A PHYLOGENETIC CLASSIFICATION OF
THE GRAPTOLOIDS

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ABSTRACT. Graptolite classification has traditionally been based upon grade groups reflecting general levels of evolutionary complexity. This has been acknowledged as unsatisfactory and the present classification, used widely in the Western world, is a hybrid between this system and what are claimed to be 'natural' groups. A phylogenetic classification, in which taxa are based upon common ancestry, produces a more objective classification with taxa that are diagnosable. We attempt a reclassification of the planktic graptolites (excluding retiolitids) using phylogenetic methods, and employ a cladistic representation of relationships to portray character distribution and decide taxonomic levels. The Graptoloidea are defined as a monophyletic group by retention of a nematophorous sicula in the adult. Hence the Anisograptidae are transferred from the Dendroidea to the Graptoloidea. The higher Graptoloidea fall into two natural suborders: the Virgellina suborder nov. and the Dichograptina Lapworth, which replace the four existing suborders. The Virgellina includes mostly scandent graptolites of monograptid, diplograptid, dicranograptid, nemagraptid, and phyllograptid groups. These are united by having a virgellar spine on the sicula. Recognition of superfamilies within the Virgellina is based upon proximal structure and development type. Seven groups at family level are recognized and it is only within these groups that thecal morphology—long used as the primary criterion for diplograptid genera—is likely to be useful for distinguishing genera. Within the Suborder Dichograptina are two superfamilies: the Glossograptacea is characterized by having isograptid symmetry and contains the families Isograptidae Harris, Pseudisograptidae Cooper and Ni, Corynoididae Bulman, and Glossograptidae Lapworth; the Dichograptacea contains three families, of which the Sigmagraptidae Cooper and Fortey is distinguished by its slender and asymmetrical proximal end, the Sinograptidae by prothecal morphology, while the Dichograptidae is subdivided by the progressive delay and suppression of dichotomies and some generic synonymy is recommended.

Although our scheme embraces all graptoloids, problems remain with determining the interrelationships between some higher order taxa, and with the pendent graptoloids. The Anisograptidae is retained as a paraphyletic group.

MOST modern graptolite workers would like to think that they classify their organisms phylogenetically. Classifications are, however, inherited from earlier workers where different concepts may have prevailed. We cannot necessarily apply our phylogenetic criteria to the available type species of genera, for example, and existing taxa may reflect judgements about whether a group is 'different enough' to be worth recognition at family level, rather then basing its status upon its common ancestry. It is perhaps surprising that there has been relatively little recent discussion about the higher level classification of the graptolites. Most Western workers have followed the *Treatise on Invertebrate Paleontology* in its two editions (Bulman 1955, 1970), and such unity of usage is useful as a convention, although Bulman himself clearly had reservations about whether the high-level classification was correct. New family level taxa were introduced by Mu (1950, 1974), but the phylogenetic basis of these is not clear.

This paper reviews some of the problems of high-level classification, and in particular the status and relationships of the Family Anisograptidae and subordinal taxa in the Graptoloidea. In our analyses we have used a cladistic method for presenting the distribution of characters within and between groups. This method has several advantages: it makes clear what characters are used to define groups which are considered to have descended from a common ancestor; it identifies likely polyphyletic groups; and it points to areas where it is profitable to seek new information. We should emphasize that a cladogram is *not* an evolutionary tree: in many cases it is possible to determine

the actual succession of graptoloid species from stratigraphic criteria, which can also be used as part of the evidence for classification. Cladograms are, however, extremely useful for examining the logic of classification, for determining the taxonomic status of subgroups, and for identifying monophyletic groups.

The principle of phylogenetic classification we follow is that taxa, be they orders, families, or genera, should as far as possible be monophyletic—that is, they include all the descendants of a *single common ancestor*. Nineteenth-century classification tended to be based upon a grade of organization of the rhabdosome that was ambiguously phylogenetic. The past fifty years has seen the breaking up of some of these grade groups. The Glossograptidae, for example, had been recognized as different from other scandent biserial graptoloids, and at present has subordinal status (Glossograptina) with two families and a few included genera. While this makes it clear that the glossograptids have little to do, phylogenetically speaking, with the diplograptids, it contributes nothing to our understanding of the phylogenetic position of the glossograptids within the Graptoloidea as a whole. As we discuss below, the glossograptids are better classified with related groups which share a common ancestor: the high level given to the group in the present classification obscures their relationships. We discuss most groups of planktic graptolites here, excluding only those with reduced periderm (Retiolitidae) which pose detailed problems beyond the scope of this paper.

CHARACTERS OF USE IN HIGH-LEVEL CLASSIFICATION

Almost all taxonomists, other than pure pheneticists, recognize that it is unprofitable to treat all characters as equal. Some characters operate at a more fundamental level than others and are considered more appropriate in the recognition of high-level groups. We believe that all graptolite workers would concur, for example, that the final number of stipes in a many-stiped graptoloid is significant at species level but scarcely at a higher level, and stipe characters (thecal spacing, stipe width and the like) are regarded similarly.

Recently (Cooper and Fortey 1982, 1983) we have emphasized aspects of sicula morphology and proximal structure in the discrimination of higher taxa, following the lead given by Bulman's (1936) classic paper; other authors (Finney 1980; Kearsley 1982) have also implicitly adopted such an approach. Graptoloids sharing distinctive small growth stages were regarded as having descended from a common ancestor, and hence as belonging to a monophyletic group capable of being characterized taxonomically. In the course of describing the proximal end structure of early Ordovician graptoloids we redefined several aspects of terminology for development type. It was shown that the isograptid development mode (with $th1^2$ dicalycal) was the primitive mode for the graptoloids, as opposed to the apparently simpler *artus* mode (with $th1^1$ dicalycal) which had been regarded as 'ancestral' on erroneous morphological grounds. Phyllograptid development was described for the first time, and the polyphyletic origin of quadriserial scandent rhabdosomes was recognized. This paper adopts the concepts and terminology introduced by Cooper and Fortey (1982, 1983), but there is no opportunity here to review all the evidence, and the reader is referred to our earlier works for details.

One way of justifying such an approach is to consider the development of the rhabdosome during astogeny as a series of 'instructions' which have to be followed after commencement of development of the metasicula (see Table 1). Characters of high taxonomic importance are those which are initiated early in the sequence: a change to a single one of these may alter the developmental programme for the rest of the rhabdosome. Conversely, characters of lesser taxonomic moment occur at the end of the development sequence: a change in one of these is effected by a genomic change which leaves the rest of the development untouched. In this category belong the thecal and stipe characteristics, and those relating to the timing and suppression of a distal dichotomy. If our list is approximately correct, it shows that the greater number of such 'instructions' operate on the first few thecae of the colony, which in turn implies that structures at the proximal end are a priori of greater taxonomic significance. On the other hand, quite small changes higher in the list can, in

TABLE 1. Scheme for progressive series of growth decisions which have to be made during the growth of the graptolite colony after the prosicular stage.

1. Initiation (or not) of virgella.
2. Point of origin and formation of initial bud.
3. Direction of growth of first theca (down, across, upward).
4. Direction of growth of distal part of sicula (straight, bend).
5. Growth of first crossing canal.
6. Growth (or not) of 'counterbalancing' lip on sicula.
7. Distal attitude of first theca (to form a pair with the sicula, or extend distally, etc.).
8. Angle subtended between thl^1 and thl^2 (acute, obtuse, greater than 180°).
9. Apertural form of first theca (flared, rectimarginate, denticle etc., usually repeated along subsequent stipes in dichograptoids).
10. Decision about proximal dicalycal theca (thl^1, thl^2, $th2^1$, or later, or suppress).
11. Decision about number of thecae before second dichotomy.
12. Second dichotomy (repeats proximal end).
13. Decision about angle between daughter stipes.
14. Do subsequent dichotomies simply repeat proximal pattern, or are extra instructions introduced (e.g. change angle, introduce additional thecae between branching events, or suppress)?
15. Decision about thecal form to determine stipe characters (three parameters sufficient for graptoloids with simple thecae, see Fortey 1983).
16. Thecal elaboration along stipe (spines, lappets, curvature, and the like).

theory at least, make a considerable difference to the aspect of the colony as a whole. Hence there is a greater chance for the parallelisms that are such a striking aspect of graptoloid history to be initiated by similar developmental switches late in astogeny—and these can only be recognized as such by examination of the more fundamental proximal development.

It follows that higher level monophyletic units within the Graptoloidea are best recognized by development mode and structure of the proximal end. Species with matching proximal end structure are best classified together within a higher taxon. This reveals their common ancestry. The level at which a taxon is recognized is *not* well characterized by its overall 'distinctiveness'—however superficially usable this may seem—but by its common ancestry.

While an entirely monophyletic classification is the aim, we admit that there are many uncertainties, mainly deriving from a lack of morphological information on species designated as types of higher groups; for some time at least it will be necessary to live with some large undivided groups and some paraphyletic high-level taxa. We show inferred relationship in cladograms (text-figs. 1–3, 7–10) and a tentative scheme showing the inferred phylogeny of the major groups discussed here is given in text-fig. 11. The implications of phylogenetic classification for the definition of the Graptoloidea as a whole are considered first.

In the following discussion the terms two, three, and four primary stipes refer to biradiate, triradiate, and quadriradiate rhabdosomes respectively. The primary stipes are in fact formed from *successive* dicalycal thecae in the proximal development of the rhabdosome; they are not produced simultaneously. In a biradiate rhabdosome, for example, the apertures of the first thecal pair lie in the first pair of stipes (first order stipes) and dicalycal thecae are separated along the stipe by a normal theca (text-fig. 4c), whereas in triradiate and quadriradiate rhabdosomes the apertural regions of one or both primary thecae lie in a second order stipe (text-fig. 4D, E).

Derived characters discussed in the text are cross-referenced to the cladograms by numbers in bold face.

