

## PHYLOGENETIC RELATIONSHIPS OF THE SILURIAN AFRO-SOUTH AMERICAN BRACHIOPODS *ANABAIA*, *HARRINGTONINA* AND *CLARKEIA*: NEW INSIGHTS FROM THEIR ONTOGENY

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*Abstract.* Hundreds of specimens of the rhynchonellide brachiopod *Clarkeia antisiensis* (d'Orbigny) recovered from the stratotype of the Tarabuco Formation of Bolivia form a complete series of growth stages providing a good opportunity for reconstructing its ontogenetic development. The fact that juvenile specimens of *C. antisiensis* are nearly indistinguishable from adult individuals of *Harringtonina australis* Boucot strongly suggests that *Clarkeia* evolved from *Harringtonina* by the heterochronic process of peramorphosis. On the other hand, adult specimens of both the Brazilian *Anabaia paraia* Clarke and the Precordilleran specimens of *Anabaia* never exceed the youngest ontogenetic stage of *Harringtonina australis*, to which share small hinge plates supported by a septalium-like structure and absence of cardinal process. The overlap of adult morphology of *Anabaia* with the juvenile morphology of *Harringtonina australis* allows interpreting this succession as an evolutionary lineage showing increasingly more peramorphic characters. This hypothesis is supported by the correlation between the stratigraphic record of taxa and the inferred developmental sequence being *Anabaia* the oldest member (Early Silurian), *Harringtonina australis* the intermediate form (Wenlock-Ludlow), and *Clarkeia antisiensis* the youngest (Pridoli). This interpretation raises a systematic problem because the leptocoeliids *Anabaia* and *Harringtonina* are currently classified within the superfamily Uncinuloidea whereas *Clarkeia* is placed among the Rhynchotrematoidea. If the hypothesis is proven, these superfamilies, as presently constituted, would be polyphyletic groups.

## INTRODUCTION

Silurian marine rocks are widespread in South America both in the Amazonas, Parnaíba, and Paraná Phanerozoic intracratonic basins and in the large Central Andean Basin peripheral to the Amazonas shield. With the exception of the Northern Andean segment of Colombia and Venezuela, most of the Silurian successions are characterized by a suite of brachiopods of which one of the most distinctive is the rhynchonellide *Clarkeia* Kozłowski, 1923, described originally from Bolivian material. Cocks (1972), in addressing the biogeography, eco-

logy, and phylogeny of this genus, popularized the name 'Clarkeia fauna' to designate this peculiar Silurian paleobiogeographic entity recorded in Argentina, Bolivia, Brazil, and South Africa. The extension of the 'Clarkeia fauna' into North Africa (Guinea, Senegal) was confirmed subsequently by Racheboeuf and Villeneuve (1992). In order to avoid confusion with the quite different brachiopod assemblages of the Devonian Malvinokaffric Realm, Benedetto & Sánchez (1996) proposed the name 'Afro-South American Realm' to replace the widely used but more ambiguous terms 'Silurian Malvinokaffric Realm' and 'Silurian *Clarkeia* fauna'.

Besides *Clarkeia*, the Afro-South American Realm is characterized by two other genera of the

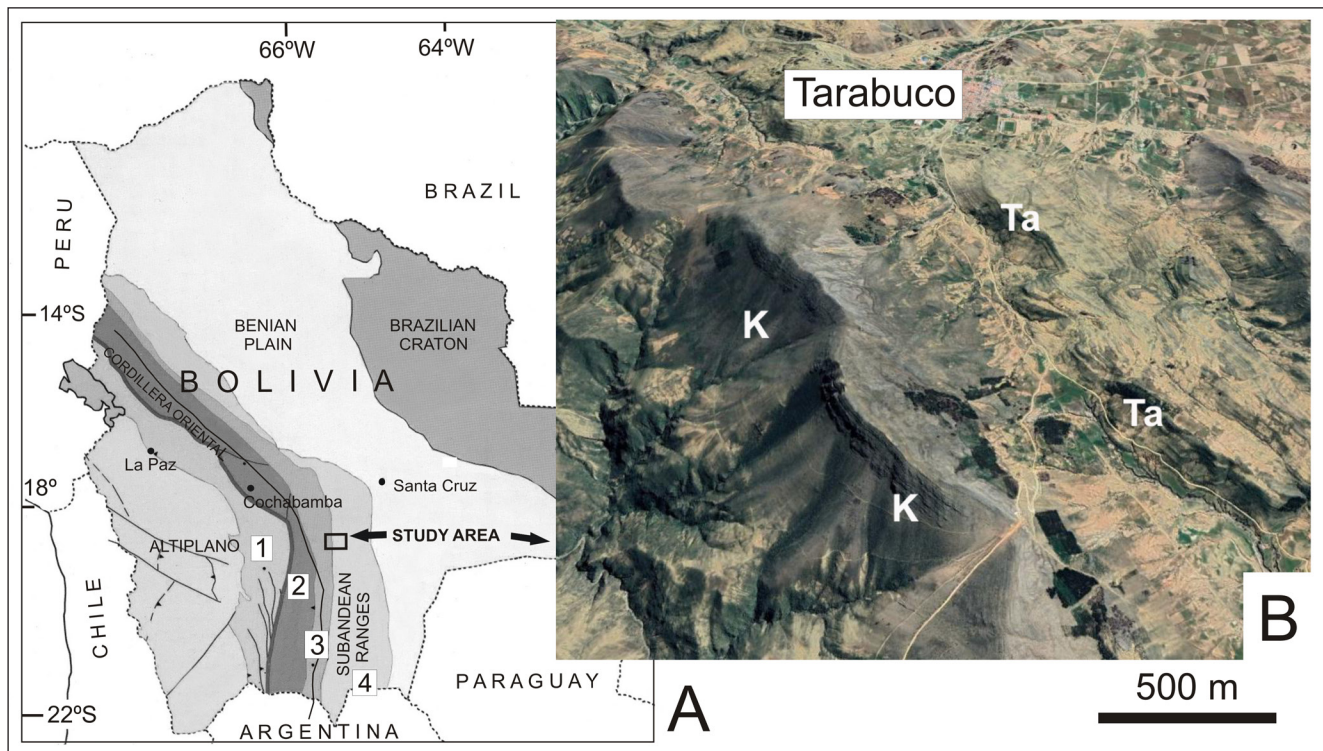


Fig. 1 - A) Geological provinces of Bolivia (simplified from Suárez Soruco, 2000) showing location of the study area. 1: Huarina fold belt; 2: Eastern Cordillera (Cordillera Oriental); 3: Interandean belt; 4: Southern Subandean Ranges. B) oblique satellite image of the Tarabuco village showing the Silurian stratigraphic succession (K: Kirusillas Formation, Ta: Tarabuco Formation).

