Notes on some species of the genus Amathia (Bryozoa, Ctenostomata)

P. J. Chimonides
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The species of the genus *Amathia* have presented difficulties of recognition for a long time. Even the most recent revisionary accounts have failed to establish the separate identity of many of the species; these have, instead, been submerged in erroneous synonymies. Fifteen species are dealt with in full. In the main, species without significant spiralling of the autozooid groups are considered. Three new species are introduced: *A. guernseii*, *A. intermedis* and *A. tricornis*. A fourth species, *A. populea* Busk MS in d'Hondt, is recognised as new. *A. distans var aegyptana* is raised to specific rank. *A. cornuta* Lamouroux (preocc.) is renamed *A. lamourouxi*. *A. obliqua* and *A. plumosa* MacGillivray are redescribed. *A. alternata* Lamx., *A. biseriata* Krauss, *A. brongniartii* Kirkpatrick, *A. lendigera* Linn., *A. pruvoti* Calvet, *A. pinnata* and *A. wilsoni* Kirkpatrick, *A. woodsii* Goldstein, are redefined with type material selected. Characters for use in taxonomic and systematic discrimination are introduced, and brief comment is made on the zoo- and palaeo-geography of the species dealt with.

Introduction

The genus *Amathia* was erected in 1812 by J. V. F. Lamouroux, consequential to the study of material collected from Tasmania and the south coast of Australia by C. A. Lesueur and F. Peron, during the years 1800–1804 (Tenison Woods 1880, d'Hondt 1979).

However, *Sertularia lendigera* of Ellis (1755) from European waters became the type species of the genus, by virtue of being Lamouroux's sole mentioned species at the introduction of the genus (I.C.Z.N. article 69(d)). The species itself was validated with the publication of the 10th edition of the *Systema Naturae* by Linneaus in 1758 (and is therefore technically that of Linneaus).

Ryland (1982) gave a revised perspective classification of the genus but there are differences between his definitions of higher categories, including *Amathia*, and the characters of the genus presented here. At the Family level, Ryland described the 'zooids' as being 'radially symmetrical, no face being partly membranous'; and at the Superfamily level, he described 'branching being irregular'. Both descriptions are inaccurate for *Amathia*. Similarly d'Hondt (1983) for the Family level, also described 'External autozoecial symmetry' as 'radiated', while at the Superfamily level, there was some ambiguity in the definitions of the characteristics employed e.g. for the 'Zoarium . . . autozoecia unconnected to their neighbours'. Clearly there is need for a review of the characters

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used in the definition of the higher taxonomic levels, although this is beyond the scope of this account.

The persistent problem has been how to differentiate between the numerous species. The brief descriptions often given are of little help, and in fact have led to some confusion. Often, widespread geographical distributions have been suggested. Where no figures or specimens are available, it is unlikely that the true identity of some species will ever be recognised. Despite the efforts of d'Hondt (1979, 1983) the picture still remains clouded.

This account attempts to establish criteria for species differentiation within the genus; to identify some species groupings based upon these criteria and in the process to discuss and correct past misconceptions.

In general, the species of *Amathia* may be assigned to either of two groupings: those with autozooids spirally disposed about the stolon; those with autozooids disposed linearly along the stolon. It is mainly the latter group which is discussed here. Where spirally disposed species are dealt with, this is mainly to obviate possible confusion with those species (i.e. *A. alternata* and *A. pruvoti*) in which marked twisting of the autozooid groups occurs along the stolon. It is in the context of comparison with *A. pruvoti* that *A. distans var aegyptana* is considered.

Definition and Assessment of Taxonomic Characters

Waters (1910) in his brief account of the genus, outlined a number of characters which may serve as a foundation on which to build an understanding of both the genus and its species. These characteristics may be added to, and arranged in what is considered here to be an order of decreasing reliability, reflecting an increase in their intraspecific variability.

List of species discrimination characteristics in order of reliability

(1) budding pattern of stolons
(2) development of any kenozooidal processes or rhizoids and their orientations
(3) arrangement of autozooids about the stolons
(4) autozooidal thickening
(5) profile of autozooids and stolons
(6) number of autozooids and proportion of stolon occupied by autozooids
(7) dimensions of components

The potentially informative characters of larval type, larval metamorphosis, ancestrula formation and initial colony development are generally not known and hence cannot be evaluated. Despite the explicit account given by Barrois (1877) for *A. lendigera*, the ancestrula and earliest astogenetic stages, for example, have not been recognised in any of the specimens examined. In some specimens it was clear that this part of the colony was absent; in others, it was impossible to see because of heavy overgrowth by the colony's own rhizoids or by spatial competitors. For these same reasons, in the following systematic accounts, no information is given on the non-erect part of the colony for the majority of species. It is possible that some colonies are the result of association between the products of more than one ancestrula, (without the necessity for fusion to have occurred, especially in the non-arborescent growth forms). Zimmer and Woollacott (1977a) suggested that the larval type of all stoloniferan ctenostomes is the same. It would appear however, that their conclusions were drawn from only three species: '*Amathia lendigera*', *Bowerbankia pustulosa* (Ellis and Solander) and *Zoobotryon verticillatum* (Delle Chiaje). Furthermore, Zimmer and Woollacott (1977*b*) pointed out that past accounts of metamorphosis of larvae in this group were inconsistent, and that 'additional work is essential to clarify the pattern(s) of metamorphosis' of the larval type. Waters' (1910) intuitive suggestion of the 'valuable assistance' which the primary zooecia might give must, therefore, be discounted for the present.

Extensive examination of several large colonies indicates that the branching pattern of stolons remains remarkably consistent within species. Differences in branching pattern may be inferred to have been microenvironmentally induced in that they tend to be sporadic, involve the development of new stolens from astogenetically early regions of the colony, and are often associated with the presence of epibionts. The budding patterns, together with kenozooidal processes, rhizoids, autozooidal thickenings and disposal of autozooids about the stolons, can give rise to characteristic colony shapes which, with familiarisation, allow identification of species by casual inspection.

The growth of a colony relies essentially on the production of the supporting 'stolonal' kenozooids. Where such a kenozooid is destined to bear autozooids, the autozooids are usually seen to develop at about the same time as the kenozooid lengthens through apical growth. Autozooid-bearing kenozooids are here termed stolons. The position of the autozooids and the proportion of stolon occupied by them is highly regular. Stolonal and autozooidal growth is considered to have ceased with the production of septa at the distal end of the stolon, and the subsequent appearance of daughter stolonal buds. The kenozooidal processes of character No. 2 in the above list appear to be growth-terminating features. These are usually distinguishable from potential autozooid-bearing stolonal kenozooids by being straighter, narrower, often tapering to a point, and frequently being subdivided by septa.

Where rhizoids are to be produced by a structure, the origin of each rhizoid is marked first by the appearance of an oval window in the cuticle. Rhizoids then develop as papilliform outgrowths of these windows, proximally directed along the colony, growing towards the colony base. The rhizoids sometimes fuse with each other en route, overgrowing and obscuring underlying stolons, and forming a trunk-like mass. Autozooids and lateral branches of overgrown stolons are often shed. When rhizoids are produced, the resulting colony form is usually arborescent.

The overall cuticular thickening of any colony appears uniform, except at the regions of the growing tips, where it is thinner. This level of cuticular thickening can differ between colonies of the same species. As this thickening is contributory to colour, it follows that colour is also variable. Within all species, there are localised areas of thickening, which tend to be constant. Thickening in the autozooids, which gives their groupings a characteristic appearance, may be used to discriminate between species. Two conditions occur: one where the walls between autozooids are differentially thickened (inner-wall thickening); the other where the outer walls are differentially thickened (outer-wall thickening) (see Fig. 1B, C).

The arrangement of autozooids on the stolon is usually described as being paired, or as a biserial row. Although this appears correct, in all specimens examined, displacement of autozooids occurs, so that the autozooids of one row interlock with the recesses between the autozooids in the other row (Dalyell, 1847 for *A. lendigera*). Very frequently, this emphasises a single proximal-most autozooid in each group. No pairing of autozooids may be confidently assigned throughout a colony in any species, and there can be odd or even numbers of autozooids in any autozooid group. In some cases, notably those with inner-wall thickening, the proximal-most autozooid tends to be larger in cross section and displaced centrally, such that it can be very difficult to assign it to a row of origin at any stage in its ontogeny.

Materials and methods

Specimens used for study were mainly those of the British Museum (Natural History), London, (BMNH) and The Manchester Museum, (MM), with additional material referred to as follows: Laboratoire de Biologie des Invertébrés Marins et Malacologie of the Muséum National d'Histoire naturelle, Paris, (LBIMM); the National Museum of Victoria, Melbourne, (NMV); the Rijksmuseum van Natuurlijke Historie, Leiden (RM); and the U.S. National Museum, Washington, (USNM).

Often, the material for study had been preserved dried, with resulting distortions. To observe the autozooidal characteristics preserved in the cuticular thickenings, it was found far better to rehydrate the specimens although it was still possible to make identifications without treatment. Rehydration was carried out using tri-sodium phosphate in 7–10% aqueous solution, with subsequent transfer to distilled water and then via a sucession of increasing concentrations of alcohol, to 80% concentration for storage. From this process, specimens regained the turgidity associated with their living state. It was from specimens in this turgid state that measurements were taken.

Some care was needed, as rupture of specimens was possible through the initial high osmotic differential established on transfer to distilled water. In some cases, specimens failed to reflate because of existing ruptures in their cuticles.

In the ensuing descriptions, anterior is used to denote the side at that location bearing autozooids, and posterior, the side opposite (see Fig. 1D, E). Dimensions are given in millimetres and are means of a minimum of 30 measurements. Where shape negated the validity of a single sample measurement, extreme dimensions are given, these also being the means of 30 measurements each. Measurements were made in ontogenetically complete components, near distal regions, avoiding where possible, astogenetically earlier (older) regions of the colony. No attempt was made to determine intra-colony variations quantitatively. Where these were noted, they were assessed subjectively.

The following abbreviations are used:

Sl.	length of stolon
Sd.	diameter of stolon, at location specified; usually midway along the proximal autozooid-free end.
Zh.	autozooid height to the highest point on the rim of thickening, of tallest autozooids, unless otherwise specified.
Zw.	autozooid width, measured along the stolonal axis.
Z/S.	the linear proportion of stolon occupied by autozooids
Zn.	the number of autozooids per autozooid group (and apparent number of 'pairs')
Tpl.	length of terminal process

Key to species

(Identification is best attempted with plentiful material.)

1	Rhizoids developed, colony frequently aborescent	2
–	Rhizoids not developed, colony not arboresecent, no terminal processes and Z/S ratio $<50\%$	13
2	Autozooidal thickening inner-wall	***brongniartii***
–	Autozooidal thickening outer-wall	3
3	Branching nearly always bifurcate	4
–	Branching primarily tri- and tetrafurcate, bifurcation may also be present	10
4	Terminal processes developed	5
–	Terminal processes not developed	7
5	A pair of lanceolate, single-kenozooidal terminal processes developed at the distal end of each autozooid group, arising in the same direction as the autozooids	***lamourouxi***
–	Lanceolate terminal processes of compound kenozooidal construction, each filament developed in place of a normal stolon, sometimes branched	6
6	Rhizoids developed postero-laterally, terminal processes never branched	***populea***
–	Rhizoids developed anteriorly, terminal processes often forked	***woodsii***
7	Autozooids re-orientated by approx. 180 deg. from stolon to stolon, polyrhizoidy (see page 335) possible	***alternata***
–	Autozooid orientation from stolon to stolon maintained within 30 deg., rhizoids paired at most	8
8	Rhizoids developed anteriorly, autozooids with marked distal inclination, autozooid group profile diminishing distally	***guernseii***
–	Rhizoids developed postero-laterally, autozooid group profile horizontally even i.e. level	9
9	Stolons curved anteriorly, curvature increasing distally, autozooid group arranged in line with stolonal axis	***biseriata***
–	Stolons straight, autozooid group set obliquely to stolonal axis	***obliqua***
10	Autozooid-bearing stolons developed laterally from a central axis of stolon-sized, or larger, kenozooids. Autozooid-bearing stolon sequences end with compound terminal processes, these often forked	***plumosa***
–	Autozooid-bearing stolons developed laterally from a central axis of other autozooid bearing stolons	11

11 Central axis stolons undergo trifurcation only; indistinguishable from lateral stolons . ***pinnata***

– Central axis stolons usually undergo tetrafurcation, a fourth autozooid-bearing stolon developed posteriorly. Central axis stolons morphologically distinguishable from lateral stolons, differences may be slight 12

12 Autozooid-bearing stolon sequences end with lanceolate, compound kenozooidal, terminal processes, each replacing a normal stolon and thus in complements of three. Pronounced difference between central axis and lateral stolons. . . . . ***tricornis***

– Autozooid-bearing stolon sequences with pinnate, compound terminal processes; each assemblage replacing stolons in other, regular positions, giving characteristic arched colony sub units. Difference between central axis and lateral stolons slight . . . . . . ***wilsoni***

13 Autozooid groups regularly twisted along stolon length . . . . ***pruvoti***

– Autozooid groups rarely showing any twist 14

14 Stolons often in rectilinear series, straight, sometimes undergoing trifurcation. Autozooid groups often remote from subsequent branching point. Autozooids usually erect . . ***intermedis***

– Stolons of variable length, usually short, sculptured and posteriorly deflected. Autozooid groups overlie subsequent branching point, autozooids inclined distally, the lean increasing distally . . . . ***lendigera***

Systematic Section

Phylum **BRYOZOA** Ehrenberg, 1831
Class **GYMNOLAEMATA** Allman, 1856
Order **CTENOSTOMATA** Busk, 1852
Genus ***AMATHIA*** Lamouroux, 1812: p. 184

Part *Sertularia* Linnaeus, 1758.
Serialaria Lamarck, 1816.
Part *Valkeria* Dalyell, 1847.
Amathella Gray, 1858.
Charadella Gray, 1858.
Serialia Gray, 1858. (errorum pro *Serialaria* Lamarck, 1816).
Spiralia Gray, 1858.
Cornalia Gray, 1858.
Amathia: Bobin & Prenant, 1956: (incomplete cum. syn., NB. Gray 1858 misquoted as 1848); Ryland, 1982; Winston, 1982; d'Hondt, 1979, 1983; Hayward, 1985.

TYPE SPECIES. *A. lendigera* (Linnaeus 1758 *sensu* Ellis 1755) Lamouroux 1812: p.184.

GENERIC DESCRIPTION. Colonies mainly erect with a creeping base, this sometimes extensive. Autozooid groups displaced towards the distal portion of the stolon. Stolons may produce rhizoids, proximally disposed. Distal, mainly growth-terminating kenozooidal processes may be developed from various positions. Autozooids with gizzards, borne on kenozooidal stolons, arising from rosette plates, in groups, connate for at least part of their length, appearing biserially arranged as a straight or spiral series.

REMARKS. The only attempt to regroup species comprising the genus *Amathia* was made by Gray (1858, duplicated 1859). Gray introduced several indeterminate subgeneric or generic groups, the type species of which were insufficiently described and not illustrated. The great majority of the limited characteristics employed are variable within species, such that none of the divisions Gray introduced exclusively defines any species group identifiable within the genus. Bobin & Prenant (1956) are followed here in assigning all species described to the genus *Amathia*.

Amathia lendigera (Linnaeus, 1758)
(Figs 6A, 7A)

? *Sertularia lendigera* Ellis, 1755: 27, pl. 15 (figs 24B, 24b).
Sertularia lendigera Linnaeus, 1758: 812.
Amathia lendigera Lamouroux, 1812: 184.
Not *Amathia lendigera*: MacGillivray, 1895: 135, pl. B (fig. 1).
Not *Amathia lendigera*: O'Donoghue & de Watteville, 1944: 430 (= *A. populea*).
Part *Amathia lendigera*: Bobin & Prenant, 1956: 280.
Amathia lendigera: Hayward, 1985: 134, fig. 45B.

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1963.1.8.3, Chichester Harbour, H. G. Stubbings collected.

OTHER MATERIAL

BMNH; 1827.11.18.8, no locality. 1852.3.16.62, Weymouth. 1882.7.7.85, no locality. 1887.7.23.5, Solent, I.o.Wight. 1891.8.7.18, Portland, Dorset. 1897.8.9.67, Weymouth Bay, Portland, 10 fthms. (18.29 m). 1899.5.1.211, ?Off Saints Bay, Guernsey? 1900.10.30.10–11, Weymouth. 1912.12.21.681, Plymouth.

MM; 7093–4, Naples. 7095, Roscoff, France. 7096–9, Swanage. 7105, Naples. 7106, St. Raphael, S. France. 7107, Rapallo (=Rapolla, Italy?).

DESCRIPTION. Colonies tend to have to have a moderately extensive creeping component of stolonal kenozooids. These are adpressed to the substratum and closely follow its profile, showing reduced branching in some places and multiple branching in others. These stolonal kenozooids are usually of irregular form and length, and only rarely bear autozooids. Bilateral palmate processes are often produced, through which adhesion to the substratum is effected. Erect components may be produced at any branching point, with or without continuation of the creeping component. The erect components develop as the characteristic autozooid-bearing stolons, arranged in the typical form of an orbicular mass, cotton-wool like in appearance, utilizing well the available free space near to the substratum. These erect components appear tangled, but are rarely so. Any erect component may resume the creeping habit on contact with the substratum. Branching in the erect part of the colony is practically always bifurcate, ranging from equally dichotomous to almost rectilinear with side branches, these appearing on alternate sides. Bifurcations typically form an angle of 90 deg. Autozooid group orientation about the stolon is not usually preserved from stolon to stolon. Daughter stolons often arise deflected anteriorly to maternal stolons. Autozooid groups, with relatively few autozooids, occurring at the extreme distal end of stolons, frequently overlapping the subsequent branching point. Stolons are often deflected posteriorly at the proximal end of the autozooid group, and also raised slightly on the anterior surface at this same region. Stolons may be of variable length. Autozooids are outer-wall thickened. Autozooid profile diminishes distally, due in part to decreasing autozooid height, and in part to increasing distal inclination of the autozooids. A proximal-most autozooid is usually prominent in each group and is displaced centrally. Where not truly central, this autozooid remains on the same side of its stolon as the direction in which that stolon was budded. The arrangements of autozooids on sister stolons are therefore mirror images of each other (see Fig. 5B). Where stolons form linear sequences, autozooid groups borne on such series tend to show an alternate sequence of autozooid displacements on successive stolons. Sometimes sister stolons carry identical autozooid displacements, these being opposite to that on their maternal stolon. No overall pattern is discernible within the colony in the occurrence of this second state of succession (see Fig. 5C). Rhizoids are absent.

Sl. 1.25–2.75
Sd. 0.75–0.97
Zh. 0.33–0.50
Zw. 0.10–0.12
Z/S. 25–50%
Zn. 8–17 (appearing as 4–8 'pairs')

REMARKS. According to Harmer (1931), the original specimens described and figured by Ellis (1755) were not kept (I.C.Z.N. article 73(b) (i), recommendation 69B). Harmer stated that specimens of *A. lendigera* were sent to Linnaeus by Ellis, but some 12 years after the publication of the nomenclaturally significant 10th edition of Linnaeus' *Systema Naturae* (1758). Two specimens, under the original name of *Sertularia lendigera*, are still in the collections of the Linnean Society of London (Nos. 1298.17 and 1298.18). The specimens are preserved pressed dry on paper, and both are labelled as 'lendigera' in Linnaeus' handwriting. From examination of these specimens, some doubt arises that Ellis and Linnaeus were sufficiently rigid in their interpretation of *A. lendigera*. Two species are present: specimen 1298.17 is identifiable as *A. semiconvoluta* (see pages 335, 338); while specimen 1298.18 is probably *A. lendigera*. Linnaeus (1758) has trustingly used Ellis' (1755) description verbatim. If the specimens originated from Ellis, Linnaeus may also have accepted their identity from him. It is possible therefore, that the mistaken identity of 1298.17 could be attributed to Ellis; neither man realising the presence of mixed material.

However, there is some evidence in support of Harmer's statement that the Linnaean specimens are not Ellis' original (1755) material. Linnaeus is reported to have been in the habit of upgrading his botanical collections, with the replacement of older specimens by new, 'some of them not conspecific by modern taxonomic standards' (Stearn, 1957), a practice which could also have been applied to herbarium preparations of 'zoophytes'. In addition, none of the figures of Ellis (1755) correspond with either of the Linnean Society specimens, in particular specimen 1298.18. Features of importance are: the arborescent and open appearance of the colony shape in figure '24b'; the number of autozooids per stolon indicated by the magnified view in figure '24B'. Although only a single line of autozooids is drawn in the latter figure, this may be interpreted as showing either: a single proximal-most autozooid with indications of the outlines of subsequent 'paired' autozooids; or possibly a line of 'all paired' autozooids. The condition depicted is readily seen in many dry preserved specimens, where only the thickened outer walls, forming the periphery, survive well. As such, 17 or 18 autozooids would be represented on three of the five stolons; 15 autozooids would be represented on one of the remaining two; and there is an inexplicable absence of autozooids on the remaining fifth and final stolon. Although notionally possible, it is very unusual for *A. lendigera* to show as many autozooids per stolon in direct succession in a colony. The importance of this analysis is that figure '24B' is claimed as an exact microscope drawing.

Harmer (1931) suggested that figures of Ellis be regarded as the lectotype of the species. However, the figures are inadequate, no rhizoids are shown, and their presence or absence is not indicated in the description. On the cumulative evidence (see above), figures '24b' and '24B' could thus be depictions of *A. intermedis* or even *A. guernseii*.

Selection of a neotype specimen is the only satisfactory way to resolve the identity of *A. lendigera*; particularly important as the species is the type of the genus. There is no indication that the Linnean Society specimen 1298.18 formed any basis for the description for the species. In addition to the uncertainties surrounding its status, 1298.18 unfortunately also lacks sufficient locality data, is not in an adequate state of preservation, and so should not be considered. Specimen BMNH 1963.1.8.3 is therefore selected here as neotype. It is preserved in alcohol, growing on *Halidrys siliquosa* as is the Linnean Society specimen. BMNH 1963.1.8.3 is erroneously listed by d'Hondt (1983) as *A. pruvoti*, a very different species (see pages 336, 337).