CLASSIFICATION OF THE ANISOGRAPTIDAE

The Family Anisograptidae has been traditionally classified in the Order Dendroidea. The intermediate grade of organization of the anisograptids has been recognized at least since Bulman (1949,
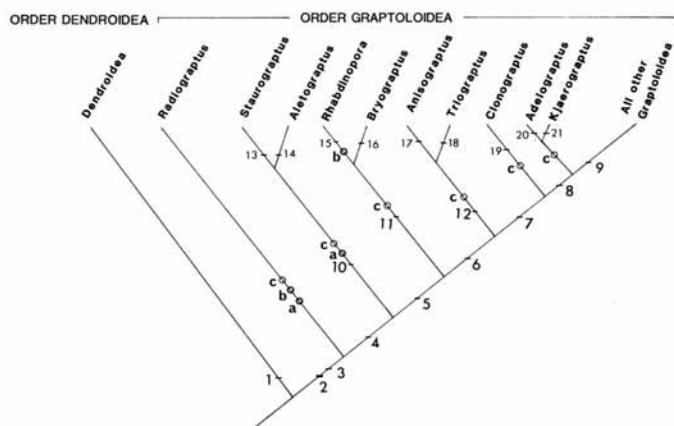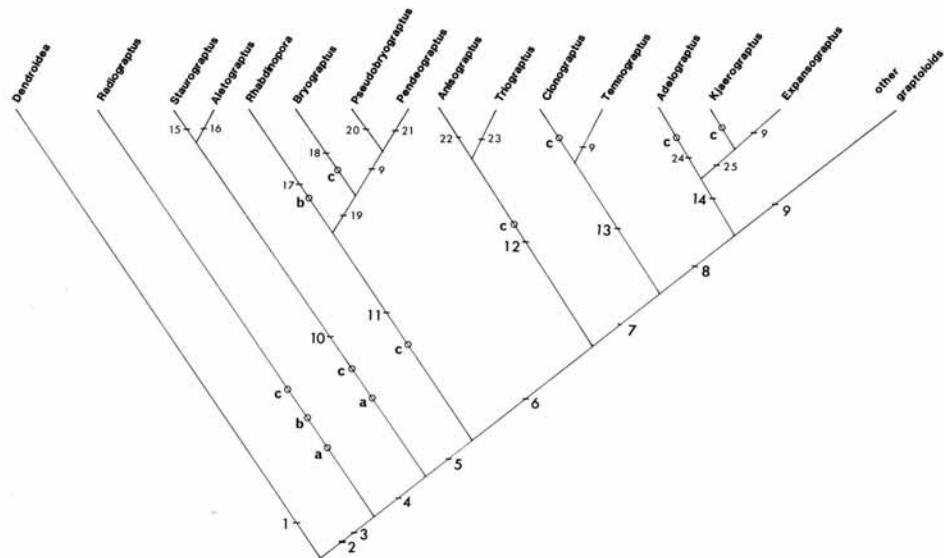
TEXT-FIG. 1. Diagram of relationships of anisograptids, assuming that loss of bithecae (9) happened only once, showing the monophyletic Graptoloidea as a definable taxon. Dashes show derived character states; circles show retained primitive character states. Derived characters are: 1, presence of rooting system; 2, sicula retains nema in adult colony; 3, bilaterally symmetrical colony; 4, dichotomies more or less regular; 5, reduction series in number of primary stipes; 6, three or fewer primary stipes (triradiate or biradiate); 7, two primary stipes (biradiate); 8, ultimate number of dichotomies fixed; 9, loss of bithecae; 10, perfect radial habit; 11, pendent habit; 12, three primary stipes (triradiate); 13, three or more orders of dichotomy; 14, suppression of distal dichotomies; 15, large conical rhabdosome; 16, stipe reduction, loss of dissepiments; 17, three or more orders of dichotomy; 18, as 14; 19, large spreading colony (three orders of dichotomy or more); 20, dichotomies delayed; and 21, only one dichotomy. Retained primitive characters are: a, four primary stipes; b, dissepiments; and c, retention of bithecae.

p. 533) described them as 'transitional between the Dendroidea and Graptoloidea'. Bulman then and subsequently emphasized the seminal role of *Dictyonema* (now *Rhabdinopora*) *flabelliforme* in anisograptid evolution. Indeed he stated that it was 'tempting to claim *D. flabelliforme* as the first ancestral graptoloid', but baulked at so doing because it would 'create problems in diagnosis and definition'. So it has remained. Equally, the 'close and intricate' (ibid., p. 534) relationship between the Graptoloidea and the anisograptids has become an accepted part of the broad view of graptolite evolution.

The diagnosis of the Anisograptidae given by Bulman in 1950 when he established the family emphasized the 'dendroid structure' of the stipes, referring to the presence of bithecae. This is, of course, a retained primitive character of the Graptolithina as a whole, and as such can scarcely be used as diagnostic. The same applies to the basically isograptid development type (Cooper and Fortey 1983). In text-fig. 1 we show a cladistic representation of the character distribution within anisograptid genera. This figure is *not* based on stratigraphic considerations but primarily on a hierarchy of primitive to derived character states, although these are usually mirrored by stratigraphic sequence. Thus, the quadriradiate condition is considered primitive, and three (6) and two (7) primary stipes (triradiate and biradiate) as derived character states (text-fig. 4), because suppression of dichotomies is regarded as a derived condition. In addition, the earliest anisograptids are unique in having two *successive dicalycal thecae* to produce the quadriradiate condition;

suppression of one of these to produce a normal dichograptid-like division on one side of the rhab-dosome is a derived condition in triradiate forms (Cooper and Fortey 1983, fig. 8). The form at the base of the cladogram is that with the greatest number of retained primitive characters (marked as circles), including four primary stipes, retention of dissepiments, and irregular dichotomies. This is the subspecies *Radiograptus rosieranus flexibilis* described recently from the base of the Ordovician in western Newfoundland (Fortey *in* Fortey *et al.* 1982). Recent interpretations of early graptolite phylogeny (ibid.; Erdtmann 1982) based on field occurrences have emphasized the secondary deri-vation of the pendent *Rhabdinopora* rhabdosome, and this is also how it appears on the cladogram. *R. flabelliformis* is not necessarily the *fons et origo* of all subsequent planktic graptolites as tradition-ally claimed, presumably from its widespread geographic occurrence in many rock sections at the base of the graptolitic sequence. The derived character linking all the anisograptids with higher graptoloids is the presence of a nematophorous sicula.

In text-fig. 1 the assumption is made that loss of bithecae (**9**) occurred only once (shown as the autapomorphy of 'all other graptoloids'). If this were the case it would at least be possible to define the Graptoloidea as used at present as a monophyletic group, but even here there are problems. Character 7—two primary stipes with the inclusion of at least one pair of thecal apertures before the first dichotomy (text-fig. 4E)—is *also* shared between two genera of anisograptids (*Clonograptus* and *Adelograptus*) and the higher graptoloids. Why should we not define the Graptoloidea as a monophyletic group having this character rather than on the loss of bithecae? If the cladogram is at all correct it is clearly preferable to extend the Graptoloidea to include all the anisograptids,

TEXT-FIG. 2. Diagram of relationships of anisograptids, this time assuming that loss of bithecae (**9**) is polyphy-letic (compare text-fig. 1). Explanation of symbols as in text-fig. 1 regarding retained primitive characters and derived characters 1-12. Derived characters 13-25 are: **13**, large spreading colony (three or more orders of dichotomy); **14**, dichotomies after dl delayed; **15**, three or more orders of dichotomy; **16**, suppression of distal dichotomies; **17**, large conical rhabdosome; **18**, stipe reduction; **19**, loss of dissepiments; **20**, small size, fewer than three orders of dichotomy; **21**, two orders of dichotomy (four or rarely three stipes); **22**, three or more orders of dichotomy; **23**, as 16; **24**, lax branching, sparse dichotomies; and **25**, only one dichotomy.

defined by the derived character of retaining a nematophorous sicula in the adult. Otherwise there is simply no rational way of separating the anisograptids from the graptoloids other than one of traditional usage.

Several authors (e.g. Bulman 1960, 1970; Erdtmann 1982) have contended that the loss of bithecae did not occur once, as shown by its treatment as a derived character in text-fig. 1, but several times. If this is the case, then the closest relatives of each such graptoloid lacking bithecae is an anisograptid *with* bithecae. A cladogram showing the distribution of characters suggested by such a hypothesis is shown on text-fig. 2. This has to incorporate several dichograptid genera with their supposedly closest related anisograptid neighbours. The classification is now even more difficult than that suggested by text-fig. 1. It becomes impossible to define the Graptoloidea as a monophyletic group if its bounds are to be taken as at present. The stippled area on text-fig. 3 shows how the Order at present defined comes out as (at least) triphyletic. The alternative, to extend the Graptoloidea to include all anisograptids to the right of *Rhabdinopora*, would leave three genera (*Radiograptus, Staurograptus*, and *Aletograptus*) as stem-group graptoloids definable, if at all, only by combinations of primitive characters. Furthermore, the notions of what should or should not be included within a monophyletic Graptoloidea will depend greatly on opinions about whether or not *Pendeograptus* and *Pseudobryograptus* share a common ancestor with *Bryograptus*, questions which are not yet resolved. None of the relationships between bithecae-bearing and graptoloid-like genera shown on text-fig. 2 are yet proved from stratigraphic or morphological grounds, so that the simpler cladogram is still a possibility.

Whichever cladogram proves to represent better the phylogenetic relationships, the implications for classification are the same: genera usually referred to the Anisograptidae are best included within the Graptoloidea. The Order then becomes definable by 'presence' characters (especially

TEXT-FIG. 3. Diagram of relationships from text-fig. 2 showing how the present concept of Graptoloidea (stippled) is polyphyletic; this is avoided by taking the phylogenetic definition proposed in this paper.

nematophorous sicula (**2**)) rather than an 'absence' character (loss of bithecae) which is in contention as polyphyletic.

The Order Graptoloidea can then be diagnosed thus: *Graptolithina retaining nematophorous sicula in adult, and with bilaterally symmetrical colonies, secondarily lost in Monograptacea.*

Remarks on some of the characters and taxa

1. *Radiograptus.* The type species *R. rosieranus rosieranus* has three primary stipes (**12**) according to Bulman (1950). The earliest species *R. r. flexibilis* Fortey *in* Fortey *et al.*, 1982 has four primary stipes—and it is this form which is shown as the sister group of the rest of the Graptoloidea on the diagrams. The type species may be derived directly from that with four primary stipes, or is conceivably independently derived, e.g. from *Rhabdinopora.* It is not shown on the diagrams because of these uncertainties.

