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The rhynchonellide brachiopod *Eocoelia* in the Llandovery of Paraguay, Paraná basin

Juan L. BENEDETTO¹

Abstract. On the basis of new material from the Llandoveryan Vargas Peña Formation the generic status of the species *Atrypina? paraguayensis* Harrington is revised. Both external morphology and internal features support the previous attribution to *Eocoelia* by Amos and Boucot and led to reject its posterior assignment to *Anabaia*. The coexistence of 'early' (e.g. coarse ornamentation) and 'advanced' (absence of dental plates) characters is suggestive of an early to intermediate stage in the phylogenetic lineage of *Eocoelia* and is consistent with a late Aeronian-early Telychian age for the Vargas Peña Formation.

Resumen. EL BRAQUIÓPODO *EOCOELIA* (RHYNCHONELLIDA) EN EL LLANDOVERYANO DE PARAGUAY, CUENCA DE PARANÁ. Se revisa el estatus genérico de la especie *Atrypina? paraguayensis* Harrington proveniente de la Formación Vargas Peña. Tanto la morfología externa como los caracteres internos de esta especie confirman la asignación previa a *Eocoelia* realizada por Amos y Boucot y permiten descartar su pertenencia al género *Anabaia* al cual fue referida con posterioridad. La combinación en *E. paraguayensis* (Harrington) de caracteres ancestrales (p.ej. ornamentación gruesa) con otros más evolucionados (ausencia de láminas dentales) sugiere un estadio temprano a intermedio en la filogenia de *Eocoelia*, infiriéndose una edad Aeroniana tardía-Telychiana temprana para las capas portadoras.

Key words. Brachiopods. Silurian. Paraguay. Paraná basin.

Palabras clave. Braquiópodos. Silúrico. Paragauay. Cuenca de Paraná.

Introduction

The occurrence of the rhynchonellide genus *Eocoelia* Nikiforova in the Silurian Afro-South American Realm (*sensu* Benedetto and Sánchez, 1996) has long been matter of controversy. Harrington (1950) first described the shelly fauna from the clays and micaceous sandstones cropping out in the Cerro Aparipí and the San Fernando Quarry, near Ypacaraí, east of Asunción. In that paper Harrington describes and illustrates some ventral and dorsal exteriors of a small ribbed brachiopod referred to the new species *Atrypina? paraguayensis*. Wolfart (1961), on the basis of few external and internal molds collected from Harrington's localities, classified this form as *Coelospira? cf. hemisphaerica* (J. de C. Sowerby). Subsequently Amos and Boucot (1963), in their revision of the Family Leptocoeliidae, reassigned this material to *Eocoelia paraguayensis*

(Harrington) and provided new illustrations showing some internal features. More recently, Gonçalves de Melo and Boucot (1990) considered that both, the Silurian 'Malvinokaffric' leptocoelids formerly referred to *Harringtonina* and Harrington's *paraguayensis* species belong to the genus *Anabaia* Clarke (1899). Then, the new combination *Anabaia paraguayensis* (Harrington) was erected to include the Paraguayan material, though no morphological details were added to the previous description by Amos and Boucot (1963).

The Llandovery brachiopod associations from the intracratonic basins of South America, such as the Paraná and the Amazonas basins, are by far less diverse than those from the Central Andean basin of northwestern Argentina, Bolivia and Peru (Benedetto *et al.*, 1992) and the Precordillera basin of western Argentina (Benedetto, 1995). Brazilian faunas are known to date only from the Trombetas Formation, which contains *Anabaia paraia* Clarke and *Heterorthella freitana* (Clarke). The composition of the Itacurubí Group fauna of eastern Paraguay is still poorly known. Gonçalves de Melo and Boucot (1990)

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reported *Clarkeia antisimensis* Kozłowski and *Heterorthisella freitana* (Clarke) and suggested that the strophomenid referred to *Australostrophia conradii* by Harrington (1950) is a parvicostellate leptostrophiid related to *Mesoleptostrophia*. The cardinalia of the material from the Eusebio Ayala Formation referred to *Clarkeia antisimensis* strongly differs from that of *Clarkeia* and consequently the taxonomic assignation of this rhynchonellide needs to be revised (Benedetto and Sánchez, 1996). Likewise, the Paraguayan *Heterorthisella* also shows morphological differences not only with the Brazilian species *H. freitana* but also with all other species described, and it seems likely that it belongs to a different genus. In this context, the main objective of this short paper is to clarify the taxonomic composition of the Paraguayan fauna, the first step being the revision of the *paraguayensis* generic assignment on the basis on new and relatively well preserved material from the Vargas Peña Shale.

