

THE SEQUENCE OF GRAPTOLITE FAUNAS

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INTRODUCTION

It was Lapworth's *Geological Distribution of the Rhabdophora* (1880) that finally established the stratigraphical value of the graptolites, but any general discussion of the succession of graptolite faunas may take as its starting-point *The Graptolite Faunas of the British Isles*, published by Miss Elles in 1922. In this, she expresses the evolutionary and philosophical conclusions reached after more than twenty years' work in collaboration with Lapworth and Miss Wood in the preparation of the famous *Monograph* (Lapworth, Elles, and Wood 1901-19). The evolutionary history of the entire group was analysed in terms of certain general trends—stipe reduction, change in direction of growth, and various trends in thecal elaboration—and stress was laid on their stratigraphical significance. The faunal section was, above all, designed to enable the stratigrapher to obtain a relatively close approximation to the age of a representative graptolite assemblage by assessing its general faunal characters, without resort to extensive specific identification. Four main faunas were recognized, and with their subfaunas have become the accepted standard; these are listed below with their original definitions:

MONOGRAPTID FAUNA

The fourth graptolite fauna is characterized pre-eminently by the enormous development of the uniserial scandent graptolites the *Monograpti*.

5. Predominance of *Monograpti* with simple thecae of the *Dichograptus* type. (Lower Ludlow zones.)
4. Acme and waning of hooked *Monograpti*. Acme of *Cyrtograpti*. (Wenlock zones.)
3. Predominance of *Monograpti* of hooked type. Acme and extinction of isolate type. Waning of lobate type. (*M. sedgwicki* to *M. crenulatus*.)
2. Predominance of *Monograpti* of isolate and lobate types. Waning of *Diplograptidae*. (*M. gregarius* to *M. convolutus*.)
1. Predominance of *Monograpti* of exclusively 'old-fashioned' types. Numerous *Orthograpti* and *Climacograpti*. (*O. vesiculosus* to *M. cyphus*.)

DIPLOGRAPTID FAUNA

The most noteworthy and characteristic feature about this third fauna is the profusion of *Diplograpti* of the *Orthograptus* type.

3. Presence of abundant *Orthograpti* with *Climacograpti* and large *Glyptograpti*. Absence of *Dicellograpti*. (*A. acuminatus* to *G. persculptus*.)
2. Presence of *Orthograpti* with *Dicellograpti* and *Climacograpti* of simple thecal type. (*D. complanatus* to *D. anceps*.)
1. Acme of large *Orthograpti*. Persistence of *Dicellograpti* and *Dicranograpti* of complex thecal type. (*C. wilsoni* to *P. linearis*.)

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LEPTOGRAPTID FAUNA

Characterized by a new element, that of elaboration of the thecal type, the older lines of evolution being temporarily arrested with the attainment of the reclined (*Leptograptus* and *Dicellograptus*) or scandent (*Glyptograptus*) position.

2. Presence of graptolites characterized by simple sigmoid thecae together with complex types. Scandent biserial forms increasingly abundant. (*M. multidentis* and *C. peltifer*.)
1. Acme of graptolites characterized by simple sigmoid thecae (absence of complex types). Reclined uniserial forms together with scandent biserial forms. (*G. teretiusculus* to *N. gracilis*.)

DICHOGAPTID FAUNA

All the earliest Graptolites are branched forms, possess simple thecae, and develop according to the *Dichograptus* plan, whilst the lines of evolution that can be traced in them are those of:

- (a) simplification in branching,
- (b) change in direction of growth (pendent to scandent).

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| Two-branched forms | { | b. Pendent series (<i>D. bifidus</i> - <i>D. murchisoni</i>). |
| | | a. Horizontal series (<i>D. extensus</i> - <i>D. hirundo</i>). |
| Many-branched forms becoming simpler | { | b. U. <i>Dichograptus</i> zone (presence of horizontal <i>Tetragrapti</i>). |
| | | a. L. <i>Dichograptus</i> zone (rarity of <i>Tetragraptus</i>). |

The scheme as a whole has justified the claims of its author. Contrary perhaps to popular belief, many graptolite zones have a restricted geographical distribution, as is only too apparent to those who attempt the correlation of graptolitic successions; and it is possible to define faunal units which are considerably bigger than zones, but which can be applied over wider areas, are more easily identified (on general characters), and also to the palaeontologist present an epitome of the geological history of the group. Discoveries of the past thirty years, however, while confirming some of the characteristics Dr. Elles employed for this purpose, have raised doubts as to the value of others. For example, it was not long before Dixon (1931) questioned the reliability of the Dichograptid faunal subdivisions, and more recently, Harris and Thomas (1940*a* and *b*) have challenged the assumed phyletic basis of the stipe-reduction series.

