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THE AFFINITIES OF *ISOGRAPTUS*, *GLOSSOGRAPTUS*, *CRYPTOGRAPTUS*, *CORYNOIDES*, AND ALLIED GRAPTOLITES

Abstract. — Numerous well-preserved specimens referred to *Glossograptus ciliatus* Emmons and *Cryptograptus marcidus* (Hall), (= C. *schaeferi* Lapworth), have been isolated from limestones of the Middle Ordovician Athens Shale of Alabama. Early growth stages of both these species show an isograptid type of development. This fact, together with new data from studies of the detailed thecal morphology, and re-interpretations of previously described species suggest that: 1) *Glossograptus* arose from an isograptid ancestor, possibly *Isograptus* itself; 2) the ancestry of the other genera of Glossograptidae can be found in *Glossograptus*: 3) cryptograptids evolved from an early glossograptid or evolved independently from an isograptid ancestor; and 4) the corynoidids evolved from *Glossograptus*. Flattened, non-isolated specimens of *Isograptus lyra* Ruedemann, which were also collected from the Athens Shale, display a pericalycal arrangement of the proximal end and are referred to a new genus, which probably arose from *Glossograptus* through divergence of the stipes.

INTRODUCTION

A primitive dichograptid-type of proximal-end development, in which theca 1^1 is the dicalycal theca and theca 1^2 originates left-handedly from theca 1^1, has been reported for *Glossograptus* (Whittington and Rickards 1969) and *Cryptograptus* (Bulman 1938, 1944). This particular type of proximal-end development has made it difficult to postulate the ancestry of the taxa within the suborder Glossograptina. New information, concerning not only the proximal-end development but also the thecal morphology and ontogeny, from specimens obtained from the Middle Ordovician Athens Shale of Alabama and re-interpretations of previously described specimens indicate that (fig. 1):

1) *Glossograptus* may have evolved from an isograptid, possibly of the *gibberulus* type.
2) The ancestry of the other genera in the family Glossograptidae can be found in *Glossograptus*.
3) *Cryptograptus* may have evolved from an early glossograptid or independently from an isograptid ancestor.
4) The corynoidids evolved directly from *Glossograptus*.