Order Rhynchonellida: *Anabaia* Clarke, 1899, and *Harringtonina* Boucot (in Berry & Boucot 1972). *Clarkeia* is currently classified in the family Eatoniiidae whereas *Anabaia* and *Harringtonina* are included in the family Leptocoeliidae. However, as shown below, an increasing amount of evidence indicates that the three genera are more closely related than previously thought, and consequently their classification should be revised. Their splitting in different families and superfamilies may be due to the fact that the strong ontogenetic changes were not taken into account in the generic diagnoses. Kozłowski (1923: 88), in his description of *Clarkeia antisiensis* had already noticed that “La région cardinale de la valve dorsale présente des aspects très différents suivant l’âge de la coquille” and described some of the differences between the cardinalia of small and large specimens. As the author stated (Benedetto 1988) such modifications affect even some morphologically ‘stable’ features (e.g. cardinal process, hinge plates) which are considered as having generic and familial diagnostic value (Savage et al. 2002). Interestingly, knowledge of ontogenetic development not only provides additional criteria for taxonomic placement at suprageneric level but

also for unraveling evolutionary lineages. The main purpose of this study, therefore, is to briefly describe the ontogeny of *Clarkeia antisiensis* (d’Orbigny, 1847) on the basis of extensive collections from the Silurian Tarabuco and Catavi formations of Bolivia and to compare it with the ontogeny of the Precordilleran *Harringtonina australis* Boucot, 1972, in order to re-assess the phylogenetic relationships between both genera. In this context, published information on the Silurian faunas of Argentina, Peru, Paraguay and Brazil (Laubacher et al. 1982; Gonçalves de Melo & Boucot 1990; Benedetto et al. 2013) is critically evaluated. This constitutes a first step towards the reconstruction of the rhynchonellide radiation that took place in the Afro-South American Realm after the end-Ordovician extinction.

## OVERVIEW

When Boucot (in Berry & Boucot 1972) erected the genus *Harringtonina* (type species *Leptocoelia acutiplicata* Kayser, 1897, non Conrad) it was classified, together with other leptocoeliids such as *Eocoelia*, *Anabaia*, *Leptocoelia*, *Australocoelia*, and *Pa-*

*cifcocoelia*, among the spiriferides of the suborder Atrypidina, following the criteria exposed by Boucot et al. (1965). However, Gonçalves de Melo & Boucot (1990: 354) cast doubts on the spiriferid affiliation of these genera as no specimens are known to have any trace of spiralia, concluding that "...there is a real possibility that the Leptocoeliidae belong to the Rhynchonellida rather than to the Spiriferida". Nearly simultaneously, Jin (1989) removed provisionally the leptocoeliids from the spiriferids to the rhynchonellids based on the presence of preseptifer crura in the related genus *Platytrichalos* from the late Llandovery of Anticosti Island. In the *Treatise* the leptocoeliids were classified within the superfamily Rhynchotrematoidea of the order Rhynchonellida (Savage et al. 2002), but most recently they were placed within the new superfamily Lepotocoeloidea by Cocks (2019) on the basis of the presence of sessile hinge plates, which occur in no other rhynchonellides. It is interesting to note that Boucot (1975: 306) and Boucot & Rhemer (1977: 1125) considered the Silurian *Harringtonina* as the ancestor of the Devonian genera *Australocoelia* and *Pacificocoelia*. The discovery in the Pridolian of the Argentinean Precordillera of *Australocoelia intermedia* (in Benedetto et al. 1992), which in some traits exhibits transitional characteristics between *Harringtonina australis* and *Australocoelia tourteloti* Boucot and Gill, 1956, supports such a phylogeny (Benedetto et al. 1992).

The relationships and taxonomic identification of the Afro-South American Realm leptocoeliids have long been controversial. An outstanding issue is as to whether *Harringtonina* Boucot is synonym of *Anabaia* Clarke, 1899 (Gonçalves de Melo & Boucot 1990) or, on the contrary, both are valid genera (Benedetto 1988, 1995, see discussion below). Also there have been numerous uncertainties regarding the generic status of *Atrypina? paraguayensis* Harrington from the Silurian of Paraguay. This species was rightly referred to *Eocoelia* Nikiforova by Amos & Boucot (1963) but subsequently it was re-assigned to *Harringtonina* by Boucot (in Laubacher et al. 1982), and then to *Anabaia* by Gonçalves de Melo & Boucot (1990). Finally, the revision of well preserved material from the Vargas Peña Formation of Paraguay led to vindicate the previous assignment of this taxon to *Eocoelia* by Amos & Boucot (1963) (Benedetto 2002). On the other hand, there is a number of Silurian rhynchonellide species from Brazil, Central Andean Basin (Bolivia, NW Argen-

tina, Perú), Precordillera, and western Africa that need taxonomic revision such as (a) *Anabaia?* sp. from the Precordilleran La Chilca Formation (Benedetto 1995), (b) *Harringtonina?* sp. from the base of the Tambolar Formation (Benedetto & Franciosi 1998), (c) *Harringtonina* n. sp. from the Lipeón Formation (upper Llandovery-Wenlock, Zapla Range, NW Argentina, Benedetto 1991); (d) a probable *Harringtonina* (illustrated but not described), from the lowermost Kirusillas Formation, Cordillera del Tunari, Bolivia (Benedetto & Suárez Soruco 1998, fig. 7), and (e) cf. *Anabaia* sp. from the lower Ludlow of Guinea (Racheboeuf & Villeneuve 1992).

