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On complex dermal elements in *Loganellia* species (Agnatha, Thelodonti) from the Upper Llandovery of Scotland (I.G.C.P. 328 Contribution)

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Abstract

Two specialized squamation types from the Upper Llandovery of Scotland are described in detail for the first time. One type occurs mainly as fused structures here referred to as scale sets. They probably belonged to the thelodont genus *Loganellia*. Their morphology is discussed and ideas are put forward about their generation, function and topography. The second squamation type is here called denticulated plate, type A and denticulated plate, type B. The morphology of these plates is compared with that of the scale sets, with which they share some characteristics. The type A plates were discovered in the branchial area of a *Loganellia* specimen and are possibly fragments of an internal dermal cover interpreted as a complex of gill rakers.

1. Introduction

In October 1990 Mr W. van der Brugghen (Almere, The Netherlands) sent me a sample of a few thousand fish scales (sample number JV 1990/82). He obtained these from a small calcareous siltstone nodule which he collected in 1990 from the upper concretionary level of the *Jamoytius* horizon (Patrick Burn Formation, Upper Llandovery) in Lesmahagow, Scotland. A considerable number of calcareous nodules in the *Jamoytius* horizon contain thelodont remains, 'either articulated individuals, patches of skin or more commonly thick layers of disarticulated denticles, probably of coprolitic origin' (Ritchie, 1968). According to Traquair (1899) two thelodonts occur in the *Jamoytius* horizon, viz., *Thelodus scoticus* Traquair (= *Loganellia scotica*) and *Thelodus planus* Traquair. Ritchie (1968) regarded the latter as a species of doubtful validity and Turner (1976) placed it in synonymy with *L. scotica*. However, the scales in the sample seem to indicate either the presence of a second *Loganellia* species or a greater morphological variety of *Loganellia scotica* scales than has been described so far. This matter will be discussed in a separate paper (Vergoossen, in prep.). Apart from *Loganellia*, the only other chordate known from the *Jamoytius* horizon is the naked, petromyzonid-like *Jamoytius kerwoodi* White. The sample also yielded some extremely small denticles fused at the base. These fused structures could not be identified with the aid of the available literature on thelodonts, although similar structures have been observed in *Loganellia* before (see section 6.1). The fused denticles or scale sets are the subject of this paper, together with the remains of very thin platelets from the branchial region of an articulated *Loganellia* sp. collected from the same upper concretionary level at Lesmahagow five years previously (sample number 1985.40 Van der Brugghen). These platelets, here called denticulated plates type A, share some characteristics with the scale

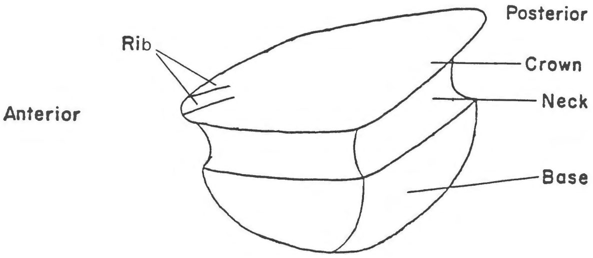

Fig. 1 Generalized thelodont scale (much enlarged).

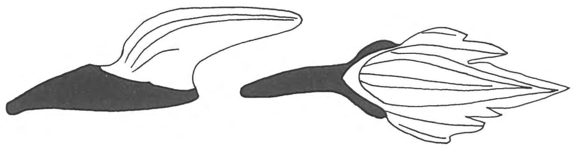

Fig. 4. Scales with anterior spur: *Thelodus trilobatus* (after Gross 1967). Base and spur have been blackened to bring out horizontal growth direction. (Much enlarged.)

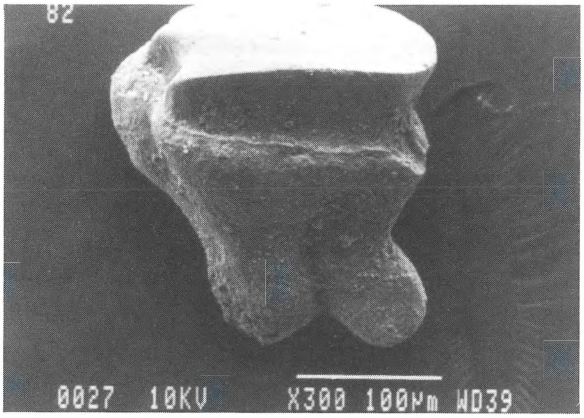

Fig. 3. Loganellia sp., rhizoid scale. Sample JV 1990/82.

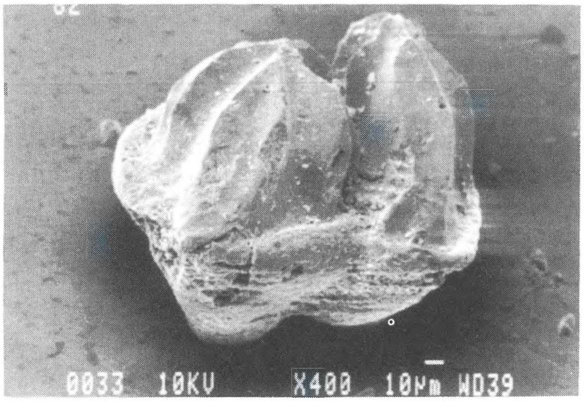

Fig. 2. Loganellia sp., twinned scales. Sample JV 1990/82.

sets. The denticulated plates proved to be extraordinarily fragile and when touched with a wet brush they simply dissolved into powder (cf. Ritchie, 1967). Efforts to isolate undamaged specimens for SEM photography unfortunately failed. For this reason the platelets could only be imperfectly studied in detail. In addition the sample contained one fragment of a more solid platelet that seems to be intermediate between the scale sets and the denticulated plates of type A. This fragment is referred to as denticulated plate, type B.

The material described here has been stored in the collection of the National Museum of Natural History at Leiden (The Netherlands). The study was carried out in the context of the International Geological Correlation Programme, project no. 328 Microvertebrates.

2. Terminology

In the morphological descriptions the terms 'dorsal' and 'ventral' have been avoided as we do not know what the dorsal and ventral sides of the scale sets and denticulated plates were. The terminology used in scale morphology is illustrated in Fig. 1.

