M]. Similar to *Idiotubus*. *Ord.(Wesenberg F.)*, Eu.(Estonia).

?**Fasciculitubus** Obut & Sobolevskaya, 1967a, p. 56 [**F. tubularis;* OD]. Robust thecae arising in irregular groups from the thecorhiza. *U.Cam.*, USSR (Sib.).

Galeograptus Wiman, 1901, p. 189 [**G. wennersteni;* M]. Rhabdosome discoidal, erect portions of autothecae associated in comparatively few (8 to 10) peripheral branches bifurcating usually once near their mid-length; proximal autothecae with umbellate apertural processes; bithecae extending along the branches. *U.Ord.-M.Sil.(Wenlock)*, Baltic-Eng.——Fig. 29,2. **G. wennersteni*, lateral view of rhabdosome; silicified boulder, Sweden (Gotland); ×3 (267).

?**Parvitubus** Skevington, 1963, p. 47 [**Azygograptus? oelandicus* Bulman, 1936, p. 46; OD]. Erect, undivided branches comprising stolothecae, autothecae and bithecae, possibly grouped on a thecorhizal base; bithecae restricted to one side of stipe, opening into autothecae. *L.Ord.(Vaginatumkalk, Ontikan*, Sweden(Öland).——Fig. 30, *1-2*. **P. oelandicus* (Bulman); *1*, basal portion of stipe; *2*, distal portion of stipe [*a*, autothecae; *bi*, bithecae], ×7.5 (214).

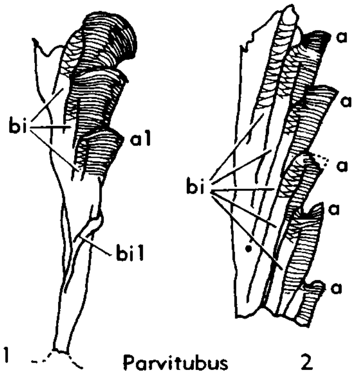

Fig. 30. Idiotubidae [*a*, autotheca; *bi*, bitheca] (p. *V*49).

CAMAROIDEA

Order CAMAROIDEA Kozłowski, 1938

[Introduced by Kozłowski in 1938 (p. 185) without diagnosis but descriptive notes in text; defined by Bulman (21) in 1938, p. 92, but first adequately described by Kozłowski (114) in 1949, p. 170]

Encrusting Graptolithina comprising autothecae and indistinct stolothecae, bithecae present in some; autothecae strongly differentiated into two parts, an inflated basal vesicle (camara) and a free tubular distal portion (collum); bithecae tubular; stolothecae forming bifurcating network above camarae or represented by extracamaral tissue surrounding stolons. *Ord.*

MORPHOLOGY

The shape of the complete rhabdosome is unknown, as is its proximal end and mode of development. As in the Graptoloidea, the dominant element is the autotheca, but sclerotized stolons are present invariably, some enclosed in stolothecae, and bithecae characterize one genus.

AUTOTHECAE

The autothecae are very sharply differentiated into distinct proximal and distal portions. The **camara** (proximal portion) is a more or less inflated vesicle or cell, whose upper wall exhibits characteristic fusellar structure in contrast to the lower surface which is structureless; the camarae, commonly embedded in extra-camaral tissue, form a sort of encrusting mosaic. At the proximal extremity of each is attached the autothecal stolon, separated from the cavity of the camara by one or more transverse partitions or septa. From one extremity also, although not necessarily the distal one, arises the slender tubular **collum,** which is morphologically equivalent to the free portion of the autothecae in the Tuboidea. Its wall shows a somewhat irregular fusellar structure and terminates in an apertural process (corresponding to the ventral process of Tuboidea and other graptolites) or more typically thins out distally to terminate in a sharp jagged edge; it has been suggested that this latter feature indicates a gradual transition in life from the sclerotized thecal wall into the soft skin of the zooid. Rarely (as in *Cysticamara accollis*). the collum is absent altogether and the thecal aperture is situated on the upper surface of the camara. Occlusion of the autothecae by a sclerotized diaphragm, generally near the base of the collum, is of very common occurrence.

BITHECAE

Where present *(Bithecocamara),* the bithecae are relatively inconspicuous tubular thecae (as in Tuboidea) which are distributed irregularly and unevenly on or near the surface of the colony.

STOLON SYSTEM

Stolothecae are present in some genera *(Bithecocamara)* as a bifurcating network of tubes near the upper surface of the colony, and even here they are never very clearly differentiated; in other genera, a stolon system occurs more or less embedded in extracamaral tissue which forms a sort of sheath, perhaps representing modified vestiges of original stolothecae. Apart from bifurcations of the stolons (and a corresponding bifurcation of the stolothecal tubes where present) no details of budding are known; it was probably irregular, and the autothecae at least possessed long autothecal stolons.

SYSTEMATIC DESCRIPTIONS

Family BITHECOCAMARIDAE Bulman, 1955

[Bithecocamaridae BULMAN, 1955, p. 42]

With all three types of thecae; autothecae with well-developed collum. *L.Ord.*

Bithecocamara KOZŁOWSKI, 1949, p. 176 [**B. gladiator;* OD]. Only genus. *L.Ord.(Tremadoc),* Eu.(Pol.).——FIG. 31,*1*. *B.* sp.; reconstr., approx. ×80 (Bulman, n).

Family CYSTICAMARIDAE Bulman, 1955

[Cysticamaridae BULMAN, 1955, p. 42]

Bithecae absent, stolothecae obscure or absent, stolons usually embedded in extracamaral tissue. *L.Ord.*

Cysticamara KOZŁOWSKI, 1949, p. 183 [**C. accollis;* OD] [=*Syringataenia* OBUT, 1953, p. 54 (type, *S. bystrowi;* M]. Stolons embedded in extracamaral tissue with fusellar structure. *L.Ord. (Tremadoc,* Eu.(Pol.); *Ontikan(Orthoceras Ls.),* Öland-NW.USSR).

Flexicollicamara KOZŁOWSKI, 1949, p. 182 [**F. bryozoaeformis;* OD]. Collum strongly bent back ventrally and fused to upper wall of camara. *L. Ord.(Tremadoc),* Eu.(Pol.).

Graptocamara KOZŁOWSKI, 1949, p. 187 [**G. hyperlinguata;* OD]. Collum provided with conspicuous apertural process. *L.Ord.(Tremadoc),* Eu.(Pol.); *Ontikan(Vaginatumkalk),* Öland.

Tubicamara KOZŁOWSKI, 1949, p. 188 [**T. coriacea;* OD]. Funnel-shaped collum with ventral apertural process; abundant cortical tissue. *L.Ord. (Tremadoc),* Eu.(Pol.).

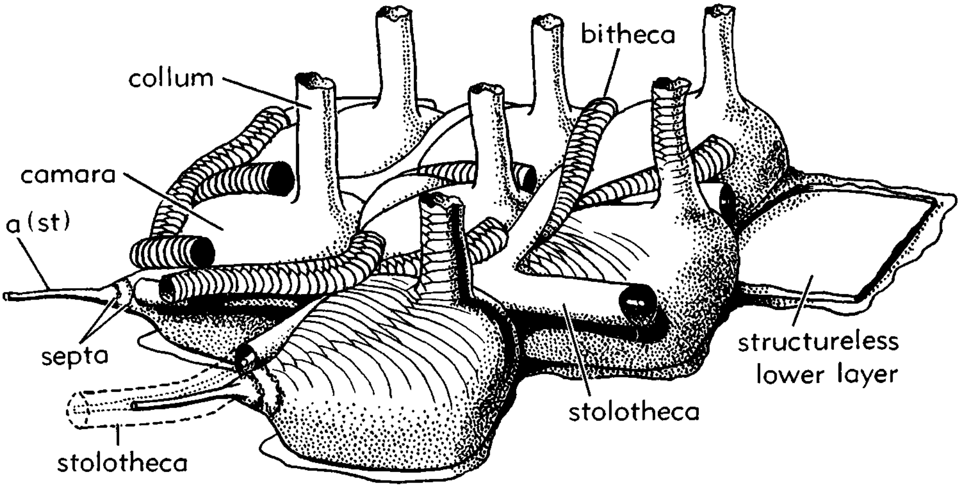

FIG. 31. Diagrammatic restoration of a camaroid, based on *Bithecocamara* KOZŁOWSKI, approx. ×80 (29). [*a(st),* autothecal stolon.]

CRUSTOIDEA

Order CRUSTOIDEA Kozłowski, 1962

[Order Crustoidea Kozłowski, 1962, p. 31]

Encrusting Graptolithina with colonies comprising autothecae, stolothecae and bithecae produced in triads; autothecae with erect (isolate) distal neck showing distinctive apertural modifications; bithecae cylindrical, adnate throughout their length; stolothecae tubular, with conspicuous well-sclerotized stolons; lower (adherent) wall of all thecae membranous, structureless; upper wall fusellar. *L.Ord.-U.Ord.*

MORPHOLOGY

The development and form of the complete colony of Crustoidea is unknown, for remains are fragmentary, but they are known to be encrusting, probably irregular and irregularly spreading; where the thecae are not in lateral contact, a thin structureless interthecal membrane is usually adherent to the substrate and continuous with the lower membrane of the thecae.

Some resemblance between the Crustoidea and Camaroidea is observed, but the former are less compact, have a more regular stolon system, and exhibit more highly elaborated apertural processes of the autothecae. *Hormograptus,* here provisionally included as an aberrant crustoid, may prove to be synonymous with *Chaunograptus* and provide a link with a number of obscure adherent forms, but the encrusting habit is of course represented in many unrelated phyla. Of all the Graptolithina, the Crustoidea constitutes the order most closely resembling morphologically the Rhabdopleurida.

AUTOTHECAE

The autothecae comprise a proximal portion in contact with the substrate, some in contact with one another laterally, with an isolate, erect, distal neck. The proximal portion is generally more or less inflated but may be almost cylindrical. It passes imperceptibly into the neck, from the distal end of which the apertural lobe is developed. This latter may be considerably enlarged and elaborated to produce a median fold and two auricular lateral folds (Fig. 32).

BITHECAE

The bithecae are slender and tubular, but vary much in length; in consequence, they may open beside, behind, or considerably in front of the autothecal aperture of the same generation. A tendency toward a right- and left-hand alternation in successive generations is seen, but this is not so regular as in the Dendroidea. Bithecal apertures are devoid of any special modification.

STOLOTHECAE

The stolothecae are slender, commonly sinuous, and distally each passes imperceptibly into the base of daughter autotheca. Externally they are distinguishable from the bithecae by their much more regular fusellar structure, with conspicuous zigzag suture. Stolons are well sclerotized, 20 to 35 microns in diameter and marked with fine transverse annulations. They exhibit well-developed nodes at the points of origin of the stolonal triads, as in the Dendroidea, but a distinctive feature is their attachment to the structureless basal wall of the stolothecae. The autothecal stolon is appreciably shorter than the bithecal stolon, and it does not terminate at the base of the theca, but penetrates to its interior. Indications of supernumerary and secondary stolons have been observed in some fragments, but their role is unknown.

GRAPTOBLASTS AND CYSTS

Vesicles or cysts may occur inside autothecae, varying greatly in size and shape, rarely filling the entire cavity of the autotheca. They may or may not be connected with the stolon, and possess blackish, structureless walls. It is possible that they represent the envelopes of degenerate zooids.

Graptoblasts (see also p. *V*136) may also occur within the autothecae of Crustoidea, completely filling the autothecal cavity, and such autothecae are devoid of normal apertural modifications. Their relationship is at present unresolved.

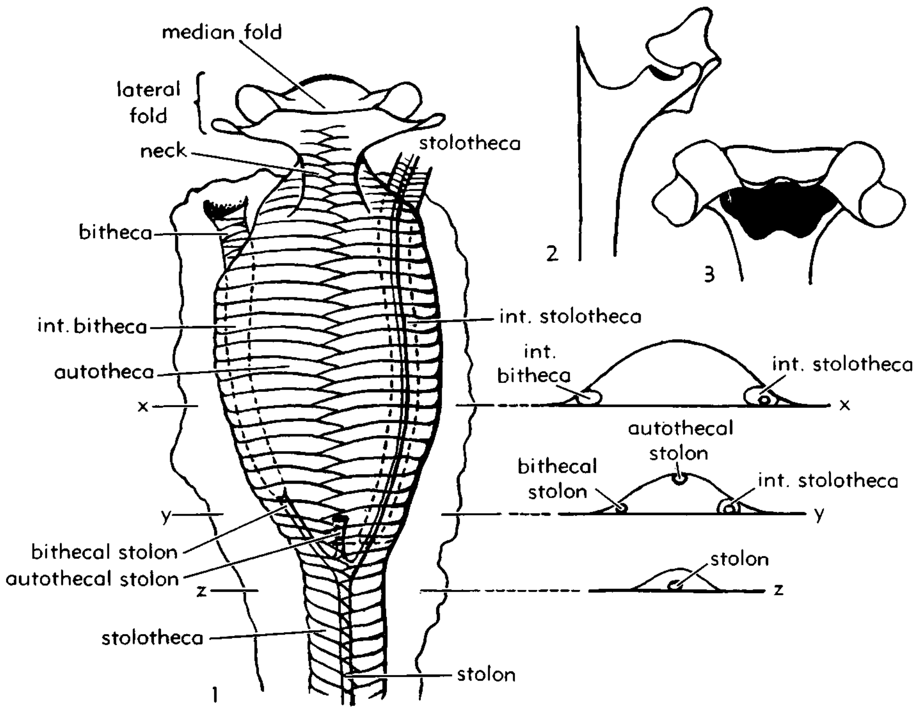

FIG. 32. Diagrammatic restoration of a crustoid thecal triad, based on *Bulmanicrusta* KOZŁOWSKI, approx. ×60.——*1.* Dorsal view of autotheca (*xx, yy, zz,* transverse sections).——*2,3.* Lateral and apertural views of autothecal apertural modification in *B. latialata* (Bulman, n).

SYSTEMATIC DESCRIPTIONS

Family WIMANICRUSTIDAE Bulman, n. fam.

Encrusting rhabdosomes comprising autothecae, bithecae, and stolothecae developed by regular triad budding; autothecae with erect distal neck and conspicuous apertural modifications; bithecae and stolothecae tubular, adnate, the latter with heavily sclerotized stolons attached to the adherent basal wall. *L.Ord.-U.Ord.*

Wimanicrusta KOZŁOWSKI, 1962, p. 42 [**W. urbaneki;* OD]. Apertural neck short or absent, apertural lobe linguiform. *L.Ord.* (glacial boulders, *?Glyptograptus teretiusculus Zone),* Eu.(Pol.).

Bulmanicrusta KOZŁOWSKI, 1962, p. 31 [**B. latialata;* OD]. Autothecae with or without well-developed neck, very large apertural lobe with median and auriculate lateral folds. *L.Ord.* (glacial boulders, *?Glyptograptus teretiusculus Zone),* Eu.(Pol.).——FIG. 32,*1-3*. **B. latialata; 1-3,* reconstr., approx. ×60 (Bulman, n).

Ellesicrusta KOZŁOWSKI, 1962, p. 38 [**E. longicollis;* M]. Autothecae with elongate neck, apertural lobe with slight lateral folds. *L.Ord.* (glacial boulders, *?Glyptograptus teretiusculus Zone),* Eu.(Pol.).

Holmicrusta KOZŁOWSKI, 1962, p. 41 [**H. sombrero;* M]. Autothecae with long neck and large flattened apertural lobe. *L.Ord.* (glacial boulders, *?Glyptograptus teretiusculus Zone),* Eu.(Pol.).

Lapworthicrusta KOZŁOWSKI, 1962, p. 44 [**L. aenigmatica;* M]. Slender autotheca without interthecal membrane and with only slight apertural modifications. *L.Ord.* (glacial boulder, *?Llanvirn*), Eu.(Pol.).

Ruedemannicrusta KOZŁOWSKI, 1962, p. 39 [**R. geniculata;* M]. Autothecae with long curved neck bearing strong internal ridges. *L.Ord.* (glacial boulders, *?Glyptograptus teretiusculus Zone),* Eu.(Pol.).

Family HORMOGRAPTIDAE Bulman, n. fam.

?Aberrant Crustoidea. Rhabdosome encrusting, irregularly branching; stolon system well developed, with triad budding commonly related to two stolothecae and an autotheca; autothecae adherent proximally, distally unknown; bithecae possibly absent or irregularly developed. *U.Ord.*

Hormograptus ÖPIK, 1930, p. 8 [*pro Thallograptus* ÖPIK, 1928, p. 35, *non Thallograptus* RUEDEMANN, 1925, p. 35] [**Thallograptus sphaericola* ÖPIK, 1928, p. 39; OD]. Only genus. *U.Ord. (Kukruse, Nemagraptus gracilis Zone),* Eu.(Est.).

STOLONOIDEA

Order STOLONOIDEA Kozłowski, 1938

[Introduced by KOZŁOWSKI in 1938, p. 185, without diagnosis but descriptive notes in text; defined by BULMAN (21) in 1938, p. 92, but first adequately described by KOZŁOWSKI (114) in 1949, p. 191]

Sessile or encrusting Graptolithina composed essentially of stolothecae and ?autothecae; stolothecae containing an exaggerated development of stolons dividing at irregular intervals and quite irregular in form. *Ord.*

MORPHOLOGY

This order is represented by extremely fragmentary remains and only an imperfect account of morphology can be given. It is, however, clearly distinguished from all other orders of Graptolithina by extraordinary development of the stolons themselves. These divide quite irregularly, in some forming whole interlacing groups (Fig. 33,*1*) and in others giving off single branches. Their course is erratic, vermiform, and they vary greatly in diameter from 50 to 350 microns. They have thick walls and the central lumen usually is filled with secondary deposit. The stolons are included in stolothecal tubes, either singly or in sheaves or groups, but these appear to have been extremely fragile and are preserved only rarely. The stolothecal tubes possess a normal though somewhat irregular fusellar structure, except on the lower surface of the encrusting forms where the thecal wall is structureless (as in Camaroidea).

The stolons appear to leave the stolothecae by pores produced by resorption, and on leaving the parent stolotheca give rise to new stolothecae or to what appear to be autothecae. Unlike most Graptolithina, where a sudden passage occurs from stolon to base of theca, the stolon here steadily increases in diameter until at a certain point the structureless substance of the stolon gives place to the fusellar structure of the theca proper. Autothecae are no more commonly preserved than stolothecae but were evidently tubular, straight or more commonly curved, with fusellar walls, opening on the surface of the colony with apertures devoid of any apertural processes.

SYSTEMATIC DESCRIPTIONS

Family STOLONODENDRIDAE Bulman, 1955

[Stolonodendridae BULMAN, 1955, p. 43]

Characters of the order. *Ord.*

Stolonodendrum KOZŁOWSKI, 1949, p. 194 [**S. uniramosum;* OD]. Large, irregularly vermiform stolons enclosed in thin-walled stolothecal tubes. *L.Ord.(Tremadoc),* Eu.(Pol.); *(?Ontikan),* Öland.——FIG. 33, *1,2*. *S.* sp., Tremadoc, Pol.; fragments of stolons, ×20 (114).

?**Melanostrophus** ÖPIK, 1930, p. 10 [**M. fokini;* OD]. Long, irregularly bent and coiled tubes in confused association; presence of growth lines demonstrated by EISENACK. *L.Ord.-U.Ord.,* Eu. (Baltic).

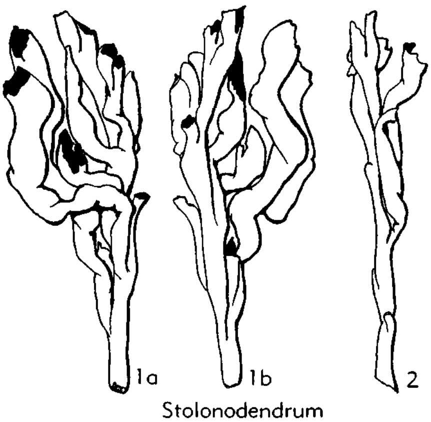

FIG. 33. Stolonodendridae (p. V53).

DENDROIDEA, TUBOIDEA, CAMAROIDEA, CRUSTOIDEA, STOLONOIDEA

TAXONOMIC POSITION UNCERTAIN

A considerable number of graptolite genera are not known in sufficient detail to be placed in the foregoing taxonomic sections. Many (e.g., *Chaunograptus*) have been described as dendroid; some (e.g., *Archaeocryptolaria*) as coelenterate (hydroid); and for others (e.g., *Dithecodendrum*) a distinct order has been proposed.

Definite pterobranch and hydroid remains are known from the Lower Ordovician and recently Kozłowski (1967) has described plausible representatives of phoronideans, Pogonophora, and what appear to be thecae of scyphozoan scyphistomae from glacial boulders of Ordovician rocks. The gross morphology of all such organisms, when poorly preserved, is little guide to their true affinity; and in the absence of detail concerning such features as the stolon system and the presence of fusellar tissue, it seems preferable to accept a large group of unclassified genera, some members of which may ultimately prove not to be Graptolithina at all.

The genera listed below vary greatly in character and in size. The majority are more or less dendroid in habit, but several are encrusting. The Dithecoidea of Obut (1964) appear to comprise autothecae only, but no stolon system has been demonstrated and they compare superficially with such genera as *Archaeocryptolaria* and others which until now have been provisionally classed as hydroids. But among these

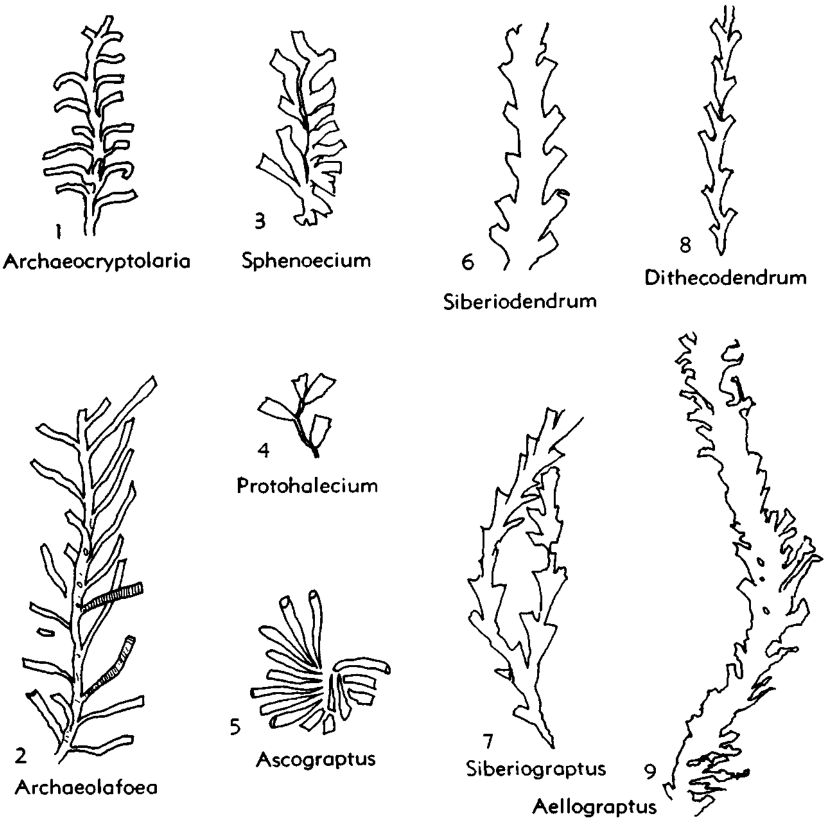

Fig. 34. Order and family uncertain (p. V55-V57).

latter, *Archaeolafoea* and *Sphenoecium* exhibit inconclusive traces of what appears to be fusellar structure, which would suggest a generally "graptolitic" affinity. Others, like *Leveillites* or *Diplospirograptus*, present superficial resemblance to algal forms, though it is perhaps doubtful whether such delicate filamentous algae could survive under the given conditions of preservation of these fossils.