To further complicate the taxonomic and phylogenetic panorama, Laubacher et al. (1982: 1165), in studying the Llandovery material from the upper Calapuja Formation of southern Peru, classified *Clarkeia* among the Leptocoeliidae and stated that 'we are left with the possibility that *Anabaia* is morphologically closer to *Clarkeia* than to *Harringtonina* and *Eocoelia*', and concluded that '*Anabaia paraia* may represent either a form generically synonymous with *Clarkeia* or alternatively a distinct genus closely related to *Clarkeia*'. According to these authors, the main similarity between both genera lies in the ventral muscle field. Based on the morphological transition between the two taxa and the fact that both coexist in the same beds, Benedetto (1988) suggested that *Anabaia* (or *Harringtonina*) *paraguayensis* was based on juvenile specimens of *Clarkeia durrelli*. The analysis of the ontogeny of *Clarkeia antisiensis* here supports this statement.

Another interesting issue is the relationship between the Late Ordovician genus *Plectothyrella* and the Silurian *Clarkeia*. Cocks (1972: 628) was the first to propose that *Plectothyrella* is more closely related to *Clarkeia* than to any other genus, giving several morphologic arguments supporting that *Clarkeia antisiensis* probably descended from the South African species *Plectothyrella haughtoni* Cocks & Brunton (in Cocks et al. 1970). The fact that the rhynchonellid from the Eusebio Ayala Formation of Paraguay (Hirnantian/ lowermost Silurian?) referred originally by Boucot et al. (1991) to *Clarkeia antisiensis* was subsequently re-assigned to *Plectothyrella? itacurubiensis* Benedetto & Halpern (in Benedetto et al. 2013), reaffirms the similarity between both taxa. Clearly, the Paraguayan species does not belong to *Clarkeia* but either accommodates well in the *Plectothyrella* diagnosis. Instead, it seems to be closer to

	PRECORDILLERA (W ARGENTINA)	SUBANDEAN RANGES (NW ARGENTINA)	ALTIPLANO/ EASTERN CORDILLERA (BOLIVIA)	EASTERN CORDILLERA/SUBANDEAN RANGES (BOLIVIA)
PRIDOLI	Los Espejos/ Tambolar Formations	Lipeon Formation	Catavi Formation	Tarabuco Formation
LUDLOW			Uncia Formation	Kirusillas Formation
WENLOCK				
LLANDOVERY	La Chilca Formation			
HIRNANTIAN	Don Braulio Fm.	Zapla Fm.	Cancañiri Formation	

Fig. 2 - Stratigraphic correlation chart of the latest Ordovician and Silurian formations of Western Argentina (Precordillera basin) and NW Argentina and Bolivia (Central Andean Basin) mentioned in the text.

the Mauritanian *Aratanea monodi* Schmidt leading to include *Aratanea* as a probable basal form of the complex phylogenetic tree of the Afro-South American rhynchonellides.

#### STRATIGRAPHIC PROVENANCE OF THE STUDIED MATERIAL

The Precordillera folded belt contains a complete succession of lower and middle Paleozoic marine rocks. Silurian strata are best exposed in the central region, between the San Juan and Jáchal Rivers, where they form a nearly continuous, up to 600 m thick succession referred by Cuerda (1965) to the La Chilca and Los Espejos Formations (Fig. 2). The La Chilca Formation consists of dark-grey shales and greenish siltstones followed by fine-grained amalgamated quartz sandstones often with hummocky cross-stratification recording deposition in an inner platform evolving to a storm-dominated shoreface setting (Astini & Piovano 1992). Shelly faunas are concentrated in several levels within the lower and middle part of the sandstone interval. The age of the base of the La Chilca Formation is diachronous, ranging from the Hirnantian (Late Ordovician) (Cuerda et al. 1988) to the Rhuddanian (Benedetto & Cocks 2009), the upper third reaching the Wenlock (Sheinwoodian-Homerian) (García Muro & Rubinstein 2015).

The Los Espejos Formation rests conformably on the La Chilca Formation by means of a sharp contact, which has been interpreted as a major marine flooding surface (Astini & Maretto 1996). The unit reaches a maximum thickness of about 500 m

in the northern part of the basin (Jáchal area) decreasing southward to less than 100 m in the San Juan River area, where the Silurian strata have been referred to the Tambolar and Los Bretes formations (Peralta 2013). The lower part of the Los Espejos Formation is dominated by olive-green laminated mudstones and bioturbated siltstones bearing a varied suite of trace fossils indicating deposition in an outer-shelf setting below storm wave base (Sánchez et al. 1991; Astini & Piovano 1992). This facies grades to siltstones and bioturbated mudstones alternating with sandstones displaying hummocky cross-stratification, interpreted as deposited in a storm-dominated inner shelf and shoreface. Shell beds are dominated by brachiopods, often associated with trilobites, gastropods, nautiloids, bivalvians, echinoderms, corals, and graptolites. *Harringtonina australis* is a ubiquitous species both in the storm beds and in the underlying open-platform green siltstones where it constitutes the 'low diversity *Harringtonina* Community' (Sánchez et al. 1991, fig. 4). Two sandstone packages bearing large-scale diffuse cross-stratification occur near the middle and the upper third of the succession, probably representing shallow-shelf sandbar complexes. The lower sandstone interval contains shell beds dominated by *Australina jachalensis* Clarke, 1913, whereas the upper interval bears *Clarkeia bodenbenderi* (Kayser, 1897). In a few localities (Cerro del Fuerte, Cerro La Chilca) the Los Espejos Formation culminates with a ca. 12-m thick unit of reddish bioturbated mudstones starting with a basal ferruginous bed containing richly fossiliferous calcareous nodules which have yielded Lochkovian brachiopods (Benedetto et al. 1992) and corals (Carrera et al. 2013).

