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Juan L. Benedetto & Ezequiel Montoya

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RESEARCH PAPER

The Afro–South American brachiopod *Castellaroina* Boucot from the Silurian of the Argentine Precordillera: its origin and phylogenetic relationships

Juan L. Benedetto · Ezequiel Montoya

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Abstract The Silurian genus *Castellaroina* and related leptostrophiids are reviewed and partially redescribed from the La Chilca, Los Espejos and Tambolar Formations of the Argentine Precordillera. The La Chilca Formation contains *Eostropheodonta chilcaensis chilcaensis* (Benedetto) and the new subspecies *Eostropheodonta chilcaensis parvula* of Rhuddanian and Aeronian–Telychian age, respectively. *Castellaroina* is represented by the type species *Castellaroina fascifer* (Kayser) and the new species *Castellaroina fuertensis*, both from beds of essentially Ludlow age. Parsimony analysis of the family Leptostrophiidae indicates that *Eostropheodonta hirnantensis* is closest to the outgroup (*Rafinesquina*) and ancestral to the entire leptostrophiid clade. *Viodostrophia*, *Palaeoleptostrophia*, *Eostropheodonta* and *Castellaroina* form a basal group characterized by having denticular plates and lacking hinge denticulation, and clearly differ from the derived denticulate forms that become dominant during the Devonian. After the late Hirnantian biotic crisis, a local radiation of endemic leptostrophiids took place in the Afro–South American Realm. Stratigraphic and morphologic evidence support that *Eostropheodonta hirnantensis*—present in the Hirnantian communities of the Precordillera basin—gave rise to the lineage leading to *Castellaroina fuertensis* nov. sp. and *Castellaroina fascifer*, being *Eostropheodonta chilcaensis parvula* nov. subsp. and *Eostropheodonta chilcaensis chilcaensis* intermediate forms. It is suggested that heterochronic processes played an important role in directing morphological changes in this evolutionary lineage.

Keywords Brachiopods · Silurian · Argentina · Precordillera · Leptostrophiidae · Phylogeny

Kurzfassung Die Gattung *Castellaroina* und weitere verwandte silurische Leptostrophiiden aus den Formationen La Chilca, Los Espejos und Tambolar der argentinischen Prekordillere werden revidiert und neu beschrieben. Die Formation La Chilca enthält *Eostropheodonta chilcaensis chilcaensis* (Benedetto) und das neue Subgenus *Eostropheodonta chilcaensis parvula* jeweils in den Stufen Rhuddanium und Aeronium-Telychium. *Castellaroina* ist durch *Castellaroina fascifer* (Kayser) und die neue Untergattung *Castellaroina fuertensis* vertreten, beide aus Schichten überwiegend ludlowischen Alters. Eine Parsimonie-Analyse der Familie Leptostrophiidae zeigt, dass *Eostropheodonta hirnantensis* der Außengruppe (*Rafinesquina*) am nächsten steht und Vorfahr des Monophylums Leptostrophiidae ist. *Viodostrophia*, *Palaeoleptostrophia*, *Eostropheodonta* und *Castellaroina* bilden die basale Gruppe, gekennzeichnet durch die Anwesenheit von zahnförmigen Platten und die Abwesenheit von Scharnierzähnen, und unterscheiden sich deutlich von den im Devon dominierenden dentikulaten Formen. Nach der biotischen Krise des späten Hirnantiums erfolgte in der Afro-Südamerikanischen Region eine lokale Radiation endemischer Leptostrophiiden. Stratigraphische und morphologische Befunde zeigen, dass *Eostropheodonta hirnantensis*—vorhanden in Hirnantischen Lebensgemeinschaften der Prekordillere—die Linie hervorbrachte, die ihrerseits zu *Castellaroina fuertensis* nov. sp. und *Castellaroina fascifer* führte, mit *Eostropheodonta chilcaensis parvula* nov. subsp. und *Eostropheodonta*

J. L. Benedetto (✉) · E. Montoya
Centro de Investigaciones en Ciencias de la Tierra
(CICTERRA), Consejo Nacional de Investigaciones Científicas
y Técnicas and Universidad Nacional de Córdoba,
Vélez Sarsfield 1611, Ciudad Universitaria,
X5016GCA Córdoba, Argentina
e-mail: jbenedetto@efn.uncor.edu

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chilcaensis chilcaensis als Zwischenformen. Heterochronie scheint eine wichtige Rolle im morphologischen Wandel dieser evolutionären Linie gespielt zu haben.

Schlüsselwörter Argentinien · Prekordillere · Leptostrophiidae · Phylogenie

Introduction

During the Silurian Period a distinctive assemblage of brachiopods referred to as the Afro–South American Realm by Benedetto and Sánchez (1996) inhabited the South American Andean basins of Argentina, Bolivia and Perú, the intracratonic basins of Brazil and the Guinea and Senegal basins of northwestern Africa. Since rocks of Silurian age are unknown from the Malvinas (Falkland) Islands, the widely used term "Malvinokaffric Realm" coined by Richter and Richter (1942) should be restricted to the Devonian faunas. The Afro–South American Realm is largely equivalent to the "*Clarkeia* shelly fauna" named by Cocks (1972) and Cocks and McKerrow (1973). This biogeographic unit developed at southern high latitudes, in opposition to the temperate/warm-water North Silurian Realm (Boucot 1975; Boucot and Blodgett 2001). It hosted low-diversity brachiopod associations in which pentameroideans are absent and spiriferids are extremely rare. The core taxa are the endemic genera *Anabaia*, *Harringtonina* and *Clarkeia* (Rhynchonellida), *Heterorthella* (Heterorthidae), *Australina* (Atrypida), *Amosina* (Chonetidina) and *Castellaroina* (Strophomenoidea), which are associated, in different stratigraphic levels and at different places, with such North Silurian taxa as *Isorthis*, *Orthostrophella*, *Salopina*, *Leangella*, *Plectodonta*, *Leptaena*, *Ancillotoechia* and *Coelospira* (Amos and Noirat 1971; Copper et al. 1988; Benedetto 1991, 1995; Benedetto and Toro 1989; Benedetto et al. 1992, 1996).

Castellaroina Boucot is the most common strophomenoid of the Afro–South American Realm. It is particularly abundant in the Los Espejos Formation of the Precordillera basin, western Argentina, from which the type species *Tropidoleptus fascifer* Kayser was collected (Kayser 1897). The genus *Castellaroina* is otherwise only known from the NW Argentina basin (*Castellaroina* sp., Benedetto 1991) and from the Bové basin of western Africa, where *Castellaroina telimelensis* Racheboeuf and Villeneuve (1992) has been reported. Since the original publication by Kayser (1897), *Castellaroina fascifer* (Kayser) has remained poorly described and illustrated (Leanza 1950; Castellaro 1959, 1966), and its phylogenetic relationships have not been elucidated. During revision of previously collected material and study of new specimens sampled from the Los Espejos Formation, the new species *Castellaroina fuertensis* was recognized. The lack of illustrations or mention of this brachiopod in the past is not surprising taking into account that its ventral interiors—which by far are the most abundant in the collections—are quite similar to those of *C. fascifer*. Likewise, in searching for potential ancestors of *Castellaroina*, the strophomenoids from the underlying Lower Silurian La Chilca Formation were restudied. As a result, those specimens formerly attributed to *Aphanomena* cf. *mullochensis* (Reed) by Benedetto (1995) were reassigned to a new subspecies of *Eostropheodonta chilcaensis* (Benedetto). Interestingly, the leptostrophiids from the Llandovery of the Precordillera show a combination of features intermediate between the latest Ordovician *Eostropheodonta hirnantensis* and the Mid–Late Silurian *Castellaroina*, which allows us to propose a phylogenetic hypothesis for the post-extinction leptostrophiid radiation in the Afro–South American Realm. The aim of this study, therefore, is to provide a detailed morphological description of *Castellaroina fascifer* on the basis of large collections from Kayser's type locality and other stratigraphic sections through the Precordillera basin, to describe *Castellaroina fuertensis* nov. sp. and *Eostropheodonta chilcaensis parvula* nov. subsp. and to discuss the origin, phylogenetic relationships and systematic placement of the genus *Castellaroina*.

