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SKIN STRUCTURE OF SMALL PAREIASAURS
With comments on their taxonomy in the Cistecephalus zone

by

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ABSTRACT

The *Cistecephalus* zone pareiasaurs all show skin armour. The features of this armour are described as found virtually complete in a small pareiasaur, identified here as an about half-grown *Pareiasaurus serridens*. Different in skin structure from this small pareiasaur is the dwarf-form, *Nanoparia pricei*. A few particulars have now been added to the known skin structure of this species. It is suggested that *Cistecephalus* zone pareiasaurs can be referred to 2 principal species: the one is *Pareiasaurus serridens* Owen, to which all the incomplete and variably grown specimens can be assigned such as the genus *Propappus* and some other species from the genera *Pareiasaurus, Anthodon* and *Nanoparia*. The other consists of the single specimen *Nanoparia pricei*. Further affinities are beyond existing evidence to settle.

INTRODUCTION

Through the presence of their armour of dermal ossicles, the pareiasaurs are the only family of Karroo Cotylosaurs in which one may study the structure of the skin. Covering the data up to that time, Boonstra (1934) reviewed and amplified our knowledge of the ossicle pattern. Most of the specimens then available in this country derived from the massive pareiasaurs (*Bradysaurus, Embrithosaurus*) of the *Tapinocephalus* zone in the lower part of the Lower Beaufort beds. A fair number of genera and species were then distinguished, many being based on individual specimens. With more available material, the effects of age, sex, post-mortem deformations of the skull, individual variation and clearer zoning have led Boonstra (1969) to reduce the numbers of valid genera and species from this zone considerably (cf. Broom, 1935).

No such reconsideration has been possible for the less massive and rarer pareiasaurs of the *Cistecephalus* zone in the upper part of the Lower Beaufort beds. As is well known, we are still hampered by types such as *Pareiasaurus serridens* of which the skull has been mislaid, *Pareiasaurus bombidens* in which the jaws were described upside down, *Propappus omocratus* which had no skull to the type specimen, and *Anthodon serrarius*, a small pareiasaur with an imperfect skull; moreover the type material, described nearly a century ago, is housed in the British Museum. Broom (1936b) was eventually prepared to refer Seeley's *Propappus omocratus* to Owen's *Pareiasaurus serridens*, thus cutting down the genera from 3 to 2. In the same year, however, Broom (1936a), described a new pareiasaurian genus from the middle *Cistecephalus* zone. It was the smallest pareiasaurian skull yet found. If it was only an immature specimen Broom suggested a relationship towards *Anthodon gregoryi*, though he preferred to regard it as a miniature form rather than a baby by giving it the generic name of *Nanoparia*, the dwarf pareiasaur. An even smaller skull was added 12 years later from the lower *Cistecephalus* zone as a new species to the same genus (Broom and Robinson, 1948). Facts concerning the genus *Nanoparia* were reconsidered and extended by Brink (1955). In this study Brink gave the only existing account of the dermal ossicles of the smaller of these two pareiasaurs, *Nanoparia pricei*.

MATERIAL

The present study on the dermal armour of small pareiasaurs is based on a hitherto undescribed specimen, kindly loaned to me from the Bernard Price Institute of Palaeontology. Catalogued as *Pareiasaurus* species, specimen No. 548, it was collected at Groot Driefontein, Murraysburg, C.P. by Mr. B. J. Kitching. Horizon: *Cistecephalus* zone. With it I was enabled to compare the type of *Nanoparia pricei* (Broom and Robinson, Cat. No. 6, Bernard Price Institute of Palaeontology).

