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LATE GRAPTOLOID FAUNAS AND THE PROBLEM OF GRAPTOLOID EXTINCTION

Abstract. — Discoveries of Early Devonian graptoloids have been continued in the past ten years in ever increasing areas, but particularly in Asia. All continents, except South America and Antarctica, have so far yielded Devonian graptoloids. Devonian graptoloid faunas appear to have a uniform composition all over the globe; there is no conclusive evidence for any biogeographic differentiation. The hitherto known morphological spectrum has broadened only insignificantly. About 25—30 Devonian graptoloid species and subspecies may be recognized at present, belonging to four genera: *Monograptus* (some 20 species), *Linograptus* (1), *Abiesgraptus* (3) and *Climacograptus* (1; represented by a sole specimen from the *hercynicus* Zone in the Carnic Alps). The *Monograptus* species are small to mediumsized, having 20—40, rarely over 60 thecae in a rhabdosome. They are robust and straight, except for a few moderately curved forms. The thecae vary from almost uniform to strikingly biform; typically they are of the type of *M. uncinatus*, at least proximally, becoming simpler towards the distal end. A minor distinctive feature of most Pragian species is the strong development of the dorsal sicular tongue. The giant *Linograptus posthumus* and *Abiesgraptus*, both of which may house up to several thousand zooids, are not found above the Lochkovian. The demonstrably highest occurrence of Devonian graptoloids is in the uppermost Pragian, though some faunas may turn out to be somewhat younger, i.e. the latest graptoloids may straddle the Siegenian-Emsian boundary only slightly. The causes for graptoloid extinction remain obscure. Extinction was a slow, stepwise historical process which — starting off at the end of the Wenlock — was marked by a number of rather sudden incisions that in summa resulted in a progressive reduction of faunal diversity. It would appear that graptoloid evolution was somehow, perhaps intimately, connected with the history of euxinic or poorly aerated seas.

Since the appearance of my paper on the graptoloids of the Upper Graptolite Slates in Thuringia (Jaeger 1959) which initiated rapid discoveries of late graptoloid faunas in many parts of the world, I gave at various occasions reviews on the last representatives of this fossil group (Jaeger 1966, 1969, 1970, 1973 and 1977a). Here I may as well consider certain aspects of the evolution of the late graptoloids, particularly results that have become apparent in the past few years. Stratigraphically, I shall confine myself to those graptoloids that are now placed in the Devonian.

1. World distribution of Devonian Graptoloidea

1.1. Devonian graptolite zones

Discoveries of Devonian Graptoloidea or their recognition have continued through the last ten years in ever increasing areas, particularly in Asia, but also in Europe, North Africa and North America. This may be seen upon comparison of fig. 1 in this paper with an older version of such a distribution map that was prepared in 1967 for the Symposium on the Silurian-Devonian boundary in Leningrad (Jaeger 1973: fig. 2). Moreover, a closer look would reveal that informations are now often much more detailed, e.g. where formerly one zone was known, several may have been recognised in the meantime. This implies that the geographical distribution of many species was extended considerably, so that most of them are now known from at 'least two continents, and half the species from four continents (Table 1). South America and Antarctica remain so far without Devonian graptoloid records.

In fig. 1 distinction is made between Lochkovian and Pragian (and possibly younger) graptoloid occurrences. In addition, each stage is subdivided into three zones as follows (in ascending order): the Lochkovian: of *M. uniformis*, *M. praehercynicus* and *M. hercynicus*, and the Pragian: of *M. falcarius*, *M. thomasi* and *M. yukonensis*.

A particular zone is plotted only if the zonal species actually occurs in a given area. This does not exclude the possible occurrence of other Devonian graptolitic levels in the same region; these cannot be placed in the zonal scheme, in my opinion, simply because of the lack of the index form.

Throughout this paper I use the stage names Lochkovian and Pragian in preference to the more traditional Rhenish stage names Gedinnian and Siegenian, as the Bohemian terms allow correlations in the graptolitic sequences to be expressed with greater precision. In spite of the important progress that has been achieved in recent years in the correlation of the Early Devonian graptolitic sequences with the non-graptolitic classical Rhenish-Ardennean Early Devonian there remains considerable latitude for the positioning of the Lochkovian-Pragian boundary, and of the Pragian within the Rhenish standard. [— Pragian after "Praga" (Latin word for Prague). The spelling "Praguian" — used by me formerly — is incorrect].

The zonal subdivision that is suggested here for the Pragian is more or less to serve the purpose of this paper. It is not believed to be the only scheme possible. It is practically identical with the local zonation of the Pragian as given for China (Mu and Ni 1975; Mu 1974: 234).

Instead of the *thomasi* Zone the Chinese authors speak of the zone of *Neomonograptus himalayensis* Mu and Ni, in which *M. thomasi* occurs. *N. himalayensis* I believe to be a synonym of *M. atopus* Bouček.

A different and perhaps more refined zonal scheme may become possible in the future. Indeed, a more detailed zonation has been suggested by Koren' (1974, 1975), but the latter was for local use. Any zonal division of the Pragian that could be claimed to be of intercontinental or
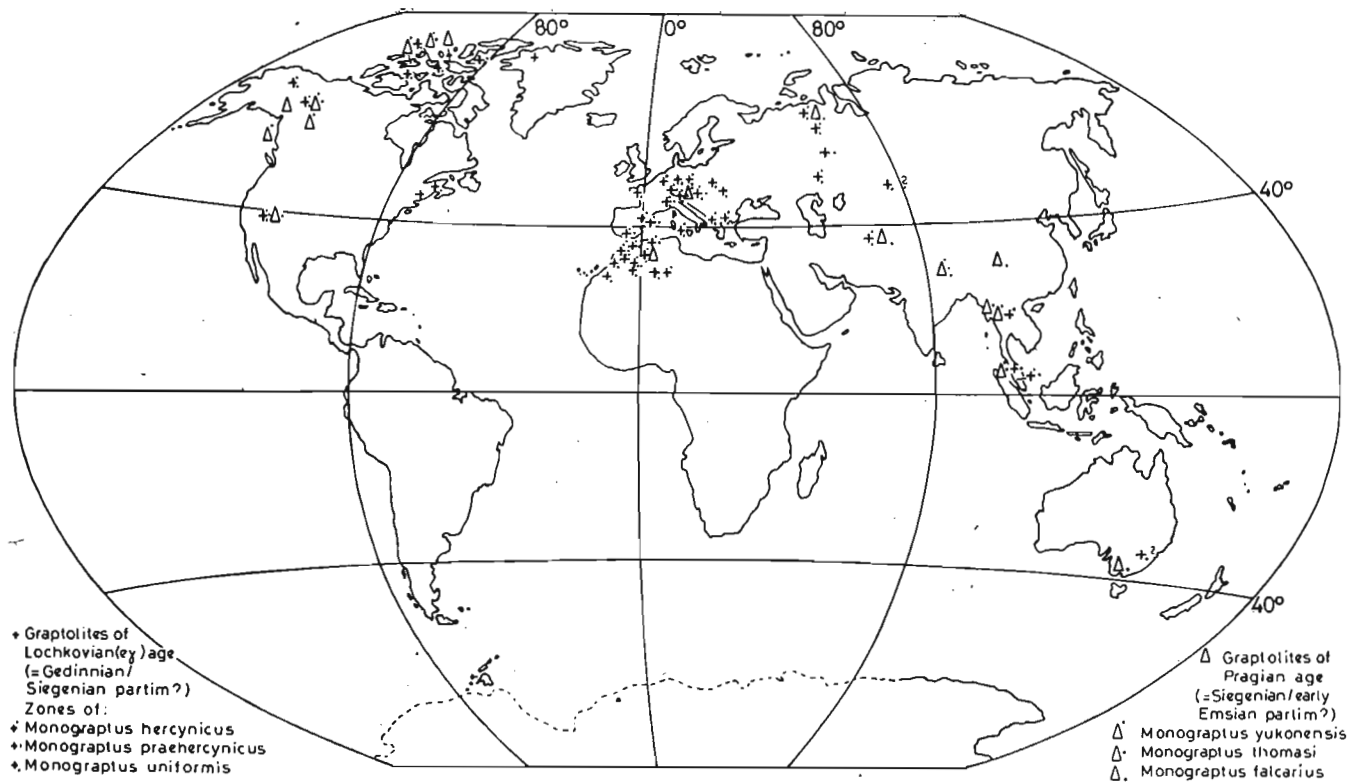
Fig. 1. World distribution of Early Devonian Graptoloidea (explanation in the text).

even global applicability has some drawbacks and must therefore be considered as tentative. Some reasons given, as to why I currently prefer this zonal scheme.

