THE DEVELOPMENT OF A DICELLOGRAPTID FROM THE BALCLATCHIE SHALES OF LAGGAN BURN

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ABSTRACT. This paper decribes the growth series, the thecal morphology, and the origin of the thecae of *Dicellograptus sp.* Points of comparison with other dicellograptids are noted.

THE material has been obtained from thin bands of nodular limestone occurring in the Balclatchie Shales of the Ardmillan Series of Laggan Burn near Girvan. The exposure is referred to in Lapworth's Girvan Succession (Lapworth 1882, p. 591, 2), in Peach and Horne (1899, p. 512), and in Bulman (1944–7, pp. i, iii). Alwyn Williams (1963) describes the stratigraphy and palaeontology of the area.

The normal technique for isolating graptolites from impure limestone was employed. Treatment with hydrochloric acid removed all the calcium carbonate, whilst concentrated hydrofluoric acid disintegrated the well-washed remaining material to a muddy sludge. The free graptolites were then isolated. Most of the specimens yielded to bleaching with concentrated nitric acid and potassium chlorate. The time taken for this process to be completed depended on the individual specimens, but usually varied between fifteen minutes and one hour. Older specimens failed to bleach readily due to secondary thickening of the periderm, and prolonged bleaching tended to destroy the growth lines.

The limestone nodules contained broken stipes (never more than four thecae in length), a few mature proximal ends, and a number of growth stages of the form described below. The rest of the fauna comprised *Dicranograptus nicholsoni* Hopkinson, *Diplograptus leptotheca* Bulman, *Climacograptus bicornis* Hall, *Climacograptus brevis* Elles and Wood, *Pseudoclimacograptus scharenbergi* Lapworth, *Orthograptus apiculatus* (Elles and Wood) Bulman, *Lasiograptus* and *Cryptograptus* in various stages of development.

The originals of the figured specimens have been placed in the Sedgwick Museum and bear the Museum's catalogue numbers.

SYSTEMATIC PALAEONTOLOGY

Family DICRANOGRAPTIDAE Lapworth
Genus DICELLOGRAPTUS Hopkinson

Dicellograptus sp.

Description. Rhabdosome broken, only a few thecae in length. Axial angle approximately 260°–320°. Overall sicular length 1·0–1·35 mm., usually 1·25 mm. (of which one-third to one-quarter is the prosicula), commonly incorporated to a varying extent into the second stipe. The tip of the prosicula prolonged into a short nema. Complete

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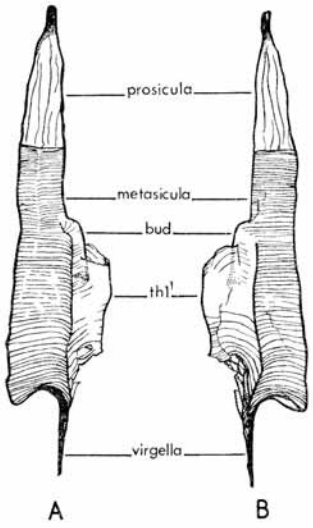


TEXT-FIG. 1. First-theca growth stage of *Dicellograptus sp.*, ×45 approx. A, Reverse side, A54471. B, Obverse.

virgella spine exceeds the metasicula length. Sicula width increases gradually to approximately 0·2 mm. at the aperture. Width of stipe at level of mesial spine on th 2^1 0·40–0·55 mm. Lengths of distal thecae 1·56–1·90 mm. All thecae examined bear mesial spines 0·25–0·30 mm. from ventral lip of aperture; free ventral wall of thecae inclined slightly outwards to mesial spine. Apertures introverted and more or less covered by apertural flanges. Width and length of excavation of th 2^2 0·12 mm. and 0·33 mm. respectively. Thecae overlap for approximately half their length.