Silurian stratigraphy and environmental settings

Palaeozoic rocks of the Precordillera folded belt are well exposed along a series of N–S trending thrust belts 150–180 km long, each of which includes Cambrian to Middle Ordovician platform carbonates followed by Upper Ordovician, Silurian and Devonian clastic marine rocks, and upper Palaeozoic glacial, shallow marine and continental deposits. Silurian strata are best exposed in the central region, between the San Juan and Jáchal Rivers (Fig. 1), where they form a nearly continuous, up to 600 m thick succession which was referred to by Cuerda (1965) as the Tucunuco Group (this name having priority over the "Cerro del Fuerte Group" mentioned by Amos 1972). It was subdivided into the lower, La Chilca Formation and the upper, Los Espejos Formation. The former ranges in thickness from 30 to 120 m. It consists of a lower interval of dark-grey shales and greenish siltstones, followed by fine-grained amalgamated quartz sandstones often displaying hummocky cross-stratification and lenticular shell beds. The overall succession shows a clear shallowing-upward trend. It has been interpreted as being deposited in an inner platform evolving to a storm-dominated shoreface setting (Astini and Piovano 1992). Shelly faunas are concentrated in several levels within the lower and middle part of the sandstone interval, where they form

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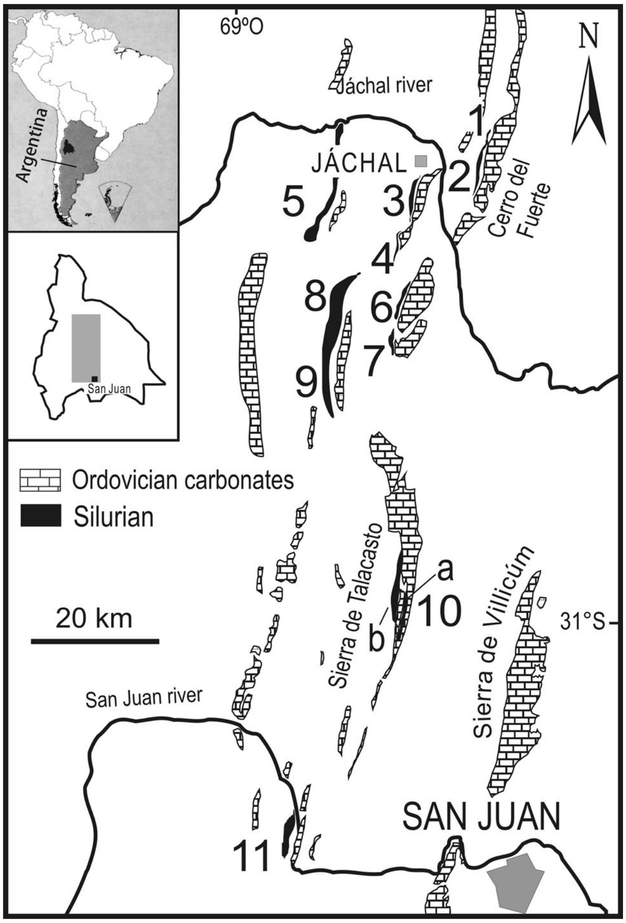

Fig. 1 Map showing Silurian outcrops of the Precordillera fold belt and location of sampled stratigraphic sections mentioned in the text. *1* Río Escondido, *2* Cerro del Fuerte, *3* Loma de Los Piojos/El Refugio, *4* Agua de Felipe, *5* Las Aguaditas, *6* Cerro Cumillango, *7* Cerro La Chilca, *8* Río de las Casitas, *9* Quebrada La Tuna/Las Chacritas, *10* Talacasto (*a* Quebrada Ancha *b* Salto Macho), *11* Tambolar

densely packed shell beds, often with incipient silicification.

The overlying Los Espejos Formation 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 a different stratigraphic unit named the Tambolar Formation was recognized (Heim 1952). 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 and Maretto 1996). Its lower part is dominated by olive-green, thinly bedded laminated mudstones and bioturbated siltstones bearing a varied suite of trace fossils (*Paleodictyon*, *Neonereites*, *Torrowangea*, *Lophochtenium*) indicating deposition in an outer-shelf setting below a storm wave base (Sánchez et al. 1991). This facies grades to siltstones and bioturbated mudstones alternating with sandstone beds averaging 30 cm in thickness but reaching up to 70 cm. Sandstone beds are sharp-based, often bearing tool and flute casts. Internally they display hummocky cross-stratification followed by mudstones with symmetrical or slightly asymmetrical wave ripples. Individual storm beds start with densely packed shell beds, usually 10–20 cm thick, in which brachiopod valves are disarticulated but rarely broken and/or abraded, suggesting short-term reworking and local provenance. Most of the strophomenoids described herein come from these coquinas. Shell concentrations also include trilobites, bivalves, gastropods, echinoderms, corals, ostracods and graptolites (Sánchez et al. 1991). This facies accumulated in a storm-dominated inner shelf transitional to shoreface. A third facies association is represented by fine to medium sized, up to 10 m thick sandstone packages, internally massive or with large-scale diffuse cross-stratification. The two main sandstone intervals, located near the medial part and towards the upper third of the Los Espejos Formation (Fig. 2), could represent shallow-shelf sandbar complexes affected episodically by high-energy oscillatory waves. The lower interval contains numerous shell beds mainly formed by *Australina jachalensis* Clarke and the new species *Castellaroina fuertensis*, whereas the upper sandy interval is dominated by *Clarkeia bodenbenderi* (Kayser). At Loma de Los Piojos (Fig. 2), the upper shell beds have yielded numerous well-preserved specimens of *C. fascifer*.

Age range of *Castellaroina* and related Precordilleran leptostrophiids

Brachiopods from the La Chilca Formation come from several shell beds within the sandy intervals. The lowest brachiopod assemblage occurs in the mixed sandstone/siltstone succession that overlies the basal graptolitiferous shale member. In most localities the fauna is dominated by *Dalmanella* aff. *testudinaria* (Dalman), *Heterorthella precordillerana* Benedetto and *Aphanomena* aff. *mullochensis* (Reed) (referred herein to *Eostropheodonta chilcaensis parvula* nov. subsp.). Graptolites from the La Chilca Formation at the Talacasto section indicate a Hirnantian age (*N. persculptus* Zone) for its lowermost part (Cuerda et al. 1988). However, a mid-Rhuddanian fauna dominated by *Hindella crassa* (J. de C. Sowerby) and *Eoplectodonta* (*Eoplectodonta*) *duplicata* (J. de C. Sowerby) was recovered from the base of the La Chilca Formation at Mogotes Azules (Benedetto and Cocks 2009). The diachronic nature of this unit has been interpreted as resulting from a rapid postglacial sea level rise onto an irregular palaeotopography inherited from the collision of the Precordillera terrane against the South American margin of Gondwana (Astini et al. 1995; Benedetto 2004). The lower, fine-grained bioclastic sandstones exposed at Cerro del Fuerte (Río Escondido