The position of the *falcarius* Zone is certainly well established at the base of the Pragian (Pai Khoi, Turkestan Range) (Koren' 1969, 1971, Erina *et al.* 1976), and the position of the *yukonensis* Zone well above the base of the Pragian (Bouček 1966; Lenz and Jackson 1971 and others). There is no evidence that the vertical ranges of *M. falcarius* and *M. yukonensis* overlap anywhere. On the contrary, there seems to be considerable gap between these two zones.

Also *M. thomasi* appears to come in well above the base of the Pragian. Again there may be a longer time span between the *falcarius* Zone and the first appearance of *M. thomasi*. This I have tried to indicate by plotting *M. fanicus* (in brackets) in between the two in the zonal column of fig. 2. However, *M. fanicus* has been recorded so far only from Central Asia (Koren' 1975) and the Canadian Arctic (Jackson *et al.* 1976). *M. thomasi* is recorded by Lenz and Jackson (1971) from immediately below the *yukonensis* Zone in Yukon.

According to Berry and Murphy (1972) and Kerr *et al.* (1977), respectively, *M. thomasi* occurs in Nevada and on Bathurst Island in the Canadian Arctic together with *M. yukonensis*. Overlapping ranges of the two species would not be surprising, but having seen the four Nevadan specimens that have been assigned to *M. yukonensis*, I am not sure of their identification. Those could well be distorted rhabdosomes of *M. thomasi*. *M. thomasi* occurs there frequently and beautifully preserved. The *M. thomasi* from Bathurst Island I identify as *M. telleri* that is indeed very similar to *M. thomasi*. (I thank Dr. R. Thorsteinsson, Geological Survey of Canada, for generously borrowing the Bathurst Island specimen to me).

The stratigraphical relationship of *M. yukonensis* and *M. thomasi* in Malaya is not known to me. There the local occurrences of these two forms seem to be mutually exclusive. In Victoria, Australia, where *M. thomasi* has a wide geographical distribution, its occurrence is out of succession in terms of graptolite zones.

Though the full interregional stratigraphical relationship of *M. thomasi* and *M. yukonensis* must be said to be unsatisfactorily known, separate plotting of their occurrences on the map allows a good deal of information to be learned. *M. thomasi* has a wide distribution in three continents (Australia, Asia, North America). *M. yukonensis* is known from four continents.

The adopted stratigraphical relationship between *M. thomasi* (below) and *M. yukonensis* (above) may be reasonably suspected also from the morphology of the two species. *M. yukonensis* could easily be thought of as a decendant of *M. thomasi*. The Australian *M. thomasi*, when followed

upwards, seems to approach the morphology of *M. yukonensis*. The Bohe-
mian *M. yukonensis*, on the other hand, does not seem to exhibit the
strong proximal recurvature which is characteristic of the typical *yuko-
nensis* from North America, nor has it the close thecal spacing of the
latter, but instead has the low thecal count of *M. thomasi*. The Bohemian
M. yukonensis could well be thought of as an intermediate between
M. thomasi and typical *M. yukonensis*.

In this context it is of interest that the common associate of the
Bohemian *M. yukonensis*, *M. atopus* Bouček, that until recently was
known only from Bohemia, was found in the Himalaya together with
M. thomasi (Mu and Ni 1975). If I understand the Chinese workers cor-
rectly, then they did not encounter *M. atopus* in the highest graptolitic
beds of Yunnan which are characterized by the occurrence of *M. yukon-
ensis fangensis*.

An even more likely descendant of *M. thomasi* might be *M. telleri* that occurs
frequently in the lower portion of the *yukonensis* Zone in northwestern Canada;
M. telleri could be described as a bigger version of *M. thomasi* with less stretched
proximal portion. *M. telleri* would mean a different and contrasting evolutionary
trend that paralleled the presumed transformation of some *M. thomasi* into *M. yukon-
ensis*. However, Koren' (1975) assigns to *M. telleri* specimens occurring as low as
the basal Pragian.

In the uppermost Lochkovian *M. kayseri* may form a zone of its own
above *M. hercynicus* or overlapping with it. *M. kayseri* occurs in its
Barrandian type area — as far as my knowledge goes — always above
the uppermost *M. hercynicus*. *M. kayseri* occurs very likely (identification
with slight reservation by Jaeger *in*: Alberti 1969: 466) in the Rabat-Tiflet
area in Morocco, there again in the uppermost Lochkovian. *M. kayseri*
may be expected to range into the Pragian (see discussion of *M. belke-
taiefensis* and *M. angueurensis* below).

1.2. Location of Early Devonian graptolite occurrences (figure 1)

In order to document the Early Devonian graptolite occurrences as
shown on the sketch-map (fig. 1) their broader locations are enumerated
in the following account accompanied by selected references, and in a few
cases also by brief comments. Quotation of a publication does not neces-
sarily imply that I agree with all the identifications given therein, even
if this will not be commented upon here.

Europe (except the Ural-Pai Khoi fold-belt). — The cluster of grap-
tolite occurrences in the middle of Europe refers to the following areas
as seen from west to east and north to south: Kellerwald Mountains and
Marburg region at the eastern edge of the Rhenish Slate Mountains
(Rheinisches Schiefergebirge) (Jaeger 1962), Harz (Jaeger: *in* Maronde
1968), Lusatia (Jaeger 1964), Saxo-Thuringian zone of the Variscan oro-

Table 1

Geographic distribution of Early Devonian graptoloid species. Some uncertain species in brackets, other doubtful or clearly synonymous species are discussed in the text. *M. langgunensis* Jones, 1973 is identical with *Monograptus* sp.n. aff. *yukonensis* from Thailand (Jaeger *et al.* 1969)

