Galesaurid cynodonts from the Early Triassic of South Africa: another example of conflicting distribution of characters in non-mammalian cynodonts

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A series of galesaurid non-mammalian cynodont specimens from the Early Triassic *Lystrosaurus* Assemblage Zone of the Beaufort Group (Karoo Basin) exhibit a mixture of characters present in different non-mammalian cynodont families. The postcanine crown morphology, lack of a completely closed osseous palate, and well-developed post-dentary bar, are distinctive galesaurid traits. However, all the specimens display an angulation between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal, a character previously reported as diagnostic for chiniquodontid cynodonts. In addition, three of the specimens exhibit a posteriorly well-projected postero-dorsal portion of the zygomatic process of the squamosal, delimiting a deep squamosal sulcus. This extended posterior projection of the squamosal, although showing different orientations, was previously recognized in cynognathid, gomphodont and tritylodontid cynodonts. This unusual combination of characters in members of the Galesauridae will most likely increase the level of homoplasy in the phylogeny of non-mammalian cynodonts.

The Karoo Basin of South Africa represents a major source of information about vertebrate life in Permian, Triassic and Early Jurassic times. The fossils from the Beaufort Group of this basin are especially significant for our understanding of terrestrial vertebrate palaeo-communities. Eight faunal associations, spanning a temporal range from the Late Permian to early Middle Triassic, have been recognized for the Beaufort Group.[1] These faunas present, as a common sign, a remarkable diversity and abundance of therapsids, with six groups recorded in the Late Permian, only three of which, dicynodonts, therocephalians and non-mammalian cynodonts (named cynodonts hereafter), survived the Permo-Triassic extinction event.[1]

The faunal associations of the Beaufort Group with their remarkable diversity of therapsids are crucial for understanding the acquisition of mammalian features during the Late Paleozoic and Early Mesozoic. Many characters typical of late mammals are evinced in different groups of cynodonts ranging from the Late Permian to the Middle Jurassic.[2] The Galesauridae is a cynodont family from the Late Permian/Early Triassic — *Dicynodon* and *Lystrosaurus* Assemblage Zones — of the Beaufort Group,[1] currently placed among the basal cynodonts essentially due to the lack of a complete osseous palate, a plesiomorphy shared with procynosuchid cynodonts.[3,4] At least three species can be recognized in the family, all of them displaying putative synapomorphies in the postcanine dentition.[3,4] The postcanines are flattened, mostly featuring a long, backwardly curved anterior cusp, and a short posterior accessory cusp.[5] Three specimens, two of them previously described as *Glochinodontoides gracilis* (National Museum, Bloemfontein, NMQR 1451; American Museum of Natural History, AMNH 2223)[6,7] and the third as *Platycraniellus elegans* (NMQR 860)[8] — all of which were later included into *Galesaurus planiceps*[9] — as well as the unpublished specimens BP/1/5064 (Bernard Price Institute, University of the Witwatersrand, Johannesburg) and NMQR 3340, are used here to draw attention to two features of galesaurids largely neglected in previous studies.

All the specimens come from the *Lystrosaurus* Assemblage Zone beds outcropping in the districts of Bethulie, Harrismith and Dewestdorp, Free State province. The Galesauridae identity for this material is indicated by the morphological pattern of the postcanine crown, lack of a complete osseous palate, and well-developed post-dentary bones (some of them showing a large and well-ossified reflected lamina of the angular). However, the five specimens show an angulation (approximately 130° or higher) between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal (Figs 1A; 2). This feature was previously recognized as diagnostic of chiniquodontids,[3,4,10,11] a late family of South American carnivorous cynodonts *sensu* Abdala and Giannini.[10] In addition, three of the galesaurid specimens (AMNH 2223, BP/1/5064 and NMQR 1451) show a posteriorly well-projected postero-dorsal portion of the zygomatic process of the squamosal, delimiting a deep squamosal sulcus (Figs 1B; 2). In the remaining two specimens this region is distorted and poorly preserved. A deep auditory groove (= squamosal sulcus) was already recognized in AMNH 2223.[7] The posterior projection of the squamosal, delimiting a deep squamosal sulcus, was previously known in cynognathid, gomphodont and tritylodontid cynodonts.[11] The orientation of the projection is, however, variable (that is, directed ventro-laterally in *Diademodon,* and posteriorly in the traversodontid *Massetognathus*). By contrast, the squamosal sulcus was considered as a moderately deep structure in the remaining sectorial-toothed cynodonts (except *Pachygenelus*), and basal galesaurids.[11]

