is not uniform and its thickness varies. In cross-section it shows triangular ridges that serve to reinforce the annular system. In this species the surface is probably formed by a network of thick ridges whose openings are closed by membranes. A fortunate section gives a picture through the equatorial plane at a very favourable angle: the chambers of the dorsal and ventral halves of the annulus touching at their flattened bases (pl. 10 fig. c). Here we see a lumen without any contents. The mesodermal contents of the capsule show indications of a rosette arrangement

of the lipid droplets around a larger centre; here they are smaller and more numerous than in the S statoblasts of *Hyalinella punctata* (pl. 8 fig. a). This rosette also indicates the former arrangement of the composing cells and represents the stage after the disappearance of the cell-walls in which the cytoplasts are not yet completely fused (see pl. 2 fig. b). The capsule and the contiguous annulus show almost the same picture as in *Plumatella emarginata* but are somewhat thinner. The inner surface of the capsule shows a quite different layer, however, which is probably an extra layer of the capsule (pl. 7 fig. b). Judged from the picture, it cannot be the innermost ectoderm. This picture can be compared to the longitudinal grain of fine-grained wood, showing the same kind of finely-waved longitudinal pattern (pl. 8 fig. b). This "grained" layer is strongly fused with the capsule and is in turn covered on its inner surface by a membrane with an exceedingly irregular profile. This membrane is composed of a darker substance containing a large quantity of irregular, forked and branched rods of a lighter substance. In some places a dissolution of these rods has caused this rod-like membrane to merge into the wavy pattern of the "grained" layer. The irregular pattern of the membrane can still be seen to some extent at these places (pl. 9 fig. a). It is not known which cells form the layers just described, but it is unmistakable that the "grained" layer originates from the rod-like layer. In the sections of this species the innermost ectodermal layer has not been observed. This statoblast was collected in November, i.e., during winter.

In cross-sections of the statoblast of *Cristatella mucedo* (pl. 10 fig. a) the chambers vary widely in size, the smallest being about one-fifth the size of the largest. The roof is wavy and, as far as can be observed, shows the same thickness throughout. Basal triangles are present on the lower and upper layers. Two ravels are partially visible (see description of the species). Pores are present in the walls. Here, too, the wall around the pores shows no thickening. In the corners of the chambers the plasma has begun to show detachment from the walls and shrinkage. The annulus and the capsule are not fused. The basal layer of the annulus again shows two zones. The inner surface of the capsule is unusually rough (pl. 9 fig. b) and resembles the highly irregular profile of the rod-like layer in *Lophopus crystallinus*. In this photograph the valve of the capsule seems to have a foamy structure. A separation is visible between the walls of the chambers. The long cells (Kaestner, 1963) excrete a surrounding layer of chitin which fuses completely with that of the adjoining cells. In the stage shown here this process is just visible. The mesodermal contents have been ruptured by cutting. The innermost ectoderm is also lacking.

To summarize the results of the electron-microscopical investigation: to the best of our knowledge, this publication contains the first published electron-microscopical photographs of the statoblasts of *Fredericella sultana*, *Plumatella emarginata*, *Hyalinella punctata*, *Lophopus crystallinus*, and *Cristatella mucedo*. These pictures concern the capsule and its valves, the annulus, the cytoplasm in the chambers, the innermost ectoderm, and the mesodermal contents.

The layer originating from the network of ridges in a sessile statoblast is of a foamy nature (*Hyalinella punctata*).

The walls of the chambers of the annulus possess pores; these pores probably form a communication system, representing a mechanism which may be related to the phenomenon of shrinkage of the cytoplasmic content of the chambers, which was demonstrated electron-microscopically; this may determine the initial submersion and later floating of the statoblasts.

In *Plumatella emarginata* and *Lophopus crystallinus* layers were discovered on the inner surface of the capsule whose nature could not be determined.

The statoblasts of the species studied have a closed outermost covering layer, except for *Lophopus crystallinus* in which this layer consists of a chitinized network of ridges with membranes.

The chambers of the annulus are more or less of the same size in *Plumatella emarginata* and in *Lophopus crystallinus*, but differ in size in *Cristatella mucedo*.

Between the dorsal and ventral halves of the annulus there is a lumen containing no material (*Lophopus crystallinus*).

The mesodermal contents include lipid droplets and remnants of cytoplasm.

The following measurements (in microns) were calculated from the photographs: *Fredericella sultana* S statoblast, thickness of valve unknown; *Hyalinella punctata* S statoblast, thickness of valve 3, thickness of crust 17; *Plumatella emarginata* F statoblast, thickness of valve 7, covering layer 5, basal layer of chambers 1, wall of chamber 0.14-0.18, roof 1.8, diameter of pores 1.4; *Lophopus crystallinus*, F statoblast, thickness of valve 2, "grained" layer (mean) 10, rod-like layer (mean) 3, wall of chamber 0.3, length of spines 5-10; *Cristatella mucedo* F statoblast, thickness of valve 2, basal layer of chambers 0.6, roof 1.2-1.4, wall of chamber 0.35, diameter of ravel 0.35.

A number of free statoblasts showed red fluorescence in ultra-violet light. This is an indication of the presence of air in the chambers of the annulus. After preparation it is impossible to say with certainty whether this air was included during the development of the chambers or entered them later, since

in spite of all the published opinions no analysis of the contents of the "air"-chambers has ever been made after the disappearance of their plasmatic content.

The histochemical investigation of the mesodermal contents and the innermost ectodermal cellular layer of statoblasts of *Pectinatella magnifica* included 20 histochemical tests and staining of microscopical sections. The reactions obtained give the following information. There is an abundant mass of building material for the formation of new adult individuals. Dispersed in the mass of organic substances were small nuclei with a fine chromatine network. Enzyme activities were low in the resting organisms; the only indication of activity of any proportions was found for lactic acid dehydrogenase, which was located directly under the chitinized capsule (in the inner ectodermal layer); this may indicate an anaerobic metabolism or an adaptation of the metabolism to conditions of low oxygen tension. In conclusion: for the development of the new generation there are available proteins, carbohydrates, (lipoids albeit not in great quantities, although the electron-microscopical investigation suggests the presence of many fat droplets), and ribonucleic acids. The metabolic activity seems to be low (Lacourt & Willighagen, 1963).

The measurements given for the statoblasts apply throughout this paper to their total size, including the annulus, and are indicated as L = total length; B = total width; l = length of capsule, b = width of capsule. The width of the annulus is understood as only that part extending beyond the capsule, here called the "optical" part; in the various species the annulus extends over the capsule to a different degree and is often characteristic, but it is the part extending beyond the capsule that determines the shape of the statoblast.

Spinoblasts. Free statoblasts equipped with spines combine two functions. They can float, but they, like sessile statoblasts, can also become attached to objects and remain anchored. Rogick (1943b) calls these "spinoblasts". Just as with her terms "floatoblast" and "sessoblast", this usage eliminates the characteristic meaning of the word "statoblast", which is the reason why I have not adopted this term.

Statoblasts represent the asexual form of reproduction by means of budding, in the sense that they are formed internally and that very early in their development the buds are surrounded by a capsule. As a rule growth of the statoblasts continues only after a dormant period.

The zoarium

The development of the zoarium takes forms ranging from a simple colony consisting of a few thin, slightly branched tubes with few widely spaced

individuals (*Fredericella sultana*) (text-fig. 6a) to a large, communal body cavity with numerous closely packed individuals (*Cristatella mucedo*) (text-fig. 10 no. 1).

The primary form of the bryozoan colony may be preserved in *Mono-bryozoon ambulans* Remane, a marine species consisting of a single functional zooid with one bud. Possibly a reduced form, it corresponds to the first zooid (the ancestrula) with a bud, the inceptive form of all zoaria. In its further development the primary zooid takes two opposite directions. This primary development is observed in *Stephanella* and *Cristatella*, to which we will return later. In the genus *Plumatella*, this phase is followed by a radial, dichotomous growth of the tubes, rapidly succeeded by a combined dichotomous and antler-like type of branching with long offshoots (text-fig. 6 b, e). In the genus *Hyalinella* the branching takes the same form but the offshoots are on the average shorter (text-figs. 6 d, 8).

The zoarium in the genus *Pectinatella* is characterized by its complete regularity: the zoarium grows from the primary zooid by repeated dichotomous branching in combination with a linear growth and antler-like branching. The zoarium remains entirely adherent; as a result, the dichotomous branching is limited by lack of space and budding is unilaterally reduced. In this genus the principle of the radial structure of the zoarium as in the genus *Plumatella* and the shortening of the tubes and the concentration of the individuals seen in the genus *Hyalinella* are combined and completely expressed. The zoarium is divided into lobes, but the *Plumatella-Hyalinella* type of branched tubes is retained (pl. 13 fig. a).

The zoarium of *Fredericella sultana* consists of a few loose tubes with little branching and few zooids (text-fig. 6 a). In the species of *Plumatella* the number of tubes is larger and they are strongly branched. There are more and more closely packed zooids (text-fig. 6 b, c). In the species of *Hyalinella* the zooids are set in closely packed rows (text-figs. 6 d, 8); the tubes show less branching. They are shortened and sometimes already fused.

In the next stage the tubes merge to form a sac-shaped lobular communal body cavity (*Lophopus* and *Lophopodella*) (pl. 13 fig. b). The lobulation is a rudimentary form of the branching that determines the formation of the zoarium in many of the Phylactolaemata. Lastly, the lobes disappear and the zoarium then consists of a long, wide tube with the zooids arranged in rows on two sides along the longitudinal axis (*Cristatella mucedo*) (text-figs. 7 b, 10 no. 2). This pattern, however, did not evolve directly. The development of the statoblasts reveals that the Phylactolaemata do not constitute a linear series, even though the zoarial forms known at present show

a remarkable consistency. But whereas *Hyalinella* and *Lophopus* form a continuous series, this is certainly not the case for *Cristatella*.

Cristatella mucedo is preceded by *Stephanella hina*, probably split off early in the *Plumatella* series. The statoblasts, like the zoaria, have a different shape. Although their branching is originally radial, the subsequent budding occurs only in two opposite directions, thus leading to a spindle-shaped zoarium. This zoarium consists of branched tubes formed by repeated dichotomous division. These tubes are not of uniform width, showing local enlargement where the zooids originate in groups (text-fig. 6e). It is probably at these sites that concentration of the zooids and reduction of the walls leads to the development of a communal body cavity (*Cristatella mucedo*). Although no intermediate form has yet been observed, its existence may be assumed.

Exactly the same zoarial origin as that of *Stephanella hina* is also described for *Cristatella mucedo*. Here too, as in *Plumatella*, the branching commences radially, after which the zoarium grows in two opposite directions (text-figs. 7b, 10 no. 1), giving rise to an elongated colony. This kind of growth reflects the primary development because the primary zooid (ancestrula) of *Plumatella* also grows first in two opposite directions. The most highly developed species appears to have retained the most primitive character. The statoblasts and the way in which the zoaria originate confirm the relationship between *Stephanella hina* and *Cristatella mucedo*. The external shape of the zoarium of *Cristatella mucedo* is highly specialized, like that of *Pectinatella* but in a different way.

Thus, certain main types can be distinguished among the zoaria: 1, the branched tubes of the *Fredericella-Plumatella-Hyalinella-Pectinatella* series (radial pattern); 2, the lobulate, sac-shaped zoaria of the *Lophopus-Lophopodella* series (more or less radial pattern); 3, the oppositionally developed, elongated zoaria of *Stephanella* and *Cristatella* (derived from a radial structure).

The evolutionary development may be summarized as follows: as starting-point, a few tubes with little branching; next, colonies of numerous, strongly branched tubes followed by a phase with tubes which become shorter and wider with reduction in the degree of branching; the continued shortening of the tubes and reduction of the walls gives rise to lobulated, sac-shaped zoaria; lastly, an elongated colony results. The lobulate and the elongated forms may divide into separate colonies; this takes place purely mechanically: the zoaria are torn apart by their own weight. It is therefore not correct to say that these zoaria possess the capacity to divide; the division is not achieved autonomously.

The number of zooids increases hugely as evolution proceeds. As compared to *Fredericella sultana*, in which the mutual separation is sometimes large (up to 30 mm) and one zooid per running 30 mm may be taken as the smallest number (although on the average there are usually more), for *Cristatella mucedo* this number is about 24. Expressed in terms of surface area, taking the tubes of *Fredericella sultana*, with a diameter of 0.4 mm, as contiguous, on a surface measuring 8 by 30 mm there would be about 20 individuals in *Fredericella sultana* as against about 120 full-grown individuals in *Cristatella mucedo*. Concentration has thus occurred with respect to the development of the zoaria and the localization of the individuals.

The polypides are small in *Fredericella sultana*, being about 1.5 mm long with about 19 to 24 tentacles; during evolutionary development they gradually become larger, reaching about 4.5 mm, and the number of tentacles gradually increases to about 100 in *Pectinatella* and is reduced to about 90 in *Cristatella mucedo*. The increase appears to be an important systematic character. Furthermore, the statoblasts become gradually larger and this enlargement keeps pace with the rise in the number of tentacles.

The cuticula is thin and rigid in *Fredericella* and *Plumatella*; in *Hyalinella* and more highly developed genera it gradually becomes thicker and softer; here it surrounds the tubes, but in *Pectinatella* and *Cristatella* it forms a soft underlayer.

The species with a simple, small statoblast like *Fredericella sultana* evolves into a number of species with increasingly larger statoblasts, ending in complicated types which do not, however, form a continuous series. As in many other groups, evolution did not follow a direct line, but here, too, the various forms show a remarkably consistent progression. The present type of the statoblast in all probability evolved from a soft, primeval statoblast, starting with a slight swelling on the funiculus (pl. 13 fig. e). The first in the series is an oval or almost round capsule consisting of two extremely small domed valves with their rims in apposition and containing a yolk-like mass. This form is called the sessile statoblast. The valves are soft and smooth in *Fredericella sultana sultana* (number of tentacles 19 to 24) (pl. 12 fig. f). In the next species, *Fredericella australiensis* (number of tentacles 24 to 30), the statoblasts are larger and stronger (pl. 12 fig. h).

The next higher genus, *Plumatella*, shows a great evolutionary advance. There are two kinds of statoblasts: the sessile, which will be indicated throughout this paper by the letter "S", and the free or floating statoblast, to be indicated by the letter "F".

The S statoblast of *Fredericella australiensis* (the genus *Fredericella* has only S statoblasts) is continued in the genus *Plumatella* as a sessile statoblast

surrounded in the median plane by a ring (annulus) (pl. 13 fig. h, i). This annulus is proportionately small in most of the species and is limited by an outer margin. Very often this annulus is called rudimentary in literature but it is better to speak of primary annulus, for from this, the more evolved swimming of the free statoblast has originated. The surface of the capsule in species of *Plumatella* is covered by a network of chitinous ridges; these ridges may become enlarged to form a nearly or entirely continuous layer. It is not correct to speak of a "perforated" layer: only when a layer was originally entirely continuous can it become perforated but this is not the sequence here. In the species of the genus *Plumatella* this layer is developed to a variable degree on the annulus of the S statoblasts (pl. 14 fig. e), but it does not become a continuous layer and, except as an exceptional monstrosity (pl. 12 fig. i), no chambers develop from it. Occasionally, isolated S statoblasts are found that completely lack the annulus, a reminiscence of the genus *Fredericella*. In the more highly evolved genera the F and S statoblasts are larger. In the species of *Hyalinella* fewer S statoblasts are found, and in *H. lendenfeldi* they have completely disappeared. The subsequent genera *Lophopus*, *Lophopodella*, *Pectinatella*, and *Cristatella* have no S statoblasts.

In the free statoblasts the annulus is markedly wider and possesses chambers on its upper (dorsal) and lower (ventral) sides. In this case the annulus is called swim-ring. It is clear that the F statoblasts must have evolved from the S statoblasts. This is also manifested by four finds of S statoblasts which actually do show a few chambers: one of *Hyalinella vaihirieae* found by Rogick & Brown (1942, pl. 1 fig. 6-8) and an S statoblast of *Hyalinella vorstmani* that I discovered in my material (pl. 12 fig. i), in which a number of chambers are present in the polar part of the annulus and a partial "swim-ring" has developed. This is not, as Rogick & Brown suggest, an intermediate form, but evidently represents a monstrosity showing the origin of the chambers. These statoblasts occur very rarely, as can be seen from the fact that up to now only four cases are known. Toriumi (1956b) found the other two in *Hyalinella toanensis* and *Plumatella fruticosa*. Microscopical examination led him to the same conclusion.

The capsule itself has not undergone marked changes; its size varies in different species, but its outline remains almost round or oval. It is mainly the annulus that has developed a variety of shapes, resulting in species-specific free statoblasts.

There is a distinct separation between the linear series formed by a number of species and certain other species that have clearly split off from it. In this sense, the ancestry of the Phylactolaemata is reflected in their

zoarium: a combination of repeated dichotomous and antler-like branching. However, within a single species single and double evolutionary developments are also demonstrable in the statoblasts. Either the F and S statoblasts are both oblong and have unquestionably evolved from a single basic pattern (e.g., in *Plumatella fruticosa*) or they differ: an oval F statoblast and an almost round S statoblast (e.g., in *Plumatella philippinensis*).

In the genera *Plumatella* and *Hyalinella* the F statoblasts are short to long oval in various ratios. In addition to a duality in their basic form, they also show a very wide variability, making it extremely difficult to distinguish a sequence. Within a single species and even within a single zoarium (proving that only one species can be involved), both elongated and wide statoblasts can be found. As a result, even though it is evident that a relationship exists, attempts to explain it sometimes seem rather laboured. In some cases reduction has taken place, in others giant forms have developed. Furthermore, there are also malformations, representing reminiscent forms and (or) intermediate stages.

In the genus *Fredericella* a tendency to split is already present, as indicated by the presence of long oval and almost round statoblasts. The almost round type is continued in the S statoblast of *Plumatella*. The long oval type has become the F statoblast of this genus. *Plumatella casmiana* (number of tentacles 23 to 41) next shows a marked degree of development. This is a highly complicated species, evidently representing a number of forms ("Formenkreis"), from which several species must have evolved. Here, a characteristic, wider statoblast of the *Plumatella*-type appears. The long oval S statoblast of *Fredericella* evolves into the long oval F statoblast and the membranaceous statoblast of *Plumatella casmiana*. This basic shape is also to be found in the F statoblast of *Plumatella philippinensis* (number of tentacles 44 to 48) and in the initial stage of the F statoblast of *Plumatella agilis* and *Plumatella fruticosa*.

Thus, there is also an elongated oval F statoblast. In addition, there is an elongated oval statoblast with a soft membrane, in which the annulus shows very little development, does not extend beyond the capsule, and consists of a small ring of chambers lying on the capsule. Is this a primitive or a rudimentary annulus? Is this soft, non-chitinized statoblast itself primitive or rudimentary? Is the soft capsule a reminiscent form of the assumed primeval statoblast, preceding even *Fredericella* but with an initial stage of annulus formation? The latter is very probably the case. *Plumatella casmiana* has the smallest number of tentacles and is the root of a division of the Phylactolae-mata. Furthermore, between all these statoblasts there sometimes occurs a somewhat shorter, somewhat triangular statoblast indicating the *Plumatella*

repens-*P. fungosa* line. Lastly, there is a single specimen with elongated poles in which the later *Hyalinella vaihiria* can be recognized.

The F statoblast of *Plumatella philippinensis* has a narrow annulus of more or less constant width and showing some elongation at the poles. The S statoblast is identical to that of *Fredericella australiensis*. *Plumatella agilis* (number of tentacles 40 to 50) has an annulus that seems to the eye slightly wider than that of *Plumatella philippinensis* but extends far over the capsule, unlike the latter in which the overlapping is slight.

Plumatella carvalhoi (number of tentacles 40 to 50) fits into this series with respect to the number of tentacles, but differs in the wide annulus of both kinds of statoblasts, like the next species, which shows longitudinal elongation. The F statoblast of *Plumatella fruticosa* (number of tentacles 30 to 50) is almost identical to that of *Plumatella philippinensis* in the initial stage (pl. 13 fig. d, pl. 14 figs b, d), but develops a highly elongated, spindle-shaped outline as a result of a strong polar elongation of the annulus. *Plumatella fruticosa* also has a relatively gigantic S statoblast with a large capsule and a wide annulus carrying a very prominent reticulation (pl. 14 fig. c). The zoarium also has an unusual shape; it is dichotomously branched and only the terminal parts show antler-like branching, but these branches are deciduous (pl. 6 fig. b). A not entirely typical F statoblast also found for this species is shorter; the annulus is narrower at the poles. This form shows a high degree of correspondence with a statoblast of *Plumatella casmiana*.

There is a remarkable, gradual increase in the number of tentacles. In *Fredericella sultana* it is 19 to 24, in *Fredericella australiensis* 24 to 30; *Plumatella casmiana* has the smallest number in the genus *Plumatella*: 23 to 41, *P. philippinensis* has 44 to 48, *P. agilis* 40 to 50, *P. carvalhoi* 40 to 50, *P. fruticosa* 30 to 50. In this respect the last four species are similar, but their statoblasts nevertheless show a progressive evolution. All these species together form what can be called the "elongated-oval series", i.e., species of *Plumatella* with an elongated oval statoblast with elongated oval capsule.

Besides this series with elongate statoblasts there is a series having medium oval statoblasts with a medium oval capsule. The smallest of these is *Plumatella javanica* (number of tentacles 20 to 45), followed by *Plumatella longigenimnis* (number of tentacles 20 to 40), *Plumatella emarginata* (number of tentacles 30 to 54), *Plumatella evelinae* (number of tentacles 44 to 64), *Plumatella toanensis* (number of tentacles 47 to 78), listed according to the number of tentacles and the size of the F statoblasts. As far as is known, this series ends with the giant species *Plumatella toanensis*.

The genus *Hyalinella* does not show such sharply defined characters. It is characterized by an usually thick, soft cuticula and a rounded oval F statoblast which continues the foregoing series. This genus comprises the species *H. vorstmani* (number of tentacles 18 to 32), *H. punctata* (number of tentacles 40 to 60), *H. indica* (number of tentacles 40 to 50), and the giant species *H. lendenfeldi* (number of tentacles 50), which shows a reduction in the number of tentacles with respect to *H. punctata*. The small number of tentacles (18 to 32), which is even lower than that of *Plumatella casmiana* (23 to 42), and the small F statoblast of *Hyalinella vorstmani* imply that this genus must have split off early in the evolution of the ordo and in all probability originated directly from *Fredericella*.

Plumatella casmiana is also probably the source of a series consisting of only two species (or only one perhaps): *Plumatella repens* (number of tentacles 40 to 60) and *Plumatella fungosa* (number of tentacles 40 to 60), with a short oval statoblast which is somewhat flattened on one side and therefore has a somewhat triangular outline. A precursor of this statoblast is sometimes already encountered in *Plumatella casmiana*. *Plumatella fungosa* has an S statoblast, sometimes of a gigantic size, measuring up to 690 μ length. Are these two species, as some investigators assume, perhaps two forms of one species? The similarity to *Hyalinella punctata* and its varieties *densa* and *prostrata* is striking. *Plumatella repens* has, on the average, somewhat smaller statoblasts; the number of tentacles is the same. The zoarium of *P. repens* consistently shows a looser structure than the massive clumps of *P. fungosa* (cf. text-figs. 6 c, 7 a), and is not entirely analogous to the open and more compact zoarium of the varieties of *H. punctata*. The sessile statoblasts differ considerably; in *P. repens* they are never as large and sometimes possess a wide annulus. In *P. fungosa* the S statoblast is sometimes of gigantic size, in which case it has no annulus; the zoaria of both species sometimes show S statoblasts of similar shape: medium sized with a narrow annulus. These two species are undoubtedly closely related, but I am nevertheless inclined to distinguish between them because among other things the tuberiform zoaria of *P. fungosa* are not found outside the holarctic region, whereas *P. repens* is a cosmopolitan species.

The zoarium in the genus *Pectinatella* has preserved the characters of the genera *Plumatella* and *Hyalinella* so strongly that it must be considered a continuation in a transcendent form. There is no communal body cavity such as is found in *Lophopus* and *Lophopodella*, in which, furthermore, the statoblasts carry only polar spines whereas the *Pectinatella* species have spines along the outer margin of their statoblasts, so that *Pectinatella* cannot be fitted into this series. The almost round gigantic shape of the

statoblast of *Hyalinella lendenfeldi* then becomes the only possible point of departure. The measurements (in microns) form a continuous series:

	length	width	size of capsule	number of tentacles
<i>Hyalinella lendenfeldi</i>	850-1000	700-800	500-600	50
<i>Pectinatella magnifica</i> (diameter)		900-1500	600-1000	60-84
<i>Pectinatella gelatinosa</i> (diameter)		1340-1750	560-630	72-106

Hyalinella vaihiriae deviates from the other species because of the elongation of the annulus at the poles. By reason of this shape, the species may be the link between *Hyalinella* and *Lophopus*; properly speaking, the only justifiable place in the system. The low number of tentacles (48) is an indication that this species belongs at the bottom of an evolutionary branch, between *Hyalinella vorstmani* and *H. punctata*. In all the species of *Lophopus* and *Lophopodella*, the immature statoblast has the same shape as that of *Hyalinella vaihiriae* (pl. 17 fig. c, g). A certain degree of polar elongation can sometimes be observed in the F statoblasts of *Plumatella casmiana* (pl. 15 fig. a), as a result of which this species seems even more likely as the starting point for the evolutionary development.

If we follow the line starting with *Hyalinella vaihiriae*, then *Lophopus crystallinus* (number of tentacles 60), in which the poles of the statoblast are pointed, must be the next stage. In the following evolutionary stage these pointed poles have become truncated and show a concave base carrying a long spine with small hooks along its edge, as found in *Lophopodella capensis* (number of tentacles 60 to 70). *Lophopodella thomasi* (number of tentacles unknown) has 3 to 6 spines on a concave base; *Lophopodella stuhlmanni* (number of tentacles 80) has 7 or 8 spines on a slightly concave, almost flat base; in *Lophopodella carteri* (number of tentacles 50 to 95) the poles are again convex and are set with 7 to 14 spines; and lastly, in *Lophopodella pectinatelliformis* (number of tentacles 50 to 70) there is a large number (36) of small hooks along the polar part of the outer margin, in analogy with *Pectinatella gelatinosa*. The lower number of tentacles and the smaller size of this last species implies a regression with respect to the other species listed, but as yet only one specimen has been found so very few data are available. The polar origin of the spines indicates the same sequence. *Lophopodella capensis* has a single spine; the base of the single spine be-

comes broader and instead of one spine there are 3 to 6 smaller spines of almost the same length; the base continues to widen and develops a transverse truncation on which 7 or 8 larger spines develop, the species *Lophopodella stuhlmanni*. The base continues to grow in size, becomes convex, and carries 7 to 14 differentiated spines of varying size: *Lophopodella carteri*. Lastly, there is a form with about 36 very small spines or hooklets: *Lophopodella pectinatelliformis*, which is analogous to *Pectinatella magnifica* and *Pectinatella gelatinosa*.

Stephanella and *Cristatella* finally form a series with perfectly round statoblasts, in which *Cristatella* must have originated from *Stephanella*, as suggested by the correspondence in structure and development of the zoaria. The evolutionary line of the Phylactolaemata does not show, at least as far as we know, any distinct origin for this series. It might conceivably be located prior to the *Plumatella* series, since *Stephanella* also already has S statoblasts. These are no longer present in *Cristatella mucedo* nor in the other, more highly developed genera. The number of tentacles (36 to 40) comes after that of *Plumatella vorstmani* (18 to 32) and the average (38) being slightly higher than that of *Plumatella casmiana* (23 to 41, average: 32). It is also possible that the series originated from this latter ancestral species. *P. casmiana* still has very thin tubes; this fact makes it conceivable that *P. casmiana* gave rise to the unusual zoarium of *Stephanella hina*. But an origin from the hypothetical species with the „primeval statoblasts”, from which diverging evolutionary lines could originate directly, is also possible. Between this primeval species and *S. hina* a species may exist that has, for example, a small, completely round statoblast with no annulus and a soft capsule. The small size of the F statoblasts of *S. hina* and the limited number of tentacles (36 to 40) are primitive characters, but the statoblast is nevertheless well developed.

The statoblast of *Cristatella mucedo* deviates completely from the *Plumatella* and *Hyalinella* type. The annulus has a radially orientated, fibrous structure; the spines are placed not on the outer margin but on the two valves of the capsule, on a ridge further in from the outer margin that also gives rise, in the S statoblasts of the species of *Plumatella*, to the excrescences by which these statoblasts often are attached to the substrate. Here we recognize once again the agreement with and the origin of the F statoblast from the S statoblast. The fibrous structure of the annulus might almost be called an “embryonic” feature, this structure must certainly be an original characteristic. The same holds for the zoarium. In its initial stage the annulus of the F statoblasts of the species of *Plumatella* shows a similar structure, remarkably enough. This can be clearly seen in pl. 14

fig. d, showing an immature F statoblast of *Plumatella fruticosa*. A more advanced stage of the F statoblast of *Plumatella philippinensis* is figured on pl. 13 fig. d.

Although no intermediary species between *Stephanella hina* and *Cristatella mucedo* (number of tentacles 70 to 90) has yet been observed, the relationship is evident, if only because the statoblast of *C. mucedo* is appreciably larger than that of *S. hina*. For all the series of the Phylactolaemata end in a giant species. Toriumi (1956b), in concluding his studies on the taxonomy of the fresh water Bryozoa, gives an ancestry with which I cannot completely agree. He composed several comparative series, on the basis of various criteria, each of them bringing him to different conclusions and a different sequence of the species. This result is not satisfying. It remains a question whether the degree of chitin formation, the nature of the cuticula, the degree of incrustation, and similar secondary characters are conclusive for the construction of a phylogenetic series. The average number of tentacles, the basic pattern of the zoaria, and the basic pattern of the statoblasts in my opinion offer more solid grounds than accidental features whose variability Toriumi himself has demonstrated. More particularly, the species *Victorella pavidata* and *Paludicella articulata*, belonging to a different ordo, should be left out of consideration. Like other investigators, I am of the opinion that the origin of the Phylactolaemata should not be looked for in these species. The Ctenostomata, which are not calcified, are also a group with primitive characters and may represent a marine parallel of the Phylactolaemata with analogous features (winter buds, hibernacula), perhaps with a common ancestor, but the Phylactolaemata must be of earlier origin.

The classification proposed by Abricossoff (1959a) is also oversimplified, and his sequence is, furthermore, not correct.

There can be no doubt that the family Plumatellidae comprises no genera other than *Plumatella* and *Hyalinella*; the (sub)genera *Afrindella*, *Australella*, *Gelatinella*, and *Stolella* must be rejected. I have demonstrated that there is a gradual transition in the characters among of these groups. In some species the septa in the tubes of the zoaria disappear, but in material of the same species found at other localities they are present. The branching of the tubes, whether it occurs to a lesser or greater degree, retains the basic antler-like form. The presence or absence of erect terminal portions of the tubes, which occurs randomly within the family of the Plumatellidae, is variable. Just because erect branches have not yet been found in the meagre material of a given species, this character nevertheless cannot be considered of specific value. We may draw tentative conclusions and pose theories — also when there is only scanty material — but we must always weigh our judge-

ments in relation to the characteristics of the entire group. The marine species *Electra pilosa* (L.), for instance almost exclusively forms zoaria which adhere entirely to the substrate, and although we sometimes find numerous offshoots we do not conclude that they represent a separate species. The cuticula has been demonstrated to be highly variable and, furthermore, the original, natural condition cannot be established with certainty in fixed material. Within a single species the cuticula has been observed both as stiff and thin and as soft and swollen. The degree of incrustation and the colour of the cuticula are not constant, and keel formation is certainly not more so. It is self-evident that the orifice of the polypides is a soft, transparent zone which contrasts with the rigid, darker cuticula, otherwise the orifice could not function; evagination of the polypide would be quite impossible if the orifice was not composed of a flexible membrane. Creases and thickening can occur in the membrane as a result of in- and evagination; and they are also dependent on the age of the polypide and the extent of evagination at the moment of fixation of the material. The orifice can also form a wide variety of angles with respect to the longitudinal axis of the tubes, at least to the extent that the twisting tubes may be said to have a longitudinal axis. And last but not least, the polypides can be found in all stages of contraction. But none of these extremely variable and uncertain characteristics can serve as the basis for establishing species or genera. Only the statoblasts have proved to be specific, although they too vary and their identification demands a great deal of experience on the part of the investigator.

In Table II the existence of series of species is expressed in the series of dimensions of the statoblasts and the series of numbers of the tentacles. These series show a natural sequence as expressed by the reasonably constant characteristics. It is therefore pointless to attempt to set up still other series based on the extremely dubious characters mentioned above. Annandale, who distinguished the genera *Afrindella*, *Australella*, and *Stolella* only to discard them for the most part later on, found an enormous field for investigation in India, where he did pioneer work. He wrote on many subjects, but his publications on the Phylactolaemata do not reflect detailed analysis and those on *Stolella* are exceptionally vague even though he discussed the subject four times. I cannot agree with Wiebach (1964) that the genus *Stolella* should be recognized on these grounds.

There is one character to which little attention has so far been given, namely the growth pattern, in other words the sequence in which buds are formed in the zoaria of the various species. Wesenberg-Lund (1937) studied this point in the species *Fredericella sultana*, *Plumatella fruticosa*, and *Pluma-*

tella fungosa, and found formulae to express their bud-formation. It is true that the arrangement of the polypides is not unimportant, but too little is known about this subject. In my opinion, however, fundamental differences are not to be expected either; the differences are more likely to be variations on the theme I have indicated in the introduction to this monograph: the development of the zoaria from the simple type of *Fredericella sultana* to the complex type of *Cristatella mucedo*. There is no reason to deny a natural sequence or to split off genera only to have to attempt later to re-insert them into the whole by means of suborders and superfamilies.

Distribution. — Table I gives a review of the distribution in the zoogeographic provinces according to the present state of our knowledge. This distribution does not entirely agree with the assumed phylogenetic development of the group. For example, the series *Hyalinella vaihirieae* — *Lophopus crystallinus* — *Lophopodella* does not occur within one province. This does not contradict the proposed phylogenetic development, any more than the opposite would be evidence for it. The distribution over the globe could have occurred in the same manner as the growth of a zoarium: on the periphery new colonies originate that may extend in all directions, while the original colony is completely lost. In the same sense the Phylactolaemata could, in the course of the aeon, more than once have migrated through the continents in their changing forms.

The distribution is strikingly homogeneous, and has its main concentration, in the southern hemisphere, or at least around and south of the equator. The list comprises 29 species, only 13 of which occur in the northern hemisphere. In both the Indian subprovince and the Ethiopian region the number is 17, the highest of all regions. This is followed by South America with 13, and Australia with 11. In the northern hemisphere, to the contrary, America has 15 (or possibly only 13, if the possibility of human influences, transport with plants, is taken into account), and the palaeartic region has 11. Japan and the surrounding region is, with respect to the Phylactolaemata, a mixed region including 4 northern species not found in southern regions (*Fredericella s. sultana*, *Plumatella fruticosa*, *P. fungosa*, and *Cristatella mucedo*), 1 virtually cosmopolitan species (*Plumatella casmiana*), 3 occurring primarily in the southern hemisphere (*Plumatella toanensis*, *Hyalinella indica*, and *Pectinatella gelatinosa*), an endemic species (*Stephanella hina*), 2 cosmopolitans (*Plumatella repens* and *P. emarginata*), and 1 species (*Hyalinella vorstmani*), which also occurs in the adjacent Indian region.

