Taxonomy and evolution of earliest Ordovician graptoloids

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The sequence, taxonomy and inferred phylogeny of earliest Ordovician graptoloids have been determined from stratigraphic sections in Newfoundland, Norway, China and elsewhere. *Rhabdinopora* is analysed in terms of population systematics and is envisaged as a diverse complex of intergrading populations that change in time (stratigraphic subspecies) and in ecological space (ecological subspecies). The main lineage, developed in sequences representing the deep shelf to continental slope environment, comprises the successive subspecies of *R. flabelliformis–parabola, canadensis, flabelliformis, anglica* and, probably, *bryograptoides* and is developed through the early and early–late Tremadoc. *R. f. parabola*, a key graptolite for correlation of the base of the Ordovician System, is described in detail. The shallow water inshore forms, *R. f. socialis* and *R. f. norvegica* are interpreted as ecological subspecies. The genus is characterized by quadriradiate development type, now known to be present in all subspecies in which the development type can be determined. The genera *Staurograptus* and *Anisograptus* are redefined and described and their species interpreted as populations with a wide range of morphologic variance. *Triramograptus atavus* gen. et sp. nov. is described from Newfoundland. The stratigraphic ranges of all species are revised and their zonal distribution presented.

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Introduction

The earliest Ordovician *Rhabdinopora* populations have proved notoriously difficult to classifiy and treat systematically. Yet they have long been recognized as of stratigraphic value, and the *Rhabdinopora flabelliformis* zone is one of those most widely recognized and quoted in the literature marking, for many, the base of the Ordovician System. The difficulty arises largely from the variability seen within even a single population on the one bedding plane:

> The variability of *Dictyonema* [= *Rhabdinopora*] is so great that hardly any two specimens ever seem exactly comparable and in any large collection of these organisms the range of variation and diverse combination of characters is bewildering (Bulman 1954, p. 7).

This may reflect genetic variance in the species, heterozygosity with a wide range of phenotypic variation or, most probably, a combination of the two. On the other hand, there often appear to be differences in modal form and morphologic range in populations from different geographic regions, leading to the plethora of subspecies, species, and even generic names found in the literature (Erdtmann 1988). In our view, the quantitative analysis of adequate populations is needed to establish with confidence the modal form of species and subspecies, estimates of the range of variation, and identification of reliable discriminatory characters. In addition, good stratigraphic sections from which can be obtained stratigraphically ordered populations are needed to evaluate the change in morphology within single lineages at the one locality. Ideally, to determine the extent of the influence of depth and facies, and the effects that changing sea level would have on faunal composition and morphology, these localities should be distributed in a two-dimensional profile across the shelf, slope and ocean floor. Finally, the patterns emerging from the above in low palaeolatitude regions should be compared with those from high palaeolatitude regions to determine how palaeolatitude influences distribution and morphology.

The limited availability and distribution of good sections with well-preserved graptolites mean that these ideals cannot be reached. However, they can be approached. Although there are still many questions left unanswered, we present here, and in a companion paper (Cooper, in prep.), the results of a first detailed attempt at such an integrated approach.

In this paper, the base of the Ordovician is taken at a level equivalent to the first appearance of the conodont *Iapetognathus* n. sp. A (Nowlan & Nicoll 1995) in the Dayangcha section of North China, that is, effectively at the base of the *Rhabdinopora flabelliformis parabola* Zone.*

Sources of material

Specimens used in the present study come from the following main localities and sections: (1) the Green

* Since the MS was submitted, the Working Group on the Cambrian–Ordovician Boundary has voted to place the boundary at the appearance of Iapetognathus n.sp. 1 in the Green Point section of western Newfoundland. This level is slightly below the Dayangcha level used in this paper (see Figs. 2, 3), but still near to the first appearance datum of planktic graptolites.

Point section in Western Newfoundland, collected by B.-D. Erdtmann and colleagues between 1981 and 1986, held at TUB Berlin (Erdtmann 1986a, b), and by J. Maletz, held at the University of Greifswald; (2) selected collections from other western Newfoundland sections, especially Broom Point North (Fortey et al. 1982); (3) the Naersnes section, south of Oslo, collections held by TUB Berlin and Oslo University (Bruton et al. 1982; Bruton et al. 1988); (4) the lower 1.6 m of the *Dictyonema* Shale at Pakerort, Paldiski (collected by D. Kaljo and R. A. Cooper), and drill cores from various borings in northern and central Estonia, held at the Academy of Sciences, Tallinn, Estonia (Kaljo et al. 1986); (5) the Eichwald collection held by the University of St Petersburg at St Petersburg; (6) the XCS section at Dayangcha, in northern China; the collections are held at, and were made by, the staff of the Nanjing Institute of Geology and Palaeontology between 1982 and 1988 (Chen et al. 1985, 1986); (7) Digermul Peninsula, northern Finmark, made by B.-D. Erdtmann, held at TUB Berlin; (8) several incomplete and fragmentary specimens from the Bliss Sandstone of New Mexico, collected by J. E. Repetski, held in the US National Museum (Taylor & Repetski 1995). A number of other localities are mentioned in the text.

Specimens with numbers prefixed GSC are held by the Geological Survey of Canada, Ottawa; PMO, in the Museum of Palaeontology, Oslo, Norway; NIGPAS, in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, China; LO, in the type collection of the Department of Historical Geology and Palaeontology, Lund University, Lund, Sweden; Va, in the collections of the Institute of Geology, Tallinn, Estonia.

Populations

From the wide range of variability described here for all species and subspecies, especially of *Rhabdinopora*, it follows that in order to be reliable, identification should be based on a population. A single specimen, unless it is a modal form, is not likely to provide a reliable basis for recognizing a species or subspecies. Whereas this makes the task of the biostratigrapher more difficult, the evolutionary succession and ecological zonation described here, and by Cooper (in prep.), allows for more precision than was previously possible, provided populations are used. As envisaged here, the genus *Rhabdinopora* is represented by a succession of populations which show progressive modal shift in time and across facies but which have widely overlapping ranges in morphology from one bed to the next, and from one ecological zone to the next.

Morphometrics

Unfortunately, proximal morphology is displayed in too few specimens to be used in population studies. Here we use characters of the rhabdosome to determine the range of variance and test the characters for their utility in interpopulation and intersubspecific discrimination. Because many of the features that have commonly been used to distinguish one rhabdosome from another are not easy to measure, a set of templates were contrived that span the range seen in the population. Hence, the complex features of mesh style, stipe sinuosity and rhabdosome form were semi-objectively quantified by classifying each specimen in the template pattern with which it most closely conformed (Figs. 11–14). In addition, standard linear and angular measurements of the rhabdosome (following previous workers, e.g. Bulman 1954) have been used.

Proximal development

Quadriradiate proximal development has proved difficult to decipher. It has been described from isolated growth stages only by Legrand (1974) in material from the Sahara (regarded as transients between forms listed as *Dictyonema sociale praeafricanum* Legrand (1973) and *D. s. mehaïgueni* Legrand (1973)). In the pattern described, th 1^1 is a normal theca and there are three successive dicalycal thecae on the th 1^2 side of the rhabdosome so that three of the first-order stipes arise on one side and one on the other (Fig. 1) producing an asymmetrical proximal end. This is in contrast to the previous model for quadriradiate structure by Bulman (1950, fig. 2h), based on flattened specimens and growth stages of *R. f. rustica* from Canada, in which two successive dicalycal thecae form on one side of the rhabdosome and one on the other leading to a more symmetrical proximal end. Although the African specimens are not free from ambiguity (Maletz 1992), they are the best available for interpreting proximal structure. Legrand's model has the advantage of simplifying the development programme of the rhabdosome (Maletz 1992), it accords with the strongly asymmetrical proximal ends seen in specimens of *R. praeparabola*, *Staurograptus dichotomous*, and some later forms, and appears to us the more probable one. Quadriradiate development is the primitive state for the Graptoloidea (Cooper & Fortey 1983; Fortey & Cooper 1986) and is characteristic of the earliest genera, *Rhabdinopora* and *Staurograptus*. It has been determined in *R. praeparabola*, *R. f. parabola*, *canadensis*, *flabelliformis* and *anglica* (herein) and *R. f. rustica* (here provisionally synonymized with *R. f. flabelliformis*) by Bulman (1954), also in *Staurograptus dichotomous* and *S. hyperboreus* (herein).

In the triradiate pattern (Bulman 1950, fig. 3; Fig. 1) theca 1^1 is a normal theca as in the quadriradiate type, and two successive dicalycal thecae (th 1^2 and th 1^3) lie on the same side of the rhabdosome so that two first-order stipes originate on one side of the rhabdosome and the third on the other. The pattern can be derived from the quadriradiate type by suppression of the last-formed dicalycal theca (th 1^4; Maletz 1992) and is a derived state

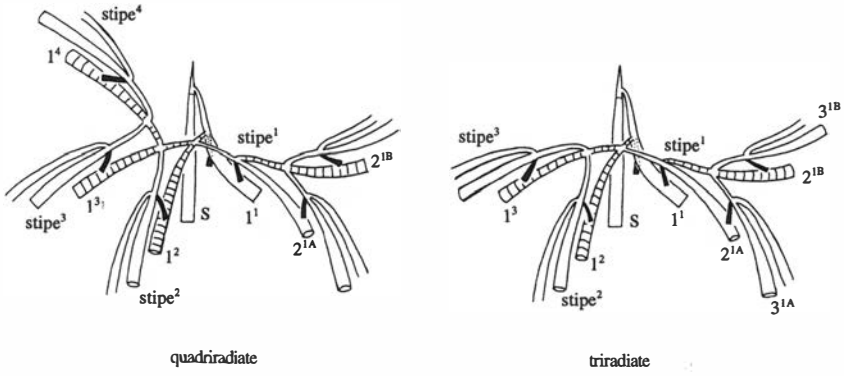


Fig. 1. Thecal diagrams of quadriradiate and triradiate proximal development types following Legrand (1974) and Maletz (1992).

in the Graptoloidea. It is characteristic of *Anisograptus*, *Bryograptus*, *Triograptus* and *Radiograptus*. It may also be present in the later species of *Rhabdinopora*, but has not yet been definitely demonstrated. In both the quadriradiate and triradiate types and, in several early biradiate species (Legrand 1964) the first dichotomy of stipe 1 is produced by dicalycal theca 3^1.

The biradiate development type is the general one among the remaining Graptoloidea and can be derived from the triradiate type by suppression of the last-formed dicalycal theca. It first appears in the stratigraphic record in the middle part of the early Tremadoc. The successive order of appearance of the quadriradiate, triradiate and biradiate development types is the basis for graptolite Assemblages 1, 2 and 3 respectively (Cooper 1979; Erdtmann 1988).

The development types are most readily determined from isolated rhabdosomes or proximal growth stages preserved in relief. They can generally be determined in isolated flattened growth stages, and in growth stages and mature rhabdosomes in the bedding plane when preserved discoidally (in dorsal view, Figs. 8, 9k, p). However, specimens preserved in lateral view generally have one or more of the first-order stipes concealed by another stipe (Fig. 9f, i; Maletz 1992) or in the rock matrix, or removed in the counterpart.

Biostratigraphic summary

The Green Point Section of western Newfoundland (Fig. 2) provides a sequence of graptolite populations through the Lower Tremadoc that is unparalleled for its completeness. It enables the succession of forms to be unambiguously determined in one region and provides a standard of comparison with early Tremadoc sequences from other regions. It represents the continental slope environment and its graptolite sequence differs in some respects from those derived from shelf and oceanic successions. The presence, absence and, in a few cases, stratigraphic range, of species in sections around the world is intimately related to the location of the sections in the shore-to-ocean depositional depth profile, to sea-level events and, to a minor extent, to palaeolatitude (Cooper in prep.). A correlation of these sequences provides the basis for compiling composite stratigraphic ranges of species and a global set of graptolite zones for the early part of the Tremadoc Series (Fig. 3).

1. *Zone of* Rhabdinopora praeparabola: The zone base is defined by the appearance of the earliest graptoloids, *Rhabdinopora praeparabola* and *Staurograptus dichotomous*, both of which range through the zone. The zone, which probably represents a relatively short time interval, is known in the relatively deep-water sequences of the continental slope in low and mid-latitude regions – western Newfoundland (Fortey et al. 1982; Erdtmann 1988), eastern New York (Landing 1993) and the Oslo region, Norway (Bruton et al. 1982).

2. *Zone of* Rhabdinopora flabelliformis parabola: The widespread appearance of the first graptolite with a well-developed meshwork, *R. f. parabola*, marks the base of the second zone, and the base of the Tremadoc Series (Rushton 1982). Near the top of the zone this subspecies is replaced, in lower slope sequences, by *R. f. canadensis*. In the upper part of the zone *R. f. socialis* appears in the upper slope to outer shelf sequences where it is is generally the oldest graptoloid. In the lower slope sequences of western Newfoundland, *Staurograptus* persists with *R. f. parabola*, whereas in the oceanic sequence of NW Canada, *Staurograptus* alone is present. The zone is known from western Newfoundland (Erdtmann 1988; Cooper, in prep.), eastern New York (forms attributable to either *parabola* or *canadensis* are described by Landing 1993), the Yukon, north-west Canada (Jackson 1975), Naersnes, Oslo, (Bruton et al. 1982), north China (Lin in Chen et al. 1985, 1986, and this paper), Taimyra, northern Russia (Obut & Sobolevskaya 1962), and Belgium (Bulman 1970; Erdtmann 1986b). It is thus represented in all latitudinal zones and in shelf to oceanic sequences.

3. *Zone of* Anisograptus matanensis: Base of the zone is defined by the appearance of *Anisograptus*, usually represented by *A. matanensis*, which here includes *A. richardsoni*, and which is widespread in upper slope to oceanic sequences. In the basal part of the zone, in slope sequences, the *R. f. flabelliformis* complex is represented by *R. f. canadensis*; it is soon replaced by *R. f. flabelliformis*

which becomes particularly abundant in shelf and upper slope successions and achieves a global distribution. Near the top of the zone, *R. f. norvegica* is found in great numbers in a narrow interval in shelf and upper slope sequences. The *Anisograptus matanensis* Zone is widespread around the world, being readily recognizable in all depth facies, and latitudinal zones.

4. *Zone of* Rhabdinopora flabelliformis anglica: The appearance of *R. f. anglica* – common in shelf to lower slope sequences – marks the base of the zone, which probably spans a relatively short time interval. *Anisograptus matanensis* generally is present in slope sequences. *R. f. norvegica* persists through the zone in shallow shelf successions. The zone can be recognized in shelf and slope sequences in all latitudinal zones.

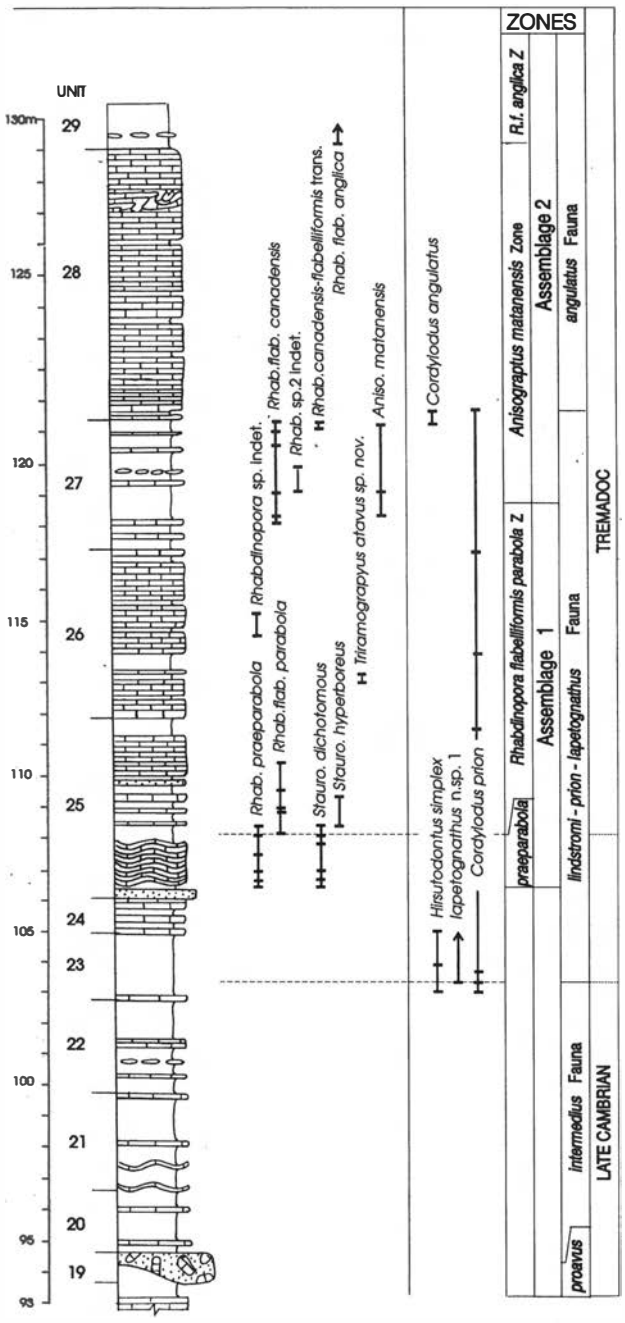


Fig. 2. Stratigraphic range of graptolites in the Green Point section, western Newfoundland, as revised herein. Lithologic column based on the measured section of Erdtmann (1986). Meterage based on Erdtmann's Green Point A section. Bed numbers of James & Stevens (1986) transposed from James & Stevens (1986) and Barnes (1992). The selected conodont ranges and cordylodid assemblage zones shown are from Barnes (1992) and Nowlan & Barnes (pers. comm.)

5. *Zone of* Adelograptus: The appearance of adelograptids, commonly of *tenellus* type (for which the name A. 'tenellus' is used here, in a broad sense), marks the base of the fifth zone. In deep-water sequences, the adelograptids are accompanied by the distinctive *Psigraptus*. In shelf sequences large multiramous biradiate forms, generally listed as *Clonograptus*, appear. The taxonomy and biostratigraphy of this zone, which represents a long time interval – possibly as long as the previous four zones combined – is poorly known. The lower part appears to be of low diversity in most successions, but in the upper part, diversity increases with the appearance of *Kiaerograptus*, *Triograptus*, several species of *Bryograptus* and *Adelograptus* and, in deep-water sequences, *Paradelograptus antiquus*.

Ecostratigraphy and classification

Long-established names of graptolite species in the early Tremadoc fall into two groups: those represented by species with pendent rhabdosomes and numerous stipes and numerous dissepiments, and those by horizontal or declined rhabdosomes, fewer stipes and few, or no, dissepiments. The first group is here referred to as *Rhabdinopora* (including *Heterograptus*), the second group includes *Staurograptus* (including *Aletograptus*) and, possibly, *Anisograptus*. The primary criteria used for generic differentiation are thus rhabdosome habit, number of stipes and presence or absence of dissepiments. Isolated growth stages suggest that sicula length, width, stipe width and, possibly, thecal overlap are also discriminating features. The present study indicates that these groups represent two main lineages that diverged soon after the appearance of graptolites.

