Research Letters / Navorsingsberigte

The first Middle Palaeozoic ostracode described from South Africa

The Devonian (Emsian–Givetian) Bokkeveld Group is well known for its characteristic Malvinokaffric cold-water marine invertebrate fauna.^{1,2} Classical fossil-collecting sites since the mid-nineteenth century, much frequented by large numbers of students and amateur collectors, occur in the road cuttings of the Gydo Pass, 15 km north of Ceres (Fig. 1). The steep slopes near the pass, which constitute the watershed between the Cold and the Warm Bokkeveld, also expose numerous fresh outcrops of the dark-grey shale, mudstone and siltstone beds of the Gydo Formation, the basal unit of the Bokkeveld Group.³

In view of the history of intensive palaeontological collecting at Gydo over the last 140 years, major new finds would be unexpected. Surprisingly, however, a brief stop at Gydo Pass during the Cape Supergroup Excursion of 1990⁴ yielded an ostracode valve (found by Dr I.G. Stanistreet), the first to be described from the Bokkeveld Group. Undescribed material is briefly listed by Oosthuizen⁵ in his preliminary report on the biostratigraphic distribution of the Bokkeveld fauna. His specimens were also from the Gydo Formation, mainly from the Prince Albert area, and superficially resemble the specimen described here.

All the sedimentological analyses to date^{3,6,7} indicate that the Bokkeveld Group largely represents deltaic sedimentation, involving the progradation of a series of lobate, wave-dominated deltas along a coastline of moderately high marine energy. The sediments deposited during the constructional phase of delta growth reflect shallow-shelf, pro-delta, delta-slope and



Fig. 1. Geological map with location of the fossil site at Gydo Pass.

delta-platform environments, and are overlain by nearshore deposits which developed during the destructive phase of the delta evolution, by marine reworking of the delta top. Palaeo-ecological analysis of the fossil taxa present at Gydo Pass indicates that the delta slope community is well represented, with the shelf community present in the lower parts of the sequence.⁸

Stratigraphically, the ostracode described here was found near the transition from the lower, more muddy half of the Gydo Formation to the upper, more sandy portion, about 54 m above the basal contact with the Table Mountain Group. It was found in association with the 'normal' Gydo marine fossil assemblage, including trilobites, brachiopods, bivalves and crinoids. This distinctive fauna is generally accepted as early Emsian to early Eifelian in age.⁹

The ostracode specimen consists of a typical 'bean-shaped' internal mould, or 'steinkern', of a giant (c. 3.5-mm-long) paleocopid ostracode, possibly belonging to the Superfamily Beyrichiacca.¹⁰ Remnants of a frill, or velum, are visible on the left side of the specimen as illustrated in Fig. 2 (identity of a left or right valve uncertain). The left lobe has been erased during preparation in the field. The lobe on the right side seems larger, but is much less prominent.

The unusually large size of the ostracode specimen as well as its overall shape and ornamentation suggest comparison with the Ludlovian to Emsian genus *Zygobeyrichia*, which may have occupied comparable ecological niches.¹¹

The Late Silurian (Pridolian) Zygobeyrichia–Halliella community of the central Appalachians in eastern North America seems indicative of a subtidal environment at or near wave base.¹² During the Early Devonian, Zygobeyrichia expanded into western and central Europe and North Africa. In Europe, the genus frequently occurs in sandy to silty shales and siltstones, together with brachiopods, bivalves, bryozoans and/or crinoids.¹³ This association is characteristic of a high-energy, shallow-marine environment above wave base ('Eifelian Ecotype').¹³ Le Fêvre¹⁴ has suggested that an Emsian ostracode assemblage including 'Zygobeyrichia?' in argillaceous silt-





Fig. 2. Internal mould of ostracode valve with remnants of frill (velum) on the left side, as well as outline drawing of specimen to scale (photograph by M. Kohler).

stones of the North African Sahara points to 'paralic' conditions (in the nearshore marine environment). A comparable shallow-marine 'restricted' environment, nearshore above wave base, may be tentatively implied for the new material from the Gydo Formation.