Criticisms such as these could be met by comparatively minor modifications, but more serious difficulties have arisen in connexion with the Leptograptid Fauna. In a recent review, Harris and Thomas (1956) have remarked that to put the Leptograptid Fauna stratigraphically below the Diplograptid Fauna 'is not warranted by observed facts' and, in effect, that we in Britain seem to have got the Leptograptid and Diplograptid Faunas inverted. To this it may be replied that they are themselves misinterpreting the basis of Elles's Leptograptid and Diplograptid Faunas. The Leptograptid Fauna was defined to include as essential components diplograptids, *Dicellograptus*, and *Dicranograptus* as well as leptograptids, united by the prevalence of some more highly modified type of theca; and the Diplograptid Fauna was largely based on the prevalence of *Orthograptus*. But it may well be felt that a terminology which admits such an interpretation is misleading. Moreover, revised correlation of graptolitic and non-graptolitic representatives of the Llandeilo and basal Caradoc has introduced further complications, because the Leptograptid Fauna can hardly now be claimed to correspond to any precise stratigraphical unit. There would seem little purpose in attempting to define and isolate a fauna between these particular limits in the absence of some compelling morphological or evolutionary reason, and for that the Leptograptid Fauna is altogether too heterogeneous.

If this be admitted, then the necessary revision becomes a more extensive problem involving the Dichograptid, Leptograptid, and Diplograptid Faunas, and affords an opportunity to recast the whole faunal sequence. As a preliminary to this it will be helpful to review very briefly the salient features in the general evolution of the graptolites.

EVOLUTION OF THE GRAPTOLITES AND ITS BEARING ON FAUNAL DIVISIONS

The relations of the Graptoloidea to the Dendroidea are incomparably better understood than they were thirty years ago, and remarkably detailed morphological studies of both these Orders have been supplemented by faunal discoveries in the Tremadoc revealing a wide range of transitional genera. There can be no doubt that the earliest graptoloid family, the Dichograptidae, was polyphyletic, and that its separation from the dendroids was a gradual process of long duration. In fact, it is becoming clear that there exists an easily recognizable transitional fauna, dendroid as to structure but graptoloid in habit, antedating the main Dichograptid Fauna. It is a fauna that is only poorly represented in this country.

Within the Dichograptidae, the pattern of evolution is now recognized as being far more complex than was hitherto realized. While reduction in the number of stipes is undoubtedly a general trend, the stipe-reduction story has evidently been greatly oversimplified and various intermediate stages are not inevitably present. But it is sufficient for the present purpose to recall that, in rocks of Arenig age, members of this family entirely dominate the graptolite assemblage and necessitate the recognition of a Dichograptid Fauna.

Along whatever lines it may have been evolved, the two-stiped dichograptid *Didymograptus* represents a relatively stable form, and to judge from the number of species, it is the most important genus of the family. From it have presumably descended the leptograptids, dicellograptids, and dicranograptids which form such a distinctive element of Middle and Upper Ordovician faunas. Details of their descent are lacking, but it is not unreasonable to regard them as a steady differentiation and radiation of late dichograptid stock. That is to say, there is stratigraphical support for the morphological evidence linking leptograptids and dicellograptids to dichograptids and anisograptids in a continuous evolutionary series.

The origin of scandent forms, biserial and uniserial, is on the contrary disconcertingly obscure and abrupt. It is unnecessary here to discuss vague theories as to their origin (Bulman 1947, p. x and 1954a), but it is relevant to admit that we no longer attach any special significance to *Dicellograptus* and *Dicranograptus* as intermediate stages in the evolution of biserial forms, and that there are even difficulties in the way of accepting *Dimorphograptus* as a direct ancestor of *Monograptus*. Yet the very abruptness of their origin, and their novelty in rhabdosome design, makes these scandent forms the more significant in the general succession of graptolite faunas. Moreover, it has been shown that the cryptograptids are so different in structure and development from the true diplograptids as to necessitate a completely separate origin, and the fact that they were almost contemporaneous only reinforces the importance of biserial forms in the faunal succession.

Now the first appearance and exuberant spread of *Monograptus* is already recognized

in the existing faunal scheme; but its curiously exact parallel, that of the biserial graptolites, is not, for it long antedates the base of Miss Elles's Diplograptid Fauna. Here surely is the feature we are seeking to replace the Leptograptid Fauna—an evolutionary event compared with which the deployment of the *Leptograpti* and *Dicellograpti* is of subfaunal importance.

To give effect to this proposal involves, as we shall find, not only expanding the former Diplograptid Fauna, but docking the tail of the Dichograptid Fauna. Consequently the revised scheme may, if adopted, create some initial confusion, for there seems no way to avoid using the same terms Dichograptid and Diplograptid Fauna with a different implication. But I believe the new faunas express as objectively as possible the known facts of morphology and stratigraphical distribution, and that they lose nothing of their value to the stratigrapher; indeed, attention has been drawn to the incoming of diplograptids as marking an important boundary in local successions by many authors before me.

Accepting the Monograptid Fauna unchanged, the four principal faunas here recognized are Anisograptid, Dichograptid, Diplograptid, and Monograptid, the last two being divided into four or five subfaunas.

1. THE ANISOGRAPTID FAUNA

The first widely distributed graptolite fauna is that of the Tremadocian comprising various epiplanktonic species of *Dictyonema* (such as *D. flabelliforme*) and their pendent and horizontal anisograptid descendants *Anisograptus*, *Clonograptus*, *Adelograptus*, *Bryograptus*, *Staurograptus*, &c. It is a transitional, but essentially a dendroid, fauna, and as such is sufficiently distinct from the Dichograptid Fauna of the Arenig to stand alone.