3. Scale sets (Figs 6–15)

3.0 Material, definition, size

Material: 77 specimens, NMNH storage numbers 383.635, 383.636, 383.637, 383.638 (SEM specimens), collected from a small calcareous siltstone nodule (sample JV 1990/82) in the upper concretionary level in the *Jamoytius* horizon of the Patrick Burn Formation (Upper Llandovery), Leshmahagow, Scotland.

Definition: scale sets consist of at least two very small crowns on

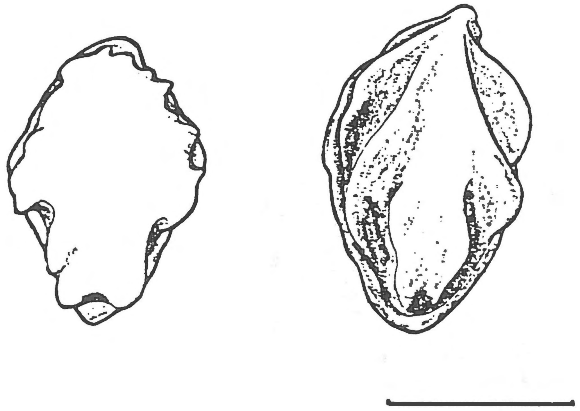

Fig. 5. Loganellia scotica, cephalo-pectoral scales, coronal view. Scale bar = 0.5 mm (after Turner 1984).

a fused base. The base is invariably hemispherical or hemispheroid. The sets are distinguished from occasionally found twinned scales (Gross 1967, Karatajute-Talimaa 1978, Turner 1991) by the fact that they may have as much as eleven crowns or more on one base.

Size: the longest specimen is a fragment with eleven separate crowns, the smallest is complete and possesses two separate crowns (Fig. 14). The highest number of crowns seen in succession in longitudinal direction is five. No specimen has been found more than three crowns wide. Storage numbers and exact measurements are given in the Appendix.

3.1 The crown

3.1.1 Arrangement of crown and shape of the scale sets

The crowns on several specimens (Fig. 8) are arranged in a straight line (lengthwise). No such arrangement is obvious from other specimens in the sample (cf. Fig. 10). The lengthwise arrangement of the crowns may give the scale sets a stringlike appearance. Short scale strings arise from arrangement of the crowns in a single row, either behind or beside each other. Evident breadthwise arrangement of the crowns is only present in the scale strings. However, the shape of many scale sets and the arrangement of the crowns on them reveals no fixed pattern (see also section 6.2.2).

3.1.2 Morphology of the crown

The crown takes the shape of an isosceles triangle. The edges of the crown are somewhat convex. Sometimes one edge is clearly more convex than the other (Fig. 12). The largest width of the crown lies at approximately one third of its length. The crown surface is flat or slightly concave; the latter especially when an anterior rib is present (Fig. 11). Anteriorly, the crown descends down to the base and narrows because its rims bend inwards (Figs 7, 9). Often the crown surface is smooth, but a short anterior rib may be present. The rib can be situated near the middle (Fig. 12) or more laterally (Fig. 10).

The crowns on a scale set all point more or less in the same direction (Fig. 7) or each crown can point in a slightly different direction (Fig. 10). The crowns do not overlap but lie free on all sides. They make a rather acute angle with the base of the scale set. Nowhere do they extend across this base (Figs 7, 8; the contrary is suggested in Fig. 11, but this is effected by the position of the camera relative to the specimen and the angle at which the scale set was photographed).

The cusps are often rounded off, probably as a result of abrasion. Originally they may have been somewhat more pointed and longer.

3.2 The neck

A neck is only present laterally and posteriorly. A sharp edge separates the crown from the neck, which is smooth and somewhat concave (Figs 14, 15). In only one specimen a short, oblique neck rib could be observed with the aid of the SEM. From the base upwards the rib runs in posterior direction (Fig. 10). Minor differences in the height of the neck are visible in Fig. 15. The necks in Fig. 14 are almost equal in height.

3.3 The base

3.3.1 Upper surface of the base (coronal view)

Originally each crown on a scale set stood in the middle of a round or oval, shallow depression which was hemmed in by a slightly raised basal rim. Relicts of such raised basal rims can be seen in Figs 7 and 9. Antero-laterally the crown nowhere projected over the basal rim around it, but the cusp of the crown may occasionally have done so (cf. Figs 7, 8). Later the basal rims were partly or wholly worn down. The lateral view of the scale set in Fig. 14 suggests that the posterior half of the basal rim is lower than its anterior half.

3.3.2 Lower surface of the base (basal view)

Under the stereomicroscope, at a maximum magnification of 160 ×, not a single pulp cavity could be detected in any of the scale sets. SEM photographs of one specimen show a number of minute openings (Fig. 6). Perhaps the smallest are the endings of the dentine tubules. Two other scale sets, not figured here, show a more or less round depression of considerable size or depth in the middle of their base. These might be remnants of pulp cavities. The conspicuous hole in the middle of Fig. 13 pierces the scale set entirely and opens onto the coronal side. A short diagonal basal groove can be seen in Fig. 6.

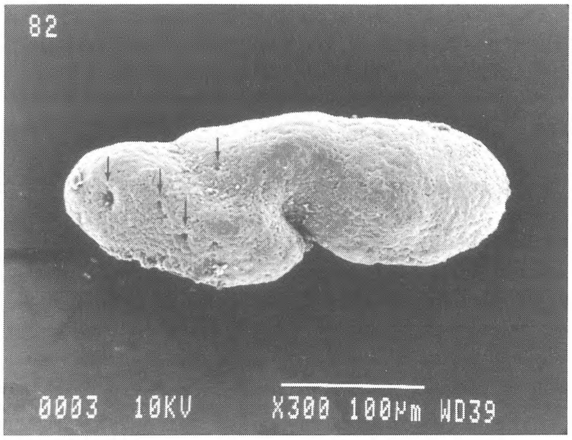

Fig. 6. Scale set: basal view. Arrows denote tiny openings, possibly of dentine tubules. Sample JV 1990/82.