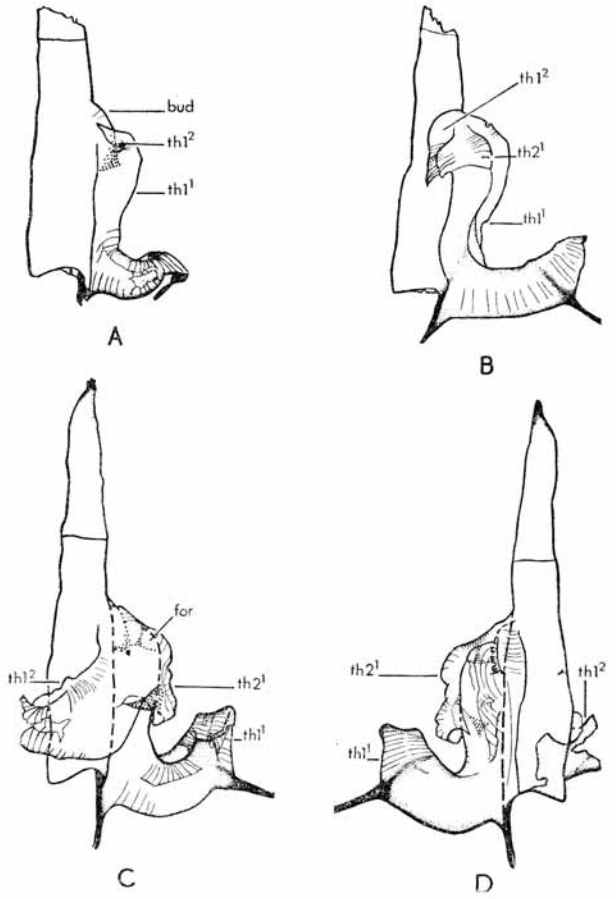
This species corresponds most closely in general form, shape of thecae, structure of proximal end, and the position of the sicula, with *Dicellograptus divaricatus* Hall (Elles and Wood 1904, p. 143, pl. XX, figs. 5*a*, 5*b*, and Elles 1940, p. 429), but bears apertural flanges not apparent in *Dicellograptus divaricatus* and is therefore not placed in this species. It is felt that no specimen of the form described below is complete enough to justify the erection of a new variety, and the existing specimens of *Dicellograptus divaricatus*, described by Elles and Wood 1904 and Elles 1940 are not well enough preserved to establish identity with these forms.

GENERAL MORPHOLOGY

The development of the early growth stages

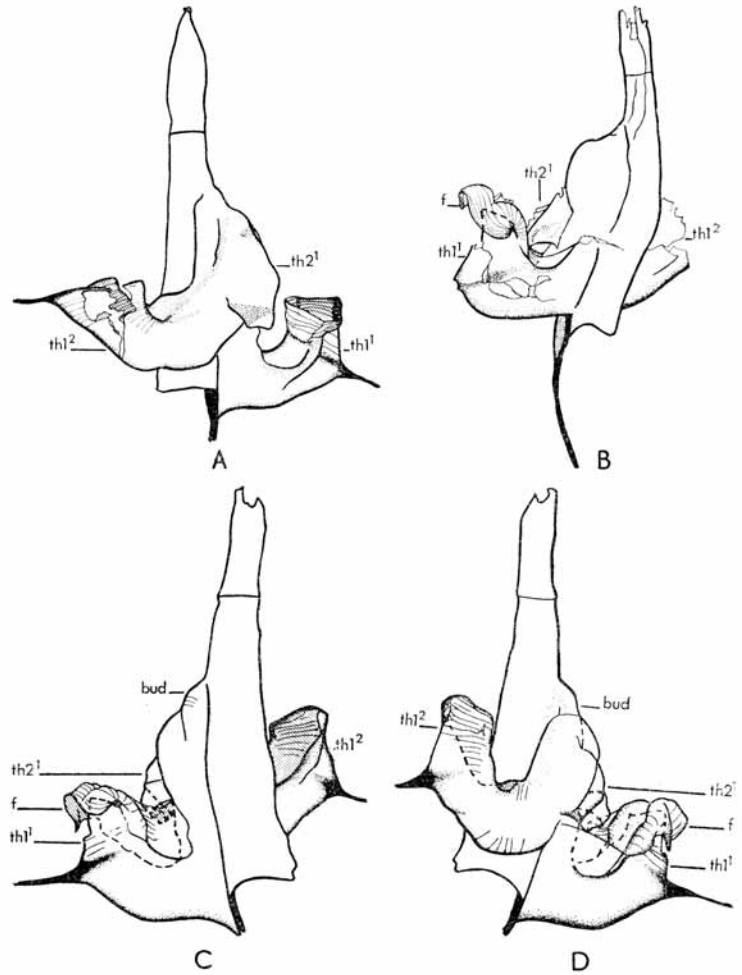
The initial bud arises from a foramen approximately half way down the length of the sicula, a little above the point of origin of the virgella. It grows down the wall of the sicula as a narrow tube, until the foramen for th 1^2 is formed, high up on the initial bud (text-fig. 1A, B). Early stages of the formation of the th 1^1 and the foramen of th 1^2 are absent. Th 1^1 now continues to grow as a much wider tube down the wall of the sicula, until just below the sicula aperture, it turns abruptly and in the form of a U is directed outwards and then upwards (text-fig. 2A, B). The space between the two limbs of the U will later be filled by th 2^1.