	Europe	Africa	Asia	Australia	America
Pragian					
M. aequabilis notoaequabilis Jaeger and Stein, 1969	×		×	×	×
(M. angueurensis, 1965)		×			
M. atopus Bouček, 1966	×		×		
(M. belketaiefensis Planchon, 1964)			×		
M. craigensis Jaeger, 1970			×		×
M. falcarius Koren, 1969			×		
M. fanicus Koren, 1975			×		×
M. langgunensis Jones, 1973			×		?
M. pacificus Jaeger, 1970					×
M. telleri Lenz and Jackson, 1971			×		×
M. thomasi Jaeger 1966			×	×	×
M. yukonensis yukonensis Jackson and Lenz, 1963			?	?	×
M. yukonensis fangensis Jaeger and Stein, 1969			×		
M. yukonensis subsp.	×				
Lochkovian					
M. aequabilis aequabilis (Přibyl, 1941)	×	×	×	?	×
M. birchensis Berry and Murphy, 1975					×
M. hemiodon Jaeger 1959	×				
M. hercynicus Perner, 1899	×	×	×		×
M. hercynicus nevadensis Berry, 1967			?		×
M. kayseri Perner, 1899	×	×			
M. microdon Reinh. Richter, 1875 (and subsp.)	×	×	×		×
M. praehercynicus Jaeger, 1959	×	×	×		×
M. ramstalensis Jaeger, 1959	×				
M. uniformis uniformis Přibyl, 1940	×	×	×		×
M. unif. angustidens Přibyl, 1940	×	×			×
M. unif. parangustidens Jackson and Lenz, 1972					×
Linogr. posthumus (Reinh. Richter, 1875)	×	×	×		×
Abiesgraptus sp. sp.	×	×	×		×
Climacograptus sp.	×				

gene in North Bavaria, Thuringia and Saxonia (Greiling 1960, 1966; Stein 1965; Jaeger 1959, 1977b), Bohemia (Horný 1962; Chlupáč *et al.* 1972), Carnic Alps (Jaeger 1968, 1975; Flügel *et al.* 1977), Sudetes (Jaeger 1959, 1964; Teller 1960; Kurałowicz 1976), Eastern Poland (Chełm boring) (Korejwo and Teller 1964) and Podolia (Obut 1968; Koren 1968; Nikiforova 1977).

Occurrences in western and southern Europe comprise Normandie (Jaeger and Robardet 1973), Northeast Spain (Greiling and Puschmann

1965), Isle of Menorca (Jaeger: *in* Bourrouilh 1973), Southern Spain (Jaeger and Robardet, in preparation) and Sardinia (Jaeger 1976); those in southeastern Europe eastern Yugoslavia (Bouček *et al.* 1976) and northwestern Bulgaria (Spassov 1963). (*M. bulgaricus* Spassov from the basal Lochkovian of Bulgaria would appear to me a genuine *M. uniformis* in a special type of preservation).

The only certain European occurrence of Pragian graptolites is near the top of the type Pragian in the Barrandian (Bouček 1966).

Another fauna believed to be Pragian was recorded by Kurałowicz (1976) from the classical section of Żdanów (Herzogswalde) in the Sudetes. This I fail to accept as Pragian. A representative collection of that fauna was placed before the participants of the Warsaw Conference. In addition, members got the chance to visit the section and collect specimens on an excursion. The graptolites that have been assigned to the Pragian species *M. falcarius*, *M. fanicus* and *M. craigensis* appear to me true *M.hercynicus* as far as they allow a safe identification to be made. Conclusive evidence for the occurrence of graptolites younger than the *hercynicus* Zone seems to be missing. An important contribution of Kurałowicz, it may be stated here that she established the occurrence of the *transgrediens* Zone in sequence with the *uniformis* Zone in the Żdanów section.

North Africa. — Lochkovian graptolites are widespread, particularly in the northern Sahara and the Atlas chains and plains in Morocco and Algeria. Proceeding from west to east and north to south the following areas of occurrence may be listed. Rif (Bourrouilh and Jaeger 1976), Massif Kabyle du Chenoua west of Algers (Bourrouilh *et al.* 1976). Rabat-Tiflet anticline (Alberti *et al.* 1966, Jaeger in Alberti 1969, 1970) and Meseta Cotiere east of Casablanca (Willefert 1966), anticline of Kasba-Tadla-Azrou in central Morocco (Willefert 1963a), Oued Dra in southwest Morocco (Willefert 1963b; Hollard 1977), Tafilalt and Moroccan-Algerian borderland (Hollard and Willefert 1961; Jaeger and Massa, 1965; Hollard, 1977), subsurface in the northern Sahara of Algeria in the triangle Laghouat-Ghardaia-Erg el Anngueur (Willefert 1962; Legrand 1965b; 1967; Planchon 1964), former Spanish Sahara (Planchon 1965), Ougarta Ranges in southwestern Algeria (Legrand, 1962, 1965b, 1977) and the western part of the Tassili N'Ajjer (central 'Sahara) (Legrand 1965a, b; 1967; Dubois and Mazelet 1965).

Pragian graptolites have been found in several borings in the triangle Laghouat — Ghardaïa — Erg el Anngueur in the northern Algerian Sahara (Planchon 1964; Legrand 1965b). There is no doubt about the age of these graptolites as they are associated with Pragian shelly fossils, and as they occur in sequence with Lochkovian rocks that yielded *M. hercynicus*. The Pragian graptolites are rare, usually fragmentary or poorly preserved. Parts of the collections were studied by the writer.

Two relatively new species are based on that material, namely *M. belketaiefensis* Planchon (1964) and *M. angueurensis* Legrand (1965b). The latter may be conspecific

with the former as Legrand himself considered. Both are reminiscent of *M. kayseri*, *M. aequabilis notoaequabilis* and *M. fanicus*. But in my opinion the state of preservation of these Saharan specimens does not allow of a safe identification. There occurs at least one additional form, i.e. the sole specimen recorded by Planchon as *Monograptus* sp. of *uniformis* type; this could possibly be *M. telleri*.

I am undecided as to *M. zeimleti* Legrand (1965b) from the Lochkovian (surface exposures) of the Sahara. *M. cravatti* Legrand (1965b), a presumed Lochkovian species, has meanwhile turned out to be the Wenlock *M. flemingi* (Legrand, personal information 1968).

Asia (inclusive Ural-Pai Khoi Ranges). — The distribution of Devonian graptolites follows the Ural-Tien Shan orogene and continues through the Himalaya and southeast Asian mountain ranges. Proceeding from northwest to southeast Lochkovian graptolites have been encountered in the following regions: Pai-Khoi (sections near Amderma at the Kara Sea and at the Malaja Oju River), Polar Ural (Kharuta River) (in both these areas graptolitic Pridolian rocks also occur), eastern slope of the Central Ural 100 km southeast of Swerdlowsk and South Ural near Orsk (Koren' 1969, 1971, 1973a, 1973b).

In Kazakhstan north of Lake Balchasch a remarkable Pridolian graptolitic sequence may as well extend into the basal Lochkovian *uniformis* Zone (and possibly higher) (Mikhajlova 1975) but further results from work in progress by Mikhajlova and Koren' are awaited.

In the Central Asian part of the Soviet Union, namely in the Turkestan and Serafshan-Gissar Ranges of the westernmost Tien Shan, Lochkovian graptolites have been described and recorded from several sections (Obut 1968, 1972; Biske and Rinenberg, 1973; Erina *et al.* 1976).

In Southeast Asia Lochkovian graptolites are known from northern Thailand (Jaeger *et al.* 1969) and several regions of peninsular Malaysia (Jones 1973).

Pragian graptolites are known from Pai Khoi (coast section at Amderma) (Koren' 1969, 1971), the Serafshan — (Magian area) and Turkestan Ranges (Rawat Jakob section) in Central Asia (Obut 1972; Koren' 1975, 1976; Erina *et al.* 1976), Himalaya in South Tibet (Jolmolungma = Mount Everest region) (Mu *et al.* 1973; Mu 1974; Mu and Ni, 1975), Yunan (Mu and Ni 1975), Sichuan (Central China) (Xiang *et al.* 1975); Burma, northern Thailand (Jaeger *et al.* 1969) and several areas in peninsular Malaysia (Jones 1973).