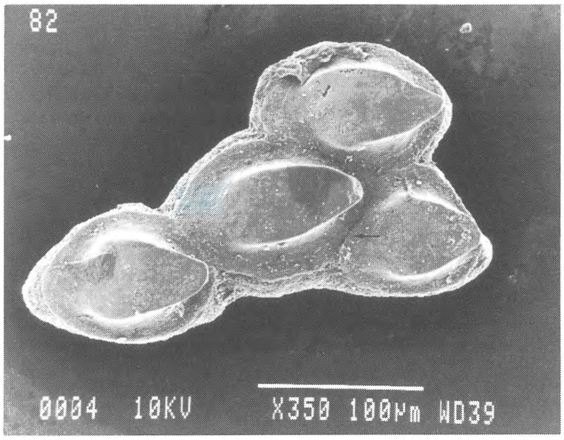

Fig. 7. Scale set: coronal view. Arrow shows continuous, raised basal rim. Sample JV 1990/82.

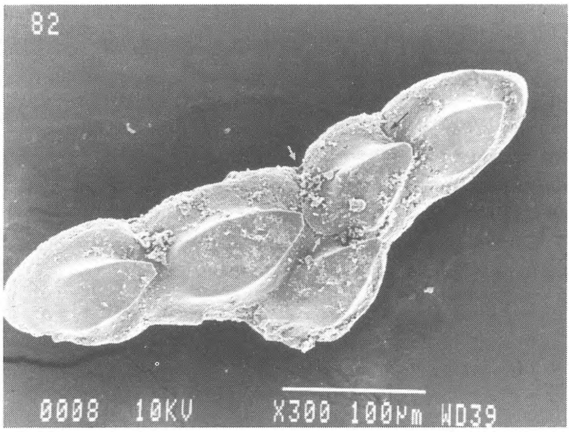

Fig. 8. Scale set: coronal view. Arrows indicate weak points (cracks) in the scale set. Here a single base and crown are being torn off. The ellipticity of the breakage pattern is characteristic. This scale set may have been broader, judging from its damaged, antero-lateral edge (bottom right). Sample JV 1990/82.

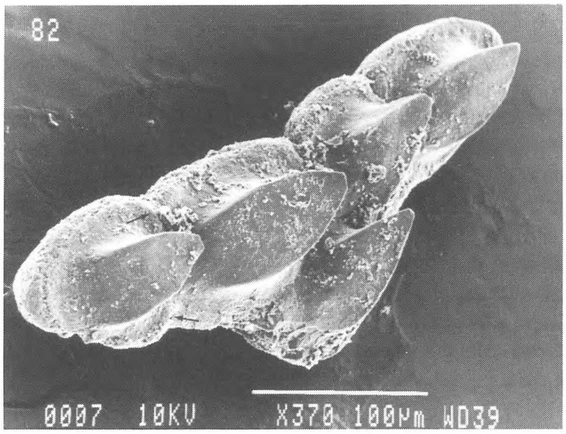

Fig. 9. Same scale set as in Fig. 8, photographed at different angle to bring out raised basal rim (marked by arrows). Coronal view.

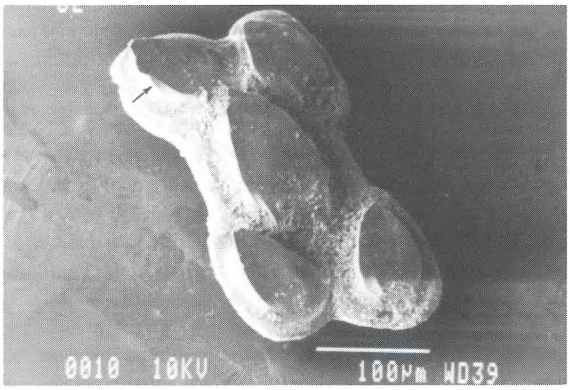

Fig. 10. Scale set: coronal view. Arrow points at neck rib. Ribs also on some of the crowns. Sample JV 1990/82.

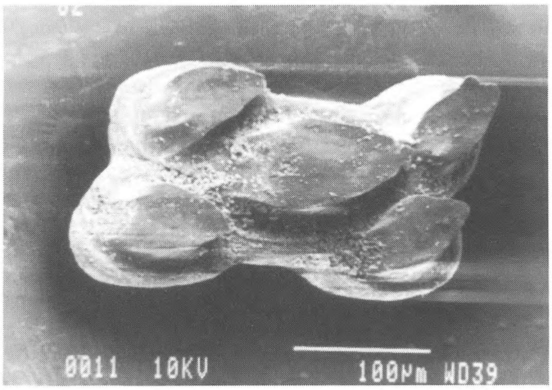

Fig. 11. Same scale set as in Fig. 10. Coronal view. The concavity of each crown differs. Notice the influence of the crown rib on the concavity.

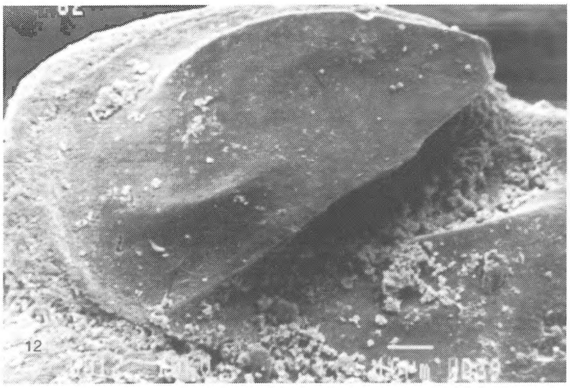

Fig. 12. Enlarged detail of Fig. 11. Scale bar = 10 μm.

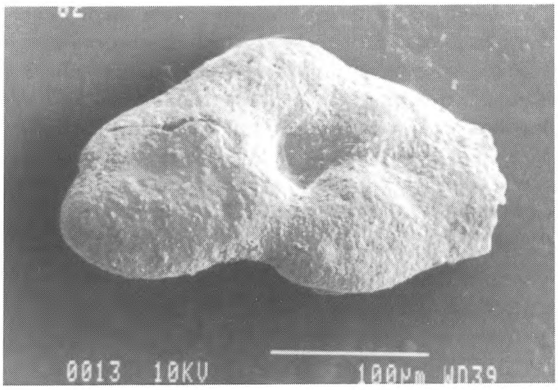

Fig. 13. Scale set: basal view showing a central hole. Sample JV 1990/82.