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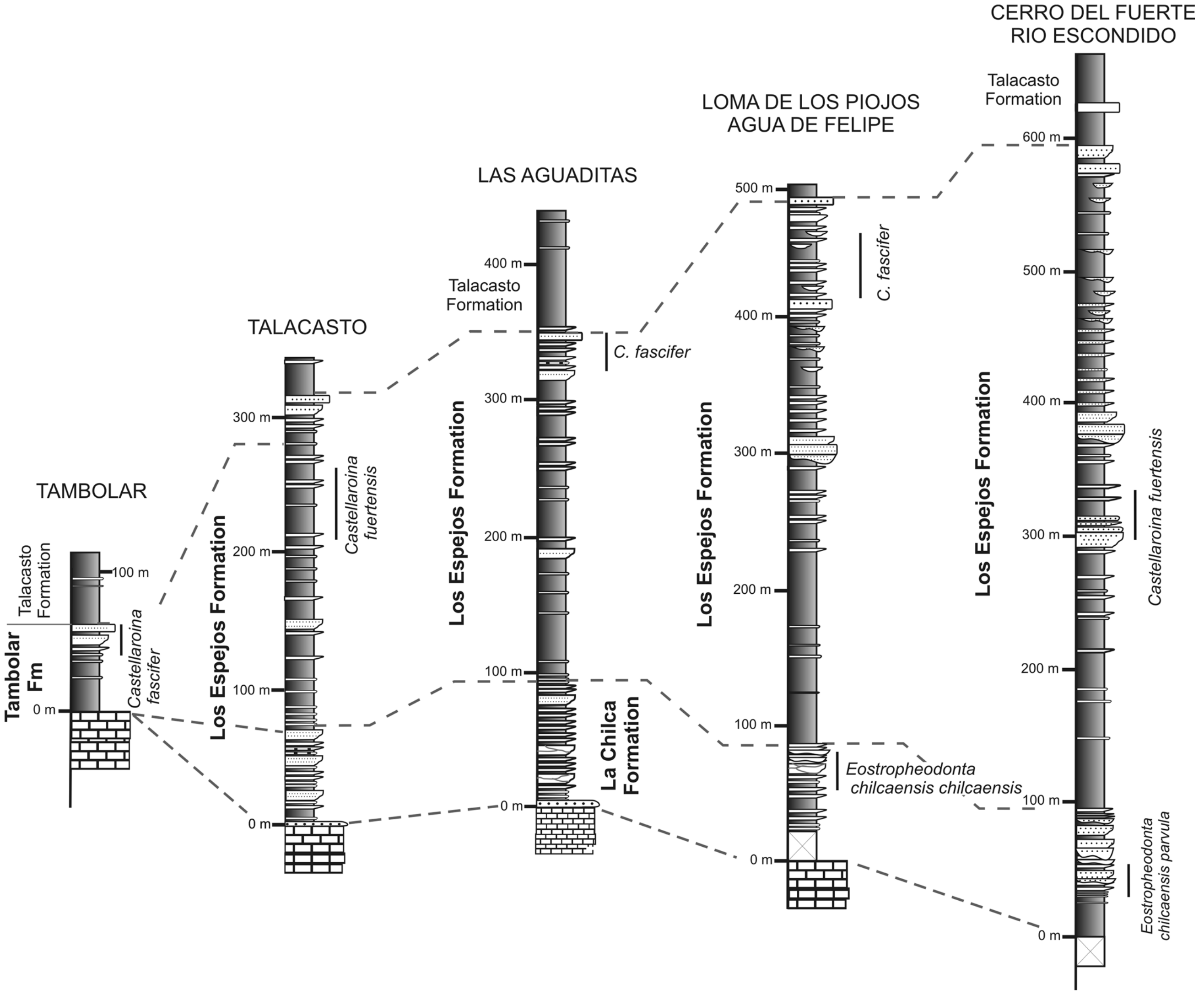

Fig. 2 Sampled stratigraphic column formations, showing stratigraphic ranges of the species discussed in the text

stratigraphic section), which have yielded abundant specimens of *Eostropheodonta chilcaensis parvula* nov. subsp., are of Rhuddanian to early Aeronian age according to the graptolites of the *Atavograptus atavus–Demirastrites triangulatus* Zones (Rickards et al. 1996) and conodonts of the *Distomodus kentuckyensis* Zone (Lehnert et al. 1999; Albanesi et al. 2006). The upper third of the La Chilca Formation is richly fossiliferous at its type locality, including shell beds bearing *Eostropheodonta chilcaensis chilcaensis* (Benedetto), *Cordatomyonia umangoensis* Benedetto and *Rostricellula* sp. The age of this interval is still poorly constrained, but taking into account the age of the underlying fauna and the few graptolites hitherto recovered within this interval (Albanesi et al. 2006), it could be Aeronian and certainly not younger than Telychian.

Fossils in the Los Espejos Formation tend to be rich in number but low in diversity. Its age range throughout the basin is difficult to constrain because of the scarcity of biostratigraphic markers. Graptolites, for instance, only occur in some fine-grained sandstone beds near the middle-upper part of the formation. Turner (1960) identified *Monograptus* aff. *vomerinus* (Nicholson) and assigned the medial part of the formation to the Wenlock Series. Cuerda (1969) reported *Monograptus uncinatus notouncinatus* Cuerda from the Talacasto section, and Albanesi et al. (2006) recorded *Saetograptus argentinus* (Cuerda) in shell beds of the upper third of the Los Espejos Formation, suggesting an early Ludlow age. The conodonts recovered from the upper half of the formation in the same locality belonging to the *Kockelella variabilis variabilis* Zone also indicate an early Ludlow (Gorstian) age (Albanesi et al. 2006). These levels can be correlated with the storm beds of the upper third of the Los Espejos Formation exposed c. 90 km to the north in the Jáchal area, which includes the

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Loma de Los Piojos section, the Las Aguaditas river section (=Cerro Blanco)—the type locality of *Castellaroina fascifer*—and the Cerro del Fuerte section (Fig. 2). The latter, located about 10 km east of Jáchal City, is the thicker and more fossiliferous stratigraphic section of the Los Espejos Formation. There, a lower Ludlow graptolite association consisting of *Monograptus uncinatus notouncinatus* Cuerda, *Saetograptus* (*Colonograptus*?) *argentinus* (Cuerda) and *Saetograptus* (*Colonograptus*?) *roemeri* (Barrande) occurs between c. 270 and 330 m above the contact with the La Chilca Formation (Benedetto et al. 1992; Rickards et al. 1996). Above these levels, Heredia et al. (2007) reported the conodont *Kockelella variabilis variabilis*. Rubinstein and Brussa (1999) provided an integrated palynomorph–graptolite record for the central part of the Silurian basin. The lowest assemblage of the Los Espejos Formation corresponds to the *Neodiversograptus nilssoni*–*Lobograptus scanicus* Zones of Gorstian age, and the A4 palynomorph zone. *Castellaroina fuertensis* nov. sp. typically occurs within this interval. The incorporation of new palynological data (acritarchs and chlorophytes) from other stratigraphic sections confirms the Ludlovian age (Gorstian–Ludfordian) for most of the Los Espejos Formation and its lateral equivalent, the Tambolar Formation, whereas the stratigraphic range of miospores suggests a slightly younger age closer to the Ludfordian–Pridolian boundary (Rubinstein and García-Muro 2013).

In the southernmost part of the Silurian basin, the c. 58-m-thick Tambolar Formation culminates with several shell beds formed almost exclusively by brachiopods, including *Castellaroina fascifer* and *Clarkeia tambolarensis* Benedetto as dominant forms, and *Salopina* aff. *missendenensis* (Straw) and *Isorthis* (*Protocortezorthis*) sp. as fairly common species. These levels are probably correlative with the upper part of the Los Espejos Formation at the Cerro del Fuerte section bearing *Plectodonta* (*Plectodonta*) *minima* Herrera and Benedetto, *Salopina sanjuanensis* Benedetto and *Isorthis* (*Protocortezorthis*) *cuyanum* Benedetto. Although the subgenus *Plectodonta* (*Plectodonta*) is suggestive of the uppermost Silurian (Pridolian), additional biostratigraphic evidence is needed to confirm that age.

The age range of *Castellaroina fuertensis* nov. sp. is thought to be approximately the same as *C. fascifer*, but correlation between the shell beds bearing *C. fuertensis* is still imprecise in detail because it is difficult to be sure over how long a time the numerous tempestite beds were deposited. At the Talacasto section, *Castellaroina fuertensis* forms both monospecific assemblages and densely packed shell beds associated with *Australina jachalensis* Clarke, *Harringtonina acutiplicata* (Kayser) and *Coelospira expansa* Benedetto. The best dated occurrence is in the Cerro del Fuerte section, from which Rickards et al. (1996) described lower Ludlow graptolites collected immediately above the sandstone interval bearing abundant *Castellaroina fuertensis* shells, near the middle part of the Los Espejos Formation.