There is great similarity between *A. lendigera* and *A. intermedis* and both resemble *A. guernseii* (see pages 316, 317). The morphologies of all three may overlap in different parts of the colony. *A. lendigera* differs from *A. intermedis* in that: it tends to have fewer autozooids per autozooid group; the autozooids have an increased distal inclination; the autozooid group profile diminishes distally more rapidly; the autozooid groups and subsequent bifurcation sites are more condensed relative to each other; it has a more compact colony form, with low incidence of rectilinear succession. Great care is needed to distinguish between the trifurcation that may occur in the erect part of the colony of *A. intermedis*, and the multiple branching, including trifurcation, which occurs in the immediate vicinity of the non-erect part of *A. lendigera*, as detachment from the substratum is frequent in preserved specimens. Non-erect stolons may usually be identified by the nearby presence of palmate processes (see Fig. 8A), and the irregular morphology associated with the creeping mode.

The displacement of the proximal-most autozooids in maternal and daughter stolons, may reflect the timing of the production of daughter stolons relative to each other. The mirror image arrangement (see Fig. 5B) possibly results from the simultaneous production of the daughters.

Most of the published records for *A. lendigera* are listed in a lengthy synonymy by Bobin and Prenant (1956). However, many of these records are unsupported by specimens available for examination and are thus equivocal. In addition, the account these authors give mentions the occurrence of rhizoids, and thus includes another species, probably *A. guernseii*.

Three specimens in the Waters Collection in the MM. (7100, 7101, 7102) from Zanzibar, are superficially similar to *A. lendigera*. However, notwithstanding the little material present, it is possible to see that the autozooid groups lack any characteristic distal inclination. In addition, the linearly disposed stolons seem to be arranged in true rectilinear fashion and lack any posterior deflection associated with stolons of their length as in *A. lendigera*. Another specimen (7104) from Menton (southern France) labelled 'A. lendigera', shows trifurcation at four stolons in almost direct succession, but conforms in most other characteristics. These stolons are all in proximity to substratum attachment sites and are probably not typical of the whole colony budding pattern. These is not enough material to be certain about this or the true identity of the specimen. The locality is, however, within the expected distribution area of *A. lendigera*. Some of MacGillivray's specimens (NMV 65387–8) marked 'British', are *A. lendigera*. Additional material (NMV 65383–5) labelled 'A. lendigera' and from Western Port, Australia, is a different species. These specimens bear little resemblance to the 'British' material, and in addition, show evidence of rhizoids. Where the rhizoids are not obvious, careful illumination is required to observe the oval window precursors. The specimens are probably early astogenetic stages of *A. lamourouxi*, but there is not enough material to be certain; the characteristic terminal processes are not present, and the identity is inferred from the branching characteristics. The 'Australian' specimens may be the material described as *A. lendigera* by MacGillivray (1895, pl. B, fig. 1), although the actual specimen figured does not appear to have been recorded.

DISTRIBUTION. *A. lendigera* is known from the Thames estuary, and along the south and west coasts of England. The species also occurs off the north coast of Africa, off Mediterranean southern France, and Naples and 'Rapallo' in Italy. Substrata recorded are rocks and the alga *Halidrys siliquosa*.

Amathia intermedis sp. nov.

(Figs. 6C, 7C)

? *Serialaria lendigera*: Johnston, 1838: fig. 40.
? *Serialaria lendigera*: Johnston, 1847: fig. 68.
? *Serialaria lendigera*: Couch, 1844: pl. 16.
Valkeria lendigera Dalyell, 1847: 249, pl. 52 (fig. 2).
? Part *Amathia lendigera*: Bobin & Prenant, 1956: fig. 124, I, IV.

Holotype: BMNH; 1887.5.2.18 part, Hastings, England.

Paratypes: BMNH; 1842.12.9.14, Belfast Bay. 1847.9.24.184, North'd (=Northumberland?) Coast. 1887.5.2.18 part, Hastings. 1963.2.10.1, Scarborough. 1985.3.2.1a, 1b, Yarmouth. 1985.3.2.2, Bournemouth. 1985.3.2.3, no locality.

ETYMOLOGY. The species at one time seemed intermediate in character between *A. lendigera* and *A. guernseii*.

DESCRIPTION. In the erect part of the colony, branching is primarily bifurcate, ranging from equally dichotomous to rectilinear series with side branches. There is a disposition to the latter condition, where at a bifurcation, one daughter stolon usually remains in line with the main axis of the maternal stolon, while the other daughter stolon appears sequentially on alternate sides. These lateral daughter stolons are produced at the same distal inclination to the maternal stolon axis as the maternal stolon autozooids. Their lateral angular inclination may be from 0–90 deg. to the orientation of the maternal autozooids, but usually ranges from 10–30 deg. Occasionally there is a trifurcation, in which, of the three daughter stolons produced, the middle one lies in the rectilinear position. The other two are produced one on either side, separated from the central one by approximately 45 deg. The autozooids on the maternal stolon bisect this angle. Autozooid groups occur towards the distal end of stolons, but there is usually a further autozooid-free portion of stolon, distal to the autozooid group. This is often axially well divided into small branches, the subdivisions orientated in the same direction as, and supporting, the daughter stolons. There is frequently a further autozooid-free length between the end of the autozooid group and this region of division, approximately equal to the diameter of one autozooid. Stolons are often straight, showing little sign of accommodating the autozooids borne. The autozooids tend to be erect, and of even height throughout the autozooid group, although autozooid group profile sometimes diminishes at the distal end. This is due in part to an increased inclination in the autozooids, and in part due to decreasing autozooid height. Autozooids are outer-wall thickened, but thinly so overall, and pale yellow brown in colour. Viewed anteriorly, a proximal-most autozooid is usually evident in each autozooid group. The occurrence of this autozooid, the pattern of autozooid displacements, and the succession states of autozooid displacements on the stolons, are identical to that found in *A. lendigera* (see page 313). The orientation of the autozooid group about the stolon is not always preserved from maternal to daughter stolons; re-orientations of up to 180 deg. may occur. No rhizoids are produced, and the colony attains a diffuse cotton-wool like appearance. The non-erect part of the colony does not appear as extensive as the erect part. Stolonal kenozooids in the non-erect part of the colony: produce branches occasionally; tend not to bear autozooids; are not of the same appearance as those of the erect part, in being elongated, sometimes twisted, and generally following the profile of the substratum. Erect components may be produced at any branching point, these assuming the normal erect growth pattern. Attachment to the substratum is effected through lateral palmate processes, often developed bilaterally from the adnate stolonal kenozooids.

Sl.	1.75–3.25	Z/S.	35–50%
Sd.	0.80	Zn.	8–29 (appearing as 4–14 'pairs')
Zh.	0.35–0.45		
Zw.	0.10		

REMARKS. *A. intermedis* resembles *A. lendigera* and *A. guernseii*, the closest similarity being with the former. *A. intermedis* may be distinguished from *A. lendigera* in having the following characteristics: trifurcations in the erect part of the colony; a tendency towards higher numbers of autozooids in the autozooid groups, and longer stolons; a staggered occurrence of autozooid groups and branching sites; a more open colony form, resulting from a higher occurrence of rectilinear succession in the stolons. *A. intermedis* may be distinguished from *A. guernseii* primarily in the fact that *A. guernseii* develops rhizoids.

As with *A. lendigera*, the displacement of the proximal-most autozooids in maternal and daughter stolons may reflect the timing of the production of the daughter stolons relative to each other (see page 314).

BMNH 1842.12.9.14, 1847.9.24.184, from Johnston's collection, are *A. intermedis*, but it is not known if any of this is his figured material (1838, fig. 40, 1847, fig 68).

DISTRIBUTION. The species is known from the east and south-eastern coasts of England, and also from Belfast Bay. The only substratum recorded is the alga, *Halidrys siliquosa*.

Amathia guernseii sp. nov.

(Fig 2A, 6B, 7B)

Holotype: BMNH; 1898.5.7.189, Saints Bay, Guernsey.

Paratypes: BMNH; 1912.12.21.682, Guernsey. 1967.8.10.2, Scilly Is. 1984.2.26.31, Gulland Rock, Padstow, Cornwall.

ETYMOLOGY. The species was first recognised in material from Guernsey.

DESCRIPTION. In the erect part of the colony, branching is primarily bifurcate, ranging from equally dichotomous, to almost rectilinear series with side branches. The angle between sister stolons remains approximately 60 deg. There is a strong disposition towards the rectilinear condition where at a bifurcation one daughter stolon tends to remain in line with the main axis of the maternal stolon; the other daughter stolon appears sequentially on alternate sides, produced at approximately the same distal inclination to the maternal stolon axis as the maternal stolon autozooids. The lateral angular inclination of this daughter stolon is about 30 deg. to the orientation of the maternal autozooid group. Autozooid groups occur at the extreme distal ends of stolons, frequently overlying the subsequent branching point. Stolons are usually shaped in accommodating the autozooids, being deflected posteriorly at the proximal end of the autozooid group. At their distal ends, stolons often broaden, as if to subdivide, providing bases for the subsequent daughter stolons, and usually curving anteriorly around the distal end of the autozooid group. Occasionally a trifurcation occurs, three daughter stolons being produced. The third stolon arises from a posterior projection at the broadened distal end of the maternal stolon; viewed anteriorly, this region retains a bilateral symmetry. At the proximal end of the autozooid group, autozooids are inclined distally at about 30 deg. to the stolon main axis. The autozooid group profile tends to be level at the proximal end of the autozooid group, decreasing at the distal end; this is due in part to increasing inclination of the autozooids, and in part to diminishing autozooid height. The profile of the rims of the autozooids usually reflects the angle of inclination in having a stepped appearance. Viewed anteriorly, a proximal-most autozooid is usually evident in each autozooid group. The occurrence of this autozooid, the pattern of autozooid displacements, and the succession states of autozooid displacements on the stolons, is identical to that found in *A. lendigera* (see page 313). The orientation of autozooids about the stolonal axis is not rigidly preserved from stolon to stolon, with variations up to 90 deg. being possible. Over an area, the sum total of such variations is to an extent self cancelling, so that autozooids, overall, face in approximately the same direction i.e. in towards a central axis, and thus a relatively sheltered colony-bounded space (see page 341). Rhizoids are produced from the anterior face of stolons, just proximal to the autozooid groups. These arise singly, or as a pair, one on either side of the stolon, at about 30 deg. to the orientation of the autozooids.

Sl. 1.75–2.75
Sd. 0.80
Zh. 0.38–0.50
Zw. 0.10
Z/S. 50%
Zn. 8–23 (appearing as 4–11 'pairs')

REMARKS. There is much overlap in the characteristics of *A. lendigera*, *A. intermedis* and *A. guernseii*, and it can be very difficult to distinguish among them unless there is an adequate amount of material. *A. guernseii* may be distinguished on the following basis: the autozooids of *A. guernseii* have a pronounced distal inclination through the entire autozooid group, whereas they tend to remain erect in *A. intermedis*; in *A. lendigera*, the condition of the autozooids is intermediate. *A. guernseii* is the only species of the three to produce rhizoids. This in turn affects the overall form of the colonies; *A. lendigera* and *A. intermedis* being diffuse, (the latter also tending to be less compact), whereas *A. guernseii*, with its aggregating rhizoid system, has a more organised and directional appearance. These differences would appear to be independent of the type of substratum. The description of *A. lendigera* given by Prenant and Bobin (1956) probably includes *A. guernseii*, as they mention the presence of rhizoids. In all three species, some twist of the stolons can occur and this is reflected in the autozooids, but it is never consistent throughout the colony, as in *A. pruvoti* (see pages 336, 337).

As with *A. lendigera*, the displacement of the proximal-most autozooids in maternal and daughter stolons may reflect the timing of the production of the daughter stolons relative to each other (see page 314).

The holotype is an alcohol-preserved specimen, originally a single colony, now divided into two fragments. The substratum is not present in any of the specimens examined.

DISTRIBUTION. The species is known only from the localities of the type material.

Amathia populea Busk MS in d'Hondt, 1983
(Figs 2B, 6D, 7D)

Amathia lendigera: O'Donoghue & de Watteville, 1944: 430.
Part *Amathia populea* Busk MS in d'Hondt, 1983: 97, pl. 3 (4).
Not part *Amathia populea* Busk MS in d'Hondt, 1983: 65, (=*A. woodsii*).

MATERIAL EXAMINED

Lectotype (selected here): BMNH; 1899.7.1.526, Natal, S.A., Busk Collection.

Paralectotypes: BMNH; 1822.8.22.1, Port Alfred, Pondoland, S. Africa. 1851.3.12.36, Port Natal, S. Africa 1899.7.1.112 C, 513, 540, Algoa Bay, S. Africa.

OTHER MATERIAL

BMNH; 1886.7.2.9, 1985.3.4.1, Algoa Bay, S. Africa. 1942.8.6.15, Isipingo Beach, Durban, S. Africa. 1963.2.14.7, Cape of Good Hope.

MM; 7061/2, Grahamstown, S. Africa. 7062/2, S. Africa. 7076/2, no locality. 7077/2, Cape Agulhas, S. Africa.

DESCRIPTION. In the erect part of the colony, branching is bifurcate; rarely, a trifurcation occurs. At a bifurcation, the two daughter stolons are produced laterally to anterolaterally, at approximately 30 deg. and 60 deg. to the maternal stolon axis, respectively. The two angular displacements may vary, but occur on alternate sides at successive bifurcations. Development in parts of the colony may be directionally biased giving rise to plumes of stolons. Plumes may be up to 7 cm. in length, with those stolons forming the central axis appearing sympodially arranged. This axis is in fact a simple linear series of stolons with lateral branches occurring on alternate sides. Side branches within a plume are usually limited to 4 or 5 stolons in sequence. As a result of daughter components frequently being produced in a slightly anterior direction, plumes are arc-shaped to cylindrical in cross-section. All sequences end with the production of paired lanceolate processes, each process made up of 2–3 sequential, progressively tapering kenozooids. Sometimes, the production of a stolon in a side branch is replaced by that of a lanceolate process. Autozooid groups reach to the distal ends of stolons, frequently overlying the subsequent branching point. Stolons are usually shaped in accommodating the autozooids, appearing raised at the proximal end of the autozooid group, becoming shallower distally and usually curving anteriorly to the region of bifurcation. Autozooids are outer-wall thickened, but they often appear cylindrical. Autozooid group profile diminishes distally, in part due to stolon shape, in part due to decreasing autozooid height. Autozooids incline distally at about 30 deg. this being displayed at the autozooid rims, the rims usually having a stepped appearance. Viewed anteriorly, a proximal-most autozooid is usually evident in each autozooid group. The occurrence of this autozooid, the pattern of autozooid displacements, and the succession states of autozooid displacements on the stolons, are identical to those found in *A. lendigera* (see page 313). As one daughter stolon tends to remain in line with its maternal stolon, the alternating sequence of autozooid displacements on linear series of stolons is more prominent. The orientation of autozooid groups is generally well preserved from stolon to stolon. Rhizoids may be produced at the proximal end of stolons, most frequently from those in the central axis regions of plumes. Where rhizoids are produced, it is as one per stolon, each arising usually from the outer faces of bifurcations, orientated at between 90–180 deg. to the autozooids on the same stolon. The resulting colony form is usually arborescent. Secondary development may occur in the erect part of the colony where stolons in the common bases of plumes resume normal budding of daughter stolons. The angular displacements described above are retained, but without maintaining the autozooid orientations about the stolons, or the directional organisation evident elsewhere in the colony. The ensuing compact, cotton-wool like, mass may engulf the plume and trunk regions.

Sl. 1.00–1.40	Z/S. 30–55%
Sd. 0.13–0.18	Zn. 6–13 (appearing as 3–6 'pairs')
Zh. 0.38	Tpl. 1.75 (2.60 max.)
Zw. 0.10–0.13	

REMARKS. An association with a sandy environment is inferred from the sand grains sometimes found accreted to rhizoids and attached epizoic worm tubes. In plume portions of the colony, the preserved orientation of the autozooid groups, and the cross-sectional profile of the regions, results in autozooids facing into a relatively sheltered colony-bounded space (see page 341).

The plume portions of *A. populea* strongly resemble the figures of *A. lemanii* in the unpublished plates of Lesueur. However, it is equally possible to draw a similarity between these figures and *A. woodsii* (see page 324) or possibly portions of *A. tricornis*.

Understandably, *A. populea* has, in the past, been confused with *A. woodsii* and *A. tricornis* (e.g. d'Hondt, 1979, 1983). It has also been confused with *A. lendigera* (e.g. O'Donoghue and de Watteville, 1944, BMNH 1942.8.6.15). *A. populea* may be distinguished from *A. lendigera* (and similar forms *A. guernseii* and *A. intermedis*) primarily through the occurrence and location of rhizoids. These do not occur in *A. lendigera* or *A. intermedis*. In *A. guernseii*, the rhizoids are produced anteriorly, just proximal to the autozooid group; whereas in *A. populea* they are produced latero-posteriorly and proximally distant from the autozooid group. *A. tricornis* and *A. populea* differ in many characteristics (see page 321).

D'Hondt (1979) placed *A. populea* Busk MS (part, without qualification) into synonymy with *A. cornuta* (*sensu* d'Hondt, 1979) along with a number of other species, including *A. australis*. D'Hondt (1983) then drew some distinction, first indicating (p.65) that *A. populea* Busk MS part from Australia is synonymous with *A. cornuta* (*sensu* d'Hondt, 1983 i.e. *A. woodsii* see pages 320, 323 *et seq.*). Later, d'Hondt (1983: p.97) also gave a brief description and a figure (p.103) of a South African specimen, BMNH 1899.7.1.526 of *A. populea* Busk MS part, so validating Busk's manuscript name, and making the name *A. populea* available for this species. D'Hondt referred to the specimen as 'A.sp.' yet appears to have remained equivocal by suggesting that this is also possibly 'a form of *A. cornuta*?' (*sensu* d'Hondt, 1983) i.e. *A. woodsii* (see pages 320, 323 *et seq.*).

A. populea and *A. woodsii* may be distinguished in the following: the form of the lanceolate processes, being simple in *A. populea*, often branched in *A. woodsii*; the autozooid to stolon ratio, being higher in *A. woodsii*; the orientation of the rhizoid origins, being latero-posterior in *A. populea* and anterior in *A. woodsii*.

Small quantities of material may be very difficult to distinguish and identify with certainty, such that even Busk made errors. Some of Busk's *A. populea*, BMNH 1899.7.1.528 from Algoa Bay, South Africa and BMNH 1899.7.1.4383 from Australia, is in fact *A. woodsii.* BMNH 1899.7.1.4383 is the only specimen in the BMNH collections from Australia labelled *A. populea*, and so is undoubtedly the material that d'Hondt (1983) refers to under the name '*A. populea* Busk, unpublished (pars: Australia)'.

All specimens labelled by Busk as *A. populea* and considered by d'Hondt (1983) are certain syntype material. D'Hondt's figured specimen, (BMNH 1899.7.1.526) is here chosen as lectotype, the remaining Busk material, except for the two misidentifications indicated above, has paralectotype status.

DISTRIBUTION. The species is known from the south-eastern coast of South Africa, possibly also occurring off southern Australia.

Amathia woodsii Goldstein, 1879
(Figs 2C, 9B, D)

Amathia woodsii Goldstein, 1879: 20, pl. 3 (fig. 5).
Amathia australis: MacGillivray, 1889: 310, pl. 185 (figs 5, 5a).
Amathia woodsii: MacGillivray, 1895: 138, pl. B (figs 5, 5a).
Part *Amathia cornuta*: d'Hondt, 1983: 65, fig. 36 (C).

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1883.11.29.27, Port Jackson.

OTHER MATERIAL

BMNH; 1861.9.20.17, Fremantle. 1897.5.1.1189, no locality. 1897.5.1.1196, Port Phillip Heads. 1899.7.1.528, 1985.3.6.1, Algoa Bay, S. Africa. 1899.7.1.4383, Australia. 1909.8.4.10, Western Port, Australia. 1963.3.28.4, Adelaide.

MM; 7075/2, Queensland.

DESCRIPTION. In the erect part of the colony, branching is bifurcate. Stolons are arranged to form rectilinear series with side branch stolons. Side branch stolons are produced on alternate sides at each subsequent bifurcation, arising with the same distal inclination as the autozooids of their maternal stolons. The lateral angular displacement of the side branch stolons can be 0–90 deg. to the autozooid orientation, but usually ranges from 10–30 deg. In parts, growth appears favoured along the rectilinear series, with side branches usually restricted to 4–5 stolon units either side. These parts of the colony have a plume like appearance. Branches end with a pair of lanceolate terminal processes, usually produced in the same orientations as stolons. The processes are made up of 3–4 sequential, progressively tapering kenozooids, often bifurcating at the distal end of the basal segment kenozooid. The lanceolate processes in which bifurcation occurs are most usually produced in the non-rectilinear position. Frequently, the production of a side branch is replaced by the production of a lanceolate process, emphasising the appearance of directional growth. Autozooid groups occur towards the distal ends of stolons, but often there is further autozooid-free part, coinciding with the production of a side branch component. Stolons may show a gentle anterior curvature, and sometimes curve around the distal autozooids of a group. Autozooid group profile diminishes distally, mainly due to decreasing autozooid height, but sometimes due in part to an increase in their distal inclination. Autozooids are outer-wall thickened, the walls appearing cylindrical. Viewed anteriorly, a proximal-most autozooid is usually evident in each autozooid group. The occurrence of this autozooid, the pattern of autozooid displacements, and the succession states of autozooid displacements on the stolons, are identical to those found in *A. populea* (see page 318). The orientation of autozooid groups is generally well preserved from stolon to stolon. Along a plume therefore, autozooids on the rectilinear sequence all face in the same direction, with lateral stolon autozooids generally facing across these. Rhizoids may be produced, one per stolon, arising near to and at about the same orientation as the autozooids. Colony arrangement is similar to *A. populea.*

Zh. 0.65
Zw. 0.10
Sl. 2.58
Sd. 0.20

Z/S. 50–70%
Zn. 8–23 (appearing as 4–11 'pairs')
Tpl. 2.50 (4.80 max.)

Remarks. Goldstein's account and figure are a very good representation of the species; the only omission is information on rhizoid production. D'Hondt (1983) placed the species in synonymy with *A. cornuta* Lamarck (1816), but there is some doubt as to the identity proposed for Lamarck's specimen by d'Hondt (1983), and the distinction between *A. cornuta* Lamarck and *A. woodsii* is here maintained (see page 323 *et seq.*).

