

Biogeography of Ordovician graptolites in the southern Appalachians

By STANLEY C. FINNEY

The graptolite fauna of the Middle Ordovician Athens Shale of Alabama shows conspicuous variation between an eastern, deep water, black shale facies and a nearby western, shallower water, calcareous facies. Although this variation involves only seven species out of a large fauna, it is distinctive. These species have very noticeable rhabdosomes and are abundant in the facies in which they occur. They characterize their assemblages and as a result the assemblages of the black shale and calcareous facies are readily distinguished. The two facies are separated by only a few tens of kilometers, and the rapid faunal variation is recognized not only in Alabama but also in Tennessee. The depth stratification model does not explain the faunal variation in which several species are restricted to the shallower water calcareous facies. Lateral fauna differentiation produced by water-mass specificity is favored as a more likely explanation.

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One hundred years ago, Lapworth (1879–1880) demonstrated the stratigraphic value of graptolites. Since then graptolite biostratigraphy has been used as the more reliable base for subdivision and inter-continental correlation of Ordovician to Lower Devonian strata. Dependence on, and confidence in, graptolite biostratigraphy was supported by the early realization (Hall 1865; Lapworth 1897) that graptolites were planktonic organisms carried around the world by oceanic currents. This engendered the belief that, once defined, the sequence of graptolite zones and the assemblages characterizing them could be recognized worldwide (Elles 1922). This assumption, however, became untenable as graptolite research outside northwest Europe intensified.

The reality of marked graptolite provincialism and its constraints on inter-continental correlation was first recognized in the Lower Ordovician graptolite sequence of Australia (Harris & Keble 1932; Harris & Thomas 1938). Subsequent research led to the recognition of: 1. Atlantic and Pacific provinces in the Lower Ordovician (Berry 1960; Skevington 1969, 1973; Bulman 1971). 2. subprovinces within both of these provinces (Jaanusson 1960; Erdtmann 1965; Skevington 1973). 3. an Upper

Ordovician fauna endemic to the northern Appalachians in contrast to a coeval cosmopolitan fauna in the rest of North America (Riva 1969; Berry 1977), and 4. gradual changes in faunal composition along paleogeographic gradients (Skevington 1974; Watkins & Berry 1977). Concomitant with these discoveries attempts were made to reconcile the observed geographic distributions with such hypothetical controls as tectonics, depth stratification, vertical and/or lateral temperature differences, water-mass specificity, depth and position of oxygen minimum zone and combination thereof. Most of these hypotheses were offered to explain large scale graptolite provincialism, but in general no studies focused on faunal variation over short distances within a single basin of deposition.

Research in the Middle Ordovician of the southern Appalachians shows that significant variations in graptolite faunas can occur over short geographic distances. Although realization of this phenomenon is not new (e.g. Watkins & Berry 1977; Kaljo 1978), some specialists might discount it because it has not previously been clearly demonstrated. The purpose of the present paper is to document this phenomenon by means of collections from the

Athens Shale in Alabama and to evaluate various hypotheses that might be used to explain it.

Geological Setting

Graptolite-rich shales of Middle Ordovician age extend almost the entire length of the Appalachians. The paleogeographic and sedimentologic history of the depositional basin of these shales, which can in general be extended through the length of the southern Appalachians, is summarized by Shanmugam & Walker (1978, fig. 5); and Neuman (1976, text-fig. 2) as follows:

1) In the lowest Middle Ordovician, shallow water carbonates were deposited on the continental shelf, near the eastern edge.

2) This deposition ceased when the shelf rapidly subsided to form a NE–SW trending basin bounded to the west by a carbonate platform and to the east by the uplifted Taconic Highlands, the source area for basal clastic sediments. The subsidence is reflected lithologically by the abrupt upward replacement of shallow water carbonates (i.e. Lenoir Formation) by graptolitic shales (i.e. Blackhouse Formation) and by the westward transgression of associated facies.

3) After an interval of pelagic sedimentation (graptolitic shales), the influx of terrigenous clastic sediments from the east increased. These sediments (i.e. Sevier Formation) comprised initially of silt and sand and later conglomerate were transported by turbidity currents. Accumulation of graptolite remains within the sediment continued.