In conclusion, *Castellaroina fascifer* is confined to the upper half of the Los Espejos Formation, though it has not been recorded from its uppermost levels. It also occurs near the top of the Tambolar Formation at the southern border of the basin. According to the graptolite, conodont and palynomorph evidence, its age is essentially Ludlow, but the possibility that *Castellaroina fascifer* extends into the Pridolian cannot be discarded. *Castellaroina fuertensis*, on the other hand, has been reported from lower Ludlow strata of the Los Espejos Formation, being absent from the Tambolar Formation. A striking feature is that the two species of *Castellaroina* have hitherto not been found associated in the same locality, which suggests a geographic isolation of populations.

Outside the Precordillera basin, the only other South American record of *Castellaroina* is in the Central Andean basin of northwestern Argentina, where *Castellaroina* sp. has been reported from the lower half of the Lipeón Formation at the Zapla anticline (Jujuy Province). The assemblage includes the brachiopods *Heterorthella zaplensis* Benedetto, *Leangella* (*Leangella*) sp., *Harringtonina* n. sp., *Clarkeia ovalis* Benedetto and *Ancillotoechia cooperensis* Amos and Noirat (Benedetto et al. 1992), associated with varied trilobites (Baldis et al. 1976; Waisfeld and Sánchez 1993) and bivalves (Sánchez 1988). As a whole, the benthic faunas suggest a late Llandovery to Wenlock age. The chitinozoans recovered from the Lipeón Formation indicate a Telychian age for its lower part, and an age not younger than early Wenlock for its middle part (Grahn and Gutiérrez 2001). A similar age has been established for the correlative Kirusillas Formation of Bolivia, which has yielded conodonts of the *Ozarkodina sagitta rhenana* Zone (Merino 1991) of Sheinwoodian (early Wenlock) age, and a brachiopod assemblage comparable to that from the lower shaly member of the Los Espejos Formation (Benedetto and Suárez-Soruco 1998).

The species *Castellaroina telimelensis* from the Bambaya Sandstone (Grès de Bambaya) of the Télimélé Group (Guinea) was referred to the Ludlow on the basis of chitinozoans, graptolites and associated brachiopods (Villeneuve et al. 1989; Racheboeuf and Villeneuve 1992; Villeneuve 2005).

Phylogenetic relationships of *Castellaroina* and systematic implications

In order to evaluate the phylogenetic relationships of *Castellaroina*, a cladistic analysis of the family Leptostrophiidae

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Table 1 Character state matrix used in TNT parsimony analysis of characters listed in the "Appendix"

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Rafinesquina	0	0	0	0	0	0	0	01	0	0	0	0	0	0	0	0	0	0	0
Leptostrophia	0	0	0	0	2	1	1	3	3	2	0	1	0	1	1	1	2	1	1
Rhytistrophia	1	0	2	2	1	1	3	3	2	1	1	0	0	1	1	1	1	2	1
Brachyprion	1	0	0	0	12	0	2	2	1	1	1	0	0	1	0	1	1	2	0
Castellaroina fascifer	1	2	01	1	1	0	2	2	0	0	01	0	1	0	0	0	1	1	0
Castellaroina fuertensis	0	2	1	1	1	0	2	12	0	0	1	0	01	0	0	0	1	0	0
Chynistrophia	0	0	0	2	2	0	3	3	2	1	1	0	0	1	1	1	1	2	1
Eomegastrophia	1	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	01	0	0
Erinostrophia	2	0	2	2	2	0	2	2	1	1	1	0	0	1	0	0	2	2	12
Eostropheodonta chilcaensis parvula	0	0	0	0	1	0	12	0	0	0	0	0	0	0	0	01	0	01	0
Eostropheodonta chilcaensis chilcaensis	0	0	0	01	1	0	12	01	0	0	0	0	1	0	0	0	1	1	0
Eostropheodonta hirnantensis	0	01	01	0	1	0	0	12	0	0	0	0	01	0	0	0	0	0	0
Gibberostrophia	2	0	0	2	1	1	3	0	2	2	1	0	0	1	1	1	1	2	1
Mesoleptostrophia	0	0	0	0	1	0	3	2	2	2	1	0	0	1	1	1	1	2	1
Paraleptostrophia	0	01	1	1	1	01	3	0	2	2	1	0	0	1	1	1	2	2	2
Protoleptostrophia	0	0	0	2	1	1	3	0	2	0	1	0	0	0	1	1	1	2	1
Viodostrophia	0	0	0	2	1	0	2	2	0	0	0	0	0	0	0	1	0	0	0
Nervostrophia	0	3	0	2	1	1	3	3	2	1	1	0	0	1	1	1	1	2	1
Palaeoleptostrophia	0	0	1	0	1	0	2	2	0	0	0	0	0	0	0	0	1	0	0

was performed using the TNT program (Tree Analysis Using New Technology) version 1.1 (Goloboff et al. 2008), selecting the heuristic search option with multiple random addition sequences and the TBR (tree branch-swapping algorithm) holding 10 trees in each addition sequence. The 19-character matrix was analyzed for 19 taxa (Table 1). Most of the coded characters are internal features, chiefly related to the articulation system (teeth, sockets, socket ridges) and muscle fields (outline, degree of impression, bounding ridges, transmuscle ridges) (see "Appendix"). Some shell features such as valve profile, ornament and rugae were also considered. All characters were treated as unordered and unweighted. The incompletely known genera *Barbaestrophia* Havlíček, *Tuvaestrophia* Kulkov, *Velostrophia* Havlíček, *Tuvaechonetes* Kulkov, *Tudiaophomena* Xian and *Tubulostrophia* Havlíček were excluded from the analysis. Following Dewing (1999), the genus *Protomegastrophia* Caster is considered a junior synonym of *Brachyprion* (*Brachyprion*), and *Eomegastrophia* as a probable subgenus of *Brachyprion*. The four Precordilleran taxa described in this paper (*Eostropheodonta chilcaensis parvula*, *Eostropheodonta chilcaensis chilcaensis*, *Castellaroina fuertensis* and *Castellaroina fascifer*) were included in the analysis in order to establish their phylogenetic relationships. The Late Ordovician strophomenide *Rafinesquina* Hall and Clarke, which lacks most apomorphies of the leptostrophiids and is considered by most authors as ancestral to the leptostrophiids and related families (Havlíček 1967; Harper and Boucot 1978; Rong and Cocks 1994), was chosen as outgroup for rooting phylogenetic trees.

Parsimony analysis resulted in eight most parsimonious trees with a length of 52 steps. The consistency and retention indices were 0.436 and 0.849, respectively. In the strict consensus (SC) tree (Fig. 3), *Eostropheodonta hirnantensis* appears closest to the outgroup and ancestral to the entire leptostrophiid clade. It shares with *Rafinesquina* the presence of dental plates, the weakly impressed muscle fields lacking bounding ridges and a similar pattern of cardinalia. The SC tree, however, does not resolve the phylogenetic relationships among *Viodostrophia*, *Eomegastrophia*, *Palaeoleptostrophia*, *Eostropheodonta chilcaensis* and *Castellaroina*, which form a polytomy that emerges as a sister group to all other leptostrophiid taxa. In four of the eight most parsimonious trees (Fig. 4), however, the Precordilleran taxa form a phyletic lineage originated from *E. hirnantensis*, the oldest known leptostrophiid. Although *Palaeoleptostrophia* appears within this phylogenetic succession, the difference in geographic distribution precludes a common origin, and it seems likely that it represents a separate lineage that evolved outside the Afro–South American Realm. This is supported by the peculiar combination of ornament, muscle fields and cardinalia seen in *Palaeoleptostrophia*.

