

ENDEMIC SOUTH AMERICAN PERMIAN BIVALVE MOLLUSCS FROM THE ECCA OF SOUTH AFRICA

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ABSTRACT—The recent discovery of a bivalve faunule in the Ecça Group of South Africa is noteworthy for comprising taxa already known from South America. This is important for demonstrating that the diverse bivalve fauna of the Paraná Basin of Brazil, Uruguay, Paraguay and Argentina was not endemic, but was restricted to a large inland sea which also covered much of southern Africa. It thus allows for an extension of the environmental setting proposed for the Estrada Nova Formation to include part of the Ecça Group, as well as providing a firmer dating of the Paraná faunas.

INTRODUCTION

In its southern outcrop, the Ecça Group comprises a thick sequence of flyschoid rocks overlying the earliest Permian glaciogenic deposits of the Dwyka Formation. Consisting of mainly dark carbonaceous shales, sandstones, siltstones, and mudstones, locally yielding elements of the *Glossopteris* flora, the Ecça Group has variously been interpreted as lacustrine (Marchant, 1978), marine (Ryan, 1968; Hart, 1964), and as reflecting euxinic sedimentation under shallow conditions of alternating fresh and brackish water (Visser and Loock, 1978). It is clear, however, that the mere extent of the basin makes it unlikely that any one environmental model can be applied to the entire depositional area, or to the sequence as a whole. What is certain, is that following retreat of the Early Permian glaciers, southern Africa was the site of an enormous, shallow, inland sea into which Ecça sediments were deposited. Moreover, as noted by Du Toit (1927), sedimentation was not confined to the southern part of Africa but extended into the then conjoined Paraná Basin of Brazil and Argentina (Figure 1). Thus, the rich and diverse bivalve faunas from the Estrada Nova Formation (Runnegar and Newell, 1971) have an important bearing on the depositional environment of the Ecça Group.

PALEONTOLOGY

We have had the opportunity of studying some bivalves from delta front deposits of the Waterford Formation (Jordaan, 1981) at

Prince Albert in the southern Cape Province. The significance of this find is that it comprises taxa long known from the Estrada Nova Formation which we have identified as *Jacquesia elongata* (Holdhaus), *Naiadopsis lamellosus* Mendes, *Casterella* cf. *gratiosa* Mendes, and *Leinzia* cf. *froesi* Mendes (Fig-

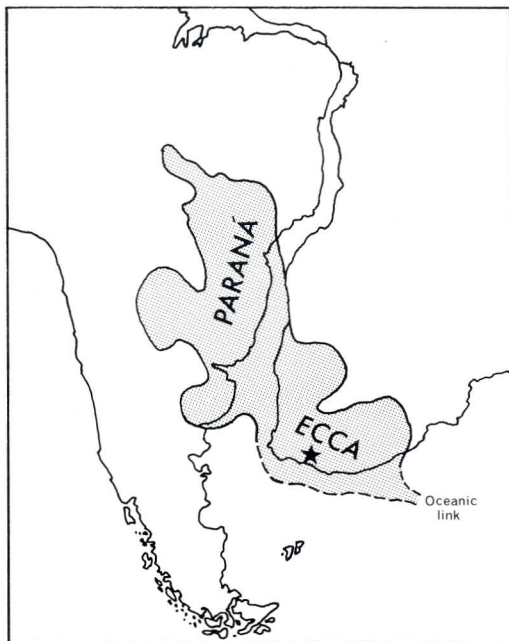


FIGURE 1—Mid-Permian paleogeographic reconstruction showing the extent of the shallow, brackish epicontinental sea that flooded Gondwana during this period. The star marks the Ecça bivalve locality discussed here.