In north-west Europe, *Dictyonema flabelliforme* constitutes a well-recognized base to the fauna, with the varieties *socialis* and *parabola* predominating in the lowermost beds. *D. flabelliforme flabelliforme*¹ follows, associated with *Anisograptus* in Norway, and with *Clonograptus* and *Adelograptus* in Sweden and Britain. In the higher part of the fauna, these anisograptids tend to occur alone, or in association with *D. flabelliforme norvegicum* (Hede 1951; Bulman 1954b). There is a rather unexpectedly local character about many of these developments, and the correlations of their various zones and subzones cannot yet be considered firmly established. Tjernvik's revision of the *Dictyonema* Shales of south Sweden (now in the press) may help to clarify the position. Norway seems to have as much in common with the maritime provinces of North America as with other parts of Europe, and holds the key to transatlantic correlation. The lowest beds with *D. flabelliforme* alone are also known from Belgium (Lecompte 1948). Koliha (1926) reported *D. flabelliforme* and *Staurograptus* in Lower Tremadoc 'of Baltic type' from Břežany, Bohemia, but Prantl and Příbyl (1949) have questioned this correlation and from their published figures I do not regard it as proved that the Anisograptid Fauna occurs here at all. The well-known dendroid fauna described by Kozłowski (1948) from the Tremadocian of Poland is quite distinct from this epiplanktonic Anisograptid Fauna.

In North America, the Anisograptid Fauna is encountered in Cape Breton (Nova Scotia), Navy Island (New Brunswick), Newfoundland, along the southern shores of the St. Lawrence, and in New York State, whilst in the west, *Dictyonema flabelliforme* by

¹ Obut (1953) has claimed that the type specimens of *D. flabelliforme* are identical with the variety that has since been called *norvegicum*, but there is some doubt about this and I am here retaining the name *flabelliforme* in its established usage.

itself has been recorded (Ruedemann 1930) from the Chushina Formation of British Columbia. The richest and best known of these assemblages is from the Matane Shales of Quebec, where *Anisograptus*, *Staurograptus*, and *Triograptus* are associated with species of siculate *Dictyonema* different from but perhaps related to *flabelliforme*, and with an early *Didymograptus*. The absence here of *D. flabelliforme* makes the exact correlation of the fauna rather uncertain, but it is probably lower Tremadoc (Bulman 1954b). The remaining faunas stand in need of revision, and records of *D. flabelliforme* cannot always be accepted at their face value; but at Green Point (Newfoundland) species of *Anisograptus* very close to those of Matane are associated with various *Dictyonema* species, one of which appears close to the Matane *canadense* while another seems at most variably distinct from *flabelliforme*.¹ The implication would appear to be that there is no great disparity in age between the *D. flabelliforme* and *D. canadense* anisograptid faunas. As claimed by Hahn (1912), Matthew's *Clonograptus proximatus*, associated with '*D. flabelliforme*' in New Brunswick, is almost certainly *Staurograptus*, and *Clonograptus* is not known for certain to occur at all in the Tremadocian of the Eastern Provinces.

Again, at Famatina and Santa Victoria, Argentina, there are several varieties of *Dictyonema flabelliforme* associated with *Anisograptus* species very close to those of Matane (Turner 1950).

All these occurrences appear to be separated from the Arenig by a considerable time interval, and the only undoubtedly Upper Tremadoc graptolites at present known are those of a small faunule described by Mosen (1925) from the *Ceratopyge* Shale near Oslo. This comprises *Triograptus*, some diminutive *Didymograptus* species, some rather fragmentary anisograptids (recorded as *Clonograptus* and *Bryograptus*, but almost certainly including *Anisograptus*), and a poorly preserved *Dictyonema*. Berry (1957 *in litt.*) has recorded *Clonograptus*, *Anisograptus*, and *Adelograptus*, again with a diminutive *Didymograptus*, from the base of the Marathon formation in Texas, which may prove to be an Upper Tremadoc fauna, and this is perhaps the only record of true *Clonograptus* from the Tremadoc of North America.

In Australia, the Anisograptid Fauna is evidently represented by the *Staurograptus* faunule (*Staurograptus* and two small species of siculate *Dictyonema*) of the basal Lancefieldian, La 1 (Harris and Keble 1928). This does not correlate readily with any of those mentioned above, but it is separated by over 1,000 feet of barren strata from the burst of *Clonograptus* and *Bryograptus* that characterizes La 2 (Harris and Thomas 1938) which may itself be Upper Tremadoc rather than lowermost Arenig. There is some evidence for the occurrence of an Anisograptid Fauna of more Atlantic type in New Zealand, where *Triograptus*, associated with various other anisograptid genera and with a *Didymograptus*, is reported by Benson and Keble (1935).

The records of *Dictyonema flabelliforme* from the Yehli formation in north China (Sun 1935), from Liaotung (Mu 1952), and from S. Chosen (Kobayashi and Kimura 1942) all appear to me doubtful, and they could well be Arenig species. Similarly, the fragmentary anisograptids figured by Mu (1955), associated with various *Dictyonema* and *Dendrograptus* species, are not very convincing; they have little in common with the true Tremadocian faunas noted above.

