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Abnormalities in the development of monograptid colonies

Lech TELLER

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Examples of abnormalities and regeneration in Wenlock Monograptidae are described and illustrated. The sicula displays deformations of the dorsal processes, swellings of virgula or extremely numerous internal rings. Some thecae reveal deformed apertures various excrescences and shortenings. Excessive growth and reduction of lateral apertures are very common. Specimens with split of virgulae have also been found. These phenomena seem to be common among graptolites but their origin is not very clear, each case requiring a separate interpretation. The only exception is regeneration whose mechanism is the best studied so far.

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INTRODUCTION

Chemical dissolving of the marly-calcareous rocks from the Wenlock section (Zawada 1 well, near town of Kętrzyn, NE Poland) produced a very rich and diversified graptolite fauna. The material contains forms with malformations which appeared during the astogeny of the colony as well as specimens whose fragments were damaged mechanically during the life time and either regenerated or scarred over. Both types of abnormalities — astogenetic and mechanical are common among Ordovician and Silurian graptolites. In the Silurian fauna such abnormalities have been recorded so far from the Llandovery and Ludlow (A. Eisenack, 1940; P. Kraft, 1926; A. H. Müller, 1975, 1977, 1980; A. H. Müller, M. Schauer, 1969; A. Urbanek, 1953, 1958, 1963, 1997; M. Walker, 1953) while in the Ordovician their occurrence seems to be less common (O. M. B. Bulman, 1932, 1970; S. R. Herr, 1971; R. Kozłowski, 1949).

For the first time the problem of abnormalities and regeneration was studied in detail by A. Urbanek (1953, 1958, 1963, 1997). In A. Urbanek's opinion abnormalities that involve only a certain number of individuals in the colony can be associated with disturbances occurring "...during the normal course of budding and development processes of the colony...". If only a single theca undergoes changes this can be "...the result of disturbances in the growth or ontogenetic development of a single individual...".

In the material studied we can trace both cases of abnormalities as well as some damaged and regenerated colonies. Besides there are several excrescences varying in shape whose origin is very hard to understand. In some instances the cause of their formation could be pathological and in others it may be due to the fact that some individuals in the colony lived in an association with chitinozoans as epibionts or were infested by some other alien organisms.

The material is housed at the Institute of Palaeobiology Polish Academy of Sciences, 00-818 Warsaw, Twarda 51/55, under the number ZPAL/GX/1–3

EXCRESCENCES

Excrescences have been recognized on several specimens of *Monograptus flemingi* (Salter, 1852). The excrescence isolated from the lob (Pl. I, Fig. 5) is situated laterally on the right side of thg of a specimen consisting of 29 thecae. It is bell-shaped, slightly widening at the base along which it is fastened to the lob. The length of the base (b) is 0.44 mm. One of the excrescence wall is arcuate, passing into a short process (p). The second wall forms a limb, which passes into a bulge in the widened part of the bell. This complicated shape of the

excrescence is due to the character of its fastening to apertual lob.

Differently shaped excrescences were found on another colony of *M. flemingi* (Salter) (Pl. II, Fig. 1). The specimen, with proximal and distal parts broken off, has only 19 medial thecae. Theca n+14 displays two excrescences, one being situated on the lob and other positioned laterally on the left side of the theca.

The excrescence on the lobe has a follicular shape. From its "opening" it widens gently to the base. The excrescence is fastened to the lob of the theca between two shovel-like lateral processes. The "opening" of the excrescence is broken, having no swelling of the margin. The slight bulginess present in the middle part allows one to conjecture that in the unflattened state of preservation the whole base of the excrescence was also bulged. In spite of the bleaching of the specimen it is very hard to trace the attachment to the lob.

The shape of the next excrescence placed laterally on the same theca resembles an elongated leaf slightly protruding beyond the dorsal line of the rhabdosome. At the base, it narrows slightly and then widens gently to form, along the lower margin, a poorly emphasized short arch, which passes into a straight line bent at the top. In the middle of the excrescence runs a slightly marked furrow. The entire structure adhers, in its lower part to the lateral side on the boundary between the pro- and metatheca, but further it diverges slightly from the rhabdosome, which is the result of a strong bending just above the place of attachment. The excrescence adhers to the lateral wall at a distance of 1.54 mm from the flattened margin of the lobe. Its length is 1.05 mm and the maximum with 0.45 mm.