4) By the upper Middle Ordovician, the influx of coarse sediments (i.e. Ottosee Formation) filled the basin and spilled over onto the western carbonate platform. Graptolites no longer lived within the basin.

The Athens Shale of Alabama represents the southernmost extension of this geological setting in the Appalachians. It crops out in a narrow band bounded to the west by the Helena thrust fault and to the east by the metamorphic front of the Piedmont Province (Fig. 1). In its eastern outcrops near Calera, it is predominantly black shale, but to the west near Centerville it is replaced by light gray to tan calcareous shale and argillaceous micrite. The

black shale facies, resting directly on shallow water carbonates (i.e. Lenoir Formation), represents pelagic sedimentation and possibly a turbiditic influx of clastics from the east (Fig. 2). The western, calcareous facies of the Athens Shale (Fig. 3), which gradationally overlies a slope facies (i.e. the Pratt Ferry Beds), accumulated at a position intermediate between the deep water black shale basin to the east and a contemporaneous shallow subtidal carbonate platform to the west (i.e. the Chickamauga Group). It is a mixture of fine clastic sediment derived from the east and carbonate mud washed eastward from the carbonate platform.

The black shale facies was extensively sampled for graptolites near Calera (locality C in Fig. 1), and graptolites were collected at many horizons in the calcareous facies (localities PF and PS in Fig. 1). Although the two facies are largely contemporaneous and have many graptolite species in common, conspicuous faunal differences do exist between them.

Graptolitic biostratigraphy

Calera section (black shale facies)

Near Calera, Alabama, the Athens Shale is represented by 75 meters of predominantly black shale that is completely exposed, is continuously and abundantly graptolitic, and was extensively sampled, in some parts at 0.2 meter intervals (Fig. 2). Most of the Athens Shale is correlated to the lower half of the *Nemagraptus gracilis* Zone with a lower boundary placed at the first appearance of *N. gracilis* at 10.5 meters above the base of the unit (Finney 1977; Finney & Bergström, in press). Below this level, the Athens Shale is assignable to the *Glyptograptus* sp. cf. *G. teretiusculus* Zone.

The Calera collections are characterized by several long-ranging, cosmopolitan species, while others are rare (e.g. *Pterograptus* sp., *Amphigraptus* n.sp. B), relatively endemic (e.g. *Apoglossograptus lyra*, *Climacograptus meridionalis*) and/or stratigraphically restricted (e.g. *D. geniculatus*, *P.* sp. cf. *P. eurystoma*, and *Leptograptus trentonensis*).

The Calera range chart (Fig. 2) consists of data combined from two measured sections (Fig. 1; see Finney 1977 for full description). In the following discussions, both sections are referred to as one by the designation Calera section.

