Late Triassic traversodontids (Synapsida: Cynodontia) in southern Africa

Bernard Battail

Muséum National d'Histoire Naturelle, Département Histoire de la Terre, USM 203 – UMR 5143 du CNRS, Paléobiodiversité et Paléoenvironnements, 8, rue Buffon, CP 38, 75231 PARIS cedex 05, France. E-mail:bbattail@mnhn.fr

Received 15 May 2005. Accepted 8 June 2006

Scalenodontoides macrodontes was described in 1957 by Crompton & Ellenberger as a new genus and species of the family Traversodontidae. For many years it was known only by its type specimen, a lower jaw from the Upper Triassic of Lesotho. The specimen was redescribed in more detail by Hopson in 1984, who established the close affinities of *Scalenodontoides* with *Exaeretodon.* In 1993, Gow & Hancox described the first skull of *Scalenodontoides,* discovered, together with fragmentary remains, in South Africa. The skull from South Africa looked very much like a skull from Lesotho, housed in the Muséum National d'Histoire Naturelle, Paris, and initially attributed, in an unpublished work, to the chiniquodontid *Belesodon* (Costedoat, 1962). Further preparation of the skull from Lesotho was carried out; the specimen proved not to belong to a chiniquodontid, but to a large traversodontid, described in this paper. A revision of the traversodont remains known from the Late Triassic lower Elliot Formation of Lesotho and South Africa leads to the conclusion that they can all be attributed to the species *Scalenodontoides macrodontes.* Detailed comparisons between *Scalenodontoides* and *Exaeretodon* confirm *Scalenodontoides* as a valid genus, with only one species, *Scalenodontoides macrodontes.* A new diagnosis of *Scalenodontoides macrodontes,* based on an analysis of all available material, is given.

Keywords: traversodontids, Lesotho, South Africa, Late Triassic.

INTRODUCTION

The family Traversodontidae was originally erected in 1936 by Huene to accommodate new forms of gomphodont cynodonts from south America. It is now known by many taxa of various sizes and skull morphologies, which share, in particular, many features in the structure of their postcanine teeth. A cosmopolitan Triassic family, the traversodontids are mostly represented in Argentina (Cabrera 1943; Romer 1967, 1972; Bonaparte 1962, 1963, 1978) and in Brazil (Huene 1935–1942; Barberena 1974; Abdala *et al.* 2002); they are also known from Tanzania (Crompton 1955, 1972), Zambia (Brink 1963; Kemp 1980), Lesotho (Crompton & Ellenberger 1957), South Africa (Gow & Hancox 1993), Madagascar (Flynn *et al.* 2000), India (Chatterjee 1982), Canada (Hopson 1984; Sues *et al.* 1992), the United States of America (Sues & Olsen 1990; Sues *et al.* 1999), Belgium (Hahn *et al.* 1988), France (Godefroit & Battail 1997), and, perhaps, Russia (Tatarinov 1973; Battail & Surkov 2000). Among the many taxa which have been described, some appear to be of dubious validity and a number of possible synonymies were suggested by Battail (1991, 58–60).

In striking contrast with South America, where Late Triassic traversodontids are numerous and relatively diversified, southern Africa has yielded up to now only very few specimens which can be attributed to Late Triassic traversodontids. The purpose of this paper is to provide a short review of the Late Triassic traversodontid material already known from southern Africa, and to describe one more specimen, a skull which, although collected long ago, had been initially misinterpreted, and had never been published. The anatomical characters of the southern African Late Triassic traversodontids are discussed and compared with other representatives of the family. These data are incorporated into a brief systematic and phylogenetic analysis.

REVIEW OF THE LATE TRIASSIC TRAVERSODONTIDS IN SOUTHERN AFRICA

Scalenodontoides macrodontes was described in 1957 by Crompton & Ellenberger as a new genus and species of the family Traversodontidae. The type specimen, the tooth-bearing portions of a huge lower jaw (Figs 1–3), was found on the northern slope of Morobong Hill, Mohale's Hoek district, Lesotho (then, Basutoland), and attributed to 'the upper Molteno Beds'. It has since been established by Turner (1972), that it comes in fact from the base of the Elliot Formation. The type specimen of *Scalenodontoides macrodontes* is housed in the Palaeontology unit of the Muséum National d'Histoire Naturelle (MNHN), Paris, under the number 1957–23. Complements to the original description, comments and comparisons were given by Hopson (1984). A second specimen referred to *Scalenodontoides macrodontes* is the right half of the anterior part of a snout, collected at a short distance from the type, and housed in the South African Musem, Cape Town (SAM K336); it was described and figured by Hopson (1984).

Crompton & Ellenberger (1957) correctly attributed *Scalenodontoides macrodontes* to the Traversodontidae, and compared it to several other genera of the same family. However, they never mentioned the genus *Exaeretodon,* described in 1943 by Cabrera. Hopson (1984) stressed the close affinities of the genera *Scalenodontoides* and *Exaeretodon* which, according to the diagnosis he gave of the genus *Scalenodontoides,* would have differed mostly in their robustness, in their skull proportions and in the relative size of their lower canines and incisors. It must be noted, however, that one of the few characters mentioned by Hopson to distinguish *Scalenodontoides* from *Exaeretodon,* namely, the presence of a chin-like ventral projection of the symphysis of the dentary, found only in *Scalenodontoides,* cannot be retained: a similar feature can indeed be observed in *Exaeretodon argentinus* and in *E. statisticae* (see for

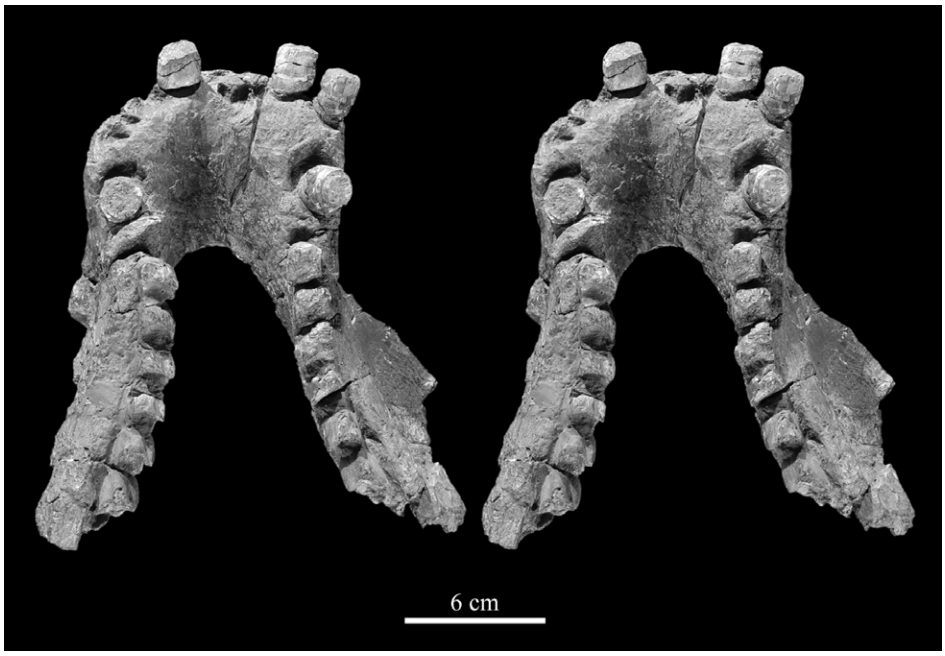

Figure 1. Stereophotograph of the type specimen of *Scalenodontoides macrodontes,* lower jaw (MNHN 1957-23), in dorsal view.

example Chatterjee 1982, figs 2 & 5). Clearly, at that stage of our knowledge of *Scalenodontoides,* the generic distinction between *Exaeretodon* and *Scalenodontoides* could be questioned.

More recently, Hancox discovered relatively abundant material attributed to *Scalenodontoides* and coming from the base of the Elliot Formation of the farm Norwood, Sterkstroom district, Eastern Cape Province, South Africa. The new material, representing at least three individuals of different sizes, was described in detail by Gow & Hancox (1993). It is housed in the Bernard Price Institute, University of the Witwatersrand, Johannesburg, and includes a complete skull (BP/1/5395 A) (Figs 4–7), an isolated parietal fragment (BP/1/5395 B), a fragment of a large snout (BP/1/5395 C), several isolated maxillary postcanines (BP/1/5395 D), and fragments of lower jaws, including one which pertains probably to the complete skull (BP/1/5395 E). The attribution of the South African material to *Scalenodontoides* is certainly correct: the piece of snout from Morobong, Lesotho, is very broad and extremely similar to the corresponding parts of the snouts from South Africa (snout of the complete skull, and isolated snout fragment); the piece of right lower jaw from South Africa has the same size and robustness as the corresponding portion of the type specimen from Lesotho; it has also a posterior mental foramen, and bears five fragmentary postcanine teeth of the same structure as the postcanines of the type. Moreover, the South African material comes from the same stratigraphic level, the base of the Lower Elliot Formation.

