

LATE ORDOVICIAN GRAPTOLITES FROM THE NORTH AMERICAN MIDCONTINENT

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ABSTRACT. Although relatively uncommon in the dominantly calcareous upper Ordovician (Cincinnatian) sedimentary rocks in the North American Midcontinent, graptolites have been recorded from many localities during some 150 years of study. A revision of these faunas, the first general review for half a century, is based on new collections from about 20 key localities as well as on museum specimens. These epicontinental faunas are locally rich in individuals but diversity is low, with only about 20 species recognized herein. Widely recorded, but poorly known and commonly misidentified species, such as *Amplexograptus manitoulinensis* (Caley), *Climacograptus putillus* (Hall) and *Rectograptus peosta* (Hall), are redescribed based on type and topotype material. Some stratigraphically important species, such as *Climacograptus nevadensis* Carter, *Dicellograptus complanatus* Lapworth, and *D. gravis* Keble and Harris, previously unknown from the Midcontinent, are also described along with a few other, more common and well-known species. Several Cincinnatian species are shown to have a previously unrecognized biostratigraphical utility. The graptolite zonal succession recognized by Riva in New York–Quebec can be applied readily to many of the sections studied, and a bipartite subdivision of the *A. manitoulinensis* Biozone appears feasible. Conodonts make it possible not only to classify the sections in terms of Atlantic conodont zones but also to establish ties between graptolite and conodont zones. Most Midcontinent graptolite faunas represent the endemic Laurentian Biofacies that differs significantly from the cosmopolitan Oceanic Biofacies of marginal areas of Laurentia. Overlap between these in Oklahoma allows correlation between separate graptolite zonal schemes. The new biostratigraphical data are used for regional correlations and for assessment of sequence stratigraphy.

FOR well over a century (since Hall 1865), geologists have collected and studied graptolites from the Cincinnatian (upper Ordovician) strata of the North American Midcontinent. Despite the long history of these studies, several important aspects of these graptolites, including the taxonomy of many species and their precise stratigraphical ranges, have remained very poorly known. This has prevented not only modern assessments of the regional palaeobiogeography and palaeoecology of these faunas but also the use of some species as reliable guide fossils. Early studies, such as those by Ruedemann (1908, 1947), Ruedemann and Decker (1934), and Decker (1935*a*, 1935*b*), documented large and apparently diverse faunas from the south-central United States. Although representing the standard of North American graptolite research during the first half of this century, these works lack several important aspects of modern taxonomic approach, such as extensive use of proximal end development for classification (Mitchell 1987). Furthermore, little, if any, attention was paid to the effects of preservation on the morphology of the rhabdosome, and no attempts were made to isolate specimens from the matrix by means of acid treatment. More recent work on upper Ordovician graptolites in the north-central Midcontinent is limited to descriptions of faunas from single outcrops (e.g. Werner and Echols 1958; Berry 1966, 1970; Berry and Marshall 1971) and of the ultrastructure of a few taxa (Berry and Takagi 1970, 1971; Herr 1971; Berry 1974). More detailed studies have been carried out in the Cincinnatian type area in the vicinity of Cincinnati in Ohio, Kentucky, and Indiana (Text-fig. 1), by Erdtmann and Moor (1973), Bergström and Mitchell (1986, 1990, 1992), Mitchell and Bergström (1977, 1991), Crowther and Bergström (1980), and Goldman and Mitchell (1991), and in the middle and upper Ordovician of Oklahoma (Arbuckle and Ouachita Mountains) from which Finney (1986) provided important information on the stratigraphical distribution of graptolites.

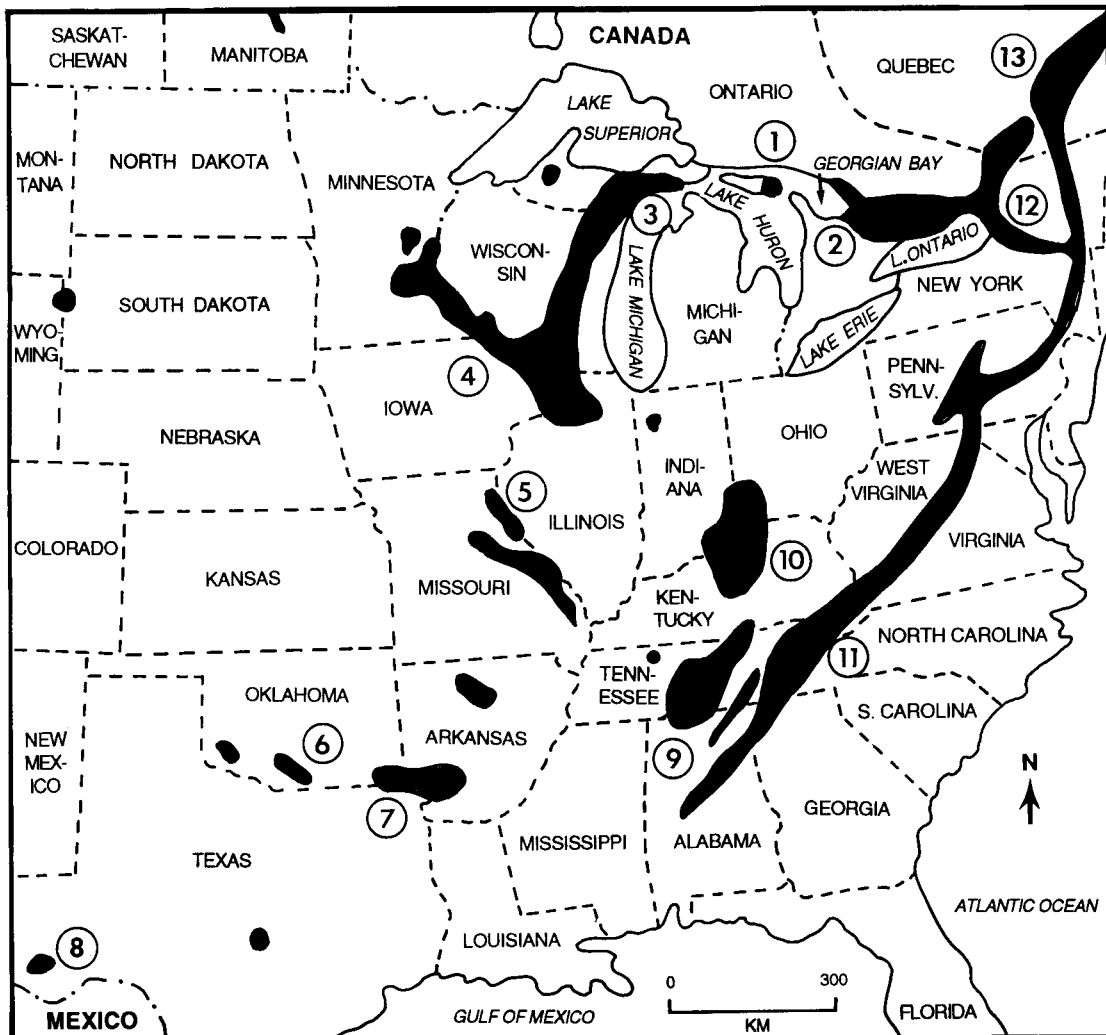
The present paper presents a comprehensive re-examination of the upper Ordovician graptoloid faunas of the North American Midcontinent, and is the first to be attempted for the whole of this vast region since that of Ruedemann (1947). Although Ruedemann's monograph on North American graptolites is still an indispensable source of information, it is out of date in several respects, especially taxonomically. Our investigation covers all the principal upper Ordovician outcrop areas from the Appalachians in the east to the Mississippi Valley in the west, and from Oklahoma in the south to southern Ontario in the north (Text-fig. 1). No upper Ordovician graptolites are known from the Nashville Dome in central Tennessee. We have not investigated the relatively few upper Ordovician graptolites described from the Canadian Arctic (Melchin 1987) nor those from Quebec and New York (Riva 1969, 1974, 1988) which are reasonably well known. Those of the Marathon uplift in western Texas were described by Goldman *et al.* (1995).

The importance of an investigation such as this one lies well beyond the need of a taxonomic reappraisal. For instance, the dark graptolitic shales, and associated carbonate rocks that were deposited over much of the Midcontinent during the late Ordovician (Bergström and Mitchell 1992) record a widespread transgressive event, which has been regarded as eustatic (see, for instance, Witzke and Kolata 1988), and it is marked as a prominent inflection point on numerous sea-level curves based on outcrop studies of North American upper Ordovician successions (see, for instance, Sloan, *in* Sloan 1987; Witzke and Kolata 1988; Johnson 1989; Ross and Ross 1992; Raatz and Ludvigson 1996; Witzke and Bunker 1996). Clearly, an accurate biostratigraphical framework is essential for reconstructing the timing and synchronicity of late Ordovician sea-level fluctuations but thus far, little up-to-date graptolite biostratigraphical information has been available from the Midcontinent for precise correlation of its many key sections, both regionally and internationally. Also, detailed geological data on the upper Ordovician graptoliferous shales have the potential to be of economic importance because these strata are thought to be the source rocks of the many significant hydrocarbon occurrences in the upper middle Ordovician of the North American Midcontinent.

Conodonts have proved very useful for local and regional correlation of upper Ordovician rocks in the North American Midcontinent, and extensive biostratigraphical work using these fossils have been carried out since the 1950s (for summaries, see Sweet 1979*a*, 1979*b*). However, several regional correlation problems have not been satisfactorily resolved. We have collected samples for conodont work at key graptolite localities, and wherever possible, also assessed published data, in several cases based on restudy of collections made by previous workers. Considerable effort has been devoted to establishing direct ties between the graptolite and conodont biostratigraphy because an integrated graptolite-conodont biostratigraphy clearly has potential of providing a considerably greater stratigraphical resolution than those based on either of these index fossil groups alone (Bergström 1986).

MATERIALS AND METHODS

The present study is based on examination of many museum and some private graptolite collections as well as extensive new collections made at about 20 key localities. Virtually all significant upper Ordovician graptolite occurrences in the Midcontinent are included, and thousands of specimens have been examined. Locality information is given in the Appendix, and graptolite species identified from 20 stratigraphical sections are listed in Table 1. For the graptolite biostratigraphical classification we follow, with one exception (eastern Oklahoma), the zonal scheme advocated by Riva (1969, 1974) that can be applied readily to the study sections. Conodont-bearing units are classified in Atlantic conodont zones (Bergström 1986). The more detailed conodont zonal scheme introduced by Sweet (1984), which is based on graphic correlation, is currently not applicable to the sections discussed herein because only one of these is included in his network of correlated sections. Finally, the term 'upper Ordovician' is used herein for the stratigraphical interval of the Cincinnati Series following long established practice in North America (Ross *et al.* 1982).



TEXT-FIG. 1. Distribution of Ordovician outcrop areas (black) discussed in the text. Key to areas: 1, Manitoulin Island, Ontario; 2, south shore of Georgian Bay, Ontario; 3, Upper Peninsula of Michigan; 4, Upper Mississippi Valley, Minnesota, Wisconsin, Illinois, and Iowa; 5, eastern and south-eastern Missouri; 6, Arbuckle Mountains, Oklahoma; 7, Ouachita Mountains, Oklahoma and Arkansas; 8, Marathon region, West Texas; 9, Nashville Dome, central Tennessee; 10, Cincinnati region, Ohio, Indiana, and Kentucky; 11, Appalachians, Alabama to Vermont; 12, Mohawk Valley and adjacent areas, New York State; 13, Saint Lawrence Lowlands, Quebec. The North American Midcontinent extends from just west of the Appalachians to beyond the left margin of the map. Note that some coastal state names are omitted because of lack of space.

BIOSTRATIGRAPHY

Manitoulin Island and Georgian Bay, Ontario

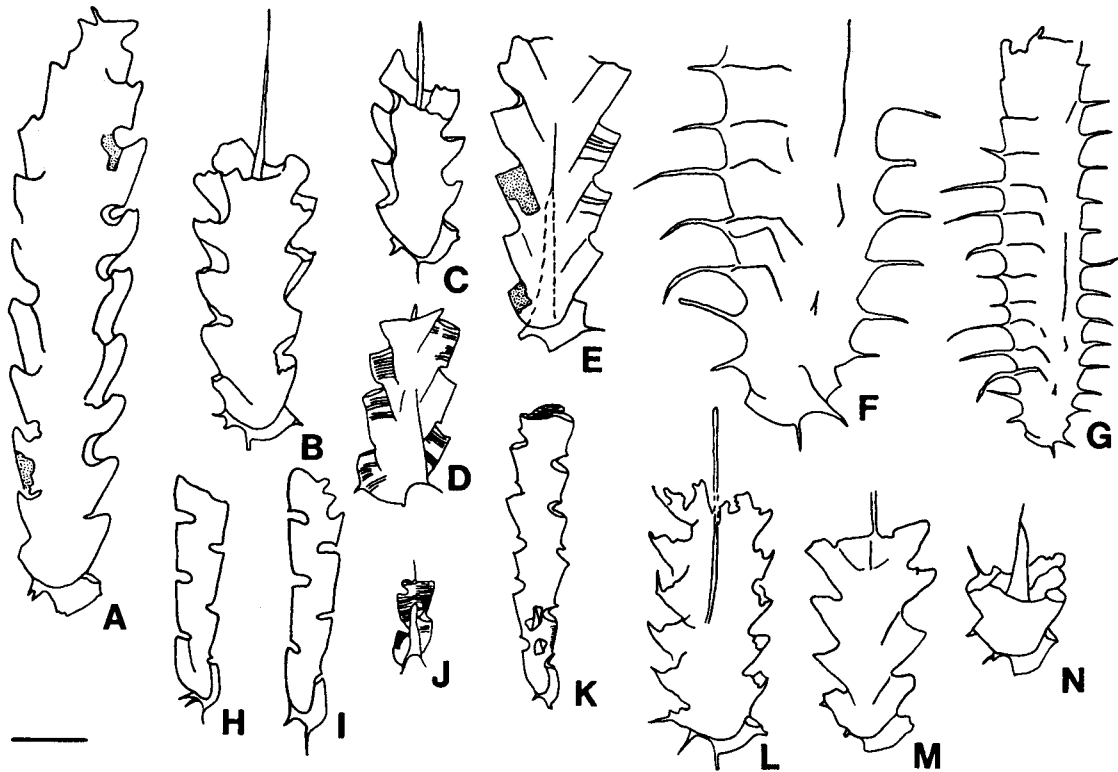
Graptolite biostratigraphy. An important succession of upper Ordovician graptolite-bearing rocks, including the Collingwood Member of the Lindsay Formation and the Blue Mountain and Georgian Bay formations, occurs in Ontario (Text-fig. 1, areas 1 and 2; Russell and Telford 1983; Lehmann *et al.* 1995). Caley (1936) published descriptions of some upper Ordovician graptolites from outcrops on Manitoulin Island and Senior (1991) recorded several species from exposures and

cores of coeval strata along the south shore of Georgian Bay. On Manitoulin Island, the Collingwood Member is a grey-weathering, black, non-calcareous shale (in contrast with its carbonate-rich equivalent along the south shore of Georgian Bay) that contains (Text-fig. 2) numerous specimens of *Geniculograptus typicalis magnificus* (Twenhofel), '*Glyptograptus*' *lorrainensis* (Ruedemann), *Orthograptus quadrimucronatus* (Hall), *O. spinigerus* (Elles and Wood), and *Rectograptus amplexicaulis* (Hall), an association indicating the upper part of the *G. pygmaeus* Biozone. A similar association, which also includes *G. typicalis*, was recorded by Senior (1991) from the Collingwood Member in exposures at Craigeith near the south shore of Georgian Bay.

The overlying Blue Mountain Formation is a blue-grey to brownish shale, a large part of which weathers to clay, with subordinate calcarenitic and calcilititic beds. Although graptolites are locally abundant, diversity is low, with only *Amplexograptus manitoulinensis* (Caley) (Text-fig. 5A–I), *Orthograptus quadrimucronatus*, and *O. eucharis* being present. The first appears about 10 m above the base of the Blue Mountain Formation at its type locality along the creek on both sides of Highway 6, about 5 km south of Little Current, and is the only graptolite present through the next 2–3 m of section. It has a similar range in drill-cores from the Little Current area. It has not been found at higher levels in the Blue Mountain Formation, nor in the overlying Georgian Bay Formation on Manitoulin Island. Senior (1991) reported the species as abundant in a 10 m interval in the uppermost Blue Mountain Formation, and a questionable specimen about 20 m above the base of the formation, in a drillcore from the Campertown area near the south shore of Georgian Bay. This species has a slightly longer, although still short, range in the St Lawrence Lowland and Anticosti Island successions described by Riva (1969; for the St Lawrence Lowland sections, see also Walters 1977 and Walters *et al.* 1982) and in the Arbuckle Mountains of Oklahoma, where it appears in the middle part of the Viola Springs Formation (Finney 1986). The occurrences in eastern North America and in Oklahoma appear to be nearly synchronous with respect to the stratigraphical range of other important index species such as *Climacograptus putillus* (Hall), *Dicellograptus complanatus* Lapworth, *Geniculograptus pygmaeus* (Ruedemann), and *G. typicalis magnificus*. The short stratigraphical range of *A. manitoulinensis* in these sections may well reflect the total range of this species and not only its local acme. However, in view of the very short range of this species at its type locality, and the lack of close graptolite control of the upper and lower boundaries of the *A. manitoulinensis* Biozone on Manitoulin Island, a reference locality of this biozone will have to be selected elsewhere. Because *A. manitoulinensis* has not been found in the lowermost Blue Mountain Formation on Manitoulin Island and south of Georgian Bay, we tentatively refer that interval to the uppermost *C. pygmaeus* Biozone.

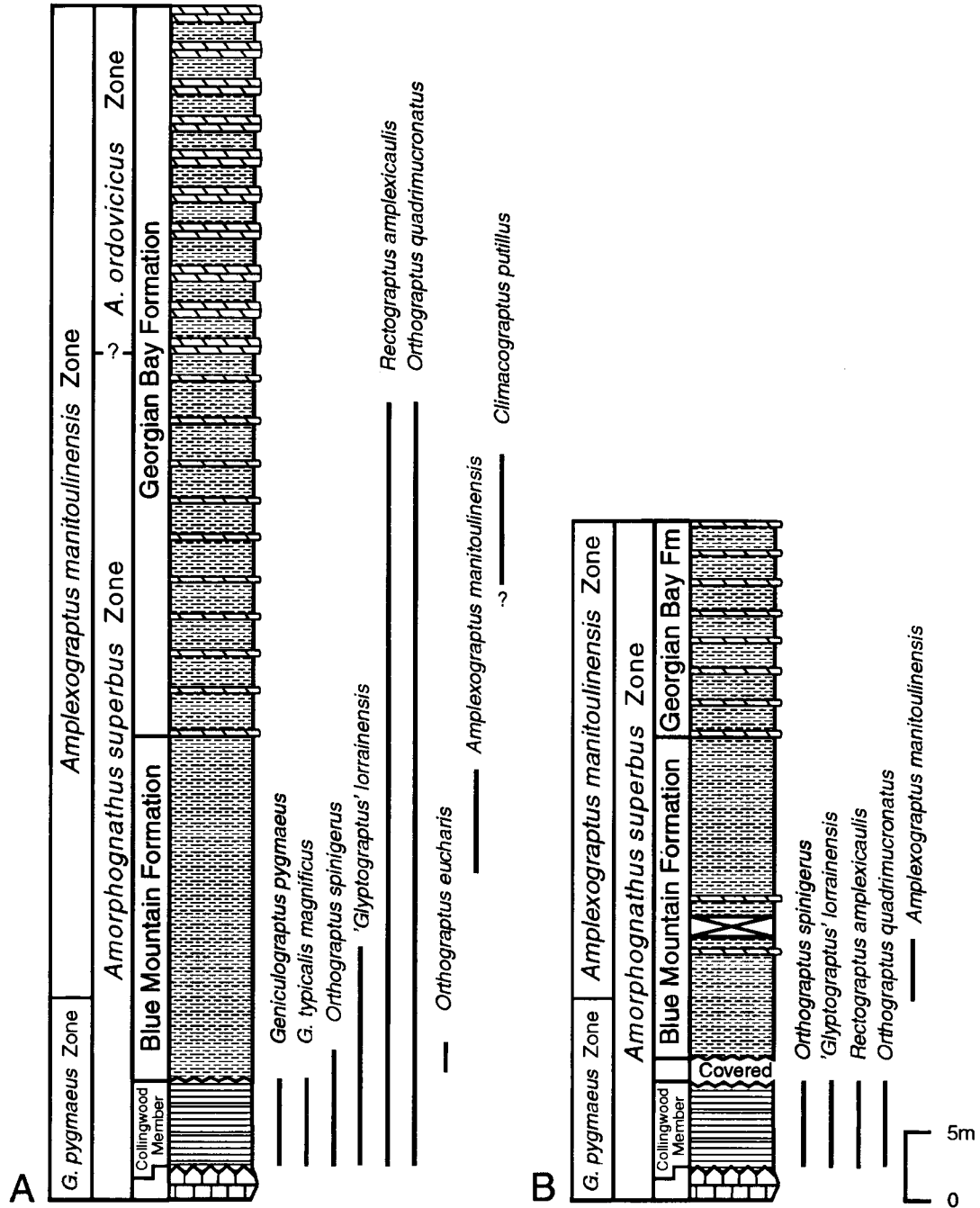
On Manitoulin Island, the Georgian Bay Formation comprises a thick sequence of interbedded grey shales and limestones that grade upward into dominantly carbonates. The contact with the underlying Blue Mountain Formation is drawn at the level of the lowermost bed of a conspicuous group of 20–60 mm thick limestone beds (Johnson *et al.* 1983). The lower portion of the Georgian Bay Formation at the shore exposure at Gorrel Point has yielded *C. putillus* (Text-fig. 5J–Z), *O. quadrimucronatus*, and *R. amplexicaulis* (Text-fig. 3). *Diplograptus similis* and *Diplograptus foliaceus gorrelensis* described by Caley (1936, pp. 66–68) from Manitoulin Island are clearly junior synonyms of *R. amplexicaulis* and *O. quadrimucronatus*, respectively. The succession of graptolite species on Manitoulin Island resembles that in coeval strata in the St Lawrence Lowlands and in the subsurface of Anticosti Island (Riva 1969, 1974; Walters 1977; Walters *et al.* 1982), where *A. manitoulinensis* is likewise succeeded by *C. putillus* (*Pseudoclimacograptus* cf. *P. clevenensis* of Riva 1969, 1974; *P. aff. clevenensis* of Walters 1977) in the upper portion of the *A. manitoulinensis* Biozone below the level of appearance of *D. complanatus*. Based on this, we interpret the upper Blue Mountain and lower Georgian Bay formations to represent the *A. manitoulinensis* Biozone. No graptolites diagnostic of Riva's (1969, 1974) *D. complanatus* Biozone are yet known from Manitoulin Island.

