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# JUVENILES OF CAVOLINIA INFLEXA (LESUEUR, 1813) AND CAVOLINIA LONGIROSTRIS (DE BLAINVILLE, 1821), THEIR DISCRIMINATION AND DEVELOPMENT (GASTROPODA, PTEROPODA)

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## ABSTRACT

In C. inflexa the mantle gland and its border show twenty-two bands. Differences in banding with C. longirostris are discussed. It appeared to be possible to discriminate the soft parts of juveniles in both species. Of special value for discrimination is the shape of the lateral appendages. The shells can be distinguished by the relative length of the caudal spine, which is longer in C. inflexa than in C. longirostris.
Different developmental stages of C. longirostris are described and those of C. inflexa are added for comparison. While for the latter species the soft parts grow larger parallel with the increment of the shell, this is not the case in C. longirostris, due to the occurrence of minute stages and shedding of the caudal spine. The differences in shedding between C. longirostris and Diacria are described.

## INTRODUCTION

Most juvenile euthecosomatous pteropods are recognizable by their embryonic shells. Nevertheless, juvenile shells of some species resemble each other closely, which is explained by similarity in their development. Van der Spoel (1967, figs. 212, 230) depicted the developing shell in Cavolina inflexa (Lesueur, 1813), and a young C. longirostris (de Blainville, 1821), which resembles the younger stages of the former.

Frontier (1966), discussing the development in C. longirostris, stated: "il est impossible de superposer les dessins de deux stades successifs de coquilles juvéniles dans leurs parties homologues". The great differences in shape of the successive life stages induced him to suppose, that the posterior part disappears gradually during the growth of the anterior parts. In the opinion of Frontier a loss of the embryonic shell at a fixed stage, as supposed by Pelseneer (1887), does not occur. The process is, according to Frontier, in all probability a flattening and stretching of the shell in dorsoventral direction. Such a process would be exceptional among Cavoliniinae. The youngest shells in the developmental series of C. longirostris do resemble juveniles of C. inflexa as well.

The purpose of the present study is in the first place to furnish means to distinguish juveniles of C. longirostris from those of C. inflexa. Discriminating characters in the shells as well as in the soft parts are described. The study of the shell and body of C. longirostris allows for a more correct description of the development in this species. For comparison, the development of the shell and the body in C. inflexa is given.

## ACKNOWLEDGEMENTS

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## MATERIAL AND METHODS

Material on which the present investigations are based came from the Caribbean near the islands of Curaçao and Bonaire, and from the Atlantic off the Guyanas. The plankton samples were taken by the M.S. "Luymes" of the Royal Dutch Navy in connection with the Cooperative Investigations in the Caribbean and Adjacent Regions (C.I.C.A.R.). The material was fixed in formalin, while after sorting, shell-bearing species were preserved in alcohol 70%. For comparison, material from the Dana Expeditions was used.

According to Van der Spoel (in press) it is possible to identify adult euthecosomatous pteropods on the ground of the bands in the mantle gland. The zones of polygonal and cuboid cells in the mantle gland are different in aspect in the various species. Rampal (1965) involved the bands in her investigation of the development of the body in Clio cuspidata (Bosc, 1802). The bands mentioned and other details in the mantle gland become very clear, when soft parts are stained for a few seconds with methylene-blue; too strong a staining can be corrected by a treatment with alcohol 70%.

All measurements were taken to the nearest 0.005 mm with an eyepiece micrometer in a Reichert stereo-binocular dissecting microscope. Shells were measured in dorsal, the bodies in ventral view. To make comparison of bodies at different stages more reliable, the size of the mantle gland was considered representative for the body size. The length of the mantle gland with flaps, but without mantle appendages (from band a to t, fig. 1) was measured, thus only less contractile parts were concerned.

Both species are represented by different formae, but in the present study the formae are not discussed separately as differences within one species proved to be neglectable.

The present material contributed much to our knowledge on the distribution of pteropods in the Caribbean. Further data on this subject will be published separately.

## STRUCTURE OF THE MANTLE

Bands visible in the mantle gland.

Mantle glands, dissected from C. inflexa and stained with methylene-blue, show under a 400 to 1000 times magnification twenty-two bands. These are from the anterior side going backwards indicated with: a, b, c, ....... u, v (fig. 1). The part which normally is referred to as mantle gland is composed of the twelve bands f to q, which are correlated below with bands described by Meisenheimer (1905), Rampal (1965) and Van der Spoel (1967).

| Band | f | g | h | i | j | k | l | m | n | o | p | q |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Meisenheimer |  | x |  | 1 |  | xx |  | 2 |  | I | 3 | II |
| Rampal | I |  | 1 | 2 |  | 3 |  | 4 |  | II | 5 | III |
| Van der Spoel |  | A' |  | A |  | I |  | B |  | II | C | III |

The bands o and q (dotted in the figs. 1, 3 and 5) and, less obviously, band g are composed of cuboid cells. The bands i, l, m, n, and p consist of polygonal cells. The other bands show other types. At a lower magnification (40 x) the complex of the f, g, and h band is seen as two bands in all stages of C. inflexa and in adults of C. longirostris, while the same complex is seen as one band in juveniles of C. longirostris. This complex is characterized in juveniles of C. longirostris by a median widening in posterior direction (figs. 5a, b), a character disappearing during growth.

Band j is not a real band of typical cells, but only a zone of cells which transforms during growth. As will be shown below, the k band (hatched in figs. 1, 3, and 5) changes from a very broad band in juveniles into a very small one in older stages. So it is comprehensible that the border of this k band is composed of disintegrating cells which constitute the j band. This hypothesis is supported by the fact that sometimes a zone comparable with j is found between the bands l and k. Moreover, in some specimens, the orientation of the cells in band l points to an active process of narrowing, explaining the presence of such "accumulation" zones. The difference between the l, m, and n bands is small. The cells slightly differ in size and staining. The band m, seen as a narrow and lighter line under low magnification, is typical of C. inflexa, but is never found in C. longirostris.