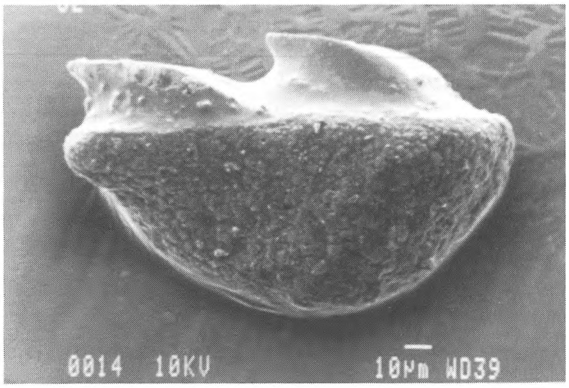

Fig. 14. Scale set: lateral view. Sample JV 1990/82.

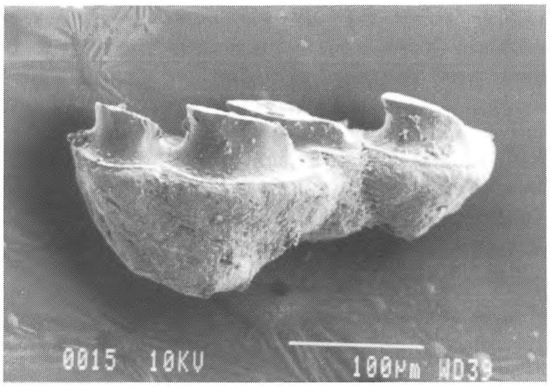

Fig. 15. Scale set: lateral view. Crowns of unequal height, smooth necks and base of unequal thickness. Sample JV 1990/82.

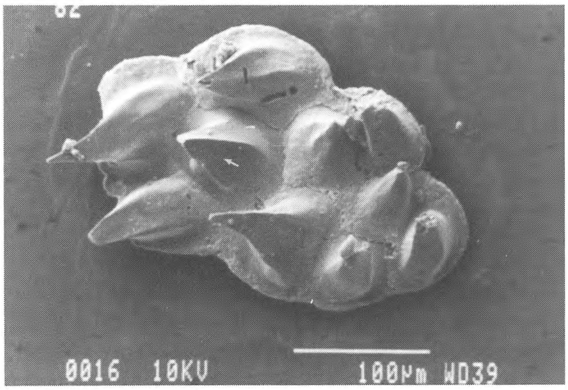

Fig. 16. Fragment of a denticulated plate, type A: coronal view. The arrow marks the lateral surface of the crown. Sample 1985.40 Van der Brugghen.

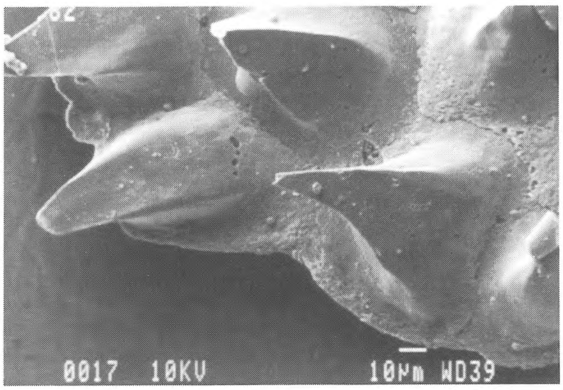

Fig. 17. Enlarged detail of Fig. 16. Different orientation of crown cusps. The crown on the lowermost right gradually slopes out, esp. so on its right side. The surface of the crowns behind it is either steep (top centre) or has a more gradual slope anteriorly (lowermost left). These features can also be observed clearly in Fig. 16. Perhaps the water current is thus forced way up the crowns and into a 'slalom' between them.

A whole range of ontogenetic stages from young to old, as known from other thelodont scales and also present among the familiar *Loganellia scotica* scales (Gross 1967, Turner 1984) of the sample under discussion, is entirely lacking. The scale sets described here are ontogenetically old, representing practically fully grown structures because the base always reaches a considerable thickness (Fig. 15). It takes up two-thirds of the total height of the scale set in Fig. 14.

3.4 Breakage

It was often difficult to judge whether scale sets represent complete or fragmentary specimens since traces of damage are not always so obvious as in Fig. 13; here an irregular edge is visible. Such an edge was left when part of the scale set broke off. The scale set shown in Fig. 6 looks undamaged; it is unlikely that it was much bigger. The scale set in Fig. 8 was probably broader anteriorly. Cracks seen in this specimen indicate that the second crown at the posterior end is being torn off. The pattern of breakage revealed here is very characteristic for the scale sets; the cracks trace an ellipse around the crown and it would seem that they follow precisely the contours of the basal rim. In a situation like this, part of the scale set might detach itself without leaving behind much evidence of its previous attachment, dependent on how firm and how complete the fusion was (see section 3.6).

3.5 Isolated scales

Three very small, isolated scales of the type that occurs in scale sets were found. Two of these belonged to scale sets and broke off at the base, leaving the same breaking edge as seen in Fig. 13. In the third specimen, however, no such damage could be observed. Its base is thick. Under the stereomicroscope no pulp opening was seen. In all probability it is a fully grown scale. See Appendix, Table 1 (specimen 383.635 N) for its size.

3.6 Morphological aspects of growth: growth contact and fusion

In the formation of scale sets and scale strings a combination of growth contact and fusion played a role. In this respect they are reminiscent of a phenomenon that has been called 'twinning' (see section 6.2.1). Clear evidence of growth contact and fusion is revealed on the lower basal surface. Here weak or pronounced swellings are often visible (Figs 6, 15). These swellings are separated by boundary lines that mark basal boundary contact during growth (Fig. 15). On the base shown in Fig. 6 the contact lines are vague; this state prevails among the collected scale sets. Basal fusion is still incomplete here. The specimen in Fig. 14 most closely approaches a state of complete basal fusion; outwardly traces of growth contact have completely disappeared. Under the most anterior crown in Fig. 15 the base of the scale set looks very much like the base of a single, fully grown scale. Apparently it was left untouched by growth contact. This was not so, however, for the basal part immediately behind it, which was deformed along the contact line as a result of pressure. Under the most posterior pair of crowns, the sigmoid basal contact line has faded away; here fusion progressed most. Apparently, differential growth processes were at work on this scale set, causing one half to fuse more tightly than the other.