2. Chitinized stolon. This is another primitive character which has been described from several anisograptids (e.g. *Rhabdinopora, Clonograptus*), and whose general presence in primitive grapto-loids is perhaps likely, but it is not widely enough described to be marked on the diagrams.

3. *Rhabdinopora.* Some members of the *flabelliformis* group have been shown to possess four primary stipes (Legrand 1974). These forms, strictly speaking, should be separated from the rest on the cladograms as the sister group of all those taxa to the right of *Rhabdinopora* s.s. The strati-graphical evidence for primary stipe reduction is so convincing, however, that they are included within the *Rhabdinopora/Bryograptus* segment, and the derived character (**3**) is taken to include the tendency for primary stipe reduction within accepted monophyletic groups to the right on the cladograms.
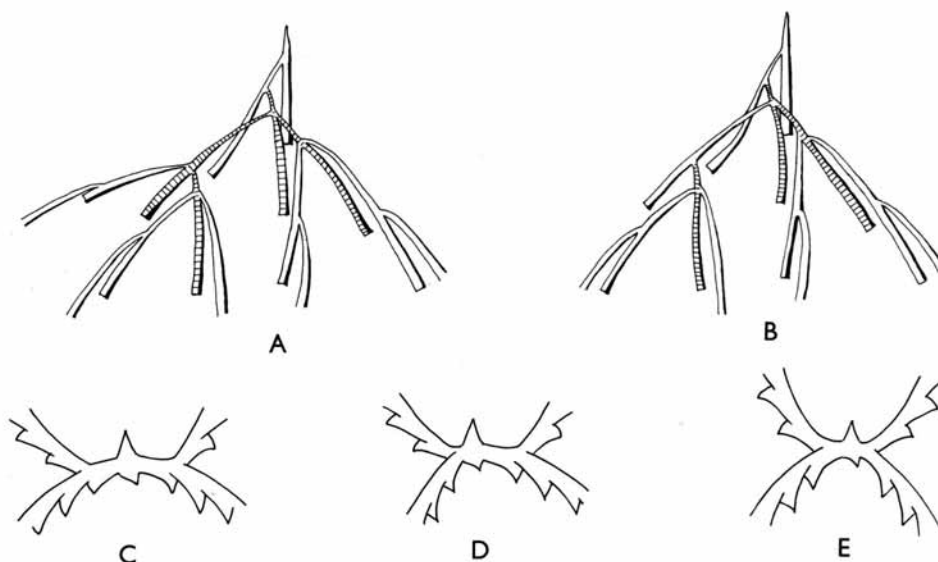
TEXT-FIG. 4. Primitive and derived conditions in anisograptid proximal ends. A, thecal diagram of the primitive quadriradiate condition ('four primary stipes'), showing successive dicalycal thecae (shaded); bithecae omitted following Cooper and Fortey (1983). B, the derived triradiate condition ('three primary stipes') with loss of one dicalycal theca. C–E, rhabdosome proximal ends showing position of apertures of the first thecal pair with respect to the stipes of the first and second orders in the C, biradiate, D, triradiate, and E, quadriradiate condition.

4. Pendent habit (**11**). For a recent view on the geological relationships of *Rhabdinopora* and *Bryograptus* see Erdtmann (1982) and Fortey *in* Fortey *et al.* (1982). Erdtmann's Subfamily Rhabdinoporinae is based primarily on the single derived character of pendent habit. Its usefulness will depend on whether the *Pseudobryograptus* and *Pendeograptus* link is confirmed; if it is, a phylogenetic taxon Rhabdinoporinae will have to include these genera.

5. Two primary stipes (**7**). All graptoloids above the acquisition of this character have, or were derived from, forms with two primary stipes. The characteristic feature is that a pair of thecal apertures open out on the 'funicle' prior to dichotomy(ies) (see text-fig. 4). This feature is also characteristic of all branched dichograptids.

Status of the Anisograptidae

If it is accepted that the Anisograptidae are to be classified within the Graptoloidea as we advocate, there remains the question of the status of this family, based as it is primarily on the retention of the primitive character of bithecae, with the addition of other primitive characters (e.g. dissepiments, irregular dichotomies) in certain early species. There now exist four subfamilies proposed within the group: Staurograptinae Mu, 1974; Anisograptinae Bulman, 1950 (*sensu* Mu 1974); Adelograptinae Mu, 1974; and Rhabdinoporinae Erdtmann, 1982. The first three are essentially formalizations of the main groupings shown on the cladogram (text-fig. 1), based on the number of primary stipes (four, three, and two respectively). The Rhabdinoporinae has to be based on pendent habit because the other character claimed by Erdtmann (presence of dissepiments) is again a primitive character.

It is doubtful whether any purpose is served by recognizing these subfamilies. The Staurograptinae and the Anisograptinae include only the nominate genera, together with one other genus each which are paedomorphic derivatives from the nominate genus (*Aletograptus* and '*Triograptus*' respectively)— and it could be argued that these are not worth generic rank. The use of Rhabdinoporinae depends on whether or not the genera *Rhabdinopora* and *Bryograptus* belong to the same phylogenetic unit as *Pseudobryograptus* and *Pendeograptus*, which is not proven. Stratigraphic evidence may also prove *Anisograptus* to have been derived from *Staurograptus*, in which case separate subfamilies would be redundant. Finally, if either of the cladograms is correct then the Adelograptinae (including *Clonograptus*, *Adelograptus*, and *Kiaerograptus*) is a paraphyletic group; this is not acceptable unless the Subfamily is classified with the rest of the graptoloids (see above), which Mu (1974) does not propose. Subfamily division in the Anisograptidae either seems to introduce excessive splitting, or is taxonomically ambiguous.

For the moment there seems to be no alternative but to retain the Anisograptidae as a paraphyletic taxon characterized by the retention of bithecae. If the polyphyletic view for the loss of bithecae (as shown in text-figs. 2 and 3) is supported by further work, at least the inclusion of the Anisograptidae within the Graptoloidea allows the whole group to be classified as monophyletic. The detailed relationship of the anisograptids to the high-level taxa in the higher graptoloids lacking bithecae (discussed below) is certainly still unclear.

CLASSIFICATION OF GRAPTOLOIDS OTHER THAN THE ANISOGRAPTIDAE

As with the anisograptids there are many problems and unanswered questions to be faced before a detailed classification of the remaining graptoloids can be attempted. Here we suggest a grouping based primarily on the structure of the sicula and proximal part of the rhabdosome (text-figs. 7–10). One problem at the outset is the polyphyletic nature of many genera. Hence it is not possible simply to list all genera and show their phylogenetic relationships on a cladogram if we are aiming towards a monophyletic classification. For this reason we have listed only those genera (appropriately qualified where necessary), species groups, subfamilies, and families for which there are good grounds to assume monophyly. Diplograptid genera are particularly difficult, based as they are primarily upon thecal morphology; the present genera are widely acknowledged to be

polyphyletic. Bulman's analogy of diplograptid evolution—a bundle of fibres (lineages) interwoven into several parallel ropes (genera)—implies that individual lineages pass from one thecal form genus to another and back again.

Bulman (1963, p. 414) wrote: 'Admittedly there has so far been little attempt to trace phylogeny, and future opportunities to carry out more detailed morphological and phylogenetic investigations will undoubtedly introduce taxonomic problems.' It is exactly these taxonomic problems that we are faced with here. The species groups shown on the cladograms are discussed briefly in the following sections, but we are conscious of many problems that remain before our graptoloid classification can be regarded as definitive. Our aim at the moment is to try to identify morphological characters that are useful in recognizing high-level monophyletic groups and to trace this distribution throughout as many sub-groups as possible.

Our main attention is given to the dichograptids, but we include diplograptids in some cladograms (text-figs. 9 and 10) to show some characters useful for establishing relationships within this latter group, and to show how they relate to Dichograptina. Lack of morphological information about some groups means that they are perforce left undivided. The 'species groups' listed in the cladograms are not necessarily of equal rank. We do not recognize a taxon exactly equivalent to the Suborder Diplograptina as used by Bulman (1970), so we refer to the biserial graptolites of this group informally as *diplograptoids* in the following discussion.

Primitive characters shared with anisograptids. There are a number of characters shared with the anisograptids, presumed to be primitive, and therefore of no direct use in recognizing groups within non-anisograptid graptoloids. These include: 1, isograptid development type; 2, simple thecal form; 3, rhabdosome with biradiate origin; 4, bilaterally symmetrical rhabdosome; 5, regular number of dichotomies in rhabdosome; 6, dicalycal thecae separated on the stipes by one or more normal thecae (i.e. not successive); 7, capacity for numerous dichotomies in the rhabdosome; and 8, stipe length unrestricted.

Suborders Dichograptina and Virgellina

At the highest level we recognize two major groups within the non-anisograptid graptoloids, based upon the presence or absence of a virgella in the sicula (text-fig. 5A–F). The Suborder Virgellina is proposed here for those graptoloids having such a spine (67); it is shown as a monophyletic group on text-figs. 7 and 8. At first glance this feature may not seem a very significant one on which to define a major division. It is, however, developed on the metasicula, that part of the colony directly developing from the larval prosicula, which is presumed to be sexually produced (all subsequent development of the colony being by asexual budding). Furthermore, the virgella is not merely a late stage apertural modification, but is present in earlier metasicular development, as shown on growth stages (Bulman 1932, pl. 2, figs. 1–20) and by deflection of growth lines (text-fig. 5A, B). It is in fact one of the earliest 'decisions' required by the developing colony (Table 1).