The Burmesian graptolites are from the Zebingyi Shale. They were originally described as the middle Silurian *M. cf. riccartonensis* and *M. dubius* (Elles in Reed 1906: 90—92). Berry (*in*: Berry and Boucot, 1972: 30) recognized these as members of the *M. hercynicus* group and compared some even with *M. atopus*. New collections made by Dr. D. Helmcke at one of Reed's localities and placed at my disposal reveal that the graptolites belong mainly or entirely to *M. thomasi*. Some of Reed's specimens that have been loaned to me by the Sedgwick Museum, Cambrigde, through the kindeness of Dr. R.B. Rickards, are also most similar to *M. thomasi* or other Pragian forms.

The Pragian sections at Amderma (Pai Khoi) and Rawat Jokob (Kik Mountains of the Turkestan Range) are remarkable in that they occur in succession with graptolitic Lochkovian and even Pridolian rocks. These are so far the only sections on the globe that exhibit an apparently continuous graptolitic record across the Lochkovian-Pragian boundary.

Certainly one of the most notable contributions to the knowledge of Devonian graptolites in recent years is the discovery of Pragian faunas in the Jolmolungma (Mount Everest) area of the Himalaya (Mu and Ni 1975). Though I oan not read the Chinese text, I feel a need to give the following comment relying on the illustrations of the graptolites that were published in several papers.

In addition to Mu and Ni describe six species and subspecies as new all of which I would affiliate to already known species. I would suggest the following identifications: the three forms described as *Neomonograptus himalayensis* Mu and Ni, *N. atopus rigidus* Mu and Ni and *N. latus* Mu and Ni appear to me all genuine *Monograptus atopus* Bouček. I am aware that Mu and Ni had to rely on the original description and illustration of *M. atopus* which is misleading. *Monograptus hyalamensis* Mu and Ni, *M. yaliensis* Mu and Ni and possibly also *M. immaturus* Mu and Ni I would label *M. thomasi*.

For the reason stated above, and because I have not seen actual specimens, my reinterpretation is given with reservation. As I have written earlier (Jaeger 1967) the Australian *M. thomasi* could be subdivided as to subspecies. Also, one or the other Himalayan form may be accorded subspecies rank. From viewing the illustrations it would appear to me that apart from the usual distortions during burial deformation by schistosity has affected the Himalayan graptolites. For me it is impossible to assess this effect on the basis of the published figures.

In conclusion, I believe the graptolites from the Jolmolungma area to be typical Pragian forms, all of which seem to compare closely with previously described species, and hence well match Pragian faunas from other parts of the globe.

Australia. — Lochkovian graptoloids are not known with certainty. Rare specimens from the Wallace Shale at Cheeseman's Greek near Orange (N.S.W.) are reminiscent of *M. uniformis*. They are accompanied by a form that could be the late Pridolian *M. transgrediens* (Sherwin 1974 written communication; see also Sherwin, this Conference, who compares the former species with *M. thomasi*. I have seen only photographs).

Pragian monograptids are of wide distribution in Victoria (Jaeger 1966, 1967). The two species that have been described, *M. thomasi* and *M. aequabilis notoaequabilis*, appeared to occur in separate horizons, but have been found at closely adjacent localities, so that they may be bound to the same general level. Work on the late monograptids of Victoria is continued by this author.

Packham (in Strusz 1972: 445) recorded *M.* cf. *yukonensis* from a locality in New South Wales.

North America. — Early Devonian graptoloids are known from the Cordilleran region in (1) Central Nevada and (2) northwestern Canada and Alaska, (3) the Canadian Arctic Islands and North Greenland (?) and (4) the northernmost Appalachians.

In Central Nevada, Lochkovian graptolites occur in several sections (some extending through the whole stage) in the following areas: Roberts Mountains, northern Simpson Park Range, Monitor Range and near Carlin (Berry 1967a, 1967b, 1970; Berry, Jaeger and Murphy 1971; Berry and Murphy 1975; Murphy 1977). Pragian graptolites have been described hitherto only from the Rabbit Hill Limestone at the type locality in the Monitor Range (Berry and Murphy 1972) (see comment above). Murphy and Jaeger collected *M. thomasi* also in the Roberts Mountains, namely in Western Assemblage rocks.

In the northern Cordilleran region of Alaska and Canada predominantly Pragian and less Lochkovian graptolite localities are known in the following four areas: (1) Southeastern Alaska (Prince of Wales Island and adjacent islands) (Churkin et al. 1970), (2) eastern Alaska close to the Canadian border, namely in the Nation-Tadonduk Rivers area (tributaries of the Yukon; Churkin and Brabb 1965), and some 250 km further north at the Porcupine River (Churkin and Brabb 1967; Churkin and Jaeger in preparation), (3) Richardson Mountains to Nahoni Ranges in the northern Yukon Territory (many sections), and (4) South Nahanni River area in the southwestern Northwest Territories (for 3—4 see Jackson and Lenz 1963; 1972; Lenz and Jackson 1971, particularly locality map text-fig. 1).

In the Canadian Arctic Islands more Pragian graptolite occurrences are known than Lochkovian. Some are in succession with Pridolian graptolites, particularly the zone of *M. transgrediens* that has a wide distribution also. With one exception none of those faunas have been described or illustrated. Most are listed in the publications of the Geological Survey of Canada. Through the kindness of Dr. R. Thorsteinsson, who identified those graptolites, I have seen some of the material. The following islands yielded Devonian Graptoloidea (from west to east): Melville Island (three areas) (Tozer and Thorsteinsson 1964: 52—64) (*M. yukonensis*, original identification *Monograptus* sp.n. A), western Prince of Wales Island (Kerr et al. 1977), Bathurst Island (half a dozen sections chiefly with Pragian graptolites) (McLaren in Fortier et al. 1963: 603—606; McMillan in Fortier et al 1963: 623—624; Tozer and Thorsteinsson 1964: 58; Kerr 1974: 23—24 and 91—144), Baillie Hamilton Island (a small island lying off the north coast of Cornwallis Island) (Kerr et al. 1977), Devon Island (Jackson et al. 1976) Ellesmere Island (Thorsteinsson in Boucot, 1960: 290; Trettin 1977, personal information). The section on Twilight Creek in the Stuart River Valley, Bathurst Island, is one of the most informative Silurian/Devonian

graptolitic sequences in the Canadian Arctis as it extends from the Lland-
overian up to the *yukonensis* zone (Kerr *et al.* 1977).

Berry *et al.* (1974) record *M.* cf. *aequabilis* from Hall•Land, North
Greenland, i.e. from strata of the Franklinian Geosyncline that are an
extension of those in adjacent northeastern Ellesmere Island. So far no
illustration was published of the single specimen on which this important
record is based.

In the northern Appalachians several Lochkovian graptolite localities
are scattered particularly over northeastern Gaspé Peninsula (Jaeger: *in*
Boucot *et al.* 1967; Lenz 1972; Jaeger 1973 and unpublished studies).
Monograptus uniformis uniformis, M. uniformis angustidens, M. microdon
and *Linograptus posthumus* occur at different localities in the Lesseps
Brook area, perhaps the most informative being the road cutting about
1,3 km west of junction of Lake St. Anne Road and Lesseps Brook as it
yielded typical *M. uniformis.* (This locality is outside the area covered by
the sketch map in Cumming 1959, fig. 8). Other localities in Gaspé, e.g.
some or all with typical *M. aequabilis*, on the basis of this species alone
could even occupy a position higher in the Lochkovian.

Lenz introduced the new subspecies *M. aequabilis gaspesiensis* Lenz 1972 for
· a form (from one locality) said to be consistently narrower and having a slightly
higher thecal count than the typical form. Without having seen the originals it is
difficult to assess that form satisfactorily. But I am aware of the considerable
variation of the dimensions in the rhabdosomes from the Forillon Peninsula (Gaspé),
which I consider as typical *M. aequabilis.* In those the number of thecae in the first
cm varies from 8 1/3—11, the maximum width of the rhabdosomes from 1,4—1,9 mm.