Alternatively, the posterior half of this specimen is somewhat older than its anterior half. It is also conceivable that scale sets could be formed in several phases if, for instance, the specimen in Fig. 15 were the end product of growth contact and fusion between two smaller, already existing scale sets.

Partial growth contact may have created the basal diagonal groove of the specimen in Fig. 6. Where no boundary contact during growth occurred, the distance between the basal constituents was not bridged and closed in consequence.

Growth contact hardly affected the upper surface of the base around each crown, because this part retained its elliptical or circular shape; plain polygonal deformations as a result of pressure during growth contact are absent. The crowns were not involved at all in the fusion process.

4. Denticulated plates, type A (Figs 16–22)

4.0 Material, definition, orientation

Material: 6 fragments (NMNH storage number 383.638) isolated from an articulated specimen of *Loganellia* sp. found in a concretion in the upper concretionary level of the *Jamoytius* horizon (Patrick Burn Formation, Upper Llandovery) in Lesmahagow, Scotland (sample 1985.40 Van der Brugghen).

Definition: a denticulated plate is a fragment of the squamation in the branchial region of a *Loganellia* sp. specimen from the Upper Llandovery of Scotland and characterized by a very thin base with many narrow and tapering crowns of minute size. The plates were probably intergrown at the base, thus forming larger units.

From the orientation of the plates relative to the surrounding scale cover it may be concluded that they are internal structures; the crowns on the plates face upwards when viewed from the splitting plane of the concretion, whereas in the rest of the entire (outer) squamation the crowns face downwards. In addition the crowns on most plates point in rostral direction whereas the crowns of the outer scales point in caudal direction. The interpretation of the denticulated plates as internal structures does not conflict with hydrodynamics; if they were part of the outer squamation, all the crowns might be expected to point more or less in the same direction (caudally) for hydrodynamical reasons. The overall impression one gets from the entire squa-

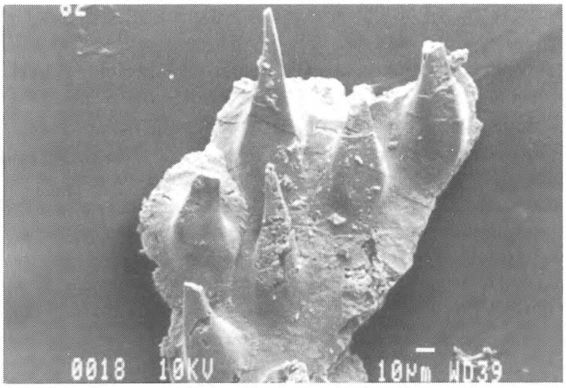

Fig. 18. Fragment of a denticulated plate, type A: coronal view. Sample 1985.40 Van der Brugghen.

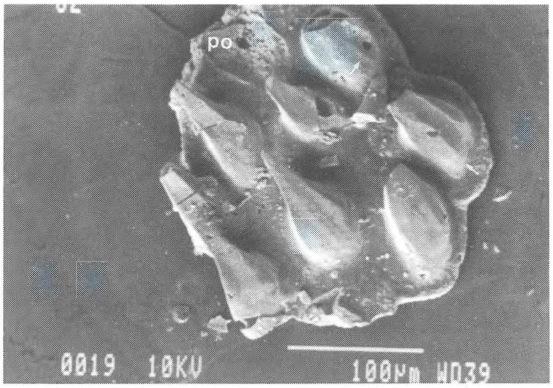

Fig. 19. Fragment of a denticulated plate, type A: coronal view; p o = possible pulp opening where a crown must have broken off. Arrows indicate ribs on upper crown surface. Behind the crown with the long median rib on its upper surface (most to the right in the photograph) lies its(?) broken off cusp. Sample 1985.40 Van der Brugghen.

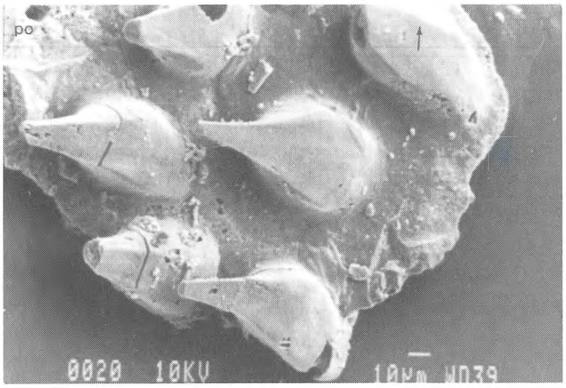

Fig. 20. Enlarged detail of Fig. 19; p o = possible pulp opening where a crown must have broken off. A rather long rib is seen on the upper surface of the crown in top right corner of the photograph (arrow). This rib is situated off-centre. A shallow, circular area surrounds the crown in the middle of the photograph.

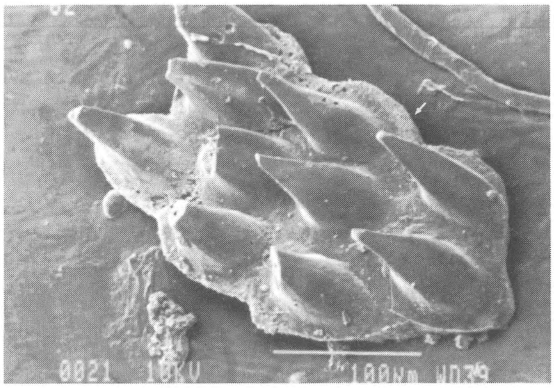

Fig. 21. Fragment of a denticulated plate, type A: coronal view. The arrow marks a well developed basal rim. Breadthwise the crowns are arranged in oblique rows. Sample 1985.40 Van der Brugghen.