With limited material, confusion could arise between *A. woodsii* and *A. populea* or *A. tricornis.* D'Hondt (1983) has referred specimens of these last two species to *A. cornuta* Lamarck (*sensu* d'Hondt 1983), i.e. *A. woodsii.* The species may be distinguished in the following: the presence of the characteristic subdivided lanceolate process in *A. woodsii*, this being simple in the other two; the production of rhizoids being near to, and in the same orientation as the autozooid group in *A. woodsii*, these being distant, and of different orientation in the other two; the budding pattern in *A. woodsii* is never as complex as in *A. tricornis*, and the predisposition to rectilinear development is more prominent than in *A. populea*, in which there is a tendency for a sympodial appearance.

According to Stach (1936) specimens from Goldstein's collection were deposited in the NMV. However, his material for *A. woodsii* is not there (NMV in litt. 6.12.1984). In view of the confusion which has arisen, there is a need for type material. The description and measurements given here are based on BMNH 1883.11.29.27 from Port Jackson, an alcohol specimen, rehydrated from the dry state. The specimen is here selected as neotype. Goldstein does not give a locality for his specimen, only mentioning that the species was found on a previous occasion at Portland, presumably Victoria State.

Distribution. The species is known from the south-eastern coast of South Africa, and from Australia, with records from Fremantle, Adelaide, Port Phillip Heads, Port Jackson and 'Queensland'.

Amathia tricornis Busk MS

(Figs 2D, 12C)

Holotype: BMNH; 1899.7.1.6600, Australia, Busk Collection.
Paratypes: BMNH 1899.7.1.4393, 4394, Australia, Busk Collection.

Etymology. Busk's MS name, probably indicating the occurrence of three terminal lanceolate processes.

Description. In the erect part of the colony, branching is mainly trifurcate, although tetrafurcation occurs in certain regions. The latter condition is associated with astogenetically early parts of the colony, which form the base and central main-axis regions. These regions tend to be composed of lengthy series of, what are here termed, type 'a' stolons. Type 'a' stolons are longer than other type 'b' stolons found in the trifurcate portions of the colony, and often bear rhizoids. Where rhizoids are produced, these arise from the proximal end of a stolon, usually singly, at between 45–90 deg. to the autozooid orientation on the same stolon. Autozooids borne by type 'a' stolons show no difference in size from those on type 'b' stolons, although the autozooid groups tend to be shorter. The linear proportion of stolon occupied by autozooids, therefore, is lower. The stolon budding arrangement, in both tri- and tetrafurcate conditions, always results in one daughter stolon lying in rectilinear succession to the maternal stolon. Two other daughter stolons are produced laterally, one on each side, at about 60 deg. to this central axis. All three of these daughter stolons bear autozooids, usually orientated in the same direction as those on the maternal stolon, with some exceptions. In the tetrafurcate condition, a fourth daughter stolon is produced, also at about 60 deg. to the central axis, but posteriorly to the maternal stolon. The autozooid group orientation of the maternal stolon is preserved in this daughter component; the autozooid group thus faces distally along the rectilinear series of the central axis (see Fig. 2D). In the tetrafurcate condition alone, the orientation of the autozooid groups along the rectilinear series is not always maintained. A repeat rotation of 90 deg. may, instead, be observed at each axial junction. The relationship of sister daughter stolons to the axial daughter stolon remains fixed, and, thus, the entire assemblage follows the re-orientation. The original orientations are recovered every fourth axial stolon unit along the sequence. In the trifurcate condition, lateral growth appears to be limited to one or two stolons in sequence each side. Development in these parts of the colony is therefore directionally biased and these parts have a plume like appearance. Branches end with the production of three lanceolate terminal processes, each made up of two or three sequential, progressively tapering kenozooids. These arise from, and lie approximately in line with, their maternal stolons. Sometimes, the central terminal process does not form, being replaced by a stolon instead. This may be repeated so that occasionally, lateral branches may be several stolons in length. On both type 'a' and type 'b' stolons, autozooid groups occur at the extreme distal end of stolons, frequently overlying the subsequent branching point. Autozooid group profile diminishes distally in all cases, mainly due to increasing distal inclination of the autozooids. In all parts of the colony, autozooids are outer-wall thickened. Along rectilinear sequences of stolons, there is a predictable repetition in the arrangement of the autozooids borne. The sequence, progressing distally, is as follows: if, in an autozooid group, there is one proximal-most autozooid prominent, this is associated with one side of the stolon; in the next stolon, no single autozooid is prominent proximally, the proximal autozooids being paired equally; on the third stolon, a proximal-most autozooid is prominent once again, but on the opposite side to that of the first stolon; on the fourth stolon, the proximal autozooids are paired as on the second stolon; the fifth stolon repeats the arrangement on the first stolon. On laterally branched stolons, a proximal-most autozooid is prominent, and is associated with the side nearest the rectilinear stolon sequence. Autozooids on stolons continuing in rectilinear series which develop from lateral branch stolons subsequently follow the predictable pattern of repetition given above.

Sl.	(a) 2.10	Z/S.	(a) 30–40%
Sd.	(a) 0.25	Zn.	(a) 8–11 (appearing as 4–5 'pairs')
Sl.	(b) 1.45	Z/S.	(b) 60%
Sd.	(b) 0.25	Zn.	(b) 10–21 (appearing as 5–9 'pairs')
Zh.	0.35		(all autozooids)
Zw.	0.10		(all autozooids)
Tpl.	2.10		

Remarks. No evidence exists, in the limited material available, that the trifurcate condition ever gives rise to the tetrafurcate condition. The colony form is inferred to be arborescent, resulting from the production of rhizoids.

None of the material held at the BMNH named *A. tricornis* in MS by Busk is misidentified. D'Hondt (1979 & 1983) erroneously placed this species in synonymy in part, with parts of *A. cornuta* (Lamarck) *sensu* d'Hondt (i.e. *A. woodsii,* see page 323), and in part, initially with *A. pinnata* (1979) (see page 330), and subsequently with *A. inarmata* (1983) (i.e. *A. biseriata,* see page 332). D'Hondt on each occasion mentioned *A. tricornis* in synonymy only, thus not making the name available at any time (I.C.Z.N. article 11e).

Among the species which may be confused with *A. tricornis* are: *A. populea*; *A. woodsii*; *A. pinnata*; *A. biseriata*. In brief, *A. tricornis* has a more complex colony construction and differs from these species in many features, for example: the bimorphic autozooid-bearing stolons; the normal occurrence of tetra- and trifurcation, including the production of triplet lanceolate processes and their permutations with autozooid-bearing stolons; autozooid and stolon re-orientations; the productions site of the rhizoids. There are also differences in the autozooid to stolon ratios.

Distribution. The species is known only from material described as being from 'Australia', sent to Busk by Miss Gore.

Amathia lamourouxi nom. nov. for
Amathia cornuta auctorem
(Figs 3A, 8C, 9A, C)

? Not *Serialaria cornuta* Lamarck, 1816: 131.
Amathia cornuta Lamouroux, 1816: 159, pl. 4 (fig. 1a, 1B).
? Not *Serialaria australis* Tenison Woods, 1877: 83, 1st fig.
? Not *Amathia australis*: Tenison Woods, 1880: 102.
Amathia cornuta: Tenison Woods, 1880: 99, fig. 3.
Not *Amathia australis*: MacGillivray, 1889: 310, pl. 185 (figs 5, 5a), (= *A. woodsii*).
Amathia cornuta: MacGillivray, 1895: 137, pl. D (fig. 1, 1a).
? *Amathia cornuta*: d'Hondt, 1979: 10, 16.
Part *Amathia australis*: d'Hondt, 1983: 65, fig. 36(F).
Not *Amathia cornuta*: d'Hondt, 1983: 65, fig. 36(C) (= *A. woodsii*).

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1887.12.10.70, Port Phillip, J. B. Wilson collection.

OTHER MATERIAL

BMNH; 1842.11.4.50, Sydney. 1899.7.1.3, New Zealand. 1899.7.1.4325, Victoria. 1899.7.1.4327, 4329–31, 4333, Australia. 1899.7.1.4328, Bass Strait. 1899.7.1.4334, Australia & New Zealand. 1985.3.10.1, Flinders Is., Bass Strait. 1985.3.24.1, mid channel, Port Phillip Heads, 15 m.

MM; 7078/2, Australia.

LBIMM; bry 2821 part, Australie Occidentale/Nouvelle Hollande (see below).

ETYMOLOGY. Lamouroux's name is used for his species of *A. cornuta* (1816), a name preoccupied by *A. cornuta* (Lamarck, 1816).

DESCRIPTION. In the erect part of the colony, branching is bifurcate. At any branching point, daughter stolons may be produced in positions ranging from almost rectilinear, to 90 deg. to the maternal stolon. A minimum separation of 90 deg. occurs between daughter stolons. These usually arise from the posterior side of their maternal stolon. Stolons are narrowed proximally and usually curved anteriorly, being reminiscent of a short, simple, cow horn. Autozooid groups occupy the greater part of stolons, and frequently overlie the subsequent branching point. Autozooid group profile usually increases proximodistally within each group, or may remain level. Autozooids are outer-wall thickened. Viewed anteriorly, a single proximal-most autozooid is evident in each autozooid group. This autozooid is usually placed just off the stolon mid-line, thus associated with either one or other side of the autozoid group. No pattern is evident from group to group, in the location of this autozooid. At the distal end of each autozooid group and contiguous with the autozooids, are produced a pair of tapering, single-kenozooid lanceolate processes. At the distal extremities of the colony, both daughter stolons tend to be produced at 90 deg. to their maternal stolons, i.e. separated from each other in equal dichotomy by 180 deg. In less distal parts of the colony, daughter stolons may be separated from each other in equal dichotomy by lesser angles. Daughter stolons produced in the linear position are less common and are associated with more central and proximal (astogenetically earlier) regions of the colony. Autozooid orientation is generally not preserved from stolon to stolon. Often there is an equal rotation by up to 90 deg. of each daughter stolon in opposite directions i.e. were both daughter stolons to lie in the linear position, their anterior faces would be away from each other. Successive daughter stolons actually lying in the linear position and forming a sequence, are all produced from the same side, i.e. in such a sequence, viewed anteriorly each time, they would all have been budded from e.g. the left side. The orientation of the autozooid groups, in such a linear sequence, is rotated by 90 deg. in the same direction, with each successive stolon. The original orientation is recovered every fourth stolon unit. Superficially, branching can appear as 'alternate' along a linear sequence. Rhizoids may be produced, usually from stolons along these linear sequences. Rhizoids are produced one per stolon, arising from a position level with, and at 90 deg. to the proximal-most autozoid, and on the same side of the stolon as the direction in which the stolon was budded.

Zh. 0.40–0.50
Zw. 0.13
Sl. 1.13
Sw. 0.25 (at the widest region)
Z/S. 75%
Zn. 11–15 (appearing as 5–7 'pairs')
Tpl. 2.00–2.25

REMARKS. No pattern has been discerned in the autozooid arrangement from stolon to stolon, other than, if the proximal-most autozooid of a group is associated with one side of the stolon, then that association may remain in both daughter stolons over a number of successive bifurcations.

The identity of *A. cornuta* auct. is inextricably associated with the collections made by Peron and Leseur, between the years 1800–1804 (see page 307), on which both Lamarck and Lamouroux worked, both of them describing a 'cornuta'.

Tenison Woods (1880) drew a distinction between his *A. australis* and *A. cornuta sensu* Lamouroux (i.e. *A. lamourouxi*) based on the understanding that Lamouroux's (1816) figure indicates a single line of autozooids. Lamouroux himself, referred in the singular to 'the largest cell of each group . . . garnished with two setaceous appendages'. The misinterpretation of a single row for a double row of autozooids, might be made as a result of a preservation artifact where, in dried specimens, the thinner central walls between autozooids collapse from view, leaving only the outer walls visible. On this basis there is no distinction between *A. australis* and *A. lamourouxi*. The additional difference claimed by Tenison Woods, in the form of the 'setaceous appendages' (his figure of 1877 shows these as being broad and less trim than those in Lamouroux's figure), might be accounted for in terms of the variation which may occur within *A. lamourouxi*. However, Tenison Woods' figure (1877) shows clearly that his specimen had undergone trifurcation. Two possibilities may account for this: the first, that under certain conditions, *A. lamourouxi* can undergo such a division; the second, that Tenison Woods did in fact have a separate species. Although the former may be possible, trifurcation has not been recognised in specimens here assigned to *A. lamourouxi*. The whereabouts of Tenison Woods' material is not known.

MacGillivray (1889) considered *A. australis* to be *A. cornuta sensu* Lamouroux, but in his description (p.310) and figure (pl. 185, figs 5, 5a) gave an acocunt of *A. woodsii*. MacGillivray (1895) subsequently recognised the error, and correctly referred to his account of 1889 as being descriptive of *A. woodsii*. At the same time, MacGillivray distinguished between *A. woodsii* and *A. cornuta*, and reaffirmed his opinion that *A. australis* was synonymous with the latter, but gave Lamouroux as the author and placing Lamarck in synonymy.

D'Hondt (1979) has found a specimen, LBIMM bry 2821, which is claimed to be the holotype of *A. cornuta* (Lamarck). D'Hondt (1979) placed *A. australis* in synonymy under *A. cornuta* (Lamarck), but without mention of *A. woodsii*. D'Hondt (1983) then placed *A. woodsii* in synonymy under *A. cornuta* (Lamarck), but excluded *A. australis*, thus revoking his opinion of 1979 and indicating that *A. australis* is different (d'Hondt's reference to 'parts' of *A. australis* at this point are enigmatic). In this reorganisation of the species, d'Hondt (1983) gave two figures: 36(C) as *A. cornuta* (Lamarck), and 36(F) as *A. australis*. Figure 36(C) is in fact *A. woodsii*, and 36(F) is *A. cornuta*, both of common usage, the latter corresponding with Lamouroux (1816), of which *A. australis* is usually taken to be a junior synonym.

D'Hondt (1983) appears to have determined *A. cornuta* (Lamarck) to be different from *A. cornuta* Lamouroux. *A. cornuta* (Lamarck) predates *A.* cornuta Lamouroux (Tenison Woods, 1880, d'Hondt, 1983). D'Hondt (1983) thus relegated *A. woodsii* as a junior synonym of *A. cornuta* (Lamarck), and assigned the name *A. australis*, as the next available name, for what was previously accepted as *A. cornuta sensu* Lamouroux.

Unless it was the only specimen involved, LBIMM bry 2821 can only be taken as the holotype if so designated at the time of introduction by the original author. Lamarck (1816) did not do this, and the number of specimens involved is not certain.

LBIMM bry 2821 is recorded as being one of three specimens of *A. cornuta* so identified by Lamarck and in the Paris Museum at the time of the compilation of the first catalogue of Bryozoa in 1867. The other two specimens appear to have been *A. cornuta sensu* Lamouroux, only 'possibly' originating from Peron and Lesueur. Their locality is given as 'Australasie'. The specimens were numbered: 172a,b,c. (photocopy of the 1867 catalogue). LBIMM bry 2821 is the only one of the three which is known to have come from Peron and Lesueur (d'Hondt in litt. 10.12.1984). The locality for this specimen is 'Australie Occidentale' (d'Hondt, 1979), and also as 'Nouvelle-Holland' (loan form 24th Jan. 1985).

D'Hondt (1979) reported that LBIMM bry 2821 carries the label 'Amathia lemanii Lesueur'. This would appear to be in the hand of Pergens, the original label having been lost or destroyed. The specimen is taken to be the same one that Pergens (1887) correlated with a figure in the unpublished plates of Lesueur, these in turn related to a manuscript of Desmarest and Lesueur, deposited at Paris in 1829 (with another slightly different version at le Havre). Pergens (1887, p. 88) ascertained that plate 13, figure 6, in the unpublished plates, is *Amathia lemanii*, and (p. 90) then gave the identification he was able to make of the species in terms of what was, to him, a valid and available name i.e. *A. cornuta* (Lamarck). Copies of the plates of Lesueur exist at the BMNH. Plate 13, figure 6, consists of three representations of the species intended, all three at different magnifications. The species represented could be *A. woodsii* or *A. populea* (see page 318); both species are capable of assuming the characteristics portrayed. Missing from the figure(s) is any information on rhizoids and on any occurrence of the characteristic subdivided terminal filaments, which might serve to distinguish between the two species. Only the actual specimen used by Lesueur will determine the true species (taken to be LBIMM bry 2821). The identity of this species is of little taxonomic consequence however, as neither plates nor descriptions have ever been published. LBIMM bry 2821 could have been the holotype perhaps, of Desmarest and Lesueur's species, but there is insufficient evidence published to suggest that it was that of Larmarck's.

In addition, Larmarck (1816) gave no figure, specimen number, or dimensions, with which a specimen may be correlated. Furthermore, the locality information (see above) for the specimen, although close, does not match exactly with that of Lamarck (or of Lamouroux). Lamarck gives 'l'Ocean asiatique' (Lamouroux gives 'Sur les Fucus de l'Australasie'). That the specimen was part of Peron and Lesueur's collections, may not in this case be sufficient; Lamarck himself is not definite as to the origins of his specimen, only 'believing' it to be from Peron and Lesueur. Pergens (1887) merely expressed his opinion that LBIMM bry 2821 is the same as *A. cornuta* (Lamarck); how he reached that conclusion is not clear. The specimen appears to be only one remaining of a number, others having gone astray since the days of Peron and Lesueur; the 1867 catalogue of the Bryozoa was compiled some 51 years after Lamarck's publication.

It is possible that LBIMM bry 2821 may be eligible for selection as lectotype of *A. cornuta* (Lamarck), if it can be shown to have been part of Lamarck's original syntype series, and formative of his opinion. However, Larmarck did also identify two different specimens as being his species, these being *A. cornuta sensu* Lamouroux (see above). These specimens might also have been eligible for selection, but are no longer to be found in the Paris Museum (d'Hondt in litt. 10.12.1984, 24.01.1985).

Further challenge to the identity proposed by d'Hondt for *A. cornuta* lies in the evidence that preceeds Pergen's opinion (1887). Tenison Woods (1880) gave information on the working relationship between Lamarck and Lamouroux concerning the *Amathia* specimens collected by Peron and Lesueur. Much of the information appears to be derived from Lamouroux's (1816) own preface and introduction. Lamouroux had 'the fullest access' to Lamarck's collection, and named at least part of this, if not all of it.

Neither Lamarck's (1816) nor Lamouroux's (1816) account of a 'cornuta' contradicts the other. However, whereas Lamouroux's account is quite explicit, and furnished with figures, such that the species he described may still be recognised; Lamarck's account is open to interpretation. The descriptions may be translated as follows:

Lamouroux, p. 159: No. 266.
(from the French)—The largest cell of each group having its free border, garnished with two setaceous appendages.
(from the Latin)—two setaceous filaments from the first rank cell
Lamarck, p. 131: No. 2.
(from the French)—I believe it (to be) from the voyage of Messieurs le Sueur and Peron. It is a

little more stout and less capillary than the preceeding [i.e. *A. lendigera*], at the extremities curved and as curls.

(from the Latin)—very branched, articulated, somewhat curled; branches alternate; curved secondary little branches; cells in distinct series; two setae at the most distant extremity.

In Lamarck's account, no orientation is given for the setae, and the description could apply to *A. cornuta* of Lamouroux, *A. woodsii* or *A. populea*. Whether the reference to the secondary branches is an indication of an arborescent growth form i.e. axial development with lateral branch system, or a reference to the stolons themselves, is not clear. In either case, the description is insufficiently distinctive. Branching is alternate in *A. woodsii* and *A. populea* and may appear so in *A. cornuta sensu* Lamouroux. Finally, Lamarck makes no mention of any subdivided terminal processes (present in LBIMM bry 2821 part) to be expected if his 'cornuta' was the equivalent of *A. woodsii*.

Although it is not possible to recognise a single species from Lamarck's description, the identity of *A. cornuta* (Lamarck) has been understood through the later accounts of the two authors: in Lamouroux (1824) and Lamarck (1836) respectively, each recognises the other's *A. cornuta* as synonymous with his own; from this derives the *A. cornuta* of common usage. It is this concordance which d'Hondt (1983) has in effect repudiated.

In the strictest sense, *A. cornuta* (Lamarck) should have been classed as a *nomen dubium*, and not used. This is historically implied by Tenison Woods (1880) who acknowledged that Lamarck probably predated Lamouroux, and so accepted *A. cornuta* (Lamarck), 'but with reference to Lamouroux only'. MacGillivray (1895) appears to have been of the same opinion (see above).

In the light of such contradictions, Lamarck's *A. cornuta* must be taken as a *nomen dubium*, and the name should no longer be used for Lamouroux's species. *A. australis* of Tenison Woods would be the next valid name available, if certainty could be attached to the identity of his species (see above). Under these circumstances, it is wiser, in the interest of long term stability, to select a new name for *A. cornuta* Lamouroux, accepting either his figures as lectotype, or perhaps selecting a neotype. It is here proposed that *A. cornuta* auct. be known as *A. lamourouxi*, with specimen BMNH 1887.12.10.70 as neotype.

DISTRIBUTION. The species is recorded from New Zealand and southern Australia.

Amathia plumosa MacGillivray, 1890
(Figs 3C, 12A, B)

Amathia plumosa MacGillivray, 1890: 110.
Amathia plumosa: MacGillivray, 1895: 139, pl. C (figs 2, 2a).
Amathia plumosa: d'Hondt, 1983: 67, fig. 36 (B).

MATERIAL EXAMINED

Holotype: NMV; H494, Port Phillip Heads, J. B. Wilson Collection.

OTHER MATERIAL

BMNH; 1963.2.12.354, 358, Western Australia. 1985.3.8.1, no locality.