More excrescence differing in shape are featured by *M. flemingi* (Salter). A fregmentary rhabdosome consisting of 27 thecae has two outgrowths. The first one (not illustrated) is on th_n+3 or th_n+4 in the proximal part. Irregular in shape, it adhers to the apertural lobe between the lateral processes. Its length is 0.83 mm and the maximum width 0.22 mm. The other excrescence attached to th_n+23 also adhers to the aperture lobe. It is irregular in shape (Pl. I, Fig. 4) and has two straight margins oriented towards each other at an angle of about 45°. The upper margin is irregularly infolded due to compression and flattening of the specimen. The lower margin (fl), however, is fused along its whole length with the outer part of the lobe between the apertural processes (lp). In the lower part of the structure a narrow reniform foramen (f) can be seen, which, when unflattened, could have been slightly ovate or round. At the present state of preservation it is hard to restore the original shape of both the excrescences.

All the described excrescences are built of a structureless skeletal material, and most probably represent chitinozoans attached to the graptolite thecae.

MALFORMATIONS OF LATERAL APERTURAL PROCESSES

Malformations of this kind are hardly visible or altogether imperceptible on specimens preseved in the rock, but they are very often observable in isolated material. Isolated specimens feature several malformed lateral apertural processes.

A specimen of *M. flemingi* (Salter) displays an aberrant process in the proximal part of th_n (Pl. II, Fig. 4). It widens in the middle part occurring a triangular shape, and it is much thicker if compared with those present on the proceeding theca.

Another left process on th_n of the same specimen (Pl. II, Fig. 3), situated more distally, was split in the terminal part into two shovel-like outgrowths. One of them is distinctly wider with a concave margin, indicative of an additional splitting. The lateral processes of all distal thecae are normal.

A complete specimen of *M. flemingi* (Salter) has 20 thecae, of which nine proximal ones were badly damaged together with the sicula. Of the remaining 10, the majority is normally built (Pl. II, Fig. 8) with the exception of th_n+18, 19 and 20, exhibiting strongly elongated right lateral processes (Pl. II, Fig. 2).

MALFORMATIONS OF THE THECAE

A different kind of malformation can be observed on a rhabdosome of *Monoclimacis flumendosae* (Gortani, 1923), (Pl. I, Fig. 10), which represents a complete well-preserved juvenile specimen consisting of five fully developed thecae. The second theca shows a disturbance of the growth. It is not only shorter than the foregoing and the succeeding ones but also slightly twisted to the left. As a result, its aperture does not lie on the symmetry plane. The lid partly covering the aperture of the theca is much bigger than that of the first theca, and its clearly thickened margin forms a roll. A very short free ventral wall is 0.15 mm long and runs almost parallel to the rhabdosome axis. The rhabdosome beneath the thecal aperture is 0.57 mm wide. The abnormal growth of the second theca is most probably connected with the disturbances in the growth of the zooid as the distal thecae developed normally.

A specimen of *M. flumendosae* (Gortani) (Pl. I, Fig. 9), features another type of disturbance of normal budding. The disturbance involves the aperture of th_2. In the normal development, the metatheca terminates with a deep excavation, displaying instead a further growth of the metatheca as well as a prolongation of the fuselli on the dorsal side. As a result the excavation is filled up with fuselli, the aperture of the theca thus becoming more vertical. The lid is missing, while the margin of the aperture forms a roll, similar to that in other thecae. Beginning with the th_3 the astogeny is normal.

MALFORMATIONS OF THE VIRGELLA

Malformations of the virgella are common among the graptolite colonies studied. A specimen of *Monograptus flemingi* (Salter) (Pl. II, Fig. 5) has, on its virgella, a short finger-like swelling while another specimen of *M. flumendosae* (Gortani) (Pl. II, Fig. 7) has a triangulate one and a considerable thickening at the tip of the virgella. Another swelling described earlier by the present author (L. Teller, 1986) is

present on a long virgella of *Monograptus belephorus* Meneghini, 1857 (Pl. II, Fig. 6).

REGENERATION

A juvenile specimen of *Monograptus antennularius* (Meneghini, 1857) (Pl. I, Figs. 12, 13) reveals a damaged apex of the prosicula. As a result of regenaration two virgulae were formed. One is very short (0.18 mm) while the other constitutes the axis of the normal growth of the colony.