Aellograptus OBUT, 1964, p. 306 [**A. savitskyi*; OD]. Elongate, unbranched or sparsely divided rhabdosomes with numerous short, projecting, cylindrical thecae. *U.Cam.*, USSR(Sib.).——FIG. 34,*9*. **A. savitskyi*; ×3 (172).

Archaeocryptolaria CHAPMAN, 1919, p. 392 [**A. skeatsi* CHAPMAN; SD BULMAN, herein]. Rhabdosome slender, branching infrequently; thecae tubular, widely-spaced, adnate proximally with conspicuous isolate distal portions. *M.Cam.*, Australia(Victoria).——FIG. 34,*1*. **A. skeatsi*, Lancefield, Victoria; ×2.5 (42).

Archaeolafoea CHAPMAN, 1919, p. 390 [**A. longicornis*; M]. Rhabdosome slender, flexuous, branching infrequently; thecae elongate, isolate, narrowing towards their bases, with indistinct traces of fusellar structure. *M.Cam.*, Australia (Victoria).——FIG. 34,*2*. **A. longicornis*, Lancefield, Victoria; ×2.5 (42).

Ascograptus RUEDEMANN, 1925, p. 18 [**A. similis*; OD]. Relatively large, conical thecae arranged spirally along an unbranched axis. *Sil.*, N.Am. FIG. 34,*5*. **A. similis*, Lockport Ls., N.Y.; ×7 (209).

Cactograptus RUEDEMANN, 1908, p. 196 [**C. crassus*; OD]. Elongate branches apparently dendroid, with prominent thecae projecting on both sides. *?Cam.*, Australia, *Sil.*, N.Am.——FIG. 35,*3*. **C. crassus*, Sil.(Clinton Sh.), N.Y.; ×1 (201).

Ceramograptus HUDSON, 1915, p. 129 [**C. ruedemanni*; OD]. Stipes apparently multiserial. *U. Ord.*, N.Am.(Can.).

Chaunograptus HALL, 1883, p. 58 [**Dendrograptus (Chaunograptus) novellus*; M]. Minute dendroid rhabdosome, usually encrusting, with short, conical thecae. *?Cam.*, *Ord.-Dev.*, N.Am.-Eu. (Czech.).——FIG. 35,*2*. *C. contortus* RUEDEMANN, U.Ord. (Richmond beds), Ind.; ×3.5 (209).

Coelograptus RUEDEMANN, 1947, p. 266 [**Inocaulis problematica* SPENCER, 1878; OD]. Similar to *Chaunograptus*, but coarser, with no recognizable thecae. *U.Sil.(Niag.)*, N.Am.(Can.).

Crinocaulis OBUT, 1960, p. 148 [**C. flosculus*; OD]. Resembling *Palmatophycus*, but with differently arranged terminal filaments. *L.Sil.*, Eu. (Est.).

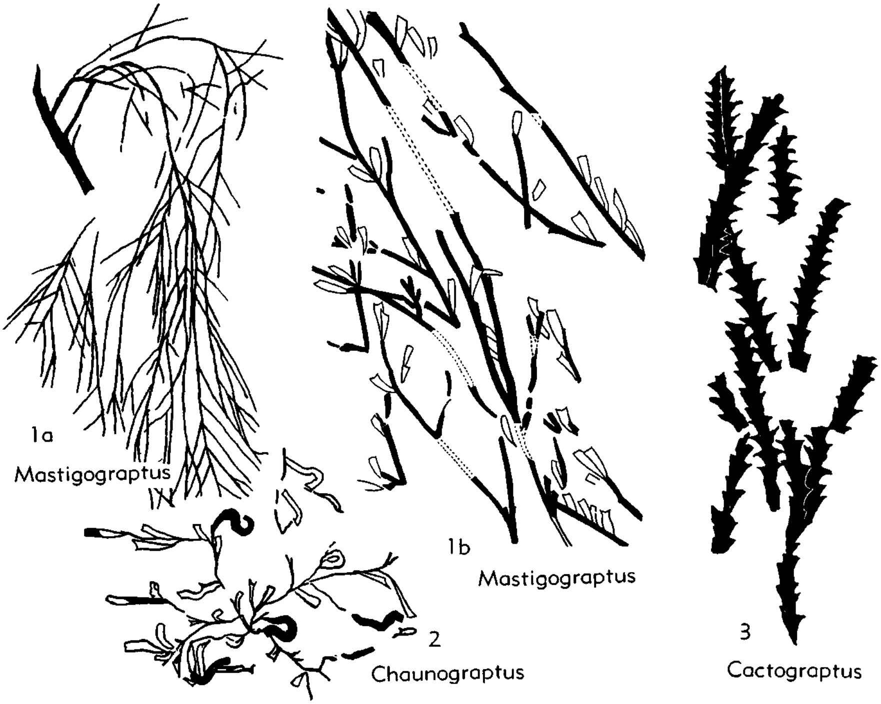

FIG. 35. Order and family uncertain (p. *V55-V56*).

Diplospirograptus Ruedemann, 1925, p. 34 [**D. goldringae;* OD]. Rhabdosome bifurcating near base to produce spirally coiled branches bearing distally a close-set brush of filamentous thecae. *Sil.,* N.Am.

Dithecodendrum Obut, 1964, p. 306 [**D. sibericum;* OD]. Slender, elongate rhabdosome; autothecae cylindrical, isolate distally, arranged biserially. *M.Cam.,* USSR(Sib.).——Fig. 34,*8*. *D. tenuiramosum* Obut; ×3 (172).

Estoniocaulis Obut & Rytsk, 1958, p. 137 [**Inocaulis järvensis* Rosenstein MS, Obut & Rytsk, 1958; OD]. Resembling *Diplospirograptus,* but with smaller terminal tufts and branched stem not spirally coiled. *L.Sil.,* Eu.(Est.).

Haplograptus Ruedemann, 1933, p. 323 [**H. wisconsinensis;* OD]. Elongate conical or vermiform thecae associated to form an irregularly dendroid rhabdosome. *Cam.-Ord.,* N.Am.

Leveillites Foerste, 1923, p. 62 [**L. hartnageli;* M]. Lateral branches set with numerous small tufts of filaments. *L.Sil.,* N.Am.(Ont.).

Mastigograptus Ruedemann, 1908, p. 210 [**Dendrograptus tenuiramosus* Walcott, 1883; OD]. Much-branched, dendroid rhabdosome with slender, dense-walled stipe (?stolothecae) and thin-walled, conical thecae apparently including autothecae and bithecae; budding in triads but arrangement uncertain and little difference between auto- and bithecae; fusellar structure with complete rings and oblique sutures. *Cam.-Sil.,* N. Am.-Eu.-?Australia.——Fig. 35,*1*. **M. tenuiramosus* (Walcott), Ord.(Utica Sh.), N.Y. *(1a);* (Eden Sh.), Ky.*(1b); 1a,* fairly complete rhabdosome, ×1; *1b,* fragment showing thecae, ×5 (209).——Fig. 36,*1,2*. *M.* sp., Ord.(glacial boulder), N.Ger.; *1,2,* two thecal groups showing fusellar structure and triad budding; approx. ×170, ×130 [*a,* autothecae; *b,* bithecae] (Andres, 1961).

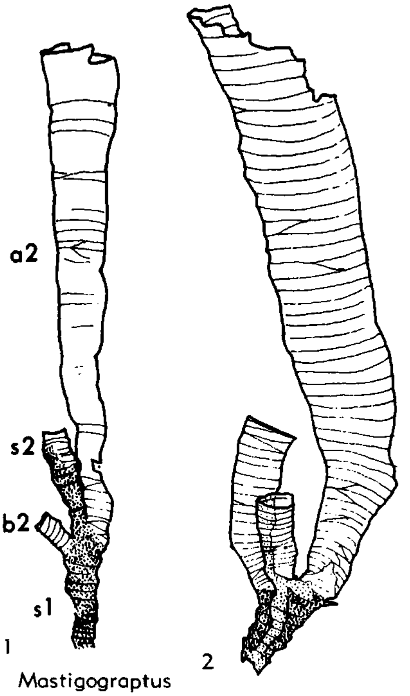

Fig. 36. Order and family uncertain [*a,* autotheca; *b,* bitheca; *s,* stolotheca] (p. V56).

Fig. 37. Order and family uncertain (p. V56).

Medusaegraptus Ruedemann, 1925, p. 29 [**M. mirabilis;* OD]. Thick main branch ending in a blunt point at the base and terminating distally in a dense mass of long, filamentous thecae. *Sil.,* N.Am.-Eu.(Czech.).——Fig. 37,*1*. **M. mirabilis,* Lockport Dol., N.Y.; ×1 (203).

Palmatophycus Bouček, 1941 (revised, Bouček, 1957, p. 148) [**P. kettneri;* OD]. Stipe terminating distally in a crown of lateral branches, each furnished with a dense mass of filamentous thecae. *M.Sil.,* Eu.(Czech.).

Polygonograptus Bouček, 1957, p. 151 [**Palaeodictyota sokolowi* Obut, 1953; OD]. An irregular network of mainly pentagonal or hexagonal meshes; thecal structure completely unknown. *U. Ord.-Sil.,* Eu.(USSR-Czech.).

Protohalecium Chapman & Thomas, 1936, p. 203 [**P. hallianum;* M]. Branching rhabdosome provided terminally with conical thecae. *M.Cam.,* Australia(Victoria).——Fig. 34,*4*. **P. hallianum,* Heathcote, Victoria; ×2 (43).

Rhadinograptus Obut, 1960, p. 151 [**R. jurgensonae;* OD]. Similar to *Mastiograptus,* but with bundle-like accumulations of slender, conical thecae. *L.Sil.,* Eu.(Est.).

Ruedemannograptus H. & G. Termier, 1948, p. 174 [*pro Streptograptus* Ruedemann, 1947, *non* Yin, 1937] [**Streptograptus tenuis* Ruedemann, 1947; SD Bulman, herein]. Irregularly branched dendroid rhabdosome with projecting, ?tubular thecae. *Ord.,* N.Am.(Tenn.)-N.Afr.(Morocco).

Siberiodendrum Obut, 1964, p. 306 [**S. robustum;* OD]. Rhabdosome robust, with short, wide, cylindrical thecae isolate distally. *M.Cam.-U. Cam.,* USSR(Sib.).——Fig. 34,*6*. **S. robustum;* ×1.5 (172).

Siberiograptus Obut, 1964, p. 306 [**S. kotujensis;* OD]. Rhabdosome slender, branching, with large, distally isolate thecae arranged biserially. *U.Cam.,* USSR(Sib.).——Fig. 34.*7*. **S. kotujensis;* ×1.5 (172).

Sphenoecium Chapman & Thomas, 1936, p. 205 [*pro Sphenothallus* Chapman, 1917, *non* Hall, 1848] [**S. filicoides;* SD Bulman, herein]. Robust, almost cylindrical thecae arranged radially (like *Fasciculitubus* Obut & Sobolevskaya) or serially, with faint traces of fusellar strucure. *M. Cam.* Australia(Victoria).——Fig. 34,*3*. **S. filicoides,* Heathcote, Victoria; ×2 (43).

GRAPTOLOIDEA

Order GRAPTOLOIDEA Lapworth, 1875

[*nom. transl.* Ruedemann, 1904, p. 573 (*ex* section Graptoloidea Lapworth, in Hopkinson & Lapworth, 1875, p. 633)] [=suborder Rhabdophora Allman 1872, p. 380]

Planktonic or epiplanktonic Graptolithina; rhabdosome generally of few stipes, always comprising only one type of theca (autotheca) without sclerotized stolons; sicula pendent in relation to apical nema, stipes pendent to scandent, uniserial or biserial, very rarely triserial or quadriserial. *L. Ord. (?Tremadoc, Arenig) - L. Dev. (Siegen., ?Emsian).*

MORPHOLOGY

GENERAL FEATURES

The Graptoloidea may be regarded best as simplified Dendroidea, to which order they are closely related through the family Anisograptidae. Such simplification, accompanying change to a pelagic mode of life, involves loss of bithecae and loss of a sclerotized stolon system; accordingly no sign is found in a graptoloid branch of the triad budding on the "Wiman rule" which distinguishes the Dendroidea. By analogy with other orders, the presence of a stolon may be inferred, but in the Graptoloidea this is not enclosed in a skeletal sheath and thus presumably was comparable with the **gymnocaulus** of *Rhabdopleura.* The proximal portion of the autotheca is morphologically equivalent to the dendroid stolotheca. The transition from one order to the other was probably gradual and may have occurred in several independent lines, and the placing of the Anisograptidae is arbitrary. Grouping this family (which includes many genera known to possess typical dendroid branch structure) with the Dendroidea leaves the typical graptoloid branch to be defined as composed of autothecae only. Following the loss of bithecae, the stipe shows a very general tendency to increase in breadth to a distal maximum.

The **sicula** gives rise laterally to a single initial bud from which ultimately the entire rhabdosome develops, and the apex of the sicula is prolonged as a slender thread known as the **nema** (or **virgula** in scandent forms) by the distal end of which the rhabdosome in general was attached. The relation between direction of growth of the branches of the rhabdosome and the nema has afforded a basis of subdivision among the Graptoloidea, and varies (Fig. 38) from pendent, through horizontal and reclined, to scandent, a general tendency in history of the group being toward attainment of a scandent direction of growth. There is likewise a general tendency toward reduction in the number of branches, the earliest genera being for the most part multiramous forms, whereas the youngest genera are composed of but one or two scandent stipes (Diplograptidae, Monograptidae). In these scandent forms it was not at

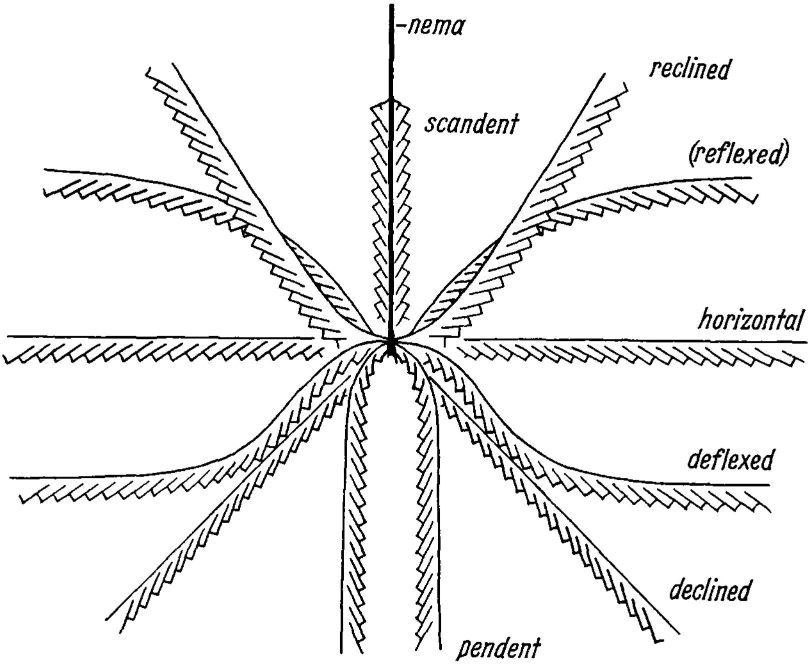

FIG. 38. Diagram illustrating relations of graptolite stipes to nema and terminology applied (21).

first recognized that the virgula is in fact identical with the nema of pendent forms. FRECH's suggested orders, Axonolipa and Axonophora, based essentially on absence or presence of an "axis," really reflect the degree of scandency attained by the rhabdosome, following the reduction in stipe number to two or one. No hard and fast line can be drawn between them, however, and the dicellograptids and dicranograptids were placed by FRECH in his Axonophora while RUEDEMANN, adopting the orders with slight modification, included them in the Axonolipa.

Biserial (axonophorous) rhabdosomes show two basically different structures. More commonly (in the Diplograptina and the Dicranograptidae) the two component stipes are oriented "back-to-back," with their dorsal sides in contact, and such rhabdosomes are termed **dipleural.** In the Glossograptina the two stipes lie "side-by-side," with one lateral wall in contact, and this structure is termed **monopleural** (JAANUSSON, 1960).

In uniserial scandent rhabdosomes (Monograptina), the stipe is commonly curved and spiral in some (plane or helical); in certain forms second- and higher-order rhabdosomes called **cladia** are developed from modified thecae or from the aperture of the sicula itself.

Loss of bithecae and particularly reduction in number of stipes results in a striking reduction in the total number of thecae in a rhabdosome. From as many as 20,000 to 30,000 in a large *Dictyonema flabelliforme,* the total falls to 2,000 or 3,000 in some *Clonograptus* species, and perhaps in a large multiramous dichograptid; averages of 100 to 200 occur in most leptograptids, dicellograptids, and diplograptids; 50 to 100 in a typical *Monograptus,* but in some no more than 10 to 20. It is also accompanied by a pronounced tendency toward thecal (apertural) elaboration. Recent morphological studies of the Graptoloidea have led to a greater appreciation of the range of complex thecal modifications, and considerable attention is now being paid to patterns of rhabdosome development. This order is outstanding for regularity in astogeny, exemplified in branching patterns, in cladia production, and in precisely controlled thecal sequences, which are discussed further in the sections on "Thecae" (p. *V*66) and on "Development of the Rhabdosome" (p. *V*71).

MUSCLE SCARS. The occurrence of muscle scars in specimens of *Climacograptus typicalis* and *Orthograptus quadrimucronatus* has been claimed by ULRICH & RUEDEMANN (1931), who used this as an argument in favor of polyzoan affinities, and later by HABERFELNER in *Monograptus* (1933). The published figures are not convincing, and we agree with KOZŁOWSKI in the view that the presence of muscle impressions in graptolites is by no means established.

GRAPTOGONOPHORES. Extrathecal structures, variously termed "ovarian vesicles," "reproductive sacs," and "graptogonophores," have been figured and described, first by HALL (1859, 1865) in *"Graptolithus whitfieldi"* (referred by RUEDEMANN to *Hallograptus bimucronatus*) and later by HOPKINSON (1871) and NICHOLSON (1866, 1872) in *Diplograptus* spp. These early figures are schematic; some represent the scopulae of lasiograptids, a peculiar spinous or fibrous development from the edges of the median septum comparable with the lacinia, whereas others probably were vesicles, having a firm outline, and seem to have been attached to the apertural region of otherwise normal thecae. Siculae and early growth stages may be abundantly associated with such specimens, and in some they appear to be attached to the vesicles by their nemata, though it is impossible to assert that they are not drifted into juxtaposition. Such capsules were claimed to represent ovicells, but their rarity and restriction to biserial graptolites is curious, and no convincing interpretation has yet been given.

SICULA

The sicula of the Graptoloidea is in general more conspicuous than that of the typical dendroids. Its significance was first recognized (LAPWORTH in HOPKINSON & LAPWORTH, 1875) and its morphology worked out (WIMAN, 1893; KRAFT, 1926; and others) in the Graptoloidea, and its role in the Dendroidea was only more recently appreciated.

The walls of the **prosicula** are strengthened not only by the spiral thread (*Schraubenlinie* of KRAFT) but also by longitudinal rods or fibers (*Längsverstärkungsleisten*) (Fig. 39,*1*). Three or four of these merge into the base of the nema, where it grows out as a hollow tube from the apex of the prosicula, and clearly serve as an anchorage for this; the remainder seem to grow from the apertural margin of the prosicula, thinning and disappearing when traced toward the apex.

The **metasicula** is sharply differentiated from the prosicula by its close-set regular growth lines, meeting in a zigzag suture down the two opposite sides (dorsal and ventral); on the virgellar or ventral side is embedded the **virgella** (Fig. 39,*2*), usually a conspicuous spine involving deposition of secondary skeletal tissue; while on the dorsal side, symmetrically placed apertural spines (or rarely, one spine) may arise when growth is complete (see Fig. 48,*6*), as also may broad lateral lappets.

In size, the sicula varies between wide limits. Usually 1.5 to 2.5 mm. in length; it attains 5 or 6 mm. in some monograptids (*Monograptus gregarius, M. acinaces*) and it may be a centimeter or more in *Cystograptus* and *Corynoides* (Fig. 39,*6*). In shape, however, the sicula varies little, apart from slight differences in length-breadth ratio, or a gentle curvature; apertural spines are not uncommon and more elaborate processes occur in a few species (Fig. 39,*5*). In *Linograptus,* an umbrella-shaped structure called the **virgellarium** occurs at the tip of the virgella and may be connected with buoyancy (Fig. 39,*7*); in *Climacograptus baragwanathi,* the virgella breaks up distally into a mass of reticulating fibers.

More or less regularly spaced internal rings (annuli) are present in the siculae (Fig. 39,*4*) and more rarely the proximal thecae of various species of *Monograptus,* and in *Linograptus* the first ring may even be situated on the prosicula. Except for the ring separating the prosicula from the metasicula, and that related to the initial bud, they are not apertural and do not correspond to periods of arrested growth; in fact, the annuli are commonly oblique to the fuselli. Their significance is not yet known; ringed and ringless forms occur in the same species and the number of rings, when present, is variable.

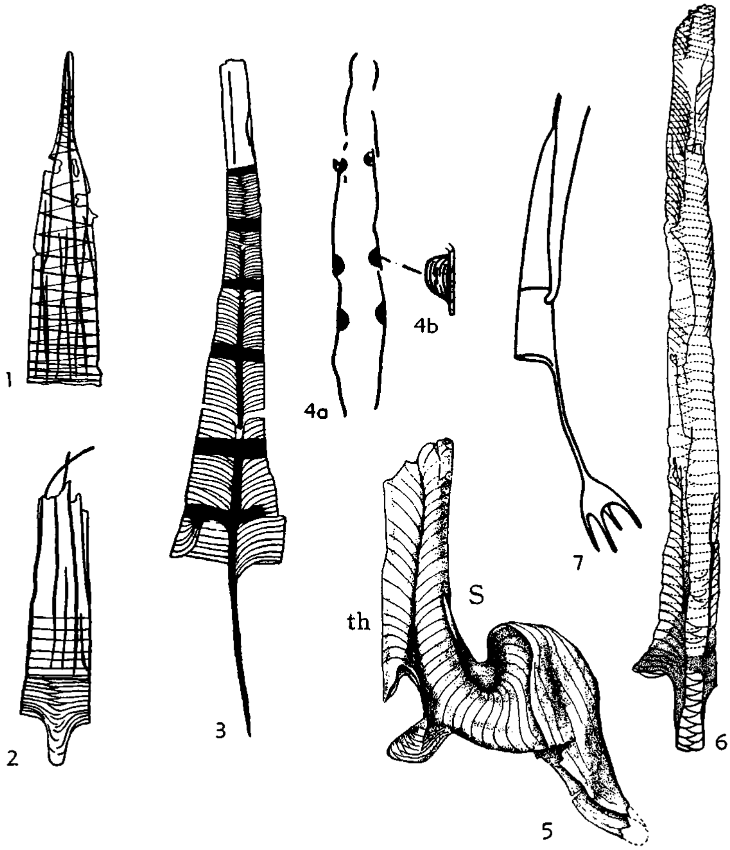

FIG. 39. Sicula in Graptoloidea.