The mantle gland border runs as a prolongation of the real mantle border along the margin of the mantle gland and consists of three zones, which are indicated in the cranial part with a, b, and c, and in the caudal part with r, s, and t. Anteriorly this border forms a typical triangular flap in C. inflexa, which is sometimes divided into two subequal lateroventral parts in juveniles. The innermost zones c and r, respectively, chequered in the figs. 1, 3, and 5 are retaining best the stain and constitute therefore the most conspicuous zones.

Zones d and e are transparent, and constitute the transition between the border and the real mantle gland. Zone u is a thickened part of the mantle, and v is the real mantle, both indicated by black in the figs. 1, 3, and 5; they cover gonad, liver, heart, and kidney in C. inflexa and in juveniles of C. longirostris.

It is possible to detect in C. longirostris, especially in the juveniles, the same components as described above, except for the already mentioned differences, as to the f, g, h, and the l, m, n complexes. Moreover, the strong curvature of the ventral part of the body prevents in adults the development of the flap with the bands as found in the more straight and flat C. inflexa. Only a membrane can be found in C. longirostris.

Lateral and anterior appendages.

In all developmental stages of both species the lateral appendages appear to be dissimilar in shape. Near the lateral sides of the mantle in C. longirostris two oblong projections are found (fig. 2a). In the youngest specimens these appendages are very close to the body. In older individuals preserved in spirit they are more distinct and expanded near the posterior part of the shell aperture, so that a gill function is most obvious. In living specimens they protrude through the posterior corners of the shell aperture. In C. inflexa long protrusions are always absent, as more rounded and folded appendages are found at the lateral sides of the mantle border (fig. 2b). The lateral appendages in both species are identical in structure with the mantle border, they bear the mantle corner glands (Van der Spoel, 1967).
In full grown C. longirostris two appendages are attached anteriorly to the cranial flap of the mantle (fig. 2a). In C. inflexa such structures are never found.

## DEVELOPMENT OF THE MANTLE AND SHELL

### Cavolinia inflexa (Lesueur, 1813)

Development of the soft parts is given in figs. 3a-d, for specimens with a shell length of 1.86, 1.90 (shown in fig. 4a), 3.18, and 4.97 mm (full grown), respectively. Increase in size of soft parts and shell runs parallel. The mantle gland with the flap shows the same growth rate as the body throughout the developmental series. The attachement of the folded lateral appendages does not reach below the k band in small juveniles. During growth these appendages shift to a more posterior position finally reaching band p. This shift of lateral appendages is already mentioned by Rampal (1965) for the single protrusion at each side, in Clio cuspidata.

There occurs a clear change in the banding of the mantle gland. Most conspicuous is the relative and absolute narrowing of the band k (hatched); in the specimen of fig. 3a this band is about three times broader than in the adult specimen of fig. 3d. At the same time the other bands of the mantle gland widen, especially the one just below the k band. This band is homogeneous in the youngest specimens, but early in the development a small m band, indicated by two interrupted lines in figs. 3b-d, develops in the complex posterior to the k band. Slightly different cells can be observed in the m band as mentioned above.

The development of the shell is given in figs. 4a-c. The animals from these shells show mantle gland lengths of 0.97 (shown in fig. 3b), 1.05, and 1.53 mm, respectively. The adult shell is not figured; one is referred to Van der Spoel (1967: figs. 103, 105).

### Cavolinia longirostris (de Blainville, 1821)

Development of the soft parts is given in figs. 5a-g. Soft parts taken from shells with a length of 1.20 (shown in fig. 6a), 1.68 (shown in fig. 6b), 2.73, 3.65 (shown in fig. 6d), and 2.73 mm (shown in fig. 6e) are depicted. The shell of specimen f was partly dissolved, but it resembles that of fig. 6e. The adult specimen g comes from a shell with a length of 4.13 mm. The size of the soft parts increases regularly and parallel with the increase of shell length only up to a certain stage. This stage is represented in fig. 5 by specimen d, in which the posterior part of the mantle (black) does no longer cover the liver, heart and kidney as it does in younger specimens (figs. 5a-c). These organs are shifted in anterior direction. Moreover, the lateral displacement of the columellar muscle can be observed in specimen d. This process is mentioned by Van der Spoel (1967) as the beginning of transformations of the soft parts, resulting in the formation of a minute stage.

In our series, this minute stage is represented by specimen e. Folds in specimen d, indicated by fish-bone lines, mark already the place where the minute stage will show the strong curvature in dorsal direction, indicated in specimens e by a fish-bone line. Specimens in minute stage are only found in shells which have already thrown off the caudal spine. Consequently the transformation in the soft and hard structures coincides, although the shift of the columellar muscle and the liver, heart, and kidney precedes the loss of the caudal spine, which is not common in Cavoliniinae.

The most conspicuous difference between C. longirostris and C. inflexa during their development is the shape of the lateral appendages. In the former species they form two oblong protrusions, while they are rounded folds in the latter species. During growth the lateral appendages shift as in C. inflexa from an anterior to a posterior position, becoming also more expanded, but in C. longirostris the shift is much more pronounced while the oblong shape persists during growth.

In C. longirostris the narrowing of the k band (hatched) is more pronounced than in C. inflexa . This may be due to the fact that for C. longirostris much younger specimens were studied or to the fact that different rates of development are concerned. In the broadening band just below band k a subdivision can never be made as it could in C. inflexa; a small band of slightly different cells as in the latter species is never found. In the specimens a and b in fig. 5 the median widening of the complex of the f, g, and h bands is clearly shown. The phenomenon is normally found in juveniles of C. longirostris but is always absent in C. inflexa.