Conodont biostratigraphy. The Collingwood Member has not yet yielded biostratigraphically diagnostic conodonts. Calcareous interbeds in the graptolite-bearing shales of the lower part of the



TEXT-FIG. 2. Graptolites of the *Geniculograptus pygmaeus* Zone. A–C, '*Glyptograptus*' *lorrainensis* (Ruedemann); OSU 48501–48503. D–E, *Rectograptus amplexicaulis* (Hall); OSU 48504–48505. F–G, *Orthograptus spinigerus* (Elles and Wood); OSU 48506. All from the Collingwood Member, Lindsay Formation; Sheguindah, Manitoulin Island, Ontario. H–K, *Geniculograptus pygmaeus* (Ruedemann); OSU 48507–48510; H–I, Collingwood Member, Lindsay Formation; Craigeith Provincial Park, Ontario. J–K, isolated uncompressed specimens; Groos Quarry Formation; Bichler Quarry, Groos, Michigan. L–N, *Orthograptus quadrimucronatus* (Hall); OSU 48511–48512; Collingwood Member, Lindsay Formation; Manitoulin Island, Ontario. Scale bar represents 1 mm (except for fig. G where it represents 2 mm).

Blue Mountain Formation (Text-fig. 3) along the creek near Highway 6 about 5 km south of Little Current contain, along with other conodont species, *Amorphognathus superbus* (Rhodes), *Aphelognathus politus* (Hinde), *Icriodella superba* Rhodes and *Periodon grandis* (Ethington). Essentially the same species association, which clearly represents the *A. superbus* Biozone, ranges upward through the lower 40 m of the Georgian Bay Formation. The precise level of the top of the *A. superbus* Biozone has not yet been established, because the index of the overlying *A. ordovicicus* Biozone, *A. ordovicicus* Branson and Mehl, has not yet been recovered from Manitoulin Island. However, based on the relations between the conodont biostratigraphy and the ranges of shelly macrofossils elsewhere in the Midcontinent, this zonal boundary is likely to be in a poorly exposed interval about 50–60 m above the base of the Georgian Bay Formation. The Manitoulin Island succession is important in terms of conodont-graptolite zone relations in providing direct evidence that the upper part of the *A. superbus* Biozone is coeval with the lower part of the *A. manitoulinensis* Biozone at the type locality of the latter graptolite species. It is appropriate to note that our new conodont data from the Blue Mountain and lower Georgian Bay formations are more detailed than, but in general agreement with, those presented by Barnes *et al.* (1978).



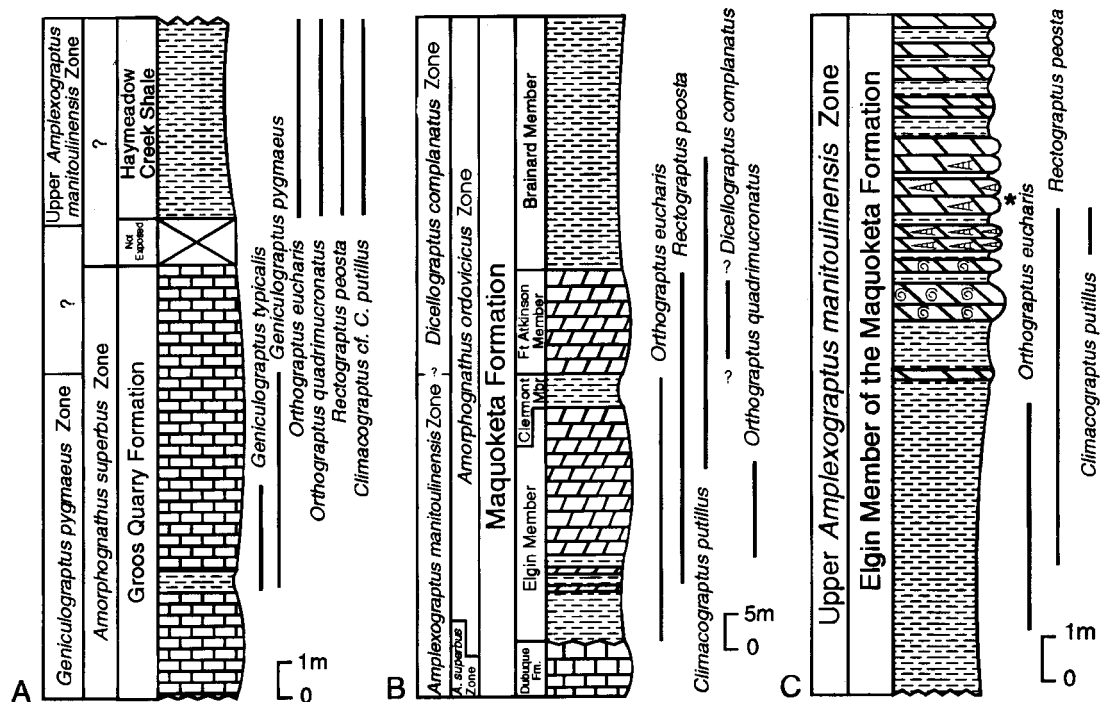
TEXT-FIG. 3. Stratigraphical columns illustrating the upper Ordovician graptolite ranges and graptolite and conodont zones in drill-cores and exposures on Manitoulin Island, Ontario. A, Ontario Geological Survey Core OGS-83-5; from near Little Current. Range of *Climacograptus putillus* is projected from its occurrence in the Gorrel Point section. B, succession at the type locality of *A. manitoulinensis* about 5 km south of Little Current. Near this locality the Collingwood Member rests directly on the Precambrian Lorrain Quartzite.

The Upper Peninsula, Michigan

Outcrops of graptolitic late Ordovician rocks are known from two areas in Delta County, Michigan, in the vicinity of Escanaba and along Haymeadow Creek (Text-fig. 1, area 3). Graptolites were recorded from shaly strata along Haymeadow Creek by Hussey (1952) and the fauna was subsequently discussed in more detail by Berry (1970). These beds, now known as the Haymeadow Creek Shale, have variously been considered to be the uppermost member of the 'Trenton Formation' or 'Trenton Group' (Hussey 1952) or the lowermost member of the Bill's Creek Shale (Hussey 1926). Hussey (1952) noted that the contact between the Haymeadow Creek Shale and the underlying limestone succession is not exposed anywhere in northern Michigan but he believed that only a thin succession of strata was missing at Bichler Quarry at Groos, 8 km north of Escanaba. Hussey (1952) classified the entire limestone succession in Bichler Quarry as the Groos Quarry Member, but Templeton and Willman (1963) referred these rocks to the Dubuque Formation, which they suggested was probably exposed in its entirety there. However, the lithological similarity to the Dubuque Formation of the Upper Mississippi Valley is not striking and, because the Bichler Quarry succession differs substantially also in age from the typical Dubuque Formation, we believe the latter formational designation is inappropriate. Following Ross *et al.* (1982), we prefer to use the term Groos Quarry Formation for these strata that are likely to be of post-'Trenton' age.

Graptolite biostratigraphy. Limestones from the upper part of the Groos Quarry Formation at Bichler Quarry (Text-fig. 2J-K) yielded three-dimensional specimens of *Geniculograptus pygmaeus* and *G. typicalis*, suggesting a *G. pygmaeus* Biozone age. At its type locality along Haymeadow Creek, the Haymeadow Creek Shale is a grey-weathering, chocolate-brown shale with sparse graptolites. A re-assessment of its graptolite fauna based on our new collections and those housed at the University of Michigan shows that it includes only *Climacograptus cf. putillus* (*C. pygmaeus* of Berry 1970) (Text-fig. 5AA), *Orthograptus eucharis*, *O. quadrimucronatus*, and *Rectograptus peosta*, a species association indicating the *A. manitoulinensis* Biozone (Text-fig. 4A). The lack of exposure of the contact between the two units prevents us from determining whether a hiatus exists at that level. Although it is possible that the graptolites from Bichler Quarry represent a low diversity fauna coeval with that in the Collingwood Member of Ontario (Senior 1991), the Haymeadow Creek section does not contain the typical lower *A. manitoulinensis* Biozone fauna such as is present in the Blue Mountain Formation of Manitoulin Island and in the Lorraine Group siltstones and shales of New York (Ruedemann 1925, 1947) and Quebec (Riva 1969, 1974; Walters 1977; Walters *et al.* 1982). It is also of interest to note that Ruedemann and Ehlers (1924) recorded *Geniculograptus pygmaeus* and a variety of *R. amplexicaulis* from slabs of shale and limestone in till near Newberry, Lucas County, about 140 km north-east of Escanaba. They interpreted these rocks as coeval with the Collingwood Formation (or Member) in southern Ontario, a unit which has been widely identified in the subsurface of the Michigan Basin (Hiatt and Nordeng 1985). Berry (1970) indicated that the Newberry rocks, which are not known to crop out *in situ*, were coeval with the Haymeadow Creek Shale (*A. manitoulinensis* Biozone) but we interpret them to be older than this unit at its type locality and to represent the *C. pygmaeus* Biozone. The Newberry rocks may be equivalent to the Groos Quarry Formation, or possibly, to the unexposed lowermost portion of the Haymeadow Creek Shale.

Conodont biostratigraphy. No conodonts are yet known from the type section of the Haymeadow Creek Shale but Votaw (1980) recorded specimens from the upper portion of the Bill's Creek Shale in the Escanaba region, including *Icriodella superba*, *Oulodus ulrichi* (Stone and Furnish), *Pseudobelodina vulgaris vulgaris* (Sweet) and *Rhipidognathus symmetricus* Branson, Mehl and Branson. This species association probably represents the *A. ordovicicus* Biozone or, possibly, the uppermost *A. superbus* Biozone. Samples from the Groos Quarry Formation in Bichler Quarry contain a relatively sparse and biostratigraphically poorly diagnostic conodont fauna, including Pa and Pb elements that probably belong to *A. superbus*, along with *Belodina confluens* Sweet,



TEXT-FIG. 4. Stratigraphical columns illustrating the upper Ordovician graptolite species succession, and graptolite and conodont zones on the Upper Peninsula of Michigan and in the Upper Mississippi Valley. A, composite section of Bichler Quarry, Groos, Michigan and the Haymeadow Creek Shale at its type locality. The contact between the Groos Quarry Formation and the overlying Haymeadow Creek Shale is not exposed and the thickness of the unexposed interval is not known. B, composite section of the Maquoketa Formation in north-eastern Iowa (after Witzke and Kolata 1988). Graptolite ranges compiled from cores and exposures in Illinois, Iowa and Minnesota. Occurrence of *D. complanatus* is projected from its inferred stratigraphical position in north-western Illinois. C, graptolite ranges in the Elgin Member of the Maquoketa Formation at Graf, Iowa. This is the type locality of *Climacograptus putillus* (Hall) and *Rectograptus peosta* (Hall). Asterisk indicates upper limit of graptolite collections made during the present investigation.

Protopanderodus liripipus Kennedy, Barnes and Uyeno, and *Periodon grandis*. We interpret this fauna as probably representing the *A. superbus* Biozone (Text-fig. 4A). This is in agreement with the graptolite evidence. The graptolite and conodont evidence suggests that the Groos Quarry Formation is probably older than the Dubuque Formation and represents an interval within the middle Edenian to the middle Maysvillian portion of the Cincinnati standard succession.

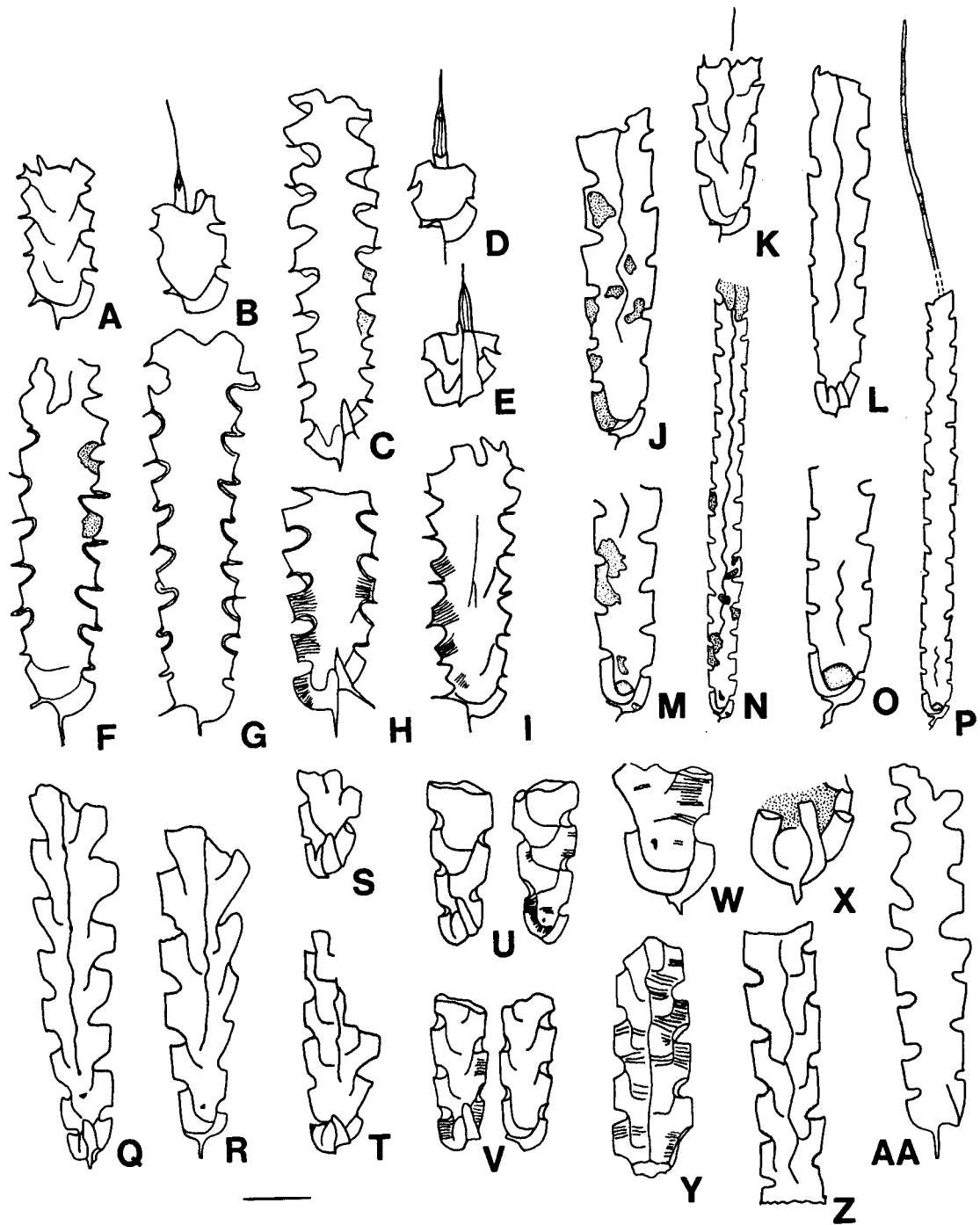
Upper Mississippi Valley in Iowa, Minnesota, Wisconsin, Illinois, and Missouri

The Cincinnati Maquoketa Group (commonly considered to be a formation in Iowa, Wisconsin, and Minnesota and a group in Illinois and Missouri) forms the topmost part of the Ordovician succession in the Upper Mississippi Valley (Text-fig. 1, area 4). The Maquoketa Group (Formation) disconformably overlies the carbonates of the Dubuque Formation in north-western Illinois and east-central Iowa where its dominant lithology is brown graptolite-bearing shale, which grades laterally in all directions into shallow-water trilobite-dominated micrites (Kolata and Graese 1983; Witzke and Kolata 1988). This facies distribution was apparently influenced strongly by the

continued development of the east-central Iowa Basin, a prominent depression that was formed during the time of deposition of the underlying Galena Group (Witzke and Kolata 1988). In north-western Illinois the lower part of the Maquoketa Group is classified as the Scales Formation, the basal part of which consists of dark brown fissile shales (the Argo-Fay Bed) that grade upwards into olive-green shales and dolomites (Kolata and Graese 1983). The Scales Formation grades westward and north-westward into the limestones and shales of the Elgin and Clermont members of the Maquoketa Group (Formation) in Iowa, Minnesota, and westernmost Illinois (Text-fig. 4b). There seems to be no unconformity at the top of the Dubuque Formation in southern Minnesota (Leverson *et al.* 1979) where the Dubuque Formation grades into the Elgin Member of the Maquoketa Formation. The Clermont Member is overlain by the Fort Atkinson Member (or Formation) that consists of massive, yellow, cherty dolomites and limestones with interbedded shales. The overlying Brainard Member and the Neda Formation (Kolata and Graese 1983) have yielded no graptolites in outcrops. However, we have seen numerous specimens of *Climacograptus putillus* in the Brainard Member in the Iowa Geological Survey drill cores W7206 (Box 26) and W30792 (Boxes 8 and 9) from central Iowa (Witzke 1987). For comprehensive recent reviews of the stratigraphy of the Maquoketa Group, especially in Illinois, see Kolata and Graese (1983) and Witzke and Kolata (1988).

