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A giant brachyopoid temnospondyl from the Upper Triassic or Lower Jurassic of Lesotho

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Key words. – Stegocephalian, Triassic-Jurassic, Southern Africa, Gigantism.

Abstract. – A jaw fragment of a giant temnospondyl from the Upper Triassic or Lower Jurassic of Lesotho (southern Africa), initially regarded as a Triassic mastodonsaurid because of its size, is redescribed in detail and considered to be a member of the Brachyopoidea (Brachyopidae + Chigutisauridae *sensu* Warren and Marsicano [2000]) based on its dental morphology, presence of a well-developed ectopterygoid tusk, and the concavity of the ventral margin of the skull in lateral view. Recognition of the specimen as a brachyopid, rather than as a chigutisaurid, is of palaeobiogeographical significance in representing one of the youngest known brachyopids from Gondwana. The Lesotho specimen is also of palaeobiological interest in that an estimate of its overall size indicates that it represents one of the largest amphibians *sensu lato* ever known.

Un Temnospondyle brachyopoïde géant du Trias supérieur-Jurassique inférieur ? du Lésotho

Mots clés. – Stégocéphale, Trias-Jurassique, Afrique australe, Gigantisme

Résumé. – Un fragment de mâchoire d'un stégocéphale géant du Trias supérieur – Jurassique inférieur ? du Lésotho (Afrique australe), autrefois rapidement attribué à un capitosaure triasique à cause de sa taille, est ici redécrit en détail et considéré comme appartenant à un brachyopoïde d'après notamment la morphologie dentaire, la présence d'un croc ectoptérygoïdien bien développé, et la concavité du bord ventral du crâne en vue latérale. Cet unique temnospondyle du Lesotho correspond à un des amphibiens *sensu lato* les plus grands connus au monde. Outre les implications paléobiogéographiques que pose la présence d'un représentant du groupe des brachyopoïdes dans le Trias supérieur – Jurassique inférieur ? du Lésotho (peut-être le plus jeune brachyopide du Gondwana), ce spécimen soulève d'intéressantes questions paléobiologiques sur le gigantisme des amphibiens en tant que tétrapodes non-amniotiques.

INTRODUCTION

In 1970, B. Battail, P. Ellenberger and L. Ginsburg discovered a skull fragment of a "grand Stégocéphale" from the uppermost part of the lower "Red Beds" (i.e. uppermost Lower Elliot Formation) at Alwinskop, near Quthing, southwestern Lesotho. This fragment was later briefly described by Dutuit and Ginsburg [1982] as a mastodonsaurid, primarily on the basis of its giant size and presumed Triassic age. However, they considered the specimen to differ from other mastodonsaurids in the absence of a sensory sulcus, its curvature in lateral view, the position of the interpterygoid vacuity and choana relative to the maxilla, and the small size of the choana. Dutuit and Ginsburg [1982] concluded by referring the specimen to the "Mastodonsauridae, *genus*, *species novae*". Until recently, the Mastodonsauridae was usually restricted to *Mastodonsaurus* and *Heptasaurus* from the Triassic of Europe [Schoch, 1999], but has recently been redefined by Damiani [2001] to encompass all taxa previously included in the Capitosauridae. The Lesotho specimen therefore represented the only known member of the Mastodonsauridae *sensu stricto* outside of Europe, and remains the only known temnospondyl from Lesotho.

In this paper, we provide a detailed redescription of the Lesotho temnospondyl following additional preparation of the specimen. This permits a reassessment of its taxonomic affinities which, in turn, provides new paleobiogeographical and palaeobiological information.

STRATIGRAPHY

According to Dutuit and Ginsburg [1982], the specimen comes from the uppermost strata of the Lower "Red Beds", in the "A7" zone of Ellenberger [1970]. The Elliot Formation (formerly "Red Beds") of the "Stormberg Group" (Karoo Basin) of southern Africa [South African Committee for Stratigraphy, 1980] is a typical non-marine, fluvio-lacustrine redbed sequence that straddles the Triassic-Jurassic boundary. It is stratigraphically subdivided into two (lower and upper) [Knoll, 2004, 2005] or three (lower, middle and upper) units [Kitching and Raath, 1984 ; Smith and Kitching, 1997].

