A dinocephalian therapsid fauna on the Ecca–Beaufort contact in Eastern Cape Province, South Africa

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Systematic exploration of outcrops of the lowermost Beaufort Group for fossils of the oldest terrestrial vertebrates of South Africa, known only from the Permian age *Eodicynodon* Assemblage Zone in Western Cape Province, has resulted in the discovery of a therapsid fauna in Eastern Cape Province that is dominated by advanced dinocephalians. The new discoveries include the skull and partial skeleton of a juvenile *Anteosaurus*, skull and skeletal elements of tapinocephalids, as well as the skull of a scylacosaurid therocephalian. The combined presence of advanced tapinocephalid dinocephalians, the anteosaur *Anteosaurus*, and scylacosaurid therocephalians suggests that the rocks of the lowermost Beaufort Group in the Eastern Cape Province can be assigned to the *Tapinocephalus* Assemblage Zone, rather than to the *Eodicynodon* Assemblage Zone, which appears to be restricted to the southwestern part of the Karoo Basin. This biozone identity permits the recognition of a younger age for the Ecca–Beaufort contact eastwards along the southern margin of the basin, thus demonstrating the diachronous nature of the Ecca–Beaufort contact in the southern Karoo.

The oldest terrestrial vertebrates of southern Africa are known only from the lowermost sedimentary strata of the Beaufort Group, which outcrop across a relatively narrow expanse between Laingsburg and Reitbron in Western Cape Province, where they conformably overlie the subaqueously-deposited rocks of the Ecca Group. These continental rocks form the lowermost vertebrate biozone of the Beaufort Group, the *Eodicynodon* Assemblage Zone.[1] The tetrapod fauna of this biozone is dominated overwhelmingly by therapsids, particularly anomodonts, which are followed in much smaller numbers by dinocephalians. The least common members are therocephalian and gorgonopsian therapsids and temnospondyl amphibians, which are represented by very fragmentary materials. Field work conducted over the past decade in an attempt to delineate the lateral boundaries of the *Eodicynodon* Assemblage Zone has produced specimens of new anomodont taxa, which have prompted a reconsideration of the biozonation of the lowermost Beaufort Group.[2] More recent field work, involving prospecting of lowermost Beaufort Group outcrops in the Northern Cape, resulted in the collection of specimens indicative of the middle-to-upper horizons of the *Tapinocephalus* Assemblage Zone. These specimens provided the first evidence for earlier geological ideas that postulated a younger age for the Ecca–Beaufort contact along the northern margin of the Beaufort Group in the southern Karoo Basin.[3] That work appears to restrict the western extent of the *Eodicynodon* Assemblage Zone fauna to the Laingsburg area. The eastern boundary of this basal vertebrate biozone, however, remained to be established with confidence, especially in light of the discovery of specimens of a new, enigmatic large species of dicynodont that were collected from the Ecca–Beaufort contact on the farm Mandalay near Klipplaat in the Eastern Cape[4] (Fig. 1).

Prior to our field work in this part of the Eastern Cape, the only evidence for the presence of dinocephalians was a single fragmentary tooth (now lost) that was tentatively ascribed to an anteosaurid. This specimen was collected from a pebble lag along the Bulrivier in the Jansenville District.[5] It was on this rather dubious evidence that Beaufort Group strata of the Jansenville area were assigned to the *Tapinocephalus* Assemblage Zone by the South African Committee for Stratigraphy.[6] We report here on dinocephalian skeletal material from lower Beaufort Group outcrops on farms north of Grahamstown and near Jansenville in the Eastern Cape (Fig. 1). Preliminary descriptions of the new material are provided here, followed by a consideration of their implications for the biostratigraphy of the Beaufort Group in this region of the Karoo Basin.

Several massively pachyostosed skull roofs (Fig. 2) and isolated postcranial elements (BP/1/5694, BP/1/5701, BP/1/5710-BP/1/5711) from the farm Delportsrivier comprise the remains of indeterminate tapinocephalid dinocephalians based on the great thickness of the cranial bone (up to 7 cm) and the remarkable thickness of the postorbital bars. Most of these materials belong to adults, but ontogenetically young individuals were present, as evidenced by a relatively small, unfused basioccipital (BP/1/5699, in part: Fig. 3), which we attribute to the Tapinocephalidae because of the broad angle (approximately 115°) at which the basitubera meet the condylar portion of the bone.

Materials collected from the nearby farm Klein Wolwefontein include numerous skeletal fragments and heavily pachyostosed skull elements of additional tapinocephalids (BP/1/5693, BP/1/5696–BP/1/5698, BP/1/5700, BP/1/5702–BP/1/5705, BP/1/5707–BP/1/5709). The latter assemblage of fossils is fairly abundant and litter a sizeable area. This could represent a tapinocephalid bonebed, an interpretation that will require comprehensive attention in the future. The cranial fragments from these two localities are characterized by the extreme pachyostosis and relatively small temporal openings found only among tapinocephalids more advanced than *Tapinocaninus* of the *Eodicynodon* Assemblage Zone. Because all South African tapinocephalids apart from *Tapinocaninus* are known only from the *Tapinocephalus* Assemblage Zone, the Beaufort Group strata of the Jansenville area can be assigned to this biozone. The well-preserved skull of a scylacosaurid therocephalian (NMQR 3484 in the National Museum) was also discovered on the farm Klein Wolwefontein at roughly the same horizon as the tapinocephalids. No fossils of dicynodont therapsids were found on any of these farms.