Graptolite biostratigraphy. In north-eastern Iowa, southern Minnesota, and north-western Illinois (Text-fig. 1) graptolites are most abundant in the brown shale facies of the Elgin Member, although they also occur in the argillaceous carbonates in this member. One of the many graptolite-bearing exposures in the Upper Mississippi Valley deserves special mention, namely the road-cut through the Elgin Member near the Little Maquoketa River at Graf, Iowa (Text-fig. 4c). At this locality, the type locality for *Climacograptus putillus* (Hall, 1865), the Elgin Member consists of a remarkable phosphatic dolomite with countless graptolites and cephalopods. Indeed, near the middle of the exposed succession there are 1–2 m of dolomitic and phosphatic limestone that is a 'graveyard' of the orthoconic nautiloid *Isorthoceras sociale* (Miller and Youngquist). For a detailed recent description of this section, see Witzke and Glenister (1987). The graptolites are very well preserved as three-dimensional phosphatic moulds. This locality was apparently at the heart of the east-central Iowa Basin where a local upwelling of phosphate-rich water (Witzke and Glenister 1987) may have resulted in plankton 'blooms' (including graptolites) upon which the cephalopods might have fed. Our graptolite collections from Graf (Text-fig. 4c) include *Climacograptus putillus* (Text-fig. 5Q–T, w–z), *Orthograptus eucharis* (Hall) and *Rectograptus peosta* (Hall). In Illinois, the Argo-Fay Bed of the Scales Formation (lowermost Maquoketa Group) has yielded abundant specimens of *O. eucharis* and no other species, but higher parts of the formation have also produced *R. peosta*. In Iowa and Minnesota, the Elgin Member of the lower Maquoketa Formation contains *C. putillus*, *O. eucharis*, *O. quadrimucronatus* and *R. peosta*. Particularly important biostratigraphically is a collection of *D. complanatus* from the Fort Atkinson Formation at Savannah, north-western Illinois, housed at the Museum of Comparative Zoology at Harvard University. Unfortunately, our efforts to find additional specimens of this index species in the Maquoketa Group exposures in the Savannah area were unsuccessful.

Graptolites from exposures of the Maquoketa Shale in north-eastern Missouri (Text-fig. 1, area 5) were described by Werner and Echols (1958), and Berry and Marshall (1971). Werner and Echols (1958) described three-dimensional phosphatic moulds of *C. putillus* that were collected from the lower Maquoketa Shale at Castlewood, 24 km south of Saint Louis. Text-figure 5U–V, Y illustrates similar specimens of *C. putillus* collected by us from a locality near Castlewood, along Highway 21. Berry and Marshall (1970) illustrated specimens identified as *Climacograptus mississippiensis* and *Orthograptus truncatus* var. *socialis* from an exposure of Maquoketa Shale along Interstate-55 near Barnhart, Missouri. Our collections from this locality contain *Climacograptus tubuliferus* (Lapworth) and *R. peosta*. The occurrence of these species suggests an upper *A. manitoulinensis* to lower *D. complanatus* Biozone age for the Maquoketa Shale in north-eastern Missouri. The low



TEXT-FIG. 5. Graptolites from the *A. manitoulinensis* Zone. A-I, *Amplexograptus manitoulinensis* (Caley); OSU 48513-48521; from the Blue Mountain Formation; 5 km south of Little Current, Manitoulin Island, Ontario. J-Z, *Climacograptus putillus* (Hall); OSU 48522-48536; M-N, same specimen; O-P, same specimen; J-P, from the Georgian Bay Formation; Gorrel Point, Manitoulin Island, Ontario; Q-T, w-z, fully three-dimensional

diversity graptolite fauna contains elements of both the endemic Laurentian Biofacies and cosmopolitan Oceanic Biofacies of Goldman *et al.* (1995).

As a whole, the species associations found in the Maquoketa Shale of the Upper Mississippi Valley match those found in the upper *A. manitoulinensis* Biozone and lower *D. complanatus* Biozone of Quebec (Riva 1969, 1974; Walters 1977; Walters *et al.* 1982) and they are also similar to those we record above from coeval strata on Manitoulin Island. We conclude that in the Upper Mississippi Valley, the lowermost portion of the Maquoketa Shale is referable to the upper *A. manitoulinensis* Biozone, and that higher parts of the unit, especially the Fort Atkinson Formation, are coeval with the *D. complanatus* Biozone.

Conodont biostratigraphy. Conodonts have long been known from the Upper Mississippi Valley in Iowa, Minnesota, Wisconsin, and Missouri, and reports have been published on those from the late Ordovician Dubuque Formation (Ethington 1957; Webers 1966; Clark and Babcock 1971), the Cape Limestone (Sweet *et al.* 1975), and the Maquoketa Group (Formation) (Branson and Mehl 1933; Glenister 1957; Webers 1966; Froming 1971; Thompson and Satterfield 1975). Apart from graphic correlation studies by Sweet (1984, 1987), little recent information is available on the upper Ordovician conodonts of this important region, and the vertical ranges of most taxa are not well documented. New collections from the Dubuque Formation, Cape Limestone, and lower Maquoketa Shale (Formation) at several localities have clarified the ranges of several key species. Of particular significance is the common occurrence of representatives of the *Amorphognathus superbus*-*A. ordovicicus* lineage in the Dubuque Formation and the Cape Limestone. The appearance of *A. ordovicicus* in the very uppermost Dubuque Formation at several localities in Iowa and Minnesota is taken as the base of the *A. ordovicicus* Biozone. The occurrence of, amongst others, *A. superbus*, along with *Belodina confluens*, *Columbodina occidentalis* Sweet, *C. penna* Sweet, *Icriodella superba*, *Periodon grandis*, *Protopanderodus liripipus*, and *Rhodesognathus elegans* (Rhodes), through most of the Dubuque Formation shows that these strata belong in the upper part of the *A. superbus* Biozone (Text-fig. 4B). Conodonts from the lowermost Maquoketa Formation, including the basal phosphatic bed, include *A. ordovicicus* (Glenister 1957; Webers 1966) indicating the *A. ordovicicus* Biozone. The lower Maquoketa Formation was assigned above to the upper *A. manitoulinensis* Biozone, and hence the base of the *A. ordovicicus* Biozone is below the top of the latter graptolite biozone. Stratigraphically higher parts of the Maquoketa Formation have yielded a not very diagnostic conodont fauna. Sweet's (1979b) record of *Plectodina florida* Sweet from the Clermont and Brainard members is of both biogeographical and biostratigraphical interest because this is a widespread species in the *A. ordovicicus* Biozone in the western Interior of North America.

At localities in east-central Missouri, the Cape Limestone yields *A. ordovicicus* (Sweet *et al.* 1975) and other species of the *A. ordovicicus* Biozone, whereas in south-eastern Missouri (Cape Girardeau County), where the Cape Limestone is substantially thicker, the lower part represents the *A. superbus* Biozone (Bergström, unpublished data). It would appear, based on both conodonts and graptolites, that not only is the Cape Limestone-Maquoketa Formation contact in Missouri at a closely similar stratigraphical level as the Dubuque Formation-Maquoketa Formation contact in Iowa and Minnesota, but also, that the relations between graptolite and conodont zones are the same in the two regions.

Arbuckle and Ouachita Mountains, Oklahoma

The late Ordovician strata in southern Oklahoma were deposited in two distinctly different

phosphatic moulds; from the Elgin Member of the Maquoketa Formation; Graf, Iowa; U-V, Y, from the Maquoketa Shale; road-cut along Highway 21, 24 km south-south-west of St Louis, Missouri. AA, *Climacograptus cf. putillus* (Hall); UMMP 57361; flattened specimen from the Haymeadow Creek Shale; Haymeadow Creek, Michigan. Scale bar represents 1 mm (except for figs N and P where it represents 5 mm and figs W and X where it represents 0.5 mm).

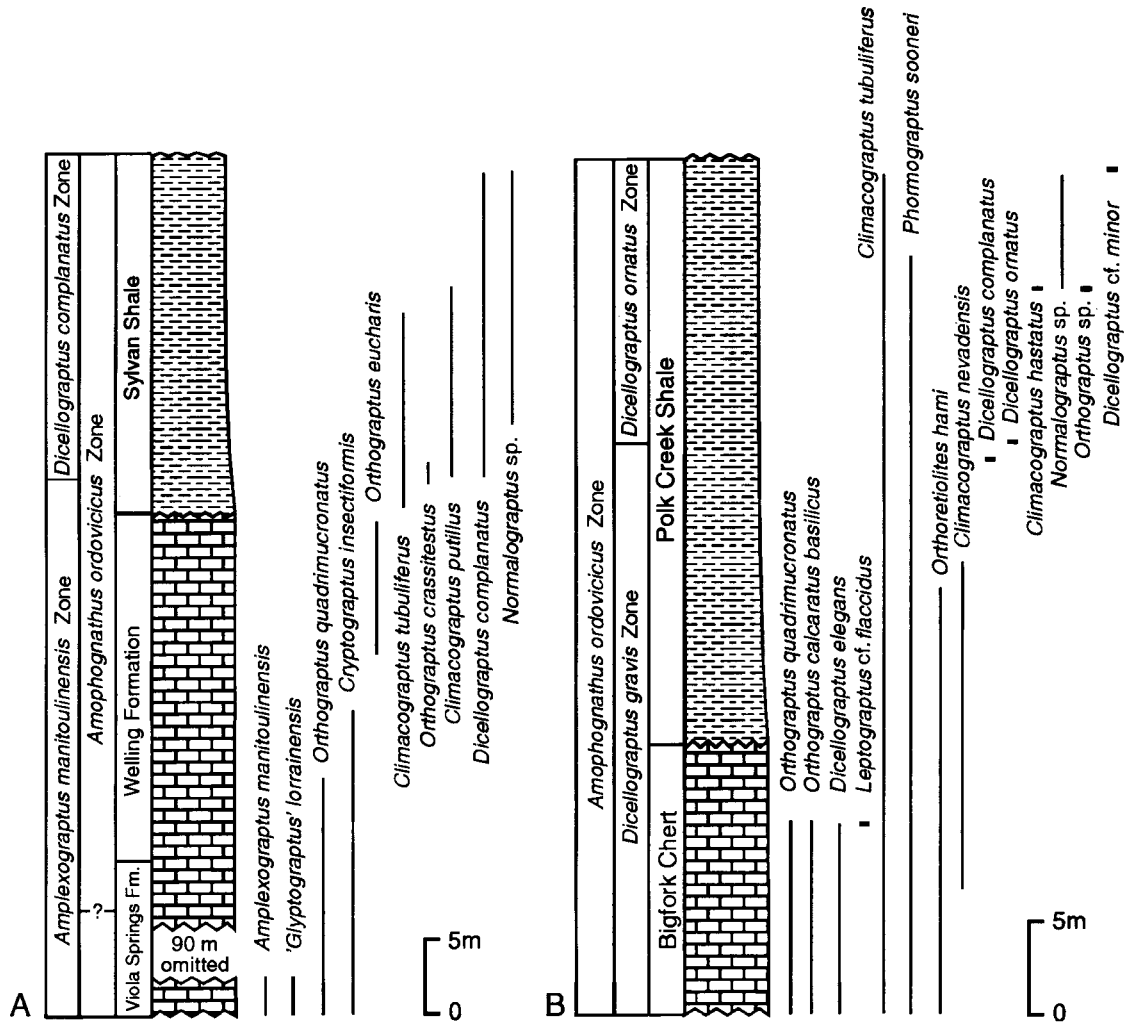
environments (Finney 1986, 1988). In the Arbuckle Mountains (Text-fig. 1, area 6), the carbonates of the Viola Group and the clastics of the overlying Sylvan Shale were laid down in an epicratonic setting within, and along, the southern Oklahoma aulacogen (Hoffman *et al.* 1974). The transition from the Viola Group limestones, which includes the Viola Springs and Welling formations, to the deeper-water Sylvan Shale represents a similar transgressive succession as the replacement of the Galena Group carbonates by the Maquoketa Group shales in the Upper Mississippi Valley. However, as is shown below, the carbonate-shale transition is stratigraphically higher in Oklahoma than in the former region. In the Ouachita Mountains in eastern Oklahoma (Text-fig. 1, area 7), the equivalents to the Viola Group-Sylvan Shale are the Bigfork Chert and Polk Creek Shale (Finney 1986), which represent a different depositional regime, namely a deep basin off the southern margin of the North American craton (Finney 1986, 1988). There are marked biofacies differences between the graptolite faunas of the two regions, which have been brought into rather close juxtaposition by late Palaeozoic thrusting.

Graptolite biostratigraphy. Pioneer studies of graptolites from the Arbuckle and Ouachita Mountains of southern Oklahoma were published by Ruedemann (1908, 1947), Ruedemann and Decker (1934), Decker (1935*a*, 1935*b*, 1936), and Whittington (1954, 1955). Based on comprehensive new collections, Finney (1986, 1988) revised the graptolite biostratigraphy of the Viola Group and Bigfork Chert. We have studied numerous collections from this region, including the type collections at the University of Oklahoma in Norman, Finney's collections, and collections made in recent years by Dr C. E. Mitchell. In the present contribution our discussion is centred on the upper Ordovician portion of the Oklahoma successions; for pertinent information about aspects of the middle Ordovician graptolite biostratigraphy of the Viola Group, see Finney (1986) and Bergström and Mitchell (1986).

In the Arbuckle Mountains, the uppermost Viola Springs Formation and the overlying Welling Formation contain (Text-fig. 6A), amongst other species, the biostratigraphically diagnostic species *A. manitoulinensis* and *O. eucharis* (Finney 1986; Goldman 1995), indicating that this interval belongs to the *A. manitoulinensis* Biozone. Collections from the Sylvan Shale made by Finney and examined by the senior author contain *Climacograptus putillus*, *C. tubuliferus*, *Dicellograptus complanatus*, *D. gravis* Keble and Harris, *Normalograptus* sp. nov., and *Orthograptus crassitestus* (Ruedemann). This association suggests a correlation with the *D. complanatus* Biozone as developed in north-western Europe (Skoglund 1963; Williams 1982*a*, 1982*b*, 1987), at Trail Creek, Idaho (Carter and Churkin 1977; Goldman *et al.* 1995), in the Marathon area, West Texas (Goldman *et al.* 1995), and in the northern Appalachian Basin (Riva 1969, 1974). Also, this interval of the Sylvan Shale corresponds to the *D. gravis* Biozone (Ea4) of the succession in Victoria, Australia (VandenBerg and Cooper 1992). Collections from the lowermost Sylvan Shale do not contain *O. crassitestus*, *C. putillus*, and the particularly significant species *D. complanatus* (Text-fig. 6A), and it is possible that this interval is coeval with the very uppermost part of the *A. manitoulinensis* Biozone.

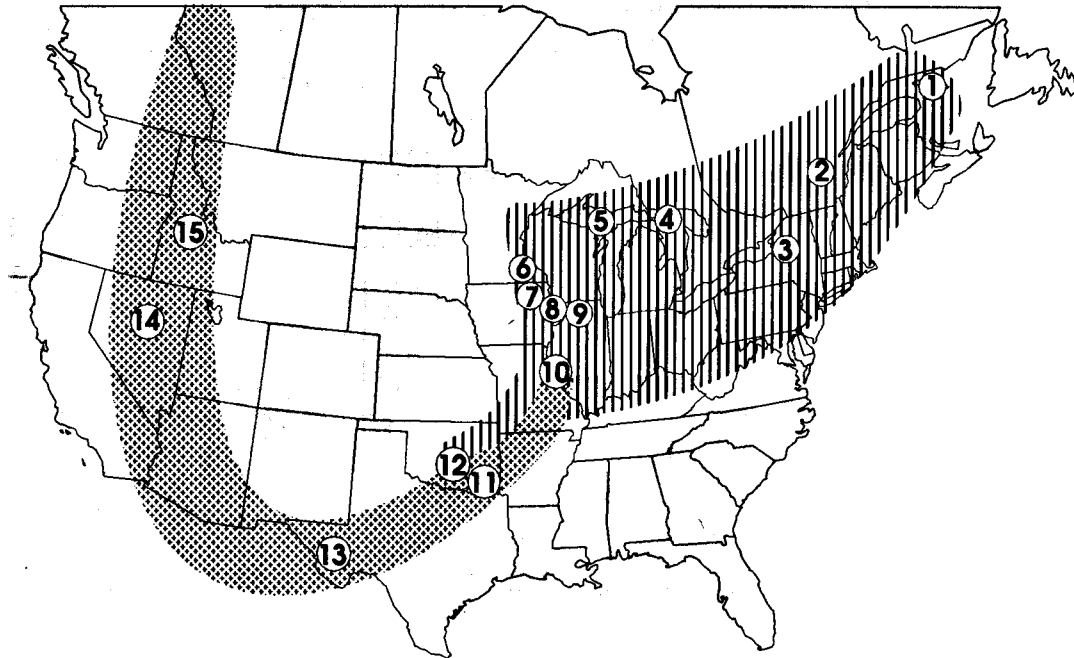
The Polk Creek Shale of the Ouachita Mountains contains a typical deep-water Pacific Province graptolite fauna (the cosmopolitan Oceanic Biofacies of Goldman *et al.* 1995). Graptolites from the Stringtown Quarry (Finney 1986), identified by the senior author, include (Text-fig. 6B) the following (distances above the base of the Polk Creek Shale): 8–10 m: *Climacograptus nevadensis* (Carter), *C. tubuliferus*, *Orthoretiolites hami* (Whittington); 14.6 m: *C. tubuliferus*, *D. complanatus*; 15.5 m: *C. tubuliferus*, *Dicellograptus ornatus* (Elles and Wood); 24 m: *Arachniograptus laqueus* Ross and Berry, *Climacograptus hastatus* T. S. Hall, *Normalograptus* sp., *Orthograptus* sp.

These collections indicate correlation with the *Dicellograptus gravis* and *Dicellograptus ornatus* biozones (Ea4 to Bo2) in the Victorian succession (VandenBerg and Cooper 1992) and the upper *Pleurograptus linearis* to *Dicellograptus anceps* biozones of southern Scotland (Williams 1982*a*, 1982*b*, 1987). The species association is virtually identical to those of the lower Maravillas Formation of West Texas (Berry 1960; Goldman *et al.* 1995) and the coeval portion of the sequence at Trail Creek, Idaho (Carter and Churkin 1977).



TEXT-FIG. 6. Stratigraphical columns illustrating the upper Ordovician graptolite successions, and graptolite and conodont zones in the Arbuckle Mountains and Ouachita Mountains, Oklahoma. A, Arbuckle Mountains sequence; graptolite ranges in the Viola Springs and Welling formations after Finney (1986). B, Ouachita Mountains sequence; graptolite ranges in the Bigfork Chert after Finney (1986).

Conodont biostratigraphy. Conodonts from the middle–upper Ordovician Viola Group (Amsden and Sweet 1983), and the upper Ordovician Sylvan Shale in the Arbuckle Mountains have been described by, among others, Oberg (1966), Sweet (1983), and Dresbach (1983), and a conodont-based graphic correlation of the Viola Springs Formation and the Welling Formation was published by Sweet (1984). Of biostratigraphical significance in the Viola Springs Formation, which is approximately 200 m thick, is the presence (Dresbach 1983) of *A. superbus* near the level of appearance of *A. manitoulinensis* in the middle part of the formation (Finney 1986). Typical specimens of *A. ordovicicus* have been collected from an interval in the topmost portion of the formation in the long section along Interstate-35 on the south side of the Arbuckle Anticline (Dresbach 1983; see also Goldman *et al.* 1995). Samples from the 80 m thick interval between the occurrences of these zonal index species have yielded (Dresbach 1983), amongst others, *Columbodina*



TEXT-FIG. 7. Distribution of late Ordovician graptolite biofacies in United States and adjacent parts of Canada. Vertical ruling and stippling represent the Laurentian Biofacies and the Oceanic Biofacies, respectively. Numbered localities and areas are as follows: 1, Anticosti Island, Quebec; 2, Saint Lawrence Lowlands, Quebec; 3, Mohawk and Black River valleys, New York State; 4, Manitoulin Island, Ontario; 5, Upper Peninsula of Michigan; 6, Rifle Hill Quarry, southern Minnesota; 7, Postville, Iowa; 8, Graf, Iowa; 9, north-western Illinois; 10, Saint Louis region, Missouri; 11, Ouachita Mountains, eastern Oklahoma; 12, Arbuckle Mountains, Oklahoma; 13, Marathon region, west Texas; 14, central Nevada; 15, Trail Creek, Idaho. Note that the two biofacies overlap in the Arbuckle Mountains. Map adapted from Finney (1986) and Goldman and Bergström (1995).

penna, *Icriodella superba*, *Plectodina florida*, and *Pseudobelodina inclinata* (Branson and Mehl), an association that is diagnostic of either the uppermost *A. superbus* Biozone or the lowermost *A. ordovicicus* Biozone. Although the precise level of the base of the latter remains undetermined, it is clearly below the base of the Welling Formation, and well below the top of the *A. manitoulinensis* Biozone; the base of the overlying *D. complanatus* Biozone is taken at the level of appearance of its zonal index, in the lowermost part of the Sylvan Shale (Text-fig. 6A). Evidently, the base of the *A. ordovicicus* conodont Biozone is within the upper *A. manitoulinensis* graptolite Biozone also in the Arbuckle Mountains succession (Text-fig. 6A).