1. Prosicula *(Diplograptus* sp. *cf. D. maxwelli)* with spiral and longitudinal lines, ×55 (255).
2. Early stage in metasicula of same, showing origin of virgella, ×55 (255).
3. Nearly adult metasicula of *Monograptus* with annuli, ×35 (256).
4. Longitudinal section *(4a)* of same showing internal position and structure *(4b)* of annuli, ×80 (256).
5. Apertural modifications of sicula of *Corynites wyszogrodensis,* ×35 (117). [*S,* sicula; *th,* theca.]
6. Elongate metasicula of *Corynoides curtus,* ×30 (23).
7. Sicula of *Linograptus posthumus* with virgelarium, ×20 (252).

In the Archiretiolitinae, the sicula is usually fully sclerotized although the rhabdosomal walls are reduced to a reticulum (and a comparable relation occurs in the dichograptid *Dinemagraptus*); but in the true retiolitids the sicula is either not sclerotized or is only represented by the delicate prosicular portion.

Further details are given below under the heading "Development."

THECAE

GENERAL RELATIONS

The form of the thecae, particularly in the apertural region, varies greatly and in fact constitutes one of the most valuable bases for the recognition of species and even genera. Outwardly, the simplest type is a straight, almost cylindrical tube partly overlapped by that which precedes it and partly overlapping that which follows it. In the past, much confusion has existed regarding the precise use of such terms as "thecae," "common canal," "interthecal septum," and others, but largely through the work of WALKER (1953), URBANEK (1953, 1958) and others, it now seems possible to define the parts with some precision. So far as concerns the periderm, each

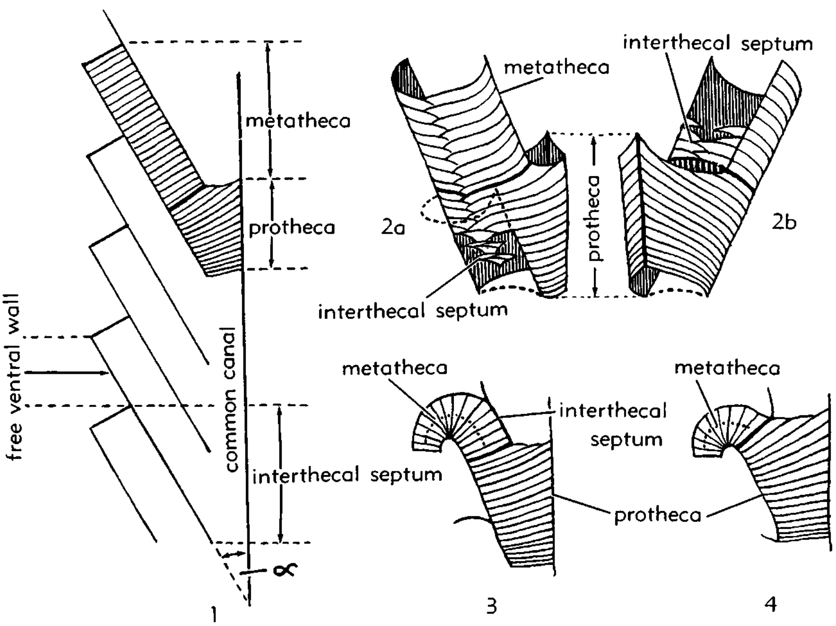

FIG. 40. Diagrams illustrating terminology of a graptolite stipe and thecae (α =angle of inclination) (29).

theca develops from the preceding theca and usually a slight but definite break or "unconformity" occurs between growth-lines of one theca and those of the next. Each theca can thus be divided into two parts, a **protheca** corresponding to the stolotheca of the dendroids and a **metatheca** corresponding to the autotheca of the dendroids[1] (Fig. 40). In the description of some highly elaborated thecae, it may be convenient to distinguish between a subapertural and an apertural portion of the metatheca (URBANEK, 1966), and in diverse graptolites, the initial portion of each protheca constitutes a distinct node which has been called the **prothecal fold.** The sum of the prothecae of a stipe, whether uniserial or biserial, constitutes the **common canal** of earlier authors (Fig. 40,*1*) and corresponds to the chain of stolothecae along the dorsal wall of a dendroid stipe. Although the common canal has thus no real entity as a structural unit, it is sometimes a useful descriptive term. A peculiar structure called the appendix occurs in *Gothograptus* (see Fig. 95,*10b*) and some other members of the Plectograptinae, where what appears to be a continuation of the common canal extends as an open tube beyond the thecate portion of the rhabdosome.

Normally, each thecal zooid buds off a single descendant zooid, but all bilateral rhabdosomes include at the proximal end at least one **dicalycal theca** (JAANUSSON, 1960) which produces two descendants, and in branched graptoloid rhabdosomes every branching division must relate to a dicalycal theca. This is further discussed in the sections headed "Development" (p. *V*71) and "Branching" (p. *V*82). The occurrence of dicalycal thecae at other points than the proximal end of a rhabdosome has not yet been investigated owing to lack of suitable material. By its nature, the dicalycal theca implies the presence of two prothecal segments, or what may be termed a prothecal and a mesothecal segment.

With minor exceptions, such as the apertural processes of certain cucullograptids, a theca remains bilaterally symmetrical in the plane of the stipe, whatever modifications in form it may undergo.

Each theca is composed of alternating right and left half-rings or fuselli, which basically meet in a zigzag suture (as in the

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[1] The term "theca" thus used corresponds to the "thecal segment" of TÖRNQUIST, 1899; the protheca corresponds to the "semitubus" and "metatubus" of MÜNCH, 1938, and metatheca to his "thecatubus."

sicula) along the dorsal and ventral sides; but irregularities are not uncommon and in particular, complications tend to be introduced where the thecae overlap—that is to say, on the interthecal septa and the median septum, where a single peridermal wall separates two distinct zooids.

INTERTHECAL SEPTUM

An interthecal septum comprises the dorsal wall of one theca, *n*, and a portion of the ventral wall of the succeeding (overlapping) theca, $n+1$. In general, the fuselli of the proximal portion are continuous with the fuselli of theca *n*, while those of the distal portion are continuous with the fuselli of theca $n+1$ (Fig. 40,*2*). Commonly intercalary fusellar segments occur, the origin of which remains uncertain; WALKER (1953) considers them a secretion of theca $n+1$, whereas URBANEK (1958) associates them with theca *n*. In some examples, ranging from didymograptid at one extreme to monograptid at the other, the growth of theca *n* is so far in advance of theca $n+1$ that the entire septum must clearly be secreted by theca *n;* but THORSTEINSSON (1955) has contended that in some cyrtograptids, the septum is wholly secreted by theca $n+1$. Finally, SKEVINGTON (1965) has claimed that in *Glyptograptus dentatus* the interthecal septa, although marked externally by grooves separating the fuselli of adjacent thecae, are absent internally, and he has attributed this to the very slight angle of inclination and close proximity of adjacent zooids; but the interthecal septa are clearly complete in known climacograptids with an even lower angle of inclination.

MEDIAN SEPTUM

The dorsal wall, where it is prothecal, is usually quite regular, but may show intercalary fuselli; it may be nonexistent where the theca (or some portion of it) is adherent to a previously secreted part of the rhabdosome such as the sicula. In dipleural biserial rhabdosomes, the dorsal wall of each stipe is represented by the median septum. Information regarding the structure of this remains scanty, but although it marks the apposition of two distinct stipes, no positive evidence indicates that it comprises more than one layer. URBANEK (1959) has related this to the fact that the terminal theca of one or other series grows slightly ahead and produces the median septum as its dorsal wall. The fuselli are close-set, inclined distally and inward toward the central nema and the structure is somewhat irregular, with numerous intercalary fuselli (see Fig. 46,*2*).

Where the median septum is complete, it arises between $th2^2$ and $th3^1$ (the first four thecae being alternating in origin), but in some biserial graptolites the septum tends to be delayed as more and more of the proximal thecae alternate in origin. The process culminates in a wholly aseptate rhabdosome which in one sense is the only truly biserial condition. Progressive delay in the origin of the septum has been shown by WAERN (1948) to have stratigraphical value in a series of forms related to *Climacograptus scalaris.* Little general stratigraphical significance is seen in the tendency, however, since many late (Silurian) forms have a complete septum, whereas aseptate forms or those with a notably delayed (incomplete) septum may occur well down in the Ordovician.

The term **cryptoseptate** has been suggested by URBANEK (1959) for the condition in *Gymnograptus linnarssoni,* for example, where the nema is attached to the rhabdosome walls by peridermal rods but a peridermal septal membrane appears to be lacking.

In other instances again, the septum may be present at first on one side of the rhabdosome only (apparently usually the obverse), thecae on the opposite side being to all appearances alternating in origin; such a condition is referred to as a **partial septum.** A stage has been reached in *Cephalograptus cometa* where the partial septum is reduced to a mere ridge on the periderm of the obverse side.

No details are yet available concerning the structure of the median septum in monopleural rhabdosomes (Glossograptina) (see Fig. 90).

PRINCIPAL TYPES

The basic types of graptolite thecae may be defined as dichograptid, leptograptid, dicellograptid, climacograptid, triangulate (and isolate), hooked, lobate and auriculate; but the extent of variation now being revealed within almost any of these types makes precise definition difficult. In the majority of these, and commonly as a result of differential growth, the main axis of the theca becomes curved and the more extreme forms involve modification of the entire apertural region. An introverted theca is one with the aperture facing inward (dorsally), in contrast to an everted aperture which faces outward (ventrally); development of the latter may result in a hooked or retroverted theca. Pronounced sigmoidal curvature of the thecal axis is usually associated with a definite **geniculum** (JAANUSSON, 1960), an angular bend in the free ventral wall, separating a supra- from an infragenicular portion. The geniculum may be the site of median or paired spines, or may be associated with median or paired flanges overhanging and restricting the aperture of the preceding theca.

Simple straight thecae (Fig. 40,*1*) characterize the uniserial stipes of the vast majority of dichograptids, many simpler monograptids, and the biserial stipes of certain diplograptids; accordingly, this has been appropriately termed the **dichograptid type.** Exceptionally, however, even dichograptids may show more advanced types (*Didymograptus leptograptoides* MONSEN and *Aulograptus*) and the sinograptids have quite highly elaborated thecae (*Holmograptus* and *Sinograptus*).

The first widespread thecal elaboration is a gentle sigmoidal curvature of the ventral wall, accompanied by elongation and reduction in the angle of inclination, which results in the so-called **leptograptid type** (Fig. 41,*1*). This finds its typical development in the Nemagraptidae, occurring also in some monograptids. Somewhat similar is the type seen in *Glyptograptus* (Fig. 41,*2*) among biserial forms.

The **dicellograptid type** is characterized by the development of a geniculum and by introversion, usually accompanied by some degree of isolation of the apertural region (Fig. 41,*3-5*). The supragenicular wall is usually convex, in some forms angularly so, and provided with a mesial spine.

A more pronounced expression of this sigmoidal curvature results in the sharply angular geniculation of many **climacograptid types** (Fig. 41,7); many diplograptids and some species of monograptids (e.g., *Monoclimacis*) show this. The supragenicular wall is usually straight; it may be parallel to the axis of the rhabdosome, or inclined distally inward or outward, rarely curved (*Pseudoclimacograptus,* Fig. 41,*6*) and with everted apertures (*Clinoclimacograptus*). It is short and inwardly inclined in *Lasiograptus* (Fig. 41,*8*) and *Gymnograptus,* and extremely short in the modified forms of this theca occurring in *Cryptograptus* and *Hallograptus.*

Thecal modifications are most conspicuous in the Monograptidae; dichograptid, leptograptid, and climacograptid types occur here, but the more extreme modifications all involve some degree of apertural "isolation." In these Silurian forms, however, the theca, as it becomes free distally, twists outward with excessive development of the dorsal lip (retroversion), in contrast to the introversion of the more extreme dicellograptids and dicranograptids of the Ordovician. Accompanying this isolation is a reduction or loss of the interthecal septum and an increase in the prothecal ratio (Fig. 40,*3,4*); thecal overlap can only be recognized in a restricted sense and ceases to have any precise descriptive or systematic value. ELLES (1922) recognized three main lines of this monograptid development (hooked, lobate, isolate); the term "triangulate" has also been applied, particularly to early stages in the isolate development. In recent years, a varied suite of modifications has been recognized which involve the development of conspicuous apertural flanges, and may be referred to collectively as auriculate.

In the **hooked type,** the isolate distal portion of each theca grows back upon itself in the form of an open hook, familiar in the widely distributed *Monograptus priodon* (Fig. 42,*1*). Typically no transverse widening of an apertural region occurs but lateral spines are commonly present. The thecae may overlap sufficiently to produce an appreciable interthecal septum, but in others provisionally included here (*M. clingani*) this may be lost.

The **lobate type** is really a very compact form of hook developed exclusively by the dorsal wall, which grows out and back over the thecal aperture like a cowl. Its highest development is seen in such species as

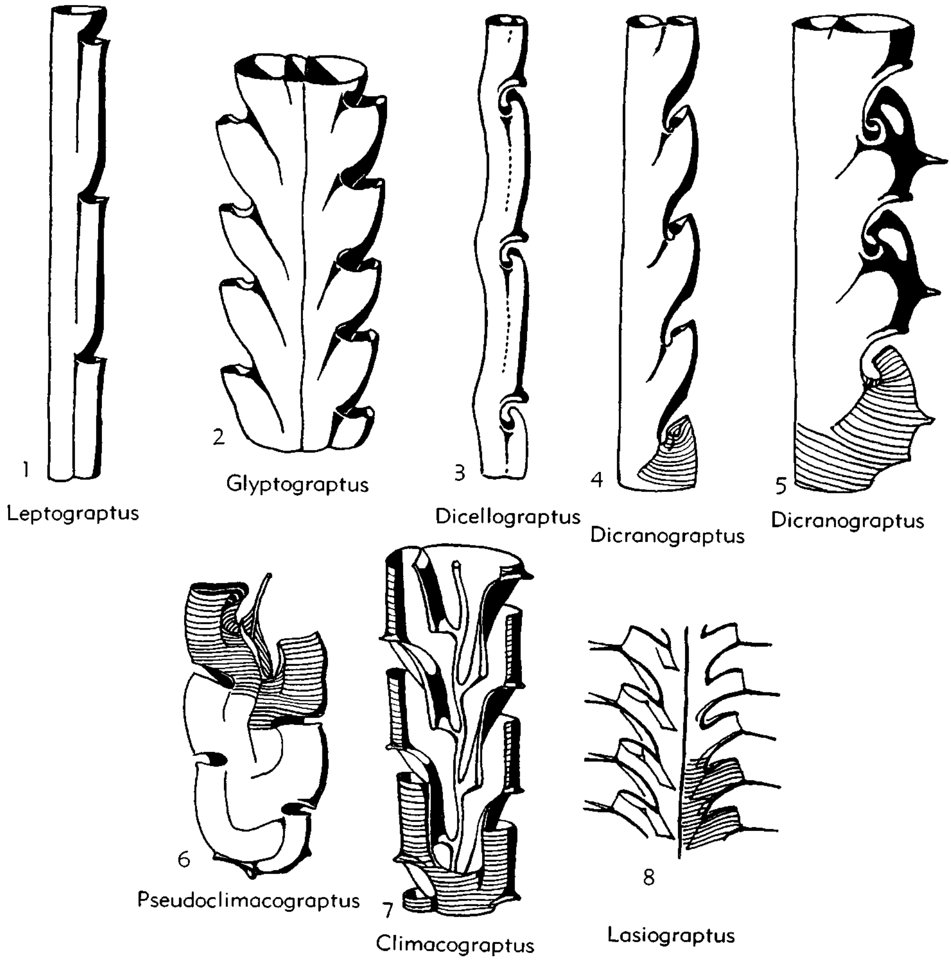

FIG. 41. Variations in graptolite thecae, mostly somewhat diagrammatic (21).

1. *Leptograptus*, ×15.
2. *Glyptograptus*, ×15.
3. *Dicellograptus geniculatus*, ×19.
4. *Dicranograptus pringlei*, ×11.
5. *Dicranograptus nicholsoni*, ×11.
6. *Pseudoclimacograptus scharenbergi*, ×22.
7. *Climacograptus typicalis*, ×19.
8. *Lasiograptus harknessi*, ×10.

Monograptus lobiferus (Fig. 42,2) and *M. becki*, where the thecal aperture is almost closed and the thecae appear in compressed material as a series of evenly spaced, rounded protuberances along the stipe. A related form is seen in *M.* sp. *cf. M. knockensis* (Fig. 42,*3*), where isolation is more strongly marked and the lobe less inflated.

In the **triangulate** and **isolate type** there is typically no trace of an interthecal septum, and the more extreme developments are so unlike normal Monograpti that they long ago received the separate generic name *Rastrites*. In less extreme development (*Monograptus spiralis* or *M. convolutus*, Fig. 42,*5*,*6*), the thecal segment is more or less triangular and the theca is distinctly hooked, but with an enrolled dorsal lip and transverse processes; the theca in profile view appears triangular, sometimes with a "flowing" apertural spine (one or other of the transverse processes), its apparent form depending on shearing). In *Rastrites* itself (Fig. 42,*7*) the straight slender thecal tubes terminate in a compact lobate aperture and are sharply differentiated from an extremely tenuous common canal, from which they extend at high angles as a row of uniformly spaced parallel tubes.

In addition to the above types, others are beginning to become known through the work of EISENACK, MÜNCH, BULMAN, and especially URBANEK on graptolites dissolved out of Silurian limestones; they are here provisionally referred to as the **auriculate group.** For the most part, these comprise long, slender thecae, with very little overlap and very short metathecal segments, of which a considerable portion of the apertural region is involved in large paired lateral lobes or auricles (cucullograptids) or a single lidlike shield developed from the dorsal margin (Fig. 42,*8*,*9*).

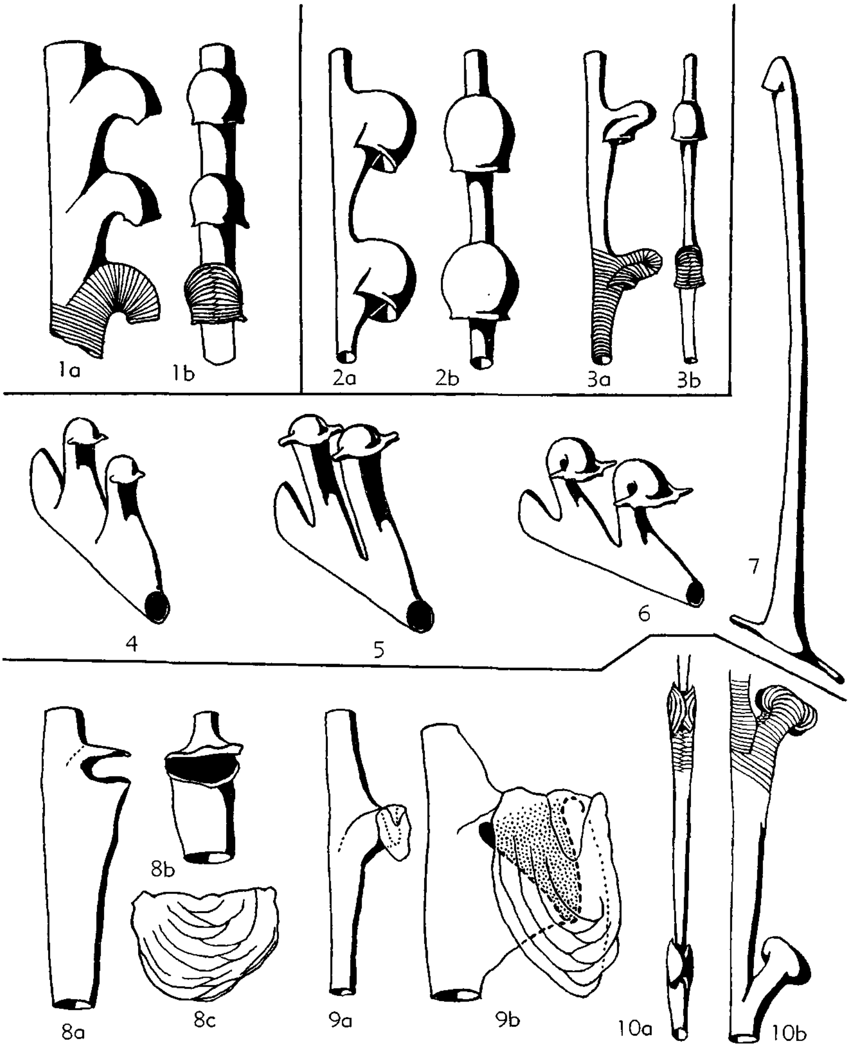

FIG. 42. Variations in monograptid thecae, somewhat diagrammatic (29).

1a,b. Monograptus priodon.
2a,b. M. lobiferus.
3a,b. M. knockensis.
4. M. triangulatus.
5. M. convolutus.
6. M. spiralis.
7. Rastrites.
8. M.sp. —— *8a,b,* ×35. —— *8c,* ×60 (Münch, 1938).
9. M. huckei. —— *9a,* ×25. —— *9b,* ×100 (Münch, 1938).
10a,b. Cucullograptus (Lobograptus) scanicus.

MONOGRAPTID TRENDS AND THEIR SIGNIFICANCE

The hooked, lobate, and isolate types of monograptid thecae appear to constitute definite trends (ELLES, 1922), each affecting large numbers of species. They were believed to operate during a comparatively short period of time and to be nonrecurrent, but some evidence indicates that hooked forms, at least, were either more persistent than originally was thought or actually reappeared after a considerable interval of time.

No graptoloid rhabdosome is composed of precisely similar thecae throughout; on the contrary, the thecae all undergo some change in form (commonly slight but in some very conspicuous) when traced along the stipe and this astogenetic succession is always remarkably regular. It is also one of the factors which complicate attempts to subdivide or define such genera as *Monograptus* on the basis of thecal form. ELLES (1922) recognized that new thecal types were introduced at the proximal end of the rhabdosome (Fig. 43), spreading distally in successive descendants, but exact data have not been available until recently and still regrettably few well-authenticated phylogenies can be cited. From the analysis of some triangulate monograptid lineages, SUDBURY (1958) was able to resolve the change into two processes, a distal spread of the new type (whereby more and more thecae acquired the new character) and a general change (whereby all thecae of the rhabdosome showed a slight and gradual trend toward the new type; Fig. 44). These processes were later referred to by URBANEK (1960) as *penetrance* and *expressivity,* respectively. In addition, SUDBURY presented some evidence that a new type might also be introduced distally. Convincing evidence of this distal introduction of new types has been provided by URBANEK (1966) in his precise work on the cucullograptids (Fig. 45). Moreover, he has attempted a biological interpretation of these evolutionary changes (URBANEK, 1960) on a morphophysiological gradient hypothesis. Briefly, he suggested that morphogenic substances, some acting as stimulators and some as inhibitors, were transmitted from the siculozooid in steadily decreasing quantities through the asexually budded succession of zooids, and that when these fell below a certain threshold level they no longer exerted any effect. Proximal introduction of a character results from increasing activity of a morphogenetic stimulator, together with a lowering of the threshold level; distal introduction results from diminishing activity of an inhibitor and a rise in threshold level. (See also section on "Cladia," p. V85.)