The SC tree shows all other taxa as forming a consistent monophyletic clade, with *Brachyprion* and *Erinostrophia* as basal forms. It includes a fairly homogeneous group of

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taxa typified by *Leptostrophia–Protoleptostrophia* and related forms, which underwent an extensive radiation in the Late Silurian and Devonian. This subclade originated from members of the basal group through the evolutionary trends envisaged by Williams (1953), and subsequently reassessed by Rong and Cocks (1994) and Cocks and Rong (2000). The apomorphies defining this clade are the progressive spread of denticles along the hinge line of both valves, the loss of dental plates and teeth, the gradual reduction and disappearance of the posterior pair of socket ridges and the placement of the anterior pair of socket ridges adjacent to the lateral margins of the cardinal process, whose lobes change in orientation from anteroventrally directed to posteriorly directed (Rong and Cocks 1994, text-fig. 19). In addition, a ventral process and deep process pits to accommodate the cardinal process lobes developed. This group clearly differs from the basal forms, which are characterized by having denticular plates and associated devices for valve articulation (e.g. crenulations, denticles, accessory sockets) but lacking hinge denticulation.

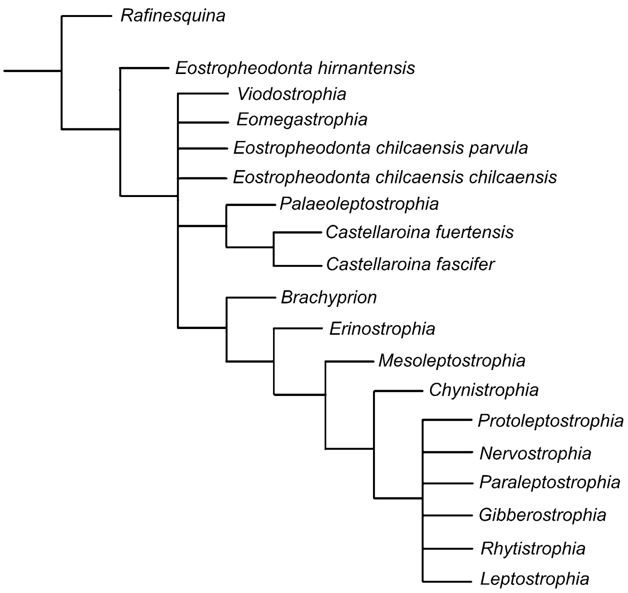


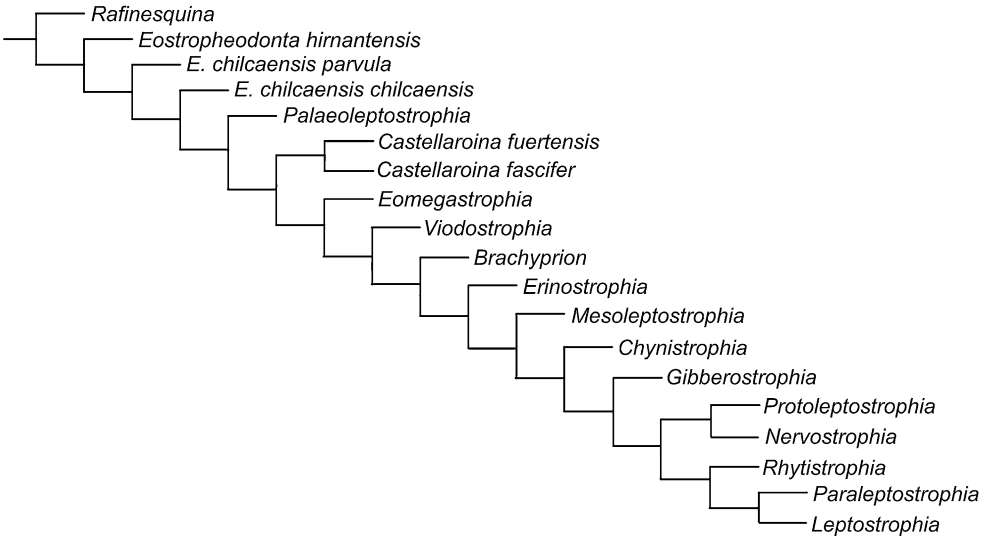
Fig. 3 Strict consensus (SC) tree resulting from the eight more parsimonious trees with a length of 52 steps

The phylogenetic relationships expressed in the SC tree are redrawn in Fig. 5, but with branch lengths calibrated to the chronostratigraphic scale. Clearly, the cladogram configuration is consistent with the known fossil record and does not require long ghost lineages.

Origin and palaeobiogeographic dispersion of *Castellaroina*

The Precordillera is unique among the high-latitude Gondwana basins in bearing a nearly continuous succession of brachiopod-rich levels ranging in age from Hirnantian to Late Silurian, and therefore it constitutes an excellent basis for studying the origin and diversification of the Afro–South American Realm. Here, we address the issue of the origin of *Castellaroina* and its further palaeogeographic dispersion. In this respect it is interesting to transcribe Boucot's opinion (in Amos 1972, p. 11): "…these Argentine shells, present within the Malvinokaffric fauna, should have no similarities to other Silurian shells, but only to an Ashgillian shell from the Old Word Province. The high endemic nature of Andean Ordovician fossils raises the possibility that *Castellaroina* was ultimately derived from an Old World source rather than a local, South American source". The Ashgillian Old World form mentioned by Boucot is *Eostropheodonta*, a genus that later was found in the Hirnantian Don Braulio Formation of the Precordillera (Benedetto 1986) and

Fig. 4 Selected cladogram among the eight more parsimonious trees



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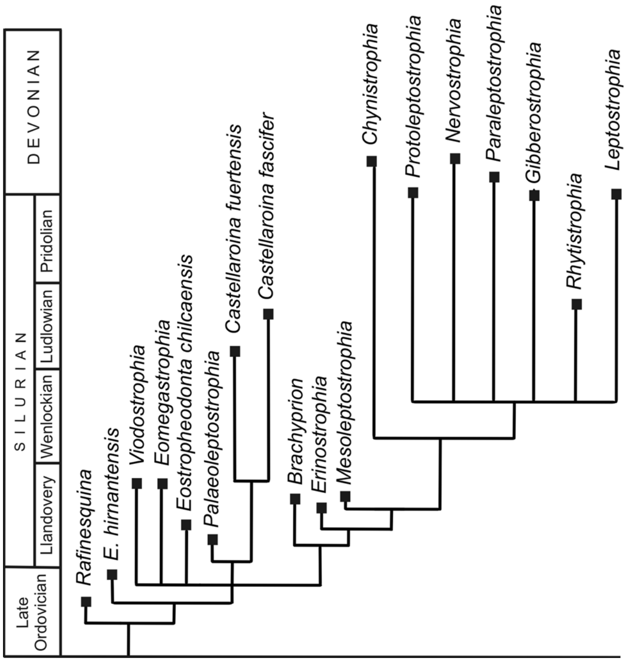

Fig. 5 Strict consensus tree calibrated with chronostratigraphic scale

subsequently in the Llandoverian La Chilca Formation (Benedetto 1995; this paper), besides numerous localities through the world (cf. Rong and Harper 1988).

On the basis of available evidence from the Precordillera basin, a phylogenetic hypothesis is proposed to account for the unresolved part of the SC tree depicted in Fig. 3. We postulate that, after the late Hirnantian biotic crisis, a local radiation of endemic leptostrophiids took place in the Afro–South American Realm (Fig. 6). In brief, our hypothesis supports that *Eostropheodonta hirnantensis*—a very common species in the open-shelf Hirnantian communities of the Precordillera basin—gave rise by heterochronic processes (paedomorphosis and peramorphosis) to the lineage leading to *Castellaroina fuertensis* and *Castellaroina fascifer*, being *Eostropheodonta chilcaensis parvula* nov. subsp. and *E. chilcaensis chilcaensis* intermediate forms (Fig. 6). The relevant role played by heterochrony in generating evolutionary trends in different organisms is widely known (McNamara 1990). Among brachiopods, phylogenetic lineages driven by heterochrony involving changes in shell size and shape, ornament, and internal structures have been recognized in extant (e.g. Pakhnevich 2009; Bitner et al. 2013), post-Palaeozoic (McNamara 1982; Laurin and García-Joral 1990; MacKinnon 2001; Jaecks 2001; Jaecks and Carslon 2001; Baker and Carlson 2010) and lower Palaeozoic taxa (Benedetto 2007, 2008; Pakhnevich 2009). The Silurian strophomenoids studied in this paper are mostly concentrated in shell beds including specimens of very different size, allowing one to reconstruct a fairly complete ontogenetic series for each species, which is a necessary condition for postulating heterochronic hypotheses. In the sample of *Eostropheodonta hirnantensis* from the subtidal mudstones of the Don Braulio Formation, adult specimens are associated with some juveniles in the same bedding plane (Fig. 12s), but ontogenetic changes in this species can also be deduced from the successive growth stages indicated by some conspicuous growth lamellae (Fig. 12p, t).