In the strict sense of the word, there are only 4 cosmopolitan species: *Fredericella sultana* with its subspecies, *Plumatella repens*, *P. emarginata*, and *Hyalinella punctata*. Three species occur in nearly all provinces: *Fre-*

Table I. Distribution of the species

	nearctic (North America)	palaeartic				Indian province	Ethiopian province	neogaea (South America)	notogaea (Australia)
		(European part)	(Asiatic part)	(North Africa)	(Japan and surrounding region)				
<i>Fredericella sultana sultana</i>	—	×	×	×	×	—	—	×	
<i>Fredericella sultana crenulata</i>	×	—	—	—	—	—	—	—	
<i>Fredericella sultana indica</i>	—	—	—	—	—	×	×	—	
<i>Fredericella australiensis</i>	×	×	—	×	—	×	×	×	
<i>Plumatella casmiana</i>	×	×	—	—	×	×	×	—	
<i>Plumatella philippinensis</i>	—	—	—	—	—	×	×	—	
<i>Plumatella agilis</i>	—	—	—	—	—	×	×	×	
<i>Plumatella carvalhoi</i>	—	—	—	—	—	—	—	—	
<i>Plumatella fruticosa</i>	×	×	—	—	×	—	—	—	
<i>Plumatella repens</i>	×	×	×	×	×	×	×	×	
<i>Plumatella fungosa</i>	×	×	×	—	×	—	—	—	
<i>Plumatella javanica</i>	×	—	—	—	—	×	×	×	
<i>Plumatella longigemmis</i>	—	—	—	—	—	×	×	—	
<i>Plumatella emarginata</i>	×	×	×	×	×	×	×	×	
<i>Plumatella evelinae</i>	—	—	—	—	—	—	×	—	
<i>Plumatella toanensis</i>	×	—	—	—	×	×	×	×	
<i>Hyalinella vorstmani</i>	—	—	—	—	×	×	—	—	
<i>Hyalinella punctata</i>	×	×	×	—	—	×	×	×	
<i>Hyalinella indica</i>	—	—	—	—	—	×	×	—	
<i>Hyalinella lendenfeldi</i>	—	—	—	—	—	—	×	×	
<i>Pectinatella magnifica</i>	×	×	×	—	—	—	—	—	
<i>Pectinatella gelatinosa</i>	—	—	—	×	—	×	—	—	
<i>Pectinatella spec.</i>	—	—	—	—	—	—	×	—	
<i>Hyalinella vaihiriaae</i>	(x)	—	—	—	—	—	—	×	
<i>Lophopus crystallinus</i>	×	×	×	—	—	—	—	—	
<i>Lophopodella capensis</i>	—	—	—	—	—	—	×	—	
<i>Lophopodella thomasi</i>	—	—	—	—	—	—	×	—	
<i>Lophopodella stuhlmanni</i>	—	—	—	—	—	×	×	—	
<i>Lophopodella carteri</i>	(x)	—	—	—	—	×	×	×	
<i>Lophopodella pectinatelliformis</i>	—	—	—	—	—	×	—	—	
<i>Stephanella hina</i>	—	—	—	×	—	—	—	—	
<i>Cristatella mucedo</i>	×	×	×	—	×	—	—	—	
	15 (13)	11	(8)	(4)	(11)	17	17	13	11
	Northern hemisphere					Southern hemisphere			

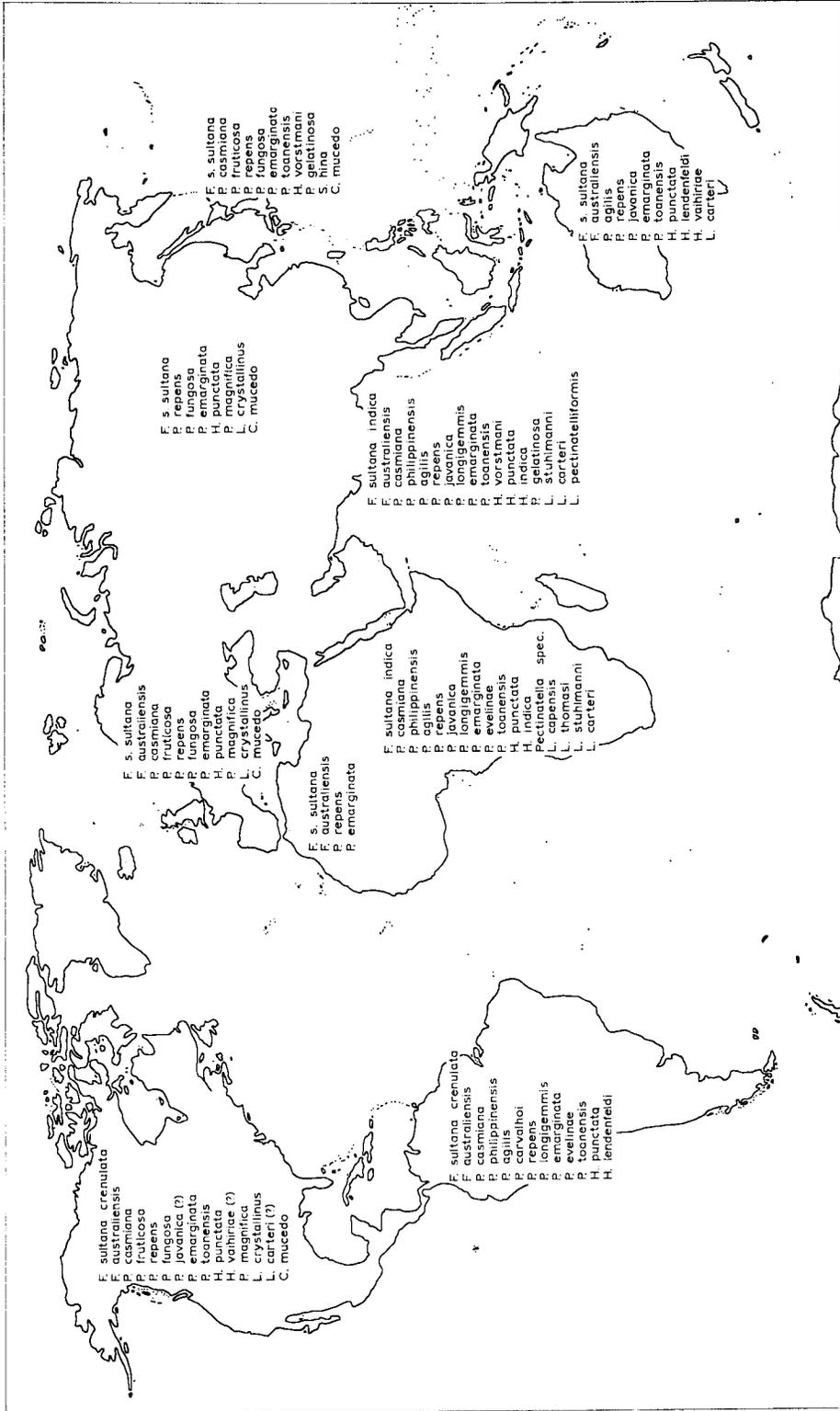


Fig. 12. Distribution of the species in the zoogeographic provinces.

Table II Measurements (in microns)

Species	S (sessile statoblast)							F (free statoblast)										Polypide number of tentacles	distribution	
	length	width	width of optical part of annulus		form	L/B ratio of S statoblast	outer margin	length	width	length breadth of capsule		width of part of annulus	optical lat./pol. ratio of ann.	diam. of chambers of ann.	L/B ratio of F statoblast	form	outer margin			
			pol.	lat.						pol.	lat.									
<i>Fredericella sultana</i> , oval	380-500	240-300	nihil	nihil	round-long-oval	1-3	smooth											19-24	cosmopolitan	
long oval ± circular <i>F. australiensis</i>	± 570 diam. 320-542	± 210 370-380 220-370	nihil	nihil	round-broadly oval	1-1.5	smooth											24-30	cosmopolitan	
<i>Plumatella casmiana</i> typical F	320-510	220-350	25-40*		rounded oval	1.5	irregularly serrated	320-453	180-280	245-330	160-210	48-85	27-40	2-3	8-10	1.6-2	broadly oval	notched	23-41	world-wide; but with discontinuity; not in Australia
<i>Plumatella casmiana</i> "thin-walled"								330-480	165-260	same as	st. bl.	(30-50 on caps.)	(1)	3	1.5-2	long oval	smooth			
<i>Plumatella philippinensis</i>	400-413	267-320	12 ± *		rounded oval	1.3	regularly serrated	365-430	212-250	260-324	176-214	53	18	3	9	1.6-2	long oval	smooth	44-48	aequatorial
<i>Plumatella agilis</i>	347	266	27 ± *		rounded oval	1.3	notched	373-530	200-310	265-306	178-237	40-66	19-26	2-2.5	8-12	1.6-1.9	long oval	very slightly notched	40-50	circumtropical
<i>Plumatella carvalhoi</i>	400	267	47-53*		rounded oval	1.5	minutely notched	328-387	210-242	180-240	156-188	74	27	2.7	9	1.4-1.8	broadly oval	partly smooth partly notched	40-50	South America
<i>Plumatella fruticosa</i>	± 700	± 270	105	23	long oval very large	2-2.6	regularly dentate	468-600	170-250	270-363	140-190	70-105	12-17	6-9	10-12	2.8	very long spindle-sh.	smooth	30-50	holarctic
<i>Plumatella repens</i>	390-600	390-515	46-58*		rounded oval	1-1.16	serrated	330-450	212-280	240-290	200-230	37-47	18-23	2	7-10	1.28	broadly oval	slightly undulating	40-60	cosmopolitan
<i>Plumatella fungosa</i>	480-690	365-500	0-23*		rounded oval	1.35	minutely serrated	350-465	230-340	210-325	184-270	70	23-35	2-3	9	1.4	broadly oval	slightly undulating	40-60	holarctic
<i>Plumatella javanica</i>	± 400	± 280	20 ± *		rounded oval	1.45	dentate	373-400	200-240	240	180	67-80	13-27	3	12	1.66-1.85	oval	smooth	20-45	Indian-Ethiopian region
<i>Plumatella longigemmis</i>	320-462	220-322	35-75*		rounded oval	1.5	notched	352-444 498-531	200-281 232-283	186-318	133-239	90-110	26-60	2-3	9-14	1.6-1.9	oval	smooth	20-40	tropical
<i>Plumatella emarginata</i>	400-590	230-320	0-16*		rounded oval	1.75	smooth	360-500	210-270	230-300	160-210	100	30	3	16	1.65-2	oval	smooth and undulating	30-54	cosmopolitan
<i>Plumatella evelinae</i>	470	315	34*		rounded oval	1.5	minutely serrated	323-466	214-290	215-311	160-218	54-78	27-36	2	?	1.5-1.7	oblique-oval		44-64	South America and Ethiopian region
<i>Plumatella toanensis</i>	333-650	227-530	12-70*		rounded oval	1.2-1.66	serrated	450-732	280-480	300-450	214-450	75-141	33-93	2.5-4	12-16	1.5-2.4	(long) oval	smooth	47-78	especially southern hemisphere
<i>Hyalinella vorstmani</i>	278-368	208-288	19 ± *		rounded oval	1.33	serrated	290-360	180-240	187	146	53	27	2	9	1.5-1.6	(long) oval	smooth and undulating	18-32	Indian region
<i>Hyalinella punctata</i>	433-585	374-468	35-46*		rounded oval	1-1.25	coarsely scalloped	232-298 431-500	200-249 282-380	166-355	160-304	33-42 61-82	20-25 28-41	1.5-2	7-9	1-1.5	round-oval	mostly smooth undulating*	40-60	world-wide but with discontinuity; not in Australia; (* very slightly notched)
<i>Hyalinella indica</i>	433-456	374-409	nihil		rounded oval	1.15	coarsely serrated	460-561	290-361	250-351	187-284	82	41	2	9	1.5	round-oval	smooth	40-50	Indian-Ethiopian region
<i>Hyalinella lendenfeldi</i>	—	—	—	—	—	—	—	850-1000	700-800	600	500	200-220	150	1.3-1.5	10-50	1.25	nearly round	smooth	50	Australia-South America
<i>Hyalinella vaihiviae</i>	410-470	293-400	13-16*		rounded oval	1-1.5	smooth	320-410	220-280	186-276	180-240	67	20	3	8-10	1.5	rhomboidal	undulating	48	Australian
<i>Pectinatella magnifica</i>	—	—	—	—	—	—	—	diam. 900-1500	—	∅ 600-1000	—	150-250*	—	12	—	—	round	smooth	60-84	holarctic
<i>Pectinatella gelatinosa</i>	—	—	—	—	—	—	—	diam. 1340-1750	—	∅ 560-630	—	445*	—	16	—	—	round	smooth	72-106	Indian region and Japanese region (unknown spec. in Ethiopian region)
<i>Lophopus crystallinus</i>	—	—	—	—	—	—	—	1200	565-630	468	386	270-366	89-122 ¹⁾	3	14	2	oval, pointed at the poles	smooth	60	holarctic (1) = without point)
<i>Lophopodella capensis</i>	—	—	—	—	—	—	—	850	550-608	∅ 440-520	—	85	35-64	1.3-2.5	10-14	1.4-1.6	oval, knotted at the poles	mostly smooth or bluntly smooth serrated	60-70	Ethiopian region
<i>Lophopodella thomasi</i>	—	—	—	—	—	—	—	875-890	642	409-437	343-363	224	140-150	1.5-1.6	16	1.4	oval, concave at the poles	dentate	unknown	Ethiopian region
<i>Lophopodella stuhlmanni</i>	—	—	—	—	—	—	—	948	854	∅ 468	—	240	193	1.25	15	1.1	nearly square	smooth	80	Indian-Ethiopian region
<i>Lophopodella carteri</i>	—	—	—	—	—	—	—	840-1300	560-900	420-538	380-510	250	200	1.25	15	1.5	broadly oval, convex at poles	minutely serrated	50-95	Indian-Ethiopian-Australian
<i>Lophopodella pectinatelliformis</i>	—	—	—	—	—	—	—	1200	900	495	435	350	232	1.5	17	1.33	oval, knotted at poles	microscopically undulating, smooth	50-70	Sumatra
<i>Stephanella hina</i>	320-340	410-460	6 ± *		rounded oval	1.3	serrated	diam. 300-370	—	∅ 210-250	—	47-58*	—	9	—	—	round	smooth	36-40	Japanese region
<i>Cristatella mucedo</i>	—	—	—	—	—	—	—	diam. 900-1250	—	∅ 776-1000	—	97-140*	—	11-16	—	—	round	frayed	70-90	holarctic and Japanese region

* annulus of about equal width throughout

*annulus of about equal width throughout

dericella australiensis, *Plumatella casmiana*, and *P. toanensis*. The species limited to the holarctic region are: *Plumatella fruticosa*, *P. fungosa*, *Pectinatella magnifica*, *Lophopus crystallinus*, and *Cristatella mucedo*. The genus *Lophopodella* is restricted mainly to the Indian and Ethiopian areas with an extension to Australia (*L. carteri*). It is striking that Australia has, as far as our present knowledge goes, only one endemic species, *Hyalinella vaihiriaae*. In North America it may have been artificially introduced. *Hyalinella lendenfeldi*, moreover, is also known from South America. A number of species occurring in other localities in the southern hemisphere are not found in Australia.

The strongest agreement is found between the Indian and Ethiopian provinces, which both have 17 species. The palaeartic region has 11. South America and Australia have 13 and 11 species respectively, but a total of 16 occurs in these regions. As far as is known, one species occurs exclusively in South America, *Plumatella carvalhoi*, but its discovery is recent.

The species of the nearctic and palaeartic regions are almost identical. In North America, *Fredericella sultana sultana* is replaced by the subspecies *F. s. crenulata*. *Plumatella javanica*, *P. toanensis*, *Hyalinella vaihiriaae* and *Lophopodella carteri* do not occur in the palaeartic region. For these species the possibility of import from the tropics to North America must be kept in mind, except for *Plumatella toanensis*, which could have penetrated from South America.

The distribution of the Phylactolaemata in its present form is an indication of the earlier existence of connections between the continents in the sense of Wegener. The present configuration of the oceans and continents could not have given rise to the present pattern of distribution. Nor can it be due, with a few rare exceptions, to human influence. The exclusive occurrence of *Hyalinella lendenfeldi* in South America and Australia is an indication of the same thing, as is, even more strongly, the composition of the fauna of the Phylactolaemata of Australia, with only one endemic species. This homogeneous distribution is, reciprocally, an indication of the great age of the Phylactolaemata.

In figure 12 the species are listed according to their occurrence in the zoogeographical provinces. Table II gives the main characteristics: the dimensions of the statoblasts and capsule, the width of the annulus, the diameter of the chambers in the annulus, the shape, the features of the outer margin, and the number of tentacles. The length/width ratio (L/B) conveys the relationship of the width to the length. The distribution is indicated for each species individually. The classification is given above (p. 3). Figure 13 outlines the ancestry of the species.

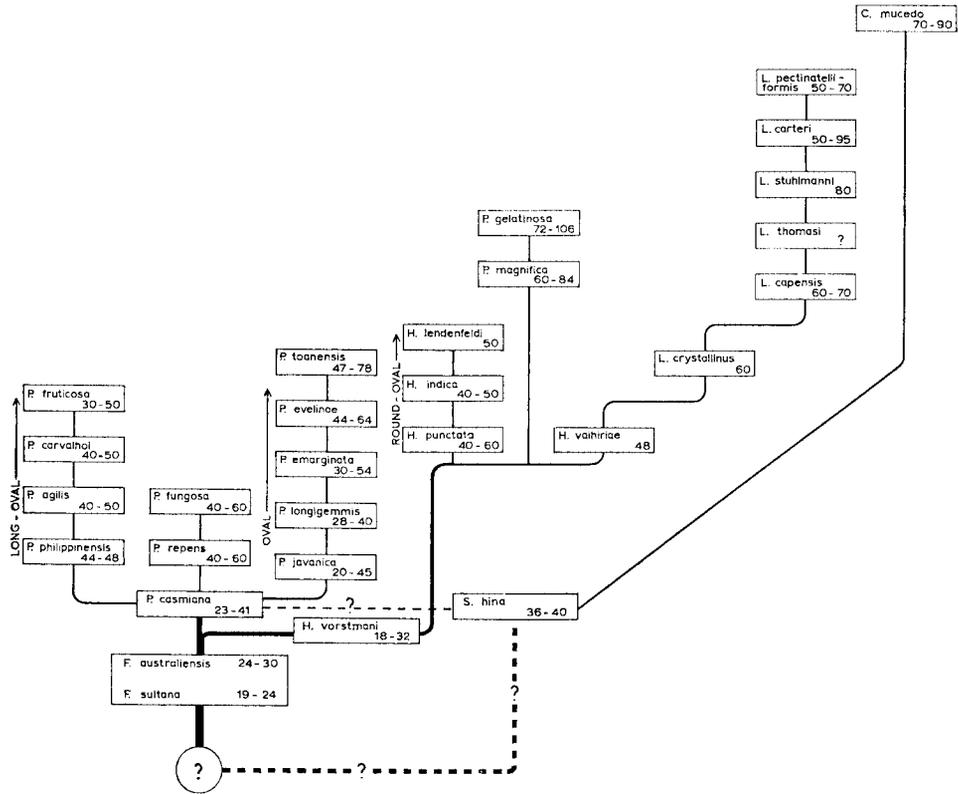


Fig. 13. Ancestry of the species of Phylactolaemata.

List of abbreviations

Material of several institutions has been examined. These institutions are indicated in the text by the following abbreviations:

RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands; ZMA, Zoologisch Museum, Amsterdam, the Netherlands; ISNB, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; ZIU, Zoologiska Institutionen, Uppsala, Sweden; NMG, Naturhistoriska Museet, Göteborg, Sweden; ZMH, Zoologisches Museum, Hamburg, W. Germany; BIS, Biological Institute, Sendai, Japan; ZSI, Zoological Survey of India, Calcutta, India; USNM, United States National Museum (Smithsonian Institution), Washington, U.S.A.; IPNC, Institut des Parcs Nationaux du Congo (now Koninklijk Museum voor Midden-Afrika), Tervuren,

Belgium; AMS, Australian Museum, Sydney, Australia; ZMB, Zoological Museum, Bogor, Indonesia; ZMK, Zoologisk Museum, København, Denmark; BM (NH), British Museum (Natural History), London, Great Britain; BM, Bergens Museum, Bergen, Norway.

Table II^a Measurements of free statoblasts with spines (spinoblast), in microns

Species	number of spines	number of hooks on each spine	shaft length	of spine width	length of hooks	width of marginal edge
<i>Lophopodella capensis</i>	1	16-26	140-175	21-12	12-16	—
<i>Lophopodella thomasi</i>	3-6	20-22	60-75	10-13	9-12	7
<i>Lophopodella stuhlmanni</i>	7-8	10-16	117	12	7	5 ⁸
<i>Lophopodella carteri</i>	7-14	6-22	20-170	8-32	7	12-24
<i>Lophopodella pectinatelli-formis</i>	36 small, on margin		13	8-4!	8 ¹ / ₂ -13	—
<i>Pectinatella magnifica</i>	10-22	2	270-100!	18-30	53-66	—
<i>Pectinatella gelatinosa</i>	140	2	24	3-6	11	6
<i>Cristatella mucedo</i> , dorsal	10-34	2	182-273	7 ¹ / ₂ -11	33-47	—
<i>Cristatella mucedo</i> , ventral	20-50					

Furthermore the following abbreviations are used: L, total length of statoblast; B, total width of statoblast; l, length of capsule; b, width of capsule; F, free statoblast; S, sessile statoblast.

SYSTEMATIC PART

Key to the species, based on the statoblasts

The descriptions and the microphotographs make an extensive key unnecessary. It will be sufficient to mention a few characters and differential features of the species. The great variability must be kept in mind; however, an average picture must be found. The number of tentacles and the distribution of the species must be taken into account. Identification cannot be made from the shape of the zoaria; this character serves at most, with restrictions, for the genus, not for the species. For example, if *Plumatella fungosa* and *Cristatella mucedo* have characteristic zoaria, it is still theoretically possible that outside Europe, or even within it, new species with the same zoarial shape but with different statoblasts could be found. In making identifications the text-figures should also be consulted for the variability. Furthermore, it should also be kept in mind that S statoblasts are not always present.

- 1a Statoblasts without spines 2
 b Statoblasts with spines 11
- 2a Statoblasts of circular shape, with annulus *Stephanella hina*
 b Statoblasts elongate or rounded oval 3
- 3a Only one type of statoblast, viz., the S statoblast *Fredericella* 4
 b Two types of statoblast, viz., the S and F statoblasts. S statoblasts as in *Fredericella* but with a narrow annulus in the median plane, with or without a reticulation. F statoblasts provided with an annulus containing chambers 5
- 4a Statoblasts small, oval or bean-shaped, seldom round, capsule valves fragile, without a trace of an annulus, outer margin a dark line within which there is a light zone *Fredericella sultana*
 b Statoblasts more solid, usually round to rounded oval, with a heavier edge, thicker valves, very dark brown *Fredericella australiensis*
- 5a F statoblasts somewhat triangular, slightly flattened on one side 6
 b F statoblasts oval 7
- 6a S statoblasts usually large, $1\frac{1}{2}$ times the length of the F statoblasts, usually without annulus but sometimes with a very wide annulus; zoarium radially branched *Plumatella repens*
 b F statoblasts larger than in the foregoing species; S statoblasts usually also large, $1\frac{1}{2}$ times the length of the F statoblasts; zoarium tuberiform *Plumatella fungosa*
- 7a F statoblasts elongate oval 8
 b F statoblasts medium oval 9
 c F statoblasts rounded oval *Hyalinella* 10
- 8a Within one and the same zoarium, variously shaped statoblasts, which, however, often occur singly: a membranaceous F statoblast with a little developed annulus, a normal F statoblast, a very narrow form of the normal F statoblast, and a form with a more elongated shape at the poles; sometimes (but seldom) a statoblast reminding of those of *P. repens* *Plumatella casmiana*
 b F statoblasts long-oval with a large, elongated-oval capsule *Plumatella philippinensis*
 c F statoblasts somewhat wider, with a smaller capsule and a wider annulus than the foregoing species; sometimes with intermediary statoblast *Plumatella agilis*
 d F statoblasts with elongated-oval capsule and very wide annulus; S statoblast also with a very wide and lobate annulus *Plumatella carvalhoi*
 e F statoblast very long and narrow, spindle-shaped, L/B = 2.8; annulus very narrow laterally, with marked polar extension: sometimes slightly shorter, showing correspondence with the narrow F statoblast of *P. casmiana*; S statoblast very large, elongated-oval with large elongated-oval capsule *Plumatella fruticosa*
- 9a F statoblasts 373-400 μ *Plumatella javanica*
 b F statoblasts 450-732 μ *Plumatella toanensis*
 c F statoblasts 352-531 μ . Capsule about twice as long as the polar width of the annulus *Plumatella longigenmis*
 d F statoblasts 360-500 μ , of a "silvery" appearance. Capsule about four times as long as the polar width of the annulus. Annulus narrow laterally *Plumatella emarginata*
 e F statoblasts 323-466 μ wide; annulus very wide laterally. Capsule about four times as long as the polar width of the annulus. Doubtful species *Plumatella evelinae*
- 10a Small (290-360 μ), rather wide annulus, polar extension twice the lateral extension; small S statoblasts with distinct annulus *Hyalinella vorstmani*

- b Size of F statoblasts varies, but not necessarily in a single zoarium: annulus equally wide in extension; F statoblasts varying from very small (230 μ , smaller than the foregoing species) to medium size (500 μ); S statoblasts seldom present, large (up to 585 μ). *Hyalinella punctata*
- c F statoblasts larger than in foregoing species (about 560 μ), annulus highly developed; S statoblasts somewhat smaller *Hyalinella indica*
- d F statoblasts very large, nearly round, (850-1000 μ); annulus of uniform width, S statoblasts unknown *Hyalinella lendfeldi*
- e F statoblasts with poles elongated *Hyalinella vaihirieae*
- 11a F statoblasts large, round, carrying spines on both sides of the capsule *Cristatella mucedo*
- b F statoblasts carrying marginal spines 12
- 12a F statoblast with spines all around the outer margin *Pectinatella* 13
- b F statoblast with spines at the poles only 14
- 13a Diameter of F statoblast 900-1500 μ , capsule large, with a small number of large marginal spines *Pectinatella magnifica*
- b Diameter of F statoblast 1340-1750 μ , capsule small, about 1/3 diameter of F statoblast, with a large number of small marginal spines *Pectinatella gelatinosa*
- 14a F statoblasts pointed at the poles *Lophopus crystallinus*
- b F statoblasts with one or more spines at the poles, carrying hooklets on edges *Lophopodella* 15
- 15a F statoblasts with one large spine *Lophodella capensis*
- b F statoblasts with concave truncation at the poles, carrying 3 to 6 spines of about the same size *Lophopodella thomasi*
- c F statoblasts with transverse truncation at the poles, carrying 7 or 8 almost identical spines *Lophopodella stuhlmanni*
- d F statoblasts with round truncation at the poles, carrying 7 to 14 spines of which the middle ones are longer than the outer ones *Lophopodella carteri*
- e F statoblasts with round polar truncation, carrying about 36 very small hooklets *Lophopodella pectinatelliformis*

A few species with medium oval and rounded oval F statoblasts resemble each other quite strongly, e.g. *Plumatella javanica* and *Hyalinella vorstmani*; and *Plumatella longigemmis* and *Hyalinella indica*. They can be distinguished as follows:

Plumatella javanica and *Hyalinella vorstmani* both are small species, the F statoblast of the latter is smaller but wider and its annulus is distinctly wider laterally.

Plumatella longigemmis and *Hyalinella indica* can be distinguished by that in the former species the capsule of the F statoblast is small, almost round and about 50 % of the total length but in *H. indica* it measures about 70 % of the total length.

H. punctata is a species in which the statoblasts vary in size and therefore it may easily be confused with several other species; however, it can at once be distinguished by the perfectly regular shape of the F statoblast, which is usually round to round-oval.

Description of genera and species

FREDERICELLIDAE Hyatt, 1868

The zoarium consists of tubes that are sparingly branched in a dichotomous manner. The lophophore is nearly round. Only one kind of statoblasts, sessile statoblasts, are present.

Fredericella Gervais, 1838

Description. — The zoarium consists of tubes which are partially adherent, sometimes furnished with a keel, and with dichotomous or antler-like branching. The cuticula is brown or grey, sometimes transparent, and with or without incrustations. The polypides have a nearly round lophophore with 20 to 30 tentacles. Only sessile statoblasts are present; they are not provided with an annulus and vary in outline from elliptical to round.

Two species belong to this genus: *Fredericella sultana* (Blumenbach, 1779) and *Fredericella australiensis* Goddard, 1909. The type species, by monotypy, is *Tubularia sultana* Blumenbach, 1779.

Fredericella sultana (Blumenbach, 1779)

(Pl. 1 figs. a, b; pl. 3 fig. a; pl. 12 figs. b, f; text-fig. 6a)

Tubularia sultana Blumenbach, 1779 (Canals in the city of Göttingen, Germany).

Fredericella sultana - Abricossouff, 1925b; 1926a; 1927a; 1927b; 1933; Allman, 1844a; 1856; Annandale, 1909b; 1910b; 1911; 1913a; 1915c; 1919-1921a; 1922b; Annandale & Kemp, 1912; Arndt, 1936; 1943; Asper, 1880; Barrois, 1893-1894; Bebnig, 1924; Berg, 1948; Du Bois-Reymond Marcus, 1946 (description and bibliography); Bonetto & Cordiviola, 1965 (partim, relation between length of statoblast and speed of water); Borg, 1930; 1936a (partim); 1940a; 1940b; 1941; Braem, 1908 (reproduction and life cycle); Brehm, 1950; Brien, 1934a; 1934b; 1952 (description of the larvae); Brown, 1933 (limnological study, physical, chemical and biological particularities); Calvet, 1904; Cant, 1936; Căpuse, 1962; Car, 1911; Chirica, 1906; Cunningham, 1920; Dartevelle, 1949; Davenport, 1899; 1904; Dendy, 1906; Despax, 1926; Dudich, 1944; 1947; 1948; Du Plessis-Gouret, 1885; Forel, 1885; Garbini, 1895; Gauthier, 1928; Gervais, 1838; Goddard, 1909; Harmer, 1913; Hastings, 1938; Heding, 1938; Houghton, 1860; Hyatt, 1866; Jullien, 1885 (monograph, synonymy); ? Keizer, 1936; Kirkman, 1901; Kolosváry, 1964; Kraepelin, 1884; 1886; 1887 (monograph); 1892 (monograph); 1893; 1914; Krzysik, 1922; Lacourt, 1949a; 1949b; Lange de Morretes, 1940; Lepneva, 1933; Levander, 1908; Linder, 1931; Loppens, 1906a; 1906b; 1908; 1910b; Marcus, 1940; Mauvais, 1927; 1942; Meissner, 1898; Mozley, 1932; Murray, 1910; Nichols, 1912; Økland, 1964; Prenant & Bobin, 1956; Rawson, 1953; Richard, 1897; Ridley, 1886; Rogick, 1934a; 1935a; 1937a; 1940a; 1940b; 1941; 1945b; 1950; Rousset, 1907; Schmidt, 1886; Schodduyn, 1925a; 1925b; Sebestyén, 1959; Spandl, 1926; Stuhlmann, 1890; Toriumi, 1941a; 1941b; 1942a; 1942b; 1951; Tretiakow, 1900; Ulmer, 1913; Vángel, 1894; Vigano, 1964; 1965; Wesenberg-Lund, 1897; 1907; White, 1917; Whitelegge, 1883; Wiebach, 1963a; Zschokke, 1900; 1910; Zykoff, 1905.

- Fredericella dilatata* Allman, 1844b (Ireland, without further specification).
Fredericella duplessisi Forel, 1885 (Swiss lakes, without further specification).
Fredericella lepnevae Abricossoff, 1927 (nomen nudum).
Fredericella pulcherrima Hyatt, 1868 (Sebago Lake, Maine, USA).
Fredericella regina Leidy, 1851 (manuscript name).
Fredericella sultana var. *cunningtoni* Rousselet, 1907 (Lake Tanganyika, Africa).
Fredericella sultana var. *jordanica* Annandale, 1913a (Lake of Tiberias, Israel).

Description. — The zoarium is free or adherent, recumbent or erect, with dichotomous and usually open branching of the tubes; the cuticula is dark brown, usually with a coarse incrustation. The polypides are few in number, with 19 to 24 short, fragile tentacles (pl. 12 fig. f). This number is susceptible to variation, however.

The statoblasts occur only in the sessile form, and are usually not numerous. They have a soft capsule and are oval to elongated-oval, greyish-brown in colour with a light border along the outer margin, which is smooth and shows no trace of an annulus. The capsule sometimes shows a hard, net-like structure. Measurements: L = 380 to 500 μ ; B = 240 to 300 μ . The statoblasts are sometimes nearly round, diameter about 370 to 380 μ , but they can also be strongly elongated, in which case the length is two or three times the width (L up to 570 μ ; B up to 210 μ). Similar statoblasts have been found in the U.S.A. (Rogick, 1937a), England (Harmer, 1913) and Japan (Toriumi, 1941a). Toriumi (1951) has demonstrated the existence of a correlation between the width of the statoblast and that of the tube from which the statoblast originates. The elongated shape is not a specific character; kidney-shaped and deformed statoblasts are also encountered. In general, and certainly in the palaeartic region, the statoblasts have a soft capsule (*F. sultana sultana*). Rogick (1937a) reported for North America that the "ripe" statoblasts are roughened on the dorsal side by a layer of chitin. Du Bois-Reymond Marcus (1946) also reported statoblasts with a thick-shelled, granular capsule from South America. Rioja (1940) found statoblasts in Mexico whose surface he described as "mamelonados", thus here too the capsule is granular.

The tubes reach a length of 10 cm (Leislott, The Netherlands; Lacourt, 1949); the distance between the zooids can amount to 30 mm (Swiss Lakes; Asper, 1880). According to reports in the literature, the cross-section of the tubes in adherent parts is 330 to 450 μ , and in free parts 240 to 330 μ . The incrustation can consist, dependent on the environment, of fine-grained material (e.g., sand; Congo, Central Russia, Japan), but is usually coarser, in which case it is composed of detritus, diatoms, sponge spicules, etc. The colour of the cuticula is nearly always dark brown but sometimes grey.

Variability. — Various formae and varieties of *Fredericella sultana* have been described. Most of such varieties and formae are based on the above-mentioned variable characteristics such as external shape, colour of the tubes, amount of incrustation, occurrence at a given depth or at a given temperature, etc. In many cases such varieties concern isolated observations outside Europe, made when there was no opportunity for longer observation. The criteria to be considered reliable and constant for distinguishing subspecies, varieties, or formae are shape, size, and degree of chitin formation in the statoblasts; the general shape of the zoarium is of secondary significance.

Fredericella sultana var. *jordanica* Annandale, 1913. According to Annandale (1913), this variety is characterized by tubes that are never long; they are usually colourless but sometimes darker and in that case thicker. None of these features is a distinct character. The holotype (Zoological Survey of India, ZEV 5455-7) consists of a single tube without polypides or statoblasts. Particulars of the statoblasts are not given by Annandale. I propose that this variety be dropped.

Fredericella sultana var. *duplessisi* Forel, 1885. The only character mentioned for this variety by Forel (1885) is the presence of free, erect branches. This shape is supposedly characteristic for the deepest part of the Swiss lakes; in the absence of a substrate the zoaria live freely in the mud. This peculiarity has also been observed elsewhere, however, and then in very shallow water (Sonsbeek, The Netherlands; Lacourt, 1949b). There is no justification for maintaining this name either.

Fredericella sultana var. *cunningtoni* Rousselet, 1907 (Lake Tanganyika, Africa). It must be concluded from the description that this is a fragile variety of *F. sultana*; statoblasts are not encountered in the type material, however, so that this variety cannot be properly characterized. I therefore propose that this variety, too, be dropped. There is a possibility that Rousselet's material belongs to *F. sultana indica* Annandale.

Fredericella lepnevae Abricossoff, 1927b. This species is not described by the author: the name must therefore be considered a nomen nudum.

To summarize, it may be concluded that all the material from the palae-arctic region (Europe, North Asia, and North Africa) belongs to the nominal subspecies *Fredericella sultana sultana*. This subspecies in all likelihood also occurs in the Australian region.

Distribution. — In this enumeration, which is based on literature and on available material, no distinction is made between the various subspecies:

Europe. The numerous authors dealing with European material of this species have mentioned it from localities all over Europe, including Great

Britain and Ireland, as well as Barra in the Outer Hebrides (Cant, 1936). The northernmost records are various localities in southern Norway (Wesenberg-Lund, 1897), the northern part of Sweden (Borg, 1941), southern Finland (Levander, 1908), northern Russia (Abricossoff, 1927b), Iceland (Heding, 1938), and islands in the Arctic Ocean, including Spitsbergen (Abricossoff, 1933, but only statoblasts). The southernmost are the deep lakes of the Pyrenees (Despax, 1926), the Alps (Asper, 1880; Du Plessis-Gouret, 1885; Forel, 1885; Linder, 1931; Mauvais, 1927; Zschokke, 1910), the Caucasus (Abricossoff, 1926a; 1927a) and Rumania (Căpuse, 1962). Finds have also been made in Spain (Brehm, 1950) and Italy (Lake Trasimeno; Vigano, 1964).

