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THE EARLY GROWTH STAGES AND ADULT STRUCTURE OF THE LOPHOPHORE OF *MACANDREVIA CRANIUM* (MÜLLER) (BRACHIOPODA, DALLINIDAE)

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(Text-figs. 1–11)

Although it has been stated (Thomson, 1927, p. 234; Elliott, 1953, p. 264) that the descending branches of the loop in dallinids, so far as is known, grow from the crura only, yet figures supporting this statement have not so far been published, not even by Beecher (1895) who described the very early stages of lophophore and loop in *Dallinella* (= *Terebratalia*) *obsoleta* (Dall). Tiny specimens of *Macandrevia cranium* dredged by R. V. 'Sarsia' have now made it possible for such figures to be published. It is a point of some importance as it is one of the characters given by Thomson (1927, p. 234) as distinguishing the Dallininae from the Mühlfeldtiinae (= Megerliinae Muir-Wood, 1955) and the Magellaniinae (= Terebratellinae, see Muir-Wood, 1955), for in the two latter groups the descending branches of the loop grow from both crura and septum to unite in the middle. At the time Thomson was writing, young growth stages of the loop of a member of the Laqueinae were not known. Since then, Konjoukova (1948, 1957) has studied the development of *Laqueus californicus*—which she placed in the Dallininae—and according to her the descending branches on reaching the septum join with it. She does not, however, figure any intermediate stages between absence of descending branches and complete ones. In 1941 Laqueinae was raised to family rank by Yabe and Hatai (see Muir-Wood, 1955, p. 93).

Palaeontologists have given the growth stages of the loop various names derived from different genera. Certain of the genera are fossil, and although familiar to palaeontologists, are unlikely to be so to many zoologists. Moreover, these terms are not fixed, several of them having been changed by successive authors, as may be seen from the table given by Thomson (1927, p. 232); since that date a further change has been made by Elliott (1953, p. 264), although not followed by Konjoukova in her 1957 monograph. It has therefore been decided to avoid them, relying on the figures to make the stages clear.

All figures have been drawn with the aid of a camera lucida. Mantle setae

have been omitted from the figures as they cover much space: at a shell length of 1·4 mm the anterior setae reach a length of about 0·8 mm.

Macandrevia cranium lacks the two carmine pigment spots, which have been found near the preoesophageal ganglion in certain other brachiopods.

THE EARLY GROWTH STAGES OF THE LOPHOPHORE AND LOOP

The fullest series of growth stages of the loop—without the lophophore—of *Macandrevia cranium* so far described and figured is that of Friele (1877) from a shell length of a little less than 3 mm to the adult. He remarked that at the former size 'a coherent apophysary system' first occurs. He had younger stages, but in a dried condition, and did not figure their brachial support. Elliott (1948) described and figured, from preserved material, the development of the lophophore and loop from a shell length of 5 mm to the adult.

Fine shell gravel from near La Chapelle Bank provided numbers of young *M. cranium* of shell length 1·0 mm onwards. Of two hauls, the first, that taken on 19 June 1956 at position 47° 37′ N., 7° 16′ W. and depth of 90–100 fathoms, was the richer of the two in tiny brachiopods, *Terebratulina retusa* and *Gryphus vitreus* occurring in addition to *Macandrevia cranium*. It was preserved on board and thus the lophophores were unfortunately in a contracted state. The second haul of 20 April 1958 from position 47° 35′ N., 7° 13′ W. at a depth of 105–110 fathoms was brought back under circulation and some young living *M. cranium* were found.

Stages of the lophophore at a shell length of 1·0–5·3 mm will be described and figured so as to join with and somewhat overlap Elliott's (1948) series. The stage of development of the lophophore to shell length varies somewhat in the La Chapelle Bank *Macandrevia*, so that length can only be taken as approximate for the stage under consideration; however, the La Chapelle Bank material shows earlier development of the loop than the specimens from Norway used by Friele (1877) and Elliott (1948).

The earliest stages were found in the preserved shell gravel and show the lophophore in the contracted state (Fig. 1).

The lophophore is trocholophous to the time when eleven pairs of filaments have developed—the last pair being short—with in addition a minute asymmetrical bud. The base of the lophophore, or lophophoral ridge, is a closed circle (Fig. 1 A), as described by Beecher (1895, p. 393) in *Dallinella* (= *Terebratalia*) *obsoleta* (see, however, Williams, 1956, pp. 260–1). The more recently formed filaments show a marked difference in length, indicating that the appearance of new ones is not as rapid as in later stages. The first few filaments to be formed arise from the body behind the mouth; then it would seem that the lophophoral ridge extends on to the brachial mantle. The mouth is a small opening lying in front of the bases of the first formed pair of

filaments, as described by me (Atkins, 1959) in *Platidia* and by Beecher (1895) in *Dallinella obsoleta*. In front of the mouth is a lobe which elongates laterally —running concentric to the bases of the filaments—to form the lip of the food groove or brachial fold. At the eleven pairs of filament stage the lip reaches to about the base of the fifth or sixth filament on each side. The length of the shell at this stage is approximately 1·0–1·2 mm. This mode of growth of the lip has been previously described in *Platidia* (see Atkins, 1959) and is contrary to that described by Percival (1944) and by Williams (1956, p. 260).

By the time twelve pairs of distinct filaments are present the lophophoral ridge is interrupted in the mid-line anteriorly and very slightly indented, there now being two distinct, but closely contiguous, growth regions (Fig. 1 B, C).