Most samples from the graptolite-bearing Bigfork Chert at Stringtown Quarry, eastern Oklahoma contain few, and biostratigraphically undiagnostic conodonts. However, a sample from the upper third of the unit includes, among others, *A. cf. ordovicicus* and is likely to represent the *A. ordovicicus* Biozone. This agrees well with the graptolite biostratigraphy in this section (Finney 1986; also see Text-fig. 6B).

The Cincinnati region in Ohio, Kentucky and Indiana

It is outside the scope of this paper to deal with the relatively well-known graptolites of this important outcrop area (for a general summary, see Bergström and Mitchell 1986), but some comments on the graptolite-conodont zonal relations are in order. Currently available data indicate

that the base of the *G. pygmaeus* Biozone is about 25 m above the base of the basal Cincinnati Edenian Stage in strata belonging to the *A. superbis* Biozone (Mitchell and Bergström 1991). Zonal conodonts occur in close association with zonal graptolites in the lower half of the *G. pygmaeus* Biozone in numerous sections in this region (Text-fig. 1, area 10) and there can be no doubt about the graptolite-conodont zone relations in this interval. The base of the overlying *A. manitoulinensis* Biozone is established less precisely, but unpublished drill-core data suggest that it is about 80 m above the base of the *G. pygmaeus* Biozone near the middle of the Maysvillian Stage in strata of the *A. superbis* Biozone (Text-fig. 8). Of particular interest for the correlation of the type Cincinnati Series is the appearance of typical representatives of *A. ordovicicus* along with *Periodon grandis*, *Rhodesognathus elegans*, and *Icriodella superba* in the uppermost Arnheim Formation (in an interval also referred to as the Dillsboro Formation) of the lower Richmondian Stage in eastern Indiana (MacKenzie and Bergström 1993, 1994; Goldman *et al.* 1995). The uppermost Arnheim Formation populations of *Amorphognathus* also contain transients to the evolutionary ancestor of *A. ordovicicus*, *A. superbis*. Moreover, only the latter species has been found in stratigraphically older parts of the Cincinnati. Based on these facts, we interpret the level of appearance of *A. ordovicicus* in the uppermost Arnheim Formation as being its first occurrence in the Cincinnati succession and that level is taken to mark the base of the *A. ordovicicus* Biozone. In the excellently exposed sections near Brookville, Indiana, *A. ordovicicus* is associated with *Arnheimograptus anacanthus* (Mitchell and Bergström), a graptolite species that elsewhere (see, for instance, Walters *et al.* 1982) is restricted to the *A. manitoulinensis* Biozone. Although absence of zonal graptolites currently makes it impossible to locate the *A. manitoulinensis*-*D. complanatus* zonal boundary precisely in the type Cincinnati, the facts at hand clearly suggest an overlap between the lower part of the *A. ordovicicus* Biozone and the upper part of the *A. manitoulinensis* Biozone in this succession. This is in agreement with the relations between conodont and graptolite zones in the Upper Mississippi Valley and Oklahoma successions described above.

Graptolite biofacies

Recently, Goldman *et al.* (1995) distinguished two distinct late Ordovician graptolite biofacies within the tropical Pacific Province in Laurentia, namely an *Oceanic Biofacies* characterized by a mixed fauna containing cosmopolitan elements of the epipelagic and mesopelagic biotopes, and a *Laurentian Biofacies* characterized by epipelagic and endemic cratonic taxa. The graptolite faunas of the Laurentian Biofacies occur in the Appalachian Basin, on Manitoulin Island and the Upper Peninsula of Michigan, and in most other parts of the North American Midcontinent. In successions representing this biofacies, Riva's (1969, 1974) upper Ordovician graptolite zone succession is readily applicable. The Oceanic Biofacies is present in the Canadian Rocky Mountains, the Great Basin, the Marathon region of West Texas, and the Ouachita Mountains of Oklahoma and Arkansas. Sequences having this biofacies are best subdivided using the zonal scheme of Victoria, Australia (VandenBerg and Cooper 1992). The Viola Group and Sylvan Shale in the Arbuckle Mountains of Oklahoma contain some elements of both biofacies, including *Amplexograptus manitoulinensis*, *Climacograptus putillus*, *C. tubuliferus* and *Dicellograptus complanatus*, which allows for correlation between the two zonal schemes. The regional distribution of these biofacies in United States and southern Canada is illustrated in Text-figure 7. The Oceanic Biofacies forms a parabolic arc from the Rocky Mountains in Canada across the Great Basin and the Marathon region in West Texas to the Ouachita Mountains in Oklahoma. The cosmopolitan mesopelagic species characteristic of this biofacies, including *C. tubuliferus*, *C. nevadensis* and most dicellograptids and dicranograptids, are off-shore species that generally are not present on the craton (Finney 1986; Goldman *et al.* 1995). However, the widespread late Ordovician transgression, which is recorded by dark shales over much of the Midcontinent (Bergström and Mitchell 1992), allowed several of these mesopelagic species to migrate into the continental interior. Examples of such migrations are the occurrences of *C. tubuliferus* and *D. complanatus* in the Sylvan and Maquoketa shales.

N. Am. Stages	N. Am. Graptolite Biozones	Conodont Biozones	Cincinnati Sequences	Manitoulin Island	Northern Michigan	Upper Mississippi Valley	Arbuckle Mtns., Oklahoma	Eastern Oklahoma	South Scotland	South Wales	Sweden	Yangtze Platform, China	Victorian Graptolite Biozones
RICHMONDIAN	<i>Dicellogr. complanatus</i>	<i>Amorphogn. ordovicianus</i>	C5	GEORGIAN BAY	STONINGTON	MAQUOKETA	SYLVAN	POLK CREEK	UPPER HARTFELL	SHOLE-SHOOK	JONSTORP	WUFENG	<i>Dicellogr. gravis</i> (Ea4)
			C4		BILL'S CREEK HAY-MEADOW CREEK		WELLING				FJÄCKA		
MAYSVILLIAN	<i>Amplex. manitoulinensis</i>	<i>Amorphogn. superbus</i>	C3	BLUE MOUNTAIN	?	DUBUQUE		BIG-FORK	LOWER HARTFELL	MYDRIM	SLAND-DROM	LIHNSIANG	<i>Dicranogr. kirkii</i> (Ea3)
			C2		GROOS QUARRY	?						PAGODA	
EDENIAN	<i>Geniculogr. pygmaeus</i>	<i>Amorphogn. superbus</i>	C1	COLLING-WOOD			VIOLA SPRINGS						<i>Climacogr. spiniferus</i> (Ea2)
	<i>Climacogr. spiniferus</i>												

TEXT-FIG. 8. Correlation of North American and Victorian upper Ordovician graptolite biozones with conodont biozones, sequence stratigraphical units in the Cincinnati region, and formations in the North American Midcontinent, southern Scotland, South Wales, Sweden and the People's Republic of China.

The Laurentian Biofacies is present in most of the eastern and central parts of North America. A typical development is in the dark shales and overlying flysch of the Taconic foredeep in New York and Quebec (Riva 1969, 1974). The cosmopolitan epipelagic elements of this biofacies (for instance, *Orthograptus quadrimucronatus* and *Rectograptus amplexicaulis*) occur abundantly at many localities in the continental interior, usually in single-species associations, and in many cases in storm deposits. Endemic species such as *Climacograptus putillus* and *Amplexograptus manitoulinensis* are present more sporadically in the Midcontinent. In the Saint Lawrence Lowlands of Quebec, where the full vertical ranges of these endemic species are best represented, the late Ordovician transgression, so apparent in the Midcontinent, is largely masked by the deposition of clastics eroded from the Taconic orogen.

Areas where these two biofacies overlap, such as the Arbuckle Mountains in Oklahoma, are of particular significance in that their successions provide the opportunity to establish ties between the two disparate zonal schemes. Our interpretation of the relationships between the various units studied by us, the zonal succession recognized in Victoria, Australia (VandenBerg and Cooper 1992) and that established by Riva (1969) is illustrated in Text-figure 8.

Summary of the upper Ordovician graptolite biostratigraphy of the North American Midcontinent and international correlation

Text-figure 9 gives the vertical distribution of the graptolites and conodonts discussed herein, and adds some significant new information to similar compilations published by Bergström and Mitchell (1986) and Goldman *et al.* (1995). It shows that several relatively common Midcontinent species have a narrow stratigraphical range and hence are useful biostratigraphically within the interval of the *G. pygmaeus*, *A. manitoulinensis*, and *D. complanatus* biozones. Of biostratigraphical interest also is that a bipartite subdivision of the *A. manitoulinensis* Biozone appears possible. The upper part has a characteristic species association, including several species absent in the lower part, such as *Climacograptus putillus*, *C. nevadensis* and *Rectograptus peosta*. The biozonal index, *Amplexograptus manitoulinensis*, appears to occur mainly in the lower part of the biozone, whereas *Arnheimograptus anacanthus* and *C. putillus* are most common in, but not restricted to, the upper part. It is premature

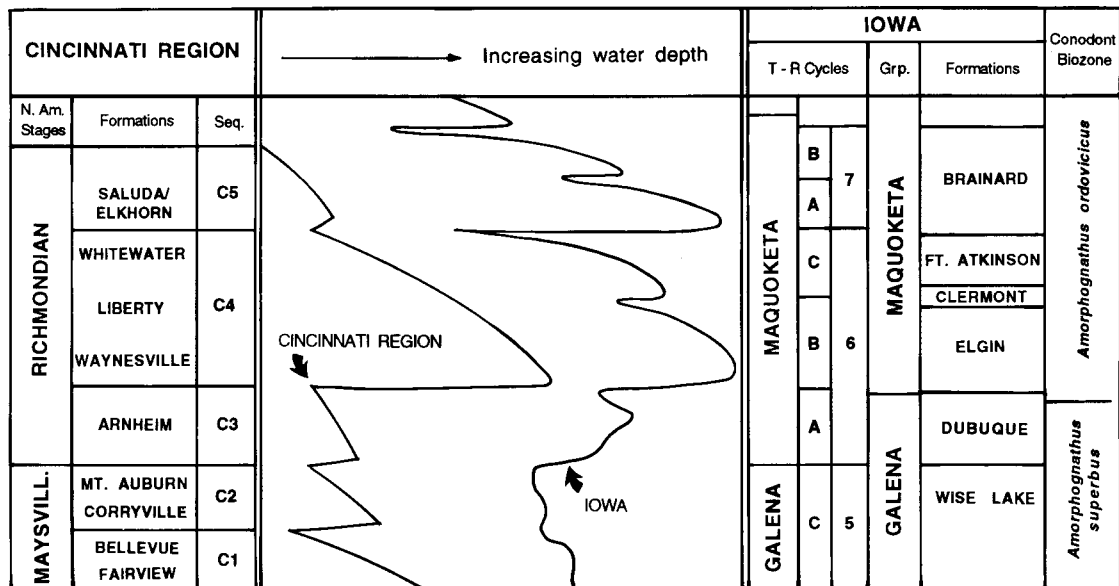
number of conodonts, which are preserved on shale surfaces and therefore difficult to identify, has been found. Of particular interest are Barnes and Williams' (1988) records of *Amorphognathus superbis* from the Lower Hartfell Shale (*P. linearis* Biozone) and *A. ordovicicus* from the lower Complanatus Band in the Upper Hartfell Shale (*D. complanatus* Biozone) at Dob's Linn. Although their identifications of these key species are based on the platform (Pa) rather than the more diagnostic holodontiform (M) elements, the reported occurrences are in agreement with the graptolite-conodont zone relations elsewhere.

South Wales. Graptolite faunas that are coeval with those of the Hartfell Shale have recently been recorded by Zalasiewicz *et al.* (1995) from a new road-cut along the A40 about 3 km west of Whitland, that exposes the Mydrim Shales and the overlying Shoeshook Limestone. The Mydrim graptolite species associations differ markedly from those of southern Scotland and the North American Midcontinent, the only species in common with the latter being the relatively long-ranging *Rectograptus amplexicaulis* and *Orthograptus quadrimucronatus*. Interestingly, C. R. Barnes (pers. comm. 1995), who is describing the conodont succession at this locality, has discovered *A. ordovicicus* in the lower Shoeshook Limestone just above an interval with graptolites considered to represent the *P. linearis* Biozone. Hence, the graptolite-conodont zone relations appear to be the same as those known elsewhere in this upper Ordovician interval.

Sweden. As described by Bergström and Mitchell (1986, fig. 6) and Goldman *et al.* (1995, fig. 6), the boundary between the *P. linearis* and *D. complanatus* zones in the Swedish succession is taken to coincide with the boundary between the Fjäckå Shale and the Jonstorp Formation. Specimens of *A. ordovicicus* have previously been recorded from the Fjäckå Shale but recently, the junior author has discovered numerous specimens of this zonal index in the upper part of the Slandrom Limestone in a previously unstudied section at Skålberget, Dalarna, central Sweden. Although the Slandrom Limestone has yielded no biostratigraphically diagnostic graptolites and the *P. linearis* graptolite fauna in the overlying Fjäckå Shale has little in common with coeval Midcontinent graptolite faunas, the conodonts provide a close correlation link with the latter region.

SEQUENCE STRATIGRAPHY AND SEA LEVEL CHANGES

In a recent study, Holland (1993; see also Holland and Patzkowsky 1996) defined five sequence boundaries in the upper Ordovician in its outcrop area in Ohio, Kentucky, and Indiana (Text-figs 8, 10). Of particular interest here is his C3/C4 sequence boundary, which coincides with the base of the Waynesville Formation in sections studied by us near Brookville in eastern Indiana. This sequence boundary is just above the base of the *A. ordovicicus* Biozone, and it is overlain by shaly strata representing a deeper-water facies deposited during a prominent sea-level rise that Holland (1993) interpreted to be eustatic. Based on conodont biostratigraphy, the base of the C4 sequence would correspond with the base of the Maquoketa Group in the Upper Mississippi Valley, which represents a change from the relatively shallower-water depositional environments of the carbonates of the Galena Group to the relatively deeper-water environments of the shales of the lower Maquoketa Group (Text-fig. 10). In Michigan and on Manitoulin Island, the corresponding horizon is probably within unexposed intervals of the Bill's Creek and Georgian Bay formations, respectively. Based on conodont biostratigraphy, the equivalent horizon in the Arbuckle Mountains of Oklahoma could be at the base of the Welling Formation, but further studies are needed to clarify whether it can be recognized with certainty. Apparently, the boundary between the Slandrom Limestone and the Fjäckå Shale in the Swedish succession represents a flooding surface of a closely similar, if not identical, age as the base of the C4 sequence. Furthermore, in the well-known succession in the Yangtze Platform region of China, the upper Pagoda Limestone has yielded conodonts of the upper *A. superbis* Biozone (Chen *et al.* 1995) and the overlying Wufeng Shale



TEXT-FIG. 10. Comparison of late Ordovician bathymetric curves from the Cincinnati region in Ohio, Kentucky, and Indiana (after Holland 1993), and Iowa (after Witzke and Bunker 1996). Note the similarity between these curves, especially in the timing of major transgressive-regressive events, which suggests that these reflect eustatic sea level changes.

contains graptolites coeval with the *D. complanatus* Biozone and conodonts of the *A. ordovicicus* Zone. In many sections, these formations are separated by the Linhsiang Formation, a thin unit of nodular limestone that has not yet produced zonal conodonts or graptolites. It would seem that the C4 sequence boundary could correspond to either the base, or more probably, the top of the latter formation but further biostratigraphical study is needed to clarify this. At any rate, the biostratigraphical and depositional data at hand from several continental plates appear to support the idea that the C4 sequence boundary indeed represents a eustatic transgression. The base of the C4 sequence is not the only level in the successions investigated that may reflect eustatic sea level changes. Although there are significant differences between some of the recently published Midcontinent upper Ordovician bathymetric curves, which is in agreement with the observation by Johnson *et al.* (1989, p. 43) that 'cyclic sequences attributed to eustatic sea-level changes have been the subject of much lively debate', two such curves, namely that of the Cincinnati succession by Holland (1993), and that of the Iowa sequence of Witzke and Bunker (1996), are of particular significance in this investigation. These curves, which are based on extensive recent studies in two regions separated geographically by a distance of about 700 km, are compared in Text-fig. 10. Their vertical alignment follows the revised correlation between the successions in the Cincinnati region and the Upper Mississippi Valley presented herein, and no change in the original curve shapes has been made. This comparison between the inferred changes in bathymetry in the two regions shows several important similarities apart from the significant transgression at the base of the Waynesville (base of the C4 sequence) and the base of the Maquoketa (base of the T-R (transgressive-regressive) cycle 6B) referred to above. These include: (1) the base of the C3 sequence appears to correlate with the base of the Maquoketa T-R cycle 6A; (2) the C4 sequence corresponds to the T-R cycle 6B-6C; (3) the C4/C5 sequence boundary appears to correspond to the base of the T-R 7A-B cycle; and (4) the top of the C5 sequence seems to correlate with the top of the T-R cycle 7. Lehmann *et al.*

(1995) observed that some recent interpretations of late Ordovician sea-level changes in the Cincinnati and Upper Mississippi regions were in conflict, but our biostratigraphy-based comparison shows a striking general similarity between recently published bathymetric curves of the successions studied in the two regions. This is noteworthy in view of the fact that these curves reflect subjective, mainly lithology-based interpretations by different investigators working in two widely separated regions. We interpret this similarity as indicating that eustatic sea-level changes exercised a very significant bathymetric control during the deposition of the late Ordovician sediments in these regions.

SYSTEMATIC PALAEOLOGY

Repositories for figured and cited material are abbreviated as follows: AMNH, American Museum of Natural History, New York; BU, the Lapworth Museum, University of Birmingham, UK; GSC, Geological Survey of Canada, Ottawa; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; OSU, Orton Geological Museum, Ohio State University, Columbus, Ohio; and USNM, United States National Museum, Washington, D.C.

Suborder VIRGELLINA Fortey and Cooper, 1986

Superfamily DIPLOGRAPTOIDEA Lapworth, 1873, emend. Mitchell, 1987

Family DICRANOGRAPTIDAE Lapworth, 1873

Subfamily DICRANOGRAPTINAE Lapworth, 1873, emend. Finney, 1985

Genus DICELLOGRAPTUS Hopkinson, 1871

Type species. By subsequent designation (Gurley 1896, p. 70); *Didymograpsus elegans* Carruthers, 1867, p. 369, pl. 2, fig. 16a.