Asia. Specimens have been found in the Siberian low-lying plains (Abricossoff, 1927b), Lake Yashil Kul in Pamir(?) (Keizer, 1936), Lake Saissan (Zykoff, 1905) and Lake Teleckoje in the Altai Mountains (Abricossoff, 1927b; Lepneva, 1933), Lake Baikal (Abricossoff, 1927b), Tchoubouk dam and lake, Ankara, Turkey (A. Geldiay in litt. 1957), Lake Huleh (Barrois, 1894; Hastings, 1938), Lake Tiberias (= Sea of Galilee) (Barrois, 1894), Ain et Tineh, Lake Tiberias, Israel (Annandale, 1913), Lake Homs, Syria (Barrois, 1894), Seistan, eastern Persia (Annandale, 1919-1921a), Lake Kumaon in the western Himalayas (Annandale & Kemp, 1912), lakes in India (Annandale 1909b; 1911), Colombo water works, Ceylon (Annandale, 1922b), Japan (Toriumi 1941a; 1942; 1951; 1956), Formosa (Toriumi, 1942b), Korea (Toriumi, 1941b).

Africa. Masyassa near Alexandria, Egypt (Kraepelin, 1893), Oued Boudjamah near Bone, Algeria (Gauthier, 1928; Borg, 1940b), Lake Tanganyika near Kibanga and Mshale (Rousselet, 1907), Tarouda River, Lake Imegha and Amguid River, all in the Hoggar Massif, altitude 2175 m, in the Central Sahara (Borg, 1936a), Lac Inférieur Gando, Albert National Park, Congo (IPNC), Lower Congo (Darteville, 1949), Congo River near Matadi (Borg, 1940a), Middle Zambesi just above the Victoria Waterfalls, Rhodesia (Kraepelin, 1914).

North America. Various sites in Canada and the U.S.A. (Brown, 1933; Davenport, 1899; 1904; Mozley, 1932; Rogick, 1934-1950; White, 1917), Jacobshavn, Greenland (Wesenberg-Lund, 1907), Lago de Xochimilco, Mexico (Rioja, 1940b).

South America (Brazil). São Paulo (Kraepelin, 1893), Umuarana (Du Bois-Reymond Marcus, 1946; 1953; 1955); Parana River (Bonetto & Cordiviola, 1965); Amazonas River system (Wiebach, 1967).

Australia and New Zealand. New South Wales (Ridley, 1886; Whitelegge, 1883), Victoria (Goddard, 1909), Adelaide, South Australia (Goddard, 1909), Christchurch, New Zealand (Dendy, 1906).

From these data the conclusion may be drawn that the species *F. sultana* has a cosmopolitan distribution, occurring from the islands in the Arctic Ocean to the subantarctic regions. Its presence has been demonstrated in the deep, cold lakes of the high mountain chains of Eurasia; in tropical waters it is far less common. However, in very large areas (South America, Indonesia) in which other are numerous, this species has been found only rarely, if at all.

Keizer (1936) mentioned the occurrence of Bryozoa in Lake Yashil Kul on the plateau of Pamir, altitude 3700 m, without specifying the species. This observation probably pertains to *F. sultana*, which has often been found in other high mountain lakes.

Kirkman's (1901) report of the occurrence of *F. sultana* in Natal is incorrect; his material proved to consist of tubes of a rotifer (Rousselet, 1907).

Borg (1940a) identified with some reserve material from Congo River as this species, since it consisted of a single tube without polypides or statoblasts.

Kraepelin (1893) mentioned the species from Punta Arenas, Patagonia. As shown by Calvet (1904) the correct locality is Islas Picton, off the southern coast of Tierra del Fuego. The material from this locality, which is preserved in the Zoological Museum, Hamburg (B 83), proved to consist of a statoblast of *Plumatella* spec.

Biology. — The substrate consists of various plant components, stones, tree bark, and wood. The zoaria can also bore into the mud, however, or grow in colonies of other species of Bryozoa or Algae. The food consists of diatoms and unicellular algae (Borg, 1936a). As can be seen from its distribution, *F. sultana* prefers low temperatures; even overwintering has been observed many times (Houghton, 1860; Schodduyn, 1925). Zschokke (1900) reported mass overwintering under the ice in Swiss mountain lakes. The species occurs above the snow-line, i.e., up to 3480 m altitude. It has been observed at a depth of 214 m, though it probably occurs at even greater depths. It is also found in very shallow water (10 cm depth, in a pool near Neora Selvatn, Iceland; 30 cm, Sonsbeek, The Netherlands). *F. sultana* also occurs in brackish water, but is then more poorly developed. The optimal temperature for development is 9° to 17° C, but it can thrive at 4° to 5° C, although sexual reproduction no longer occurs at these temperatures (Wesenberg-Lund, 1897; Kraepelin, 1914). Higher water temperatures also inhibit development.

The population of a biotope can vary greatly from one season to another; some seasons may show such a very heavy growth that all other organisms are being crowded out, in others the growth is very minor.

Borg (1941) called *F. sultana* the most common species of the waters of the Swedish mountains. Toriumi (1951) demonstrated that the shape of the zoarium and the zoecia, the nature of the cuticula, the number of tentacles, the presence or absence of a keel, etc., are influenced by external conditions; however, he considered the presence or absence of a net-like structure (reticulation) on the statoblasts to be of taxonomic value. This I can only confirm.

Concerning the benthos of alpine lakes, Zschokke (1910) put forward the following hypothesis: "... dass die Tiefenfauna der großen Wasserbecken des Alpenfußes aus zwei Elementen besteht, aus eurythermen Kosmopoliten des Flachwassers, die noch heute den Weg auf den tiefen Seegrund finden, und aus Ueberresten einer stenothermen Kaltwasserfauna der Eiszeit, die postglacial in der Seetiefe Zuflucht suchten".

Kraepelin (1886) said with respect to *F. sultana* "... während die Schweizer Seen seit geologischen Zeiträumen Formen beherbergen". This is highly probable, but it can hardly be longer than since the Ice Age.

Subfossil statoblasts of *F. sultana* are known from Quaternary deposits in Denmark, Norway, Sweden, Finland, and northern Germany, and they have also been found in peat deposits (pollen analysis). *F. sultana* was not, for instance, common in the "pine period" (Wesenberg-Lund, 1907).

Fredericella sultana sultana (Blumenbach, 1779) (Pl. 12 fig. f)

Fredericella sultana sultana - Abricossoff, 1927 (Oka River near Muron, Russia).

Material. — Europe. The Netherlands: material from various sites (RMNH, ZMA; Lacourt, 1949b). Belgium: material from various localities (ISNB; Lacourt, 1949a). Sweden: Uppland-Trehörningen (ZIU), Smaland (NMG).

Asia. Turkestan: without further specification (ZMH, B 1632, no statoblasts). Japan: Sendai (BIS). Israel: Lake Tiberias (ZSI, ZEV 5455-7, type material of *F. sultana* var. *jordanica* Annandale, 1913a); from the same locality, material without statoblasts (ZMH, B 119).

Description. — The nominal subspecies is principally distinguished from the two other subspecies by the capsule of the statoblast, which is not thickened or granular. For further details, reference is made to the description of *F. sultana* and the characters of *F. sultana indica* and *F. sultana crenulata*.

Distribution. — As stated in the description of *F. sultana*, the distributional area of the nominal subspecies includes the entire palaeartic region and probably Australia.

Fredericella sultana indica Annandale, 1909 (Pl. 13 fig. f)

Fredericella indica Annandale, 1909b (Lake Igatpuri, Western Ghats, India)

Material — Asia. India: various localities (USNM, no. 5156; ZSI, nos. 67, 73; ZMH, B 111).

Africa. Egypt: Masyassa, near Alexandria (ZMH, B 77). Congo (IPNC, coll. Damas, no. 40).

Description. — Annandale (1909b) distinguished this subspecies from the nominal subspecies as follows: "in general a delicate form, cuticula minutely roughened, sometimes with small sandgrains incrustated; nearly colourless but imperfectly transparent; tentacles about 20; statoblast as *F. sultana* in general, surrounded by a stout chitinous ring; the lower valve smooth, the upper valve minutely granulated; the prominences of the upper valve being star-shaped and the apex rounded. Of course they are so, being originated from polygonal ridges which grow and fuse".

Annandale gave no measurements, but the above-mentioned material from the U.S. National Museum (no. 5165) includes statoblasts. These are smaller than those of *F. sultana sultana* and have a granular surface. The measurements are: L 292 to 363 μ , B 175 to 211 μ .

Kraepelin (1914) reported material of *F. sultana* from Rhodesia in which the statoblasts were two-thirds the size of those of the typical subspecies. The Congo material also has small statoblasts, measuring 315 \times 182 μ ; both valves show reticulation. *Fredericella sultana indica* is thus smaller than *F. sultana sultana*; the statoblasts are darker in colour and show a retiform surface pattern.

Distribution. — Asia. Shasthancottah Lake, Travancore (Annandale, 1909b); Kumaon Lake, western Himalayas (Annandale & Kemp, 1912).

Africa. Rhodesia (Kraepelin, 1914), Congo (IPNC, unpublished).

Basing myself on these data I agree with Toriumi (1951) in considering *F. sultana indica* a tropical subspecies, whose distribution is limited to the Indian and Ethiopian regions.

Fredericella sultana crenulata Du Bois Reymond-Marcus, 1946 (Text-fig. 9)

Fredericella sultana crenulata Du Bois-Reymond Marcus, 1946 (Umuarana, Campos de Jordão, São Paulo, Brazil); Bonetto & Cordiviola, 1965.

Fredericella sultana - Rogick, 1937a; Rioja, 1940b.

Description. — The following details of this subspecies are taken from Du Bois-Reymond Marcus' description. Statoblasts are numerous, up to six

in one zoecium, dark brown, broad ellipsoid. Size: L 325 to 382 μ , B 265 to 305 μ , both valves show a thick, granulated layer of chitin. The rim (= outer margin) is crenulate with denticles; this crenulation is shown in all forms of this subspecies.

I do not consider the unilateral or bilateral covering of the statoblast by a thick chitinized layer as characteristic. The criterion is whether or not the capsule is thickened.

Distribution. — Rioja (1949b) also reported material of *F. sultana* from Mexico in which the statoblasts are "mamelonados" on the surface. Rogick (1937a: 102, fig. 1B) mentioned for North America specimens of *F. sultana* in which the statoblasts show a "roughened surface". The illustrations provided by Du Bois-Reymond Marcus and Rogick show almost complete agreement. In all probability, *F. sultana crenulata* is distributed over all of North and South America. Unfortunately, I have not been able to study material of this subspecies myself.

***Fredericella australiensis* Goddard, 1909**

(Pl. 12 fig. h; pl. 13 fig. e)

- Fredericella australiensis* Goddard, 1909 (Pott's Hill Waterworks); Annandale, 1911.
Fredericella sultana var. *transcaucasica* Abricossoff, 1927a (Lake Madatapeen in district of Tiflis, Caucasus).
Fredericella australiensis var. *transcaucasica* - Du Bois Reymond-Marcus, 1953 (descriptions and illustrations); Rogick, 1945b (idem).
Fredericella sultana - Borg, 1936a (partim); Bonetto & Cordiviola, 1965 (partim).
Fredericella sultana f. *major* Borg, 1936a (mountainous region of northern Sweden).
Fredericella sultana var. *grandigemmis* Abricossoff, 1927b (in ponds near Ropsche in the Leningrad district, USSR).
Plumatella (Afrindella) testudinicola Annandale, 1912a (Ganges River near Rajmahal, Allahabad, and Fatheghay); Annandale 1912b; Abricossoff, 1927b; Sokolov, 1931.
Fredericella australiensis var. *australiensis* - Rogick, 1945b (description with illustrations, Church Butte, Uinta County, Wyoming, USA).
Fredericella australiensis var. *browni* Rogick, 1945b (Church Butte, Uinta County, Wyoming, USA); Du Bois-Reymond Marcus, 1953 (description with illustrations); Du Bois-Reymond Marcus, 1955.
 ?*Fredericella walcottii* Hyatt, 1866 (species incerta; Georgetown, Mass., USA).
Fredericella spec. Whitelegge, 1889 (near Port Jackson, Australia).

Material. — Europe. Belgium: La Voer (ISNB, nos. 9541-8).

Asia. India: River Ganges, near Rajmahal (ZSI, ZEV 5023/73).

Australia. Sydney Watersupply (AMS).

Description — The zoarium is partially adherent, the tubes are initially dichotomously branched and then develop antler-like branching; the cuticula

is brown and transparent, sometimes incrustated; the polypides are short and thick with 24 to 30 tentacles.

Only S statoblasts are present, often in large numbers. They are round or a broad ellipse, sometimes kidney-shaped, and reddish-brown or black in colour. The surface is smooth and shows no reticulation, although it is sometimes (in Asiatic material) granulated. The capsule is surrounded by a substantial chitinized ring from which it is separated by a deep peripheral groove. The outer margin is smooth. Measurements: L 320 to 542 μ , B 220 to 370 μ .

Synonymy —It has long been an open question whether there is a second *Fredericella* species. The description of *Fredericella australiensis* (Goddard, 1909) is far from convincing, and the validity of this species has long been doubted, including by me. However, a re-examination of the material from La Voer, Belgium (ISNB, no. 9541-8) has convinced me that a second *Fredericella* species indeed occurs. It is characterized by a sturdy, thick, short polypide with 22 thick tentacles not longer than 0.8 mm. The diameter of the tentacles is 23 μ , that of the tubes 292 to 409 μ . The cuticula has a clear grey colour and carries a rough incrustation. *F. sultana sultana* has a thinner and more delicate polypide, and the diameter of its tubes is not more than 292 μ (for comparison see pl. 12 fig. b and pl. 13 fig. e, and Borg's (1930: 112, fig. 152) figure of *F. sultana*). In my opinion, the Belgian material is to be called *Fredericella australiensis*; it corresponds in all details with Australian material from the Sydney waterworks, and I consider this material to be identical to that described by Goddard (1909), originating from the Pott's Hill waterworks. The Australian material differs from *F. sultana sultana* not only in the above mentioned characters but also by the larger, darker statoblasts, which have thicker valves. According to Goddard, the Australian material consistently shows one statoblast for each branching; In the var. *browni* which is not otherwise to be distinguished from the species, the statoblasts are more numerous (Rogick, 1945 b).

Du Bois-Reymond Marcus (1953) made a distinction between the common sessile statoblasts (sessoblasts of Rogick, 1943b), in the tubes attached to the substrate, and sessile statoblasts, lying free in the tubes (piptoblasts). The latter are somewhat larger. The question of whether these piptoblasts actually differ from the sessoblasts, I am unable to answer. They have not yet been studied microscopically. They could, however, be formed by better-fed polypides.

The description of *F. sultana* f. *major* from the northern part of Sweden given by Borg (1936a) and of *F. sultana* var. *grandigemmis* from ponds near Ropsche, district Leningrad, USSR, given by Abricossoff (1927b) are

very incomplete but very probably pertain to *F. australiensis*. *F. sultana* f. *major* is described as being generally larger and having more tentacles (28 to 32); no particularities concerning the statoblasts are given. For *F. sultana* var. *grandigemmis*, Abricossoff reported that the statoblasts are very large.

Some of the material reported by Borg (1936a) from the Sahara unquestionably belongs to *F. australiensis*. This is also the opinion of both Rogick (1945b) and Du Bois-Reymond Marcus (1953).

Judging from description, measurements and figures Bonetto & Cordiviola (1965: 262, fig. 6) also recorded *F. australiensis* from the river Uruguay, South America. *F. sultana* is recorded from the river Paraná. The characters of both species of *Fredericella* are discussed and the authors conclude that only one species, *F. sultana*, exists. The gap between maximum and minimum measurements of statoblasts of material from the two localities mentioned above, however, is far too large to allow the inclusion of all the material in one species. Length measurements of the statoblasts of material from the river Uruguay falls within the limits of those of *F. australiensis* and this material in my opinion distinctly belongs to the latter species.

Whitelegge (1889) in all likelihood already saw material of *F. australiensis*: concerning material found in and near Port Jackson he said: "This is closely allied to *F. sultana*, but the statoblasts are nearly round and not bean-shaped. In Shea's Creek, Waterloo Swamps, abundant in 1884. The same or another species is found in Parramatta Park near the footbridge". It is also possible that Hyatt (1866), judging from his drawing of the zoarium, has already found this species in Georgetown, Mass., U.S.A. He described this material as *F. walcottii*. Its branching pattern agrees with that of *F. australiensis*. Hyatt did not observe statoblasts, however, and consequently this species cannot be identified with certainty.

Annandale (1912a: 148) gave the following description of *Plumatella testudinicola*: "Zoaria forming quite flat, oval or circular lichenoid patches with undulating or sinuous borders and in some instances as much as 10 cm in diameter; consisting of zooecia laying parallel and closely adjacent in one plane and radiating in branches from a common centre. Zooecia entirely recumbent, narrow, elongate, with the orifice opening almost vertically; the proximal part a little flattened, without dorsal keel or furrow; the ectocyst densely covered with minute sand-grains, translucent brownish, indistinctly annulated, paler on the distal than on the proximal part. Polypide not observed.

Statoblasts. — Only fixed statoblasts are apparently developed. They occur in great profusion, entirely filling many dead zooecia and arranged in moniliform series. As the dorsal wall of the zooecium decays they are left adhering

with their ventral wall to the host's carapace and reproduce the pattern of the zooecium, often almost completely. They are, as a rule, broadly oval, measuring about 0.52×0.35 mm, but sometimes they are circular and occasionally kidney-shaped. The surface is polished and without a trace of reticulation and the capsule is surrounded by a stout chitinous ring separated from it by a deep peripheral groove; the colour is black or very dark brown".

Although Annandale placed his material in the genus *Plumatella*, he did point out that the statoblast resembles that of *Fredericella*. He reported S statoblasts, but thought that the species had adapted itself to the special substrate (carapaces of four species of tortoises, viz., *Kachuga lineata* (Gray) (= *K. kachuga* (Gray)), *K. dhongoka* (Gray), *K. smithii* (Gray), and *Hardella thurjii* (Gray), and that the F statoblasts had become superfluous in this situation. The adaptation is supposed to have been recent and rather sudden. I cannot subscribe to Annandale's speculations. All characters point to the genus *Fredericella*, and in my opinion we are concerned here not with an adapted species of *Plumatella* but a true *Fredericella*. There is no reason to assume that F statoblasts would simply disappear. The Phylactolaemata as a whole are a sessile group: according to Annandale's standpoint, there would be no reason for the existence of F statoblasts in any species whatever. In the genus *Fredericella*, Annandale's species is certainly synonymous with *F. australiensis*. Only the unusually compact zoarium could, as an expression of a positive rheotropism, be a reaction to the unusual substrate.

Summarizing, I am of the opinion that all material referred to above and described under various names belongs to only one species: *F. australiensis*.

In contrast to Rogick's views (1945b), I see no grounds for a further division of the species *F. australiensis*. Rogick's argumentation for subdivision "based on the great similarity to each other so far as the shape of their statoblast was concerned and their slight but distinct differences as regards the nature of the ectocyst and the number of tentacles", can, in my opinion, only be explained as an argument for the uniformity of the material.

Distribution — In addition to the localities mentioned above in the synonymy, *F. australiensis* has also been found in the following localities: Europe. La Voer, Belgium (ISNB).

Asia. Waterworks of Buchara (Abricossoff, 1927b; Sokolov, 1931).

Africa. Streams in the Hoggar Massif in the central Sahara, altitude 2175 m (Borg, 1936a).

South America. Lake Titicaca and surroundings in the Andes Mountains on the borders of Peru and Bolivia (Du Bois-Reymond Marcus, 1933).

Australia. Sydney Waterworks (AMS).

The pattern of distribution revealed by these data is cosmopolitan in nature but with great discontinuities, probably the species has been repeatedly overlooked.

Measurements of the statoblasts (in microns)

Author or locality	Name	Length	Width
Abricossoff, 1927a	<i>F. sultana</i> var. <i>transcaucasica</i>	470	315
Rogick, 1945b	<i>F. australiensis</i> var. <i>browni</i>	331-461	266-367
Du Bois Reymond Marcus, 1953	idem	320-380	280-320
idem	idem, piptoblasts	340-420	250-370
Borg, 1936a	<i>F. sultana</i> (part)	370-430	220-270
Sydney Waterworks (AMS)	<i>F. australiensis</i>	386-421	257-328
Annandale, 1912a	<i>P. testudinicola</i>	520	350
Summarized		320-542	220-370

The measurements of the material described by Borg as *F. sultana* f. *major* and by Abricossoff as *F. sultana* var. *grandigemmis* are not known.

Biology. — *F. australiensis* occurs to a depth of about 7 m. In the Andes mountains this species is found in lakes up to an altitude of 4100 m. The material from the Ganges was found on the carapaces of tortoises, and was collected during the cold, wet season.

PLUMATELLIDAE Allman, 1856

The zoarium consists of tubes that are often branched, chiefly in an antler-like manner. The lophophore is horseshoe-shaped. There are two kinds of statoblasts, sessile and free statoblasts.

Plumatella Lamarck, 1816

The zoaria consist of tubes which are partially adherent; they are dichotomous with antler-like branching and may become compact masses; the cuticula is usually hard, and brown or grey; translucent to opaque and often incrustated. The polypides have a horseshoe-shaped lophophore carrying 20 to 80 tentacles. There are two types of statoblasts: an oval sessile statoblast with a less developed primary annulus and "swim-ring" statoblasts, long to medium oval and provided with a ring of chambers. As type species I designate *Tubipora repens* Linnaeus, 1758.

The genus *Plumatella* may be divided into three groups to which I assign the following species.

I: *P. casmiana* Oka, 1907; *P. philippinensis* Kraepelin, 1887; *P. agilis* (Marcus, 1942); *P. carvalhoi* (Marcus, 1942); *P. fruticosa* Allman, 1844.

II: *P. repens* (Linnaeus, 1758); *P. fungosa* (Pallas, 1768).

III: *P. javanica* Kraepelin, 1906; *P. longigemmis* (Annandale, 1915); *P. emarginata* Allman, 1844; *P. evelinae* (Marcus, 1941), and *P. toanensis* (Hozawa & Toriumi, 1940).

I. Species of *Plumatella* with elongate-oval statoblasts:

***Plumatella casmiana* Oka, 1907**

(Pl. 13 figs. g, h, i, j, k, l; pl. 15 fig. a)

Plumatella casmiana Oka, 1907b (partim; Kasumi Ga-Ura, Japan); Annandale, 1915a; 1922; Behning, 1924; Lacourt, 1948; Rogick, 1941a; 1943a (abundant data); Rogick & van der Schalie, 1950; Sebestyén, 1961; Toriumi, 1955a (taxonomic study); Vorstman, 1928a; Wiebach, 1963a (various types of statoblasts), 1963b.

Plumatella casmiana rossica Abricossoff, 1927b (Lake Ladochowo, Saratow district, U.S.S.R.).

Plumatella repens var. *casmiana* - Toriumi, 1941a; 1942b.

Plumatella repens var. *flabellum* type *casmiana* - Toriumi, 1941b.

Plumatella repens var. *annulata* Hozawa & Toriumi, 1940 (Mu-tan-k, Manchuria); 1941; Rogick & Brown, 1942.

Plumatella annulata - Lacourt, 1955b.

Plumatella ruandensis Wiebach, 1964 (Lake Bulera, Ruanda).

Stolella indica - Wiebach, 1964 (p.p., Lake Bango near the mouth of the Congo River, nr. 64, fig. 32, 33).

Material. — Asia. Japan: pond in Goshogawara (BIS); Kasumi Ga-Ura (ZMB, no. 16). Java: without further specification (ZMB). India: Bhim Tal, Kumaon, W. Himalayas (ZMH, B 109); Nagpur, C.P. (ZSI, no. 69).

Africa: Congo, Mabue (IPNC).

America. U.S.A.: Lake Erie (RMNH). Netherlands Antilles: Curaçao and Klein Bonaire (RMNH). Guatemala: San Pedro River near Paso Caballo, Dept. Peten, and Pasion River, east of Ceibol, Alta Vera Paz (RMNH).

Description — The zoarium is open to compact, entirely adherent, small; consisting of short, slender radially branched tubes. The cuticula is thin, light yellow, and little or not incrustated. The polypides are irregularly distributed: few in the older parts of the zoarium and sometimes growing thickly in the younger parts. The tentacles vary in number from 23 to 41.

This species was originally described as having atypical F statoblasts (pl. 13 fig. g) with a very soft, membranaceous capsule. Later an S statoblast was found (pl. 13 fig. h). Toriumi (1942a) and Rogick (1943a) both reported finding a normal F statoblast (pl. 13 fig. j) in a zoarium in which they had found S statoblasts. I myself found still other forms, that prove this species to be a Formenkreis. The atypical "thin-walled" F statoblast (Rogick, 1943a) is very long and narrow, with a light yellowish-brown coloration and a membranaceous capsule; the contents are transparent; the annulus is very

narrow and consists of 4 to 5 rows of chambers which do not extend beyond the capsule; the network on the annulus is very scantily developed, the margin is smooth. The measurements are: L 330 to 480 μ , B 165 to 260 μ ; the annulus has the same width throughout: 30 to 50 μ ; the diameter of the chambers is 3 μ . Typical F statoblasts are oval, dark brown, translucent; the capsule is relatively large, the annulus narrow, being about 2 to 3 times wider at the poles than laterally; the margin is notched. Measurements: L 320 to 453 μ , B 180 to 280 μ ; the annulus is 48 to 85 μ wide at the poles and 27 to 40 μ laterally; the diameter of the chambers is 8 to 10 μ ; the capsule measures l 245 μ , b 160-210 μ .

Among these statoblasts a wide, almost triangular statoblast is sometimes, although seldom, found (pl. 13 fig. k). Rogick & van der Schalie (1950: 141, pl. 1 figs. 8-9) have illustrated similar but not typical F statoblasts, which they term "capsuled statoblast", but this term is actually applicable to all other statoblasts with exception of the thin walled type. They resemble the "*P. repens*" form and represent a branch of the "*P. repens*" series. *P. casmiana* is a precursor of *P. repens* and not one of its varieties.

In addition to the typical oval F statoblast, I have found elongated-oval statoblasts in one and the same zoarium (pl. 13 fig. l); in these statoblasts the capsule has a long-oval shape and the annulus is narrower at the poles. If these statoblasts are considered apart from the typical form, they give the impression of belonging to another species entirely. If the entire polar width of the annulus is considered (i.e., not only the part extending beyond the capsule, the so-called optical part), the difference is not so great and the total length of the narrow form exceeds the described length either very little or not at all. In the Phylactolaemata it is often very small differences that determine the species. Furthermore, the occurrence of two differently-shaped F statoblasts within one species, the type with oval and that with parallel outlines, complicates matters in many species. In this species in particular it has required much prolonged effort to isolate the facts. Originally, only material with membranaceous statoblasts was known as *P. casmiana*; the material with typical F statoblast was described as *P. annulata*, and the true relationship was only found by Toriumi accidentally. Add to these the aberrant long, narrow-oval form of the typical F statoblast, plus the above-mentioned short "*repens*"-like form which gives the species its fourth appearance, remember also the occasionally found "*vaihiriæ*"-like form and it is easy to understand how the original confusion could arise. I have even come across material from the Sedang Garut fishpond in Java in which there are statoblasts with a shape similar to *P. philippinensis* but with a more highly developed annulus reaching further over the capsule.

The S statoblast is rounded-oval, sometimes with an incomplete annulus occasionally showing an incomplete reticulation: the surface is granular; the margin is irregularly notched. Measurements: L 320 to 510 μ , B 220 to 350 μ , the width of the annulus varies between 25 to 40 μ .

Toriumi (1941a: 418, text-fig. 5a, b) gave illustrations of two F statoblasts of different size. The great differences between them are not indicated by the accompanying measurements. In a later publication Toriumi (1942b) mentioned L = 350 to 460 μ , which is in better agreement with the pictures. It follows from this that in one and the same region, i.e., Japan, the size can differ widely. This is also evident from the measurements given by Rogick (1941a) for North American material: 330 to 480 μ .

Rogick (1943) and Toriumi (1955) are of the opinion that the membranaceous statoblast belongs to a summer generation; only the empty valves were to be found in winter, whereas the F statoblasts remained intact. This is conceivable, but the membranaceous statoblast is unquestionably an imperfect form.

Wiebach (1963a) has discussed the different kinds of statoblasts and the various denominations used for them. His suggestions for a detailed terminology for the various types deserve consideration.

Synonymy. — For *P. casmiana rossica* Abricossoff (1927b) the measurements fall within the limits of variability, and thus it is pointless to make distinctions. This subspecies should therefore also be discarded.

Toriumi (1955a) came to the conclusion, in a detailed study on this species, that *P. repens* var. *annulata* Hozawa & Toriumi (1940) is synonymous with the species under discussion here. The “*annulata*” form was originally considered to be a variety of *P. repens*, but Toriumi later found the typical and the membranaceous statoblasts in a single zoarium, which proves them to be identical. I myself have split off the variety “*annulata*” from *P. repens*, and have already cited it in a discussion of Caribbean material as a separate species (Lacourt, 1955b).

Rogick & Brown (1942: figs. 15, 16) also gave an illustration of this type of statoblast which has been found to belong to *P. casmiana*. Wiebach (1964: figs. 18, 19) found only this type of statoblast in material from Central Africa, on which he based a new species, *Plumatella ruandensis*; but the material that he included under this species has all the characteristics of *P. casmiana*. In table II, in which I have collected all the characters and measurements, the location of a sample of material can be found for almost all cases. For a length of the F statoblast of 342 to 378 μ , a width of 180 to 218 μ , and a number of tentacles of about 20, there appear to be three possibilities, i.e., *P. casmiana*, *P. javanica*, and *Hyalinella vorstmani*. Com-

parison with the descriptions and the plates indicates that the material examined by Wiebach fits entirely within the Formenkreis of *P. casmiana*. The statoblast of *H. vorstmani* is exclusively broadly oval and that of *P. javanica* slender, leaving the statoblast of *P. casmiana*. The degree of connection of the capsule by the annulus as described by Wiebach also agrees completely with what is shown in the figures of Rogick & Brown (1942) and Rogick & van der Schalie (1950) as well as by my microphotograph of the F statoblast (pl. 15 fig. a).

The "Medianschnitt-Diagramm" devised by Wiebach (1964) may prove to be a useful criterion, if applied with care and based on the study of sufficient material, but a variation between 15° and 24° such as Wiebach mentioned for *P. emarginata* according to our present knowledge, is already too large to be reliable. Because my investigations were already approaching completion, it was no longer possible for me to apply this characteristic in the present monograph.

In an earlier publication (Lacourt, 1948), I mentioned *P. casmiana* as a synonym of *P. philippinensis* because of the great similarity of some of the statoblasts, but I am now of the opinion that they are different species.

Wiebach (1964) assigned a group of specimens (IPNC nr 64) to *Stolella indica*, a non-existent species. He gave two illustrations of the F statoblasts, but without any further data. For other material, which he also assigned to *S. indica* (cf. Wiebach 1964: figs. 34, 35, nrs 65, 66) but which belongs to *Plumatella agilis*, he provided measurements. From the illustrated form it may perhaps be inferred that all the statoblasts shown have roughly the same length (Wiebach in any case assigns them all to one species). This leads me to the conclusion that the statoblasts in his figures 32 and 33 must belong to *P. casmiana* and to the "*repens-fungosa*"-like branch. It is to be regretted that Wiebach, who has provided a very useful publication (1964) based on excellent material, has nevertheless classified some of that material erroneously.

Distribution. — Europe. Various localities in Russia, including Jeruslan River (Annandale, 1915a), Lake Ladochowo in the district of Saratow (Abricossoff, 1927b), Talovka River (Behning, 1924). Hungary: Lake Balaton (Sebestyén, 1961). France: Arles, Bouches-du-Rhône (Wiebach, 1963a). Germany: Ryckflusz near Greifswald (Wiebach, 1963a).

Asia. Various localities in Japan, including Lake Biwa (Annandale, 1922a), the pond Goshogawara, Aomori prefecture (Toriumi, 1955a). Indonesia: lakes and ponds on the Garut plateau, West Java (Vorstman, 1928a). India: Nagpur, C.P. (ZSI), Bhim Tal, Kumaon, western Hima-

layas (ZMH). Mu-tan-k, Manchuria (Hozawa & Toriumi, 1941). Korea (Toriumi, 1941b). Formosa (Toriumi, 1942b).

Africa. Mabue, north of Lake Upemba, Congo (IPNC). Lake Bulera, Ruanda (Wiebach, 1964).

North America. Lake Erie (Rogick, 1941a; 1943a). Michigan and Indiana (Rogick & van der Schalie, 1950).

Central America and West Indies. Guatemala: San Pedro River near Paso Caballo in the Peten department (RMNH) and Pasion River east of Ceibol, Alta Vera Paz (RMNH). Netherlands Antilles: Curaçao and Klein Bonaire (Lacourt, 1955b).

It may be concluded from these distributional data that the species is probably cosmopolitan but shows great discontinuities. In Australia it has so far not been found.

For the palaeartic region it was long known only from the Volga region (Abricossoff, 1927b; his precise description makes confusion with other species impossible). Now that Wiebach (1963a) has found this species in western Europe, it must be assumed that it had been overlooked.

Biology. — The main substrate for the species is water plants, but it is also to be found on stones and shells of freshwater snails.

Plumatella philippinensis Kraepelin, 1887

(Pl. 14 fig. b; text-fig. 1a, b)

Plumatella philippinensis Kraepelin, 1887 (Libmanan River, Philippines); Lacourt, 1948; 1955a (part); Loppens, 1908.

Plumatella fruticosa - Vorstman, 1928a (not *P. fruticosa* Allman, 1844).

Plumatella (Afrindella) persica Annandale, 1919-1921a (Randa River near Jellalabad, Seistan); Borg, 1936.

Stolella evclinae - Marcus, 1942 (not *Stolella evclinae* (Marcus, 1921)).

Afrindella philippinensis-Wiebach, 1964.

Material. — Asia. Philippines: Libmanan River, Luzon, on *Vallisneria* (ZMH, B 92, leg. F. Jagor, don. Mus. Berlin 1886). India: Belgachi, Calcutta (as *P. repens* var. *coralloides* in *Spongilla carteri*) (ZMH, B 113, don. N. Annandale, 1907); Rajshal, eastern Bengal (ZMH, B 118, don. N. Annandale, 1907); Belgachia, Calcutta (USNM no. 5173); Zoological Gardens, Calcutta (USNM, no. 5172). Indonesia, Java: Sedang near Garut, Lake of Pendjalu, Botanical Gardens Bogor, Ponds near Leles, (ZMB resp. nos. 032, 034, 061, 074b); Pond Botanical Gardens in Bogor, and Lake of Leles, Garut (ZMA).

Africa. Kadia, Lac Kisale, Congo (IPNC).

Further, a slide of the type or paratype with the label "*Plumat. philippinensis* Statobl. Brl. Musesum" (ZMH); and four zoaria from the Botanical Gardens in Amsterdam (ZMA, May, 1898).

Description. — The zoarium is small, up to about 50×40 mm. In the initial phase branching is regularly dichotomous, thereafter it is characterized by markedly antler-like and fan-shaped growth: adherent with erect terminal parts, compact. The cuticula is fragile, translucent, dark brown, and according to present knowledge not incrustated. The number of tentacles is 44 to 48.

The F statoblasts are numerous, small, elongated-oval with parallel sides, regular in outline, angular at the poles; yellowish brown with a narrow dark ring around the capsule, which is relatively large; the annulus is narrow with an indistinct reticulation; 3 times wider at the poles than laterally; the annulus partially overlaps the capsule ventrally; the outer margin is smooth. Measurements: L 365 to 430 μ , but sometimes very long, up to 471 μ ; B 212 to 250 μ , L/B 1.6-2; the width of the annulus is 53 μ at the poles, 18 μ laterally; the diameter of the chambers is 9 μ . Some statoblasts are shorter than those of the typical form (text-fig. 1b): the annulus in these is somewhat wider at the poles and its network is more distinct. Thus, these statoblasts show a resemblance to the F statoblast of *P. casmiana*. S statoblasts are larger than the capsule of the F statoblast, rounded oval with a narrow annulus of equal width: the outer margin is regularly notched. Measurements: L 400 to 413 μ , B 267 to 320 μ ; the annulus is 12 μ wide. This species was described by Kraepelin in a footnote and consequently failed to become generally known, which explains various erroneous identifications.