Stratigraphy, age and correlations

Silurian rocks in Paraguay are represented by the Itacurubí Group that includes, in ascending order, the Eusebio Ayala, Vargas Peña and Kari'y (or Cariy) Formations. The first Paleozoic fossils mentioned by Beder and Windhausen (1918) and the majority of the macrofossils later recognized by several authors came from the whitish to grayish clay and subordinate sandstone named Vargas Peña Shale (Wolfart, 1961). This unit crops out discontinuously along the western border of the Ypacaraí graben (Degraff *et al.*, 1981) as well as in the Eusebio Ayala locality, c. 60 km to the east of Asunción (text-fig.1). Apart from brachiopods, the Vargas Peña Formation has yielded trilobites, gastropods, bivalves (Harrington, 1950;

Wolfart, 1961), conulariids (Babcock *et al.*, 1990), tentaculitids (Godoy Ciguel, 1988), graptolites (Turner, 1959; Harrington, 1972), chitinozoans (Wood *et al.*, 1989) and land spores (Gray *et al.*, 1992).

The specimens described in this paper were collected in the Vargas Peña Shale at its type locality in the San Fernando Quarry (also known as the 'Vargas Peña Clay Pit'), a few meters above the Eusebio Ayala reddish micaceous sandstones. Although this rhynchonellide has been reported from the underlying sandstones (Wolfart, 1961; Boucot *et al.*, 1991) it is absent from our samples.

On the basis of graptolites identified by Turner and Bulman (personal communication cited in Harrington, 1950) as *Climacograptus innotatus brazilensis* Ruedemann and *Diplograptus modestus* Lapworth, Harrington (1950) assigned the Vargas Peña Shale to the early Llandovery ('Valentian'), modifying the Early Devonian age postulated by Beder and Windhausen (1918). This age assignment was widely accepted until the 90's when Rickards (in Gonçalves de Melo and Boucot, 1990) suggested that the Vargas Peña graptolites are Aeronian (middle Llandovery, *convolutus* Zone) rather than Rhuddanian in age. The organic-walled microfossils (spores, phytoplankton and chitinozoans) recovered from the same climacograptid-bearing levels of the Vargas Peña Shale indicate a slightly younger, late Aeronian to middle Telychian age (Gray *et al.*, 1992), though according to Grahn *et al.* (2000) and Grahn and Gutiérrez (2001) the lower part of the Vargas Peña Shale extends into the Rhuddanian. The finding of the graptolite *Monograptus gregarius* in the Pitinga Shale of the Trombetas Formation in the Amazonas basin also suggests an Aeronian age for this classical unit bearing climacograptids of the *innotatus* group (Jaeger, 1976; Gray *et al.*, 1992).



Figure 1. Schematic geologic map of the Lago Ypacaraí region showing the Itacurubí Group outcrops (stippled pattern) and the location of the collecting site (asterisk). / Mapa geológico esquemático de la región del lago Ypacaraí mostrando los afloramientos del Grupo Itacurubí (en puntillado) y la localización del sitio fosilífero (asterisco).

Brachiopod taxa have proved inconclusive for stage-level age determination. *Heterorthella*, for example, is recorded from the latest Ashgill (?) (Disa member of the Cedarberg Formation, South Africa; Cocks and Fortey, 1986) to the Pridoli (Tarabuco Sandstone of Bolivia; Benedetto, 1991) but, as can be judged by the associated graptolites in the Paraná and Amazonas basins, the species *H. freitana* seems to be restricted to the mid-Llandovery. However, no biostratigraphic considerations can be made on the Paraguayan *Heterorthella* until its specific status has been established. The genus *Eocoelia* has a greater biostratigraphic significance because of its well-defined morphological trends through the early-mid Silurian of the North Atlantic Province (Ziegler, 1966; Doyle *et al.*, 1991). These changes involve mainly the rib strength and the articulatory mechanisms. As stated below, the nearly complete reduction of dental plates displayed by *E. paraguayensis* is a distinctive feature of several species younger than *E. hemisphaerica*, but the rib strength is more comparable to that of *hemisphaerica-intermedia* species group. The particular combination of features of the Paraguayan species suggests an early (but not earliest) to intermediate stage within the *Eocoelia* phylogeny, so that a late Aeronian-early Telychian age can be assumed for the Vargas Peña Shale. This age assignment is slightly younger than that suggested by the monograptids and is more consistent with the evidence from the organic-walled microfossils studied by Gray *et al.* (1992).