Dicellograptus complanatus Lapworth, 1880

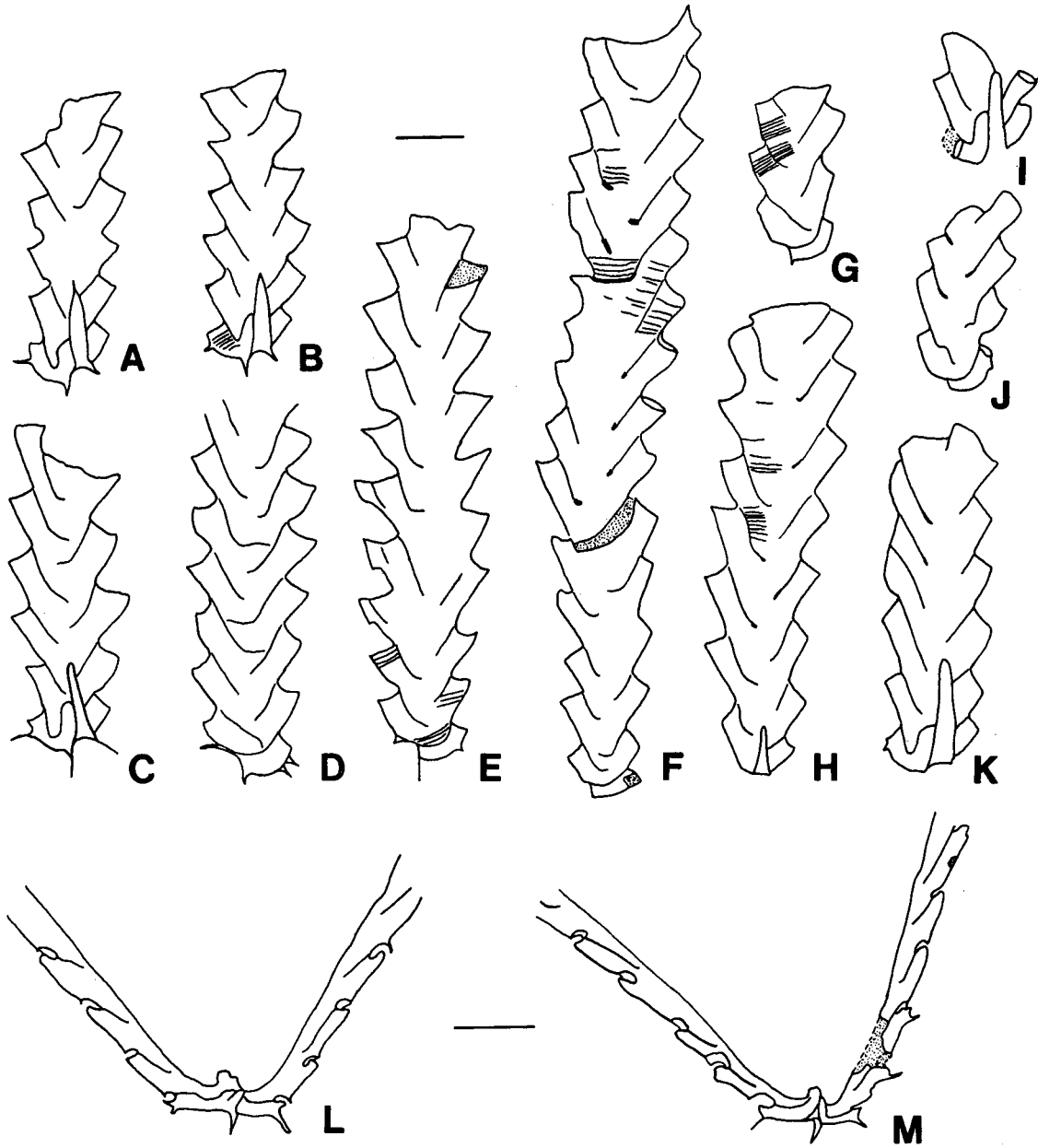
Text-figure 11L-M

- 1880 *Dicellograptus complanatus* Lapworth, p. 160, pl. 5, fig. 17a-17e.
 1904 *Dicellograptus complanatus* Lapworth: Elles and Wood, p. 139, pl. 20, fig. 1a-1d; text-fig. 84a-e.
 1908 *Dicellograptus complanatus* Lapworth: Ruedemann, p. 294, pl. 18, fig. 1; text-figs 208-209.
 1935b *Dicellograptus complanatus* Lapworth; Decker, p. 702 (*partim*), fig. 1a-e (*non* fig. 2g).
 1947 *Dicellograptus complanatus* Lapworth; Ruedemann, p. 376, pl. 62, figs 4-10.
 1963 *Dicellograptus complanatus* Lapworth; Skoglund, p. 33, pl. 1, fig. 3; text-fig. 10A-E.
 1970 *Dicellograptus complanatus* Lapworth; Toghil, p. 12, pl. 4, figs 1-5; pl. 5, figs 1-5; pl. 6, fig. 1; text-figs 2g-1, 4b.
 1983 *Dicellograptus complanatus* Lapworth; Koren' and Sobolevskaya, p. 101, pl. 25, figs 5-9; text-fig. 31.
 1987 *Dicellograptus complanatus* Lapworth: Williams, p. 71, figs 3a-h, 5a-c, 6g.
 1991 *Dicellograptus complanatus* Lapworth; Williams, p. 589, pl. 1, figs 12-13; text-fig. 71-q.

Lectotype. BU 1072b, designated by Toghil (1970, p. 13); Lower Complanatus Band, Dob's Linn, Scotland.

Material. Two complete specimens and numerous stipe fragments from the Sylvan Shale, Sycamore Creek, southern Oklahoma (collected by S. C. Finney), and four specimens (MCZ 9428-9431) from the Fort Atkinson Formation, Maquoketa Group, town of Savannah, Carroll County, Illinois.

Description. Stipes are 0.4-0.5 mm wide at the aperture of th_2^1 , increasing to an average of 0.7 mm wide distally; stipes diverge at an angle of approximately 60°. Thecae simple, numbering 5-7 in the proximal 5 mm,



TEXT-FIG. 11. A-K, *Rectograptus peosta* (Hall, 1861); OSU 48537-48541, 48595-48600; A-E, flattened specimens; Fort Atkinson Formation, Maquoketa Group; Savannah, Illinois; F-K, fully three-dimensional phosphatic moulds; Elgin Member, Maquoketa Formation; Graf, Iowa. L-M, *Dicellograptus complanatus* Lapworth, 1880; MCZ 9429-9430; Fort Atkinson Formation, Maquoketa Group; Savannah, Illinois (drawings of L-M by C. E. Mitchell). Scale bars represent 1 mm.

decreasing to 4-6 in 5 mm distally, with long, straight supragenicular walls. Th¹₁ and th¹₂ diverge horizontally from the sicula and bear prominent mesial spines; th²₁ grows horizontally and then bends sharply upward, while th²₂ grows continuously upward. Mesial spines commonly present on second and third thecal pairs.

Thecal apertures slightly introverted proximally, becoming nearly horizontal distally. Axil slender and rectangular.

Remarks. The four specimens (MCZ 9428–9431) labelled *Dicellograptus* cf. *D. complanatus* now appear to be misplaced (F. Collier, pers. comm. 1994). The specimen label lacks precise locality information and the name of the collector, and the present authors were unable to find additional specimens from exposures at Savannah. Lithological descriptions of the slabs containing the specimens provided by C. E. Mitchell (pers. comm. 1994), who had previously examined and identified the material, matched precisely the lithology of the sections we examined at Savannah. Figures of the specimens (Text-fig. 11L–M) were generously donated by C. E. Mitchell. Based on these we feel that the specimens represent *D. complanatus*.

Dicellograptus complanatus was revised and redescribed by Williams (1987), and our specimens agree well with his description.

Stratigraphical and geographical occurrence. *Dicellograptus complanatus* is the key index species of the eponymous biozone in Europe (Skoglund 1963; Nilsson 1977; Williams 1982b, 1987) and North America (Berry 1960; Riva 1969, 1974), and it has also been reported from Russia (Keller 1956; Koren' and Sobolevskaya 1983). *D. complanatus* is a cosmopolitan mesopelagic species, and part of the Oceanic Biofacies of Goldman *et al.* (1995).

Dicellograptus gravis Keble and Harris, 1925

Text-figure 15D

- 1925 *Dicellograptus gravis* Keble and Harris, p. 516, pl. 70, fig. 2a–b.
 1972 *Dicellograptus alector* Carter, p. 46, pl. 1, figs 9, 11–12, 15; text-fig. 2a, g.
 1977 *Dicellograptus alector* Carter; Carter and Churkin, p. 18, pl. 3, figs 8, 12–13, 17.
 1987 *Dicellograptus alector* Carter; Williams, p. 77, figs 4b, 5d–h.

Syntypes. Geological Survey of Victoria nos 24004 and 24085, from the upper Eastonian (Ea 4) at Mt Easton, Victoria. Specimen 24085 is here selected as the lectotype.

Material. One well preserved specimen from the lowermost Sylvan Shale in Rayford Quarry (Section Q of Alberstadt 1973), southern Oklahoma (collected by S. C. Finney).

Description. Axial angle approximately 30°. Axil rectangular and stout. Stipe width 0.56 mm at the level of the th1¹ aperture, increasing to 0.92 mm at the aperture of th8¹. Th1¹ and th1² with apertural spines; all subsequent thecae with prominent mesial spines. Supragenicular walls with a distinct bend at the position of the mesial spine. Thecal apertures strongly introverted proximally, less so distally. The free portion of the sicula missing, apparently from resorption.

Remarks. We follow Cas and VandenBerg (1988) in synonymizing *Dicellograptus alector* with *D. gravis*.

Stratigraphical and geographical occurrence. *Dicellograptus gravis* is the nominal species for Ea4 in the Victorian graptolite succession (Cas and VandenBerg 1988). Goldman *et al.* (1995) suggested that the *D. gravis* Biozone is also an appropriate name for Carter and Churkin's (1977) *C. tubuliferus* Biozone as well as for the coeval part of Zone 13 of Berry (1960) in the basal Maravillas Formation of the Marathon region in West Texas. Williams (1987) recorded the co-occurrence of *D. gravis* with *D. complanatus* in the Mill Formation, Upper Whitehouse Group, at Myoch Bay in the Girvan area, Scotland.

While this is the only species of *Dicellograptus* occurring in S. C. Finney's collections from the lower Sylvan Shale at Rayford Quarry, other sections of Sylvan Shale have yielded numerous specimens of *D. complanatus*. *D. gravis* is a cosmopolitan mesopelagic species and part of the Oceanic Biofacies of Goldman *et al.* (1995).

Family DIPLOGRAPTIDAE Lapworth, 1873, emend. Mitchell, 1987
Subfamily CLIMACOGRAPTINAE Frech, 1897, emend. Mitchell, 1987

Genus CLIMACOGRAPTUS Hall, 1847, emend. Mitchell 1987

Type species. By original designation; *Graptolithus bicornis* Hall, 1847.

Remarks. Considerable confusion continues to plague the taxonomy of several middle and upper Ordovician *Climacograptus* species. The primordial astogeny of such biostratigraphically important taxa as *Climacograptus caudatus* Lapworth, *Climacograptus tubuliferus* Lapworth, *Climacograptus nevadensis* Carter, and *Climacograptus putillus* (Hall) has been variously interpreted (see, for example, Mitchell 1987; Riva 1988; Riva and Ketner 1989) with resultant taxonomic obfuscation.

Mitchell (1987, p. 361, text-fig. 5) described and illustrated the primordial Pattern D astogeny of *Climacograptus caudatus* based on three-dimensional isolated growth stages from the Viola Springs Formation in southern Oklahoma. The salient characters of Pattern D astogenetic growth include a short, broad sicula bearing only a virgella, and a characteristic prosicula composed of only one or two vertical rods that merge with the nema. Th1¹ grows down along the sicula and then turns sharply upward with its metatheca pressed against its protheca. Th1² is prosoblastic and grows across the reverse side of the sicula in a broad symmetrical arch. The crossing canal of th2¹ appears as a small hood that fuses along the sicula axis with an upward-growing flange from the crossing canal of th1². This fusion of hood and flange is marked by a short list and accompanies the differentiation of the prothecae of th2¹ and th2². In mature or semi-flattened rhabdosomes, Pattern D astogeny can be recognized by the broad, evenly rounded arch formed by th1² on the reverse side of the sicula, and by a distinct dimple in the position of the list formed by the fusion of the th2¹ crossing canal with the upward-growing flange from th1² (Text-fig. 5U, w). Other taxa exhibiting Pattern D primordial astogeny referred to *Climacograptus* by Mitchell (1987) include *C. tubuliferus*, *C. putillus* and *C. styloideus*.

Riva (1988), believing that *C. putillus*, *C. tubuliferus*, *C. styloideus*, and *C. nevadensis* possess Pattern H primordial astogeny, referred these species to a new genus, *Scalarigraptus* (a junior synonym of *Normalograptus* Legrand, 1987). Additionally, Riva, in Riva and Ketner (1989) established the monotypic genus *Ensigraptus* for Pattern D climacograptinids lacking spines on their first two thecae, with *Climacograptus caudatus* as type species. Williams (1991) noted that in specimens of *C. tubuliferus* figured by Williams and Bruton (1983, fig. 15a, n) th1² showed early downward growth, a feature consistent with Pattern D proximal development but not found in Pattern H (in which th1² grows directly upward from th1¹), and re-assigned *C. tubuliferus* to *Climacograptus*. It is appropriate to note that Riva, in Riva and Ketner (1989) did not discount the possibility that better preserved specimens of *C. tubuliferus* might reveal Pattern D primordial astogeny. Williams (1991) also chose to retain *C. caudatus* in *Climacograptus*, but did not synonymize *Ensigraptus* with *Climacograptus*. We agree with Williams' (1991) revisions and think that the presence and number of spines on the proximal thecae are important characters for differentiating species but are not consistent enough to define genera. We are not convinced that the loss of proximal thecal spines occurred only once in the evolutionary history of *Climacograptus*, and it may well represent a character 'acquired' independently by several species.

Goldman *et al.* (1995) illustrated well-preserved specimens of *C. nevadensis* from the lower Maravillas Formation of the Marathon region that clearly exhibit Pattern D development. We retain *C. nevadensis* in *Climacograptus* and redescribe it based on additional material from the Polk Creek Shale of Oklahoma. Topotypes and other specimens of *Climacograptus putillus*, an often misidentified species, also exhibit Pattern D early astogeny and are redescribed below.

Climacograptus nevadensis Carter, 1972

Text-figure 13E-G

- 1963 *Climacograptus* aff. *C. innotatus* Nicholson; Churkin, pl. 2, fig. 27.
 1972 *Climacograptus innotatus nevadensis* Carter, p. 47, pl. 1, figs 1, 8; text-fig. 2b-f.
 1992 *Normalograptus tubuliferus nevadensis* (Carter); VandenBerg and Cooper, fig. 10b.
 1995 *Climacograptus nevadensis* (Carter); Goldman *et al.*, figs 2a-c, 3a-c.

Holotype. USNM 164439, from the Jacks Peak Formation of the Valmy Group, Chicken Creek, Elko County, Nevada.

Material. Twenty specimens, from exposures of the Polk Creek Shale at the Stringtown Quarry, southern Oklahoma. Comparative material from the lower Maravillas Formation in the Marathon region, West Texas was also examined.

Diagnosis. Pattern D climacograptine with prominent genicular flanges; rhabdosome septate, widens gradually throughout. Nema long, thin; virgella also long and thin.

Description. Rhabdosomes up to 10 mm long, gradually increasing in width from an average of 0.8 mm at the aperture of th^1 to a maximum of 1.6–1.8 mm distally. Thecae climacograptid, numbering 7–8 in the proximal 5 mm, decreasing in number to 5.5–6.5 in 5 mm distally. Supragenicular walls 0.4–0.45 mm long proximally, increasing to 0.6–0.65 mm distally with a prominent flange or spine up to 0.6 mm long at their base. Thecal apertures shallow, semicircular, slightly everted. Nema long and thin. Virgella moderately long and slender. Primordial astogeny is Pattern D of Mitchell (1987).

Remarks. *C. nevadensis* can be differentiated from *C. tubuliferus* by its distinct genicular flanges, shorter rhabdosome, wider proximal end, and thin as opposed to broad nema. It may be separated from *Paraclimacograptus innotatus* by its Pattern D (as opposed to Pattern I) primordial astogeny, or in poorly preserved material, by its much wider proximal end.

Stratigraphical and geographical occurrence. *Climacograptus nevadensis* is common in Ea3 to Ea4 strata of the Victoria (Australia) graptolite succession (VandenBerg and Cooper 1992), the lower Maravillas Formation of West Texas (Goldman *et al.* 1995), and in the *D. gravis* Biozone of Idaho and Nevada (Churkin 1963; Carter 1972; and see Goldman *et al.* 1995 for a revision of the late Ordovician graptolite zonation). *C. nevadensis* is a cosmopolitan mesopelagic species and part of the Oceanic Biofacies of Goldman *et al.* (1995).

Climacograptus putillus (Hall, 1865)

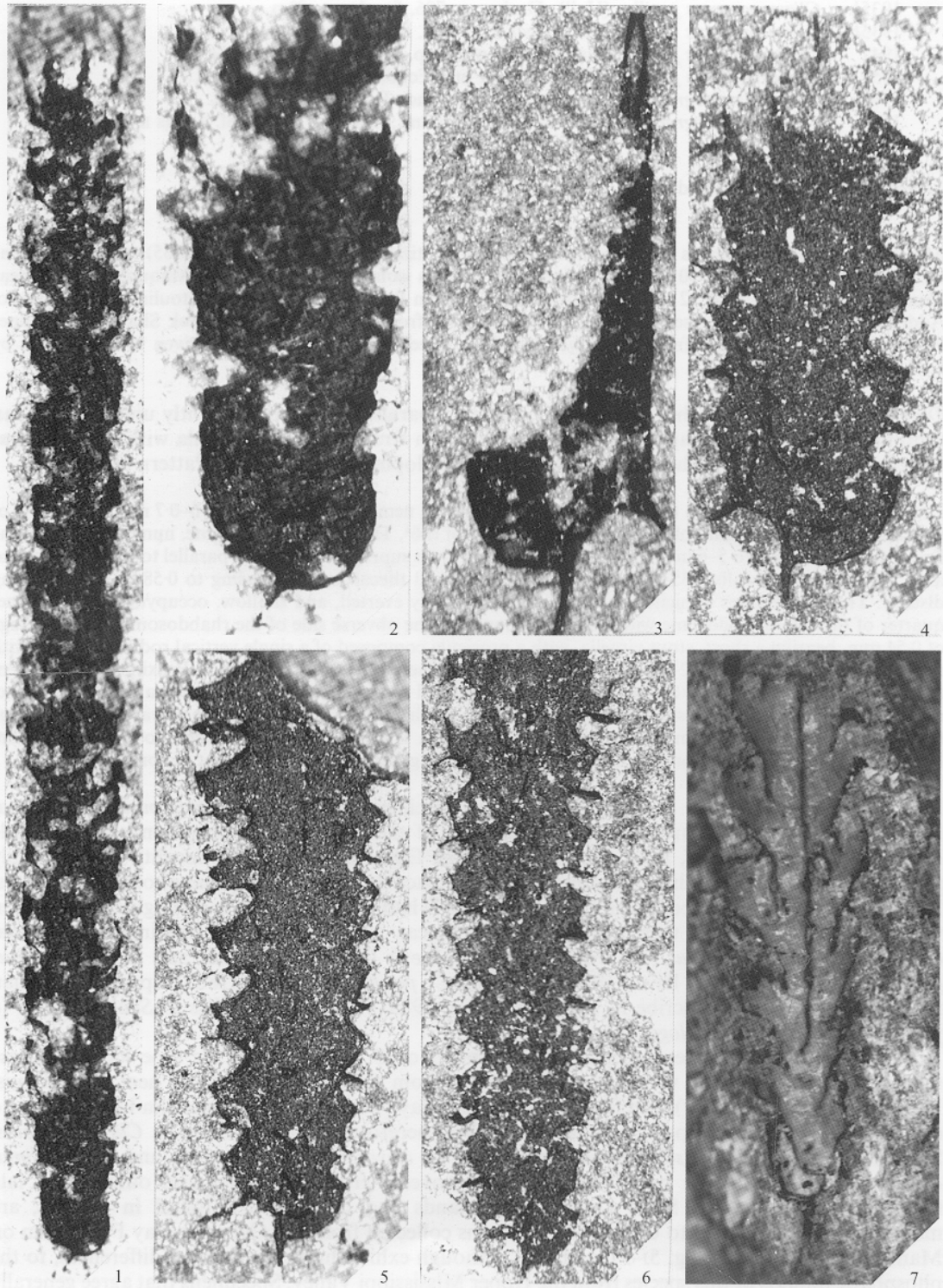
Text-figures 5J-Z; Plate 1, figures 1–2, 7

- 1865 *Graptolithus putillus* Hall, pp. 27, 44, pl. A, figs 10–12a.
 1908 *Climacograptus putillus* (Hall); Ruedemann, p. 415 (*partim*), figs 368–370 (*non* 371–377).
non 1913 *Climacograptus putillus* Hall; Hadding, p. 49, pl. 3, figs 15–17. [= *Normalograptus haddingi* (Glimberg, 1952)].
 1925 *Climacograptus putillus* (Hall); Ruedemann, p. 60 (*partim*).
non 1935 *Climacograptus putillus* (Hall); Thorslund and Askund, p. 18, pl. 1, fig. 6 [= *Normalograptus haddingi* (Glimberg, 1952)].

EXPLANATION OF PLATE I

Figs 1–2, 7. *Climacograptus putillus* (Hall, 1865); 1–2, OSU 48525; Georgian Bay Formation; Gorrel Point, Manitoulin Island, Ontario; $\times 15$ and $\times 45$. 7, OSU 48527; Elgin Member, Maquoketa Formation; Graf, Iowa; $\times 18$.

Figs 3–6. *Amplexograptus manitoulinensis* (Caley, 1936); OSU 48561, 48513, 48521, 48562; Blue Mountain Formation; 5 km south of Little Current, Manitoulin Island, Ontario; note pattern G proximal end development and the prominent genicular flanges; $\times 50$, $\times 30$, $\times 25$ and $\times 18$.