Identification of BPI Specimen 548. Figs. 1-3 give details of the skull shape, sutures and molar teeth and Table 1 gives comparative skull measurements. Most of the measurements suggest that *Pareiasaurus serridens* is roughly twice the size of this unnamed specimen. There are 3 relative differences: in the latter the maxilla is much shorter, the pineal opening is much farther forward and the cheek development is much less. Holding the maxillary tooth row horizontal, the posterior portion of the skull roof in BPI 548 shows a marked downward shelving, which starts sloping postero-ventrally from a ridge which connects a boss behind the pineal with the two tabular bosses. In this respect it closely resembles the skull shape

of Boonstra's (1934) neotype of *P. serridens*. Of course, if one tips the snout ventrally, the slope is less conspicuous a feature on the occiput (cf. the published side-view of *Anthodon gregoryi*). Table II sets out some of the data on *Cistecephalus* zone pareiasaur skin ossicles. It is clear that the recognised specimens are again about twice the size of the unnamed skull. The body length from snout to pubis here would be approx. 850 mm. Double this in the adult length would at least be about 5½ feet. From the relative scale size it could certainly be more, though this is in keeping with the presumed size of *P. serridens*.

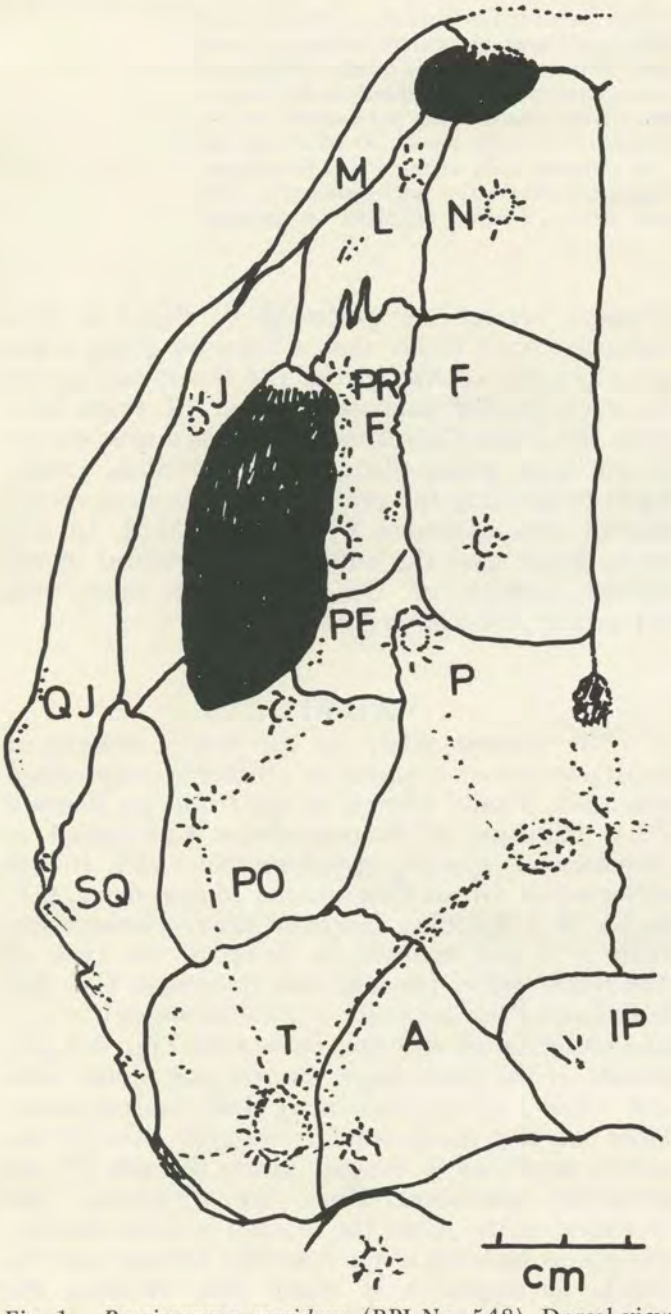


Fig. 1. *Pareiasaurus serridens* (BPI No. 548). Dorsal view with suture and boss patterns. At the occipital margin the single neck scute is shown, which touches the problematic "element A" of Broom, here considered to be a lateral post-parietal or the tabular according to Parrington. See p. 22 for abbreviations.

There therefore seems to be good reason to regard this specimen as an almost half-grown *Pareiasaurus serridens*.

Status of related genera and species.