In general among graptoloids the sicula is not highly variable in morphology: elaboration of the aperture is known in *Corynites* (Kozlowski 1956) and many monograptids, but in the bulk of the graptoloids variation is largely confined to overall size (other than dorsal apertural processes produced at a late stage in metasicular development). The presence or absence of a virgella is one of the very few structural features of sicular morphology, if not the only one, that can be recognized and readily used in taxonomy, at least in our present stage of knowledge. Its presence serves to unite the whole group of diplograptids s.l., monograptids, dicellograptids, and nemagraptids with the one group of 'dichograptoids' that has a diplograptid-like proximal end (Cooper and Fortey 1983, fig. 5)—the phyllograptids—while at the same time excluding the glossograptids, now thought to be derived from *Pseudisograptus* (Cooper and Ni 1986). It is significant that the development and structure of the virgella is apparently closely similar in Phyllograptidae and the remaining virgellinids (cf. text-fig. 5A, B). The change in origin of thl[1] from the antivirgellar side (in Phyllograptidae) to the virgellar side (in the remaining virgellinids) is not accompanied by a change in the virgella itself—another reason why we believe it to be monophyletically derived and of high taxonomic value.
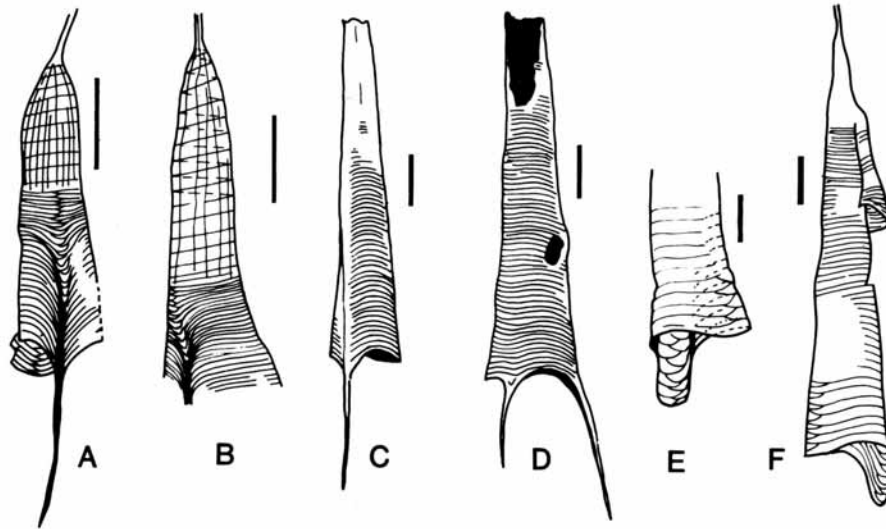
TEXT-FIG. 5. The virgella and analogous structures. A, *Xiphograptus formosus formosus* (Bulman), partially grown metasicula showing early formation of virgella (after Skevington 1965, fig. 19). B, *Dicranograptus nicholsoni* Hopkinson, showing early formation of virgella (after Bulman 1944, text-fig. 20). C, D, *Climacograptus typicalis* Hall, partially grown (C) and fully grown (D) metasicula showing late development of dorsal spines (after Bulman 1932, pl. 1, figs. 1, 4, respectively). E, *Corynoides* cf. *gracilis* Hopkinson, distal end of mature metasicula showing lamelliform ventral process (after Bulman 1947, text-fig. 39m). F, *Pseudisograptus geniculatus* (Skevington), complete but immature sicula showing extended ventral process (after Skevington 1965, fig. 52). Scale bars represent 0·2 mm.

The change in side of origin of th1^1 is likely to have accompanied the change from a prosicular to a metasicular origin (discussed below).

The presence of a virgella spine may or may not be a character with particular adaptive importance for the developing colony, but it should be noted that it is quite legitimate to use even a relatively minor character in the recognition of a major group. The character need only signify a speciation event in the early history of an evolving plexus; if the character is retained in descendants of the first species having it, then it becomes of taxonomic importance regardless of theories about its function. The taxonomic level which the character serves to define is really a matter of the diversity and size of the subsequent speciation—in the case of the Virgellina more than half the known graptoloids.

Our grouping of forms with a virgella differs fundamentally from previous high-level groupings, hence we coin a new subordinal name—Virgellina. The nearest existing concept for this group is possibly Axonophora Frech, 1897 (as reviewed by Mu 1950, 1974), which, however, excluded the Nemagraptidae, Dicranograptidae, and Phyllograptidae. For the other suborder (discussed below) we use Dichograptina Lapworth, 1880, in order to avoid conceptual confusion with the Didymograptina Lapworth, 1880, which was used in the *Treatise* (Bulman 1970) to include the Nemagraptidae, Dicranograptidae, and Phyllograptidae—all families which are included within the Virgellina here. There are outstanding problems in the relationships between the Dichograptina (in which we include the Glossograptacea and the Dichograptacea) and the Virgellina; this is indicated by an

unresolved trichotomy on text-figs. 7-10. A strictly cladistic treatment would accord Glossograp-tacea and Dichograptacea subordinal status like that of Virgellina in view of this trichotomy; we prefer for the moment to unite these two superfamilies within a Suborder Dichograptina, even though this is based upon a shared primitive (absence of virgella) character rather than a derived character, at least until more is known about the phylogenetic history of these graptolites.

Discussion of characters

Isograptid symmetry (**55**). The Dichograptina is divided into two major groups. The superfamily Glossograptacea is characterized by having isograptid symmetry, i.e. the sicula and thl^1 form a symmetrical pair (text-fig. 6c, D), and the axis of rhabdosome symmetry passes between them (Cooper 1973). The primitive condition is found in the remaining Dichograptina; the axis of rhabdosome symmetry passes through the sicula itself, and the sicula and thl^1 form an asymmetrical pair.

Development type. Development type refers to the thecal budding arrangement at the first dichotomy in the rhabdosome (Cooper and Fortey 1983). The primitive condition shared with dendroids and early graptoloids is the isograptid development type; this type prevails in the great majority of Dichograptina and in the Family Phyllograptidae of the Virgellina. It has been shown that in species whose thecal budding pattern is known at distal dichotomies (i.e. at formation of branches) the pattern replicates the isograptid development type (Cooper and Fortey 1983). Thus only one development type is employed throughout the entire development of the rhabdosome. Deviation from the isograptid type goes in one of two directions. First, the dicalycal theca may appear earlier in the sequence and may be thl^1 instead of thl^2. This produces what has been termed the *artus* development type, and is found in some pendent didymograptids of Arenig to Llanvirn age, together with odd species like *Kinnegraptus kinnekullensis* and *Oncograptus upsilon*. Secondly, the dicalycal theca may appear later in astogeny and be $th2^1$ (**72**) or a later theca, collectively referred to as diplograptid development type by Cooper and Fortey (1982). Further work is needed to characterize the various development types found in this group, but the delayed dicalycal theca serves as a useful apomorphic character to define superfamilies Diplograptacea (and Dicranograptacea). In Monograptidae the initial dichotomy is lost and the character has no chance of expression, but we know that *Glyptograptus* s.s., which has it, is the sister group of monograptids.

Proximal structural types. We rely heavily on proximal structural types in defining major groups within the non-anisograptid graptoloids. These types are discussed and described in the outline of the proposed classification below and are illustrated in text-fig. 6.

The earliest diplograptaceans, the '*Glyptograptus*' *austrodentatus* group of species (which differs from the type species *G. tamariscus*), have a strong downward component of growth in their early thecae (thl^1, thl^2, and $th2^1$), giving the proximal end a square symmetrical outline. Particularly in later diplograptids, thl^2 and $th2^1$ have a less prominent downward component of growth giving the proximal region a more pointed outline. A morphological transition between one and the other was claimed by Bulman (1936, pp. 88-93, text-fig. 29), who later named and described them as the *streptoblastic* and *prosoblastic* type respectively (Bulman 1963). Commonly associated with the streptoblastic type is the left-handed origin and strongly sigmoidal growth path of thl^2. The streptoblastic type is found in *Dicaulograptus hystrix*, *Gymnograptus retioides*, *Pseudoclimaco-graptus* spp., as well as the *austrodentatus* group. The prosoblastic type is typified by such forms as *Orthograptus apiculatus* (described by Bulman 1946), *O. gracilis* (*sensu* Bulman 1932, and *Amplexograptus maxwelli* (*sensu* Walker 1953).