Th 1^2 grows at first upwards and inwards, and then, curving round in the form of a hood is directed downwards close to th 1^1 and the reverse sicula wall (text-fig. 2A, B). Th 2^1 arises from the virgella side of the earliest downwardly directed part of th 1^2 when th 1^2 is still in the early stage of growth. Th 1^1 now appears as a more or less complete split tube; the dorsal wall is present, but seemingly only until the level of the mesial spine. Th 1^2 continues growth downwards, at first more or less parallel to the initial bud, and later obliquely across the reverse sicula wall, until, just before reaching the aperture, it turns outwards and then upwards in a similar manner to th 1^1. The space between the two arms of the U formed in this way will be filled by th 2^2 (text-figs. 3A, 4A).



TEXT-FIG. 2. Second- and third-theca growth stages of *Dicellograptus sp.*; all ×45 approx. A, Reverse side, A54472. B, Reverse, A54473. C, D, A54474; C, Reverse; D, Obverse.

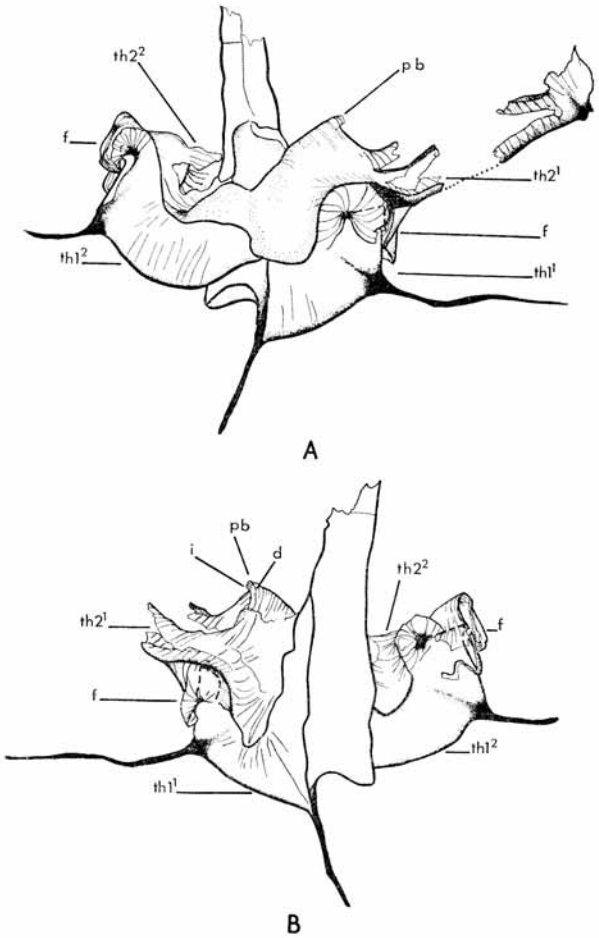
Th 2^1 grows downwards close to th 1^2 and th 1^1 until approximately the level of the mesial spine on th 1^1. The aperture is directed slightly inwards. A thickened diaphragm of chitin occurs within the tube and whilst the exact nature of this is uncertain (text-figs. 2C, D, 3A, B, C, D), it is most probably related to the origin of th 2^2. An upward-growing flange unites with the initial portion of th 2^1 (text-fig. 3 D) producing two apertures from which develop the later portion of th 2^1, on that side facing th 1^1, and the initial part of th 2^2. Th 2^1 grows abruptly upwards filling the space formed by the U shape of th 1^1 (text-figs. 3B, C, D). Th 2^2 grows across the sicula, and obliquely upwards