Another kind of regeneration was found on a specimen of *Monograptus flexuosus* (Tullberg, 1833) (Pl. I, Figs. 1–3). The proximal part of the colony consists of a complete first theca, two vestigial thecae replacing the second theca, as well as of the third and fourth normal thecae. The demaged area runs obliquely through the protheca of the primary second theca. It was scarred over with fusellar tissue but instead of a normally developed theca there appear two vestigial thecae (Pl. I, Fig. 2, $th_{2.1}$ and $th_{2.2}$) oriented in opposite directions. The left theca (Pl. I, Fig. 2, $th_{2.1}$) has a straight long protheca while the metatheca narrows uniformly, terminating with a (Pl. I, Fig. 2, ap) round aperture directed upwards.

The opposite vestigial theca (Pl. I, Fig. 2, $th_{2.2}$) built of normal fuselli forms only a short tubular process. Its upwardly directed concavity could have been the aperture (Pl. I, Fig. 2, ap). It is surrounded by a lappet (Pl. I, Fig. 2, l) which narrows its opening.

Both vestigial thecae have their apertures directed opposite to the first theca. The next theca (th_3) grows normally and a part of its protheca can be already seen.

The damage (Pl. I, Fig. 2, Da) of the rhabdosome most probably occurred during the development of th_2 or even during the growth of its protheca. The shape and the opposite direction of growth of the vestigial thecae are very difficult to interpret. They may be related to the degree of damage and to the resulting disturbances of the astogenetic development. It seems that at the place of damage two additional buds appeared to produce two vestigial thecae. The budding after the regeneration proceeded normally according to the monograptid pattern.

The regeneration of a damaged lateral wall of the first theca can be also seen in a specimen of *M. flumendosae* (Gortani) (Pl. I, Fig. 11). After the development of the first theca of the juvenile specimen the right lateral wall of the protheca was damaged over quite a large area. The regeneration started already before the second theca was formed. The regenerated tissue in the form of narrow stripes was deposited both in the lower part of the damaged wall and in its right upper corner. One could infer that the filling up of the damaged area occurred simultaneously from both sides. But it is also possible that the graptolite zooid may have died because of the injuries.

A juvenile *M. flumendosae* (Gortani) (2 1/2 th) shows an abnormal development of the metasicular aperture (Pl. I, Fig. 7). A distinct apertural process is missing while the margin is thickened and slightly turned round. The thecae are developed normally.

Two other specimens of the same species (Pl. I, Figs. 6, 8) exhibit mechanical damages of the parapertural dorsal side of the metasicula. Both damages are very similar, implying that this part of the metasicula was probably "plucked" or "snapped" off by an unknown organism. The slightly torn fragments were somewhat displaced and later the damage was healed.

OTHER ABNORMALITIES

Three Wenlock specimens of *Monograptus dubius* (Suess, 1851) *s.l.* from Homerian — *Cyrtograptus lundgreni* Zone, reveal numerous sicular rings both in the pro- and metasicula. Sicular rings have been recorded and described several times in different Monograptidae and can be hardly regarded as abnormalities (A. Urbanek, 1953, 1958, 1997; M. Walker, 1953). In our case, however, their number is exceptional varying from 10 to 14. The specimen illustrated in Pl. II, Fig. 11 has 13 sicular rings, that in Pl. II, Fig. 10 has 11, that in Pl. II, Fig. 12 as many as 14, while the specimen in Pl. II, Fig. 13 has only 10.

A small porus (Pl. II, Fig. 9) on the junction of pro- and metasicula of *Cyrtograptus radians* Tornquist, 1887 shows that the porus itself was not completly closed after budding of the first theca.

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NIEPRAWIDŁOWOŚCI W ROZWOJU KOLONII U MONOGRAPTIDAE

Streszczenie

Przytoczono i omówiono nieprawidłowości w rozwoju astogenetycznym u wenlockich kolonii graptolitów. W obrębie sikuli stwierdzono deformacje wyrostków dorsalnych, zgrubienia na wirgelli oraz liczne pierścienie sikularne. Niektóre teki wykazują deformacje apertur, krótsze lub nienormalnie długie wyrostki aperturalne, a także narośla, które stanowią najprawdopodobniej przytwierdzone chitinozoa. Napotkano także kolonie z rozdwajającą się wirgulą oraz kolonie zregenerowane po uprzednim uszkodzeniu.