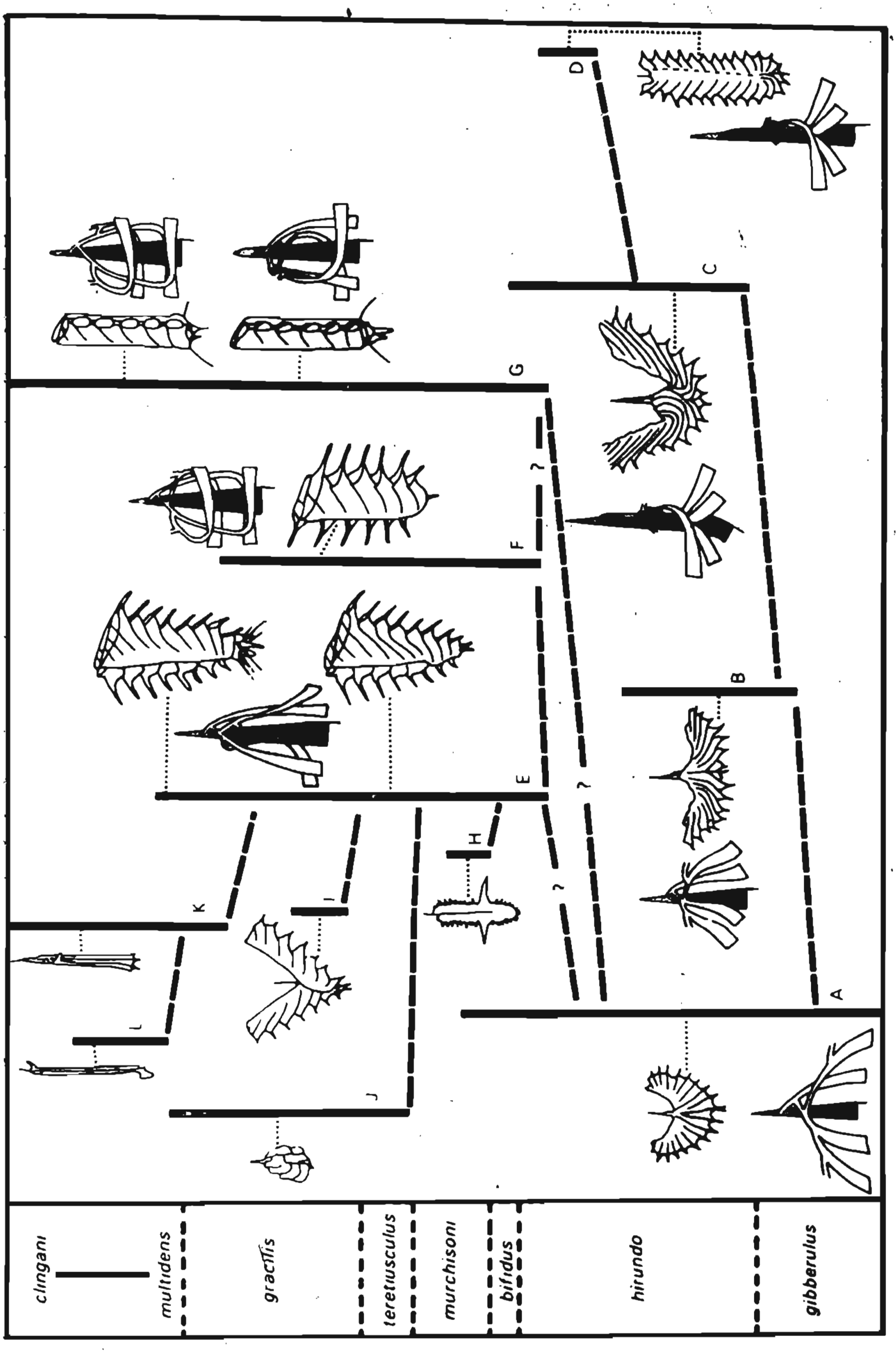

Fig. 1. Proposed phylogenetic scheme. British graptolite zones used for biostratigraphic divisions. *A* — *Isograptus*, represented by *I. gibberulus*. *B* — *Maeandrograptus*, represented by *M.? geniculatus*; *C* — *Pseudisograptus*, represented by *P. manubriatus*; *D* — *Apiograptus*, represented by *A. crudus*; *E* — *Glossograptus*, represented by *G. holmi* (lower) and *G. ciliatus* (upper); *F* — *Paraglossograptus*, represented by *P. proteus*; *G* — *Cryptograptus*, represented by *C. marcidus* (lower) and *C. tricornis* (upper); *H* — *Lonchograptus*, represented by *L. ovatus*; *I* — *Apoglossograptus*, represented by *A. lyra*; *J* — *Nanograptus*, represented by *N. lapworthi*; *K* — *Corynoides*, represented by *C. calicularis*; *L* — *Corynites*, represented by *C. divnoviensis*.

The Athens Shale crops out in northeast-southwest trending fold belts throughout the central and southern Appalachian Mountains (fig. 2). A calcareous facies of this formation occurs at a locality in Alabama that is known as Pratt's Syncline, and numerous well-preserved specimens, referred to *Glossograptus ciliatus* Emmons and *Cryptograptus marcidus* (Hall), have been obtained from this calcareous facies by means of acid treatments. In addition, non-isolated specimens that are conspecific with Ruedemann's (1947) *Isograptus lyra* and which I will asign to a new genus in the family Glossograptidae were collected at a nearby locality known as Calera, Alabama.

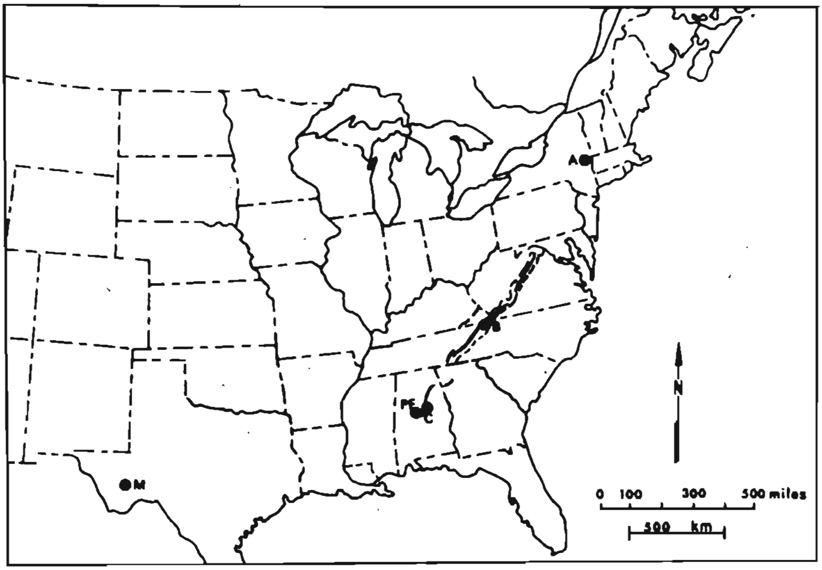

Fig. 2. Map of portion of the United States showing outcrops of Middle Ordovician rocks in the Southern Appalachians and some notable localities of Middle Ordovician graptolites. (*A*) Albany, New York; (*B*) Bristol, Tennessee; (*C*) Calera, Alabama; (*PF*) Pratt's Ferry and Pratt's Syncline, Alabama; (*M*) Marathon Region, Texas.

The information presented here represents only a preliminary report on a small part of a study of the graptolites of the Athens Shale in Alabama (Finney 1977). The entire graptolite fauna and the biostratigraphy of the Athens Shale in Alabama will be described in a forthcoming paper (Finney, in preparation). This graptolite fauna is indicative of the lowermost part of the *Nemagraptus gracilis* Zone. Altogether, sixteen species and nine genera are represented by thousands of specimens, which were isolated by means of acid treatment, and an additional ten species and six genera are represented by non-isolated specimens. The Alabama specimens illustrated in this paper are stored in the Orton Geological Museum at The Ohio State University, Columbus, Ohio, and the museum numbers of these specimens carry the prefix OSU.

PROXIMAL-END DEVELOPMENT IN *GLOSSOGRAPTUS*

The available isolated specimens of *Glossograptus ciliatus* are transparent and display growth lines (fig. 3). They represent a nearly complete series of growth stages showing development from the initial budding of theca 1^1 to the origin of the sixth pair of thecae. Theca 1^1 has a prosicular origin (fig. 3a). Theca 1^2 originates right-handedly from theca 1^1 (fig. 3 m), and it is the dicalycal theca, giving rise to both theca 2^1 and theca 2^2 (fig. 3g—3l). The first two thecae grow directly downward along the sicula; whereas succeeding thecae grow in a clockwise direction around the sicula, when the rhabdosome is viewed from the proximal end. The proximal-end development is of the isograptid type because of the right-handed origin and dicalycal nature of theca 1^2 and the presence of two crossing canals (fig. 4*b*). This type of development is very different from that interpreted for *Glossograptus holmi* by Whittington and Rick-