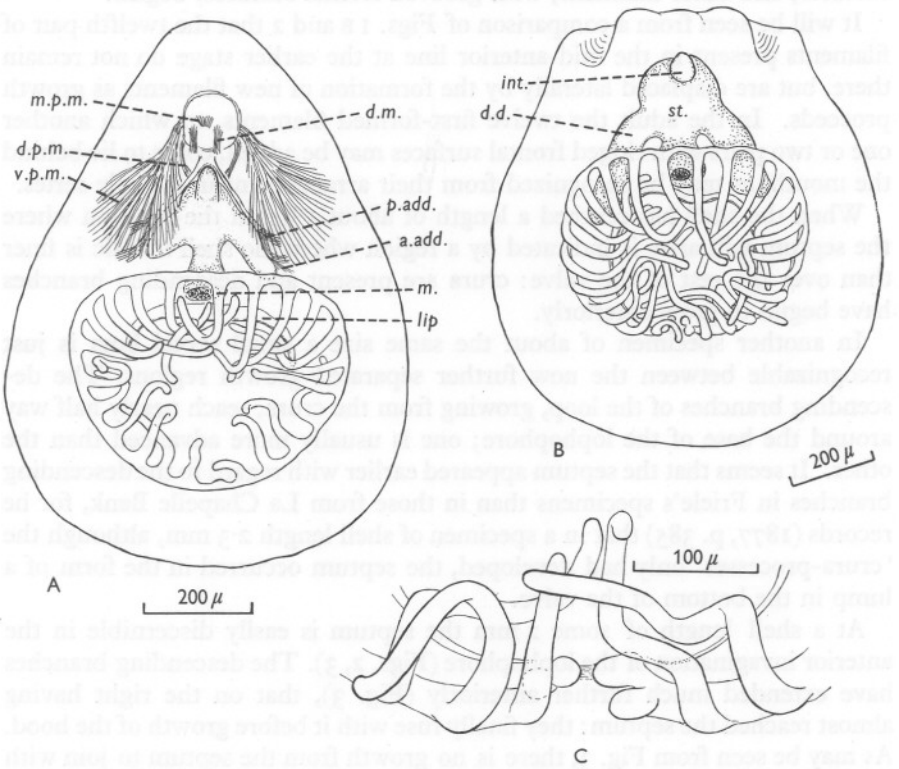

Fig. 1. *Macandrevia cranium*. A, Entire animal of shell length 1·0 mm viewed ventrally: lophophore trocholophous. B, Brachial valve of specimen of shell length 1·35 mm with very early schizolophe: muscles omitted. In both A and B the lip of the food groove (*lip*) is turned outwards exposing the mouth (*m.*). C, Growing region of the lophophore of a specimen of shell length 1·25 mm; the lip of the food groove is merely a slight ridge anteriorly. *a.add.*, anterior adductor muscle; *d.d.*, digestive diverticulum; *d.m.*, diductor muscle; *d.p.m.*, dorsal pedicle muscle; *int.*, intestine; *m.p.m.*, median pedicle muscle; *p.add.*, posterior adductor muscle; *st.*, stomach; *v.p.m.*, ventral pedicle muscle. Stained with eosin and drawn while in cedar wood oil.

The filaments are still in a single row and all have ridged frontal surfaces. In addition to the twelve pairs of recognizable filaments are two pairs of minute buds (Fig. 1 B, C) and not the one minute asymmetrical bud as in the trocholophous stage. No crura or septum can be recognized. The growth of the lip of the food groove has caught up, or nearly so, with that of the filaments, and it extends to about the base of the last formed filament on each side. Shell length is now 1·2 –1·4 mm.

From this stage onwards, as the invagination of the lophophore deepens, the rate of growth of new filaments is accelerated, the growing region bearing closely gradated buds (Fig. 2). When twelve to fourteen pairs are present, differentiation into an alternating series of inner filaments, with ridged frontal surfaces, and outer filaments, with grooved frontal surfaces, begins.

It will be seen from a comparison of Figs. 1 B and 2 that the twelfth pair of filaments present in the mid-anterior line at the earlier stage do not remain there, but are displaced laterally by the formation of new filaments as growth proceeds. In the adult the twelve first-formed filaments, to which another one or two pairs with ridged frontal surfaces may be added, come to lie behind the mouth, as may be recognized from their arrangement in a single series.

When the shell has reached a length of about 1·9 mm the position where the septum will arise is indicated by a region where the shell mosaic is finer than over the rest of the valve: crura are present and descending branches have begun to grow anteriorly.

In another specimen of about the same size a small septal boss is just recognizable between the now further separated growth regions. The descending branches of the loop, growing from the crura, reach nearly half way around the base of the lophophore; one is usually more advanced than the other. It seems that the septum appeared earlier with regard to the descending branches in Friele's specimens than in those from La Chapelle Bank, for he records (1877, p. 385) that in a specimen of shell length 2·3 mm, although the 'crura-processes' only had developed, the septum occurred in the form of a lump in the bottom of the valve.

At a shell length of some 2 mm the septum is easily discernible in the anterior invagination of the lophophore (Figs. 2, 3). The descending branches have extended much further anteriorly (Fig. 3), that on the right having almost reached the septum: they finally fuse with it before growth of the hood. As may be seen from Fig. 3, there is no growth from the septum to join with the descending branches growing from the crura. The descending branches are calcareous ribbons vertical to the valve floor, and so appear extremely narrow in dorsal and ventral view; they run slightly above the valve floor.