Pareiasaurus steenkampensis Seeley, 1908 was described on a collection of scutes from Steenkamp's Poort south of Fraserburg. The horizon according to Mr. J. W. Kitching would be in the *Cistecephalus* zone. The scutes look exactly like the scutes from No. 548 except for being twice the size. Boonstra (1934) was convinced that these were not the scutes of *Bradysaurus*. It therefore seems obvious that the status of "Incerta sedis" given by Boonstra to this species can be replaced by synonymy with *P. serridens*.

Pareiasaurus serridens Owen 1876. Richard Owen described this genus and species from a skull cast. The accompanying pelvis with overlying scutes was assigned to the same genus by Watson (1914) after Owen had incorrectly described it as coming from a *Dicynodon*. The scutes described from Boonstra's neotype (1934) are double-sized versions of those in our "unknown" species.

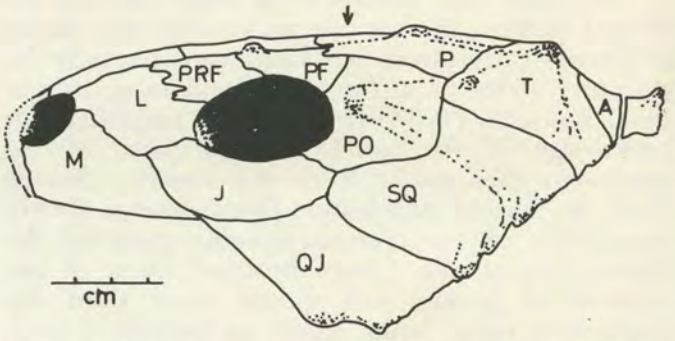


Fig. 2. *Pareiasaurus serridens* (BPI No. 548). Lateral view. To show the contact at the back of the skull between element A and the neck scute, the snout is turned slightly medially, foreshortening the skull length slightly. Arrow at the top indicates the front edge of the pineal opening.

Propappus omocratus Seeley. Watson considered that the scutes of this genus were very like those of *P. serridens*, and Broom (1935) considered on other grounds that Seeley's genus and species was probably synonymous with *P. serridens*. In *Propappus parvus* the scutes are less gross in outline and embellishment. So are those which in this paper we are calling a small *P. serridens*.

Anthodon serrarius Owen. Scutes are undescribed in Owen's account. Boonstra illustrates scutes which could not be distinguished from either *P. serridens* or *Anthodon gregoryi*. However he does describe the boss on the scutes as standing up in a way which sounds like a funnel on a flattish base. This is what we have found in *Nanoparia*.

Anthodon gregoryi Broom 1930. As in the above, the dermal armour is merely alluded to and not fully described or illustrated. The type of this species comes from the *Cistecephalus* zone north

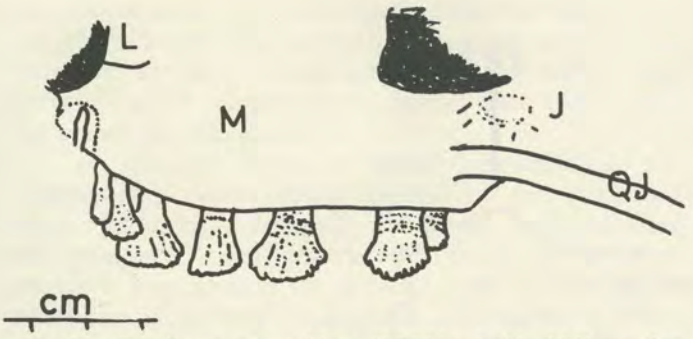


Fig. 3. *Pareiasaurus serridens* (BPI No. 548). Oblique view of left maxilla showing tooth row. The most anterior tooth is seen as a root in the socket under the nasal opening without a crown. Overlap of the teeth is shown, the front edges of the teeth lying medial to the back edge of the next tooth ahead. The seventh tooth space is vacant, making a probable total of 9 cheek teeth.

of Graaff-Reinet (the farm Vlakteplaas near Bethesda Road Station) and is in the American Museum of Natural History. As indicated, this pareiasaur is about three-quarters the size of *P. serridens,* has big heavy cheek plates and a rather short obtuse maxilla. The pineal opening is relatively far back according to skull measurements, but it lies actually behind the frontoparietal suture. Short as Broom's paper is, there are several conflicting statements in it, nor was he happy about the placing of this genus and species. Prepared as I am to consider the unknown specimen BPI No. 548 as a half-grown *Pareiasaurus serridens,* this *A. gregoryi* of Broom would do equally for a $\frac{2}{3}$ grown specimen.