Almost all previous students of the *Rhabdinopora* group have commented on the variability of the species or subspecies, and listed morphological transients between them. Brögger (1882) noted that Kjerulf's (1865) variety *norvegicum* was linked to the forma typica *flabelliforme* by morphological transients. Bulman (1954, p. 16) noted transients that connect *flabelliformis* with *norvegica*, *socialis* and *anglica*, and *anglica* with *bryograptoides*. Erdtmann (1982) regarded *norvegica* as a gerontic growth stage of *flabelliformis*, with continuous intergradation between them. Erdtmann (1988) and Fortey et al. (1982) have remarked on the overlap between populations of *flabelliformis* and *rustica* (=*canadensis*). Our observations confirm these morphologic transitions which make the assignment of names to populations frequently a difficult, and somewhat arbitrary, operation. For this reason, we follow Bulman (1954) and regard the

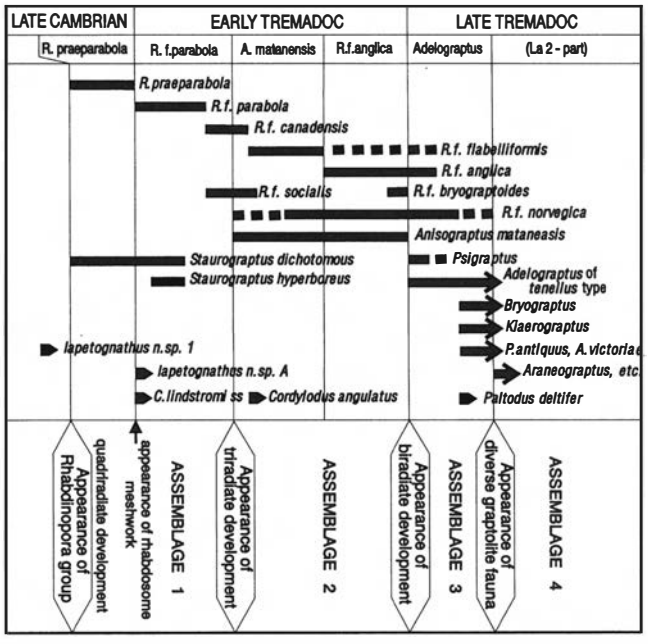


Fig. 3. Ranges of graptolite subspecies based on taxonomic revisions herein and global correlation of Tremadoc graptolite sequences (Cooper, in prep.). The ranges are composites, derived from the ranges of taxa in shelf, slope and oceanic sequences from around the world. The first appearance levels of some key conodont taxa are shown.

several forms here recognized as subspecies rather than as species.

On the other hand, on any one bedding plane it is rare to find more than a single form. In more than 1200 slabs from the *Dictyonema* Shale of Estonia examined by one of us (RAC) the forms *flabelliformis*, *socialis*, *norvegica* and *anglica* were recognized but on no slab was there clearly more than one population represented. Occasionally, one form will alternate with another in successive beds (e.g. *norvegica* and *flabelliformis*). Where more than one form is listed from one locality (e.g. Bulman 1954, text-fig. 3) they are commonly either transients or forms that lie adjacent to each other in the morphologic series, such as *flabelliformis* and *anglica*. In no case has the co-ocurrence of two forms in a single bed been substantiated by population analysis.

A variety of reasons for this mutual exclusivity have been suggested including geographic differentiation (geographic subspecies, Bulman 1970; Skevington 1973), stratigraphic differentiation (stratigraphic subspecies, Bulman 1954) and habitat differentiation in the water mass ('ecological subspecies'); or gerontomorphism and ecological separation of growth stages (Erdtmann 1982).

Cooper (in prep.) has proposed a model for the distribution of *Rhabdinopora* forms in time and space (Fig. 4) that envisages them as a diverse complex of intergrading populations, each characteristic of a particular horizon (stratigraphic subspecies) or ecological zone (ecological subspecies). The ecological zones are primarily related to water depth and distance from shore. The succession of forms found in any given locality or region will be the result of the complex interplay between stratigraphic succession (evolutionary change), the position of the locality within the shore to ocean profile, and lateral facies migration such as caused by sea-level change and local tectonic displacements.

We treat the restricted inshore forms, particularly *Rhabdinopora flabelliformis norvegica* and *R. f. socialis*, as ecological subspecies, because they represent central morphotypes (modal forms) of populations occupying an environment marginal to that of the most abundant and diverse graptolite populations, in a pattern that repeats itself on different continents or regions. However, we cannot discount the possibility that they are merely ecophenotypes (or envirotypes *sensu* Chauffe & Nichols 1995) of other subspecies, growing and living in an extreme environment. In this case they should not carry separate taxonomic names. Unfortunately, we know of no way to test this hypothesis with the present material. It is convenient to distinguish the forms nomenclaturally here, but the alternative interpretation (ecophenotypes) should be regarded as possible, too.

Phylogeny

Detailed morphology of the proximal region and of the thecal and stipe structure are known in very few specimens of *Rhabdinopora*, and are lacking altogether in some species and subspecies. From those recovered in the present study, it appears that proximal morphology is useful for distinguishing the main lineages although it is relatively uniform within them. The main evidence for phylogenetic relationship within the *Rhabdinopora* group must therefore come from precise biostratigraphy and from rhabdosome morphology. Fortunately, most subspecies are known from relatively large populations and the succession of populations is finely controlled in several sections around the world, particularly those of western Newfoundland, providing excellent control of change in populations with time. *Staurograptus* and its derivatives, on the other hand, are known from both well-preserved isolated material and the usual bedding-plane preservation.

The lowest populations at Green Point and Naersnes represent the earliest planktic graptolites (graptoloids)

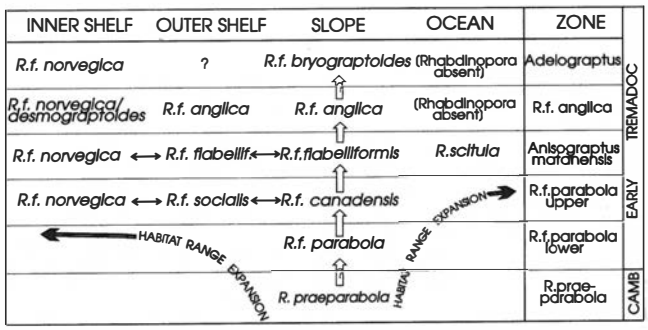


Fig. 4. The succession of *Rhabdinopora flabelliformis* subspecies in time and in ecological space. Open arrows indicate inferred evolutionary transitions, double-ended arrows indicate transitions in ecological space.

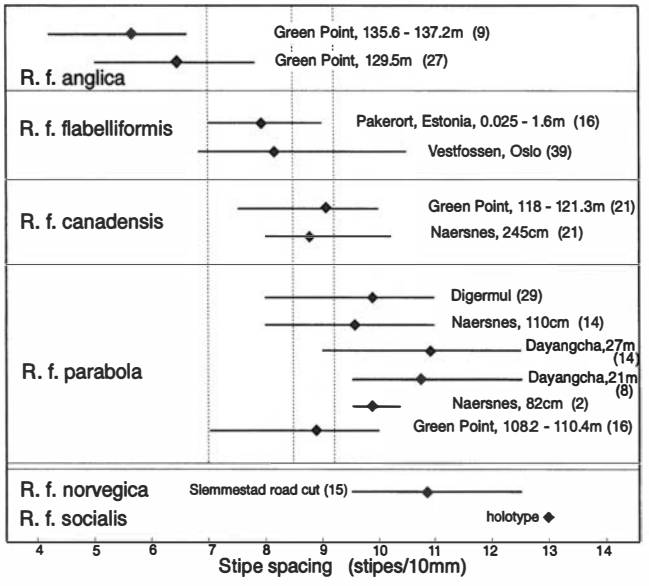


Fig. 5. Stipe spacing, measured in the mature part of the rhabdosome, in populations of *Rhabdinopora flabelliformis* subspecies. The mean value and range are given for each. Details of localities are given in the text, sample meterage is shown for samples from measured sections. The number of specimens measured is given in parentheses for each population.

known in the world. Rhabdosome shape is very variable, and, in Green Point populations, ranges from strongly pendent (*praeparabola* type) to horizontal (*Staurograptus* type). Dissepiments are present in both types but are seen only in a few of the most mature specimens, where they are always scattered, rare and distally placed. Specimens preserved in the shale appear to range in morphology continuously from one type to the other. At the extreme end of the range in horizontal forms is Fortey's *Radiograptus rosieranus flexibilis*. However, isolated specimens from this level at Green Point indicate that there are two types of proximal ends present, differing in sicula length and width and in stipe width. The more robust proximal ends represent *Rhabdinopora praeparabola* and the less robust, *Staurograptus*. Two species are therefore recognized at this earliest level – *Rhabdinopora praeparabola* and *Staurograptus dichotomous* (which here includes *R. r. flexibilis*). At higher levels in the *R. praeparabola* Zone, at Green Point, the two species are more clearly identified. They are inferred to each give rise to a clade; (1) rhabdinoporids of the *flabelliformis* group (from *praeparabola*) and (2), *Staurograptus hyperboreus* and, possibly, *Anisograptus* and its derivatives, (from *S. dichotomous*).

(1) The first well-developed rhabdosome meshwork is seen in the following species, *Rhabdinopora flabelliformis parabola* at the base of the *parabola* Zone. Its obvious ancestor is *R. praeparabola*, from which it is readily derived by an increase in the number of proximal dichotomies and by the more regular insertion of dissepiments. However, a sequence of populations showing the transition is not yet known and it therefore remains provisional.

As discussed above, the various subspecies of *Rhabdinopora* are interpreted as comprising a diverse complex of intergrading populations that change in time (stratigraphic subspecies) and in ecological zone (ecological subspecies). The main lineage, which developed in the deep water of the continental slope, is comprised of the successive subspecies of *Rhabdinopora flabelliformis* – *parabola*, *canadensis*, *flabelliformis*, *anglica* and, probably, *bryograptoides* (Fig. 4). There is a general and progressive increase in mean stipe spacing (Fig. 5) throughout the series that appears to be useful for subspecies discrimination. There is also a general, but very variable, increase in mean spacing of dissepiments and in 'openess' of the meshwork from *parabola* to *anglica* (Fig. 6). Bulman & Rushton (1973) have suggested that bithecal morphology may be useful for subspecies discrimination in *Rhabdinopora* but we have too few specimens showing bithecae to test the idea. From this main lineage is derived the shallow-water, shelf (ecological) subspecies *socialis* – at about the level of *R. f. canadensis* – and *norvegica* – at about the same level or slightly higher. In the farthest offshore zone, the oceanic realm, only diminutive forms are present – *R. scitulum* of Australasia.

(2) In the later populations of *Staurograptus dichotomous* some specimens show delayed development of distal dichotomies, resulting in longer initial stipes. If this trend is continued, the result is the rhabdosome of *Staurograptus hyperboreus*. Suppression of one of the initial dichotomies of *Staurograptus* would result in the rhabdosome of *Anisograptus*, and this may indicate the origin of that genus. However, there appears to be a

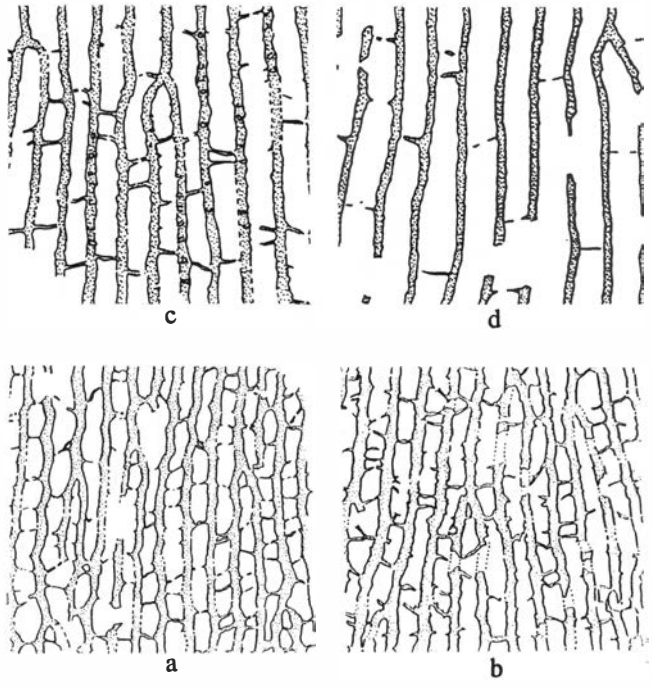


Fig. 6. Meshwork in *Rhabdinopora*. (a) *Rhabdinopora flabelliformis parabola*, NIGPAS 92680; (b) *Rhabdinopora flabelliformis canadensis*, GSC 115796; (c) *Rhabdinopora flabelliformis flabelliformis*, (d) *Rhabdinopora flabelliformis anglica* specimen figured by Bulman (1927 pl. 1, fig. 7), somewhat restored. All ×3.5.

stratigraphic gap between the youngest occurrence of *Staurograptus* (mid-*parabola* Zone) and the earliest occurrence of *Anisograptus* (*Anisograptus matanensis* Zone), at least in western Newfoundland, and an independent origin for *Anisograptus* from the *Rhabdinopora* lineage, perhaps through a 'triradiate Rhabdinopora' such as *Radiograptus*, remains a possibility. Derivation of the later anisograptids and their daughter group, the sigmagraptines, from *Anisograptus* seems more certain but needs to be documented by detailed study of the proximal morphology and careful analysis of stratigraphic collections through the late Tremadoc.

Systematic descriptions

Order Graptoloidea Lapworth (in Hopkinson & Lapworth 1875)

Family Anisograptidae Bulman 1950

The scope and relationships of the Family Anisograptidae have been discussed by Bulman (1950), Mu (1974), and its status and nature by Erdtmann (1982), and by Fortey & Cooper (1986) who regarded it as a paraphyletic stem group for the Graptoloidea.

Genus *Rhabdinopora* Eichwald 1855

1986 *Heterograptus* n. gen.; Lin (*in* Chen et al. 1986) (pars), pp. 241–242. (See Bulman 1927 and Erdtmann 1982 for full synonymy and discussion of nomenclature)

Type species. – *Gorgonia flabelliformis* Eichwald 1840, designated by Eichwald in 1855.

Diagnosis. – Pendent multiramous anisograptids with dissepiments, proximal development quadriradiate.

Discussion. – Until more details of proximal morphology and structure are available, the diagnosis must be based largely on rhabdosome characters. Except for early members of its earliest species, *R. praeparabola*, the genus is distinguished from all other genera by its quadriradiate structure combined with the presence of a well-developed meshwork that enables even distal rhabdosome fragments to be readily identified. *R. praeparabola*, in which dissepiments are either rare or lacking, is distinguished from its closest morphological match, the coeval *Staurograptus dichotomous*, by its pendent rhabdosome form and larger sicula.

The genus *Heterograptus* Lin (*in* Chen et al. 1986) was synonymized with *Staurograptus* by Erdtmann (1988, p. 339). However, material described by Lin as *Heterograptus antiquus* is here included in *R. flabelliformis parabola*.

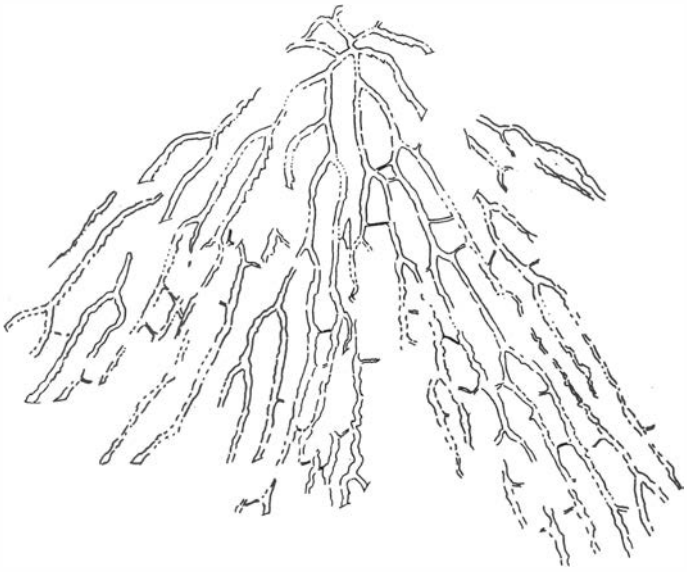


Fig. 7. Rhabdinopora flabelliformis flabelliformis. Cable Canyon, Bliss Sandstone, New Mexico, showing quadriradiate proximal structure. Specimen JER C5 15-16. ×2.7.

Heterograptus radiatus, the type species of *Heterograptus* (see Lin *in* Chen et al. 1986, p. 241) appears to be a *nomen nudum* and status of the name *Heterograptus* is uncertain. It is here regarded as a junior synonym of *Rhabdinopora*.

Proximal structure. – Proximal structure in the type species, *R. f. flabelliformis*, is known only from a single flattened specimen from the Bliss Sandstone in New Mexico, in which the proximal region is preserved discoidally to show four initial stipes (Fig. 7). However, quadriradiate, triradiate and biradiate structures have each been claimed to be represented in different subspecies of the genus (Erdtmann 1988). Quadriradiate structure has been established in several subspecies of *Rhabdinopora flabelliformis*, including *R. f. flabelliformis* (herein), *R. f. parabola* (herein), *R. f. canadensis* (herein), *R. f. anglica* (herein) and *R. f. rustica* (Bulman 1950), and in *R. praeparabola* (herein), but the presence of triradiate and biradiate structures is less certain.

Bulman (1927) described triradiate structure (= 'three primary stipes') in specimens of *R. f. anglica* from the transition beds of Shropshire and it is largely on the basis of this description that a triradiate structure has been established as present in the genus. However, several specimens of the subspecies in Green Point are preserved in dorsal (discoidal) view and clearly show quadriradiate proximal structure (Figs. 19e, f). The specimen on which Bulman primarily based his interpretation (Bulman 1927, pl. 1, fig. 7) was refigured by him and reinterpreted in 1949 (fig. 3). It is isolated from the matrix and clearly shows the origin of three of the initial stipes. One of these, however, that based on theca 1^2, is broken off at the base of theca 1^2, so that its subsequent

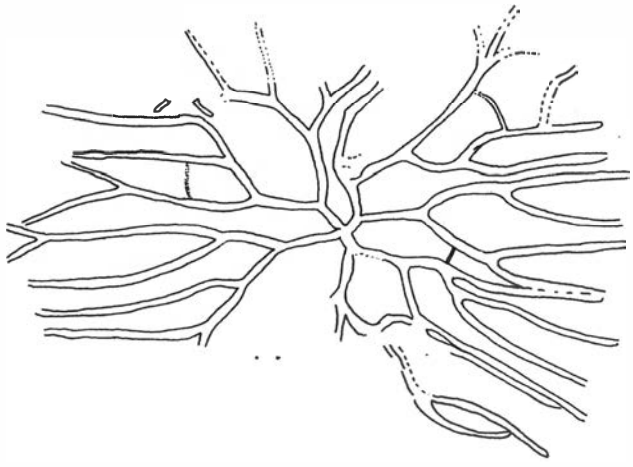


Fig. 8. Rhabdinopora praeparabola. GSC 115797, mature, discoidally preserved specimen showing quadriradiate proximal end and dissepiments. Green Point, 107.9 m. ×3.

development cannot be seen. Although Bulman's deduction that this rhabdosome could not be quadriradiate was reasonable in terms of his model of quadriradiate proximal structure (Bulman 1950, fig. 2h), the new interpretation of quadriradiate structure (discussed above) leaves open the possibility that the broken stipe is actually stipe 3 (based on theca 1^3 rather than 1^2) which might have branched again, immediately after its point of fracture. This, of course, would imply that the specimen represented a quadriradiate type.