DESCRIPTION. The branching pattern on the erect part of the colony is based on both bi- and trifurcation. Trifurcation is associated with non autozooid-bearing stolonal kenozooids, forming angularly undulating 'main-stems'. At the distal end of each of the main-stem constituent stolonal kenozooids, are produced: a single continuing stolonal kenozooid, deflected by approximately 30 deg. towards the central axis of the main-stem; two (autozooid-bearing) side branch stolons, one each side. The side branch stolons are produced in the same plane as their maternal stolonal kenozooid, but diverge from each other equally, by an approximate total angle of 60 deg. The autozooids borne on these side branch stolons face the main-stem, and the stolons themselves are curved anteriorly. Subsequent branching from these side branch stolons is usually bifurcate, although new main-stem sequences may be produced, showing the associated trifurcation. Development along side branches is usually limited; 2–3 stolons in a sequence is usual, but up to 8 stolons in succession may occur. The orientation of autozooid groups along any such sequence remains the same. These side branches end with the production of a pair of usually dichotomously branched lanceolate processes. These are made up of sequential, progressively tapering kenozooids. Where the processes are branched, this occurs at the distal end of the base segment kenozooid. This may be repeated in one or both of the next resultant segments. Rarely, a lanceolate process may trifurcate. On occasions, the production of a stolon in a side branch is replaced by the production of a lanceolate process. Development in such cases, therefore, tends to be directionally biased. The colony is composed of such quasi-cylindrical assemblages, circular in cross-sectional profile, and somewhat reminiscent of 'feather boas'. These may be supported on a trunk-like part of the colony, resulting from the production of rhizoids (see page 309). Rhizoids are produced in two ways: they may be produced from the proximal end of main-stem kenozooids, sometimes singly, although more often as an adjacent pair, in the same orientation as the side branch stolons lying immediately proximal; they may be produced from autozooid-bearing stolons, at approximately 120 deg. to the orientation of the autozooid group on the same stolons. Where autozooid groups develop in side branches, these occur towards the distal ends of stolons, but often there is a further autozooid-free portion. This portion is about the same length as the diameter of, and coincident with the production of, a daughter component. Autozooid group profile tends to remain level and autozooids are outer-wall thickened. Where a proximal-most autozooid of a group is evident, its occurrence, and the pattern of autozooid displacements from stolon to stolon, are similar to those of *A. lendigera* (see page 313) except that the second succession state does not appear to occur.

kSl. 1·45 (main-stem kenozooidal stolons)
kSd. 0·19–0·29 (main-stem kenozooidal stolons)

Sl. 1·03–1·61
Sd. 0·15–0·26
Zh. 0·32
Zw. 0·10

Z/S. 55–65%
Zn. 7–17 (appearing as 3–8 'pairs')

Remarks. The species is so distinctive that it does not appear to have been confused with any other. The slide mounted specimen NMV H494, is accepted here as the holotype of *A. plumosa* MacGillivray (1890), and as that figured by MacGillivray (1895). The label on the slide carries the information: 'H494 *Amathia plumosa* McG P.P.H. fig J.B.W.'. This in agreement with the original description in which the locality is given as 'Port Phillip Heads', from the collection of J. B. Wilson. The description given here is based on the above specimen. Some supplementary information is derived from BMNH 1963.2.12.354 and BMNH 1963.2.12.358, these agreeing well with the holotype.

There is some indication that the repeated branching in the lanceolate processes coincides with the development of a lanceolate process in substitution for an expected stolon, although there is no certainty to this. Autozooid groups are orientated about main-axis stolons to face into relatively sheltered, colony-bounded space (see page 341).

Distribution. The species is known only from Australia, recorded from 'western' Australia and the type locality of Port Phillip Heads in the south-east.

Amathia obliqua MacGillivray, 1985

(Figs 3D, 8B)

Amathia obliqua MacGillivray, 1895: 135, pl. B (figs 2, 2a).

Material examined

Syntypes: NMV; H493 (old number 65391), H493 (old number 65392), Port Phillip heads, J. B. Wilson Collection.

Other material

MM; 7108/2W, Port Phillip.

Description. In the erect part of the colony, branching is bifurcate with repetitive gradual variation evident in the branching angle. This ranges from equal dichotomy, to the condition where the daughter stolons are produced at angles to the maternal stolon axis of 30 deg. and 60 deg. respectively. This variation occurs over a sequence of four stolon units, i.e. if one daughter stolon is angled at 60 deg. to the right of a maternal stolon, the same angular displacement appears, to the left of a maternal stolon, four stolon units further on in a stolon sequence. The original angular displacements are recovered after a further sequence of four stolon units. In between each of these stages, there is an intermediate, equally dichotomous condition. Over the entire sequence, a sigmoidal pattern in stolon arrangement may be observed. Autozooid groups occur towards the distal ends of stolons, but usually there is a further autozooid-free portion beyond the group, of variable length. Stolons tend to be straight, but sometimes the distal autozooid-free portion may be twisted slightly or deflected anteriorly, or both. Autozooid groups are set obliquely on the stolons. The autozooid group points in the same direction as that, in which the bearing stolon itself was budded i.e. viewed anteriorly, on a right hand daughter stolon, the autozooid group starts proximally on the left of the stolon and finishes distally on the right, and vice versa. Autozooid group orientation is generally well preserved from stolon to stolon, though variations of up to 30 deg. may occur. Autozooids are outer-wall thickened, and the autozooids of any one group tend to be about the same height. Autozooid group profile therefore tends to be level. A single proximal-most autozooid is usually prominent in each autozooid group. Its occurrence, and the pattern of autozooid displacements from stolon to stolon, are similar to those of *A. lendigera* (see page 313) except that the second succession state does not appear to occur. Rhizoids may be produced, one per stolon, from mid-way along the proximal autozooid-free end. These are orientated at about 90 deg. to the autozooids, on the outer faces of stolons at a bifurcation i.e. on the side of a stolon away from its sister stolon.

Zh. 0·39 Z/S. 65%
Zw. 0·11 Zn. 11–21 (appearing as 5–10 'pairs').
Sl. 1·16–2·13
Sd. 0·13–0·20 (immediately proximal to the autozooids)

Remarks. Little material is available for study, therefore little is known of the colony form, other than from MacGillivray's original description. It is inferred, from the presence of rhizoids, that the colony attains an arborescent form. MacGillivray's (1895) description seems to bear this out, the colony being 'attached by the bases of main stems by radical tubes, the branches being quite free and not intertwining or climbing over other objects'. MacGillivray made no mention of the non-erect part of the colony. Neither of the two slide specimens from the NMV, H493 (65391, 65392) matches the figure of MacGillivray (1895) exactly. There is however a very close resemblance to specimen H493 (65391). Some of this colony fragment has broken away which may account for the lack of congruence with the figure.

As with many other species of *Amathia*, *A. obliqua* has been confused with *A. lendigera* (by MacGillivray 1895). The presence of rhizoids and their orientation, the development pattern of autozooid groups and the overall colony form, serve to distinguish this species from *A. lendigera* (and also from *A. intermedis* and *A. guernseii*).

Distribution. The species is recorded only from the Port Phillip Bay region in Australia.

Amathia wilsoni Kirkpatrick 1888
(Figs 4D, 10C, D)

Amathia wilsoni Kirkpatrick, 1888: 18, pl. 2 (figs 4, 4a).
Amathia wilsoni: MacGillivray, 1895: 139, pl. D (figs 2, 2a, 2b).
Amathia wilsoni: d'Hondt, 1983: 67, fig. 36 (A).

Material examined

Syntype: BMNH; 1888.5.17.7, Port Phillip, J. B. Wilson Collection.

Other material

BMNH; 1821.5.24.16, 1985.3.12.2, Portland, Australia. 1882.7.7.54, Wilsons Promontory. 1886.6.8.3, Port Phillip 1910.10.17.31–32 part, north end Victoria Tasman Cable, <50 fthms. (91.44 m). 1963.2.12.361, Australia 1963.2.12.366, Holdfast Bay nr. Adelaide. 1985.3.12.1a,b, Flinders Is. 1985.3.18.3, Hobart, Tasmania.

MM; 7136/3W, off Shark Is., Port Jackson. 7137/3W, Port Phillip.

Description. In the erect part of the colony, branching is based on tri-, tetra- and pentafurcation. The colony is constructed of three types of stolons, here termed 'a', 'b' and 'c' (see below). Often, the region of branching, of a maternal stolon, is prominently thickened. Pentafurcation appears to be associated with external influence such as injury or the presence of an epibiont. Tetrafurcation is associated with astogenetically early regions, forming the base and main-axis regions of the colony. Main-axis regions are composed of type 'a' stolons. Trifurcation is associated with side branches which develop from main-axis regions. It is not possible to predict with certainty, the direction in which stolons will be produced at pentafurcation. In both the tetra- and trifurcate conditions however, one resultant component is produced in linear succession, and two others are produced laterally, one on each side. These are lateral side branches, composed of type 'b' stolons and are produced at an angle of about 60 deg. to the central axis. In the tetrafurcate condition, the fourth component, comprising type 'c' stolons, is produced posteriorly to its maternal stolon in the central axis, also at an angle of about 60 deg. This is a posterior side branch. Development along the side branches is limited and ends with the production of pinnately arranged, tapering kenozooids. The component kenozooids of such pinnate groupings are arranged as: three in linear succession, with an opposed lateral pair at both inter-kenozooidal junctions. In the lateral side branches, the pinnate kenozooids are usually produced after a 'linear' succession of three stolons; in the posterior side branch, after only one. The orientation of autozooids about the stolon along a main-axis sequence remains the same; this same orientation is preserved in the posterior side branch. In the lateral side branches, the autozooid group orientation is also preserved from stolon to stolon, but the autozooids are usually re-orientated to face distally along the main-axis; also in these branches, only one stolon, of a possible three, is usually produced at each branching point. On one side of the main-axis, viewed anteriorly, this is in the extreme right position; on the other side of the main-axis, this is in the extreme left. In each case, the other two positions are replaced by a pinnate terminal kenozooid group. The stolons along a lateral side branch are thus deflected anteriorly at each junction, in relation to the main-axis stolons. The branches therefore form inward facing arches across the anterior surface of the main-axis stolons. The resulting form is a long 'cylindrical' plume, reminiscent of snake vertebrae with ribs. The colony is composed of a number of these plumes, arising from various positions. Autozooid groups occur towards the distal ends of stolons. In the main-axis stolons, there is a further, distal, autozooid-free portion to each stolon, usually corresponding in length to the width of a daughter stolon. In the side branches, the autozooids frequently overlap the subsequent branching point. All stolons may be curved anteriorly. Autozooids are outer-wall thickened, but the thickening differential is usually low. Autozooid group profile tends to be level. The arrangement of autozooids in groups along main-axis stolons is, to some extent, predictable. A proximal-most autozooid may be evident in a group, and is associated with one side of the stolon. This autozooid loses its prominence over the next few stolons, the proximal autozoids of the groups appearing equally paired. Eventually, a proximal-most autozooid becomes prominent once more, but this time is associated with the opposite side of its stolon. Such a sequence is estimated to occur over 5 stolon units. The original condition is regained after a sequence of 10 stolon units. Side branches, where produced, have autozooid groups each with a prominent proximal-most autozooid associated with the side of its stolon nearest the main-axis stolons. This arrangement is preserved in subsequent autozooid groups along a side branch, unless a main-axis sequence is produced. Rhizoids may develop, one per stolon, from the proximal most end of, usually, main-axis stolons. Each rhizoid is produced at about 30 deg. to the orientation of the autozooids on the same stolon.

Sl. (a) 2·44 Z/S. (a) 50%
Zn. (a) (14–25 (appearing as 7–12 'pairs')

Sl. (b) 1·60 Z/S. (b) 80%
Zn. (b) 18–28 (appearing as 9–14 'pairs')

Sl. (c) 1·13 Z/S. (c) 80%
Zn. (c) 18–28 (appearing as 9–14 'pairs').

Sd. 0·35 (all stolons)
Zh. 0·35 (all stolons)
Zw. 0·13 (all stolons)

REMARKS. The cuticle in some specimens is seen to bear numerous cyst-like bodies, whose structure and function have yet to be determined. These cysts appear to be associated with the distal, astogenetically later (most recently budded) parts of the colony.

The branching pattern and resulting shapes in parts of the colony are quite distinct. The overall result is that autozooids face into a relatively sheltered colony-bounded space. This arrangement may have some protective advantage (see page 341).

D'Hondt (1983) places *A. verticillata* Waters MS and *A. delicatissima* Busk MS in synonymy with *A. wilsoni*. Only the latter assertion is completely correct. The only apparent record of *A. verticillata* MS is of slide MM 7137, bearing the legend 'so named by Kirkpatrick . . . KP. afterwards called it *Amathia wilsoni* K'. *A. verticillata* is, thus, merely Kirkpatrick's MS name for what he subsequently described as *A. wilsoni*. The slide was part of Water's collection, from which the confusion probably arises. There appears to be no other record of *A. verticillata* Waters MS.

In the original description by Kirkpatrick (1888), a BMNH specimen from Port Jackson is apparently indicated. No such specimen has been found. The entry in the account is somewhat anomalous, in that the account deals with 'Polyzoa from Port Phillip'. It seems likely that Kirkpatrick was referring to an additional specimen, then held in the collections at the BMNH, but whose whereabouts cannot now be determined, simply of the same identity as that which he described. At the beginning of the account, Kirkpartrick stated that he was describing new species from a collection made by J. B. Wilson from Port Phillip, subsequently sent to the BMNH. Specimen BMNH 1888.5.17.7 matches this description in being part of such a collection, and is indicated as type material in catalogue and registration records, in Kirkpatrick's own hand. This specimen is clearly syntype material.

DISTRIBUTION. The species is known from the south-eastern region of Australia, ranging from Holdfast Bay near Adelaide to Port Jackson near Sydney and Hobart, Tasmania. The record from Flinders Island is not clear; it could refer to the island off Tasmania or that in the Great Australian Bight.

Amathia pinnata Kirkpatrick, 1888
(Figs 3B, 10A, B)

Amathia pinnata Kirkpatrick, 1888: 19, pl. 2 (figs 5, 5a).
Amathia pinnata: MacGillivray, 1895: 136, pl. C (figs 1, 1a).
Part *Amathia pinnata*: d'Hondt, 1979: 16.
Part *Amathia inarmata*: d'Hondt, 1983: 67, fig. 36 (G).
Not *Amathia inarmata*: d'Hondt, 1983: 67, pl. 2 (fig. 1) (= *A. biseriata*).

MATERIAL EXAMINED

Lectotype (selected here): BMNH; 1888.5.17.8 A, Port Phillip, J. B. Wilson Collection.
Paralectotypes: BMNH; 1888.5.17.8 B, C, Port Phillip, J. B. Wilson Collection.

OTHER MATERIAL

BMNH; 1847.6.23.14, Tasmania. 1884.11.14.5–12 B, Port Phillip. 1886.6.8.1, Griffths Point, Port Jackson. 1963.2.12.363, George Town, ?Tasmania? 1985.3.28.1, Port Phillip Heads, 15 m. 1985.3.30.2, Algoa Bay, S. Africa.
MM; 7109/2W, Port Phillip.

DESCRIPTION. In the erect part of the colony, branching is regular and almost always trifurcate. This results in a typically compound pinnate arrangement. At any branching point, one daughter stolon is produced in rectilinear succession, and two others are produced laterally opposing, at an angle of about 60 deg. to the centre. Stolons tend to be straight. Autozooids are distally located, occupying the greater part of stolons. Autozooid groups develop as far as the subsequent branching point, but do not overlie it. Autozooid group profile tends to be level, and autozooids are outer-wall thickened, although there is a tendency for both differential and overall thickening, not to be great. Autozooid group orientation from stolon to stolon is generally well preserved. The arrangement of autozooids on stolons lying in rectilinear succession is to some extent predictable. Viewed anteriorly, a proximal-most autozooid may be prominent in an autozooid group, and is associated with one side of the stolon. Over successive stolon units, each autozooid group shows rearrangement so that this autozooid loses prominence. The proximal autozooids thus appear equally paired, until a proximal-most autozooid becomes prominent once more, this time associated with the opposite side of the stolon. Such a series appears to occur over a sequence of 4 stolon units. The original condition is recovered on the seventh or eighth stolon unit. In lateral daughter stolons, a single proximal-most autozooid is prominent in the autozooid group, this being associated with the side of the stolon nearest the rectilinear series, i.e. for a right-branched stolon, the proximal-most autozooid is nearest the left side of its stolon, and vice versa. Autozooid groups on stolons subsequently produced from a lateral daughter stolon, display the same organisation along resultant rectilinear series and lateral components. Terminal lanceolate processes may occasionally be produced; each one is made up of a tapering series of three kenozooidal sub-units. These terminal lanceolate processes are usually produced simultaneously as a group of three, each process replacing a normal stolon. Rhizoids may be produced, approximately mid-way along the proximal autozooid-free part of the stolon. These arise singly or as a pair, one on either side of the stolon, at about 30 deg. to the autozooid orientation. Colonies may be large and arborescent.

Zh. 0·45 Z/S. 80%
Zw. 0·13 Zn. 18–49 (appearing as 9–24 'pairs')
Sl. 1·50–3.25 Tpl. 1·50
Sd. 0·35 (just proximal to the autozooid group)

REMARKS. Measurements of this species given by Kirkpatrick (1888) appear to originate from the same material as he figured. There is, however, some discrepancy between the figures and the description, as it is possible to infer 18 autozooid 'pairs' from his figure, whereas he described the range as being from '12-16'.

Kirkpatrick's figure corresponds to a specimen which is obviously a fragment from a larger colony. However, this specimen and another which greatly resembles it, are obviously not from other material stored in the same container and bearing the same registration number. All these specimens are Kirkpatrick's *A. pinnata*, as is borne out by catalogue and registration records in Kirpatrick's own hand. There is a suggestion, in the stolon shape and rhizoid production site, that the registration may harbour two species. *A. pinnata sensu stricto*, is taken as the morph which corresponds with Kirkpatrick's figure; the registration of these components receiving the suffixes A and B (the remaining component the suffix C). Component A is the figured specimen, and is here designated the lectotype, the remaining portions, B and C, being paralectotypes. Provisionally, all three components are accepted as being *A. pinnata*.

This species is one of a number that were considered by d'Hondt (1979, 1983) to be synonymous with one another, the grouping also including: *A. biseriata*; *A. tricornis* (part); *A. brongniartii*; *A. cygnea* MS; *A. 'polycistica'* MS; *A. desmarestii* MS (see page 331). D'Hondt (1979) indicated *A. pinnata* Kirkpatrick 1888, as the senior synonym of this group. D'Hondt (1983) then indicates that *A. inarmata* MacGillivray 1887, is the senior synonym of the same compositional group, thus subordinating *A. pinnata* as a junior subjective synonym. *A. pinnata* is in fact not synonymous with any of the species in this grouping, being a separate and distinct species (see pages 332, 333).

DISTRIBUTION. The species is known from the south-eastern region of Australia, ranging from Port Jackson, to Port Phillip Heads and Tasmania, also being recorded from Algoa Bay, South Africa.

Amathia biseriata Krauss, 1837

(Figs 4B, 11C, D)

Amathia biseriata Krauss, 1837: 23, fig. 1 (a, b, c).
Not *Amathia biseriata*: Busk, 1852: 385.
? *Amathella biserialis* Gray 1858: 320 (? errorum pro *Amathia biseriata* Krauss, 1837).

Amathella uniserialis Gray, 1858: 320.
Amathia inarmata MacGillivray, 1887: 183.
Amathia biseriata: Kirkpatrick, 1888: 17.
Amathia inarmata: MacGillivray 1889: 309, pl. 183 (fig. 4).
Amathia biseriata: MacGillivray, 1895: 137, pl. B (fig. 4).
part *Amathia pinnata*: d'Hondt, 1979: 16.
part *Amathia inarmata*: d'Hondt, 1983: 67, fig. 36 (G).

MATERIAL EXAMINED
Neotype (selected here): BMNH; 1887.12.10.90, Port Phillip, J. B. Wilson collection.

OTHER MATERIAL
BMNH; 1899.7.1.4317, 4318, 1963.2.12.357, Australia. 1899.7.1.4319, New Zealand. 1965.8.12.19, Jervis Bay, Huskisson, N.S.W. 1985.3.14.1, no locality.
NMV; H492 (1–9), Port Phillip Heads.
RM; 1808, Port Natal, Africa.

DESCRIPTION. In the erect part of the colony, branching is always bifurcate. Viewed anteriorly, at each branching point, one daughter stolon tends to lie approximately in line with the maternal stolon, although deviations of up to 20 deg. may occur. The other daughter stolon is usually produced laterally, at an approximate angle of 45 deg. to the main axis of the maternal stolon. The side on which a lateral branch appears, alternates at each successive bifurcation. Stolons have a slight constriction near the proximal end and are usually curved anteriorly, the curvature becoming progressively more acute distally, to bend around the distal end of the autozooid groups. The stolon tends to remain in contact with the distal side of the autozooids. Where this is not so, this portion of the stolon remains autozooid-free. Daughter stolons produced in the 'linear' position, arise from the distal end of the maternal stolon; lateral daughter stolons are produced from the most sharply curved region of the maternal stolon. The distal region of the maternal stolon may show some axial subdivision to bear the daughter stolons, more so when it is not in contact with the distal face of the autozooids. Autozooid groups on maternal stolons are rarely developed distal to the origin of the lateral daughter stolon, or where the stolon shows division. Autozooids are outer-wall thickened, the thickening sometimes being accentuated at the rims. Autozooid group profile appears level, sometimes slightly concave centrally, or diminishing slightly proximodistally along the stolon. A single proximal-most autozooid is evident in each group, slightly broader than the rest, usually placed just off the mid-line, and thus associated with one or other side of the stolon. No pattern has been discerned in the location of this autozooid from stolon to stolon. Sometimes both daughter stolons show the same autozooid arrangement as on their maternal stolon; sometimes the opposite; sometimes combinations of the two. Autozooid orientation is generally well preserved from stolon to stolon. Rhizoids may be produced, one per stolon, arising from a position level with, or just proximal to, the proximal-most autozooid of the autozooid group. The orientation of the rhizoids is between 90–135 deg. to the autozooid group, occurring on the same side of the stolon as the direction in which that stolon was budded. Stolons and their autozooid groups become shorter nearer the distal (astogenetically later i.e. most recently budded) regions of the colony.

Sl.	2·05	Z/S.	75%
Sd.	0·32	Zn.	5–25 (appearing as 4–12 'pairs')
Zh.	0·35		
Zw.	0·11		

REMARKS. The autozooid pattern from stolon to stolon remains elusive in this species, primarily due to the difficulties of observation over the number of stolon sequences necessary.