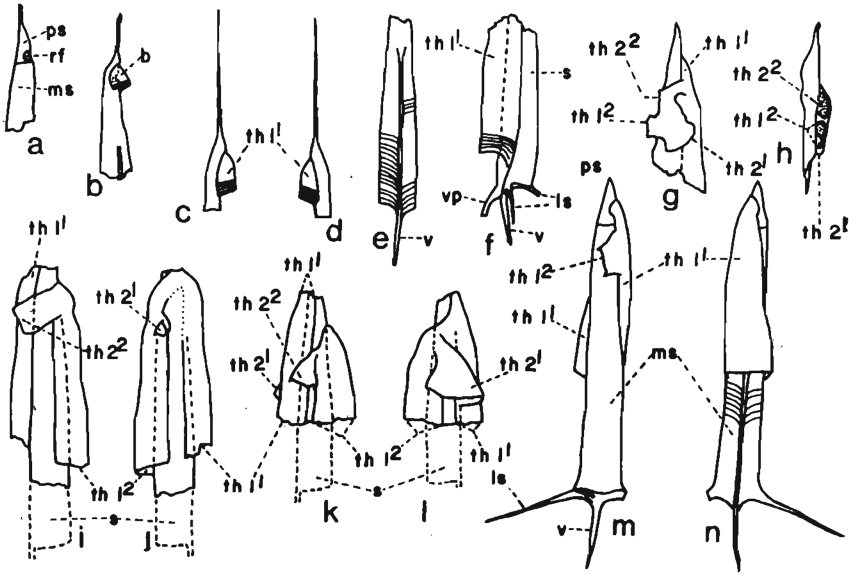

Fig. 3. *Glossograptus ciliatus* Emmons. Isolated specimens representing early growth stage: *a* prosicula and proximal end of metasicula, ca. X28 (OSU 33134); *b* prosicula and proximal end of metasicula with initial bud of theca 1^1, ca. X28 (OSU 33135); *c, d* ventral and dorsal aspects showing growth of theca 1^1 as a split tube, ca. X28 (OSU 33136); *e* distal end of metasicula, ca. X28 (OSU 33137); *f* left-lateral view of metasicula and theca 1^1, ca. X28 (OSU 33138); *g, h* dorsal and left-lateral aspects of fragment showing thecae 1^2, 2^1, and 2^2, ca X28 (OSU 33139); *i, j* left-and right-lateral aspects of fragment showing thecae 2^1 and 2^2 budding from theca 1^2, ca. X28 (OSU 33140); *k, l* left-and right-lateral aspects of fragment showing thecae 2^1 and 2^2 budding from theca 1^2, ca. X28 (OSU 33141); *m, n* dorsal and ventral aspects of sicula with thecae 1^1 and 1^2, ca. X28 (OSU 33142). Abbreviations: *b* initial bud of theca 1^1, *ls* lateral spine of sicular aperture, *ms* metasicula, *ps* prosicula, *rf* resorption foramen of initial bud, *s* sicula, *v* virgella, *vp* ventral apertural process.

ards (1969) in which theca 1^2 has a left-hand origin and theca 1^1 is the dicalycal theca (fig. 4*a*). However, their interpretation was not based on early growth stages but on young colonies and fragments of the proximal end, which are black, opaque, and rarely show growth lines. On the basis of their illustrations and an examination of their figured specimens, I believe that Whittington and Rickards specimens can be re-interpreted to show an isograptid type of development or a slight modification of that type of development.

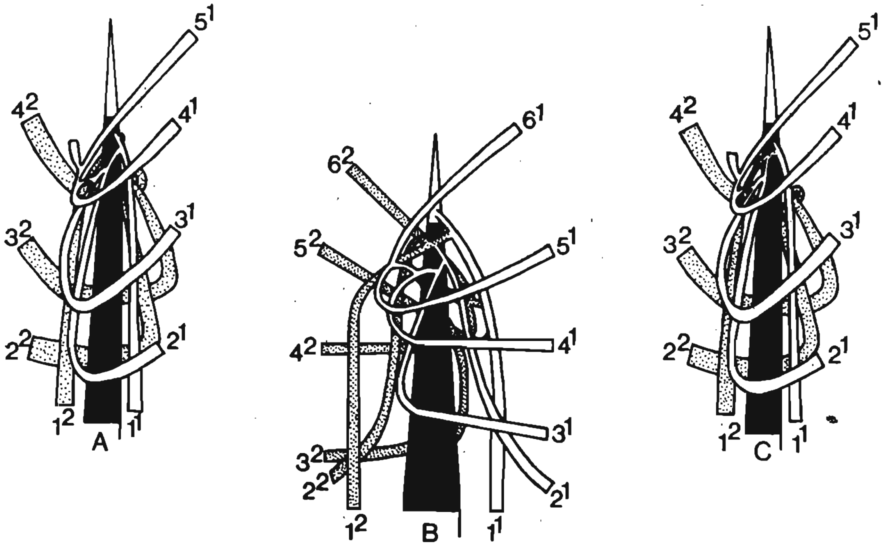

Fig. 4. Thecal diagrams to illustrate development, first thecal series open, second series stippled: *A* — *Glossograptus holmi*, after Whittington and Rickards (1969); *B* — *Glossograptus ciliatus*, based on present material; *C* — *Glossograptus holmi*, alternative interpretation.