The presence of a biradiate structure (Erdtmann 1988) was based on the specimen from Green Point featured in Fig. 17b. Other *Rhabdinopora* specimens in the same bed have quadriradiate structure and the specimen, if indeed it is biradiate, is likely to represent a structural variant rather than characterize a particular subspecies.

The conclusion therefore must be that neither a triradiate nor a biradiate structure has yet been conclusively demonstrated as characteristic of any species of *Rhabdinopora*. Quadriradiate structure, on the other hand, has been shown to be present in *R. praeparabola*, *R. f. flabelliformis*, *R. f. parabola*, *R. f. canadensis*, and *R. f. anglica* and can be taken as the primitive state, and most commonly occurring condition, in the genus.

Rhabdinopora praeparabola (Bruton, Erdtmann & Koch 1982) Figs. 8, 9a–f, 10b, c, e, f, 16a

1982 *?Dictyonema* n. sp. Bruton et al., pl. 2, figs. 6, 9, text-fig. 3.
1982 *Rhabdinopora? praeparabola* n. sp. Erdtmann, pl. 1, figs. 6, 8–10, pl. 2, fig. 2?
1982 *Dictyonema flabelliforme* subsp. A, Fortey et al., pl. 1, fig. 4.
?1986 *Dictyonema proparabola* sp. nov. Lin (*in* Chen et al.), pp. 238–240, pl. 62, figs. 1–8, ?pl. 65, fig. 11, text-fig. 95.
1986 *?Rhabdinopora praeparabola*, Erdtmann, p. 78, pl. 1, fig. 1, text-fig. 1.
1988 *?Rhabdinopora praeparabola*, Erdtmann, 1988, figs. 6A–D, 7A–D.
1993 *Rhabdinopora flabelliformis praeparabola*, Landing, figs. 3.1–3.8.

Material. – Small collections of 7–10 specimens from the type locality, Naersnes, Norway, and from Dayangcha (Bed 13P), and larger collections from several horizons at

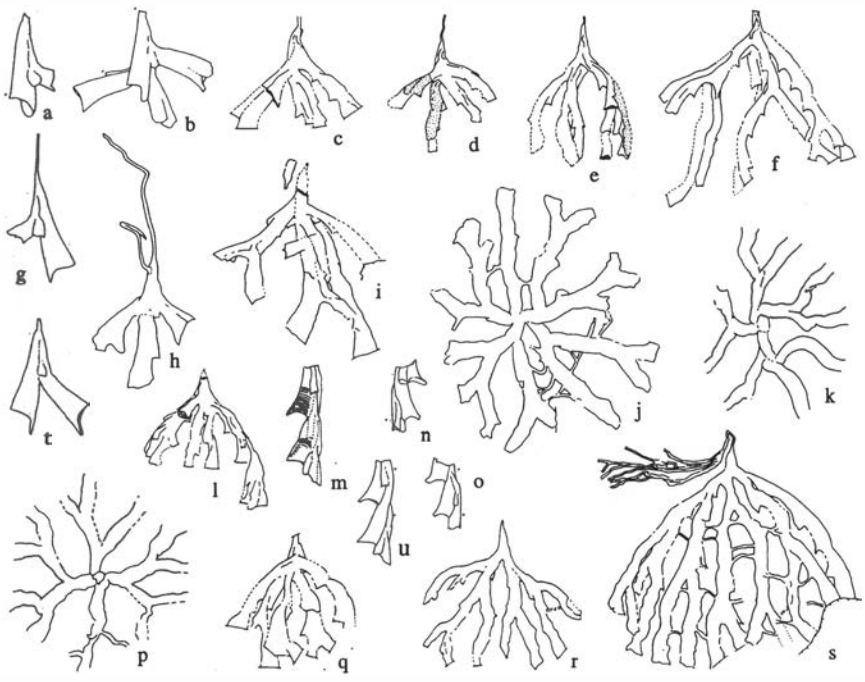


Fig. 9. Rhabdinopora praeparabola. (a) Isolated growth stage, GSC 115798, Green Point, 106.4 m. ×14; (b) Isolated growth stage, showing at least three first-order stipes, GSC 115799, Green Point, 106.4 m. ×14; (c) PMO 155.447, N/52 cm/005. Naersnes section, Norway. ×7; (d) GSC 115800, Green Point, 106.6 m. ×7; (e) GSC 115801, 107.5 m. ×7; (f) GSC 115802, partly exfoliated specimen, Green Point, 106.4 m. ×7; *Rhabdinopora flabelliformis parabola.* (g) Isolated growth stage, GSC 115803, Green Point, 108–108.2 m. ×14; (h) PMO 155.448, juvenile, Digermul, north Norway. ×8; (i) GSC 115804, Green Point B, 2.33–2.39 m. ×8; (j) PMO 155.449, Digermul, north Norway. ×9; (k) Specimen of Fig. 10d, showing quadriradiate structure. NIGPAS 92689, Dayangcha, ×9; (l) GSC 115805, Green Point B, 2.53 m, ×7; (m, u) Cleared and uncleared views of stipe fragment showing bithecae and dendroid stipe structure, GSC 115806, Green Point, 108–108.2 m, ×11; (n, o) GSC 115807, stipe fragment shown from both sides, Green Point, 108–108.2 m, ×11; (p) NIGPAS 92659, Dayangcha, ×9; (q) GSC 115808, Green Point B, 2.33–2.39m, ×7; (r) NIGPAS 98619, Dayangcha, ×7; (s) PMO 155.450, Digermul, ×7; (t) GSC 115809, isolated sicula and first theca showing strongly developed rutelli, Green Point, 108–108.2 m. ×14.

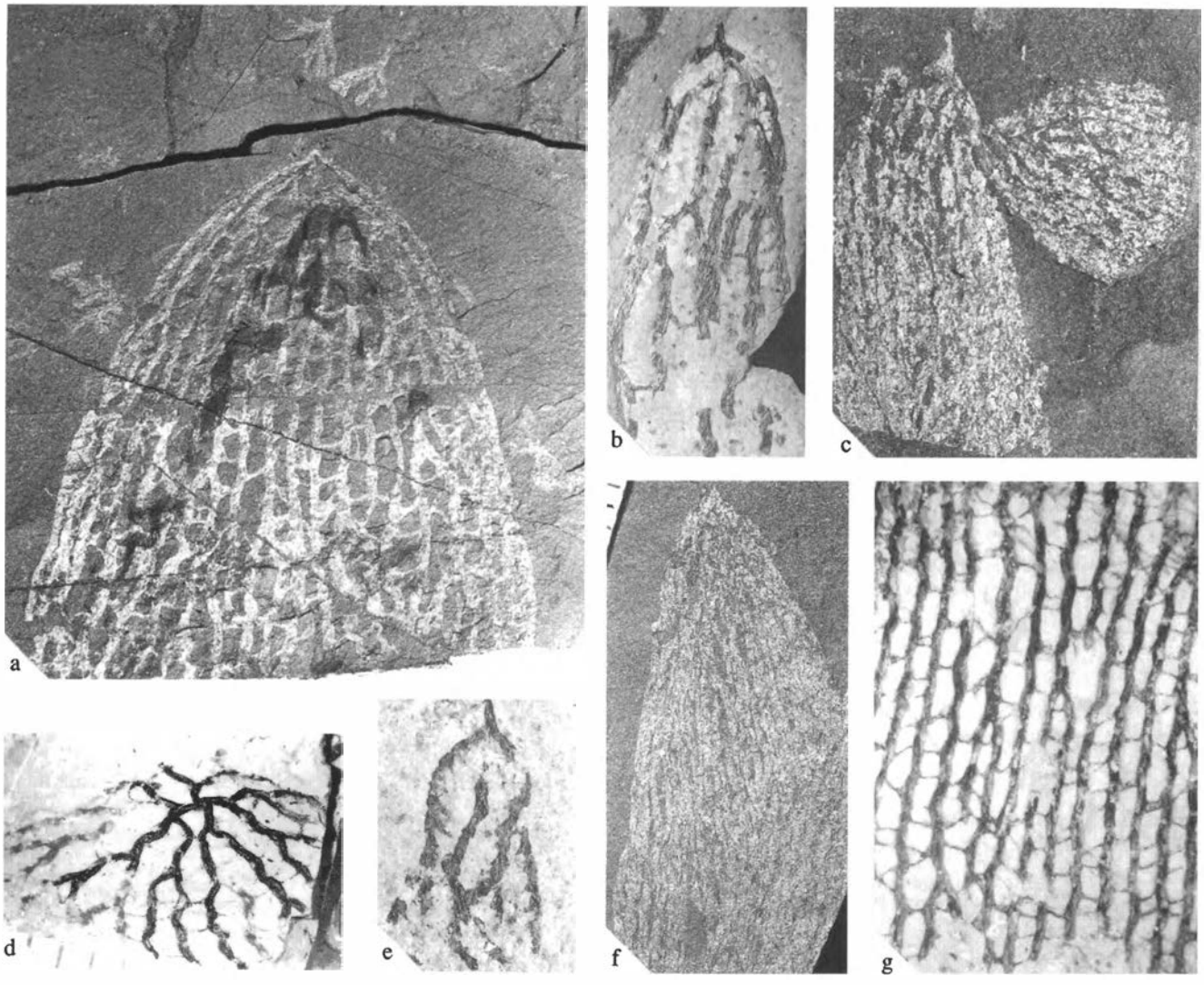


Fig. 10. (a) *Rhabdinopora flabelliformis parabola*, holotype, PMO 61.772, two juveniles are seen on the slab, ×3. (Bulman 1954, pl. 1, fig. 3); (b) *Rhabdinopora praeparabola*, GSC 115810, Green Point, 106.4 m, ×5. (Erdtmann 1986, fig. 137b); (c) *Rhabdinopora praeparabola*, PMO 107.888, ×5; (d) *Rhabdinopora flabelliformis parabola*, NIGPAS 92689, proximal end in partial relief, showing quadriradiate structure, Dayangcha, ×5; (e) *Rhabdinopora praeparabola*, GSC 115811, Green Point, 106.4m, ×5. (fig. Erdtmann 1986, fig. 137c); (f) *Rhabdinopora praeparabola*, holotype, PMO 107.882, ×3. (Erdtmann 1982, pl. 1, fig. 8); (g) *Rhabdinopora flabelliformis parabola*, NIGPAS 92680, showing mesh character, ×4.6.

Green Point between the 106.20 m and 108.40 m levels, and at Broom Point South. All of the material is flattened and preserved in shale. However, several specimens and growth stages from Green Point show proximal rhabdosome structure and general morphology.

Diagnosis. – *Rhabdinopora* with loose flexuous stipes, rare distal dissepiments and pendent to declined rhabdosomes.

Description. – Isolated flattened growth stages (Figs. 9a–b) show that the sicula is about 1.6 mm long, 0.36 mm wide at the aperture, and bears a prominent rutellum. The first theca arises low on the prosicula and bends sharply outwards at sicula mid-length; a small sicula bitheca terminates at the point of separation. The second and third thecae diverge from near the sicula aperture and the proximal region is strongly asymmetrical. Later growth stages are represented in the *in situ* material (Figs. 9c–f) and show the origin of the four initial stipes from the region of the sicula. The proximal region appears either symmetrical or asymmetrical depending on the orientation of the rhabdosome before burial. The initial stipes diverge at angles varying from low, in the Naersnes forms, which have strongly pendent rhabdosomes, to high in most of the Green Point specimens, which have a more parabolic or open cone shape. Details of the initial thecal budding pattern cannot be determined, but several specimens are preserved to show a quadriradiate proximal structure (Figs. 8, 9d, f). A nema is commonly present and is always undivided.

The rhabdosome is pendent to declined and usually preserved in lateral view, but discoidal (dorsal view) preservation is common in growth stages and occasionally found in mature specimens (Fig. 8). Rhabdosomes are generally small, rarely exceeding 20 mm in length. Stipes are flexuous, 0.3 mm in lateral width in specimens from the lower part of its stratigraphic range at Green Point and 0.4 mm wide at higher levels, also in

topotypes from Naersnes and specimens from Dayangcha. The number of terminal stipes varies greatly from 7 or 8 in the strongly pendent forms to 15–30 in the more conical forms. Scattered distal dissepiments are generally present in the larger specimens.

Thecae have concave ventral margins and denticulate apertural margins. Thecal spacing is unknown.

Discussion. – This species which, together with *Staurograptus dichotomous*, comprises the earliest known graptoloid is represented in Norway (Erdtmann 1982), western Newfoundland (Erdtmann 1988), eastern New York (Landing 1993), Belgium (Erdtmann 1986b) and, possibly, China. Several of the specimens from the early (20.85 m) level in the Dayangcha section, including those assigned to *Dictyonema* proparabola sp. nov. by Lin (*in* Chen et al. 1986) match the species but the preservation is too poor, and their numbers too few, to be certain that they are not end members of a variable population of *parabola*.

With few, or no, dissepiments to hold the stipes together in a regular pattern, stipes are flexuous and loose and the rhabdosome is consequently very variable in form. Populations from Green Point and Dayangcha differ from the Naersnes topotypes only in having slightly less prominent siculae, and less consistently pendent rhabdosomes. In general, they share the key characteristics of relatively small rhabdosomes with few dissepiments or none at all, and loose flexuous stipes and all forms are here regarded as belonging to the one, variable species.

Rhabdosomes from the earliest horizon (106.4 m) at Green Point have slender stipes (0.3 mm in lateral width), openly conical proximal ends, and more distantly spaced dichotomies and are transitional in morphology towards *S. dichotomous*, present in the same bedding planes. The sicula, however, is longer and broader than in *S. dichotomous*, and growth stages of the two species are readily distinguished (Figs 9a, b, 22a–d). In higher horizons at Green Point the rhabdosomes become more robust and resemble the Naersnes specimens.

Rhabdinopora flabelliformis flabelliformis (Eichwald 1840) Figs. 6c, 7

1840 *Gorgonia flabelliformis* Eichwald, p. 207, not illustrated.
?1842 *Gorgonia flabelliformis*, Eichwald, pp. 45–47, pl. 1, fig. 6.
1865 *Dictyonema graptolithinum* Kjerulf, p. 1, figs 4, 5.
1882 *Dictyonema flabelliformis*, forma *typica*, Brögger, pp. 31–36, pl. 12, figs. 17–19.
1909 *Dictyonema flabelliformis*, Westergård, pp. 57–59, pl. 3, figs. 1–6.
1927 *Dictyonema flabelliforme*, Bulman, pp. 12–26, pl. 2, figs. 3, 4, text-figs. 13, 14.
1949 *Dictyonema flabelliforme*, Bulman, pp. 33–40, text-figs. 1–4.
?1950 *Dictyonema rustica* Bulman, pp. 77–79, pl. 5, figs. 1–5, pl. 8, figs. 1, 12, 13; text-fig. 2.
1954 *Dictyonema flabelliforme*, Bulman, pp. 14–17, pl. 2, figs. 1–5, text-figs. 4a–d.
1966b *Dictyonema flabelliforme*, Bulman, pp. 417–413, text-figs. 1–3.
1973 *Dictyonema flabelliforme patulum* Bulman & Rushton, pp. 18–20, textfig. 4a, b, ?c, pl. 2, figs. 1, 5, 6, pl. 3, figs. 1, 2.
1982 *Rhabdinopora flabelliformis*, Erdtmann, pp. 129–136, pl. 2, figs 4–6, 9 (with full synonymy, excluding references to *R. f. socialis* and *R. f. norvegica*)

Type specimen. – Status of the type specimen is uncertain. Eichwald's original description of *Gorgonia flabelliformis* is brief and not diagnostic; no particular specimen was identified and no illustration was given. The locality mentioned for the new species was the Thonschiefer of Baltischport (the *Dictyonema* Shale of Paldiski) in Estonia (Eichwald 1840, p. 22), but the species was also (p. 207) said to occur at Odinsholm (=Osmussar, Estonia) and Pulkowka near Zarskoje (about 25 km south of Leningrad). In 1842 Eichwald presented his first and only figure of the species but said only that it was from the 'Thonschiefer, wie Estland'. In later papers (Eichwald 1854, 1855, and 1860) several further localities in the Baltic area were mentioned, including Reval (=Tallinn), as further collections of the species came into his possession. Because of the vagueness of the original description and the diagrammatic nature of the 1842 illustration there was considerable confusion about the identity of the species (Salter 1858; Brögger 1882). In 1882 Brögger figured (from Norway) a specimen that he regarded as the *forma typica* of the species and, for the next 70 years, this was the most widely accepted and used concept for the species (Bulman 1927, 1954).

In 1953 Obut announced that he had refound the type specimens in the Eichwald collection in the Museum of St. Petersburg University. He selected the specimen labelled 1/28a2 as the best match with Eichwald's 1842 figure and designated it as a lectotype. He claimed that the specimen represents *Dictyonema norvegicum* Kjerulf 1865 and that the name *D. graptolithinum* Kjerulf 1865 should in future be used for the *forma typica* of Brögger. The label (apparently in Eichwald's handwriting) that accompanied the specimen indicates (in German) that it came from the *Obolus* Sandstone at Reval (Tallinn), which therefore became the type locality. Obut did not discuss the fact that this locality was not among those listed by Eichwald in the original description of *Gorgonia flabelliformis*.

Bulman (1966b) agreed with Obut that Kjerulf's *Dictyonema norvegicum* and Eichwald's *Gorgonia flabelli formis* are synonyms but, on grounds of stability of nomenclature, Bulman (1966a, b, 1967) appealed to the International Commission on Zoological Nomenclature

to overrule the Rule of Priority and retain the name *flabelliforme* for the *forma typica* and thus in effect to nullify Obut's (1953) nomination of lectotype. This would have the effect also of maintaining the traditional usage of both *flabelliforme* and *norvegica*. Bulman regarded Paldiski as the type locality and illustrated (1966a, text-fig. 1) a specimen from that locality held by the British Museum, which he nominated as a neotype. Apart from a comment by Obut (1974) objecting to Bulman's submission, and comments by Skevington (1973) and Legrand (1983) in support, there has been no further discussion in the Bulletin of Zoological Nomenclature and a ruling on the topic has yet to be made. Almost all subsequent workers have followed Bulman and retained the traditional usage (references cited in Erdtmann 1982). Thus for over 100 years, the name *flabelliforme* has been mainly used for the form identified by Brögger as the forma typica of the species.

Eichwald's original collection was re-examined in October 1995 (by RAC) in an effort to find a more suitable specimen for neotype – in particular, a specimen from one of the three original localities mentioned by Eichwald, in which the proximal portion of the rhabdosome is preserved. Unfortunately, no specimen could be found in which this part of the rhabdosome was preserved and those fragments referrable to *flabelliformis, forma typica*, listed as *Dictyonema graptolithinum* by Obut (1953), are considerably inferior to the specimen chosen by Bulman.