¹ I am indebted to Professor Whittington for photographs and specimens of this material which is now being systematically collected and described.

The presence of small but apparently genuine *Didymograptus* species in the Anisograptid Fauna is of considerable interest in its bearing on dichograptid evolution. It also suggests that, when any considerable upper Anisograptid Fauna is discovered, true dichograptids may well be found to constitute a significant element in it, and the Anisograptid Fauna will be seen to merge gradually into the Dichograptid Fauna. Already it is known that the lowermost beds of the Arenig (other than in Britain) characteristically yield an abundance of *Clonograptus* and *Bryograptus*. It has never been proved that these Ordovician species possess bithecae and are in fact true dendroids, and if they do not they should logically be distinguished generically from their Tremadoc representatives; but this will hardly assist the stratigrapher in his general assessment of the fauna.

2. THE DICHOGRAPTID FAUNA

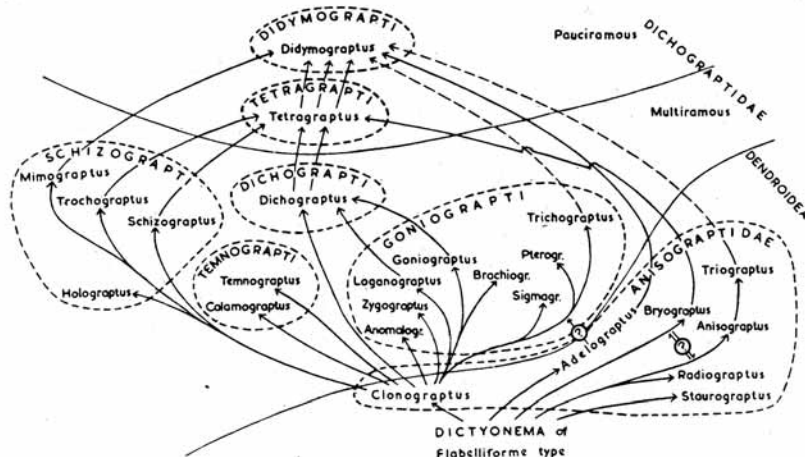
The generally accepted zoning of the Arenig in Britain is essentially that of Elles (1904), but owes much to the work of Marr (1894) on the Skiddaw Slates and is closely linked with the evolutionary concepts of Nicholson and Marr (1895). From the latter originated the idea that the two-stiped genus *Didymograptus* is a stage, independently attained from multiramous dichograptid ancestors by many different lines of descent through various *Dichograptus* and *Tetragraptus* species. The inference was that Arenig strata will show successive concentrations of *Dichograptus*, *Tetragraptus*, and *Didymograptus*. Elles (1922) qualified this by pointing out that the pendent series evolves more slowly than the horizontal series, but in the zonal scheme of the *Monograph* and in Elles (1922) a *Dichograptus* zone finds its place at the base, and in 1933 two horizontal *Tetragraptus* subzones were introduced between it and the *extensus* zone.

This faunal sequence was challenged by Dixon (1931), who found little stratigraphical evidence for such a precise transition in the Skiddaw Slates, claiming that many of the species concerned are long-ranged and that many-branched dichograptids are not necessarily indicative of a low stratigraphical horizon. Recently, in some still unpublished work, Jackson (1956) has again failed to find any stratigraphical support for the existence in the Skiddaw Slates of the *Dichograptus* and *Tetragraptus* zones, although he confirms the presence of the upper three *extensus*-subzones of Elles 1933. The *Dichograptus* zone has never been recorded elsewhere, and I think it must be agreed that there is no stratigraphical evidence for its existence. Nor does there seem strong evidence as yet for the occurrence of any marked concentration of *Tetragraptus* in the lower portion of the British Arenig.

Abroad, Harris and Thomas (1940*a* and *b*) criticized the theoretical concepts underlying this part of the faunal scheme, considering it improbable that *Loganograptus* is an intermediate between *Clonograptus* and *Dichograptus*. If I read them aright, they even doubt the close relation of *D. octobrachiatus* to any *Clonograptus* species, although accepting that some rare *Dichograptus* species with a long funicle and second-order stipes may logically be derived by stipe reduction from a *Clonograptus* ancestor. These authors further suggested that some *Tetragraptus* and *Didymograptus* species might well be derived from *Schizograptus* and *Trochograptus* ancestors, and regarded the table of dichograptid descent then current as greatly over-simplified. The possibility of direct derivation of *Didymograptus* species from Anisograptid ancestors has also been suggested (Bulman 1941, 1950*a*), and all these complications are incorporated in the tentative phylogenetic table, text-fig. 1.

Finally, as Dixon and others have observed, many of the common species such as *T. quadribachiatus*, *Dichogr. octobrachiatus*, &c., have a long vertical range extending through the Dichograptid Fauna as here restricted and even beyond. What little reliable information is available concerning relative generic abundance at successive levels does not seem very encouraging for widespread correlation.