In northern Maine the occurrence of *M. microdon* (Berry 1967: 964)
is suggestive of the *uniformis* or *praehercynicus* Zone. However, as the
microdon lineage is now known to extend into the Pridolian, and as it is
extremely difficult to distinguish between Lochkovian and Pridolian
forms, a Pridolian age for this occurrence may not entirely be outruled.

1.3. Generalizations

From a consideration of the world distribution of Devonian graptoloids
several generalizations seem to emerge. These were suggested earlier
(Jaeger *et al.* 1969), but stand now on a broader and safer basis.

1) Early Devonian Graptoloidea (including the faunas younger than
the *hercynicus* Zone) were still of world-wide distribution, and

2) were of extremely uniform composition the world over down to
the species level; biogeographic differences do not appear to be esta-
blished.

Certain differences between local faunas, such as the record of dif-
ferent subspecies of *M. yukonensis* from different continents, or the
current restriction of a certain species to one area only, e.g. *M. pacificus*
to southeastern Alaska, may have temporal rather than biogeographical

significance, or may be simply an effect of uneven knowledge (thus *M. hemiodon* is known with certainty only from Thuringia, *M. ramstalensis* from Thuringia and Bulgaria, i.e. from sections with an unusually complete graptolitic record).

The following example may serve to illustrate how uniform the composition of a certain Early Devonian fauna may be even in distant sections. When sampling through the *uniformis* Zone at Coal Canyon, Simpson Park Range, Nevada, I was struck by the observation, that there not only are the species the same as, say, Thuringian species, but that their relative frequency, i.e. the quantitative composition of the fauna, is closely comparable in those two so distant regions. The most common form is to be *M. uniformis* which occurs frequently in several beds. Also common is *M. microdon*, but this is not found in every graptolite-bearing layer. One or two bedding planes yielded abundant *Linograptus posthumus*. After some time *M. aequabilis* was found in one bed; this species is neither rare nor frequent. The listed four forms are those species that are typically met with everywhere in the *uniformis* Zone.

2. Age of latest graptoloids

A detailed survey of the correlation of the highest graptoloid occurrences is beyond the scope of this paper. But a few words may be written. If all the data from various fossil groups, such as brachiopods, conodonts and tentaculitids are taken together, it would appear that no conclusive evidence has been adduced for an age younger than Pragian for any known Devonian graptoloid. But from circumstantial evidence, a range above the Pragian might well be considered for some faunas.

Here a few remarks may be made on the datum rendered by pelagic tentaculitids that have received biostratigraphic significance recently, and that are at many localities directly associated with the latest graptoloids. In various sections all over the globe the latest graptoloids occur on the same bedding plane together with *Nowakia acuaria* (Reinh. Richter) that does not range beyond the top of the Pragian, at least in the Barrandian type area of the stage. For example, *M. yukonensis* in the Cordilleran region of Canada, *M. langgunensis* and *M. thomasi* in Malaya are associated with *N. acuaria*. Mu *et al.* (1973) record *N. acuaria* from the formation that yields the latest graptoloids in the Himalaya. *M. thomasi* in Burma and *M. yukonensis* in Malaya are among others associated with a species of *Metastyliolina* that is close to the Pragian *Metastyliolina lardeuxi* Alberti (det. G. Alberti). Also the latest Australian graptoloids seem to be associated with Pragian, namely late Pragian tentaculitids; but the result of current studies is awaited.

Whether or not the succession of Early Devonian pelagic tentaculitids compares closely in distant sections of the globe, has yet to be established. For instance, in southeast Asia *Nowakia acuaria* is associated with abundant styliolinids (soft-shelled pelagic tentaculitids), an observation that is unexpacted from Central European experience. Could such be suggestive of somewhat different ranges of important tentaculitid species in different continents?

In the Barrandian, the Pragian graptoloids occur in strata 3-5 m below the top of Pragian. If my suspicion is right that on phylogenetic and comparative biostratigraphic considerations (discussion under 1.1) the Pragian graptoloids of the Barrandian are less advanced than, say, faunas with the typical *M. yukonensis* or with *M. yukonensis fangensis* and *M. langgunensis*, then the respective North American, southeast Asian and Yunnan graptoloid faunas could well range higher, possibly even into the Zlichovian.

3. Morphology of Devonian Graptoloids

About 25-30 Devonian graptoloid species and subspecies may be currently recognized belonging to four genera: *Monograptus* (some 20 species), *Linograptus* (1), *Abiesgraptus* (3) and *Climacograptus* (1). (The latter is based on a single specimen from the *hercynicus* Zone in the Carnic Alps.) By far the majority of species as well as rhabdosomes pertain to *Monograptus*, but *Linograptus* and *Abiesgraptus* may also occur in profusion in many beds of the zones of *M. uniformis* and *M. praehercynicus*, e.g. in Thuringia, Barrandian, Carnic Alps, Sardinia, Menorca, Morocco, Ural, Nevada and Malaya.

In addition to the species sketched in fig. 2 or listed in Table 1, many others have been described in recent years. Most of those are discussed in the foregoing (1.2) and considered as synonyms, or as insufficiently known. Identification of many Devonian species is a matter of fine judgement, particularly when found in the usual state of preservation as flattened films in tectonized black shale. Safe comparison and identification is often rendered impossible when the preservational conditions differ greatly. Many species of the *uniformis* and *praehercynicus* type, though quite distinct as adults, may not be identifiable as juveniles in any state of preservation, and as adults when they are tectonically deformed, or as single specimens.

In fig. 2 no attempt is made to assign species to lineages. The Lochkovian *Monograptus* species belong certainly to at least four or five lineages as follows: (1) *M. microdon*, (2) *M. aequabilis*, (3) *M. ramstalensis*, (4) *M. uniformis* and (5) *M. praehercynicus*- *M. hercynicus*, with *M. birchensis* (?), *M. hemiodon* (?) and *M. kayseri* (?), i.e. the latter lineage may be branched, or this species group could consist of more than one lineage. *Linograptus* and *Abiesgraptus* form a further lineage that is with certainty somewhat branched.

The late Pragian graptoloids belong to at least four lineages: (1) *M. aequabilis* (possibly with *M. fanicus*), (2) *M. atopus*, (3) *M. yukonensis* — *M. langgunensis* and (4) *M. thomasi* — *M. telleri*; this latter may have ramified repeatedly, and may have given rise to the *yukonensis* lineage with which it coexists. *M. falcarius* represents a fifth lineage (=*hercynicus* lineage) that became extinct in the early Pragian. Four species are the maximum to be found on one bedding plane in the Pragian.

In spite of the very many new discoveries of Devonian graptoloids,

the considerable geographical extension of discoveries, and the achieved stratigraphical progress, the hitherto known rather narrow morphological spectrum of Devonian faunas has changed only insignificantly through the last ten years.