For the following reasons we advocate (and adopt here) acceptance of Bulman's recommendations, of his nomination of neotype, and of adopting the Pakri Peninsula (Pakerort) near Paldiski as type locality: (1) Paldiski is specifically mentioned with the first mention and description of the species by Eichwald and Reval is not. (2) The doubt about the validity of Obut's lectotype, arising from the uncertainty that the nominated specimen was from Eichwald's (1840) type series (*sensu* International Code of Stratigraphic Nomenclature). (3) A consistent usage of the names *flabelliforme* and *norvegica* for over 100 years is maintained.

Material. – Over 50 rhabdosomes, all fragmentary, from the lower 1.6 m of the *Dictyonema* Shale at Pakerort, Paldiski, Estonia (the type locality); several hundred fragmentary specimens from drill cores through the *Dictyonema* Shale of Estonia; over 30 mostly fragmentary specimens from the Tøyen and Hammersborg sections of Oslo; over 60 specimens from the Alum Shale, Skarahagen near Vestfossen, Oslo region; 10 incomplete specimens from the Bliss Sandstone of New Mexico.

Description and Discussion. – A full description of the subspecies has been given by Bulman (1954), and also by Erdtmann (1982) who, however, included the form here listed as the subspecies, *R. f. norvegica*. As envisaged here, the subspecies accords well with Bulman's description which follows Brögger's concept of the *forma typica*, except that rhabdosome shape and dissepiment spacing are both thought to be variable characters and should be interpreted broadly in diagnosis. Specimens from the lower 1.6 m of the *Dictyonema* Shale at Pakerort, Estonia, show a wide range in mesh character, but stipe spacing ranges from 7 to 9, averaging 8, in 10 mm (Fig. 5) as in the Norwegian material. Dissepiments are generally widely spaced throughout most parts of the rhabdosome but locally become crowded or duplicated. Stipes are generally 0.3–0.4 mm in lateral width, and thecae are spaced 14–16 in 10 mm. Specimens from Estonian drill cores match those from Paldiski but those from higher levels in the drill cores grade into *R. f. anglica* (Fig. 20; Kaljo et al. 1986), with wider stipe spacing.

A large population from the Alum Shale at Skarahangen near Vestfossen in the Oslo district has stipes spaced at from 6.8 to 10.5, averaging 8.2, in 10 mm (Fig. 4). Most specimens have thickened stipes and dissepiments and a few specimens approach *R. f. norvegica* in this feature. They may represent a population transitional towards *R. f. norvegica*.

Specimens from the Deanshanger and Tattenhoe borecores in central England, on which Bulman & Ruston (1973) based the subspecies, *Dictyonema flabelliforme patulum*, are said to differ from the *forma typica* in having broader rhabdosomes, broader and more closely set dissepiments, and four, rather than three, initial stipes. However, rhabdosome shape and dissepiment spacing are here regarded as variable characters, of limited diagnostic value, and quadriradiate structure is now known to be present in all subspecies of *R. flabelliformis* in which proximal structure is known. The British specimens have 8–8.5 stipes in 10 mm, most closely matching *R. f. flabelliformis* as envisaged here, and are synonymized accordingly.

Dictyonema rusticum Bulman (1950) apparently was based on a small number of specimens from the Matane region of Quebec. Only two relatively complete specimens and two fragmentary or distorted specimens were illustrated. The specimens resemble most the immature growth stages of *R. f. flabelliformis* but because no population characteristics are known, they are only provisionally included here. Kjerulf's (1865) variety *graptolithinum*, was synonymized with *R. f. flabelliformis* by Bulman (1954) and is included here.

Of particular interest are the two small collections (10 specimens) from a thin shale band in Bliss Sandstone of New Mexico (Taylor & Repetski 1995). Although most are incomplete, they have the characteristic *flabelliformis* meshwork with average stipe spacing of 7.8 and 8.5 in 10 mm respectively. One specimen (Fig. 7) shows the proximal region in discoidal view and clearly reveals a quadriradiate proximal structure. The occurrence is also of interest as the only record of any member of the *R. flabelliformis* group in the Ordovician equatorial shelf region.

The subspecies has a global distribution; it is found in continental shelf and slope environments and in high to low palaeolatitude regions (Cooper, in prep.).

Rhabdinopora flabelliformis parabola (Bulman 1954) Figs. 6a, 9g–p, 10a, d, g, 11–15, 16b–o, 25g, h, j

1954 *Dictyonema flabelliforme parabola* sp. nov. Bulman, pp. 25–27, pl. 1, figs. 1–5, text-fig. 9.
1962 *Dictyonema parabola*, Obut & Sobolevskaya, p. 72, pl. 1, fig. 1.
1970 *Dictyonema flabelliforme belgica*, Bulman, pp. 215–8, figs. 1–4.
1982 *Dictyonema flabelliforme parabola*, Bruton et al., pl. 2, figs. 1, 5.
1982 *Rhabdinopora parabola*, Erdtmann, pl. 2, figs. 1–2.
1982 *Dictyonema flabelliforme parabola*, Fortey et al., p. 105, pl. 1, figs. 5–6.
?1982 *Dictyonema flabelliforme flabelliforme*, Fortey et al., p. 104, pl. 1, figs. 7, 10.
?1982 *Dictyonema flabelliforme rusticum*, Fortey et al., p. 105, pl. 1, fig. 8.
1985 *Dictyograptus parabolus*, Yu et al., pp. 21–2, pl. 3, figs. 10–11.
1985 *Dictyograptus flabelliformis belgicus*, Yu et al., pl. 3, figs. 1–2.
1985 *Dictyonema flabelliforme parabola*, Lin (*in* Chen et al.), pp. 58–59, pl. 1, figs. 1, 4, 5, pl. 3, figs. 1, 6, 7, pl. 4, figs. 1, 2, 4, pl. 7, figs. 1, 2.
1985 *Dictyonema flabelliforme*, Lin (*in* Chen et al.), p. 57, pl. 3, fig. 8, pl. 4, fig. 3.
1985 *Dictyonema flabelliforme sociale*, Lin (*in* Chen et al.), pp. 59–60, pl. 3, figs. 2, 3, pl. 5, figs. 1–3, pl. 8, fig. 2.
1985 *Dictyonema praeparabola*, Lin (*in* Chen et al.), p. 60, pl. 1, figs. 2, 6, 8.
1985 *Radiograptus* sp., Lin (*in* Chen et al.), pp. 61–62, pl. 1, fig. 9, pl. 2, figs. 1–4.
1985 *Staurograptus dichotomous* Lin (*in* Chen et al.), pp. 62–63, pl. 1, figs. ?3, 7, pl. 2, figs. ?6, ?7, pl. 3, fig. 5.
1986 *Dictyonema flabelliforme*, Lin (*in* Chen et al.), pp. 232–235, pl. 57, figs. 1–4, 7, pl. 58, figs. 1–5.
1986 *Dictyonema flabelliforme eosociale* ssp. nov. Lin (*in* Chen et al.), pp. 236–238, pl. 59, figs. 3–5, pl. 60, figs. 1–4, pl. 61, figs. 1–5, 7, 8, text-fig. 94.
1986 *Dictyonema proparabola* sp nov. Lin (*pars*) (*in* Chen et al.), pp. 238–240, pl. 62, figs. 7, 8.
?1986 *Heterograptus antiquus* gen. et. sp. nov. Lin (*in* Chen et al.), pl. 64, figs. 1–4, text-fig. 97.
?1986 *Staurograptus dichotomous priscus* ssp. nov. Lin (*in* Chen et al.), pl. 66, figs. 1–5, text-fig. 100.
1986 *Heterograptus antiquus* Lin (*in* Chen et al.), pp. 242–245, pl. 64, figs. 1–4, text-fig. 97.
1986b *Rhabdinopora parabola*, Erdtmann, pp. 80–82, pl. 1, figs. 2–5, text-fig. 2.
1988 *Rhabdinopora parabola*, Erdtmann, pp. 338–339, figs. 7E–F.

Material. – Small to moderate-sized populations (10–30 specimens) from Naersnes (82 cm and 110 cm), Green Point (several horizons between the108 and 110.3 m levels), and Dayangcha (20.85, 26.85 and 27 m levels), and an exceptionally large and well-preserved population, comprising several hundred complete specimens, from the Digermul Peninsula, northern Finmark. All material is partially to completely flattened, but details of morphology can be seen in several of the specimens from Green Point and from Dayangcha.

Description – proximal and thecal characters. – The sicula is 1.3 mm long and bears a strongly projecting rutellum. Theca 1^1 originates high on the sicula and diverges sharply from it at mid length. A small sicular bitheca terminates at this point of divergence (Figs. 9g, t). From growth stages, the structure of the proximal region is consistent with the quadriradiate pattern described by Legrand (1974) and Maletz (1992), although preservation is insufficiently good for it to be certain. Stipes have a typical dendroid structure with autothecae originating laterally, and alternately, along the stipe. Autothecae have prominent rutelli. Bithecae alternate on either side of the rhabdosome, are short fine tubes, and terminate 0.4–0.6 mm from the autothecal apertures (Figs. 9m–o, u).

Rhabdosome characters – Digermul population. – Rhabdosome outline form ranges widely, from broadly parabolic to narrow cone shape with 66% ($\pm$ one SD from the mean) of specimens occupying a reasonably narrow band (Fig. 12). The most common shape conforms with shape template patterns 2A and 3A (Fig. 11).

The broader forms have a greater number of stipes at any given level (Fig. 13) and there is no correlation between rhabdosome width and interstipe distance so stipe density is not related to the expansion rate of the rhabdosome. The range in interstipe distance through the population, however, is considerable – 0.35–0.8 mm in the mature part of the rhabdosome. Mean stipe spacing ranges from 8 to 11 in 10 mm and averages 9.92 (Fig. 5). The numbers of stipes counted at various distances from the apex give a measure of the frequency of dichotomy throughout the rhabdosome (Fig. 13). In the distal parts of rhabdosomes there is a suggestion of bimodality in stipe number (Fig. 13c). This is not reflected in rhabdosome width and further investigation is needed to determine the significance, if any, of this feature.

Rhabdosome length generally does not exceed 40 mm but in rare specimens reaches 70 m. Stipe lateral width ranges from 0.35 to 0.5 mm and stipes are generally straight to moderate in sinuosity. There is no correlation between rhabdosome length and stipe width or dissepiment width, suggesting that in this population at least, secondary cortical overgrowth does not significantly contribute to the last two characters.

Dissepiments in most specimens are moderately inclined and widely spaced to moderately spaced in the submature part of the rhabdosome, and moderately inclined, close to very closely spaced in the mature part of the rhabdosome (Fig. 14). Dissepiments are present within 1–2 mm of the distal tips of growing stipes in

mature rhabdosomes, suggesting that they form soon after thecal maturity. There is no evidence of later dissepiment insertion.

Other populations. – Specimens from the 108–110.3 m interval in the Green Point section are broadly parabolic (shape template 4A). In stipe width, mesh character, stipe sinuosity, dissepiment width, and rate of branching they lie close to the Digermul modes.

At 0.82 m in the Naersnes section, a single exceptionally broad rhabdosome is found that lies well within the range of the Digermul population in most characters, but which plots at the extreme (wide) end of the range for rhabdosome width. It is here included in the species (as the earliest known specimen of *parabola* at Naersnes), although it is broader than any other of the (later) Norwegian specimens. Eight measured specimens from the 1.10 m level in the Naersnes section plot well within the range of the Digermul population for rhabdosome width and shape, mesh character, diseppiment width, and stipe sinuosity. Stipe width ranges from 0.4 to 0.6 mm, extending slightly beyond the Digermul range. Stipe spacing is closely similar, averaging 9.9 and 9.6 in 10 mm in the lower and upper horizons respectively.

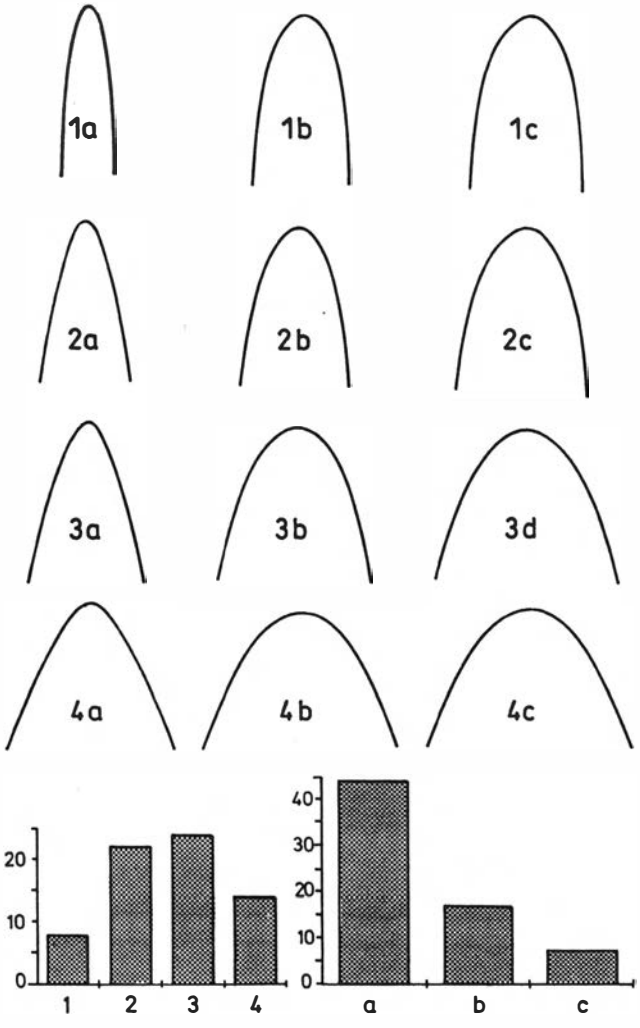


Fig. 11. Templates for rhabdosome shape (×0.5), and distribution of 68 Digermul specimens of *Rhabdinopora flabelliformis parabola* among the templates; 1–4, angle of stipe divergence; a–c, sharpness of stipe divergence.

At Dayangcha, eight measured specimens from the earliest, 20.85 m (HDA 13O) level, plot well within the range of the Digermul population, ranging in shape template pattern from 1A to 4A. At the 26.85 and 27.1 m levels (HDA 19), rhabdosomes match the more parabolic Digermul specimens. Modal stipe width in the Chinese specimens is 0.3 mm rather than 0.4 mm, but otherwise they match well with the modal Digermul forms. Average stipe spacing is 11.2 in 10 mm.

Other features. – Nematic structures are present in several of the populations of *R. f. parabola*. In specimens from Naersnes, Digermul and the upper (26.85–27.1 m) level at Dayangcha, the nema apparently divides, producing two or more threads (Figs 9s, 15d, 16h). In extreme examples there may be 10 or more threads developed. In the lower (20.85 m) level at Dayangcha, a three-vaned structure is present in several specimens (Figs. 16d, e; Lin *in* Chen et al. 1986) and Erdtmann (1988, fig. 6D) has described a similar vaned appendage in a specimen from Green Point. Erdtmann (1986b) and Bulman (1970) have described nematic threads in specimens from the Stavelot Massif in Belgium. Vaned, threaded or float structures have been widely reported as proximal appendages in *Rhabdinopora* (Størmer 1933, 1935; Hahn 1912, Bulman 1929; Bulman & Størmer 1971). They generally are present in some, but never in all, specimens of any population and are not generally regarded as of taxonomic significance by most workers.

Discussion. – Although it is widely variable in most characters the species, as envisaged here, is distinguished by its small size, the irregularity of its meshwork, its commonly parabolic rhabdosome outline, the closeness of spacing of stipes, its generally sinuous stipes, and the common development of nematic threads or vanes. In terms of rhabdosome shape, spacing of dichotomies, stipe width, interstipe distance, and mesh character, the holotype (Fig. 10a) and topotypes of *parabola* lie well within the range of the Digermul population, although towards the larger, more robust, more parabolic end of that range.

Apart from those specimens tentatively referred to here as *R. praeparabola*, all graptolites from the early, HDA 13O (20.85 m) level at Dayangcha most probably belong to the subspecies, as do all specimens from the HDA 19 (26.85–27.1 m) level in the same section. This includes forms listed by Lin (*in* Chen et al. 1985, 1986) under 14 species and subspecies names assigned to the genera *Dictyonema*, *Radiograptus*, *Heterograptus*, *Staurograptus*, and *Anisograptus*. *Heterograptus antiquus* Lin and *Staurograptus dichotomous priscus* Lin are probably conspecific with *parabola* but their holotypes are too poorly preserved to be certain. *D. flabelliforme eosociale* Lin is here synonymized with *R. f. parabola*.

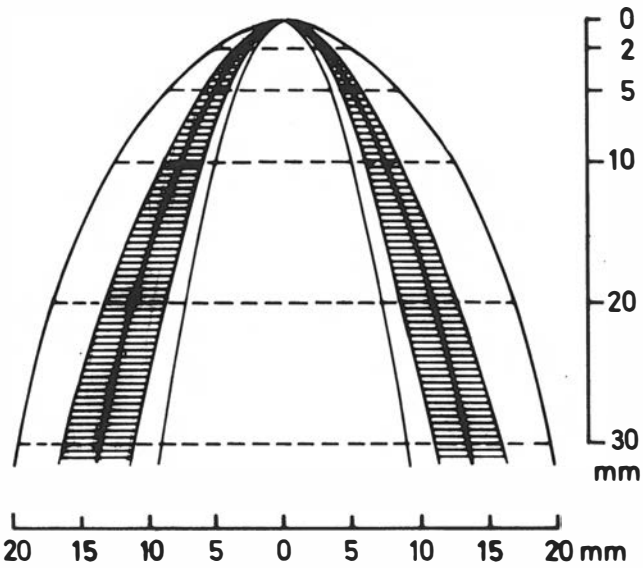


Fig. 12. Variability in the rate of expansion of the rhabdosome in the Digermul population, *Rhabdinopora flabelliformis parabola*. Heavy line shows the mean rhabdosome shape, shaded area gives one standard deviation from the mean, and the thin lines give the range.

Rhabdinopora flabelliformis canadensis (Lapworth 1898) Figs. 5, 6b, 17a, c, 18, 21f, h, ?25c, i

1898 *Dictyonema canadense* Lapworth, p. 194, fig. 67.
1927 *Dictyonema canadense*, Bulman, text-fig. 4a.
1950 *Dictyonema canadense*, Bulman, pp. 72–73, pl. 4, figs. 1–11, 12?, pl. 7, fig. 24?, pl. 8, figs. 3, 14–16.
1982 *Dictyonema flabelliforme rusticum*, Fortey et al., pl. 1, fig. 8, ?7.
1982 *Dictyonema flabelliforme sociale*, Bruton et al. (pars), pl. 2, figs. 2, 8, 10.
1982 *Dictyonema flabelliforme sociale*, Bruton et al. (pars), pl. 2. fig. 5
1988 *Rhabdinopora flabelliformis rustica*, Erdtmann, p. 339, figs. 8A–D.