MORPHOLOGY

The Post-Parietal Region The weathered state of the occiput in many specimens has made the region between the tabulars and the parietals difficult to interpret. It is the region where the transverse occipital canal or occipital commissure of the lateral line system would lie—identifiable as such in Stegocephalians (Schmalhausen, 1968), and liable therefore to form centres of ossification in the cranial roof independently of the dermal bone system over the body.

The cotylosaurs clearly show a variable degree of separation or fusion of the two stegocephalian post-parietals leading to 3 possibilities: (a) A median unpaired bone (dermo-supra-occipital, interparietal, post-parietal), (b) a paired bone (post-parietal on either side), (c) a median unpaired plus a paired bone—the situation seen here and described by Broom in *Nanoparia pricei.*

One could call the set of 3 bones between the tabulars and behind the parietals respectively the left and right lateral post-parietal and the median post-parietal. This removes the uncertainty left by Broom (1936) for what he called "element A," to which the name lateral post-parietal seems appropriate.

Broom's "element B," an ossification on the posterior cranial margin seen so far only in *Nanoparia pricei,* lies in our specimen where an inturned piece of the squamosal is seen. If element B does not belong to the squamosal, it can then be a supratemporal, not normally extant here as a separate bone. At this mobile point one would not expect an attachment to the dermal armour, and indeed there is none.

After choosing to interpret the occipital bone pattern as an expression of variability in the interparietal complex, Parrington's (1962) view was brought to my notice. He prefers to regard the interparietal in pareiasaurs as having shrunken to the small oval median bone here described, and the tabular as having slid inward to the occiput, also with some inevitable loss of size. The large prominent bone lateral to this which Broom,