TEXT-FIG. 3. Second- and third-theca growth stages of *Dicellograptus sp.*, showing flanges (*f*) over the aperture of the first theca; all ×45 approx. A, Reverse, A54475. B, Obverse, A54476. C, Obverse, A54477; D, Reverse.

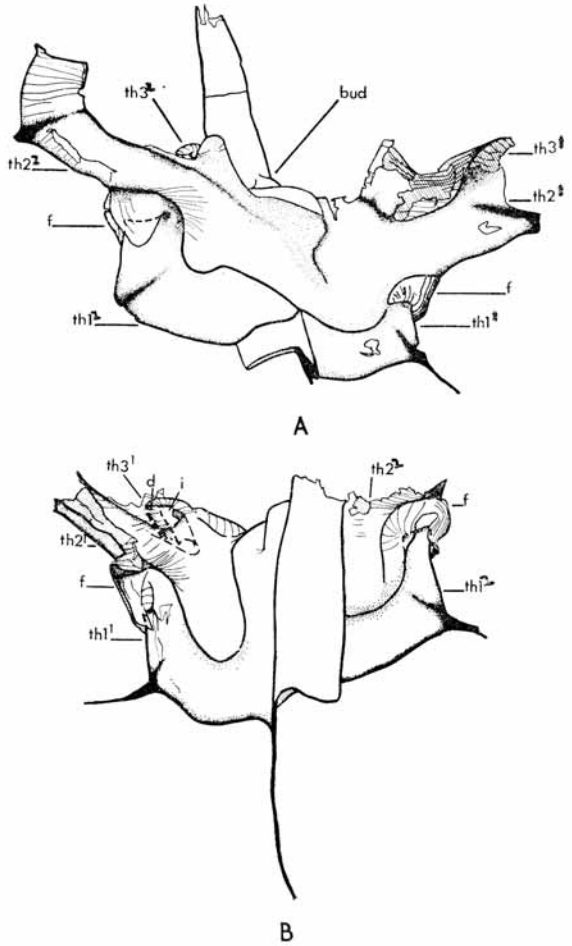
between the limbs of th 1^2 (text-figs. 4A, 5A). Th 3^1 arises from th 2^1 and th 3^2 from th 2^2 (text-fig. 5A).

The development of *Dicellograptus sp.* may be closely compared with those of *Dicellograptus divaricatus* var. *salopiensis* Elles and Wood (Strachan 1959), *Dicellograptus geniculatus* Bulman (Bulman 1932), *Leptograptus sp.* (Whittington 1955), and