GOLDMAN and BERGSTRÖM, *Climacograptus*, *Amplexograptus*

- 1935b *Climacograptus putillus* (Hall); Decker, p. 706, figs 1m-o, ?2m.
 1935b *Climacograptus ulrichi* (Hall); Decker, p. 707, fig. 2e.
 1947 *Climacograptus putillus* (Hall); Ruedemann, p. 434, pl. 72, figs 29-42.
 1958 *Climacograptus putillus* (Hall); Werner and Echols, p. 1026, figs 1-2.
 1969 *Pseudoclimacograptus* cf. *P. clevensis* Skoglund; Riva, p. 526, fig. j-k.
 1977 *Pseudoclimacograptus* aff. *P. clevensis* Skoglund; Walters, p. 948, pl. 4, figs D-E.

Lectotype. Not yet designated.

Material. Over 100 specimens preserved as internal phosphatized moulds from Hall's (1865) type locality near Graf, Iowa; approximately 50 internal phosphatized moulds isolated from the Lower Maquoketa Shale near Saint Louis, Missouri; and 12 specimens from the Georgian Bay Formation on Manitoulin Island, Ontario. Additional, but less well preserved material was collected from the Haymeadow Creek Shale in the Upper Peninsula of Michigan, and from the Sylvan and Polk Creek shales of Oklahoma (given to the authors by S. C. Finney).

Diagnosis. Rhabdosome short, narrow (< 1.2 mm), parallel-sided, with a gently undulose median septum. Thecae climacograptine, slightly everted, with straight genicula. Sicula with a short, stout virgella; $th1^1$ and $th1^2$ without spines. Proximal development representing Pattern D astogeny.

Description. Rhabdosome up to 16 mm long (excluding the nema), widening from 0.6-0.7 mm at the level of $th1^1$ aperture to a maximum of 0.8-1.0 mm at the level of $th6^1$. Thecae climacograptine, numbering 6-7 in the first 5 mm, decreasing to 5-6 in 5 mm distally, having straight supragenicular walls parallel to the rhabdosomal axis. Supragenicular walls 0.35-0.45 mm long in the second thecal pair, increasing to 0.58 to 0.68 mm long distally. Thecal apertures semicircular, horizontal to slightly everted, and shallow, occupying less than one-quarter of the total rhabdosome width. Sicula exposed on the obverse side of the rhabdosome for an average of 0.54 mm, bearing a short, stout virgella, with a prosicula composed of a single vertical rod that merges with the nema. Sicula aperture 0.2-0.25 mm wide. Length of the entire sicula unknown. Proximal development follows Pattern D primordial astogeny. The broad rounded arch of the $th1^2$ crossing canal, and the distinct dimple of the position of the list formed by the fusion of the $th2^1$ crossing canal with the upward growing flange from $th1^2$, are shown clearly in well preserved specimens (Pl. 1, figs 1-2, 7). A gently undulose median septum begins at the level of the second or third thecal pair. A long slender nema is present in some specimens.

Remarks. Hall's (1865, pl. A, figs 10-12a) type specimens of *Climacograptus putillus* are distal fragments from an exposure of the Elgin Member of the Maquoketa Formation near the Little Maquoketa River at Graf, Iowa (Text-fig. 4c). The Elgin Member at this locality is remarkably phosphatic and the graptolites are preserved as spectacular three-dimensional phosphatic moulds. Riva (1974) noted that Ruedemann (1908, 1925, 1947) had great difficulty in distinguishing between various small graptolites with climacograptine thecae and had referred specimens of several different taxa to *C. putillus* (e.g. *Normalograptus brevis* (Elles and Wood) and *Geniculograptus pygmaeus* (Ruedemann)). Riva (1974) restricted *C. putillus* to Hall's (1865) upper Ordovician material but did not redescribe it, and later (Riva, 1988) referred *C. putillus* to *Scalarigraptus* (a junior synonym of *Normalograptus*).

We have collected numerous complete specimens of *C. putillus* from the type locality. These specimens (Text-fig. 5Q-T, w-z), as well as others from the Maquoketa Shale near Saint Louis, Missouri (Text-fig. 5U-v, Y), and from the Georgian Bay Formation on Manitoulin Island, Ontario clearly show a Pattern D primordial astogeny. We therefore retain *C. putillus* in *Climacograptus*. Specimens described as *Pseudoclimacograptus* cf. *P. clevensis* by Riva (1969) and *Pseudoclimacograptus* aff. *P. clevensis* by Walters (1977), recovered from well cores and outcrops of late Ordovician strata in the Saint Lawrence Lowlands and on Anticosti Island in Quebec, are morphologically identical to *C. putillus* specimens collected from the Georgian Bay Formation on Manitoulin Island (Text-fig. 5J-P), and also, although exhibiting preservational differences, to the phosphatic moulds of this species from the Upper Mississippi Valley. Specimens that agree generally

with the morphology of *C. putillus*, but are too poorly preserved to show the undulose median septum or proximal end details, occur in the Sylvan Shale of Oklahoma (Ruedemann 1908; Decker 1935b).

Stratigraphical and geographical occurrence. *Climacograptus putillus* first appears in the uppermost *Amplexograptus manitoulinensis* Biozone in the Saint Lawrence Lowlands of Quebec and on Anticosti Island (Riva 1969, 1974; Walters 1977) and Manitoulin Island. Exposures of the lower Maquoketa Group (Formation) in the Upper Mississippi Valley also yield specimens of *Orthograptus eucharis*, *Rectograptus peosta*, and, at one locality (Savannah, Illinois), *Dicellograptus complanatus*. This suggests an age of upper *A. manitoulinensis* to lowermost *D. complanatus* biozone for the lower Maquoketa Group (Formation). *C. putillus* is not known outside Laurentia (specimens assigned to *C. putillus* by Hadding (1913) and Thorslund and Asklund (1935) from the middle Ordovician of Sweden belong to *Normalograptus haddingi* (Glimberg, 1952)). It is an endemic epipelagic species (Goldman *et al.* 1995).

Climacograptus tubuliferus Lapworth, 1876

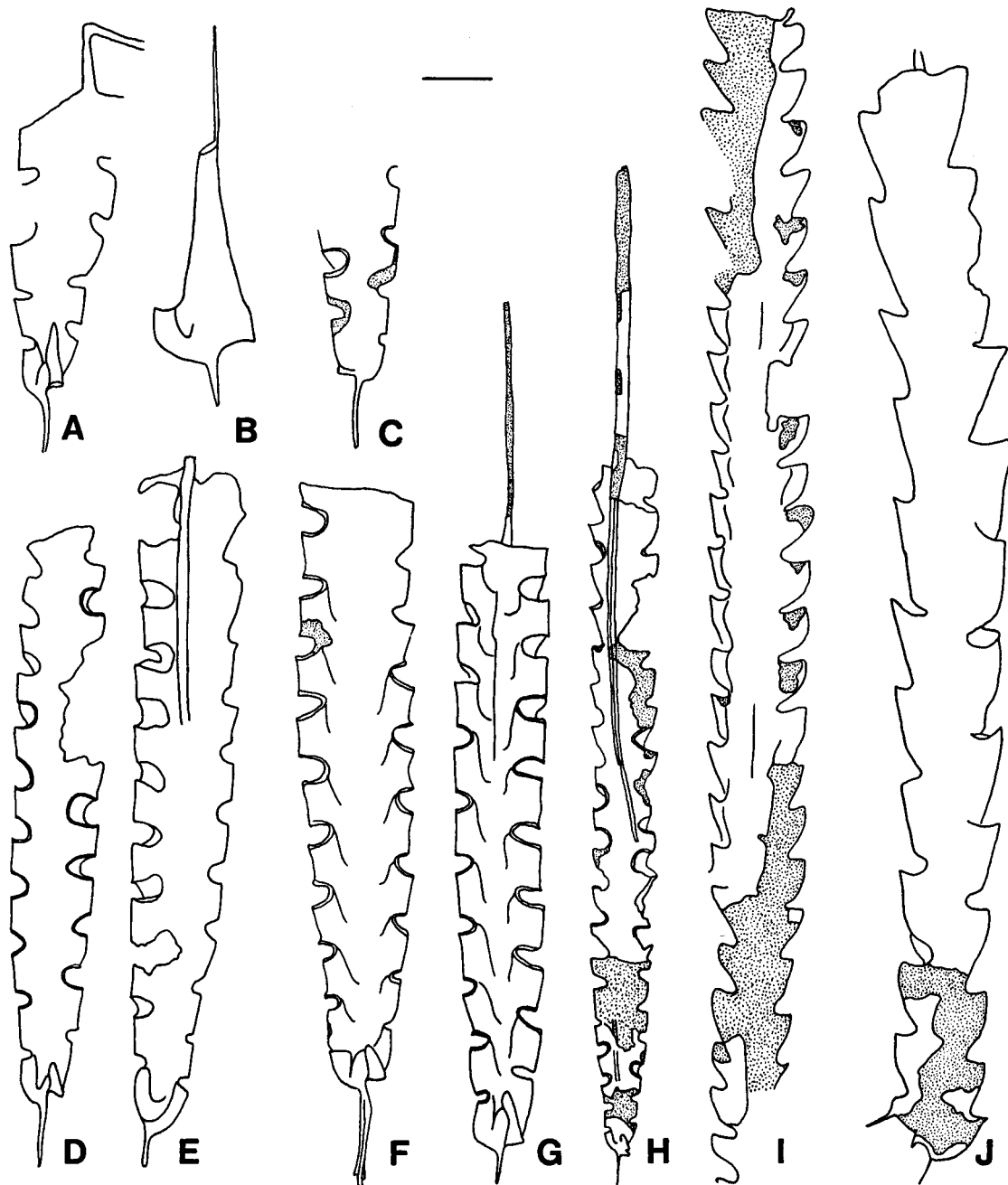
Text-figures 12A–H, 13A–D, I–K, Plate 2, figures 1–3

- 1876 *Climacograptus tubuliferus* Lapworth, pl. 2, fig. 49.
 1877 *Climacograptus scalaris* var. *tubuliferus* Lapworth; Lapworth, pl. 6, fig. 33.
 1902 *Climacograptus tubuliferus* Lapworth; Hall, p. 55, pl. 13, fig. 5; pl. 14, fig. 4.
 1906 *Climacograptus tubuliferus* Lapworth; Elles and Wood, p. 203, pl. 27, fig. 8a–d; text-fig. 134a–c.
 1908 *Climacograptus mississippiensis* Ruedemann, p. 414, pl. 28, figs 12–13; text-figs 366–367.
 1908 *Diplograptus crassitustus* Ruedemann, p. 354, text-fig. 299.
 1908 *Climacograptus ulrichi* Ruedemann, p. 413, text-fig. 364.
 1935b *Climacograptus mississippiensis* Ruedemann; Decker, p. 704, figs 1j–l, 2l.
 1935b *Diplograptus crassitustus* Ruedemann; Decker, p. 702, figs 1f–i, 2h.
 1947 *Climacograptus tubuliferus* Lapworth; Ruedemann, p. 440, pl. 75, figs 54–56.
 1947 *Climacograptus mississippiensis* Ruedemann; Ruedemann, p. 431, pl. 74, figs 3–9.
 1947 *Diplograptus crassitustus* Ruedemann; Ruedemann, p. 415, pl. 71, figs 3–9.
 1955 *Climacograptus tubuliferus* Lapworth; Harris and Thomas, p. 40, pl. 1, figs 10–12.
 1960 *Climacograptus tubuliferus* Lapworth; Berry, p. 85, pl. 19, fig. 5.
 1963 *Climacograptus tubuliferus* Lapworth; Ross and Berry, p. 132, pl. 10, figs 1–2.
 1977 *Climacograptus tubuliferus* Lapworth; Carter and Churkin, p. 23, pl. 7, fig. 5.
 1982a *Climacograptus tubuliferus* Lapworth; Williams, p. 245, fig. 11a–n.
 1983 *Climacograptus tubuliferus* Lapworth; Williams and Bruton, p. 170, figs 12c–e, 15a–n.
 1983 *Climacograptus tubuliferus* Lapworth; Koren' and Sobolevskaya (*partim*), pl. 41, figs 1–3; text-fig. 51 (*non* pl. 40, figs 6–11).
 1986 *Climacograptus tubuliferus* Lapworth; Finney, p. 453, fig. 13a, c.
 1987 *Climacograptus tubuliferus* Lapworth; Williams, p. 80, figs 4f, h–i, 6g, 7o–q.
 1988 *Scalarigraptus tubuliferus* (Lapworth); Riva, fig. 2i–j.
 1989 *Normalograptus tubuliferus* (Lapworth); Riva, *in* Riva and Ketner, p. 87, figs 10a–i, 11a–e.
 1991 *Climacograptus tubuliferus* Lapworth; Williams, p. 593, pl. 1, figs 2–4, ?5; text-fig. 8a–c.
 1995 *Climacograptus tubuliferus* Lapworth; Goldman *et al.*, figs 2D–E, 3D–F.

Lectotype. BU 1193 g, designated by Riva (*in* Riva and Ketner 1989, fig. 10h); from the Lower Hartfell Shale (*Pleurograptus linearis* Biozone) of Hartfell Spa, southern Scotland.

Material. Fifty specimens from the Sylvan and Polk Creek shales of southern Oklahoma (collected by S. C. Finney); holotype and paratype material of *C. mississippiensis* and *D. crassitustus* (USNM 54268, 242263, 240638, 340636) also from the Sylvan Shale; and the holotype of *C. ulrichi* (USNM 54276a–b) from the Maquoketa Shale near Spencer, Missouri.

Diagnosis. Large, Pattern D climacograptine with a long, thick nema commonly exhibiting a three-veined structure. Rhabdosome widening gradually from a very narrow proximal end. Virgella long, commonly lodged within a short tubular downgrowth of the sicula (parasicula). Rhabdosome widening gradually from 0.64 mm proximally to 2.5 mm distally.



TEXT-FIG. 12. Graptolites from the Sylan Shale. A-H, *Climacograptus tubuliferus* Lapworth, 1876; A-E, OSU 48542-48545, 48594; Sycamore Creek, Oklahoma (Section J of Alberstadt 1973). Note the single prosicular rod in B, indicating Pattern D proximal development. F-G, holotype and paratype of *Climacograptus mississippiensis* Ruedemann, 1935b; USNM 54268, 242263; USGS collection 241; near Davis, Oklahoma; specimens in partial relief and slightly compressed laterally. H, USNM 240638; same locality as F-G. I-J, *Orthograptus crassitestus* (Ruedemann, 1908); H, paratype, USNM 240638; same locality as F-G; specimen flattened. I-J, holotype and paratype; USNM 54266, 235604; USGS collection 241; near Davis, Oklahoma. In addition

Description. Proximal end very narrow, characterized by Pattern D primordial astogeny. Thecae with slight outward inclination, straight to slightly rounded supragenicular walls, and numbering 6–7 in 5 mm proximally, decreasing to 4–5 in 5 mm distally. Thecal apertures horizontal, semicircular, and narrow. Rhabdosome displaying a delayed median septum, beginning at the seventh thecal pair. Nema long, wide, and often displaying a three-vented structure (Text-fig. 13A–B). Virgella long, narrow, commonly enclosed within a short parasicula.

Remarks. The holotype and paratypes of *Climacograptus mississippiensis* Ruedemann (USNM 54268 and 242263, respectively; Text-fig. 12F–G) are well preserved specimens of *C. tubuliferus* in partial relief. Hence, *C. mississippiensis* is a junior synonym of *C. tubuliferus*. Similarly, the holotype (Ruedemann 1908, p. 413, fig. 364) of *Climacograptus ulrichi* Ruedemann (USNM 54276a) is a specimen of *C. tubuliferus*, although several specimens on the reverse side of the slab appear to be referable to *C. putillus*. Paratypes of ‘*Diplograptus*’ *crassitestus* Ruedemann on the slab USNM 240638 (Ruedemann 1908, p. 354, fig. 299; Text-fig. 12H) also belong to *C. tubuliferus*. However, the holotype (USNM 54266), and other paratype specimens of ‘*D*’. *crassitestus* (Text-fig. 12I–J) belong to the *Orthograptus calcaratus* species group and are redescribed below.

Climacograptus tubuliferus can be differentiated from *Climacograptus caudatus* Lapworth by its narrower proximal end, wider three-vented nema, delayed median septum (specimens of *C. caudatus* are septate from the third thecal pair), and its shorter, less well developed parasicula. An accurate assessment of the differences between *C. tubuliferus* and *C. styloideus* Elles and Wood requires a revision of the latter using well preserved and large populations of specimens.

Stratigraphical and geographical occurrence. *Climacograptus tubuliferus* is an abundant element in the cosmopolitan mesopelagic Oceanic Biofacies of Goldman *et al.* (1995). It is common in the Lower Hartfell Shale of Scotland (*Pleurograptus linearis* Biozone; Williams, 1982a), the lower Maravillas Formation of West Texas (Zone 13 of Berry 1960; the *D. gravis* Zone of Goldman *et al.* 1995), the Sylvan and Polk Creek shales of Oklahoma, and in the *D. gravis* through *C. uncinatus* zones in Victoria (VandenBerg and Cooper 1992). An offshore, deeper water species, it is absent from the Appalachian Basin and most of the craton in North America.

Subfamily ORTHOGRAPTINAE Mitchell, 1987

Genus AMPLEXOGRAPTUS Elles and Wood, 1907

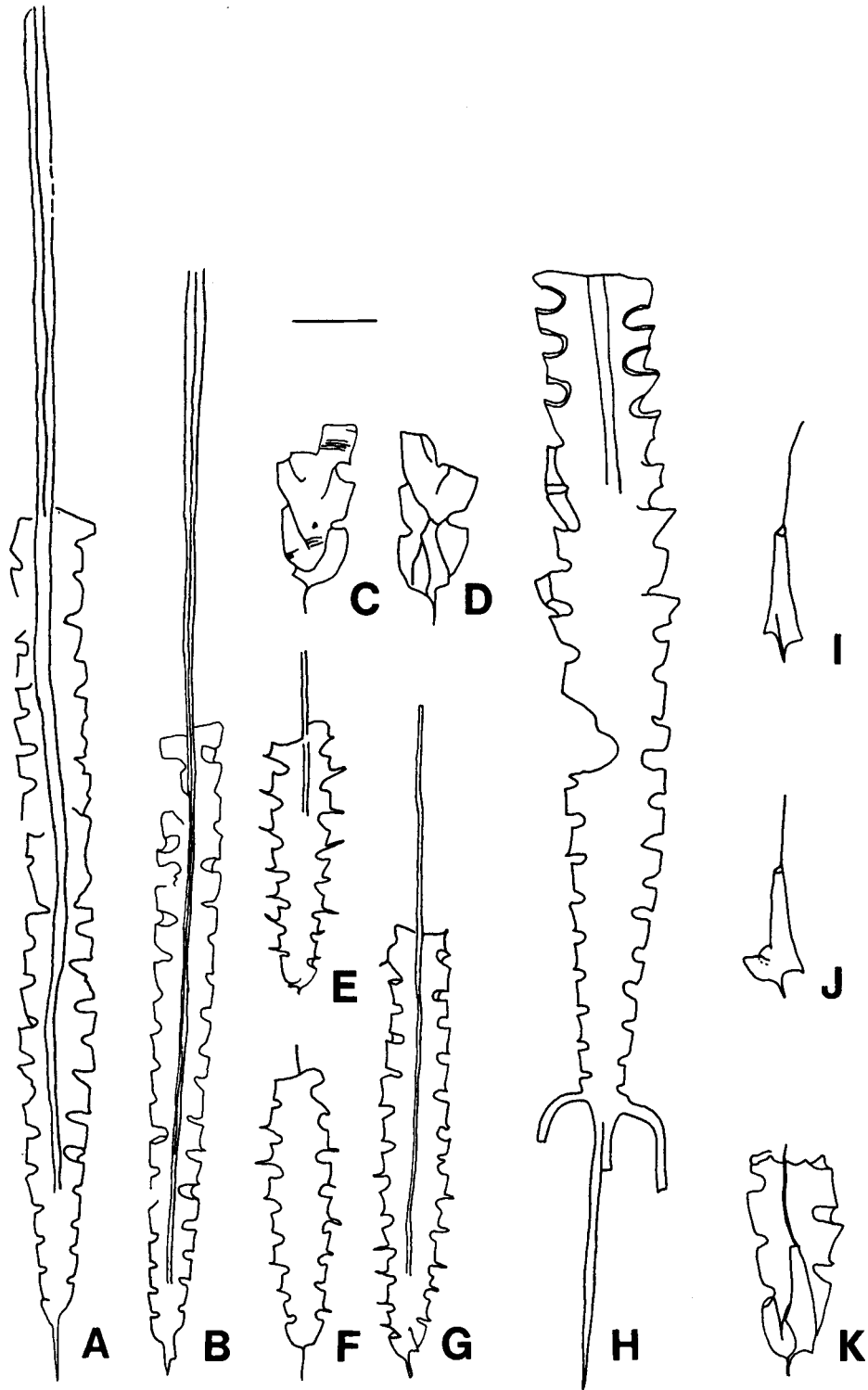
Type species. By original designation; *Diplograptus perexcavatus* Lapworth, 1873.