This species is one of a number that were considered by d'Hondt to be synonymous with one another. D'Hondt (1979) indicated that *A. pinnata* Kirkpatrick 1888, was the senior synonym of this group, inclusive of *A. biseriata*, and then (1983) indicated that *A. inarmata* MacGillivray 1887 was the senior synonym of the same compositional group. Both assertions are erroneous. The inclusion of the name *A. desmarestii* in this group is of little consequence as Lesueur never published his work. The name itself is not valid in being published only in synonymy (I.C.Z.N. article 11e). Of the other species in this group: *A. tricornis* is a separate and distinct species (see page 321), with a more complex colony composition than the rest; *A. cygnea* Busk MS, and *A. polycistica* (sic) Busk MS, are here considered to be synonymous with one another as *A. brongniartii* (see page 333); *A. pinnata* is also a separate and distinct species, in which trifurcate branching predominates. There are no indications, in any of MacGillivray's accounts of *A. biseriata*, of the trifurcate branching pattern shown by d'Hondt (1983), who reproduced MacGillivray's (1895) figure of *A. pinnata*. In fact, MacGillivray and Krauss both stated that the branching pattern in *A. biseriata* is dichotomous. Supplementary features which may be used to distinguish between *A. biseriata* and *A. pinnata* are: the site of rhizoid production; the occurrence of terminal kenozooids in the latter species. Were *A. biseriata* and *A. pinnata* synonymous, then *A. biseriata* would be the senior synonym (cf. d'Hondt 1979). *A. biseriata* however, is synonymous with *A. inarmata*, but again, it is *A. biseriata* which is the senior synonym. In this case, Krauss' publication predates that of MacGillivray by 50 years. Furthermore, MacGillivray (1895) accepted his species to have been the same as that of Krauss. MacGillivray's syntypes are held in the NMV (H492 1–9), and all 9 specimens are *A. biseriata*.

MacGillivray (1895) appears to have been under the misconception that Krauss' material of *A. biseriata* originated from south Africa, when in fact it was from New Holland i.e. western Australia. It is probable that MacGillivray (1895) was actually referring to material received from 'Pergens' (MacGillivray, 1889).

Krauss' (1837) description and figures are here considered to be more than adequate to distinguish his species from any other; his only mistake was to make the assumption that the rhizoids produced the stolons and their autozooids. Krauss' material does not appear to have survived. In view of the subsequent confusion, selection of a neotype is necessary. BMNH 1887.12.10.90 (although from Port Phillip) is selected here.

DISTRIBUTION. The species is known from south Africa, southern Australia and New Zealand.

Amathia brongniartii Kirkpatrick, 1888
(Figs 4A, 11A, B)

Amathia brongniartii Kirkpatrick, 1888: 18, pl. 2 (figs 3, 3a).
Amathia brogniartii (sic): lapsus calami MacGillivray, 1895: 136, pl. B (figs 3, 3a).
Part *Amathia pinnata*: d'Hondt, 1979: 16.
Part *Amathia inarmata*: d'Hondt, 1983: 67.
Not Part *Amathia inarmata*: d'Hondt, 1983: 67, fig. 36G, (=*A. pinnata*).

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1888.5.17.6, Port Phillip, J. B. Wilson Collection.

OTHER MATERIAL

BMNH; 1838.2.26.13, 1847.6.23.4, 1899.7.1.4379, 4381, Tasmania. 1887.4.27.19, Port Jackson, N.S.W. 1887.12.10.98A (part), Port Phillip, Vict. 1899.7.1.4419, 6601, Swan Is. ?Bass Strait? 1927.9.26.21, Swan Is., Banks Strait. 1984.12.4.1, Portsea Pier, Victoria, 2 m. 1985.3.16.1, Victoria. 1985.3.16.1.2a,b, Flinders Is. ?Tasmania?

NMV; 65397, Port Phillip Heads, Vict.

MM; 7074, Lane Cove, Port Jackson, N.S.W.

DESCRIPTION. In the erect part of the colony, branching is always bifurcate. At each branching point, one daughter stolon tends to continue in line with the maternal stolon, often giving rise to rectilinear series, although deviations by up to 15 deg. may occur. The other daughter stolon of each birfurcation arises laterally, often anterolaterally, appearing on alternate sides along a series, at an angle of between 20–50 deg. to the axis of the maternal stolon. Stolons are usually straight and tend to have a slight constriction near the proximal end. The distal end of a stolon does not usually show any axial subdivision or widening to bear daughter stolons; more often, the maternal stolon shows some abbreviation into a wedge shape to accommodate these. The autozooid groups develop as far as, and often overlie the subsequent branching point. Autozooids are markedly inner-wall thickened, with a thin walled exterior. The autozooids are usually, large, prismatic, and pentagonal in section. Viewed anteriorly, the walls between the autozooids, being much thicker, give a characteristic zig-zag backbone appearance to the autozooid groups. Autozooid group profile ranges from gently arched upwards to level with the autozooids shorter at each end of the group. A single proximal-most autozooid is evident in each autozooid group, slightly broader than the rest, usually just off the mid line and thus associated with one or other side of the stolon. Viewed anteriorly, this autozooid is always on the side nearest the sister stolon. Autozooid orientation from stolon to stolon is generally well preserved. Rhizoids may be produced, one per stolon, from a position level with or just proximal to the proximal-most autozooid of a group. These arise at about 110–160 deg. to the autozooid orientation on the same stolon, and on the same side of the stolon as the direction in which the stolon was budded. Stolons and their autozooid groups appear to be shorter nearer the distal (astogenetically newer) regions of the colony.

Sl. 1·75–4·00 Z/S. 80%
Sd. 0·25 Zn. 10–39 (appearing as 5–18 'pairs')
Zh. 0·48
Zw. 0·15

REMARKS. This species was considered by d'Hondt to be a junior synonym of: (1979) *A. pinnata*; then (1983) of *A. inarmata. A. brongniartii* differs from *A. pinnata* in many features, such as: the autozooidal thickening; the sites of rhizoid production; the basic branching pattern. *A. inarmata* is itself a junior synonym of *A. biseriata* (see page 332). Kirkpatrick (1888) and MacGillivray (1895) indicated differences between *A. biseriata* and *A. brongniartii* in their accounts. The two species may be distinguished quite readily by: the shape of the stolons; to some extent, the site of rhizoid production; the autozooidal thickening, this last being the most prominent difference.

A. brongniartii appears to display a large variation in stolon length and attendant number of autozooids borne. Such variation may be seen within single colonies. However, colonies may often show good uniformity in stolon lengths, whether long, short or intermediate. Busk, in his unpublished notes and figures stored at the BMNH, considered the possibility that the extremes of the size range might be discrete. He appears to have called colonies with short stolons and lower autozooid number *A. cygnea* (up to 20 autozooids, equivalent to 8–12 'pairs'), with more diminutive versions as *A. cygnea var. nana.* Colonies with higher numbers of autozooids (24–36 units, equivalent to 12–18 'pairs') and longer stolons, he called *A. polycystica.* In Busk's material, the specimens which might be *A. polycystica* tend to be dark coloured, but other than this there seems to be nothing which distinguishes them taxonomically. (Busk's notes make no recognition of the *A. brongniartii* in the unpublished plates of Lesueur).

Kirkpatrick (1888), in his account of *A. brongniartii*, erroneously credited the species to Desmarest and Lesueur, citing Lesueur's figures and Pergens' (1887) collations as his reference for the identity and name. As Desmarest and Lesueur never published their work, the Pergens mentions the name only in synonymy, Kirkpatrick is the authority for the species (I.C.Z.N. article 11e). As Kirkpartick did not consider himself the author of the species, he did not choose any type specimens. Kirkpatrick's figures, like those of Lesueur, are of insufficient quality to be utilised as reliable references. Kirkpatrick's figures hardly show any detail at all, whilst Lesueur's figures (pl. 13 fig. 5) show curved stolons and tube-like autozooid anteriors, both characteristics of *A. biseriata.* At the same time however, Lesueur shows approximately 20 'pairs' of autozooids, a number high enough to be associated with *A. brongniartii.* Understandably, confusion has arisen and so it would seem appropriate that a neotype be designated. BMNH 1888.5.17.6 is, therefore, selected as neotype. This specimen is the only one labelled as *A. brongniartii* by Kirkpatrick in the collection made by J. B. Wilson from Port Phillip. This collection is the subject of Kirkpatrick's publication of 1888.

Specimen NMV 65397 is believed to have been before MacGillivray at the time of his writing his 1895 account of *Amathia* species (in litt. NMV. 30th May 1983.). The specimen is undoubtedly *A. brongniartii* Kirkpatrick, thus MacGillivray's name 'A. brogniartii' is simply a misspelling, as his synonymy indicates.

DISTRIBUTION. The species is known from south-eastern Australia, ranging from Tasmania to Port Jackson.

Amathia alternata Lamouroux, 1816
(Figs 4C, 13A, B)

Amathia alternata Lamouroux, 1816: 160.
Amathia alternata: Lamouroux, 1821: 10, pl. 65 (figs 18, 19).
Amathia alternata: Lamouroux, 1824: 44.
Not *Amathia alternata*: Osburn, 1932: 444, pl. 1 (fig. 4).
Part *Amathia convoluta*: Maturo, 1957: 22, fig. 11.
Not part *Amathia convoluta*: Maturo, 1957: 22, fig. 10.
Amathia alternata: Winston, 1982: 108, fig. 8.

MATERIAL EXAMINED

Neotype (selected here): USNM; 6307 (part), Albatross Stn. 2619, off Cape Fear, North Carolina.

OTHER MATERIAL

BMNH; 1964.7.10.1A,B, New River Inlet, North Carolina.
1964.7.10.2, Alligator Harbour, North Carolina.

DESCRIPTION. In the erect part of the colony, branching is always bifurcate. At each branching point, one daughter stolon tends to continue in line with the maternal stolon, forming a linear series. The other daughter stolon is produced at approximately 45 deg. to the maternal stolon axis at that location, at between 45–90 deg. to the orientation of the distal autozooids there. Branching may appear equally dichotomous at times. Daughter stolons are produced from the posterior side of the maternal stolon, this showing some abbreviation into a wedge shape to accommodate them. Stolons are: narrowed proximally, additionally having a proximal constriction; often curved posteriorly, also undergoing a slight twist along their length. The linearly disposed stolons may thus appear as an undulating progression. Any twist in these is normally reflected in the autozooids borne, changing the orientation between proximal and distal autozooids in a group by up to 90 deg. At times, this may give the impression that autozooid groups are simply arranged obliquely on the stolons. Autozooid groups may, however, be arranged along the stolonal axis without any evidence of twist at all in either component. Where the twist, proximodistally along a stolon, is clockwise, the left daughter stolon is produced in the 'lateral' position, and with anticlockwise twist, the right. The direction of twist is generally well preserved from stolon to stolon (although both directions may be found in the same colony). Lateral daughter stolons are thus produced from the same side of stolons along any linear sequence. The spatial orientation of these lateral branches is determined by the maternal axis and autozooid orientation at that point. Autozooid orientation changes by 100–180 deg. from stolon to stolon. This is taken from the distal autozooids on the maternal stolon to the proximal autozooids on each of the two daughters. Autozooids frequently overlie the subsequent branching point and are outer-wall thickened. Autozooids are inclined at about 60 deg. to the stolonal axis, and group profile is level or gently convex. A proximal-most autozooid is frequently evident in each group. Viewed anteriorly, this is associated with the side of the stolon in which the direction of twist occurs e.g. the right side, with clockwise twist proximodistally. Rhizoids may be produced at any point on a stolon from the constriction to beneath the proximal autozooids. A polyrhizoid condition may result, where any number of rhizoids, up to a maximum of 5, possibly more, may be produced from a single stolon, at any orientation. Two orientations appear more frequently occupied by rhizoids: within 10 deg. of the proximal autozooid orientation on the same stolon; approximately 180 deg. to the proximal autozooid orientation.

Zh. 0·42   Z/S. 85%
Zw. 0·10   Zn. 24–57 (appearing as 12–28 'pairs')
Sl. 1·45–3·87
Sd. 0·29–0·35 (just proximal to the autozooid group)

REMARKS. In the non-erect part of the colony, secondary thickening of stolons may occur. This has the appearance of a sleeve developing along existing stolons.

A. alternata can display a consistent, if only slight, spiral nature, and the species has been confused with *A. convoluta sensu* Lamouroux, and possibly also with *A. semiconvoluta*

Lamouroux. As no type material exists, it may also be possible to confuse *A. alternata* with other spiral-autozooid group species, for example *A. tortuosa* Tennison Woods or *A. connexa* Busk.

Maturo (1957) described and gave representative figures, under the name of *A. convoluta* (*sensu* Lamouroux), of material collected at Fort Macon on Bogue Banks, USA. This material was noted to have 'straight autozooid groups, alternately placed from one internode to the next', and to be the same as a specimen in the USNM labelled *A. spiralis*, from Albatross Stn. 2619, off Cape Fear, North Carolina. The latter, USNM 6307 (part), has been examined here. Portions of this specimen have autozooids arranged and placed in the way Maturo describes and illustrates for the Fort Macon material. This specimen, Maturo's account, and the description given here, conform with Lamouroux's brief description of *A. alternata* in 1816, his subsequent account of 1821, in which he presents figures (pl. 65, figs 18, 19), and his final account in 1824.

Lamouroux's (1821) figures lack important information, and, in not being published at the same time as the original description, are clearly not eligible for any type status. Lamouroux's collection was destroyed during the Second World War (d'Hondt in litt. 27.10.1982), but material from his collection obtained via Busk, and labelled *A. alternata* is stored at the BMNH as 1897.7.1.6606. This material was originally stored dried and pressed, but has subsequently been rehydrated, and is at present stored in alcohol. As recorded on a label with the material, examination by Dr F. Maturo before rehydration revealed only two bryozoan species, these being other than *A. alternata*, possibly *A. brasiliensis* Busk and *Zoobotryon verticillatum*. Since rehydration, the absence of *A. alternata* is here confirmed, and the identity of the two other species established as *A. wilsoni* and *A. semiconvoluta*.

The packet originally enclosing the specimens bears the names 'A. alternata' and 'Amerique' in what is taken to be Lamouroux's handwriting. The locality mentioned does not disagree with that of Lamouroux's accounts (1816, 1821, 1824) of *A. alternata*, (the most specific locality given being the Sea of Antilles in 1824). The two species found enclosed in the packet, however, are not expected from this region; all other records of *A. wilsoni* are from southern Australia. Similarly, all other records for *A. semiconvoluta* are from the Mediterranean, the species possibly extending as far along the west African coast as Nigeria. It is unlikely that *A. wilsoni* would have been confused with *A. alternata* by Lamouroux, as the species has many distinguishing features and lacks alternate autozooid group placings. It may be possible to confuse dried *A. semiconvoluta* with *A. alternata*, but this is considered unlikely of Lamouroux, as he is the author of both species. Lamouroux introduced *A. alternata* in 1816, redescribed the species in 1821 and again in 1824 when he introduced *A. semiconvoluta*, the descriptions for the two species appearing on the same page. It is to be assumed that the author was capable of recognising and distinguishing his own species. The fate of any *A. alternata* that may have been present in BMNH 1897.7.1.6606 is open to speculation. The circumstances of Busk's acquisition of specimens enveloped in paper bearing Lamouroux's writing are unknown.

In the interests of nomenclatural stability, a neotype is required. Specimens considered eligible are: those in the BMNH under 1964 registrations, all from North Carolina, donated and identified by Dr F. Maturo as *A. alternata*; specimen USNM 6307 (part); Maturo's Fort Macon material. The whereabouts of the Fort Macon material (Maturo 1957) is not known. The neotype selected, therefore, is specimen USNM 6307 (part) from Cape Fear, off North Carolina, at 15 fthms. (27.43 m) this being the earliest recorded specimen surviving. The polyrhizoid condition is not readily apparent in this specimen, but it does show the possible variation in the arrangement of autozooid groups.

The difference between *A. alternata* and *A. semiconvoluta* are as follows: the degree of 'spirality' that may occur is much greater in *A. semiconvoluta* (180–270 deg., cf. *A. alternata* 0–90 deg.); the orientations of the distal end of one autozooid group and the proximal end of the next are within 10 deg. of each other in *A. semiconvoluta*, but a distinctive 100–180 deg. in *A. alternata*; a lower linear autozooid to stolon ratio of 50% for *A. semiconvoluta*, compared to about 85% in *A. alternata*. Although rhizoids may appear at similar orientations in both species, only *A. alternata* shows polyrhizoidy with rhizoids in proximity to the autozooids (and, additionally, a slightly wider bifurcation angle between daughter stolons). In *A. semiconvoluta* the rhizoids appear at the proximal-most end of the stolons, at about the same orientation at which the preceeding autozooid group terminates, or displaced by 180 deg., or when two rhizoids are present on the same stolon, at both orientations. *A. semiconvoluta* is understood from the following specimens: BMNH; 1885.12.5.12,13, Marseilles. 1888.11.9.4, Naples. 1899.5.1.290, 1912.12.21.687, Adriatic. 1899.7.1.6606pt., ?locality?

The other species mentioned above i.e. *A. convoluta*, *A. tortuosa* and *A. connexa*, are also distinguishable from *A. alternata* by their degree of spirality. This is significantly greater than *A. alternata* in all cases. Problems might arise, however, in distinguishing these three species from each other, and establishing their validity.

A. convoluta is understood from BMNH 1899.7.1.6607. This specimen is from Lamouroux's collection, obtained via Busk, and is labelled 'Amathia convoluta, Australasia' in what is accepted to be Lamouroux's handwriting. There is nothing to contradict its identity from any of Lamouroux's descriptions. The specimen also conforms with MacGillivray's (1895) account of the species, corroborated by his opinion on Busk 1884 (pl. 6. fig. 2, there misidentified as *A. spiralis*). However, there is nothing to suggest that MacGillivray ever saw BMNH 1899.7.1.6607 at any time. This specimen is noted as 'type' in the catalogue of the BMNH, though no formal declaration of its purported status has ever been made. It is possible that the specimen was formative of Lamouroux's opinions of the species and thus a 'type' but there can be no certain evidence for or against this notion. However, the specimen appears to be the only extant material which bears an unchallengeable identification, attributable to the original author. D'Hondt (1983) indicated that Lamarck's name for the species (*Amathia crispa*), as the senior synonym, should instead be used.

DISTRIBUTION.The species is recorded off North Carolina, USA, and, from Lamouroux's (1824) record, from the Caribbean.

Amathia pruvoti Calvet, 1911
(Fig. 13D)

Amathia pruvoti Calvet, 1911: 59, fig. 2.
Amathia pruvoti: Bobin & Prenant, 1956: 287, fig. 128.
Amathia pruvoti: d'Hondt, 1983: 67, fig. 35F.
Amathia pruvoti: Hayward, 1985: 136, figs 46A, B.

MATERIAL EXAMINED

Type: LBIMM; Bry 8205, Calvet collection: no locality.

OTHER MATERIAL

BMNH; 1882.7.7.1–2, Trieste. 1882.7.7.–, Mediterranean.
1885.12.5.14, Montpellier. 1889.7.27.48, 1890.7.22.8 part, Studland Bay, Dorset. 1975.7.1.15, Emborios Bay, Chios, 90 ft. 1984.2.26.102, Dhiaporia Rock, Chios, 100 ft.

DESCRIPTION. In the erect part of the colony, branching is always bifurcate. Daughter stolons appear to diverge equally, lying at approximately 60 deg. to each other, thus giving the impression of equal dichotomy. In fact, at each branching point, one stolon tends to be budded in a linear position and is subsequently deflected, whilst the other is produced laterally. The linearly disposed daughter stolon may be wider than its sister, with little deflection, at times giving a strong impression of rectilinear progression. In all stolons, there is a slight constriction near the proximal end. The distal end does not show any axial subdivision or widening to bear daughter stolons; however, it often shows some abbreviation into a wedge shape to accommodate these. Autozooid groups sometimes overlie the subsequent branching point. However, it is more usual for the autozooid group to only develop as far as the branching point, or, alternatively, 'stop short' and be followed by an autozooid-free portion of stolon, about the width of an autozooid in length. Stolons tend to be straight proximally although often slightly curved posteriorly and undergoing an axial twist in the region of the autozooids. The twist in the stolon is usually reflected in the autozooids borne, changing the plane of their orientation, between the proximal-most and distal-most autozooids, by approximately 90 deg. The plane in which the subsequent bifurcation occurs is also affected to the same degree. The twists are normally predictable. Viewed anteriorly, in the left-branched daughter stolon, the twist is usually clockwise in a proximodistal direction, and anticlockwise in a right-branched daughter. These twists generally occur irrespective of the twist which occurs in the maternal stolon. However, there can be variations to this. Occasionally, both daughters may twist in the same direction, this being opposite to that of their maternal stolon. Occasionally, the inverse to the normal condition occurs, where a left daughter twists anticlockwise and the corresponding right daughter twists clockwise. Autozooids are outer-wall thickened. Autozooid group profile, where discernible, is level proximally, diminishing distally, resulting from decreasing height and increasing distal inclination of the autozooids. A single proximal-most autozooid is evident in each autozooid group, usually off centre to the axis of the stolon. Viewed anteriorly, this autozooid is always associated with the same side of the stolon, as the direction in which the autozooid group twists, e.g. the right side, with clockwise twist proximodistally. Autozooid orientation from stolon to stolon, changes by 180 deg. between the distal autozooids of the maternal stolon and the proximal autozooids of each of the two daughter stolons. No rhizoids are known, and the erect part of the colony appears as a diffuse cotton-wool like mass. Sometimes, erect components of the colony come into contact with the substratum, and their characteristic stolonal shape is lost. These components do not bear autozooids; as stolonal kenozooids (see page 309), they become elongated and twisted, occasionally branching and producing clumps of flattened lateral processes. Further erect components may be produced at any time and these may resume the normal erect growth pattern.

Sl.	2.40–3.75	Z/S.	60%
Sd.	0·13–0·15	Zn.	21–31 (appearing as 10–15 ‘pairs’)
Zh.	0·40		
Zw.	0·13		

REMARKS. Apart from the ancestrula, little is known of the non-erect portion of the colony. It is assumed that this would resemble the contact-modified erect stolons and their growth behaviour. No occurrence of two autozooid groups on the same stolon has been encountered in any of the material examined (cf. Calvet, 1911). Such an instance would be contrary to the present concept of the genus.

There is a specimen at the LBIMM, bry 8205, originating from the Station Zoologique de Cette, Université de Montpellier. This is latterly documented (e.g. LBIMM loan form 26th Oct 1983) as ‘the probable type of *A. pruvoti*: Calvet (Cette), with a handwritten label of the author carrying the name *A. semiconvoluta*’. The justification for regarding LBIMM bry 8205 as the type specimen of *A. pruvoti* Calvet, is not given. The specimen is, however, well preserved, and would serve as an excellent basis on which to recognise the species in future. It is proposed here that the specimen be accepted as the type specimen of the species. If no historical justification for its claimed status as a ‘type’ is available (see below), it is here selected as neotype, obviating the confusion that has arisen between *A. pruvoti* and *A. lendigera* (*sensu lato*).