Although the transition from 'mammal-like reptiles' to mammals is one of the best examples of macro-evolutionary change in the fossil record,[2,12] conflict exists as to the best explanation for the origin of mammalian features. Among therapsids, cynodont is the lineage that is believed (at least in all recent monophyletical hypotheses on mammal origins[2,3,11–15]) to include the sister taxon of Mammalia (= Mammaliaformes *sensu* Rowe[14]). Even when coincidental in this premise, sound controversy remains as to which precise group among cynodonts is the sister-group of Mammaliaformes.[4,11–20] A probable cause of these disagreements is the distribution of characters in cynodont taxa, that determine a high level of homoplasy in the phylogeny of the group.[3,17,20–22]

Other cases of conflicting distribution of characters in cynodonts were also recently documented in the South American Triassic: *Prozostrodon brasiliensis*[23,24] and *Ecteninion lunensis.*[20] The first species, recovered in outcrops of the Santa Maria Formation in southern Brazil, was originally proposed as *Thrinaxodon brasiliensis*[23] because of the similar postcanine crown pattern, particularly in the lower teeth, with *Thrinaxodon liorhinus.* On the contrary, other features of *Prozostrodon brasiliensis* are shared with late eucynodonts such as chiniquodontids, tritheledontids, tritylodontids and even morganucodontids (for example, long osseous palate, ilium plate with a reduced posterior process).[24,25] In *Ecteninion lunensis* from the Ischigualasto Formation in western Argentina, the conflictive nature of character distribution in cynodonts is also dramatically manifest: the cavum epiptericum floor in the basicranium is extensively developed, a feature shared with basal mammals[26,27] and with the traversodontid *Exaeretodon*;[28] the osseous palate is short

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Fig. 1. Specimen BP/1/5064. **A**, Right lateral view of the skull; the arrow indicates the angulation between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal; **B**, lateral view of the posterior portion of the left zygomatic arch with the arrow indicating the squamosal sulcus. Abbreviations: J, jugal; M, maxilla; Sq, squamosal; v, vertebra. Scale 2 cm.

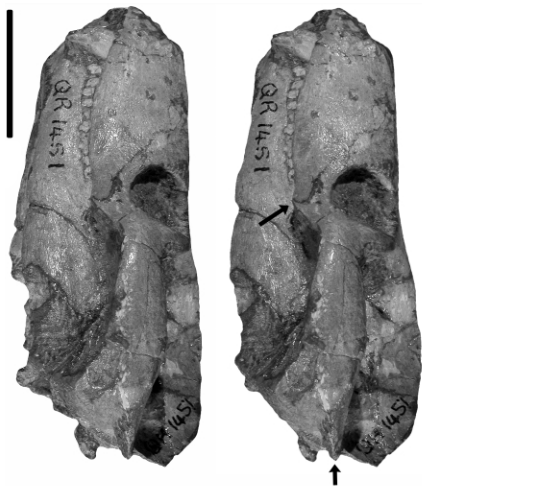

Fig. 2. Specimen NMQR 1451. Stereopair of left lateral view. Arrows indicate the angulation between maxilla and jugal, and the squamosal sulcus. Scale 3 cm.

as in *Thrinaxodon,* and the sectorial border of the postcanines closely resemble those of the tritheledontid *Pachygenelus.*[20]

The new morphological information on galesaurids provided here will certainly represent an increment in the already high level of homoplasy acknowledged in cynodont phylogeny. Thus, conflicting distribution of characters, frequently recognized in different branches of Eucynodontia, is also recorded in basal cynodonts of the Epicynodontia clade.[11] In addition, the Galesauridae (and cynodonts featuring an incomplete osseous palate) appear to be a more heterogeneous group than previously recognized.

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