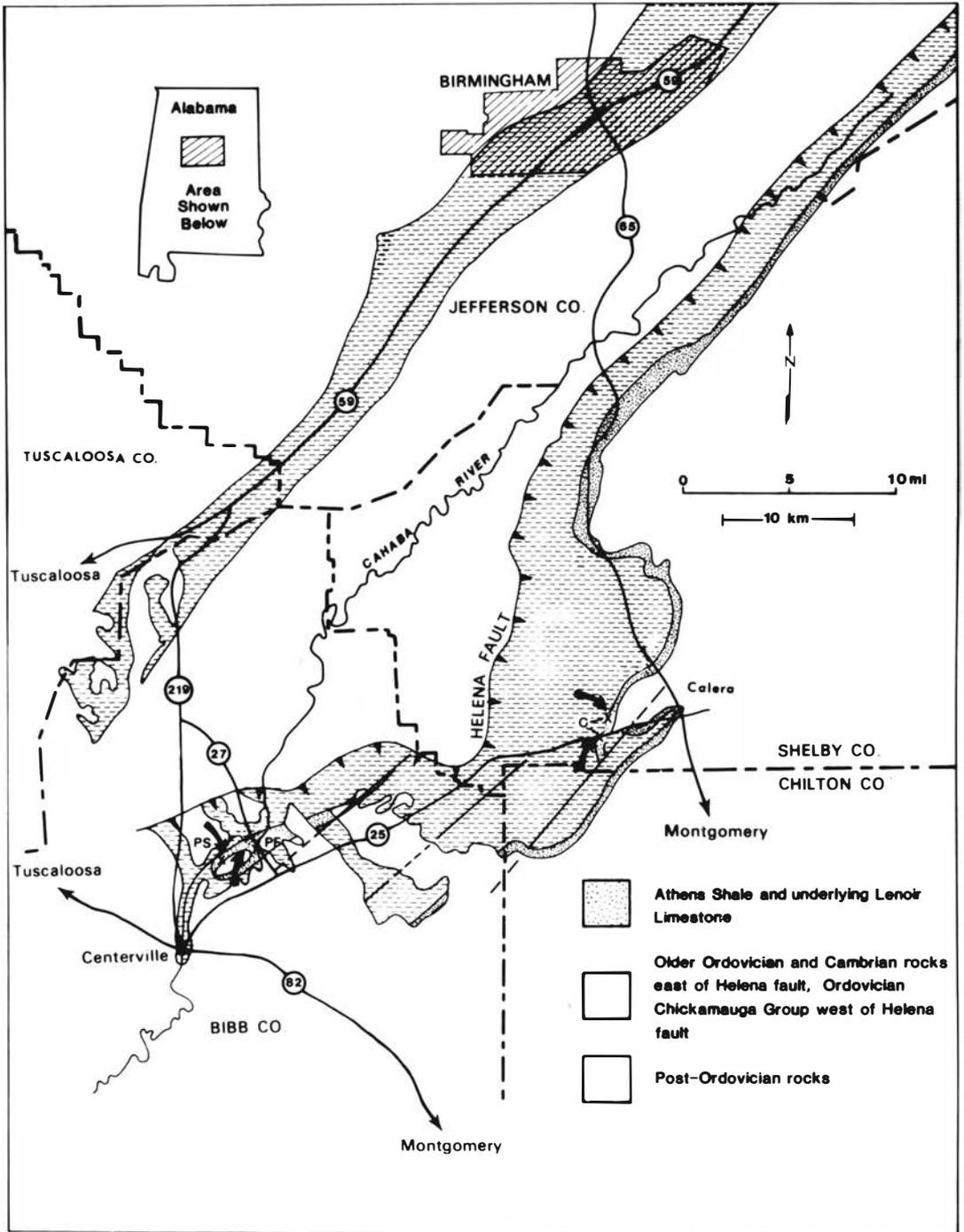