A more refined classification of proximal structural types is applied to all diplograptoids by Mitchell (in press), and incorporates features of growth and construction such as the formation of a cowl during the early development of thl^2 and its daughter $th2^1$, and the formation of a ventral plate which grows up and eventually joins the cowl to form the second 'crossing canal'. Nine proximal patterns (termed A—I) are recognized and fully explained by Mitchell (in press). The terms streptoblastic and prosoblastic therefore no longer seem useful, and in our cladograms
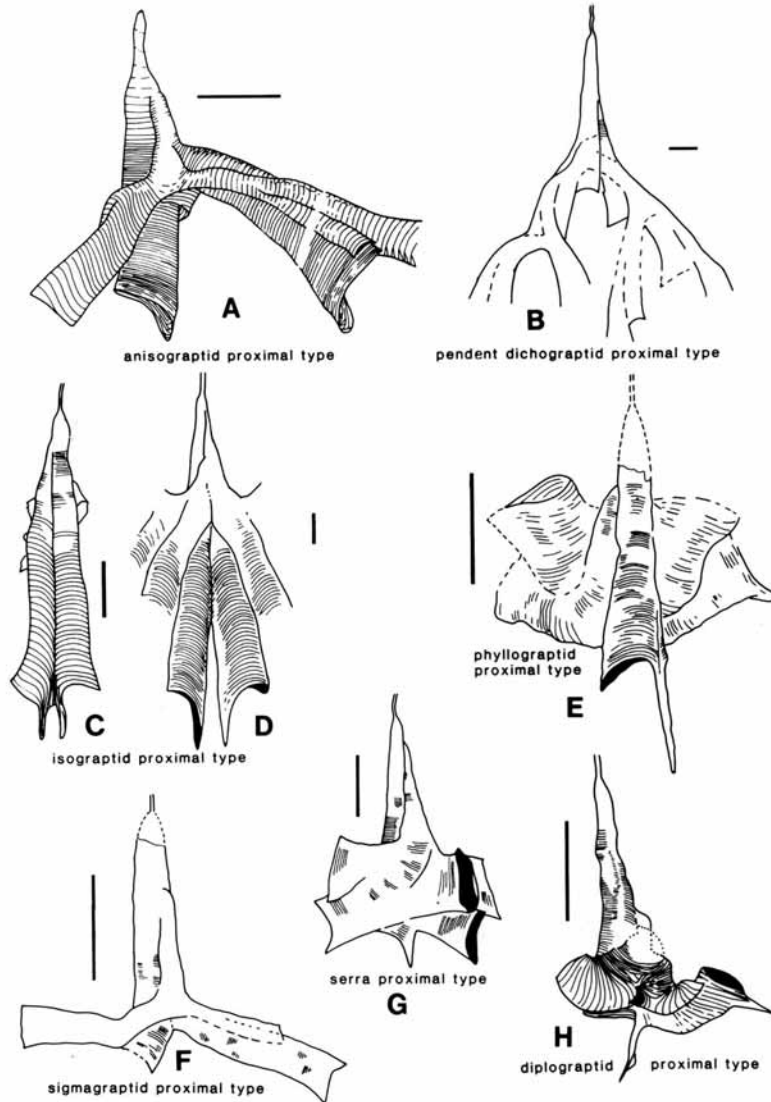
TEXT-FIG. 6. Proximal structural types used in classification. A, anisograptid listed as *Clonograptus tenellus?* by Hutt (1973, fig. 6c). B, *Tetragraptus* (*Pendeograptus*) *fruticosus* Hall (after Cooper and Fortey 1982, fig. 30f). C, *Pseudisograptus geniculatus* (Skevington) (after Skevington 1965, fig. 53b). D, *Isograptus* '*gibberulus*' (Nicholson *sensu* Bulman 1932, pl. 8, fig. 2). E, *Phyllograptus typus* Hall (after Cooper and Fortey 1982, fig. 71f). F. *Sigmagraptus praecursor* Ruedemann (after Cooper and Fortey 1982, fig. 61c). G, *Tetragraptus* (*Tetragraptus*) *phyllograptoides triumphans* Cooper and Fortey (1982, fig. 22b). H, '*Glyptograptus*' *dentatus* (Brongniart) (after Skevington 1965, fig. 61a). Scale bars represent 0·5 mm.

(text-figs. 7 and 8) we employ Mitchell's proximal patterns instead, and follow his mapped distribution of these among the diplograptoids.

Cladia (**73**). Cladia are branches formed at the apertural margin of the sicula or a theca; they differ fundamentally in their mode of origin from the branches produced by dichotomous division. They are known in the Cyrtograptidae and have recently been found in the Nemagraptidae (Finney 1985). The capacity for production of cladia presumably appears with the change in development type from isograptid to diplograptid. If this inference is correct it can be predicted that branching in the Dicranograptidae (e.g. in rare specimens of *Leptograptus*, and in *Ordosograptus*) is cladial rather than dichotomous.

Biseriality and monoseriality. The primitive state for the Graptoloidea is monoseriality. Among the Dichograptina scandency was attained at least six times independently if the relationships shown in text-figs. 7 and 8 are correct (independent lineages would be found for *Pseudophyllograptus*, *Phyllograptus*, *Pseudotrigonograptus*, *Skiagraptus*, *Cardiograptus*, and the Glossograptidae), producing biserial, triserial, or quadriserial forms. Among the Virgellina it is possible that scandent biserial rhabdosomes were also attained more than once, but our cladograms and inferred phylogenetic tree (text-fig. 11) suggests that this was not so (**74**). If stratigraphic evidence is accepted that the '*G.*' *austrodentatus* group is ancestral to the Diplograptacea, then it follows that biseriality is an apomorphic character for the whole group, and that monoseriality has been secondarily acquired in the nemagraptids and dicranograptids (**86**) and, of course, in the Monograptacea (**79**).

Prosicular and metasicular origin of thl^1 (**70**). A prosicular origin of thl^1 is primitive, being shared by the Anisograptidae (Hutt 1974) and the early Dichograptina and Virgellina (Cooper and Fortey 1982). Unfortunately, preservation is rarely good enough to determine the point of origin of the first theca, but a prosicular origin seems to be more general among the Dichograptina, whereas a metasicular origin is general (with apparently no exceptions) among the Dicranograptacea and Diplograptacea (**70**). A prosicular origin is retained in the Phyllograptidae. A metasicular origin is regarded as a synapomorphy for the Monograptacea and the Diplograptacea. Its rare appearance in certain Dichograptina (e.g. *Didymograptus artus*) is, therefore, considered to be a parallelism.

Stipe reduction and dichotomy delay. Stipe reduction has long been regarded as an important 'trend' in graptolite evolution. More fundamental, in terms of the rhabdosome development programme, is the number of orders of dichotomy present, since rhabdosomes with, for example, three orders of dichotomy may have five, six, seven, or eight terminal stipes (e.g. *Dichograptus octobrachiatus*). We therefore discuss the branching dichograptinids in terms of the pattern, distribution, and number of orders of dichotomy. The first order is termed d1, the second order d2, and so on for ease of reference.

There is no doubt that the capacity for many orders of dichotomy, as expressed in the multiramous dichograptinids, is a primitive character shared with the anisograptids. It is present in the sister group of the higher Graptoloidea (*Clonograptus*; text-fig. 1). Furthermore, this assumption is supported by at least one stratigraphically based lineage known from several sections around the world, this being *Pendeograptus fruticosus* in which first four, then three, then two stiped forms appear in upward sequence. Recognition of the primitive nature of multistiped rhabdosomes is important for establishing relationships among the Dichograptacea. In the primitive state dichotomies are *consecutive* (defined under branching styles) at least for the first several orders, and this state is modified by delaying a particular dichotomy, for example d3, such that the stipe segment between d2 and d3 contains several thecae instead of just one. The least modification of the primitive state is a delay in distal dichotomies (**36**). Suppression of a dichotomy can be regarded as an indefinite delay, and more fundamental changes to the rhabdosome are introduced by the more proximal position of a suppressed or delayed dichotomy (**29, 30, 34–44, 46, 49–51,** and **54**). The ultimate state is the suppression of dichotomy d1, resulting in the single-stiped rhabdosome of *Azygograptus*.

Branching style. Terms to denote styles of branching in a rhabdosome were given by Cooper and Fortey (1982, table 2). In *progressive* branching, each of the two daughter stipes resulting from a dichotomy divides again, whereas in *monoprogressive* branching (**52, 53**) one stipe remains undivided (e.g. *Sigmagraptus, Pterograptus,* and *Brachiograptus*). Dichotomies can be *consecutive,* when dicalycal thecae are separated along the stipe by a normal 'unicalycal' theca, or *delayed,* when two or more thecae separate dicalycal thecae.

Monoprogressive branching usually follows one or more orders of progressive branching in the proximal regions of the same rhabdosome, either in a regular ordered manner, as in *Goniograptus,* or in an irregular manner, as in *Clonograptus* or *Zygograptus,* where occasionally stipes of a relatively early order remain undivided while their sister stipes go on to several further orders of dichotomy. Distal dichotomies of multistiped rhabdosomes, particularly those with progressive branching, are commonly somewhat delayed; this is necessary to avoid overcrowding of stipes. A single early dichotomy may be delayed, as in *Zygograptus* (**35**), or all dichotomies after one, two, or three orders of consecutive dichotomy may be delayed, as in *Mimograptus* (**40**), *Temnograptus* (**38**), and *Orthodichograptus* (**37**) respectively.

No distinction is made here, so far as branching type is concerned, between 'lateral' and 'dichotomous' branching (see Bulman 1970, pp. V82–85). All branching is produced by dichotomy (also referred to as dichotomous division or stipe division) and the difference between lateral and dichotomous branching is the result of the directions of growth of the two daughter stipes. The distinction has little influence on subsequent decisions in a development programme and is unlikely to have much taxonomic importance.


CLASSIFICATION OF THE DICHOGRAPTINA

Dichograptacea

The major group of dichograptinids is the Superfamily Dichograptacea (text-fig. 7), which lacks isograptid symmetry. Four subfamilies can be distinguished on the basis of proximal end structure.

In the Subfamily Sigmagraptinae Cooper and Fortey, 1982 (text-fig. 6F) the sicula and early thecae are slender, especially the prothecal segment of th2^1, and thl^1 and thl^2 diverge from the sicula at different levels; these features can be referred to as the *sigmagraptine proximal end* (**47**). Relationships within the subfamily are based on branching characteristics: forms with monoprogressive branching (**52, 53**) have one or two initial progressive (normal) dichotomies, e.g. *Sigmagraptus* (?synonym of *Thamnograptus* Hall) and *Goniograptus* respectively, and in the case of *Yushanograptus* the second dichotomy is delayed (**54**); *Laxograptus* has only progressive dichotomies, but all are irregularly delayed (**50**); *Acrograptus* can be regarded as a sigmagraptine in which dichotomy d2 has been suppressed, and could thus be more closely related to either the *Laxograptus* or *Sigmagraptus* clades.

The Subfamily Tetragraptinae Mu, 1950 includes forms with a massive structure on the reverse side of the rhabdosome formed by the crossing canals thl^2, th2^1, and the proximal portion of th2^2. This proximal end can be referred to as a *T. serra proximal type* (**28**) and is displayed by *T. (T.) serra, T. (T.) reclinatus,* and *T. (T.) phyllograptoides* (see Cooper and Fortey 1982, fig. 22; text-fig. 6G herein). Reclined stipes and suppression of distal dichotomies appear to accompany the feature. The *T. (T.) serra* species group, *T. phyllograptoides, Pseudophyllograptus cor,* and the remaining *Pseudophyllograptus* spp. all belong within this group; the relationships among them have been discussed by Cooper and Lindholm (1983) and are shown on text-fig. 7. *Dichograptus solidus* may represent a member of the group in which dichotomy d3 has not been suppressed; it is suppressed in all others.