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The Lower Elliot Formation encompasses the biostratigraphically defined *Euskelosaurus* Range Zone of Kitching and Raath [1984], and has traditionally been assigned either a Carnian or Norian age (late Triassic) according to faunal and floral data [e.g. Ellenberger, 1970 ; Cooper, 1982 ; Kitching and Raath, 1984 ; Olsen and Galton, 1984 ; Gauffre, 1993 ; Anderson *et al.*, 1998]. Lucas and Hancox [2001] reviewed the vertebrate and ichnological evidence and settled on a Norian age (late Triassic) for the Lower Elliot Formation.

The Upper Elliot Formation *sensu* Knoll [2005] includes the Middle and the Upper Elliot Formation *sensu* Kitching and Raath [1984]. It encompasses the biostratigraphically defined *Massospondylus* Range Zone of Kitching and Raath [1984], and is regarded as early Jurassic in age. Knoll [2005] regarded the "A7" zone of Ellenberger [1970], the horizon from which the specimen was recovered, as belonging to the lowermost part of the Upper Elliot Formation, hence as early Jurassic in age. In the absence of a consensus view on the stratigraphic subdivision of the Elliot Formation, we refer to the Lesotho specimen as Upper Triassic/Lower Jurassic in age.

SYSTEMATIC PALEONTOLOGY

Order TEMNOSPONDYLI Zittel, 1887-1890
Infraorder STEREOSPONDYLI Zittel, 1887-1890 [*sensu* Yates and Warren, 2000]
Superfamily BRACHYOPOIDEA Lydekker, 1885 [*sensu* Warren and Marsicano, 2000]
Brachyopoidea indet.

figures 1-2

Material. – A temnospondyl skull fragment, reposited in the Muséum national d'Histoire naturelle, Paris, and numbered "Lesotho 1970" (hereafter abbreviated L1970).

Description. – The specimen is a large skull fragment (fig. 1) whose maximum dimensions are 22 cm in length, 10 cm in width, and 6 cm in height. It consists of strongly ossified, thick bones of the skull roof and palate, some marginal teeth, a large palatal tusk and its replacement alveolus, part of the margin of a palatal fenestra, and, possibly, the partial edge of an additional opening. Dutuit and Ginsburg [1982] interpreted L1970 as an anterior snout fragment of the right side of a skull which included premaxilla, maxilla, vomer, a vomerine tusk, the antero-lateral edge of the interpterygoid vacuity, and the antero-lateral edge of the choana (fig. 2A).

We believe Dutuit and Ginsburg's [1982] interpretation to be erroneous based largely on the positions of the supposed margins of the interpterygoid vacuity and choana. First, the palatal margin could not be that of the interpterygoid vacuity because of its close proximity to the marginal tooth row, leaving no room for the presumed palatine bone between them. It is more likely that the margin pertains to an anterior palatal fenestra, a choana, or a subtemporal fenestra, the outer margins of which are usually in closer proximity to the marginal dentition than are interpterygoid vacuities. However, the absence of teeth and, in particular, tusks around this margin argues against the hypotheses of a choana or an anterior palatal fenestra, because tusks and/or teeth are always found adjacent to these vacuities in temnospondyls. Hence, the margin probably represents part of the subtemporal fenestra. Second, the identification of a choanal margin by Dutuit and Ginsburg [1982] is tenuous, because the "margin" does not appear to be of finished bone and hence may not be a real edge, the "margin" is located more dorsally than ventrally, and the presumed choana is located too far medially. We suggest that this "margin" may be an eroded edge of a dorsal opening, most likely an orbit. We therefore reinterpret L1970 as a fragment of the right side of a skull just anterior to the subtemporal fenestra, and includes the antero-lateral margin of that fenestra, marginal teeth of the maxilla, part of the ectopterygoid including its tusk, and, possibly, part of the right orbital margin dorsally (fig. 2B).

In dorsal view (fig. 1A), the maxilla displays ornamentation composed of antero-posteriorly elongated, parallel ridges and grooves, as is present in many temnospondyls. There is no trace of either sutures or sensory canals on this surface, although the bone is not well preserved.