All these factors combine to discredit the former scheme of faunal subdivision and to make hazardous any alternative proposals. The Dichograptid Fauna as a whole remains a satisfactory and readily recognizable assemblage of species belonging to a wide range of multiramous and pauciramous dichograptid genera, and the fact that practically everything belongs to a single family gives it unity. It is not so well differentiated from the



TEXT-FIG. 1. Diagram illustrating tentatively the phylogeny of *Tetragraptus* and *Didymograptus*. (Reproduced from *Treatise on Invertebrate Paleontology*, Pt. V, fig. 49.)

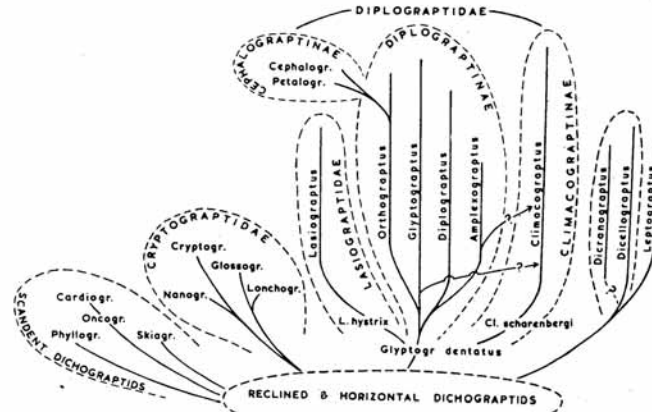
underlying Anisograptid Fauna but that uncertainty can exist, for example, as to the correct placing of the La 2 fauna in Australia, but that is inevitable from the close relations of the Dichograptidae to the Anisograptidae. What is in doubt is whether any general principle of universal subdivision can profitably be attempted. Short of any formal scheme, however, it may be noted that *Clonograptus* species and *T. approximatus* frequently occur in abundance near the base of the Fauna; that declined didymograptids and *Phyllograptus* are well represented near the middle; and that the first appearance of tuning-fork didymograptids (*protobifidus* and allied forms) and *Isograptus* reliably indicate the upper part (with *Glyptograptus dentatus*, *Cardiograptus*, and *Oncograptus* locally). Zoning, on a regional basis, has proved entirely reliable, and the zoning of the Bendigonian, Castlemainian, and Chewtonian of Victoria is an almost ideal example, but exact correlation over long distances may not always be easy.

3. THE DIPLOGRAPTID FAUNA

Introduction. In Britain, the Diplograptidae make their first appearance with *Glyptograptus dentatus* near the top of the Arenig, being known from the Shelve Church Beds

and the *hirundo* zone of Shropshire, the upper part of the *extensus* and the *hirundo* zones of the Skiddaw Slates, and the *hirundo* zone of Anglesey. The spread of this and allied forms (such as *Amplexograptus* and *Climacograptus*) is rapid (see text-fig. 2), and coincides with the rise of *Cryptograptus* and *Glossograptus* to form a distinctive biserial association in the *bifidus* fauna. Their presence in this country is to a great extent masked by the extraordinary profusion of tuning-fork graptolites; but subtract these pendent didymograptids from any representative Llanvirn Fauna and there remains a distinctive diplograptid element.

That this is equally true of Scandinavia is clearly brought out in the memoirs of Ekström (1937) and Hede (1951, p. 48) for south Sweden, and Størmer (1953, p. 44) for



TEXT-FIG. 2. Diagram illustrating tentatively the phylogeny of the principal genera of biserial graptolites. *Amplexograptus* should have been shown as originating independently from *Glyptogr. dentatus* before *Diplograptus*. (Reproduced from *Treatise on Invertebrate Paleontology*, Pt. V, fig. 50.)

the Oslo area. It also applies to the Lower Llanvirn of Belgium (Bulman 1950b), though not so satisfactorily to France and Bohemia.

A diplograptid fauna closely similar to that of north-west Europe is again represented in the *dentatus* beds of Levis and Deepkill, where it overlies the *bifidus* beds (Raymond's zones C2 and C3, and Deepkill beds 3-5). I suggest that these *dentatus* beds are the true equivalent of our Lower Llanvirn, from which it would follow that the *bifidus* zone of eastern North America is to be correlated with our Upper Arenig. No biserial graptolite of any kind is known below the *dentatus* zone in eastern North America, where the *bifidus* zone is exclusively dichograptid; and the limited composition of the biserial element in the *dentatus* zone itself implies a position near the base of the Diplograptid Fauna. It seems to me that the correlative value attaching to the diplograptids is superior to that of *D. bifidus*, which is an intermediate member of an unusually slowly evolving stock (*protobifidus*-*bifidus*-*murchisoni*), to the successive stages and offshoots of which it is notoriously difficult to give precise definition.¹

¹ In the zonal and other repercussions of this view, it must not be overlooked that the type of *D. bifidus* (Hall) came from the Levis Shales of Quebec.