Fig. 2 A and B of the same lophophore stage, the one drawn living and the other preserved, show the great difference in appearance of the lophophore resulting from preservation without narcotizing (see also Atkins, 1959, p. 128). The individual shown in Fig. 2 B has the septum and descending branches

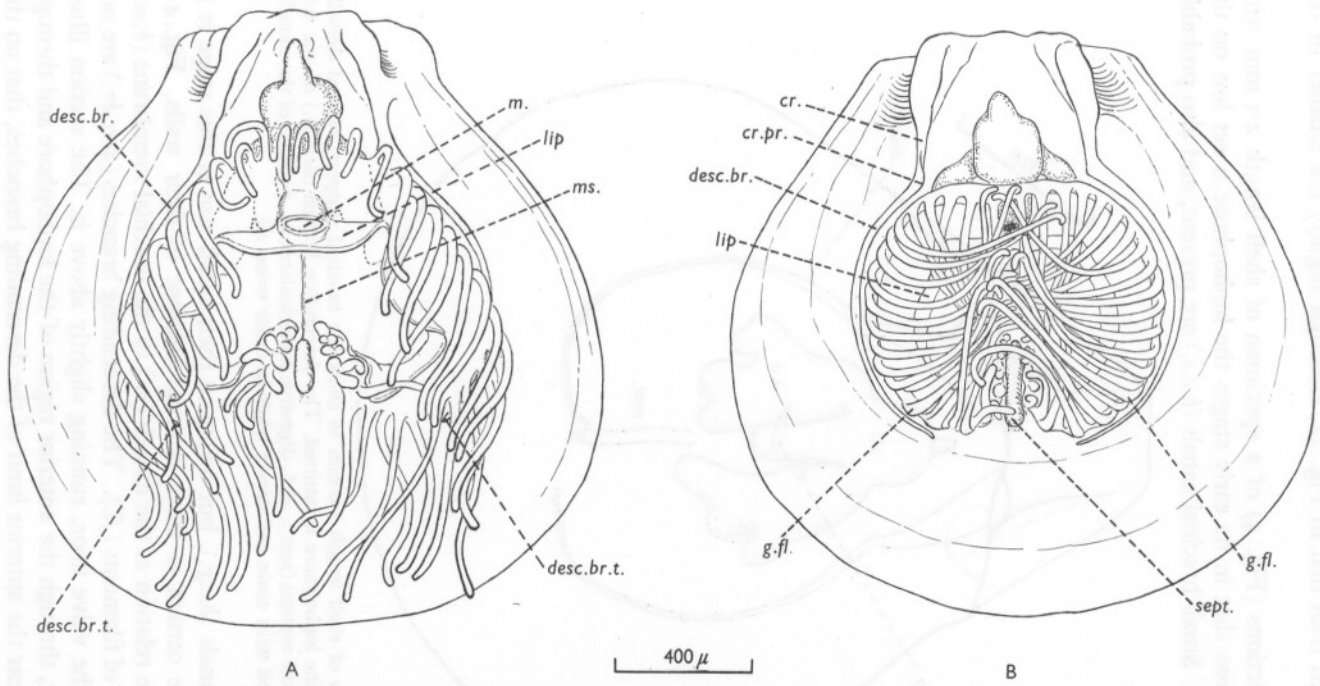

Fig. 2. *M. cranium.* A, Brachial valve, with schizolophe, of specimen of shell length of 2·25 mm, drawn living and fairly well expanded. B, Brachial valve with schizolophe in contracted state, thus exposing the well advanced descending branches of the loop. The septum as yet shows no development of a hood. Specimen of shell length 2·1 mm, drawn preserved without narcotizing. Differentiation into a double series of filaments has begun, the first outer grooved filament on each side is indicated (*g.fl.*). *cr.*, one of the crura; *cr.pr.*, crural process; *desc.br.*, descending branch of the loop; *desc.br.t.*, tip of descending branch; *lip*, lip of the food groove; *m.*, mouth; *ms.*, mesentery; *sept.*, septum.

further developed than that in Fig. 2A, although slightly the smaller of the two.

Transverse sections (Fig. 4) of a specimen of shell length 2·1 mm with schizolophe, shows that in its early stages the lophophore is set low on the brachial mantle. Small brachial canals (*b.c.s.*) are present, and also probably