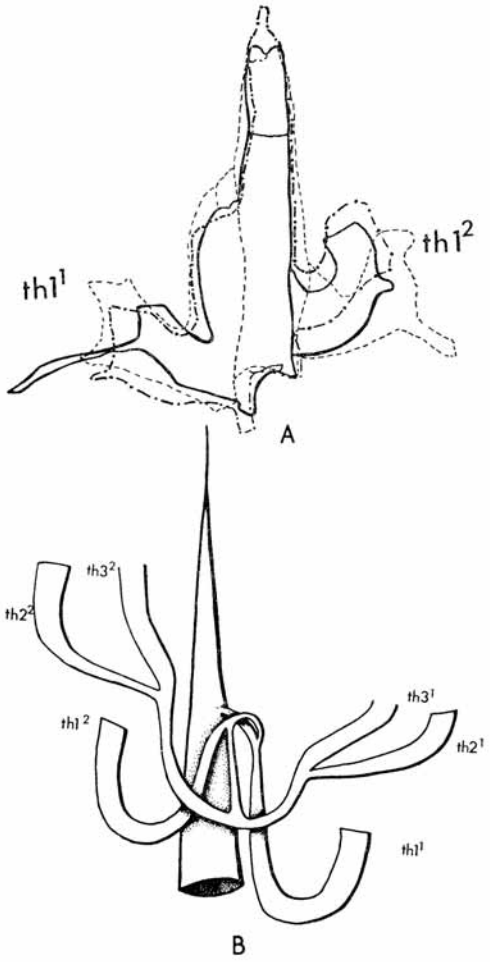
TEXT-FIG. 4. Fourth-theca growth stage and developing prothecal base of fifth theca of *Dicellograptus sp.* A, Reverse side, B, Obverse side of same specimen, A54478, ×45 approx. *pb*, prothecal base; *i*, inner wall of prothecal base; *d*, dorsal wall of prothecal base; *f*, flange.

Dicranograptus nicholsoni Hopkinson (Bulman 1944). In all these forms the initial upward growth of th 1^2, its hood-like curvature down, and the downgrowth of the first formed part of th 2^1 imparts to the proximal end a close resemblance to that of *Glyptograptus dentatus* and other primitive diplograptids (Bulman 1944). The form described in this paper resembles more closely *Dicranograptus nicholsoni* Hopkinson, than the



TEXT-FIG. 5. Fifth- and sixth-theca growth stage of *Dicellograptus sp.*; ×45 approx. A, Reverse side, A54479. B, Obverse side, A54480. Both show prothecal base of youngest theca; *i*, inner wall of prothecal base; *d*, dorsal wall of prothecal base; *f*, flange.

other forms referred to above in the compactness of the proximal end. Only a small portion of th 1^1 and th 1^2 show horizontal growth, and the distal portions are directed upwards and even occasionally inwards (text-fig. 6A). Variation in the growth of the sicula and the first two thecae are shown by the three superimposed outlines of text-fig. 6A.



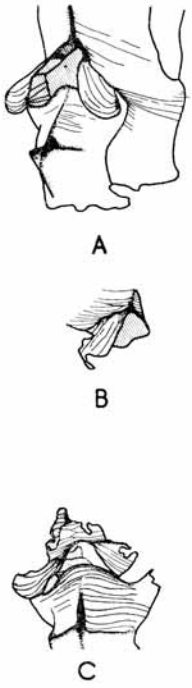
TEXT-FIG. 6. Variation in growth of intitial bud and first two thecae of *Dicellograptus sp.* shown by three superimposed outlines: A, Obverse side, solid line, A54481, dashed line, A54482; dot-dash line, A54483. B, Diagram of growth of proximal thecae. Both ×45 approx.

Thecal morphology

The adult thecae overlap for half their length, which varies from 1·56 mm. to 1·99 mm. The greatest width of the stipe (at the level of the mesial spine) varies from 0·58 to 0·76 mm. The more proximal thecae are smaller. The free ventral wall of the thecal segment

inclines slightly outwards as far as the mesial spine, approximately 0·5 mm. from the aperture, to which it then inclines inwards (text-fig. 7). All the thecae examined have a mesial spine, and one theca (text-fig. 7) appears to have two. The breadth of the thecae is not constant, narrowing considerably above the aperture of the preceding theca until the mesial spine is reached, after which it quickly expands to the wide apertural lip