The Devonian *Monograptus* species are small to medium-sized, having 20—40, rarely over 60 thecae in a rhabdosome. Typically, they are robust and straight, except for a few forms that are partially or totally recurved (*M. yukonensis, M. langgunensis, M. falcarius*) or strikingly incurved (certain *M. microdon*). All have hooded thecae of the type of *M. uncinatus* (implying certain modifications), either throughout the rhabdosome length or at least in the proximal portion, the minimum being on well-developed hood in *M. aequabilis* and *M. atopus*. In the latter the hood is a rather flat lid that leaves only a slit-like thecal aperture.
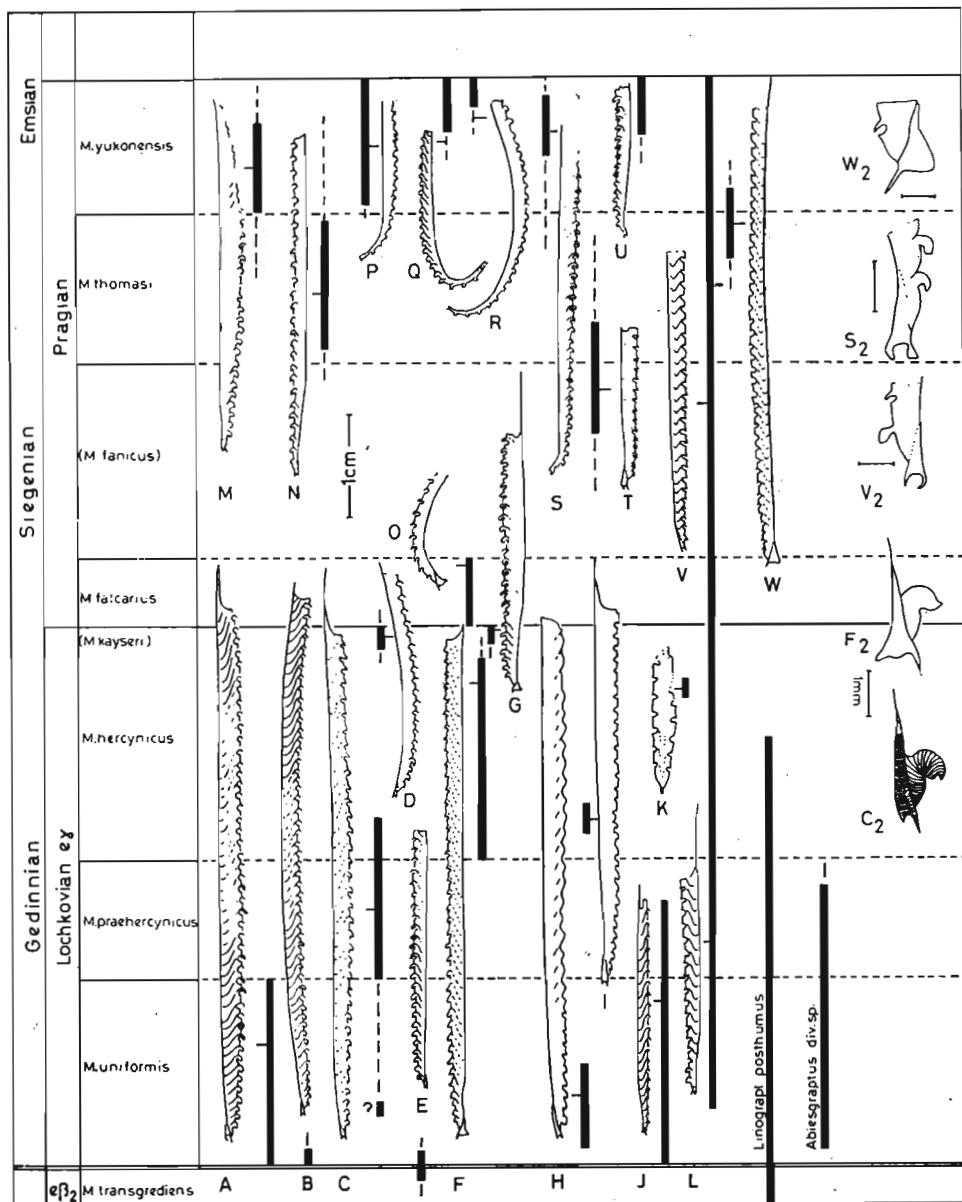
M. uncinatus type theca means: the thecal aperture is roofed by an unpaired, more or less arched mesial shield or hood without spines. This hood is the ventral extension of the dorsal thecal wall as can be seen when studying the astogeny of Devonian species. Typically, full length growth of a certain theca, including formation of the hood is completed before growth of the next theca begins (Jaeger 1959: 90—91, pl. 4: 1 and others). In *M. microdon*, even in very distal thecae growth of the hood is accomplished before any fusellus of the succeeding theca is formed. Consequently, the apertural hoods should be constructed of normal fuselli, as is the

Fig. 2. Ranges and sketches of Devonian graptoloid species. Ranges for most of the Pragian forms tentative. Sketches slightly diagrammatic. Broken lines, particularly for interthecal septa, are conjectural, i.e. not clearly observed in the depicted specimen, but known from others. All specimens more or less flattened. Drawn to scale. Catalogue numbers G ... refer to collection of Palaeontological Museum, Humboldt-University, Berlin.
A — M. uniformis uniformis Přibyl. Lejškov, Bohemia. G 337; *B — M. uniformis angustidens* Přibyl. Čertovy schody, Bohemia. G 573; *C — M. praehercynicus* Jaeger. Ramstal, Thuringia. G 65a. C_2. *M.* cf. *praehercynicus* Jaeger. Čertovy schody Bohemia, *uniformis Zone*. G 574c; *D — M. kayseri* Perner. Jižne od Cikanky, Bohemia. UUG Prague, coll. Chlupáč. Composite figure; *E — M. birchensis* Berry and Murphy. West of Coal Canyon, Simpson Park Range, Nevada. G 622a; *F, F_1 — M. hercynicus hercynicus* Perner. Ramstal and Gräfenwarth, Thuringia. G 15 and G 410; *G — M. hercynicus nevadensis* Berry. West of Coal Canyon, Simpson Park Range. Nevada. G 623; *H — M. ramstalensis* Jaeger. Ramstal, Thuringia. G 29; *I — M. hemiodon* Jaeger. *Ibidem*, G 153; *J — M. microdon microdon* Reinh. Richter. *Ibidem*. Composite figure; *K — Climacograptus* sp. Bischofalm, Carnic Alps. Coll. Univ. Graz; *L — M. aequabilis aequabilis* (Přibyl). Lejškov, Bohemia. G 194; *M — M. telleri* Lenz and Jackson. Royal Creek, Yukon. After Lenz and Jackson 1971, pl. 1: 14; *N — M. thomasi* Jaeger. 19 Mile Quarry, Yarra Track, Victoria. After Jaeger 1966, fig. 1a; *O — M. falcarius* Koren. Amderma, Pai Khoi. After Koren, 1971, fig. 3A; *P — M. yukonensis yukonensis* Jackson and Lenz. Royal Creek, Yukon. G 506.1; *Q — M. yukonensis fangensis* Jaeger and Stein. Road section Chiengmai-Fang, Thailand. After Jaeger et al., 1969, fig. 1D; *R — M. langgunensis* Jones. *Ibidem*, fig. 1J; *S. S_2 — M. craigensis* Jaeger. Port St. Nicholas, Prince of Wales Island, southeastern Alaska. G 624; *T — M. fanicus* Koren. Darai-Khurd, Serafschan, Bed 12. G 625; *U — M. pacificus* Jaeger. Port St. Nicholas, Prince of Wales Island, southeastern Alaska. After Churkin et al, 1970: fig. 7A; *V — M. aequabilis notoaequabilis* Jaeger and Stein. 20 Mile Quarry, Yarra Track, Victoria. After Jaeger, 1966: fig. 1d. V_2. Port St. Nicholas, Prince of Wales Island, southeastern Alaska. After Churkin et al., 1970: fig. 9J; *W, W_2 — M. atopus* Bouček. Stydlé vody, Bohemia. G 508.

dorsal thecal wall. Construction of hoods of broad fusselli can be demonstrably seen in the following species that I have etched out of the rock. *M. uniformis, M. aequabilis, M.* cf. *praehercynicus, M. hercynicus* and *M. microdon.* But the fusellar structure can be observed also in sufficiently preserved specimens of the listed species, and also in *M. thomasi* (at least) when lying on the rock.