An important discovery is a medium-sized therapsid from the farm The Grant 39, north of Grahamstown. This specimen (AM 4950 in the Albany Museum), comprising the greater part of a skull, is characterized by heeled incisors and by a postorbital bar that is slightly pachyostosed dorsally, a combination of features which strongly suggest that AM 4950 is an anteosaurid dinocephalian. Although the skull of AM 4950 (Fig. 4) is only about half the size of those of adult *Anteosaurus*, we regard the specimen as a provisional member of that genus because of the

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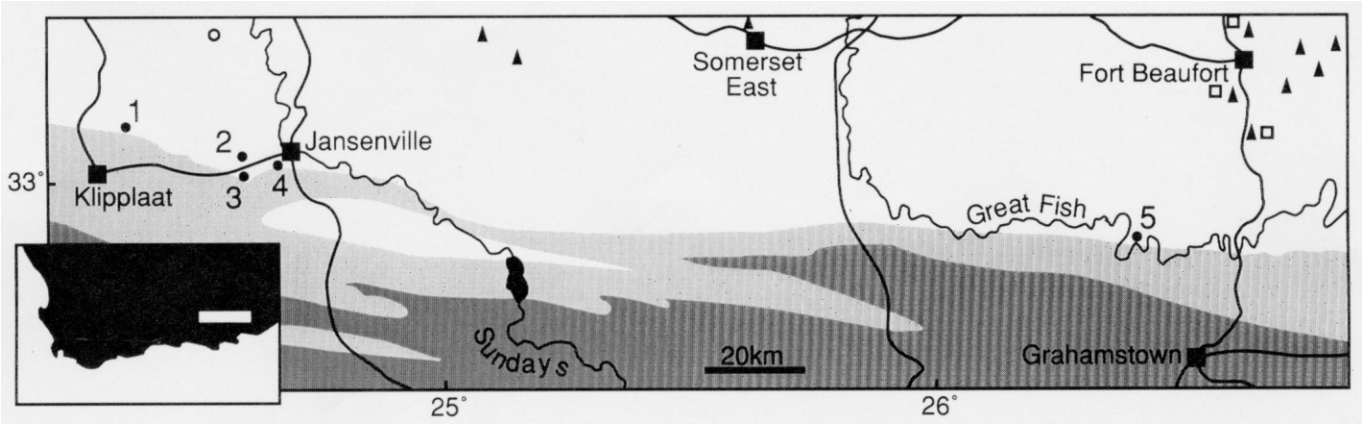

Fig. 1. Map of the study area showing position of fossil localities relative to the Ecca–Beaufort contact in Eastern Cape Province. Clear, Beaufort Group; light grey shading, Ecca Group; medium grey shading, Dwyka Group and Cape Supergroup; squares, towns and settlements; open squares, localities mapped by Kitching[13] as 'old *Endothiodon* zone' (now *Tropidostoma* Assemblage Zone[6]); triangles, *Cistecephalus* Assemblage Zone localities;[13] open circle, anteosaurid-tooth locality at Bulrivier.[5] Key to new fossil localities: 1, Mandalay; 2, Mörester; 3, Klein Wolwefontein; 4, Delportsrivier; 5, The Grant 39.

general build of the skull roof, which resembles that illustrated for *Anteosaurus magnificus*.[7] Consonant with the relatively small size of AM 4950, and our provisional assignment to *Anteosaurus*, juvenile status is indicated by the observation that the exposed neural arch is not fused to its associated centrum. Additional, albeit fragmentary large bones that are preserved in the same strata elsewhere on the farm probably represent indeterminate dinocephalians. As in the Jansenville district, no dicynodonts were recovered.

The presence of advanced tapinocephalid dinocephalians, together with *Anteosaurus* and scylacosaurid therocephalians, is indicative of *Tapinocephalus* Assemblage Zone horizons, and the location of such material this far east along the Ecca–Beaufort contact serves greatly to extend the known distribution of the *Tapinocephalus* Assemblage Zone fauna. The conspicuous absence of dicynodonts at these localities is puzzling, especially given their relatively high numbers in the *Eodicynodon* Assemblage Zone and most other strata of the Beaufort Group. Two partial skulls of a new species of large dicynodont were recovered from lowermost Beaufort strata in the Klipplaat district, west of Jansenville.[2,4] Those specimens confirm that dicynodonts are indeed present on the Ecca–Beaufort contact in the Eastern Cape, but the lack of association with known taxa is not helpful for biostratigraphy.[2]

Systematic field collection in the *Tapinocephalus* Assemblage Zone[8,9] suggests that the biozone (as it is currently regarded[10]) can be divided into two informal units: (1) a lower unit where dinocephalians are much more common than dicynodonts, and (2) an upper level where dicynodonts greatly outnumber dinocephalians. The lack of dicynodonts in our study areas suggests to us that the lowermost Beaufort sediments near Jansenville and those north of Grahamstown are provisionably referable to the lower dinocephalian-dominated strata of the *Tapinocephalus* Assemblage Zone.