Synonymy. — I consider *P. persica* to be a synonym of *P. philippinensis*. As judged from the not entirely distinct illustrations provided by Annandale (1919-1921a), which I had enlarged for better comparison with my own photographs, and the description, which agrees in details with the species under discussion, no doubt can be entertained here despite the fact that no type material of *P. persica* is available. Nor is *P. persica* a variety of *P. emarginata*, as Borg (1936) assumed. Annandale's assumption that the zoarium is composed of two layers, the lower layer containing S statoblasts and the upper F statoblasts, is of course incorrect. There is no second layer. The S statoblasts are always located in the basal parts of the tubes, which branch "further up". Annandale gives smaller sizes for the F statoblasts: L 289 to 374 μ , B 170 to 204 μ . The S statoblasts, like those of other species, according to Annandale vary widely in size. L 340 to 544 μ , B 255 to 272 μ .

The illustrations in Vorstman's paper (1928a) cannot represent *P. fruticosa*; they concern the species under discussion (Lacourt, 1955a).

At one time I assigned the material identified by Marcus as *P. fruticosa* to *P. philippinensis* (cf. Lacourt, 1955a). From the present state of our knowledge, I now believe it should be assigned to *Hyalinella punctata*: the regularity of the width of the annulus, which reaches far over the capsule dorsally, is

to be found only in *H. punctata*; the annulus does not always extend so far over the capsule, but this feature has been seen in European material.

Marcus (1942) later published new illustrations of his "*Stolella evelinae*". Comparison with his earlier publication (Marcus, 1941) gives the impression, however, that the second set of pictures concern another species. The statoblasts are longer, as is the capsule, and the annulus is narrower at the poles. To the extent that drawings can represent statoblasts accurately, I am of the opinion that the material in Marcus' 1942 publication should be assigned to *P. philippinensis*. These statoblasts closely resemble the adjacent illustration of *P. agilis*, a species to which *P. philippinensis* is closely related.

Wiebach was of the opinion (1964: 24) that my identification of sample 18/20 from Lake Kisale (preserved in IPNC) is erroneous. He points to a difference consisting of 2 to 3 additional rows of air chambers in the annulus of a statoblast in the Kisale material as compared to the usual type, but this type of F statoblast was already known to me from other material and it was on that basis that I made my identification. There is also too much variation in the "Medianschnitt-Diagram", which has not yet been sufficiently worked out.

Distribution. — Asia. The species was originally described for the Libmanan River and Lake Buhi on Luzon, Philippines (Kraepelin, 1887). It is also known from various places on Java, Indonesia (ZMB, ZMA, see above). India: Randa River near Jellalabad, Seistan (Annandale, 1919-1921a); Calcutta (ZMH, USNM); Rajshal, East Bengal (ZMH).

Africa. Kadia, Lake Kisale, Congo (IPNC). Lake Mohasi and Lake Lohango, Ruanda (Wiebach, 1964).

South America. Rio Ribeiro de Iguape, São Paulo, Brazil (Marcus, 1942).

All known localities are situated equatorially.

In May 1898 four zoaria were found in a hothouse of the Botanical Gardens, Amsterdam (Lacourt, 1955a). This, of course, is not a natural habitat.

Biology. — The stems and leaves of waterplants are used as substrate, but shells also serve this purpose.

Plumatella agilis (Marcus, 1942)

(Pl. 11 figs. a, b; pl. 15 fig. b; text-fig. 2a, b, c.)

Stolella agilis f. *typica* and f. *iheringi* Marcus, 1942 (described in detail with illustrations: São Paulo, in a tank on the grounds of the Department of Natural Sciences of the University).

Hyalinella agilis - Lacourt, 1955b.

Stolella indica - Wiebach, 1964, figs. 34, 35 (partim).

Plumatella javanica - Wiebach, 1967.

Material. — Asia. India, Calcutta (ZMH, B 114; ZSI, ZEV 3760/7, nos. 63, 74, 76, 77). Java (ZMB, nos. 004, 020, 025, 027, 033, 046, 057, 067, 071).

Africa. Congo (IPNC).

America. West Indies (RMNH, coll. Wagenaar Hummelinck, nos. 44, 66, 100).

Australia. Moorooka and Caboolture, near Brisbane (RMNH, leg. E. F. Riek).

Description. — The zoarium is open to compact, with antler-like branching of the tubes with cock's comb-shaped parts. The polypides are arranged in linear series which curl outwards, giving them the appearance of very small cock's combs. The number of tentacles in f. *typica* is 40 to 50, in f. *iheringi* 35 to 45, and about 50 in the Australian material. Length 3 to 5 mm. The F statoblasts are rather large and oval. Sometimes a slightly smaller F statoblast with a narrower annulus and parallel sides occurs (text-fig. 2 c). The capsule is large with a narrow annulus which partly covers the capsule on both sides but more on the ventral side; 2 to 2½ times wider at the poles than laterally. A form with a larger capsule and narrower annulus is rarely seen (text-fig. 2 b). The outer margin is smooth with a few indentations.

Measurements (in microns)

forma <i>typica</i>	L 380-440	B 216-258	L/B 1.5-2	1.71
forma <i>iheringi</i>	460-530	265-310	1.61-1.87	1.75
Caribbean Islands	373-427	200-240	1.86-1.78	1.82
Australia	413-427	240-254	1.68-1.72	1.70

Summarized: L 373 to 530 μ , B 200 to 310 μ ; capsule: l 265 to 306 μ , b 178 to 237 μ . L/B 1.6 to 1.9.

The annulus measures 40 to 66 μ at the poles, 19 to 26 μ wide laterally; the diameter of the chambers is 8 to 12 μ . The S statoblasts are rounded-oval or oval, with a narrow, equally wide annulus; the capsule and the annulus are both covered with a reticulation, the outer margin is notched. L 347 μ , B 266 μ , the annulus is 27 μ wide. Initially, no S statoblasts were known, but they were found in material from Bonaire and Java, supplementing the description.

Synonymy. — The zooids are often piled up on one another without an elongated part. There is therefore no reason whatever to maintain the genus *Stolella*, which is based on elongated zooids. Elongated zooids occur in many species, for example in *Fredericella* and *Hyalinella*. The cuticula shows widely differing appearances depending upon ecological circumstances, as

has been demonstrated for various species (Toriumi, 1956b). *Stolella agilis* f. *iheringi* is a form with a slightly larger statoblast. The number of tentacles and the size of the statoblasts is also variable in the Phylactolaemata. The formae *typica* and *iheringi* should therefore be discarded.

The giant form "*Stolella agilis tica*" is not a *Stolella agilis* at all. It is clear from comparison with the measurements and the drawing of Du Bois-Reymond Marcus (1953) that this is the large species *Plumatella toanensis*, also found by Rioja (1940a) in Mexico and published by him as *H. punctata*. This also explains the histological characters deviating from *P. agilis* described for this material by Du Bois-Reymond Marcus (1953).

Wiebach (1964) has recorded material under the name *Stolella indica*, some of which belongs to *P. agilis*. *S. indica* is a synonym of *H. punctata* rather than an independent species. The material assigned by Wiebach to *S. indica* belongs to two species. Examination of his illustrations shows conclusively that the short, wide, irregular statoblast in his figs. 32 and 33 and the regular, elongated statoblast in figs. 34 and 35 must belong to two different species. Despite the great variability of the statoblast, the range never shows such extremes. The measurements given by Wiebach for the specimens in figs. 34 and 35, i.e., $465 \times 270 \mu$ with an L/B value of 1.7, fall within the limits of the range of the statoblast of *P. agilis*; the localities of the finds fall within the known distributional area of the species; and the outlines of the statoblasts coincide. Wiebach gave no further information concerning the statoblasts shown in figs. 32 and 33, but they in all probability belong to *P. casmiana*.

Wiebach (1967) reported upon material from the Amazonas river system as *P. javanica*. I consider this material to be identical with *P. agilis*. Wiebach's figures of the various statoblasts agree with mine of the latter species, especially with the outlines of my text-figure 2. Wiebach reported his material from an area, viz., central Brazil, whence *P. agilis* was already known.

Distribution. — South America: southern and central Brazil, viz., Arredores de Porte Alegre in Rio Grande do Sul State, University grounds of São Paulo, São Paulo State, and Fortaleza, Ceará State (Marcus, 1942); Amazonas River system (Wiebach, 1967). Netherlands Antilles: Curaçao, Aruba, and Bonaire (Lacourt, 1955b).

Asia. India: Mangaldai, Assam (ZSI); Burhanpur, C. P. (ZSI); Bagra Hoshangabad, C. P. (ZSI); Shalimar, Lahore (ZSI); Calcutta, Zoological Gardens (ZMH). Indonesia: several localities in Java, viz. Kawa Kamodjaa, Tji Binung, pond in Botanical Gardens of Bogor, Lake Pendjaloe, Tji Tajan Lake near Lembang, Lake Tjigombong, Rawa Bening (ZMB).

Africa. Congo: "Albert National Park" (IPNC); Lake Bango, near the mouth of the Congo River; Lake Kisale (Wiebach, 1964).

Australia. Moorooka and Caboolture, near Brisbane (RMNH). This demonstrates the circumtropical distribution of the species.

Biology. — The substrate consists of living and dead water plants. On Aruba and Bonaire this species was found between algae in temporary ponds with a varying chlorinity.

Plumatella carvalhoi (Marcus, 1942)

(Pl. 15 figs. c, d)

Hyalinella carvalhoi Marcus, 1942 (an aquarium in São Paulo).

Plumatella repens var. *osburni* Rogick & Brown, 1942 (partim, excl. syn).

Material. — Pasion River in Guatemala (RMNH, don. Miss M. D. Rogick), identified as *P. repens* var. *osburni*, which this species resembles but from which it differs by a larger capsule of the F statoblast. Marcus (1942) found no S statoblasts, but these are numerous in the Guatemala material; this has been used to supplement the description.

Description. — The zoarium consists of linear series of zooids with antler-like branching; the cuticula is gelatinous and transparent; the polypides have 40 to 50 tentacles.

The F statoblasts are broadly oval with large capsules; the annulus is 2 to 2½ times wider at the poles than laterally; the outer margin is not entirely smooth, showing ravel here and there. L 328 to 387 μ ; B 210 to 242 μ ; the capsule is elongated oval, l 180 to 240 μ , b 156 to 188 μ ; the annulus is 50 to 74 μ at the poles, 27 to 32 μ wide laterally; the diameter of the chambers is 9 μ .

The S statoblasts are rounded-oval with a very wide annulus, carrying an extremely well-developed wide meshed reticulation; this reticulation is also visible on the capsule. The width of the annulus is equal, with an irregular, wavy outline: the outer margin is minutely notched. Measurements: 400 \times 267 μ , capsule 294 \times 173 μ , annulus 47 to 53 μ wide; diameter of the chambers 9 to 16 μ .

Distribution. — South and Central America. In addition to the type-locality, the species has also been found in the Pasion River east of Ceibol, Alta Vera Paz, Guatemala. This may concern an endemic species.

Biology. — The species is found on *Elodea* and other water plants.

Plumatella fruticosa Allman, 1844

(Pl. 11 fig. e; pl. 14 figs. a, c, d; pl. 15 fig. e; text-figs. 3a, b, 6b)

Plumatella fruticosa Allman, 1844b (Ireland, without further specification); Abricossoff, 1925a; 1925b; 1926b; 1927b; 1933; Allman, 1847; 1856; Annandale, 1908a;

1909b; 1912b; Borg, 1930; 1941; Braem, 1890; Cant, 1936; Căpuse, 1962; Carl, 1943; Carter, 1859; Hejsková, 1948; Hora, 1926; Kolosváry, 1964; Kraepelin, 1906; Lacourt, 1949a; 1949b; 1955; Levander, 1905; 1908; Marcus, 1940; 1942; Neistwestnova-Shadina, 1928; Murray, 1910; Prenant & Bobin, 1956 (synonymy); Protic, 1936; Schmidt, 1886; Sebestyén, 1959; Toriumi, 1941a; 1942a; 1954b (taxonomy); Vigano, 1964a; 1965; Vorstman, 1928a; 1928b; Wesenberg-Lund, 1897; 1907; Whitelegge, 1899; Wiebach, 1952 (expulsion statoblasts); 1953; 1954b (reproduction); 1958a (biology).

Alcyonella fruticosa - Goddard, 1909.

Plumatella coralloides Annandale, 1911.

Plumatella emarginata var. *fruticosa* - Pateff, 1924.

Plumatella princeps var. *fruticosa* - Davenport, 1899; 1904; Kraepelin, 1887; Richardson, 1925; Tretiakow, 1900.

Plumatella repens var. *fruticosa* - Carl, 1943; Rioja, 1940a; Rogick, 1934a; 1935a; Toriumi, 1941a; 1942a.

Plumatella repens - Annandale, 1907b (not *Tubipora repens* L., 1758).

Material. — Europe. The Netherlands: Beilerstroom and Dwingelosevaart in the province of Drente (RMNH). Denmark: island Seeland (ZMK).
Asia. Japan: pond near Sendai (BIS).

North America. Lake Beautiful, Forbidden Plateau, Vancouver Island, B.C., Canada (Provincial Museum Victoria, B.C.).

Description. — The zoarium is shrubby or consists of long tubes, adherent along only a small part of their extent, branching antler-like in the terminal parts. These terminal parts show a remarkable structure; usually, the branches are shed, leaving nothing more than stumps behind (text-fig. 6b); the ends of the tubes are swollen. The cuticula is dark reddish-brown, transparent, stiff, brittle, and sometimes incrustated. The polypides carry 30 to 50 tentacles.

The F statoblasts are elongate to spindle-shaped and numerous; the annulus is very wide at the poles, where it is 6 to 9 times wider than laterally; laterally, the annulus is very narrow. The network of the chambers is extremely distinct; the outer margin is smooth. L 468 to 600 μ , B 170 to 250 μ ; the annulus is 70 to 150 μ wide at the poles and 12 to 17 μ laterally; capsule l 270 to 363 μ , b 140 to 190 μ ; diameter of the chambers 10 to 12 μ . Once, a smaller form has been found in Upper Lake on Vancouver Island; it is less distinct and has been found together with a not quite characteristic S statoblast, but there is no doubt that this material belongs to *P. fruticosa*. There is resemblance with the narrow form of the statoblast of *P. casmiana* (compare pl. 13 fig. i with pl. 15 fig. e).

The very large S statoblasts are of gigantic dimensions: elongated-oval, L/B 2 to 2.6. The outer margin is undulating or angular: the annulus is wide, about 4 times wider at the poles than laterally, with a distinct reticulation; the outer margin shows a regular dentation. Measurements: L 430 to 702 μ ;

B 180 to 270 μ ; the annulus is 105 μ wide at the poles, 23 μ laterally; capsule l 526 μ , b 222 μ ; the diameter of the reticulation is 14 to 16 μ ; in one case a statoblast measured 960 \times 480 μ .

Distribution. — Europe. Almost everywhere from the coast of the Arctic Ocean as far south as the Pyrenees and the Balkans: Murmansk coast (Wesenberg-Lund, 1907). Ura, Lapland (Levander, 1908, statoblasts only). Southern Finland north to 63° N (Levander, 1908). Russia, but not yet in the northeastern part of the country (Abricossoff, 1927b). Norway (Wesenberg-Lund, 1907). Sweden (Borg, 1941). Central and western Europe, including Great Britain and Ireland (including Barra, Outer Hebrides: Cant, 1936), as far south as the Pyrenees (Allman, 1856). Lago Trasimeno in Italy (Vigano, 1964a). Yugoslavia (Protic, 1936). Balta Greaca, Rumenia (Căpuse, 1962). Bulgaria (Pateff, 1924).

Asia. Turkestan? (Abricossoff, 1927b). Japan (Toriumi, 1941a; 1942a).

North America. Canada: Upper Lake, Forbidden Plateau Area, Vancouver Island, B.C. (Carl, 1943). U.S.A.: Lake Erie (Rogick, 1935a) and a number of other localities (Davenport, 1899; 1904; Richardson, 1925; Rogick, 1934a; 1935a). Mexico: Lago de Xochimilco (Rioja, 1940a).

P. fruticosa is evidently restricted to the holarctic region, but has not yet been found in North Africa. Little is known about its occurrence in Asia, where the species has been found with certainty in Japan (Toriumi, 1954 b). Abricossoff (1927b) made a vague mention of its occurrence in Turkestan. There is no evidence of its presence in other parts of the world. The fairly numerous reports of the species from the Indian area and South America (Annandale, 1908a-1912b; Carter, 1859; Hora, 1926; Vorstman, 1928a; Marcus, 1942) are based on erroneous identifications and concern *P. philippinensis*. The extensive material of the Zoological Survey of India that I examined did not include *P. fruticosa*, but *P. philippinensis* was well represented. The sample from Calcutta (USNM nr. 5173) is likewise not this species but *P. philippinensis*, most investigators having overlooked the latter species. Annandale's (1910b) statement "statoblasts the length being twice the greatest breadth" might refer to *P. fruticosa*. But further on he added "the swim-ring, however, is as a rule not much broader at the ends than at the sides" which clearly shows that his material is not the present species but *P. philippinensis*. The illustrations given by Marcus (1942) and Vorstman (1928a, 1928b) clearly show their identification to be incorrect (Lacourt, 1955). The report made by Whitelegge (1889) from Port Jackson in Australia (see Goddard, 1934) is dubious since his description states: "the statoblasts resemble those of *P. fruticosa* in shape and are much narrower than those of *Alcyonella fungosa* (= *P. fungosa*)". Narrow statoblasts,

equalling those of *P. fungosa* in length, might belong to a species such as *P. emarginata*, and it is therefore possible that Whitelegge's material belongs to such a species but not to *P. fruticosa*. All these facts lead to the conclusion that *P. fruticosa* does not occur outside the holarctic province.

Biology. — Wesenberg-Lund (1897) observed no hibernation in northern Europe and saw no larvae, but the statoblasts were already formed in June. This species is also found in brackish water, e.g., in Lake Liesch-Morast, an alkaline lake with saline water in the northern Donaubanschaft in Yugoslavia at an altitude of 100 m, the depth of the lake being 1.3 m, with many marine and brackish-water algae as relics of the Pliocene inland sea (Protic, 1936). The bathymetric occurrence of the species ranges from the surface to a depth of several metres. *P. fruticosa* is a rather rare species, which as a rule is also not numerous locally.

II. Species of *Plumatella* with inequilateral statoblasts:

Plumatella repens (Linnaeus, 1758)

(Pl. 12 fig. a; pl. 15 figs. f, g; text-fig. 6c)

Tubipora repens Linnaeus, 1758 (without specification of locality).

Plumatella repens - Abricossoff, 1924; 1925a; 1925b; 1926b; 1927b; 1933; Allman, 1844; 1856; Annandale, 1907b; 1910b; 1915c; Arndt, 1943; de Beauchamp, 1939; L. S. Berg, 1925; K. Berg, 1938; 1948; Borcea, 1924; 1926; Borg, 1930; 1936; 1936a; 1941; Brehm, 1950; Brezeanu & Prunescu-Arions, 1962; Brown, 1933 (internal budding and limnology); von Büren & Leiser, 1962; Cant, 1936; Căpuse, 1962; Car, 1911; Chirica, 1906; Cunnington, 1920; Davenport, 1899; 1904; 1918 (in Ward & Whipple); Deevey, 1942; Dendy, 1906; Despax, 1926; Dudich, 1944; 1947; 1948; Garbini, 1895; Gasser, 1962; 1962a (histochemistry of statoblast; histology, cytology and histochemistry of ectoderm); Gauthier, 1928; Geldiay, 1949; Goddard, 1909; De Guerne, 1888; Hejsková, 1948; Hickman & Scott, 1933; Hrabě, 1942; Jullien, 1885; Knight Jones, 1954; Kolaczkowska, 1936; Kolosváry, 1964; Kraepelin, 1914; Lacourt, 1949a; 1949b; Lamarck, 1816; Lange de Morretes, 1940; Levander, 1908; Linder, 1904; Loppens, 1906a; 1908; 1910a; 1910b; Machado, 1942; Main, 1953; Marcus, 1940; Margalef, 1948; 1955; Meuche, 1939; Murray, 1910; Nichols, 1912; Oka, 1907b; Økland, 1964 (biology); Osburn, 1940; Pateff, 1924; Prenant & Bobin, 1956 (synonymy); Rawson, 1953; Remy, 1928; Richard, 1896; 1897; Ridley, 1886; Rioja, 1940; 1940a; Robertson, 1900; Rogick, 1934a; 1935a; 1937a; 1940a; 1941 (modifications of growth); Rogick & Brown, 1942; Rogick & van der Schalie, 1950; Rousselet, 1907; Sars, 1896; Schmidt, 1886; Schodduyn, 1925a; 1925b; Scott & Duthie, 1895; Sebestyén, 1959; Seurat, 1922; Toriumi 1941a; 1942a; 1955 (taxonomy and synonymy); Ulmer, 1913; Valkanov, 1932; Vängel, 1894; Viganò, 1964a; 1965; 1966; Wesenberg-Lund, 1879; 1907; White, 1917 (biology); Whitelegge, 1883; Wiebach, 1953; Zirpolo, 1925; Zschokke, 1900; Zykoff, 1905; 1908.

Plumatella polymorpha var. *repens* - Kraepelin, 1887; Arndt, 1926; Barrois, 1893-1894; Davenport, 1899; 1904; Kraepelin, 1892; 1893; M. Meissner 1893; 1897; 1898; Wal. Meissner, 1904; Richardson, 1925; Trauberg, 1940; Tretiakow, 1900; Zykoff, 1890.

Plumatella casmiana Oka 1907b (partim).

Material. — Europe. Many localities in the Netherlands (RMNH; ZMA; Zoologisch Laboratorium, Amsterdam; Lacourt, 1949b). Many localities in Belgium (ISNB, Lacourt, 1949a). Denmark (Bergens Museum, Norway).

America. Aquarium tanks in New Jersey and New York (American Museum of Natural History). Lake Erie (RMNH, don. Rogick). Poor House Pond, Halifax, Nova Scotia (RMNH).

New Zealand. Christchurch (USNM 5476).

Description. — The zoarium is adherent and consists of long tubes growing radially and repeatedly branched in an open manner, but sometimes very compact with erect tubes. The cuticula is light yellow to clear brown; the polypides carry 40 to 60 tentacles.

The F statoblasts are small, broadly oval, flat on one side, with a nearly circular capsule which often carries a reticulation. The annulus is not wide; it is twice as wide at the poles, where it is somewhat elongated, as laterally, and twice as wide dorsally as ventrally; dorsally half its width overlies the capsule. Some examples show a narrow border (about 5 μ wide) around the annulus; the outer margin is slightly wavy in correspondence with the hexagonal chambers. Measurements: L 330 to 450 μ , B 212 to 280 μ ; L/B 1.28. Capsule l 240 to 290 μ , b 200 to 230 μ ; annulus 37 to 47 μ wide at the poles, 18 to 23 μ laterally; the diameter of the chambers is 7 to 10 μ . Aberrant F statoblasts are unknown.

Author	region	F statoblast		S statoblast	
		length	width	length	width
Trauberg (1940)	Latvia	254-364	182-275	309-491	236-431
Hickman & Scott (1933)	Tasmania	377-677	377-677	447	338
Toriumi (1941a, 1942a, 1955)	Japan	330-410	240-310	—	—
"	Fouta-numa crater lake	370-450	290-330	—	—
Lacourt	Western Europe	330-450	212-280	390-600	390-515

A cuticular striation as found in the present species, characterizes species with a soft cuticula such as *H. punctata* and *P. casmiana*. Further study of a much more abundant material and of ecological conditions might provide an explanation of the great diversity in the state of the cuticula and the chitin formation of the capsules of the statoblasts of different species described in the detailed discussion by Toriumi (1955). The measurements given by Trauberg (1940) for Latvian material are smaller than those generally found. Hickman & Scott (1933) found larger statoblasts in material from Tasmania; their description and the measurements of the sessile statoblasts point to the species under discussion, but their report is nonetheless dubious; the large

statoblasts of their specimens resemble strongly those of *H. punctata*, whose zoarium sometimes resembles that of *P. repens*. Toriumi (1955) has published measurements of Japanese material. Variations in a cosmopolitan species are of course to be expected. Measurements (in microns) of my material and those from literature are listed above.

The S statoblasts are large and rounded oval, the annulus is wide, with a uniform width; the capsule of old statoblasts shows reticulation; the outer margin is notched. Measurements: L 390 to 600 μ , B 390 to 515 μ ; capsule l 410 to 500 μ , b 330 to 350 μ ; annulus 46 to 58 μ wide roundabout. L/B 1.25.

Synonymy. — The old literature contains many synonyms, as must be expected in a time in which the exchange of information was difficult and chauvinism was prevalent, even in the field of biology. Jullien (1885) and Prenant & Bobin (1956) have published a list of the synonyms. Various so-called varieties appear to have been based only on developmental stages. Toriumi's retention (1941a) of var. *typica* does not seem justified. Nor can I agree with Toriumi (1955) that *P. fungosa* is a phenotype of *P. repens*. The statoblasts of *P. fungosa* are larger on the average and do not fall within the range of variation of those of *P. repens*. Furthermore, the developmental pattern of *P. fungosa* is essentially different. The fusion of the tubes (agglutination of the ectocyst; Toriumi, 1955: 62) in the *Plumatella* group only occurs in *P. fungosa*. Toriumi further based his conclusion on various obscure descriptions given by old authors, which could best be left out of consideration.

Distribution. — Europe. Throughout Europe including the large and small western islands, like the Hebrides and the Shetlands, the Pyrenean and Balkan peninsulas, and, in Italy, Lake Trasimeno and Sicily. In the north the species has been found, be it only as statoblasts, in Lake Kopustjaur on the Kola Peninsula, Lake Bolschoje Sidorowskoje on the Beluschi Peninsula, and Novaja Semlja, South Island (Abricossoff, 1933), and in the Advent Bay region of Spitsbergen (Richard, 1897). Eastwards it is known as far as the Volga River (Abricossoff, 1927b).

Asia. Siberia: West Siberia, drainage system of the Irtish, Lake Saissan, Lake Baikal (Berg, 1915); Pamir Mountains (Marcus, 1940); Amur, Ussurian region (Abricossoff, 1927b). Japan: a number of localities (Oka, 1907; Toriumi, 1941a; 1942a; 1955). Korea (Toriumi, 1941b). China: Shanghai (Zschokke, 1900). Vietnam: Tonkin (Richard, 1894). India: Calcutta (Annandale, 1907b). Syria: Oronto River (Barrois, 1897). Turkey: Tsoubouk Dam near Ankara (Geldiay, 1949).

Africa. West Africa: Azores (Richard, 1896), Canary Islands (Richard, 1898); Senegal (Ridley, 1886); Niger (Ridley, 1886). North Africa: Algeria,

oueds near Algiers and Bône (Gauthier, 1928; Seurat, 1922); marshes of Kharezas (Sars, 1896). East Africa: White Nile (Meissner, 1897); Upper Nile (Ridley, 1886); Victoria Nyanza, Edward Nyanza and Albert Nyanza (Cunnington, 1920; Kraepelin, 1893; 1897; Meissner, 1893; Ulmer, 1912); Lake Tanganyika (Rousselet, 1907); Bibisande in Ugogo Uniamwesi (Meissner, 1898). South Africa: Neudamm (Kraepelin, 1914).

North America. From Kadiak, Alaska (Robertson, 1900) throughout all of North America (Brown, 1933; Davenport, 1899; 1904; Rogick, 1934-1941; White, 1917; USNM) to Lago de Patzcuaro and Lago de Xochimilco, Mexico (Rioja, 1940; 1940a).

South America and West Indies. Brazil: São Paulo (Kraepelin, 1893); Gualyba near Porto Alegre, Rio Grande do Sul (Kraepelin, 1897; Lange de Morretes, 1940). Peru: Lake Titicaca (de Beauchamp, 1939). Puerto Rico (Rogick & Brown, 1942; Osburn, 1940).

Australia and New Zealand. Australia: Moore Park, New South Wales (Whitelegge, 1883); Queensland, Victoria, and South Australia (Goddard, 1909; Hickman & Scott, 1933); Punch Bowl Reservation near Launceston, Tasmania (Hickman & Scott, 1933). New Zealand: Napier (Hamilton, 1879); moat at Christchurch (USNM 5476).

Thus, *P. repens* is a cosmopolitan species which, judging by its occurrence at high northern latitudes, can tolerate low temperatures and would therefore occur less frequently in tropical regions. In agreement with this is the small number of localities in the Indian region. The almost complete absence in South Africa is striking, especially in contrast to the numerous localities in the African Lake Region. These latter are possibly to be explained by avian transport of the statoblasts (de Guerne, 1888), but not all the species of Phylactolaemata found in the migrational areas of birds occur in the Great Lakes.

In a summary of the distribution of *P. repens*, Seurat (1922) also mentioned Malacca and the Philippines, but I have been unable to find the source of these data.

Biology. — This species occurs mainly on large, flat substrates; often on the underside of the leaves of waterlilies; it was once found on a breakfast plate and on a plate of glass, and also on sluice walls; it occurs on many other substrates as well.

Meuche (1939) pointed out that *Plumatella* occurs on substrates carrying little or no other growths, and he thought that some species instinctively settle on the substrate that they require: thus, *P. fungosa* on strong, firmly secured substrate such as branches and roots, and *P. repens* chiefly on a flat substrate. My observations indeed supply grounds supporting this view.

Berg (1938) confirmed the opinion advanced by Wesenberg-Lund (1897) that where *P. repens* occurs in a particular area, *P. fungosa* is lacking. I myself have never found the two species in the same area in The Netherlands. *P. repens* was the only of the two species found in the Vecht River region in the province of Utrecht, while *P. fungosa* was met with in the peat-bog ponds around the village of Roelofarendsveen in the province of South Holland.

P. repens is common almost everywhere it occurs and is also found in brackish water. Its bathymetric distribution is usually limited to the upper layers; it is found down to a depth of 3 m, and in exceptional cases to a depth of 30 m. As to altitude, the species occurs from slightly below sealevel (The Netherlands), to high altitudes, in mountain lakes in the Alps up to the snow-line, and in the Pamir Mountains up to 3950 m at temperatures never higher than 10° C. A range of pH has been measured between 7.9 and 8.4.

The main growth period falls in low-lying regions between June and October and lasts about 22 weeks: in the mountains from July to September, lasting 8 to 10 weeks. In the north, e.g., in Denmark this period extends from August to September, in Australia from October to December, and in Calcutta during the rainy season.

Marcus (1941; 1942) observed the expulsion of statoblasts through a vestibular pore in South America specimens. Wiebach (1953) made the same observation in Europe. This phenomenon has since been observed in holarctic species: *P. fruticosa*, *P. emarginata*, *P. repens*. Knight-Jones (1954) found dexioplectic metachronism (relations between metachronism and the direction of ciliary beats in Metazoa) only in adults of *P. repens*.

According to De Guerne (1888), all kinds of organisms, including statoblasts, can stick to the feet, bill, and feathers of birds and thus be distributed over large areas. The result, however, is not so extensive as De Guerne suggested; if it were, the aquatic fauna would be more uniform throughout the world.

Subfossil statoblasts of *P. repens* are known from peat deposits. Deevey (1942) reported statoblasts found in boring samples of sediments taken from the bottom of Linsby Pond (Connecticut, U.S.A.) with a maximum age of 11390 years.

Plumatella fungosa (Pallas, 1768)

(Pl. 12 fig. d; pl. 15 figs. h, i; text-fig. 7a)

Tubularia fungosa Pallas, 1768 (Stariza River, Russia).

Plumatella fungosa - Abricossoff, 1925a; 1925b; 1927a; 1927b; Annandale, 1907b; 1919b; Barrois, 1894; Becker, 1938; Bertrand, 1950; Borcea, 1924; 1926; 1931; Borg

1930; 1941; Braem, 1897 (reproduction); 1911a (parasites); Brien, 1952 (larvae); Căpuse, 1962; Car, 1911; Carrada, 1964; Chirica, 1906; Davenport, 1899; 1904; 1918; Dudich, 1947; Du Plessis-Gouret, 1885; Harmer, 1913; Hassell, 1842; Hejsková, 1948 (positive thermophilia and negative phototropism); Hozawa & Toriumi, 1941; Hurrell, 1927; Hyatt, 1866; Lacourt, 1949a; 1949b; Lee, 1936; Levander, 1908; Marcus, 1940; 1950; W. Meissner, 1904; Prenant & Bobin, 1956 (synonymy); Rioja, 1940; Rogick, 1935a; 1937a; Schmidt, 1886; Schröder, 1913 (parasites); Sebestyén, 1951; 1959; Trauberg, 1940; Vigano, 1964a; 1965; 1966; Wesenberg-Lund, 1897 (biology); 1907; White, 1917 (biology); Zykoff, 1890; 1905.

Alcyonella fungosa - Allman, 1856; Du Plessis-Gouret, 1885; Laurie, 1901.

Plumatella polymorpha var. *fungosa* - Kraepelin, 1887; Barrois, 1893-1894; Davenport, 1899; 1904; 1918 (in Ward and Whipple); Neistwestnova-Shadina, 1928; Trauberg, 1940; Zykoff, 1890.

Plumatella repens var. *fungosa* - Annandale, 1910b; Braem, 1911a; Dudich, 1944; 1948; Hozawa & Toriumi, 1941; Loppens, 1906a; 1908; 1910a; 1910b; Rogick, 1935a; Schmidt, 1886; Toriumi, 1955; Vängel, 1894.

Material. — Numerous localities in The Netherlands (RMNH, ZMA, the zoological laboratories of the Universities of Leiden and Amsterdam; Lacourt, 1949b). Specimens from a number of localities in Belgium (ISNB; Lacourt, 1949a).

Description. — The zoarium is spindle- or bulb-shaped when growing on cylindrical substrates; cushion-like or hemispherical on flat substrates, sometimes lobulate. It consists of tubes that are attached to each other over their entire length. The polypide has 40 to 60 tentacles.

The F statoblasts are broadly oval, somewhat irregular in outline, and angular; they are flatter on one side and therefore irregularly triangular. The capsule is almost round; the annulus is 2 to 3 times wider at the poles than laterally and extends far over the capsule dorsally, leaving an open space with a diameter of about $\frac{1}{3}$ the length of the statoblast; the outer margin is slightly undulated. Measurements: L 350 to 465 μ , B 230 to 340 μ ; L/B 1.4; capsule l 210 to 325 μ , b 184 to 270 μ . Extreme measurements: L 291 to 491 μ , B 210 to 432 μ . The annulus is 70 μ wide at the poles, 23-35 μ laterally; the diameter of the chambers is about 9 μ . Aberrant F statoblasts are not known.

The S statoblasts are rounded-oval, usually with a narrow annulus of equal width. In an older stage the annulus is covered with a thick reticulation. The outer margin is finely notched. Measurements: L 480 to 690 μ , B 365 to 500 μ . Extreme measurements: L 364 to 800 μ , B 291 μ . The width of the annulus is about 23 μ .

The spindle-shaped zoaria sometimes reach a length of $1\frac{1}{2}$ m, the bulb-shaped ones a diameter of 10 cm. The spindle-shaped form has been supposed to originate from numerous sessile statoblasts whose tubes become fused. However, they could probably also develop from free statoblasts and larvae,

via an originally '*repens*'-like young zoarium, by means of heavy branching and a compact, erect growth of the tubes (Braem, 1911a). The growth of the zoaria sometimes seems to be inhibited or to take an abnormal course, which may have been the case for the material from Issuk-Kul in Turkestan (Braem, 1911a). This material is also discussed by Abricossoff (1927b) and Marcus (1950). According to Braem's (1911a) description, it is nevertheless this species. Large zoaria showing zones in cross-section have been interpreted as colonies that had persisted for several years, the zones indicating hibernation (Wesenberg-Lund, 1897). Braem (1911a) excluded this possibility on the basis of his own observations: the zoaria never survive their first year. I agree with Braem that these zones are the result of interrupted growth due to external causes during the season; traces of injury can sometimes be seen on the surface. Other causes are also undoubtedly present, such as variations in the temperature or chemical conditions of the water, etc. The zones are pathological phenomena, and therefore of little importance.

