ON THE STRUCTURE OF THE SKIN IN *URANOCENTRODON (RHINESUCHUS) SENEKALENSIS*, VAN HOEPEN

By G. H. Findlay

In the famous collection of fossil remains of the labyrinthodont *Uranocentrodon*, housed since 1911 in the Transvaal Museum, the bony skin armour from the ventral surface of the body of at least six individuals has been preserved. In spite of this lavish quantity of material only a few notes on the osseous skin structure were included in van Hoepen's (1915) description, and all later papers have passed it by almost completely.

The two most recent contributions with full bibliographies on the skeleton of *Uranocentrodon* are those of Romer (1947) and Watson (1962).

Most of the sandstone slabs from the *Lystrosaurus* (basal Triassic) zone of Senekal which contain this skin material have been grouped together for many years in a large closed display case. Three slabs apparently unconnected with each other had not been cemented into the display and were separately available at the Museum for detailed study. They proved to belong together, and fitted to yield a strip of armour some 25 inches long down the ventral midline and in places up to 4 inches broad on one or other side of the midline. On these portions the present study is mainly based. They had been presented to the museum by the Municipality of Senekal after the main collection had been purchased.

The complete skeleton of *Uranocentrodon* in the National Museum, Bloemfontein, has a length between the limb girdles of some 40 inches, clearly covered by ventral armour which extends laterally to a maximum of 5–6 inches from the midline. From these measurements, it may be concluded that the study material available which comprised this 25 inch strip gave a fairly extensive view of the skin structure, pending opportunities to compare it in detail with the rest of the collection.

Orientation of Specimens

The dermal ossicles in *Uranocentrodon* form an inverted-V or chevron pattern, with the point of the chevron lying in the ventral midline directed like an arrowpoint towards the head end of the animal. In the specimen studied the bilaterally diverging lines of bones meet at an angle of 60° at the anterior end of the specimen falling to 50° over the slenderer parts farther back. The angles of divergence from the midline itself decline therefore from 30° to 25° respectively.

Mostly it was the internal aspect of the skin armour which showed uppermost on the stone slabs from Senekal. In some cases the skin had obviously slipped out of line with the vertebral column and was clearly indented from above by displaced parts of the axial skeleton.

Because the ossicles overlap one another, it is their medial ends which are seen on the internal surface of the armour, and their lateral ends on the external surface. Therefore if the free ends of the ossicles point towards the midline, it is the internal surface which is being examined. By establishing the midline, the direction of divergence and the pointing directions of the free ends of the ossicles, one can orientate the specimen in all planes. Confirmation may be obtained from the position and orientation of the vertebral column where present.

When the midline is not visible on the specimen, as is the case in some of the slabs collected at Senekal, the morphology of the individual bony ossicles must be used to determine the facing of the specimen.

Anatomy of the Typical Dermal Ossicle

The dermal ossicles may be considered as belonging to two regional types: those which lie away from the ventral midline, comprising up to 8 clear rows in our material, and those which abut on the midline itself, limited naturally to a single row contributed from either side.

The *laterally placed ossicle* (Fig. 1), seen from the internal or dorsal aspect, has a smoothly pointed flame-shaped medial end (G). Its lateral end (C) after narrowing somewhat, exhibits a thin saucer-like expansion with a slight anterior deflection. These ends are frequently broken off in the specimens. Such an ossicle measures about 35 mm. from end to end. Although both ends taper, the ossicles measure about 5–6 mm. across at the centre where they are broadest. The most conspicuous feature of the ossicles, and indeed the only feature to work from if the ends are missing, is a conical buttress (F) running along the posterior edge of the ossicle. This cone (Fig. 1F) has its apex near the posterior edge of the spoon or saucer-like lateral end of the ossicle where it is about 1 mm. broad, and it swells evenly in thickness to a breadth of 2–3 mm. just medial to the midpoint of the ossicle. Here the buttress flattens out over the posterior part of the flame-shaped medial end of the ossicle.

This buttress converts the dorsal aspect of the ossicle into a grooved or gutter-like channel (E). In the gutter-like part of the ossicle, two structures are clearly housed. One is the next most lateral ossicle of the same row, whose flame-shaped medial end lies about 8 mm. away from the inner tip of the ossicle in which it lies (Fig. 1). The posterior edge of the overlying ossicle impinges on the anterior facing of the conical buttress, while its anterior edge abuts on or overrides the buttresses in the next headward row of ossicles (Fig. 1). The second group of structures which lie in the guttered surface of the internal aspect of the scale are the grooves and foramina presumably for nerves and vessels. These lie tucked in the angle formed where the ossicle rises up to form the buttress. Here they would be sheltered from and protected by the overlying ossicle (Fig. 5).

The medial or flame-shaped end of the ossicle shows on its inner aspect a number of grooves suggesting muscular, ligamentous or tendinous attachments passing horizontally forward, interspersed with vascular grooves and foramina.

The external aspect of the dermal armour could not be directly studied in plan view, but sections cut through one of the slabs at right angles to the line of the laterally placed ossicles showed the following features. The outer surface was saw-toothed in cross-section (Fig. 2), the ossicles having roughly the shape of angle irons with the angle pointing to the outer surface of the animal. The pattern was occasionally ratchet-like, with the short slope of the ratchet formed by the posterior buttress of the scale.