The recognition of what appears to be *D. bifidus* 'identical with that at Levis' in the *Oncograptus*-*Cardiograptus* series of Marathon by Berry (*in litt.* 1957) would on this view agree with the position allotted to the Yapeenian by Harris and Thomas (1938), and with the record of *Oncograptus* associated with an (admittedly fragmentary) Arenig fauna in western Ireland (Cummins 1954).

There is, however, one record (Simpson Group of Oklahoma, Decker 1935) in North America of the association of a pendent didymograptid (*artus*) with a biserial form ('*Amplexograptus maxwelli*'), and in a later paper Decker (1941) suggested that the Deepkill species might perhaps be *protobifidus*.

In South America (Bulman 1931; Lemon and Cranswick 1956), *Glyptograptus*, *Amplexograptus*, and cryptograptids are abundantly associated with pendent didymograptids in assemblages of Llanvirn age, but the collections reported upon lack a proper stratigraphical control.

In Australia, the pendent dichograptid series (*Tetragr. fruticosus*, *D. protobifidus*), after being so well developed and zonally important in the Bendigonian and Castlemainian, ends abruptly in the overlying beds. There are no representatives of *D. bifidus* or *murchisoni*, and the early diplograptid fauna of Harris and Thomas's 'Middle Ordovician' (M.O. 1-4) is rendered all the more conspicuous by their absence. It is of interest to note here that the form described by Ekström as *A. maxwelli* from the *bifidus* zone of Sweden is identified by Hede (1951, p. 48) and Nilsson (1951) as *A. cf. differtus* H. and T. from M.O. 2.

From the Kopalinski beds of the Chu-Iliiski mountains of Kazakhstan, Keller (1956) has described a fauna consisting of *Diplograptus*, *Climacograptus*, *Cryptograptus*, *Glossograptus*, and *Trigonograptus* associated with *Loganograptus*, *T. quadribrachiatus*, and a few extensiform didymograptids which he correlates with the Llanvirn. The index fossils of the two zones which he recognizes are biserial forms; and biserial graptolites are used as zonal and subzonal indices in the Ningkuo Shale for a fauna which Hsü (1934), in my opinion rightly, correlates with the *bifidus* zone.

This then is the evidence on which it is claimed that the Diplograptid Fauna, logically defined, begins at the base of our Llanvirn, the Upper Didymograptus Shales of Scandinavia, the *dentatus* zone of eastern North America, and the 'Middle Ordovician' of Australia. Its upper limit remains the same as that of Elles 1922, for it persists until in turn replaced by the development of monograptids in the *vesiculosus* zone of the Lower Llandovery. The total fauna is extremely diversified, embracing the gradual development and waning of various elements, which permit the recognition of four subfaunas, but the boundaries between them are seldom sharp.

A. The Glypto-Amplexograptid Subfauna

To those accustomed to having the emphasis firmly placed on pendent didymograptids the name given to this subfauna may strike a jarring note; but, with the possible exception of French and Bohemian Llanvirn, the diplograptid element is important and in many parts of the world tuning-fork graptolites have already disappeared before its commencement.

On my interpretation, the base of this (and hence of the Diplograptid Fauna) is not marked by the incoming of *Glyptograptus dentatus* (which occurs in the *extensus* zone and may locally be quite abundant in the *hirundo* zone¹), but by its association with other

¹ D. E. Jackson (1956) records nearly 50 per cent. of *G. dentatus* in the *hirundo* zone faunas of the Skiddaw Slates at some localities.

diplograptid genera. Species of *Glyptograptus*, *Amplexograptus*, and *Climacograptus* are characteristic; *Diplograptus* s. str., *Hallograptus*, and *Lasiograptus* may also occur, together with *Cryptograptus* and *Glossograptus* (see text-fig. 2), and the enigmatic *Trigonograptus* may persist into the lower beds.

Dichograptids are represented, especially in the lower part of the subfauna, by the 'tailings' of the Dichograptid Fauna, and near the base commonly outnumber the diplograptid element. They include horizontal, declined, and pendent didymograptids, *Tetragraptus*, *Dichograptus*, *Loganograptus*, *Phyllograptus*, and the multiramous *Pterograptus*, *Trichograptus*, and *Brachiograptus*. In any one region, they are not as a rule so well represented as this collective list would suggest. For example, in Britain, declined and especially pendent *Didymograptus* form the bulk of the dichograptid element; in Scandinavia, pendent forms in profusion are characteristically associated with *Pterograptus* and *Janograptus*; in Australia, the pendent didymograptids are conspicuously absent, but declined forms with some *Tetragraptus*, *Pterograptus*, and *Brachiograptus* appear to make up the bulk of the non-diplograptid assemblage; in the *dentatus* zone of North America, the dichograptid element consists of extensiform didymograptids, *Tetragraptus*, *Dichograptus*, and rather commonly *Loganograptus*.

Dicellograptus makes its first appearance in this subfauna, being reported from as low as the *bifidus* zone in Britain (*D. moffatensis*) and rather higher in Sweden (*D. vagus*). *Dicranograptus* appears in the uppermost part (*D. rectus* in Britain and *D. irregularis* in Sweden).