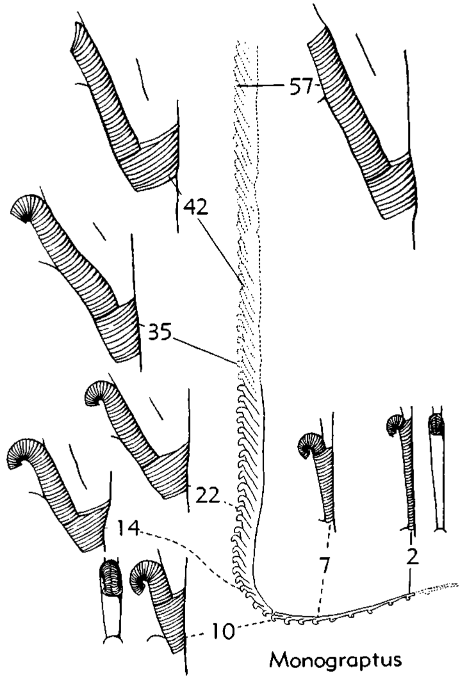

FIG. 43. Thecal changes along rhabdosome of *Monograptus argenteus* (NICHOLSON); outline of rhabdosome, ×2; enlarged thecae, ×10 (29).

The few examples so far described are all monograptid, but comparable phenomena seem to be of general occurrence among Graptoloidea, especially dicellograptids and diplograptids.

APERTURAL PROCESSES, SPINES AND LOCALIZED THICKENING OF PERIDERM

Certain species of most graptolite genera show a development of apertural spines associated with some or all thecae of the rhabdosome, and spines may also be developed at other points, such as the ventral wall of a theca (mesial spines) of rarely

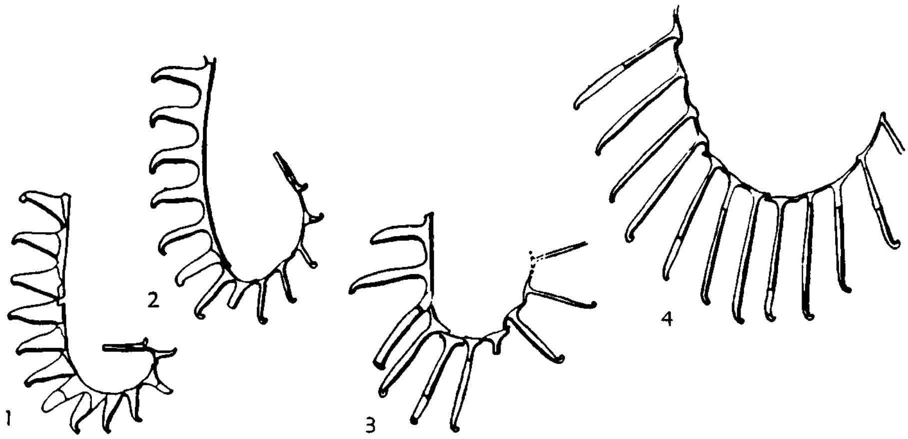

FIG. 44. Proximal introduction and distal spread of new thecal type in triangulate monograptids, all ×5 (230).——*1. Monograptus triangulatus separatus.*——*2. M. triangulatus triangulatus.*——*3. M. triangulatus extremus.*——*4. Rastrites longispinus.*

laterally (e.g., *Dicaulograptus*) or from the dorsal wall of a stipe (e.g., *Didymograptus nodosus*) or even along the edges of the septum (e.g., *Nymphograptus,* see Fig. 93,*4*).

Apertural spines are usually median in position and unpaired, and every gradation is found between a blunt denticle and slender aciculate spine; they are laid down in the manner of the sicular virgella (Fig. 39,*2*) and strengthened by deposition of secondary tissue. Such spines are particularly associated with the first two thecae of the rhabdosome (especially in dicellograptids and biserial genera) and in *Climacograptus bicornis,* where these spines are unusually large, the first two thecae may become completely involved, with their distal portions growing back along the spines. In other *Climacograptus* species, comparable spines are associated with flanges *(C. papilo,* see Fig. 70,*11)*.

More rarely, apertural spines are paired structures (e.g., *Orthograptus quadrimucronatus* and various monograptids) and these are not produced from overlapping, alternating fuselli but arise as localized secretions of lateral fuselli (monofusellar tissue), as in *Saetograptus chimaera* (see Fig. 101,*3*). In some varieties of the *O. quadrimucronatus* groups, the spines of one particular thecal pair may be exaggerated in length.

Somewhat more complicated are the dorsal and lateral spines described by WHITTINGTON & RICKARDS (1969) as hollow structures associated with the microfusellar hood overhanging the apertures in *Glossograptus.*

The most remarkable spinous developments occur among the lasiograptids (see Fig. 93) where apertural and mesial spines of great length may break up distally to form an interlacing network **(lacinia)** outside the thecal apertures. Such structures are presumably of cortical tissue.

Spines usually have been regarded as protective in function and RUEDEMANN (1947) has observed that they are commonly placed at exposed portions of the rhabdosome; but the possible relationship of apertural processes to the lophophore of the graptolite zooid, both as supporting structures and hydrodynamic tunnels related to feeding, has been pointed out by URBANEK (1966).

LOCALIZED THICKENING. Certain graptolites show a marked thickening of parts of the periderm along structural lines, accompanied by attenuation or reduction of intervening areas of the test; the "shell" or box construction of the normal rhabdosome is replaced by a structural framework **(clathria)** of **lists** (strengthening rods) carrying only the most delicate cuticular "skin" or in extreme cases none at all. This is associated commonly with a profuse development of spines (apertural, mesial and lateral), in some breaking up into a filamentous network **(lacinia)** beyond the limits of the rhabdosome proper. Such features are developed to a varying extent in the Diplograptidae, Glossograptidae, and Lasiograptidae; and the recent discovery of *Dinemagraptus* shows that comparable features were developed even in the Didymograptina.

A thickened selvage on the apertural margin (apertural list) occurs generally; this may be extended laterally (pleural lists) and distally (mesial list) to form a bent ring, strengthening the aperture. Such is found in some climacograptids and more particularly in amplexograptids, and may be continued into mesial and apertural spines, as in the lasiograptids. The latter usually exhibit also at least the beginnings of parietal lists along edges of the interthecal septum, and an aboral list formed by thickening of the inner edge of the septum. Completing this framework (or clathria) a longitudinal list may occur along each lateral wall of the rhabdosome, and, except where thecal overlap is almost total, a longitudinal list also appears connecting the mesial with the apertural list along the mid-ventral line of each theca.

Among the Retiolitidae, the clathria supports a delicate skeletal network, the **reticulum;** in well-preserved specimens this seems

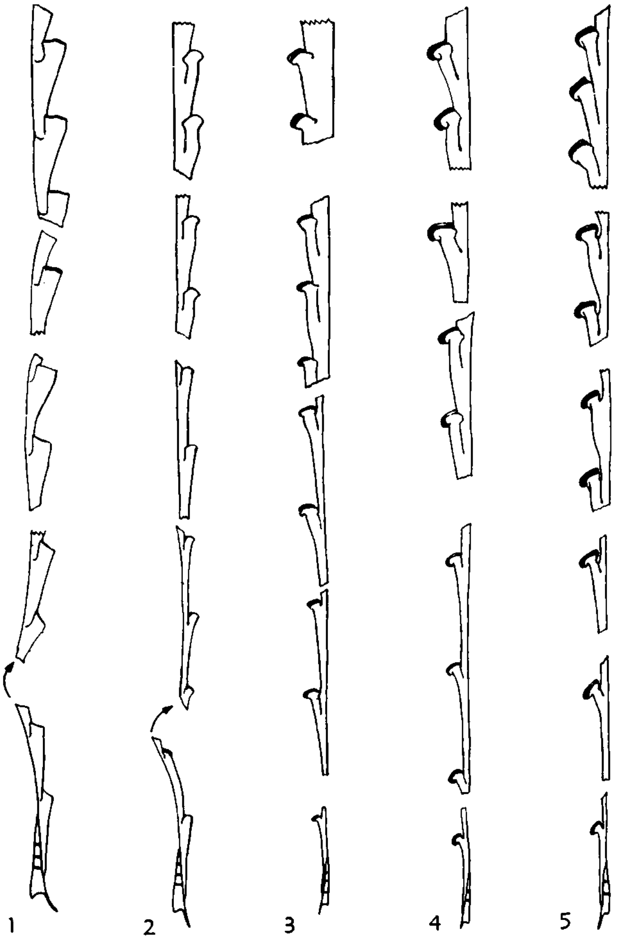

FIG. 45. Distal introduction and proximal spread of new thecal type in cucullograptids; all ×20 (253).——*1. Cucullograptus (Lobograptus) progenitor.——2. C. (L.) simplex.——3. C. (L.) scanicus parascanicus.——4. C. (L.) scanicus amphirostris.——5. C. (L.) scanicus scanicus.*

to be covered by an exceedingly thin, possibly structureless, film, but its relation to the normal graptolite periderm are obscure.

The three structures, clathria, reticulum and lacinia, need not be closely correlated; *Retiolites,* with perfect reticulum and clathria, has no lacinia; in *Nymphograptus* and most *Lasiograptus,* the clathria is associated with a well-developed lacinia; and in *Plegmatograptus nebula* the clathria is barely developed, the reticulum being distinct but irregular and the lacinia well developed.

NEMA

Among the Dichograptidae, with the exception of *Phyllograptus, Cardiograptus* and *Oncograptus,* a threadlike nema commonly extends from the apex of the prosicula and probably served (as suggested by Lapworth) for fixation of the rhabdosome, at least in juvenile stages; examples are known where it terminates distally in a somewhat irregular attachment disc. In the genera *Leptograptus* and *Dicellograptus,* the nema is usually so short that it is not obvious how it can have served, at a mature stage of astogeny, for attachment of the rhabdosome; and *Dicranograptus* appears to have lacked a nema. Among the Diplograptidae, a nema is invariably present as a central axis, then commonly referred to as the virgula, embedded in the median septum or in aseptate forms lying freely in the cavity of the common canal and in some species anchored by fusion to the bases of the interthecal septa (Fig. 46,*1*). Even where embedded in the median septum, additional strengthening lists may be developed (also in the median septum) connecting the nema with the lateral walls of the rhabdosome (Fig. 46,*2*). In monograptids, the nema is embedded in the dorsal wall of the stipe. Its relations in cladia-bearing monograptid genera are described elsewhere (p. *V*85).

The doubtful relations of the nema in retiolitids have been resolved largely by the work of Eisenack (1951) and it is now known that the "straight axis" in the lateral wall of *Retiolites* is the true nema. In other retiolitids it may be free and axial in position, and in still others it ends blindly within the rhabdosome, perhaps continued as an unsclerotized thread.

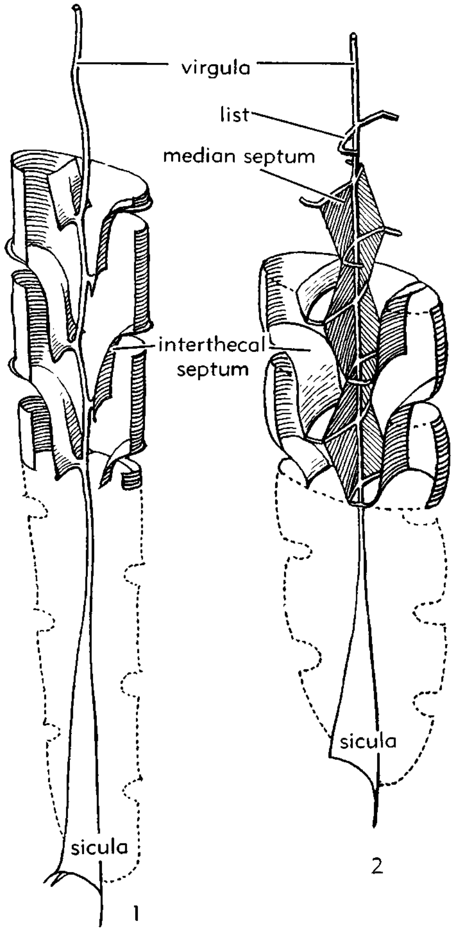

Fig. 46. Stereograms showing relations of virgula to median septum and interthecal septa in biserial graptolites (19).——*1.* Aseptate, *Climacograptus typicalis.*——*2.* Septate, *Pseudoclimacograptus scharenbergi.*

Several biserial graptolites possess what has been interpreted as a float at the distal end of the nema; this is discussed in the section on buoyancy, p. *V*93.

The nema of the neanic and adult rhabdosome replaces the embryonic *nema prosiculae* (Fig. 39,*1*), which is a hollow tubular projection from the apex of the prosicula. Lengthening of the *nema prosiculae* occurs during growth of the sicula; subsequent breakage and replacement of this by a regenerative nema has been described by Urbanek as "almost normal" in some monograptids, but in other graptolites the one appears to have developed from the other. Whether the nema remains hollow or becomes a solid rod is disputed, though the latter seems the more probable; and without doubt the nema can continue to lengthen during astogeny and this must be due to the presence of some covering layer of living tissue. Lengthening is convincingly demonstrated in synrhabdosomes comprising colonies in all stages of development, including young growth stages with very short nemata. Irregular flanges and thickenings may occur (e.g., *Climacograptus parvus*) on the outside of the nema in addition to the terminal "float" (see Fig. 69).

REGENERATION

Graptolites possessed considerable powers of regeneration of damaged skeletal tissue and examples are to be found in any large collection of fossils dissolved from the matrix (KRAFT, 1926; BULMAN, 1932; EISENACK, 1940; KOZŁOWSKI, 1949; URBANEK, 1958; etc.). Where the repair is to damage at the growing edge of the rhabdosome, it is effected by normal fuselli (though the growth lines are of course unconformable to those of the undamaged tissue). In other places on the rhabdosome, where it could no longer be repaired by that portion of the zooid concerned with the secretion of fusellar tissue, it is composed of a structureless film presumably comparable with cortical tissue and secreted by some part of the organism responsible for cortical tissue.

Prosiculae are particularly susceptible to injury in early stages of growth; indeed, a

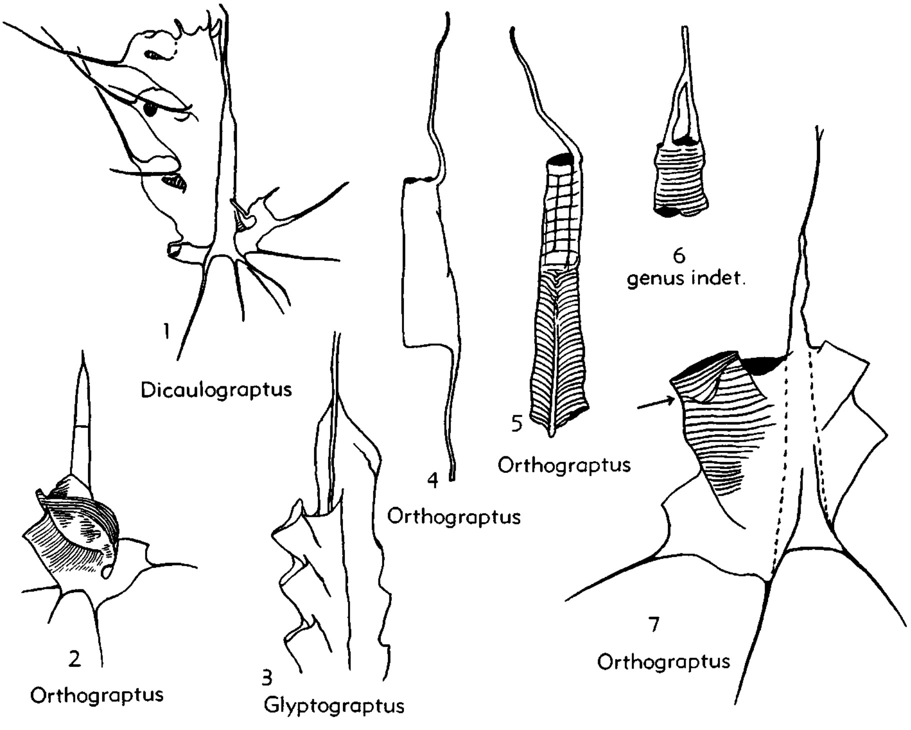

FIG. 47. Malformations and regeneration in graptolites.

1. Suppression of stipe above second-formed theca *(th1²)* in biserial rhabdosome, *Dicaulograptus hystrix,* ×18 (19).

2. Malformation of proximal end, *Orthograptus gracilis,* ×13 (19).

3. Suppression of one stipe in biserial rhabdosome at distal end, *Glyptograptus dentatus,* ×10 (19).

4. Loss of prosicula, virgula attached to metasicula open at both ends, *O. gracilis,* ×30 (19).

5. Damage to prosicula open-ended distally, *O. gracilis,* ×40 (56).

6. Loss of prosicula, bifurcating virgula attached to metasicula, genus indet., ×30 (56).

7. Regeneration of damaged theca, *O. gracilis,* ×30 (126).

high proportion of diplograptids and monograptids possess regeneration nemata and URBANEK has concluded that in *Saetograptus chimaera* it is almost invariable. Damage to the graptolite rhabdosome in general is usually ascribed to some unknown predator, but may be due to wave action, and damage to the nema appears to have been due to insecure attachment during initial stages in the change from planktonic siculae (with nonfunctional nema prosiculae) to the epiplanktonic attachment of neanic stages.

The most remarkable instances of regeneration, involving the development of an entire colony (pseudocladium), have been described by URBANEK (1963) in the linograptids; this process is related to the development of cladia and is discussed further in that section (p. *V*89).

ABNORMALITIES IN DEVELOPMENT

Regularity in development of the graptolite rhabdosome is one of the most distinctive features of the group, but malformations due to some pathological cause and not to damage and regeneration are also known. Some examples concern single thecae only and generally affect the shape of the aperture or apertural processes; others affect several thecae before normal development is resumed. It is not clear whether the example illustrated in Figure 47,*1* is truly pathological, or follows damage to *th*2^1; but the normally biserial rhabdosome has been converted to an exceptional uniserial colony.

URBANEK (1958) has described monograptid siculae with "twin pores," one lying on either side of the virgella, which may be due to some acceleration in the budding process. In another example, abnormality in *th1* (in *Saetograptus chimaera*) is associated with an abnormal budding process; *th2* is completely partitioned off from *th1* and a lateral resorption foramen in the first and another foramen in the second theca mark the points of exit and re-entrance of the stolon, which in its extrathecal course remained unprotected by any sclerotized skeleton.

Thecal occlusion, commonly recorded in dendroids and camaroids, is rare among the Graptoloidea.

DEVELOPMENT[1]

GENERAL DISCUSSION

Development commences with the secretion of the prosicula, of which three stages have been recorded (KRAFT, 1926). The earliest of these (Fig. 48,*1*) consists of a delicate bottle-shaped object, usually 400 to 500 microns in length, open at the base and closed at the neck or *nema prosiculae*. It is faintly marked with a spiral thread *(Schraubenlinie)* which may be coiled indifferently right- or left-handedly; this spiral thread may be strengthening, or perhaps (according to KRAFT) marks the line of fusion of a continuous spiral growth band. In the second stage (Fig. 48,*2*), a group of three or four longitudinal strengthening fibers is laid down from the *nema prosiculae* to the aperture of the prosicula. Finally (Fig. 48,*3*), secondary longitudinal fibers are secreted between the primaries, extending one-half to two-thirds the way from the aperture to the *nema prosiculae* and the growth of the prosicula then is complete. A ring of secondary tissue may (rarely) be developed at the margin of the prosicula, marking a pause in growth.

An entirely new structure, the metasicula, then begins to appear (Fig. 48,*4*,*5*). This contrasts sharply with the prosicula in its incremental mode of growth, being composed of normal peridermal fuselli laid down in alternating growth bands with typical zigzag suture along opposite (dorsal and ventral) sides. Rarely, the ventral and dorsal zigzag sutures, according to KOZŁOWSKI (1954), may be absent at the commencement of the metasicula. These growth bands tend to extend forward along the ventral side (Fig. 48,*4*), resulting in a rounded projection and later a short spine, which is finally reinforced to form the virgella spine. In nearly all dichograptids, a true virgella is absent and is represented only by a blunt or rounded ventral process. KOZŁOWSKI (1949) has suggested that the actual spine formation is deferred progressively in stratigraphically younger forms; BARRASS (1954) has claimed that the late formation in *Climacograptus* contrasts with an early formation in *Diplograptus (s.l.)*. When growth of the metasicula is com-

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[1] *See* footnote on page *V*32.

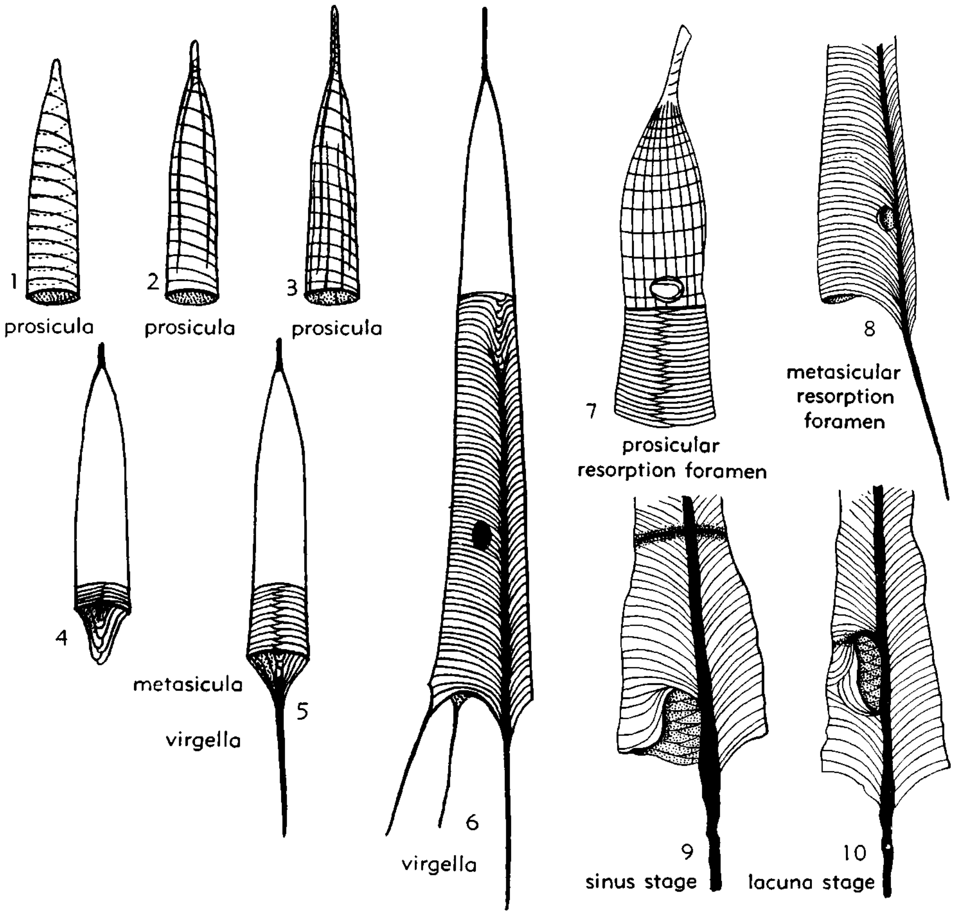

FIG. 48. Diagrams illustrating development of sicula and initial bud (*7-10* from 123, 126, and 249).