The *midline ossicles* differ in having broadly expanded medial ends (Fig. 3) by contrast with the tapering flame-shaped medial ends of the laterally placed ossicles. These ends lie along the midline, each overlapping alternately with the one from the opposite side. The expanded end of each ossicle can be divided into two areas: an anterior portion which points forward and dorsally, and exhibits the markings of vessels and ligaments, and a posterior portion, which continues laterally into the end of the ossicle buttress, and is flattened or hollowed out dorsally over the midline to receive the ventral surface of the next most caudal ossicle from the opposite side.

The ossicles whose medial ends form the midline differ somewhat in shape according to their position. Those placed farthest forward are squarish with a straight anterior edge at right angles to the midline. They also give the impression of being tilted from the horizontal, so that their posterior edges would point backwards and downwards on the outside of the body along the midline. Farther back the midline scales are flatter and less massive, and have the shape of miniature mutton chops which lie without tilting on a level with the rest of the scales (Fig. 4).

Construction of the Armour

As the ossicles in succeeding rows are of roughly equal length, their lateral ends lie in a straight line which is more or less parallel to the ventral midline. In any particular row of ossicles the next most lateral ossicle reaches the exterior aspect of the armour in the following manner. The anterior edge of any ossicle touches the buttress of the more headward ossicle but diverges from this edge of contact at point A, Fig. 1, as it tapers laterally. An angle of divergence of some 10°–15° is formed (Fig. 1), and through this cleft along the anterior free margin of the ossicle the body of the next ossicle escapes laterally, being partly held behind in the cavity of the outer end of the more medial ossicle. This supporting cavity lies roughly in line with the 10°–15° point of divergence at the front edge of the ossicle so supported. A double imprint is therefore sometimes seen on the matrix here—that of the oblique divergence of the more medial scale, and the groove formed by the ridged outer surface of the escaping lateral scale.

The arrangement described ensures that no external portion of the armour could be displaced in any direction on its own without hinging on another part of the armour for movement and support.

Significance of the Ventral Armour

The armour which clothes the entire ventral surface of *Uranocentrodon* between the limbs would probably function as a protector of the internal organs from even and uneven pressures on the ground, and at the same time be of some mechanical use when the animal was either lying at rest or walking. The special structure of the armour suggests that it may well have served several such functions.

For example, the posterior buttress of the ossicle structure would counteract denting from the outside. It would also resist and transmit forward and backward pressures in the rows of ossicles. The inverted V–shaped arrangement of the ossicle rows, the backward and downward projections of the midline ossicles and the tougher posterior edge of the external aspect of the lateral ossicles are all features which make one think of the gripping tread of a motor tyre. Such a tread would principally prevent a backwardly slipping movement, and the slanting rows of scales would check a sideways slip in either direction. This arrangement would be useful for crawling up or lying on a sloping bank. Furthermore, it is perhaps worth pointing out that in walking on its widely separated limbs, the *Uranocentrodon* probably also exhibited fish-like undulations of the spine for which the inverted V–pattern would be useful. In a forward swerve to the right, the left hand ossicle rows would slide the longest distance with their ridges lying in line with the direction of movement. This would minimise friction. The right hand rows would at the same time move a comparatively short distance obliquely to the line of movement. The friction on the right side would actually be greater, but would be offset by the shortest sliding distance and the possibility that the simultaneous stride on the foot of this side would raise this part of the body somewhat off the ground.

Nature of the Epidermal Covering

It seems rather unlikely that the bony armour just described was either naked or projected even partly through the epidermal surface. A tough overlying dermis with a thick epidermal covering would adequately transmit the surface distortions to the underlying bony shield—and this is the arrangement seen over other sculptured and ossicular dermal bones in living amphibia.

There is an interesting possibility that the epidermis over the bony ridges was capped by a horny layer just as is the case in certain fresh-water fish. Van Hoepen was able to follow the ventral armour in some of his *Uranocentrodon* specimens round to the dorsum of the fossilised remains, where he found the ossicles gradually replaced by reddish brown non-bony rings which he took to be horny scales. This seems indeed to be the most likely interpretation.

Having found small bright red powdery patches near the outer surface of the scales while cleaning the present specimen, it seemed worth considering if this could also represent keratin. Because of the high sulphur content of keratin Dr S. H. Haughton suggested the following mechanism to me—conversion of ferruginous mud to ferrous sulphide at the sites of decomposing keratin with subsequent conversion of the ferrous sulphide to haematite. This would give the site of keratin deposits a reddish tint after all traces of keratin had disappeared.

The perforated centres of the horny rings described by van Hoepen, which are still clearly seen in his mounted exhibit, would possibly have been the sites of glandular openings on the surface.

Bloodvessels and nerves to the ventral body surface could reach it from the dorsum and sides of the body, and also to a small extent from channels which perforate the ossicles or escape between the outer free ends of the ossicles.