Shell development for C. longirostris is given in figs. 6a-e. The animals from these shells show a mantle gland length of 0.75 (shown in fig. 5a), 0.90 (shown in fig. 5b), 1.12, and 1.94 mm (shown in fig. 5d). The soft parts from shell e are given in fig. 5e, while soft parts like given in fig. 5f are found in shells like in fig. 6e. The adult shell is not figured; one is referred to Van der Spoel (1970: fig. 25).

Very fine cracks are common along the lateral ribs of the caudal spine in juveniles. Although these cracks occur occasionally in species which show no loss of the caudal spine, they indicate in the present species the area where the spine will break. The loss of a caudal spine results in a clear caudal spine mark in juveniles as shown in fig. 6e. In some specimens even an opening is left at the place of rupture. The occurrence of a rupture and existence of minute stages was already discussed by the second author (Van der Spoel, 1967: 178). In juveniles as well as in adults this mark, 0.75-0.82 mm in length, is situated at about 0.30 mm behind the posterior edges of the shell aperture. The shell diameter 0.30 mm below these aperture edges is about 0.80 mm in specimens as shown in fig. 6d. Thus the adult shape of C. longirostris specimens evidently develops as a continuation of the series of juveniles given in fig. 6. The length of the caudal spine that is thrown off is about 1.2 mm. Shell length in specimens which have already lost the caudal spine is usually about 2.6 mm, as a consequence, the length of shells with the caudal spine still intact must be 1.2 + 2.6 mm. The three eldest juveniles found with a caudal spine, show a shell length of 3.7, 3.7, and 3.8 mm, so that the above mentioned interpretation becomes far more acceptable. That only such a small number of older juveniles with an intact caudal spine could be found will be due to the short time during which this stage exists. The caudal spine is always thrown off in adults of C. longirostris.

In the samples, shells of young specimens of both species were found in different conditions: besides very transparent and flexible shells more opaque and solid specimens were found; this phenomenon is also described by Frontier (1966). To what extent preservation fluids will be responsible for these differences is uncertain. Both kinds of shells were found in the same sample, and as their treatment was similar one cannot consider the different condition of the shells due to an artefact. Probably calcification starts at different times in the population, or the differences are due to small differences in age. Frontier (1966) stated that it is not clear whether coastel populations are represented by other juveniles than oceanic ones. And it is neither known if populations from deeper layers are represented by other juveniles than those from surface layers. Since calcification of the shell is, according to Van der Spoel (1967), a secondary process, it is not amazing that shells of comparable age but in different conditions are collected. Juveniles of C. longirostris were often surrounded by a jelly-like mass, called the extra-pallial fluid.

## DISCRIMINATING CHARACTERS

### Shells

In whichever condition the shells were found, they were usually measurable, which made it possible to compose a graph of the ratio between the length of the caudal spine (which is here considered to be the part of the shell posterior to the shell aperture) and the total shell length. This ratio is found to differ in the two species, already distinguished by their soft parts as mentioned before. The relative length of the spine is always longer in C. inflexa than in C. longirostris (fig. 7). However, of the latter species smaller specimens have been collected than of the former, which made it impossible to compare all stages of the developmental series of both.

### Soft parts

In specimens of C. longirostris with a mantle gland of about 0.53 mm or more in length the lateral appendages are each characterized by two oblong protrusions (fig. 2a). The cranial mantle flap is rounded with, in the juveniles, a dark-staining band of more or less uniform width. In older, stained juveniles of C. longirostris it is possible to recognize cranially to this flap the first development of two appendages, which become more distinct in older animals (fig. 2a). On the cranial border of the flap in the specimens of figs. 5d, e, and g, the two appendages can be observed. A median widening in caudal direction of the complex of bands just below this flap can be found in the younger juveniles (figs. 5a, b). All these characters are absent in C. inflexa.

In specimens of C. inflexa with a mantle gland of 0.9 mm or more in length the lateral appendages are composed of two rounded folds only (fig. 2b). The cranial mantle flap has a somewhat triangular shape, with in the juveniles a triangular dark-staining band. (figs. 3a, b, c).

## DISCUSSION

The shedding of the caudal spine in C. longirostris is a process distinctly different from that described for Diacria (cf. Van der Spoel, 1967, 1968). Though the development of the minute stage is identical in C. longirostris and Diacria, the mechanism which effects the loss of the caudal shell part is more primitive in the former.

First of all there is no real preformed place of rupture visible in the shell, and secondly there is no distinct closing mechanism. The rupture of the shell results in a hole in the posterior part of the adult shell. This opening is closed afterwards. This explains the absence of specimens with a closing membrane and still a caudal spine persisting.

In Diacria usually a collar-like ring of shell material is found posteriorly around the closing membrane. The ring or collar is never found in Cavolinia which is explained by the fact that the adult shell closes at the level where the opening, caused by rupture, occurs, and not at a preformed place. In Diacria the place of rupture is determined by pure accident but the place of the closing membrane is fixed. In C. longirostris the place of rupture is preformed and the place of the closing membrane is determined by the rupture itself.

The two series of development given in figs. 3 and 5 are the first in which the development of the soft parts in a species through a minute stage is shown. Fig. 5d gives the first part of retraction; fig. 5e shows a real minute, while fig. 5f gives a minute in development towards an adult.