The Los Espejos Formation has been referred essentially to the Ludlow Series on the basis of its palynomorph and graptolite content (Rickards et al. 1996; Rubinstein & Brussa 1999; García Muro et al. 2015, and references therein). Conodonts recovered from the upper half of the formation belonging to the *Kockelella variabilis variabilis* Zone also support an early Ludlow (Gorstian) age (Albanesi et al. 2006). Based on the brachiopod association Benedetto et al. (1992) referred the top of the Los Espejos Formation at Cerro del Fuerte to the Pridolian. This is consistent with the late Ludfordian-early Pridolian age based on conodonts from the southern part of the basin (named the Tambolar Formation) (Mestre 2009), and the miospores recovered from the upper part of the Los Espejos Formation (García-Muro et al. 2014). Subsequently, terrestrial palynomorphs of Pridolian age were identified near the top of this formation at the Talacasto and Cerro del Fuerte sections (García Muro & Rubinstein 2015).

In the Andean-Subandean ('Interandean') belt (Suárez Soruco 2000) (Fig. 1) the Silurian succession encompasses the Kirusillas and Tarabuco formations (Fig. 2). The basal Cancañiri diamictite has long been considered of Llandoveryan age (Díaz Martínez & Graham 2007, and references therein), but evidence from correlatable glacial deposits of NW Argentina (Zapla Formation) suggests a latest Ordovician (Hirnantian) rather than Silurian age for the main glacial event (Benedetto et al. 2015). The Kirusillas Formation of the Eastern Cordillera is made up by a monotonous succession of dark-gray shales interbedded with sandstones towards the top (Fig. 1). On the basis of brachiopods, graptolites and palynomorphs this unit is mostly Ludlow in age (Limachi et al. 1996). It is conformably overlain by the Tarabuco Formation, which consists of gray to greenish fine-grained cross-stratified fossiliferous sandstones interbedded with micaceous shales. The more common brachiopods are *Clarkeia antisiensis* and *Heterorthella freitana* Clarke, 1899, but they disappear approximately 40 m below the top of the formation. According to the chitinozoan recovered from the *Clarkeia*-bearing beds in the stratotype near Tarabuco, its age is essentially Pridolian, whereas the uppermost shales (the Chululuyoj Member) bearing *Amosina tarabucensis* Racheboeuf, 1992, and chitinozoans reach the Lochkovian (Racheboeuf et al. 1993). The Silurian succession of the Huarina Fold Belt (Altiplano and Eastern Cordillera) en-

compasses the Uncia and Catavi formations (Fig. 2). The former consists of laminated shales and subordinated sandstones which could be an equivalent of the Kirusillas Formation, whereas the upper Catavi sandstones contain brachiopod assemblages including *Clarkeia antisiensis* closely comparable to those from the Tarabuco Formation.

Studied specimens of *Harringtonina australis*, some of which were illustrated and discussed in a previous paper (Benedetto 1988), come from the uppermost levels of the Los Espejos Formation (ca. 10 m below the contact with the Talacasto Formation) at Quebrada Ancha (Talacasto), and from the upper 30 m of the Los Espejos Formation at the Cerro del Fuerte section. The material of *Clarkeia antisiensis* comes from the Tarabuco Formation about 1.5 km NW of the Tarabuco village (Fig. 1). A substantial part of this collection was sampled during the field trip of the 2<sup>nd</sup>. Meeting of the IGCP 193 'Silurian and Devonian of South America' held at Sucre in 1983. A collection of *C. antisiensis* from the the Catavi Formation was sampled by P. Racheboeuf at km 69.3 of the road Cochabamba-Confital. All illustrated specimens are deposited in the paleontological collection of Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Consejo Nacional de Investigaciones Científicas y Técnicas and Universidad Nacional de Córdoba (institutional abbreviation CEGH-UNC). A juvenile dorsal valve is deposited in the Museo de Paleontología, Universidad Nacional de Córdoba (institutional abbreviation CORD-PZ). Illustrated material of *Anabaia paraia* is housed in the paleontological collection of the Museu Nacional do Rio de Janeiro (institutional abbreviation MN).

## CLARKEIA IN SPACE AND TIME

Sánchez and Benedetto (1993) addressed the stratigraphic and biogeographic distribution of *Clarkeia*, perhaps the more ubiquitous core taxon of the Afro-South American Realm. The type species *C. antisiensis* is widespread in the Upper Silurian of Bolivia, both in the Altiplano and Cordillera Oriental, leading Suárez Riglos (1975) to recognize the *Clarkeia antisiensis* Biozone. Although this species is unknown in Paraguay and Argentina it has been recurrently cited in the literature. As stated above, the Paraguayan material of '*Clarkeia antisiensis*' was re-

assigned to *Plectothyrella? itacorubiensis* Benedetto and Halpern. The Lipeón Formation (upper Llandoverry-Wenlock) of the Subandean ranges of NW Argentina has yielded the minute species *Clarkeia ovalis* Benedetto (1991). The Early Silurian of southern Peru contains *Clarkeia durrelli* Boucot (in Laubacher et al. 1982), a species relatively close to *C. antisienensis*. In the Precordillera basin of Western Argentina the genus *Clarkeia* underwent a significant speciation event (Benedetto et al., 1996). The oldest species yet reported are *Clarkeia bodembenderi* (Kayser) and *Clarkeia deflexa* Benedetto et al., 1996, of Ludlovian age. The large species *Clarkeia tambolarensis* Benedetto et al., 1996, occurs in Ludfordian/Pridolian beds exposed in the southern portion of the basin (Tambolar area), whereas the hyperpliate *Clarkeia alta* Benedetto et al., 1996, is confined to beds of Pridolian age at the top of the Los Espejos Formation at Cerro del Fuerte. Recently, however, this species has been recorded from the overlying reddish siltstones of earliest Lochkovian age, which constitutes the first well-constrained record of *Clarkeia* in the Lower Devonian in the Precordillera basin. The presence of a single species of *Clarkeia* in the Silurian of Bolivia may reflect the lack of detailed taxonomic studies of the abundant material from the Catavi and Tarabuco formations rather than a low rate of speciation in the Central Andean basin.

There are no reports of *Clarkeia* in the intracratonic basins of Brazil. Outside South America, the species *Clarkeia puilloni* (Barrois) has been described from Pridolian beds of the Armorican Massif of western France (Mélou & Rachaboeuf 1977; Babin et al. 1979), and *Clarkeia* sp. occurs in the lower Ludlow Téliimélé Group (Bambaya Sandstone) of Guinea, West Africa (Racheboeuf & Villeneuve 1992). *Clarkeia* has also been reported from probable Lower Devonian strata of East Senegal (Drott et al. 1979), associated with the typical Afro-South American chonetid *Australostrophia* (Racheboeuf & Villeneuve 1989), but the species remains unidentified.