The zoaria sometimes show shrubby projections (*forma coralloides* Allman, 1856) which may represent new colonies originating from larvae, but this has not yet been established. No report has been made of the presence of statoblasts in these projections for *P. fungosa*, and the possibility remains that they originate from larvae of other species.

The zoaria also sometimes show massive offshoots consisting of bundles of closely fused tubes. In these cases the surface remains rounded, however, in contrast to other species, for example *Hyalinella punctata*, in which the terminal parts of the tubes are free. It is a fact that somewhat irregular, imperfectly rounded oval statoblasts of *H. punctata* cannot be distinguished from those of *P. fungosa*; in compact zoaria of *H. punctata* this has undoubtedly led to erroneous identifications. The identification must therefore also be based on the character of the zoarium of *P. fungosa*, even though a few typical statoblasts are always present in any given zoarium.

Wesenberg-Lund (1897) gave the name "*forma repens*" to the zoaria of *P. fungosa* with massive offshoots; this denomination should be discarded because of its confusion with *P. repens* and because the naming of developmental forms serves no useful purpose. The older authors created great confusion by naming all kinds of developmental forms, which furthermore themselves show many different transitions. Seemingly, various species can show the same zoarial shapes. *P. fungosa* "*forma repens*", the "*fungoid*" form of *H. punctata*, the compact zoaria of *P. repens*, *P. emarginata*, etc. all resemble each other. For this reason, only the uncomplicated zoarial forms should be primarily described; the complications can be given secondary

attention, but identification must consistently depend upon the statoblasts.

Small statoblasts are sometimes reported. I am inclined to wonder, however, whether some of the reports of small statoblasts of *P. fungosa* do not concern those of compact colonies of *P. repens* (L.), whose statoblasts have the same shape as those of *P. fungosa* but are smaller. However, *P. fungosa* can always be recognized from the completely fused tubes, being the only *Plumatella* species yet known with this characteristic.

Trauberg (1940) gave measurements of $291 \times 218 \mu$ for the statoblasts of material from the Baltic region, but since the measurements given by this author for other species are consistently smaller than those of most authors, there might be some question as to the accuracy of his measurements. On the other hand, most of the reports of *P. repens* var. *fungosa* concern *P. fungosa*, as indicated by the descriptions. Their authors have considered the species *P. fungosa* as nothing more than a variety of *P. repens* and in this instance mistakenly attributed too little value to the shape of the zoarium.

Distribution. — Europe. In the older literature, various species have unmistakably been confused, but it can be concluded from the abundant trustworthy data that *P. fungosa* occurs virtually throughout Europe, including Great Britain and Ireland, and as far east as the Ural and the Caucasus. In the north it is found in southern Finland up to 63° N. latitude, but not in the northern part of Russia (Abricossoff, 1927b), and in the south as far as Lago Trasimeno in Italy, Sardinia, Croatia and the Danube, but it has not yet been found in the Iberian, Italian and Balkan peninsulas, nor is it known from North Africa.

Asia. U.S.S.R.: West Siberia (Abricossoff, 1927b); Saissan Lake and Irtisch (Zykoff, 1905); Baikal Lake (Abricossoff, 1927b); Issyk-Kul in the Kara-Su, Turkestan (Braem, 1911a). Manchuria: Mukden City (Hozawa & Toriumi, 1941). China: Peking (Lee, 1936). Syria: marshes of the Oronto River near Lake Homs (Barrois, 1894).

North America. The species occurs throughout North America (Davenport, 1899; 1904; 1918; Hyatt, 1866; Rioja, 1940; Rogick, 1935a; 1937a; White, 1917; USNM).

The northern and southern limits of the species are still unknown. Annandale's supposition that the species occurs in the Indian region so far has not been confirmed.

Biology. — *P. fungosa* avoids the superficial water layers and reaches a depth of several metres. Its altitudinal range is very great, extending from below sealevel (The Netherlands) to an altitude of 2116 m in mountain lakes.

This species is found exclusively on sturdy, firmly-embedded, or compact

substrates: branches, roots, stones, bridge supports, walls (Becker 1938); often also on shells of Gastropods and fresh-water mussels, like *Anodonta*, *Unio*, *Dreissena* (on the siphonal side), once it was found on *Astacus leptodactylus* Eschscholtz; never on green parts of plants. It has also been found on live *Cardium*, *Balanus* and reed stalks in the brackish Lake Zmeica in Rumania near the coast of the Black Sea (Borcea, 1931) and in western Europe in the vicinity of harbours, even in polluted water (Borg, 1930). Trauberg (1940) reported that the zoaria sometimes acquire a dark bluish-green colour from the alga *Phormidium fragile* (Meneghini). According to Bertrand (1950), 1 kilogram dry weight of this species contains 16.8 milligrams of vanadium. *Plumatella fungosa* sometimes shows the presence of parasites: Schröder (1913) mentioned the microsporidean, *Nosema bryozoides* Korotneff, *Buddenbrockia plumatellae* O. Schröder and species of Haplosporidia. Braem (1911a) also found the first two species.

III. *Plumatella* species with medium-oval statoblasts:

***Plumatella javanica* Kraepelin, 1906**

(Pl. 15 fig. j)

Plumatella javanica Kraepelin, 1906 (pond near Tjitajam on Java); Annandale, 1910b; 1910c; 1911; Loppens, 1908; Toriumi, 1952d; Vorstman, 1928a; 1928b; Wiebach, 1964 (Medianschnitt-Diagram of statoblasts).

Plumatella emarginata - Hastings, 1929a (not *P. emarginata* Allman, 1844).

Material. — Asia. India (ZSI): Chaibassa; Lucknow; Puela waterworks; Pashok, eastern Himalayas; Siripur, Saran District, Bengal (USNM 5174); Lake Labugama on Ceylon (ZSI P. 161/1, erroneously as *P. longicemmis*). Java: a number of localities including Tjitajam near Bogor (ZMH, B 98, syntype, don. Kraepelin); Botanical Gardens, Bogor (ZMB, ZMA). Sumatra: Ajer Teganang (ZMB).

Polynesia. Lake Vaihiria, Tahiti (British Museum, don. A. B. Hastings).

America. East Sister Island, Canada (RMNH, don. M. D. Rogick). I found this material of *P. javanica* among other material sent me by Miss M. D. Rogick.

Description. — The zoarium is compact, and entirely adherent; it has very thin, parallel, long main branches, which are often further divided, forming a felty blanket. The cuticula is extremely fragile, dark brown, transparent, sometimes incrustated with detritus. The polypides are usually arranged linearly and are numerous; the number of tentacles is 20 to 45.

The F statoblasts are numerous, oval to elongated oval, and of variable shape but aberrant forms are unknown. The capsule is almost round; the annulus reaches far over the capsule dorsally and is about 3 times wider at

the poles than laterally; the outer margin is smooth. Measurements: L 373 to 400 μ , B 200 to 240 μ ; the width of the annulus is 67 to 80 μ at the poles, and 13 to 27 μ laterally. Capsule l 240 μ , b 180 μ ; the length of the bare space is 107 to 133 μ , its width \pm 80 μ ; the diameter of the chambers is 12 μ .

The S statoblasts are not numerous; they are rounded-oval, sometimes large and elongated, with or without a narrow annulus that is of constant width. The surface of the statoblast is entirely covered by a reticulation; its outer margin is dentate. Measurements: L \times B about 480 \times 280 μ ; the annulus is 20 μ wide. The diameter of the spaces in the reticulation is 8 μ . Abnormal statoblasts of about 427 \times 267 μ have been observed.

The polypides sometimes show a proximal elongation also found in other species. *Plumatella javanica* could be called a "small *P. emarginata*" form, distinguishable from *P. emarginata* by the thinner, closely packed tubes, the compact habit, and the smaller statoblasts. This resemblance misled Hastings when she identified material of *P. javanica* from Lake Vaihiriae on Tahiti as 'probably *P. emarginata*'.

Distribution. — Asia. India: northern part of the Indian peninsula to the Himalayas, including Calcutta and Travancore (Annandale, 1910b), Lucknow (ZSI); Darjeeling District (ZSI); Mangaldai in Assam (ZSI); Puela waterworks in Bengal (ZSI); Siripur, Saran District, Bengal (USNM). Ceylon: Lake Labugama (ZSI). Burma: Shneli River, Northern Shan States (ZSI). China: Mong Pan, Yunnan (Annandale, 1910c). Indonesia: Ajer Teganang, Sumatra (ZMA); a number of localities on Java (Vorstman, 1928a; 1929b; Kraepelin, 1906; ZMA, ZMB).

Africa. Lake Upemba, Congo (Wiebach, 1964).

Polynesia. Lake Vaihiriae, Tahiti (Hastings, 1929a).

North America. East Sister Island, Lake Erie (RMNH, don. Rogick).

P. javanica thus occurs predominantly in the Indian province with a possibly artificial distribution in North America.

Biology. — This species is common where it occurs and is found on waterlilies, submerged wood and stones. It may have been imported into North America along with tropical plants.

***Plumatella longigemmis* (Annandale, 1915)**

(Pl. 15 fig. k; text-fig. 4a, b, c, d)

Plumatella (Hyalinella) punctata var. *longigemmis* Annandale, 1915a (pond on Barkuda Island in Lake Chilka, Garjam District, Madras Presidency).

Plumatella longigemmis - Annandale, 1922b; Marcus, 1942.

Plumatella bombayensis Annandale, 1908b; 1910b.

Plumatella repens var. *osburni* Rogick & Brown, 1942 (partim, description and figures, Pasion River near Ceibol, Alta Vera Paz, Guatemala).

Plumatella osburni - Toriumi, 1952c (taxonomy).

Hyalinella osburni - Lacourt, 1955b.

Plumatella pseudostolonata Borg, 1940a (Tschinua Senze, Congo).

Plumatella auricomis - Lacourt, 1948 (not *P. auricomis* Annandale, 1913).

Plumatella emarginata - Monod, 1950 (not *P. emarginata* Allman, 1844).

Material. — Asia. Type-material from Barkuda Island (ZSI 6671/7; ZMB 28). Lake Labigama, Ceylon (ZSI P 162-1). India: Igatpuri Lake (USNM 5166 as *P. bombayensis*); Bhim Tal, Kumaon (USNM 5167); Calcutta, Zoological Gardens (USNM 5172). Indonesia: Lake of Madiun, E. Java, and Botanical Gardens, Bogor, West Java (ZMB 003, 015).

Africa. Congo: Lac Ndalaga and Lac Lukulu (IPNC); Mabue, (IPNC). Bibisande in Ugogo Uniamwesi, E. Africa (only statoblasts, ZMH B 78 and 79).

West Indies. Netherlands Antilles: Aruba and Bonaire (RMNH). Through the kindness of Mr. C. Barnard Lewis, Curator of the Kingston Museum I received from Mr. Horace Vendryes, biologist connected with the Water Commission at Kingston, Jamaica, a communication (15.VI.1946) with microphotographs of an F statoblast and of a polypide with about 30 tentacles from Jamaica. The shape of the statoblast, the number of tentacles, and the transparent cuticula indicate that this material belongs to the present species. This locality is consistent with the other known localities of the species in the Carribean.

Description. — The zoarium is adherent, with erect terminal parts; the tubes show antler-like branching. The cuticula is transparent and thick, with strong or without incrustation; the number of tentacles is 20 to 40.

The F statoblasts are medium large, oval to broadly oval, sometimes narrow and with parallel sides, with a relatively small capsule which is almost round (see fig. 4, illustrating different outlines). The annulus is very wide, broadly rounded at the poles where it is 2 to 6 times wider than laterally; the lateral width is variable. The annulus extends halfway over the capsule; the outer margin is smooth. Measurements: L 352 to 444 μ , B 200 to 281 μ ; capsule l 186 to 250 μ , b 133 to 187 μ . The width of the annulus is 90 to 110 μ at the poles, and 26 to 60 μ laterally; the diameter of the chambers is 9 to 14 μ . L/B = 1.6-1.9. In material from the Congo, I found the following measurements of the F statoblasts: L 498 to 531 μ , B 232 to 283 μ ; capsule 327 \times 199 μ ; width annulus 106 μ polarly, 17 μ laterally; the diameter of the chambers is 14 μ . As in many species, the width varies. For the African material in the Hamburg Museum measurements of the statoblasts are: L \times B = 429 \times 286 μ ; of the capsule l \times b = 286 \times 214 μ .

The S statoblasts are round to rounded oval with a wide to very narrow

primary annulus of constant width, or with the annulus irregularly lobulated and turned upwards; the capsule and the annulus are both covered with a reticulation, which as a rule is very distinct on the annulus but can be absent; it is present in all African material. The outer margin is minutely serrated and notched. Measurements: L 320 to 462 μ , B 220 to 322 μ ; capsule l 260 to 375 μ , b 180 to 250 μ (but 150 to 160 μ in the Hainan material examined by Toriumi, 1952c); the annulus is 35 to 75 μ wide.

The zoarium may have an open form with long tubes but can also be compact. Typically, the F statoblasts are wide, but narrow ones also occur. These narrow statoblasts may have suggested the name "*longigemmis*" to Annandale. The diameter of the capsule is 54 to 57% of the length of the statoblast. *P. longigemmis* can be distinguished from *H. punctata* by its smaller capsule and the greater polar width of the annulus for the same total length of the statoblast.

Synonymy. — With some reservations, I consider *P. bombayensis* synonymous with *P. longigemmis*. Annandale's description of the F statoblasts of the former species as "elongate, often irregular outline; the swim-ring well developed and broad; the central capsule profusely and regularly tuberculate" is not clear. Annandale compared *P. bombayensis* with "*P. polymorpha*" and "*P. princeps*". To judge from the illustrations of F statoblasts of *P. bombayensis* (cf. Annandale, 1908b), however, there is no direct relation between these species, and *P. bombayensis* must be considered identical with *P. longigemmis*. This implies that S statoblasts of *P. longigemmis* are also known from Annandale's description of those of *P. bombayensis*. The material of *P. bombayensis* in the U.S. National Museum contains only S statoblasts; no type material seems to exist in the collection of the Zoological Survey of India. Annandale's rather cursory treatment of the Bryozoan material makes often certain identification impossible. Consequently, the identity of the two species cannot be proved though this is very probable.

H. osburni clearly is a synonym of *P. longigemmis*. This is evident from a comparison of the statoblasts; the descriptions, which I originally prepared from material of both "species" separately, agree in details. The character of the zoarium, the shape and the measurements of the F statoblasts and the capsule are the same in both descriptions. The statoblasts vary slightly in width and outline, as they do also, for example, in *P. emarginata*; in that species statoblasts can be found that are broadly oval to elongated, varying from a rounded outline to a form with parallel sides in a single zoarium. My 1955 paper gives an illustration of the latter shape, but the oval form is also present, as in some Caribbean material.

There is no good reason to consider *H. osburni* a variety of *P. repens* as

did Rogick & Brown (1942). The F statoblasts bear no resemblance whatever to those of *P. repens*: the small capsule and wide annulus as well as the thick, transparent cuticula, which, however, according to Rogick & Brown's description can also be thin, characterize the present species as valid. Annandale did not know the S statoblasts of this species.

P. pseudostolonata also is a synonym of *P. longigemmis*. In the material described as *P. pseudostolonata*, the annulus of the F statoblasts is somewhat narrower and the proximal parts of the zooids somewhat thinner and in some cases elongated; but these are not features on which to establish a separate species. The cuticula is not thick nor hyaline. Thin proximal parts of zooids occur in other species as well. In his description of African material, Borg (1940a) stated that the branching of the tubes often occurs in pairs: 'often', thus not consistently. In many cases what one author describes as absolute, proves to be absolutely different elsewhere. The structure of the zoaria has been demonstrated to be extremely variable, even within one species. Many factors, such as origin from a statoblast or a sexual form of reproduction, age, ecological differences as temperature, etc., all have an influence on the shape, which then cannot be considered to be specific. S statoblasts are also known for *P. pseudostolonata*. Given the sparse localities of the material in Asia and Africa, the scattered literature and the absence of a summary, duplications in the descriptions of a species were to be expected. I place this species in the genus *Plumatella* on account of the oval shape of the statoblasts and the variable character of the cuticula.

Distribution. — Asia. India: Balka Lake (ZSI); Igatpuri Lake, Western Ghats, Bombay Presidency, 2000 feet altitude (USNM); Bhim Tal, Kumaon (USNM); Calcutta (USNM). Ceylon: Colombo Waterworks and Lake Labigama (ZSI). China: Hainan Island in the South China Sea and Formosa (Toriumi, 1952e). Indonesia: Java (ZMB).

Africa. Lac Malaga, Lac Lukulu, Mabue-rive nord du Lac Upemba, all in the Congo (IPNC); waterworks of Jos, Nigeria (Monod, 1959); Bibisande in Ugogo Uniamwesi, E. Africa (ZMH).

West Indies. Netherlands Antilles: Aruba and Bonaire (Lacourt, 1955b). Waterworks of Kingston, Jamaica (C. B. Lewis in lit.). The known localities of this species lie between the two yearly isotherms of 25° C. It is a tropical species.

Since Borg (1940a) described his material (as *P. pseudostolonata*), few new data for Africa have been added. I did, however, find material in two collections from the Congo (IPNC, Congo Museum).

Monod (1950) found this species in Nigeria, identifying it as *P. emarginata*. From his illustrations, which show elongated statoblasts, however, it is

clear that his material cannot be *P. emarginata*; the shape, the L/B ratio and capsule/annulus relationship leave no doubt that it actually belongs to the present species. Some of the reports of the occurrence of *P. emarginata* in the regions of the Great Lakes in Africa must also pertain to *P. longigemmis*. The two species show a great resemblance, and in earlier years some identifications were unquestionably erroneous.

Biology. — In Aruba and Bonaire, *P. longigemmis* was found in December 1936 in temporary pools with algae, with a salinity of 40 to 200 mg Cl/l. In India it was found growing during the rainy season (November).

Plumatella emarginata Allman, 1844

(Pl. 3 fig. b; pl. 4 figs. a, b; pl. 5 figs. a, b; pl. 6 figs. a, b; pl. 12 fig. e;
pl. 15 fig. l)

Plumatella emarginata Allman, 1844 (Ireland, without further specification); 1856; Abricossouff, 1925a; 1925b; 1927a; Annandale, 1907b; 1907c; 1910a; 1911; 1922b; Annandale & Kemp, 1912; Aplin, 1860; Arndt, 1943; Berg, 1948; Borcea, 1924; Borg, 1930; 1932; 1936; 1936a; 1940b; 1941; Braem, 1890; Brehm, 1950; Brown, 1933 (limnology); 1936; Căpuse, 1962; Carter, 1859; Chirica, 1906; Cunningham, 1920; Davenport, 1904; Dudich, 1944; 1948; Harmer, 1913; Hastings, 1929; 1929a; 1938; Hejsková, 1948; Hickmann & Scott, 1933; Hilgendorf, 1874; Kalaczkowska, 1934; Kolosváry, 1964; Kraepelin, 1887; 1892; 1906; Lacourt, 1949a; 1949b; Lange de Morretes, 1940; Lee, 1936; Linder, 1931; Loppens, 1908; 1910a; 1910b; Marcus, 1940; 1942; W. Meissner, 1904; Murray, 1910; Prenant & Bobin, 1956 (synonymy); Rogick, 1937a; Sebestyén, 1959; Silen, 1954; Smedley & Dover, 1927; Toriumi, 1952b (taxonomic study, statoblasts, illustrations); 1954a (cuticula); Trauberg, 1940; Ulmer, 1913; Vigano, 1964a; 1965; 1966; Vorstman, 1928a; 1928b; 1930; Wesenberg-Lund, 1897; White, 1917; Wiebach, 1953 (vestibular pore).

Plumatella aplinii MacGillivray, 1860 (Richmond, Australia); 1889; Ridley, 1887; Whitelegge, 1889.

Plumatella jugalis Allman, 1844 (Ireland, without further specification); Toriumi, 1952a (zoaria originating from larvae).

Plumatella princeps var. *emarginata* - Kraepelin, 1887; Annandale, 1910a; Apstein, 1907; Arndt, 1926; Davenport, 1899; 1904; Goddard, 1909; Kraepelin, 1893; 1914; M. Meissner, 1893; 1898; Richardson, 1925a; Valkanov, 1932; Zykoff, 1902.

Plumatella repens var. *emarginata* - Hozawa & Toriumi, 1941; Rioja, 1940; Rogick, 1934a; 1935a; 1937a; 1940a (measurements and illustrations); Rogick & Brown, 1942; Rogick & van der Schalie, 1950; Toriumi, 1941a; 1941b; 1942a; 1942b; Vängel, 1894.

Material. — Europe. The Netherlands (Lacourt, 1949b; RMNH; ZMA); Belgium (Lacourt, 1949a; ISNB).

Asia. India: India (ZSI); Bhim Tal, Kumaon, Himalayas (USNM 5167); Calcutta, Zoological Gardens (USNM 5172; ZMH B 112). Japan: Sendai (RMNH). Indonesia: Botanical Gardens, Bogor and Goa Lalai, Tji Bodas, Java (ZMA, ZMB).

North America. Lake Erie, U.S.A.; East Sister Island, Canada (RMNH, don. M. D. Rogick).

Australia. Caboolture near Brisbane (RMNH, don. E. F. Riek).

Description. — The zoarium is partially adherent, with long, antler-like branching of the tubes, which diverge from a centre. Also compact colonies with very heavily branched tubes are met with, while a combination of both forms also occurs. The tops of the zooids are transparent or white and sometimes show a groove; the cuticula is dark brown and free of incrustations. The polypides are packed close together, about 2 mm long; the number of tentacles is 30 to 54.

The F statoblasts are usually very numerous, forming strings. Their shape is oval, the capsule is almost round; the annulus is 3 times wider at the poles than laterally. The width of the statoblasts varies; when small, the sides are almost parallel and the outline is somewhat pointed at the poles; when wide, the poles are rounded but there are no aberrant forms. L/B varies from 1.65 to 2. The capsule is sometimes granular. Dorsally, the annulus reaches far over the capsule, leaving only a small space uncovered. The network of the annulus is very distinct except in material from the tropics where it is less so. In contrast to other species, the colour is not straw-yellow but silver-white (pl. 12 fig. e).

The statoblasts have about the same size all over the world. F statoblasts: L 360 to 500 μ , B 210 to 270 μ ; extreme sizes have been reported: 364 \times 127 μ (Latvia, Trauberg, 1940); and 702 \times 250 μ (Swiss lakes, Linden, 1939). Capsule l 230 to 300 μ , b 160 to 210 μ ; the annulus is 100 μ wide at the poles, 30 μ laterally; the dimensions of the dorsal space are: length 94 to 104 μ , width 70 to 94 μ ; the diameter of the chambers is 16 μ ; the outer margin is smooth and wavy.

The S statoblasts are rounded oval, with a narrow annulus that is everywhere of the same width. There are some indications of a reticulation. The annulus is sometimes missing. The average sizes are: L 400 to 590 μ , B 230 to 320 μ . Extreme sizes: L 340 to 819 μ , B 145 to 368 μ ; capsule l 370 to 450 μ , b 250 to 320 μ . The annulus is about 16 μ wide; the outer margin is smooth.

Toriumi (1952b) thought that immature forms could be distinguished as to species. Here it should be mentioned once again that zoaria without statoblasts cannot be identified with certainty. In a taxonomic study, Toriumi (1952b) gave a more detailed treatment of the structure of the zoarium at various stages and developed under various conditions, as well as of the polypide and the measurements and shape of the statoblasts, the text being accompanied by many illustrations. Toriumi (1952a) also discussed the germinate form —

P. jugalis —, i.e., the colonies originating from larvae. The '*jugalis*' form also occurs in other species, however.

Synonymy. — A great many names have all proved to be synonyms based on minor deviations or local growth forms (cf. Prenant & Bobin, 1956). These names are often used in combination with the species name to denote varieties.

Under the name *P. princeps*, Kraepelin (1887) combined two easily recognizable species that later authors treat separately.

Some authors (see above) consider *P. emarginata* to be a variety of *P. repens*; this is not justified: the oval F statoblast of the former differs essentially from the almost round statoblast of the latter.

Harmer (1913) distinguished between the varieties *muscosa* and *spongiosa* on the basis of minor size differences of the statoblasts. Apart from the fact that the measurements given by him are too few in number, it has been repeatedly demonstrated that ecological conditions play a role here. The number of tentacles also varies in local forms over the entire world.

Distribution. — Europe. *P. emarginata* is found nearly everywhere in Europe, including Great Britain and Ireland; in the south as far as Spain and Italy (Lake Trasimeno); in the southeast as far as Bulgaria and the Caucasus but not north and east of a line drawn from central Sweden through the Baltic countries and through central Russia along the Volga. This line corresponds with the January isotherm of -10° C.

Asia. U.S.S.R.: The upper course of the Jenisej (Arndt, 1926); Lake Baikal (Abricossoff, 1927a); Ussurian Region (Abricossoff, 1927a); Turgai Region (Abricossoff, 1927a). China: Dairen City, Manchuria (Hozawa & Toriumi, 1941); Peking (Lee, 1936). Korea (Toriumi, 1941b). Japan (common, Toriumi, 1941a; 1942a). Formosa (Toriumi, 1942b). Israel: Lake Huleh (Hastings, 1938). Jordan: pond in southern part (Hastings, 1938). India: Himalaya Mountains; Punjab; Bulandshahr, Central Provinces; Bombay; Calcutta; Ganges River; Assam (Annandale, 1910a). Burma: Shan States; Rangoon (Annandale, 1910a). Thailand (Annandale, 1910a). Malaya: Malay Peninsula (Annandale, 1910a); Ampang waterworks at Kuala Lumpur (Smedley & Dover, 1927). Ceylon (Annandale, 1922b). Indonesia: Lake of Singkarak, Sumatra (Vorstman, 1930); Java (Vorstman, 1922a; 1928b); Macassar, Celebes (ZMA).

Africa. North Africa: a pond in southern Tunisia (Borg, 1936a). Great Lakes area of Central Africa: Bibisande in Ugogo Uniamwesi between Tabora and Lake Victoria; Towalio and Ngomé on, and the island of Sosswé, Lake Victoria; Vitskúmbi, Albert Edward Lake; Kassenga and Kiwi, Albert Lake (M. Meissner, 1898); Lohango Lake (Ulmer, 1913). South Africa:

Great Fish River, a short distance south of Seeheim, S.W. Africa (Kraepelin, 1914); Florida Lake near Johannesburg (Hastings, 1929); Gundzana Bach north of Satara Camp, Krüger Park, eastern Transvaal (Borg, 1936).

North America. A number of widely separated localities (Rogick, 1934a; 1935a; 1937a; 1940a; White, 1917; Rogick & van der Schalie, 1950; Davenport, 1899; 1904; Richardson, 1925a). Mexico: Lago de Patzcuaro (Rioja, 1940); Xtoloke Cenote, Chichen Itza, Yucatan (Brown, 1936). Lake Peten, Guatemala (Rogick & Brown, 1942).

South America. Brazil: Rio Grande do Sul (M. Meissner, 1893); Rio Camaquan, Arredores de Blumenau (Kraepelin, 1887).

Australia and New Zealand. Mary River, Conondale, Queensland (Godard, 1909; Silén, 1954). Waterloo Swamps, Parramatta, New South Wales (Whitelegge, 1889). Woollli Creek, Cooks River near Melbourne, Victoria (Whitelegge, 1889). Torrens River near Adelaide, South Australia (MacGillivray, 1889). Tasmania (Hickmann & Scott, 1933). Hutton, New Zealand (Ridley, 1887).

In Eurasia the species has not been reported from the northern part of Russia, together with the adjacent West Siberian region and the northern part of East Siberia, but it has been found to the south of this area as far as Peking. Also in many localities in the Indian region and two isolated localities in the Middle East. In North America widely-separated localities suggest the probability of a general occurrence, in the north as far as Ontario. Thus, the distribution on the northern hemisphere is roughly limited by the January isotherm of -10° C, from central Sweden running over Leningrad and Moscow, through Asia north of Korea and Japan, and in America through Ontario.

In Africa, all localities are from the region of the Great Lakes with the exception of one in the north and a few places in South Africa.

In South America it occurs at widely separated localities. In Australia there are comparatively many places in the eastern half of the country. Hastings' record (1929) for Tahiti is based on an erroneous identification.

Several records give the impression that they do not always concern this species. The resemblance to other species outside Europe must certainly have led to faulty identifications in a number of cases, for instance in the Tahitian material that I have examined, which appeared to belong to *P. javanica*. This does not change the general picture, however, although I consider the occurrence of the species in Australia dubious.

P. emarginata is thus a cosmopolitan species, but one governed by a certain minimum temperature, e.g., -10° C.

Biology. — In addition to the familiar substrates such as submerged plants,

branches, etc., this species is frequently found on Gastropod shells, e.g., *Paludina* sp., and on those of Lamellibranchs such as *Unio* and *Anodonta*. Some authors see this as a symbiosis between the Bryozoa and the Molluscs; the current created in the water by the Molluscs in taking up food also carries food to the Bryozoa. Zykoff (1902) mentioned fist-sized and even larger clumps of *P. emarginata* on *Vivipara fasciata* Müll. in the Volga River. This resembles *P. fungosa* but the statoblasts of the species under discussion differ sufficiently from the others as to make erroneous identification almost impossible. The bathymetric distribution reaches to a depth of 11 m. The species also occurs in mountain lakes to an altitude of 1500 m. In southern Europe the growth period begins in April; in Calcutta in the cold rainy season. The species is able to live in only a few inches of water as e.g., in Lake Peten, Guatemala (Rogick & Brown, 1942). On a smooth substrate its spreading is maximal; the best developed specimens are found in protected spots (Berg, 1948).

Plumatella evelinae (Marcus, 1941)

(Pl. 11 fig. c)

Stoella evelinae Marcus, 1941 (Arredores da cidade da Pirassununga, São Paulo, Brazil), (anatomy, histology, reproduction, physiology and parasites); 1942.

Hyalinella africana Wiebach, 1964 (Lake Mohasi, Ruanda).

?*Plumatella* spec. Brown, 1936.

Material. — Two statoblasts, found among material of other species from the Pasion River, Guatemala, since lost, probably belong to the present species; one of these statoblasts is figured here. As I am not very familiar with this species, fewer data are available than for other species. I am not even completely satisfied that it is a good species.

Description. — The zoarium consists of tubes with antler-like branching; the cuticula is thin and transparent. In the terminal young parts the polypides are situated in groups of 2 or 3; they are placed closer together in the older parts. The number of tentacles is 44 to 64.

The F statoblasts are irregularly oval, oblique of outline with a large capsule. Measurements: L 323 to 466 μ , B 214 to 290 μ . Capsule l 215 to 311 μ , b 160 to 218 μ . L/B = 1.26-1.91. The annulus is about twice as wide at the poles as laterally: the diameter of the chambers is not known. The outer margin is notched (Wiebach, 1964, fig. 44).

S statoblasts were reported from Yucatan by Brown (1936, fig. A) and described as nearly circular, almost identical with "*P. princeps spongiosa* Kraep" but not definitely identified. I interpret these as sessile statoblasts of *P. evelinae*. According to Brown, the capsule is short-oval with an irregular

annulus; the outer margin has not been described. No measurements are known. Brown's fig. B is closest to Marcus's (1941) fig. 54B. This would then be the second record of the species from America. Brown gave no exact measurements but mentioned that the F statoblast in his material is "almost identical with *P. polymorpha fungosa* Kraep." [= *P. fungosa* Pallas]; this implies that the measurements agree with those of Marcus.

Wiebach (1964) in a recent paper has given more exact information of this species under the name *Hyalinella africana*. According to his description and fig. 48 the S statoblast is rounded oval and has an irregular wavy outline; the surface sometimes shows a weak reticulation; the outer margin is minutely serrated. Measurements: L 470 μ , B 315 μ ; the width of the annulus is virtually constant, about 34 μ .

There is no reason to maintain the genus *Stolella*. Many species of *Plumatella* have long "pseudostolons" that are no true stolons; furthermore, the interstices are later occupied by polypides, as in the present species. As judged from the illustrations published by Marcus (1942) in a further paper on this species, this later material cannot belong to *P. evelinae*. There are distinct differences in the figures in the two successive publications. I consider that the material from Sul do Estado de Minas Gerais, Brazil, should be assigned to *P. philippinensis*.

The discovery of a vestibular pore through which the statoblasts can escape (Marcus, 1941) is not so startling: Wiebach (1952) found the same phenomenon in *P. fruticosa* in Europe, and it may well be normal for many, if not all, species of Phylactolaemata. Certainly no separate species should be based on it. It should also be remembered that the same discovery had already been made by Meyen (1828), although, as so often happens, it was ignored. Hyatt (1864), who cited Meyen, in any case said the following on this point: 'No orifices for the expulsion of the ova [= statoblasts] have been as yet positively demonstrated. Meyen (Isis 1828: 1228) chronicles the escape of the eggs [= statoblasts] of *Alc. stagnorum* [= *P. fungosa*] from an opening in the vicinity of the anus. But this is, probably, erroneous, since, as observed by Mr. Hancock "the great size of the egg forbids the possibility of its escape without the destruction of the polypid". It now appears that Meyen's observation was in all likelihood correct.

Synonymy. — Wiebach (1964, figs. 44, 45, 48) has described material from Central Africa as *Hyalinella africana* n.sp. His illustrations correspond to those of Marcus (1941, fig. 54B) and those of Brown (1936, figs. A, B), showing the same wavy, oblique outline of the statoblast and irregular outline of the capsule in Brown's illustration, and although the number of tentacles (24 to 32) is considerably lower than the number mentioned by Marcus, which

is 44 to 46, the data in Table II shows that this number varies widely. Wiebach has mentioned a large number of species in his publication, but does not seem to know *P. evelinae*. In my opinion, his species is identical with *P. evelinae*. His measurements of the statoblast are also in agreement with those of *P. evelinae*. Even though an identical statoblast is associated with different zoarial characteristics, I do not consider this sufficient grounds to justify the description of a new species, and certainly not on the basis of material as meagre as that now available.

If I am correct in this opinion, we now also know the S statoblast of *P. evelinae*, and a lacuna in Table II has accordingly been filled. Furthermore, the species is now known to occur in Africa.

Distribution. — South and Middle America. In addition to the type-locality there is — with the reservation that, as I have mentioned above, I have not seen the material — another American locality: Country Club Cenote, Merida, Yucatan, Mexico (Brown, 1936) and possibly Pasion River, Guatemala (see under Material). The species in all probability also occurs in Africa: Lake Mohasi, Ruanda (Wiebach, 1964). No definite conclusions can be drawn here because too few data are available.

Biology. — This species is found on plants close to the surface of the water.

Plumatella toanensis (Hozawa & Toriumi, 1940)

(Pl. 16 figs. a, b; text-fig. 5a, b, c)

Hyalinella toanensis Hozawa & Toriumi, 1940 (Mishanfu, Manchuria); 1941; Toriumi, 1941a; 1941b; 1942a; 1942b.

Gelatinella toanensis - Toriumi, 1955e (taxonomy).

Hyalinella punctata - Rioja, 1940a (not *H. punctata* (Hancock, 1850)).

Hyalinella punctata phase *prostrata* - Vorstman, 1928a.

Stoella agilis subsp. *tica* Du Bois-Reymond Marcus, 1953 (vestibular pore and histology).

Material. — Asia. Japan: pond near Sendai (RMNH, ZMH B 1715). Indonesia: Tji Gombong Lake, Java (ZMA; ZMB, Br 076; 084).

Africa. Lac Magéra, Ndalaga, Bitá, Congo (IPNC, 294, 327, 369, 373; unpublished data).

South America. Lake Peten, Guatemala (RMNH, don. M. D. Rogick).

Australia. Queensland: Enoggera Reservoir, Oxley Creek, Norman Creek, Conondale, all near Brisbane (RMNH, don. E. F. Riek). New South Wales: pond in Moore Park, Sydney; Woolli Creek near Sydney; Cambewarra Reservoir near Nowra (AMS U 108, G 11136, G 2692, G 11138; RMNH). Tasmania: Punch Bowl Creek near Launceston (Tasmanian Museum; RMNH).