Text-figure 3b of Whittington and Rickards (1969) shows that theca 1^1 extends proximally onto the right-lateral wall of the sicula. Because of the position of the proximal end of theca 1^2 and the visibility of the left-lateral wall of the sicula between the proximal parts of theca 1^1 and theca 1^2, I can only interpret a right-hand origin of theca 1^2 from theca 1^1. The available specimens do not show the origin of theca 2^1, but theca 2^2 appears to arise from the right-hand side of theca 1^2, and theca 2^1 might develop from the left-hand side of theca 1^2. Therefore, instead of showing a dichograptid-type of development, I believe that the available specimens of *Glossograptus holmi* show an isograptid type of proximal-end development (fig. 4c) or a slight modification of an isograptid type of development, depending on the position of the dicalycal theca.

PROXIMAL-END DEVELOPMENT IN *CRYPTOGRAPTUS*

Cryptograptus marcidus (Hall) is here considered to be a senior subjective synonym of the well-known species *C. schaeferi* Lapworth. The available isolated specimens of *C. marcidus* are very fragmentary and often flattened, but they do reveal the essential features of the proximal-end development (fig. 5). The initial bud of theca 1^1 originates high up on the ventral, virgellar side of the metasicula (fig. 5*i*), and theca 1^2 has a right-hand origin from theca 1^1 (fig. 5*e*—5*h*). One, rather poor, fragmentary specimen shows that both theca 2^1 and theca 2^2 develop from theca 1^2 (fig. 5*k*—5*l*). Thus, *C. marcidus* with its right-hand origin and dicalycal nature of theca 1^2 has an isograptid-type of proximal-end development (fig. 6*b*). Both theca 1^1 and theca 1^2 grow directly downward along the sicula. A comparison of the initial directions of growth of theca 2^1 and theca 2^2 in the early growth stages with the orientation of their apertures in mature specimens indicates that the second pair of thecae have a spiral direction of growth in their initial parts.

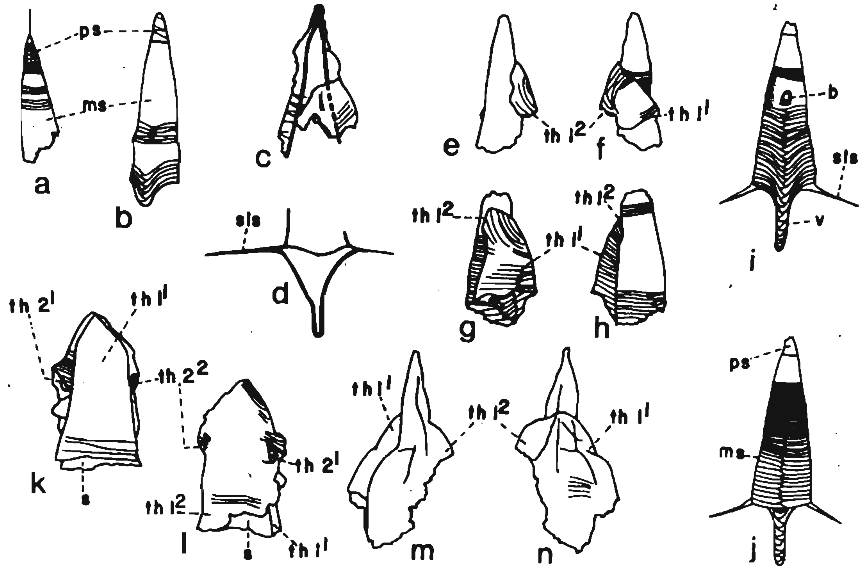

Fig. 5. *Cryptograptus marcidus* (Hall). Isolated specimens representing early growth stages: *a* prosicula and proximal end of metasicula, ca. X28 (OSU 33184); *b* ventral aspect of prosicula and metasicula, ca. X28 (OSU 33185); *c* apex of sicula in specimen with very deteriorated periderm showing longitudinal sicular lists, ca. X28 (OSU 33186); *d* list structure that rims sicula, ca. X28 (OSU 33187); *e f* proximal end of sicula showing origin of theca 1^2 from theca 1^1, ca. X28 (OSU 33188); *g, h* fragment showing middle part of sicula with thecae 1^1 and 1^2, ca. X28 (OSU 33189); *i, j* ventral and dorsal aspects of sicula with initial bud, ca. X28 (OSU 33190); *k, l* ventral and dorsal aspects of fragmentary specimen showing the budding of thecae 2^1 and 2^2 from theca 1^2, ca. X28 (OSU 33191); *m, n* ventral and dorsal aspects of sicula, theca 1^1, and theca 1^2 with deteriorated periderm. ca. X28 (OSU 33192). Abbreviations as in fig. 3.

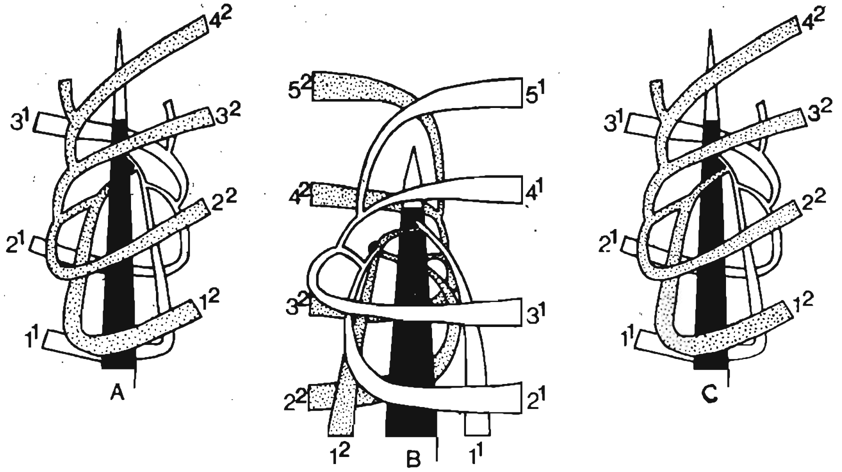

Fig. 6. Thecal diagrams to illustrate development, first thecal series open, second series stippled: *A — Cryptograptus tricornis*, after Bulman (1944); *B — Cryptograptus marcidus*, based on present material; *C — Cryptograptus tricornis*, alternative interpretation.