In ventral view (fig. 1B), the maxilla is approximately 40 mm wide and bears 13 large tooth loci of which six are occupied by teeth, all broken in their upper parts and showing pleurodont implantation. Their bases vary between 15-20 mm in diameter and are sub-circular in section, becoming more rounded toward their upper part. A slight decrease in tooth size posteriorly supports the hypothesis that the fragment belongs to the right side of a skull. In section, all teeth display a conspicuous pulp cavity and moderate infolding of the dentine. The adjacent ectopterygoid is thick and robust, although its surface is somewhat damaged. Anteriorly it bears a huge tusk adjacent to an equally large, deep replacement pit. The tusk is about 30 mm in diameter at its base and circular in section throughout, and, in contrast to most temnospondyls [Warren and Davey, 1992], shows pleurodont implantation via a distinct dorsal expansion or swelling of the ectopterygoid around the antero-lateral margin of the tusk. As with the marginal teeth, the tusk also bears a conspicuous pulp cavity but shows more complex infolding of the dentine. Neither a tooth row nor denticles appear to have been present on the ectopterygoid. Posteriorly, a small, slightly curved margin of the subtemporal fenestra is present.

In lateral view (fig. 1C), the fragment is distinctly concave, so that the skull may have sloped downwards in the region of the subtemporal fenestra. Contrary to Dutuit and Ginsburg [1982], there is no evidence that the teeth were recurved posteriorly as is shown in their lateral view.

Discussion. – The Lesotho fragment belongs to a very large temnospondyl from the Upper Triassic or Lower Jurassic of southern Africa. It clearly pertains to an adult individual based on the pattern of dermal ornamentation, the ossification of the bones and their thickness, and the degree of infolding of the teeth [Boy and Sues, 2000 ; Steyer, 2000, 2003].

In contrast to the hypothesis of Dutuit and Ginsburg [1982], the Lesotho temnospondyl is unlikely to pertain to the Mastodonsauridae [*sensu* Damiani, 2001] because in all adult members of that taxon the marginal teeth are densely packed and strongly antero-posteriorly compressed (both being especially marked in large specimens), the ectopterygoid tusk is absent, and a complete tooth row is present on all palatal bones [Warren and Davey, 1992 ; Damiani, 2001]. In addition, mastodonsaurid marginal teeth are more complexly infolded