It should be noted that there is some difference between Calvet’s description (1911) and specimens subsequently recognised as *A. pruvoti*, including specimen LBIMM bry 8205. Calvet described stolons as lying in rectilinear series. This condition is not readily apparent in the majority of specimens, except in two specimens from Chios, BMNH 1975.7.1.15, 1984.2.26.102, and in these there is also little evidence of the proximal stolonal constriction. It is not possible to be certain of what Calvet meant when he described the ‘stature’ of *A. pruvoti* as ‘erect’, then drawing a comparative difference between it and *A. lendigera*, when the colony budding patterns of the two species are in fact very similar. It is possible that the supposed distinction may reflect an opinion that *A. lendigera* has a higher proportion of the non-erect colony component, or that the erect part of *A. lendigera* tends to be spatially more condensed. In both species, there is some variation in the overall length of stolons. This variation appears less extensive in *A. pruvoti*. The most obvious difference between the two species, however, lies in the disposition of autozooids about the stolons. A degree of twist is usually present in *A. pruvoti*, and an autozooid-free distal portion of the stolon often occurs.

Calvet also drew a comparison with *A. semiconvoluta*. The differences in the erect part of the colony between this species and *A. pruvoti* are that, in *A. semiconvoluta*: the curvature of the stolon beneath the autozooids is much shallower, if present at all; the autozooid height tends to be equal throughout the autozooid group; the autozooid group is more spiralled, undergoing twists of 180–270 deg.; the orientations of the distal end of the autozooid group on the preceeding stolon, and the proximal ends of the next, on the succeeding stolons, occur within 10 deg. to each other; the direction of spiral tends to be preserved from maternal to daughter stolons, although both directions may be found in the same colony; branching is always bifurcate (as in *A. pruvoti*) but one daughter stolon is always linearly disposed, giving rise to definite rectilinear series, with the other daughter stolon produced anterolaterally at about 30 deg. to the stolon axis and distal autozooid orientation; when the autozooid twist, proximodistally, is clockwise, the right hand daughter stolon is in the rectilinear position, and with anticlockwise twist, the left hand daughter stolon acquires the rectilinear position; autozooid groups always overlie the subsequent branching point; rhizoids are produced from the proximal end of stolons. Further characteristics of *A. semiconvoluta* are as follows: rhizoids arise singly, either in the same orientation as the proximal-most autozooids, or at 180 deg. to this (see pages 335, 336, Figs 5A, 13C); when two rhizoids per stolon are produced, these arise as one from each orientation; the production of rhizoids would enable the colony to attain an arborescent form, but this has not been confirmed.

There is, in addition, some similarity between *A. pruvoti*, *A. distans* Busk, *A. distans var. aegyptana* d'Hondt and *A. brasiliensis*, each of which is a distinct entity. The distinction between the species may be found in the following characteristics. In the last three, the autozooid groups are more spiral, usually describing a 360 deg. rotation about the stolon in *A. brasiliensis* and *A. distans*, slightly less (270–360 deg.) in *A. distans var. aegyptana*. Of this group, *A. brasiliensis* is the only one which produces rhizoids, these arising at the proximal end of stolons, orientated within 10 deg. to the proximal autozooids on the same stolon. *A. distans var. aegyptana* has the distinction of producing autozooid groups in which the direction of spirality remains preserved from maternal to daughter stolons i.e. all clockwise or all anticlockwise, whereas one of two other patterns prevail in *A. pruvoti*, *A. distans* and *A. brasiliensis*. Using the distal-most autozooids as the orientation reference, and viewing anteriorly: in *A. pruvoti* and *A. brasiliensis*, the left daughter stolons carry autozooids arranged clockwise in a proximodistal direction, and the right daughters, anticlockwise; in *A. distans*, the left daughter stolons carry autozooids arranged anticlockwise, and the right daughters, clockwise. The distinctions are made with reference to type material:

For *A. distans*: BMNH 1887.12.9.926, Bahia, 10–12 fthms. (18.29–36.58 m.).
For *A. brasiliensis*: BMNH 1887.12.9.927, Bahia, 10–20 fthms. (18.29–36.58 m.).
For *A. distans var. aegyptana*: BMNH 1926.9.6.25, Suez Canal.
For *A. pruvoti*: LBIMM bry 8205, no locality.

In conclusion, *A. distans var. aegyptana* should be considered as a species in its own right, and is here raised to specific rank as *Amathia aegyptana*.

Harmer (1915) drew attention to the similarities between *A. distans* and other species, including *A. pruvoti*. However, his understanding of *A. distans*, particularly in the degree of spirality which may occur, is here considered insufficiently rigorous. Unfortunately, it is Harmer's understanding which is followed by Bobin and Prenant (1956) and d'Hondt (1983).

DISTRIBUTION. The species is known mainly from the Mediterranean, with some material from Studland Bay in Dorset, England.

Discussion

It is readily apparent that there is a considerable degree of regularity and possible colony integration within species of the genus *Amathia*. Some of this is reflected in the consolidation of a colony by rhizoids. These grow back, sometimes fusing with each other, and ultimately interact with the substratum to provide support. The various arborescent growth forms that result can only be maintained through continued sustenance of these rhizoids, and of any underlying stolons which will usually have lost their feeding autozooids. This implies nutrient transfer to them, and thus a potential ability for self repair.

The most basic and obvious level of intergration, however, is the clustering of autozooids into groups on septa-bound kenozooidal stolons, to form intercommunicating functional units. These can show changes of characteristics with astogeny. Changes may be gradual, as in stolon lengths and autozooid numbers in *A. biseriata*; or discontinuous, as in the autozooid complement per stolon in parts of *A. tricornis*.

In the majority of cases, the polypide appears capable of retracting to about the level of the highest part of its associated thickened walls. This suggests that a degree of protection may be afforded by the thickening, and has some analogy to the situation found in other, calcified, bryozoans. It is not clear whether the mineral salts reported to be found in the body walls of *Amathia* (Ryland 1970) are associated with any particular feature, such as this autozooidal thickening.

From the autozooidal organisation evident, there are indications that some further analogy may be drawn between species of *Amathia* and other bryozoans, in terms of colony integration and co-ordinated behaviour. Together with regular budding patterns and specific orientations of autozooids, the localised autozooidal thickening carries with it implications for the achievement of lophophore eversion (and retraction). The thickened areas of cuticle might resist the deformation required by the autozooid to change its volume and effect these actions. There is little constraint on independent action of autozooids in those groups with inner wall thickening; the outer face of each autozooid is able to move freely in response to the volume changes necessary. In groups with outer wall thickening, the implied compliant boundaries for each autozooid are those walls contiguous with other autozooids. Thus, attempted changes in the colume of any one autozooid might impinge on the status of those adjacent. If these adjacent autozooids resist a change, then the eversion in the original autozooid will be hindered. It may be inferred, therefore, that in some species with outer wall thickening, feeding may be a group activity. Advantages of group feeding would lie in combined feeding currents, enhanced by specific autozooid orientations within colony bounded space, (Winston 1979, McKinney 1984). Independent autozooid behaviour is more likely if: the thickened outer wall has localised weak patches acting as diaphragms; the wall is sufficiently folded to allow concertina-like accommodation of volume change; the thickening differential is low; there are co-ordinated inverse volume changes of autozooid pairs. It cannot be discounted, however, that collective feeding may occur in either wall-type grouping, simply by co-operation of autozooids. Confirmation of possible patterns of feeding behaviour, however, requires the observation of living colonies.

In the autozooid groups, no pairing of autozooids may be confidently assigned throughout a colony in any species (see page 309). Although the concept of biserial rows loses some ground, it cannot be discounted completely. There is thus equal possibility that the arrangement of autozooids into groups may have evolved in any of three ways: by unification of two separate single rows of autozooids with subsequent modifications; by the linear organisation of randomly clumped autozooids; by spatial condensing, with alternate displacement, of one single row of autozooids. All three hypothetical initial conditions have some analogues in extant ctenostomes; the first in *Zoobotryon*, the last two in species of *Bowerbankia*. Tenuous indications for origins via the third category may be inferred from the order of autozooid production on stolons. Autozooids in a group are developed in distal sequence, often making their appearance laterally displaced on alternate sides. It is possible, however, that this simply reflects the fact that growth proceeds distally through a sequence of interlocked autozooids, as autozooids may also be seen to be produced as equal pairs.

As with many colonial organisms, a large epifauna is frequently associated with colonies of *Amathia*, presumably deriving benefit from the microenvironment of the colony interiors (see below). The colonies serve as a substratum for some organisms and as shelter for others. Great numbers of other bryozoans, coelenterates, crustaceans, annelids, algae, foraminifera and molluscs, are often found. In this context, the record of *Amathia* body walls containing calcium salts (Ryland 1970) needs re-investigation from material in which the absence of any encrusting calcareous epibionts is ensured, as these can be extremely diaphanous. It is not known if any of the associations are species-specific, or what other levels of interdependence may occur. The ecological criteria which determines distribution and survival of the species of *Amathia* are known in only most general terms, and nothing is known of the relative ecological requirements which epibionts and 'hosts' may have. All that might have been expected is that numbers of epibionts might be related to some simple factor, such as the degree of shelter a colony provides. However, Murray (1970) reported that the entire life-cycle of the gastropod *Marginella minutissima* is spent with Australian *A. biseriata*. In this case, the *Amathia* colony serves both as food substrate as well as the physical substratum. Murray's concluding suggestion was that it is the occurrence of the bryozoan which actually determines the mollusc's distribution.

The observable specific variation, and the limited numbers of recognisable characters perceived in these non-rigid animals, has made past workers, for example MacGillivray (1895), Hastings (1927), d'Hondt (1979, 1983), variably reluctant to accept the existence of certain species. As a result it has been suggested that some species, for example *A. lendigera* and *A. distans*, are almost ubiquitous. Wide geographic distributions, continuous or discontinuous, are not unknown amongst marine animals (Ekman 1967, Cook and Lagaaij 1973), and the genus has been reported from nearly all marine regions except the polar and subpolar seas. However, there is no evidence that any species of *Amathia* has ever achieved and maintained a cosmopolitan distribution. Any indications to the contary seem based on misidentifications. The problem is compounded in one instance; for two specimens, *A. wilsoni* and *A. semiconvoluta* ex Lamouroux collection (BMNH 1899.7.1.6606 parts), there is doubt that the locality data and specimens actually belong together (see page 335).

Although Rao and Ganapati (1975) reported '*Amathia distans*' as 'an important fouling species at the Visakhaptnam Harbour', species of *Amathia* are not noted as fouling the hulls of sea going vessels, and there is no indication that shipping has any effect (cf. Ryland 1970) on distribution. From the information available (albeit that this reflects the situation around the turn of the century, when many of the specimens studied were collected) the species determined appear to have distributions which reflect modern oceanic current flows (see below). This is not unexpected, as *Amathia* colonies are sessile, and the geographic distribution of species would be greatly dependent on dispersal of colony fragments and larvae by water currents.

Taken simplistically, the maintenance of widespread distributions suggests the need for adequate gene flow to help preserve the biological unity of each species (Sheppard 1975, Speiss 1977), and may be influenced by physical criteria. To some extent, this would involve the effects of sperm dispersal. Assuming some general similarity of ctenostomes with other Bryozoa, the free-swimming life of the lecithotrophic larvae (Barrois 1877, Nielsen 1971, Zimmer and Woollacott 1977), might be estimated at about 24 hours. Records of lecithotrophic larval life in Cheilostomata range from 20–75 minutes as in *Parmularia* (Cook and Chimonides 1985), to a maximum of 3–5 days as in *Crassimarginatella falcata* (Cook 1985). Under the same assumption of similarity, sperm life might be estimated as up to 1 hour (Marcus 1926 for *Electra pilosa*, Silén 1966 for *Electra posidoniae*). Lecithotrophic larval life in Bryozoa is generally held to be short and dispersal limited (Ryland 1976, Farmer 1977, Hayward and Cook 1983). Similarly, the contribution sperm dispersal makes towards preventing speciation must also be limited.

It is difficult to assess what contribution fragmentation makes towards species distribution; for the present, it is possible only to speculate on the effects of the factors involved. It is unlikely that colonies of *Amathia* would be susceptible to the same shear forces that might cause rigid, calcified colonies to fail structurally (Cheetham and Erikson 1983). The shape of *Amathia* colonies results partly from the exoskeletal function of locally thickened cuticles, but derives mainly from turgor pressure of the various coelomic fluids acting on the cuticles. The cuticles are flexible but non-elastic. Such an essentially hydrostatic support system would be capable of a great deal of deformation with subsequent recovery. Structural failure results when drag forces exceed tensile strength. Tensile strength of alcohol preserved specimens examined appeared subjectively high. The failure, near a bifurcation, of single stolons taken from distal tips of a specimen of *A. brongniartii* from Victoria Australia (BMNH 1984.12.4.1), was recorded at 80 grams.

Additional resistance to fragmentation is likely in colonies with dense branching. In these, water flow effects are prevented from acting directly on all the constituent components, and the effective drag of a colony is less than expected (Cheetham and Erikson 1983). Under this condition, much water flow would be redirected around the colony, and this would place some emphasis on the external hydrodynamic profile that a colony presents. A possible reaction to this is suggested in the fact that autozooids are often arranged to face into the relatively sheltered space within the colony interior, as for example in *A. wilsoni*, *A. woodsii*, *A. populea* and *A. guernseii.*

The characteristics of flexibility, reasonable tensile strength and hydrodynamic reaction are, however, the very features which have allowed *Amathia* species to spread into the kind of high energy environments, for example, much of southern Australia (Thomas and Shepherd 1982, King and Shepherd 1982) where, if only under severe storm conditions, fragmentation of colonies themselves must occur. In less extreme circumstances, for some species, fragmentation of the possible algal substratum might occur, setting entire colonies adrift.

The longevity of adult colony pieces, is potentially much greater than that of the larvae and sperm. Under laboratory conditions at the BMNH, specimens of *Flustrellidra hispida* survived for over 6 months without their original algal substratum, which had rotted away. The colonies adopted a highly mishaped globular form, approximately 1·5 cms. maximum dimension, lying free on the gravel filter bed of their container. These colonies could be bowled around by very mild water movement, while the great majority of the autozooids forming their surfaces, retained the ability to feed.

As colony fragments of *Amathia* do not readily float, it is to be expected that they will be transported well only whilst they are kept clear of the sea floor. Transportation and being kept clear of the sea floor will take place only as long as there is the appropriate energy in the water currents. More distant dispersal is possible if rafting on a more bouyant substratum, such as algae, occurs (Cheetham 1966, Cook and Lagaaij 1973). The success of any dispersals would require the eventual deposition of species in some suitable environment. Three levels of failure seem possible: that destination environments outside the recorded distribution are unsuitable (in which case, under certain circumstances, it is not impossible that remnants of at least some of these failures might be found); that dispersals do not reach wider transportation currents; that dispersals do reach wider transportation currents but suffer mortality en route, through loss of the 'raft' as the alga dies and rots. *A. lendigera* and *A. pruvoti* can be algal epibionts. These species, if any, would be expected to have achieved very wide distributions, but this does not appear to be the case. Their distributions instead appear similar to those of well documented Lusitanian faunas (Hardy 1959, Ekman 1967, Tait 1986, Currie 1983) (cf. *A. semiconvoluta* recorded from the west coast of Africa to the Mediterranean).

Regardless of the dispersal method of fragmentation products, direct survival of fragments would mainly be favoured by a low energy environment. Higher energy environments might allow survival only through subsequent release of larvae and their settlement. No colonies have been encountered where direct re-establishment of fragments is recognised to have occurred. It is quite possible, however, that colony fragments of variable size may re-attach and grow, and even that arborescent colonies resume their posture and growth form with the aid of rhizoids, in a process analogous to that observed in *Parmularia* (Cook and Chimonides 1985). However, whatever the frequency of fragmentation and outcome of subsequent events, the effects on distribution appear, for the present, to be of little significance.

The earliest record of fossil *Amathia* is from the Late Cretaceous, with a species appearing in the Maastrichtian of The Netherlands (Voigt 1972, Cheetham and Cook 1983). The genus is not associated with very deep water, the deepest record encountered being 150 fathoms (275 metres approx.) for specimens collected off Bahia during the Challenger Expedition. It seems likely, therefore, that the genus achieved its present day tropical to cold-temperate distribution via shelf waters through Tethys and the Tehuantepec Channel, and to have traversed these regions before their closure in the mid Miocene (Ekman 1967, Cook and Lagaaij 1973, Haq 1981). It is obvious that more evidence is required to support these suggestions, although this may not be readily available, as non-boring ctenostomes have a poor preservation record (Cheetham and Cook 1983).

It is interesting to note that some of the species recognised, *A. pinnata*, *A. woodsii*, *A. biseriata*, seem to have been recorded exclusively from both south Africa and southern Australia. Parallels exist for other bryozoan species (Hayward and Cook 1983). This distribution is almost certainly the resultant of palaeogeographic factors rather than of modern current flows (see below), and implies that the genus was established and speciated by the time Africa has moved into relative isolation from its Antarctic association. This does not extend the theoretical age of the group much beyond the Maastrichtian however (see above).

Although the imprecision of past records is criticized, the interpretation here of both *A. brongniartii* and *A. pinnata* from Australia, as two single species, rather than as species complexes, is prehaps lenient even on present evidence. Similarly, the specific genetic unity implied in each case for *A. biseriata*, *A. woodsii* and *A. pinnata* in both south Africa and southern Australia, although accepted here, must be viewed with caution. No linking distributions are recorded and gene flow through dispersal of sperm, larvae and colony fragments is not favoured over such distances and locations, and would not prevent divergence from occurring. Additionally, long term genetic stability of species is implied.

In general, it may be said that the members of the genus have had time to become distributed widely. There has also been enough time for the effects of isolation and isolating mechanisms in demes to have come into play (Schopf 1977, Speiss 1977). Furthermore, if the cryptic speciation indicated by Thorpe and Ryland (1979), for species of the ctenostome *Alcyonidium*, has any parallel in this ctenostome group, further subdivisions within many of the groupings proposed here should be expected.

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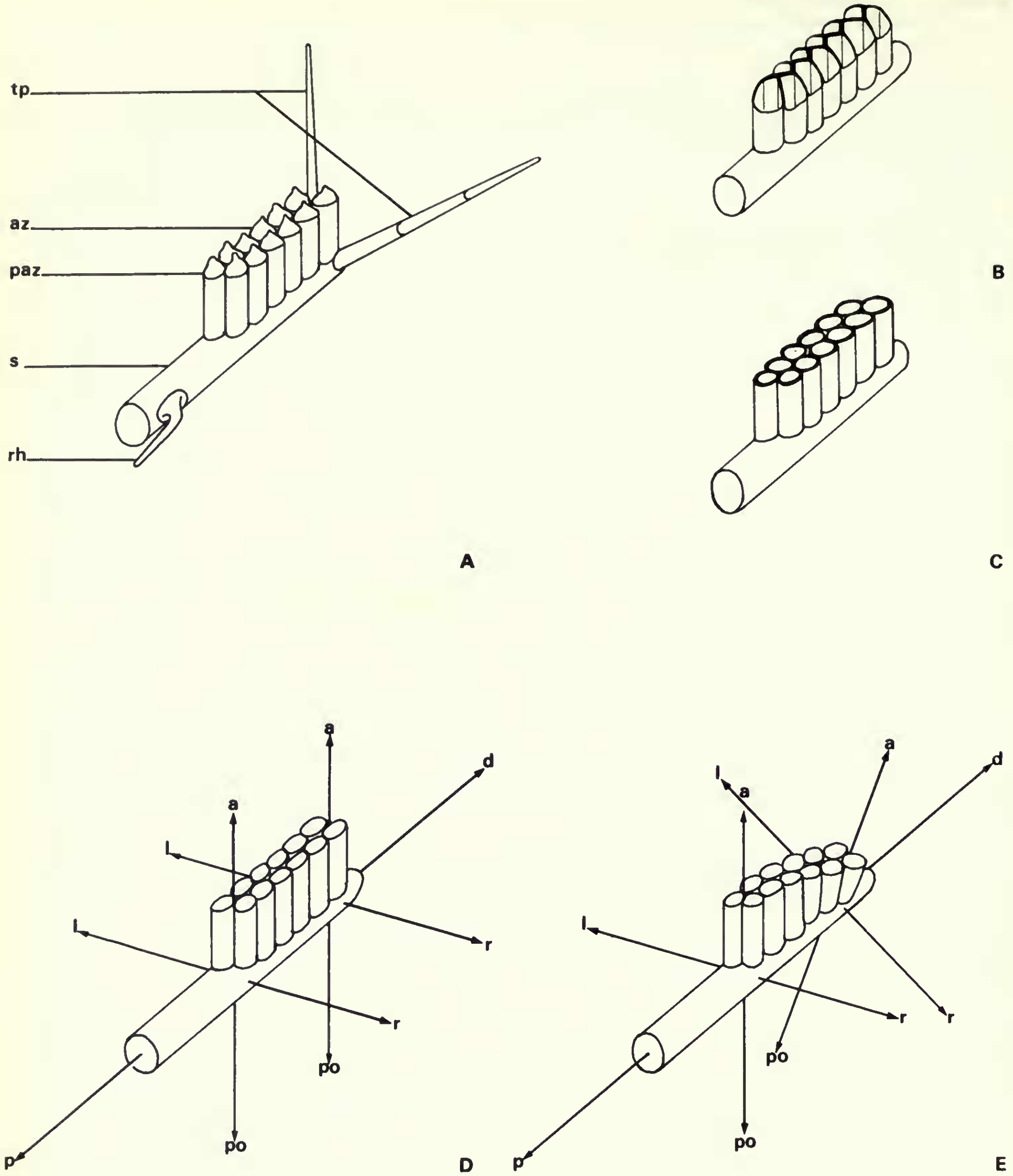

Fig. 1 Schematic representation of erect colony components with reference orientations: (A) *az* autozooecia, *paz* proximal-most autozooid, *rh* rhizoid, *s* stolon, *tp* terminal process; (B.) interior wall thickening; (C.) exterior wall thickening; (D, E.) *a* anterior, *d* distal, *l* left lateral, *p* proximal, *po* posterior, *r* right lateral.