The very small juvenile shells of C. inflexa and C. longirostris resemble each other at first sight, but they differ distinctly as to their caudal spine length. Specimens of about 1.8 mm and larger have a longer spine in C. inflexa than in C. longirostris. Although, no doubt this difference will also exist in individuals of both species from other regions, one has to be aware that in different areas growth rate is not comparable. Working with other material, the meristic differences have to be studied again. Juveniles of C. inflexa collected by the Dana Expedition off the coast of Spain (40° 11' N, 12° 11' W), affirm this supposition. Geographic or clinal variation may also influence meristic differences between the two species (Van der Spoel, 1970). Most important and less variable are the differences in morphology of the soft parts, which distinguish both species.

The smallest specimen of C. inflexa found has a shell length of 1.86 mm while for C. longirostris specimens a shell length of 1.00 mm was found. This difference is probably due to the fact that most juveniles of C. longirostris were still surrounded by extra-pallial fluid, while those of C. inflexa were always without this fluid, which may have decreased the catchability. Moreover, there may exist a diffenence in ontogenetic migration besides a difference in the vertical distribution of the two species, which may contribute to the discrepancy in the minimum length of both species found, but this is still unknown.

The horizontal distribution of the juveniles of both species agrees with that of the adults in the area investigated. Juveniles of both species are found together or separately in different samples, but in both cases they occur always together with the adults of the same species. In the area off the Guyanas juveniles of C. longirostris have been found only.

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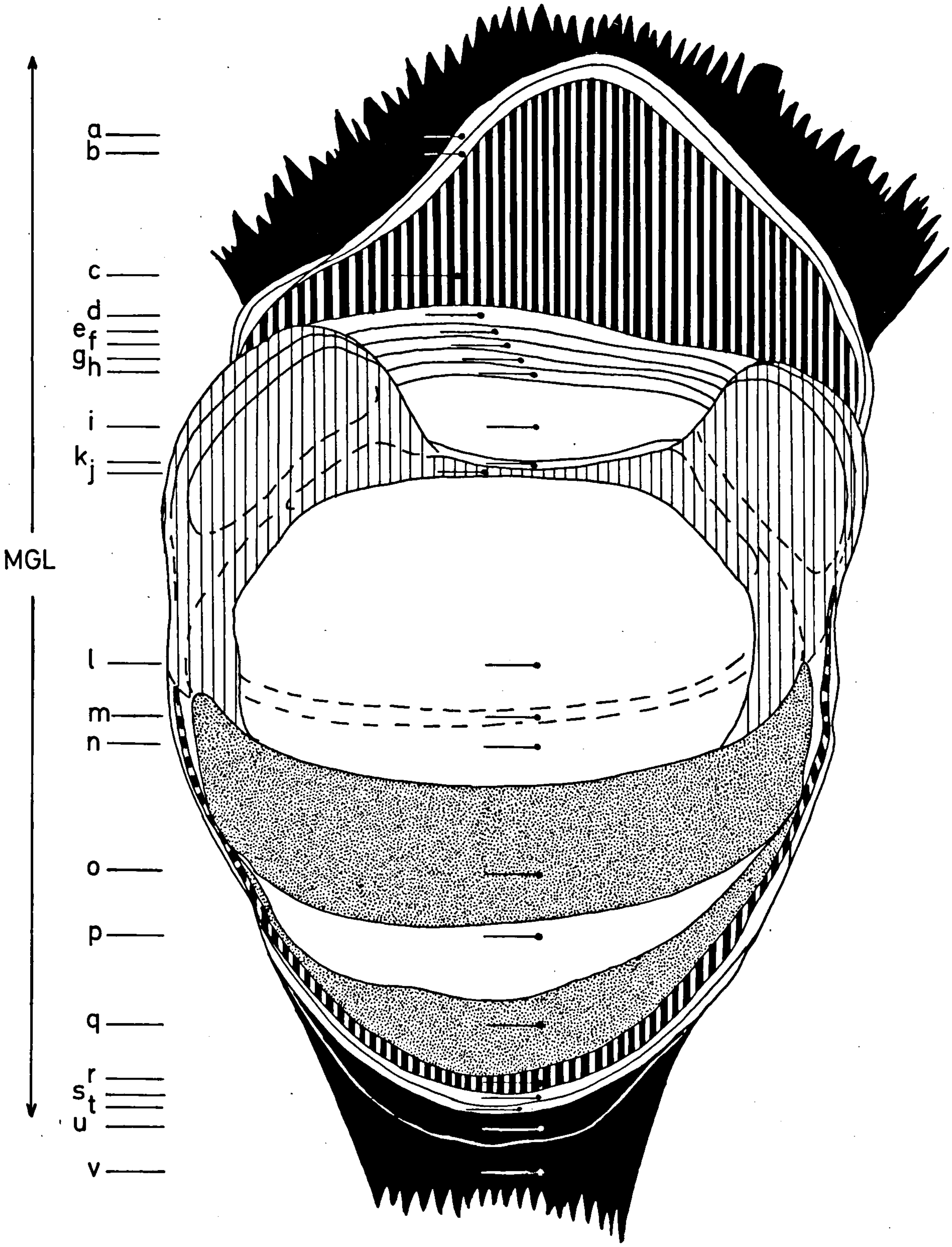

Fig. 1 Diagram of the bands in the mantle gland of **Cavolinia inflexa**. MGL: measured length of the gland; a-v: bands in the mantle.