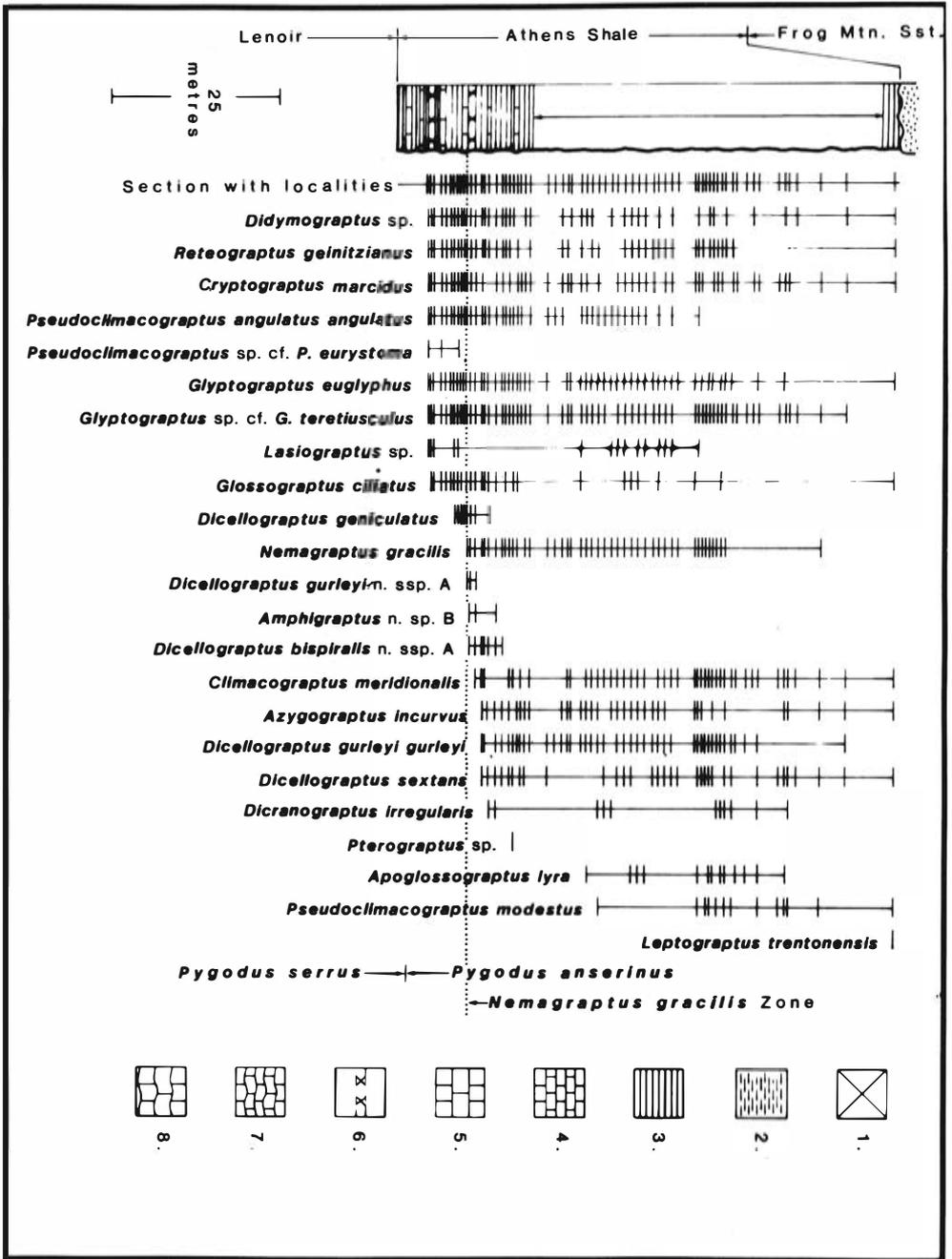