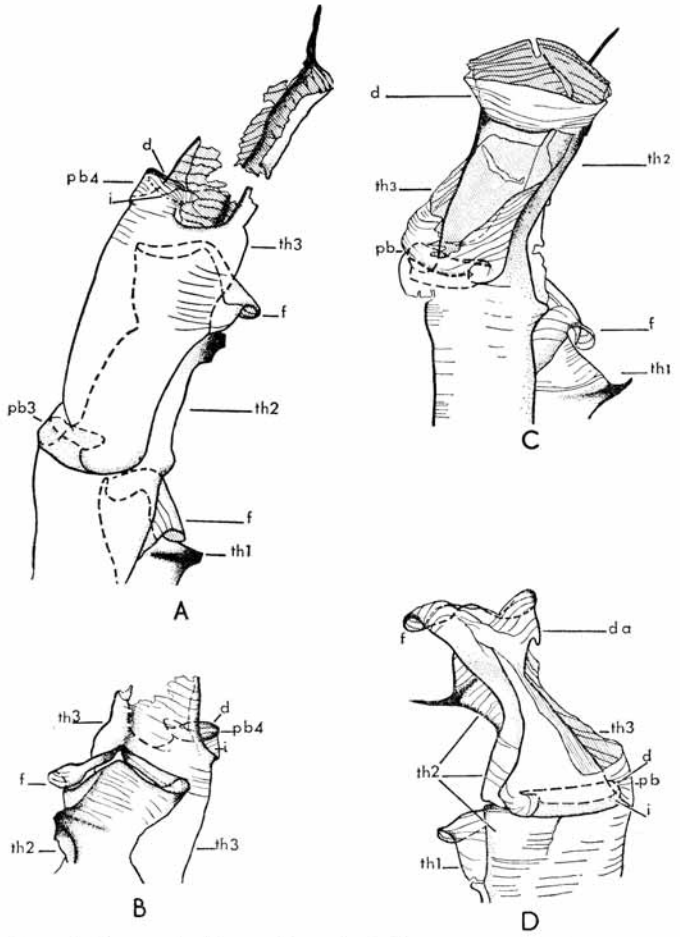
TEXT-FIG. 7. Fragment of stipe of *Dicellograptus sp.* showing adult thecae, A54484; ×22 approx.



TEXT-FIG. 8. Fragments of thecae of *Dicellograptus sp.* showing the aperture and the flanges over the aperture, ×45 approx. A, A54484. B, A54485. C, 54486.

(text-fig. 7). Lists are developed longitudinally along the mid-ventral line of each theca and transversely at the level of the mesial spine. The aperture is oblique and introverted and lies in a deep excavation. The ventral wall of the lip of the aperture is not straight but forms a broad, low, mid-ventral lappet. The aperture is more or less covered by two oblique, downwardly and outwardly directed flanges, one on either side, situated below the geniculum of the succeeding theca (text-figs. 7, 8).

The flanges are composed of fuselli, similar in thickness and width to those of the stipe in general. The growth lines of these flanges (of which there are approximately six), are more or less parallel to the free outer edge. Although there is no projecting flange from the mid-ventral area, thickening, as well as the convergence of the growth



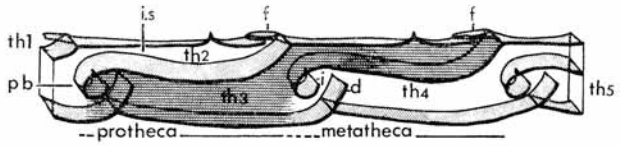
TEXT-FIG. 9. Stages in the growth of the protheca of *Dicellograptus sp.*; all ×45 approx. A, B, Dorsal and ventral sides of the same specimen, A54487. C, Dorsal, A54488. D, Dorsal, A54489. *pb*, prothecal base; *i*, inner wall of prothecal base; *d*, dorsal wall of prothecal base; *f*, flange.