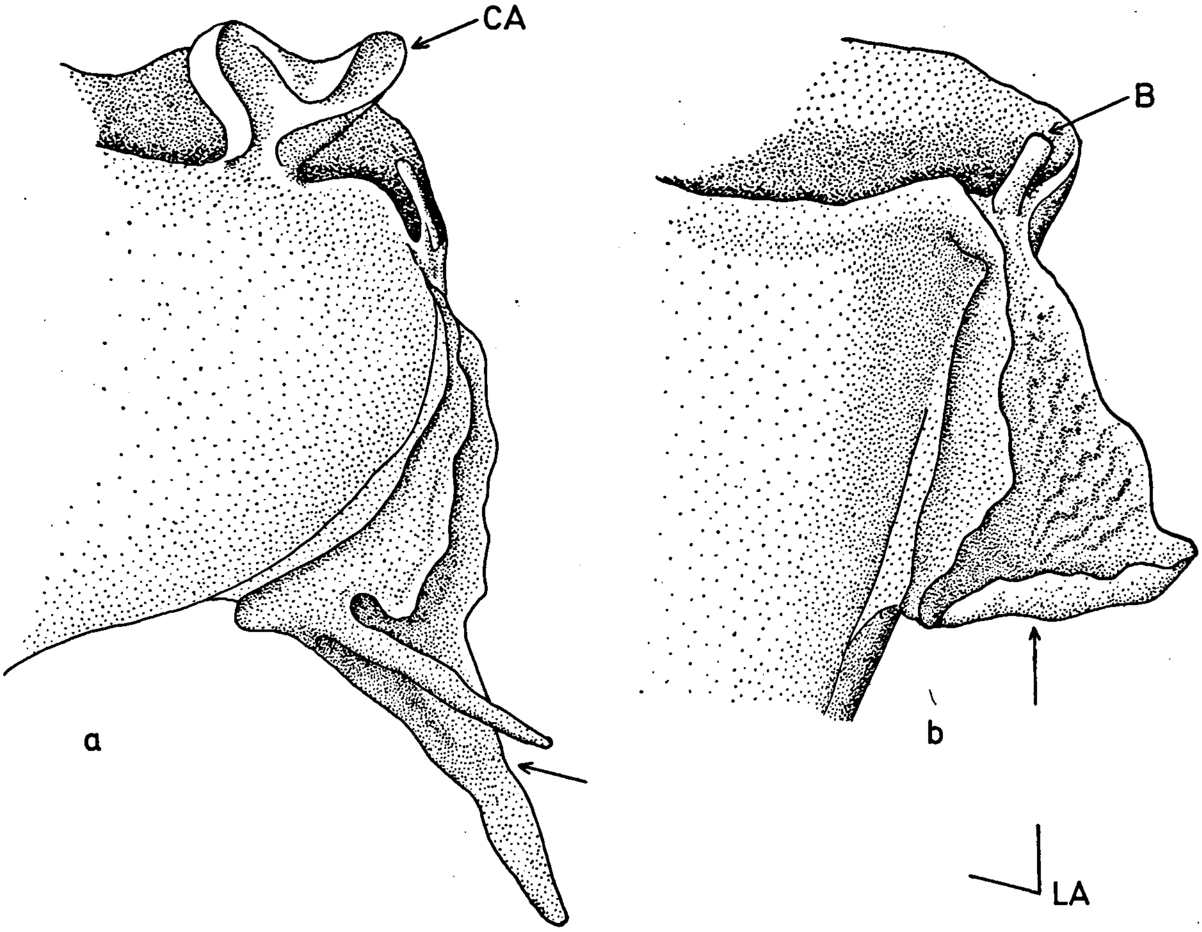

Fig. 2 Mantle appendages in Cavolinia longirostris (a) and Cavolinia inflexa (b). B: balancer; CA: cranial appendage; LA: lateral appendages.

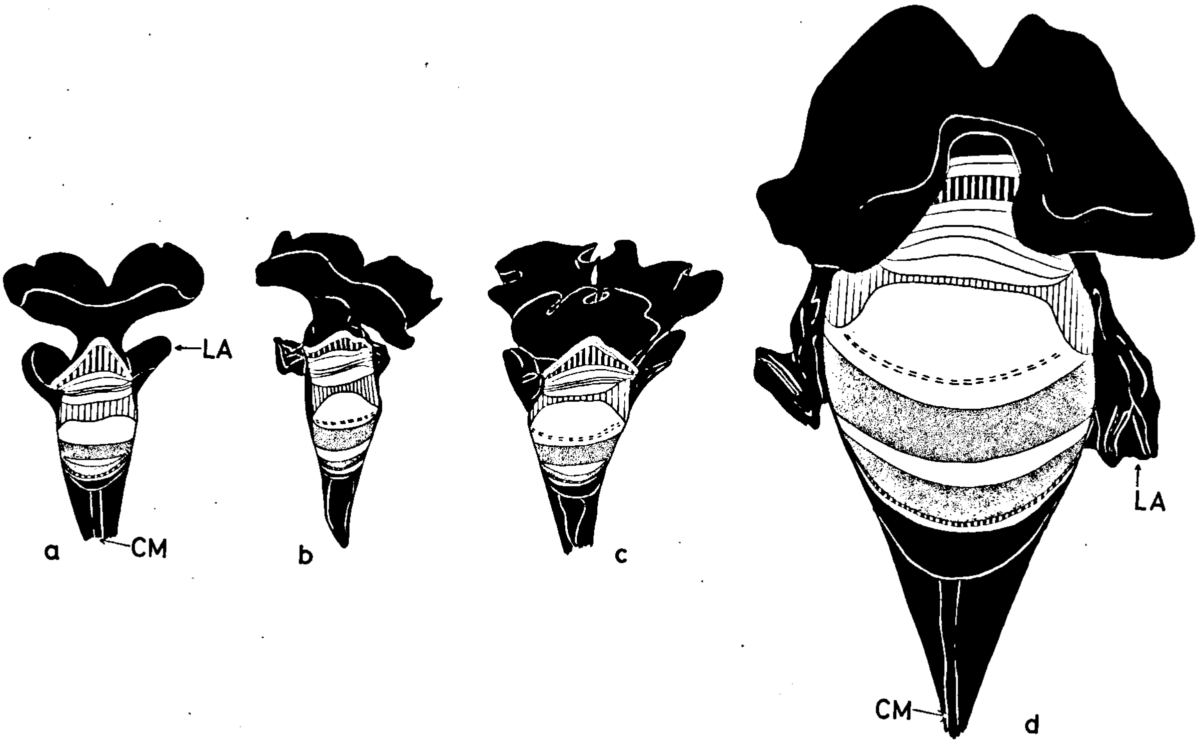

Fig. 3 Development of the soft parts in ventral view in Cavolinia inflexa. The length of the mantle gland in the specimens a, b, c, and d is 0.90, 0.97, 1.35, and 2.66 mm, respectively.