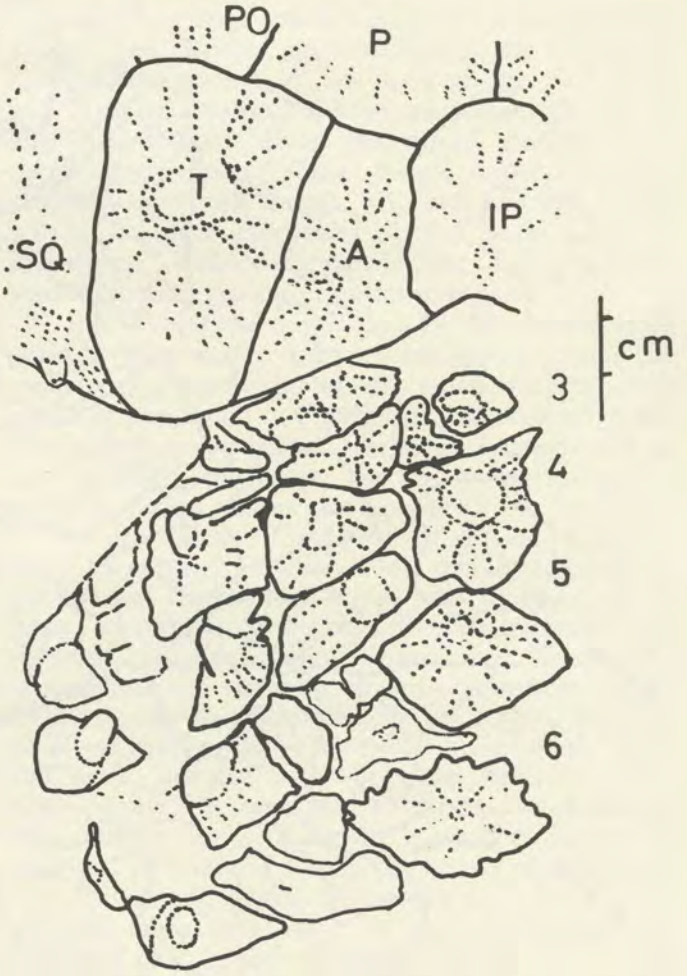


Fig. 4. *Pareiasaurus serridens* (BPI No. 548). The left cervical scutes, dorsal view. It is presumed that the first midline scute overlies the 3rd vertebra (3), and the succeeding transverse rows respectively over cervical 4–6 vertebrae as numbered. The midline row lies opposite the interparietal, the 1st lateral anteroposterior row opposite Broom's "Element A" with which it makes contact, the 2nd lateral anteroposterior row leads back from the tabular and the 4th is roughly in line with the squamosal.

Robinson, Brink and myself preferred to keep as the tabular, normally placed at the paroccipital



Fig. 5 *Pareiasaurus serridens* (BPI No. 548). Scutes over the shoulder girdle, dorsal view. The midline, anterior and posterior ends, are indicated by the heavy arrows. The positions of the scutes overlying the vertebrae 7–11 are numbered as such and the corresponding oblique scute rows spreading from them on either side are indicated by the small tailed and numbered arrows.

prominence in the procolophonids, becomes Parrington's supratemporal; this in turn requires an increase in the nomenclature of the supra- and intertemporal elements in these and other diadectomorph cotylosaurs.

To choose between these possibilities, i.e. fragmenting either the occipital or the temporal bony elements respectively with ensuing size changes, my own interpretation as given here requires less change in relative size of the bony units in question. For want of more decisive evidence, the view which favours less violent changes in the final surface areas and outlines of bone seems for the time being superior. I have therefore allowed it to stand beside Parrington's, knowing that he says "l'identification de l'os temporal unique des Pareiasauriens typiques et des Procolophonides est une problème extremement difficile." A study of comparative suture-line lengths from actual specimens seems to me to be a suitable way of looking at probable trends in bone size over the cranial vault—a pursuit not embarked upon here.

A last possibility remains, viz. a separation of the tabular itself into two ossification centres, one carrying the boss and the other catering for the element A in the occipital declivity.

Skin Structure. The dermal ossicles or scutes are the only guide to the structure of the pareiasaurian skin. It has long been known that the ossicles are closely related in position and number to the underlying vertebrae and ribs. This is also seen in the present specimen, where the last 7 pre-sacral, 4 sacral and one or two caudal vertebrae can be correlated with the overlying scutes.

There are 18 rows of pre-sacral scutes. The exact number of pre-sacral vertebrae is not known in this specimen, but assuming there are 20 as in most pareiasaurs, it means that the first two cervicals are not covered by scute rows.

Referring to Table III, total lengths of scute rows as measured groupwise anteroposteriorly in middorsal line are given in column B where they are measured batch by batch. The numbers of rows per batch is given in column A; column C is equal to B divided by the number of units in A. The same plan is followed in columns D, E and F for the vertebrae, so far as they are exposed. From the table it is clear that the smallest midline scutes at the root of the tail are half the size of the largest ones over the middle of the back, (figures in column C). The figures in the table suggest that the skin (column C) was slightly too small for the underlying vertebral column (column F) which it had to cover. However the fossil shows marked dorsoventral compression making the vertebral column convex ventrally, increasing its apparent length, and the skin is depressed ventrally, decreasing its anteroposterior length somewhat. The ossicles are not more marked over the limb girdles, as is said to be the case for some other species. Perhaps they are at times better preserved over the underlying girdles so as to give this impression.

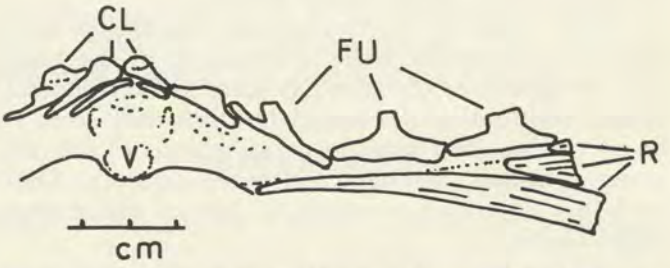


Fig. 6. *Nanoparia pricei.* Fracture through the dorsal wall at the front of the 9th central scute articulating with the 8th oblique row of scutes. Vertical sections through the scutes are shown, indicating funnel-like bosses, overlapping and overriding of scutes and of the rib rows.