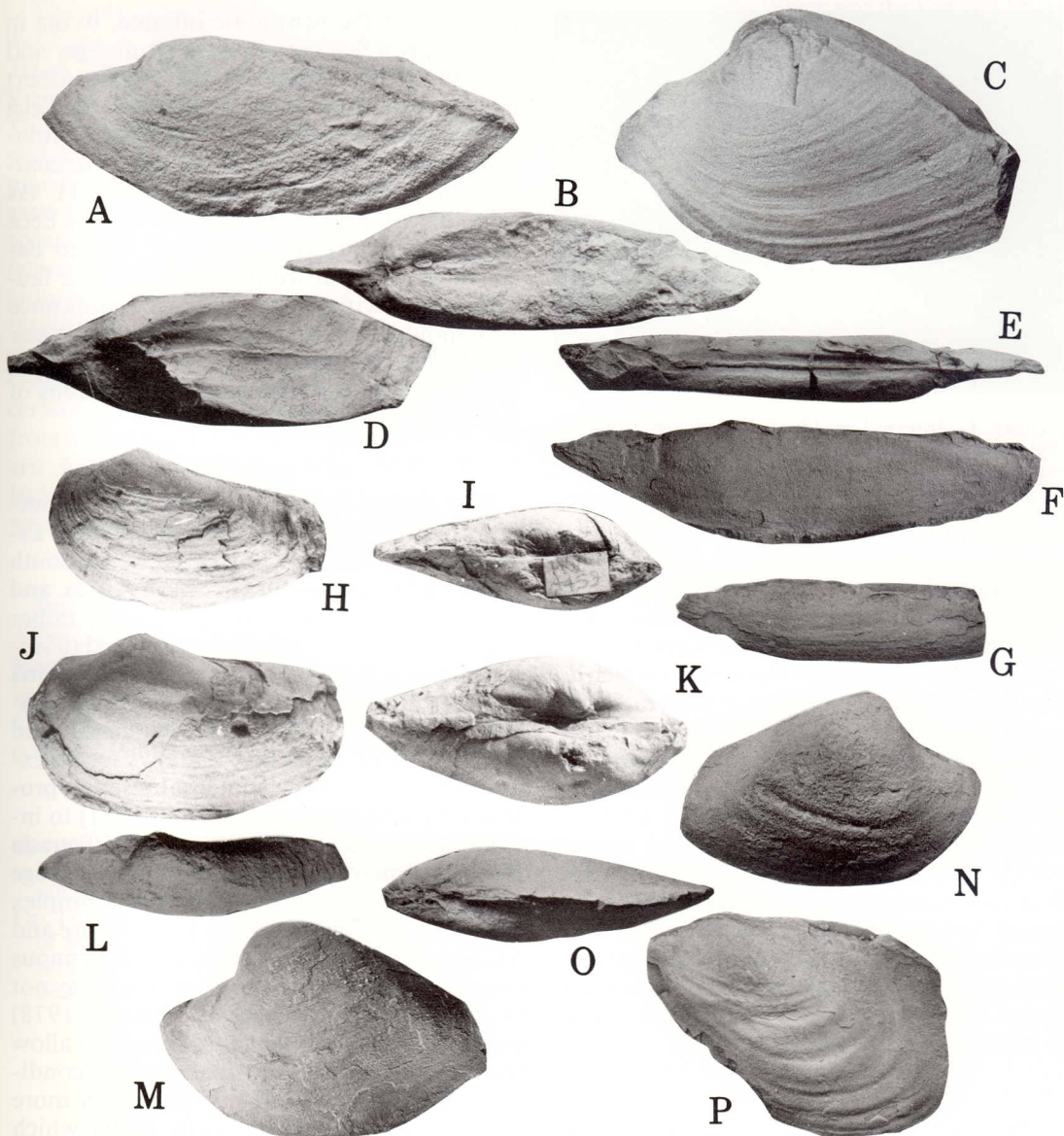


FIGURE 2—A–D, *Jacquesia elongata* (Holdhaus). E–G, *Leinzia* cf. *froesi* Mendes. H–K, '*Unio*' *alettaensis* Rilett. L–N, *Casterella* cf. *gratiosa* Mendes. O–P, *Naiadopsis lamellosus* Mendes. With the exception of H–K, which are housed in the Geological Survey, Pretoria, the remaining specimens are in the South African Museum, Cape Town. All $\times 0.8$.

ures 2, 3). We have also seen a fragment of a valve whose ornament compares favorably with that of *Pyramus cowperesoides* (Mendes). There can be little doubt as to the identification of *Jacquesia elongata*, while the *Casterella* differs from Mendes' species only in being slightly more produced anteriorly. The

Ecce *Naiadopsis*, like much of the remainder of the fauna, are preserved in internal molds and thus do not show the pronounced umbonal carina which is such a feature of the external shell of *N. lamellosus*. However, scattered tubercles on the internal mold (Figure 3) provide evidence for the muscle at-



FIGURE 3—Internal mold of *Naiadopsis lamellosus* Mendes showing muscle attachment pits in the umbonal region, $\times 0.6$.

tachment pits seen in *N. lamellosus*. We are confident of this identification and are thus able to verify that *Naiadopsis* is an equivalve genus. Lack of conspicuous ornament and straight dorsal margin allies the Ecça *Leinzia* most closely to *L. froesi* Mendes, of which *L. gigantea* Mendes may be a synonym (Runnegar and Newell, 1971). While the Prince Albert specimens, being internal molds, do not show the pronounced posterodorsal crest figured for the holotype (Mendes, 1949), a slight, rounded ridge is present. The overall outline and proportions agree well with the Brazilian material. Although *Leinzia* was assigned 'family uncertain' by Runnegar and Newell (1971), the Ecça material strongly resembles a very elongate *Jacquesia* (compare Figure 2A, B with 2 E, F) and hence might be referable to the Megadesmidae.