Systematic paleontology

Specimens described and illustrated in this paper are housed in the paleontological collection of the Cátedra de Estratigrafía y Geología Histórica, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina (prefix CEGH-UNC).

Order RHYNCHONELLIDA Kuhn, 1949

Superfamily RHYNCHOTREMATOIDEA Schuchert, 1913

Family LEPTOCOELIIDAE Boucot and Gill, 1956

Genus *Eocoelia* Nikiforova (in Nikiforova and Andreeva, 1961)

Type species. *Atrypa hemisphaerica* J. de C. Sowerby, in Murchison 1839, p. 637, pl. 20, fig. 7.

Eocoelia paraguayensis (Harrington, 1950)

Figures 2.A-2.P

1950 *Atrypina?* *paraguayensis* Harrington, p. 62-64, pl. 1, figs. 9, 10, 13-16.

1961 *Coelospira?* *hemisphaerica* J. de C. Sowerby; Wolfart, p. 65-66, pl. 2, figs. 8-11.

1963 *Eocoelia paraguayensis* (Harrington, 1950). Amos and Boucot, p. 448, pl. 64, figs. 12-15; pl. 65, figs. 1, 2.

non 1982 *Harringtonina paraguayensis* (Harrington, 1950); Laubacher, Boucot and Gray, p. 1157-1161, pl. 3, figs. 1-30.

1990 *Anabaia paraguayensis* (Harrington, 1950). Gonçalves de Melo and Boucot, p. 365-366.

Material. Twelve ventral valves and five dorsal valves preserved as internal and external molds, CEGH-UNC 17369-17376.

Description. Medium-sized (averaging 8.8 mm wide and 1.9 mm deep), planoconvex to weakly concavoconvex, wider than long shells (average width/length ratio: 1.17); maximum width at valve midlength; cardinal extremities obtuse, rounded; anterior margin evenly rounded. Ventral valve weakly carinate, about one-quarter as deep as long. Dorsal valve flat to gently concave. Ornament of twelve to sixteen rounded, simple ribs, narrower and weaker in the postero-lateral corners; mesial rib in the ventral valve and corresponding dorsal intercostal space somewhat wider than the rest; concentric growth lamellae conspicuous anteriorly. Delthyrial cavity deep with a short pedicle callist. Teeth large, robust, oval in outline, without evidence of crural fossettes. Dental plates absent or poorly developed, attached to shell wall by callus. Hinge plates thick, raised almost perpendicularly on a low notothyrial platform, diverging anteriorly at about 55°. Median ridge broad and low becoming indistinct on the anterior half.

Remarks. Two aspects must be considered in the present taxonomic analysis: the generic assignment of the Paraguayan material and the validity of Harrington's *paraguayensis* species. Concerning the generic status, the general shape, convexity, costation as well as the dorsal internal morphology showing discrete hinge plates and absence of cardinal process are all distinctive features of the genus *Eocoelia* to which it was assigned by Amos and Boucot in 1963. The re-assignment of this form to the genus *Anabaia* by Gonçalves de Melo and Boucot (1990) is not supported by morphological evidence from previous descriptions and from the specimens studied herein. According to Gonçalves de Melo and Boucot (1990, p. 365) "*Anabaia* differs from *Eocoelia* in the convex nature of its brachial valve, whereas that of the latter is flat." However, in his original description of *Atrypina?* *paraguayensis* Harrington (1950, p. 62) stated that the dorsal valve is very gently convex. Likewise, Wolfart (1961, pl. 2, figs. 10, 11) illustrated two slightly concave dorsal valves and Amos and Boucot (1963, p. 448), in redescribing *Eocoelia paraguayensis*, stated that its dorsal valve "is flat to slightly convex". The stronger convexity of the dorsal valve of *Anabaia*, however, is not the only differential character with *Eocoelia*, the following can be added:

(1) The ornamentation in *Anabaia* consists of 3 or 4 strong ribs or plications on either flank while in