The fossilised neck region is dorsoventrally compressed. Round the outsides of the scutes the hemicircumference of the neck at the first scute row is about 130 mm. Scutes are present the whole way round; apart from the dorsal midline scute there are probably four lateral scutes meeting ventrally over the throat. The 2nd and 3rd lateral scutes lie over the side of the neck, and are prominent. They have projecting outer surfaces which increase the outer circumference.

Fig. 4 gives the dorsal view of the cervical scale pattern. One notes a transverse gap between the median post-parietal and the small median scute which is presumed to overlie the 3rd cervical spine. The lateral post-parietal overhangs a scute lying in the 1st lateral position. Through compression the laterally facing scutes also appear in the top view.

In general the formation of distinct bosses is not a prominent feature of this specimen. Many of the cranial bones and scutes rise to blunt elevations, like the summit of a flattish barnacle, but rounded mushroom-like knobs and funnel-like protrusions are virtually absent. Prominent bosses are seen only in the lateral cervical region. There is no direct continuity between the bones of the head and neck, yet the anteroposterior lines of scutes have a general resemblance to the cranial elements. The midline units lie in the median post-parietal axis, the first lateral row in the lateral post-parietal line, the second lateral row in line with the tabular and the third row more or less in line with the scalloped back corner of the squamosal.

Succeeding this, the scute pattern in the dorsal region up to the level of the forelimb is shown in Fig. 5. Here as in the cervical region one recognises a herring bone pattern of scute rows at 45° to the midline: in general the scutes can be attributed to roughly equidistant positions, though the units may be subdivided. This means that two scutes may appear at a site where only one appears at a comparable site elsewhere.

Between the limb girdles, the scutes follow much the same pattern, the rows lying along the curved axes of the ribs. The scutes are largest in

their transverse axis, reaching the maximum sizes quoted in Table II. There appear to be at least 5 lateral scutes in each row (lateral to the median scute) covering the back and flanks.

There can be no doubt that the scutes were also present on the belly. Flattening of the body and disruption of the skin has scattered the ventral, caudal and limb scutes somewhat, but they seem to be of the smallest type in these regions (Table II), being rounded, nodular and more discrete. They probably extended to within 40 mm of the midline if not closer.

At the level of the 16th pre-sacral vertebra an estimate of the transverse hemicircumference of the squeezed body was about 420 mm. Transition to the smaller scute type took place about 220 mm from the dorsal midline.

The principal scutes have a radial structure. Designed like a limpet, they rise externally to a central point which is at times finely rough as if to anchor an overlying cap of horn. The centre may be little elevated or quite flat. From this centre radial undulations or flounce-like ridges diverge which give the edge of the scute a fluted appearance, or a pattern of flat radial arms like a starfish. In these scutes a distinct radial arrangement of bone fibres can also be seen, corresponding to the gross structure. These bony striae often have slit-like lacunae in them filled with matrix. A feature of many scutes is an oval matrix-filled depression on the outer surface like a small oblique cavity, 1-3 mm at the opening. It often lies under the shelter of the central boss. When some of these cave-like depressions were cleaned out they were found to be quite smooth and usually blind. Concerning the direction of its opening, the facing of the hollow area and its position on the scute, no pattern was discovered. They were not related in direction to the bone fibres and appeared more to be an encapsulation in a scute. Minor depressions and pockets were common over scute surfaces as well.

The most prominent part of the scute was not always situated at the centre for radial growth of the bone. An elevation or boss was often quite eccentric relative to the growth centre and situated occasionally at the edge of the scute. Likewise the little pockets or sacs on the scute could even be shared, as it seemed, across adjoining scutes.