Zaobserwowane zjawiska wydają się być częste wśród kolonii graptolitów, a obserwować można je łatwiej na materiale wyizolowanym chemicznie ze skały. Przebadany materiał pochodzi z profilu wenloku otworu Zawada 1 (NE Polska).

EXPLANATIONS OF PLATES

PLATE I

Figs. 1–3. *Monograptus flexuosus* (Tullberg)
Regenerated fragment of damage rhabdosome with two vestigial thecae oriented in opposite direction; Fig. 1 — damaged part of the rhabdosome enlarged; Fig. 2 — camera lucida drawing of the damaged part: $th_{2.1}$, $th_{2.2}$ — vestigial thecae, th_2, th_3 — normal thecae, Da — damaged area, pth — protheca, mth — metatheca, ap — aperture, l — lappet; Fig. 3 — fragment of rhabdosome with the damaged part; 1590.6–1597.7 m; Figs. 1, 2 — x 10, Fig. 3 — x 3.5

Figs. 4, 5. *Monograptus flemingi* (Salter)
Fig. 4 — lateral view of the left side of the excrescence attached to the lob of th_n+23; Fig. 5 — camera lucida drawing of an excrescence isolated from the apertural lobe of th_8; ex — excrescense, fl — fused line, lp — lateral process, f — foramen, b — base, t — tonque, p — process; 1555.9–1562.0 m; x 120

Figs. 6, 8. *Monoclimacis flumendosae* (Gortani)
Mechanical demage of the parapertural dorsal side of the metasicula; 1590.6–1597.7 m; Fig. 6 — x 15, Fig. 8 — x 5

Fig. 7. *Monoclimacis flumendosae* (Gortani)
Abnormal development of the metasicular aperture; 1597.7–1603.1 m; x 10

Figs. 9, 10. *Monoclimacis flumendosae* (Gortani)
Malformed second theca; vi — virgella, msi — metasicula, psi — prosicula, ab — thickend margin, l — lid; 1597.7–1603.1 m; Fig. 9 — x 22, Fig. 10 — camera lucida drawing, x 12

Fig. 11. *Monoclimacis flumendosae* (Gortani)
Damaged lateral wall of the first theca; 1590.6–1597.7 m; x 30

Figs. 12, 13. *Monograptus antennularius* (Meneghini)
Damaged apex of the prosicula; Fig. 13 — camera lucida drawing; vi — virgella, dp — dorsal process, msi — metasicula, lt — longitudinal threads, rv — regenerated virgula, psi — prosicula; 1597.7–1603.1 m; x 15

All samples from the Wenlock of the Zawada 1 well section (NE Poland)

PLATE II

Figs. 1, 2, 8. *Monograptus flemingi* (Salter)
Fig. 1 — differently shaped excrescences attached laterally to the protheca of th_n and to the apertural lobe, x 10; Fig. 2 — ventral view of elongated right and normal left processes, x 15; Fig. 8 — ventral view with normally developed processes, x 10; 1562.0–1568.1 m

Figs. 3, 4. *Monograptus flemingi* (Salter)
Fig. 4 — aberrant left processes on th_n situated in the proximal part; Fig. 3 — more distally; 1546.5–1552.7 m; x 50

Fig. 5. *Monograptus flemingi* (Salter)
Swelling of the virgella; 1562.0–1568.1 m; x 50

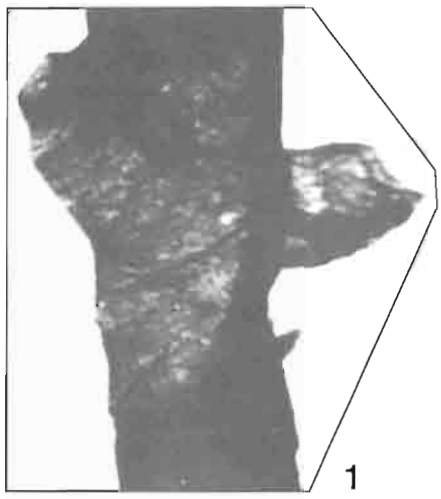
Fig. 6. *Monograptus belephorus* (Meneghini)
Swelling on a long virgella; 1603.1–1609.1 m; x 70

Fig. 7. *Monoclimacis flumendosae* (Gortani)
Triangulate swelling on the virgella; 1590.0–1597.7 m; x 50