Material. – Twenty-one specimens from the 2.45–2.5 m level in the Naersnes section, and 21 specimens from the 118–121.2 m level in the Green Point section. Isolated specimens are available from the Green Point B section at 9.25–10.00 m (comparable to the 115.5–116.5 m level in Green Point A).

Description. – Rhabdosome shape is variable, commonly parabolic, as in *parabola* (most specimens conforming with shape template 4a), but ranging from widely conical (Fig. 18f) to forms which become parallel sided distally (Fig. 18h). Rhabdosome length is usually 50–60 mm, but can reach over 150 mm in the largest specimens. Stipes are spaced from 7.5 to 10.2 in 10 mm, averaging 8.82 in the Naersnes population and 9.04 in the Green Point population (Fig. 5). Stipe width is 0.4–0.5 mm in dorsal view. Stipes are straight to moderately sinuous. Dissepiments are thin, commonly paired, and perpendicular to slightly inclined; their spacing varies widely both within a single rhabdosome and from specimen to specimen, but commonly averages at 1 to 2 per millimetre. There is no evidence of secondary dissepiment insertion, or of secondary cortical overgrowth of stipes. The overall pattern of rhabdosome meshwork is similar to that of *R. f. parabola*. Neither stipe spacing nor mesh character shows any consistent variation with rhabdosome shape.

From a few well-preserved flattened growth stages and proximal fragments, sicula length is 1.6 mm. The rhabdosome is clearly quadriradiate (seen in several specimens) and expands rapidly by rapid dichotomy. Proximal morphology is similar to that of *R. f. parabola*. Thecal spacing, given by Bulman, is 11–12 in 10 mm.

Discussion. – The lectotype, designated by Bulman (1950), is from the Matane region, Quebec and his description is based on specimens from this region. Apart from rhabdosome shape, which is known to be variable, the description matches well with the material described here, particularly in mesh character and stipe spacing. Stipe spacing in the Matane material ranges from 8 to 10 in 10 mm and averages 9.1, very close to the average spacing of 8.8 and 9 in the Naersnes and Green Point populations respectively. Thecal apertures were not clearly seen in the present material and the peculiar apertural spines described by Bulman could not be determined. However, this feature should be confirmed in well-preserved isolated material before it can be regarded as diagnostic for the subspecies. Bulman states that rhabdosome length can reach over 60 mm.

In specimens from Green Point, dissepiments form within 1 mm of the rhabdosome periphery and are not more closely spaced proximally than distally. Stipes show no evidence of secondary cortical thickening. The subspecies most closely resembles its immediate predecessor, *R. f. parabola*, and differs in reaching a much greater rhabdosome length and in having slightly wider average stipe spacing, as well as occupying a higher stratigraphic interval. A few specimens from high in the *A. matanensis* Zone at Green Point have widely spaced stipes and approach the succeeding subspecies, *R. f. flabelliformis*. They are listed here as transients between *canadensis* and *flabelliformis*. One specimen (Fig. 17b) appears to have biradiate symmetry, but because it has been distorted during preservation its *rhabdosome* characters cannot be compared with other forms and is listed simply as *Rhabdinopora* sp. However, the specimen is of interest in possibly indicating, in these early *Rhabdinopora* populations, occasional variants with few initial stipes (Erdtmann 1988).

Specimens from 2.45 to 2.5 m above the base of concretion 2N in the Naersnes section, listed as *R. f. parabola* and *R. f. sociale* by Bruton et al. (1982) more closely match *canadensis* as defined here. The form described from the Hatch Hill Formation of eastern New York (Landing 1993) as *R. f. rustica* probably also belongs to the present subspecies.

Rhabdinopora flabelliformis anglica (Bulman 1927) Figs. 5, 6d, 19, 20, 21e

1927 *Dictyonema flabelliforme* var. *anglica* Bulman, text-figs. 16, pl. 1, figs. 1, 3, 5–8, pl. 2, figs. 5–8.
1949 *Dictyonema flabelliforme* var. anglica, Bulman, fig. 3.
1954 *Dictyonema flabelliforme anglicum*, Bulman, pp. 17–18, pl. 4, figs. 3, 5, text-fig. 5a.

Material. – More than 36 specimens from the 129.4–30.9 m and 135.8–145.2 m intervals at Green Point, and about 15 specimens from various drill cores through the *Dictyonema* Shale of Estonia.

Description. – Isolated flattened growth stages from Green Point show the sicula to be a gradually expanding cone, 1.3 mm long and 0.35 mm wide at the aperture. There is no pronounced rutellum. Theca 1^1 originates high on the sicula (Figs. 19a, b) and diverges sharply from it, leaving 0.4 mm of the ventral wall free. Theca 1^2 grows down and across the sicula, diverging from near the sicula aperture, thus producing a markedly asymmetrical proximal end (Fig. 19c), as in *R. praeparabola* and *R. f. parabola*. A sicula bitheca is present (Fig. 19a) Development is quadriradiate (Figs. 19e, f).

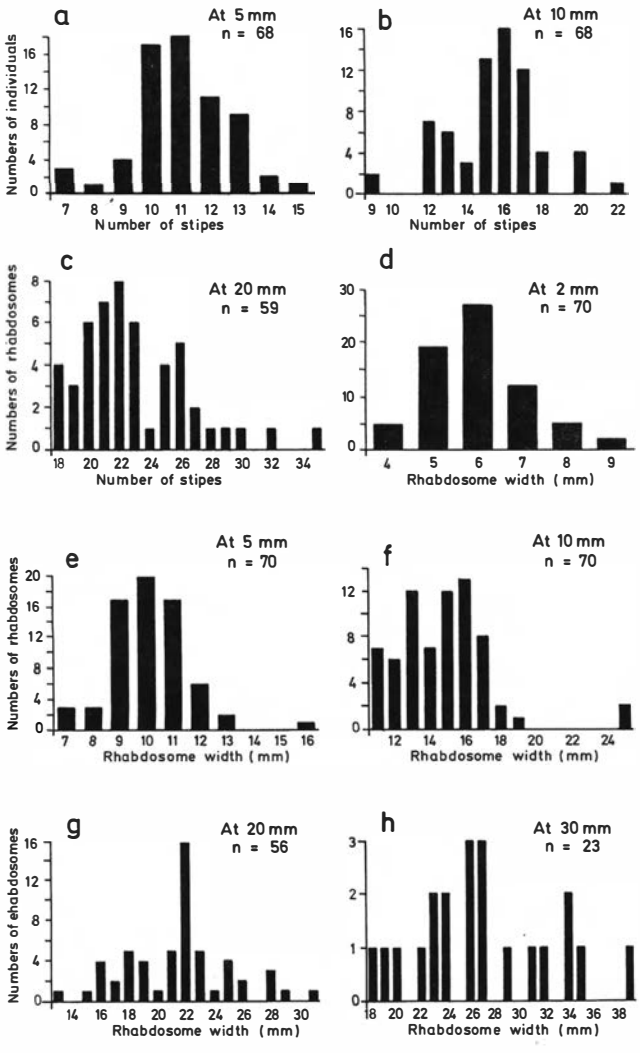


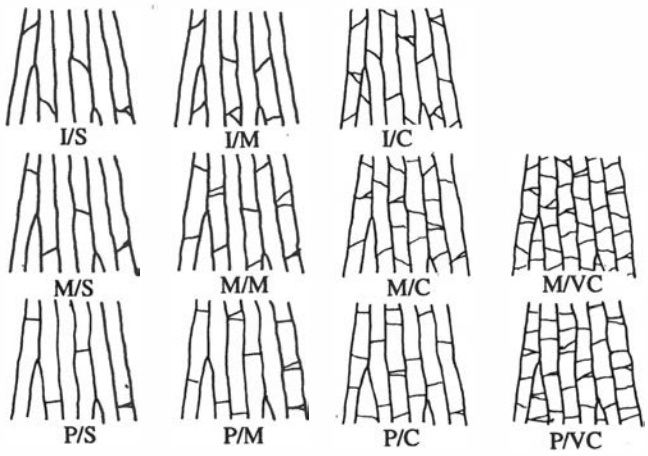
Fig. 13. Frequency distribution of branching rate, and rhabdosome expansion rate in the Digermul population of *Rhabdinopora flabelliformis parabola.*

The rhabdosome is widely variable in shape, ranging from broad cones up to about 40 mm long in the earliest forms at Green Point, to narrow cones reaching well over 100 mm in length in the younger populations. Stipes are straight, 0.3–0.4 mm in lateral width in early populations, becoming broader in later populations, and spaced from 4.5 to 7.8 in 10 mm, averaging 6.4 and 5.71 in 10 mm in the lower and upper intervals respectively at Green Point (Fig. 5). Dissepiments are generally perpendicular, thin and widely spaced, averaging 2–3 in 10 mm. The meshwork thus has a very open appearance, is similar in both the broad- and narrow-coned rhabdosomes, and is quite distinctive. Thecal spacing ranges from 10.5 in 10 mm in specimens from the lower interval at Green Point, to 13/cm in specimens from the upper (129.4–30.9 m) interval. In the Estonian material, they average 14–15 in 10 mm, and Bulman quotes 15–16 in 10 mm in the Shropshire type material. Stipe morphology and structure have been described by Bulman (1927).

Discussion. – Specimens from the lower interval at Green Point are broadly conical and often preserved in dorsal view. They resemble *Radiograptus rosieranus* in rhabdosome form, under which name they were listed by Erdtmann (1988). Their quadriradiate proximal structure enables distinction from *Radiograptus* which, is triradiate (Bulman 1950).

The species here encompasses a wider range of variability in morphology than that described by Bulman (1954) in the Norwegian material, including forms with relatively widely spaced stipes. Significance of the wide range in thecal spacing, reported here, is not certain but all forms have the characteristic meshwork of *anglica* with widely spaced stipes and dissepiments. In proximal structure, the isolated Green Point specimens (representing the early population, with widely spaced thecae) fit well with those from Shropshire (Bulman 1927, pl. 2, fig. 7). The range in rhabdosome form shown by the Green Point populations is wider than envisaged by Bulman (1927, text-fig. 12).

R. f. anglica most closely resembles its predecessor, *R. f. flabelliformis*. The present study suggests that mean stipe spacing may be a useful discriminator between the two forms, with the boundary between them lying at about seven stipes in 10 mm (Fig. 5). The rhabdosome of *anglica* can readily be derived from that of *R. f. flabelliformis* by increase in average stipe spacing and reduction in number of dissepiments, and transients with intermediate values in these characters are known (Fig. 20; Bulman 1954). The modal forms of the two subspecies are distinct, but populations of one subspecies overlap those of the other in most characters. For this reason, the two are commonly reported to overlap in stratigraphic range (Bulman 1954; Kaljo et al. 1986). The transition from *flabelliformis* to *anglica* in the succession of populations through the *Dictyonema* Shale of Estonia strongly points to *flabelliformis* as the ancestor of *anglica*.



Mesh Character

	Proximal				Distal			
I	7	6	2		5	1	3	
M	15	18	7		4	9	12	20
P	10	0	2	1	2	6	2	4
	S	M	C	VC	S	M	C	VC

Fig. 14. Templates for mesh character, and numbers of Digermul specimens of *Rhabdinopora flabelliformis parabola* for each template.

If the trend towards reduction in number of dissepiments and increased stipe spacing is continued, and the total number of stipes reduced, the result is the rhabdosome of *Rhabdinopora flabelliformis bryograptoides* (Bulman 1954), and it is significant that this form is found in the stratigraphically highest beds in the Tøyen section of Oslo. We have not examined specimens of this form, but Bulman noted that it is 'a morphological intermediate between *D. flabelliforme* and *Bryograptus*', and it could well represent a final stage in the *Rhabdinopora* evolutionary series.

Notes on other rhabdinopora species

1. *Rhabdinopora flabelliformis multithecatum* Bulman 1954. This form matches *R. f. anglica* as described here, especially the younger Green Point populations with widely spaced stipes, in all respects except for the close spacing of its thecae, given by Bulman as 18–20 in 10 mm and the extended apertural spines. Bulman refers to only a single specimen in the Oslo sequence, the lectotype (PMO 62.412, 62.415, counterparts), as definitely representing the species but, unfortunately, it is a loose slab and the stratigraphic horizon of the form is uncertain.

2. Matane species. Bulman's (1954) recognition of six species of which five were new, among collections from six localities in the Matane region of Quebec, depended heavily on rhabdosome outline shape as a diagnostic character. One of these, *D. canadense* Lapworth is here thought to be conspecific with populations at Green Point (as believed by Bulman) and Norway and is here redescribed under the name *Rhabdinopora flabelliformis canadensis*. His species, *D. cristatum* and *D. lapworthi*, both appear to lie within the range of morphologic variation of this subspecies in stipe spacing and general mesh character, as well as proximal structure, and are regarded as junior synonyms. As discussed earlier *D. rustica* is provisionally synonymized with *R. f. flabelliformis*. *D. clarki* apparently is based on a single narrow acutely coned specimen of uncertain affinity. *D. cyathiforme* is distinguished primarily by its slender, very closely spaced stipes (15 in 10 mm) and closely spaced and regular dissepiments, together producing a fine rhabdosome meshwork. It seems most closely related to *R. f. socialis* (Salter).

3. *Rhabdinopora flabelliformis socialis* (Salter 1858). The close spacing of stipes (11–13 in 10 mm) and the fine densely packed dissepiments are the main distinguishing characters of this species. This is characteristic of continental shelf environments and first appears at about the same level as *R. f. canadensis*, in the uppermost *R. f. parabola* Zone. It precedes *R. f. flabelliformis* stratigraphically in shelf sequences (e.g. Shropshire, Stubblefield & Bulman 1927; and Norway, Bulman 1954) and has been regarded as the ancestor of *flabelliformis* (Bulman 1954). However, in deeper water environments, *R. f. canadensis* precedes *flabelliformis* (Cooper, in prep.) and because it lies morphologically between the early form *R. f. parabola* and *flabelliformis* itself, it is here regarded as a more likely ancestor. *R. f. socialis* is regarded as an ecological subspecies adapted to shallow (shelf) waters, grading laterally and vertically into other subspecies of *Rhabdinopora flabelliformis* (Cooper, in prep.)

4. *Rhabdinopora flabelliformis norvegica* (Kjerulf 1865). This form is characteristic of shallow and mid-shelf environments, reaching into outer shelf or upper slope environments only during times of sea level minima (Cooper, in prep.). It is not known from oceanic or deeper water environments and is confined to the Balto-Scandian region. It is distinguished chiefly by its broad stipes and broad, closely spaced dissepiments, consistent with survival in a high-energy environment. In extreme forms the stipes and dissepiments are so thickened that the spaces between them are reduced to small round holes (Bulman 1954, figs. 8a–e). Stipes are generally spaced about 9–12 in 10 mm. A population from Slemmestad, Norway (Fig. 21a), averages 10.9 stipes in

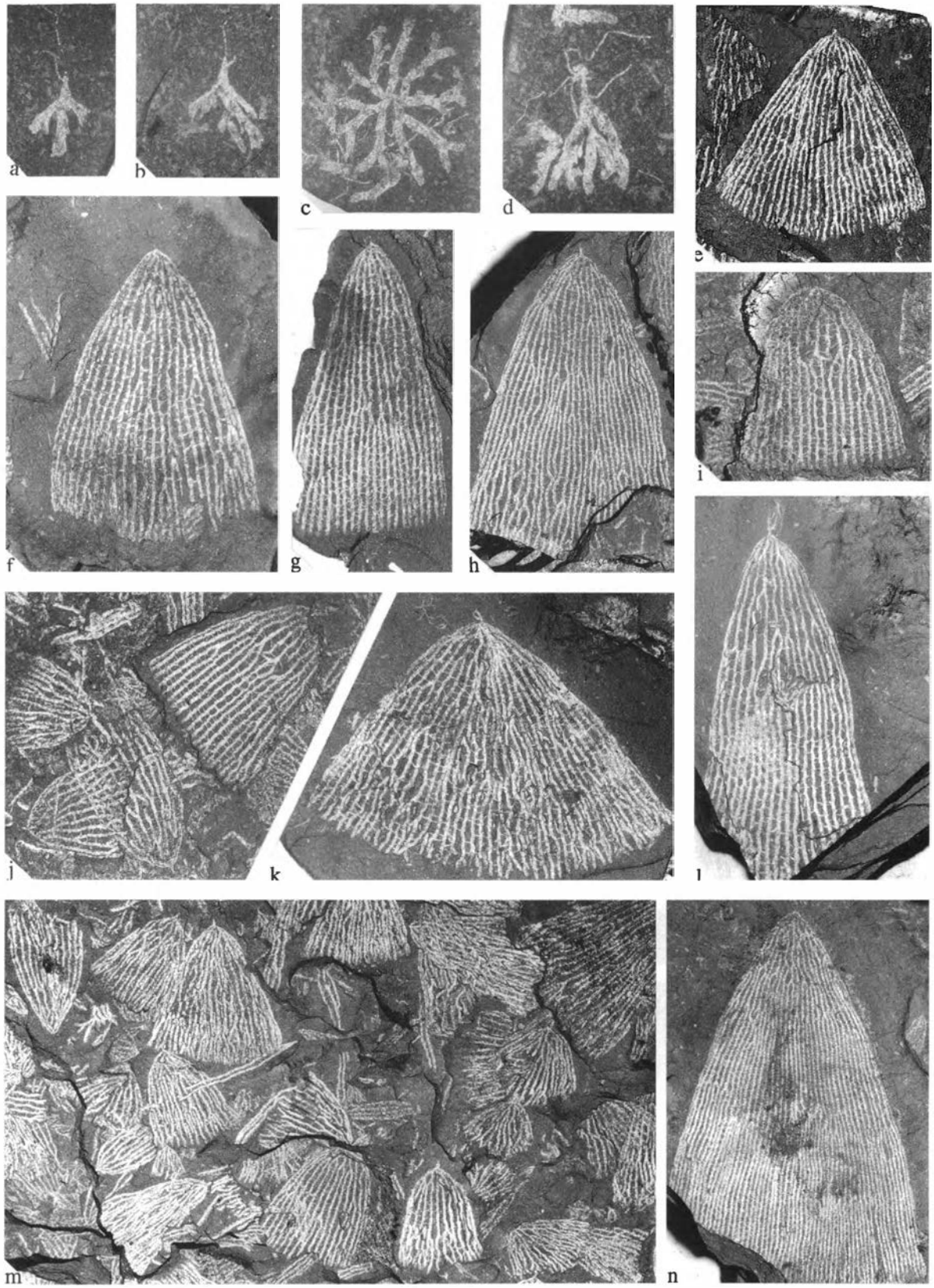


Fig. 15. Rhabdinopora flabelliformis parabola, Digermul, Norway population. (a) Developmental stage, PMO 155.451a, ×5; (b) Developmental stage, PMO 155.452, ×5; (c) Developmental stage, discoidal view, PMO 155.449, ×5; (d) Developmental stage, PMO 155.451b, ×5; (e) Modal form, PMO 155.453, ×1.5; (f) Modal form, PMO 155.454, ×1.8; (g) Narrow rhabdosome, PMO 155.455, ×1.5; (h) PMO 155.456a, ×1.2; (i) Specimen with parabolic outline, PMO 155.456b, ×1.5; (j) Modal form, PMO 155.457, and several immature specimens, ×1.5; (k) Broad rhabdosome with relatively wide stipe spacing, PMO 155.458, ×1.5; (l) Narrow rhabdosome, PMO 155.159, ×1.8; (m) Group of specimens on the bedding plane, PMO 155.460, × l; (n) Exceptionally large rhabdosome with relatively close stipe spacing, PMO 155.461, ×1.