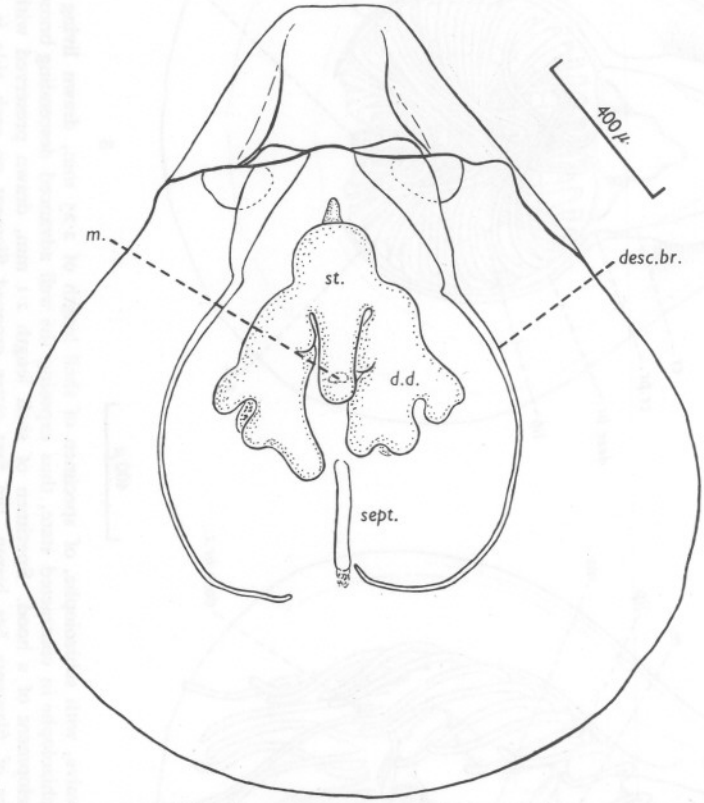

Fig. 3. *M. cranium* of shell length 2·0 mm to show the brachial support, viewed dorsally through the shell: the lophophore is omitted. The descending branch (*desc.br.*) of one side has almost reached the septum (*sept.*). *d.d.*, digestive diverticulum; *m.*, position of the mouth; *st.*, stomach. Stained with eosin and drawn while in cedar wood oil.

great brachial canals (*b.c.g.*), but owing to their small size at this stage it is impossible to be certain as there is some collapse of their walls. Fig. 4A clearly shows the relation of the mouth (*m.*) to the brachial membrane (*b.m.*) and to the circle of filaments (*fl.*). The descending branches (*desc.br.*) are not confluent with the valve floor, running slightly above it. The section illustrated in Fig. 4C, through the anterior region of the lophophore and through the septum, is near the anterior limit of the descending branches, that on the right alone being present.

As growth of the lophophore proceeds the position of the descending branches shifts inwards. A late schizolophous stage, with lateral arms deflected, at a shell length of 2·2 mm is illustrated (Fig. 5A). The, as yet widely curved, descending branches have united with the septum, which is slightly grooved ventrally—the grooving precedes formation of the hood—and is split anteriorly. Konjoukova (1957, pp. 63–4) has noted that anterior division of the septum is characteristic of the development of the brachial apparatus of the Dallininae, in which she included *Laqueus*.

In another specimen of about the same size and lophophore stage as that shown in Fig. 5A the descending branches make an acute angle with the

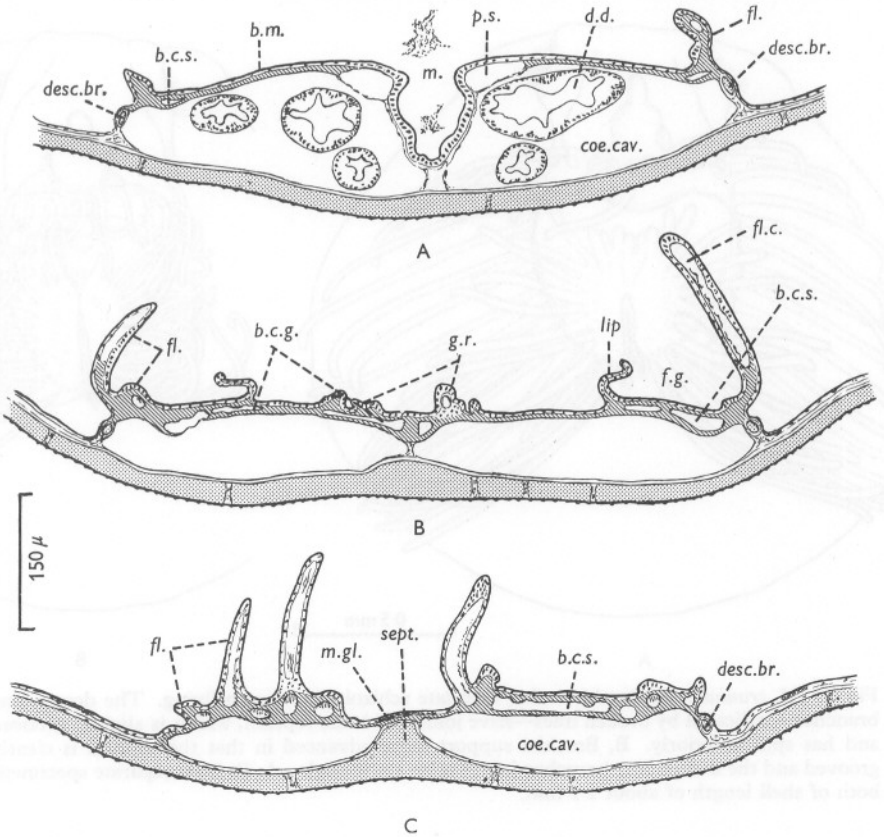

Fig. 4. *M. cranium* of shell length 2·1 mm. Transverse sections through schizolophe to show its relation to the dorsal mantle and shell, (A) through the mouth (*m.*), (B) through the twin growing regions (*g.r.*) and (C) through the anterior region of the lophophore and the septum (*sept.*). *b.c.g.*, great (?) and *b.c.s.*, small brachial canals; *b.m.*, brachial membrane; *coe.cav.*, coelomic cavity; *d.d.*, tubule of digestive diverticulum; *desc.br.*, descending branch of the loop; *f.g.*, food groove; *fl.*, filament and filament base; *fl.c.*, filamentar canal; *lip*, lip of the food groove; *m.gl.*, mucous gland cells; *p.s.*, perioesophageal sinus. Supporting substance diagonally hatched.

septum (Fig. 5 B). This is the youngest stage of the brachial support described by Friele (1877) at a shell length of a little less than 3 mm, nearly agreeing with his fig. 1.