1-3. Prosicula.
4,5. Beginning of metasicula and formation of virgella.
6. Completed sicula with apertural spines, virgella and resorption foramen.
7. Prosicular resorption foramen, *Didymograptus* sp., ×65.
8. Metasicular resorption foramen, *Orthograptus gracilis,* ×45.
9. Sinus stage in monograptid, *Pristiograptus bohemicus,* ×65.
10. Lacuna stage in same, ×65.

plete, apertural spines, almost invariably paired, may develop on the dorsal side opposite the virgella (Fig. 48,*6*), but more elaborate apertural modifications occur rarely (Fig. 39,*5*). The presence of annuli among monograptids has already been mentioned (p. *V*59).

POSITION AND FORMATION OF PORUS

The **porus,** or pore through which the initial bud passes to the exterior, may be situated either in the prosicula or metasicula. In primitive and geologically early forms, such as many dichograptids and as in all known dendroids, it is prosicular (Fig. 14,*1,2;* 48,*7*) but in typical graptoloids it is metasicular (Fig. 46,*8*) in position, and seemingly the pore tends generally to arise progressively lower down on the metasicular wall until it comes to lie quite close to the aperture. Normally it is placed close to the virgella and on its (biologically) right-hand side; but in *Didymograptus formosus* (see Fig. 51) the prosicular pore lies on the side opposite to the virgella, which becomes incorporated in the ventral wall of the $th1^{2}$ and *D. rozkowskae* and *D. artus* appear to be other exceptions.

Two methods of pore formation are discriminated. Most commonly, and invariably when it is prosicular in position, a pore is produced by resorption, as clearly demonstrated by its relation to growth lines (or the spiral line on the prosicula). But in *Monograptus* it is contemporary with adjacent sicular tissue, being formed as a notch in the transient apertural margin, later closed by forward-bending growth bands. EISENACK (1942) termed these successive phases the **sinus** and **lacuna stages;** and where sicular annuli occur, the "budding ring" forms an apertural thickening to the proximal rim of the sinus. The formation of pores in dimorphograptids is not known in detail, but they do not appear to have acquired the sinus type of formation.

INITIAL BUD

The initial bud grows out from the porus and down the side of the sicula, except in monograptids and most dimorphograptids where it is erect. As in the dendroid stolotheca no true inner wall is present and the bud is a split tube fused at its edges to the sicula (see Fig. 50,2). Growth bands initially extend uninterruptedly from side to side, but later alternate to produce a median zigzag suture. All varying types of graptolite rhabdosome are derived from this single initial bud by different methods of branching.

In the development of a bilateral rhabdosome two buds must be borne by a single zooid, inhabiting the **dicalycal theca.** This may be the first-formed theca, $th1^{1}$, but it tends to be progressively deferred in the thecal succession; as a consequence of this delay, the earliest thecae acquire an alternating arrangement, growing across the sicula on the reverse side to open on the side opposite that of their origin. The proximal (prothecal) portions of such thecae constitute the **crossing canals.** If $th1^{1}$ is the dicalycal theca, there is one crossing canal, $th1^{2}$. If $th1^{2}$ is the dicalycal theca, there are technically two crossing canals, $th1^{2}$ and $th2^{1}$ (Fig. 49), though the second may be short and inconspicuous. When the $th2^{1}$ is the dicalycal theca, there are three crossing canals ($th1^{2}$, $th2^{1}$ and $th2^{2}$). With the ultimate stage of this process, no dicalycal theca is developed and all thecae either alternate to form an aseptate diplograptid rhabdosome or form a uniserial monograptid rhabdosome.

LATER DEVELOPMENT[1]

Recognition of four main types of development—dichograptid, leptograptid, diplograptid and monograptid—is due to ELLES (1922), but the structural detail now becoming revealed as a result of more modern techniques indicates a more complex range of rhabdosomal development. Stages in these main types recognized by BULMAN (e.g., 1955) retain some value as concise descriptive terms, but the concept of the dicalycal theca introduces a necessary discontinuity into what was formerly regarded as continuous gradual change.

The proximal end development is now known with full growth-line detail from transparencies in nearly 40 species of graptolites, of which the majority are biserial or monograptid. In the dichograptid type, where $th1^{1}$ is dicalycal, the first daughter theca, $th1^{2}$, may be either right- or left-handed, as in many dendroids; but a biologically right-handed origin is more usual, with $th1^{2}$ growing across the front of the sicula oriented with the virgella on the right (Fig. 49). In the isograptid type of development (*minutus, extensus* and *gibberulus* stages of Fig. 49) and presumably also in the leptograptid type, $th1^{2}$ is again right-handed in origin and the dicalycal theca is $th1^{2}$ (or possibly $th2^{1}$ in some leptograptids). In all the various examples of the diplograptid type so far described, $th1^{2}$ originates differently and the few known dicranograptids resemble the diplograptids in this respect. Here $th1^{2}$ arises behind $th1^{1}$ (left-handedly) and consequently grows around and across the front of $th1^{1}$ as well as of the sicula (Fig. 49). But as in isograptids and leptograptids, subsequent budding "fans out" in various ways on the reverse side, leaving the sicula largely free on the obverse side. All these developments have been collectively termed **platycalycal** (BULMAN, 1968). In contrast to them, the biserial rhabdosomes of *Cryp-*

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[1] *See* footnote on page *V*32.

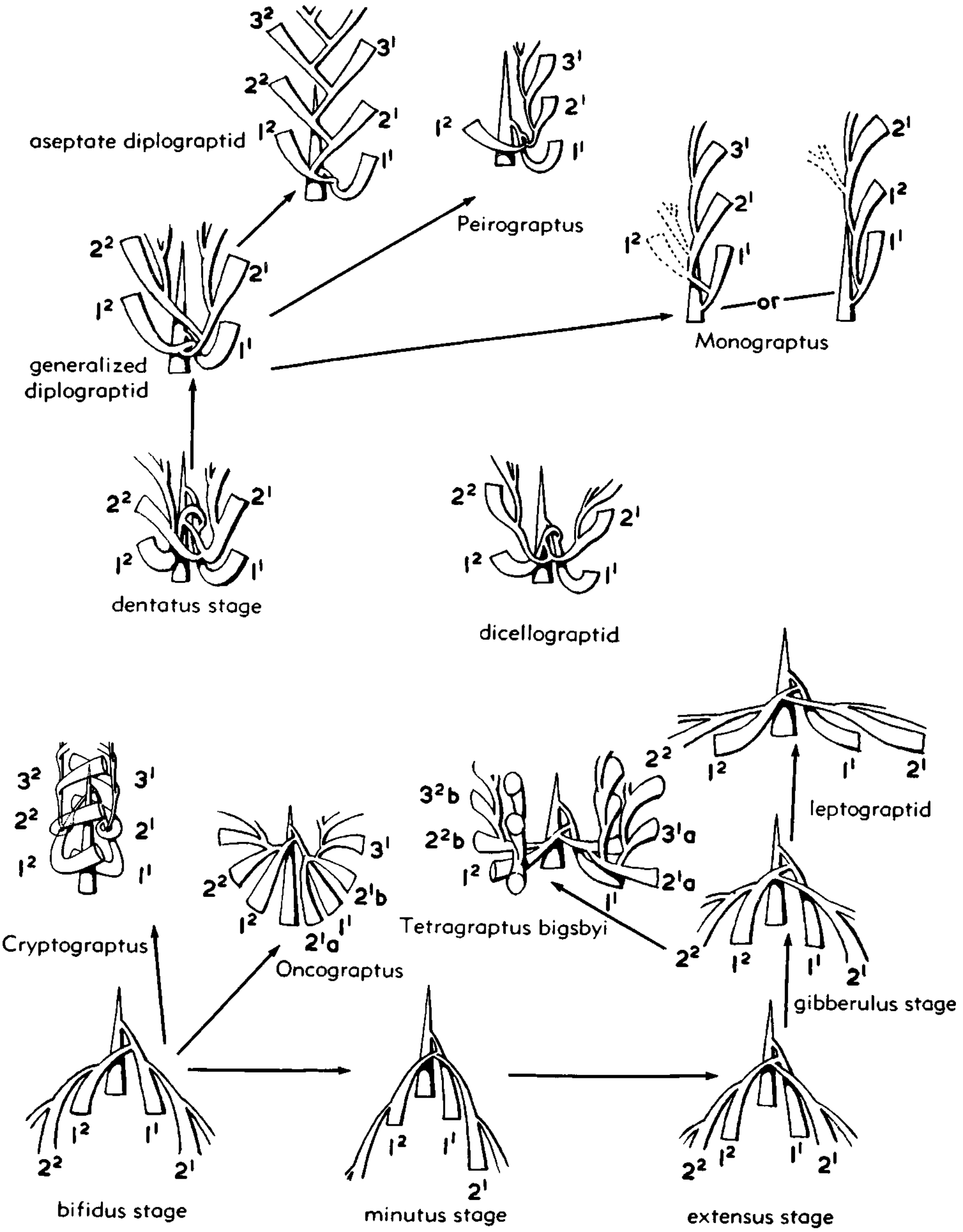


FIG. 49. Thecal diagrams illustrating progressive trends in development of the proximal end. Thecae are numbered according to convention in manner indicating their order of budding in different series, as $th1^1$ (first-formed theca developed from sicula, $th1^2$ (next-formed theca, budded from $th1^1$), $th2^1$ (third-formed theca, budded from $th1^1$ or $th1^2$) and so on. Bifidus stage relates to dichograptid type of development; isograptid type includes *minutus, extensus,* and *gibberulus* stages (Bulman, n).

tograptus and *Glossograptus* develop from a dicalycal $th1^1$ but with $th1^2$ originating left-handedly and growing behind the sicula (Fig. 49); during the course of development the sicula becomes largely enclosed and concealed on both sides, and in this **pericalycal** type of proximal end the terms obverse and reverse have little meaning.

DICHOGRAPTID TYPE

A type of graptolite development characterized by a single crossing canal was originally defined by ELLES (1922) as dichograptid type, for it was believed to characterize the bulk of the Dichograptidae. ELLES recognized the occurrence of a second crossing canal in *Didymograptus (Isograptus) gibberulus,* however, so that this species subsequently was separated along with other comparable species as the isograptid type (BULMAN, 1932).

The dichograptid type, now defined as a platycalycal mode of development with $th1^1$ as the dicalycal theca and a single crossing canal, is in fact relatively rare. The *minutus* stage (BULMAN, 1955) must be transferred to the isograptid type, leaving the dichograptid type with content of the *bifidus* stage alone. Details are known in only two examples, *Didymograptus rozkowskae* (Fig. 50,*1-3*) and *D. artus* (SKWARKO, 1967), but a number of pendent didymograptids, including *D. bifidus,* undoubtedly developed on this plan. An unusual modification is seen in *Parazygograptus* (Fig. 50,*4*), where $th1^1$, after producing a right-handed bud $th1^2$, undergoes no further development and the crossing canal is not associated with presence of a dicalycal theca.

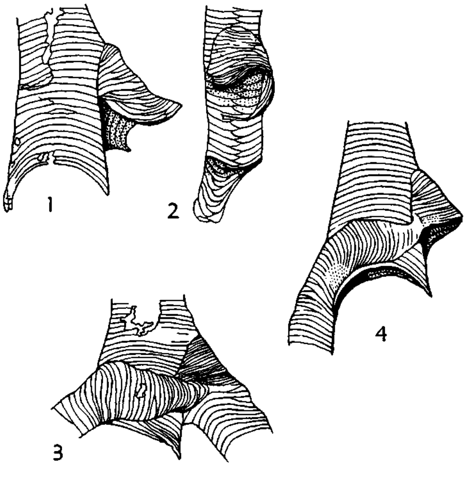


FIG. 50. Dichograptid type of development (*bifidus* stage) (116).——*1,2. Didymograptus rozkowskae,* initial bud and right-handed origin of $th1^2$.——*3. D. rozkowskae,* single crossing canal.——*4. Parazygograptus erraticus,* modified *bifidus* stage with abortive $th1^1$. All ×35.

ISOGRAPTID TYPE

In the isograptid type, the third theca ($th2^1$) lacks any connection with the first ($th1^1$) but develops from $th1^2$, which is the dicalycal theca originating right-handedly from $th1^1$. This type, with two crossing canals, is widespread and full structural details are known for *Didymograptus formosus* (Fig. 51), *D. minutus* (Fig. 52), *Aulograptus cucullus, Isograptus geniculatus* and *Tetragraptus* sp. cf. *T. bigsbyi* (Fig. 53); numerous well-preserved though not transparent proximal ends further extend the range of its occurrence.

Perhaps little purpose justifies attempting to distinguish between the *minutus, extensus, gibberulus* and *hirundo* stages (Fig. 49) which were based mainly on the precise levels of origin of $th2^1$ and $th2^2$; it is possible, if not indeed probable, that the dichograptid and isograptid types of development originated independently and stand in parallel rather than serial relationship to one another. The relationship of both to the anisograptid (dendroid) proximal end is obscure and critical evidence from such forms as *Kiaerograptus* is not yet available.

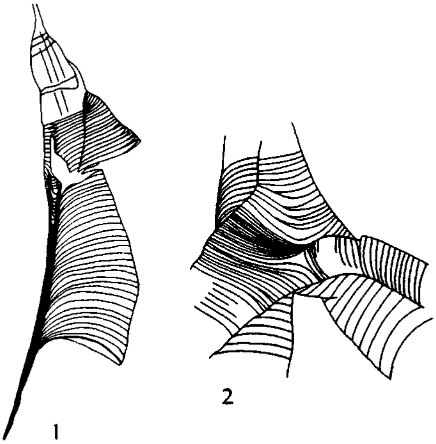


FIG. 51. Isograptid type of development (*extensus* stage), *Didymograptus formosus* (215).——*1.* Prosicular foramen and initial bud on anti-virgella side of sicula, ×43.——*2.* Crossing canal of $th1^2$ (right-handed) and $th2^1$, ×47.

LEPTOGRAPTID TYPE

Least well-known of all types of proximal end development in graptolites is that named leptograptid type. It was originally

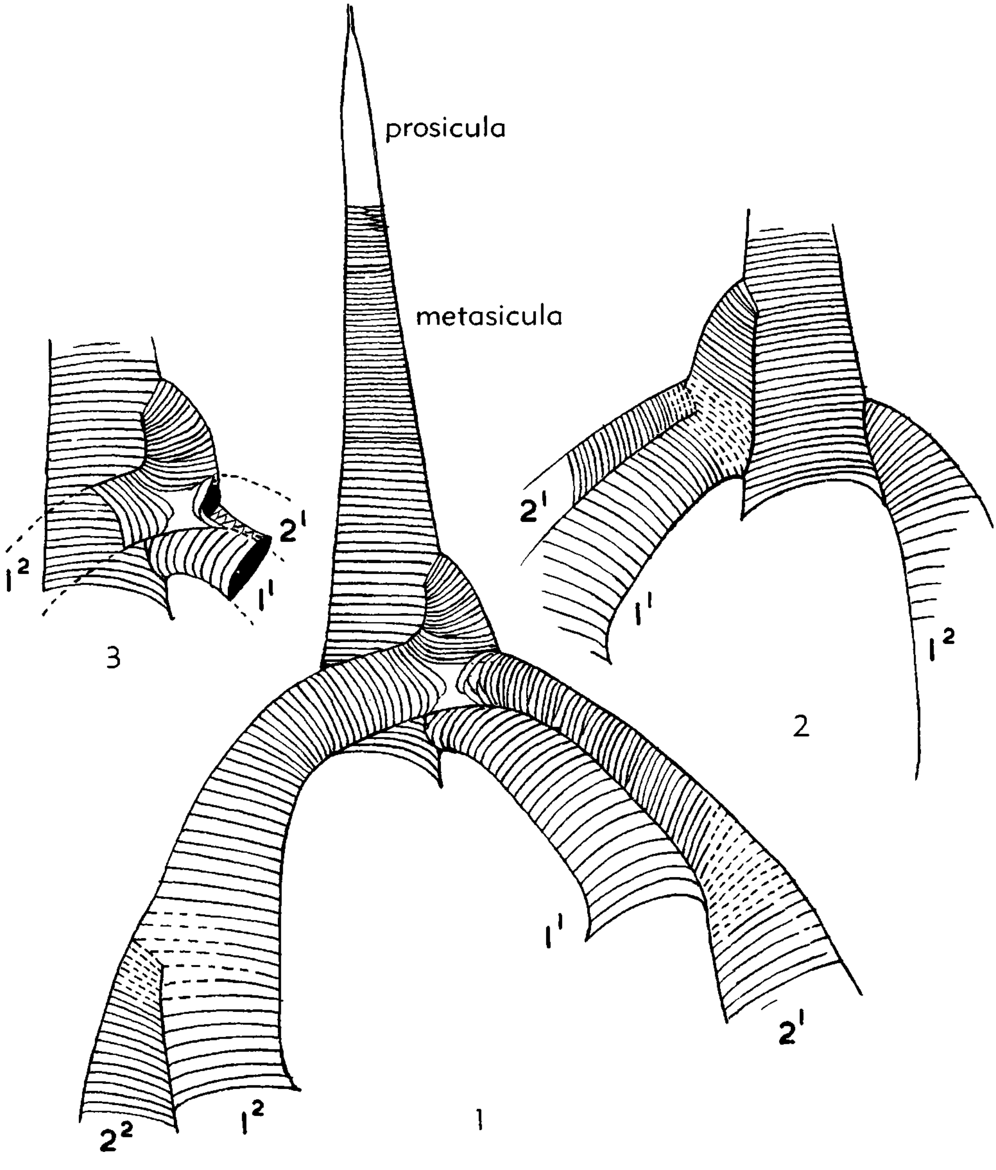


FIG. 52. Isograptid type of development (*minutus* stage), *Didymograptus minutus*.——*1*. Reverse aspect with single crossing canal.——*2*. Obverse aspect, ×40 (91).——*3*. Hypothetical growth stage. [Growth lines where doubtful shown by broken lines.]

defined by the presence of two crossing canals and the horizontal instead of downward direction of growth of even the earliest thecae as reported by ELLES (1922), but her accompanying diagram (Fig. 39) could be interpreted only in terms of three crossing canals. The leptograptid type was later accepted as possessing two or three crossing canals, with a horizontal or even slightly reclined direction of growth of the earliest thecae (BULMAN, 1955) and taken to include certain *Dicellograptus* species. These latter are here excluded and transferred to the diplograptid-dicranograptid type on the basis of the mode of origin of *th1*^{2}.

If species of *Leptograptus* should prove to exhibit a righthanded origin of the dicalycal *th1*^{2} (Fig. 49), then the development would appear to represent a simple modification of the geologically earlier isograptid type. But if the mode of origin of the dicalycal theca proves to be left-handed, as in *Dicellograptus* and *Dicranograptus,* subsequently growing across *th1*^{1} and the sicula, it would hardly be possible to separate this type from the diplograptid-dicranograptid type described below.

DIPLOGRAPTID TYPE

The compact proximal end of a biserial diplograptid rhabdosome includes a wide variety of forms and some 15 species are known in complete detail, with many more in rather less perfect preservation. In all cases some upward component in the growth direction of at least the distal portion of each proximal theca is generally well marked, and the prothecal portions of at least the first three thecae constitute crossing canals. Thus the dicalycal theca is *th2*^{1} or some later theca. The origin of *th1*^{2} is left-handed, the prothecal portion forming a hood which grows across the parent *th1*^{1}*,* as well as the sicula, and the development is platycalycal (Fig. 54).

In species of *Dicellograptus* the scandent element in thecal growth is less extreme and the sicula may lie exposed in the axil

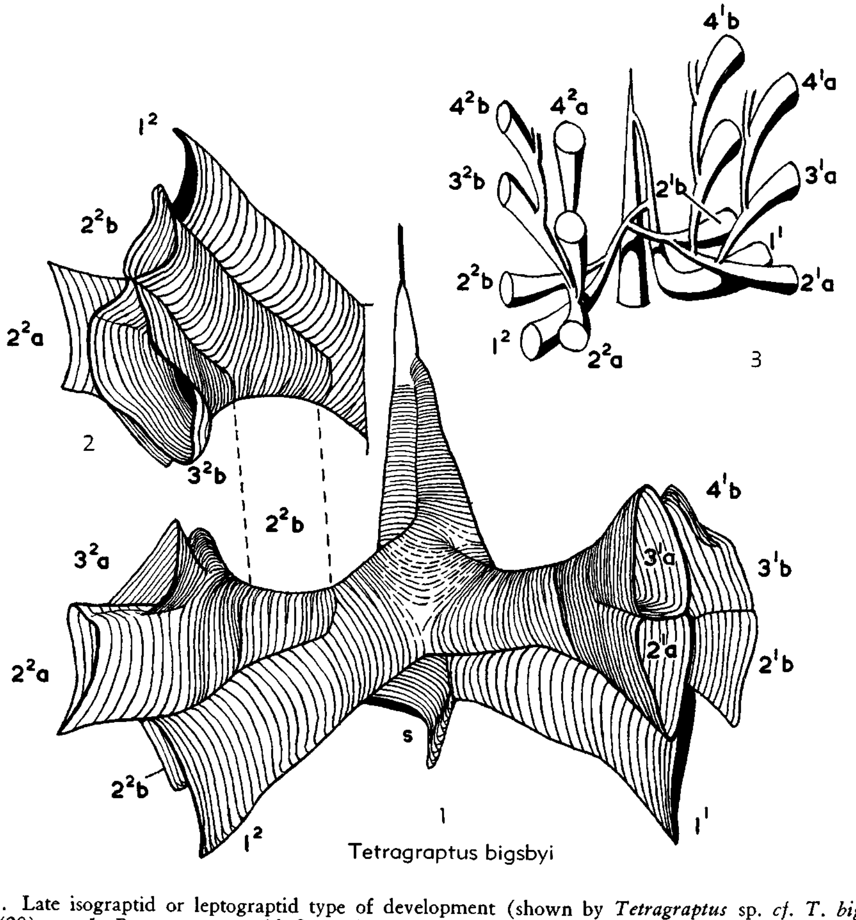


FIG. 53. Late isograptid or leptograptid type of development (shown by *Tetragraptus* sp. *cf. T. bigsbyi,* ×30) (29).——*1.* Reverse aspect with 2 crossing canals.——*2.* Obverse aspect of left side to demonstrate relations of *th2*^{2}*a, th2*^{2}*b,* and *th1*^{2}.——*3.* Thecal diagram illustrating relations of early thecae and mode of branching. [Growth lines where doubtful shown by broken lines. Sicula, *s*.]

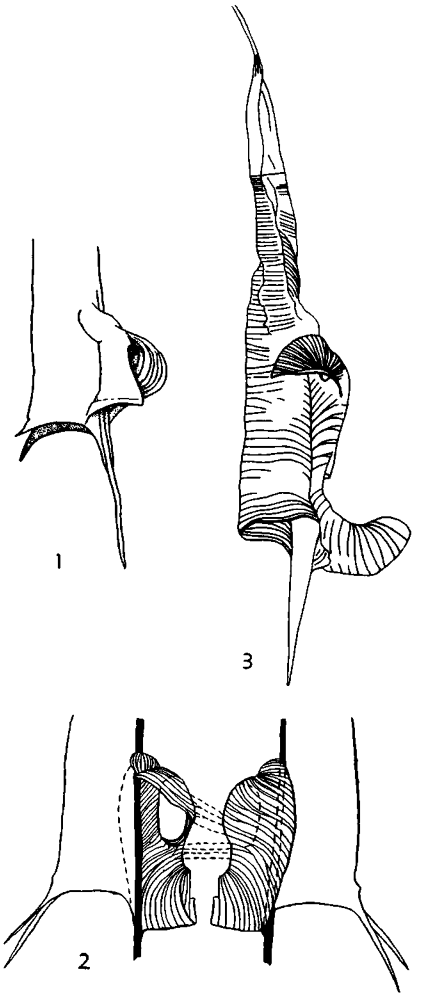


Fig. 54. Early stages of diplograptid development showing left-handed origin of $th1^2$ and growth of crossing canal across $th1^1$ and sicula.——*1. Orthograptus gracilis,* initial bud and partly formed foramen of $th1^2$ (cf. Fig. 50), ×30 (19).——*2. Amplexograptus cf. A. maxwelli,* reverse and obverse views of completed foramen of $th1^2$, ×40 (255).——*3. Glyptograptus austrodentatus oelandicus,* reverse view of slightly later stage, ×35 (215).

of the rhabdosome, though in many forms it is incorporated in the dorsal wall of one stipe (Fig. 55). *Dicranograptus* is typically diplograptid and theoretically at least the dicalycal theca could be some theca later than $th2^1$ (Fig. 56).