lines in this region, suggests that the flanges are continuous one with the other. This is confirmed by the development. It is here, where the flanges appear least protective, that the ventral lip of the aperture rises to form a broad lappet. A closer study of the flanges in the mature stipe, and also of the stages of their development, suggests that they are a continuation of the fusellar system of the dorsal wall of the metatheca, rather than a derivative of the ventral wall of the succeeding protheca. For example, the dorsal wall

of a theca in the region of the aperture is continuous with the flange over the aperture, so that it is impossible to say where one begins and the other ends (text-figs. 3B, C, D; 4; 9D). The growth lines of this wall and those of the flange are seemingly conformable, converging over the aperture towards the lateral edge. Growth lines of the ventral wall of the succeeding theca rise upwards and converge towards the dorsal wall of the aperture of the preceding theca, suggesting the presence of the latter (and the flanges with which it is continuous (during the growth of the former.

The development of the flanges of the proximal thecae

Th 1^1 appears to be a more or less complete split tube when th 1^2 is in an early stage of growth, and it is not until th 1^2 has reached the formation of a spine that a wall across the dorsal part of the aperture becomes distinct. A thick band of chitin is present at the base of the dorsal wall of the aperture, and is common along the lateral edge of



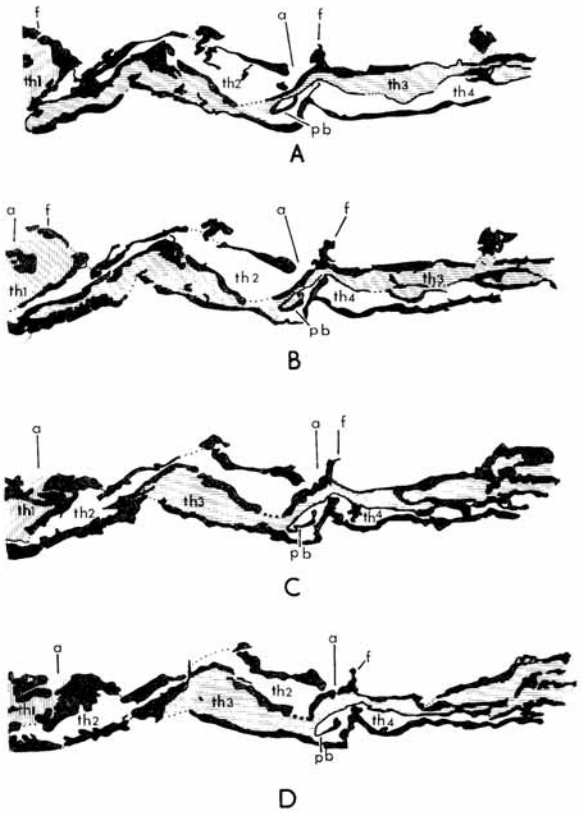
TEXT-FIG. 10. Diagrammatic longitudinal section of fragment of stipe of *Dicellograptus sp.*, th 3 is shaded. Protheca and metatheca refer to th 3, ×30 approx. *pb*, prothecal base; *i*, inner wall of prothecal base; *d*, dorsal wall of prothecal base; *i.s.*, interthecal septum.

the former (text-fig. 3A). Growth now continues and flanges develop over the aperture. The specimen shown in text-fig. 3C, D has complete dorsal wall and flanges of th 1^1 when th 2^1 is at an early stage of development. Th 1^2 is seemingly as yet a split tube.