The skull described by Gow and Hancox is in good condition, but it has been very dorsoventrally compressed. In its general proportions, it displays a few conspicuous features: the snout is very broad, the skull roof is very broad between the orbits, and the temporal region is remarkably short. These cranial proportions appear as

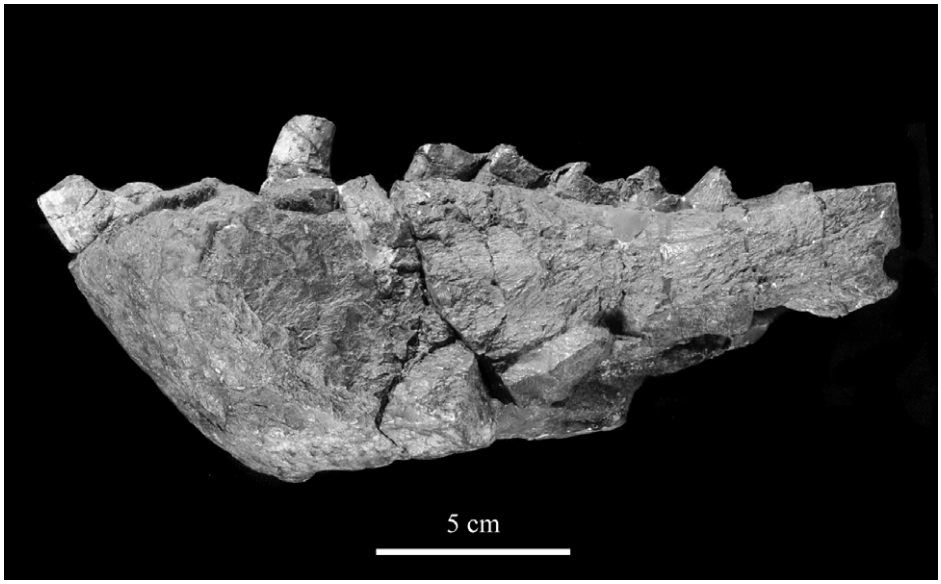

Figure 2. Photograph of the type specimen of *Scalenodontoides macrodontes,* lower jaw (MNHN 1957-23), left lateral view.

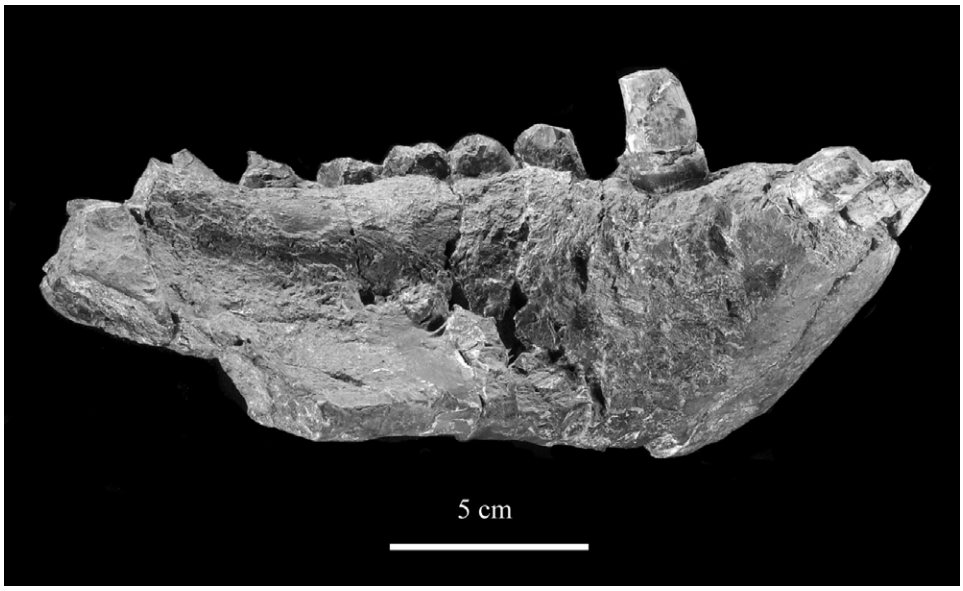

Figure 3. Photograph of the type specimen of *Scalenodontoides macrodontes,* lower jaw (MNHN 1957-23), right lateral view.

quite different from those of *Exaeretodon*, in which the snout is more slender and has a more marked constriction behind the canine, the interorbital width is much more reduced, and the temporal fossae are much more elongated. But the most obvious difference is the existence, in *Scalenodontoides* only, of what Gow & Hancox named a nuchal table: 'In all other cynodonts, parietals, squamosals, and tabulars combine to form a sharp crest separating the

Figure 4. Photograph of the skull of *Scalenodontoides macrodontes* (BP/1/5395 A), dorsal view.

Figure 5. Photograph of the skull of *Scalenodontoides macrodontes* (BP/1/5395 A), ventral view.

occiput from the temporal openings. In *Scalenodontoides* the parietals form a broad, coarsely rugose horizontal shelf, barely overhanging the temporal openings, but forming an extensive shelf above the occiput. Smoothly concave lateral indentations are present where the parietals drop vertically to be overlapped by the squamosals which then wrap around onto the anterior surface as far as the borders of the posttemporal fenestrae.' (Gow & Hancox 1993, 162–164). That unique nuchal table is considered by Gow & Hancox as establishing the generic distinctiveness of *Scalenodontoides.*

The study by Gow & Hancox (1993) of the upper dentition of the South African specimens shows that, as in the snout fragment from Lesotho, there are only three incisors immediately followed by the canine. More important perhaps is the first description of upper postcanines of *Scalenodontoides.* In the skull, only the last postcanine of each row is preserved. In addition, identifiable isolated postcanines include five right uppers and four left uppers. In crown view, the upper postcanines all display a more or less geniculate shape, and can be described as composed of two lobes, one labial lobe and one lingual lobe, which meet in an angle; three in-line labial cusps flank a very steep shearing plane; the central labial cusp is the main one, the anterior and posterior accessory labial cusps are connected to the crest that descends from the main labial cusp; the central part of the crown is occupied by a basin surrounded by a rim which is thicker on the lingual side. The interpretation of the last postcanines which remained *in situ* in the skull is difficult, as 'these teeth had suffered some wear through use, and unfortunately they are impacted into their sockets and have been deformed' (Gow & Hancox 1993, 165). It is worth noting, however, that the last left upper postcanine displays a narrow bridge connecting the labial and lingual lobes, and that the latter is posterior, rather than medial, to the labial lobe (see Gow & Hancox 1993, fig. 8 top right).

THE LARGE CYNODONT SKULL FROM LERIBE (LESOTHO)

Introduction

A large cynodont skull had been found in 1955 by F. Ellenberger near Leribe, northern Lesotho, in the lowermost part of the Elliot Formation (base of the 'Lower Red Beds'). That skull, now housed in the Muséum National d'Histoire Naturelle (MNHN), Paris, under the number 1955–25, is not very well preserved, and was partly

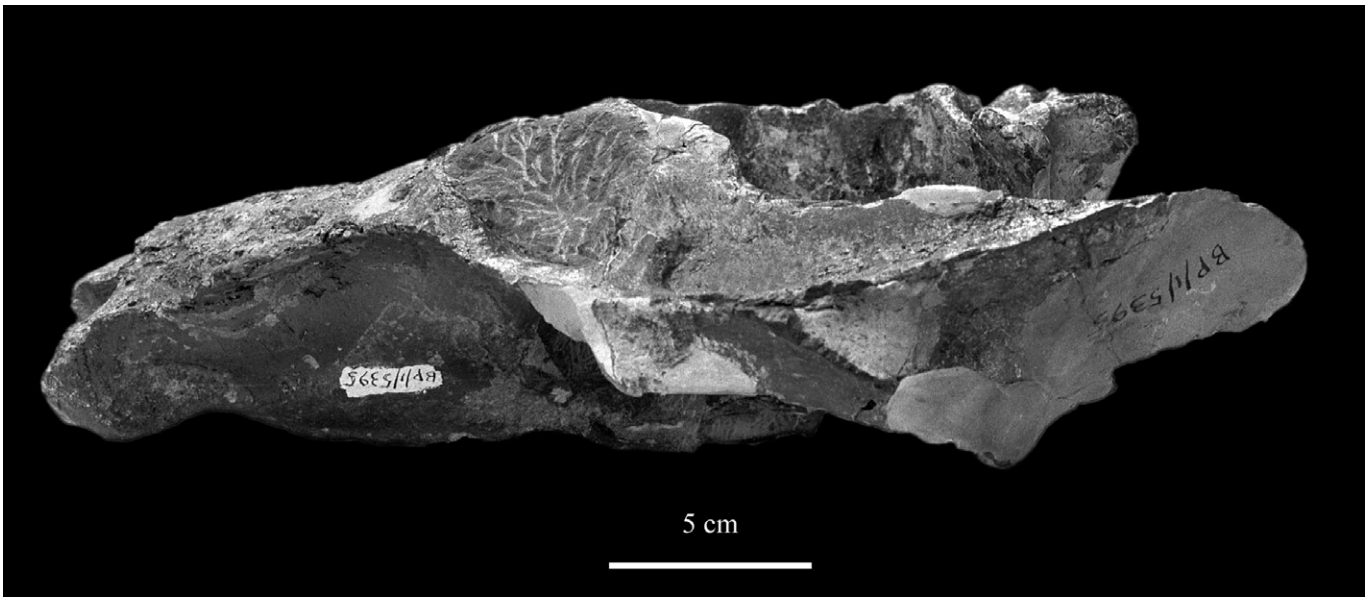

Figure 6. Photograph of the skull of *Scalenodontoides macrodontes* (BP/5395 A), left lateral view.

embedded in an extremely hard matrix. Without any further preparation, it was briefly described in an unpublished work by Costedoat (1962), and compared by her, mainly on the basis of similarities in size and in the structure of the skull roof, with the chiniquodontid *Belesodon* from Brazil.