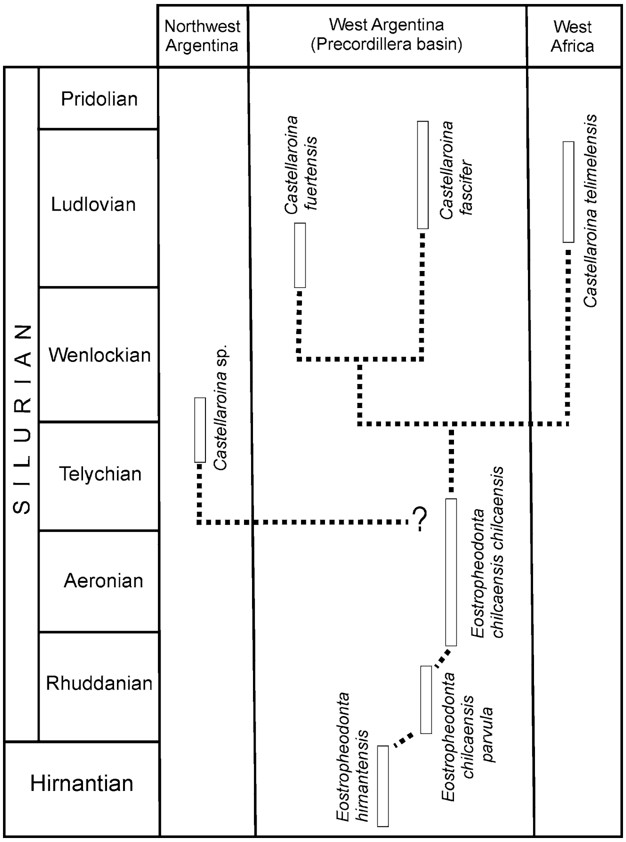

Fig. 6 Inferred phylogeny of studied Silurian leptostrophiids from Precordillera, NW Argentina, and N Africa

Since *Eostropheodonta chilcaensis parvula* occurs a few metres above the Ordovician–Silurian boundary, the first issue refers to the possibility that it evolved from *Eostropheodonta hirnantensis*. Ornament of the dorsal valve in both species is finely parvicostellate, with sporadic bifurcations, which are more frequent in juvenile than in mature shells. Although both species are very close in outline and ornament, adult shells of *Eostropheodonta chilcaensis parvula* are consistently smaller. Internally, the muscle fields of both species are similar, except that in *E. c. parvula* impression of ornament is lacking or diffuse. The smaller valves of *E. hirnantensis* from the Don Braulio Formation available for study have short and thin dental plates, becoming thicker and longer with growth. A similar ontogenetic progression can be seen in the Polish specimens illustrated by

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Temple (1965). The cardinalia of both species are also similar. Perhaps the main difference in the adult forms lies in that the cardinal process lobes in *E. hirnantensis* tend to be subelliptical in outline and often are joined posteriorly, whereas in *E. c. parvula* they are more elongated and do not meet in contact. Unfortunately, the ontogeny of the dorsal valve of *E. hirnantensis* is still poorly known, but late juveniles ("adolescent" according to Baker and Carlson 2010) show somewhat slender cardinal process lobes. Although incomplete, this evidence is compatible with the assumption that *E. c. parvula* evolved from *E. hirnantensis* through the heterochronic phenomenon of paedomorphosis, which accounts for the smaller size, reduced dental plates, delicate cardinalia and absence of crenulations and/or denticles. We can speculate that *E. c. parvula* originated from isolated populations of *E. hirnantensis* surviving the end-Ordovician extinction event. Its small size (adult shells are 10 mm wide on average) could be related to the postglacial elevation of seawater temperature, which was considered by MacKinnon (2001) as a factor favouring selection of diminutive sexually mature individuals. However, unfavourable environmental conditions (i.e. shallow waters periodically reworked by storms) also could have been responsible for the reduction of size.

The transition from *E. c. parvula* to *E. c. chilcaensis* occurs in some tens of metres of amalgamated sandstones within the La Chilca Formation. Their ancestor–descendant relationship is supported by the wide overlap between the extreme morphologic variants of both forms. Small specimens of *E. c. chilcaensis* are always unequally parvicostellate and hardly differentiable from juveniles of *E. c. parvula*, but ornament becomes subequally parvicostellate with growth. Likewise, cardinalia of juveniles of *E. c. chilcaensis* are comparable to those of adults of *E. c. parvula* (cf. Figs. 11q, 12o). During ontogeny, the posterior socket ridges of *E. c. chilcaensis* become more prominent than anterior, crenulations usually develop along the anterior pair of socket ridges, and dental plates become thicker than in *E. c. parvula*. The tendency for the dorsal costellae to increase by dichotomy rather than by insertion is evident in the ramicostellate ornament of *Castellaroina fuertensis* and becomes fully developed in the fascicostellate pattern of *Castellaroina fascifer*. Back in the lineage, branching is developed only on the juvenile portion of the dorsal valve of *Eostropheodonta chilcaensis*, suggesting a paedomorphic origin for this kind of ornament. However, most features of the Late Silurian descendants, such as the increase of shell size (*C. fascifer* reaches up to 32 mm wide), acquisition of strong crenulations along the socket ridges combined with pits on the teeth, hypertrophy of posterior socket ridges, more prominent dorsal median ridge and muscle bounding ridges, and more deeply impressed and best delimited muscle scars, all can be ascribed to the operation of peramorphic processes.

The persistence of short dental plates in *Castellaroina* sp. from NW Argentina is consistent with its occurrence near the Llandovery–Wenlock boundary, but its phylogenetic relationships with the Precordilleran lineage cannot be established at present because of the scarcity of material.

The Silurian marks the beginning of the increased endemism of the Afro–South American Realm shelly faunas, the endemic brachiopod genera attaining 14 % of the total in the Llandovery and about 42 % by the Wenlock/Ludlow (Benedetto and Sánchez 1996). If our phylogenetic hypothesis is correct, *Castellaroina* originated in the Precordillera basin and then migrated into the North African Bové basin. Benedetto et al. (2013) postulated an epicontinental seaway connecting the Paraná basin of Paraguay–Brazil with the Ghana and Bové basins of Guinea, Guinea Bissau and Senegal of West Africa. Such a dispersal pattern seems to have been active since the end-Ordovician postglacial sea-level rise. During this sea-level highstand, the early Llandovery graptolitic black shales of the lower part of the Télimélé Group were deposited (Villeneuve and Da Rocha Araujo 1984), followed by sandstones bearing a typical Afro–South American brachiopod assemblage, including *Castellaroina telimelensis* (Racheboeuf and Villeneuve 1992). Overall, this succession is similar to that of Precordillera. If *Castellaroina* reached NW Africa following this migratory route, it implies a connection between the Precordilleran and Paraná basins through the Central Andean basin, where *Castellaroina* occurs. However, the lack of records of Wenlock–Ludlow brachiopods from Paraguay and Brazil, together with the apparent absence of *Castellaroina* in the richly fossiliferous Silurian successions of Bolivia, make this connection highly speculative.

Systematic palaeontology

Studied specimens are deposited in the palaeontological collection of the Centro de Investigaciones Paleobiológicas (CIPAL), Universidad Nacional de Córdoba, institutional abbreviation CEGH-UNC. Other material examined is housed at the Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, institutional abbreviation CORD-PZ.