There are two important features of these specimens of *Cryptograptus marcidus* that have aided in a re-interpretation of the proximal-end development of *C. tricornis* (Carruthers). First of all, the initial growth lines of theca 1^2 are subparallel to the axis of the sicula, reflecting a horizontal initial direction of growth of theca 1^2 (fig. 5*f*—5*g*). Secondly, the sicular aperture and the margins of the virgella are rimmed by a list to which are connected the lateral spines of the sicular aperture and two longitudinal rods that extend to the apex of the prosicula (fig. 5*c*—5*d*).

Bulman (1938, 1944) reported a primitive dichograptid-type of proximal-end development for *Cryptograptus tricornis* in which theca 1^1 is the dicalycal theca and theca 1^2 has a left-hand origin (fig. 6*a*). Bulman's interpretation of the left-hand origin of theca 1^2 is based on "Traces of what may represent growth-lines on the corssing canal . . . on very few specimens . . .". However, these growth lines, as shown in Bulman's text-figure (Bulman 1944: fig. 15), are oriented exactly like those on the crossing canal of theca 1^2 in the specimens of *C. marcidus*. Bulman describes a list structure that borders the margins of the sicula in *C. tricornis*, and although it differs somewhat from that of *C. marcidus*, the two can be homologized. In *C. marcidus*, the list structure is always present on the dorsal, antivirgellar margin of the sicula (compare figs. 5*d* and 5*j*). If the same is true for Bulman's specimens of *C. tricornis*, then his transverse cross-bar (Bulman 1944: fig. 15) represents the dorsal, anti-virgellar margin of the sicular aperture and the Y-shaped sicular spine on the opposite side of the sicular margin must represent the virgella. Thus, Bulman would have theca 1^1 originating on the anti-virgellar side of the sicula. The arrangement of the lateral sicular spines and the longitudinal rods in the sicular list structure of *C. tricornis* closely resembles that in *C. marcidus*. Therefore, this comparison of the list structure, together with the growth-line evidence leads me to believe that Bulman's thecal designations for *C. tricornis* should be reversed such that the initial bud of theca 1^1 is located on the virgellar side of the sicula. With a reversal of Bulman's thecal designations, the list structure, the origin of theca 1^1, and the orientation of the growth lines on the crossing canal would have the same arrangement in both *C. tricornis* and *C. marcidus*, and such an arrangement in *C. tricornis* requires theca 1^2 to have a right-hand origin from theca 1^1 (fig. 6*c*). Theca 1^1 is the dicalycal theca in Bulman's specimens, but the proximal-end development of *C. tricornis* can be easily derived from the isograptid-type of development by an advance in the position of the dicalycal theca.

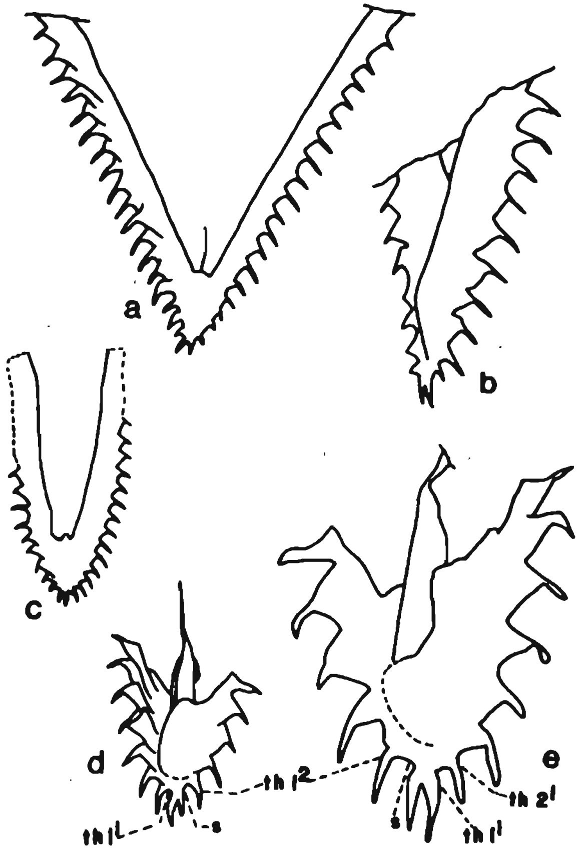

Fig. 7. *Apoglossograptus lyra* (Ruedemann). Non-isolated specimens: *a* lateral aspect showing nema free within axil, ca. X2.2 (OSU 33164); *b* lateral aspect of specimen preserved in partial relief and showing overlap of stipes in proximal end, ca. X4.5 (OSU 33165); *c* lateral aspect, apex of prosicula visible in axil, ca. X2.2 (OSU 33166); *d* lateral aspect of young rhabdosome showing sicula enclosed by the two stipes, ca. X4.5 (OSU 33167); *e* lateral aspect of rhabdsome showing sicula enclosed by the two stipes, ca. X9.2 (OSU 33168).

ISOGRAPTUS LYRA RUEDEMANN

Calera, Alabama is the type locality of *Isograptus lyra* Ruedemann. I have collected more than 40 specimens from this locality, and after examining these specimens and Ruedemann's (1947) type specimens, I believe that the species *lyra* should be assigned to a new genus, which I will formally name *Apoglossograptus* in a forthcoming paper (Finney, in preparation). The name of this genus reflects my belief that this species evolved directly from a species of *Glossograptus*, possibly the species *ciliatus*, by a separation of the two thecal series in a scandent biserial rhabdosome in such a way that they from two reclined stipes.