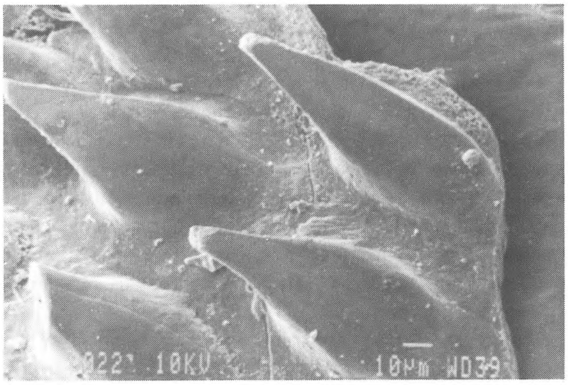

Fig. 22. Enlarged detail of Fig. 21. Notice the concave surface of the rightmost crown. The concavity is narrow and extends longitudinally and medially across two-thirds of the surface, from anterior into posterior direction. The thinness of the base is excellently visible at the right edge of the plate.

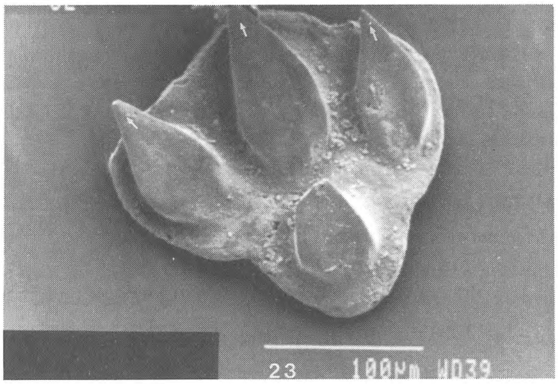

Fig. 23. Fragment of a denticulated plate, type B: coronal view. The arrows show the orientation of the crowns. Notice the slight differences in anterior and central concavity of each crown. Sample JV 1990/82.

mation on this specimen is that its arrangement has not been too much disturbed.

Detailed information on the *Loganellia* specimen mentioned here will be given by Mr W. van der Brugghen in a forthcoming paper.

4.1 The crown

4.1.1 Cross section of the crown

The cusps of several crowns have broken off. Cross sections of crowns are revealed in Figs 17, 20, 21. They are roughly rectangular in appearance. The more or less straight sides of this rectangle correspond to the upper and lateral surfaces of the crown in cross section. The lower surface of the crown is always markedly convex and in cross section it produces the most curved side. This structure of the crown with its four surfaces differs essentially from the crowns on a scale set.

The crowns did not break off at the same place, providing cross sections that slightly differ from each other.

The crowns also show minor morphological variations. Some are narrower than others (cf. the crowns in Fig. 22), some are robuster (cf. Figs 16 and 18), or the degree of concavity of one or more crown surfaces may differ, even on the same crown.

4.1.2 The four surfaces of the crown

The crowns are narrower and more pointed than those of the scale sets. Ribs may be seen on the upper surface of at least two crowns in Fig. 19. One of these ribs is rather long. As a rule, however, the four surfaces of the crown seem to be smooth. Crowns may have a concave surface where others have developed a rib, e.g. the rightmost crown in Fig. 22. Here the concavity is narrow and extends longitudinally and medially across two thirds of the surface.

The upper surface is at its widest close to the base. From the point where it is widest, one or both lateral rims may faintly bend inwards. The resulting constriction is always less conspicuous than in the scale sets.

Of the four surfaces the upper is often broader than the lateral surfaces. But the plate in Fig. 16 also has a crown with one lateral surface (here indicated by an arrow) that is at least as broad as the upper.

4.1.3 Crown rims

These may be:

- sharp or blunt
- straight, convex or concave (combinations occur on one and the same crown).

4.1.4 Number and arrangement of the crowns

The largest plate fragment possesses 10 crowns. The plates reached a maximum width of 3 to 4 crowns. The crowns were arranged in straight lines parallel to the length of the plate (Fig. 21) and in occasionally somewhat oblique lines parallel to its breadth (Figs 18, 19, 21). The crowns stand free on all sides. Mostly they are evenly distributed over the base (Fig. 21) at a distance that may slightly vary (Fig. 22). In the specimen seen in Fig. 19 the differences in distance are more marked because a crown seems to be lacking parallel to the breadth. Compare with the plate in Fig. 21, where in the posterior half a crown seems to have been inserted.

4.1.5 Orientation of the crown cusps

The plate shown in Fig. 21 presents a more uniform view than the plate in Fig. 16. This is due to the more regular shape of the crowns and to the direction in which the cusps point. Mostly the cusps run parallel to the length of the plate, but in Fig. 16 they indicate at least two different directions depending on where the crown is situated on the plate (left or right in the picture).

4.1.6 Holes and cavities

On one plate at least two cross sections of crowns reveal the existence of an internal cavity (Figs 19, 20). Two other crowns on this plate have holes in their upper surface providing a view through into a hollow space. On the same plate there is a hole where a crown was present. Here a pulp opening may have been preserved. In one specimen (Fig. 16), the holes in one of the crowns may be attributed to the destructive activities of a boring organism.

4.2 The neck

There is no neck or constriction around the base of the crown.

4.3 The base

The base has undulating rims and is flat and extremely thin. The extraordinary thinness is best illustrated at the right margin of the plate in Fig. 22. Notice the ellipticity of the base around the crown at the left lateral margin in Fig. 18; that part is still fixed to the plate but it might break off along the elliptical line. Around the largest crown in Fig. 22 the base is vaguely circular. Special attention is drawn to the base in Fig. 16. Here it would seem that the upper surface of the base has come off in very thin layers, leaving the characteristic pattern of undulating (elliptical or circular) breaking edges even on the upper surface of the base. The plate in Fig. 21 has one lateral, well developed, slightly raised basal rim (marked by an arrow) enclosing a shallow, semi-elliptical depression.

Rows of pulp openings are visible in the arrangement of the plates on the articulated specimen. This could not be further studied.

5. Denticulated plates, type B (Figs 23, 24)

5.0 Material

Sample JV 1990/82 (see introduction) contained one fragment of a denticulated plate that shares characteristics of both the plates described in section 4 and the scale sets described in section 3. (NMNH storage number 383.638). It has probably been preserved because it is rather solid. The posterior end has broken off. About its position nothing is known.