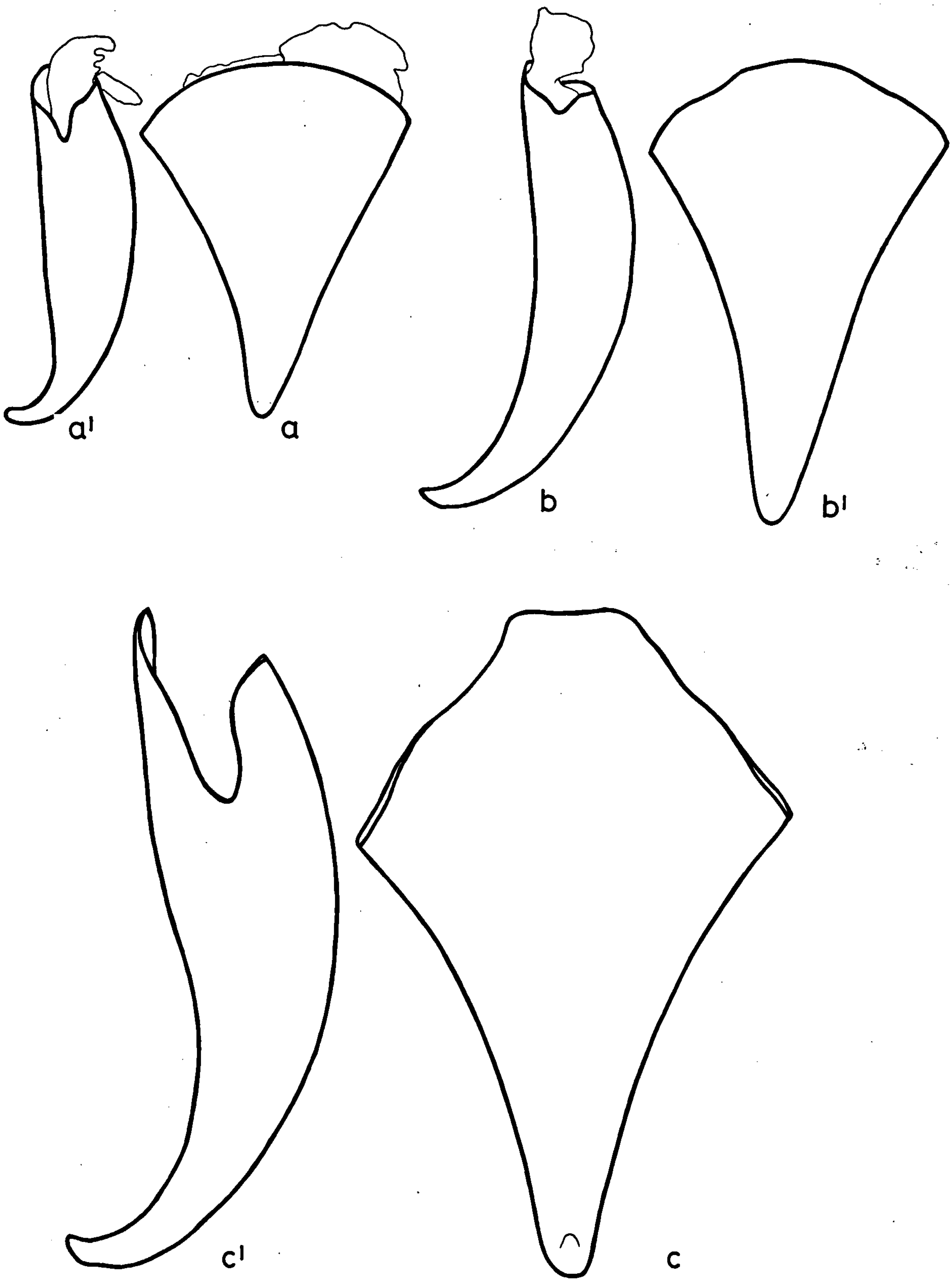

Fig. 4 Development of the shell in Cavolinia inflexa. The length of the specimens a, b and c in dorsal view (or a', b', and c' in lateral view) is 1.90, 2.36, and 3.40 mm, respectively.