All the available specimens are flattened on shale surfaces, but a few retain some relief and show the pericalycal arrangement of the proximal end (fig. 7). Although the stipes are reclined and diverge from the proximal end, the sicula is enclosed between the two stipes. The apertural portions of the most proximal thecae are ascending. This feature reflects the semi-circular direction of growth of the proximal thecae and allows specimens of this genus to be distinguished from specimens of *Isograptus*.

Several of the available specimens represent early growth stages (fig. 8). Although these specimens are flattened on shale surfaces, the outlines of thecae can be discerned and show that theca 1^2 originates righthandedly from theca 1^1. Although I am not certain as to the origin of theca 2^1 and theca 2^2, it appears that they both might develop from theca 1^2.

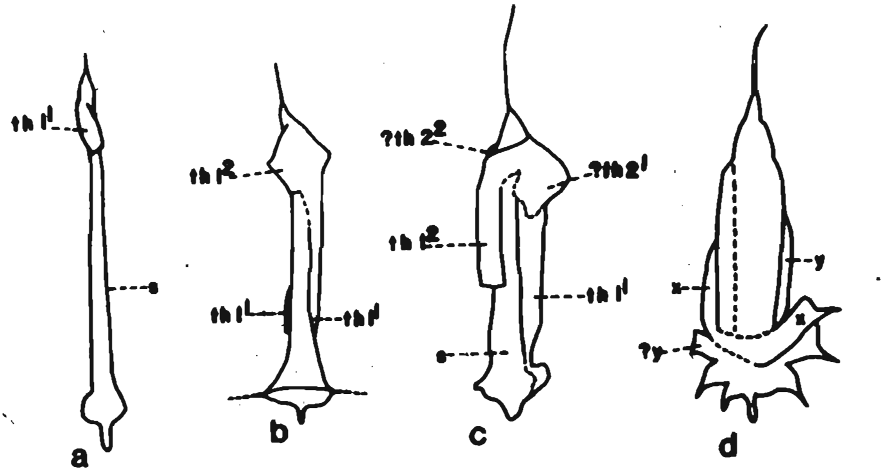

Fig. 8. *Apoglossograptus lyra* (Ruedemann). Non-isolated specimens representing early growth stages. *a* ventral aspect of sicula with theca 1^1, ca. X10 (OSU 33169); *b* dorsal aspect of sicula showing right-hand origin of theca 1^2 from theca 1^1, ca. X10 (OSU 33170); *c* dorsal aspect of sicula with thecae 1^1, 1^2, ?2^1, and ?2^2, ca. X10 (OSU 33171); *d* lateral aspect of specimen showing clockwise direction of growth of thecae about sicula ca. X10 (OSU 33172).

Because of overlapping stratigraphic and geographic ranges and both quantitative and qualitative morphological similarities, it seems highly probable that *Apoglossograptus lyra* evolved directly from *Glossograptus ciliatus* by means of a separation of the thecal series.

INTERPRETATION OF PHYLOGENETIC RELATIONSHIPS

As I mentioned in my introductory remarks, the interpretations of a primitive dichograptid-type of proximal-end development has made it difficult to postulate the ancestry of the taxa within Glossograptina. After presenting new information and re-interpretations for an isograptid-type of proximal-end development for *Glossograptus* and *Cryptograptus*, I feel obliged to attempt an interpretation of the phylogenetic relationships of the taxa within the suborder Glossograptina (fig. 1). Several of these interpretations must still be considered highly speculative because only a few of the taxa discussed here are represented by well-preserved isolated specimens.

The isograptid-type of proximal-end development of *Glossograptus* (fig. 1*E*), together with such additional features as a long, narrow sicula, a prosicular origin of theca 1^1, and long, slender thecae with considerable overlap and spatula-shaped ventral apertural processes, strongly favours an isograptid ancestry (fig. 1A) for *Glossograptus*. In *Isograptus gibberulus*, theca 1^1 grows directly downward along the ventral, virgellar wall of the sicula, and theca 1^2 grows around to and down along the dorsal wall of the sicula (see Bulman 1932). The structural plan of the proximal-end of *Glossograptus* could easily be derived from that of *I. gibberulus* by a clockwise direction of growth about the sicula of the second, third, and fourth pairs of thecae.

The structural plan of *Glossograptus* seems to characterize all the other genera of the family Glossograptidae. *Lonchograptus* (fig. 1*H*), which has been described only on the basis of specimens flattened on shale surfaces, is remarkably similar in outline to *Glossograptus*. The sole difference between the two genera seems to be the single pair of long, stout spines of *Lonchograptus*. Superficially, *Nanograptus* (fig. 1*J*) differs from *Glossograptus* by its small rhabdosome that consists of no more than 5 pairs of thecae. However, Hadding (1915) has described and illustrated early growth stages of *Nanograptus lapworthi*, which show an isograptid-type of proximal-end development. *Paraglossograptus* (fig. 1*F*) has been described on the basis of isolated specimens. It differs from *Glossograptus* by the upward curvature of the first two thecal apertures, the presence of a lacinia, and a metasicular origin of theca 1^1. Except for these differences, *Paraglossograptus* is similar to *Glossograptus*. The right-hand origin of theca 1^2 in *Paraglossograptus* (see Whittington and

Rickards 1969) indicates an isograptid-type of proximal-end development or a slight modification of that type of development, depending on the position of the dicalycal theca, which is presently unknown. As previously mentioned, *Apoglossograptus* (fig. 1*I*), which is here assigned to the family Glossograptidae, resembles a glossograptid in which the two thecal series have separated.