After the description of the skull of *Scalenodontoides* by Gow and Hancox, I realized that the skull from Leribe, Lesotho, was very similar to it, and that, most probably, it had originally been misinterpreted. Further preparation of the skull from Leribe was carried out; the specimen proved not to belong to a chiniquodontid close to *Belesodon*, but to a large traversodontid.

Description

The state of preservation of the cynodont specimen from Leribe is rather poor. The specimen consists of a large skull without lower jaw (Fig. 8–11). It was found in several pieces. The snout is extremely weathered, and its contact with the rest of the skull is not very good. The skull has not been compressed, but it is distorted, it bears numerous fractures and cracks, and most sutures are not visible. The bone is often difficult to distinguish from the matrix, which is very hard and could not be entirely removed. Only two teeth (right upper postcanines) are preserved.

The basal length of the skull, about 28 cm, is approximately equal to its maximum width. In size and general proportions, the specimen agrees very well with the skull of *Scalenodontoides* described by Gow & Hancox.

Little can be said of the snout, except that it is massive, short and very broad. The dorsal surface of the skull, between the level of the anterior border of the orbits and the level of the posterior part of the temporal openings, is remarkably similar to that of the South African skull: the skull roof is very broad between the orbits (minimum interorbital distance: 12 cm), and the postorbitals have a

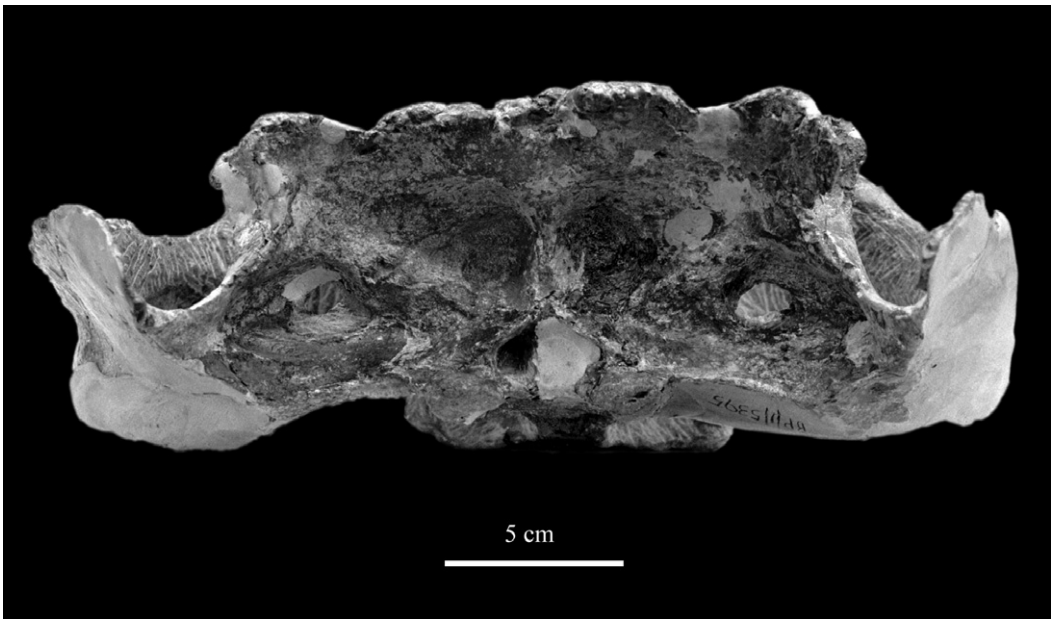

Figure 7. Photograph of the skull of *Scalenodontoides macrodontes* (BP/5395 A), occipital view.

Figure 8. Photograph of the skull of *Scalenodontoides macrodontes* (MNHN 1955-25), dorsal view.

strong dorsal ridge bordering the temporal openings; however, the medial ridge of the frontals is less pronounced than on the South African skull, and no pineal foramen could be found in the Leribe specimen. The temporal region is very short. The cranial arches – suborbital and postorbital bars, zygomatic arch – are extremely robust. As in the *Scalenodontoides* skull from South Africa, the lateral surface of the jugal is depressed behind the orbit. Only the left zygomatic arch is preserved; its posterior surface is weathered, and therefore the posterior process of the squamosal is not preserved.

The occipital region of the skull from Lesotho has been somewhat distorted, but still displays clearly the same structure as that of any other cynodont, with two sharp occipital crests meeting the posterior part of the sagittal crest. The left part of the occipital plate is still coated with a plane layer of very hard matrix, through which one would have expected to see a horizontal shelf of bone protruding, if a nuchal table had been present; the right part of the occipital plate has been partially prepared, and, similarly, no evidence of a nuchal table could be found. The occipital region of the skull from Lesotho is therefore very different from that of the South African skull, even if two common features can be found: the medial part of the occipital crest is almost horizontal (in most cynodonts, the occipital crest descends regularly from the sagittal crest to the squamosal), and, seen in dorsal view, the two occipital crests meet in a very obtuse angle (in most cynodonts, they meet in a more closed angle).

The ventral surface of the skull is neither well preserved, nor fully prepared. The secondary palate is complete and well developed. As in other advanced traversodontids, the postcanine row is displaced medially. Owing to the bad state of preservation of the snout, the total number of the postcanines could not be established. Only two postcanines are preserved, the antepenultimate and the last one of the right side. Behind the pterygoid flanges, the basicranial axis is broad and short. The occipital condyles