5.1 The crown

There are four crowns on the plate. The crowns are arranged parallel to its length and breadth. The cusp of the crown on the utmost left has an orientation different to the rest. The most anterior crown has broken off, but its cross section is not rectangular. The crowns make a uniform impression and are almost identical to those on the scale sets:

- they have the form of an isosceles triangle with convex edges,
- there is a remarkable anterior narrowing,
- there is a (vague) anterior rib on the central crown. The rib is positioned laterally.
- they are concave (anteriorly).
- they are widest at one third of their length,
- they make an acute angle with the base.

5.2 The neck

As in the scale sets a neck is present only on the lateral and posterior part of each crown.

5.3 The base of the plate

The base is very thin but somewhat thicker than the base of the denticulated plates type A. It has an undulating rim. No pulp opening was observed.

6. Discussion

6.1 References to very small scales and platelike structures in thelodont literature

References in the literature to very small scales and platelike structures in the thelodonts are exceptionally rare.

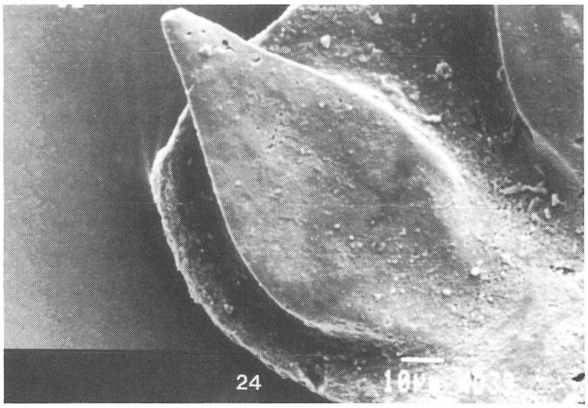

Fig. 24. Enlarged detail of Fig. 23.

In his description of the scales of *Loganellia taiti,* Gross (1967) mentions: (1) extremely small but normally shaped body scales; they are situated on the ventral side in strictly defined areas, (2) locally large quantities of very tiny and very thin plates on the foremost part of the trunk. They are covered with minuscule little thorns more or less resembling the crowns of body scales but without a free base. According to Gross these plates were apparently in communication with some organ in the areas where they occur and served the purpose of opening this organ.

Gross' illustrations of the plates do not permit the conclusion that they are identical with one of the types described in this article. The type B plate comes nearest to his illustrations.

Turner (pers. comm.) is not sure that Gross did see *L. taiti.* In her opinion his illustrations are of the *L. scotica* type and no clear *L. taiti* scales like those given by Stetson (1931).

Turner (1984, 29) interpreted the 'fan-shaped structures made up of longitudinal rows of minute scales each 0.1 mm long or less' on the ventral surface of the cephalothorax in a *Loganellia scotica* specimen as 'part of an internal pharyngo-branchial filtering system, acting as gill rakers'. These fans are less than 0.4 mm in length. Later (loc. cit., 38) she writes that the fan-shaped structures within the bounds of the cephalothorax can be explained as part of 'an internal buccopharyngeal scale-covering comparable with that in sharks'. Some of such scales 'might have been modified as gill rakers' (loc. cit., 241).

Ritchie (1963 – vide Turner, loc. cit., 29) explained the fan-shaped structures in the same *Loganellia scotica* specimen as external branchial flaps or as part of the flexible membrane on the ventral side (loc. cit., 38). When discussing the branchial remains of the *Loganellia scotica* specimen in plate 2.1.C. (loc. cit.) Turner states that Ritchie (1963) interpreted the minute scale-covered patches (between the branchial apertures) as 'interapertural bars'. Finally, in the text to plate 2.2 (loc. cit.), Turner writes about 'a large buccopharyngeal area sparcely covered with minute scales with patches devoid of scales' and 'the remnants of four or five fan-shaped structures bearing rows of minute scales which might be a zone of transitional scales between trunk and oralo-branchial fenestra (A. Ritchie, 1963)' or 'internal branchial structures akin to gill rakers' with the anterior minute scales lining the buccopharyngeal cavity. Virtually the same ideas are repeated in Turner (1991), but in less detail.

Up to now Turner has neither figured nor given morphological descriptions of any of these minute scales or fan-shaped structures but she informed me that the scale sets and denticulated plates are similar to the structures that she observed in the branchial region of *Loganellia scotica.*

6.2 Interpretations of the generation, function and topography of the scale sets

6.2.1 Twinning and basal spurs compared with the scale sets

Fused scales are occasionally found in samples containing thelodont scales. This is called 'twinning' because in most cases two scales have grown together (Gross 1967, Karatajute-Talimaa 1978, Turner 1991). Usually they have a joined base and separate crowns. Two such twinned specimens were present in sample JV 1990/82 (Fig. 2). The histological aspects of this phenomenon have so far never been studied in detail.

In many thelodonts, among them *Loganellia scotica,* the scales may show a tendency to produce a rhizoid base. The roots are interpreted as an extra firm anchorage of the scales in the corium (Turner 1984, 1991). These roots may reach considerable dimensions (Fig. 3) and some are much longer than others, even on the same specimen. Clearly, rhizoid formation shows a preferential growth effort of the base in vertical direction and affected some parts of the base more than others. Of course rhizoid formation is not possible in places where the skin is very thin. Finds of twinned bases with preserved and well-developed roots are not known to me.

Another way of producing firmer anchorage is the formation of an anterior spur on the base (Fig. 4). Here too, the dimensions may be considerable. What is so striking about many spurs is the growth effort of the base in horizontal direction. Such horizontal growth might excellently suit the need of firmer anchorage in places where the skin is thin. Finds of twinned bases with intact and well-developed spurs are not known to me either.

According to T. Märss (pers. comm.) the generation of roots or spurs depended on the part of the body (and skin) where the scale was situated and the flexibility of that part of the body (and skin). More specifically, their generation also depended on the thickness of the skin in the region where they occurred. The generation of the scale sets could be explained as a horizontal extension of the anchoring surface in the manner of spur formation. The process would be limited to a specific body area where the skin was rather thin (e.g. the gill area, the fin webs, etc.).

Finally, it should be pointed out that in the sample under discussion there are many examples of rhizoid formation among the ordinary *Loganellia scotica* scales. But not a single example of horizontal spur formation has been noticed!