#### REMARKS ON THE *CLARKEIA ANTISIENSIS* ONTOGENY

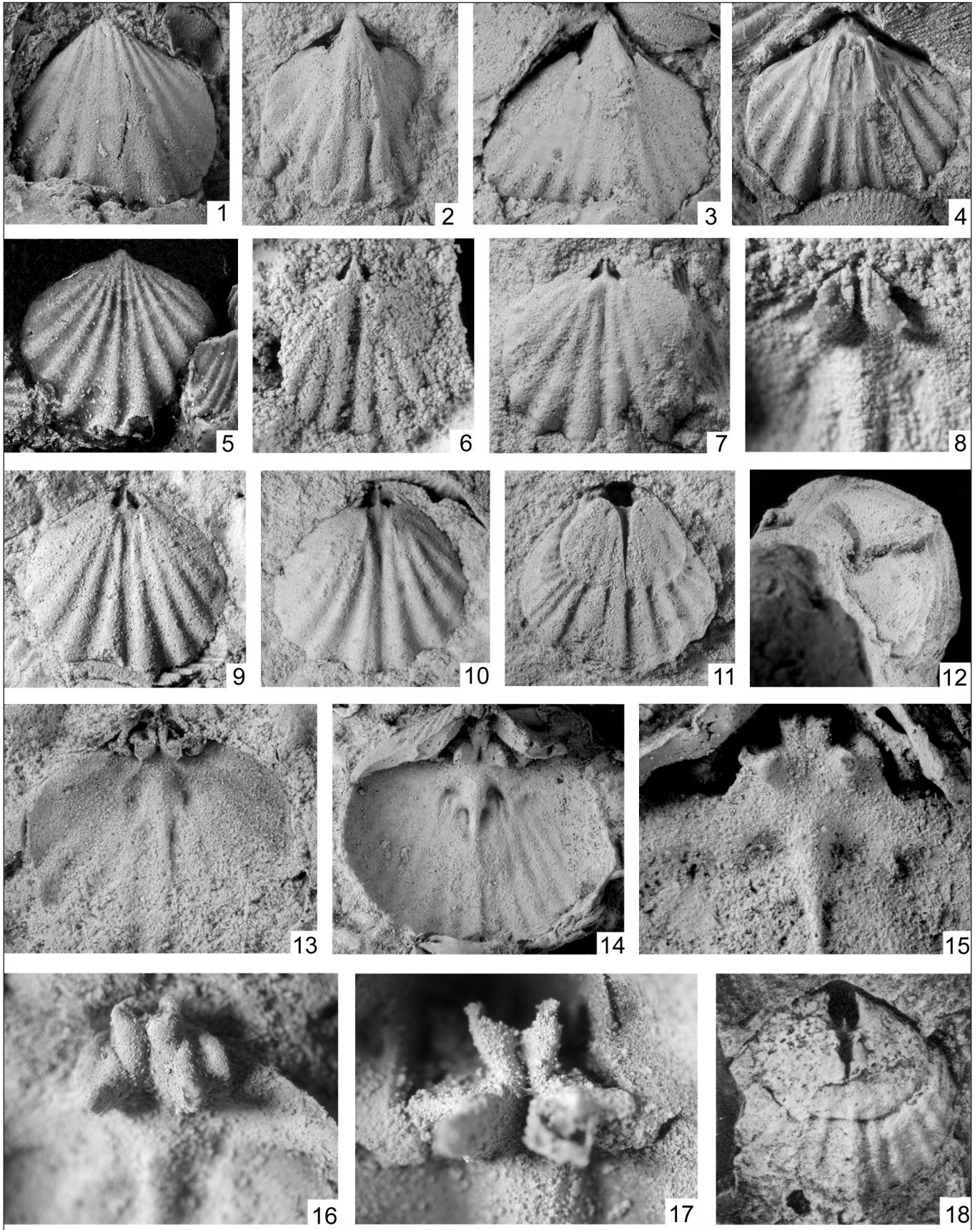
Material recovered from the Tarabuco Formation consists of hundreds of specimens ranging in size from a few millimeters to up to 20 mm long.

Many specimens are conjoined internal molds so that internal features can be accurately known by means of latex replicas. Such a complete series of successive growth stages provides a good opportunity for reconstructing to some detail the ontogeny of *Clarkeia antisienensis* (Fig. 3).

**Exterior.** Smallest shells (up to 7 mm long) are subcircular in outline, planoconvex in lateral profile. The ornament of the ventral valve consists of three rounded simple costae on flanks and one bisecting the median sulcus, all of which rapidly enlarged towards the margin (Fig. 3.1). The median sulcus becomes deeper and broader on the anterior third of the valve, and the anterior commissure becomes uniplicate. The dorsal valve bears two median costae and 3-4 costae on flanks. All costae are simple, broad, rounded in profile, separated by equally rounded intercostal furrows; the two median costae are situated in the same plane than those on flanks but rise towards the margin to form a low fold, which corresponds to the ventral sulcus (Fig. 3.5). With growth, the shell outline tends to become suboval, slightly longer than wide, and convexity

Fig. 3 - 1-17) *Clarkeia antisienensis* (d'Orbigny, 1847).