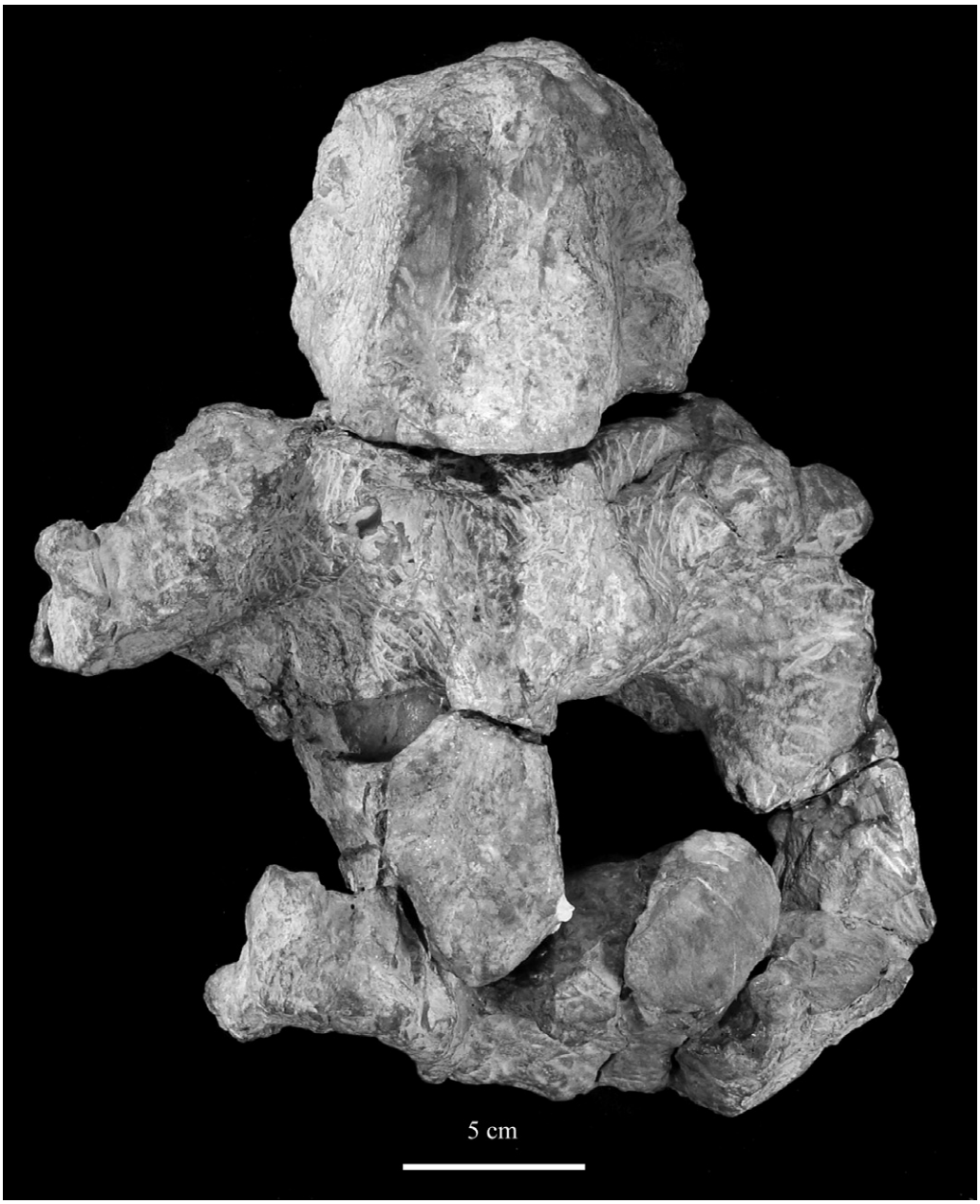

Figure 9. Photograph of the skull of *Scalenodontoides macrodontes* (MNHN 1955-25), ventral view.

are very damaged, especially the right one; they are widely separated. The paroccipital process, relatively well preserved on the left side, is extremely massive.

Dentition. Little can be said of the antepenultimate postcanine, which is very damaged. Its outline in occlusal view is similar to that of the postcanines of *Scalenodontoides* described by Gow & Hancox, 1993, fig. 6e, but it seems to have been narrower anteroposteriorly. The last postcanine (Figs 12–16) has a crown which has suffered only little wear, and it has been fully prepared. Its root is not preserved. Its setting in the tooth row is particular, the main axis of the occlusal surface of the crown being orientated almost anteroposteriorly, rather than obliquely as in the antepenultimate postcanine: the 'lingual lobe' is thus posterior, rather than medial, to the 'labial lobe'. For comparative purposes, the terms labial and lingual have, however, been retained in the description which follows. The two lobes are very well individualized, they are separated by a narrow constriction, marked, behind the posterior accessory labial cusp, by a fold of enamel which penetrates deeply between them. The anterior accessory labial cusp is not very distinct from the main labial cusp. The posterior accessory labial cusp, very small, is situated low on the crown; it rises from a cingulum and is connected to a blunt ridge which descends from the main labial cusp. The lingual lobe bears several ill-defined, low cusps. The postero-external wall of the crown is bordered with a cingulum. The last upper postcanine of the skull from Lesotho is similar to the last left postcanine of the *Scalenodontoides* skull from South Africa in its anteroposterior orientation, and in the presence of a constriction between the two lobes.

Discussion

Owing to its relatively poor state of preservation, the traversodontid skull from Lesotho could not be described in as much in detail as the skull from South Africa. It is higher than the skull from South Africa (but the latter has

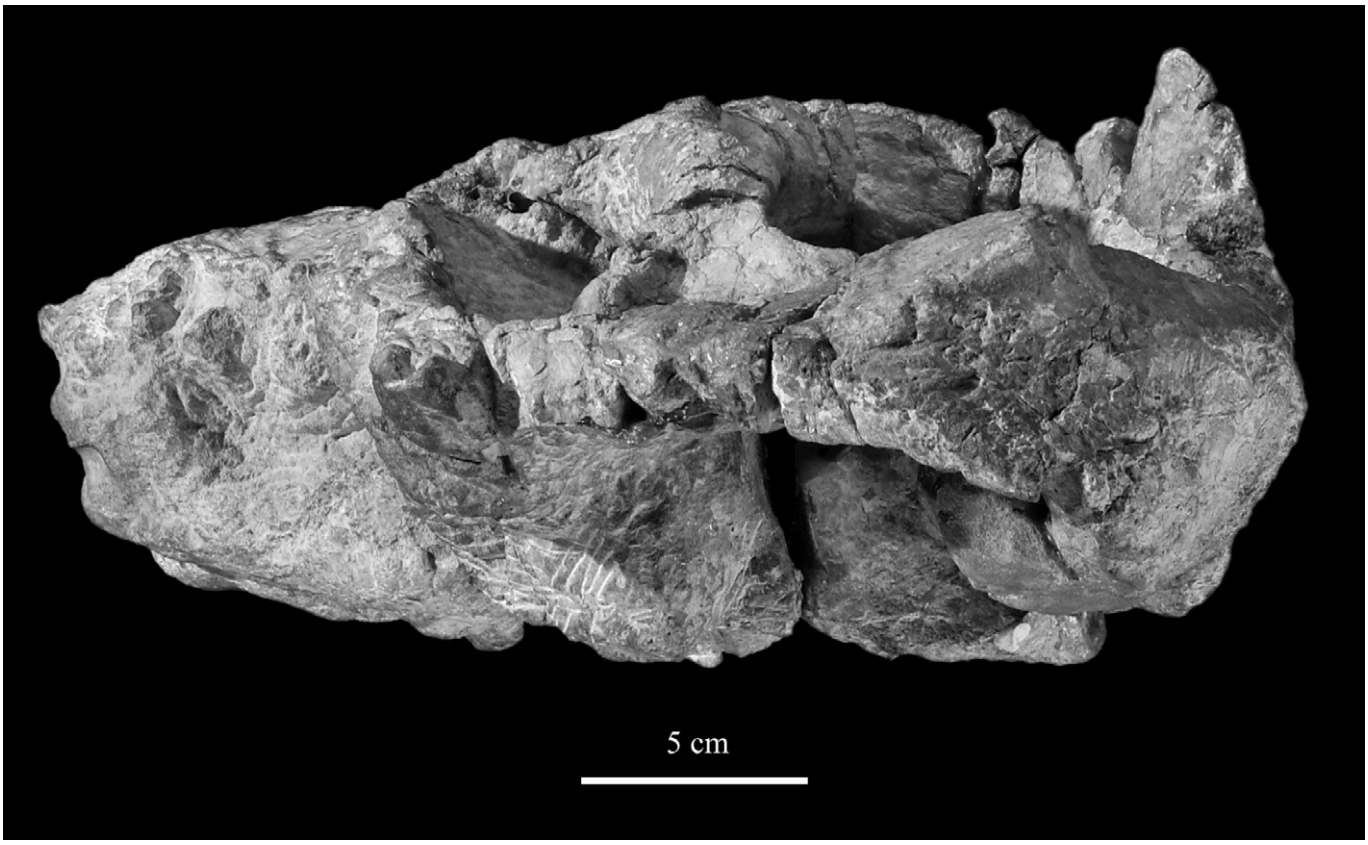

Figure 10. Photograph of the skull of *Scalenodontoides macrodontes* (MNHN 1955-25), left lateral view.

been dorsoventrally compressed), and it has a more massive paroccipital process. Every other character observable on the skull from Lesotho agrees very closely with the corresponding character of the skull from South Africa, with one noticeable exception: a conspicuous nuchal table is present in the skull from South Africa, but totally absent in the skull from Lesotho. Does that only difference, sharp as it may seem, warrant the attribution of the skull from Lesotho to a new taxon? I do not think so, and am inclined to believe that it could rather be ascribed to sexual dimorphism, keeping in mind the fact that, in living tetrapods, sexual dimorphism often expresses itself by a major differ-