The Subfamily Dichograptinae Lapworth, 1880 retains a primitive, generalized dichograptid proximal end and is subdivided on the pattern and distribution of dichotomies. The group is characterized by the regularity of its branching, at least until delayed dichotomies are introduced at higher levels. At the lowest level a delay in dichotomy d2 (**35**) results in the rhabdosome of
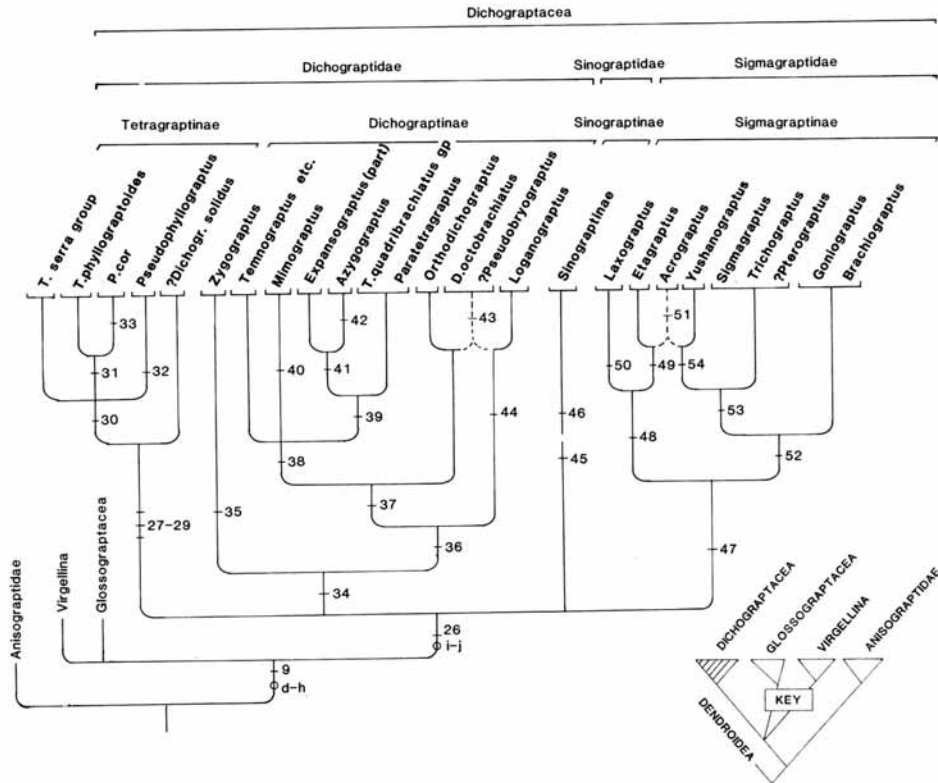
TEXT-FIG. 7. Cladogram of relationships of the main species groups included within the Superfamily Dichograptacea. Suggested groupings at subfamily and family level are indicated. All groupings are monophyletic. Derived characters are: **26**, ultimate number of orders of dichotomy in the rhabdosome limited (generally not exceeding seven); **27**, reclined stipes; **28**, *serra*-type proximal end; **29**, dichotomy d4 suppressed; **30**, dichotomy d3 suppressed; **31**, partially scandent; **32**, fully scandent; **33**, proximal gape; **34**, branching pattern regular (lost where dichotomies become delayed); **35**, dichotomy d2 delayed; **36**, dichotomies after d4 delayed; **37**, dichotomies after d3 delayed; **38**, dichotomies after d2 delayed; **39**, dichotomy d3 suppressed; **40**, dichotomies after dl delayed; **41**, dichotomy d2 suppressed; **42**, dichotomy dl suppressed; **43**, dichotomy d4 suppressed; **44**, five or more stipes attained by proximal dichotomy; **45**, prothecal folds; **46**, dichotomy d4 suppressed; **47**, sigmagraptine proximal end; **48**, all dichotomies delayed; **49**, dichotomy d4 suppressed; **50**, dichotomies irregularly delayed; **51**, dichotomy d2 suppressed; **52**, monoprogressive branching after dichotomy d2; **53**, monoprogressive branching after dichotomy dl; and **54**, dichotomy d2 delayed. Primitive retained characters are: **d**, prosicular origin of thl[1]; **e**, progressive (normal) branching pattern; **f**, generalized dichograptid proximal end; **g**, isograptid development type; **h**, capacity for large number of dichotomies; **i**, lack virgella; and **j**, asymmetry of sicula and thl[1].

Zygograptus. A progressive delay in dichotomy, starting from distal and working towards proximal dichotomies, characterizes the multiramous genera *Orthodichograptus, Temnograptus,* and *Mimograptus* (**37, 38,** and **40**). Suppression of dichotomies can also be traced progressively from distal to proximal through the classical series *Loganograptus-Dichograptus octobrachiatus,* tetragraptids of the *quadribrachiatus* and *approximatus* groups, and extensiform didymograptids (**39, 41, 43,** and **44**). It becomes clear that on the basis of these branching characteristics there is little justification for maintaining all the members of the *Temnograptus* group (i.e. *Temnograptus* Nicholson, *Schizograptus* Nicholson, *Trochograptus* Holm, *Holograptus* Holm, and probably *Calamograptus* Clark) as distinct genera; *Temnograptus* (or *Schizograptus*) takes priority.

Two minor groups are also distinguished on text-fig 7. The sinograptids are characterized by the exaggerated development of prothecal folds (**45**), and relatively few stipes. Little is known of their proximal structure, but it appears to be of a generalized dichograptid type; hence their position on the cladogram is not certain. They could, for example, form a sister group with that containing *Dichograptus octobrachiatus*; this would assume that suppression of dichotomy d4 is a more primitive character than the acquisition of prothecal folds. They are tentatively shown as a separate sister group (Subfamily Sinograptinae Mu, 1957) to the three main groups above. A second minor group comprises the Arenig species referred to *Clonograptus,* such as *C. persistens* and *C. magnificus.* Little is known about the morphology of these forms; they retain primitive (clonograptid) branching characteristics but bithecae have not been seen. They may prove to be a distinct group lacking the regularity of branching and limited numbers of orders of dichotomy that characterize the four main groups; on the other hand, they may prove to be nothing more than stratigraphically late *Clonograptus.* They are not shown on the cladogram because of these uncertainties. Another group of species not shown is the pendent plexus (*Didymograptus s.s., Pendeograptus,* and *Pseudobryograptus*). *Didymograptus* is known on stratigraphic grounds to have had two evolutionary 'bursts', distinguished by Cooper and Fortey (1982) as the subgenera *Didymograptus (Didymograptus)* with artus development and *Didymograptus (Didymograptellus)* with isograptid development. The main problem in establishing their relationships is in assessing whether or not the pendent habit is of phylogenetic significance. If it is a derived character for the whole group, then the suppressed dichotomy d2 in *Didymograptus* s.l. has been independently derived and its sister group is *Pendeograptus.* As discussed above, *Pendeograptus* and *Pseudobryograptus* could in turn relate to the anisograptid group Rhabdinoporinae. We are not certain whether this is the case, however, and if the pendent habit was acquired more than once the closest relatives of pendent *Didymograptus* might be found in dichograptid groups such as *Expansograptus* or *Corymbograptus.* We leave the group unassigned because of these uncertainties.

Finally, we note that the relationships among the four dichograptacean subfamilies are far from clear, and the relative order of the advanced characters which distinguish them is uncertain. In particular, Dichograptinae is retained on the basis of primitive, rather than derived characters, and its relationship to Tetragraptinae may be subject to change when more is discovered about the detailed structure of these early graptoloids.