Fig. 9. *Cyrtograptus radians* Tornquist
Small porus on the junction of pro- and metasicula; 1555.9–1564.0 m; x 25

Figs. 10–13. *Monograptus dubius* (Suess) *s.l.* with numerous sicular rings
Fig. 10 — x 30, Figs. 11, 13 — x 20, Fig. 12 — x 25; 1546.5–1552.7 m

All samples from the Wenlock of the Zawada 1 well section (NE Poland)



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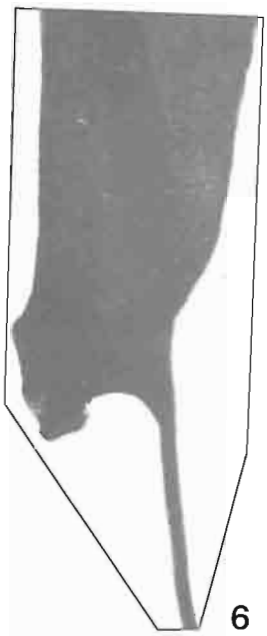

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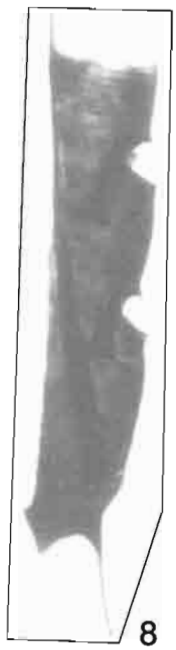

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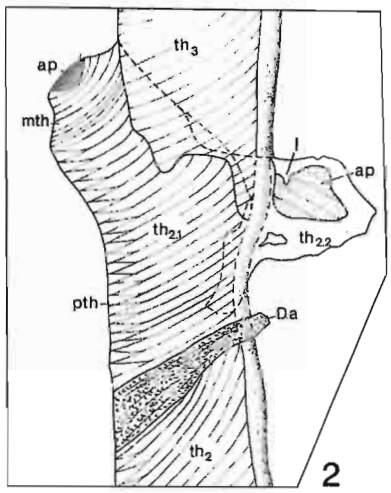

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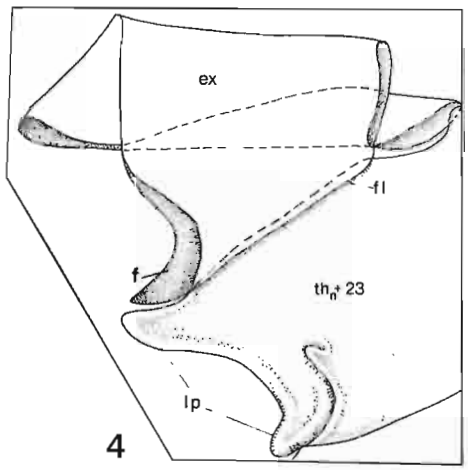

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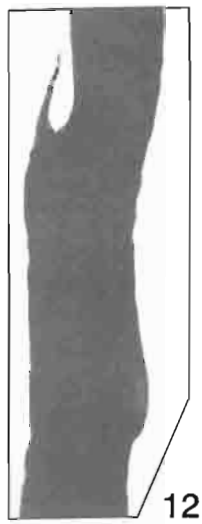

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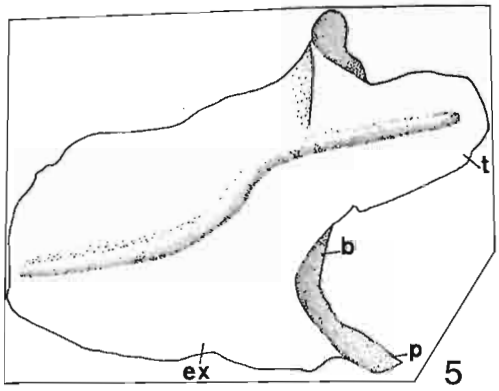

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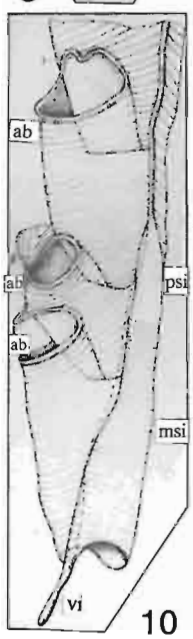