Amplexograptus manitoulinensis (Caley, 1936)

Plate 1, figures 3–6; Text-figure 5A–I

- 1875 *Diplograptus hudsonicus* Nicholson; Nicholson, p. 38, fig. 15 [suppressed specific name; ICZN opinion 1561].
- 1936 *Climacograptus manitoulinensis* Caley, p. 65, fig. 1.
- 1947 *Climacograptus manitoulinensis* Caley; Ruedemann, p. 431, pl. 73, fig. 55.
- 1969 *Climacograptus manitoulinensis* Caley; Riva, p. 526, fig. 6g–h.
- 1973 *Amplexograptus* aff. *A. prominens* Barrass; Jackson, p. 2, fig. 2b, e–f.
- 1977 *Climacograptus manitoulinensis* Caley; Walters, p. 937, pl. 3, figs a–b, g.
- 1986 *Climacograptus manitoulinensis* Caley; Finney, fig. 8o–p.
- 1988 *Pseudoclimacograptus manitoulinensis* (Caley); Riva, fig. 5g–j.

to *C. tubuliferus* and *O. crassitestus*, USGS collection 241 contains many fragments of *Dicellograptus complanatus*. Scale bar represents 1 mm (except for fig B where it represents 0.5 mm and figs H–J where it represents 2 mm).



TEXT-FIG. 13 For caption see opposite.

Type specimen. Caley (1936, fig. 1) illustrated three specimens, but designated no holotype. From these we select the middle one in his figure 1 as the lectotype. According to Caley (1936, p. 66) his specimens were collected at Lot 12, concession XII, Howland Township (which is near Highway 6 about 5 km south of Little Current), and deposited in the Royal Ontario Museum, Toronto.

Material. Several hundred topotype specimens from the Blue Mountain Formation along the creek that crosses Highway 6, 5 km south of Little Current, Manitoulin Island, Ontario, Canada.

Diagnosis. Rhabdosome short, narrow, aseptate; thecae amplexograptid, with short, outwardly inclined supragenicular walls, and very prominent genicular flanges. Th1¹ is U-shaped, and lacks a spine. Primordial astogeny is Pattern G of Mitchell (1987).

Description. Rhabdosome short, generally with less than 15 thecal pairs and less than 10 mm long; widens from 0.80–0.90 mm at the level of the th1¹ aperture to 1.15–1.25 mm at th6¹; long specimens reach a maximum width of 1.5 mm. Thecae amplexograptid, with short, outwardly inclined supragenicular walls and large prominent genicular flanges; closely packed, numbering 8–9 in the first 5 mm, decreasing to 7–8 in 5 mm distally. Supragenicular wall lengths vary from 0.28–0.36 mm at th1¹ to 0.40–0.44 mm distally. Thecal apertures everted, lacking lappets. Sicula with a virgella and paired anti-virgella spines, 1.80–2.0 mm long, and exposed for an average length of 1.0 mm on the obverse side of the rhabdosome. Prosicula short with very prominent vertical rods and thin periderm. Th1¹ growing down along the sicula and then turning upward in a broad smooth arch, and lacking the sub-apertural or mesial spine characteristic of most amplexograptids.

Remarks. Riva (1987b) recognized *Climacograptus manitoulinensis* Caley, 1936 to be a junior synonym of *Diplograptus hudsonicus* Nicholson, 1875. However, because the latter name had not been used for more than a century, he applied to the ICZN in 1987 (Case 2596) for a conservation of the former, widely used, species name, and the ICZN ruled in his favour in 1989 (ICZN Opinion 1561).

Riva (1987a) placed *A. manitoulinensis* in *Paraclimacograptus* Přibyl along with *A. decipiens* (Riva) based on the prominent genicular elaborations and spineless th1¹ exhibited by these species. The type species of *Paraclimacograptus*, however, is *P. innotatus* (Nicholson), a Silurian species with Pattern I early astogeny. Thus, neither *A. manitoulinensis* nor *A. decipiens* (specimens of which exhibit Pattern G development) belong to *Paraclimacograptus*. *A. manitoulinensis*, *A. decipiens*, and *A. prominens* Barras are differentiated from all other *Amplexograptus* species by their prominent genicular elaborations and spineless th1¹. Specimens of *A. manitoulinensis* can be differentiated from those of *A. decipiens* by their possession of genicular flanges as opposed to paired genicular spines, and from those of *A. prominens* by their Pattern G as opposed to K proximal astogeny, lack of lappets and much narrower rhabdosome.

Stratigraphical and geographical occurrence. *Amplexograptus manitoulinensis* is the predominant element and nominal species of Riva's (1969, 1974) *A. manitoulinensis* Biozone. It has been reported by Walters (1977) from the Nicolet River Formation of the Saint Lawrence Lowland of Quebec, and by Finney (1986) from 113 m above the base of the Viola Group at Rayford Quarry (Alberstadt's (1973) Section Q) in southern Oklahoma. *A. manitoulinensis* has not been recorded from outside North America and belongs to the Laurentian Biofacies of Goldman *et al.* (1995).

Genus ORTHOGRAPTUS Lapworth, 1873

Type species. By original designation; *Graptolithus quadrimucronatus* Hall, 1865.

Remarks. Relationships between the taxa within *Orthograptus* have historically been based on thecal morphology. Elles and Wood (1907, p. 220) divided *Orthograptus* into three informal groups:

TEXT-FIG. 13. Graptolites from the Polk Creek Shale, Stringtown Quarry, Oklahoma. A–D, I–K, *Climacograptus tubuliferus* Lapworth, 1876. OSU 48546–48552. E–G, *Climacograptus nevadensis* Carter, 1972; OSU 48553–48555. H, *Climacograptus hastatus* Hall, 1902; OSU 48556. Scale bar represents 2 mm (A–B, E–H) or 1 mm (C–D, I–K).

the *quadrimucronatus* group (specimens whose thecae bear paired apertural spines and are rectangular in cross section), the *calcaratus* group (specimens whose thecae bear paired apertural horns and are sub-rectangular in cross section), and the *truncatus* group (= *amplexicaulis* group, see Riva 1974; specimens whose thecal apertures lack elaboration and are oval in cross section). According to Elles (1922) these groups also had separate ancestries; she believed that the *quadrimucronatus* group evolved from a species of *Glossograptus*, and the *calcaratus* and *amplexicaulis* groups from *Glyptograptus* (now *Hustedograptus*) *teretiusculus*. Elles' suggestion of a polyphyletic origin for *Orthograptus* is consistent with the view of evolution by orthogenesis that was pervasive in graptolite studies during the first half of this century.

Ruedemann (1908, 1947) also believed that there was a close phylogenetic relationship between the spinose orthograptids of the *quadrimucronatus* group and *Glossograptus*, and placed them within that genus. His (1908, 1947) classification was not, however, adopted outside North America (e.g. Harris and Thomas 1955), and was subsequently abandoned there as well (Berry 1960; Ross and Berry 1963). Přibyl (1949), concerned about the apparent polyphyletic origin of *Orthograptus*, erected *Rectograptus* to include the non-spinose *calcaratus* and *amplexicaulis* group orthograptids. Use of Přibyl's genus has been sporadic.

The problem with all the preceding classifications is that they were based on phylogenies constructed from thecal characters and not astogenetic similarity. Mitchell (1987) reunited all three groups within *Orthograptus*, recognizing a common ancestry based on a similar early astogeny (Pattern G). He (1987, p. 378) rejected the segregation of the non-spinose orthograptids into *Rectograptus*, noting that the 'taxon is defined on the basis of the loss of a single, relatively simple character, and there is no reason to assume that such a loss should be unique'.

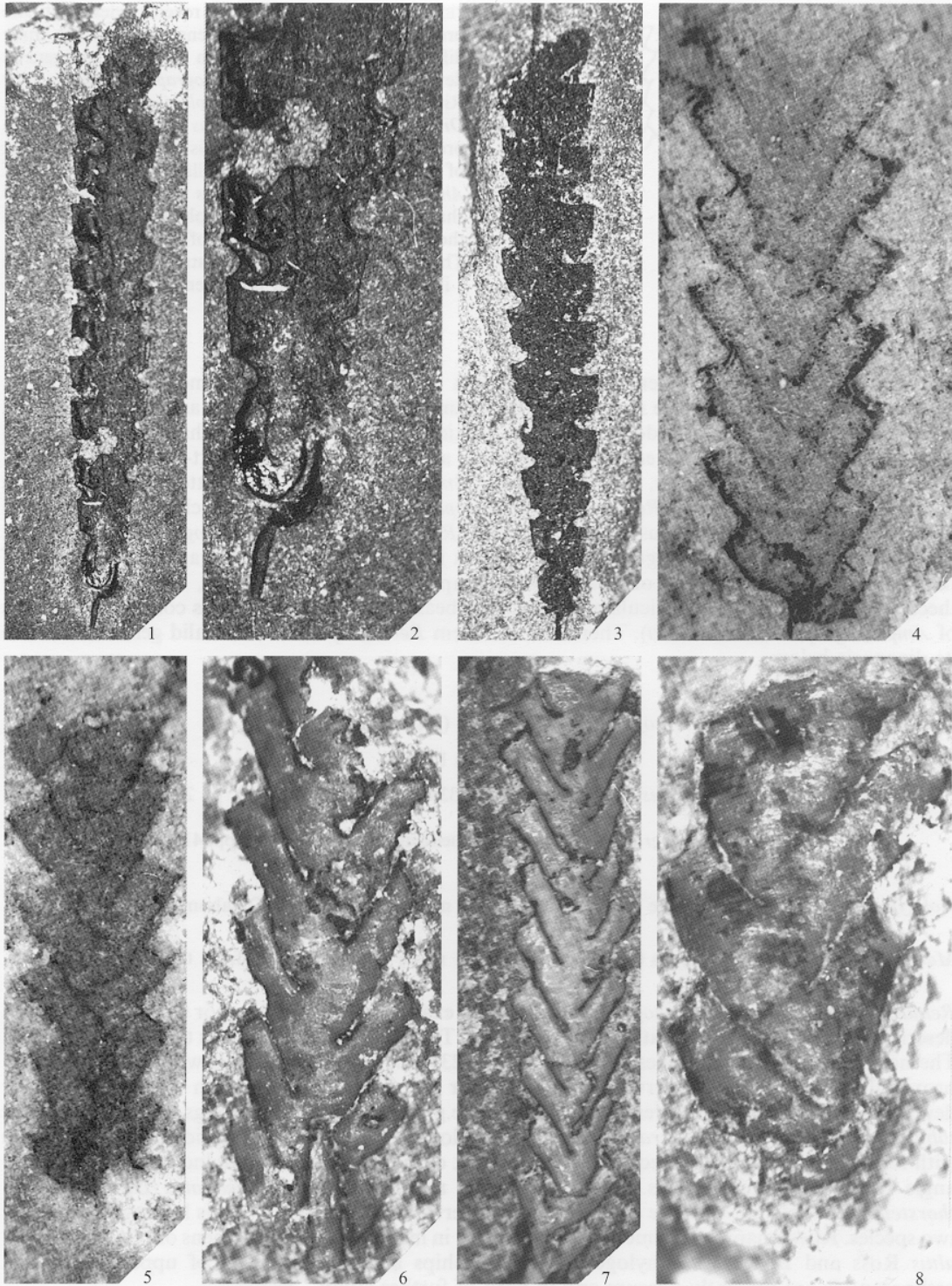
We agree with Mitchell's (1987) contention that the absence of a character is a poor basis for establishing a new taxon; however, a close examination of the morphology of the *amplexicaulis* group orthograptids shows sufficient differences from the morphology of other *Orthograptus* taxa (particularly in the proximal end) to warrant its inclusion in a separate genus. The proximal end of *Rectograptus amplexicaulis* bears a striking resemblance to that of *Amplexograptus* (Riva, 1987a, p. 929; Text-fig. 14C-D). The initial three to six thecal pairs in *R. amplexicaulis* are geniculate and strongly resemble the early thecae in specimens of *Amplexograptus*. In both taxa, $th1^1$ grows down along the sicula and then turns upward in a rather sharp 'U', its aperture facing upward as opposed to outward as in *Orthograptus*. $th1^2$ grows horizontally across the base of the sicula on the reverse side of the rhabdosome and then turns sharply upward, its aperture being either in contact with the sicula or very close to it, leaving only a short portion of its metatheca exposed in the obverse view. $th1^1$ has a prominent mesial spine and $th1^2$ does not bear a spine. The sharp upward bends in the first two thecae impart a rectangular shape to the proximal end in *Rectograptus* and *Amplexograptus* (Text-fig. 14A-D). Additionally, *Rectograptus amplexicaulis* is aseptate (the *quadrimucronatus* and *calcaratus* groups are generally septate), and the thecal margins are straight and everted, as opposed to being lobate and horizontal.

In *Orthograptus*, the first two thecae grew upward at a much gentler angle than in *Rectograptus*, causing their apertures to face outward and not upward, and $th1^2$ has a much longer portion of its metatheca visible on the obverse side of the rhabdosome. $th1^1$ and $th1^2$ both have apertural spines

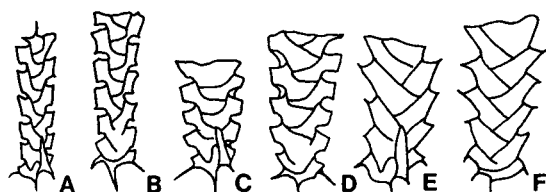
EXPLANATION OF PLATE 2

Figs 1-3. *Climacograptus tubuliferus* Lapworth, 1876; Sylvan Shale; Sycamore Creek (Section J of Alberstadt 1973), Arbuckle Mountains, Oklahoma; 1-2, OSU 48563; note pattern D proximal end development; $\times 10$ and $\times 25$. 3, OSU 48564; $\times 10$.

Figs 4-8. *Rectograptus peosta* (Hall, 1861); 4-5, OSU 48540, 48537; Fort Atkinson Formation, Maquoketa Group, Savannah, Illinois; $\times 18$. 6-8, OSU 48565-48567; three-dimensional internal moulds; Elgin Member, Maquoketa Formation; Graf, Iowa; $\times 25$, $\times 13$ and $\times 35$.



GOLDMAN and BERGSTRÖM, *Climacograptus*, *Rectograptus*



TEXT-FIG. 14. Obverse and reverse views of the proximal portion of specimens representing three different genera with Pattern G early astogenetic development. A–B, *Amplexograptus praetypicalis* Riva; C–D, *Rectograptus amplexicaulis* (Hall); E–F, *Orthograptus quadrimucronatus* (Hall). Note that the proximal end in *Rectograptus* is of similar size to that of *Orthograptus* but of similar shape to that of *Amplexograptus*. *Rectograptus* and *Amplexograptus* share a spineless $th1^2$, amplexograptid proximal thecae, and a short exposure of $th1^2$ in obverse view. These characters are not restricted to the species illustrated but occur consistently in these genera.

(although the $th1^2$ spines were secondarily lost in the youngest end members of the *O. quadrimucronatus* lineage). The more gentle curvature of the first two thecae as they turn upward imparts a smoother, more rounded shape in the proximal end of *Orthograptus* that contrasts sharply with the rectangular proximal end of *Rectograptus* and *Amplexograptus* (Text-fig. 14A–F).

Thus, although *Orthograptus*, *Rectograptus* and *Amplexograptus* all have Pattern G astogeny, the proximal ends of specimens of *Rectograptus* and *Amplexograptus* share several characters not found in *Orthograptus*. Whilst obviously closely related, *Rectograptus* and *Amplexograptus* also exhibit important differences. In *Rectograptus*, only the first few thecae are amplexograptid, whilst most of the rhabdosome is composed of straight orthograptid thecae. Additionally, although the early thecae of *Rectograptus* are geniculate, they do not bear the prominent lappets common in species of *Amplexograptus* (Riva 1987a). Therefore, we deem *Rectograptus* to be a valid genus and revise its diagnosis below.

Orthograptus crassitestus (Ruedemann, 1908)

Text-figure 12I–J

- 1908 *Diplograptus crassitestus* Ruedemann, pp. 334 (*partim*), text-fig. 300; pl. 25, fig. 6; *non* text-fig. 299.
 1947 *Diplograptus (Mesograptus) crassitestus* (Ruedemann); Ruedemann, pp. 415 (*partim*), pl. 71, fig. 3; *non* figs 4–9.

Holotype. USNM 54266, from the Sylvan Shale, 3.2 km north of Dougherty, Oklahoma.

Material. Holotype and paratypes (USGS collection 241 made by E. O. Ulrich) from the above locality.

Remarks. The material of *Orthograptus crassitestus* examined by us is too poor to permit a detailed description, but several observations may be made. The type material includes two distinct species. The holotype and two paratypes (USNM 235604–235605) are orthograptids with Pattern G or K proximal astogeny (the preservation is too poor to differentiate between these two similar developmental patterns). The rest of the material (e.g. USNM 240638) belongs to *Climacograptus tubuliferus*. Specimens of *O. crassitestus* exhibit a long, slender, gradually widening rhabdosome with long, gently sinusoidal thecae. The thecae lack cusps or spines and are inclined at a very low angle to the rhabdosome axis. *O. crassitestus* is reminiscent of *O. fastigatus* Davies and *O. thorsteinssoni* Melchin, with the exception of an apertural spine on $th1^2$ that is lacking in the latter two species. Ruedemann's specimens are also similar in morphology to specimens of '*Glyptograptus altus* Ross and Berry. The phylogenetic relationships among this group of upper Ordovician orthograptids are presently obscure and in need of further study.

Stratigraphical and geographical occurrence. *Orthograptus crassitestus* is known only from the Sylvan Shale of Oklahoma. Specimens of *C. tubuliferus* and *D. complanatus* co-occur with *O. crassitestus*, suggesting that it occurs in the *D. complanatus* Biozone.

Orthograptus eucharis (Hall, 1865)

Plate 3, figures 1–5; Text-figure 15A–C

1865 *Retiograptus eucharis* Hall, p. 16, pl. 14, fig. 9.

1995 *Orthograptus eucharis* (Hall); Goldman, pp. 530, figs 15·6–15·7, 17·1–4 [with full synonymy].

Holotype. GSC 13623 (synrhabdosome), from the Pointe Blue Shales on Lake St John, Quebec.

Material. Hundreds of flattened and isolated three-dimensionally preserved specimens from the lowermost Maquoketa Group (Formation) in the Upper Mississippi Valley, and several flattened specimens from the Haymeadow Creek Shale of northern Michigan.

Diagnosis. *Orthograptus* with small, narrow, parallel-sided, aseptate rhabdosome that tends to narrow distally; th¹ with apertural spine, th² lacking a spine, subsequent thecae with paired apertural spines. Periderm attenuated. Primordial astogeny is Pattern G of Mitchell (1987).

Description. Rhabdosomes short (rarely more than ten thecal pairs), narrow, parallel-sided, maintaining a mean width of 0·9 mm throughout or narrowing distally; aseptate; thecae inclined to the rhabdosome axis at an angle of 35–40°; th¹ with single apertural spine, th² lacking a spine, subsequent thecae with paired apertural spines. Sricula averages 1·96 mm in length and 0·33 mm in apertural width, and is visible in observe view for a mean distance of 0·92 mm before becoming enclosed within the rhabdosome. Periderm attenuated, especially along the free ventral walls of the thecae.

Remarks. This species has been revised by Goldman (1995).