At a somewhat greater shell length, 2·8 mm, the lophophore is still schizolophous, but the ventral, abfrontal, surfaces of the lateral arms have widened. The hood, although narrow is clearly distinguishable. Long, spinous, processes have developed from the anterior end of the septum. This would correspond to Friele's fig. 2. Elliott (1953, p. 269) has noted the spiny nature of many dallinid loops, mature and immature, a feature almost completely lacking in the Terebratellidae.

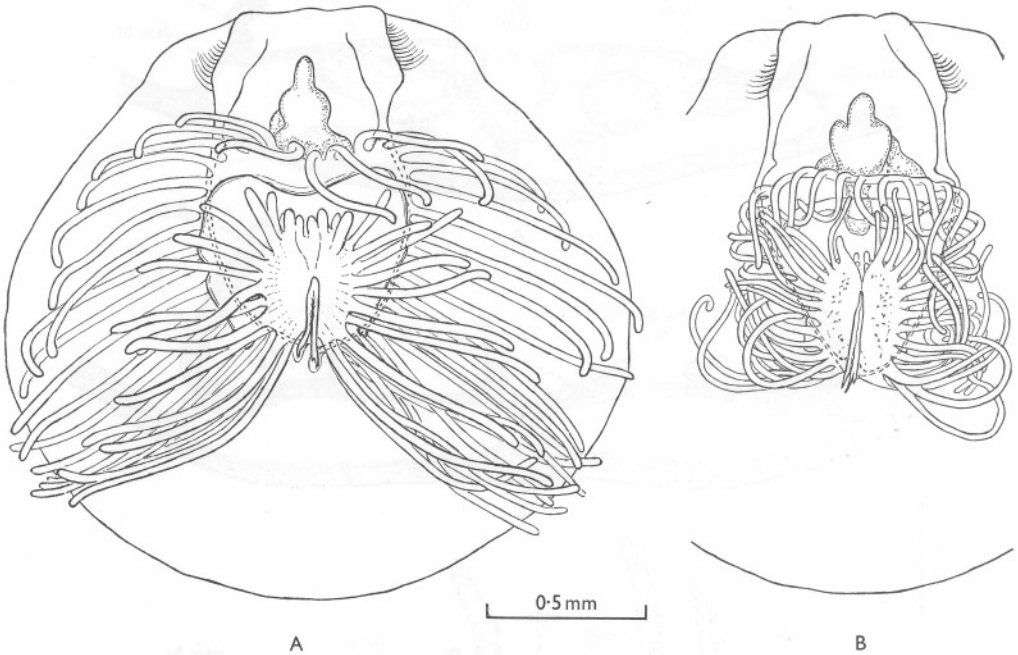

Fig. 5. *M. cranium*. A, Brachial valve with late schizolophe, drawn living. The descending branches—indicated by broken lines—have joined with the septum, which is slightly grooved and has split anteriorly. B, Brachial support more advanced in that the septum is clearly grooved and the descending branches join it at an acute angle. A, B, from separate specimens both of shell length of about 2·2 mm.

At a shell length of 3·5 mm (brachial valve 3·35 mm) the lophophore is zygolophous (Fig. 6). The hood has widened posteriorly and by resorption of its posterior closed end, the transverse band (*t.b.*) has been formed. The anterior spinous processes have increased in number. This stage was drawn from a living individual obtained from La Chapelle Bank region in September 1954. The condition of the brachial support corresponds to Friele's fig. 3.

The transverse sections of this stage, illustrated in Fig. 7, show the relation of the brachial support, and particularly of the hood, to the lateral arms. The somewhat oblique section shown in Fig. 7 A passes through the growing region (*g.r.*) of one side. At this size the great brachial canals (*b.c.g.*) are clearly distinguishable.

At a shell length of 4·2 mm (brachial valve 3·6 mm) the lophophore (Fig. 8 A) is at about the same stage of development as at the smaller shell size (Fig. 6). Growth of the hood, however, has advanced, its lower margins having diverged widely, and is now at about the stage shown in Friele's (1877) fig. 4 (brachial valve 4·5 mm long) and Elliott's (1948) fig. 2 (of shell length 5·5 mm).

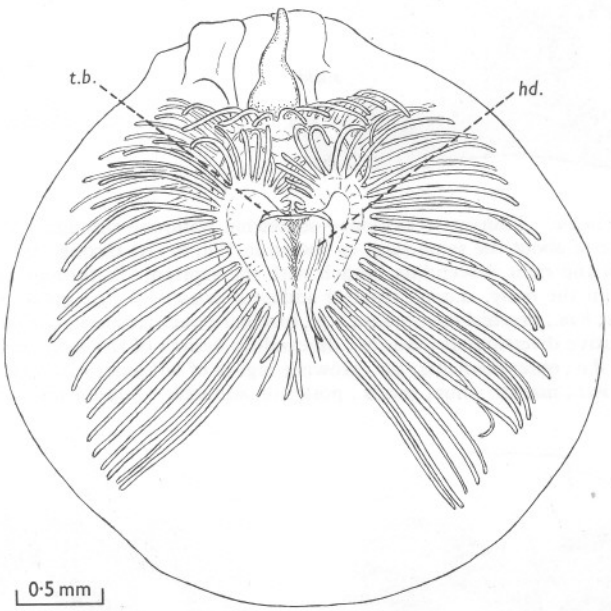

Fig. 6. *M. cranium* of shell length 3·5 mm. Brachial valve with zygolophe, drawn living. The hood (*hd.*) has widened posteriorly and the transverse band (*t.b.*) is distinct. The anterior spinous processes are long. The dorsal filaments of the lateral arms have been omitted so as to avoid confusion.