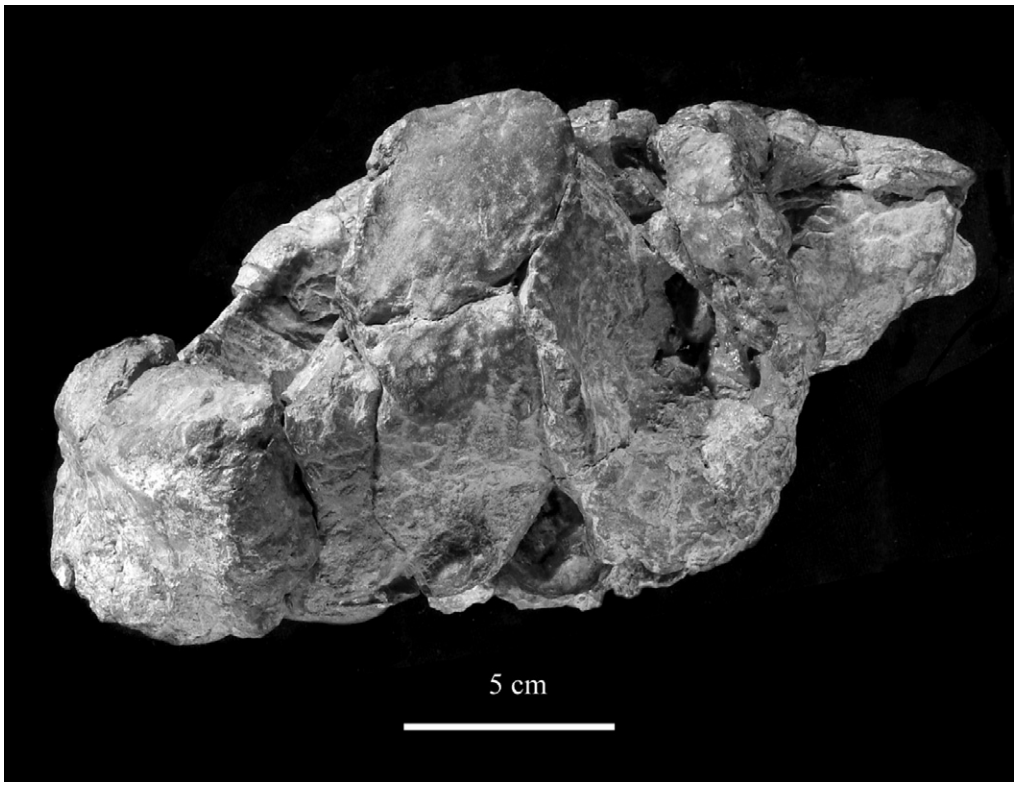

Figure 11. Photograph of the skull of *Scalenodontoides macrodontes* (MNHN 1955-25), occipital view.

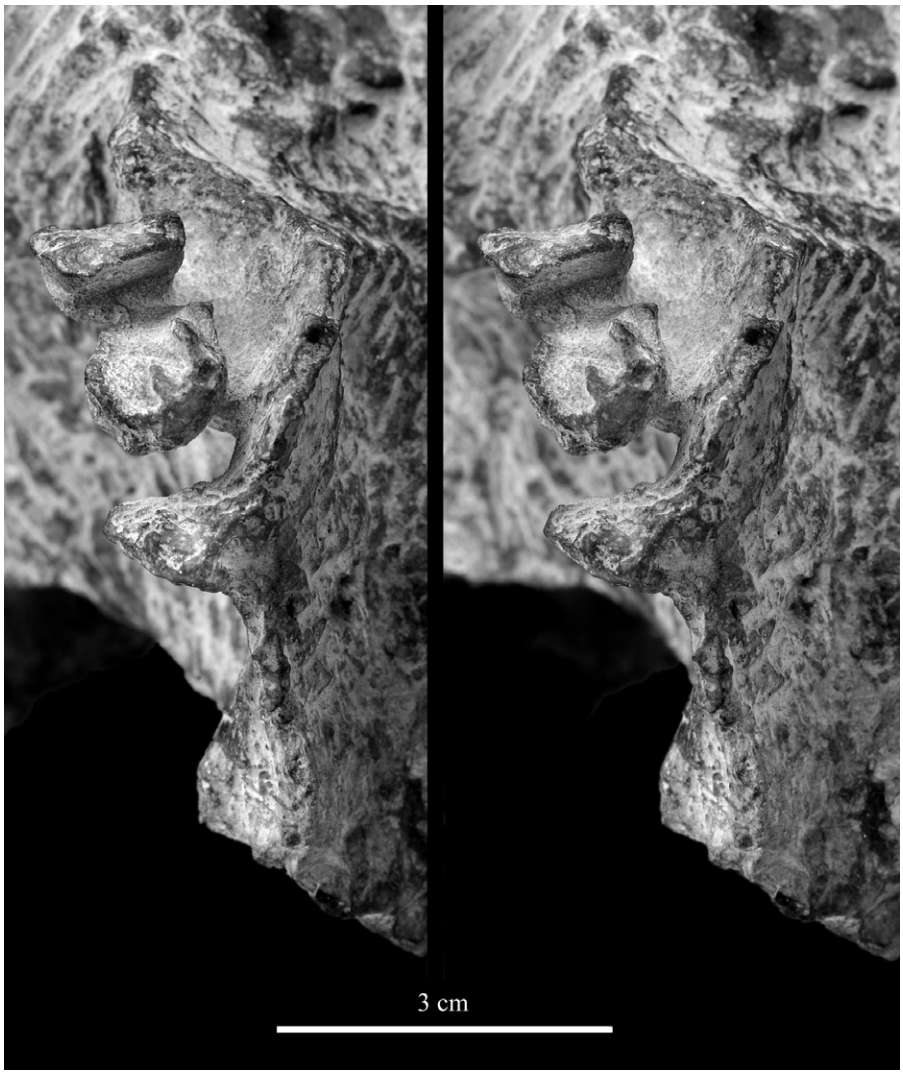

Figure 12. Stereophotograph of the last right upper postcanine of *Scalenodontoides macrodontes* (MNHN 1955-25), occlusal view.

ence dealing with just one character (presence or absence of horns, in many antelope species, for example).

If my conclusions are accepted, all the traversodontid specimens known from the Lower Elliot Formation may be attributed to the species *Scalenodontoides macrodontes.* If they are not, it becomes impossible to determine if it is the skull from South Africa or the skull from Lesotho which belongs to *Scalenodontoides macrodontes.*

THE GENUS SCALENODONTOIDES

Comparisons and phylogeny

In 1984, Hopson re-examined *Scalenodontoides macrodontes,* and convincingly demonstrated that *Scalenodontoides* was a close relative of *Exaeretodon.* In the same paper, he described the fragmentary remains of a huge traversodont found in the Upper Triassic beds of the Wolfville Formation of Nova Scotia, Canada. The largest piece was a partial lower jaw – the horizontal ramus of a right dentary with a small portion of the left dentary adjacent to the symphysis – similar in size and robustness to the corresponding part of the type specimen of *Scalenodontoides macrodontes.* It was chosen as the type specimen of a new species, provisionally placed in the genus *Scalenodontoides* and named ?*Scalenodontoides plemmyridon.* Unfortunately, neither the type specimen, nor the two other dentaries from the same locality, attributed to the same species, had kept their postcanines. An isolated tooth, interpreted as a right lower postcanine, was tentatively assigned to ?*Scalenodontoides plemmyridon.* It is composed of 'a tall, transversely-widened, anterior blade bearing three principal cusps, and a low, anteroposteriorly-narrow, posterior heel' (Hopson 1984, 196).

The problem, well understood and explained by Hopson, was the following: the postcanines of *Scalenodontoides* would have been expected to be similar to those of *Exaeretodon* but, instead, that isolated tooth, wider than long, with anteroposteriorly compressed main cusps, could rather be compared with a lower postcanine of a very different genus, *Massetognathus.* A few years later, a new traversodont tooth, an isolated left upper postcanine, was discovered in the Wolfville Formation of Nova Scotia; it is characterized, in particular, by its anteroposterior compression, by the presence of three large cusps on a vertical transverse ridge, and by a low anterior cingulum. It had then became clear that only one species of large traversodont was represented in the Wolfville Formation and that the isolated postcanines, in view of their sizes and shapes, could be referred to it. These isolated postcanines, upper as well as lower, are far too different, in