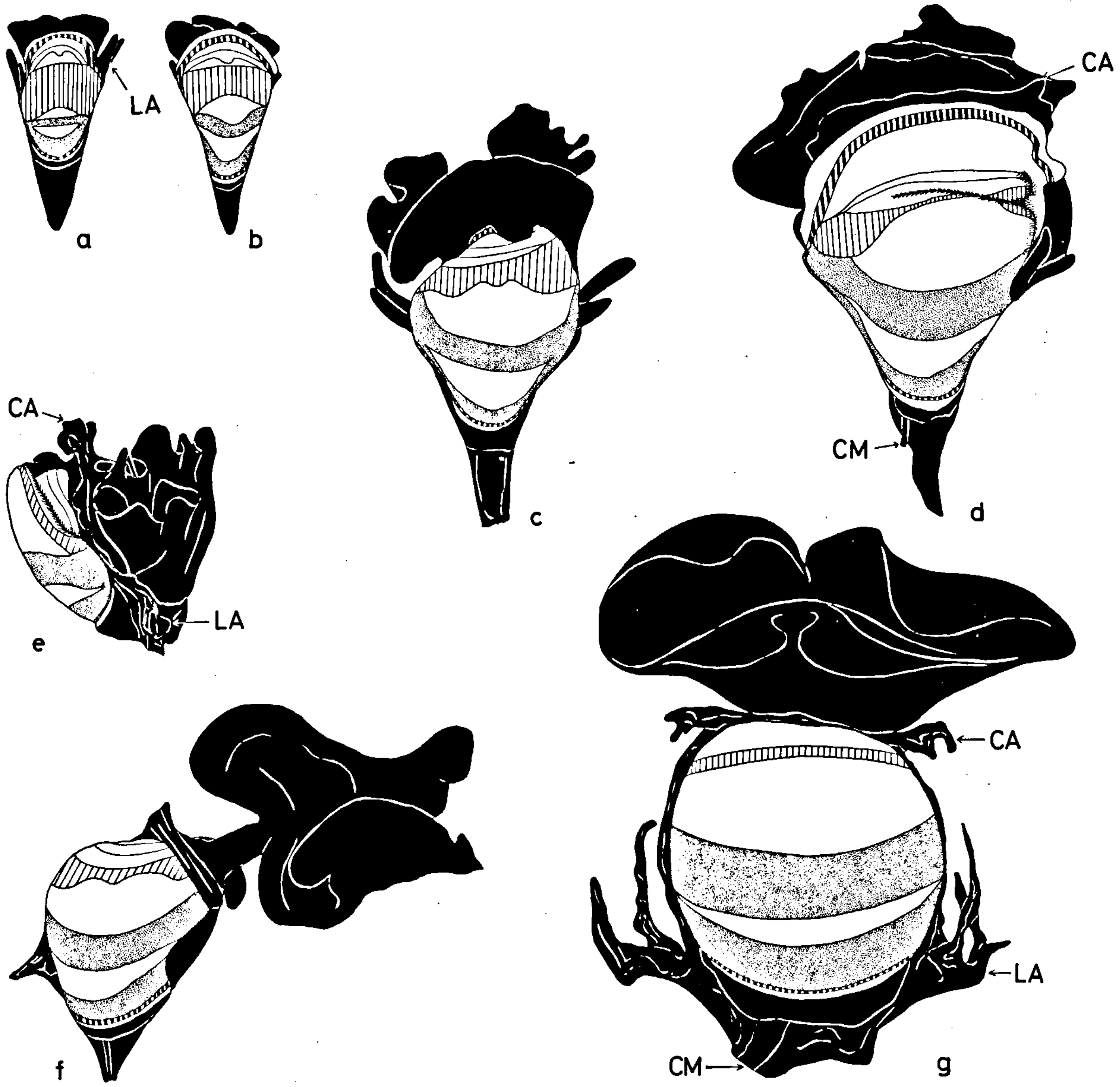

Fig. 5 Development of the soft parts in Cavolinia longirostris. The length of the mantle gland of the specimens a, b, c, d, e, f, and g (in ventral view except for specimen e) is 0.75, 0.90, 1.42, 1.94, 1.20, 1.40, and 1.70 mm, respectively.