The diplograptid development may be divided into two groups, **streptoblastic** and **prosoblastic** (Bulman, 1963). In the former, $th1^2$ is recumbent S-shaped, with an initially upward direction of growth, followed by a pronounced downward direction of the middle portion before the theca finally turns upward again at its distal end (Fig. 56). Associated with this, the initial portion of $th2^1$ has a pronounced downward direction of growth. This peculiar twisted configuration of the second and third thecae was originally described as the "*dentatus* stage," but later it was recognized in numerous genera including *Dicellograptus, Dicranograptus, Glyptograptus, Pseudoclimacograptus, Dicaulograptus,* and *Gymnograptus.* The prosoblastic type appears to develop from this by a gradual straightening-out of $th1^2$ and $th2^1$; $th2^1$ comes to grow entirely upward (Fig. 57) and ultimately (e.g., *Climacograptus brevis*) even $th1^2$ may grow upward from its origin. The process appears to occur independently in many different lineages and within a single genus.

The dominantly upward growth of the early thecae, coupled with some delay in separation of $th1^2$ and later thecae, leads to a condition in which the crossing canals pass across the nema rather than the sicula, which latter tends to be far more completely exposed even on the reverse side (e.g., *Cephalograptus,* see Fig. 91,*8*).

Independent of this straightening-out of the initial parts of early thecae, the separation of two linear series of thecae by a median septum may be progressively delayed as more and more of the proximal thecae alternate and the number of crossing canals steadily increases (Fig. 58); the dicalycal theca shifts progressively distally and the rhabdosome eventually becomes aseptate.

The development of the retiolitids remains imperfectly understood. One group, the Archiretiolitinae, appear to develop on lines generally similar to the diplograptids; the sicula is fully sclerotized, but it is difficult to trace the relations of later thecae owing to reduction of the periderm (see Fig. 95, 96). The Retiolitinae and Plectograptinae present a different appearance. The sicula is unsclerotized or at most represented by the prosicula (Fig. 59,*10*) and the familiar early growth stages are replaced by the **ancora** and **corona stages** (Fig. 59,*1-6*).

MONOGRAPTID TYPE

In the monograptid type (Fig. 60) a downward direction of growth no longer affects even the initial bud, which grows upward from its first appearance, following a nonresorption type of porus. The origin of this development presents another unsolved problem. To convert a biserial to a uniserial scandent rhabdosome requires the reduction and loss, or reorientation, of ***th1²*** in addition to the disappearance of a dicalycal theca (see p. *V*108). Most dimorphograptids appear to be aseptate (or cryptoseptate) and thus to lack a dicalycal theca, which could give rise by its suppression to a monograptid rhabdosome (Fig. 61).

PERICALYCAL TYPE

The development of *Cryptograptus* and *Glossograptus* is strikingly different from that of the biserial diplograptids. As in the dichograptid type, the first theca ***th1¹*** is dicalycal and there is but a single crossing canal (Fig. 62). Theca ***th1²*** appears always to originate left-handedly (unlike the dichograptids) and instead of crossing over ***th1¹*** and the sicula (as in the diplograptids) it grows down the back of the sicula on what corresponds to the obverse side, and the bases of the two monopleural stipes enclose the sicula in front and behind. Hence this type of development has been called **pericalycal.** A left-handed origin of ***th1²*** is not in itself sufficient to produce pericalycal budding and a monopleural rhabdosome, but the few known examples of monopleural astogeny are all left-handed. In *Cryptograptus* ***th1¹*** and ***th1²*** are curved distally slightly upward and in fact curve right around the sicula (Fig. 62,*1-3*); but in

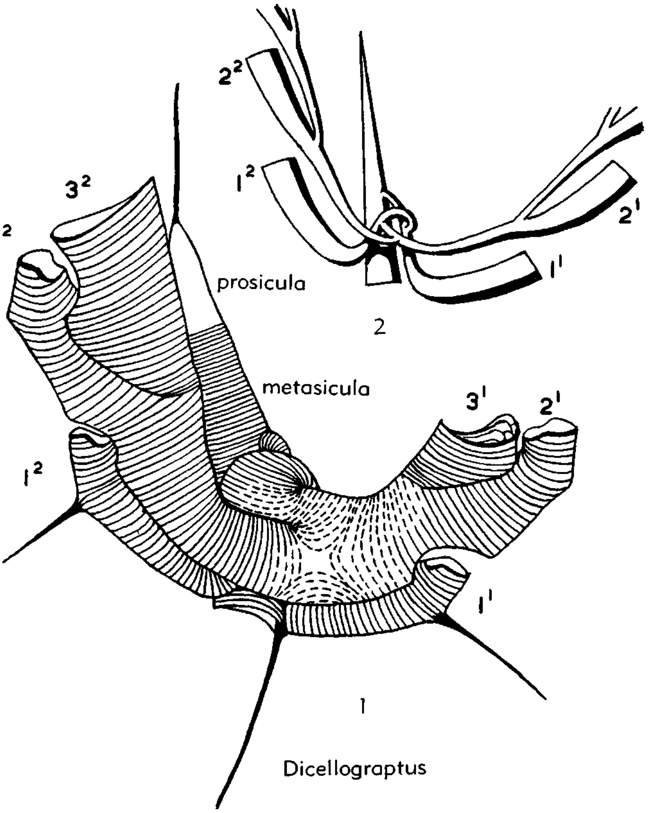


FIG. 55. Diplograptid type of development (illustrated by *Dicellograptus* sp., ×40) (29).——*1*. Reverse aspect showing 3 crossing canals.——*2*. Thecal diagram. [Growth lines where doubtful shown by broken lines.]

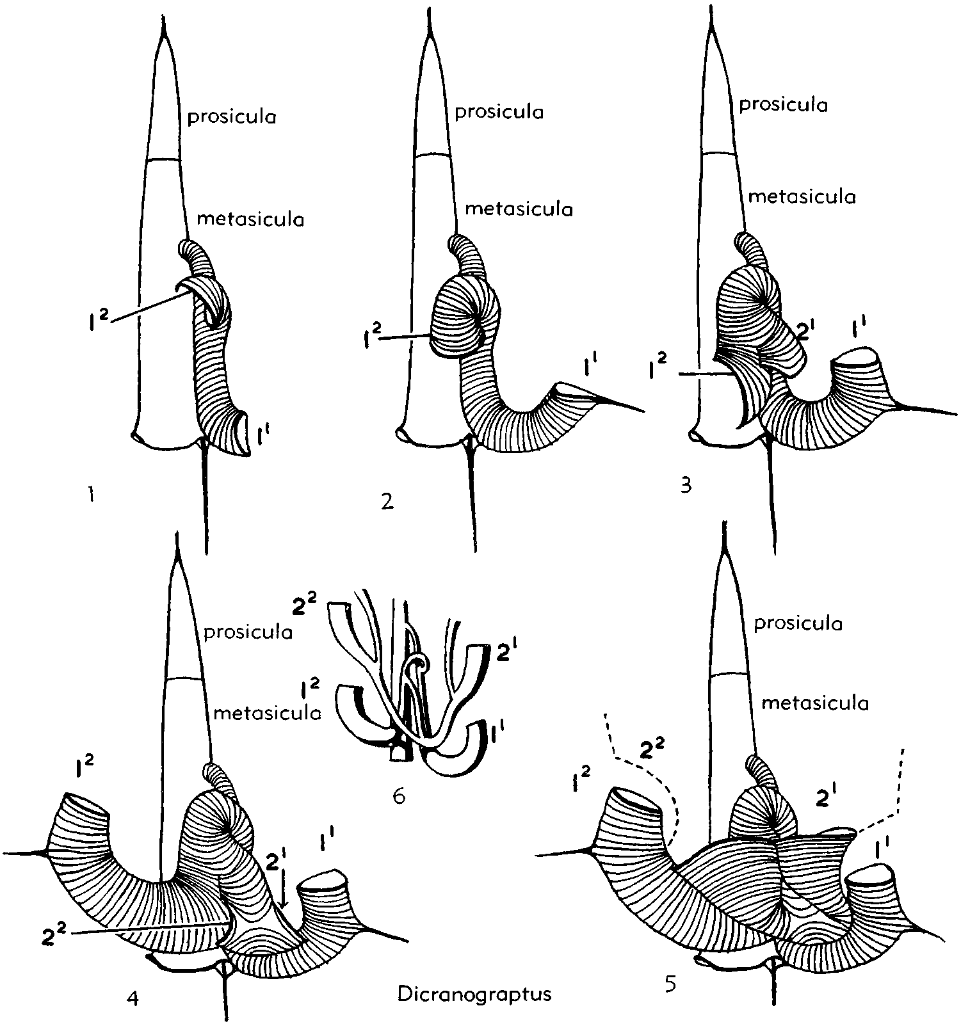


FIG. 56. Diplograptid type of development.——*1-6*. Series of growth stages of *Dicranograptus nicholsoni* illustrating *dentatus* stage, growth lines slightly schematic, *ca.* ×30 (29).

Glossograptus the first two thecae (in *G. sinicus* perhaps the first four thecae) appear to be straight, opening proximally on either side of the sicula (Fig. 62,*4*); and in *Skiagraptus* (Fig. 62,*5*), which has been interpreted on a similar plan, all the thecae are nearly straight.

In contrast to the platycalycal type of astogeny, where collectively the formation of the dicalycal theca is progressively delayed and ultimately eliminated, the evidence suggests that here the dicalycal theca cannot be other than *th*1^1. In this connection the development of *Isograptus manubriatus* is of some interest; the proximal thecae show an unusual curvature reminiscent of a *Glossograptus* and even encroach the sicula to some extent on the obverse side; but the astogeny is clearly based on the isograptid type, with *th*1^2 originating righthandedly and the development does not constitute a true transition between platycalycal and pericalycal types (Fig. 63).

Oncograptus and *Cardiograptus* are biserial forms with dichograptid affinities

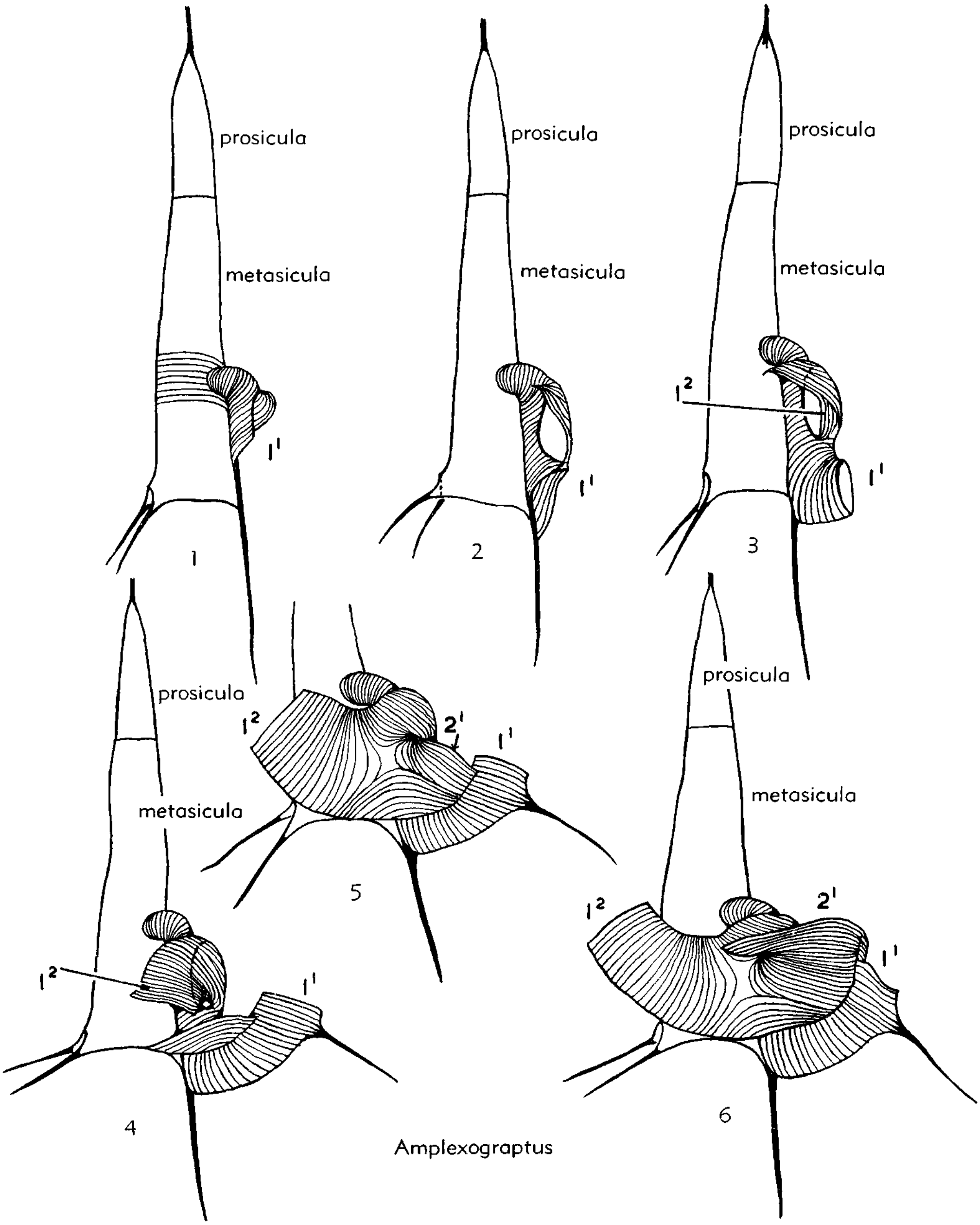


FIG. 57. Diplograptid type of development.——*1-6.* Series of growth stages of *Amplexograptus* sp. *cf. A. maxwelli,* slightly schematic, ×40 (255). [*3* shows disconformity between *th*1^2 and *th*1^1; *5* shows disconformity between *th*2^1 and *th*1^2.]

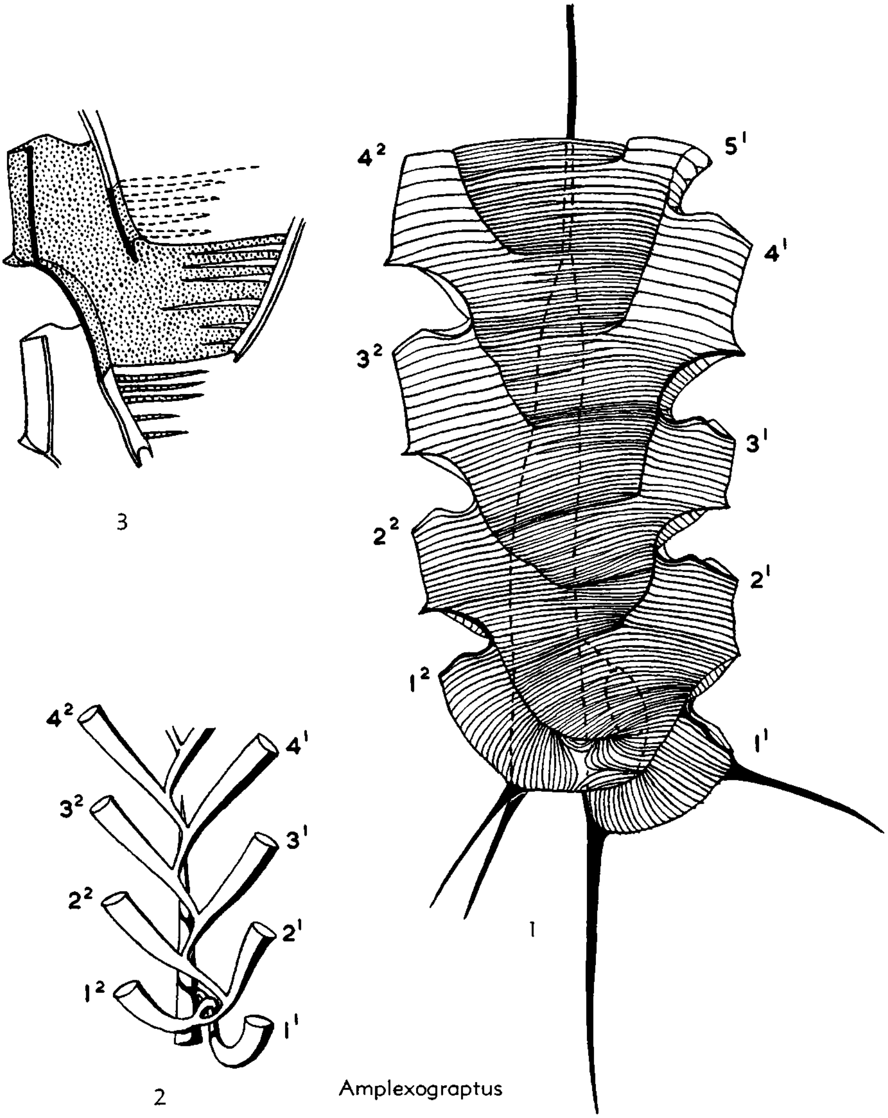


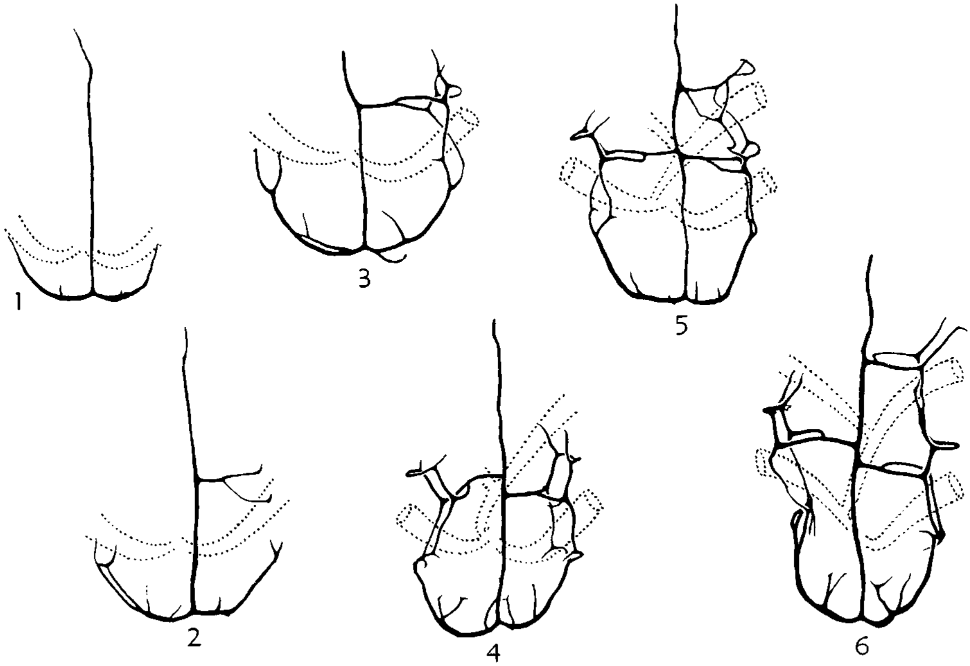
FIG. 58. Diplograptid type of development illustrated by *Amplexograptus* sp. *cf. A. maxwelli,* ×40 (255).——*1.* Proximal end of rhabdosome.——*2.* Thecal diagram.——*3.* Diagram showing growth relations of adjacent thecae and formation of interthecal septum.

and possibly dichograptid or isograptid development (like the scandent *Phyllograptus*), but few details are available.

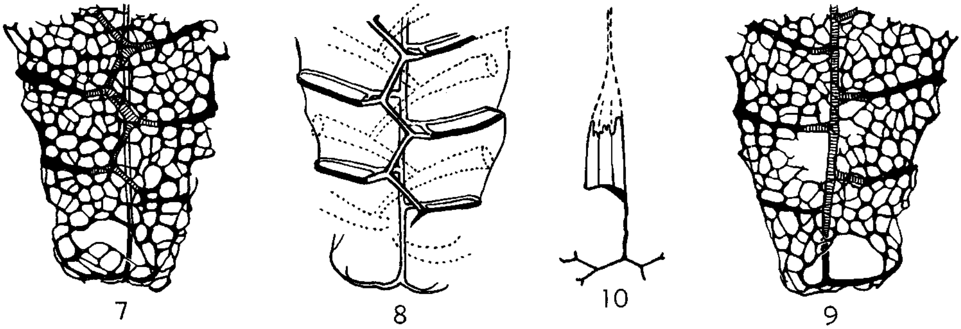
BRANCHING OF RHABDOSOME

Branching in the graptolite rhabdosome may be either dichotomous or lateral; in the former, the two branches diverge symmetrically, whereas in the latter one branch continues the original direction of growth and the other is thrown off laterally. Lateral branching (e.g., *Trichograptus, Nemagraptus, Pleurograptus*) is less common than dichotomous; the two types may occur in the same rhabdosome (e.g., *Schizograptus*) and may (as in *Goniograptus*) be difficult to distinguish.

Reduction in number of branches is a general tendency in graptolite evolution. Indeed, it is a process carried to completion within the Dichograptidae and almost to completion within dendroid Anisograptidae (*see* also Phylogeny, p. *V*103). Nicholson & Marr (1895) suggested that this reduction was to insure a more adequate food supply to the zooids; whether or not this was a factor, symmetry and balance seem to have exerted a controlling influence throughout and a pronounced tendency leads toward regularity in the pattern of the rhabdosome (Bulman, 1958).



Gothograptus



Retiolites

Fig. 59. Retiolitid development.——*1-6.* Series of growth stages of *Gothograptus tenuis* showing (1) ancora stage and (3) corona stage, approx. ×20 (57).——*7-9.* Proximal end of *Retiolites geinitzianus* showing corona, reticula and clathria, ×20 (Bulman, n).——*10.* Prosicula and ancora stage of *R. geinitzianus,* ×20 (Kühne, 1953).