The last lophophore stage to be described here (Fig. 8 B) is at a shell length of 5·3 mm (brachial valve 4·6 mm). The lophophore is early plectolophous, with one small coil to the spiral arm. In the figure the dorsal part of the spiral arm has been omitted so that the loop should not be entirely hidden. The loop is in the stage shown in Friele's fig. 7, which according to Elliott (1948) corresponds to his figs. 4 and 5. Friele gave the length of his brachial valve as 5·6 mm; Elliott the length of his pedicle valve as 7·0 mm. The freeing of the loop from the septum, and the gradual thinning and disappearance of the

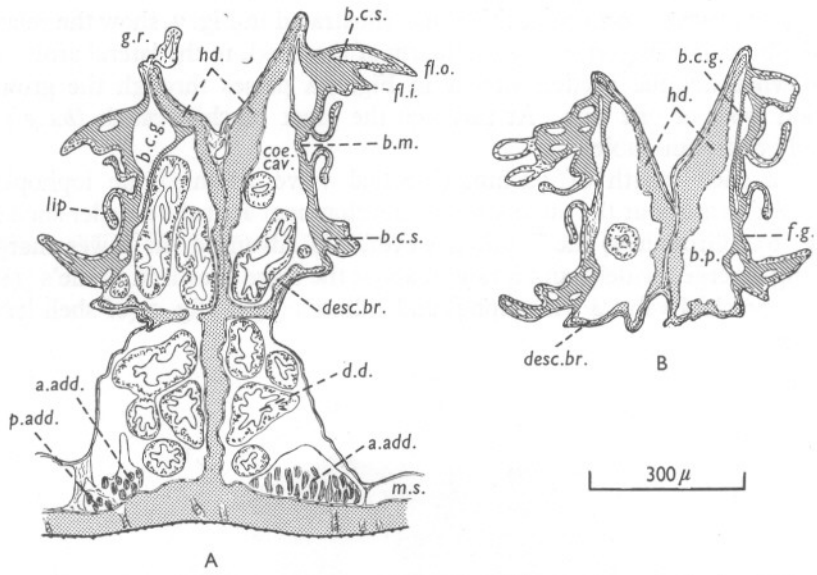

Fig. 7. *M. cranium.* Transverse sections—somewhat oblique—through the brachial valve with zygolophe of about the same stage as shown in Fig. 6, (A) through the hood (*hd.*) and the junction of the right descending branch with the septum, (B) through the lateral arms where free from the body. *a.add.*, anterior adductor muscle; *b.c.g.*, great and *b.c.s.*, small brachial canals; *b.m.*, brachial membrane; *b.p.*, brachial pouch; *coe.cav.*, coelomic cavity; *d.d.*, tubule of digestive diverticulum; *desc.br.*, descending branch of the loop; *f.g.*, food groove; *fl.i.*, inner and *fl.o.*, outer filaments; *g.r.*, growing region of left side; *hd.*, hood; *lip*, lip of the food groove; *m.s.*, mantle sinus; *p.add.*, posterior adductor. Supporting substance shown hatched.

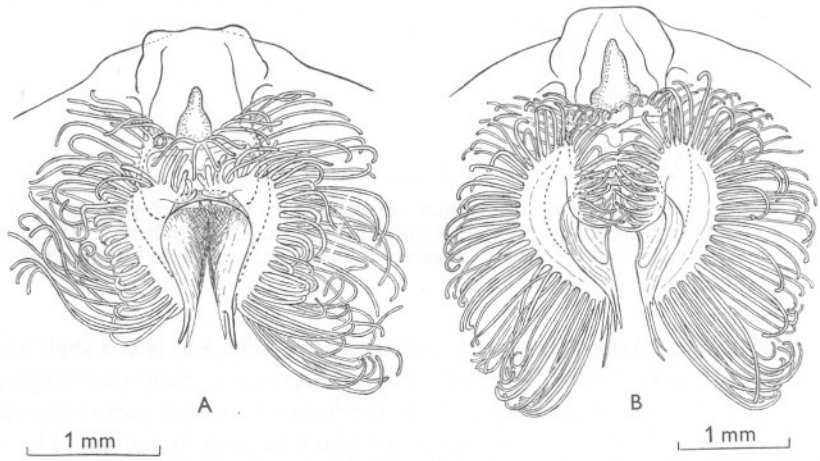

Fig. 8. *M. cranium.* A, Specimen of shell length 4·2 mm: part of the brachial valve with zygolophe, drawn preserved, unnarcotized. The hood is more advanced than that shown in Fig. 6, its lower margins having diverged. B, Specimen of shell length 5·3 mm; early plectolophe with spiral arm of one coil, the dorsal half of which has been omitted for the sake of clearness. The hood shows large lacunae. Preserved after narcotizing and drawn while in cedar wood oil.

latter takes place at this stage; it has been described by Friele (1877, pp. 381–2) and Elliott (1948, p. 301).