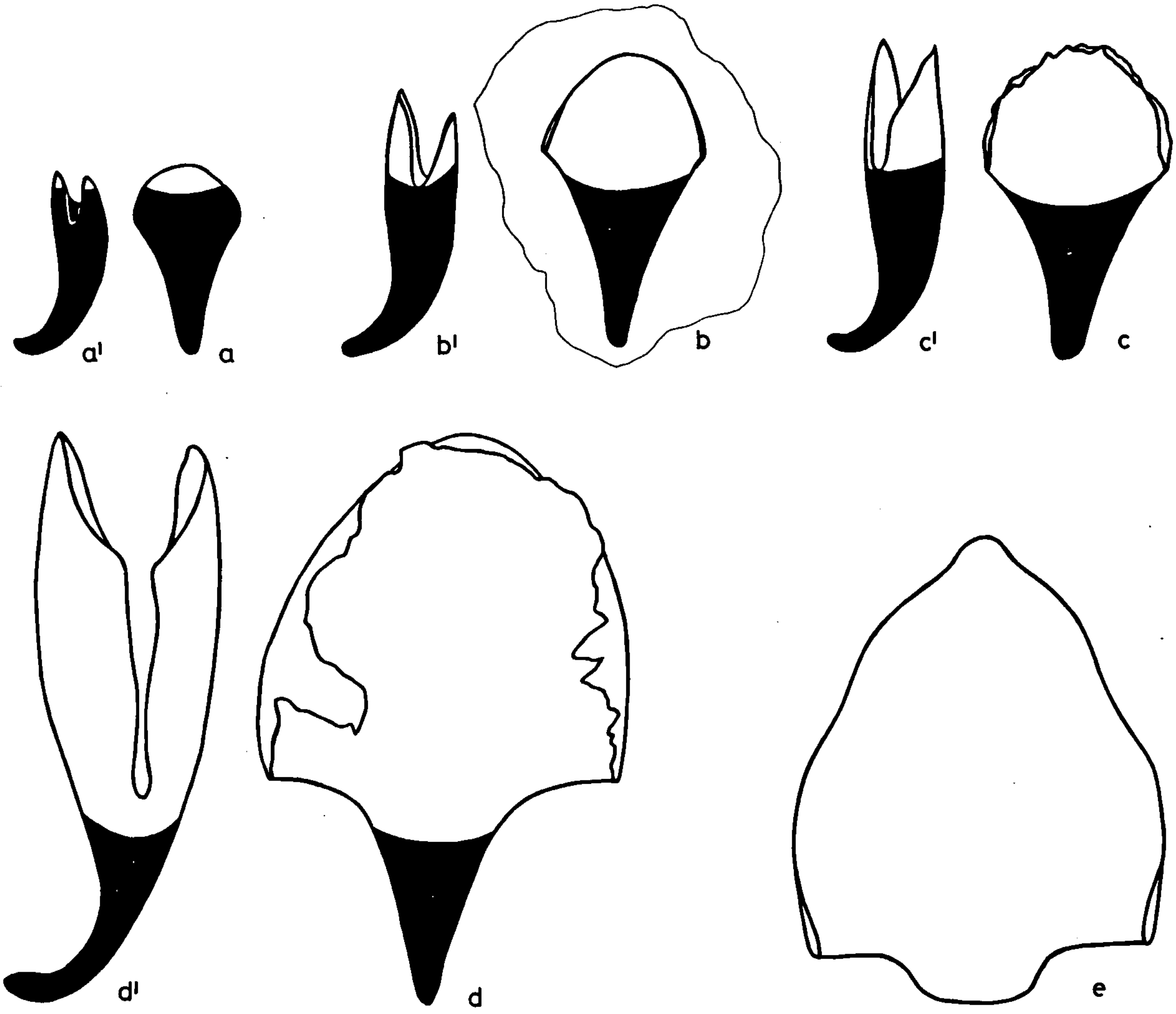

Fig. 6 Development of the shell in **Cavolinia longirostris**. The length of the specimens a, b, c, d, and e in dorsal view (or a', b', c', d', and e' in lateral view) is 1.20, 1.68, 1.94, 3.65, and 2.73 mm, respectively. The parts which will be thrown off are indicated in black.

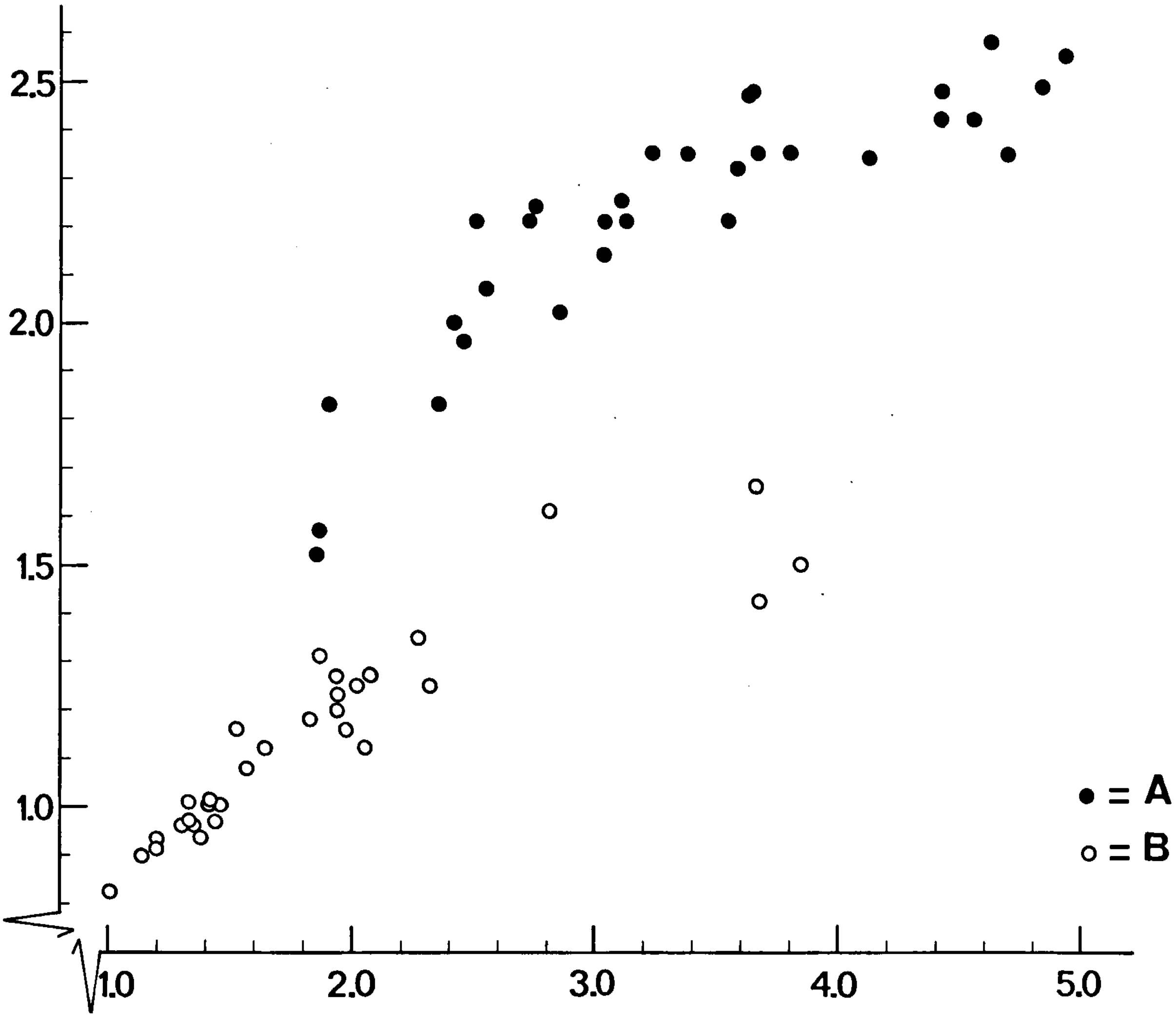

Fig. 7 Graph of shell length (x axis) against caudal spine length (y axis) in mm for Cavolinia inflexa (A) and Cavolinia longirostris (B) from the Caribbean area.