As it is here constituted, the family Glossograptidae includes a large range of variation in the general appearance of the rhabdosome. Basically, however, all the genera in the family Glossograptidae have: 1) an isograptid-type of proximal-end development, or a slight modification of this type of development, 2) a pericalycal arrangement of the proximal end, 3) a monopleural arrangement of the thecal series, 4) curved thecae in the proximal end and relatively straight distal thecae, and 5) simple, long, narrow thecae with ventral apertural processes. The structural plan of *Glossograptus* is one from which those of the other genera can be derived by a very few morphological changes: *Lonchograptus*, by the development of one pair of enlarged spines; *Nanograptus*, by arrested development of an early astogenetic stage; *Paraglossograptus*, by a change from a prosicular to a metasicular origin of theca 1^1, by the addition of a lacinia, and the curvature of the distal portions of the first two thecae; and *Apoglossograptus*, by a separation of the two thecal series.

The family Cryptograptidae, as represented by its only genus *Cryptograptus* (fig. 1*G*) seems to differ significantly from the family Glossograptidae. These differences are: 1) the relatively shorter sicula, 2) the metasicular origin of theca 1^1, 3) the spiral direction of growth of the initial parts of theca 2^1 and theca 2^2, and 4) the short free ventral wall of the thecae. Superficially, these differences suggest an origin of *Cryptograptus* that is completely independent of that of *Glossograptus*. However, on closer examination, the structural plan of *Cryptograptus* can be derived from that of the glossograptids.

The metasicular origin of theca 1^1 and the initial direction of growth of theca 1^2 in *Cryptograptus* is remarkably similar to that shown by a specimen referred to *Paraglossograptus proteus* by Whittington and Rickards (1969) and Rickards (1972). By adding extreme curvature to the initial portions of theca 2^1 and theca 2^2, the proximal-end morphology of *Glossograptus* approaches that of *Cryptograptus*. In *C. marcidus*, each theca has a short free ventral wall situated directly above the base of a distinct ventral apertural process. This thecal morphology is intermediate between that of *Glossograptus*, which lacks a free ventral wall but includes a ventral apertural process and that of *C. tricornis*, which lacks a ventral apertural process but includes a free ventral wall.

The final group of graptoloids to be discussed is the family Corynoididae. While studying the earliest growth stages of *Glossograptus*, I noted the remarkable similarity of these specimens to certain species of *Cory-*

noides. In fact, I have synonymized Ruedemann's (1947) *Corynoides tricornis* with *Glossograptus ciliatus* because I believe that the specimens referred to this particular species are early growth stages of *G. ciliatus* (Finney 1977). Bulman (1944, 1947) has described isolated specimens of two species of *Corynoides*. The similarities between these specimens and the earliest growth stages of *G. ciliatus* are as follows (fig. 9):

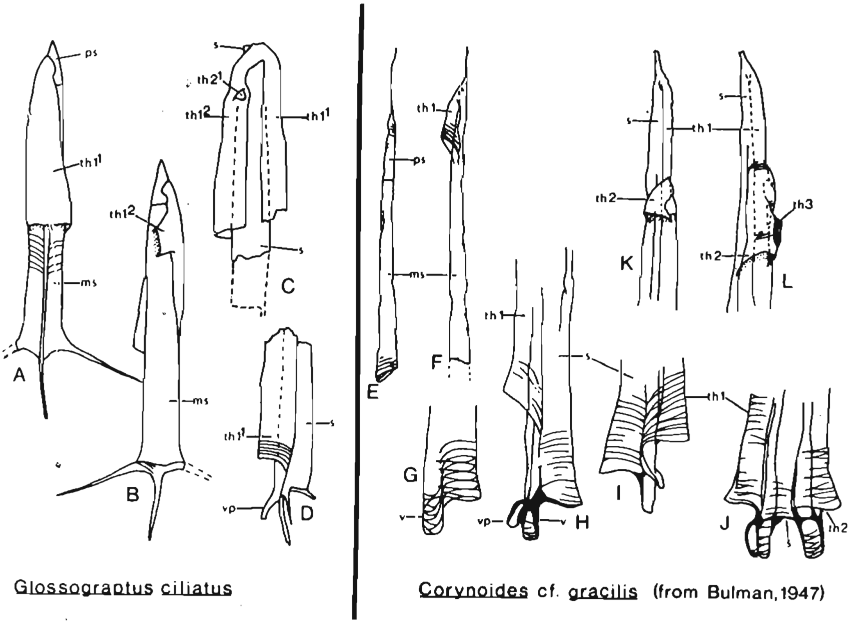

Fig. 9. Selected, isolated specimens of *Glossograptus ciliatus* and *Corynoides* cf. *gracilis* showing similarities in proximal-end development. *A—D*, same specimens as shown in figs 3*n*, 3*m*, 3*j*, and 3*f*, respectively. *E—J*, taken from Bulman's (1947) text-figs. 39B, 39J, 39K, 40E, 40F, 40J, 40A, and 40B, respectively.

1) The prosicula is very small, accounting for only a small fraction of the length of the sicula (figs 9*a* and 9*e*).

2) The metasicula is long and narrow, and the virgella, which is formed by the downward curvature of the growth lines along one side of the sicula, originates high on the metasicula (figs 9*d*, 9*e*, 9*g*).

3) The virgella, especially at maturity, is a lamelliform process with its lateral margins turned upward forming a wide U-shaped cross-section. At maturity, the lateral edges of the virgella are dark black, which suggests the presence of cortical deposits (figs 9*a* and 9*h*).