The only scutes having prominent knob-like surface elevations were, as noted above, those on the sides of the neck. No scutes were dissected out, but they showed a layered structure, again reminiscent of a barnacle shell.

Besides the scutes with a plainly radial structure there were "secondary" scutes in the rows or parts of the main scutes which merely showed a curling and crinkling structure with depressions and folds. The canals entering these were round, and radial bone structure was not always evident. Their dells were sometimes in continuity with the sac-like cavities of the radial scutes. These same features were recognisable in the cranial bones—a radial structure with a central (e.g. tabular) or eccentric (e.g. lateral post-parietal) prominence, and the lettuce-leaf-like bone without such features (e.g. postfrontal).

Being radial structures arising from growth centres, the resulting junctions between scutes were necessarily of an overall linear and angular type. The junctions were closest over the mid-back but became progressively looser over the sides and ventral surface of the body. Spaces between scutes took several forms—zigzag sutures 1-2 mm across, vertical gaps with scalloped borders, and oblique shelving overlaps with variable and sometimes fairly large spaces between. Cranial suture lines vary of course in the same general way.

Nanoparia pricei **Broom and Robinson.**

The skin and skull structure leaves little doubt that this specimen is quite different from *Pareiasaurus serridens*, although the same may not be said with confidence for *N. luckhoffi*. Thus: (a) Despite the very small size of the animal and its scutes, the development of bosses is striking. There are large mushroom-like bosses, funnel-shaped prominences and blunt thorn-like outgrowths on the skull and scutes. By comparison the skull and scutes of *Pareiasaurus serridens* are rather smooth. (b) The first lateral pair of scutes lying beside the central row touch in the midline behind the central scute and have bosses shaped like a pair of kidneys, one on either side of the midline as illustrated by Brink (1955). The central scutes are just over 14 mm apart, and the vertebrae likewise. The distances change negligibly over the preserved row of 13 scutes. (c) Brink's diagrammatic representation (*loc. cit.*) of the scute pattern suggests a highly improbable gap in the lateral scute rows, which leaves an area uncovered by scutes for some 40-50 mm on either side of the midline series. A little cleaning and an examination of existing fractures in the specimen showed that the scute rows were in fact complete, being merely buried in the matrix above the dorsoventrally flattened rib cage. A section (Fig. 6) shows a complete series, with funnel-like bosses. The medial edge of the scutes lies external to the outer edge of the next most medially placed scute—the opposite of a tile-type of overlap. (d) There is considerable overlap of scale rows and ribs.

One could perhaps make out a case for there being only one species of *Nanoparia*. However, the skin can contribute nothing to this question at present. Broom himself regarded *N. luckhoffi* as possibly a small *Anthodon gregoryi* (= *P. serridens*), which if accepted would leave *N. pricei* as the only species in the genus.

CONCLUSIONS

From a study of the skin in the *Cistecephalus* zone pareiasaurs, the genera *Pareiasaurus* Owen and *Nanoparia* Broom appear to be valid. Being the smaller animal, *Nanoparia* has a more striking

armour; one is reminded that the most striking horny growth of any pareiasaur is that of the small form *Elginia* from Scotland. It seems desirable to place the following into synonymy with *Pareiasaurus serridens: P. steenkampensis, Propappus omocratus* and *Anthodon gregoryi.* The present study could contribute nothing to the placing of other specimens referred to the genus *Anthodon.*

Growth changes as surmised for *P. serridens* comprise a proportional enlargement of the scutes, vertebral column and skull generally, except that the cheeks become disproportionately larger and the skull longer with age. A relatively backward shift of the pineal opening is seen, and the maxillae may come to lodge more cheek teeth.

The structure of the scutes in *P. serridens* indicates the existence of two separate influences in scute structure: these are respectively the ossification centre, presumably dermally determined, and the placing of the boss and the cavities upon the scute surface, presumably epidermally determined. The purpose of the boss is clearly defensive, but the nature of the cavity present on many scutes is uncertain. These excavations have the smoothness that one sees in the bone near the intracranial venous sinuses, but it is hard to guess what such vulnerable cavernous bloodspaces would be doing on the outside of the body. A cutaneous gland pocket is a possibility, though it is unusual to find gland lobule nestling in such a type of bony cavity. More possibly I fancy that all the irregularities are under the control of growth stimuli from a variegated epidermis and do not point to any special organs contained therein.