Fig. 1. Index map of central Alabama showing distribution of Ordovician rocks and location of sections at Pratt's Ferry (PR), Pratt's Syncline (PS) and Calera (C).

Fig. 2. Range chart and stratigraphic column of *Calera* section. Taxonomy is after Finney (1977, 1978, 1980). Symbols: 1. Covered interval; 2. Mudstone, generally calcareous; 3. Shale, black shale and calcareous shale; 4. Thin to medium bedded micrite; 5. Thick bedded micrite; 6. Bentonite; 7. Medium bedded fossiliferous limestone with wavy bedding surfaces, i.e. Pratt Ferry Beds; 8. Massively bedded fossiliferous limestone with wavy bedding surfaces, i.e. Lenoir Limestone.



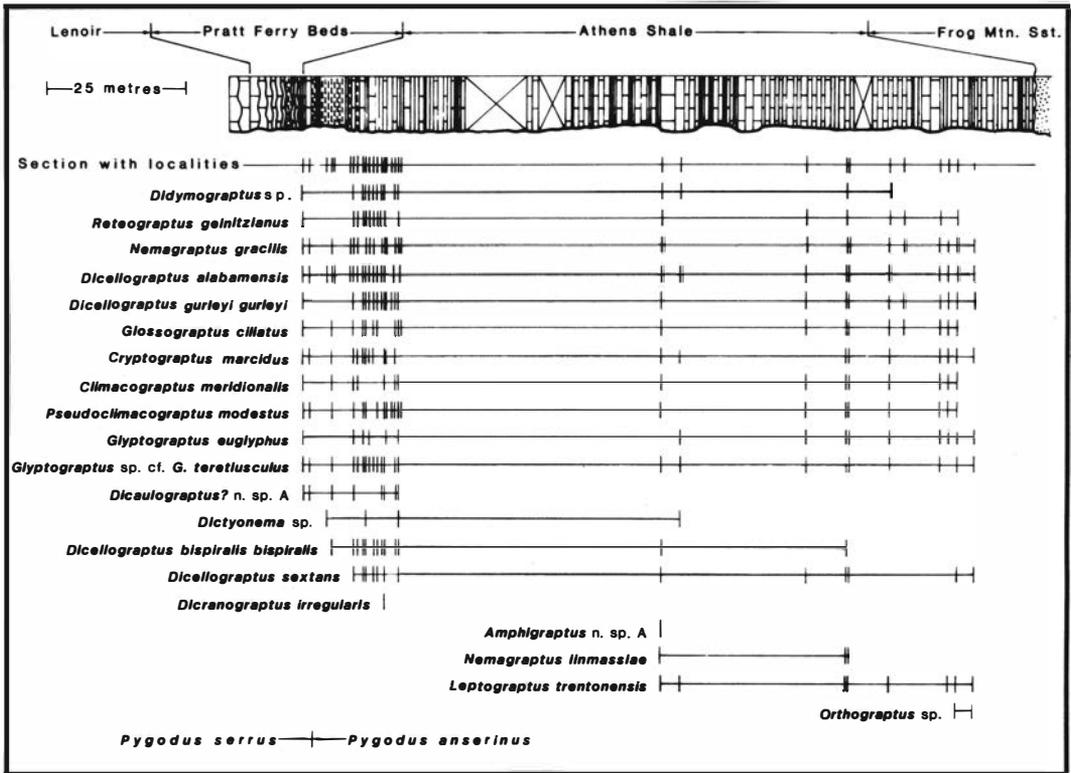


Fig. 3. Range chart and stratigraphic column of Pratt's Ferry - Pratt's Syncline section. Taxonomy is after Finney (1977, 1978, 1980). Symbols as in Fig. 2.

Pratt's Ferry and Pratt's Syncline Sections (calcareous facies)

The range chart for the calcareous facies (Fig. 3) is also a compilation of data from two measured sections (see Finney 1977). Only the lowest 25.5 meters of the Athens Shale is exposed at the Pratt's Ferry section. It is rich in graptolites and was sampled at 22 levels. The nearby Pratt's Syncline section includes the entire 134-meter thickness of the Athens Shale. Its lowest 25 meters is lithologically identical to the Pratt's Ferry section. Its middle and upper parts are dominated by micrites. Shale interbeds are few and thin. Graptolites were found at only twelve horizons that are stratigraphically above the Pratt's Ferry section. However, at these horizons they are abundant and well-preserved. In the following discussions the

Pratt's Ferry and Pratt's Syncline sections are referred to collectively as the PF-PS section.

As at Calera, the graptolite collections are characterized by several long-ranging, cosmopolitan species, while others are rare (e.g. *Dicranograptus irregularis*, *Amphigraptus* n.sp. A, *Nemagraptus linmassiae*), relatively endemic (e.g. *Dicaulograptus?* n.sp., A, *Dichellograptus alabamensis*, *D. bispiralis*), and/or stratigraphically restricted (*Leptograptus trentonensis* and *Orthograptus* sp.).

The presence of *Nemagraptus gracilis* in the lowest graptolite collection and *Orthograptus* sp., which helps define the base of the *Climacograptus bicornis* Zone (Finney & Bergström in press), in the highest collection indicates that the calcareous facies is entirely within the *N. gracilis* Zone.

Correlation of sections

Comparison of species composition, graptolite ranges, and conodont ranges between the Calera and PF–PS sections shows that, while the black shale and calcareous facies differ somewhat in age, they are largely equivalent. The base of the Athens Shale is diachronous reflecting the basal subsidence and westward transgression exhibited in the Middle Ordovician throughout the Appalachians. The levels of the first appearance of *gracilis* Zone graptolites and of the *Pygodus serrus* – *P. anserinus* conodont zone boundary demonstrate that graptolite shales of the eastern black shale facies began accumulating before those of the western calcareous facies. The top of the Athens Shale is an unconformity and was eroded to different levels in the two areas before deposition of the Devonian Frog Mountain Sandstone. The level of first appearance of *Leptograptus* in the two sections indicates that the top of the Athens Shale at Calera is correlative with a level within the lower half of the PF–PS section. Thus, although the PF–PS and Calera sections are largely correlative, the Calera section extends to a lower biostratigraphic level than the PF–PS section, and the PF–PS section extends to a higher level than the Calera section.