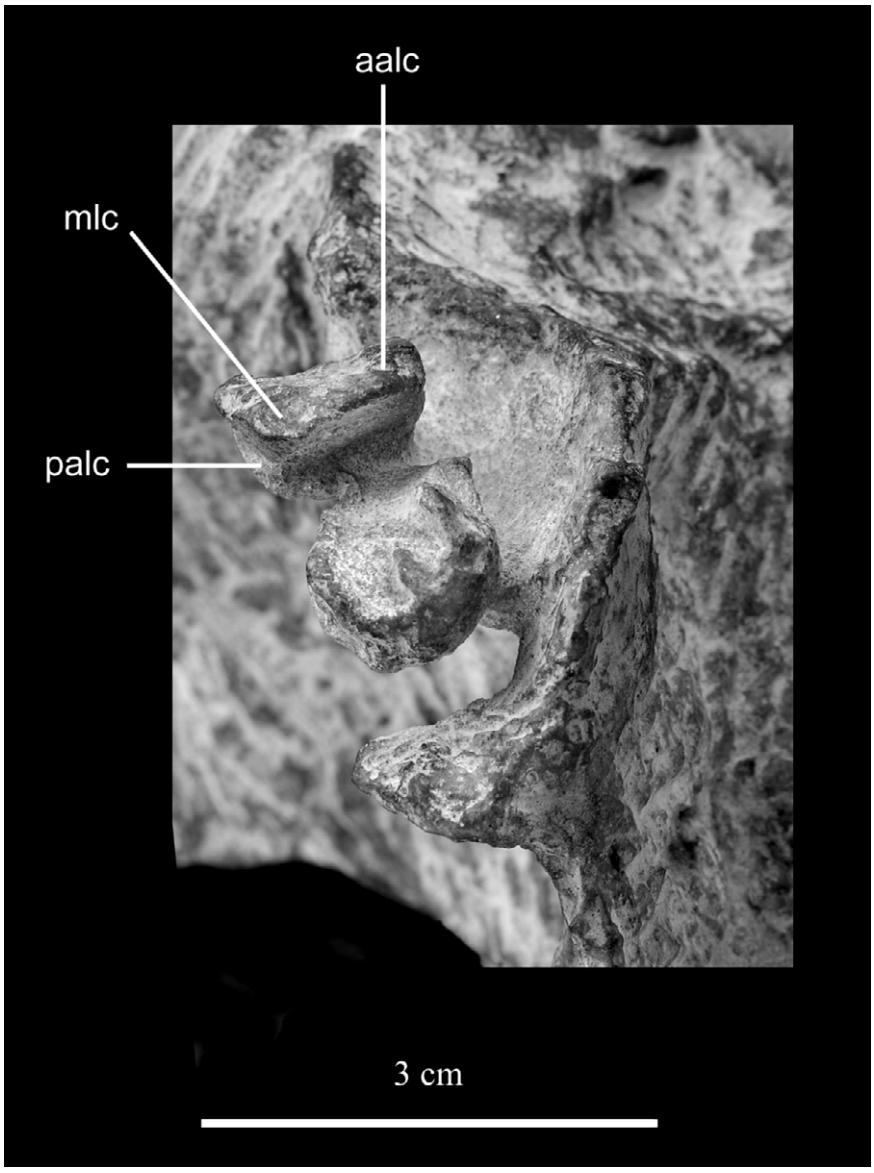

Figure 13. Photograph of the last right upper postcanine of *Scalenodontoides macrodontes* (MNHN 1955-25), occlusal view. Abbeviations: aalc, anterior accessory labial cusp; mlc, main labial cusp; palc, posterior accessory labial cusp.

their structure, from those of *Exaeretodon,* to belong to such a close relative of *Exaeretodon* as *Scalenodontoides.* Consequently, the traversodont from Nova Scotia was transferred by Sues, Hopson & Shubin (1992) to the new genus *Arctotraversodon.* The possibility of a close relationship between the three North American genera *Arctotraversodon, Boreogomphodon* and *Plinthogomphodon* has been suggested by Sues, Olsen & Carter (1999) on the basis of similar features of the upper postcanines. Finally, only one species remains in the genus *Scalenodontoides,* the type species *Scalenodontoides macrodontes.*

Hopson (1984, 1985) could define, within the traversodontids, a clade, comprising *Gomphodontosuchus, Exaeretodon* and *Scalenodontoides,* characterized by the following features of the postcanines: (A) upper postcanines (1) a very oblique orientation of the postcanines in the maxilla; (2) lack of a central cusp on the posterior transverse ridge; (3) a high anterior wall bounding the central basin; (4) a prominent internal ridge anterior to the main internal cusp. (B) Lower postcanines (1) the anteroexternal cusp is wider than the anterointernal cusp; (2) the anterointernal cusp is inclined obliquely backwards; (3) the crown in occlusal view has a trapezoidal rather than rectangular outline.

The recently described genus *Menadon,* from Madagascar, belong also to this clade (Flynn *et al.* 2000).

Menadon, Exaeretodon and *Scalenodontoides* are united by a few synapomorphies: internarial bar incomplete; enlarged incisors, the lower being procumbent; reduction of upper incisors from four to three. *Exaeretodon* and *Scalenodontoides* have a closer relationship, as they share additional synapomorphies: lack of small anterior postcanines; outline of the upper postcanines geniculate in occlusal view, with very distinct labial and lingual lobes; presence of a posterior accessory labial cusp on the upper postcanines, observable at least on the last ones. As stated by Hopson as early as 1984, *Exaeretodon* appears as the sister genus of *Scalenodontoides.* But thanks to the description of more material since then, the differences between the two genera can now be more clearly pointed out.

The skull of *Scalenodontoides* is different in shape and proportions from that of *Exaeretodon:* its snout is shorter

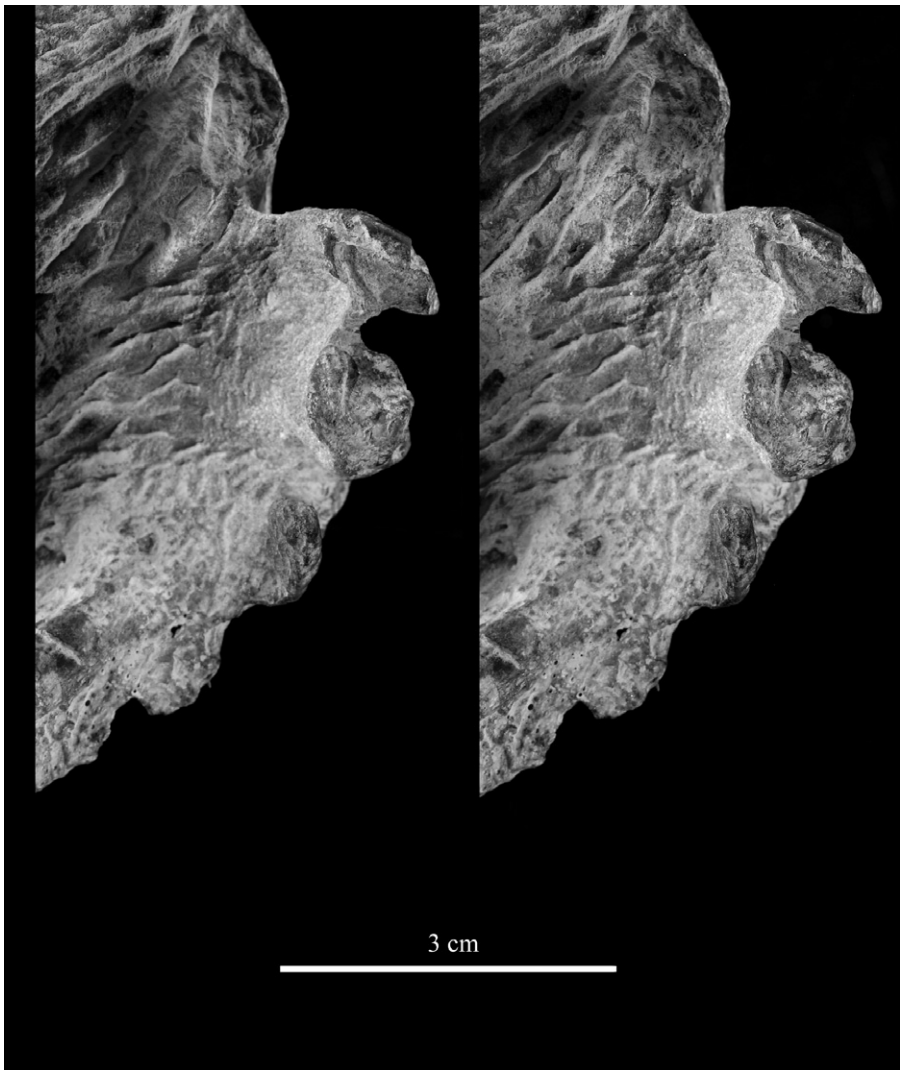

Figure 14. Stereophotograph of the last right upper postcanine of *Scalenodontoides macrodontes*(MNHN 1955-25), postero-external view.

and broader, its temporal region is much shorter; its occipital crests meet in a very obtuse angle; its lower jaw is more massive. A very conspicuous cranial feature, a nuchal table running across the top of the occiput, distinguishes also *Scalenodontoides* from *Exaeretodon;* but it seems to be present only in certain individuals, and could be a character linked to sexual dimorphism (see above).

The dentition is very similar in *Exaeretodon* and *Scalenodontoides.* A few differences can, however, be noted. In all the genera of the clade to which *Scalenodontoides* pertains (*Gomphodontosuchus, Menadon, Exaeretodon* and *Scalenodontoides*), the upper postcanines are orientated obliquely in the maxilla, rather than transversely as in other traversodonts (*Massetognathus,* for example). In *Exaeretodon,* the obliqueness of the orientation of the postcanines increases slightly, but regularly, from front to rear in the tooth row. In *Scalenodontoides,* there is a sharp change of orientation of the last postcanine, which has the main axis of its crown orientated almost anteroposteriorly, rather than obliquely. The labial and lingual lobes of the last upper postcanine, as recorded in both *Exaeretodon* and *Scalenodontoides,* are clearly distinct, being demarcated by an angulation between them, but in *Scalenodontoides* this demarcation is further emphasized by a constriction. On the upper postcanines of *Exaeretodon* and *Scalenodontoides* which have not suffered extensive wear through use, a posterior accessory labial cusp can be seen. It has been described in detail by Abdala *et al.* (2002) in *Exaeretodon:* 'In unworn teeth, the labial posterior accessory cusp is completely isolated from the crest that descends from the main labial cusp .... Thus, two basins characterize the unworn postcanine: the principal one formed by the anterior accessory labial cusp and the main labial cusp, and a posterior small one formed only by the posterior accessory labial cusp.' (Abdala *et al.* 2002, p. 320 and fig. 9). In *Scalenodontoides,* as can be seen on the last postcanine of the skull from Lesotho and on the moderately worn isolated postcanines from South Africa described by Gow & Hancox (1993), the posterior accessory labial cusp, small and very low, is connected by a crest to the main labial cusp and does not form a small basin. The postero-external wall of the crown of the last upper postcanine is bordered by a well developed cingulum in *Scalenodontoides;* such a cingulum does not exist in *Exaeretodon.* The lower postcanines are also slightly different in *Exaeretodon* and *Scalenodontoides.* As noted by Hopson, 'in crown view, the ridge which passes back from the apex of the lingual cusp to the heel describes a distinct curve, concave lingually [in *Scalenodontoides*], whereas in *Exaeretodon* ... the ridge is straight.' (Hopson 1984, 183).