Description. — The zoarium is nodular, compact, with a thick synoecial

cuticula and an irregular surface from which the terminal portion of the zooecia projects. The measurements are about 5×15 cm, with a thickness of 4 cm. The zooids are arranged linearly. The polypides are straight and about 3 mm long. The evagination is about $\frac{3}{4}$ of their length; the tentacles are about half as long as the polypides and number 47 to 78. Toriumi (1955) found "widely open branching", but only in "reared colonies", and assumed that this can also occur "in the field under certain environmental conditions". This is indeed the case for the Australian material, which has no thick cuticula and consists of short tubes of about 30 mm, with space between the zooids. The branching shows a repeated dichotomous and an antler-like pattern.

The F statoblasts are oval to elongated, often with a large blunt process in the centre of the ventral side. The capsule is rounded-oval to round. The annulus is $2\frac{1}{2}$ to 3 times wider at the poles than laterally and dorsally it covers most of the capsule; the outer margin is entirely smooth. According to Toriumi (1941), the statoblast is covered with minute spines. I did not find these, but observed at most a few small ragged excrescences. The presence of minute spines may be a regional characteristic, in the same sense that the statoblasts of *F. sultana* have chitinous valves of varying thickness in different parts of the world. Moreover, the name "spines" seems to be somewhat exaggerated in this case.

The measurements of the statoblasts vary, as can be seen from the following list.

Author	Region	Measurements (in microns)		
		L	B	L/B
Toriumi, 1955e	Japan	450-620	280-380	1.6
AMS and coll. Riek	Australia	507-732	294-453	1.6
Vorstman, 1928a	Java	666-720	280-360	2-2.4
Rioja, 1940a	Mexico	440-640	290-390	1.5
RMNH, don. Rogick	Mexico	500-700	350-480	
diameter of chambers 12-16	min.-max.	440-732	280-480	1.5-2.4
		l	b	
Toriumi, 1955e	Japan	300-380	240-290	
AMS and coll. Riek	Australia	346-413	254-294	
Vorstman, 1928a	Java	320-333	214-240	
Rioja, 1940a	Mexico	320-450	300-450	
	min.-max.	300-450	214-450	

The S statoblasts are short-oval to round, black, with an annulus composed of a chitinous lamella with a reticulation; the capsule is granular on both sides, with or without a blunt process in the centre of the ventral side; the outline is serrated. The measurements (in microns) vary in these statoblasts, too:

Author	Region	L	B	annulus	L/B
Toriumi, 1955e	Japan	460-650	390-530	20-70	1.2
RMNH, coll. Riek	Australia	400-413	240-280	12-16	1.5-1.66
Vorstman, 1928	Java	333	227	14	1.47
RMNH, don. Rogick	Guatemala	333-400	267-280	14	1.25-1.4
	min.-max.	333-650	227-530	12-70	1.2-1.66

The F statoblasts are highly variable and show a diversity similar to that of the F statoblasts of *P. longigemmis*. They are short-oval to ellipsoid, or have an angular outline, or are almost rectangular with parallel sides (text-fig. 5a, b, c). The material from Java has long, narrow statoblasts; their large measurements make it certain that the material belongs to *P. toanensis* (pl. 16 fig. b).

Synonymy. — I see no reason whatever to assign this species to a separate genus as suggested by Toriumi (1955a). *P. toanensis* fits perfectly within the genus *Plumatella*, by reason of its size being a giant form and standing at the end of a series. For further remarks on the synonymy see below under Distribution.

Distribution. — Asia. China: Toan, Manchuria (Hozawa & Toriumi, 1940; 1941). Japan: general (Toriumi, 1941a; 1942a). Korea: Bukeiko (Toriumi, 1941b). Formosa (Toriumi, 1942b). Indonesia: Lake of Tji Gombong, Java (Vorstman, 1928a).

Africa. Congo (see under Material, IPNC).

Central and South America. Lago de Xochimilco, Mexico (Rioja, 1940a). Guatemala: Lake Peten (RMNH). Peru: Lagunilla Lagunilla near Lake Titicaca (du Bois-Reymond Marcus, 1953).

Australia. A number of localities (see under Material) (RMNH, AMS, Tasmanian Museum).

The Australian Museum, Sydney, and Mr. E. F. Riek, Brisbane, provided me with unidentified material from Australia. Some of this material belongs to the present species, indicating its occurrence in Australia, where it was previously unknown.

Among the material from Guatemala sent me by Miss M. D. Rogick I also found this species. The species is also known from Mexico whence Rioja (1940a) reported it as *P. punctata*. Rioja's material cannot belong to that species because, unlike *P. punctata*, Rioja's specimens have a very large, elongated-oval statoblast of 700 μ length. His material therefore must belong to the present species. The same holds for the material of Vorstman (1928a) from Java and also identified as *P. punctata*. The statoblasts in her material are also very large and have a very elongated shape, forming the connecting link between the forms inhabiting the continents of the southern hemisphere.

Du Bois-Reymond Marcus (1953, pl. 4 fig. 24-26) identified as *Stolella agilis* ssp. *tica* a large form whose measurements and shape show it to belong to the present species. The measurements given (L 440 to 640 μ , B 290 to 390 μ) fall within the limits of those of *P. toanensis*. The identity of her material is also demonstrated by her illustrations. The locality of her material (near Lake Titicaca, Peru) is the first to be known from S. America, the nearest localities being in Mexico and Guatemala.

Thus, the distribution comprises the southern hemisphere, from where it penetrates in two adjacent northern areas of the holarctic region, viz., Japan and Central America.

Biology. — The zoaria grow around the stems of water plants like *Elodea*, primarily in quiet water in small lakes and ponds; they also occur on clumps of algae and on small gastropod shells (e.g., Hydrobiinae).

Hyalinella Jullien, 1885

The characteristics are the same as those of the genus *Plumatella*, except that the cuticula is usually transparent and thick, the tubes are less strongly branched, the zooids usually arranged linearly, the free statoblasts more regular in shape and rounded-oval, and the sessile statoblasts less numerous or lacking.

To this genus belong *H. vorstmani* (Toriumi, 1952), *H. punctata* (Hancock, 1850), *H. indica* (Annandale, 1915), *H. lendenfeldi* (Ridley, 1886), and *H. vaihirieae* Hastings, 1929.

As type-species for this genus I select *Plumatella vesicularis* Leidy, 1854, a junior subjective synonym of *P. punctata* Hancock, 1850.

Hyalinella vorstmani (Toriumi, 1952)

(Pl. 12 figs. g, i)

Plumatella vorstmani Toriumi, 1952d (Japan, without further specification).

Plumatella javanica Kraepelin sensu Vorstman, 1928a (partim), Toriumi, 1952 d.

Material. — Asia. Java: pond in Botanical Gardens of Bogor; Tji Ampoerdarat; Lake of Tjigombong (ZMB 008, 0021, 058, 072; ZMA). India (ZSI).

Material from ZMB, set aside because it strongly resembled, but was not identical to, *P. javanica*, was found to belong to this species.

Furthermore, a small number of specimens from the ZSI collection must be assigned to this species. This material, which I have been able to study, later was no longer available; consequently, exact localities cannot be given.

Description. — The zoarium is adherent, open to compact; the terminal parts are somewhat erect, the tubes branch first dichotomously and then in antler-like manner; the cuticula is transparent to semi-opaque, light to dark

brown, little or not at all incrustated; the polypides have 18 to 32 tentacles.

The F statoblasts are small and broadly oval with a small round capsule; the annulus is twice as wide at the poles as laterally; the outer margin is smooth and wavy; it partially covers the capsule dorsally and ventrally.

Measurements: L = 290 to 360 μ , B = 180 to 240 μ ; the annulus is 53 μ wide at the poles, 27 μ laterally. Capsule 187 \times 146 μ ; the diameter of the chambers is 9 μ .

The S statoblasts are small, rounded-oval, with a wide lamella of equal width and showing little reticulation. The capsule carries a fine reticulation; the outline is minutely serrated. Measurements: L = 278 to 368 μ , B = 208 to 288 μ , the annulus is 19 μ wide. One S statoblast has, on the lamella at one pole, a number of irregularly shaped chambers developed over a distance of 56 μ (pl. 12 fig. i).

H. vorstmani differs from *P. javanica* by the smaller F statoblasts, which are also more rounded. On the basis of this round shape I place this species in the genus *Hyalinella*, in which it is the species with the smallest statoblasts and the smallest number of tentacles, therefore occupying the place at the beginning of the series.

Synonymy. — Toriumi (1952b) has indicated his reasons for basing *P. vorstmani* on the material of Vorstman (1928a), which was published under the name *P. javanica*. Examination of Vorstman's material convinced me that on the whole Toriumi was correct, but a portion of that material nevertheless belongs to *P. javanica*.

Distribution. — Asia. "Japan and its vicinity, twenty-seven localities" (Toriumi, 1952d). India (ZSI). Indonesia: Java (see under Material) (ZMB).

Thus, to the best of our knowledge, *H. vorstmani* is limited to the Indian province.

Biology. — The stems and leaves of water plants serve as substrate for this species, as well as the shells of Mollusca.

***Hyalinella punctata* (Hancock, 1850)**

(Pl. 2 figs. a, b; pl. 11 fig. f; pl. 12 figs. c, j, k; text-fig. 8)

Plumatella punctata Hancock, 1850 (Bromley Lough, Northumberland, England); Vigano, 1965.

Hyalinella punctata - Abricossouff, 1927b; Allman, 1856; Annandale, 1907a; 1907b; 1910b; 1911; 1916; Borg, 1930; 1936; 1936a; Borner, 1928; Braem, 1890; Calvet, 1904; Cant, 1936; Čapuse, 1962; Chirica, 1906; Coates, 1936; Davenport, 1904; Dudich, 1944; 1948; Heding, 1938; Hejsková, 1948; Jenkin, 1936; Kolaczowska, 1934; Kraepelin, 1887; 1893 (biology and description); 1914; Lacourt, 1949a; 1949b; Lange de Morretes, 1940; Levander, 1900; 1908; Loppens, 1908; Marcus, 1940; 1942; Mauvais,

- 1927; Murray, 1910; Prenant & Bobin, 1956 (synonymy); Remy, 1928; Rioja, 1940a (error); Rogick, 1934a; 1935a; 1937a; 1939 (larvae); 1940a (illustrations and measurements); 1941b (resistance to desiccation); 1945a (culture from statoblasts, growth data); Rogick & van der Schalie, 1950; Schmidt, 1886; Sebestyén, 1959; Sokolov, 1931; Toriumi, 1941a; 1941b; 1942a; 1942b; 1955d (taxonomic study); Tretiakow, 1900; Vorstman, 1928a (error); 1928b; 1930; Wesenberg-Lund, 1897; White, 1917; Wiebach, 1936a.
- Plumatella (Hyalinella) bigemmis* Annandale, 1919a (Hamun-i-Helmand near Lab-i-Baring, Seistan, Persia); Abricossoff, 1926a.
- Plumatella vesicularis* Leidy, 1854 (Schuylkill River, Philadelphia, U.S.A.); Allman, 1856; Jullien, 1885; Vángel, 1894.
- Plumatella vitrea* Hyatt, 1868 (Cambridge, Mass., U.S.A.); Borcea, 1924; Jullien, 1885.
- Plumatella fungosa* subsp. *kamtschadalica* Abricossoff, 1927b (Lake Chalachtirka and Lake Krestowoje, Kamchatka, USSR).
- Plumatella incrustata* Abricossoff, 1927b (River Koladshir, where it flows out of the Marka-Kul in the Semipalatinsker Region, Siberia).
- Plumatella longa* Abricossoff, 1927b (Lake Krasikorvo and Lake Kursin, Kamchatka, USSR).
- Plumatella repens* var. *minuta* Toriumi, 1941a (Tokyo); 1941b; 1942a; 1955e.
- Hyalinella minuta* - Toriumi, 1955c.
- Stolella indica* Annandale, 1909a (outskirts of Calcutta); 1910b; 1911; 1915b; Borg, 1941; Marcus, 1941; Rogick, 1943b; Rogick & van der Schalie, 1950.
- Stolella himalayana* Annandale, 1911 (Malwa Tal, Kumaon, Western Himalayas); 1915b; Annandale & Kemp, 1912; Rogick, 1943b.
- Plumatella auricomis* - Annandale, 1915c (not *P. auricomis* Annandale, 1913).
- Plumatella fruticosa* - Marcus, 1942 (not *P. fruticosa* Allman, 1844).

Material. — Europe. The Netherlands: a number of localities (RMNH; ZMA; Lacourt, 1949b). Belgium (ISNB; Lacourt, 1949a). Norway: Natlandsvann (Bergens Museum, Bergen). Denmark: Frederiksborg (ZMK). Sweden: Uppland, Trehorningen, (ZIU). U.S.S.R.: Volga Region (British Museum (Natural History) 14.6.10, 1, *part* Dr. Behning as *Plumatella auricomis*).

Asia. Japan: Asamushi Aonori (RMNH, don. Toriumi), Sendai (ZMH, B 1714 as *Hyalinella minuta*). Persia. (ZSI, P. 92/1, type of *Plumatella bigemmis*). India: Calcutta (USNM 5168, 6311; ZMH, B 113 as *H. minuta*); Madras (ZSI, ZEV 4925/7 as *Stolella indica*); Malwa Tal, Kumaon. (ZSI, ZEV 4813/7, as *Stolella himalayana*). Indonesia: Java (ZMB, Br 062, as *Hyalinella minuta*); Rawah Galapan (ZMA, as *H. minuta*); Rawah Galapan and Botanical Gardens, Bogor (ZMA).

Africa. Congo: Kajanza and Kasinga (IPNC). Southern Rhodesia: Matje omklope near Bulawayo (RMNH, don. D. H. Eccles, Cape Town).

Australia. Punch Bowl Creek, Tasmania (RMNH, Tasmanian Museum).

Description. — The zoarium consists of a number of tubes with little

branching, sometimes it forms irregular strings of fused tubes, sometimes compact adherent masses with erect terminal parts. The cuticula is transparent and thick, not incrusted. The tubes have no septa. The polypides are placed close together in a linear arrangement. The number of tentacles is 40 to 60.

The F statoblasts occur in two sizes plus transitional forms; they are rounded-oval, strikingly regular in outline, and medium brown in colour. The capsule is almost round, the annulus is 1 to 2 times wider at the poles than laterally. L/B 1-1.4. The outer margin is predominantly smooth and somewhat wavy. Measurements of the large form: L 431 to 500 μ , B 282 to 380 μ ; of the small form, L 232 to 298 μ , B 200 to 249 μ . The capsule is about $5/7$ L; the annulus is $1/7$ L wide at the poles, $1/10$ L laterally; the diameter of the chambers is 7 to 8 μ .

S statoblasts are rarely found; they are large, nearly round, dark brown to black. The annulus is very little developed, of equal width with an indication of a reticulation; the outer margin is scalloped. Measurements: $585 \times 468 \mu$, the annulus is 35 to 46 μ wide.

The zoaria reach a diameter of 20 cm; exceptionally they are bulb-shaped when the zoarium has grown around a branch, but the tubes are not fused. Two developmental forms have been distinguished in the literature: a summer generation, forma *prostrata*, with an open zoarium and small F statoblasts, and an autumn generation, forma *densa*, of a compact form and with large statoblasts. However, statoblasts differing in size are found together in one and the same zoarium and, furthermore, in both forms of zoaria. Annandale (1910b, 1911) found *H. punctata* in the Indian province throughout the year, without differentiation into a summer and autumn generation.

The phenomenon of the differently-sized statoblasts has not been explained. The shape of the F statoblasts is not always regular: the outline is sometimes flattened on the sides, in which case they cannot be distinguished from those of *P. fungosa* (see under that species). There are cases of F statoblasts of a divergent size with an annulus of constant width but narrower than normally or unusually wide. The interrelationship of the species of Phylactolaemata is sometimes demonstrated by the formation of F statoblasts deviating completely from the specific form. It is a remarkable thing that these F statoblasts have the same oval shape in various species of the genera *Plumatella* and *Hyalinella*. The statoblasts shown in pl. 12 fig. k occur proportionately the most frequently; for the rest they are a rather rare phenomenon. This undifferentiated statoblast corresponds to the elongated-oval basic form found in the former series of species, especially in *P. agilis*,

but I have also seen it in *P. philippinensis*, *P. fungosa*, and *P. emarginata*.

In many species giant statoblasts also occur. According to some authors, the cuticula is somewhat contractile. Possibly in agreement with this, I have found that the cuticula is not equally transparent and thick in all specimens, it is sometimes less thick and somewhat brittle, as in the species of *Plumatella*. This may be the consequence of ecological conditions.

Synonymy. — *Plumatella bigemmis* Annandale is a synonym of *H. punctata*. I have examined the type material and found it to be identical. The dimensions of the F statoblasts of *P. bigemmis* fall between the large and the small sizes of those of *H. punctata*: L 357 to 374 μ , B 255 to 272 μ . The material recorded by Abricossoff (1926a) also falls within these limits. The dimensions of the S statoblasts of *P. bigemmis* also coincide with those of *H. punctata*: L 459 to 561 μ , B 425 to 459 μ . Annandale based his species on extremely small differences: ectocyst (= cuticula) more translucent; statoblasts less variable; and annulus wider at the poles; but all these differences lie within the limits of variability.

P. fungosa subsp. *kamtschadalis* Abricossoff (1927b) must be considered identical with *H. punctata*. Although Abricossoff reported the tubes to be fused, he added that the zoaria form fairly massive clumps, i.e., these are evidently not as solid as in *P. fungosa*. Furthermore, the compact zoaria of almost all species of *Plumatella* and *Hyalinella* are rather massive. But Abricossoff puts special emphasis on the wide F statoblasts, with L/B 1.2, which in *P. fungosa* varies between 1.4 and 1.6. This fact, together with the description of the zoaria, led to the above conclusion.

The material from the Volga region identified by Annandale (1915c) as *P. auricomis* belongs to *H. punctata*. I have seen part of the material preserved in the British Museum (Natural History) and this unquestionably belongs to the present species.

P. incrustata Abricossoff (1927b) is a synonym of *H. punctata*: the colonies are irregularly shaped and rather compact; the tubes are wide, the cuticula colourless, the F statoblast wide-oval, with an annulus of equal width. Measurements: L 400 to 472 μ , B 320 to 360 μ , thus differing only slightly from *H. punctata*.

P. longa Abricossoff (1927b) is also a synonym. The zoarium consists of strings of tubes as already described. The F statoblasts are wide oval, almost round; the annulus is of equal width; L 432 to 456 μ , B 360 to 384 μ . I have not seen any material of this species so I remain ignorant of the width of the annulus, but in both cases the description corresponds to that of *H. punctata*, the sizes of the statoblasts are in agreement, and the description of the statoblasts as being wide oval with equally wide annulus

indicates that we have to do with *H. punctata*. The few microns difference, as in *P. incrustata*, were certainly not sufficient reason to establish two new species.

H. punctata prostrata, *H. minuta*, *Stolella indica*, and *S. himalayana* are also synonyms: 1) in all three the cuticula is (ordinarily) thick and soft; 2) in all three the zoarium has a virtually open form; and 3) in all three the statoblasts are identical. With respect to point 2, Toriumi (1941a) emphatically stipulates the open form for *H. minuta*, and the extended proximal part is even taken by Annandale (1909a) as the basis for his genus *Stolella*. Rogick (1943b) accepts it as characteristic for the identification of her material. The branching is irregular and antler-like; the illustrations (Toriumi, 1941a, figs. 7 and 8; Rogick, 1943b, figs. 1-8; Annandale, 1915b) actually agree entirely with Kraepelin's illustration (1887, p. 127, pl. 4 fig. 115), which is reproduced by Borg (1930, fig. 164), the latter showing the colony somewhat schematically, the former in more detail. As has been repeatedly said here, the extended proximal part of the zooids has no specific importance. Toriumi (1955e) mentioned it as occurring occasionally, but normally the zooecia of *H. minuta* are as closely packed as in *H. punctata*. Borg (1940a) based his *P. pseudostolonata* on the occasionally present extended proximal parts: they also occur sometimes in *H. punctata*. In *Stolella indica* they are the rule but sometimes "somewhat difficult to detect" (Annandale, 1909a). This is a primitive character, normally occurring in *Fredericella sultana* as large distances between the zooids, and only occurs now and again in the series of the Phylactolaemata. Extended zooids alone are not a character on which to base a species. The manner of branching of the zoarium in *S. indica* is mainly antler-like, albeit "retarded" and extended, and often irregular. However, the various taxonomic studies by Toriumi (1951-1956) have clearly demonstrated the variability and purely relative value to be attached to the extension of zoaria. For *H. minuta*, Toriumi (1941a) emphatically mentions antler-like branching. What Rogick (1943b) included under *S. indica* corresponds, with respect to its shape, with the figure given by Kraepelin (1887). For unknown reasons, the zooids in some cases become extended. It is not quite clear to me how Rogick was able to recognize *S. indica* in another hemisphere, in view of the fact that in his description Annandale mentioned only the name, the long proximal parts of the zooids, and a statoblast resembling *H. punctata*. Borg (1941) correctly calls this vague description worthless because it lacks illustrations and measurements. The detailed description promised by Annandale never appeared. Rogick (1943b) otherwise correctly considered *S. indica* and *S. himalayana* to be synonyms.

The number of tentacles on the polypides agrees: 26 to 39 for *H. minuta*, 30 to 35 for *S. indica*, and 40 to 60 for *H. punctata*. Although few exact data are available on this point, we may assume that the number for the small form of *H. punctata* is lower than for the large form. In the Phylactolaemata series, increasing size of the polypide and statoblasts coincides with an increase in the number of tentacles. Vorstman (1928a) mentioned a number of about 28; roughly speaking, 28 to 45 tentacles may be supposed to be present. Although the number of tentacles is of course a relative character, dependent on various factors, the numbers in the material discussed here do not contradict each other.

Lastly, the F statoblasts are of the same shape with a difference in size falling within the known size limits of *H. punctata*. *H. punctata prostrata*: L 232 to 370 μ (calculated average size), B 200 to 290 μ , L/B 1.15 to 1.30. *H. minuta*: L 265 to 300 μ , B 190 to 230 μ ; L/B 1.30 to 1.40. *S. indica* (cf. Rogick 1943b): L 350 to 410 μ , B 240 to 280 μ ; L/B 1.45. The L/B ratio for the entire *H. punctata* material is 1 to 1.40. A microphotograph of the original *H. punctata* statoblast is shown on plate 12 fig. j. Toriumi's picture of *H. minuta* (1941a) represents a small form of this statoblast. Rogick's illustrations (1943b) of *S. indica* represent the oval F statoblast of *H. punctata*. The diameter of the chambers is 7 to 8 μ , and the outer margin of the statoblasts is smooth in all forms. I have seen material of *H. minuta* and, very fortunately, material of *S. indica*. The F statoblast has all the features of that of *H. punctata*. In this material the tubes have a constant width and the zooids are arranged in linear series, as in *H. punctata*. Some material of *S. himalayana* was also available, but very little. It has a soft cuticula and small F statoblasts, identical to those of *H. punctata*. S statoblasts are rare in this species and always large; none are known for *H. minuta* but those known for *S. indica* are rather large, and agree with those of *H. punctata*. They are not present in the specimen of *S. himalayana*. Rogick (1943b) gave as measurements 470 to 560 μ .

The three species described above appear to be identical in all characters; they are distinctly synonymous. The diversity of the zoaria and the differently-sized statoblasts misled some authors in former times as well as later.

H. punctata forma *prostrata* of Vorstman (1928a) is another species (*P. toanensis*); the illustration given by Rioja (1940b) of *H. punctata* does not concern this species, his material also being *P. toanensis*. Marcus (1942) reported *Plumatella fruticosa* from the southern part of the state of São Paulo, Brazil. I have already referred to the fact that, judged from the illustration, this cannot be *P. fruticosa*, and at that time assigned the material to *P. philippinensis* (cf. Lacourt, 1955a). In the present state of

our knowledge, I believe that Marcus's material belongs to *H. punctata*.

Distribution. — Europe. Throughout Europe, including Scandinavia, Great Britain, the island of Barra in the Outer Hebrides, and Iceland. The species has not yet been found in the northern part of Russia; southwards it extends as far as Rumania. It also does not occur in the Iberian, Italian, and Balkan peninsulas.

Asia. U.S.S.R.: Kamchatka (Abricossoff, 1927b); Semipalatinsker region (Abricossoff, 1927b); Turga region, Turkestan (Abricossoff, 1927b); Staraja Buchara, Turkestan (Sokolov, 1931); Samarkand, Usbekistan (Sokolov, 1931). Persia (Annandale, 1919a). Japan (Toriumi, 1941a; 1955c). Korea (Toriumi, 1941b). Formosa (Toriumi, 1942b). India: Madras (ZSI); Calcutta; the Himalayas; Kumaon Lakes; Bulandshahr in the United Provinces; the whole of the Indo-Gangetic plain (Annandale, 1907a-1915; Annandale & Kemp, 1912). Indonesia: Rawa Galapan and Tjigombong Lake, Java (Vorstman, 1928a; 1928b); Botanical Gardens, Bogor, Java (ZMB); Toba Lake, Sumatra (Vorstman, 1930).

Africa. Congo (IPNC). Kenya: Naivasha Lake (Jenkin, 1936). Southern Rhodesia (RMNH).

North America. Throughout North America (Davenport, 1904; Rogick, 1934a to 1945; Rogick & van der Schalie, 1950; White, 1915); the northern limit being not yet definitely known.

South America. Harberton Harbour, southern Tierra del Fuego (Calvet, 1904).

Australia. Punch Bowl Creek, Launceston, Tasmania (Tasmanian Museum).

Despite the numerous reports, I initially had grave doubts that *H. punctata* did actually occur outside the holarctic province, i.e., in the tropics, or is even cosmopolitan. The species of Phylactolaemata are difficult to recognize and identifications require much experience. The small form of *H. punctata* has been identified as *H. minuta* and the large form can easily be confused with *H. indica*. Looking back, I now even doubt some of my own identifications. Material of the Hamburg Museum, originating from the waterworks at Neudamm near Windhoek in S.W. Africa, was erroneously identified; it belongs to *H. indica*. I fear that a number of other identifications, based on material no longer available, were probably also mistaken, having been done in a period in which the European species were considered to occur all over the world. It is now my impression that the small form occurs in the tropics, analogous to the smaller form of *Fredericella sultana*. The data for *Stolella indica* and *Hyalinella minuta* furnished no new information, their range coincides with that of *H. punctata*. Nevertheless, *H. punctata*

proves to be cosmopolitan, albeit its occurrence is discontinuous.

Biology. — The substrate consists of leaves and stems of water plants, branches, bark, wood, and stones. The bathymetric distribution runs from about 25 cm to a few metres; the species has also been found at an altitude of 1890 m in mountain lakes in Kenya. It lives in water with temperatures ranging from 18 to 25° C and a pH of 9 to 9.4, and has also been found in brackish water (near Antwerp; in the Frische Haff on the Baltic; and in a ditch on the island of Walcheren, The Netherlands).

Hyalinella indica (Annandale, 1915)

(Pl. 17 fig. a)

Australella indica Annandale, 1915b (Ferozpoore, a rain-water pool on the banks of the River Sutlej near the Kaiser-i-Hind railway bridge); Abricossouff, 1927b.

Australella indica var. *sibirica* Kluge, 1949.

Hyalinella indica - Hastings, 1929a.

Plumatella emarginata - Borg, 1936 (not *P. emarginata* Allman, 1844).

Material. — Africa. Gunzana Bach, East Transvaal (Natur Museum Senckenberg, SMF 795, F. Haas S. 31-8-1931). Waterworks of Neudamm near Windhoek, S.W. Africa (ZMH, B 96, Michaelsen leg. 15.5.1911, part of a zoarium with both types of statoblasts).

Asia. India (ZSI, 33, 65, 73).

Description. — The zoarium consists of several main stems, recumbent and adherent. The lateral branches are arranged symmetrically in pairs, joining the main stem at an acute angle, growing to a massive, somewhat nodular zoarium with a radiate dendritic appearance. The cuticula is colourless and hyaline; a thick synoecial chitinous layer fills the interstices in the zoarium. The polypides are hook-shaped, slender, placed in linear series; the tentacles number 40 to 50, they are moderately elongate.

The F statoblasts are broadly-oval and of medium size; the capsule is rounded-oval. The annulus is two times wider at the poles than laterally; it is curved in cross-section. The outer margin is smooth. According to Annandale (1915b) the measurements are: L 460 μ , B 290 μ , capsule l 250 μ , b 187 μ . The material from the Senckenberg Museum has the following measurements: L 526 to 561 μ , B 316 to 363 μ ; l 351 μ , b 281 μ ; the annulus is 82 μ wide at the poles, 41 μ laterally; the diameter of the chambers is 9 μ . The S statoblasts are almost round; they have no annulus or only a primary border; they are dark brown and show a reticulation along the edge; the outer margin is coarsely notched. L 433 to 456 μ , B 374 to 409 μ .

In the drawing given by Annandale (1915b: 166, figs. 1, 1a, 1b) the curvature of the statoblast in fig. 1a is exaggerated and does not agree with his fig. 1b. The junction of the annulus and the capsule is not drawn cor-

rectly: it is shown as convex instead of concave and too large in proportion to the capsule. The eccentrically-placed capsule is an exception seen occasionally in other species as well; it is not a specific character. Annandale's illustrations of the zoarium are very good. *H. indica* is distinguished from *H. punctata* by the smooth surface of the zoaria, its regular structure, and the synoecial cuticula; in addition, the F statoblasts are larger than those of *H. punctata* but the capsule is smaller. The S statoblasts are smaller than those of *H. punctata*.

The type material was very limited in quantity and could not be put at my disposal. Very fortunately, however, the Senckenberg Museum possesses a specimen from Africa, definitely belonging to *H. indica*, although Borg (1936) had mistakenly identified it as *P. emarginata*. Therefore, this species could be described here in detail and its systematic position ascertained. Annandale (1915b) found no sessile statoblasts, but they are present in the African material. Further, a specimen from the Hamburg Museum (B 96), identified as *H. punctata*, also proved to belong to *H. indica*, and thus another African locality could be recorded for it.

Synonymy. — Annandale's reasons for establishing the genus *Austrolella*, based on the present species, are obscure. The material of this species examined by me has all the characteristics of the genus *Hyalinella*, i.e., the rounded-oval F statoblasts and the thick cuticula. I fully agree with Hastings (1929a), who placed this species in the genus *Hyalinella*. Annandale (1919a) himself later also discarded the name *Austrolella*.

Austrolella (*H.*) *indica* var. *sibirica* Kluge (1949) cannot be recognized because there is no published description and only one illustration, which is insufficient to establish the status of this form. This name must be considered a nomen dubium.

Distribution. — Asia. India: Lahore, Punjab (Annandale, 1915b); two more localities in India (ZSI).

Africa. "Tümpel des Gunzana Baches", near Satara Camp, Krüger Park, East Transvaal (Natur Museum Senckenberg). Waterworks at Neudamm near Windhoek, S.W. Africa (ZMH). Abricossoff (1927b) also mentioned the species from the Satanchua River, which empties into Lake Chanka, E. Siberia, but I am inclined to doubt the accuracy of his identification. *H. indica*, namely, is a tropical species. Several species bear a strong resemblance to each other, and forty years ago there was even less information available than now.

The range of *H. indica* occupies the Ethiopian and Indian regions.

Biology. — The only reported substrate for this species is the shell of a fresh water mussel, *Aspatharia wahlbergi wahlbergi* (Krauss).

Hyalinella lendenfeldi (Ridley, 1886)

(Pl. 17 fig. b; text-fig. 6d)

Lophopus lendenfeldi Ridley, 1886 (Parramatta River, New South Wales).*Lophopus lendenfeldi* - Annandale, 1907b (error); Colledge, 1917; Goddard, 1909; Kraepelin, 1892; 1893; Whitelegge, 1889.*Australella lendenfeldi* - Annandale, 1910b; 1915.*Hyalinella lendenfeldi* - Annandale, 1919a; Loppens, 1908; Hastings, 1929a.*Lophopus jheringi* Meissner, 1893a (Rio Grande do Sul, Brazil); Kraepelin, 1893; Loppens, 1908.*Australella jheringi* - Annandale, 1915b; Kraepelin, 1914.*Hyalinella jheringi* - Annandale, 1919a.*Pectinatella* (?) *jheringi* - Hastings, 1929a; Marcus, 1942; Lange de Morretes, 1940.

Material. — Australia. Parramatta River, New South Wales (British Museum (Natural History), fragment of type, 86.9.22.10, without statoblasts).

South America. Rio Grande do Sul, Brazil (Zoological Museum Berlin, 554, type of *Lophopus jheringi* Meissner; ZMH, B 84, H. von Ihering don., August 1893).

Description. — The zoarium consists of a number of closely-packed tubes, which are branched here and there in a radial arrangement; they are sometimes narrow and without polypides. Their diameter is up to 35 μ . The cuticula is transparent, tough, and about 1 mm thick. The polypides are up to about 2½ mm in length, protruding out of the zoarium; arranged in a linear manner; here and there grouped together as a beginning of branching. The tentacles, about 50 in number, are about 1 mm long.

Only F statoblasts are known. They are large, rounded-oval and dark brown. The capsule is rounded-oval. The annulus is wide with a constant width. The outer margin is smooth. Measurements: L 850 to 1000 μ , B 700 to 800 μ , L/B 1.25; capsule 600 × 500 μ ; width of annulus 200 to 220 μ at the poles, 150 μ laterally; the diameter of the chambers is 10 to 50 μ .

Ridley (1886) gave a detailed description, later supplemented by Hastings (1929a), from the holotype in the British Museum (Natural History). In Ridley's illustration, however, the tentacular crown is figured too large. The stolon he mentioned does not exist: this was the stalk of a hydroid (see Annandale, 1915b). Kraepelin (1893) remarked that, according to the measurements given by Ridley, the statoblast is drawn too narrow.

Meissner (1893) illustrated the statoblasts with an irregular outline; such outlines do sometimes occur. He called the surface of the zoarium bushy, but in his figure of the lower side of a zoarium a *Pectinatella*-like, radial-dichotomous structure is visible.

Synonymy. — Most fortunately, the Zoological Museum of Berlin still possesses the type material of *Lophopus jheringi* Meissner, which was placed at my disposal. The material proved to be identical to *H. lendenfeldi*. The type material of *H. lendenfeldi* sent me by the British Museum (Nat. Hist.) did not include statoblasts. Kraepelin (1893), even in his time, considered the two species to be identical. This opinion is supported by the fact that the measurements and descriptions of the two species are the same. It is fortunate that in this case both authors provided not only the diameter of the entire statoblast, but also the width of the annulus, which are virtually the same: 200 μ and 220 μ for the poles, laterally both 150 μ . For the same lengths and widths of the statoblasts, the capsules can be of unequal size, but this is not the case here. The descriptions of the zoaria are the same in all the main features.

Annandale's report (1907b) of the occurrence of this species at Bhim Tal-Kumaon must pertain to statoblasts of *Lophopodella carteri* from which the spines had broken off. This is quite clear from the description of the zoarium and the figure of the statoblasts: "the zoarium a small mound of jelly, polypides in palmate formation, margins [of statoblast] generally broken". His *Lophopus lendenfeldi* var. *himalayanus* is also unquestionably *Lophopodella carteri*.

H. lendenfeldi has been placed in various genera, but according to its habitus and statoblast it belongs in the genus *Hyalinella*.

Distribution. — In addition to the type-localities of *H. lendenfeldi* and *H. jheringi*, this species has also been found in Parramatta Park near the footbridge at Port Jackson, N.S.W., Australia (Whitelegge, 1889). The distribution of the species, like that of other species, might point to an original interconnection of the continents. *H. lendenfeldi* has not been rediscovered since the early reports.

Biology. — In Australia the material was found in deep water on the stalks of water plants (Whitelegge, 1889).

***Hyalinella vaihiriae* Hastings, 1929**

(Pl. 17 fig. c; pl. 18 fig. c)

Hyalinella vaihiriae Hastings, 1929a (Lake Vaihiriae on Tahiti, description and branching pattern); Rogick & Brown, 1942 (description and measurements).

Material. — Polynesia. Lake Vaihiriae, Tahiti (RMNH, don. Miss A. B. Hastings).

America. Bear River, U.S.A. (RMNH, don. Miss M. D. Rogick).

Australia. Oxley Creek, Brisbane (RMNH, don. E. F. Riek).