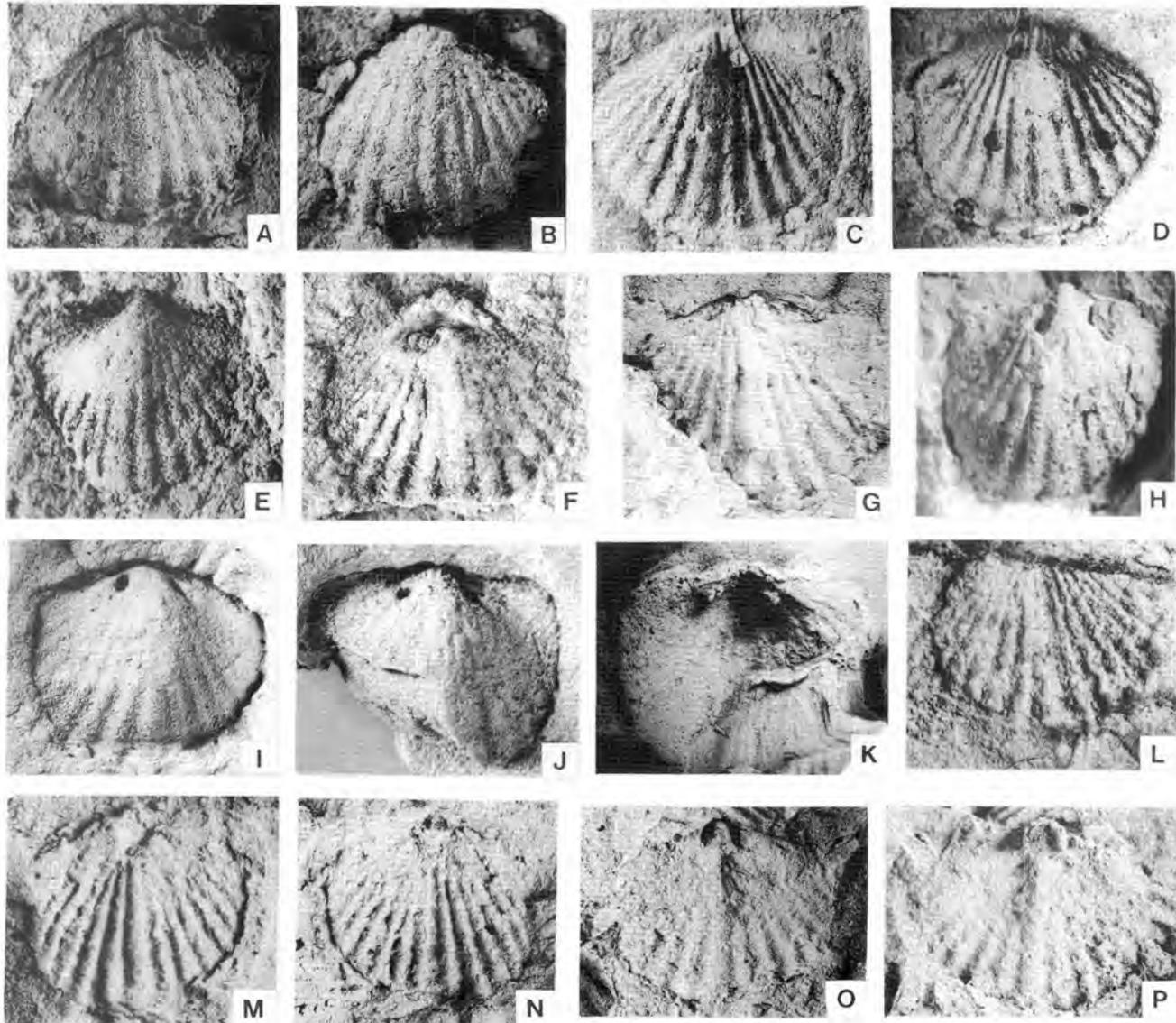


Figure 2. A-P, *Eocoelia paraguayensis* (Harrington, 1950). A, latex cast of ventral external mold, CEGH-UNC 17376a, x 4/ réplica de caucho del exterior de una valva ventral; B, latex cast of ventral external mold, CEGH-UNC 17376b, x 4/ réplica de caucho del exterior de una valva ventral; C, D, ventral external mold and latex cast, CEGH-UNC 17370, x 3.5/ molde externo de una valva ventral y réplica de caucho; E, exterior of ventral valve, CEGH-UNC 17375, x 4/ exterior de una valva ventral; F, exterior of ventral valve, CEGH-UNC 17375b, x 4/ exterior de una valva ventral; G, exterior of ventral valve, CEGH-UNC 17376d, x 4/ exterior de una valva ventral; H, ventral internal mold, CEGH-UNC 17371, x 4/ molde interno de valva ventral; I, ventral internal mold corresponding to the external mold of figures C and D, CEGH-UNC 17369, x 4/ molde interno de valva ventral correspondiente al molde de las figuras C y D; J, K ventral internal mold and latex cast, CEGH-UNC 17374, x 4/ molde interno y réplica de caucho de una valva ventral; L, latex cast of ventral valve exterior, CEGH-UNC 17373, x 7/ réplica de caucho del exterior de una valva ventral; M, N, dorsal external mold and latex cast, CEGH-UNC 17375b, x 4/ molde externo y réplica de caucho de una valva dorsal; O, P, dorsal internal mold and latex cast, CEGH-UNC 17376c, x 4/ molde interno y réplica de caucho de una valva dorsal.