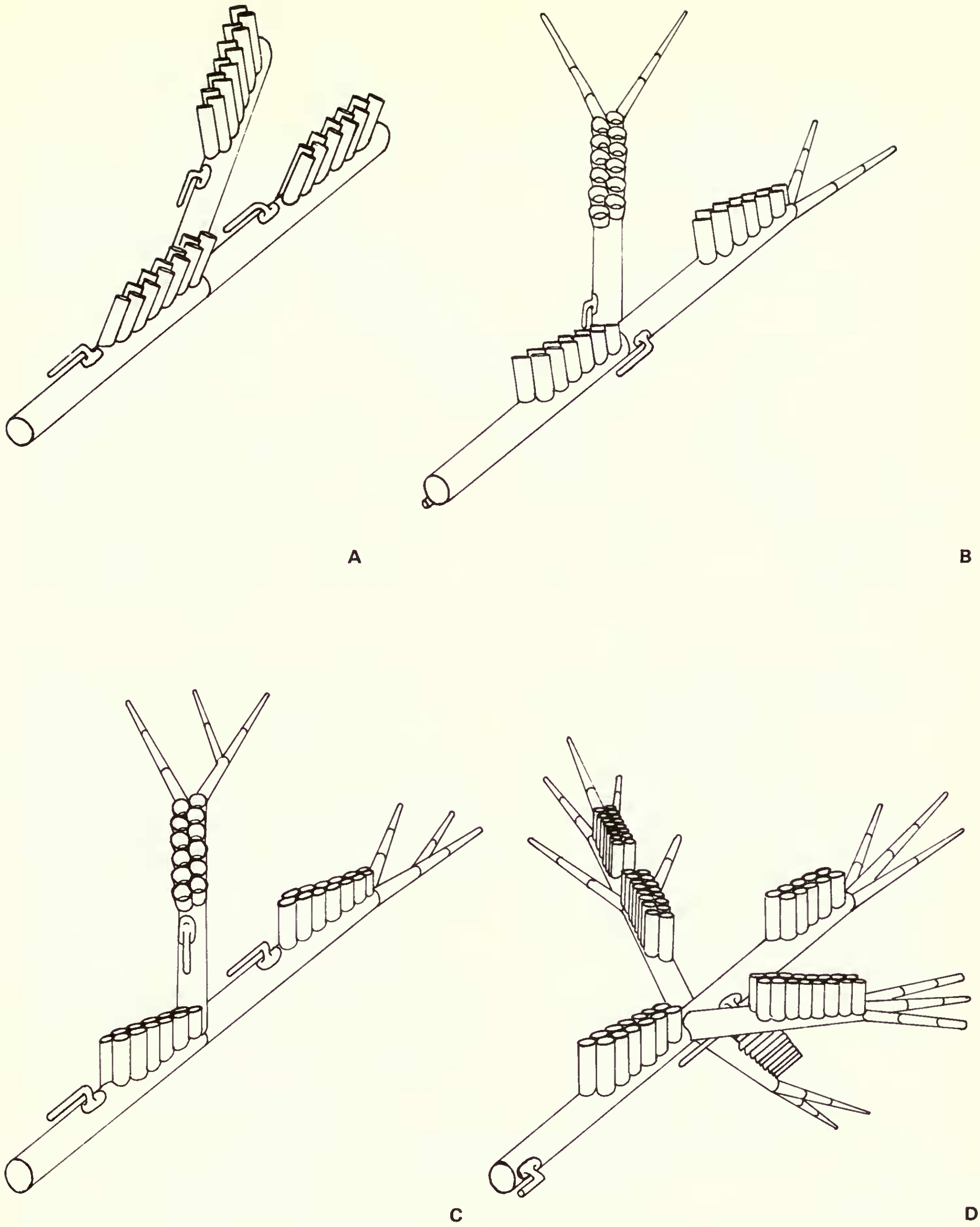

Fig. 2 Relative orientations of autozooecia and rhizoids about the stolon: (A.) *A. guernseii*; (B.) *A. populea*; (C.) *A. woodsii*; (D.) *A. tricornis*.

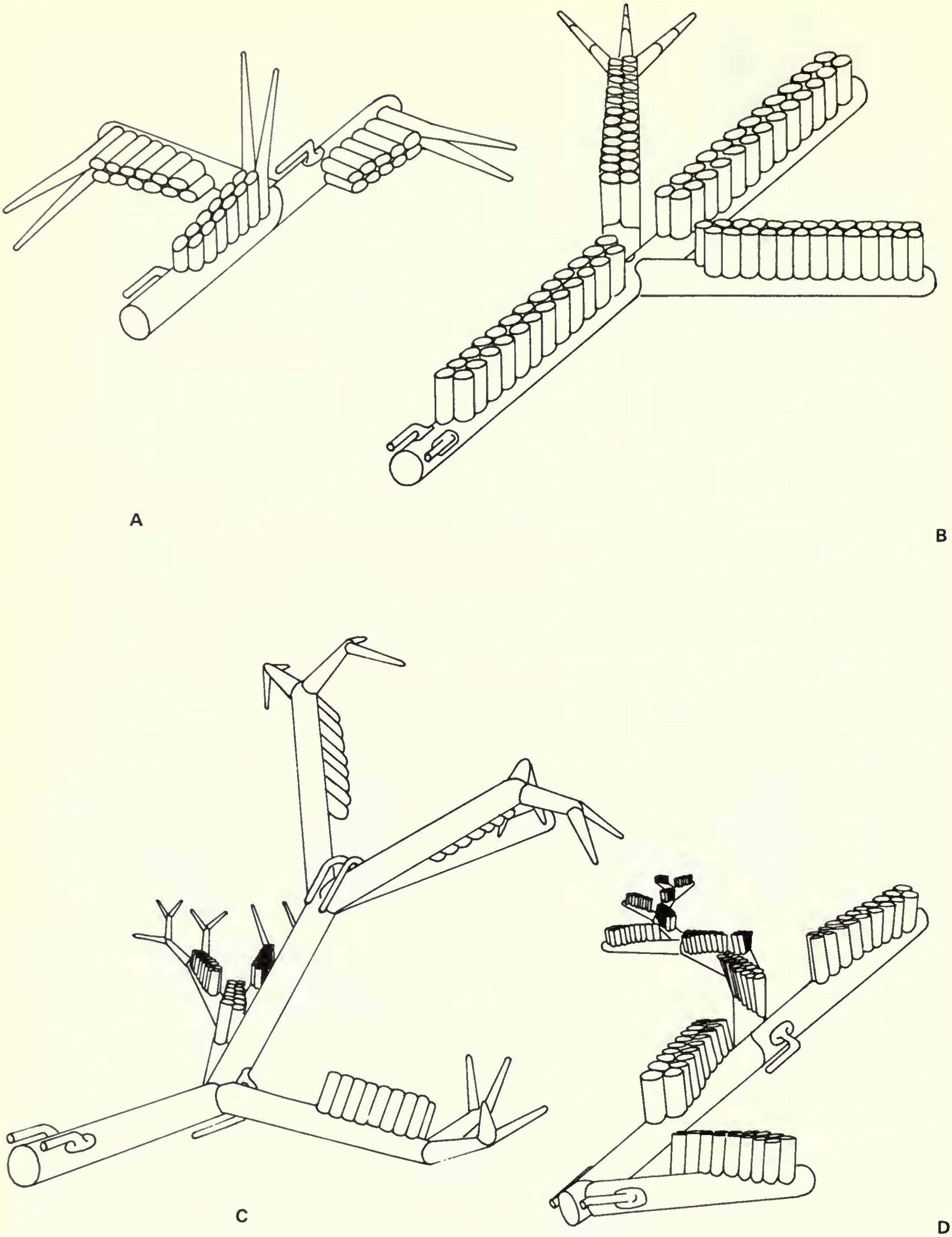

Fig. 3 Relative orientations of autozooecia and rhizoids about the stolon: (A.) *A. lamourouxi*; (B.) *A. pinnata*; (C.) *A. plumosa*; (D.) *A. obliqua*.

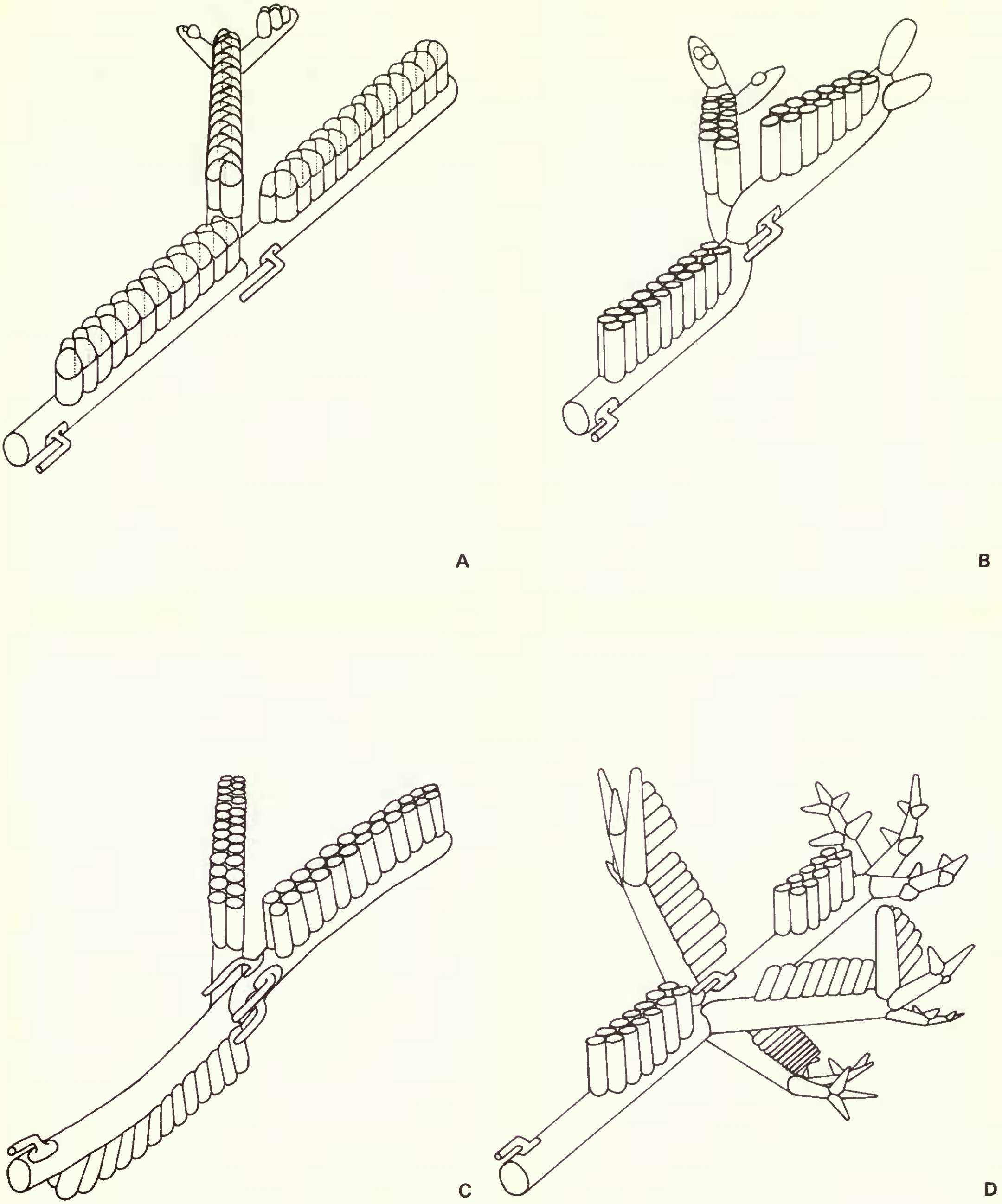

Fig. 4 Relative orientations of autozooecia and rhizoids about the stolon: (A.) *A. brongniartii*; (B.) *A. biseriata*; (C.) *A. alternata*; (D.) *A. wilsoni*.

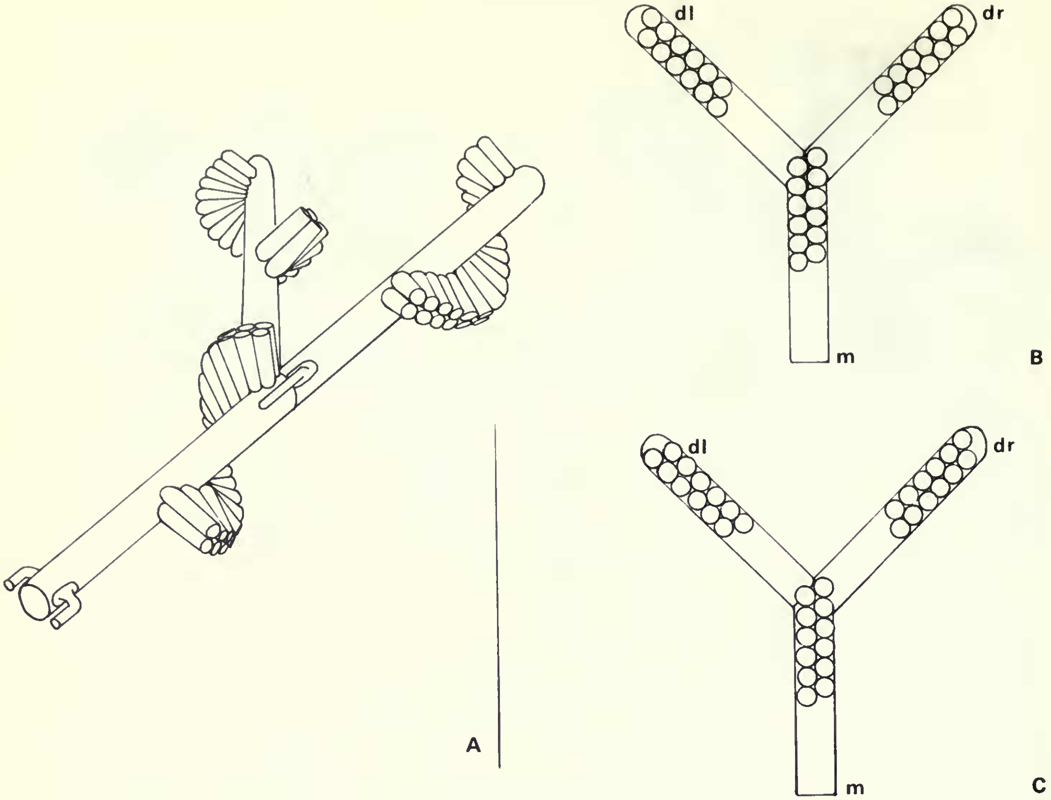

Fig. 5 (A.) Relative orientations of autozooecia and rhizoids about the stolon in *A. semiconvoluta*. Exemplified by *A. lendigera*: (B.) normal autozooid arrangement on a triad of maternal and daughter stolons with sister stolons carrying autozooid displacements to each other; (C.) alternative autozooid arrangement on a triad of maternal and daughter stolons, the daughter stolons carrying identical displacements, both opposite to the condition on the maternal stolon. *dl* left daughter stolon, *dr* right daughter stolon, *m* maternal stolon.

Fig. 6 (A.) *A. lendigera* BMNH 1942.8.6.15, Neotype, Chichester Harbour, UK. × 18; (B.) *A. guernseii* BMNH 1898.5.17.189, Holotype, Guernsey, *Guernsey*, UK × 17; (C.) *A. intermedis* BMNH 1887.5.2.18, Holotype, Hastings, UK × 27; (D.) *A. populea* BMNH 1899.7.1.526, Lectotype, Natal, South Africa, site of rhizoid origin arrowed × 44.

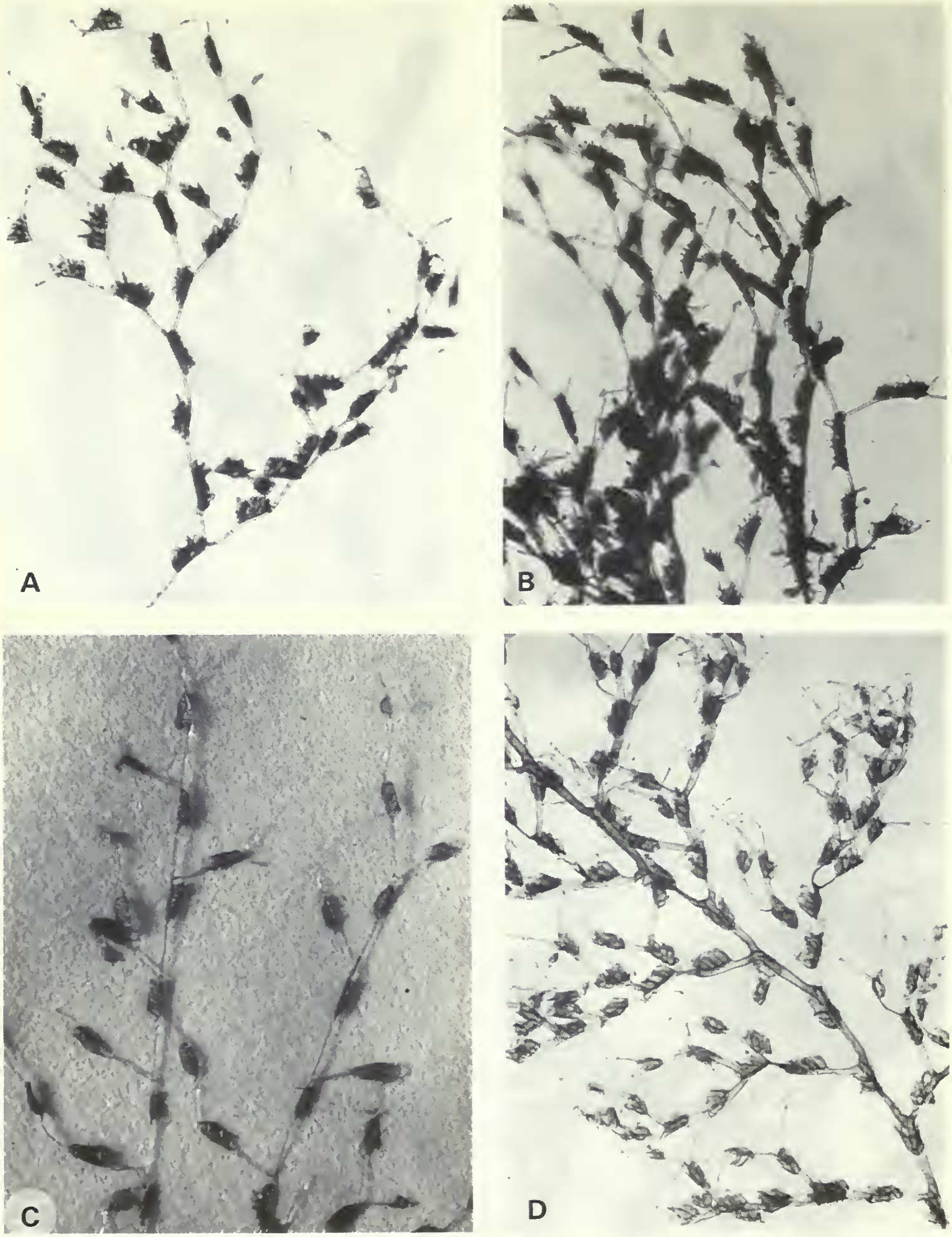

Fig. 7 (A.) *A. lendigera* BMNH 1942.8.6.15, Neotype, Chichester Harbour, UK ×8; (B.) *A. guernseii* BMNH 1898.5.17.189, Holotype, Guernsey, UK ×8; (C.) *A. intermedis* BMNH 1842.12.9.14, Belfast Bay, N. Ireland ×6; (D.) *A. populea* BMNH 1899.7.1.526, Lectotype, Natal, South Africa ×8.

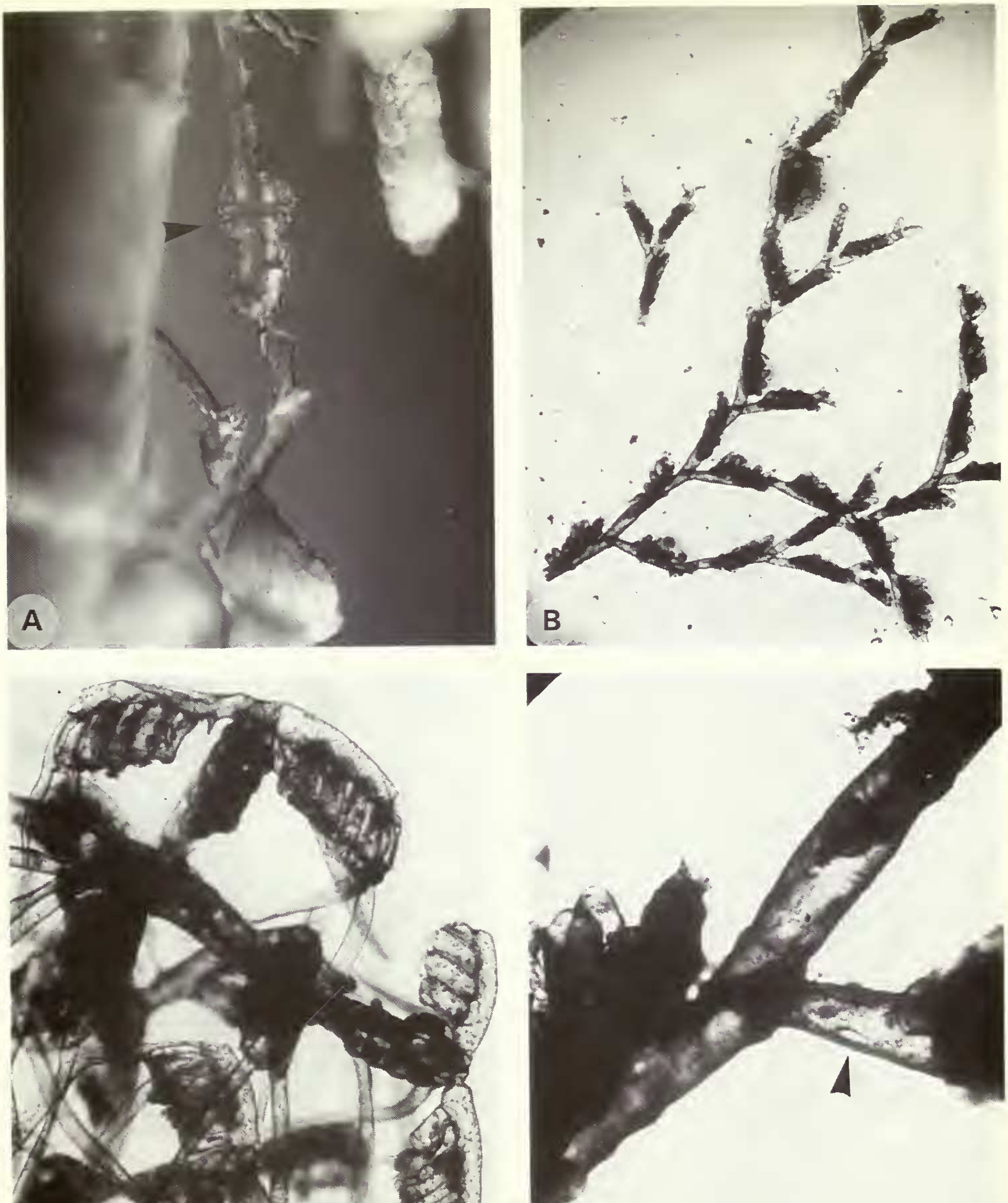

Fig. 8 (A.) *A. lendigera* BMNH 1942.8.6.15, Neotype, Chichester Harbour, UK, palmate processes × 28; (B.) *A. obliqua* NMV H493 (65391) Syntype, Port Phillip Heads, Aus. × 10; (C.) *A. lamourouxi* BMNH 1887.12.10.70, Neotype, Port Phillip, Aus. × 20; (D.) *A. obliqua* NMV H493 (65391) Syntype, Port Phillip Heads, Aus., site of rhizoid origin arrowed × 57.