Glossograptacea

The acquisition of isograptid symmetry (**55**) (isograptid proximal type; text-fig. 6c, D) appears to be accompanied by a reclined attitude of stipes and to characterize a broad group within the Dichograptina, the Superfamily Glossograptacea Lapworth, 1873 (text-fig. 8). The pseudisograptids have been described and discussed by Cooper and Ni (1986) and shown to share several features with the Glossograptidae, including partially developed pseudopericalycal (defined by Cooper and Ni) proximal structure. Fully developed pseudopericalycal structure (**65**) is confined to the Glossograptidae. The pseudisograptids and glossograptids were regarded as sister groups, and the Suborder Glossograptina Jaanusson was therefore downgraded to subfamily level; the Subfamily Pseudisograptinae was accepted as a paraphyletic stem group. The Corynoidinae were paedomorphically derived (**66**) from a glossograptid (either pseudisograptine or glossograptine) and share the extended ventral apertural processes with that group. Together the three subfamilies comprise the family
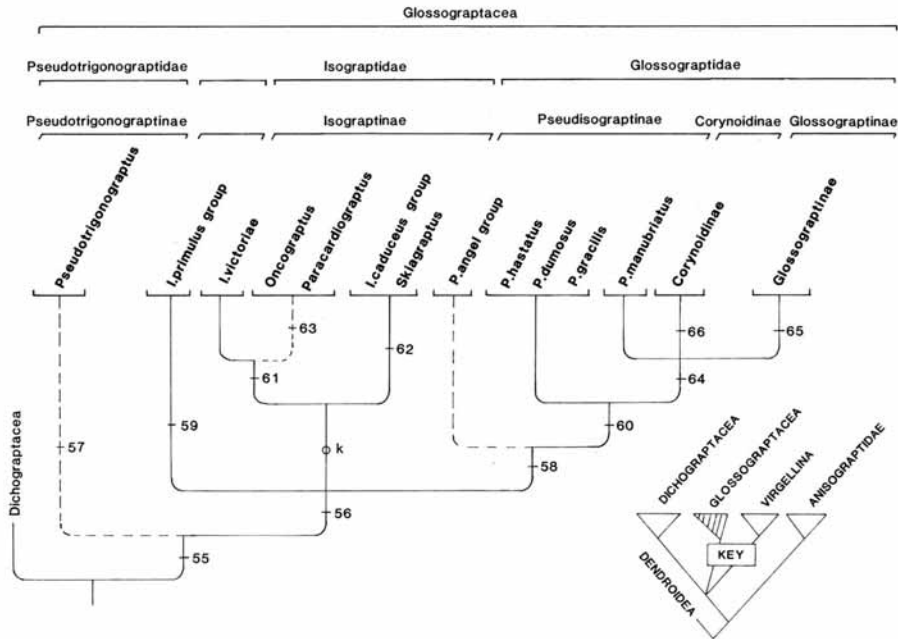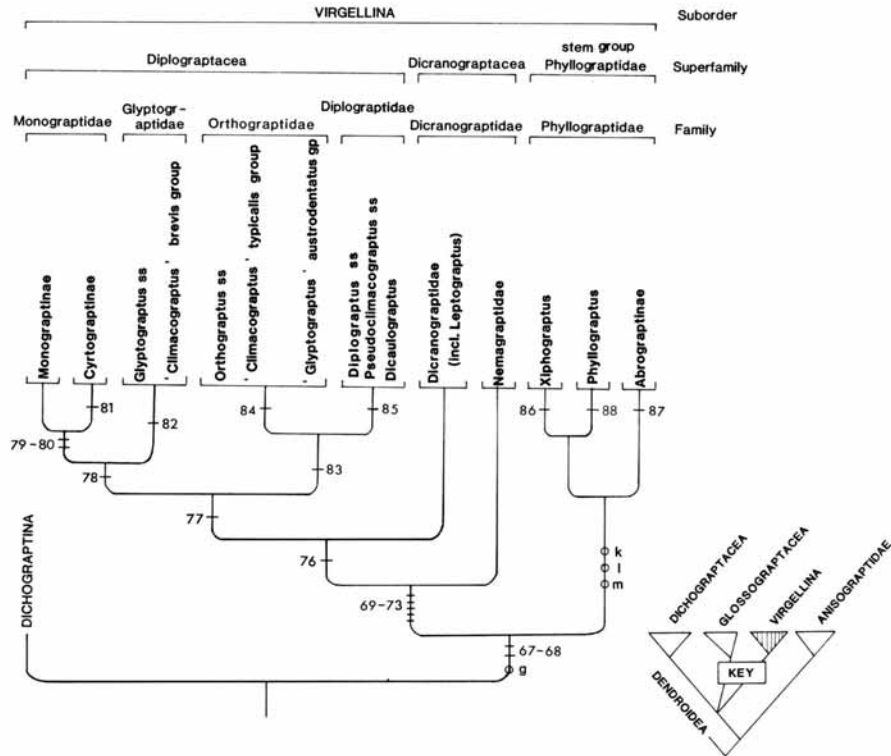
TEXT-FIG. 8. Cladogram of relationships of the main species groups included within the Superfamily Glossograptacea. Suggested groupings at the subfamily, family, and superfamily levels are indicated. All groupings are monophyletic except for the Pseudisograptinae which is retained as a paraphyletic stem group following Cooper and Ni (1986). Derived characters are: **55**, isograptid symmetry of sicula and thl[1]; **56**, dichotomy d2 suppressed; **57**, scandency; **58**, presence of manubrium; **59**, high initial angle of inclination of thecae; **60**, well-developed manubrium; **61**, smoothly rounded ventral margin; **62**, sicula and thl[1] project ventrally; **63**, partial or complete scandency; **64**, advanced manubriate thecal form (see Cooper and Ni 1986); **65**, pseudopericalycal proximal structure (see Cooper and Ni 1986); and **66**, paedomorphism. Retained primitive characters are: **k**, low initial angle of inclination of thecae.

Glossograptidae. Cooper and Ni regarded the subfamily Isograptinae *sensu* Cooper and Fortey, 1982 to be the sister group of the Glossograptidae, but the isograptines may be diphyletic (Cooper 1973; Cooper and Fortey 1982). The species group containing *I. primulus* Harris, *I. scandens* Cooper and Fortey, and the Swedish *I. 'gibberulus'* (*sensu* Bulman 1932) is thought to have been independently derived and is shown separately on text-fig. 8. Although the *I. victoriae* group is thought likely to be more closely related to the Glossograptidae than to the *I. primulus* group, we know of no characters (other than the primitive one of low initial thecal inclination) that unite the Isograptinae and the Glossograptidae without also including the *I. primulus* group; these are therefore shown as an unresolved trichotomy on text-fig. 8.

CLASSIFICATION OF THE VIRGELLINA

All members of the Virgellina carry a virgellar spine on the sicula (**67**). The suborder is divided in the first instance on the structure and development of the proximal end (text-figs. 9 and 10). The

primitive isograptid development type is retained by only one group, the stem group Phyllograpti-
dae, which also retains the prosicular origin of thl[1] and simple dichograptid thecae. *Phyllograptus*
and *Xiphograptus* are the only two genera included with certainty, together with an unnamed
reclined tetragraptimorph from Victoria (Vandenberg *in* Vandenberg and Stewart 1984). This no
doubt reflects the lack of knowledge of sicular structure in the large majority of forms currently
included in Dichograptacea, and the full list of Phyllograptidae is likely to prove larger. Tentatively
included in the family is the Abrograptidae Mu, 1958, in which the periderm has become so reduced
that it is no longer possible to interpret such features as development type and proximal structure;

TEXT-FIG. 9. Cladogram of relationships among species groups and genera included within the Suborder
Virgellina, assuming that the right-handed origin of thl[2] in the Nemagraptidae is a primitive character
shared with the Dichograptina. Suggested groupings at family and superfamily level are shown; all are
monophyletic except for the Dicranograptidae. Derived characters are: **67**, virgella present; **68**, dicho-
tomy d3 suppressed; **69**, dichotomy d2 suppressed; **70**, metasicular origin of thl[1]; **71**, sigmoidally curved
thecae; **72**, th2[1] dicalycal; **73**, capacity for cladia generation; **74**, biserial; **75**, simple sicula with dorsal
sinus; **76**, left handed origin of thl[2]; **77**, complication of sicular apertural margin; **78**, asymmetrical
proximal end; **79**, dichotomy dl suppressed; **80**, sinus origin of thl[1], **81**, cladia present (or potentially
so); **82**, type B proximal pattern; **83**, symmetrical proximal end; **84**, type A proximal end; **85**, type C
proximal end; **86**, partial or complete monoseriality; **87**, reduction of periderm; and **88**, scandency.
Retained primitive characters are: **k**, thl[2] dicalycal; **1**, prosicular origin of thl[1]; and **m**, dichograptid
thecae.
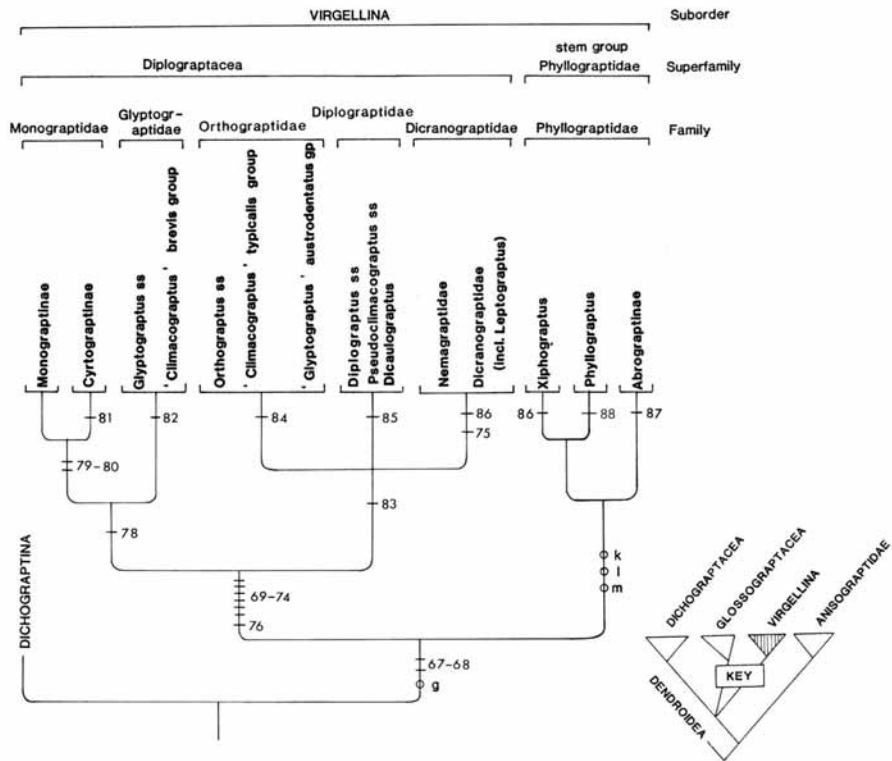
TEXT-FIG. 10. Same as text-fig. 9 except that the Nemagraptidae and Dicranograptidae form a group sharing partial or complete monoseriality. This arrangement has the advantage of comprising only monophyletic taxa and being consistent with stratigraphy.

a virgellar spine, however, is apparently present. Finney (1980) has suggested that the biserial form *Reteograptus* belongs within the family. '*Azygograptus*' *incurvus* Ekström (Finney 1980, text-figs. 9 and 10) also bears a virgella and should be included.

In all the remaining Virgellina an isograptid development type has been modified by a delay in the dicalycal theca which, instead of being thl^2 becomes $th2^1$ (72), $th2^2$, or a later theca. The loss of a capacity of (normal) isograptid branching and, instead, the acquisition of a potential for cladia generation appears to accompany this change.

The approach to the problem of diplograptoid classification adopted by Kearsley (1982, 1985) and Mitchell (in press) is entirely consistent with the principles of graptolite classification set out here. The group is subdivided on features of the proximal end, particularly sicular structure, proximal symmetry, and pattern of proximal construction, and we largely follow Mitchell (in press) to whom reference should be made for explanation and definition of his nine constructional patterns A–I and synapomorphies.