Description. — The zoarium consists of linear series of zooids, often branched, compact, adherent, with erect terminal parts. The cuticula is thick. The polypides have about 48 short tentacles. The F statoblasts are oval and elongated at the poles. The dorsal side is markedly convex. The capsule is round. The annulus is narrow, about 3 times wider at the poles than laterally. The outer margin shows very fine undulations, being almost entirely smooth. Measurements: L 320 to 410 μ , B 220 to 280 μ . The annulus is 67 μ wide at the poles and 20 μ laterally. The diameter of the chambers is 8 to 10 μ . The S statoblasts are oval to rounded-oval; they have a narrow primary annulus of equal width; the capsule and the annulus are covered with a primary reticulation; the outer margin is smooth. The measurements of the rounded-oval statoblasts are L 410 to 470 μ , B 320 to 400 μ ; of the oval statoblasts 293 \times 453 μ ; the annulus is 13 to 16 μ wide.

Distribution. — Australia. Queensland: Oxley Creek, Brisbane (RMNH).

Polynesia. Lake Vaihiria, Tahiti (Hastings, 1929a; RMNH).

America. Bear River, Utah, in Box Elder County where highway U.S. 30 crosses the river (RMNH).

In this species, as in some other species (e.g., *P. philippinensis*, cf. Lacourt, 1955), transport from Australia could be considered, e.g., with plants for hot houses. Because of the scarcity of data, I still tentatively take *H. vaihiriae* to be an endemic Australian species.

Biology. — This species is found in large numbers locally. The Bear River locality in the U.S.A. was in very muddy, alkaline water. The substrate consists of dead branches and stones.

PECTINATELLIDAE nov. fam.

A number of zoaria are placed together on a common, gelatinous base. The zoaria forming a rosette; the tubes branch in a radiate manner. Only free statoblasts are present, these are nearly round and carry marginal spines.

Pectinatella Leidy, 1851

The small, rosette-shaped zoaria have a radial structure; large numbers of them arise from a common base. Only free statoblasts are known; they are large and round, carrying anchor-shaped spines localized marginally. Type by monotypy: *Cristatella magnifica* Leidy, 1851. To this genus also belongs *Pectinatella gelatinosa* Oka, 1890.

Pectinatella magnifica (Leidy, 1851)

(Pl. 11 fig. d; pl. 17 fig. d; text-fig. 7c)

Cristatella magnifica Leidy, 1851b (a stream in the neighbourhood of Philadelphia).

Pectinatella magnifica - Allman, 1856; Borg, 1930; Borodin, 1928; Braem, 1911; 1913; 1913a (statoblasts, variability, spines); Brandwein, 1938 (culture); Brooks, 1929

(anatomy, histology, motion, experimental germination); C. J. D. Brown, 1933 (limnological study); Căpuse, 1962; Davenport, 1900 (statoblasts, variability, spines); 1904; 1918 (in Ward & Whipple); Deevey, 1942; Dudich, 1944; 1948; Henchman & Davenport, 1913 (statoblasts, variability, spines); Hincks, 1880; Honigmann, 1927; Hrabé, 1934; Hyatt, 1866; Jara, 1955; Judd, 1951; Jullien, 1885; Kraepelin, 1887 (description); Lacourt & Willighagen, 1966 (histochemical investigation); Leidy, 1851c; Loppens, 1908; 1910a; Marcus, 1940; Osler, 1883; Prenant & Bobin, 1956; Richardson, 1928; Rogick, 1934a; 1935a; 1937a; 1940a; Rogick & Brown, 1942; Schachanowskaja, 1929; 1930; Sebestyén, 1959; Weltner, 1906; White, 1917; Wilcox, 1906 (origin, motion, negative phototropism); Williams, 1921 (larval colonies).

Material. — America. U.S.A.: Lake Hopatcong, New Jersey, and Yonkers Reservoir, Yonkers, N.Y. (American Museum of Natural History, New York and RMNH); East Waseham, Mass., U.S.A. (British Museum (Natural History), 28.4.26).

Europe. Germany: Bille near Hamburg (ZMH. B 29); Scharmützelsee near Berlin (RMNH).

Description. — The zoaria are always grouped together in large numbers on a gelatinous communal base. They arise from a small number of solitary specimens which by fission form a large number of closely packed zoaria; these secrete a chitinous cuticula, forming a large collective mass ("Tierstock" (Borg, 1930) or 'Cormus polyblastus' (Kraepelin, 1887)), which is bulb- or spindle-shaped and can reach a diameter of 200 mm. Each zoarium is rosette-shaped and shows a radial structure; initially round, compression later gives the zoaria an irregularly angular shape. A zoarium may have up to 10 lobes, and shows a central cavity in which no polypides are found. Around the orifices lie cuticular glands secreting a white substance, appearing as spots on the surface; the function and effect of these glands is not yet known. The polypides are about 1 mm thick and have 60 to 84 tentacles. *P. magnifica* has only F statoblasts; these are discoidal, round or slightly oval, or in the shape of optically rounded-off rectangles resulting from bending around two axes. They carry 10 to 22 (usually 14) spines, originating from the outer margin. These spines are flat, lamellar, restricted to the dorsal valve, and end in a double, or in rare cases triangular, hooklet; the annulus is grey and of equal width; the capsule is brown, round or slightly oval; the outer margin is smooth. Measurements: the diameter is 900 to 1500 μ , the width of the annulus is $\frac{1}{6}$ to $\frac{1}{7}$ of the diameter of the statoblast; the length of the spines depends on their number: 270 μ when there are few, decreasing to 100 μ when there are many; the width of the shaft is 18 to 30 μ , that of the hooks is 53 to 66 μ ; the diameter of the chambers is about 12 μ ; the diameter of the zoaria 20 mm.

Distribution. — Europe. Germany: Elbe River near Hamburg; Havel;

Oder near Frankfurt; lakes around Berlin; Silesia (Borg, 1930; Braem, 1911; 1913; Honigmann, 1927; Kraepelin, 1887). Czechoslovakia: Bohemia, e.g., in the river Moldau near Prague (Hrabé, 1934; Schachanowskaja, 1919). "Between the Elbe and the Oder, but not in Hungary" (Sebestyén, 1959). Rumania: Lake Snagov (Căpuse, 1962).

Asia. Turkey, at Erğirdir Lake in the Lake District (written communication from R. Geldiay, 1957).

North America. U.S.A. In the eastern part of the country, as far south as Florida; in the region of the Great Lakes and bordering states of the U.S.A. and Canada (Brooks, 1929; Davenport, 1900; 1904; Hyatt, 1866; Richardson, 1928; Rogick, 1934a to 1940a; White, 1917; Williams, 1921; USNM; American Museum of Natural History, New York; British Museum (Natural History)).

Central America. Pasion River, Guatemala (Rogick & Brown, 1942; statoblasts). This species always occurs in large numbers. Its occurrence in Europe is assumed to be due to importation from America. Zoaria and statoblasts are thought to have been deposited in the harbour of Hamburg during the cleaning of fresh-water tanks of a ship from America. It has been pointed out that the European localities are all along the main shipping lanes, from which distribution to the surrounding waters is possible. Borg (1930) asked for evidence on this point, but how can this be provided? The fact that the species was not found in Europe before 1883 is of course not conclusive evidence but it does constitute a strong indication. Recent penetration into Europe of several marine and brackish water organisms, whether or not by artificial means, is also known. The further spread and increase in central Europe, for example in Silesia, is an indication in this sense. The species is not cosmopolitan. Hyatt's designation of it as '*Pectinatella carteri*' was erroneous; he confused it with *Lophopodella carteri*. It is extremely difficult to draw any conclusions about the distribution of this species because of the discontinuity in its occurrence. Is this a nearctic species imported by man in the palaearctic region or a holarctic species with a scattered distribution? Recently, a new locality has been found in Rumania; the occurrence in Europe now shows a chain of localities from Hamburg across Europe to Asia Minor. The species is conspicuous and will not easily be overlooked. Nevertheless, I now doubt whether it really has been imported in Europe and Asia.

Biology. — The substrate of the species includes wood and stones. *P. magnifica* is never found on the green parts of plants. The bathymetric distribution is supposed to go to a depth of 7 metres, but most reports give 3 metres. This is a thermophilic species requiring a temperature of a least

20° C to thrive (Marcus, 1940) and often occurs in places with a southern exposure. It has been reported that low temperatures during the development of the statoblasts cause a higher number of spines, which then remain small; the available amount of material must therefore be distributed over more spines; when the spines are fewer in number they are twice as large (Braem, 1913a).

The species is also found near spillways in dams, i.e., in running water; this is not necessarily an indication of positive rheotropism but rather a question of settlement in a favourable place to which a continuous current of water carries food. This food consists of plankton, small infusoria, and diatoms.

In cavities in the gelatinous bases of the colonies Brooks (1929) found flatworms, protozoans, snails, and crustaceans. According to Borodin (1928), a rotting process caused by bacteria takes place in the gelatinous base; this process attracts infusoria that serve as food for the polypides.

For a colony measuring 280 × 190 mm, Jara (1955) found a weight of 5050 grams, a volume of 5007 cm³, a specific gravity of 1.0085 and mentioned a water temperature of at least 4° C; he says further: "the gelatinous base of the zoarium showed many spots of various size, coloured green, red, reddish brown; seen under a microscope the spots were found to be agglomerations of vegetal Protozoa belonging to Euglenineae, Cryptomonadineae and Volvocineae; moreover the base showed concentric streaks lighter in colour". Deevy (1942) found subfossil statoblasts in a sediment in Connecticut, U.S.A., with a probable age of 11300 years.

***Pectinatella gelatinosa* Oka, 1890**

(Pl. 17 figs. e, f)

Pectinatella gelatinosa Oka, 1890 (ponds on the grounds of the Imperial University, Tokyo); Annandale, 1908a; Hastings, 1929a; Kraepelin, 1892; Loppens, 1908; Oka, 1907; Toriumi, 1941a; 1941b; 1942b; 1956 (taxonomical study, variability); Vorstman, 1928a; West & Annandale, 1911.

Pectinatella burmanica Annandale, 1908a (Lake of Kawkareik, interior of Amherst district, Tenasserim, Lower Birma); 1910a; 1910b; 1911; 1912b; Hastings, 1929a; Vorstman, 1928a.

Material. — Asia. Indonesia: Botanical Gardens of Bogor (ZMB, ZMA). Burma: Kawkareik (ZSI, 100; ZMB). India: Sur Lake, Orissa (ZSI, ZEV 3079/7; USNM, 5169); Japan: Arinoika, pond near Kyoto (RMNH, don. Toriumi).

Description. — The zoaria are always multiple, also originating by fission and placed on a communal chitinous base which is very thick (about 50 mm)

and transparent. The zoaria are fused and embedded in the cuticula, the shape is roughly oval or hexagonal; the diameter is about 20 mm. The tubes are arranged radially, the centre is depressed and has no polypides. The polypides are about 5 mm long. The number of tentacles is 72 to 106; the aperture lies on a protuberance which projects above the cuticula and carries a network of ridges forming hexagonal compartments.

There are only F statoblasts. These are dark brown, large, round or somewhat bent around two axes at right angles to each other, so that the statoblast gives the optical effect of being rectangular with rounded corners. The margin carries about 140 very small spines; the dorsal and ventral halves of the annulus each carry spines which do not coincide. The spines arise from the annulus and carry two hooks. The annulus is here a disk covering the capsule on both sides; in the part of the annulus overlying the capsule the chambers are smaller than in the remaining portion; the capsule is almost round; the outer margin is smooth. Measurements: the diameter is 1340 to 1750 μ ; the annulus has an equal width of 445 μ ; the border is 6 μ wide; the diameter of the capsule is 560 to 630 μ ; the length of the spines is about 24 μ and their width 3 to 6 μ ; the length of the hooks is 11 μ ; the diameter of the chambers 16 μ .

Composite colonies measuring about 75 cm in length and about 10 cm thick have been found. The radial structure of the zoaria derives from a repeated, initially spirally, dichotomous branching from a primary zooid, to form a round zoarium. When this spiral structure is realized there are no more zooids at the centre of the zoarium, but in the reproductive zone at the periphery they are closely packed, giving the zoarium a bowl-shaped appearance. Constrictions in the zoarium indicate division and reproduction, as in the previous species.

Synonymy. — The statoblasts sometimes show pseudolobes that are true malformations; the hooks may also be deformed. Hastings (1929a) later also distinguished two species, *P. burmanica* and *P. gelatinosa*, based on these malformations and even compared *P. gelatinosa* to *Lophopodella carteri* var. *himalayana* Annandale; the latter name, however, was also based on a pathological form. In this case there are no parallel species and there is no question of two species, only of synonyms. Annandale (1908a) considered *P. gelatinosa* and *P. burmanica* to be two different species because of the rounded-rectangular statoblasts of the former and the rounded statoblasts of the latter, but this difference is not essential. The statoblasts may be flat, but the annulus may also curve upwards somewhat at the edges; this difference is not specific, however.

Distribution. — Asia. India: Sur Lake, Puri District, Orissa (ZSI);

pond in the northern Central Provinces (Annandale, 1910a). Ceylon (Annandale, 1910a). Formosa (Toriumi, 1942b). Korea (Toriumi, 1941b). Japan: a number of localities (Toriumi, 1941a; 1956). Indonesia: West Java (Vorstman, 1928a).

It is striking that this Asiatic species has so far been found only in coastal regions. The locality in the Botanical Gardens in Bogor, Java, is in all likelihood secondary since the situation in such gardens is always artificial because of the importation of plants. The species occurs mainly in the Indian region.

Biology. — The growth period lies between July and December, larvae then being found in large numbers. The species lives in association with sponges. It has been reported to occur at times in impoverished forms with only a few (two or three) zoaria measuring 10 mm, but these could have been juvenile zoaria also.

West & Annandale considered it possible that the algae *Dactylococcopsis pectinatellophila* W. West and *Microcystis orissica* W. West produce the gelatinous investment of the compound colonies. Although algae can secrete a gelatinous envelope, the Phylactolaemata secrete their own chitinous cuticula; therefore, this is probably a case of symbiosis (see also under *P. magnifica*). When the zoaria are crushed a poison (?) is set free; no analysis of this poison has yet been given, but it has a very quick, toxic, lethal action on small fish (Oda in litt.; Rogick, 1957). Recent investigations on this poison are reported upon by Tenney & Woolcott (1964) and Collins, Tenney & Woolcott (1964), whose papers I unfortunately have not been able to consult.

Pectinatella spec.

(Pl. 13 fig. a)

Material from Lac Bita and Lac Lukulu in the Congo (IPNC, unpublished) proved on examination to belong to a species of *Pectinatella*, showing that the genus *Pectinatella* occurs in Africa as well as in Europe, America, Asia.

Description. — The zoaria have a radial structure, as regular as if crystalized out; the outline is angular. The examined material was in an advanced stage of development, about 60 μ m in cross-section. Unfortunately, no statoblasts were present, which is striking considering the size of the zoaria. The polypides are about 2½ mm long and about ½ mm thick, with a number of indistinct gastric folds; the number of tentacles is about 75. Leaves of *Nenuphar* served as substrate.

LOPHOPODIDAE Rogick, 1935

The zoarium is a small gelatinous mass. The tubes branch in a radiate

manner. Only free statoblasts are present; these are pointed or carry spines at the poles.

Lophopus Dumortier, 1835

The zoarium is sac-shaped or lobulate; the cuticula is transparent, not incrustated. There are only free statoblasts; these are elongate and pointed at the poles.

Type species by monotypy: *Tubularia crystallina* Pallas, 1768.

Lophopus crystallinus (Pallas, 1768)

(Pl. 7 figs. a, b; pl. 8 figs. a, b; pl. 9 fig. a; pl. 10 figs. b, c; pl. 17 figs. g, h)

Tubularia crystallina Pallas 1768 (pond near country residence Sorghvliet, outside the Hague, Holland).

Lophopus crystallinus - Abricossoff, 1925a; 1926a; 1936a; Allman, 1856; van Beneden, 1848; Berg, 1938; 1948; Borg, 1930; Braem, 1890; Căpuse, 1962; Chirica, 1906; Davenport, 1899; 1904; 1918 (in Ward & Whipple); Davidson, 1910; Despax, 1926; Dudich, 1944; 1948; Dumortier, 1835; Hollowday, 1947; Kraepelin, 1887; Lacourt, 1949a; 1949b; Laurie, 1901; Loppens, 1906a; 1906b; 1908; 1910a; 1910b; Makarow, 1941; Marcus, 1934, (biology, morphology, physiology, development and taxonomy); 1940; Pateff, 1924; Prenant & Bobin, 1956 (synonymy); Rogick, 1946; Schodduyn, 1925b; Sebestyén, 1959; Vigano, 1964; 1965; Wesenberg-Lund, 1895; 1897; Wilcox, 1906; Zirpolo, 1925; Zykoff, 1890.

Lophopus trembleyi Jullien, 1885 (no locality given).

Material. — Inclosure near Frederiksborg, Denmark (UZW).

Description. — The zoarium is sac-shaped in the young stage, gradually becoming lobulate and reaching a size of about 40 mm; there are no septa; the cuticula is soft and completely transparent without incrustation, as lying loose on the ectocyst. The polypides number 6 or 7 to a lobe, the number of tentacles is 60. The statoblasts are large, elongate, and pointed at the poles. The annulus is wide and grayish-brown; the capsule is brown and nearly round. The annulus is 3 times wider at the poles than laterally, excluding the points; dorsally, the annulus completely covers the capsule but ventrally it covers only a small portion of it. The statoblast is surrounded by an extremely narrow strip of the annulus; the outer margin is entirely smooth. Measurements: L about 1200 μ , B 565-630 μ ; the capsule measures 468 \times 386 μ , the diameter of the chambers is 14 μ ; the width of the strip 2½ μ .

Discussion. — When full-grown, the zoarium may be semi-globular. In a younger stage it is hemispherical; the lobes spread like fans. New zoaria are produced by constriction of parts of the old ones. Chirica (1906) found 3 adjacent zoaria connected by a tube consisting of the ectocyst and cuticula. This observation evidently pertains to a fission in which the parts chanced

to remain connected longer than usual. Various malformations have been described. The annulus may be rudimentary, the polar points may be double, and the shape of the statoblast may be almost round (Marcus, 1934).

Distribution. — Europe. The species is found over a large part of Europe including Great Britain and Ireland; in the east it reaches the Balkans and southwestern Russia, as far as the estuaries of the Dniestr and the Dniepr rivers; it has not been found in Greece. In the north its range extends no further than Jutland, Denmark; in the southwest it reaches to, but not beyond, the Pyrenees.

Asia. Anselis, Persia (Abricossoff, 1926a).

North America. U.S.A.: Schuylkill River near Philadelphia (Kraepelin, 1887); Illinois River (Davenport, 1899); Lake Erie (Rogick, 1946).

Thus, *L. crystallinus* has a limited, holarctic distribution. Loppens (1908) mentioned the species from Sweden, but this must be erroneous; Borg (1941) in any case did not mention it. Zykov (1890) reported it from the vicinity of Moscow, but according to Abricossoff (1925a) his material was incorrectly identified.

Abricossoff (1936a) pointed out that the eastern boundary of the range of the species in Europe as well as in North America and Asia virtually coincides with the -4° C January isotherm. He supported this opinion with the fact that this species has not been found in European Russia in spite of extensive hydrobiological investigations; in these investigation an abundant Bryozoan material was collected, but *L. crystallinus* was always absent. Its occurrence in the estuary of the Dniepr (Makarow, 1941), reported later, falls on the boundary.

Biology. — The substrate consists of water plants. The development already begins in water of 9° C. The bathymetric distribution reaches from just under the surface to a depth of about 2 m. The species is also found in high mountain lakes (Lac d'Orédon, Hautes Pyrenées, 1869 m; Despax, 1926), but it nowhere is common, being usually even rare. The zoarium is capable of some locomotion, up to a rate of 60 mm in 12 hours (Wilcox, 1906; Wesenberg-Lund, 1897). This species can tolerate temperatures as low as 0° C, so that hibernation of the zoaria is possible (Marcus, 1934; Sebestyén, 1959). Hollowday (1947) found living zoaria under a layer of ice. Allman (1856) observed unknown organisms, which he took to be parasites; this was confirmed by Marcus (1934).

Lophopodella Rousset, 1904

The zoarium consists of a small patch of chitinous substance, sometimes more or less deeply lobed; the cuticula is gelatinous and soft, not incrustated.

The tubes are repeatedly and dichotomously branched, radiating from a centre; no septa are present. Only F statoblasts are known; these are oval, curved longitudinally, and provided at the poles with one or more spines whose edges, with one exception, carry small hooks.

The type, by monotypy, is *Lophopodella thomasi* Rousset, 1904. Further species belonging to this genus are: *L. capensis* (Sollas, 1908); *L. stuhlmanni* Kraepelin, 1914; *L. carteri* (Hyatt, 1866); and *L. pectinatelliformis* Lacourt, 1959.

Lophopodella capensis (Sollas, 1908)

(Pl. 13 fig. b, c, d; pl. 16 fig. c)

Lophopus capensis Sollas, 1908 (Valkenberg Vlei near Capetown).

Lophopodella capensis - Borg, 1936; 1936a; Hastings, 1929; Jenkin, 1936; Kraepelin, 1914; Loppens, 1908; Marcus, 1934; Sollas, 1908 (larvae, statoblasts).

Lophopusella capensis - Abricossoff, 1959a.

Material. — S. Africa. Florida Lake, Johannesburg, Transvaal (ZMH); Pans near Rietfontein and near Johannesburg, Transvaal (British Museum (Natural History) 28.6, 24.1, 28.12.8.1); Neudamm near Windhoek (ZMH B 97, don. W. Michaelsen, 1911).

Description. — The zoarium is broadly oval with constrictions, about 23 mm long; it consists of radially arranged tubes. The cuticula is thin, with little or no incrustation, transparant, but sometimes yellowish or turbid. The orifice of the polypides is placed at the end of a short, cylindrical protuberance which is bordered by a narrow ridge. The polypides are regularly distributed along the periphery of the zoarium, which has no polypides in the centre; their length is about 3 mm. The number of tentacles is 60 to 70.

The statoblasts are elliptical but truncated at the poles, which carry a long spine. The spine is expanded at the base and studded on each side with a double row of recurved hooklets which at the expanded base extend along the edge of the statoblast. The spines are flattened in the same plane as the statoblast; they consist of two layers which can become detached. The hooklets are usually placed alternately along the edges of these layers, which do not always coincide. The spines either have the same width along the entire length or become pointed at the tips. The capsule is brown and round; the annulus is greyish-yellow and reaches far over the capsule, leaving a round or oval bare space of about a third the diameter and it is 1.3 to 2.5 times wider at the poles than laterally. There is no border along the annulus, or only an extremely narrow one, the resulting outer margin is smooth or very bluntly serrated. Measurements: L 850 μ , B 550 to 608 μ . The diameter of the capsule is 440 to 520 μ , the length of the spines 140 to 175 μ , their width 21 to 12 μ ,

but $47\ \mu$ at the base. The hooklets are 12 to 16 μ long; the diameter of the chambers is 10 to 14 μ .

The cuticula is described as thick and hard, but examination of the material revealed the zoarial cavity to be very large, as a result of which the zoarium seems swollen; the cuticula, to the contrary, is thin and wrinkled. The base of the spines may be straight, convex, or markedly concave.

Kraepelin (1914) distinguished var. *michaelseni*, with more hooklets on the spines of the statoblasts, an almost round capsule, and a somewhat angular outline. Hastings (1929) was of the opinion that Kraepelin's drawing of this variety was exaggerated; she observed transitional forms. It holds here, as for all species, that variability is of great importance, and the differences used by Kraepelin to distinguish var. *michaelseni* are too small to justify its retention.

Synonymy. — Abricossoff (1959a) proposed a new genus, *Lophopusella*, for this species because the statoblast has only one spine. This is phylogenetically unjustified; in a series, singular or multiple spines do not constitute an essential difference; this feature serves to distinguish between species but should not serve as a basis for genera.

Sollas (1908) originally placed *Lophopodella capensis* in the genus *Lophopus*, in which it does not belong because the statoblasts of *Lophopus*, although pointed at the poles, carry no spines.

Distribution. — Africa. Mountain Lake near Neudammer Berg near Neudamm, north-east of Windhoek, S.W. Africa (Kraepelin, 1914); in the Pans of Transvaal; Lake Christie; Florida Lake near Johannesburg; Rietfontein Pan; near Rietfontein in Grass Pan; Mud Pan; Brak Pan; Avenue Pan Benoni (Hastings, 1929); Naivasha Lake in Kenya (Jenkin, 1936). All the finds made so far are located in South Africa except the one in Kenya. No localities between these two are known. *L. capensis* is therefore an Ethiopian species.

Biology. — The substrate consists of stems and leaves of plants and of stones; the bathymetric distribution extends to a depth of 18 m. The species is also found in mountain lakes to an altitude of 1890 m (Kenya). The main growth period is from April to May, at temperatures between 18° and 25° C. It is also found in brackish water and in water with a pH of up to 9.4. Large zoaria, measuring from 20 to 30 cm in diameter, are mentioned in the literature, but these do not exist: such cases represent a large number of zoaria very close together but without a communal base. A number of unicellular algae are sometimes lodged on the outside of the gelatinous cuticula (Sollas, 1908).

Lophopodella thomasi Rousselet, 1904

(Pl. 17 fig. i)

Lophopodella thomasi Rousselet, 1904 (a temporary vlei in the old watercourse or omurambi at Tamansu, Ovamboland, South West Africa); Barnard, 1927; Borg, 1936; Loppens, 1908; Rousselet, 1907; Wesenberg-Lund, 1939.

Material. — Rhodesia (British Museum (Natural History), Rousselet coll. 1917.I.I.179).

Description. — The zoarium is an oval patch of stiff gelatinous substance measuring $6\frac{1}{2} \times 3$ mm; branching tubes radiating from the centre; the cuticula is hard and thick; the polypides are numerous, protruding all around the edge and the surface of the zoarium, leaving a central space free; the number of tentacles is unknown.

The statoblasts are greyish-brown, elliptical, curved in the direction of the longer axis, truncated at the poles and bent inwards, furnished with 3 to 6 spines carrying on their lateral edges 20 to 22 minute, closely-set, curved hooklets. The spines are almost all the same length except for the outermost, which are much shorter; the two layers coincide. The capsule is very nearly circular. The annulus covers the capsule entirely on the dorsal side, and on the ventral side it leaves a bare central space, measuring half the diameter of the capsule. The annulus is 1.5 times wider at the poles than laterally. The statoblast is surrounded by a very narrow border; the outer margin is sometimes serrated. Measurements: L 857 to 890 μ , B 642 μ ; capsule l 409 to 437 μ , b 343 to 363 μ ; the length of the spines is 60 to 75 μ , their width 10 to 13 μ ; the hooklets are 9 to 12 μ long, the diameter of the chambers is 16 μ ; the border is 7 μ wide.

Distribution. — Africa. In addition to the type locality, the species has been found in the Hunyani River, Salisbury, Southern Rhodesia. "The species is up to now only known from two localities which are relatively widely separated. But they are situated in the drainage systems of two rivers, the Kunene and the Zambesi which are considered to have been more or less intimately connected in times past. The occurrence in these two localities may be a prove that these riversystems were once connected" (Barnard, 1927). This species thus is restricted to the Ethiopian region.

Lophopodella stuhlmanni Kraepelin, 1914

(Pl. 16 figs. d, e)

Lophopodella stuhlmanni Kraepelin, 1914 (dry river-bed near Bibisande, Ugogo-Uniamwesi, between Tabora and Victoria Nyanza, Africa); Borg, 1936; 1936a; Hastings, 1929.

Lophopodella carteri Kraepelin, 1893; 1914; Ullmer, 1913; Vorstman, 1928a (partim).
Pectinatella carteri Kraepelin, 1893; Meissner, 1898.

Material. — Indonesia: Botanical Gardens, Bogor, Java (ZMA, ZMB).
E. Africa: Bibisande (type locality, ZMH, B 7879, 1 statoblast).

Description. — The zoarium is oval in outline, shallowly lobed; about 8×6 mm; the cuticula is yellowish, hyaline, thin and very soft, with hardly any incrustation. When invaginated the orifice of the polypides is situated on a short protuberance which projects obliquely and is surrounded by a wide, thick ridge. The polypides can be almost completely evaginated; they number up to 7 per lobe and are large; the ventricle has 12 to 14 gastric folds; the number of tentacles is about 80. Kraepelin's description is incomplete and is amplified here from the available material.

The statoblasts are wide and nearly rectangular. The poles are flatly truncated, with an angular transition to the sides and carry 7 or 8 spines, each bearing 10 to 16 small marginal hooklets. The spines are of more or less uniform length, the medium spines somewhat longer. The capsule is round and brown; the annulus is greyish-yellow and extends over $\frac{1}{4}$ of the diameter of the capsule. It forms a border of constant width without any reticulation; the outer margin is smooth but sometimes serrated at the corners. Measurements: L up to 948 μ , B up to 854 μ . The diameter of the capsule is 468 μ ; the diameter of the chambers 15 μ . The spines are 117 μ long, of constant width up to 12 μ . The hooklets measure 7 μ , the border is 58 μ wide. The annulus, spines, and hooklets may show malformations.

The differences between the statoblasts of this species and those of *L. carteri* are the following:

In *L. stuhlmanni* the statoblast has a flat polar truncation, while in *L. carteri* the poles are rounded, the basic shape of the statoblast of the former species is rectangular, but more oval in *L. carteri*. The spines in *L. stuhlmanni* are nearly all of the same length, while in *L. carteri* the median spines are about twice as long as the outermost.

Distribution. — Asia. Indonesia: Botanical Gardens, Bogor, Java (by transport?) (ZMA, ZMB).

Africa. Mohasi Lake west of Victoria Nyansa? (Kraepelin, 1914). In Africa this species has only been found in the region of the Great Lakes.

Examination of the material collected by Vorstman in the Bogor Botanical Gardens, some of which is preserved in the Zoological Museum in Amsterdam, revealed that this material, which was identified as *L. carteri* (cf. Vorstman, 1928a), also includes statoblasts of *L. stuhlmanni*. Thus, this species also occurs in Java, but as always, the question remains whether occurrence in botanical gardens may be considered autochthonous.

According to Kraepelin (1914), the two colonies described by Ulmer (1913) as *Lophopodella carteri* belong to the present species, as does the

material on which Kraepelin (1893) based his report. It later also appeared that the material published as *Pectinatella carteri* also belongs to *L. stuhlmanni* (Kraepelin, 1893; Meissner, 1898). Thus, *L. stuhlmanni* is also an Ethiopian species with a probably artificial occurrence in the Indian province.

Biology. — Zoaria are found throughout the year but not always statoblasts are present. Fully developed colonies may divide into two parts; they are capable of locomotion but only at an extremely slow speed.

Lophopodella carteri (Hyatt, 1866)

(Pl. 16 fig. f)

Pectinatella carteri Hyatt, 1866 (freshwater-reservoir near Bombay); Jullien, 1885; Meissner, 1898.

Pectinatella davenporti Oka, 1907 (Kasumiga-Ura near Tokyo); 1907a; Annandale, 1911.

Lophopodella carteri - Annandale, 1910b; 1911; 1912; 1919-1921b; Annandale & Kemp, 1912; de Beauchamp, 1936; Borg, 1936; Dahlgren, 1934; Kraepelin, 1914; Lee, 1936; Loppens, 1908; Masters, 1940; Oda, 1954; 1954a; 1955; 1959 (number of spines not of generic nature); Rao, 1929; Rogick, 1934b (description and distribution); 1935a; 1935b (development); 1936 (variability of statoblasts); 1937b (finer anatomy, behaviour, and reactions); 1938 (viability of dried statoblasts); 1957; Roussetlet, 1904; 1907; Takahasi, 1934; Tenney & Woolcott, 1962; 1962a (literature, distribution, biology); Toriumi, 1941a; 1941b; 1942b; 1956a (taxonomical study, variability, montrosities of statoblasts, seasonal variation and temperature); 1963-1964 (intra-specific variation of the "spinoblast"); Ulmer, 1913; Vorstman, 1928a; West & Annandale, 1911.

Lophopodella carteri var. *davenporti* - Borg, 1936a; Rogick, 1934b.

Lophopodella carteri var. *himalayana* - Annandale, 1911; Rogick, 1934b.

Lophopodella carteri var. *typica* Rogick, 1934b; 1935b; 1937b; 1938.

Lophopodella picta Bretnall, 1920 (Nepean River, Australia).

Lophopus spec. Carter, 1859 (tank near Bombay); Mitchell 1862.

Lophopus brisbanensis Colledge, 1917 (freshwater streams near Brisbane); Hastings, 1929.

Lophopus carteri race *himalayanus* - Annandale, 1908a; 1908b.

Lophopus himalayanus - Annandale, 1908a.

Lophopus lendenfeldi Annandale, 1907b.

Lophopus lendenfeldi var. *himalayanus* Annandale, 1907a (Bhim Tal, Kumaon, Western Himalayas).

Material. — Asia. Indonesia: Botanical Gardens, Bogor (ZMA); Java, a number of specimens (ZMB). Japan: pond near Sendai (BIS); Lake Biwa (ZMK). India: Puella Waterworks, Bengal (ZSI, 55); Bhim Tal, Kumaon, Himalayas (ZMH, don. Annandale, B 110).

Australia. Nepean River, Queensland (Australian Museum, U 711, as *L. picta*).

Description. — The zoarium is small, about 10×4 mm; sac-shaped and round in the initial stages, oval when fully developed. The ectocyst is thick, soft, and hyaline, not incrustated. The protuberance of the polypide is short, the orifice is surrounded by a thick ridge. The diameter of the polypide is 410 to 700 μ . The polypides are arranged concentrically, 5 to 6 per lobe, 20 to 45 per zoarium and are about $4\frac{1}{2}$ mm in length. The number of tentacles is 50 to 95, they are about $1\frac{1}{2}$ mm long and 20 to 30 μ thick.

The statoblasts are broadly-oval, curved along two axes; they are rounded at the poles, which carry 7 to 14 spines decreasing in size from the middle towards the sides. The spines have 6 to 22 marginal hooklets which are curved towards the capsule. The capsule is dark brown and nearly round. The annulus is light brown, extending partially over the capsule, and has an almost constant width. It is encircled by a wide border with an incomplete reticulation; the outer margin is minutely serrated. Measurements: L 840 to 1300 μ , B 560 to 900 μ ; capsule l 420 to 558 μ , b 380 to 510 μ . The annulus is 250 μ at the poles and 200 μ laterally. The spines are 20 to 170 μ long and 8 to 32 μ wide. The hooklets are 7 μ long. The diameter of the chambers is 15 μ ; the border is 12 to 24 μ wide.

Larger zoaria occur, measuring up to 15 mm (Vorstman, 1928a). According to Annandale (1907a), stellate and round cells are found in the cuticula, as described by Ridley (1886) for *Hyalinella lendenfeldi*. Various authors report that different parts of one polypide sometimes have a different colour (Bretnall, 1920), but these colours have been found to be dependent on the nature and degree of digestion of food and the age of the polypide. Obviously they have no specific value.

The statoblasts may be numerous, sometimes 2 to 3 to a polypide, sometimes completely filling the zoaria. The spines are formed of two layers, originating from the two valves; these layers do not always coincide and the number of spines on the two valves may differ. The hooklets, too, do not always coincide. The number of spines varies widely and can be as high as 25.

Malformations and abnormalities occur fairly often in the statoblasts of this species. The spines may be double or Y-shaped, curved or thickened. They may also be entirely absent or very few in number; in such cases the whole statoblast is usually deformed. The polypide is then small and the number of tentacles lower (30). The hooklets are usually comma-shaped but sometimes anchor-shaped; they may be irregularly situated or be partially absent. Even a tripolar statoblast has been observed (Rogick, 1936), as well as a few covered with spines (Toriumi, 1956a). A unipolar statoblast has also been described.

I have mentioned these deformations only because they can be misleading, and have already led to the designation of at least one new species, by Annandale (1907a). He proposed a new variety, *L. lendenfeldi* var. *himalayanus*, later even raised to specific rank (*Lophopus himalayanus* Annandale, 1908a), but later dropped both (1910b). This deformation is also not a 'link' between *Lophopodella capensis* and *Lophopus cristallinus* as Sollas (1908) thought, but only a developmental abnormality. These deformations, furthermore, should not influence our concept of variability, but they can elucidate the mutual relationships among the species.

Synonymy. — Hyatt placed this species in the genus *Pectinatella*, but the statoblasts of that genus have spines around the entire circumference whereas *L. carteri* has spines at the poles only.