Although it has been found that some variation occurs in the shell length at which a certain stage of lophophore and loop is attained, it will have been seen that the loop is in a more advanced stage at a lesser shell size in the La Chapelle Bank specimens than in those of Friele and Elliott. Elliott's *Macandrevia cranium* came from the Hardangerfjord, Norway (1948, p. 316); those of Friele (1877) apparently from the same country.

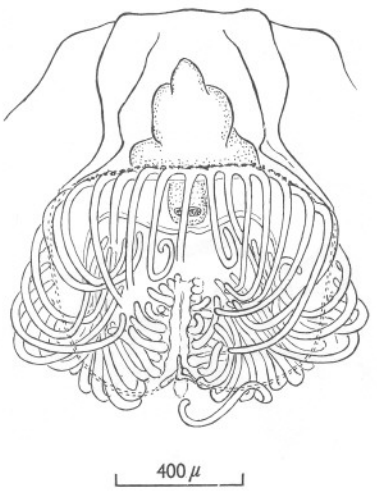

Fig. 9. *M. cranium* of shell length 2·3 mm. Schizolophe with abnormal septum, restricted to a small three-pronged structure at the junction with the descending branches (indicated by broken lines). Stained and drawn while in cedar wood oil.

The development of the brachial support of *M. cranium* is marked by exceptionally early growth of the descending branches of the loop and a late development and early disappearance of the septum.

In *Dallinella* (= *Terebratalia*) *obsoleta*, the only member of the Dallinidae in which the very early stages of the loop have been figured, a septum is present before the development of the crura, and a hood appears on the septum before growth of the descending branches begins (Beecher, 1895).

In *Laqueus californicus*, placed by Konjoukova (1957) in the Dallininae, but by Yabe and Hatai in 1941 (see Muir-Wood, 1955) in the Laqueidae, the septum also appears before the descending branches, as may be seen from her fig. 27 (p. 40).

Small individual with an abnormal septum. One individual of shell length 2·3 mm, with advanced schizolophe, had an abnormally developed septum (Fig. 9). A small calcified region, irregularly three-pronged in shape, occurred

at the junction of the descending branches with it. The remainder of the septum appeared to be represented by connective tissue only. The median dorsal mesentery was clearly visible running up its centre.

THE ADULT LOPHOPHORE

The adult lophophore is plectolophous, supported by a long calcareous loop: spicules are entirely lacking. As the shell is long the lateral and spiral arms are long. The loop extends to the extreme end of each lateral arm, and a spine projects anteriorly. The position of the twin growing regions at the apex of the spiral arm is shown in transverse section in Fig. 10A. From the sections illustrated in Fig. 10 the very largely tubular structure of the lophophore of

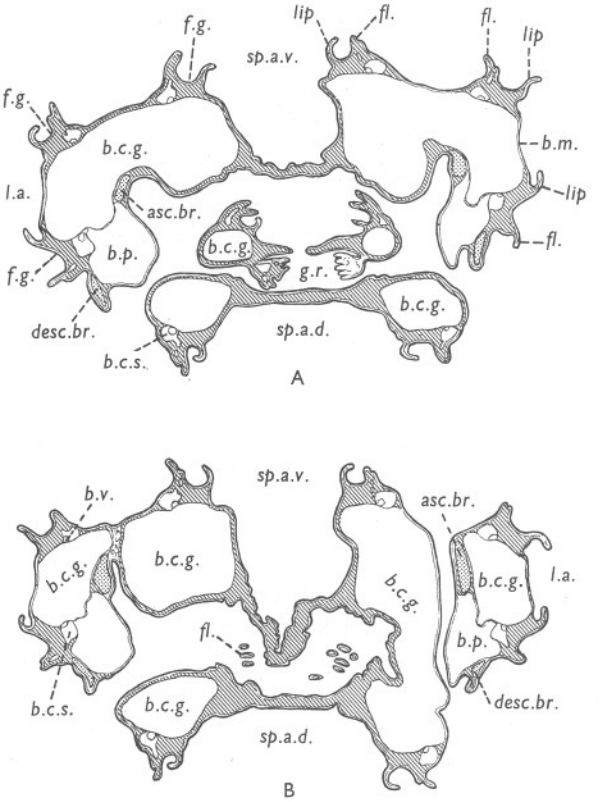

Fig. 10. *M. cranium* of shell length 17 mm. Transverse sections through adult plectolophe. A, Section through the twin growing regions of the lophophore (*g.r.*) at the apex of the spiral arm. The great brachial canals of the lateral and spiral arms are in communication. B, a section anterior to A, with the spiral and lateral arms becoming separate. *asc.br.*, ascending branch of the loop; *b.c.g.*, great and *b.c.s.*, small brachial canals; *b.m.*, brachial membrane; *b.p.*, brachial pouch; *b.v.*, 'blood' vessel; *desc.br.*, descending branch of the loop; *f.g.*, food groove; *fl.*, filament; *l.a.*, lateral arm; *lip*, lip of the food groove; *sp.a.d.*, dorsal and *sp.a.v.*, ventral side of first coil of spiral arm. Supporting substance shown hatched.

Macandrevia cranium is apparent. There is so little tissue that on fixation a certain amount of distortion occurs, for instance the brachial membrane connecting the opposite rows of filaments of the ventral part of the first coil of the spiral arm is probably too deeply indented.