In view of some criticisms in the literature I may as well remind those authors that the first to describe *M. uniformis,* Přibyl (1940), erected this species as a variety

of *M. uncinatus*, as did independently Münch (1942), who named it *M. uncinatus latus*. In his revision of *M. hercynicus*, Přibyl compared the thecae of this species also with those of *M. uncinatus*. To him and others, including myself, who studied actual specimens of those and other Devonian species, there was never any doubt about the character of their thecae. Even those older and recent workers in five continent who studied Devonian monograptids, but mistook them for Silurian forms, usually identified them as the Ludlow *M. uncinatus* (and varieties) or the Wenlock *M. riccartonensis* that somewhat resembles *M. uncinatus*.

The thecae vary from almost uniform (*M. uniformis, M. microdon*) to strikingly biform becoming simpler towards the distal end; at least the size of the hoods may somewhat decrease. (*M. microdon* possesses fully developped, peculiarly specialized hoods — these are closely pressed against the ventral wall — along the whole rhabdosome length, but the outline of the hoods of the initial thecae is slightly different.)

In the long-ranging *M. aequabilis* and others the distal thecae are climacograptid, in *M. ramstalensis* they are even dichograptid, i.e. simple as in *M. dubius*.

A peculiarity of most Pragian species is the excessive development of the dorsal tongue of the sicula. This minor morphological feature is characteristic also of the early Lochkovian *M. uniformis*. However, one of the youngest species, *M. atopus*, does not possess a dorsal tongue at all, but has a sicula of unique shape (fig. 2 W_2).

Several species (*M. thomasi, M. telleri, M. craigensis, M. pacificus, M. yukonensis*) show a tendency towards proximal protraction and correlative isolation of thecae — an old trend in graptoloid evolution, particularly in the Llandovery, when it was, however, much more pronounced.

Viewed against the background of graptolite phylogeny the Devonian *Monograptus* association appears to be the most monotonous and uniform monograptid fauna that ever inhabited the seas, thus demonstrating the "programme-evolution" or "Zeitsignatur" in graptolite history. Morphology was governed by one universal fashion with such small latitude for variation as has not been seen before.

In addition to the some 20 species and subspecies of the uniserial *Monograptus* that may be recognized at present in the Devonian, there occur the normally giant rhabdosomes of *Linograptus posthumus* and *Abiesgraptus* both housing up to several thousand zooids. The true *Abiesgraptus* is confined to the two basal Lochkovian zones, though attempts towards its evolution are known from earlier strata. *Linograptus posthumus* pertains to a long-ranging lineage that started in the Ludlow and lasted to the zone of *M. hercynicus*. The Devonian *Linograptus* is characterized by a predominance of four-branched rhabdosomes as compared with the Silurian specimens that typically exhibit variable and often higher stipe numbers. The 4-branched *Linograptus* rhabdosome appears to be predisposed and even a prerequisite to give rise to *Abiesgraptus*. (*L. posthumus* occurs frequently also in the Australian Ludlow (Jaeger 1967), but this

occurrence is not plotted in Table 1 as it is to show the Devonian distri-
bution.)

Though both genera were cosmopolitical in the Lochkovian, neither
Linograptus nor *Abiesgraptus* has turned up in beds younger than the
hercynicus Zone. The *absence* of these two genera in the Pragian is the
most distinctive gross feature of the graptoloid faunas of this stage.

4. Origin of Devonian graptoloids

The actual ancestors of the majority of *Monograptus* species that ap-
pear at the base of the Lochkovian, so to say "out of the blue" (as is the
rule for earlier graptolite faunas also), remain obscure. But the roots of
such species as *M. birchensis, praehercynicus, hercynicus, kayseri, tho-
masi, telleri, yukonensis, pacificus*, probably also *uniformis* and others
belonging to this plexus (though the immediate phylogenetic relationships
for most of them appear to me unclear) might easily be sought for in such
species as *M. uncinatus* of the early Ludlow and *M. similis* from the
ultimus Zone and others. It is difficult to distinguish *M. similis* from the
later *M. praehercynicus* and *M. birchensis*, all three being of very general-
ized (unspecialized) morphology. Throughout the Ludlow and Pridoli there
occur sporadically and unevenly distributed over the globe, and not yet
well understood, species with *uncinatus* thecae.

On a global scale the Pridolian graptoloids are less well known than the Loch-
kovian faunas. Although such species as *M. transgrediens* has demonstrably a world-
wide distribution, there are some indications of a regional differentiation in contrast
to the Devonian faunas. For instance, the spinous *M. willowensis* (Berry and Murphy)
from the uppermost Pridoli of Nevada was quite unexpected in such stratigraphical
level. The record of late Ludlow and Pridolian graptolites in Nevada is very poor
(except for *M. willowensis*), but the rare specimens to be found belong usually to
the *uncinatus* group. The common *M. birchensis* even crosses the Silurian/Devonian
boundary (Berry and Murphy 1975).

Some data from Alaska seem to point in the same direction. The interval between
the Ludlow and the basal Devonian appears to be dominated by graptolites with
uncinatus type thecae (Churkin and Brabb 1967: 235).

In conclusion, graptolites of the *uncinatus* group that are of sporadic
occurrence in the European Pridolian could well be better represented
elsewhere in that time span.

I would consider it both unnecessary and unlikely to envisage a *Mono-
graptus* with simple dichograptid thecae as the typical ancestor that by
way of the early Pridolian *M. ultimus* led to the Devonian forms of the
uniformis-hercynicus group (Hutt *el al.* 1972: 172 and Rickards *et al.*
1977: 78 ff.). Both *M. ultimus* and the late Pridolian *M. transgrediens*
(which latter obviously belongs to a lineage different from *M. ultimus*)
have thecae with ear-shaped extensions of the lateral thecal walls
(*M. transgrediens* only proximally) (Jaeger 1975, 1977a). I failed to detect
any tendency towards astogenetic or phylogenetic dorsal coalescence of
the lateral apertural processes. Moreover, the construction of the rhab-

dosome of *M. ultimus* is rather different from that of any known Devonian species.

The unique *M. microdon* has a forerunner in the middle of the Pridoli (still to be described properly; Jaeger 1975). For a time I was inclined to regard the middle Pridolian form even as conspecific with the Lochkovian *M. microdon*. Still farther back near the Ludlow/Pridoli boundary we find *M. kallimorphus* Kraatz (*M. balticus* Teller would appear to be a younger synonym) as a likely member of such lineage.

M. ramstalensis is the only species for which I can see the need and likelihood for a derivation from a *dubius*-type species. But neither morphological nor temporal intermediates are known.

At any event, such forms as the small, highly specialized *M. ultimus* would appear to be most unlikely ancestors for the big *M. ramstalensis* well understood, species with *uncinatus* thecae.

The Ludlow species "with Devonian morphological affinities" as described by Rickards and Palmer (1977) I do not hesitate to identify with *M. haupti* Kuehne, a common and long-ranging species that extends through most of the Ludlow. This shows the development of small supra-apertural hoods in a few proximal thecae in a very late astogenetic phase, namely after the rhabdosome has attained a length of over 20—30 thecae. Accordingly, the hoods of *M. haupti* are clearly not homologous with the apertural hoods of *M. uncinatus*. This mode of growth I believe to be not at all typical of any hitherto known Devonian species.