Although the scute may be subdivided in *P. serridens*, the scutes are so large that no mammal could develop a warm fur coat at the rate of one hair set per scute field. The cotylosaurian scute pattern therefore offers no framework for the suppleness or multiplicity of mammalian hair units.

Finding now that the pareiasaurian scute pattern extended round on to the belly, it becomes easier to derive the turtles from the short bodied dwarf pareiasaurs as Gregory (1946) had proposed when *Elginia* was the only dwarf pareiasaur known. The broad ribs of *Nanoparia pricei* may make a better possible intermediate than the *Tapinocephalus* zone specimens of *Eunotosaurus,* whose claims as an ancestral chelonian have been recently diminished by Cox (1969). In *Eunotosaurus* the presence of dermal armour was shown moreover to be an error of observation, and the ribs exhibit a regional sculpturing which in no way resembles the patterns described here in the pareiasaurian skin or skull.

ACKNOWLEDGMENTS

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ABBREVIATIONS TO ILLUSTRATIONS.

A = Broom's element A.
CL = Central and first lateral scute bosses.
F = Frontal.
FU = Funnel shaped bosses on lateral scute rows.
IP = Interparietal (median).
J = Jugal.
L = Lacrimal.
M = Maxilla.
N = Nasal.
P = Parietal.
PF = Postfrontal.
PO = Postfrontal.
PRF = Prefrontal.
QJ = Quadratojugal.
R = Ribs (3 overlapping sections).
SQ = Squamosal.
V = Vertebral body.

Table I

COMPARATIVE SKULL MEASUREMENTS (mm)

	P. serridens[1]	*A. serrarius*[1]	*A. gregoryi*[2]	*Unknown No. 548*
Median length	318	255	± 240	± 170
Width, greatest	260	135	295	200
Interorbital distance, smallest	180	110	123	78
A-P orbital length	—	—	48	42
Occiput–postr. edge pineal	105	?	34	69
Premaxilla–antr. edge pineal	260	135	± 186	93
Intertabular width	200	110	—	104
Postr. orbit to postr. border cheek	150	124	—	73
Tabular boss to cheek angle	225	175	—	122
Vertical overhang of cheek maxilla border	140	50	—	29
Dentigerous length (maxillary)	180	125	116	± 66
Teeth	14	14	11 "post-canines" ?	10 "post-canines"

[1] After Boonstra [2] After Broom.

Table II

COMPARATIVE SURFACE MEASUREMENTS OF SCUTES

	P. serridens[1]	*Propappus parvus*[1]	*P. omocratus*[1] = *P. serridens*	*Anthodon*[1] *Sp.*	*"Pareiasaurus steenkampensis"*[2]	*Unknown No. 548*
Largest						
Length	67	60	50	64	57	30
Breadth	58	37		45	40	25
Medium						
Length	53	50		54		20
Breadth	45			40		20
Small						
Length	47		± 10		35	10 – 15
Breadth	40				25	8 – 10

[1] After Boonstra [2] After Seeley

Table III

AVERAGE ANTEROPOSTERIOR LENGTHS OF MIDLINE SCUTE ROWS AND VERTEBRAE COMPARED (SPECIMEN No. 548)

Region	*Set of Scute rows rows according to number of underlying vertebra*	*Combined length of of Rows (mm)*	*Average length of scutes over the region (mm)*	*Set of Vertebrae*	*Total length of set (mm)*	*Average length per vertebral body in region (mm)*
Code	A	B	C	D	E	F
Cervical	3 – 6	86	21,5	1 – 6	—	—
Dorsal	7 – 11	116	23,2	7 – 14	—	—
	12 – 16	156	31,2	14 – 16	97	32
	17 – 20	100	25	17 – 20	120	30
Sacral	21 – 24	76	19	21 – 24	100	25
Caudal	25 – 29	75	15	25 – 26	35	17,5