Eocoelia the modal rib number is greater than twelve, usually 14 to 18.

(2) *Anabaia* bears a characteristic dorsal fold and a corresponding ventral sulcus resulting in an unipli-cate commisure; this feature is only weakly developed in certain populations of *E. hemisphaerica*.

(3) The ventral muscle scars in *Anabaia* are heart-shaped and more deeply impressed than in *Eocoelia*.

(4) *Anabaia* possesses well-developed, blade-like dental plates and umbonal chambers which are present only in the earliest species of *Eocoelia*.

In summary, morphological evidence does not support the assignment of the Vargas Peña specimens to the genus *Anabaia* and validates the previous assignment to *Eocoelia* by Amos and Boucot (1963).

The species *Atrypina? paraguayensis* was not formally diagnosed by Harrington (1950) but he stated that the Paraguayan specimens differ from *Coelospira hemisphaerica* (J. de C. Sowerby), the type species of *Eocoelia*, by its less circular shell outline. Ziegler (1966, p. 535) pointed out that "The *Atrypina* (?) *paraguayensis* of Harrington ... cannot at present be

distinguished from *E. hemisphaerica*", and seemingly Wolfart (1961) referred the material from Paraguay to this species. Amos and Boucot (1963), however, considered that *paraguayensis* is a valid species. Certainly, *E. paraguayensis* more closely resembles *E. hemisphaerica* in shell outline and ornamentation pattern but slightly differs in having a somewhat coarser mesial rib. This difference alone is not sufficiently important to differentiate the Paraguayan specimens. In fact, some degree of enlargement of both, the ventral mesial rib and the corresponding dorsal mesial furrow, may occur in populations of different *Eocoelia* species (i.e. *E. curtisi* from Venezuela, Boucot *et al.*, 1972, pl. 28, fig. 20-21). Internally, however, *E. paraguayensis* differs from *E. hemisphaerica* in the almost complete absence of dental plates, the broader dorsal median ridge and the less divergent hinge plates (c. 90° in *E. hemisphaerica* and c. 45° in *E. paraguayensis*). It resembles *E. intermedia* (Hall) in the reduction of umbonal cavities and the obliteration of dental plates, but differs in having somewhat stronger ribs which show a less marked tendency to fade out in the posterolateral areas. In this respect *E. paraguayensis* can readily be distinguished from the later members of the *Eocoelia* lineage, such as *E. curtisi* Ziegler and especially *E. sulcata* (Prouty) and *E. angelini* (Lindström) in which the radial ornamentation is vestigial and confined to the umbonal region (Ziegler, 1966; Basset and Cocks, 1974; Cocks and Worsley, 1993). The subspecies *E. curtisi immatura* Doyle *et al.*, 1991 represents a transitional stage between the strongly-ribbed earliest forms and the weakly ornamented younger species. Although the Scottish subspecies is rather similar to *E. paraguayensis* in the rib pattern, it differs in having deep crural fossettes cutting the medial face of teeth.

Finally it is important to note that the combination of 'early' (relatively strong ribbing) and 'advanced' (absence of dental plates) characters in *E. paraguayensis* suggests that the evolutionary trend of *Eocoelia* was not clearly linear, at least considering species from outside of the North Atlantic Region. But in general, the coexistence of internal features such as the robust teeth lacking crural fossettes and the incipient dental plates with a well-developed external ornamentation suggests that the Paraguayan species attained the 'intermedia' or early 'curtisi' evolutionary stage.

Acknowledgments

I wish to thank Enrique Villas and Fernando Alvarez who acted as reviewers and provided valuable comments and suggestions to improve this work.

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Recibida: 2 de julio de 2001.

Aceptada: 21 de marzo de 2002.