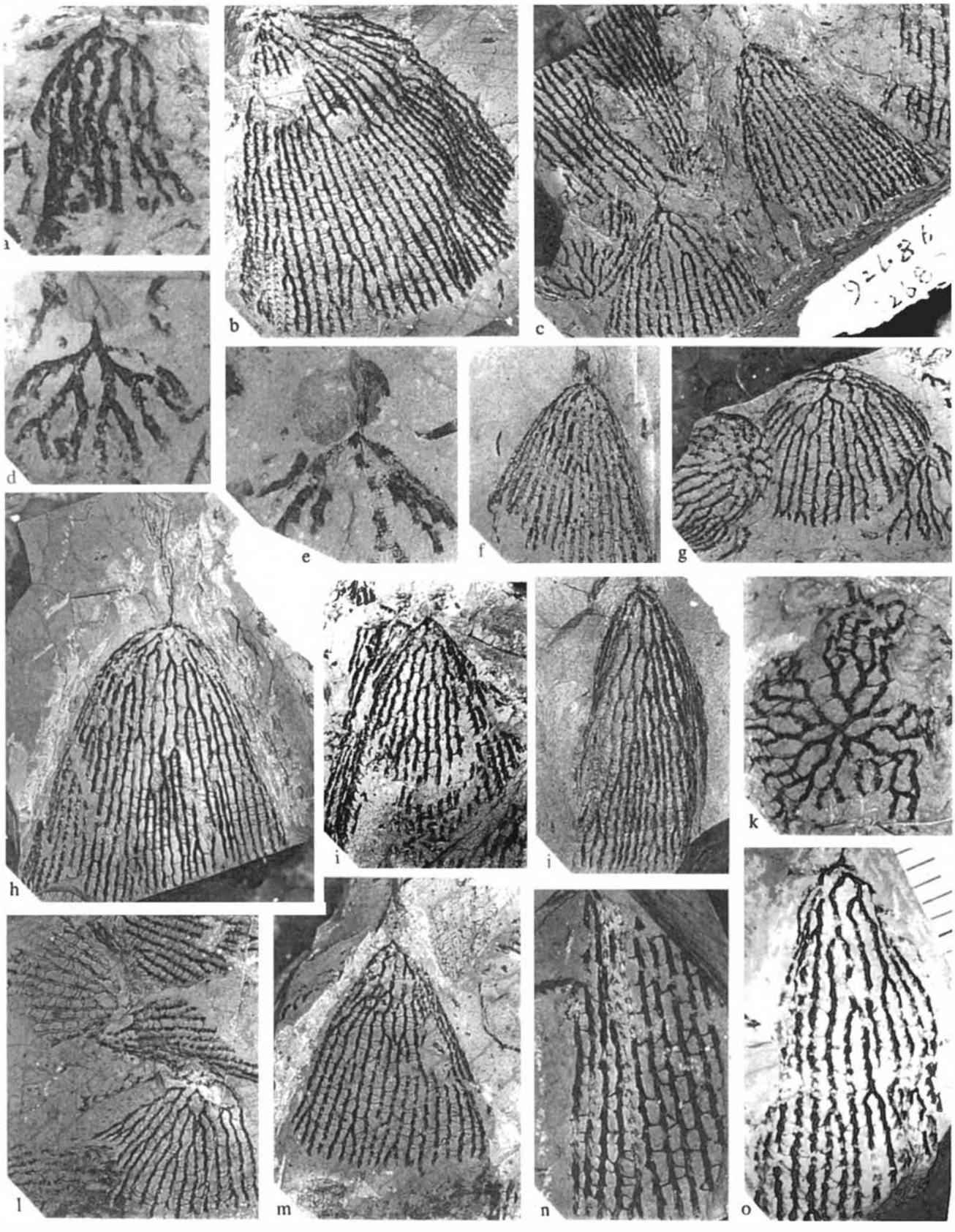


Fig. 16. Rhabdinopora flabelliformis parabola, R. praeparabola, Dayangcha. (a) *R. praeparabola*?, NIGPAS 98654, holotype of *Dictyonema proparabola* Lin, ×6. (b–o) *R. f. parabola*. (b) NIGPAS 92680, ×3. (c) Group of complete and fragmentary rhabdosomes, NIGPAS 92686/92687, ×3. (d) Developmental stage showing quadriradiate structure and nematic vane structure, NIGPAS 98619, ×8.5; (e) Specimen showing nematic vane structure, NIGPAS 98618, ×8.5; (f) NIGPAS 98646, paratype of *Dictyonema flabelliforme eosociale*, ×3?; (g) Two rhabdosomes obliquely preserved showing quadriradiate structure, NIGPAS 92659, ×3; (h) Large specimen with divided nema, NIGPAS 92662, ×3; (i) Paratype of *Dictyonema flabelliforme eosociale*, NIGPAS 98642, ×3?; (j) Holotype of *Dictyonema flabelliforme eosociale*, NIGPAS 98633, ×3; (k) Discoidally preserved specimen, NIGPAS 92661, ×6; (l) Group of fragmentary rhabdosomes, NIGPAS XXXXX, ×3. (m) NIGPAS 92676, ×3; (n) Fragmentary rhabdosome showing mesh structure, NIGPAS 92682, ×6. All specimens with the exception of that of 161 figured by Lin (in Chen et al. 1985); (o) Relatively narrow specimen, NIGPAS 92669, Shandaopu Quarry, 9 km NE of Dayangcha town, ×4.5.

10 mm, and ranges from 9.5 to 12.5 (Fig. 5). Dissepiments are spaced 7–12 in 10 mm. However, little is known about other features of morphology and the proximal end of the rhabdosome is not known from well-preserved material. Growth stages are also unknown. Confusion about its nomenclature in relation to the lectotype of *R. f. flabelliformis* is discussed above.

Although the subspecies is commonly found in a short interval in the late *Anisograptus* Zone and early *R. f. anglica* Zone (Cooper, in prep.), it has been reported from a wide stratigraphic range; the earliest records are about at the level of *R. f. canadensis* (late *parabola* Zone) and the latest are from the *Adelograptus* Zone (Hede 1951; Tjernvik 1958). It generally is found as broken rhabdosome fragments concentrated in dense mats in thin beds and often alternates with other subspecies of *R. flabelliformis*. It is therefore unlikely to be of regional stratigraphic value but is useful locally (Kaljo et al. 1986). The specimen figured in Fig. 21a is the most complete one found so far.

As discussed under the classification, the inshore shallow water forms, *R. f. norvegica* and *R. f. socialis*, are regarded as ecological subspecies living in a marginal environment that grades into the more offshore and deeper water environment in which early Tremadoc graptolites were most abundant and diverse.

5. *Rhabdinopora flabelliformis desmograptoides* (Hahn 1912) is a similarly poorly known, and geographically even more restricted, species that also appears to be characteristic of the inshore environment. Although it is accorded stratigraphic value by Tjernvik (1958) in Scania, its stratigraphic range is not well established elsewhere. The form differs from *R. f. norvegica* chiefly in having less closely spaced diseppiments. The specimen figured by Tjernvik (1958) has stipe spacing of apparently exceptional width; however, the scale is X2 and not X1.5 as given, and the correct stipe spacing is 10.5 in 10 mm.

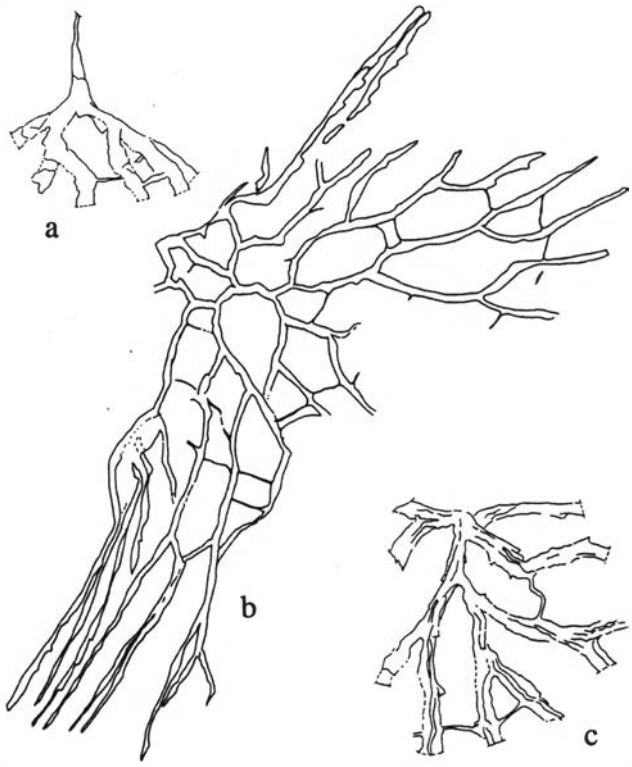


Fig. 17. (a, c) *Rhabdinopora flabelliformis canadensis*, western Newfoundland. (a) Developmental stage, GSC 115812, Green Point, 118.2 m, ×6. (c) Proximal region showing quadriradiate structure, GSC 115813, Green Point, 120.21 m, ×7. (b) *Rhabdinopora* sp. indet., with an apparently biradiate proximal structure, GSC 115814, Green Point, 120.12 m, ×3.

6. *Rhabdinopora scitulum* (Harris & Keble 1928). The close spacing of stipes and a small rhabdosome size suggest affinity of this form, known only from Australia, with *R. cyathiformis* Bulman, consistent with the records of *Anisograptus* associated with each species. But the tufted nematic threads in *R. scitulum* are remniscent of those in *R. f. parabola* and the affinities of the Australian form need further investigation.

Genus *Staurograptus* Emmons 1855

Type species: *Staurograpsus dichotomous* Emmons (by monotype)

1855 *Staurograpsus* (new genus); Emmons, p. 108
1962 *Aletograptus* gen. nov.; Obut & Sobolevskaja, p. 76

Diagnosis. – Quadriradiate anisograptid with horizontal to subhorizontal rhabdosome; distal dichotomies irregularly spaced; dissepiments rare and scattered distally in some mature and gerontic specimens of early species, otherwise lacking altogether.

Description. – The rhabdosome is multiramous, horizontal to subhorizontal, with quadriradiate proximal development. In dorsal (apical) view the four first-order stipes diverge from the sicula at 90° to each other. They are produced by successive dicalycal thecae in the fashion described by Maletz (1992), wrapping around the sicula (Fig. 22a, b; 25a, b). Scattered distal dissepiments are present in some mature to gerontic specimens of *S. dichotomous*, but are lacking in other specimens and in all other species.

Proximal development is of isograptid type with prosicular origin of theca 1^1. The proximal end is strongly asymmetrical, with stipe 1 originating higher on the sicula and stipes 2 to 4 at successively lower levels. The sicula gradually widens towards the aperture and has a barely developed rutellum. The thecae are slender with short rutelli and possess a moderate thecal overlap. Bithecae are present, accompanying all thecae. They are generally small and inconspicuous.

Remarks. – The genus *Staurograptus* was described by Emmons (1855) for a small graptolite showing four short primary stipes, of one to two thecae each, in a cruciform arrangement, and dichotomies to the third order. Larger

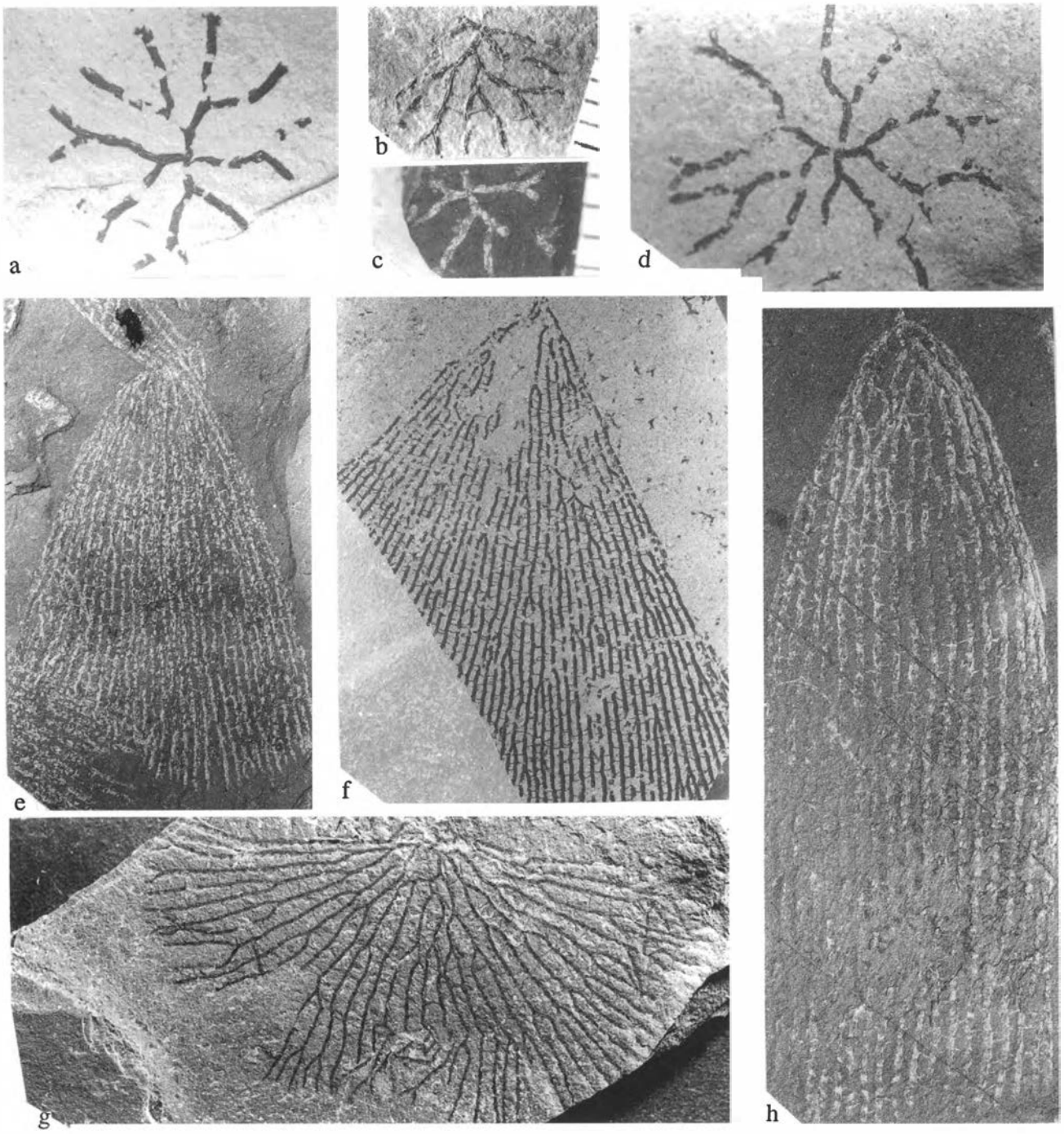


Fig. 18. Rhabdinopora flabelliformis canadensis, Newfoundland and Norway. (a) GSC 115815, Green Point N section, discoidally preserved juvenile without dissepiments, showing quadriradiate structure, ×5. (b) Juvenile, GSC 115816, Green Point, 120.12 m, proximal end in partial relief, ×3.5. (c) Juvenile, PMO 155.462, Naersnes, Norway, juvenile, ×5. (d) Discoidally preserved juvenile showing dissepiment on lower right stipe, GSC 115817, Green Point N section, ×5. (e) Modal form, PMO 155.463, Naersnes, Norway, ×1.5. (f) Wide-coned specimen, GSC 115818, Green Point, ×1.5. (g) Broken discoidal preservation, GSC 115819, Green Point, 119.86 m, ×1.8. (h) Parallel-sided rhabdosome, SM-A/48193a, ×2.8. (figured by Erdtmann 1982).

specimens showing higher orders of branching were included in *S. dichotomous* by Ruedemann (1904, 1947), whose description has been used as the basis of recognition of the genus *Staurograptus* by most subsequent workers. The genus is here redefined, and includes large gerontic specimens, referred to as *S. dichotomous*, bearing dissepiments. The number of distal stipes seems to be unlimited and specimens with stipes up to the eighth order have been found.

Aletograptus, which here includes forms with long-delayed second-order dichotomies, is synonymized with *Staurograptus*. The type material of *Aletograptus hyperboreus* (Obut & Sobolevskaja 1962) consists of small specimens, in which the distal dichotomies are not yet developed or are not preserved in the fragmentary material.

Staurograptus dichotomous Emmons, 1855 Figs. 22a–s, w, x, 25a, b, e

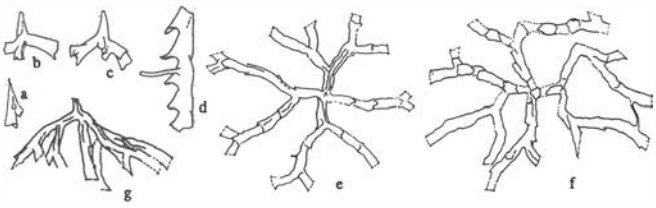


Fig. 19. Rhabdinopora flabelliformis anglica. Green Point, western Newfoundland. (a) Isolated growth stage, sicula with incomplete first theca, and sicular bitheca, GSC 115820, Green Point N section, ×10. (b, c) Isolated developmental stages in reverse (b) and obverse (c) views, showing at least three first-order stipes, GSC 115821, 115822, Green Point N section, ×10. (d) Isolated stipe fragment with dissepiment, and most thecal apertures broken off, GSC 115823, Green Point N section, ×10. (e–f) Proximal ends of discoidally preserved specimens showing quadriradiate proximal structure, GSC 115824, and GSC 115825, Green Point N section, 0.25–0.8 m, both ×7. (g) Proximal end, GSC 115826, Green Point N section, 0.25–0.8 m, ×7.