- 1: juvenile ventral valve exterior, latex cast CEGH-UNC 27071b (X3).
- 2: juvenile ventral internal mold CEGH-UNC 27062 (X3).
- 3: juvenile ventral internal mold CEGH-UNC 27051 (X3).
- 4: adult ventral internal mold CEGH-UNC 27070 (X2).
- 5: juvenile dorsal exterior, latex cast CEGH-UNC 27071 (X3).
- 6: early juvenile dorsal internal mold CEGH-UNC 27064 (X7).
- 7-8: juvenile dorsal internal mold (X3) CEGH-UNC 27066a, and latex cast showing cardinalia (X9).
- 9: juvenile dorsal internal mold CEGH-UNC 27056 (X4).
- 10, 15: adult dorsal internal mold CEGH-UNC 27066b (X2), and detail of cardinalia, latex cast (X6).
- 11: dorsal internal mold of large adult specimen CEGH-UNC 27055 showing growth discontinuity (X1.5).
- 12: lateral view of large adult specimen CEGH-UNC 27052 showing growth discontinuity and shell curvature (X1.5).
- 13: latex cast of juvenile dorsal interior CEGH-UNC 27065 (X5).
- 14: latex cast of dorsal interior, intermediate ontogenetic stage CEGH-UNC 27072a (X4).
- 16: detail of cardinalia, latex cast of adult specimen CEGH-UNC 27060 (X10).
- 17: detail of cardinalia, latex cast of adult specimen CEGH-UNC 27069 (X10).
- 18) *Clarkeia durrelli* Boucot (in Laubacher et al., 1982) (upper Calapuja Formation, Peru), internal mold of adult dorsal valve USNM 303915 showing growth discontinuity (X2.5) (from Laubacher et al. 1982, pl. 5, fig. 23).



increases to reach a mean thickness/length ratio = 0.40. The number of costae in the sulcus increases to three by bifurcation of the primary median rib and subsequently to four by interpolation of a new rib on the external side of parental costae. In the dorsal valve, each of the two primary costae bifurcates at about 6–8 mm from the umbo, but dichotomy can be delayed up to the midlength of adult shell. In some populations ribs do not increase in number through ontogeny, so that mature individuals bear a single rib in the sulcus and two ribs on the fold. However, in most medium to large individuals the fold bears anteriorly four subequal rounded to subangular costae. The anterior commissure is faintly plicate or serrate. Rib number on the flanks of both valves increases to 6–8 either by lateral branching or by dichotomy. Noteworthy, in many specimens the point of rib bifurcation on the fold is marked by a strong growth discontinuity located at 7–9 mm from the umbo, dividing the shell into a nearly planoconvex ‘juvenile’ region with few low simple costae and a convex ‘adult’ region characterized by stronger and more numerous ribs arising sporadically by dichotomy and/or interpolation (Fig. 3.11, 3.12). Such a discontinuity also coincides with a sharp deflection of valves leading to a gradual increase of shell convexity (Fig. 3.18), which can be related to a change from an umbo-down subvertical position to a semi-infaunal mode of life with the posterior part of the shell partially buried into the sediment.

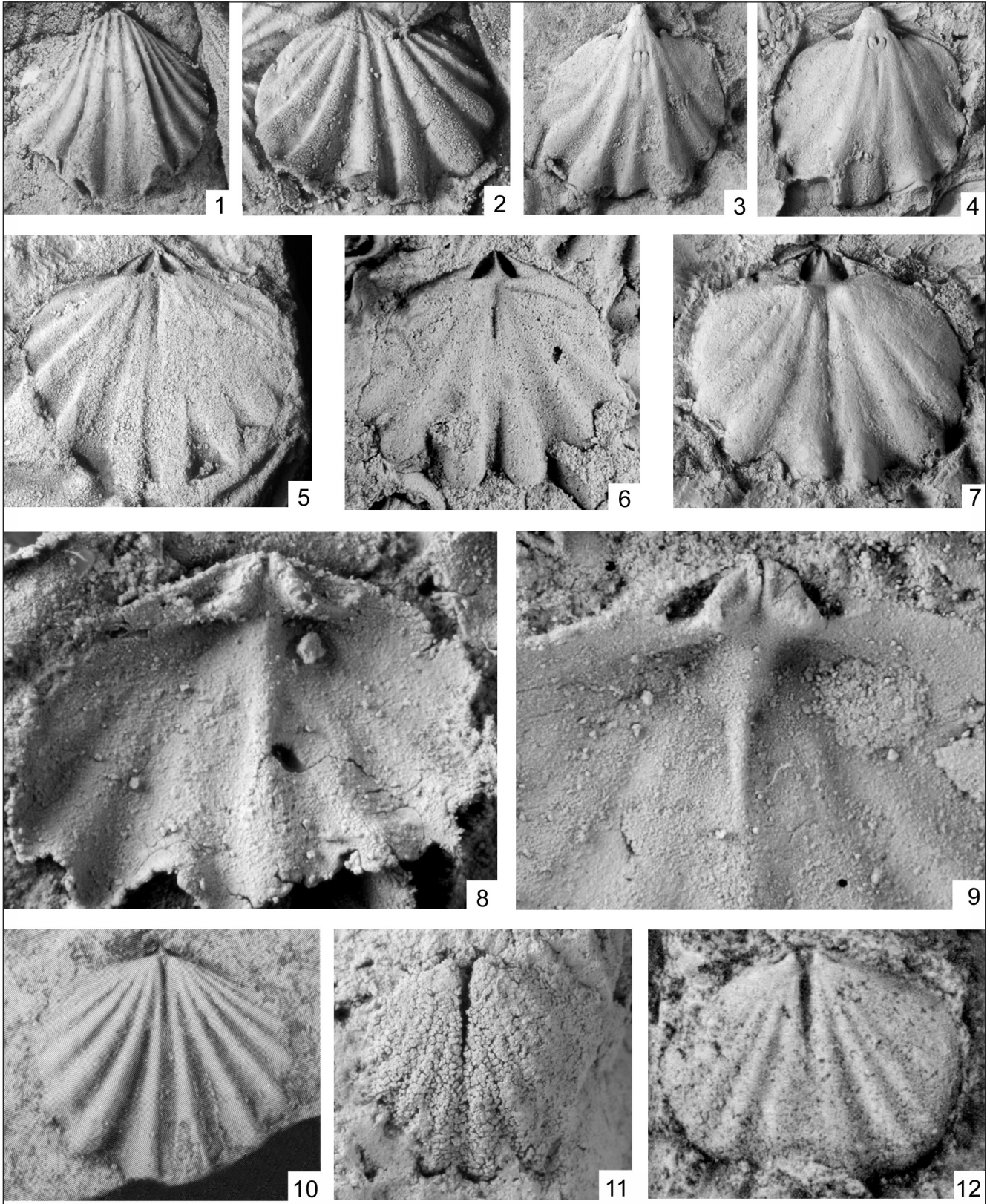
**Ventral interior.** In small individuals (up to about 7 mm long) diductor scars are faintly impressed and bounded posterolaterally by low extensions of dental plates, reaching anteriorly 40–50% of the valve length. The adductor scars are small, suboval, surrounded by poorly defined diductors (Figs. 3.2–3.3). Teeth are small, rounded, supported by well-defined blade-like dental lamellae. In medium-sized individuals dental plates thicken and become partially obliterated by secondary deposits, and the periphery of diductor scars is better defined. As size increases the dental plates become almost completely masked by secondary deposits and the muscle field expands laterally to become approximately as long as wide (Fig. 3.4). The adductor scars are prominent because of extensive deposition of secondary shell within the apical chamber.