Comparison with other South African Labyrinthodonts

Of the South African stereospondylous labyrinthodonts, skin scutes have been described only by Kitching (1957) for *Laidleria*. Mr Kitching had nevertheless observed their presence in *Lydekkerina* as well, and lent me a specimen for study. The ossicles in this specimen were scanty and disarranged, but the best developed examples were about 6 mm. long and 1 mm. broad—a length to width ratio of 1:6 exactly as in *Uranocentrodon*, and there was a slight suggestion of the finer structural features such as the posterior buttress, the flame-shaped medial and the rocker-like lateral end. The ossicles of *Lydekkerina* were one-sixth the length of those in *Uranocentrodon* (6 mm. as compared with 35 mm.). This size difference was about equal to the ratios in total body length between *Lydekkerina* and *Uranocentrodon*, respectively (15 inches and 6–7 feet).

Reports from elsewhere allow limited comparisons. The closest resemblances are towards *Onchiodon* (*Sclerocephalus*) *labyrinthica* as described by Credner in 1893. In this case the scales are of somewhat similar construction with a length of 15 mm. for an animal 1.3 metres long.

Summary

The structural and functional features of the dermal armour of the ventral body surface of *Uranocentrodon* are discussed, chiefly based on one specimen acquired by the Transvaal Museum after the first examples had been described.

Acknowledgments

My thanks are due to Dr C. K. Brain, Dept. of Palaeontology, Transvaal Museum, for loan of the specimens, and to the C.S.I.R. Photobiology Group, whose facilities were used in making this study.

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EXPLANATION OF TEXT FIGURES

Fig. 1. Semi-diagrammatic reconstruction of four dermal ossicles on ventral body surface of *Uranocentrodon*. Dorsal facing (i.e. internal surface). A—point of lateral divergence from buttress of next most headward scale. B—point of medial divergence of next most tailward scale. C—kidney-shaped lateral end of scale. E—neuro-vascular groove. F—posterior buttress, enlarging medially. G—flame-shaped medial end. θ—point of escape to the outside from the most lateral ossicle in each row. Total length from tip of C to tip of G about 37 mm.

Fig. 2. Section through five complete ossicle rows, middle row defective. Ventral surface below, embedded in sandstone matrix. Anterior end to left. Photograph shows angle-iron-like or ratchet-like construction of ossicles, with posterior buttress showing as a thickening making up the right-hand portion of the ossicle. Section also shows manner by which anterior (left) border of scale approaches posterior border of buttress by means of a sharp edge at the middle of the buttress.

Fig. 3. Midline portion of midline ossicle seen from dorsal aspect. Dish-like area of bone with extension to posterior buttress on the left. Straight anterior edge defective. Overlying distal scale belonging to right-hand scale removed.

Fig. 4. Midline view farther back than figure 3. Flame-shaped medial ends of left-hand ossicle rows running obliquely up from left. Emerging from beneath them the dilated midline ossicle row (damaged), resembling inner end of mutton chop in shape. Overlapping ossicles alternately from right side not shown.

Fig. 5. Dorsal view of left-side ossicle row showing in centre the lateral end (to the left) of one ossicle rising up from C to point A (as in figure 1) with the posterior conical buttress (with small gap in it) on its lower or posterior edge. The buttresses of other ossicles show the tendency to broaden towards the right (midline).

Fig. 1

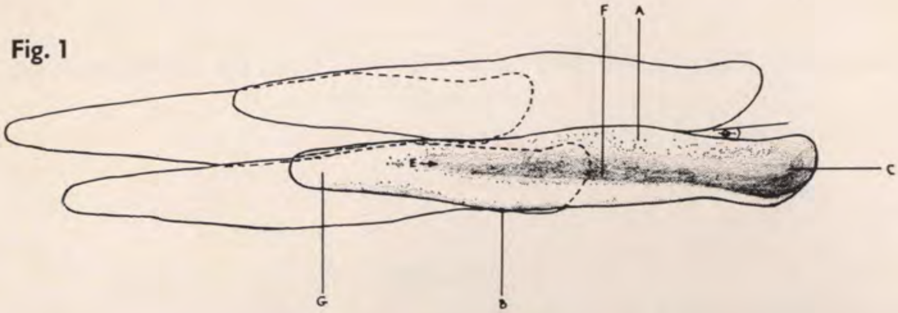

Fig. 3

Fig. 5

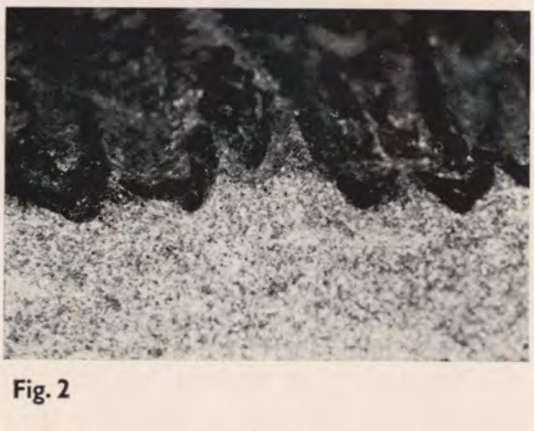

Fig. 2

Fig. 4