Stratigraphical and geographical occurrence. *Orthograptus eucharis* is the most common graptolite in the lower Maquoketa Group (Formation). It is abundant in both the dense black shale (Argo-Fay Bed) that marks the base of the Maquoketa Group in north-western Illinois (Kolata and Graese 1983) and in the Elgin Member in north-eastern Iowa and southern Minnesota. In Quebec, Michigan, and Oklahoma, specimens of *O. eucharis* occur in the uppermost *G. pygmaeus* to *A. manitoulinensis* Biozone (Riva 1969, 1974; Finney 1986). *O. eucharis* is unknown from outside North America and is an endemic epipelagic species and part of the Laurentian Biofacies of Goldman *et al.* (1995).

Orthograptus quadrimucronatus (Hall, 1865)

Text-figures 2L–N, 14E–F

1865 *Graptolithus quadrimucronatus* Hall, p. 144, pl. 13, figs 1–10.

1877 *Diplograptus quadrimucronatus* (Hall); Lapworth, p. 133, pl. 6, fig. 20.

1907 *Diplograptus (Orthograptus) quadrimucronatus* (Hall); Elles and Wood, p. 223, pl. 28, fig. 1a–d; text-fig. 145a–f.

1936 *Diplograptus foliaceus gorrelensis* Caley, p. 66, fig. 2.

1947 *Glossograptus quadrimucronatus* (Hall); Ruedemann, p. 452 (*partim*), pl. 78, figs 1–2; (*non* figs 3–5).

1995 *Orthograptus quadrimucronatus quadrimucronatus* (Hall); Goldman, p. 525, figs 10·1–10·19, 11·1–11·6, 15·1–15·5, 17·5–17·9 [see for full synonymy].

Syntypes. GSC 1898a–b, d from the Pointe Blue Shales on Lake St John, Quebec.

Material. Several specimens from the Georgian Bay Formation on Manitoulin Island, and the lower Maquoketa Group in the Rifle Hill Quarry, Fillmore County, Minnesota.

Diagnosis. *Orthograptus* with short single apertural to sub-apertural spines on $th1^1$ and $th1^2$; subsequent thecae with paired apertural spines, none of consistently unusual length; rhabdosome septate, gradually widening. Primordial development is Pattern G of Mitchell (1987).

Remarks. This species has been revised recently by Goldman (1995).

Stratigraphical and geographical occurrence. *Orthograptus quadrimucronatus* is common in the *C. americanus* through *A. manitoulinensis* biozones in North America. It also occurs ubiquitously in the upper middle and upper Ordovician world-wide. Due to its rather long range, *O. quadrimucronatus* has limited biostratigraphical utility. Specimens collected from the Georgian Bay Formation and from the Lower Maquoketa Group (Formation) are from the *A. manitoulinensis* Biozone. *O. quadrimucronatus* belongs to the cosmopolitan epipelagic Oceanic Biofacies of Goldman *et al.* (1995).

Genus RECTOGRAPTUS Přibyl, 1949

Type species. By original designation; *Graptolites amplexicaule* Hall, 1847.

Revised diagnosis. Rhabdosome aseptate, with amplexograptid proximal thecae and orthograptid distal thecae; $th1^1$ with mesial to subapertural spine, other thecae non-spinose; thecal apertures smooth, straight, non-lobate, lacking spines or cusps; proximal end amplexograptid-like with $th1^1$ and $th1^2$ sharply upturned imparting a rectangular shape. Primordial astogeny is Pattern G of Mitchell (1987).

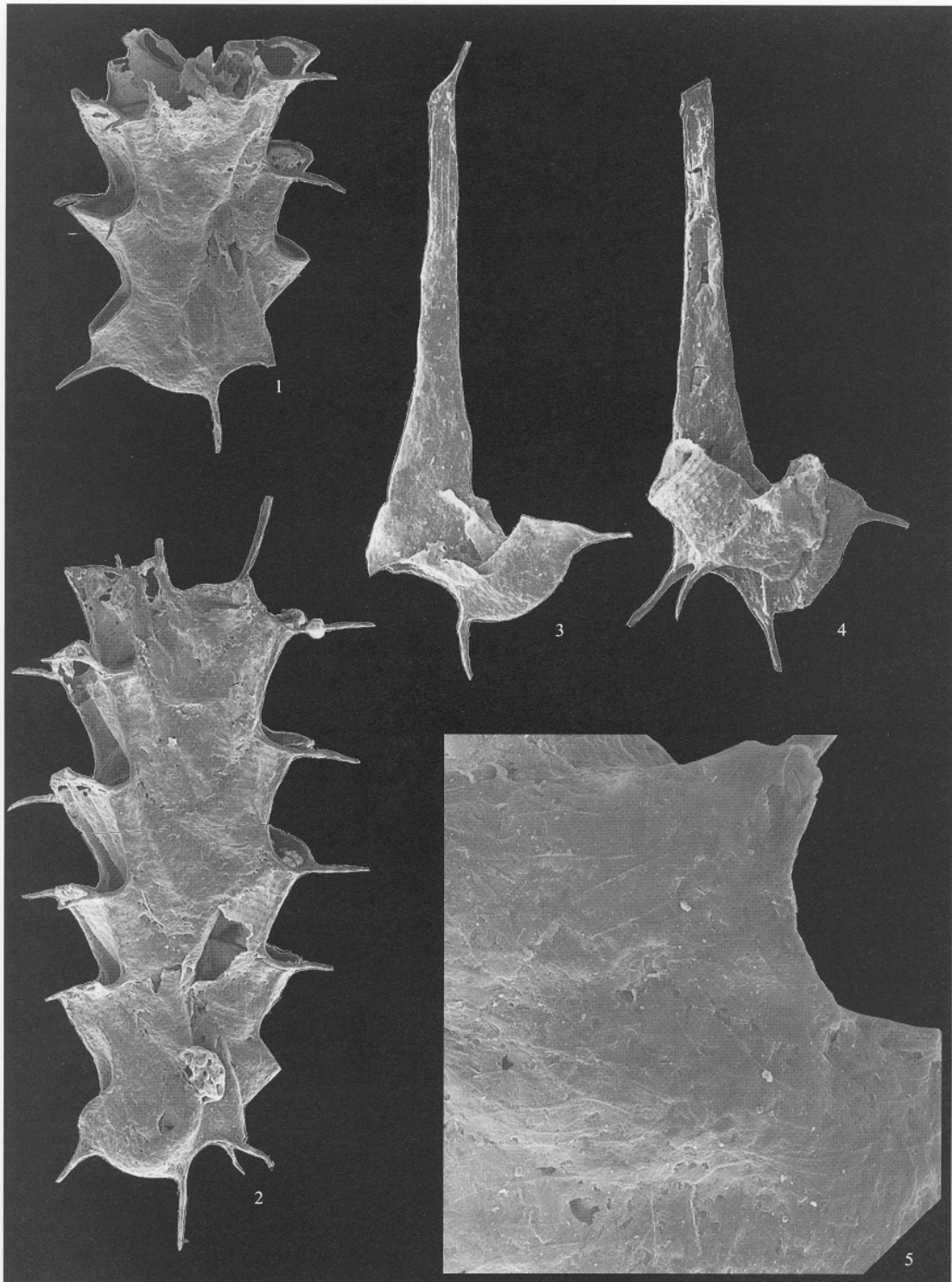
Rectograptus peosta (Hall, 1861)

Plate 2, figures 4–8; Text-figure 11A–K

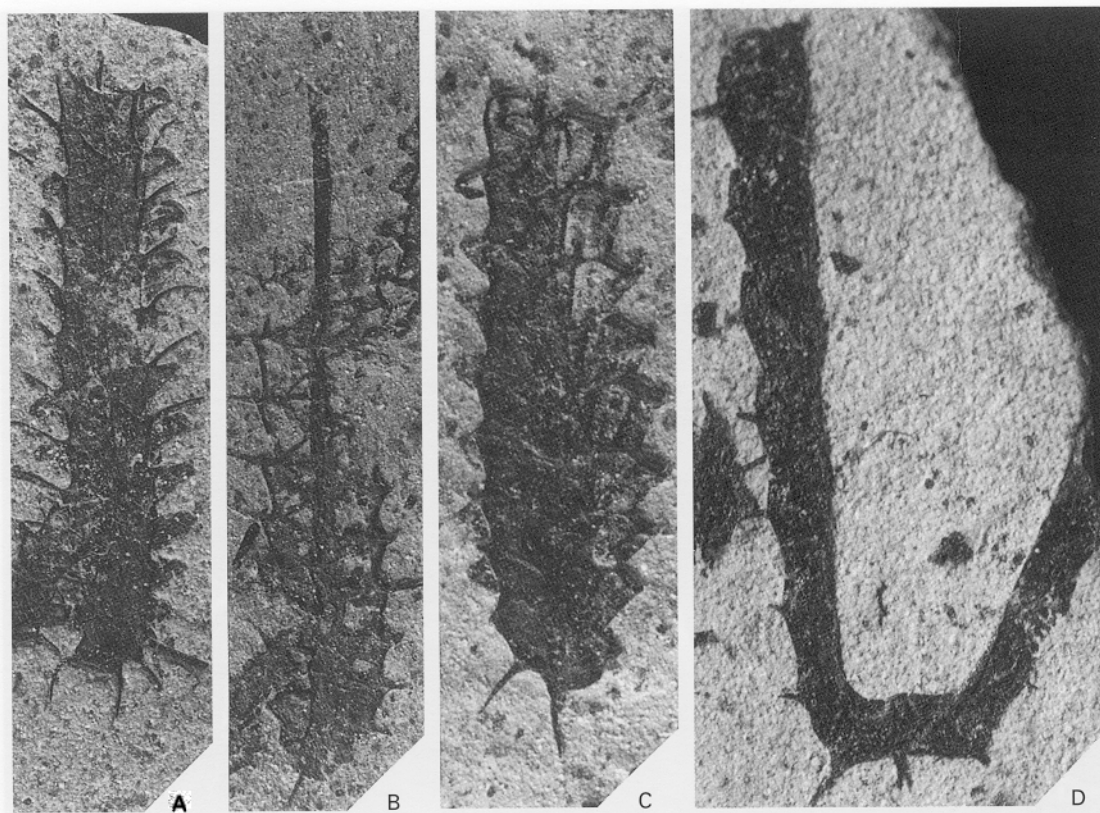
- 1861 *Graptolithus* (*Diplograptus*) *peosta* Hall, p. 17.
 ?1861 *Retiolites gracilis* Roemer, p. 31, pl. 5, fig. 1.
 ?1880 *Diplograptus socialis* Lapworth, p. 166, pl. 4, fig. 13a–c.
 1895 *Graptolithus* (*Diplograptus*) *peosta* Hall; Whitfield, p. 47, pl. 5, fig. 12.
 ?1907 *Diplograptus* (*Orthograptus*) *truncatus* var. *socialis* (Lapworth); Elles and Wood, p. 237, pl. 29, fig. 7a–e; text-fig. 157a–d.
 1908 *Diplograptus peosta* (Hall); Ruedemann, p. 372, pl. 25, fig. 17.
 1915 *Diplograptus peosta* (Hall); Hadding, p. 16, pl. 2, figs 12–14.
 1947 *Diplograptus* (*Glyptograptus*) *peosta* (Whitfield); Ruedemann, p. 408 (*partim*), pl. 69, figs 22–25, ?figs 26–27, 28a; non pl. 69, figs 28–31.
 ?1963 *Orthograptus truncatus* var. *socialis* (Lapworth); Ross and Berry, p. 151, pl. 11, fig. 21.
 ?1963 *Orthograptus gracilis* (Roemer); Skoglund, p. 46, pl. 4, fig. 6, pl. 5, figs 5, 7, text-fig. 11 [includes synonymy list of *O. gracilis*].
 ?1970 *Orthograptus truncatus socialis* (Lapworth); Toghil, p. 24, pl. 13, figs 7–9, pl. 16, fig. 7.
 1971 *Orthograptus truncatus* var. *socialis* (Lapworth); Berry and Marshall, p. 256, text-fig. 3a–c.
 ?1987 *Orthograptus socialis* (Lapworth); Williams, p. 81, figs 7c–m, 8f–h.
 ?1991 *Orthograptus socialis* (Lapworth); Williams, p. 595, pl. 2, figs 16–17; text-fig. 91–n.

EXPLANATION OF PLATE 3

Figs 1–5. *Orthograptus eucharis* (Hall, 1865); SEM photomicrographs; Elgin Member, Maquoketa Formation, Clermont, Iowa. 1–2, OSU 48568–48569, $\times 45$. 3–4, OSU 48570–48571; note the upward growing flange from $th1^1$ that meets the $th1^2$ crossing canal to construct the $th1^2$ protheca; $\times 60$. 5, OSU 48572; note cortical bandages; $\times 190$.



GOLDMAN and BERGSTRÖM, *Orthograptus*



TEXT-FIG. 15. A–C, *Orthograptus eucharis* (Hall, 1865); OSU 48557–48559; Elgin Member, Maquoketa Formation; Postville North Quarry, Iowa; note the reduced periderm; $\times 12$. D, *Dicellograptus gravis* Keble and Harris, 1925; OSU 48560; lower Sylvan Shale; Rayford Quarry, Oklahoma; note the mesial spines present on the thecae, and the distinct bend of the supragenicular wall; $\times 15$.

Type specimen. Not yet designated.

Material. Over 100 specimens from outcrops of the lower Maquoketa Group (Formation) in Iowa and Illinois (see Table 1).

Diagnosis. Slender *Rectograptus* species, aseptate, widening from 0.84–1.00 mm at the $th1^1$ aperture to 1.16–1.36 mm at the sixth thecal pair, to a maximum of 1.56 mm in long specimens. $Th1^1$ bears a single apertural spine; $th1^2$ and subsequent thecae are spineless; thecae straight, simple, with everted apertures, inclined to rhabdosome axis at a low angle (approximately 25°).

Description. Thecae number 7–8 in the proximal 5 mm, decreasing to 5–6 in 5 mm distally in long specimens. Sicula 1.88–2.0 mm long, exposed on the obverse side of the rhabdosome for about half its total length. Primordial astogeny is Pattern G of Mitchell (1987).

Remarks. A plethora of species similar to *R. peosta* have been described from North America and Europe (e.g. by Elles and Wood 1907; Ruedemann 1947; Ross and Berry 1963). Many of these taxa have undoubtedly been erected on the basis of preservational differences, stratigraphical position and national origin. A lack of definable characters makes the task of sorting out their taxonomy

TABLE 1. Occurrence of upper Ordovician graptolite species at each of the investigated localities in the North American Midcontinent. Numbers correspond to localities in Appendix.

Species	Locality																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Dicellograptus complanatus</i>	X	.	.	.	X	X	.	.	X
<i>Dicellograptus gravis</i>	X
<i>Amplexograptus manitoulinensis</i>	.	X
<i>Climacograptus nevadensis</i>	X
<i>Climacograptus putillus</i>	.	X	X	cf	X	.	.	.	X	.	.	X	.	.	.
<i>Climacograptus tubuliferus</i>	X	X	X	X	.	.	X
<i>Geniculograptus typicalis</i>	X	X	.	.	X
<i>Geniculograptus pygmaeus</i>	X	X	.	.	X
<i>Orthograptus crassitestus</i>	X	.	.	X
<i>Orthograptus eucharis</i>	.	X	.	X	.	X	X	X	X	X	.	X
<i>Orthograptus quadrimucronatus</i>	.	X	X	X	.	.	X
<i>Orthograptus spinigerus</i>	.	X
<i>Rectograptus amplexicaulis</i>	.	X	X
<i>Rectograptus peosta</i>	.	.	.	X	X	X	X	X	.	X
' <i>Glyptograptus</i> ' <i>lorrainensis</i>	.	X
<i>Normalograptus</i> sp. nov.	.	.	X	X	X	X	.
<i>Orthoretiolites hami</i>	X	.	.	.	X	.	.	.
<i>Phormograptus sooneri</i>	X

troublesome. *Rectograptus peosta* can be differentiated from *R. amplexicaulis* (Hall) by its shorter sicula, more slender rhabdosome and lower angle of thecal inclination. *R. peosta* is similar in its dimensions to *Rectograptus socialis* (Lapworth) and is probably a senior synonym of that taxon. Also, *R. peosta* is closely similar to, and may be conspecific with, *R. gracilis* (Roemer), which occurs in coeval strata in Baltoscandia (Skoglund 1963). Compared with the latter, *R. peosta* appears to have a slightly narrower rhabdosome and thecae are inclined to the rhabdosome axis at a slightly smaller angle (25° versus 35°), but the significance of these small differences needs further evaluation.

Stratigraphical and geographical occurrence. *Rectograptus peosta* is common in the *A. manitoulinensis* and *D. complanatus* biozones in North America, and in the *D. complanatus* Biozone of Scotland (Williams 1987). *R. peosta* is a cosmopolitan epipelagic species and occurs in both Oceanic and Laurentian biofacies of Goldman *et al.* (1995).

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APPENDIX: GRAPTOLITE LOCALITY DETAILS

1. Eastern Boundary of Craiglieth Provincial Park, south shore of Georgian Bay, Craiglieth, Ontario; Collingwood Member of the Lindsay Formation.
2. Ontario Geological Survey Drill Core 83-5 and exposures along Highway 6, 5–7 km south of Little Current, Manitoulin Island, Ontario; Collingwood Member of the Lindsay Formation, Blue Mountain and Georgian Bay formations.
3. Gorrel Point, shoreline bluffs, 4 km north-east of Gore Bay, Manitoulin Island, Ontario; Georgian Bay Formation.
4. Haymeadow Creek, northern part of Sec. 19, T. 42 N., R. 20 W., Upper Peninsula of Michigan; Haymeadow Creek Shale.
5. Bichler Quarry, Sec. 1, T. 39 N., R. 3 W., Groos, Upper Peninsula of Michigan; Groos Quarry Formation.
6. Rifle Hill Quarry, NE1/4 NW1/4 sec. 35, T. 102N., R. 12 W., Fillmore County, Minnesota; Elgin Member, Maquoketa Formation.
7. Exposure along a small creek beneath County Highway B 60, SW1/4 NW1/4 sec. 35, T. 95 N., R. 7 W., 1.6 km east of Clermont, Fayette County, Iowa; Elgin Member, Maquoketa Formation.
8. Postville North Quarry, SW1/4 SW1/4 sec. 16, T. 96 N., R. 6 W., Allamakee County, Iowa; Elgin Member, Maquoketa Formation.

9. Graf railroad cut, S1/2 NW1/4 SW1/4 sec. 29, T. 89 N, R. 1 E., Dubuque County, Iowa; Elgin Member, Maquoketa Formation.
10. Illinois Central Railroad Cut, SW1/2 NE1/4 SW1/4 sec. 26, T. 29 N., R. 2 E., Scales Mount, Jo Davies County, Illinois; Scales Formation, Maquoketa Group.
11. Outcrop in bluff, north of intersection of State Route 84 and U.S. Route 52, SW1/2 SW1/4 NW1/4 sec. 11, T. 25 N., R. 3 E., Savannah, Carroll County, Illinois. Fort Atkinson Formation, Maquoketa Group.
12. Mt Carroll Quarry, north side of U.S. Route 52, SW1/2 NE1/4 SW1/4 sec. 10, T. 24 N., R. 4 E, 4 km south-west of Mt Carroll, Carroll County, Illinois; Scales Formation, Maquoketa Group.
13. Road-cut along Highway 21, 24 km south-south-west of St Louis, Missouri; Maquoketa Shale.
14. Road-cut along Interstate 55, just north of the Barnhart (Highway M) interchange, SW1/4 SE1/4 sec. 19, T. 42 N., R. 6 E., Jefferson County, Missouri; Maquoketa Shale.
15. Amis Construction Company Quarry, north end of Black Knob Ridge, centre of the N1/2 sec. 16, T. 1 S., R. 12 E., Stringtown, Atoka County, Oklahoma; Bigfort Chert and Polk Creek Shale.
16. Sycamore Creek, Section J of Alberstadt (1973), sec. 27, T. 3 S., R. 4 E., Troy Quadrangle, Oklahoma; Sylvan Shale.
17. Ideal Cement Quarry, sec. 36, T. 3 N., R. 5 E., Alhoso Quadrangle, near Lawrence, Oklahoma; Sylvan Shale.
18. Rayford Quarry, Section Q of Alberstadt (1973), sec. 28, T. 1 S., R. 2 E., Dougherty Quadrangle, Oklahoma; Sylvan Shale.
19. U.S. Geological Survey Collection 241, Middle of sec. 34, T. 1 S., R. 2 E., approximately 3 km north of Dougherty, Dougherty Quadrangle, Oklahoma; Sylvan Shale.