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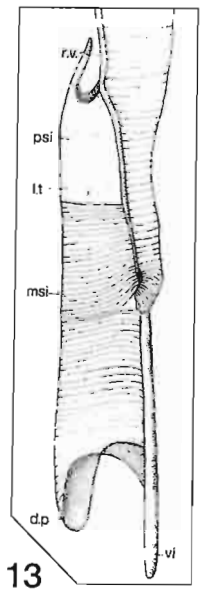

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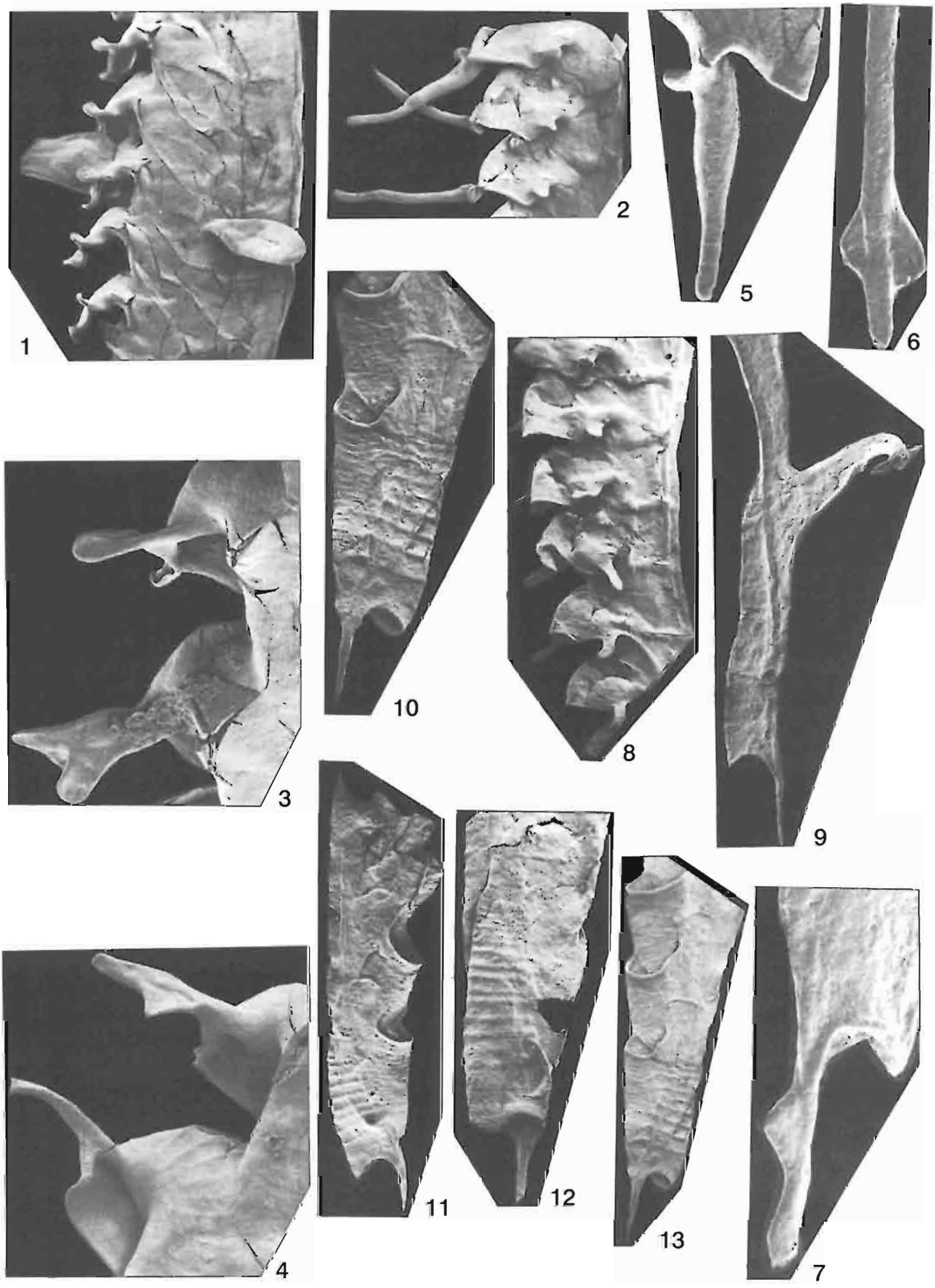

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