As the rocks of the *Tapinocephalus* Assemblage Zone of the Beaufort Group conformably overlie those of the Ecca Group at the localities near Jansenville and north of Grahamstown, it is evident that the Ecca–Beaufort contact in this part of the basin is younger than in the Western Cape Province, where it is formed by the lower boundary of the *Eodicynodon* Assemblage Zone. These findings complement recent field work on the Ecca–Beaufort contact in Northern Cape Province, where the discovery of specimens of dinocephalians and *Eunotosaurus africanus* provided the first evidence for ideas[11,12] that posit a younger age for the Ecca–Beaufort contact northwards along the western margin of the basin.[3] Together with the report of *Eunotosaurus* in

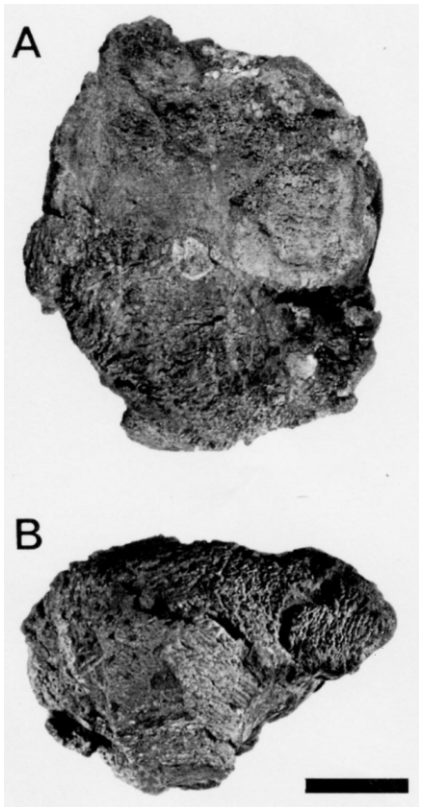

Fig. 2. Photographs of BP/1/5711, a partial tapinocephalid skull roof from Delportsrivier in (**A**) dorsal and (**B**) right lateral views. Anterior is to the right in both views. Scale bar equals 5 cm.

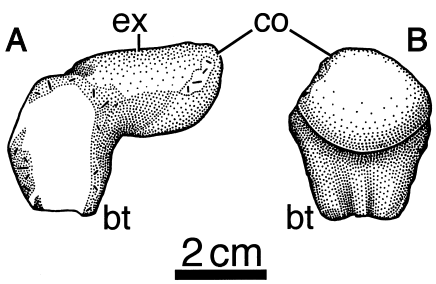

Fig. 3. BP/1/5699 (in part), isolated basioccipital of juvenile tapinocephalid from Delportsrivier in (**A**) left lateral and (**B**) occipital views. bt, basituber; co, condylar portion; ex, sutural surface for exoccipital.

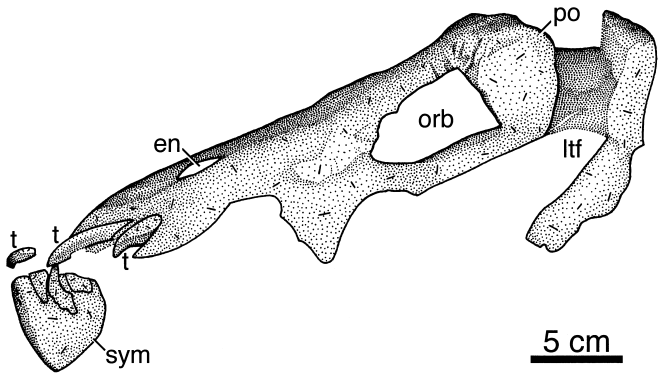

Fig. 4. Skull roof and lower jaw of AM 4950, partial juvenile skull of *Anteosaurus* from The Grant 39, as exposed in left lateral view. en, external naris; ltf, lateral temporal fenestra; orb, orbit; po, postorbital bar; sym, symphysial region of lower jaw; t, tooth. Three teeth implanted in the lower jaw are not labelled.

the Carnavon area, this paper highlights the use of tetrapod fossils in showing the diachronous nature of the Ecca–Beaufort contact in the Karoo Basin. This phenomenon was long suggested by geologists,[12] but could only now be verified with the incorporation of palaeontological evidence. It is now evident that the oldest rocks of the Beaufort Group, those of the *Eodicynodon* Assemblage Zone, are restricted to the southwestern part of the basin between Laingsburg and Reitbron. Continued palaeontological research on the Ecca–Beaufort contact in the Karoo Basin will enhance biostratigraphic resolution of the lower Beaufort and lead to more refined basin development models.

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