Class **Strophomenata** Williams et al. 1996
Order **Strophomenida** Öpik, 1934
Superfamily **Strophomenoidea** King, 1846
Family **Leptostrophiidae** Caster, 1939
Genus ***Castellaroina*** Boucot (in Amos 1972)

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Type species. Tropidoleptus fascifer Kayser 1897, p. 291, fig. 13–16.

Emended diagnosis. Gently to moderately concavoconvex shell with costellae increasing principally by intercalation in the ventral valve (parvicostellate) and by bifurcation in the dorsal valve (ramicostellate or fascicostellate). Teeth and socket ridges with crenulations. Denticles confined to the posterodorsal face of teeth. Dental plates absent or vestigial. Ventral muscle field large, subtriangular, open anteriorly, deeply impressed posteriorly, bounded by coarse pseudopunctae. Ventral process usually well developed. Dorsal muscle field gently to moderately impressed, divided by a broad median ridge. Cardinal process lobes slender and elongated.

Species included. Castellaroina fascifer (Kayser, 1897) from the Los Espejos Formation of the Precordillera (San Juan Province, western Argentina); *Castellaroina fuertensis* nov. sp. (this paper); *Castellaroina telimelensis* Racheboeuf and Villeneuve (1992), from the Grès de Bambaya, Télimélé Group (Guinea, western Africa); *Castellaroina* sp., from the Lipeón Formation, Sierra de Zapla, Jujuy Province, northwestern Argentina (Benedetto 1991).

Castellaroina fascifer (Kayser, 1897) (Figs. 7a–v; 8a–o)
1897 *Tropidoleptus fascifer*, Kayser, 1897, p. 291, figs. 13–16.
1913 *Tropidoleptus fascifera* Kayser, Clarke, 1913, pp. 337–340, figs. 1–5.
1950 "*Tropidoleptus*" *fascifera* Kayser, Leanza, p. 161, pl. 1, figs. 6–8.
1959 *Strophodonta* (*Brachyprion*) *fascifer* (Kayser), Castellaro, pp. 48–51, pl. 1, figs. 1–11.
1966. *Strophodonta* (*Brachyprion*) *fascifer* (Kayser), Castellaro, pp. 30–31, figs. a–f.
1972 *Eostropheodonta (Castellaroina) fascifer* (Kayser), Boucot (in Amos, p. 11).
1978 *Castellaroina fascifer* (Kayser), Harper and Boucot, p. 83.

Material. Las Aguaditas river section (topotype material): CEGH-UNC 19150–19180, 25687; Loma de Los Piojos section: CEGH-UNC 19131–19149, 25688; a slab with one internal mould of dorsal valve and two internal moulds of ventral valve, CORD-PZ 8205. Tambolar section: CEGH-UNC 19181–19222.

Diagnosis. Shell moderately concavoconvex. Dorsal valve ornament of initially simple flattened primary ribs enlarged forward, repeatedly bifurcated to form conspicuous bundles separated by narrow interspaces. Teeth and socket ridges with crenulations. Denticles confined to the posterodorsal face of teeth. Dental plates absent. Ventral muscle bounded posteriorly by raised extra-muscular areas covered by coarse pseudopunctae. Dorsal muscle field gently to moderately impressed divided by a broad median ridge.

Fig. 7 a–v *Castellaroina fascifer* (Kayser). **a**, **b** Ventral valve ▶ external mould and latex cast (CEGH-UNC 19133); **c** dorsal valve exterior, latex cast (CEGH-UNC 19154); **d** ventral valve exterior, latex cast (CEGH-UNC 19131); **e** ventral valve exterior, latex cast (CEGH-UNC 19131); **f** ventral valve exterior (CEGH-UNC 19191); **g** dorsal valve exterior (CEGH-UNC 19151); **h** dorsal valve exterior, latex cast (CEGH-UNC 19177); **i**, **j** dorsal valve exterior and latex cast (CEGH-UNC 19141); **k** dorsal valve exterior (CEGH-UNC 1977); **l**, **p** ventral valve internal mould and lateral view (CEGH-UNC 25687); **m** dorsal valve exterior, latex cast (CEGH-UNC 19177); **n** dorsal valve exterior, latex cast (CEGH-UNC 19186); **o** ventral valve internal mould (CEGH-UNC 19148); **q**, **v** ventral valve internal mould and detail of latex cast showing accessory sockets (CEGH-UNC 19201); **r**–**u** ventral valve latex cast (**r**), detail of teeth and accessory sockets (**s**), ventral view of internal mould showing infilling of pits (**t**) and oblique view of the same mould showing denticles along the posterior wall of teeth (CEGH-UNC 19202). **a**–**r** *scale bar* 5 mm; **s**–**v** *scale bar* 2 mm

Remarks. The genus *Castellaroina* was erected as a subgenus of *Eostropheodonta* by Boucot (in Amos 1972, p. 11) with type species *Tropidoleptus fascifer* Kayser, 1897, from the Las Aguaditas (or "Aguadita") River, SW Jáchal. In erecting the subgenus, Boucot noted that *Castellaroina* resembles *Eostropheodonta* in most features but differs in lacking dental plates. Subsequently, Harper and Boucot (1978) elevated *Castellaroina* to generic rank based on its fasciculate ornament in which costellae increase by bifurcation, whereas in *Eostropheodonta* they increase mainly by insertion. The suite of species morphologically similar to *Eostropheodonta* but having parvicostellate ornament were included by Bergström (1968) in its new genus *Aphanomena*. Despite the generalized use of rib branching patterns in the taxonomy of "stropheodontoids", their taxonomic value has been a matter of debate since Rong and Cocks (1994) noted that ornament in *E. hirnantensis* is highly variable, with multicostellate, unequally parvicostellate or fascicostellate specimens even in the same population, concluding that this feature is of questionable taxonomic value at supraspecific level. On this basis, the family Eostropheodontidae proposed by Havlíček (1967) and redefined by Harper and Boucot (1978) was not recognized in the revised *Treatise* (Cocks and Rong 2000), and the genus *Aphanomena* was synonymized with *Eostropheodonta*, which was classified in the family Leptostrophiidae. The ornament of *Castellaroina fascifer*, however, is highly distinctive among the leptostrophiids and constitutes one of its diagnostic features. Examination of numerous well-preserved exteriors of both valves from different Precordilleran localities revealed a very narrow range of variation in the ribbing pattern. A peculiarity is that the ornament of the ventral valve is the exact counterpart of that of the dorsal. The dorsal valve is