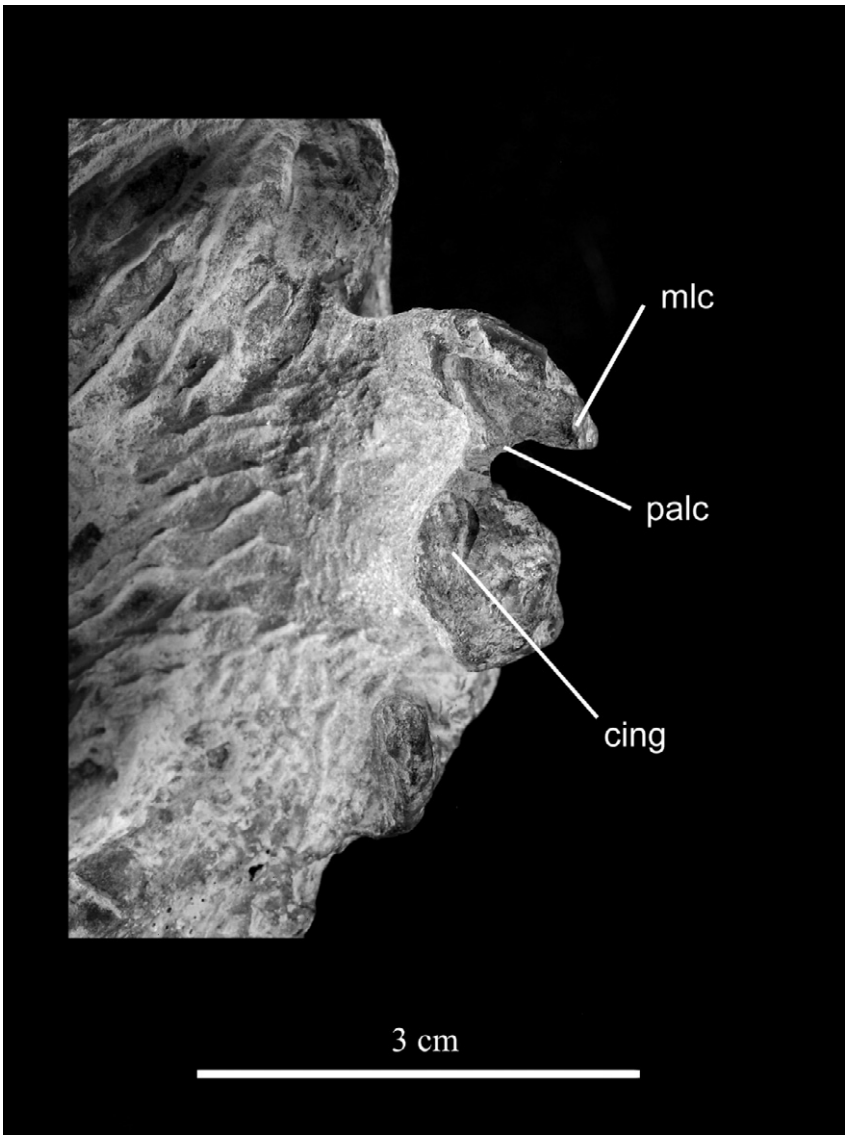

Figure 15. Photograph of the last right upper postcanine of *Scalenodontoides macrodontes* (MNHN 1955-25), postero-external view. Abbreviations: cing, cingulum; mlc, main labial cusp; palc, posterior accessory labial cusp.

SYSTEMATIC PALAEONTOLOGY

Synapsida
Therapsida
Theriodontia
Cynodontia
Traversodontidae

Scalenodontoides Crompton & Ellenberger, 1957

Scalenodontoides macrodontes Crompton & Ellenberger, 1957

Holotype. Specimen No. 1957–23 in the palaeontology unit of the Muséum National d'Histoire Naturelle, Paris. Paired dentaries lacking the region behind the postcanines.

Referred specimens. The right front half of a large snout, No. SAM K336, in the collection of the South African Museum, Cape Town. A complete skull with a fragment of lower jaw, the front part of a large snout, a sagittal crest and isolated postcanines, No. BP/1/5395 in the collection of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. A skull lacking the lower jaw, No. 1955–25 in the palaeontological unit of the Muséum National d'Histoire Naturelle, Paris.

Horizon and localities. The type specimen and the partial snout housed in the South African Museum were found a short distance apart; they come from Morobong, Mohale's Hoek district, Lesotho. Originally attributed by Crompton & Ellenberger (1957) to 'the upper Molteno Beds', they are in fact from the base of the Elliot Formation, as shown by Turner (1972). The material housed in the Bernard Price Institute was scattered over a wide area, but comes from only one locality, the farm Norwood, Sterkstroom district, Eastern Cape Province; it was found 'at the base of the Elliot Formation immediately above its contact with the underlying Molteno Formation' (Gow & Hancox 1993). The skull without lower jaw kept in the Muséum National d'Histoire Naturelle was indicated by Ellenberger as having been found near Leribe, Leribe district, Lesotho, at the base of the 'Lower Red Beds', that is to say, in the lowermost part of the Elliot Formation. Thus, all recorded specimens come apparently from the same level: *Scalenodontoides macrodontes* seems to characterize a very narrow stratigraphic interval at the base of the Late Triassic Lower

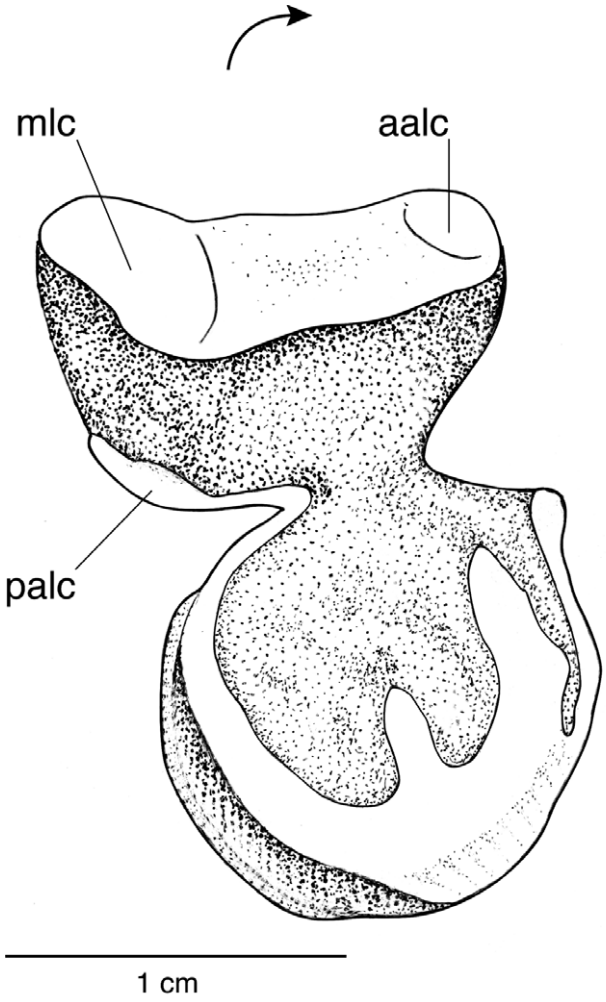

Figure 16. Occlusal view of the last right upper postcanine of *Scalenodontoides macrodontes* (MNHN 1955-25). Abbreviations as in Fig. 13.

Elliot Formation (see Kitching & Raath 1984, fig. 2).