The Ludlovian through Emsian ostracode assemblages with Zygobeyrichia occupied a relatively small area between the palaeoequator and palaeolatitude 40°S, according to palaeo-geographic maps.¹⁵ Between these palaeolatitudes they only occurred along the southern and south-eastern shore of Laurasia and the northern shore of Gondwana.¹² South Africa was situated between palaeolatitudes 60° and 75°S during the Early–Middle Devonian.¹⁵ The unexpected presence of ostracodes comparable with Zygobeyrichia at such high southern palaeolatitudes could have a bearing on the interpretation of palaeocurrents during the Early–Middle Devonian.

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Relationships between stable carbon and nitrogen isotope ratios in bone collagen of African ungulates

 ${}^{13}C/{}^{12}C$ ratios in bone collagen of ungulate browsers from African savanna habitats are largely determined by the consumption of C₃ vegetation depleted in ${}^{13}C$; in contrast, the bone collagen of grazers feeding primarily on savanna grasses characterized by the C₄ photosynthetic pathway is less depleted in ${}^{13}C.{}^{1-11}$ ${}^{15}N/{}^{14}N$ ratios in terrestrial herbivores from African savannas are inversely related to rainfal. 12,13 This phenomenon apparently results primarily from increasing ${}^{15}N$ concentration in the tissues of animals stressed by drought. 14,15 In this study we report relationships between carbon and nitrogen isotope ratios of both grazers and browsers, and demonstrate a pattern which holds for ungulates from both southern and East Africa.

Carbon and nitrogen isotope ratios were obtained from the collagen fraction of bone after dissolution of the inorganic phase in 0.2 M HCl and removal of lipids. Carbon dioxide and N₂ were produced by closed-tube combustion and cryogenic separation.¹⁶ Isotope ratios from CO₂ and N₂ were measured on a VG 602E mass spectrometer. Carbon and nitrogen isotope ratios are reported as δ^{13} C and δ^{15} N values, expressed as parts per thousand (‰) relative to the PDB standard and air N₂, respectively. Error is < 0.2‰ for δ^{13} C and < 0.5‰ for δ^{15} N values.

The ungulate samples used in this study include browsers and grazers from modern and archaeological (Holocene) contexts. Steenbok (Raphicerus campestris), grysbok (R. melanotis), duiker (Sylvicapra grimmia), bushbuck (Tragelaphus scriptus), kudu (T. strepsiceros), eland (Taurotragus oryx), black rhino (Diceros bicornis), giraffe (Giraffa camelopardalis) as well as elephant (Loxodonta africana) are all primarily browsers. Ungulates which are primarily if not entirely grazers include zebra (Equus burchelli and E. zebra), hartebeest (Alcelaphus lichtensteini), blue wildebeest (Connochaetes taurinus), bontebok and blesbok (Damaliscus dorcas), gemsbok (Oryx gazelle) as well as buffalo (Syncerus caffer). Opportunistic ungulates include bushpig (Potamochoerus porcus) and impala (Aepyceros melampus), which browse and graze. Most of the samples are from southern Africa (n = 165), including data from a Holocene sequence in southern Africa,¹⁷ supplemented by $\delta^{13}C$ and $\delta^{15}N$ values obtained from previously published literature on ungulates from East Africa, notably $\delta^{13}C$ and $\delta^{15}N$ values for 47 individual specimens from that region of the continent,^{3,7} as well as mean $\delta^{13}C$ and $\delta^{15}N$ values for several taxa reported by Ambrose and de Niro.² A principal objective of this study is to demonstrate patterning for such herbivores considered as a whole, rather than for any particular species.

Regression analyses were undertaken on carbon and nitrogen isotope ratios for large samples of ungulates from southern Africa, using the UCT database. Regression analyses were not undertaken on the East African isotope data as they had either been summarized as means in the published literature,² or on account of the fact that some of the raw data from East Africa had been published in figures rather than in tables.³

The consumption of C₃ plants by browsers is reflected by δ^{13} C values ranging mainly between -25 and -16‰; by contrast grazers from African savanna habitats have carbon isotope values ranging mainly between -16 and -6‰. This distinction applies to browsers and grazers from both southern Africa^{4,8} and East Africa.^{2,3} For specimens with δ^{13} C values ranging between -25 and -16‰, δ^{15} N tends to increase as δ^{13} C becomes more positive, reflecting an enrichment in both δ^{15} N