Geographic faunal variation between Calera and PF–PS sections

Graptolite collections from the Calera and PF–PS sections may have many common species. However, several species are restricted to either the Calera or the PF–PS section, and this makes the assemblages of the two sections distinctive.

Some of the faunal restriction is due to age differences. For example, the biostratigraphic ranges of *Pseudoclimacograptus* sp. cf. *P. eurystoma*, *Dicellograptus geniculatus*, *D. gurleyi* n. ssp. A, and *D. bispiralis* n. ssp. A are too low for them to appear in the PF–PS section, and the range of *Orthograptus* sp. is too high for it to appear at Calera. Differences involving *Amphigraptus* n. sp. A, *Amphigraptus* n. sp. B, *Nemagraptus linmassiae*, *Lasiograptus* sp., and *Pterograptus* sp. are no doubt due to the scarcity of available specimens. Conspicuous differences between the sections still remain, and

these must be due to ecological factors restricting the geographic ranges of seven other species. These species and their geographic and stratigraphic distributions are as follows (all have been or will be described by Finney 1978, 1980, in preparation):

1) *Pseudoclimacograptus angulatus angulatus* Bulman is abundant through most of the Calera section. Its long rhabdosome and distinctive apertural excavations make it easy to recognize. Its complete absence from the PF–PS section is noticeable especially because it is a cosmopolitan species.

2) *Azygograptus incurvus* Ekström is common in 40 collections from the Calera section where distinctive rhabdosomes, each consisting of a single strongly curved stripe, cover bedding planes. Although cosmopolitan, the species is absent in the PF–PS section.

3) *Dicranograptus irregularis* Hadding is a common species in the middle of the Calera section distinguished by a short biserial proximal end. A single specimen was found in the PF–PS section. Its scarcity there is surprising in light of the many specimens collected at Calera and its worldwide distribution.

4) *Apoglossograptus lyra* (Ruedemann) is common in the upper part of the Calera section but completely absent in the PF–PS section. It has a conspicuous rhabdosome consisting of two proximally monopleural but distally diverging stipes.

5) *Dicellograptus alabamensis* Ruedemann has a large distinctive rhabdosome with a spinose proximal end often thickened with cortical tissue and appearing to be biserial (Ruedemann 1908, pl. 20, figs. 1–2). It is abundant throughout the PF–PS section. Its complete absence at Calera is conspicuous especially because it occurs in Virginia and Texas.

6) *Dicellograptus bispiralis bispiralis* (Ruedemann) has a distinctive rhabdosome composed of two helical stipes with extremely introverted thecae. It is abundant throughout the PF–PS section. Yet, it is absent at Calera even though it has been recorded in Tennessee (Decker 1952).

7) *Dicaulograptus?* n. sp. A is peculiar because its biserial rhabdosome displays torsion and it is easily recognized by its highly spinose and introverted thecae. It occurs only in the lower part of the PF–PS section. But because

it is so abundant there and so distinctive, its absence from an equivalent interval at Calera is readily noticed. The species is known from Tennessee (S. Finney personal collections).

The differences between the assemblages of the Calera and PF-PS sections, involving only seven species, is not great. However, it is conspicuous because these seven are so morphologically distinct and so abundant that they readily distinguish assemblages from the sections in which they occur.

The faunal differences occur over a geographic distance of 43 kilometers. If adjusted for structural shortening, the distance is 70 kilometers. The faunal variation is thus surprising and significant because the seven species that do not co-occur in well sampled, correlative sections only a few tens of kilometers apart in Alabama have been reported from localities hundreds and thousands of kilometers away from Alabama.