1855 *Staurograpsus dichotomous* n. sp. – Emmons, p. 109, pl. 1, fig. 21
1904 *Staurograptus dichotomus* Emmons – Ruedemann, p. 614, pl. 2, figs. 1–20, text-fig. 34
1904 *Staurograptus dichotomus* var. *apertus* var. nov. – Ruedemann, p. 616, pl. 2, figs. 21–24
1947 *Staurograptus dichotomus* Emmons – Ruedemann, p. 290, pl. 46, figs. 10–18
1947 *Staurograptus dichotomus* var. *apertus* Ruedemann – Ruedemann, p. 291, pl. 46, figs. 19–21
?1962 *Anisograptus richardsoni* Ruedemann – Obut & Sobolevskaja, p. 75, pl. 2, fig. 1
?1962 *Anisograptus* sp. – Obut & Sobolevskaja, pl. 2, fig. 2 (no description)
1982 *Radiograptus rosieranus flexibilis* n. ssp. – Fortey (*in* Fortey et al.), p. 104, pl. 1, figs. 1–3, 11–12, text-fig. 5
non 1986 *Staurograptus* cf. *dichotomus* Emmons – Lin (*in* Chen et al.), p. 244, pl. 65, figs. 1–5, 8–10, 13, 14, text-figs. 98, 99 (=*Rhabdinopora flabelliformis parabola*)
non 1986 *Staurograptus dichotomus priscus* subsp. nov. – Lin (*in* Chen et al.), p. 245, pl. 66, figs. 1–5, text-fig. 100 (=*Rhabdinopora flabelliformis parabola*)
1988 Form-species *Staurograptus dichotomus* Emmons – Erdtmann, p. 341, figs. 9A, 10C–F
1988 Form-species *Staurograptus* (*Radiograptus*) *flexibilis* (Fortey) – Erdtmann, p. 344, figs. 7, 9B–F, 10A–B

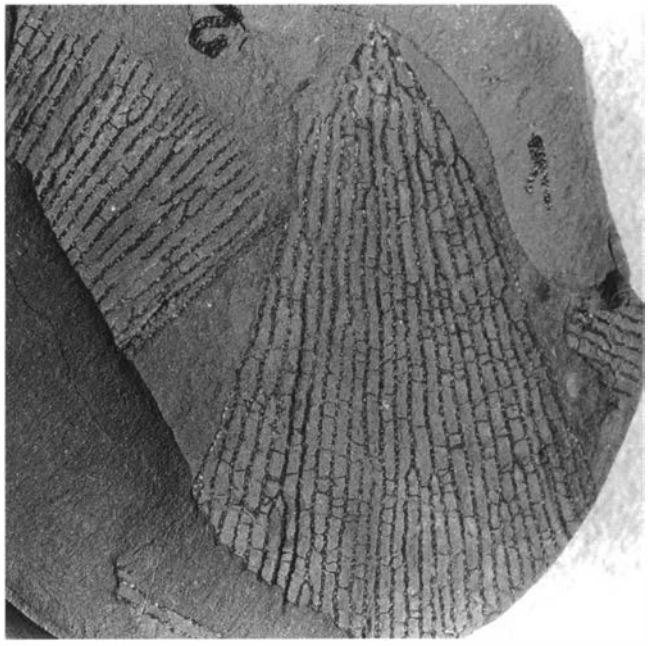


Fig. 20. Rhabdinopora flabelliformis anglica, morphologically an early member with relatively close spaced stipes; Va 1042, borehole Nõva, 3.1 m below the top of the *Dictyonema* Shale (=Türisalu Formation), Estonia, coll. E. Kivimägi.

Type specimen. – The type specimen, presumably housed in the New York State Museum (Albany, New York), was not available for study. The type locality is known only as the 'Taconic shales of Rensselaer county, New York'. *Staurograptus* is recorded at several localities in this area of New York State by Ruedemann (1947).

Material. – Several hundred specimens from the interval 106.40–108.45 m in the Green Point section in the collection of Erdtmann (TU Berlin). Isolated specimens from the 108.00–108.20 m level at Green Point. In addition, more than 50 specimens from the Petite Blanche River (RPB) or Rivière Petite Blanche on the Gaspé peninsula of Québec (Landing et al. 1986) in the collections of J. Maletz (University of Greifswald) and B.-D. Erdtmann (TU Berlin). Landing et al. (1986) noted the presence of *Anisograptus matanensis* Ruedemann and *Anisograptus matanensis tetragraptoides* Bulman from this locality. The graptolites are found in a thin black shale layer a short distance above a level with conodonts of the *Rossodus manitouensis* Zone. They thus represent stratigraphically higher beds than are known for the species elsewhere.

Description–proximal morphology. – Isolated flattened specimens from Green Point show that the sicula is slender, with a short and inconspicuous rutellum. The conus and cauda of the prosicula (Hutt 1974) are clearly differentiated (Fig. 25a), but the exact length of the prosicula cannot be determined, as the specimens are only partly transparent and growth lines are difficult to see near the apex of the sicula. The proximal end shows typical isograptid development with theca 1^2 being the first dicalycal theca. Theca 1^1 originates high on the sicula and bends sharply away from it at sicula mid-length, giving the proximal region a strongly asymmetrical appearance. Just before its point of flexure, it produces theca 1^2 on one side and a conspicuous sicular bitheca on the other side (Fig. 22a, b). Development mode (sinistral or dextral) cannot be determined in the flattened material. Theca 1^2 grows downwards along the sicula and crosses over to reach its dorsal side. From the region of the sicular aperture three stipes start to grow, their points of origin wrapping around the sicular aperture (Fig. 25a, b) consistent with the quadriradiate devel-

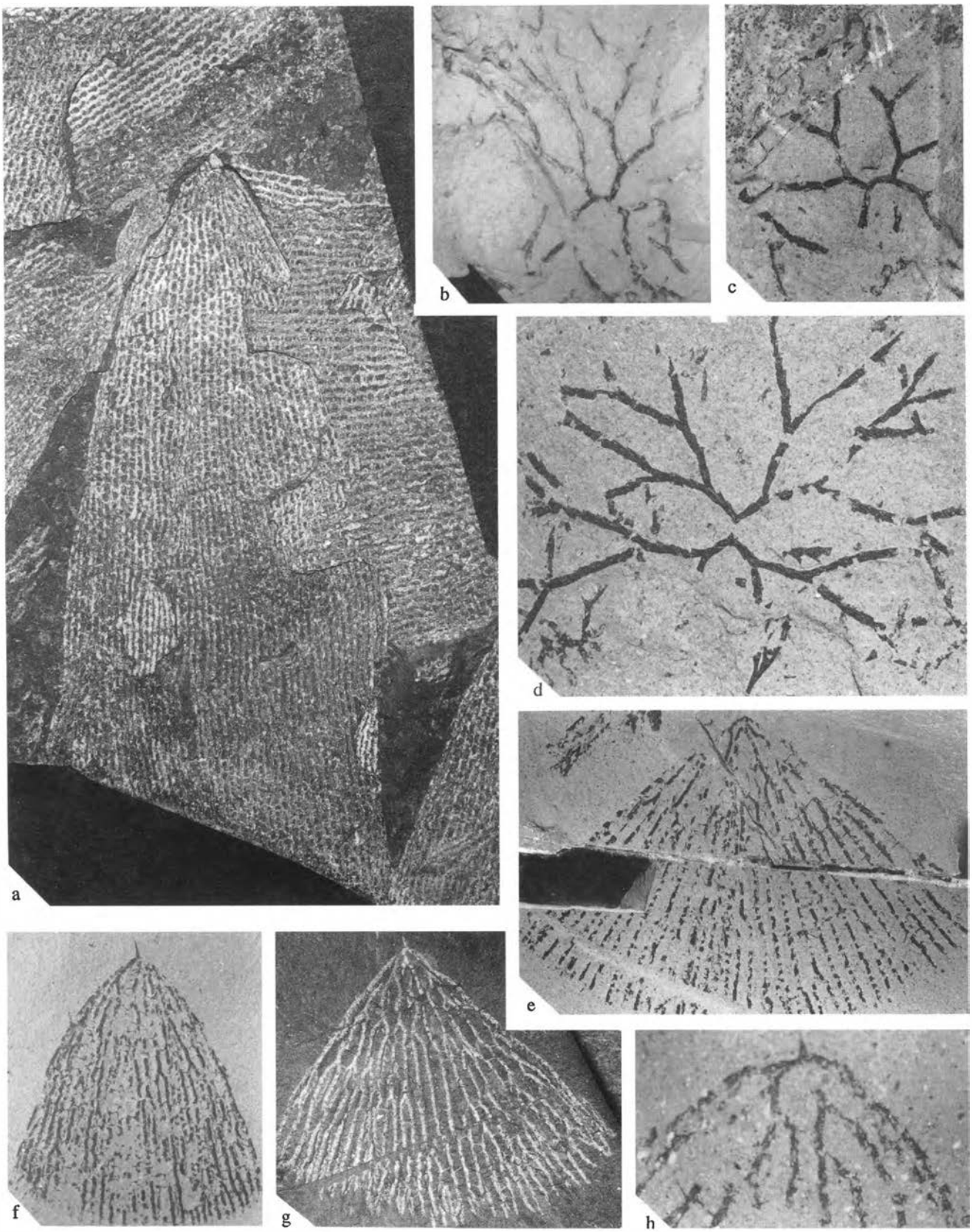


Fig. 21. (*a*) *Rhabdinopora flabelliformis norvegica*, the most complete specimen yet found, with fragments of several other specimens, PMO 155.464, Rortunet Senter, Slemmestad, Norway, ×1.5; (b) *Anisograptus matanensis*, NIGPAS 92702, Dayangcha, ×4.4; (c) *Anisograptus matanensis*, NIGPAS 92702, Dayangcha, ×4.4; (d) *Anisograptus matanensis*, GSC 115827, Green Point, 118.2 m, ×3.8; (e) *Rhabdinopora flabelliformis anglica*, GSC 115828, Green Point, ×1.7; (f) *Rhabdinopora flabelliformis canadensis*, GSC 115829, Green Point, ×1.5; (g) *Rhabdinopora flabelliformis flabelliformis*, Lo 7511, Ottenby, Öland, Sweden, ×1.5; (h) *Rhabdinopora flabelliformis canadensis* proximal end of a larger specimen, GSC 115830, Green Point, 120.81 m, ×5.

opment model outlined above and by Legrand (1974) and Maletz (1992).

Description of Green Point populations. – Rhabdosomes are of typical *Staurograptus* (cruciform) shape, commonly developed only to two or three orders of dichotomy. Lateral stipe width is generally 0.3–0.4 mm. Stipe length ranges widely, even among stipes of the same order in a single specimen (compare second-order stipes in Fig. 22g). First-order stipes are generally of 1–2 thecae (1–2 mm) each, but longer stipes are present in some specimens (compare the Quebec population described below). In most rhabdosomes, stipe length increases with stipe order. At least eight orders of stipes have been observed.

The thecae are long and slender, with an inclination of about 15–20° and a short rutellum. They are spaced 9–10.5 in 10 mm. Dorso-ventral stipe width, measured in isolated stipe fragments, is up to 0.7 mm. Stipe structure is of general dendroid type with a bitheca associated with each theca, alternating on either side of the rhabdosome. Dissepiments are present in some mature specimens with more than five orders of stipes (Figs. 22l, p). The dissepiments are thin and hairlike, sometimes bifurcate, and are irregularly distributed throughought the rhabdosomes. The dissepiments closest to the proximal end connect third-order stipes. It therefore appears that dissepiments are a gerontic feature and are produced at a fairly late stage in the growth of the colony.

Remarks on Green Point population. – Judging from the illustrations of Emmons (1855) and Ruedemann (1947) the type specimen of *S. dichotomous* is a poorly preserved juvenile and could belong to either *Rhabdinopora* or *Staurograptus*, as juveniles of the two genera are indistinguishable in discoidal preservation. The mature form of the rhabdosome of *Staurograptus dichotomous* and variation within the species was not described by Emmons (1855). Ruedemann's (1947) concept of the species is therefore adopted here and used for the Green Point material. This material includes juveniles and mature specimens and enables the development to be observed.

Ruedemann (1904) distinguished *S. dichotomous* var. *apertus* on its fewer terminal stipes His material, from Schaghticoke, New York, includes *S. dichotomous* s. s. and the pauciramous forms very likely represent intraspecific variants. Specimens described as *Anisograptus richardsoni* and *Anisograptus* sp. by Obut & Sobolevskaja (1962) clearly have a quadriradiate proximal development. They are here provisionally included in *S. dichotomous*, but the possibility cannot be excluded that they represent immature *Rhabdinopora* instead. *Radiograptus rosieranus flexibilis* Fortey (Fortey et al. 1982) is closely comparable with specimens regarded here as mature forms of *Staurograptus dichotomous* with dissepiments. The type material comes from the Broom Point South section and represents the earliest planktic graptolite species in the succession (Fortey et al. 1982, text-fig. 12). This level corresponds with the *R. praeparabola* Zone in the Green Point section.

Comments on the Québec population. – All graptolites present are referred to as *Staurograptus dichotomous*. They clearly show a quadriradiate proximal end with several distal dichotomies (Figs. 22m–o, q–s, w, x). The maximum number of stipe orders counted is 5 (Fig. 22n) and no dissepiments were seen. A single specimen with a triradiate proximal end (Fig. 22n) is interpreted as a quadriradiate form that failed to develop all proximal dichotomies rather than representing a distinct genus. Compared with the Green Point populations, the dichotomies are more widely spaced resulting in larger rhabdosomes with a smaller number of stipes. The first-order stipes range from 1 mm to 5 mm (Figs. 22r, x), generally lying between 2 and 4 mm. Apart from their somewhat more widely spaced dichotomies, the Québec specimens fit well with the Green Point population and they are here referred to as the same species. The wider spacing of dichotomies may represent evolution within the *S. dichotomous* lineage, and may therefore prove to have stratigraphical value. The rhabdosome of *S. hyperboreus* could represent the result of a similar trend.

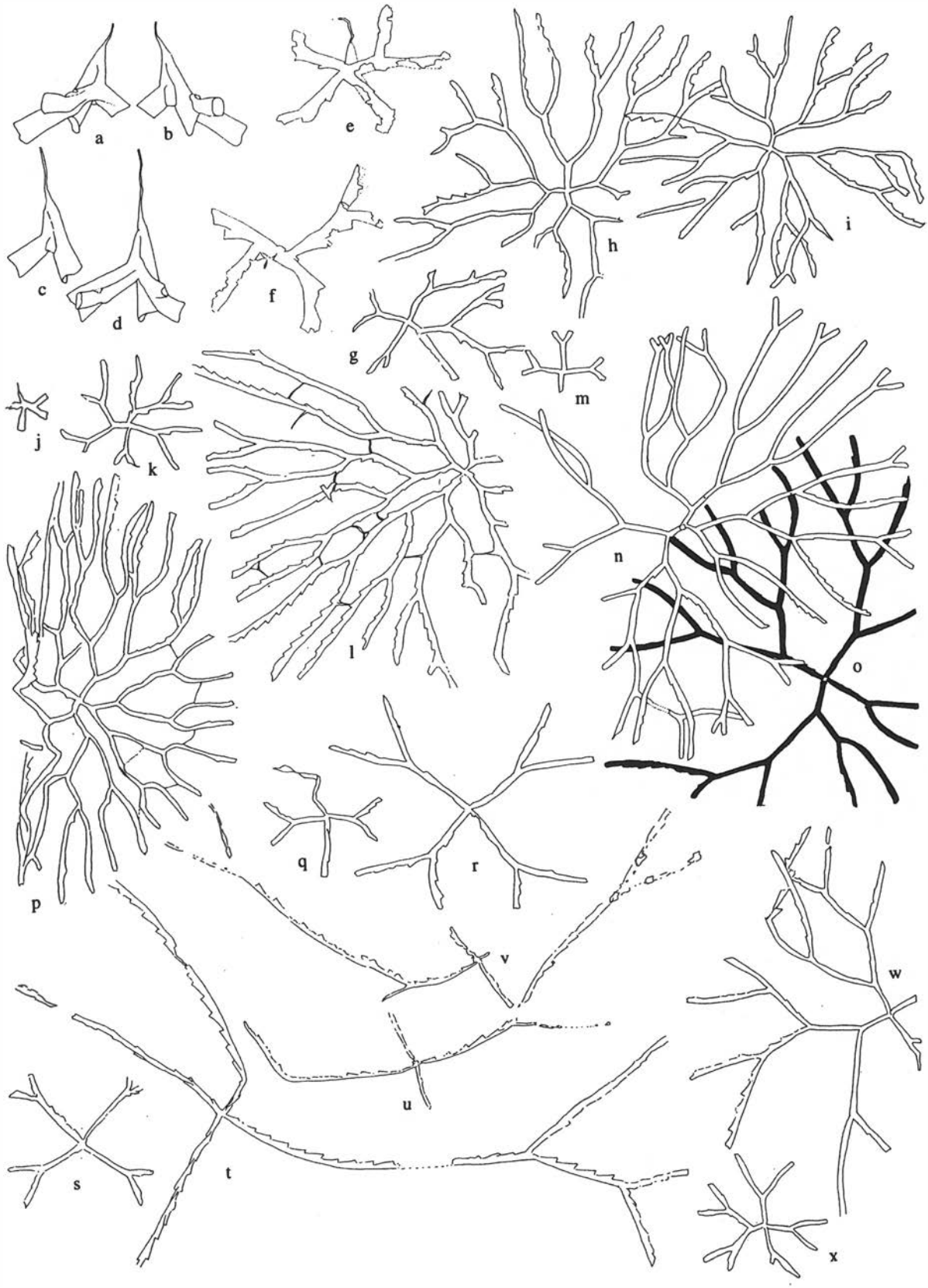
Staurograptus hyperboreus Obut & Sobolevskaja 1962, figs. 22t–v.
1962 *Aletograptus hyperboreus* sp. nov. – Obut & Sobolevskaja, pp. 76–77, pl. 2, figs. 6, 7.
?1962 *Triograptus canadensis* Bulman – Obut & Sobolevskaja, p. 76, pl. 2, figs. 3–5.

Type specimens. – The type material of *Aletograptus hyperboreus* comes from the Taimyr Peninsula, Arctic Russia, and consists of two fragmentary specimens showing four first-order stipes, but no distal dichotomies.

Material. – Several specimens from the 108.45 m–110.5 m interval in the Green Point section.

Description. – The rhabdosome has up to three orders of stipes. First-order stipes are long, usually 5–7 mm (Figs. 22u, v), up to a maximum of 17 mm (Fig. 22t), before bifurcating. The second-order stipes, in some specimens, are shorter than the first-order stipes. The stipes are slender and carry about 9–10 thecae in 10 mm, as in *S. dichotomous*. Stipes are generally poorly preserved and lateral stipe width is estimated at 0.6–0.7 mm. Details of the proximal development are not known.

Remarks. – The species is distinguished by having long-delayed second-order dichotomies, seen only in mature specimens. The type material of *Aletograptus hyperboreus* is indistinguishable from those Green Point specimens in which the second-order dichotomies are not seen because of fragmentary preservation, or immaturity. *S. hyperboreus* may be interpreted as derived from *Staurograptus dichotomous* by delay of the distal dichotomies. As far as can be distinguished, it is similar all other characters.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The specimens of *Triograptus canadensis* described by Obut & Sobolevskaja (1962) are here interpreted as fragmentary specimens of *S. hyperboreus*. They show *ca.* 90° angles between the stipes and slender thecae like those of *S. hyperboreus*, and also come from the same horizon. They are unlikely to represent the younger form, *Triograptus*.

Genus Triramograptus n. gen. Erdtmann (*in* Cooper et al.).

Type species. – *Triramograptus* atavus n. sp. Erdtmann (*in* Cooper et al.).

Diagnosis. – Robust, triradiate, reclined anisograptid with three stipes of no more than eight to nine thecae each.

Description. – see *Triramograptus atavus* n. sp. The genus is monotypic.