4) Theca 1^1 originates from a foramen in the right-lateral wall of the prosicula and develops as a split tube, that is, without its own ventral wall. Early in its development, theca 1^1 grows around to and then down and in contact with the virgellar wall of the sicula (figs 9*a* and 9*f*).

5) As theca 1^1 approaches, but before it reaches, the level of the sicular aperture, a process is produced from the base of the sicular vir-

gella. This process is similar in appearance to the sicular virgella; it diverges from the sicular virgella, and it eventually serves as a ventral apertural process of theca 1^1 (figs. 9*d*, 9*h* and 9*i*).

6) After theca 1^1 grows around to the virgellar wall of the sicula and before it grows halfway down the sicula, theca 1^2 (Bulman's theca 2) originates right-handedly from theca 1^1 (figs 9*b* and 9*k*).

7) Theca 1^2 grows down the anti-virgellar wall of the sicula and develops its aperture on the opposite side of the sicula from theca 1^1. Theca 1^2, as with theca 1^1, is provided with a ventral apertural process that resembles closely the sicular virgella (fig. 9*j*).

8) The third theca originates left-handedly from, and high up on, theca 1^2 (figs 9*c* and 9*l*).

On the basis of these similarities, *Corynoides* (fig. 1*K*) shows close affinities to *Glossograptus*, and could have evolved from *Glossograptus* by means of arrested development at a very early astogenetic stage. In turn, *Corynites* (fig. 1*L*) may have evolved from *Corynoides* by the development of elaborate apertural flanges on the sicula.

Previous workers have suggested an isograptid ancestry for the family Corynoididae, but they have been troubled by the large stratigraphic gap between the youngest isograptid and the earliest corynoidid. *Glossograptus* spans this gap, and with my interpretation of a glossograptid ancestor for *Corynoides*, I will propose that the family Corynoididae be assigned to the suborder Glossograptina (Finney, in preparation).

CONCLUSION

To summarize, I suggest that:

1) *Glossograptus* might have evolved from an isograptid ancestor, possibly of the *gibberulus* type. It is also possible to derive the biserial, monopleural rhabdosome of *Apiograptus* (fig. 1*D*) from an isograptid of the *gibberulus* type by way of *Maeandrograptus* (fig. 1*B*) and *Pseudisograptus* (fig. 1*C*), however I believe this to be a dead-end lineage that does not lead to *Glossograptus*, as some authors suggest (Harris and Thomas 1935; Thomas 1960).

2) The ancestry of the other genera of Glossograptidae can be found in *Glossograptus*.

3) The Cryptograptidae might have evolved from an early glossograptid or possibly independently from an isograptid ancestor.

4) The Corynoididae could have evolved directly from *Glossograptus*.

An examination of the stratigraphic ranges of these taxa in North America, Britain, Baltoscandia, and Australia shows that the ranges are compatible with the proposed phylogenetic scheme.

A significant feature of the entire phylogenetic scheme proposed here is the similarity of the thecal morphology and ontogeny, as well as it can be determined, among all the various taxa. The thecae can be characterized morphologically as straight, long and narrow, and of the orthograptid type with ventral apertural processes. Except for structural modifications in *Cryptograptus*, namely the short free ventral wall, the variations in the thecae among the various taxa seem to be entirely quantitative, involving such parameters as length to width ratios, degree of straightness or curvature, inclination to stipe axis, amount of overlap, et cetera. What little is known of the thecal ontogeny seems to confirm the high degree of similarity of the thecae in all the taxa in the proposed phylogenetic scheme (fig. 1).

This thecal ontogeny is best known on the basis of growth lines for Skevington's (1965) *Maeandrograptus*? *geniculatus*. In this species, there is an abrupt change in the growth line density at the boundary between the metatheca and protheca. This change has been interpreted as representing an abrupt increase in the rate growth of the theca. The metatheca then develops without its own ventral wall until its lateral walls are at, or near, the aperture of the preceding theca, then it develops its own ventral wall. The growth lines on this ventral wall are continuous with those on the lateral walls, yet they project distally in advance of the corresponding growth lines on the lateral thecal walls. Thus, the ventral wall develops as a distally tapering process in advance of the lateral and dorsal walls of the theca. When fully developed, the ventral wall forms a ventral apertural process.

Thecal ontogenies, essentially similar to that summarized above for *Maeandrograptus*? *geniculatus*, are revealed by growth-line evidence in *Glossograptus ciliatus*, *Cryptograptus marcidus*, and the species of *Corynoides* described by Bulman (1944, 1947). Similar thecal ontogenies are also interpreted on the basis of partly developed thecae on "growing tips" of specimens representing *Isograptus* (Bulman 1932: pl. 8: 3, 4), *Pseudiosograptus* (Cooper 1973: fig. 22c), and *Apoglossograptus* (figs 7*d* and 7*e*).

Recent ultrastructural studies on graptolites strongly suggest that the periderm is secreted within an epithelial evagination. Thus, the ontogeny of a theca, as it is revealed by growth-line evidence, is probably associated closely with the ontogeny of the zooid that secreted the theca. This association lends itself to two further speculations. First, the development of the ventral wall in advance of the other walls of the theca and its distally tapering shape may be related to some particular soft part of the zooid. Second, the constancy of the thecal ontogeny throughout the proposed phylogenetic scheme (fig. 1) suggests that, except for *Cryptograptus*, the evolutionary changes involved primarily the morphology of the colony, or rhabdosome, and not the morphology of the zooids, or thecae. These evolutionary changes are consistent with a pelagic mode of life, which in the case of graptoloids probably placed the greatest selective pressure on the shape of the colony.

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