Other localities in the southern Appalachians

Decker (1952) recorded graptolites from many localities in eastern Tennessee and southwestern Virginia. In addition, USGS field parties, University of Tennessee graduate students, S. Bergström and S. Finney have also made many collections from the Middle Ordovician shale basin in this region. The seven species listed above occur in several of these collections, in most instances in the same associations as the Calera and PF-PS sections. This demonstrates that there are other sections in close proximity (tens of kilometers) that appear to display the same faunal variation as in Alabama. These sections have not been systematically collected so that detailed correlations and comparisons cannot yet be made. They do however show that the geographic differentiation of the graptolite fauna extends throughout the southern Appalachians.

Cause of faunal variation

The graptolite variation so clearly demonstrated in Alabama must be a reflection of ecological controls. The extensive systematic collecting and precise correlations rule out collecting failures and age differences as the cause. Tecto-

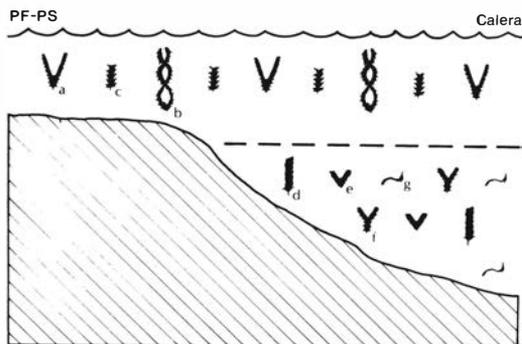


Fig. 4. Depth stratification model in which *Dicellograptus alabamensis* (a), *D. bispiralis bispiralis* (b), and *Dicaulograptus* ? n. sp. A (c) inhabit upper layers of water column and can thus occur in the PF-PS region and *Pseudoclimacograptus angulatus angulatus* (d), *Apoglossograptus lyra* (e), *Dicranograptus irregularis* (f), and *Azygograptus incurvus* (g) are restricted to deeper water and thus cannot occur in the PF-PS region. This model is invalidated by absence of fossils of *D. alabamensis*, *D. bispiralis bispiralis*, and *Dicaulograptus* ? n. sp. A at Calera.

nic controls, such as the juxtaposition of once widely separated basins of deposition by plate tectonics that was proposed to explain some graptolite provincialism (Skevington 1973) can also be disregarded because the Alabama localities and those in Tennessee and Virginia were deposited in a single basin of deposition.

Many ecological factors have been proposed to explain graptolite provincialism. Large-scale controls, in particular the latitudinal distribution of climatic belts favored by Bulman (1964, 1971), Boucek (1972), and Skevington (1974) as the cause of global variation, are not appropriate because the variation in Alabama is sharp, occurs over a small distance, and is repeated several hundred kilometers away in Tennessee. Other possible ecological controls can be grouped into two categories that involve either a vertical differentiation of the graptolite fauna or a lateral differentiation.

Depth stratification or vertical zonation of graptolites was first proposed by Berry (1962) and later used by Skevington (1969), Berry & Boucot (1972), Erdtmann (1976), and Kaljo (1978) to explain geographic variation. Cisne & Chandlee (1982) recently invoked it in order to relate lateral and vertical variations in abun-

dance of various taxa to changing water depths, i.e. transgressions, regressions, and topography. Depth stratification has been attributed to vertical changes in water temperature (Berry & Boucot 1972), light intensity, nutrient supply, water turbulence, and the position of the oxygen minimum zone (Erdtmann 1976; Cisne & Chandlee, 1982).

Berry (1974, 1977; Watkins & Berry 1977) later attributed geographic variation to a lateral differentiation of the graptolite fauna. This variation occurring across and within a basin of deposition was due to water-mass specificity, i.e. the differentiation of surface water masses and the restriction of graptolite species to them.