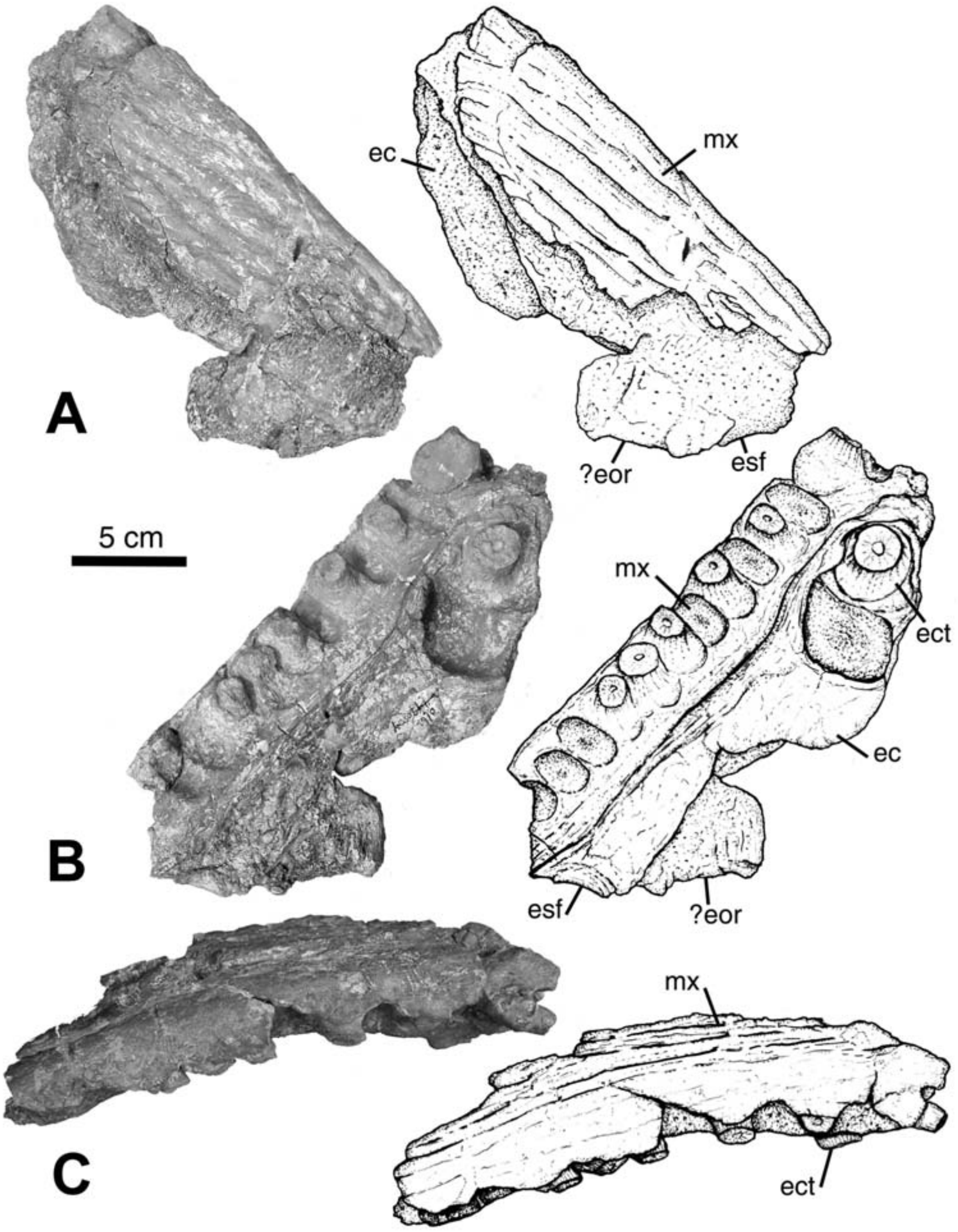

FIG. 1. – Brachyopoidea indet., MNHN L1970, skull fragment, Upper Triassic -? Lower Jurassic of Lesotho. Photographs (left) and interpretive drawings (right) in dorsal (A), ventral (B), and lateral (C) views. Anatomical abbreviations: ec, ectopterygoid; ect, ectopterygoid tusk; eor, edge of orbit; esf, edge of subtemporal fenestra; mx, maxilla.

FIG.1. – *Brachyopoidea indet., MNHN L1970, fragment de crâne, Trias supérieur - ? Jurassique inférieur du Lesotho. Photographies (gauche) et schémas interprétatifs (droite) en vues dorsale* (A), *ventrale* (B) *et latérale* (C). *Abréviations :* ec*, ectoptérygoïde* ; ect, *croc ectopterygoïdien* ; eor*, marge de l'orbite ;* esf*, marge de la fenêtre subtemporale ;* mx*, maxillaire.*

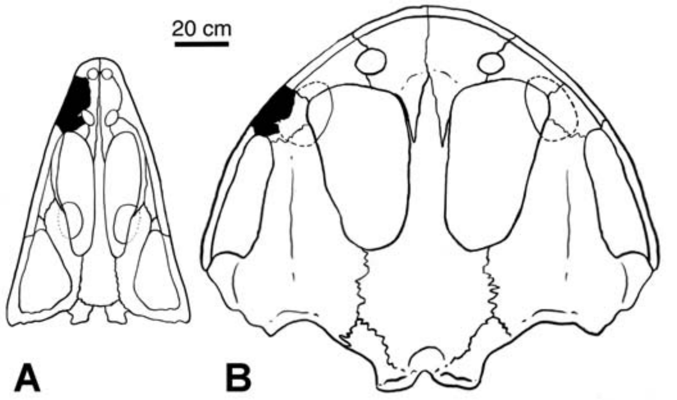

FIG. 2. – Outline diagrams showing the position and orientation of MNHN L1970 (in black) superimposed on (A), a mastodonsaurid skull as interpreted by Dutuit and Ginsburg [1982, modified], and (B), a brachyopoid skull as interpreted by the present authors. Both skulls are represented in palatal view.