In the combination of hooded thecae proximally and simple *dubius*-type thecae distally, the Lochkovian *M. ramstalensis* is indeed reminiscent of the Ludlovian *M. haupti*. Unfortunately, the astogeny of *M. ramstalensis* is not known. The smallest complete rhabdosome of my collection (No. g 157) has 23—24 thecae. It shows already the complete set of hooded proximal thecae (th$_{1-4}$ with fully grown hoods, th$_{5-7}$ with hoods of decreasing size). This implies that the hoods in *M. ramstalensis* are formed in a much earlier astogenetic stage than in *M. haupti*. The hooded proximal parts of *M. ramstalensis* cannot be distinguished from the coeval *M. uniformis*, nor could be distinguished juveniles of the two species, provided that the initial thecae of *M. ramstalensis* exhibit the same mode of growth as the thecae of *M. uniformis*. Juvenile *M. uniformis* are common in the bed that yielded adult *M. ramstalensis* as well as adult *M.uniformis*. It appears to me likely that juveniles of *M. ramstalensis* have not been found simply because they cannot be distinguished from juvenile *M. uniformis*.

Originally (Jaeger 1959: 131—132) I have envisaged *M. ramstalensis* as the likely immediate ancestor of *M. uniformis*. But after what is known to-day I would doubt such hypothesis as less probable; rather I would consider *M. ramstalensis* as a separate lineage with unknown root (*M. transgrediens?*), and an interesting example of convergent evolution towards a Devonian type of rhabdosome which ended blindly at an early evolutionary stage.

In this context it may be mentioned that the narrow rhabdosomes of *M. uniformis angustidens* grade into the broad typical *M. uniformis* low in the *uniformis* Zone, and that the imbrication structure of thecae that is typical of the distal rhabdosome portion of both subspecies appears to have evolved gradually early in the *uniformis* Zone, but became more pronounced in higher levels of the zone. Observation of

gradation of *M. uniformis angustidens* in *M. uniformis uniformis* would appear incompatible with an immediate phylogenetic linkage of *M. ramstalensis* and *M. uniformis*.

Linograptus* and *Abiesgraptus* form a lineage that can be continuously traced back to the early Ludlow *M. nilssoni*.

5. Extinction of graptoloids

Extinction of whole faunas, animal classes and even phyla is one of the very few major features of evolution, and therefore should be given due consideration on a symposium like this. However, by its very nature the phenomenon of extinction is extremely difficult to assess; it will perhaps always remain a wide field for speculations.

Graptolites are found in a wide variety of marine rocks (varying from black euxinic clays free of carbonate to white organic limestones, and from finest muds to coarse, conglomeratic graywackes). This indicates a wide variety of marine environments. But they show a preservational preference for black (graptolitic) shales. Black euxinic shales or at least rocks deposited on less well aerated sea bottoms are most favourable for the preservation of graptolites, because the organic periderm is rapidly destroyed by oxidation. But it would appear that euxinic seas or oceanic areas with less aerated bottoms, with low energy environment, were also more favourable for the life of planktic graptolites than other environments. With other words, the evolution of the planktic graptolites may have been somehow connected and correlated with the generation of vast stretches of more or less stagnant waters. Did they profit from the development of large areas of *Sargassum*-like seaweed and/or did they (or some of them) manage to thrive near the interface between the fully aerated surface waters and the non-oxigenated bottom waters? Or were they somehow adapted to certain specialities of the physics of such seas of which we have not the slightest notion?

The middle to late Llandovery maximum diversity of Silurian graptolites (after the drastic faunal break at the Ordovician-Silurian junction) coincides with the maximum areal extent of the Silurian transgression in Europe and North Africa, and the maximum extent of euxinic seas and black mud deposition in these two continents (Jaeger 1976).

The great crisis in graptolite evolution at the end of the Wenlock (with only two common species that survive, and indications of rare other retiolitid survivors) coincides with a geologically sudden areal reduction of the more or less euxinic seas in Europe and North Africa, and a temporary distinct weakening of euxinic conditions in persisting euxinic areas (e.g. Thuringia). This geological event I would consider as the most plausible cause for the crisis in graptolite evolution at the end of the Wenlock. This geological event that is clearly to be recognized in parts of two continents, may have been a global event, with specific effects on graptolites also in less graptolitic facies. It is interesting to note that coeval

benthic faunas show at the same time maximum diversity (Barrandian, Holy Cross Mountains).

The stepwise evolution of the Ludlow graptolite fauna (as imposing as it may have been) did not reach the diversity of the former Wenlock fauna which in fact was only the tail of the magnificient late Llandovery fauna.

The end of black mud deposition even in the interior parts of the Palaeotethys geosyncline between Europe and North Africa in about the middle of the Ludlow coincides rather closely with the extinction of the last retiolitids and the spinous monograptids of the *M. chimaera* group.

The renewed extension of euxinic seas about the Silurian-Devonian boundary coincides with the beginning of the rather important evolution of the Lochkovian graptoloids. The end of the Lochkovian marks the end of euxinic deposition for a long time to come in all of the Palaeotethys area in Europe. It also means the extinction of several Lochkovian graptoloid lineages, including the spectacular *Linograptus* and *Abiesgraptus*, thus resulting in a further impoverishment of the graptoloid faunas.

Though the Pragian graptoloids are still world-wide in distribution, their diversity is lower than any earlier Silurian-Devonian fauna. Therefore they were still more in danger of extinction at times of drastic ecological changes.

In conclusion, the process of extinction of the graptoloids was a slow, stepwise, longlasting historical process. This was marked by a series of more or less drastic and even sudden incisions that appear to have been caused by geological, especially climatic events. These can be demonstrated on a regional scale, but may be global. Such incisions led in total to a progressive reduction of the diversity of graptoloid faunas, thus increasing the danger of final extermination. The latter has yet to be analysed more precisely on a global scale, i.e. the local extinction data have to be determined more exactly than appears possible now.

Of course, graptoloid evolution was also subjected to biotic selection forces of various sorts. At a time when *M. hercynicus* was believed to be the last true graptolite, one could be struck by the coincidence of the apparent extinction of graptoloids and the burst of pelagic tentaculitids. To-day graptoloids and the small pelagic tentaculitids are known to have well co-existed for many millions of years. Obviously, the graptoloids occupied an ecological niche different from that of the tentaculitids. Therefore the tentaculitids survived the final crisis in graptoloid history that led to the extermination of the last graptoloids.

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DISCUSSION

A. Lenz:

Age range of *M. yukonensis* in northern and Arctic Canada, the age of *M. yuko-
nensis* as deduced from conodonts and brachiopods is confined entirely to the Pra-
gian. No post-Pragian graptolites that is Zlichovian, are presently known from the
Cordilleran or Arctic regions.

L. Sherwin:

Dr. Jaeger, would you care to comment upon the stratigraphic range of *Mono-
graptus thomasi*?

Dr. Jaeger's reply to dr Sherwin: The Australian and South-east Asian occurrences
of *M. thomasi* are more or less out of succession, but a general Pragian age is
indicated by the associated tentaculitids. A more precise fix-point is rendered by
the discovery of *M. thomasi* in beds immediately below the first occurrence of
M. yukonensis in the Yukon Territory, Canada (Lenz and Jackson 1971) which is
still Pragian as is suggested by the associated tentaculitids and other fauna. In
Nevada, *M. thomasi* is known from beds (Rabbit Hill Limestone) overlying strata
that are demonstrably coeval to the *hercynicus* Zone.

In conclusion, a Pragian age for *M. thomasi* would appear to be well established
in many regions, but how much of the Pragian is covered by the *thomasi* biozone
is not yet clear.