**Dorsal interior.** A continuum of morphologic transformations takes place through growth making it difficult to establish discrete ontogenetic

stages. The smallest specimens (up to about 7 mm long), possess very simple cardinalia consisting of a pair of disjunct, slender slightly diverging hinge plates welded on a low subtriangular notothyrial platform. At this earliest stage there is no evidence of cardinal process and myophragm, and the muscle field is indistinct (Fig. 3.6, 3.9). With growth, hinge plates enlarge and extend anteriorly becoming gradually elevated above the valve floor to which are welded posteriorly by callus deposits forming a pseudoseptalium. At this stage the more significant modification is the appearance of a pair of short ridges on the inner (medial) margin of hinge plates, which represent the embryonic state of the complex adult cardinal process of *Clarkeia antisimensis*. Initially, such a double ridge is confined to the posterior part of the hinge plates (Fig. 3.8) but with growth it extends along the entire plate. Simultaneously, a second prominent oblique ridge developed along the external margin of each hinge plate, representing the inner socket ridge, and the outer socket ridges arise delimiting elongate shallow sockets (Fig. 3.8). In medium-sized individuals, the ventral face of hinge plates becomes concave and swells distally giving support to bulbous crural bases (Fig. 3.13), which in the internal moulds are visible as a pair of deep subcircular holes of variable diameter. The double-ridged cardinal process grows posteroventrally forming a short tubular structure (Fig. 3.14). As deposition of secondary material increases the notothyrial platform thickens

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- Fig. 4. 1–10) *Harringtonina australis* Boucot, 1972. 1, juvenile ventral valve exterior, latex cast CEGH-UNC 27076 (X3). 2: dorsal exterior CEGH-UNC 27073, latex cast (X5). 3: adult ventral internal mold CEGH-UNC 27050b (X3). 4: adult ventral internal mold CEGH-UNC 27050d (X3). 5: juvenile dorsal internal mold CEGH-UNC 27050a (X6). 6, early adult dorsal internal mold CEGH-UNC 27049a (X6). 7–8: adult dorsal internal mold CEGH-UNC 27050 (X2.5), and latex cast showing detail of cardinalia (X10). 9: juvenile dorsal internal mold, latex cast CEGH-UNC 27049b (X10). 10: early juvenile dorsal internal mold CORD-PZ 9227 (X9).
- 11) *Anabaia* sp. (La Chilca Formation, Precordillera) dorsal internal mold CEGH-UNC 27077 (X9).
- 12) *Anabaia paraia* Clarke, 1899 (Trombetas Formation, Brazil), adult dorsal internal mold MN 3313a-I (X5).





and its anterior margin welded with a prominent myophragm, which fades anteriorly to disappear towards the valve midlength. In some specimens a vestige of the early double-ridged cardinal process is still visible on the posterior region of the notothyrial platform welded to the strongly enlarged concave inner socket ridges (Fig. 3.14). In mature specimens, the base of the cardinal process is a massive structure bifurcated distally (Fig. 3.15), often bearing a median sulcus which is interpreted as a relic of the double-ridged structure of the younger stages (Fig. 3.16). A pair of subparallel posteriorly directed tubular cardinal lobes developed in the largest individuals (Fig. 3.17). Their distal surfaces may be variably sulcate conferring to the cardinal process a quadrilobate aspect (Fig. 2.16). Trifid cardinal processes as those described and illustrated by Kozłowski (1923: 88, fig. 5) have not been observed in our material. One can speculate that the illustrated structure corresponds actually to a simple but prominent cardinal process bearing distally a pair of deep sulci giving a trifid aspect, but given that this structure is highly variable further investigation is required to clarify the issue. In general, crura are broken at their bases, but in a few large individuals they are preserved as long slender, simple, ventrally curved structures falling within the radulifer type (Jin 1989).

## TAXONOMIC AND PHYLOGENETIC IMPLICATIONS

Although the ontogeny of *Harringtonina australis* is relatively well-known (Benedetto 1988), new extensive collections provided additional data to reconstruct the development of adult cardinalia. Its description, however, is out of the scope of this study; the main traits of its ontogeny are mentioned herein for the sole purpose of comparing with the ontogeny of *C. antisiensis*. In brief, the early and intermediate ventral and dorsal valves of *H. australis* are nearly identical both externally and internally to the earliest ontogenetic stages of *C. antisiensis*, the resemblance being particularly striking in the cardinalia (cf. Fig. 4.8 with Fig. 3.8). In the smallest valves of *H. australis* (ca. 4–6 mm long) it consists of two short thin, disjunct hinge plates bounding medially the sockets, and the cardinal process is absent or rudimentary (Fig. 4.9). At a slightly later