Two major groups can be recognized on the basis of proximal symmetry. First, a symmetrical proximal end (83) is shared by two families, Diplograptidae and Orthograptidae. The Orthograptidae includes, in addition to *Orthograptus* s.s., '*Climacograptus*' *typicalis* and related species, and

'*Glyptograptus*' *austrodentatus*. It is distinguished by having a type A proximal pattern (**84**), which becomes modified to types G or F in some species. The Diplograptidae includes *Diplograptus* s.s., *Pseudoclimacograptus* s.s., *Dicaulograptus* and related species. It is distinguished by having a type C proximal pattern (**85**), modified to types D or E in some species. The second major group has an asymmetrical proximal end (**78**) and comprises two families. The Family Monograptidae includes the monograptids and cyrtograptids, here grouped in one family because the only basis for distinction between them is the presence of cladia (**81**)—a primitive character at this level—in the 'Cyrtograptidae'. The family is defined by having dichotomy dl suppressed (**79**) and thl^1 arising from a sinus in the developing metasicula rather than through a resorption foramen (**80**). The strong upward direction of growth of thl^1 links it with the second family, the (paraphyletic) Glyptograptidae, which includes *Glyptograptus* s.s. and '*Climacograptus*' of *brevis* type, and has type B proximal pattern (**82**), modified to types H or I in some species.

Insertion of the Nemagraptidae and the Dicranograptidae in the cladogram presents some problems. Finney (1985) established that the Nemagraptidae have th2^1 dicalycal, and that branching is by the formation of cladia rather than by dichotomous division. He showed that *Leptograptus* has dicellograptid type thecae and proximal structure, and transferred the genus to the Dicranograptidae. We suggest two alternatives. In the first (text-fig. 9) the right-handed origin of thl^2 in the Nemagraptidae is regarded as a primitive character shared with the Dichograptina, and the Nemagraptidae is accordingly regarded as a sister group to the Diplograptacea and Dicranograptidae. The Dicranograptidae shares with the Nemagraptidae a 'simple' dorsal apertural margin on the sicula, but shares with the Diplograptacea a left-handed origin of thl^2 (**76**); it is therefore a sister group of the Diplograptacea. The Nemagraptidae and Dicranograptidae are grouped on the cladogram as the paraphyletic Superfamily Dicranograptacea, which is considered preferable to each being assigned to a separate and monotypic superfamily. This arrangement, however, conflicts with the stratigraphic order of appearance of the characters (text-fig. 11); dorsal spines (or other modifications) on the sicula aperture (**77**) and left-handed origin of thl^2 *precede* a simple sicular aperture (in nemagraptids) in the stratigraphic record by a gap equivalent to the whole of the Llanvirn Series.

In the other alternative (text-fig. 10) the simple sicula and partial or complete monoseriality define a group comprising the Nemagraptidae and the Dicranograptidae. This group is a sister group to both the Diplograptidae and the Pseudoclimacograptidae in an unresolved trichotomy; all three, however, share a symmetrical proximal end (**83**). This arrangement results in a monophyletic Dicranograptidae (including the Nemagraptidae) and is consistent with stratigraphy if the simple sicula is regarded as a derived character state.

At the superfamily level a revised definition of the Diplograptacea is suggested to include the Family Monograptidae (which comprises both monograptids and cyrtograptids). To distinguish the Monograptidae at superfamily level leaves a paraphyletic Diplograptacea—hence we regard it as in principle more satisfactory to recognize an enlarged, monophyletic Diplograptacea as shown.

This grouping of forms with a virgella cuts across the traditional grouping based on thecal type. Hence forms with glyptograptid thecae are present in each of the groups discussed above, as are forms with climacograptid thecae. Thecal form may well prove useful in recognizing phylogenetically based genera within each group, but it is of little use in discerning the major groups themselves.

We have made no attempt to include the Retiolitidae in our classification because current investigations into their phylogenetic relationships would make their inclusion premature. For example, a discussion of relationships of the Retiolitidae and some minor diplograptid families, such as the Lasiograptidae and the Peiragraptidae, is given by Mitchell (in press).

OUTSTANDING PROBLEMS

1. The relationship between Virgellina, Glossograptacea, and Dichograptacea needs to be clarified. A careful search for forms with a virgella in the early Arenig, for example, might reveal further characters, in an ancestral or early species, useful for linking the Virgellina with one of

TEXT-FIG. 11. Phyletic tree of the main families and subfamilies of the Order Graptoloidea (excluding the pendent dichograptids and retiolitids) derived from phylogenetic relationships (as shown in cladograms, text-figs. 1–3, 7–10) and stratigraphic data.

the other groups. At present no more than two orders of dichotomy are known in any Virgellina species and it is possible that the ancestral species lay within one of the pauciramous dichograptid groups.

2. The relationship between members of the pendent 'dichograptids', including *Pendeograptus*, the *Didymograptellus* group, and the *Didymograptus* (*murchisoni*) group is quite uncertain, as is the question of whether all these members constitute a monophyletic group. Is the pendent habit a feature shared with the pendent anisograptids, or has it been independently derived? If one or all of these forms are derived from an anisograptid such as *Bryograptus*, and are therefore more closely related to it than to other Dichograptina, they should be classified in a separate group which includes *Bryograptus* and *Rhabdinopora*.

3. There is a considerable morphological gap between the stem group Phyllograptidae and the remaining members of the Virgellina, across which several new characters are acquired, i.e. a change of the dicalycal theca from thl^2 to $th2^1$, suppression of dichotomy d2, change to metasicular origin of thl^1, change to sigmoidal curvature of thecae, and acquisition of the potential for cladia generation. Our cladograms (text-figs. 9 and 10) suggest that eventually a form possessing some, but not all, of these characters might be found.

4. Regrouping of diplograptoid species into groups with comparable structure (see Mitchell, in press). Thecal morphology may well be useful for recognition of genera within these groups, but as they stand at present, most diplograptoid genera are strongly polyphyletic. Elucidation of the relationship between these groups based on proximal structure requires a careful survey of the available data on proximal morphology.

5. Further study is needed to clarify the relationships of groups with reduced periderm—the Retiolitidae and Abrograptidae.

SUMMARY OF PROPOSED CLASSIFICATION

Listed below is the proposed classification of the Graptoloidea together with characters (or character states) useful for diagnosis. A phyletic tree showing the stratigraphic ranges of taxa is given in text-fig. 11.

Order GRAPTOLOIDEA: graptolites in which the nema is retained in the adult stage.

Suborder DICHOGRAPTINA Lapworth, 1873: graptoloids lacking bithecae and virgella.

Superfamily DICHOGRAPTACEA Lapworth, 1873 (emend.): dichograptinids lacking isograptid symmetry, number of orders of dichotomy in rhabdosome limited.

Family DICHOGRAPTIDAE Lapworth, 1873 (emend.): dichograptaceans lacking prothecal folds and sigmagraptine proximal end.

Subfamily DICHOGRAPTINAE Lapworth, 1873 (emend.): generalized dichograptid proximal end, branching pattern regular (but lost when dichotomies become delayed).

Subfamily TETRAGRAPTINAE Mu, 1950 (emend.): proximal region of *serra*-type, reclined stipes, dichotomy d4 suppressed.

Family SINOGRAPTIDAE Mu, 1957: characters of subfamily.

Subfamily SINOGRAPTINAE Mu, 1957: pronounced prothecal folds.

Family SIGMAGRAPTIDAE Cooper and Fortey, 1982: characters of subfamily.

Subfamily SIGMAGRAPTINAE Cooper and Fortey, 1982: sigmagraptine proximal region.

Superfamily GLOSSOGRAPTACEA Lapworth, 1873 (emend.): isograptid symmetry.

Family GLOSSOGRAPTIDAE Lapworth, 1873 (emend.): presence of manubrium.

Subfamily GLOSSOGRAPTINAE Lapworth, 1873: pseudopericalycal or pericalycal proximal structure.

Subfamily CORYNOIDIDAE Bulman, 1944: development arrested at th3, sicula and first theca elongated.

Subfamily PSEUDISOGRAPTINAE Cooper and Ni, 1986: paraphyletic, includes forms with manubrium but lacking pseudopericalycal structure.

Family ISOGRAPTIDAE Harris, 1933 (*sensu* Cooper and Fortey 1982): characters of subfamily

Subfamily ISOGRAPTINAE Harris, 1933 (*sensu* Cooper and Fortey 1982): biramous, reclined, thecae with initially low angle of inclination.

Family nov. (includes the '*I.*' *primulus* group of species): biramous, reclined, thecae with initially high angle of inclination.

Family PSEUDOTRIGONOGRAPTIDAE nov.: scandent, triserial or quadriserial. (Type species: *P. ensiformis.*)

Suborder VIRGELLINA nov.: graptoloids with virgella.

Superfamily DIPLOGRAPTACEA Lapworth, 1873: dorsal margin of sicula bears spines.

Family MONOGRAPTIDAE Lapworth, 1873 (incorporates Cyrtograptidae): thl[1] arises via sinus in metasicula, monoserial.

Family GLYPTOGRAPTIDAE Mitchell, in press (includes *Glyptograptus* s.s., *Climacograptus brevis* group): type B proximal pattern (or modified to types H or I).

Family DIPLOGRAPTIDAE Lapworth, 1873 (emend.) (includes *Orthograptus* and *Diplograptus* s.s., *Climacograptus typicalis* group, '*Glyptograptus*' *austrodentatus* group): type A proximal pattern (or modified to types G or F).

Family DICRANOGRAPTIDAE Lapworth, 1873 (emend.) (includes Nemagraptidae Lapworth, 1873): simple sicula with dorsal sinus, partial or complete monoseriality. [In the alternative cladogram, text-fig. 9, the family alone comprises the Superfamily Dicranograptacea.]

Family PSEUDOCLIMACOGRAPTIDAE Mitchell, in press (includes *Pseudoclimacograptus* s.s., *Dicaulograptus*): type C proximal pattern (or modified to types D or E).

Stem group PHYLLOGRAPTIDAE: characters of family.

Family PHYLLOGRAPTIDAE Lapworth, 1873 (emend. Cooper and Fortey 1982): isograptid development type, simple (dichograptid) thecal form, prosicular origin of thl[1].

Suborder not assigned

Family ANISOGRAPTIDAE Bulman, 1950: paraphyletic group, sicula retains nema in adult stage, bithecae present, rhabdosome more or less bilaterally symmetrical, and quadriradiate, triradiate or biradiate.

GRAPTOLOIDEA *incertae sedis*

Group containing the pendent dichograptids.

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