6.2.2 Diversification

One cannot discuss the generation of the scale sets without considering three aspects of their morphology (see also sections 3.0 and 3.1.1):

(1) the total number of crowns on the scale sets is subject to substantial variation (2–11 or more),
(2) apart from the observation that the maximum width of the scale sets seems to be restricted to three crowns, no clear patterns can be distin-

guished in the lengthwise and/or breadthwise distribution of these crowns across many scale sets,

(3) some scale sets look like short strings whose crowns are arranged in a single row, either behind or beside each other.

If the scale sets were generated in a specific (restricted) body area, the induction of fusion within this body area was apparently controlled by mechanisms that admitted of considerable diversification to meet the specific requirements of this body area. Such diversification might be needed e.g. in a tail with zonation of the squamation (cf. Turner 1991).

6.2.3 External versus internal position of the scale sets

Apart from the arguments that have been advanced in the preceding sections, the following considerations should be taken into account when – in the absence of complete fish with unmistakable and preserved scale sets – the topography of the scale sets is discussed.

- Each crown on a scale set possesses some of the characteristics that T. Märss (1986) summarized for cephalo-pectoral scales of the outer squamation, to wit, (1) it is smooth, (2) the base protrudes beyond its antero-lateral edges, (3) a short anterior rib may be present.
- Still, the crowns on scale sets differ in appearance from ordinary, cephalo-pectoral scales in *Loganellia scotica* (Fig. 5). Perhaps this is due to their special position and function within the cephalo-pectorus: e.g., within the branchial area or apparatus.
- The diversification in the morphology of the scale sets (section 6.2.2) would be tied up with considerable flexibility demands in the body area where they grew. In the external squamation such flexibility would be required in branchial flaps or fin webs. An argument in favour of the latter possibility is the stringlike appearance of some scale sets: they might have formed some sort of rods or 'rays' (cf. Woodward 1920, Stetson 1931, Turner 1991).
- The orientation of the crowns on a scale set, together with the presence of an anterior rib on a concave crown, may have played a role in conducting the watercurrent into a certain direction (cf. the pit organ scales in modern sharks, Reif 1985).
- In the *Loganellia* specimen of Mr W. van der Brugghen the external squamation consists of tightly fitting scales; there is no space between the crowns. An important functional aspect of the crowns of scale sets might be related to the fact that they are not adjoined. So water probably flowed between the crowns. A water current between the crowns is functional in feeding or filtering. Therefore the scale sets may have functioned in combination with the denticulated plates in a feeding and/or filtering apparatus.

6.3 Functional interpretation of the denticulated plates, type A

Since the base of the denticulated plates, type A is so thin and flat it may be argued that the skin was very thin where the plates were anchored. In modern sharks the skin of the gill slits is very thin (Reif 1985). In *Cethorinus maximus* 'each of the five gill arches on either side has a double row of very densely spaced, bristle shaped gill rakers. There are probably several hundred gill rakers in one row' (loc. cit., 81). Thus it is conceivable that the plates covered cartilaginous gill arches (cf. Turner 1991) in *Loganellia* and functioned in gill slits where the narrow and pointed crowns could serve the purpose of filtering or catching.

6.4 Identification of scale sets and denticulated plate, type B on genus level

Only histological research can definitely prove that the scale sets and denticulated plates, type B belonged to the thelodont genus *Loganellia*. They are here referred to *Loganellia* on the following grounds:

(1) the faunal list of the *Jamoytius* horizon and the relative abundance of the various faunal elements (Ritchie 1968) do not permit inclusion in any other animal known from the horizon,

(2) disarticulated (in)vertebrate remains other

than scales of *Loganellia* have never been reported from calcareous nodules with disarticulated thelodont remains in the *Jamoytius* horizon,

(3) rare references in the literature on thelodonts make a case for the existence of complex dermal elements in *Loganellia,*

(4) the denticulated plates, type A (occurring in *Loganellia* sp.) and the scale sets share the following characteristics: various crowns on a common base, the crowns lie free on all sides, undulating basal edge, (raised) basal rim, the elliptical or circular shape of the upper basal surface around each crown, pattern of breakage.

7. Conclusion

Of the squamation types described here, the scale sets most resemble external scales, but there are also considerable differences in size, age, crown and fusion frequency. In the material at hand no gradual transitions in size or crown features have been noticed between scale sets and cephalo-pectoral/postpectoral scales.

It is likely that the denticulated plates of type A are internal structures functioning in a branchial system, probably as gill rakers. No definite opinion can be expressed on the topography or function of the denticulated plate, type B. However, since the plate of type B seems to be intermediate between the scale sets and the plates interpreted as gill rakers, it is tentatively concluded here that there is a gradual transition from the gill rakers to the scale sets. Transitional structures might have fitted into the undulating basal rims of the plates and sets and formed an uninterrupted and perhaps (partly) interlocking scale covering. The transition from denticulated plates to scale sets would be marked by an increasing thickness of the base and a decreasing number of crowns.

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Appendix: Measurements of scale sets in sample JV 1990/82

Table 1. Size of scale sets in measuring units (0.5 mm is ± 25 measuring units)

Storage number	Number of crowns lengthwise	Length	Smallest and largest breadth corresponding to number of crowns breadthwise		
			1	2	3
383.635A	5	22.5	4–7		
B	5	21	4	9	
C	5	21	4	7	
D	5	19.5	4.5	7	
E*	4	23		7–10	
383.638A	4	23	5	8	
383.635F	4	19	4		9
383.638B	3	18	6.5	10	
383.635G*	2	16		8	11
H	2	13	4.5		11.5
J*	2	11.5	4		9.5
K	2	10.5	5.5		
L	2	10	5.5		
M	2	10	5.5		
383.638C	2	10			
383.635N	–	8	5		
O	–	7			14.5

* Broken lengthwise
383.638A is SEM Fig. 8
383.638B is SEM Fig. 10
383.638C is SEM Fig. 14

Table 2. Crown sizes of scale sets in μm

Figure	Number of crowns, arranged from largest to smallest L = length; B = breadth									
	1		2		3		4		5	
	L	B	L	B	L	B	L	B	L	B
7	105	52.5	95	50	92.5	52.5	92.5	46.25		
8	100	50	75	40.6	75	39	68.7	46.8	65.6	40.1
10	172.7	90.9	128.2	68.2	127.2	63.6	118.2	65.9	95.5	54.5

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