PALEOECOLOGY

The Ecça bivalves were collected by R. Oosthuizen, from dark grey limestone pods in the Waterford Formation. Although the material seems to comprise an admixture of the *L. froesi* and *Pinzonella neotropica* assemblages of Runnegar and Newell (1971) which are believed to be ecologically distinct, the Ecça shells were closely associated, *Naiadopsis* and *Leinzia* occurring together in the same hand specimen. What may be significant, however, is the occurrence of both isolated and conjoined valves, together with the fact that *Jacquesia*, *Leinzia*, and *Casterella* have more or less well developed permanent posterior gapes. They were, therefore, prob-

ably part of the benthonic infauna, living in water only a few meters deep (Runnegar and Newell, 1971). However, the Prince Albert locality was close to the depocenter for Ecça sedimentation, while the Waterford Formation displays trace fossils of the *Cruziana-Skolithos* ichnofacies (Jordaan, 1981). As such, there is a strong possibility that the Ecça faunule is a mixed assemblage, flushed basinwards by delta-front instability. The faunule is thus without bathymetric significance and should not be used to determine water depths for the depocenter. Nor should it be used to refute the ecological observations of Runnegar and Newell (1971).

BIOGEOGRAPHY

The significance of the Ecça find is fourfold: firstly, it indicates that the diverse Estrada Nova fauna is not endemic to South America but also occurs in South Africa, and hence forms part of a geographically rather widespread fauna. This fauna evolved in isolation and is thus endemic to the Ecça/Paraná Basin, while retaining affinities with the marine Permian of Australia (Runnegar and Newell, 1971). Secondly, it allows for an extension of the environmental model proposed by Runnegar and Newell (1971) to include the Ecça Basin. Thus, Ecça/Estrada Nova sedimentation occurred within a huge inland sea of brackish water with complex salinity gradients, as well as temperature and oxygen stratification. Thirdly, the tenuous oceanic connection of the Ecça trough lay not to the north-west (Visser and Loock, 1978) but to the east, and was insufficient to allow the development of normal marine conditions. Finally, the Ecça find permits a more precise dating of this unusual fauna which Runnegar and Newell (1971, p. 17) consider "... is not a typical marine fauna of the early Triassic, and for the present it seems more reasonable to conclude that the fauna is Permian rather than Triassic in age." The present material firmly establishes the Permian age of the Estrada Nova fauna since the Waterford Formation, at the top of the Ecça succession, is conformably overlain by fluvial deposits of the Beaufort Group, rich in late Kazanian tetrapods (Cooper, 1981). Consequently, a mid- to early late Kazanian age is indicated for the Ecça bivalve assemblage.

The only other bivalve to be described from the Ecça is '*Unio alettaensis* Rilett (Figure 2H-K) from the fluviodeltaic deposits of the Vryheid Formation in Natal (Rilett, 1952). This unit represents a postgradational clastic wedge into the Ecça basin and hence the non-marine origin of the bivalve is by no means assured. Indeed, it was allegedly closely associated with the ammonoid *Paraceltites? bowdeni* (Rilett) (Teichert and Rilett, 1974), although this association has recently been repudiated (McLachlan, 1977). Notwithstanding these problems, '*Unio alettaensis* bears a close morphological resemblance to certain species of *Myonia*, a genus also known from Brazil and the marine Permian of Western Australia. Unfortunately, dentition, or lack of it, in '*U. alettaensis* is unknown and we cannot be positive of this identification.

ACKNOWLEDGMENTS

We wish to thank R. Oosthuizen of Prince Albert, and A. Keyser (Geological Survey of South Africa) for allowing us to study material in their care, and N. D. Newell (American Museum of Natural History) for his comments on the draft of this paper.

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MANUSCRIPT RECEIVED MARCH 17, 1983

REVISED MANUSCRIPT RECEIVED DECEMBER 22, 1983