The usual canals are present in the lophophore. Small brachial canals (*b.c.s.* Figs. 10, 11), arising from the perioesophageal lacunae, run at the bases of the filaments to which they give off branches. Within the small brachial and the filamentar canals are 'blood vessels', with fine muscle fibres in their walls. The great brachial canals (*b.c.g.*) each ends in a blind sac on each side of the oesophagus (see also Hancock, 1858, p. 807). In the lateral arms they do not extend as far anteriorly as do the small brachial canals, which are continuous around the blind end of the arms. Posteriorly the great brachial

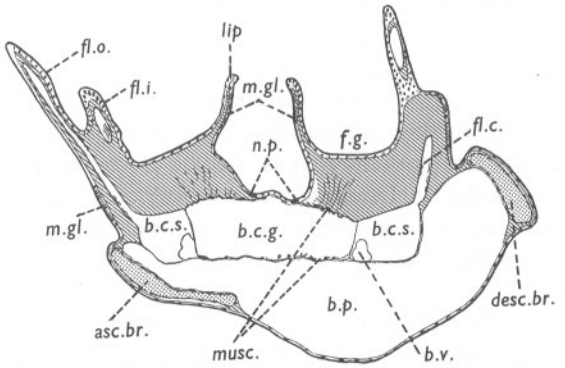

Fig. 11. *M. cranium*. Transverse sections of lateral arm of an adult. *fl.c.*, filamentar canal; *fl.i*, inner and *fl.o.*, outer filaments; *m.gl.*, mucous gland cells; *musc.*, muscle fibres; *n.p.*, principal nerve. Other lettering as in Fig. 10.

canals of the lateral and spiral arms are continuous (Fig. 10A), as noted by Hancock; anteriorly they become separate (Fig. 10B). In each lateral arm a brachial pouch, a continuation of the coelomic cavity, extends anteriorly to its extremity, reaching beyond the great and small brachial canals. In Figs. 10 and 11 it is impossible at the magnification shown to indicate the various tissues.

Muscle fibres are present in the walls of the canals, chiefly beneath the supporting substance under the food grooves and the filaments. Here they are mainly transverse in direction and on contraction compress the supporting substance, so that in sections it appears to have fibres running normal to the food groove. Contraction of these muscle fibres also causes the brachial membrane to be thrown into folds. In the lip of the food groove muscle fibres are present below the epithelium.

Nerves are difficult to distinguish in sections of the lophophore, indeed only the principal nerve (*n.p.*) could be certainly identified: its position is shown in Fig. 11.

The distribution of mucous gland cells on the lophophore is similar to that in other plectolophes examined. They occur: (1) in an abfrontal tract below the bases of the filaments; (2) on the brachial membrane of the arms; and (3) on the walls, including the lip of the food groove.

The filaments are in the usual double alternating series, the outer with grooved and the inner with ridged frontal surfaces. Behind the mouth twelve to fourteen pairs of filaments are in single series and have ridged frontal surfaces: these filaments are short. Longitudinal muscle fibres are present in the walls of the filamentar canals, chiefly in a frontal group, in which the fibres are striated.

The body of the lophophore is entirely ciliated, except possibly for mucous cells. The outer surfaces of the filaments are entirely ciliated, the cilia being in four tracts: frontal, abfrontal and paired lateral.

The ciliary feeding mechanism of *M. cranium* has been briefly described (Atkins, 1956) and it is intended to publish a full account separately.

In the various growth stages resulting in the plectolophe of the adult, new filaments are formed in two immediately adjacent regions, one on each side of the mid-line. The two growing regions remain close together in all developmental stages and in the final plectolophe are situated at the apex of the spiral arm. There is no interpolation of filaments, and yet the lateral arms increase in length commensurate with growth in length of the shell. It appears that there is a shifting around of the filaments, together with the underlying brachial canals, so that those on the ventral side of the lateral arms move around on to the dorsal side, while filaments which were originally situated on the spiral arm will move around on to the ventral side of the lateral arm. The two opposite rows of filaments of the spiral arm are distinct in that one set belongs to the left side of the body and one to the right: there are two distinct great brachial canals. In the lateral arms there is a single great brachial canal for the two rows of filaments on opposite sides of the arms: the two tubes having as it were coalesced (Hancock, 1858).

To account for the forward growth of the lateral arms in the lophophore of terebratulaceans and terebratellaceans, Williams (1956, pp. 261–3) suggested that growth in the median zone is temporarily suppressed, while two secondary growth regions arise in the antero-lateral positions of the lophophore. This suggestion seems to be unfounded. Secondary growth zones would presumably be marked by the presence of short filaments and filament buds, but such have been found only in the twin growing regions in the median indentation of the schizolophe in all brachiopods studied, including *Terebratella inconspicua* which Williams figured (1956, fig. 5 (1)). And far from growth being suppressed in the median zone, it becomes accelerated, as the presence of crowded filament buds shows (see Fig. 2). The growth of new filaments appears to be so rapid that their migration anteriorly and laterally to form the lateral arms does not keep pace with it, and the growing

regions turn either anteriorly, and finally ventro-dorsally, as in plectolophes, or laterally, as in spirolophes, encroachment on the mouth thus being avoided.

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SUMMARY

The early growth stages of lophophore and loop of *Macandrevia cranium* at a shell length of 1·0–5·3 mm are described. Figures are given to show that in this dallinid the descending branches of the loop grow from the crura only and fuse with the septum. The figures also show that only the two primary growth regions persist, and that no secondary growth zones arise.

The growth of the brachial support is marked by exceptionally early development of the descending branches of the loop and a late development and early disappearance of the septum.

The structure of the adult plectolophous lophophore is described.

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