The development of the thecal segment

Each thecal segment consists of a protheca, which 'corresponds approximately at least with the stolotheca of the Dendroidea' (Bulman 1951) and a metatheca which corresponds approximately to the autotheca of the Dendroidea. The protheca commences growth at approximately the level of the aperture of the second preceding theca (text-fig. 10). It has a free dorsal wall, and a ventral wall which is the interthecal septum lying between it and the metatheca of the preceding theca. The metatheca has a free ventral wall, and a dorsal wall which is the interthecal septum lying between it and the protheca of the succeeding theca. It has an aperture distally which communicates with the exterior. The development of the protheca involves the formation of a structure here named the prothecal base (text-figs. 10, 4, 11, 5, 9). This has the form of a cylinder flattened dorso-ventrally, and curving inwards such that the plane of its aperture is parallel to the direction of the stipe (text-figs. 5B, 9B). The dorsal wall of the cylinder (labelled *d*), is continuous with the dorsal wall of the preceding protheca. The ventral inner wall of the cylinder (labelled *i*), is continuous with the interthecal septum. Text-fig. 4A, B shows the prothecal base of th 3^1 developing from the distal portion of the protheca of th 2^1. Th 2^1 although broken, is almost complete, but it is uncertain whether the dorsal wall of the metatheca (i.e., the interthecal septum between it and the new unformed protheca) is formed. The thickened and slightly frayed nature of the ventro-

lateral edges suggest that it was formed, but not preserved. An inner wall appears to be present, although the relationship between it and the developing dorsal wall of the prothecal base and the lateral wall of the preceding protheca is obscure. Although in



TEXT-FIG. 11. Part of longitudinal section series of *Dicellograptus sp.*, specimen A54491; section interval 10 μ, ×45 approx. *a*, aperture; *f*, flange; *pb*, prothecal base. A, B, C, D, section numbers 21, 20, 18, 17 respectively.

text-fig. 9A, B the metatheca of th 3 has only reached the stage of the formation of a spine, the prothecal base of th 4 is more advanced than the last example. It has more growth lines and is now curving inwards due to greater deposition of chitin dorsally than laterally. The aperture of the prothecal base of this specimen can be seen in ventral view (text-fig. 9B). The rim of the inner wall proximally, the growth relationships between this, the interthecal septum, the dorsal wall, and the lateral wall, are not clear. Some time after the completion of the prothecal base, the dorsal and lateral walls, and perhaps the

interthecal septum of the new protheca, develop. The space between the prothecal base and the metatheca of the preceding theca is filled by deposition of chitin in a manner suggested by the growth lines (text-figs. 9C, D). At first deposition is more or less parallel to the incurling edge of the prothecal base, but later, when the most distal part of the structure is reached, bands of chitin are laid down over the dorsal part, forming the new dorsal wall of the developing protheca, as well as continuing laterally. Text-fig. 5B shows the lateral wall just beginning to extend back over the dorsal wall of the prothecal base. It is at a slightly later stage of development in text-figs. 9C, D.

Thus the ventral wall of the metatheca is more or less complete (text-figs. 4A, 5A) when the prothecal base of the succeeding theca is just beginning to form. It is possible that the

TEXT-FIG. 12. Proximal part of the rhabdosome of *Dicellograptus sp.*, A54481; × 22 approx.

interthecal septum is also present as a thin and easily destroyed membrane. A thickened band of chitin is common across the base of the dorsal part of the aperture of the metatheca (as it is in the proximal thecae), and may suggest a discontinuity of growth in this region. The dorsal wall of the aperture of the metatheca becomes apparent as the lateral and dorsal walls of the new succeeding protheca are forming, developing in a similar manner to those of the proximal thecae. The wall extends over the aperture and forms the flanges (text-figs. 9C, D).

The interthecal septum

The interthecal septum lies between the protheca of one thecal segment and the metatheca of the preceding segment. Longitudinal sections of the stipe (text-figs. 10, 11) show that it is continuous proximally with the inner wall of the prothecal base, and distally with the dorsal wall of the aperture and consequently the flanges over the aperture. The zooid (or zooids) responsible for the formation of the septum, apertural flanges, and the inner wall of the prothecal base, is not known, but since the flanges over the aperture of one theca are complete when the succeeding protheca is at an early stage of growth (text-figs. 3B, C, D; 9D) it seems likely that the zooid responsible for their formation was the zooid over whose aperture the flanges lie.

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