Revised diagnosis. A very large traversodontid. Skull very robust, approximately as broad as long. Snout short and broad. Internarial bar incomplete. Skull roof very broad between the orbits. Temporal region remarkably short. Temporal opening wider than long. Occipital crests almost horizontal in their medial portion, and meeting, in dorsal view, at a very obtuse angle; they can be followed by a robust, overhanging nuchal table composed mostly by the parietal. Occipital condyles widely separated. Lower jaw massive; symphysis broad, long and deep. Upper dentition with only three, large, incisors. Upper postcanines orientated obliquely in the maxilla, except the last one, which has the main axis of its crown orientated almost anteroposteriorly. Labial and lingual lobes of the last upper postcanines clearly distinct and demarcated one from another by a constriction. On the upper postcanines, the posterior accessory cusp is linked by a crest to the main labial cusp, and does not form a basin. The postero-external wall of the crown of the last upper postcanine is bordered by a cingulum. Lower dentition with three very large, procumbent incisors. Lower canine orientated slightly posteriorly. In the lower postcanines, the anterolabial cusp is much larger than the anterolingual cusp; the posterior basined heel is relatively short; in crown view, the ridge which passes back from the apex of the lingual cusp to the heel describes a distinct curve, concave lingually.

CONCLUSIONS

Only one traversodont is known from the Late Triassic Elliot Formation of Lesotho and South Africa, namely *Scalenodontoides macrodontes.* Since the description of this taxon by Crompton & Ellenberger (1957), on the basis of a lower jaw only, additional material, mainly cranial, could be attributed to it. Its study confirms the conclusion drawn as early as 1984 by Hopson, that *Scalenodontoides* is the sister taxon of *Exaeretodon. Scalenodontoides* appears, however, far more different from *Exaeretodon* than could be initially expected. The unique nuchal table, described by Gow & Hancox (1993), the very unusual skull proportions (very broad skull, extremely short temporal region), and distinctive features of the dentition, leads me to consider it indeed as a valid genus. *Scalenodontoides* is also the only cynodont in which pronounced sexual dimorphism can be suggested.

From a biostratigraphic point of view, *Scalenodontoides macrodontes* is interesting, as it characterizes only a short interval in the lowermost part of the Elliot Formation. Finally, the new assignment of the skull from Leribe, Lesotho, has consequences on biogeographical interpretations: as this skull had originally been attributed to a large chiniquodontid, the presence of *Belesodon* sp. in the Upper Triassic of southern Africa was sometimes mentioned in the literature (see for example P. Ellenberger 1970). It appears now that there is no evidence of the existence of such a chiniquodontid in Africa.

I am grateful to Didier Geffard, Philippe Loubry and Charlène Letenneur for their very efficient technical assistance with the illustrations and the preparation of the manuscript. I thank J. Neveling for many helpful comments.

REFERENCES

ABDALA, F., BARBERENA, M.C. & DORNELLES, J. 2002. A new species of the traversodontid cynodont *Exaeretodon* from the Santa Maria Formation (Middle/Late Triassic) of southern Brazil. *Journal of Vertebrate Paleontology* **22**(2), 313–325.

BARBERENA, M.C. 1974. *Contribuição ao conhecimento dos cinodontes gonfodontes (Cynodontia-Tritylodontoidea) do Brasil.* Ministério de Educação e Cultura, Universidade Federal do Rio Grande do Sul. Tese Livre Docente.

BATTAIL, B. 1991. Les Cynodontes (Reptilia, Therapsida): une phylogénie. *Bulletin du Muséum national d'Histoire naturelle, 4ème série, C* **13**(1–2), 17–105.

BATTAIL, B. & SURKOV, M.V. 2000. Mammal-like reptiles from Russia. **In**: Benton, M.J., Shishkin, M.A., Unwin, D.M. & Kurochkin E.N. (eds), *The Age of Dinosaurs in Russia and Mongolia,* 86–119. Cambridge, Cambridge University Press.

BONAPARTE, J.F. 1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguellii,* Cabrera y su comparación con Diademodontidae, Tritylodontidae y los cinodontes sudamericanos. *Publicaciones del Museo Municipal de Ciencias Naturales i Tradicionales de Mar del Plata* **1**, 135–202.

BONAPARTE, J.F. 1963. La familia Traversodontidae (Therapsida-Cynodontia). *Acta Geológica Lilloana* **4**, 163–194.

BONAPARTE, J.F. 1978. El Mesozoico de América del Sur y sus Tetrápodos. *Opera lilloana* **26**, 1–596.

BRINK, A.S. 1963. Two cynodonts from the Ntawere Formation in the Luangwa valley of Northern Rhodesia. *Palaeontologia africana* **8**, 77–96.

CABRERA, A. 1943. El primer hallazgo de terápsidos en la Argentina. *Notas del Museo de la Plata* **8**, 317–331.

CHATTERJEE, S. 1982. A new cynodont reptile from the Triassic of India. *Journal of Paleontology* **56**, 203–214.

COSTEDOAT, D. 1962. *Etude de quelques Reptiles fossiles.* Unpublished

Diplôme d'Etudes Supérieures, Université de Paris.
CROMPTON, A.W. 1955. On some Triassic cynodonts from Tanganyika. *Proceedings of the Zoological Society of London* **125**, 617–669.
CROMPTON, A.W. 1972. Postcanine occlusion in cynodonts and tritylodontids. *Bulletin of the British Museum of Natural History, Geology, London* **21**, 27–71.
CROMPTON, A.W. & ELLENBERGER, F. 1957. On a new cynodont from the Molteno Beds and the origin of the tritylodontids. *Annals of the South African Museum* **44**(1), 1–13.
ELLENBERGER, F. 1955. Note préliminaire sur les pistes et les restes osseux de Vertébrés du Basutoland (Afrique du Sud). *Comptes Rendus de l'Académie des Sciences de Paris* **240**, 889–891.
ELLENBERGER, P. 1970. Les niveaux paléontologiques de première apparition des mammifères primordiaux en Afrique du Sud et leur ichnologie. Etablissement de zones stratigraphiques détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias supérieur à Jurassique). **In**: *Second Gondwana Symposium, South Africa, July to August 1970, Proceedings and Papers*, 343–370.
FLYNN, J.J., PARRISH, J.M., RAKOTOSAMIMANANA, B., RAKOTOSAMIMANANA, L., SIMPSON, W.F., & WYSS, A.R. 1999. New traversodontids (Synapsida: Eucynodontia) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* **20**(3), 422–427.
GODEFROIT, P. & BATTAIL, B. 1997. Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France). *Geodiversitas* **19**(3), 567–631.
GOW, C.E. & HANCOX P.J. 1993. First complete skull of the Late Triassic *Scalenodontoides* (Reptilia Cynodontia) from southern Africa. **In**: Lucas, S.G. & Morales M. (eds), *The Nonmarine Triassic. New Mexico Museum of Natural History & Science Bulletin* No. 3, 161–168.
HAHN, G., LEPAGE, J-C. & WOUTERS, G. 1988. Traversodontiden-Zähne (Cynodontia) aus der Ober-Trias von Gaume (Süd-Belgien). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* **58**, 171–186.
HOPSON, J.A. 1984. Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. *Palaeontologia africana* **25**, 181–201.
HOPSON, J.A. 1985. Morphology and relationships of *Gomphodontosuchus brasiliensis* von Huene (Synapsida, Cynodontia, Tritylodontoidea) from the Triassic of Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1985**, 285–299.
HUENE, F. von 1935–1942. *Die fossilen Reptilien des südamerikanischen Gondwanalandes.* München, C.H. Beck.
KEMP, T.S. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa. Journal of Zoology* **191**(2), 193–239.
KITCHING, J.W. & RAATH, M.A. 1984. Fossils from the Elliot and Clarens Formations (Karoo Sequence) of the northeastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. *Palaeontologia africana* **25**, 111–125.
ROMER, A.S. 1967. The Chañares (Argentina) Triassic reptile fauna. III. Two new gomphodonts, *Massetognathus pascuali* and *M. teruggii. Breviora* **264**, 1–25.
ROMER, A.S.1972. The Chañares (Argentina) Triassic reptile fauna. XVII. The Chañares gomphodonts. *Breviora* **396**, 1–9.
SUES, H-D., HOPSON, J.A. & SHUBIN, N.H. 1992. Affinities of ?*Scalenodontoides plemmyridon* Hopson, 1984 (Synapsida: Cynodontia) from the Upper Triassic of Nova Scotia. *Journal of Vertebrate Paleontology* **12**, 168–171.
SUES, H.D. & OLSEN, P.E. 1990. Triassic vertebrates of Gondwanan aspect from the Richmond Basin of Virginia. *Science* **249**, 1020–1023.
SUES, H.D., OLSEN, P.E. & CARTER, J.G. 1999. A Late Triassic traversodont cynodont from the Newark Supergroup of Northern Carolina. *Journal of Vertebrate Paleontology* **19**(2), 351–354.
TATARINOV, L.P. 1973. Cinodonty gondvanskogo oblika v srednem triase SSSR. *Paleontologicheskij Zhurnal* (2), 83–89.
TURNER, B.R. 1972. Revision of the stratigraphic position of cynodonts from the upper part of the Karroo (Gondwana) System in Lesotho. *Geological Magazine* **109**, 349–360.