Oka (1907) described a form under the name *Pectinatella davenporti* as being distinguished by a higher number of spines (18 to 20) of the statoblast and a seemingly somewhat more sturdy polypide. This is only a developmental form. The larger number of spines does not justify specific differentiation because it is the result of ecological circumstances. The variability of the number of spines has been discussed for *Pectinatella magnifica*. Here too the number of spines varies but there is no second species. *Lophopus brisbanensis* Colledge, 1917, found in Brisbane, Australia, is almost certainly identical with the present species, although the inadequate description and indistinct drawings make identification impossible. The large number of polypides, 30 per lobe, and the absence of the epistome seem contradictory but could be the result of inaccurate observation or description. One lobe cannot accommodate 30 polypides unless the entire zoarium consists of a single lobe. The number of tentacles is not mentioned but, to judge from the highly-developed lophophore in the drawing, it was probably large. Colledge (1917) gave no measurements, neither for the polypide nor for the statoblasts. The type material has apparently been lost, or at least could not be found in the Australian Museum. But two facts support my suggestion: the poles of the statoblast are reported to show about ten short, serrated filaments and *L. carteri* occurs in Australia. I am therefore of the opinion that the name *Lophopus brisbanensis* should be placed in the synonymy of *Lophopodella carteri*.

Bretnall (1920) described a new species as *L. picta*. The type material of the Australian Museum, which I have examined, is identical to *Lophopodella carteri*. *L. picta* is therefore a synonym.

Distribution. — Asia. Persia: Nassarabad in Seistan (Annandale, 1919-1921b). India: Igatpuri Lakes in Western Ghats, Bombay Presidency (Annandale, 1908a); Bombay (Annandale, 1911); Madras (Annandale,

1910b); Puela waterworks in Bengal (ZSI). Burma: Indawgyi Lake (Rao, 1929). China: Peking and Soochow in the Province of Kiangsu (Lee, 1936; Annandale, 1919-1921b). Korea (Toriumi, 1941b). Formosa (Takahasi, 1934; Toriumi, 1942). Japan: Sendai and Lake Biwa (Toriumi, 1941a). Indonesia: Botanical Gardens, Bogor, Java (Vorstman, 1925a).

Africa. Kenya: railway station 6, Athi River near Nairobi (de Beauchamp, 1936).

North America. U.S.A.: Princeton, New Jersey (Dahlgren, 1934); Lake Erie (Rogick, 1934a; 1934b); Ohio (Masters, 1940); Pennsylvania (Rogick, 1957); Louisville, Kentucky (Rogick, 1957); Virginia (Tenney & Woolcott, 1962).

Australia. Queensland: Besides in the Nepean River, also in a freshwater creek in Brisbane (Colledge, 1917).

The principal distribution is in the South-Asian province where the localities lie in a curve running from Persia to Japan, with which Java and Australia are associated (keeping in mind that a botanical garden is always a dubious location).

De Beauchamp's record (1936) from Africa seems correct from his description, in which he quotes Kraepelin (1914), who noted the differences between the various species of *Lophopodella*. The other localities in Africa would seem to concern *L. stuhlmanni* (cf. Kraepelin, 1914).

According to Masters (1940), *L. carteri* was imported into the United States with tropical plants ordered by an importer in Independence, Ohio. The distribution is thought to have started from there and from Princeton, New Jersey, where the same importer had other nurseries and where Dahlgren was the first to find the species.

There must certainly have been a few cases of transportation, although this is difficult to prove. A species can escape notice for a long time, be discovered at a late date, and yet be autochthonous. But here we are concerned with a tropical species.

L. carteri has a preponderantly Indian distribution with records from Ethiopian and Notogaen regions, in addition to which there is a probably artificial nearctic distribution.

Biology. — Leaves and stems of water plants, undersides of stones, pieces of wood, and the snail *Viviparus bengalensis* (Lamarck) serve as substrate. Judged from the literature, the bathymetric distribution is not extensive; one of the records of *L. carteri* was in the remnant of a ditch, 6 inches deep. It has also been found in waters of mountains, in the Himalayas, and near Nairobi at an altitude of 1500 m. The zoaria are capable of slow locomotion, about 3 to 4 inches per day (Lee, 1936; Rogick, 1934b; Takahasi,

1934; Vorstman, 1928a), but it is not clear whether all the authors themselves observed the phenomenon.

The peak periods vary according to the region, in America from July to September (Rogick, 1934b), in Australia, February (Brettnall, 1920), in Seistan, December (Annandale, 1911), in Formosa from March to July (Takahasi, 1934), in Lake Biwa, November (Toriumi, 1941a), in Java from November to May (Vorstman, 1928a), and in Nairobi, November (de Beauchamp, 1936). Fully developed zoaria divide and the parts develop into complete zoaria, as can be seen from the photograph of *L. capensis* (pl. 13 fig. b).

West & Annandale (1911) found an alga, *Tolythrix lophopodellophila* W. West, living in symbiosis with *L. carteri*. Rogick's record (1934b) may concern the same phenomenon; she states: "The colony is enclosed in a thin transparent ectocyst which is often surrounded by a gelatinous substance to which debris adheres". The term "ectocyst" is employed erroneously here: the part referred to is the cuticula which is not incrustated in this species. Rogick also states that the gelatinous substance is not always present, but that when present it is incrustated. This may be a case in which the alga was included in the assumed importation.

If the zoaria are damaged a substance is liberated which has a very quick and lethal toxic action on small fish (Rogick, 1957).

Toriumi (1956a) assumed the existence of a number of strains on the basis of experimental cultures in which he found constant differences in a number of groups. This observation may be analogous to the occurrence of races of cattle and laboratory animals produced by breeding. Definite conclusions, however, require a basis of many critical observations. In his *L. carteri* material Toriumi also observed statoblasts resembling those of *L. stuhlmanni* and *L. thomasi*, which again demonstrates the close relationship between the species of *Lophopodella*.

Oda investigated the variability of the statoblasts (1955) and the occurrence of "double monsters" (1954), as well as the development of double monsters under artificial conditions (1954a). He made an experimental study of the germination of statoblasts of this species under various conditions: rapid and prolonged drying, freezing, x-ray irradiation, treatment with hydrochloric acid as a stimulant, germination after prolonged quiescence, oxygen consumption, and influence of light and temperature (Oda, 1959). According to his results, the radiosensitivity of the developing statoblast-rudiments is greater than that of the buds. From this it may be inferred that the rudiments of statoblasts are more embryonic in nature than the buds (Oda, 1954). What Oda means by 'rudiments' are apparently

developmental phases of the statoblast. He refers to "small bead-like swellings", which are the first primordia and their later stages, but they are not rudiments.

Lophopodella pectinatelliformis Lacourt, 1959

(Pl. 17 figs. j, k)

Lophopodella pectinatelliformis Lacourt, 1959 (Patua, Sumatra).

Material. — 2 slides, type material from Patua, Sumatra (RMNH).

Description. — The zoarium consist of a lobate gelatinous mass, about 4 mm in diameter. The lobation originates from the base, but also probably, is a result of incisures of the border; in peripheral lobations they do not reach very far into the lumen and give the impression of being cicatrices of healed fissures. The polypides are about $2\frac{1}{2}$ mm long, the tentacles number 50 to 70 and are about half as long as the total length of the polypide. The invagination is complete. The statoblasts are oval; the poles are truncated-convex and studded with about 36 very small, anchor-like processes on both valves. The processes do not coincide and are continued on the sides, where they number 4 or 5. The capsule is nearly round, brown, and minutely granulated. The annulus is straw-coloured, covering a small part of the capsule on both sides; the outer margin has microscopic undulations but is smooth. The measurements of the statoblasts are $1200 \times 900 \mu$, of the capsule $495 \times 435 \mu$. The length of the shaft of each processus is 13μ , the width of the anchor 17 to 20μ and the diameter of the chambers 17μ .

There is little material available of this species, which has only been found once. In consequence, the data concerning measurements of the statoblasts and the number of tentacles are very few.

STEPHANELLIDAE nov. fam.

The zoarium is round or spindle-shaped. The zooids are arranged in groups. The lophophore is nearly round. Two kinds of statoblasts are present. The free statoblast is circular in outline.

Stephanella Oka, 1908

The zoarium consists of a gelatinous mass and is adherent, the tubes are thin and repeatedly dichotomously branched. The zooecia are cylindrical and erect; the diameter of the zooecia is greater than that of the tubes. The cuticula is very thick, soft, transparent and contiguous, it carries little incrustation.

Statoblasts. Both types are present. The F statoblasts are circular and

flat; they have no spines. The S statoblasts are rounded-oval with a small annulus. The type species, by monotypy, is *Stephanella hina* Oka, 1908.

***Stephanella hina* Oka, 1908**

(Pl. 18 fig. b; text-fig. 6e)

Stephanella hina Oka, 1908 (a pond near the railroad station of Mejiro, Japan); Loppens, 1908; Toriumi, 1941a; 1941b; 1942a; 1955b (peak period, germination of statoblasts; taxonomical study); 1956.

Material. — Japan: Mejiro near Tokyo (ZMH B 103, part of Oka's type); Sendai, (ZMH B 1716); Tokyo (British Museum (Natural History), Rousselet coll. 1917.1.1.168); pond near Sendai (RMNH, don. Toriumi).

Description. — For the zoarium of the species the characters are the same as those of the genus.

The F statoblasts are numerous and round; the capsule is brown. The annulus is of constant width and carries a border of constant width; the outer margin is smooth. The chambers are more regularly hexagonal than in the other species. Measurements: the diameter is 300 to 370 μ , the diameter of the capsule 210 to 250 μ . The annulus is 47 to 58 μ wide. The diameter of the chambers is 9 μ ; the width of the border is 5 μ .

The S statoblasts are rounded-oval with a small primary annulus. Capsule and annulus are reticulated; the outer margin is serrated. L 410 to 460 μ , B 320 to 340 μ ; the annulus is about 6 μ wide.

The zoarium, depending upon the substrate, is spindle-shaped or seemingly lobulate, 50 to 60 mm long and 6 mm thick. In the distal parts, i.e., in the growth zone, the zooids are single. In the central part they are situated in groups on parts of the tubes swollen locally due to budding on the walls and from the zooids. In this species budding does not occur over the entire length of the tubes but leads to groups of zooids. Oka (1908) mentioned stolons and stalked zooids, but this is incorrect. The tubes, which in *Plumatella* ordinarily have the same diameter, in *Stephanella* are very thin and locally swollen. I consider this to be a primitive character. The polypides are clustered in groups of about 6 individuals, about 3½ mm long. The length of the tentacles is about 1½ mm. The diameter of the zooids is about 2 mm, but only ½ mm without the cuticula. The diameter of the tubes is 1 mm; the length of the branches is about 2 mm.

The polypide shows no deviations from the *Plumatella* type but the number of tentacles is small, being 36 to 40. The lophophore consequently is so small that the tentacles stand in a ring, with an indentation on the anal side. This gives the polypide a resemblance to that of *Fredericella* and, according to Oka (1908) and Toriumi (1956), *Stephanella* should therefore be placed

between *Fredericella* and *Plumatella*. This cannot be correct because 1) there is no similarity between the statoblasts, and 2) the cuticula of the two species shows extreme differences. The round F statoblasts of *Stephanella* are an evolutionary development preceding that of *Cristatella mucedo*.

Oka's description indicates that the zoarium is radially branched in its initial stages; budding later takes place in two opposite directions, giving the zoarium a spindle shape. This growth pattern is exactly the same as that of *Cristatella mucedo*. The characteristics of the zoaria and statoblasts of the two species lead to the conclusion that *S. hina* is a precursor of *C. mucedo*. Both species belong to a single series whose starting point is not yet known.

Distribution. — Asia. Japan: four ponds in the Tohoku district (Toriumi, 1941a); Hokkaido (Toriumi, 1942a); Sendai (RMNH). Korea (Toriumi, 1941b; statoblasts only).

This species seems to be an endemic form, known so far only from a limited area located on the boundaries of the holarctic and Indian provinces.

Biology. — Oka mentioned colour differences in various parts of the digestive tract, here too caused by the diet. According to Toriumi (1955), the statoblasts germinate between 9° and 11° C; the peak period falls in December and January (Oka, 1908).

CRISTATELLIDAE Allman, 1856

The zoarium is elongate, without branching. The polypides are arranged in longitudinal rows. Only free statoblasts are present; these carry spines on both halves of the capsule.

Cristatella Cuvier, 1798

The zoarium is elongated with parallel sides, not branched, gelatinous and colourless. There are only F statoblasts; these are circular and have an annulus. The statoblasts carry spines originating from the dorsal and ventral valves.

Type species, by monotypy, *Cristatella mucedo* Cuvier, 1798.

Cristatella mucedo Cuvier, 1798

(Pl. 9 fig. b; pl. 10 fig. a; pl. 17 fig. l; pl. 18 fig. a; text-figs. 7b, 10)

Cristatella mucedo Cuvier, 1798 (type locality Europe, not further specified); Abricossoff, 1924; 1925a; 1925b; 1926b; 1927b; 1933; Allman, 1844b; 1856; Arndt, 1936; Becker, 1938; L. S. Berg, 1925; K. Berg, 1938; Borg, 1930; 1941; Borner, 1927; Braem, 1888; 1890 (histology, development, reproduction, and structure of statoblast); 1893; 1913; 1913a; von Buddenbrock, 1910 (development of statoblast); Cant, 1936; Căpuse, 1962; Carl, 1943; Davenport, 1904; 1918 (in Ward & Whipple); Davidson, 1910; Deevey,

1942; Despax, 1926; Dudich, 1944; 1948; Du Plessis-Gouret, 1885; Gerwerzhagen, 1913b (nervous system); Heding, 1938; Hejsková, 1948; Hozawa, 1939; Hurell, 1927; Jullien, 1888; Kemper, 1930; Kolaczkowska, 1936; Kraepelin, 1887; 1892 (detailed monographic treatment); Lacourt, 1949a; 1949b; Laurie, 1901; 1942; Levander, 1908; Loppens, 1906a; 1906b; 1908; Marcus, 1940; Margalef, 1948; Mauvais, 1927; W. Meissner, 1904; Munthe, 1941; Murray, 1910; Neistwestnova-Shadina, 1928; Nichols, 1912; Oda, 1954a; Parker, 1913; Perret, 1925; Prenant & Bobin, 1956 (synonymy); Rawson, 1953; Rogick, 1935a; 1937a; Schachanowskaja, 1930; Schmidt, 1886; Schodduyn, 1925a; 1925b; Schölzel, 1951 (development of statoblasts and larvae, studied with intra-vital staining methods); Scott & Duthie, 1895; Sebestyén, 1959; Sherren, 1898; Svetlov, 1935; Toriumi, 1941a; 1942a; 1943; Trauberg, 1940; Tretiakow, 1900; Valkanow, 1932; Vängel, 1894; Vignano, 1964a; 1965; Wesenberg-Lund, 1897; 1907; White, 1917; Zschokke, 1900; Zykoff, 1890.

Cristatella mucedo var. *idae* and var. *genuina* Kraepelin, 1887; Braem, 1888.

Cristatella ophioidae Hyatt, 1866 (structure and biology); Kraepelin, 1887; Loppens, 1908.

Material. — Europe. Various localities in the Netherlands (Lacourt, 1949b; RMNH; ZMA) and Belgium (Lacourt, 1949; INSB); Gjetanger, Norway (Bergens Museum).

Description. — The zoarium is elongated and worm-shaped, it lacks branching and lobes. The cuticula is light grey and very thin, forming an underlayer for the zoarium. The polypides are arranged in three rows on both sides of the longitudinal axis of the zoarium. The medially situated rows consist of degenerated polypides; anterior to the outermost row is a zone of proliferation in which new individuals continually develop (text-fig. 10 nos. 1, 5). The tentacles number between 70 and 90, but usually 73 to 75. The diameter of the zoarium is 5 to 10 mm.

The statoblasts are round in outline and elongated-oval in cross-section. The capsule is round and brown in colour: the annulus is greyish-yellow. Both valves of the annulus carry a ring of spines, round in cross-section with forked points carrying up to 6 small hooks; the spines number 10 to 34 dorsally and 20 to 50 ventrally. The spines do not originate from the outer margin as in other species but from the valves, arising from a ridge situated inwards from the annulus (text-fig. 10 nos. 2, 3, 4). This position corresponds to the place of the excrescences found on the capsule of sessile statoblasts in *Plumatella* and by which the statoblasts become attached to the substrate. In the present species the annulus is narrow and less developed, extending only slightly over the capsule. It consists of a fibrous substance with radially directed fibres; the network formed by the chambers becomes coarser and more irregular towards the outer margin. The outer margin is frayed by the presence of very small projections. Electron-microscopical examination has shown these ragged projections to arise from the roof of the chambers (pl. 10 fig. a). Measurements: the diameter of the statoblasts

is 970 to 1250 μ ; the width of the annulus is $1/9$ to $1/10$ of this diameter. The length of the spines is 182 to 273 μ ; the width of the shaft is $7\frac{1}{2}$ to 11 μ . The spines extend beyond the edge of the statoblast dorsally by 150 μ and ventrally by 130 to 180 μ ; the length of the hooklets is 33 to 47 μ . The diameter of the chambers is 11 to 16 μ ; the length of the projections is $2\frac{1}{2}$ μ .

The cuticula is secreted in a very thin state, the chitin flows down, and piles up into a layer several millimetres thick under the zoarium. The zoarium forms a communal body cavity for the polypides, a coenocelial space wherein only rudimentary septa are present, serving as a system of trabeculae.

Braem (1888, 1890) demonstrated that the principle of branching found in *Cristatella* in the initial stages is the same as that in *Plumatella*, but the main stem remains short, the lateral branches grow out, and the segment acquires a truncated outline. The radial branching leads to a round zoarium; then, passing a butterfly-shaped, lobate stage in which growth occurs in two opposite directions, an elongated zoarium develops. According to various reports, in this final stage the zoarium can attain lengths of 20 cm and even up to 40 cm, and divide by fissure into a number of new, independent zoaria.

The number of spines on the statoblast can vary widely. The varieties *genuina* and *idae* are based on this feature. The extremes, however, overlap. The development is influenced by various factors: diet, temperature, light, chemical composition of the water, and seasonal effects, i.e., ecological factors which also influence the number of tentacles. These influences are still poorly understood and few or no experiments have been performed (cf. *Pectinatella magnifica*). Schachanowskaja (1930) saw a relationship between the number of spines and the circumference of the statoblasts in the sense that an increase of the circumference is accompanied by an increase in the number of spines, in contrast to *Pectinatella magnifica* in which, according to this author, the number of spines remains constant for variable sizes of the statoblast. This opinion is incorrect, however, because the number of spines in the latter species is not at all constant. Kraepelin (1887) held the opinion that *Cristatella* and *Pectinatella* are still in an evolutionary phase in which the characters are not yet completely developed.

Svetlov (1935) discussed the question of whether an organism is a unit, a group of mutually interdependent individuals, or a number of independent individuals. The locomotion of the colonies suggests a physiological equality of the poles of the colony, *Cristatella* usually creeps in the direction of the sagittal axis, but is capable of moving in all directions. No posterior or anterior pole can be distinguished. *Cristatella* colonies are not bilateral but rather dissymmetrical forms. When cut longitudinally they heal; when cut in other directions they also heal if the fragment includes part of the margin

of the colony. On this basis Svetlov considered *Cristatella* colonies to be complete organic individuals composed of subordinate elements retaining their original characters. In this connection I would only remark that there is no division of functions.

Synonymy. — Braem (1888) and Kraepelin (1887) considered the names *C. idae*, *C. genuina*, and *C. ophioidea* as synonyms, because the differences were too small. I am in agreement with this.

Distribution. — Europe. Finland: Solkajewi Lake, Lapland (Levander, 1908, statoblasts). U.S.S.R.: Umba River near the village of Umba on the Kandalaksha Coast of the White Sea, Kola Peninsula (Abricossoff, 1926; 1933). Iceland (Heding, 1938; statoblasts). Further, throughout Europe to the Pyrenees (Despax, 1926). Switzerland: Swiss Lakes (Du Plessis-Gouret, 1885). Italy: Lago Trasimeno (Vigano, 1964a). The Balkan Mountains (Valkanov, 1932). Rumania: delta of the Danube (Căpuse, 1962). Great Britain and Ireland; Shetlands Islands (Scott & Duthie, 1895); Hebrides (Cant, 1936).

Asia. U.S.S.R.: West Siberia, Altai Mountains and Baikal Lake (Abricossoff, 1927b; 1933; Arndt, 1936; Berg, 1925; Munthe, 1941); Chalaktir Lake, Kamchatka (Braem, 1893; statoblasts). Japan: Lakes Raitisi and Bakko, Sachalin (Toriumi, 1941a); Japanese Islands (Toriumi, 1941a, 1942a; Hozawa, 1939).

North America. Canada: Go Home Bay, Ontario (USNM); Vancouver Island (Carl, 1943); Great Slave Lake (Rogick, 1937a); Lake Erie (Rogick, 1935a); near Quebec (White, 1917). U.S.A. (Hyatt, 1866; Davenport, 1904).

Our present knowledge of the distribution gives the following picture: in the north, the range is limited, at least in Europe, by the northern timber-line. In the East Siberian region this species is not found in the cold area of the January isotherm of -40° C. The localities in West Siberia, the Altai Mountains, and Lake Baikal lie outside this boundary. To the south, the mountain chains in Europe and Asia determine the boundary. The report of the occurrence of the species in the Lake of Tiberias, Israel, probably got into the literature through a mistake of Zschokke (1900). He mentioned Barrois (1893-1894) as source, but there such a record cannot be found. The species occurs throughout North America from Vancouver Island to Quebec. The northern and southern boundaries in America are not clear, but in the Great Slave Lake the timber-line is approached. Thus, *C. mucedo* must be considered a holarctic species.

Fossil statoblasts have been found in quarternary layers in Norway, Finland, Denmark, the northern part of Germany, and Switzerland (Wesen-

berg-Lund, 1907). They have also been recorded for the Dryas and Ancylus periods in Sweden (Borg, 1941), and they have been found in peat layers from the Dryas period in Lapland (Levander, 1908) as well as in sandy late glacial peat in The Netherlands (Florschütz, written communication, 1947). Statoblasts also occurred in a sediment from the bottom of Linsly Pond, Conn., U.S.A. (Deevey, 1942).

Biology. — In central Europe the peak period is from August to September; according to other reports there is a brief, explosive development in April and October with unusually large numbers of statoblasts, e.g. in the Jura Lakes (Perret, 1925). According to White (1917), *C. mucedo* is common in North America, but he failed to observe seasonal variations in number.

The development of the zoaria can vary greatly from year to year, as I have myself observed in Sonsbeek, Arnhem, The Netherlands. For many years *C. mucedo* and *F. sultana* have both been present in this locality; in one year the stream bed is entirely covered with *Cristatella* colonies, and in the following year *F. sultana* appears in similar numbers and *P. emarginata* is also represented, but there are only few *Cristatella* colonies.

The bathymetric distribution extends from 0 to 20 m; statoblasts have been found at a depth of 100 m. The species is found on every kind of substrate but particularly on water plants; this is related to its frequent littoral occurrence.

C. mucedo thrives at temperatures between 9 and 30° C. It can, however, support lower temperatures, as indicated by its occurrence up to the northern timber-line and in high mountain lakes near the snow-line (Wesenberg-Lund, 1907; Lago Taneda in the Alps at 2293 m, Zschokke, 1900). *C. mucedo* is highly dependent on fresh-water and cannot survive in brackish water, but it does occur in peat lakes with very acid water, e.g., in Mecklenburg in Germany (Becker, 1938).

The zoaria are capable of locomotion, apparently by the movements of the tentacles, since the zoarium possesses no muscles. When it becomes detached from the substrate, the zoarium may assume a spiral shape. *C. mucedo* is supposed to show little reactivity to external stimulation.

Evidently by chance, the zoaria sometimes serve as food as a clump of statoblasts, 2 cm in diameter, has been found in the stomach of the Scaup Duck, *Aythya marila* (L.) (Bergens Museum).

DOUBTFUL SPECIES

Plumatella auricomis Annandale, 1913

Plumatella auricomis Annandale, 1913a (El Almania, Lake Tiberias, Palestine); Annandale, 1915c; Abricossoff, 1927b; Behning, 1924; Hastings, 1938; Hozawa & Toriumi, 1941; Lacourt, 1948.

Annandale originally described only the S statoblasts of this species, but these are not characteristic; various species have S statoblasts of the same kind. In a later paper (1915c) Annandale mentioned F statoblasts as well, but gave neither an adequate description nor illustrations. Moreover, Annandale (1915c) could not know later on with certainty that he had the same species before him. The type material in the British Museum (Natural History), 1936.6.24.2, and the material of the Zoological Survey of India (5473) includes no F statoblasts.

7

In contradiction to my earlier opinion about this species (Lacourt, 1948), I must now conclude that a species without F statoblasts is unrecognizable and that the name *P. auricomis* should be considered a nomen dubium. *P. auricomis* is certainly not identical with *P. pseudostolonata*.

The material from the Volga region (Annandale, 1915c) belongs to *H. punctata* (cf. p. 90). The reports of Abricossoff (1927b) and Behning (1924) refer to this material. The material from the Belgian Congo (Lacourt, 1948) belongs to *P. longigemmis* (cf. p. 74). The material of Hozawa & Toriumi, 1941, cannot be identified.

***Plumatella tanganyikae* Rousselet, 1907**

Plumatella tanganyikae Rousselet, 1907 (Lake Tanganyika); Annandale, 1911; 1919-1921b; Annandale & Kemp, 1912; Borg, 1936; 1936a; Cunningham, 1920; Lacourt, 1948; 1951; Loppens, 1908; Rao, 1929; Ulmer, 1913; Wiebach, 1965.

For the same reason as given for *P. auricomis*, this species must also be considered dubious. The S statoblast is identical to that of *P. auricomis*.

The material in the British Museum (Natural History) (31.5.06, Rousselet coll., 1917.1.1.25 (holotype) and items 1.6.06 Rousselet coll. 1917.1.1.25 and 27.8.18.4) is not conclusive, nor was the material from ZMB (B 102). A specimen from ZMH (B 111), probably attributable to Annandale and identified as *P. tanganyikae* subsp. *bombayensis*, is *Fredericella sultana* subsp. *indica*.

Wiebach (1965) argued that the specific name *Afrindella* (= *Plumatella*) *tanganyikae* be maintained, although earlier he has agreed with me that when F statoblasts are lacking it is impossible to describe a species (1946: 7). I do not think that there are grounds to change my opinion. The granulation and further chitin-formation of a statoblast is dependent on various ecological factors and on the "age" of the statoblast. The opinion of Wiebach that *P. tanganyikae* is an archaic species because it has only an S statoblast and a low number of tentacles, cannot be summarily rejected but requires confirmation by evidence from culture experiments, to prove that no F statoblasts

develop during reproduction. On the other hand, the S statoblast under discussion is already so highly developed that it can no longer be called archaic. An analogous case is found in the species *Stephanella hina*; this species, too, has a low number of tentacles, the lophophore has a small bend, and there is a well-developed S statoblast, but *Stephanella hina* nevertheless has an F statoblast, that is small but completely developed.

Plumatella orbisperma Kellicot, 1882

Plumatella orbisperma Kellicot, 1882 (near Buffalo); Rogick & van der Schalie, 1950.

According to the latter two authors, this species cannot be identified. The type material is apparently no longer extant, since the authors do not mention it, and they were unable to provide any further data on the species. The name should be considered a nomen dubium.

Various species of *Plumatella* and *Hyalinella* have almost identical sessile statoblasts, with the same size and shape; in the absence of free statoblasts they cannot be identified. Statoblasts that could not be identified have been found in the following places:

Europe. Volga region (Annandale, 1915c).

Asia. Amur area, Siberia (M. Meissner, 1897); Mishanfu-Dalai Nor and Buir Nor, Manchukuo (Hozawa & Toriumi, 1941); China: Ningpo, Canton, Hunan, and Siang Kiang (M. Meissner, 1897); vicinity of Shanghai, China (Richard, 1894); Yokohama, Japan (M. Meissner, 1897); vicinity of Lao-Kay, Kebao and Janina Lake, Tonkin (Richard, 1894); Inner Lake Talé Sap, Singora, Thailand (Annandale, 1916); Indawgyi Lake, Birma (Rao, 1929); Igatpuri and Kumaon Lake, India (Annandale, 1911); canal at Cuttack, Orissa, India (Annandale & Kemp, 1912); El Almanyia, Lake Tiberias, Israel (Annandale, 1913a); Manila, Philippines (M. Meissner, 1897); Loka, Celebes (ZMA, leg. M. Weber).

Africa. Bibisande, East Africa (Stuhlmann, 1890); Towalio, Victoria, Albert and Albert-Edward Lakes, East Africa; Nile delta, Nile, upper Nile and White Nile, Egypt (M. Meissner, 1893); Lake Tanganyika (Rousselet, 1907); Canary Islands (Richard, 1898); Athi River near Nairobi, E. Africa (De Beauchamp, 1936); Niger River, Senegal (M. Meissner, 1893).

America. Rio das Almas, Tocantin basin, Goiás and Rio São Francisco, Baiá, Brazil (Lange de Morretes, 1940); Piston Isle, southern Tierra del Fuego (Kraepelin, 1893; Calvet, 1904, erroneously as *F. sultana*).

Australia and New Guinea. B River, Kaiser Wilhelmsland, Territory of New Guinea (M. Meissner, 1897); Murray River, Australia (M. Meissner,

1897); Horse Pond, Moore Park, Sydney and Duck Creek, Clyde (Whitelegge, 1889).

To summarize, statoblasts not mentioned for individual species have been found in the following regions: Asia (Amurland; interior of China; Tonkin; Siam; Luzon; Celebes). Africa (drainage basin of the Nile, Niger, and Senegal Rivers; Canary Islands). South America (interior of Brazil). Australia (Murray River in southern Australia; eastern New Guinea).

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Plate 1

Fredericella sultana (Blumenbach). a, section through capsule of S statoblast; b, innermost ectoderm (E) and mesodermal content (electron-micrographs).

Plate 2

Hyalinella punctata (Hancock). a, section through capsule with adhering crust of S statoblast; b, mesodermal content (electron-micrographs).

Plate 3

a, *Fredericella sultana* (Blumenbach), ectodermal cells, strongly magnified ($\times 8400$); b, *Plumatella emarginata* Allman, pore in wall of chamber of F statoblast (electron-micrographs).

Plate 4

Plumatella emarginata Allman. a, section through capsule (K), basal layer (bl) and internal lining (ib) of F statoblast; b, chamber with shrinking cytoplasm (electron-micrographs).

Plate 5

Plumatella emarginata Allman. a, roof layer of annulus of F statoblast; b, aberrant chambers and pore, general view (electron-micrographs).

Plate 6

Plumatella emarginata Allman. a, internal lining of capsule, strongly magnified; b, mesodermal content (electron-micrographs).

Plate 7

Lophopus crystallinus (Pallas). a, pores in walls of chambers, still containing rest of cytoplasm; b, "grained layer" (hl) and rod-like membrane (st 1), K = capsule (electron-micrographs).

Plate 8

Lophopus crystallinus (Pallas). a, mesodermal content of capsule; b, "grained layer" (hl), rod-like membrane (st 1) and capsule (K) (electron-micrographs).

Plate 9

a, *Lophopus crystallinus* (Pallas), transition between "grained layer" and "rod-like" membrane (see arrow); b, *Cristatella mucedo* Cuvier, section through capsule (K) and part of annulus (electron-micrographs).

Plate 10

a, *Cristatella mucedo* Cuvier, section through annulus and capsule (K); b, c, *Lophopus crystallinus* (Pallas), section through annulus; b, roof layer (see arrow); c, line along which the statoblast will split when development starts (T) (electron-micrographs).

Plate 11

a, *Plumatella agilis* (Marcus), evaginated polypide, catching a prey; b, *Plumatella agilis* (Marcus), invaginated polypide; c, *Plumatella evelinae* Marcus, F statoblast; d, *Pectinatella magnifica* (Leidy) statoblast, darkfield illumination; e, *Plumatella fruticosa* Allman, S statoblast in polarized light; f, *Hyalinella punctata* (Hancock), S statoblast in polarized light.

Plate 12

a, *Plumatella repens* (Linnaeus), orificium in closed condition; b, *Fredericella sultana* (Blumenbach), zooid; c, *Hyalinella punctata* (Hancock), F statoblast, small form; d, *Plumatella fungosa* (Pallas), gelatinous envelope of F statoblast, light field illumination; e, *Plumatella emarginata* Allman, F statoblast with the characteristic reticulation; f, *Fredericella sultana sultana* (Blumenbach), S statoblast; g, *Hyalinella vorstmani* (Toriumi), F statoblast; h, *Fredericella australiensis* Goddard, S statoblast; i, *Hyalinella vorstmani* (Toriumi), S statoblast with aberrant chambers on the annulus; j, *Hyalinella punctata* (Hancock), F statoblast; k, undifferentiated statoblast, occurring in this shape in various species of *Plumatella*.

Plate 13

a, *Pectinatella spec.*, zoarium; b, *Lophopodella capensis* (Sollas), zoarium; c, *Lophopodella capensis*, initial stage of statoblast; d, *Lophopodella capensis*, initial stage of annulus formation; e, *Fredericella australiensis* Goddard, zooid; f, *Fredericella sultana indica* Annandale, S statoblast; g, *Plumatella casmiana* Oka, membranaceous statoblast; h, *Plumatella casmiana* Oka, S statoblast; i, *Plumatella casmiana* Oka, S statoblast with wide annulus and reticulation; j, *Plumatella casmiana* Oka, F statoblast, typical shape; k, *Plumatella casmiana* Oka, F statoblast, precursor of *P. repens*; l, *Plumatella casmiana*, F statoblast, narrow form.

Plate 14

a, *Plumatella fruticosa* Allman, F statoblast, typical shape; b, *Plumatella philippinensis* Kraepelin, F statoblast; c, *Plumatella fruticosa* Allman, S statoblast; d, *Plumatella fruticosa* Allman, F statoblast, immature stages.

Plate 15

a, *Plumatella casmiana* Oka, F statoblast, *P. vaihirieae*-precursor; b, *Plumatella agilis* (Marcus), F statoblast; c, *Plumatella carvalhoi* (Marcus), F statoblast; d, *Plumatella carvalhoi* (Marcus), S statoblast; e, *Plumatella fruticosa* Allman, F statoblast of an appearance resembling that of *P. philippinensis* Kraepelin and *P. casmiana* Oka; f, *Plumatella repens* (Linnaeus), F statoblast; g, *Plumatella repens* (Linnaeus), S statoblast; h, *Plumatella fungosa* (Pallas), F statoblast; i, *Plumatella fungosa* (Pallas), S statoblast; j, *Plumatella javanica* Kraepelin, F statoblast; k, *Plumatella longigemmis* (Annandale), F statoblast; l, *Plumatella emarginata* Allman, F statoblast.

Plate 16

a, *Plumatella toanensis* (Hozawa & Toriumi), F statoblast; b, *Plumatella toanensis* (Hozawa & Toriumi), F statoblast, elongated form; c, *Lophopodella capensis* (Sollas), statoblast; d, *Lophopodella stuhlmanni* Kraepelin, statoblast; e, *Lophopodella stuhlmanni* Kraepelin, spines of statoblasts, with hooklets, highly magnified; f, *Lophopodella carteri* (Hyatt), statoblast.

Plate 17

a, *Hyalinella indica* (Annandale), F statoblast; b, *Hyalinella lendenfeldi* (Ridley), F statoblast; c, *Hyalinella vaihirieae* Hastings, F statoblast; d, *Pectinatella magnifica* (Leidy), statoblast; e, *Pectinatella gelatinosa* Oka, statoblast; f, *Pectinatella gelatinosa* Oka, spines of statoblast, highly magnified; g, initial stage in the formation of F statoblast in *Lophopus* and *Lophopodella*; h, *Lophopus crystallinus* (Pallas), statoblast; i, *Lophopodella thomasi* Rousselet, statoblast; j, *Lophopodella pectinatelliformis* Lacourt, statoblast; k, *Lophopodella pectinatelliformis* Lacourt, spines on statoblast, highly magnified; l, *Cristatella mucedo* Cuvier, statoblast, initial stage of chambers.

Plate 18

a, *Cristatella mucedo* Cuvier, initial stage of statoblast, showing fibrous structure of the annulus; b, *Stephanella hina* Oka, F statoblast; c, *Hyalinella vaihirieae* Hastings, S statoblast.