FIG. 2. – *Crânes de temnospondyles montrant la position et l'orientation du fragment étudié (MNHN L1970, ici en noir) en le considérant comme* (A) *un mastodonsauridé d'après Dutuit et Ginsburg [1982, modifié], ou comme* (B) *un brachyopoïde d'après les présents auteurs. Les crânes sont représentés en vue palatale.*

and show a smaller pulp cavity in section [Warren and Davey, 1992] than in L1970. Similarly, metoposaurids lack the ectopterygoid tusk and a complete tooth row is present on all palatal bones [Warren and Davey, 1992]. In the Trematosauroidea and Plagiosauroidea, a reduced palatal tooth row, often consisting of unevenly-sized large teeth, is present, while plagiosauroids also lack palatal tusks [Warren and Davey, 1992]. Moreover, plagiosauroid teeth are simple in section with little infolding of the dentine [Warren and Davey, 1992], unlike in L1970.

Morphologically, the Lesotho temnospondyl most closely resembles the Brachyopoidea (*sensu* Warren and Marsicano [2000]: Chigutisauridae + Brachyopidae), especially in the morphology of the marginal teeth, the presence of an ectopterygoid tusk, and in the concavity of the skull fragment in lateral view which is similar to that in the region between the maxilla and the cheek in brachyopoids. Significantly, amongst Mesozoic temnospondyls, only brachyopids show a marked reduction or complete absence of palatal teeth, an autapomorphic character of that group [Warren and Marsicano, 2000], whereas chigutisaurids possess a tooth row on the palatal elements [Warren and Davey, 1992]. We conclude that the Lesotho temnospondyl pertains to a brachyopoid temnospondyl, and, most likely, to a brachyopid.

Two features of the Lesotho temnospondyl warrant additional remarks. First, scaling L1970 against skulls of more complete brachyopoids [Warren and Hutchinson, 1983; Warren and Marsicano, 2000] suggests a skull in excess of 100 cm in midline length (fig. 2B and see below). In contrast, the estimated midline length of the largest known brachyopoid, the chigutisaurid *Koolasuchus cleelandi* [Warren *et al.*, 1997], is 65 cm, and thus significantly smaller than the Lesotho temnospondyl. Second, the pleurodont implantation of the ectopterygoid tusk may be unique and thus autapomorphic for L1970, so that it may represent a new species. However, pending the discovery of more complete material we consider it prudent to designate the Lesotho temnospondyl as Brachyopoidea indet.

PALEOBIOGEOGRAPHY

The attribution of the Lesotho temnospondyl to the Brachyopoidea (Chigutisauridae + Brachyopidae) is also supported by palaeobiogeographic data. The Chigutisauridae appear to have been endemic to Gondwana, with representatives in the Lower Triassic of Australia [Warren, 1981], the Upper Triassic of Argentina [Marsicano, 1999] and India [Sengupta, 1995], the Upper Triassic (Lower Elliot Formation) and Lower Jurassic (Upper Elliot Formation) of South Africa [Warren and Damiani, 1999], and the Lower Jurassic and Lower Cretaceous of Australia [Warren and Hutchinson, 1983; Warren *et al.*, 1997]. The Brachyopidae, on the other hand, had a cosmopolitan distribution during the Triassic and were particularly diverse in Australia [Warren and Marsicano, 2000] and South Africa [Damiani and Rubidge, 2003], whereas all post-Triassic members of that group appear to have been Laurasian [Warren *et al.*, 1997]. Remarkably, only a single brachyopid has been reported from the Upper Triassic: mandibular and postcranial remains from Argentina [Marsicano *et al.*, 2000].

The brachyopid material from the Upper Triassic of Argentina indicates that the family was contemporaneous with chigutisaurids in the Upper Triassic of western Gondwana. Similarly, the Lesotho temnospondyl suggests that large brachyopids lived alongside large chigutisaurids in the Upper Triassic or Lower Jurassic of central Gondwana. Furthermore, if the Lesotho temnospondyl is indeed of early Jurassic age, it could represent the first post-Triassic brachyopid from Gondwana.