Focusing attention on the Diplograptid element results in linking faunally the Llanvirn with the Llandeilo, for the palaeontological break between the *murchisoni* and *teretiusculus* zones (Elles 1940, p. 411) is little more than the extinction of tuning-fork graptolites. In consequence, diplograptids come to dominate the upper part of the fauna almost completely, but the Llandeilo diplograptid element contains nothing new above specific level. It also gives some support to Størmer's choice (1953) of this horizon as marking the base of the Middle Ordovician, corresponding with Australian practice.

B. The Nema-Dicellograptid Subfauna

Here we find a fairly sharp and certainly easily recognizable base with the incoming of *Nemagraptus gracilis*, and with this also the whole character of the fauna changes; *Dicellograptus* and *Dicranograptus* species now assume numerical importance and even dominance. In the *gracilis* zone of Britain, there are listed (Lapworth, Elles, and Wood) eight species of *Dicellograptus* and five of *Dicranograptus*; in the *peltifer* zone, nine of *Dicellograptus* and ten of *Dicranograptus*. Coinciding with this also is the first appearance of *Leptograptus*. Diplograptids are still more abundant (nineteen species are listed in Lapworth, Elles, and Wood for the *peltifer* zone), but the only significant generic change in this element of the fauna is the appearance of rare *Orthograptus*.

Scandinavia, North America, Australia, and China all furnish closely analogous assemblages. *N. gracilis* itself has an almost worldwide distribution; *Dicellogr. sextans*, *C. peltifer*, and many others are also remarkably widespread and together give the impression of unusually free inter-communication at this time.

C. The Ortho-Dicellograptid Subfauna

I use this term to include the remainder of the Ordovician portion of the Diplograptid Fauna, which comprises various species of *Orthograptus* associated principally with

Dicellograptus, *Dicranograptus*, *Leptograptus*, and *Climacograptus*. Its lower limit coincides with the appearance of *Orthograptus* in abundance represented by the *truncatus*, *calcaratus*, and *quadrimumcronatus* groups; its upper limit with the final disappearance of axonolipous graptolites.¹ *Orthograptus*, *Climacograptus*, and *Dicellograptus* range throughout, but *Dicranograptus* and *Leptograptus* are restricted to the lower portion.

The above association renders an assemblage of this age readily identifiable,² but there may be some uncertainty as to the base of the subfauna. Thus the *vasae* and *molestus* zone faunas of Sweden and the *wilsoni* zone fauna of Scotland would be assigned to the underlying subfauna on general faunal characteristics, while the assemblages from the upper part of the *multidens* shales of Shropshire and south Wales might be identified as belonging to this subfauna on account of their rather more conspicuous orthograptid element. But faunal assemblages at this horizon have proved difficult to the specialist employing the full resources of zonal correlation (Jaanusson and Strachan 1954), and Nilsson (1953) has recorded a peculiar mixed assemblage from Sularp (Scania) which suggests a transitional fauna between the *gracilis* and *clingani* zones.

Pleurograptus linearis has a curious distribution, occurring abundantly in south Scotland, but not elsewhere in Britain or in Europe, yet it is recorded from North America and Australia. The more widely distributed *C. styloideus* has been used as an alternative index fossil, and most of the species characteristic of the lower part of the subfauna are widely distributed.

The upper part of this subfauna has everywhere the characters of an impoverished fauna, with dwarf varieties of *Climacograptus* and *Orthograptus* associated with the last survivors of *Dicellograptus*. The index fossil of one zone (*complanatus*) is, however, a remarkably widespread species, recorded from many areas in North America, Europe, Asia, and Australia.

D. The Ortho-Climacograptid Subfauna

This small subfauna is closely linked, even to a considerable degree of specific identity, with the subfaunas above and below, and is in all respects transitional though it can very easily be defined. Like all Silurian graptolite assemblages, it is composed solely of scandent forms, but the genus *Monograptus* has not yet appeared, so that it is entirely biserial or uni-biserial. I have named it the Ortho-Climacograptid Subfauna, but one of its most characteristic features is the reappearance of *Glyptograptus* and *Diplograptus* (= 'Mesograptus'). Whether these are generically identical with their Ordovician namesakes is perhaps questionable; the gap between Ordovician and Silurian *Diplograptus* has been almost bridged by some rare forms described by Davies (1929) from the *linearis* and *complanatus* zones, but there is no sign of *Glyptograptus* between the *wilsoni* and *anceps* zones.

Structural modifications at the proximal end beginning at this horizon lead to the production of such genera as *Akidograptus* and *Dimorphograptus*; the first of these is confined to the base of this subfauna and is widely distributed, the latter only becomes abundant in beds above, where it is also joined by *Rhaphidograptus*.

¹ Axonolipa was a term proposed by Frech (and adopted by Ruedemann) for graptolites without a virgula (i.e. graptolites with an exposed nema), in contradistinction to the Axonophora or graptolites with a virgula. It thus furnishes a convenient comprehensive term for all other than scandent graptolites.

² In American faunal lists (e.g. Ruedemann 1947), the abundance of *Orthograptus* is very often concealed by the mistaken reference of such species as *quadrimumcronatus* to *Glossograptus*, and various members of the *truncatus* group to *Amplexograptus*.