Remarks. – The genus is represented by a single species with uncertain phylogenetic relationships, present in a narrow stratigraphic interval in the Lower Tremadoc (*parabola* Zone) of western Newfoundland. From the strong development of the rutellum, the robust thecae and the wide stipes, the sole species, *T. atavus*, matches *Rhabdinopora* rather than *Staurograptus*. It is here interpreted as a species with a strongly reduced rhabdosome, probably derived from a quadriradiate *Rhabdinopora* by suppression of all dichotomies after the second one. The genus and species represents the earliest undoubtedly triradiate graptolite but apparently has no descendents and is regarded as an early experiment in triradiate structure. For this reason it is not regarded as signalling the appearance of diverse triradiate lineages, which takes place in the following (*Anisograptus matanensis*) zone, and Assemblage 2.

With its reclined stipes it anticipates a trend in graptolite evolution otherwise first seen in late Tremadoc assemblages (e.g. *Triograptus*, *Psigraptus*).

Triramograptus atavus n. sp. Erdtmann (*in* Cooper et al., figs. 23, 25d, f.

Type specimens. – GSC 115854 from the Martin Point section is here nominated as a holotype. The specimen occurs with several other specimens on a slab of dark brown shale. It is completely flattened and shows little detail of its rhabdosomal development. The specimen comes from the 53.00 m level in the Martin Point section as described by Erdtmann (1986a).

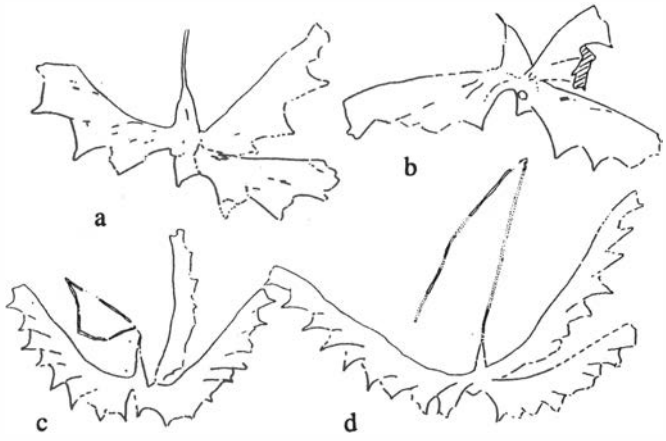

Fig. 23. Triramograptus atavus Erdtmann n. sp. (a) GSC 115854, holotype, Martin Point, western Newfoundland, ×9; (b) GSC 115855, paratype, Martin Point, western Newfoundland, ×9; (c) GSC 115856, Green Point B section, 6.6–6.7 m, ×4; (d) GSC 115857, Green Point B section, 6.6–6.7 m, ×4.

Material. – Many specimens from the Green Point B and Martin Point sections, mostly preserved as flattened films; several flattened specimens isolated from the shales at Green Point B, at the 6.60–6.70 m level (comparable with 113.00–113.10 m of the Green Point A section).

Description. – Generally, the three stipes are moderately reclined (Fig. 23c, d), reaching a length of about 8 mm, and with 8–9 thecae in the largest specimen. Stipe dorsoventral width is 1–1.5 mm and is constant throughout the length of a stipe. The thecae show a conspicuous rutellum when completely developed. Mature specimens show a fairly long nema, more than 15 mm long in one specimen. The nema is neither thickened nor divided. The proximal structure is triradiate, shown by both the isolated specimens (Figs. 25d, f) and by the shale material. The sicula bears a conspicuous rutellum, similar to that of *Rhabdinopora*. Stipe 1 originates at about the mid-length of the sicula, whereas stipes 2 and 3 start from near the sicular aperture. A prominent sicular bitheca is seen below the arch formed by the sicula and the ventral side of theca 1^1. Isolated specimens show that

Fig. 22. Staurograptus specimens. a–s, w, x: *Staurograptus dichotomous* Emmons. (a, b) GSC 115831, isolated, flattened specimen, showing at least three first-order stipes and a strongly asymmetrical proximal end. Green Point, 108.0–108.20 m; (c) GSC 115832, isolated juvenile, Green Point A, 108.0–108.20 m; (d) GSC 115833, isolated proximal end, Green Point A, 108.0–108.20 m; (e) GSC 115834, Green Point A, 106.80 m, quadriradiate proximal end; (f) GSC 115835, Green Point A, 106.40 m, quadriradiate proximal end in shale; (g) GSC 115836, Green Point A, 108.00–108.20 m, juvenile; (h, i) GSC 115837, 115838, Green Point A/786, 108.00–108.20 m, two associated specimens of medium size; (j) GSC 115839, Green Point A, 108.00–108.20 m, juvenile; (k) GSC 115840, Green Point A, 108.00–108.20 m, juvenile; (p) GSC 115841, Green Point A, 108.00–108.20 m, mature specimen with dissepiments; (l) GSC 115842, Green Point A, 108.00–108.20 m, mature specimen with dissepiments; (m) GSC 115843, Rivière Petite Blanche, Gaspé Peninsula, Québec; (q) GSC 115844, Rivière Petite Blanche, Gaspé Peninsula, Québec; (r) GSC 115845, Rivière Petite Blanche, Gaspé Peninsula, Québec, specimen with comparably long first-order stipes; (n, o) GSC 115846, 115847, Rivière Petite Blanche, Gaspé Peninsula, Québec, unusual triradiate specimen associated with a typical quadriradiate specimen (in black); (s) GSC 115848, Rivière Petite Blanche, Gaspé Peninsula, Québec, specimen with long first-order stipes and distal dichotomies; (w) GSC 115849, Rivière Petite Blanche, Gaspé Peninsula, Québec, largest specimen; (x) GSC 115850, Rivière Petite Blanche, Gaspé Peninsula, Québec, small specimen with short first-order stipes; t–v: *Staurograptus hyperboreus* (Obut & Sobolevskaja). (t) GSC 115851, large specimen showing two distal dichotomies on one stipe, Green Point A/005, 108.45 m; (u, v) GSC 115852, 115853, Green Point 108.45 m level, both specimens are associated on one slab. Magnifications: A–D: ×12; E, F: ×6.5; G–X: ×3.

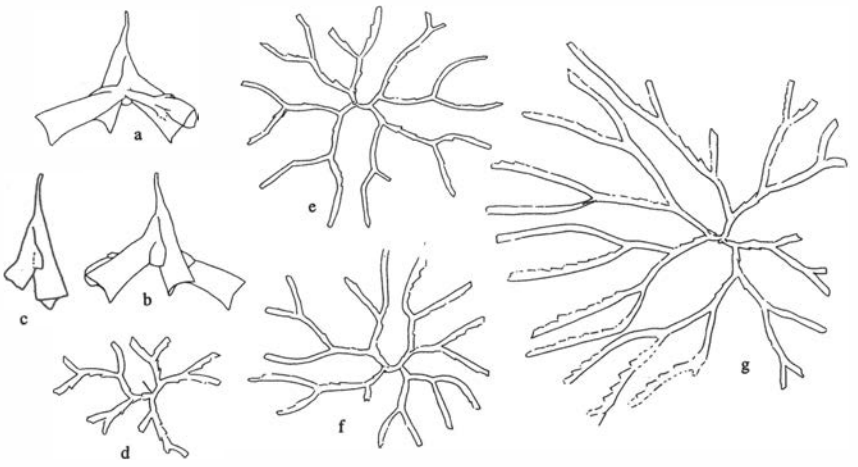

Fig. 24. Anisograptus matanensis. Ruedemann. (a, b) GSC 115858, isolated, flattened specimen, showing the strongly asymmetrical proximal end with a sicular bitheca and a possible distal branching at stipe 1. Green Point A/216, 118.20 m; (c) GSC 115859, isolated juvenile, showing short rutellum on sicula, Green Point A/216, 118.20 m; (d) GSC 115860, Green Point A, 118.20 m; (e) GSC 115861, Green Point A, 119.86 m; (f) GSC 115862, Green Point N, 137 m; (g) GSC 115863, Green Point A, 118.20 m. Magnifications: A–C: ×17; D–G ×3.2.

thecal bithecae are invariably present in association with all thecae. A more detailed description, especially of the proximal end development is in preparation (Maletz & Cooper, in prep.).

Remarks. – The species is easily identified by its reclined rhabdosome habit and short stipes. A few rhabdosomes are preserved in dorsal (apical) view and show the triradial arrangement of stipes which meet at angles of about 120°. The species is known only from western Newfoundland, where it is confined to a short time interval in the *Rhabdinopora flabelliformis parabola* Zone, at two localities. The species was reported as ?*Psigraptus* cf. *canadensis* by Erdtmann (1986, text-fig. 136; 1988, fig. 3) in the range chart for the Green Point section. With its broad stipes and prominent sicula, the species is distinct from *Triograptus canadensis* (Bulman 1950), a triradiate species with thin stipes, less than 0.7 mm wide, which most resembles a reduced *Anisograptus*. The relationship to *Triograptus osloensis* var. *minor* (Ruedemann 1947) from Matane and Newfoundland is unclear. The latter is found associated with a tetragraptid at St. Paul's Inlet, western Newfoundland, and may represent a three-stiped tetragraptid. The specimens described and figured by Rudemann (1937, 1947) are specifically indeterminable.

Genus *Anisograptus* Ruedemann, 1937

1937 *Anisograptus* gen. nov.; Ruedemann, p. 61
? 1984 *Toyenograptus* gen. nov.; Li, p. 579 (type species, *Anisograptus isolatus* Bulman 1954)

Type species. – *Anisograptus matanensis* Ruedemann, 1937 (original designation)

Diagnosis. – Triradiate anisograptid with horizontal to subhorizontal rhabdosome form; spacing of dichotomies highly variable; number of stipes unrestricted; development based on dicalycal thecae 1^2 and 1^3.

Included species. – *Anisograptus matanensis* Ruedemann 1937, *Anisograptus richardsoni* Bulman 1941 (synonym of *A. matanensis*), *Anisograptus ruedemanni* Bulman 1941, *Anisograptus monseni* Bulman 1941, ?*Bryograptus retroflexus* Brögger 1882 (see Bulman 1941, p. 113), ?*Clonograptus* (*Staurograptus*) *heres* Westergård (see Bulman 1941, p. 114), *Didymograptus primigenius* Bulman 1950 (syn. of. *A. matanensis*), *Anisograptus norvegicus* Bulman 1954 (syn. of *A. matanensis*), *Anisograptus grandis* Bulman 1954 (?synonym of *A. matanensis*), *Anisograptus isolatus* Bulman 1954, *Anisograptus flexuosus* Bulman 1941 (synonym of *A. matanensis*).

Remarks. – The genus *Toyenograptus* was erected with minimal discussion by Li (1984) based on the isolated thecal apertures in *Anisograptus isolatus* Bulman. The type species of the genus is known from only one locality in Norway and needs to be redescribed in detail before the taxonomic value of this genus can be evaluated. In the meantime it is here taken as congeneric with *Anisograptus*.

Anisograptus matanensis Ruedemann, 1937 Figs. 21b–d, 24, 25k–m

1937 *Anisograptus matanensis* n. sp. – Ruedemann, p. 62, figs. 6–9
1941 *Anisograptus matanensis* Ruedemann – Bulman, p. 108, pl. 2, fig. 5

Fig. 25. Isolated graptolite specimens from Green Point. (a) GSC 115864, *Staurograptus dichotomous*, juvenile, Green Point A, 108.00–108.20 m; (b) GSC 115831, *Staurograptus dichotomous*, juvenile, Green Point A, 108.00–108.20 m; (c) GSC 115865, *Rhabdinopora flabelliformis canadensis*, quadriradiate proximal end showing that stipes 2–4 wrap around the sicular aperture in a loop, Green Point B; (d) GSC 115866, *Triramograptus atavus* Erdtmann n. gen. n. sp., Green Point B/277, 6.60-6.70 m, proximal end showing triradiate development; (e) GSC 115867, Green Point A, *Staurograptus dichotomous*, stipe fragment, 108.00–108.20 m; (f) GSC 115868, *Triramograptus atavus* Erdtmann n. gen. n. sp., Green Point B, 6.60–6.70 m, proximal end; (g) GSC 115869, Green Point A, 108–108.2 m, *Rhabdinopora flabelliformis parabola*., stipe fragment; (h) GSC 115870, *Rhabdinopora flabelliformis parabola*, sicula with conspicuous rutellum, Green Point A, 108–108.2 m; (i) GSC 115871, *Rhabdinopora flabelliformis canadensis*, large proximal with quadriradiate development clearly seen, three stipes originate close to the sicular aperture, Green Point B, 9.25–10 m; (j) GSC 115872, *Rhabdinopora flabelliformis parabola*, fragment of a sicula showing the long rutellum, Green Point A, 108–108.2 m; (k) GSC 115873, *Anisograptus matanensis*, Green Point A, 118.20 m, proximal end showing triradiate development; (l) GSC 115874, *Anisograptus matanensis*, Green Point A, 118.20 m, juvenile; (m) GSC 115875, *Anisograptus matanensis*, Green Point A, 118.20 m, proximal end with strongly asymmetrical development, stipe 1 originates from middle of sicula, whereas stipes 2 and 3 originate close to the sicular aperture. Magnification ×40 for all specimens.


a
b
c
d
e
f
g
h
i
j
k
l
m

1941 *Anisograptus richardsoni* n. sp. – Bulman, pp. 109–110, pl. 2, fig. 6, text-figs. 2a, b
1941 *Anisograptus flexuosus* n. sp. – Bulman, pp. 110–111, pl. 2, figs. 1–4, text-fig. 3
1947 *Anisograptus matanensis* Ruedemann – Ruedemann, pp. 291–292, pl. 47, figs. 1–8
1947 *Anisograptus richardsoni* Bulman – Ruedemann, pp. 292–293, pl. 47, fig. 10
1947 *Anisograptus flexuosus* Bulman – Ruedemann, p. 292, pl. 47, fig. 9
1950 *Anisograptus matanensis* Ruedemann – Bulman, pp. 80–83, pl. 7, figs. 5–12, text-figs. 4a–g, 5
1950 *Anisograptus richardsoni* Bulman – Bulman, pp. 85–87, pl. 6, figs. 8–12, text-fig. 7
1950 *Anisograptus matanensis* var. *tetragraptoides* nov. – Bulman, pp. 83–84, pl. 7, figs. 14–17, pl. 8, figs. 4, 11, text-fig. 11
1950 *Anisograptus flexuosus* Bulman – Bulman, pp. 84–85, pl. 6, figs. 13–15, pl. 7, fig. 13, pl. 8, fig. 10, text-fig. 6
?1950 *Didymograptus primigenius* sp. nov. – Bulman, pp. 93–94, pl. 7, figs. 22, 23, pl. 8, fig. 6
1954 *Anisograptus norvegicus* sp. nov. – Bulman, p. 29, pl. 7, figs. 1–5, text-figs. 11a, b

Type specimens. – The type material comes from Matane, Quebec. It is probably housed in the New York State Museum (note by Bulman in Ruedemann 1947, p. 292), but was not available for study.

Material. – Many flattened shale specimens from the Green Point section. Abundant isolated flattened specimens have also been recovered from the 118.00–118.10 m interval of the Green Point section.

Description – proximal end. – The sicula consists of a slender cone with a fairly short rutellum. The conus and cauda are clearly differentiated, but the length of the prosicula cannot be determined. The conus is at least 0.2 mm long, as is the cauda. The complete sicula measures 1.2–1.4 mm long including the cauda. Theca 1^1 originates at approximately the midlength of the prosicula. Theca 1^1 widens rapidly and bends sharply outwards at sicula midlength. Theca 1^2 and the sicular bitheca originate just above this point of flexure. The sicular bitheca grows down to the indentation with theca 1^1 and its aperture can be seen in reverse view. The sicular bitheca is fairly conspicuous in most specimens. Theca 1^2 grows down and across the sicula to reach its dorsal apertural margin and is dicalycal. Theca 2^1 originates early in the development of theca 1^2, growing back across the sicula and along the dorsal side of theca 1^1. The second daughter theca of theca 1^2, the dicalycal theca, theca 1^3, originates close to the sicular aperture and is the first theca of stipe 3. The proximal end is therefore strongly asymmetrical with two successive dicalycal thecae growing in the same direction around the sicular aperture and building up the triradiate condition of the proximal end (Fig. 25n). Stipe 1 invariably subdivides after one autotheca, as in *Staurograptus dichotomous* and *Rhabdinopora*. The other first-order stipes are generally of only one or two thecae each.

Description of rhabdosome. – In dorsal (apical) view the three stipes diverge at angles of about 120° to each other. The length of stipes is highly variable both within a single rhabdosome and from rhabdosome to rhabdosome. Within a single specimen, however, stipe length generally increases with increasing number of stipe order. At least six orders of stipes have been observed. Stipes reach a dorsoventral width of 0.5–0.6 mm and a lateral width of about 0.9–1.0 mm. The thecae possess short rutelli and are inclined at about 20–25°. There are 9.0–10.5 thecae in 10 mm. Thecal budding is of normal dendroid triad type with a bitheca associated with each autotheca, alternating along the stipes.

Remarks. – Variability of branching pattern in *Anisograptus* makes differentiation of the several species assigned to this genus difficult. In his description of *A. flexuosus*, Bulman (1950, p. 85), for example, stated that the species is probably related to *A. matanensis*, as there are specimens morphologically intermediate between the two. The species is here regarded as a highly variable one and the several forms differentiated by Bulman (1941, 1950, 1954) as distinct species or subspecies are here regarded as intraspecific variants. They include *A. richardsoni*, *A. flexuosus*, *A. matanensis* var. *tetragraptoides*, and *A. norvegicus*.

Anisograptus ruedemanni Bulman (1941) may be a synonym but is not investigated here. The species is said to differ from *A. matanensis* by its consistently longer first-order stipes, a more declined rhabdosome, and wider stipes (Bulman 1941, p. 112), thus, paralleling the changes seen in the evolution of *Staurograptus*. The two-stiped *Didymograptus primigenius* may consist of a fragmentary *Anisograptus matanensis* or an abnormal specimen with only a single dicalycal theca.

Radiograptus rosieranus Bulman, 1950

1950 *Radiograptus rosieranus* sp. nov. – Bulman, pp. 89–90, pl. 6, figs. 1–3, text-fig. 8

Type specimen. – GSC 9871, Cape Rosiers, the only specimen of this species ever described and figured. The specimen is said to be associated with fragments of anisograptids, probably representing *A. richardsoni* and *A. matanensis* (Bulman 1950, p. 89).

Remarks. – Bulman (1950, p. 90) stated that the branching of *Radiograptus rosieranus* ressembles that of *Anisograptus richardsoni*, but is more robust. The robustness of the stipes, however, could be interpreted as a consequence of rhabdosome maturity. Other characters, such as the spacing of stipes, thecal details and presence of thin dissepiments are identical to those of the early populations of *Rhabdinopora flabelliformis anglica* from

Green Point. Discoidally preserved specimens of *R. f. anglica* are identical to *R. rosieranus* except for their triradiate rather than quadriradiate proximal structure. This leads to the possibility that *R. rosieranus* is an aberrant specimen of *R. f. anglica* in which theca 3^1 failed to produce a dicalycal theca. Until further specimens of the species are found, its identity remains provisional.

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