THE LARGEST KNOWN AMPHIBIAN ?

In this paper, the term “amphibian” is used in the traditional, broad sense to refer to all non-amniote tetrapods. The best preserved brachyopoid, and one of the largest known, is *Siderops kehli* from the Lower Jurassic of Australia [Warren and Hutchinson, 1983]. It was at least 2.7 m in total length, and its skull was about 70 cm broad. By comparative scaling, the near-complete skeleton of *Siderops* allows an assessment of the overall size of the Lesotho specimen. Scaling the Lesotho brachyopoid against *Siderops* suggests a skull width of about 1.7 m, and an estimated body length of about 7 m (fig. 3), a record amongst amphibians *sensu lato* !

The largest living amphibian ever recorded is a specimen of the Chinese giant salamander *Andrias davidianus* that reached 1.8 m in length [Chang, 1936]. Yet many

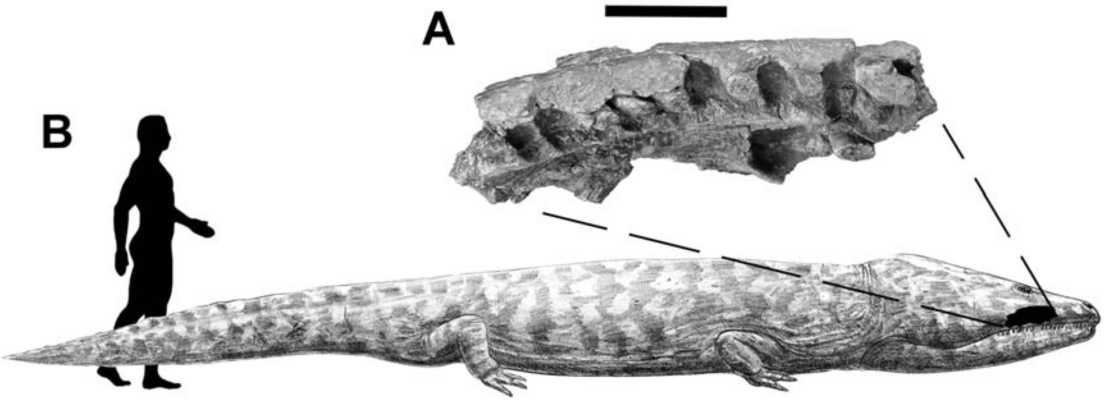

FIG.3. – Brachyopoidea indet., MNHN L1970, Upper Triassic -? Lower Jurassic of Lesotho, skull fragment in dorsolateral view (A), and hypothetical life reconstruction of the entire animal by A. Bénéteau (B). Scale bar = 5 cm.

FIG. 3. – *Brachyopoidea indet., MNHN L1970, Trias supérieur - ? Jurassique inférieur du Lesotho, fragment de crâne en vue dorsolatérale* (A), *et reconstitution hypothétique de l'animal entier par A. Bénéteau* (B). *Echelle = 5 cm.*

amphibians from the late Palaeozoic and early Mesozoic were of considerably larger size, such as the Triassic temnospondyl *Mastodonsaurus giganteus*, which grew to about 6 m in length [Schoch, 1999].

Our reassessment of the Lesotho brachyopoid, arguably the largest amphibian ever recorded, leads us to reflect on the biology of these giant tetrapods. Brachyopoids were secondarily aquatic, predatory temnospondyls, with distinctively parabolic skulls, powerful jaw muscles and huge teeth [Warren, 2000]. Later members of the group grew to a considerable size, as exemplified by the Lesotho form. Their growth was continuous throughout life, as in most ectothermic land vertebrates. Brachyopoids were among the dominant predators in fresh water environments, and their large size may have limited the competition with contemporaneous semi-aquatic carnivores such as metoposaurid temnospondyls, early crocodilians [Warren *et al.*, 1997], or phytosaurs. This probably contributed to their survival until the early Cretaceous, well beyond the extinction of all other known temnospondyls at the close of the Triassic.

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