growth stage the hinge plates thicken and enlarge, and a ridge begins to grow progressively from the posterior region of each plate (Fig. 4.8) forming in mature or gerontic specimens a more or less prominent double-ridged cardinal process (Benedetto 1988, pl. 1, fig. 15; this paper Fig. 4.8). Such morphology of cardinalia is closely comparable to that seen in the early (but not earliest) growth stages of *C. antisiensis* (Fig. 3.8, 3.13). As stated in the description of ontogeny above, as growth continued the two ridges merged each to another originating a tubular cardinal process projected first posteroventrally and then posteriorly, becoming bifid distally in large adult specimens (Fig. 3.15, 3.17). Noteworthy, such a transformation of *Clarkeia antisiensis* cardinalia coincides with a significant change in the rate and direction of shell growth (ontogenetic allometry) (Fig. 3.12). This deflection is marked on both valves by a prominent growth discontinuity (Fig. 3.11), which was also noted by Boucot in *Clarkeia durelli* (in Laubacher et al. 1982, pl. 5, fig. 23, reproduced here in Fig. 3.18). Shape transformations of cardinalia in *Clarkeia* could be related to a change in life position from attached umbo-down attitude to a reclined mode, as the increase of shell convexity and strengthening of the commissure suggest. The pre-discontinuity stage in *C. antisiensis* is characterized by a gently biconvex shell with a single rib in the sulcus and a pair of ribs defining anteriorly a low fold. It should be noted that this stage of *C. antisiensis* is nearly indistinguishable from adults of *Harringtonina australis* (cf. Figs. 3.1, 3.5 with Figs. 4.1, 4.2). It is likely that such specimens have been referred in the literature to *Harringtonina australis* (or '*Anabaia*' *australis*). So far, there is no conclusive evidence of the presence of this species in the Tarabuco and Catavi formations, pending of confirmation its record in the Kirusillas Formation. The same reasoning is valid for the specimens attributed to '*Anabaia*' (or *Harringtonina*) *paraguayensis* from the Llandoverly upper Calapuja Formation of Peru (Laubacher et al. 1982) which in our opinion corresponds to the juvenile 'pre-discontinuity' stage of *Clarkeia durelli*.

*Anabaia* Clarke, 1899, is a still poorly known genus, the type material of *Anabaia paraia* was illustrated by Clarke (1899, pl. 2, figs. 1–9) by hand-drawing figures, and more recently both valves were re-illustrated by Gonçalves de Melo & Boucot (1990, figs. 1–10; a dorsal interior is reprodu-

ced here in fig. 4.12). Additional photographs were kindly sent to me from the National Museum of Rio do Janeiro, but unfortunately no dorsal latex casts are available, which are crucial to confirm the validity of the genus. Following the Gonçalves de Melo & Boucot (1990)'s criterion, Savage et al. (2002) considered *Harringtonina* as a junior synonym of *Anabaia*, which is defined as having small crural plates welded to a prominent myophragm forming a septalium-like (pseudoseptalium) structure, and lacking evidence of cardinal process. Although in other features (ornament, ventral interiors) both genera are very similar, adults of *Harringtonina* clearly differs from *Anabaia* in having a well-defined cardinal process welded to the inner margins of hinge plates, supporting the validity of the two taxa. Relevant for its phylogenetic connotation is the fact that the earliest ontogenetic stages of *Harringtonina* lack of any trace of cardinal process and possess a pair of short hinge plates welded to the myophragm (Fig. 4.10) like mature specimens of *Anabaia paraia* (Fig. 4.12). Such septalium-like structure is particularly evident in the Rhuddanian specimens from the Precordillera considered by Benedetto (1995, pl. 61, fig. 22; this paper Fig. 3.11) as a possible new species of *Anabaia*.

## CONCLUSIONS AND FUTURE RESEARCH

In recent years the crucial role that changes occurring during ontogeny play in generating intrinsic phenotypic variation within a species – which is the target for natural selection and hence in generating micro and macroevolutionary trends – has been widely accepted (e.g. McNamara & McKinney 2005; Smith 2003). Processes involving heterochrony, defined as changes over time in the rate and timing of development, are ubiquitous in several taxonomic groups. In the last years significant advances have been made in detecting heterochronic processes in different Ordovician brachiopods as productorthids (Benedetto 2008) and plectorthoideans (Benedetto 2007; Benedetto & Muñoz 2016). On the basis of the ontogeny of *Clarkeia antisiensis* described herein, the case for a close phylogenetic relationship between *Harringtonina* and *Clarkeia* is compelling. The fact that juvenile specimens of *C. antisiensis* are nearly indistinguishable from adult individuals of *Har-*

*ringtonina australis* strongly suggests that *Clarkeia* evolved from *Harringtonina* by peramorphosis. On the other hand, adult specimens of the Brazilian *Anabaia paraia* (and also the Precordilleran *Anabaia* sp.) never exceed the youngest ontogenetic stage of *Harringtonina australis*, to which share small hinge plates supported by a septalium-like structure and absence of cardinal process. This evident overlap of the adult morphology of *Anabaia* with the juvenile morphology of *Harringtonina australis* and, in turn, of the adult morphology of the latter with the juvenile traits of *Clarkeia antisiensis* lead us to interpret this succession as an evolutionary lineage showing from ancestors to descendants increasingly more peramorphic characters. This interpretation is supported by the close correlation between the stratigraphic record of taxa and the inferred developmental sequence, being *Anabaia* the oldest member (Lower Silurian, probably mid-Llandovery), *Harringtonina australis* an intermediate form (Wenlock-Ludlow), and *Clarkeia antisiensis* (Pridoli) the youngest.

This hypothesis may give more integrative insight into the phylogenetic relationships of these genera, but it needs to be corroborated by more detailed morphological studies, in particular of *Anabaia* and some still poorly known related forms. This interpretation generates an intricate taxonomic problem because the leptocoeliids *Anabaia* and *Harringtonina* are currently classified within the superfamily Uncinuloidea whereas *Clarkeia* is placed in the Rhynchotrematoidea (Savage et al. 2002). If the hypothesis supported here is correct the latter superfamily, as well as the family Eatoniidae, as presently constituted, would be polyphyletic groups.

Concerning to the Silurian-Devonian rhynchonellide radiation in Gondwana, some other relevant issues remain to be resolved: (1) the role of the Late Ordovician genus *Plectothyrella* in the post-extinction diversification of rhynchonellides; (2) the phylogenetic placement of *Aratanea* in relation to the *Anabaia-Harringtonina-Clarkeia* evolutionary lineage; (3) the origin from *Harringtonina* of a quite different lineage leading to the Devonian genera *Australocoelia* and *Pacificocoelia*; and (4) the taxonomic identity of a number of rhynchonellide species recovered from upper Llandovery-Wenlock strata, and the possibility that some of these forms might be intermediate between *Anabaia* and *Harringtonina australis*.

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