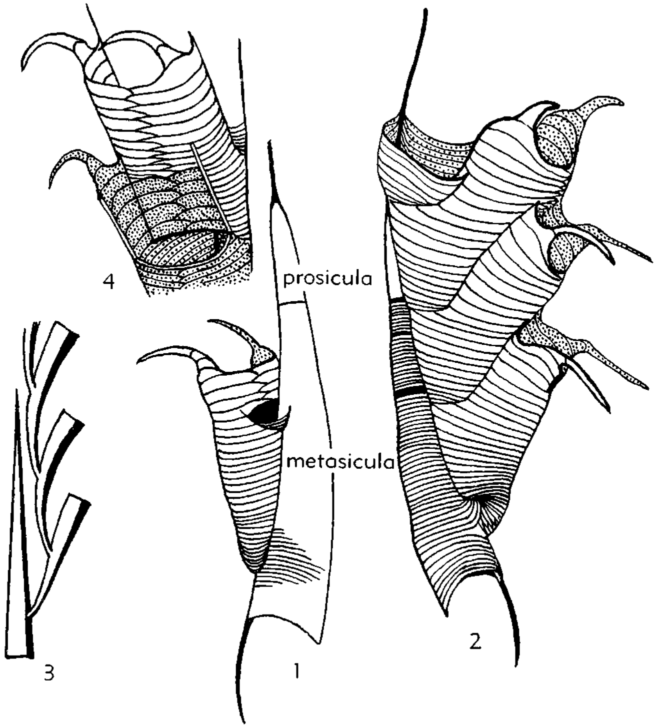


FIG. 60. Monograptid type of development illustrated by *Saetograptus chimaera* (256).——*1,2*. Early growth stages showing annular deposits in metasicula, primary notch and initial bud, and growth relations of successive thecae, ×30.——*3*. Thecal diagram.——*4*. Diagram illustrating formation of interthecal septum.

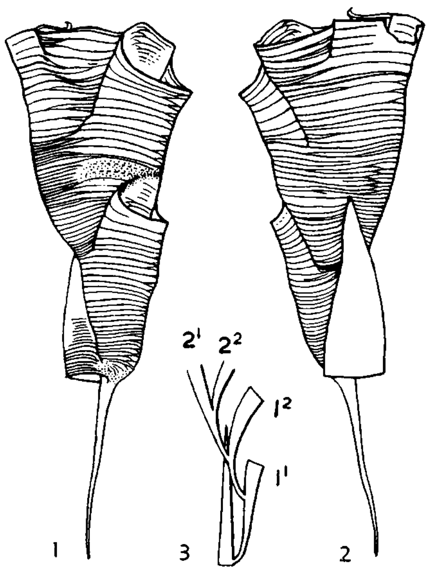


FIG. 61. Proximal end of *Dimorphograptus* sp. ——*1*. Reverse view, ×32.——*2*. Obverse view, ×32.——*3*. Thecal diagram. The order of succession of thecae is clearly shown, but diplograptid homologies in *3*, the thecal diagram, are conjectural (Bulman, n).

The actual process of branch division is very little known. In the Dendroidea, since a branching node consists of two stolothecae and an autotheca, it is due ultimately to the development of two autothecae in place of an autotheca and bitheca (Fig. 13). In the Graptoloidea, since only one type of theca is present, it must be due to the development of a dicalycal theca. *Tetragraptus* sp. cf. *T. bigsbyi* (Fig. 53) is the only graptolite rhabdosome so far known in which growth-line evidence indicates details of the branching division, and here the dichotomy appears as a replica of the isograptid proximal and development; the dicalycal theca constitutes the basal theca of one branch, while the predicalycal theca is carried over into the other at its basal theca, and a sort of crossing canal,

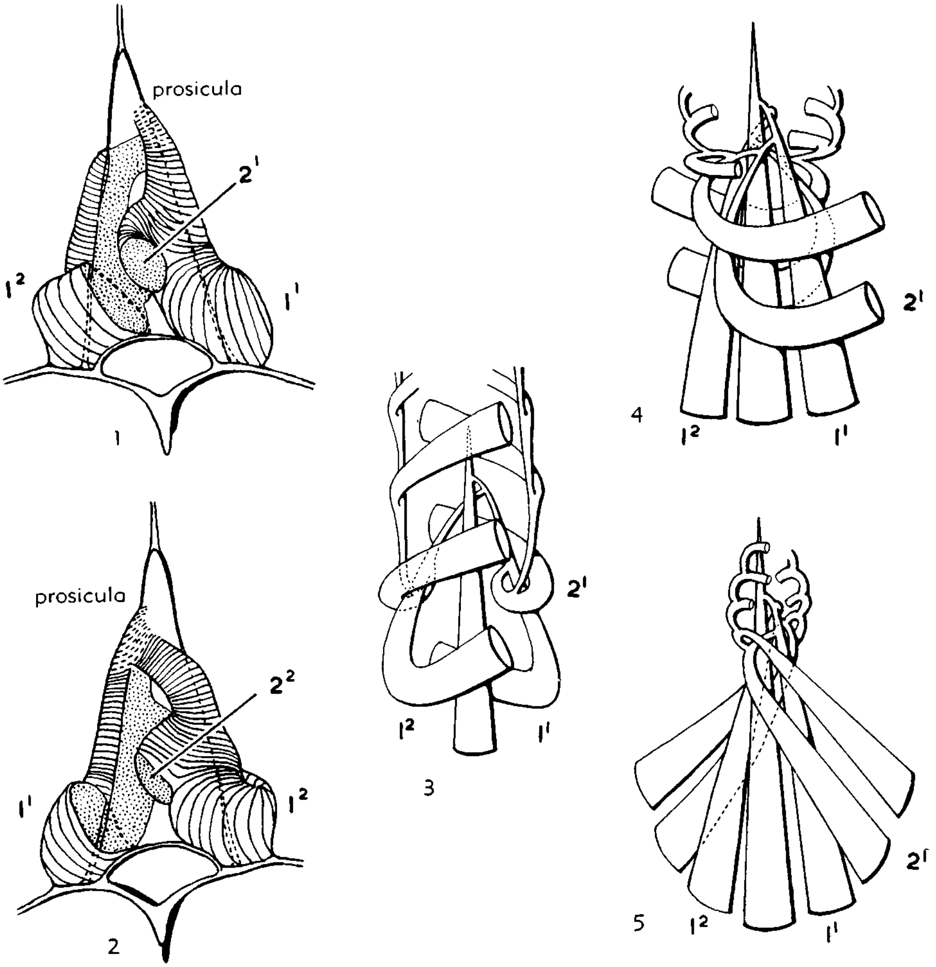


FIG. 62. Pericalycal type of development (23; *4* and *5* based on 261).——*1,2. Cryptograptus tricornis,* "obverse" and "reverse" aspects, ×20.——*3.* Thecal diagram of *C. tricornis.*——*4.* Thecal diagram of *Glossograptus holmi.*——*5.* Thecal diagram of *Skiagraptus* sp.

$th3^1b$ occurs. SKEVINGTON's dichograptid sp. *a* (1965) is closely comparable, as also is JAANUSSON's *Goniograptus* sp. (Fig. 64). What appears superficially here as lateral branching is seen to be dichotomous, and the main stipe is composed of dicalycal thecae alternating with the proximal ends of normal-type thecae which open on the lateral branches (Fig. 64,*3*). Those biserial graptolites which possess a complete septum may still be regarded as essentially two-stiped and the stipes may (pathologically) develop independently of one another (Fig. 47,*3*).

Details of lateral branching are virtually unknown. It occurs among Lower Ordovician dichograptids and again among the nemagraptids of the Upper Ordovician. All these examples may prove to be early instances of cladia production (see below) and it has even been suggested that *Janograptus* is a "pseudo-*Didymograptus*" with a sicular cladium.

CLADIA

The development of cladia in various monograptid genera has been investigated

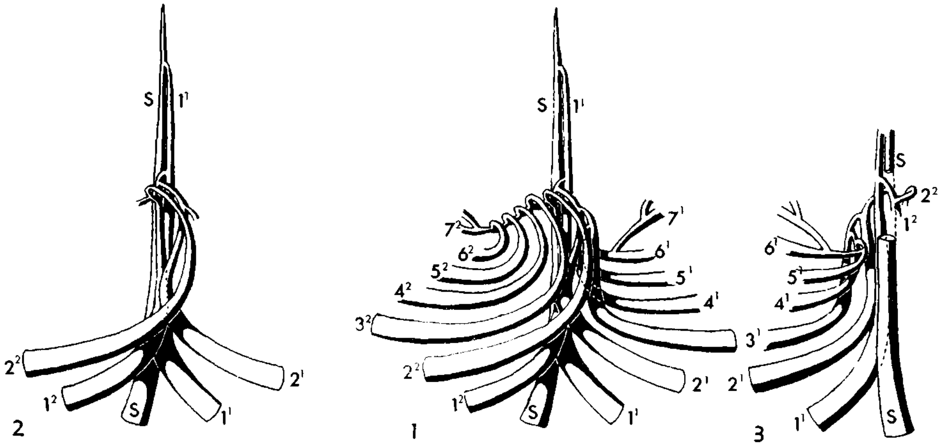


FIG. 63. *Isograptus manubriatus* (35).——*1*. Thecal diagram (reverse view).——*2*. Thecal diagram omitting *th*3^1 and subsequent thecae.——*3*. Thecal diagram (obverse view) omitting distal portions of *th*1^2 and later thecae of that series. [*S*, sicula.]

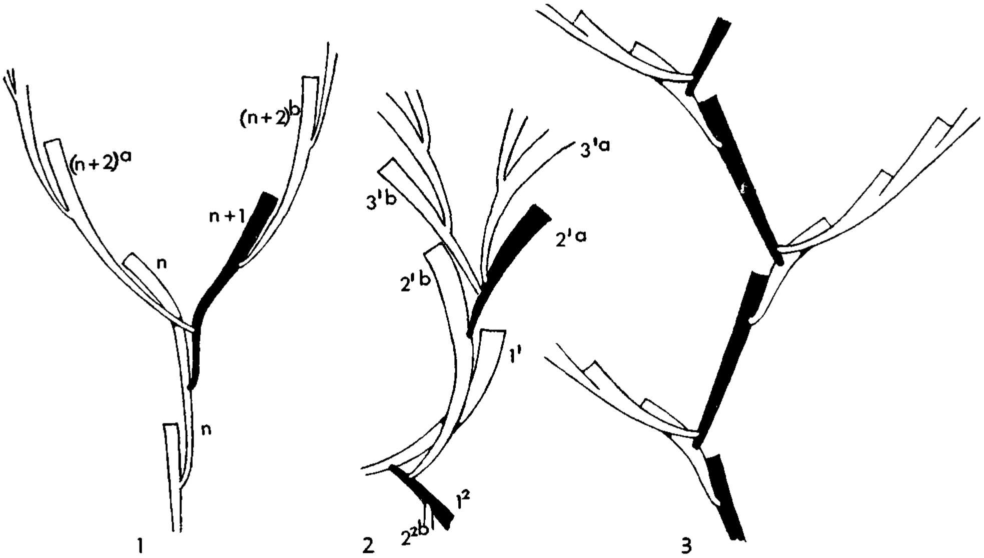


FIG. 64. Graptoloid branching.——*1*. Dichograptid sp. *A* of SKEVINGTON (215).——*2*. *Tetragraptus cf. T. bigsbyi* (Bulman, n).——*3*. *Goniograptus* sp. (104). [Dicalycal thecae shown solid black; *n* indicates an arbitrary number.]

in recent years by STRACHAN (1952), THORSTEINSSON (1955), TELLER (1962), and especially URBANEK (1963). The suggestion that the "bilateral" *Diversograptus* rhabdosome results from the production of a sicular cladium was confirmed by STRACHAN and the mode of development of thecal cladia in *Cyrtograptus* was described in detail by THORSTEINSSON; later work has centered mainly around *Neodiversograptus* and *Linograptus*.

Stages in the development of thecal

cladia in *Cyrtograptus* are well illustrated by THORSTEINSSON's data for *C. rigidus* var., shown in Figure 65. The first indication is commonly the elongation of one (obverse) of the lateral apertural spines of the mother theca, which is destined to become the pseudovirgula of the cladium. This is followed or accompanied by the appearance of the initial flange, and then the ventral hood, which by their ankylosis produce both the tubular initial portion of the cladium and a secondary aperture to the mother theca, the cladial activity retaining at the same time unrestricted communication with the cavity of the parent theca. The cladium appears, therefore, to be developed from an asexually produced bud on one of the mainstipe thecae.

For any given species, the thecal number of the mother theca (counted from the proximal end) is nearly constant and a more or less constant number of thecae (some three or four) are added to the distal end before the beginnings of cladial generation become manifest. Furthermore, the process of development outlined above occupies a time represented by the formation of several more thecae, so that by the time

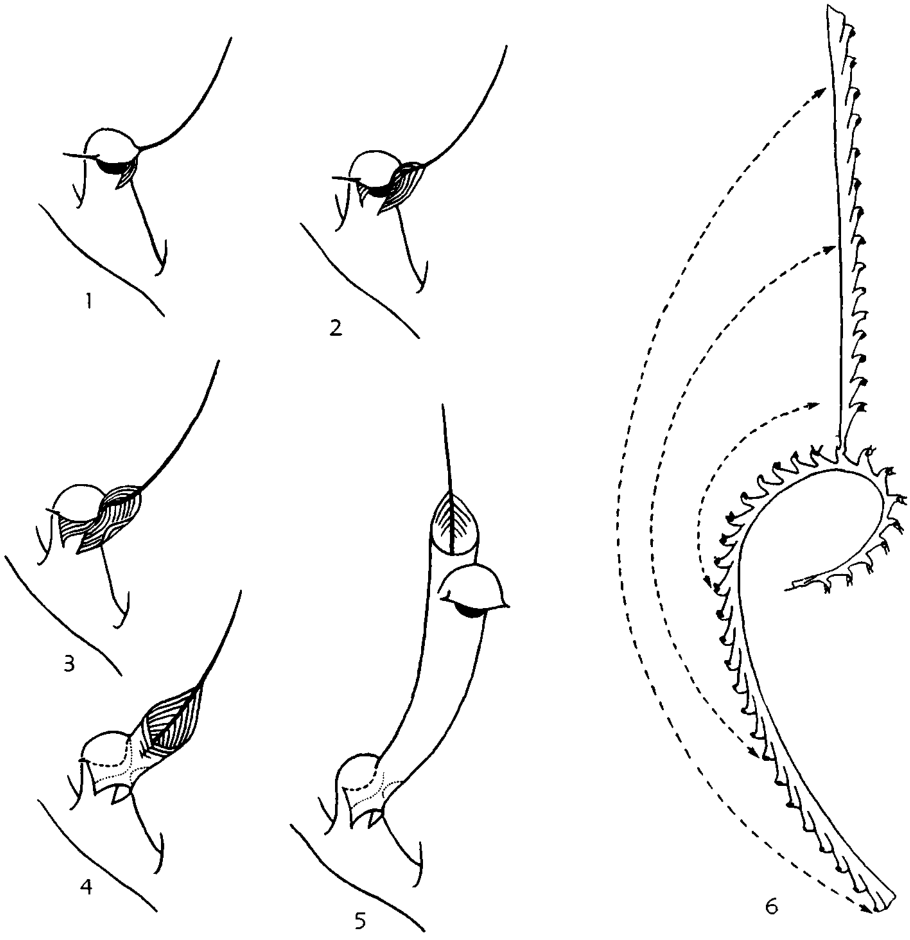


FIG. 65. Cladial generation in *Cyrtograptus rigidus* var. (236).——*1-5.* Successive stages, somewhat schematic.——*6.* Diagram of mature rhabdosome, showing thecal relations of cladium and main stipe, ×2.

the first cladial theca is completed, the position of the mother theca has become seventh or eighth from the distal end. Progressive change in thecal form is usual in cyrtograptids and the characters of the first cladial theca correspond closely to those of the contemporary theca on the main stipe; subsequent growth of the cladium keeps in step with the main stipe and any further changes in thecal characters on the main stipe are paralleled by the cladial thecae (Fig. 65,*6*). Thus, at any time, thecae of the same size and shape are developing at both the free ends of the rhabdosome. The same principle seems to apply to more complicated cyrtograptids and to those with several "orders."

Sicular cladia are comparable in that each initial thecal tubule is based on an elongate apertural spine which becomes the pseudovirgula of the cladium. Full details are not yet available for *Diversograptus,* but in *Neodiversograptus* the pseudovirgula is either a symmetrical dorsal apertural spine of the sicula (Fig. 66) or an asymmetrical spine produced from one of a pair of rounded lappets; it is never the virgella. Stages are not known in quite the same detail as for sicular cladia. In *Linograptus* (exemplified by *L. posthumus*), four or more sicular cladia are produced; the first and second are based on apertural sicular spines, the third and fourth on spines arising from the adapertural plate (a thickened basal expansion of the preceding cladial tubule). The internal cavities of the first thecae of all cladia communicate with the cavity of the sicula, not with one another, and must have been budded independently and directly from the siculozooid (Fig. 67,*5*).

Unlike the thecal cladia of *Cyrtograptus,* the sicular cladia of *Linograptus* are produced in rapid succession. The number of thecae on the main stipe (procladium of URBANEK) and first sicular cladium is equally balanced by the time their second thecae are fully developed; the second sicular cladium has originated by *th4-th5* and the third by *th6-th7*. This preserves an approximate balance about the virgellarium as the assumed organ of buoyancy (Fig. 67,*1*).

In *Diversograptus* a few, and in *Sinodiversograptus* many thecal cladia are produced in addition to the sicular cladium, but the most extreme complication is represented by *Abiesgraptus* (see Fig. 104). The latter has four principal stipes (three of which appear to be sicular cladia) at right angles, and on one sicular cladium and the "main stipe" (procladium) paired thecal cladia arise at regular intervals.

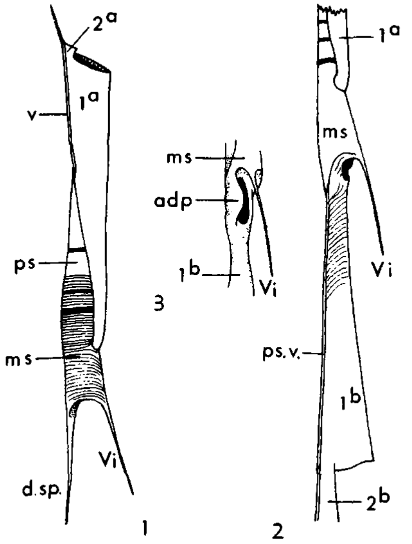


FIG. 66. Production of sicular cladium in *Neodiversograptus beklemischevi,* ×25 (252).——*1.* Sicula and first 2 thecae.——*2.* Initial thecae of cladium (1^b, 2^b).——*3.* Same, ventral view, showing opening of sicula and adapical plate. [1^a, 2^a, thecae of main stipe (procladium); *adp,* adapical plate; 1^b, 2^b, thecae of sicular cladium (metacladium); *d.sp.,* dorsal sicular spine; *ms,* metasicula; *ps,* prosicula; *ps.v.,* pseudovirgula; *v,* virgula; *Vi,* virgella.]

URBANEK (1963) has interpreted these as representing stages in monograptid astogeny. Some analogy can be inferred between the primary bud of monograptids, which does not emerge from a resorption foramen but arises as an apertural bud (*via* sinus and lacuna stages) and the apertural budding of a cladium, either sicular or thecal, which justifies the use of the term **procladium** for the main stipe. This represents a stable astogenetic phase; elaborations are subsequently introduced by the development of **metacladia** (thecal or sicular), resulting in the series: 1), monograptid stage, with procladium or main stipe only; 2), cyrtograptid stage, with thecal cladia only; 3), diversograptid stage, with

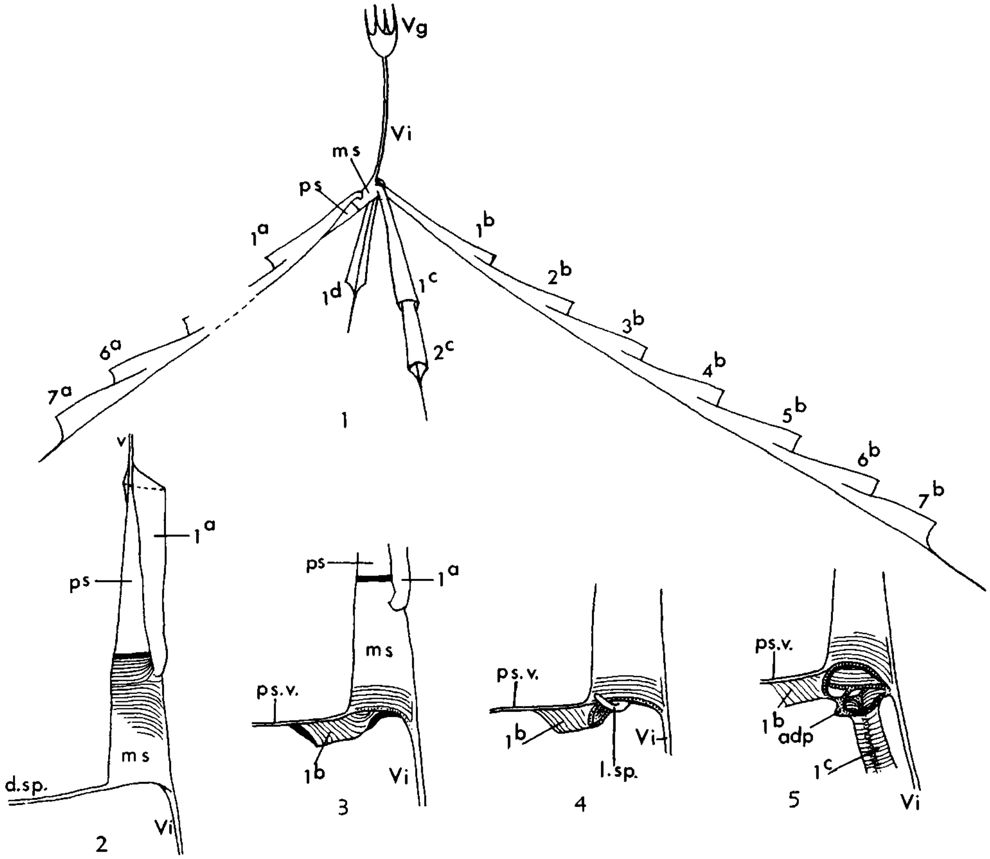


FIG. 67. *Linograptus posthumus* (252).——*1.* Restoration of early stage of development, with 3 sicular cladia.——*2-5.* Stages in development of main stipe (procladium) and first 2 sicular cladia (metacladia). [1^a-7^a, thecae of main stipe; 1^b-7^b, thecae of first sicular cladium; 1^c, 2^c, thecae of second sicular cladium; 1^d, first theca of third sicular cladium; *l.sp.*, lateral spine which becomes pseudovirgula; *Vg*, virgellarium. Other letters as in Fig. 66.]

one sicular cladium; 4), linograptid stage, with numerous sicular cladia; and 5), abiesgraptid stage, with numerous sicular and thecal cladia.

Finally, reference may be made to bipolar monograptid colonies which lack a sicula, investigated by BOUČEK and PŘIBYL (1953), JAEGER (1960) and URBANEK (1963). Various examples have been described, including *Cucullograptus (Lobograptus) scanicus,* but interpretations of such colonies are as yet hypothetical; it seems probable that they represent examples of regeneration involving the formation of **pseudocladia** following serious injury. On this interpretation (illustrated diagrammatically in Fig. 68), the regenerated pseudocladium, removed from the morphogenetic influence of the siculozooid, will exhibit thecal characters of the distal portion of the original stipe; the degree of contrast between the original stipe and the pseudocladium at their junction will depend mainly upon the level at which amputation occurred.