4. THE MONOGRAPTID FAUNA

No changes are here proposed in the definition or subdivision of this fauna as outlined by Miss Elles (p. 159). The thecal elaboration trends used at this level have proved more reliable than the others. This may be partly the result of a less exacting time-scale, and the total assemblage is less complicated, for whether or not *Monograptus* be polyphyletic, it certainly does not compare with the intricate plexus of dichograptid descent.

MONOGRAPTID FAUNA	E monograptids of simple thecal type	L. Ludlow	Llandovery	SILURIAN
	D hooked monograptids and <i>Cyrtograptus</i>	Wenlock		
	C hooked and lobate types dominant			
	B triangulate and lobate types dominant			
	A simple thecal types + diplograptids and <i>Dimorphograptus</i>			
DIPLOGRAPTID FAUNA	D Ortho - Climacograptid subfauna		Bala	ORDOVICIAN
	C Ortho - Dicellograptid subfauna	<i>D. clingani</i>		
	B Nema - Dicellograptid subfauna	<i>N. gracilis</i>		
	A Glypto - Amplexograptid subfauna	Llandeilo and Llanvirn		
DICHOGRAPTID FAUNA			Arenig	
ANISOGRAPTID FAUNA			Tremadoc	

TEXT-FIG. 3. Simplified diagram showing the succession of graptolite faunas and subfaunas, related to the standard British Lower Palaeozoic succession.

The Llandovery succession of simple thecal type (associated with diplograptids), followed in turn by dominantly triangulate and isolate, and dominantly hooked and lobate, has never been seriously questioned. These subfaunas are widely distributed, but it is of interest to note how poorly developed are the faunas of this age in North America, where *Dimorphograptus*, *Cephalograptus*, *Petalograptus*, *Rastrites*, and such common species as *M. triangulatus* and *M. lobiferus* are as yet unknown (Ruedemann 1947). There is evidence, however (Thorsteinsson *in litt.*), that they are well represented in arctic Canada.

The cyrtograptid element associated with hooked monograptids characteristic everywhere of the graptolitic Wenlock, has a more restricted distribution, but the final graptolitic subfauna of the Lower Ludlow is again widespread. The complicated cladia-bearing genera *Linograptus* and *Abiesgraptus* occur in the Ludlow, and *Monograptus* trails away with such species as *uniformis* and *hercynicus* in the Upper Ludlow of Thuringia and Bohemia.

The faunas proposed are shown in outline in text-fig. 3, and are defined in rather more detail below.

4. MONOGRAPTID FAUNA
Scandent uniserial rhabdosomes (Monograptidae) with diplograptids in lower part and subordinate retiolitids throughout.
- Llandovery {
- E. L. Ludlow: monograptids of simple thecal type.
 - D. Wenlock: cyrtograptids and hooked monograptids.
 - C. Monograptids with hooked and lobate thecae: *sedgwicki* to *crenulatus* zones.
 - B. Monograptids with triangulate and isolate thecae: *gregarius* and *convolutus* zones.
 - A. Monograptids of simple thecal type: diplograptids and dimorphograptids abundant in lower part: *vesiculosus* (*atavus* and *acinaces*) and *cyphus* zones.
3. DIPLOGRAPTID FAUNA
Comprises main development of Diplograptidae, Lasiograptidae and Archiretiolitinae with cryptograptids: development and extinction of *Dicellogr.* and *Dicranogr.*, and at base last dichograptids.
- D. Ortho-Climacograptid subfauna: diplograptids (including *Glyptograptus* and *Diplograptus*) with *Akidogr.* and *Dimorphogr.*: *persculptus* and *acuminatus* zones.
 - C. Ortho-Dicellograptid subfauna: diplograptids (especially *Orthograptus*, *Climacograptus*) with *Dicellogr.*, *Dicranogr.*, and *Leptogr.* in lower part, and *Dicellogr.* in upper part: *clingani* to *anceps* zones.
 - B. Nema-Dicellograptid subfauna: abundant diplograptids (incl. *Diplograptus*) with *Dicellogr.*, *Dicranogr.*, and *Leptogr.* *N. gracilis* in lower part: *gracilis* to *wilsoni* zones.
 - A. Glypto-Amplexograptid subfauna: early species of most diplograptid genera, especially *Glyptogr.* and *Amplexogr.*, with *Cryptogr.*, *Glossogr.* and late dichograptids: *bifidus* to *teretiusculus* zones.
2. DICHOGRAPTID FAUNA. An exclusively dichograptid assemblage of multiramous and pauciramous genera, except for *Clonograptus* and *Bryograptus* near base and *G. dentatus* in highest portion: *extensus* (*deflexus*, *nitidus*, *gibberulus*) and *hirundo* zones.
1. ANISOGRAPTID FAUNA. A dendroid assemblage characterized by sciculate *Dictyonema* associated with and followed by pendent and horizontal anisograptids (*Anisogr.*, *Stauogr.*, *Clonogr.*, *Bryogr.*, *Triogr.*, &c.); some small didymograptids are known: L. Tremadoc (*Dictyonema* Shales) and U. Tremadoc (3aβ Norway; ? La 2 Austr., &c.)

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