The Alabama data are best explained by a lateral differentiation of the fauna. The Calera section was probably a deeper water site of sedimentation than the PF-PS section because of the timing of sedimentation and its lithology. The depth stratification model (Fig. 4) can, therefore, account for the restriction of *Pseudoclimatograptus angulatus angulatus*, *Apoglossograptus lyra*, *Dicranograptus irregularis*, and *Azygograptus incurvus* to Calera if they are restricted to a deeper water habitat. However, it cannot explain the restriction of *Dicellograptus alabamensis*, *D. bispiralis bispiralis*, and *Dicaulograptus?* n. sp. A to the PF-PS section. These species must have lived at shallow depths in the sea to occur at the PF-PS section, but this would not have prevented them from inhabiting waters overlying those with deep water species. In fact, they should also occur at Calera. Proponents of the depth-stratification model (Erdtmann 1976; Cisne & Chandlee 1982) explain the absence or scarcity of shallow-water species in deep-water strata by the selective destruction of the rhabdosomes of shallow-water species during their long drift to the deep burial site. However, the large durable rhabdosomes of the shallow-water species in Alabama and their easy preservation and abundance in the oxygenated and biologically-rich (and thus predator and scavenger rich) environment of the shallow-water carbonate facies, strongly suggest that at least some of these rhabdosomes should survive the passage to the deep burial site. Their complete absence from the deep-water facies, which was so extensively collected at Calera, indicates that they were

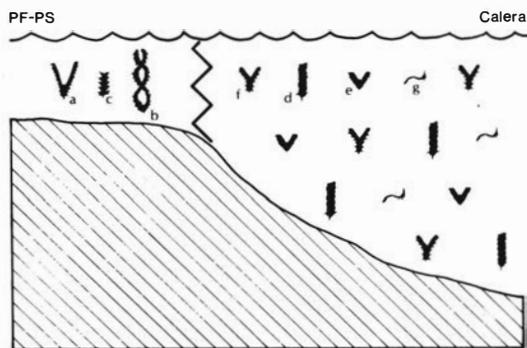


Fig. 5. Lateral differentiation in which characteristic species are confined to water masses overlying either the Calera region or the PF-PS region. Letters denoting species as in Fig. 4.

not present in the waters overlying the area. The abundance of *Cryptograptus marcidus* throughout both the PF-PS and Calera sections (Figs. 2, 3) also argues against selective destruction. Among the more than 30 species for which I have studied isolated material, this species has the thinnest, weakest periderm. It is usually preserved on shale surfaces only as a faint film while the periderm of other species on the same bedding surfaces stands up in relief. If any species should show selective destruction in either a shallow, oxygenated environment or during sinking to a deep burial site, then it should be *C. marcidus*. Yet, it does not in the Athens Shale. Finally, if the Athens graptolites were depth stratified, then the manner of initial appearance of graptolites in each section should reflect the gradual deepening of the sea at these localities as it transgressed westward. While the gradual incoming of species in the Calera section might be taken as evidence of this phenomenon, the sudden appearance of many species in the PF-PS section argues against it. The fact that several species are restricted to the shallow water PF-PS section and absent at Calera can be instead easily explained by a lateral differentiation of the fauna (Fig. 5).

The waters overlying the Calera and PF-PS sections would no doubt have differed in turbidity and salinity as reflected by their lithology and inferred from their paleogeographic po-

sitions. Barry (1974, 1977) has pointed out that studies of modern faunas (e.g. Fager & McGowan 1963) show that plankton are often restricted to oceanic water masses with specific hydrographic characteristics. Although it appears so in Alabama, these water masses and their restricted faunas need not be precisely reflected by the character of the underlying sediments. In Tennessee, assemblages such as those at Calera occur in both black shale and calcareous facies.

Conclusions

Graptolites are difficult to analyse paleoecologically. They have no closely related extant analogue, either taxonomically or morphologically. Furthermore, because they were pelagic, rocks containing their remains provide few clues to the nature of their habitat. The Alabama example is not to show that biogeographic variation is consistently associated with calcareous and black shale facies or due exclusively to water-mass specificity, but just that it can indeed exist over short geographic distances and in this case is easily explained by water-mass specificity. In spite of this demonstrated variation, graptolites are still valuable biostratigraphic tools. For example, the base of the *gracilis* Zone at Calera has been utilized by Finney & Bergström (in press) as a standard against which graptolite and conodont data have been used to evaluate the base of the zone in New York, Texas, Scotland, Wales, Scania, and Australia.

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