SYNRHABDOSOMES

In 1865, HALL figured a stellate group of *Lasiograptus* [*Retiograptus*] *eucharis* united by their virgulae, and in 1895, RUEDEMANN described a large series of such associations

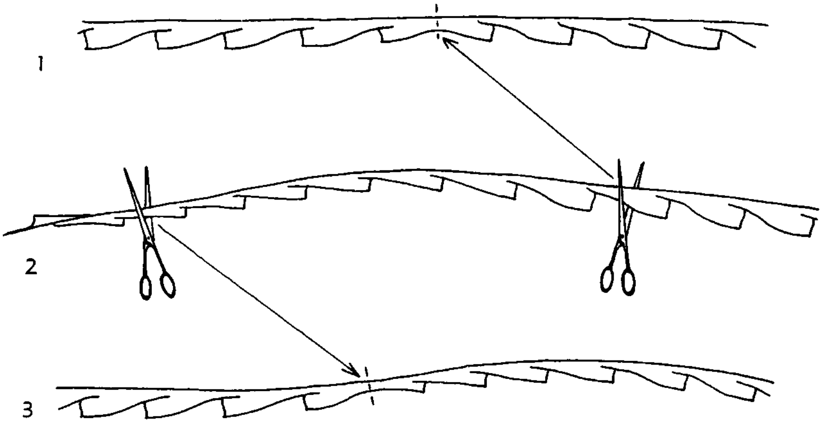


FIG. 68. Astogenetic succession of thecae in normal monograptid colony *(2)* and relations of thecae in pseudocladia regenerated after breakage at 2 different points on the rhabdosome *(1,3)* (252).

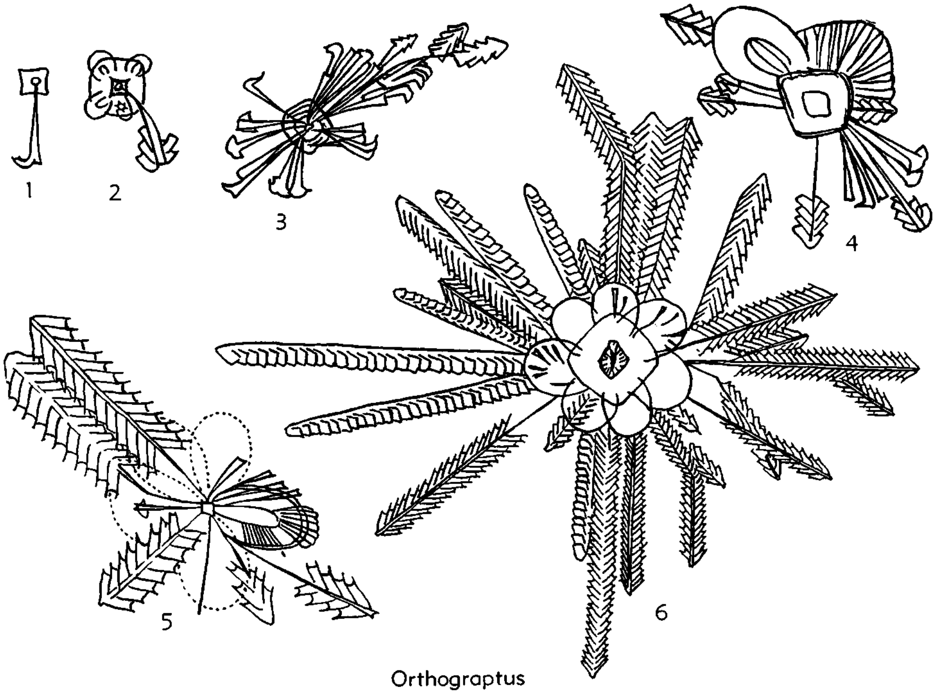


FIG. 69. Development of synrhabdosome in *Orthograptus* sp. (200).——*1-4*. Successive stages, ×3.——*5*. Partially developed synrhabdosome, ×4.——*6*. Fully developed synrhabdosome, ×1.

belonging to various biserial graptolites and attempted to relate them to the life cycle. This paper of RUEDEMANN's still provides the best and most completely illustrated description of these synrhabdosomes, as he called them; but a new interpretation has lately been suggested by KOZŁOWSKI.

The synrhabdosome consists essentially

of a stellate group of rhabdosomes in various stages of development, surrounding a central, almost square disc; and in better-preserved specimens this squarish disc partially overlies and is surrounded by several oval or circular discs which apparently contain bundles of siculae. In addition to this more or less adult arrangement, however, a series of immature stages was discribed: a single sicula or a single rhabdosome attached by its virgula to the squarish disc (Fig. 69,*1*); groups of siculae or very young rhabdosomes so attached (Fig. 69,*2-4*); and finally groups of rhabdosomes in all stages of development attached to the disc, with the subsidiary oval discs and their included siculae (Fig. 69,*6*). RUEDEMANN named the oval discs gonangia, and considered that the central disc was in fact a vesicle or float; but it might have been adhesive (a disc of attachment).

According to KOZŁOWSKI (1949), a clue to the interpretation of these synrhabdosomes is to be sought in the formation of buds on the peduncle (in some on a sterile peduncle) in *Cephalodiscus.* Admittedly these buds, though they may be so numerous as to form a circlet, do not remain attached to the maternal zooid; but in *Cephalodiscus* the organism itself does not form true colonies. The suggestion then is that synrhabdosomes result from a comparable process of budding from the apical portion of the original sicula, the buds here remaining associated. If this is true, the siculae of synrhabdosomes are not strictly comparable with the sexually produced siculae of normal rhabdosomes and should lack a differentiated prosicula portion; this point has not yet been verified. Such asexually produced siculae were termed *pseudosiculae* by KOZŁOWSKI.

Synrhabdosomes are comparatively rare, and are known only in a few species of biserial graptolites.

PALEOECOLOGY

The view that the true graptolites or Graptoloidea were sessile organisms, living erect with the sicula embedded in the mud of the sea bottom, rests upon a total misconception of the nature of the proximal end and long has been abandoned; the current view, that they were floating organisms, was first expressed by HALL (1865) and later developed by LAPWORTH (1897). In his classic paper, LAPWORTH draws a comparison with the Recent Sargasso Sea, picturing the graptolite rhabdosomes attached distally by their nemata to masses of floating weed, the periodic foundering of which supplied both carbonaceous matter and graptolite remains to the slowly accumulating, fine-grained black shales. This theory explains the significance of the nema and accounts for the wide geographical distribution of the graptolites (one of their most distinctive features), for their relation to the enclosing sediments, and to some extent for the lithology of the rocks in which they most commonly occur.

SIGNIFICANCE OF GRAPTOLITIC FACIES

Graptoloidea are not exclusively associated ecologically with any particular type of sedimentary environment, but their remains may occur in almost any kind of sediment, shallow or deep, to which they have sunk or drifted. Nevertheless, their most distinctive association is with black muds devoid of almost any other fossils, and this occurrence constitutes the "graptolitic facies."

These euxinic black shales represent a type of sediment that is not confined to the Lower Paleozoic but occurs at various horizons through the geological column, and the problem of its origin is a general one to which considerable attention now is being given. But of modern black mud conditions catalogued by DUNHAM (1961), few are in any way comparable. While they owe much of their sooty black color to the presence of carbon, such shales also may have a high iron-sulphide content (which imparts a black color) and must have accumulated under anaerobic conditions. Few analyses are available, but as much as 11 percent carbon and 7 percent sulphur has been recorded. Some more recent analyses indicate 7 to 8 percent carbon, but others show only 3 to 3½ percent; even this is some 15 times the amount present in normal shales. Pyrite infilling graptolite rhabdosomes in full relief indicates that the sulphide was syngenetic.

The essential condition is complete lack of bottom circulation so that dissolved oxygen, soon exhausted, cannot be replenished; while a high proportion of decaying organic matter may be contributed by animal and plant remains falling from the superficial aerated layers. Depth of water in itself has little or no controlling effect. At the present time, comparable conditions

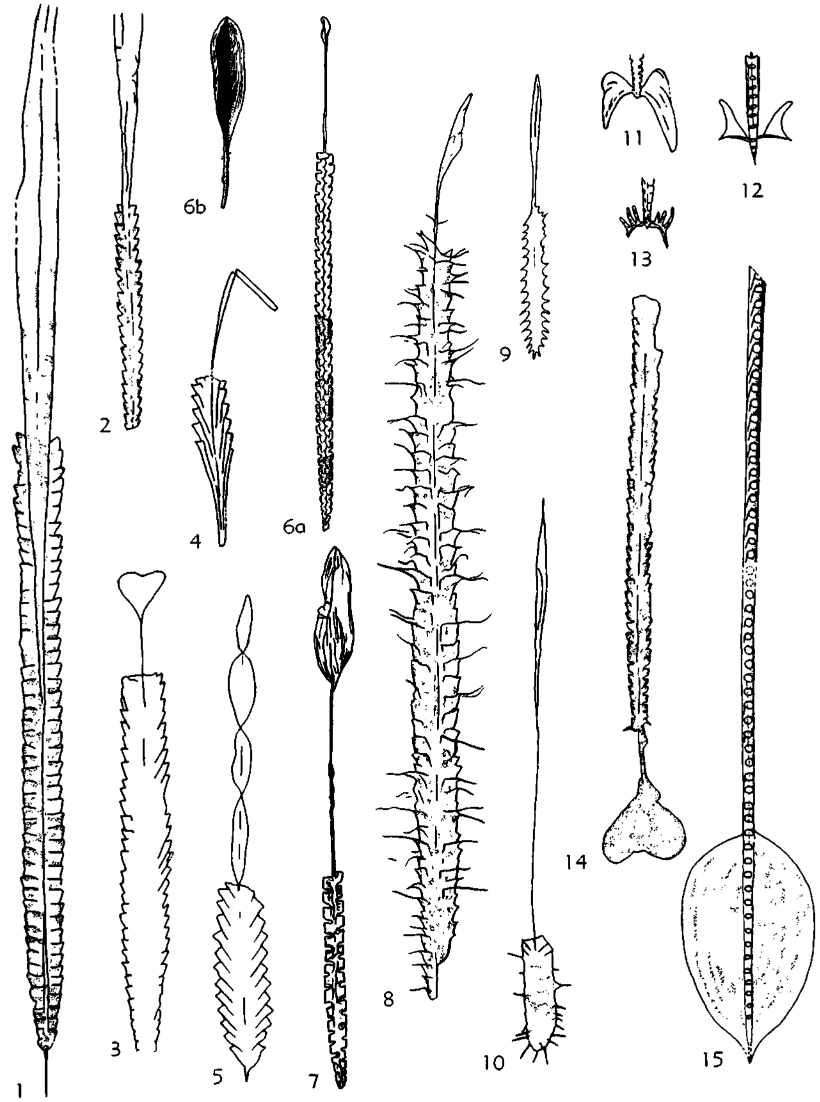


FIG. 70. Distal and proximal structures associated with buoyancy of graptolite rhabdosomes; all figures, except *6b*, ×1.5 (34).

1. *Cystograptus vesiculosus.*
2. *Glyptograptus dentatus appendiculatus.*
3. *Diplograptus decoratus.*
4. *Cephalograptus tubulariformis.*
5. *Petalograptus speciosus.*
6a,b. *Pseudoclimacograptus scharenbergi* (*6a,* rhabdosome; *6b,* "float," ×5.5).
7. *Climacograptus parvus.*
8. *Hallograptus mucronatus nobilis.*
9. *Cryptograptus tricornis schaeferi.*
10. *Glossograptus ciliatus.*
11. *Climacograptus papilio.*
12. *C. ensiformis.*
13. *C. venustus.*
14. *C. antiquus bursifer.*
15. *Monograptus pala.*

occur in the Black Sea (HUNDT, 1938), but also in narrow landlocked embayments such as the Norwegian fjords (STØRMER, 1938; STRØM, 1936) and even in coastal lagoons (SCUPIN, 1921; GRABAU, 1929).

It is certainly probable that such embayments and deltaic lagoons existed in the past, and reasonable to assume that graptolite remains might have drifted in from the open seas and accumulated there; but the extensive literature describing parallel grouping and current orientation of rhabdosomes (HUNDT, 1933-38; KLÄHN, 1930; KRAFT, 1926) and even ripple marks, rain prints and sun cracks in graptolite shales (FREBOLD, 1928; ÖPIK, 1929) probably gives an exaggerated impression of their importance. More or less uniform, haphazard distribution of graptolites in shales occurring over large areas is considered far more characteristic by RUEDEMANN (1935), SCHMIDT (1935), STRØM (1936), RAYMOND (1942), and many others. That suitable conditions might develop in large seas and even oceans, especially in a warm or temperate climate and with submarine barriers to restrict bottom circulation, is admitted by STRØM, and in at least one instance (WILLIAMS & BULMAN, 1931) the existence of such barriers is considered probable on wholly independent grounds.

It is true, however, that graptolite remains often are confined to thin layers separated by considerably greater thicknesses of unfossiliferous strata generally of different lithology. Many of these successions are now recognized to be turbidites, which introduces the possibility of current transport of rhabdosomes as well as or instead of gravity settling.

RUEDEMANN (1925b) has pointed out also that another class of graptolite shale exists, representing conditions which, though unfavorable, were by no means lethal to bottom life. Such shales as the Utica (in contrast to the Hartfell or Normanskill) contain some benthonic organisms and a variety of animals other than graptolites. Even these, however, contrast with nongraptolitic (e.g., Lorraine) shales in the nature of other organisms, seaweeds and cephalopods with small arthropods and horny brachiopods predominating in the one, but polyzoans, brachiopods, and benthonic mollusks in the other. Such "mixed" shales probably represent depositions in quiet waters beyond the littoral zone, where muds probably were carried out by strong undertow.

It is likely enough that no general explanation will account for all occurrences of these types of graptolite shale, however, but that each deposit must be assessed individually on its lithological and faunal characteristics and in relation to its general stratigraphical background. But it is a safe generalization that typical graptolite shales represent conditions more or less inimical to bottom life, and that graptolites themselves owe their distinctively wide geographical distribution to their superficial drifting mode of life.

BUOYANCY MECHANISM

Until recently, it has been assumed that graptolites were epiplanktonic organisms, living attached by their nemata (or virgulae) to floating seaweed comparable in magnitude and buoyancy to the modern *Sargassum*. On this analogy, the almost universal distribution of graptolites would necessitate an almost universal spread of *Sargassum*-type weed throughout the Lower Paleozoic. In several graptolites, however, no nema has even been recorded (e.g., *Dicranograptus, Phyllograptus*), at least in the adult, and in other examples the size and weight of the rhabdosome or length of the nema which would be required (e.g., most *Dicellograptus* species) or the mechanics of nematic support in relation to center of gravity and other factors (e.g., *Monograptus turriculatus*, see Fig. 72,3, *Cyrtograptus*) makes an epiplanktonic mode of life somewhat dubious (BULMAN, 1964). It is recognized, moreover, that in a wide range of biserial graptolites the distal prolongation of the virgula into a so-called "float" suggests that a truly planktonic mode of life was quite common.

The existence of living tissue external to the skeleton, which has to be postulated on other grounds, may have played some part in the buoyancy of graptolite rhabdosomes, more plausibly, perhaps, through the occurrence of gas bubbles in this tissue than a development of fat bodies. In all cases, the so-called floats, originally believed to be bladderlike, are now known to consist of two, or more usually three, vanes attached to the distal end of the nema, but these may well have supported vesicular tissue (Fig. 70) and comparable masses may have been related to the web structures of certain dichograptids (Fig. 71). The well-developed tufts of scleroproteic fibers commonly interpreted as "root fibers" in such forms as *Dictyonema flabelliforme* might equally well be related to an aggregation of buoyant tissue. The occurrence of thin-walled plates or vanes, commonly associated with the virgella or with prominent apertural spines at the proximal end of a rhabdosome (Fig. 70,*11-15*), suggests that, unless they acted as stabilizers, such species had a reversed orientation and floated "upside down" (see also the virgellarium of linograptids, Fig. 67,*1*).

In other instances, the peculiar configuration of the rhabdosome (Fig. 72) suggests possible gyratory movement in response to slight eddies in the water which could have been a significant factor in flotation.

Convincing attachment discs have been figured by RUEDEMANN, mainly in immature rhabdosomes (Fig. 73), and bearing in mind that immature dicranograptids (in the early biserial stage) may possess a short nema, it does seem possible that epiplanktonic attachment in juvenile stages may have been quite frequent. Such minute rhabdosomes, however, would not have required masses of buoyant weed comparable to *Sargassum*, but could have availed themselves of much smaller and more widely distributed planktonic algae. In synrhabdosomes, likewise, it is the juvenile stages, comprising numerous siculae and very early growth stages, which show the most convincing discs of attachment

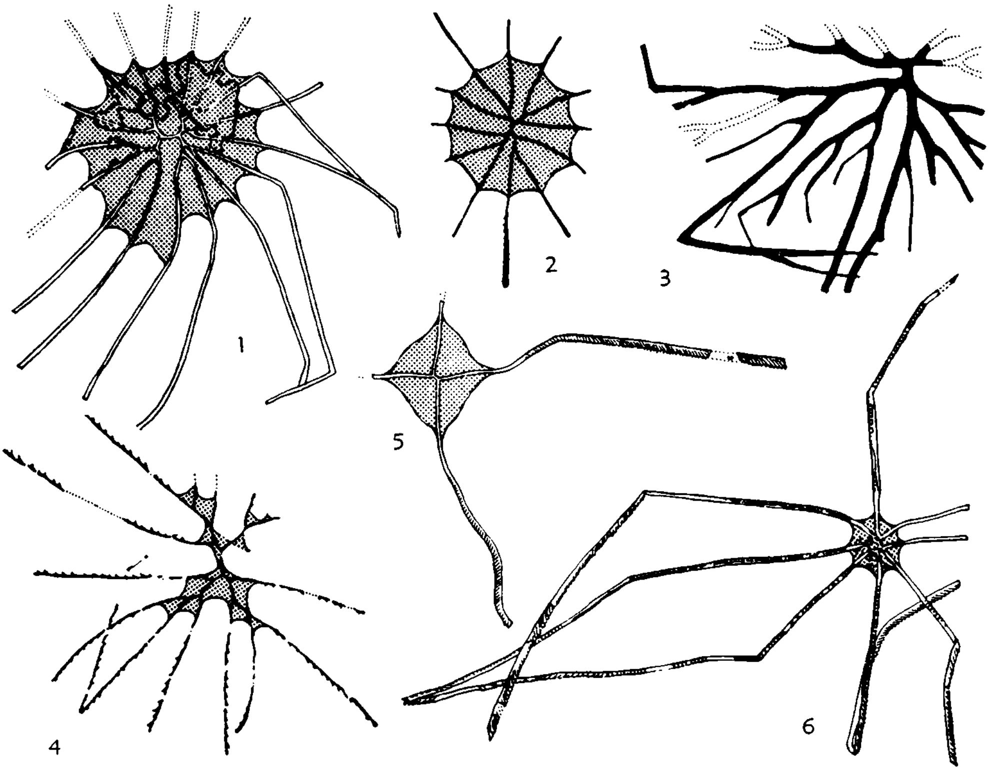


FIG. 71. Proximal web structures in various graptolites (34).——*1. Loganograptus logani,* ×0.75.——*2. L. kjerulfi,* ×0.5.——*3. Clonograptus callavei* with flanges extending along sides of stipes, ×1.——*4. Goniograptus palmatus,* ×0.75.——*5. Tetragraptus headi,* ×0.33.——*6. Dichograptus octobrachiatus,* ×0.33.

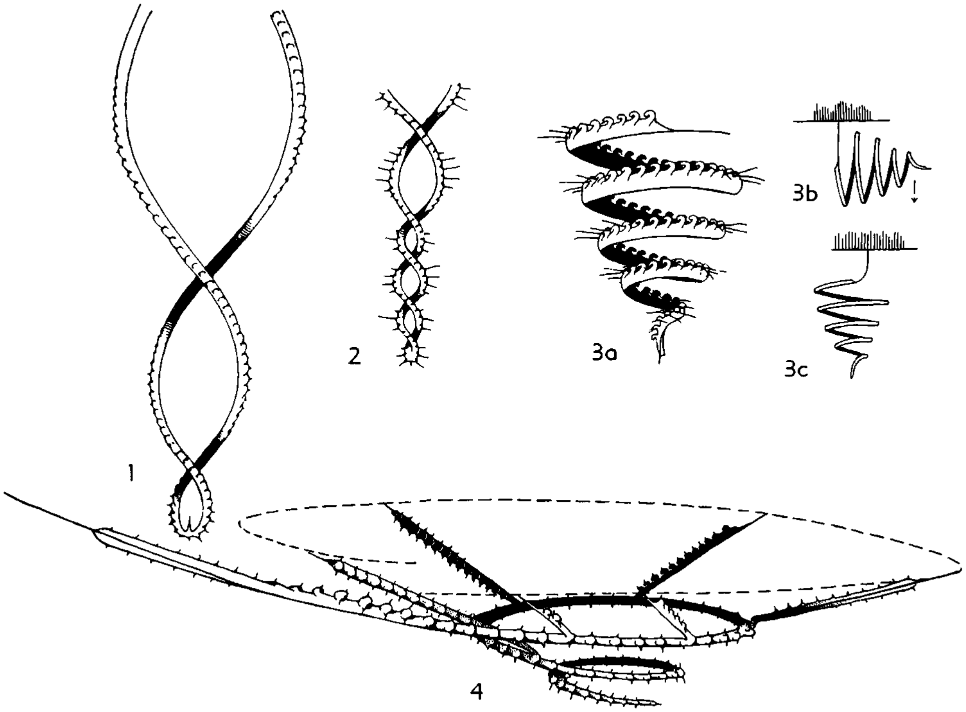


FIG. 72. Rhabdosome forms suggestive of gyratory motion (34).——*1. Dicellograptus caduceus,* ×2. ——*2. Dicranograptus furcatus bispiralis,* ×2.——*3. Monograptus turriculatus; 3a,* rhabdosome, ×3.5. ——*3b,c,* diagrams to show how attachment would distort nema *(3c)* so that growing rhabdosome could not attain regular helical form, unless oriented in defiance of gravity *(3b),* diagram.——*4.* Immature *Cyrtograptus* rhabdosome, based on *C. solaris,* ×3.

(Fig. 69,*1-4*); most adult examples show nothing centrally other than a tangle of slender fibers and it is unlikely that the synrhabdosome association constitutes primarily a buoyancy mechanism.

GEOGRAPHIC DISTRIBUTION

Since the distribution of the Graptoloidea during life was essentially dependent upon current drifting, the distribution of their fossil remains may be practically worldwide, almost coextensive with that of the rocks of a particular age. Nearly all families, the majority of genera, and some species are almost cosmopolitan; *Nemagraptus gracilis* and *Monograptus turriculatus* are examples of such species. It does not follow, however, that all graptolites are more or less universal in their occurrence and to judge by present records, many have a decidedly restricted distribution.

Partly, no doubt, this may be attributed to imperfect collecting and recording; but evidence of the existence of faunal provinces is found and on a much smaller scale, of geographical races, though the erratic distribution of some graptolites is not read-

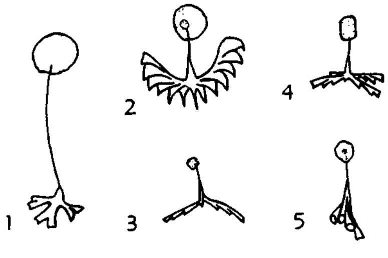


FIG. 73. Rhabdosome suspension; discs of attachment in immature rhabdosomes; all figures ×2 (201).——*1. Dictyonema flabelliforme.*——*2. Tetragraptus similis.*——*3. Adelograptus lapworthi.* ——*4. Staurograptus dichotomous.*——*5. Tetragraptus fruticosus.*