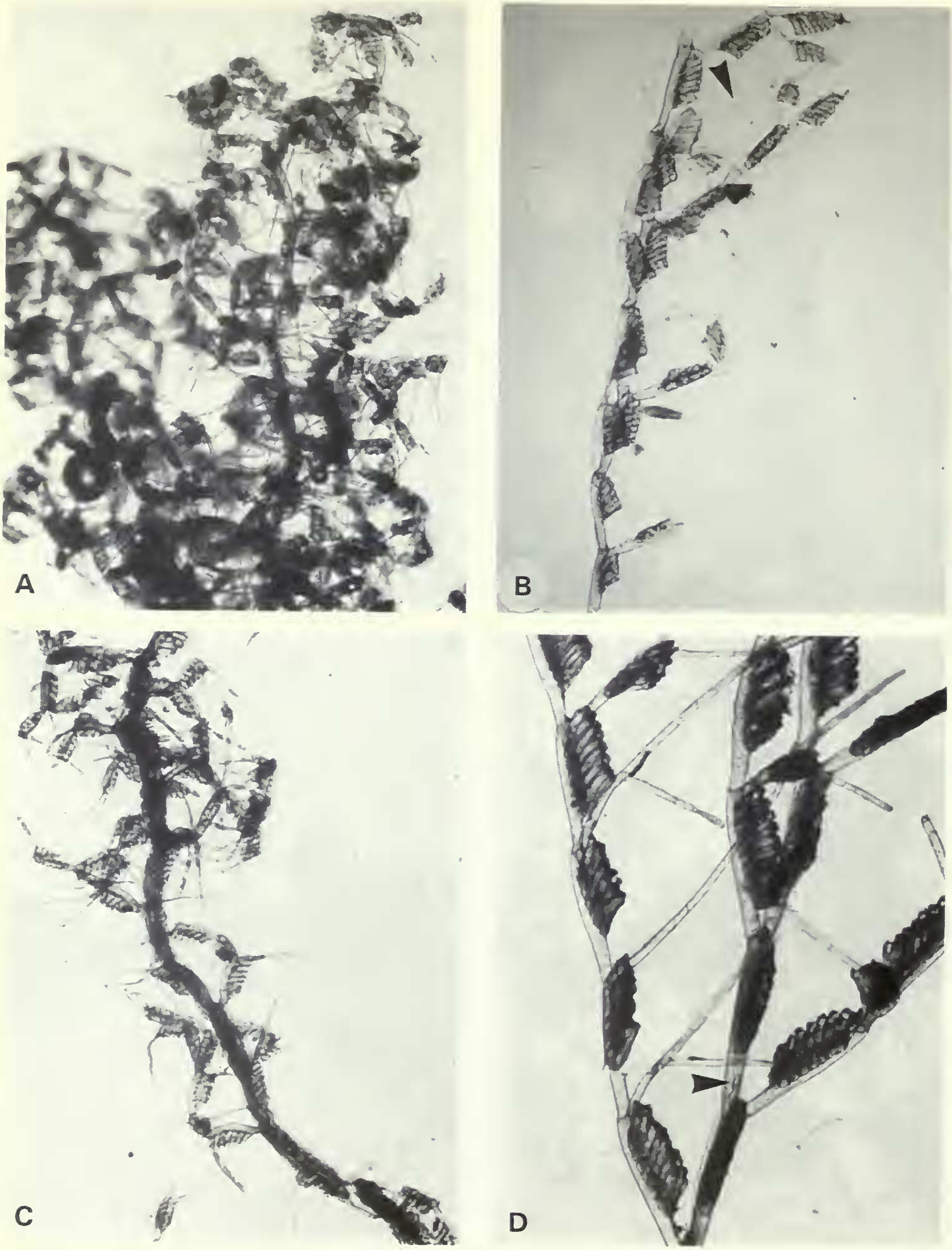

Fig. 9 (A.) *A. lamourouxi* BMNH 1887.12.10.70, Neotype, Port Phillip, Aus. × 8; (B.) *A. cornuta* sensu d'Hondt (*A. woodsii*) LBIMM 2821 part, 'l'Ocean asiatique', bifurcate terminal process arrowed × 8; (C.) *A. lamourouxi* BMNH 1899.7.1.3, New Zealand, apparent alternate branching × 7; (D.) *A. woodsii* BMNH 1883.11.29.27, Neotype, Port Jackson, Aus., rhizoid origin arrowed × 13.

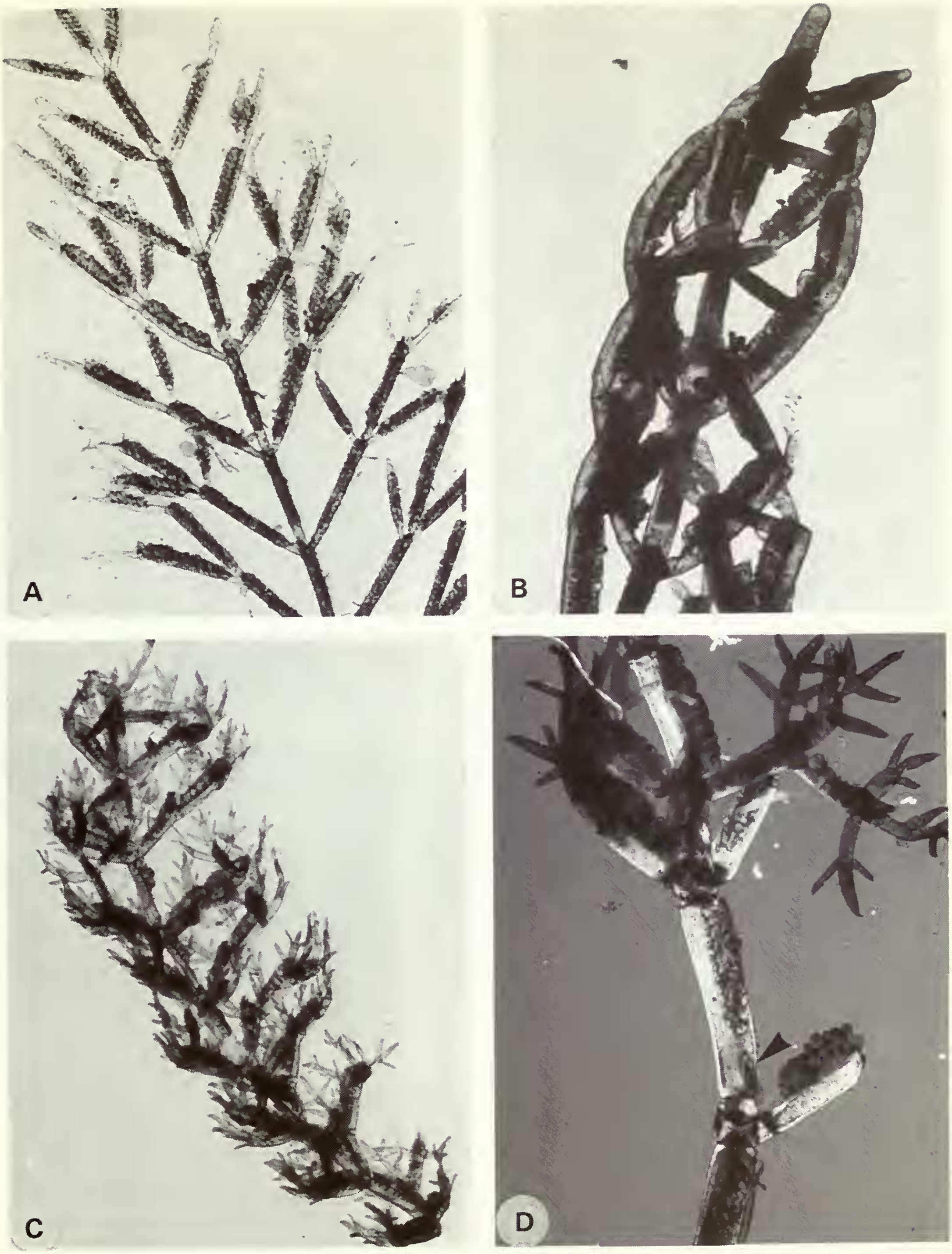

Fig. 10 (A.) *A. pinnata* BMNH 1888.5.17.8 A, Lectotype, Port Phillip, Aus. × 6; (B.) *A. pinnata* BMNH 1888.5.17.8 C, Port Phillip Aus. × 8; (C.) *A. wilsoni* BMNH 1888.5.17.7, Syntype, Port Phillip, Aus. × 5; (D.) *A. wilsoni* BMNH 1888.5.17.7, Syntype, Port Phillip, Aus., rhizoid origin arrowed × 11.

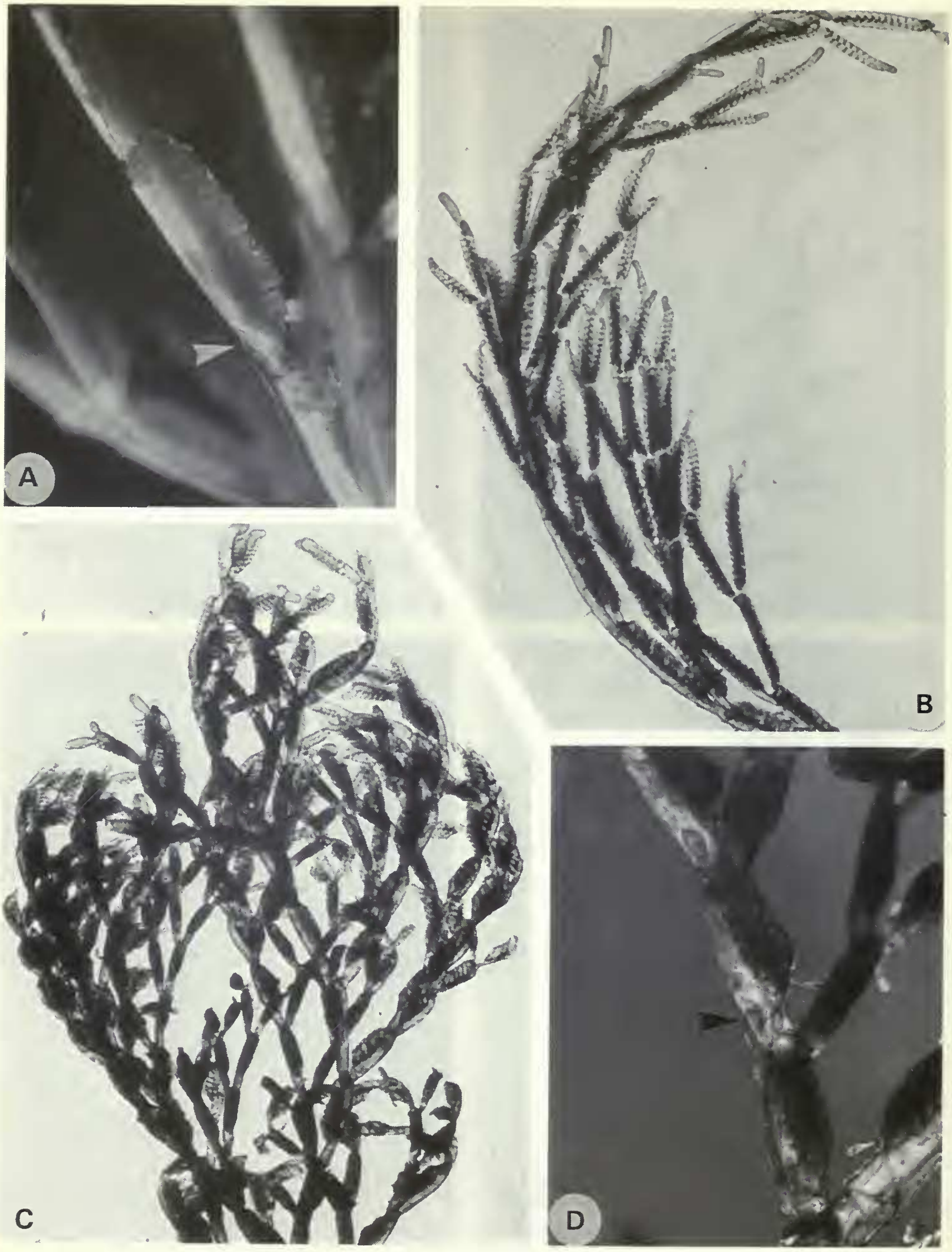

Fig. 11 (A.) *A. brongniartii* BMNH 1888.5.17.6, Neotype, Port Phillip, Aus., rhizoid origin arrowed ×20; (B.) *A. brongniartii* BMNH 1888.5.17.6, Neotype, Port Phillip, Aus. ×8; (C.) *A. biseriata* BMNH 1887.12.10.90, Neotype, Port Phillip, Aus. ×8; (D.) *A. biseriata* BMNH 1887.12.10.90, Neotype, Port Phillip, Aus., rhizoid origin arrowed ×20.

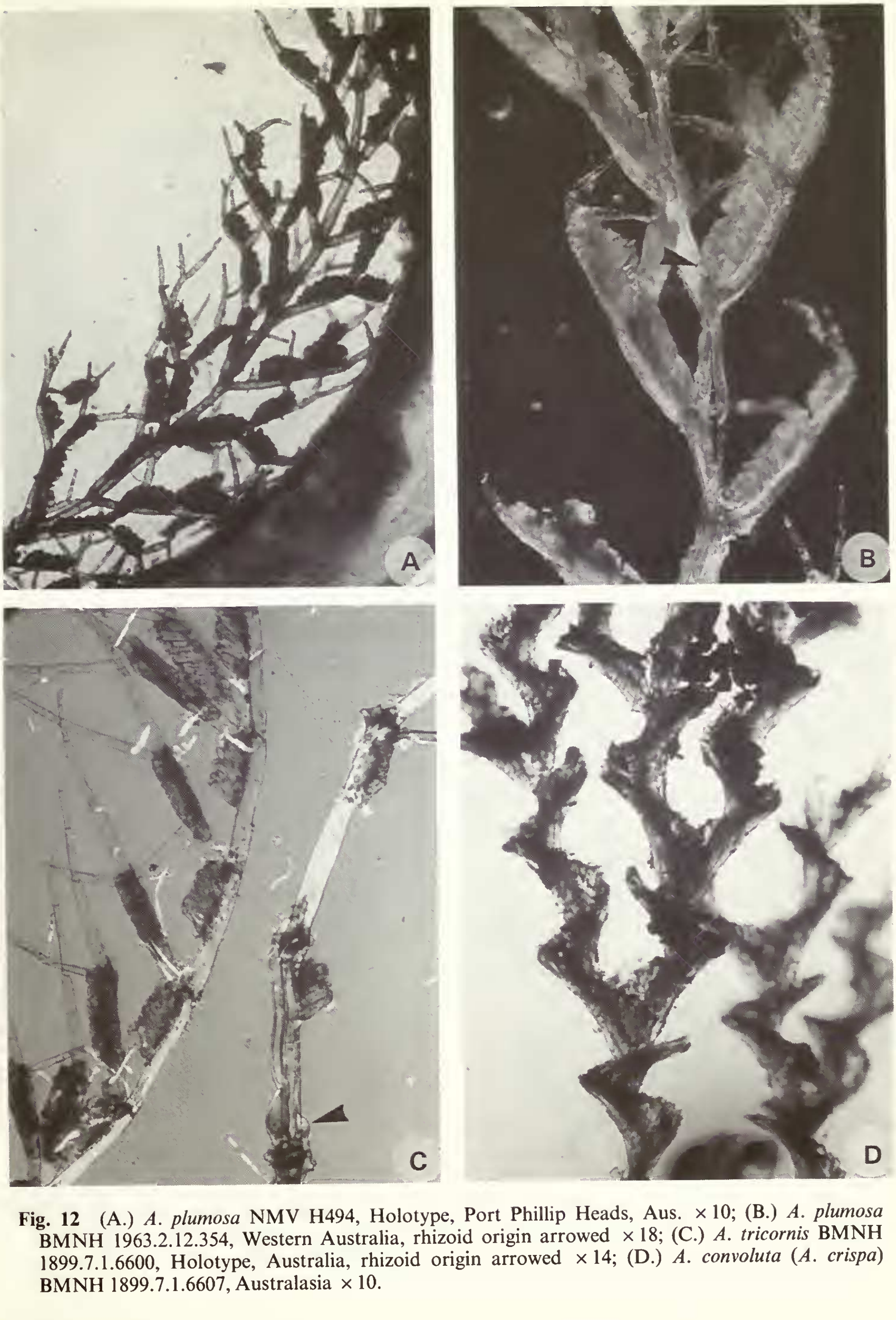

Fig. 12 (A.) *A. plumosa* NMV H494, Holotype, Port Phillip Heads, Aus. × 10; (B.) *A. plumosa* BMNH 1963.2.12.354, Western Australia, rhizoid origin arrowed × 18; (C.) *A. tricornis* BMNH 1899.7.1.6600, Holotype, Australia, rhizoid origin arrowed × 14; (D.) *A. convoluta* (*A. crispa*) BMNH 1899.7.1.6607, Australasia × 10.

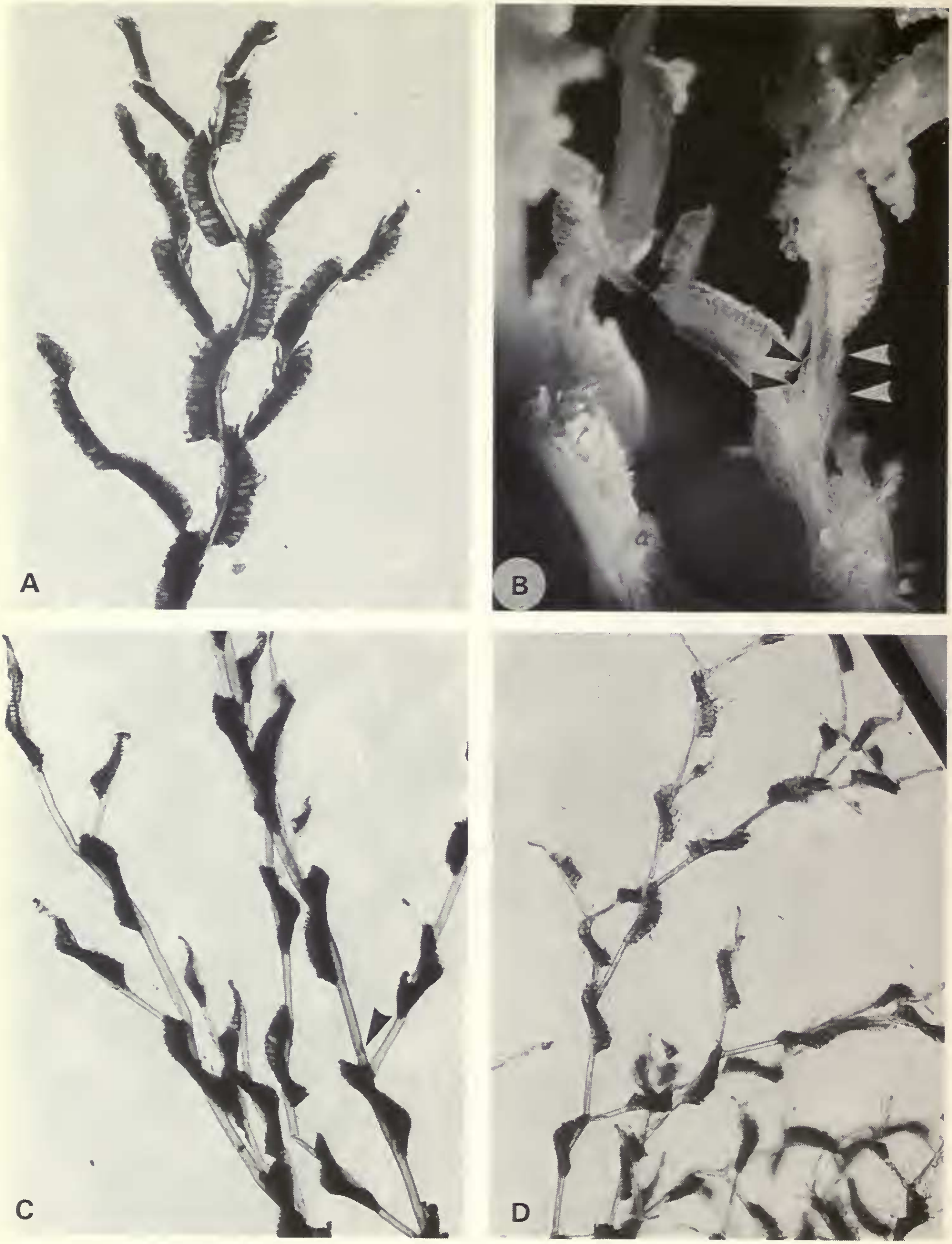

Fig. 13 (A.) *A. alternata* USNM 6307, Neotype, Cape Fear, N.C. USA ×4 (B.) *A. alternata* BMNH 1964.7.10.1A, New River Inlet, N.C., USA, showing polyrhizoid condition, the rhizoid origins indicated × 10; (C.) *A. semiconvoluta* BMNH 1912.12.21.687, Adriatic, rhizoid origin arrowed × 6; (D.) *A. pruvoti* LBIMM Bry 8205, Type × 8.