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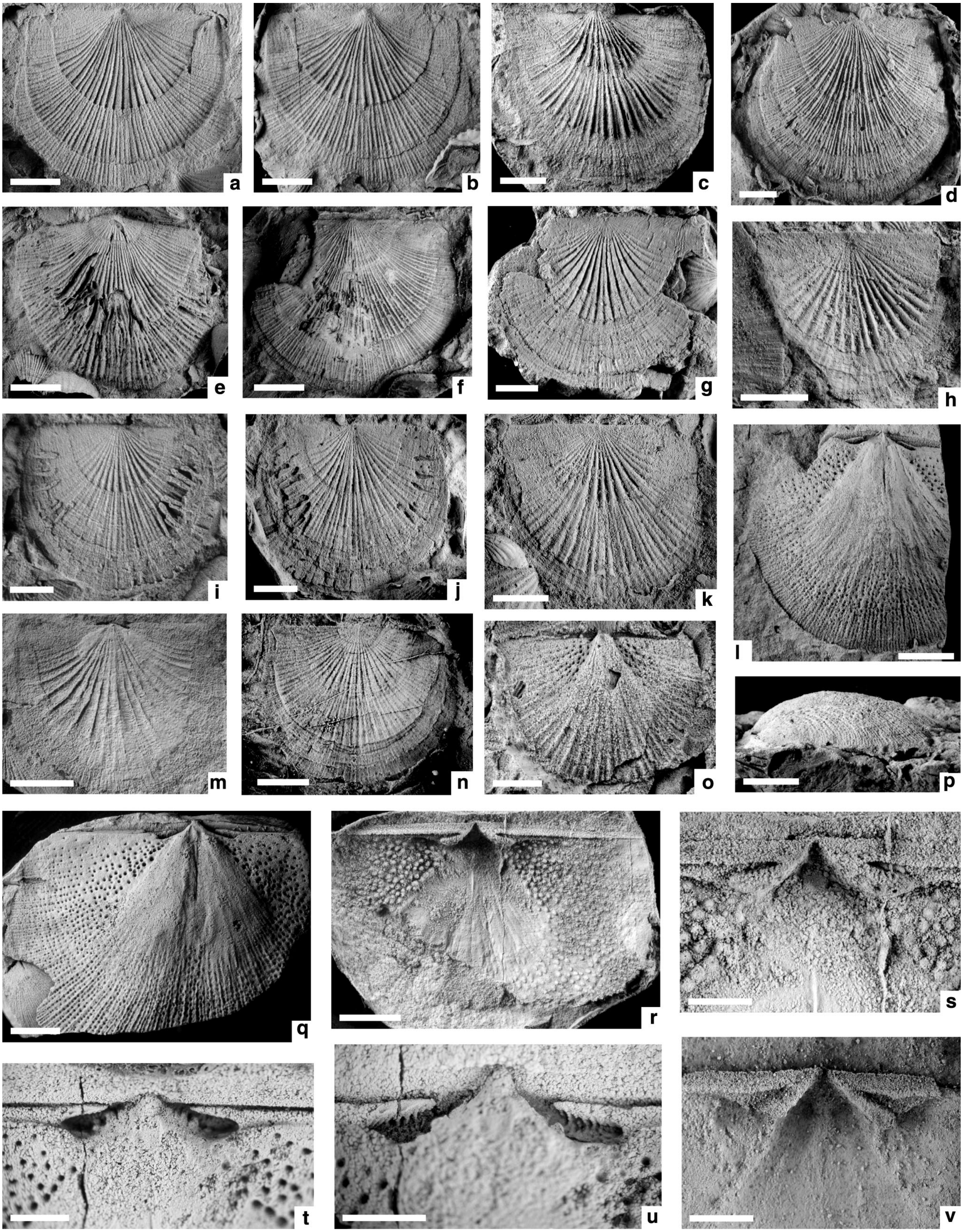

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characterized by initially simple, large, flat-topped costae which bifurcate repeatedly, originating a strongly fasciculate pattern. A remarkable feature is that the point of bifurcation coincides approximately with two marked growth lamellae developed at about one-third and two-third valve length, respectively. Most individuals also display a marginal area with diffuse radial ornament bearing closely spaced growth lines. In contrast, ornament on the ventral valve is always parvicostellate, the costellae increasing nearly exclusively by insertion. The primary costellae are simple and narrow, and they are separated by interspaces larger than ribs. As in the opposite valve, addition of new costellae occurs mostly at their intersection with the first and second prominent growth lamellae.

All specimens of *C. fascifer* of our collections lack dental plates. In the largest individuals, teeth are underlied by thick secondary deposits that are in continuity with the muscle bounding ridges, which could be interpreted as short plates. However, in our opinion, true dental plates are absent. This is the most important character to differentiate *Castellaroina* from *Eostropheodonta*. However, as shown below, variation in the dental plates from vestigial to short and thick observed in the Llandovery species *E. chilcaensis* brings into question the utility of this feature as a criterion for generic (and/or suprageneric) recognizance.

Impression of muscle fields in *C. fascifer* also appears as a rather variable feature. Examination of ontogenetic series, for instance, reveals that the ventral muscle field ranges from poorly defined in juvenile forms to deeply impressed and delimited laterally by a series of large pseudopunctae in medium to large specimens. Comparison between adult shells from different stratigraphic levels and localities also reveals a substantial intraspecific variation in the muscle fields. In this respect, *C. fascifer* clearly differs from *Palaeoleptostrophia*, *Eomegastrophia* Cocks and *Viodostrophia* Villas and Cocks, in which the ventral muscle field outline is always poorly defined. *Viodostrophia*, moreover, exhibits strong, straight muscle bounding ridges in both valves (cf. Villas and Cocks 1996), which are absent in *C. fascifer*.

The presence in *C. fascifer* of denticles for up to half hinge width mentioned in the abbreviated diagnosis of the revised *Treatise* (Cocks and Rong 2000, p. 282) has not been observed in the numerous specimens examined in this study. Instead, there are denticular plates (sensu Rong and Cocks 1994, p. 655) bearing 8–10 well-defined denticles on the posterodorsal faces of teeth and a few subcircular pits on their anterodorsal faces, whose counterpart is a series of prominent crenulations on the inner (anterior) socket ridges. In this respect, as Rong and Cocks (1994) pointed out, *Castellaroina fascifer* resembles *Palaeoleptostrophia*, from the Lower Silurian of Scotland and Wales, in having denticular plates and lacking dental plates. Together, *Eomegastrophia* Cocks and *Viodostrophia* are the only leptostrophiids undoubtedly lacking hinge-line denticles. *Castellaroina* shares with *Brachyprion leda* (Billings)—its type species—the absence of dental plates and the presence of denticular plates, but the latter differs in having a variable number of small denticles along the hinge line [e.g. *Brachyprion semiglobosa* (Davidson) reillustrated by Hoel (2011)]. In *Erinostrophia*, considered as a subgenus of *Brachyprion* by Hoel (2011), denticles are still more numerous, spreading along up to one-third of the hinge. Another difference is that in *Brachyprion* the diductor scars are shorter than in *C. fascifer* and tend to be suboval or kidney shaped in outline rather than subtriangular. The same is true for *Protomegastrophia*, recognized as a valid genus by Cocks and Rong (2000) on the basis of its strongly concavoconvex profile, but considered by Dewing (1999) and Hoel (2011) as a junior synonym of *Brachyprion* (*Brachyprion*).

Fig. 8 **a–o** *Castellaroina fascifer* (Kayser). **a** Ventral valve internal mould (CEGH-UNC 19152); **b**, **c** ventral valve internal mould and latex cast, details of cardinalia (CEGH-UNC 19199); **d** ventral valve internal mould (CEGH-UNC 19179); **e**, **f** dorsal valve internal mould and latex cast (CEGH-UNC 19131); **g** dorsal valve internal mould (CEGH-UNC 25688); **h–j** dorsal valve internal mould and latex cast, details of cardinalia (CEGH-UNC 19137); **k** dorsal valve internal mould (CEGH-UNC 19131); **l** dorsal valve internal mould (CEGH-UNC 19181); **m** dorsal valve internal mould (CEGH-UNC 19193); **n–o** dorsal valve internal mould and latex cast, details of cardinalia (CEGH-UNC 19192). **a**, **b**, **d–i**, **k–m**, **o** *scale bar* 5 mm; **j** *scale bar* 3 mm; **c**, **n** *scale bar* 2 mm ▶

The dorsal interior of *C. fascifer* is characterized by posteroventrally directed cardinal process lobes not united at their base, covered posteriorly by a chilidium supported by a thin ridge. In some species of *Eostropheodonta*, for instance *E. conradii* (Harrington), from the Hirnantian of Paraguay, the cardinal process lobes are on average more elongate than in other species of the genus (Benedetto et al. 2013). However, the cardinal process lobes in *Castellaroina* tend to be considerably more slender and elongated than in *Eostropheodonta*, in which they are nearly suboval in cross-section. This is particularly evident in *C. fuertensis*, whose cardinal process lobes are plate-like and widely separated medially. In *Palaeoleptostrophia* the cardinal process lobes are proportionally shorter, robust, closer one to another, and slightly converging on to the median ridge.

In *C. fascifer* the deep dental sockets are bounded by ridges whose internal faces are concave (half-pipe shaped), partially surrounding the teeth to prevent lateral valve skewing. The posterior socket ridges may be unusually strong, and they probably correspond to the "…pair of additional enigmatic ridges fused with the hinge line and posterior to the socket ridges" mentioned by Rong and

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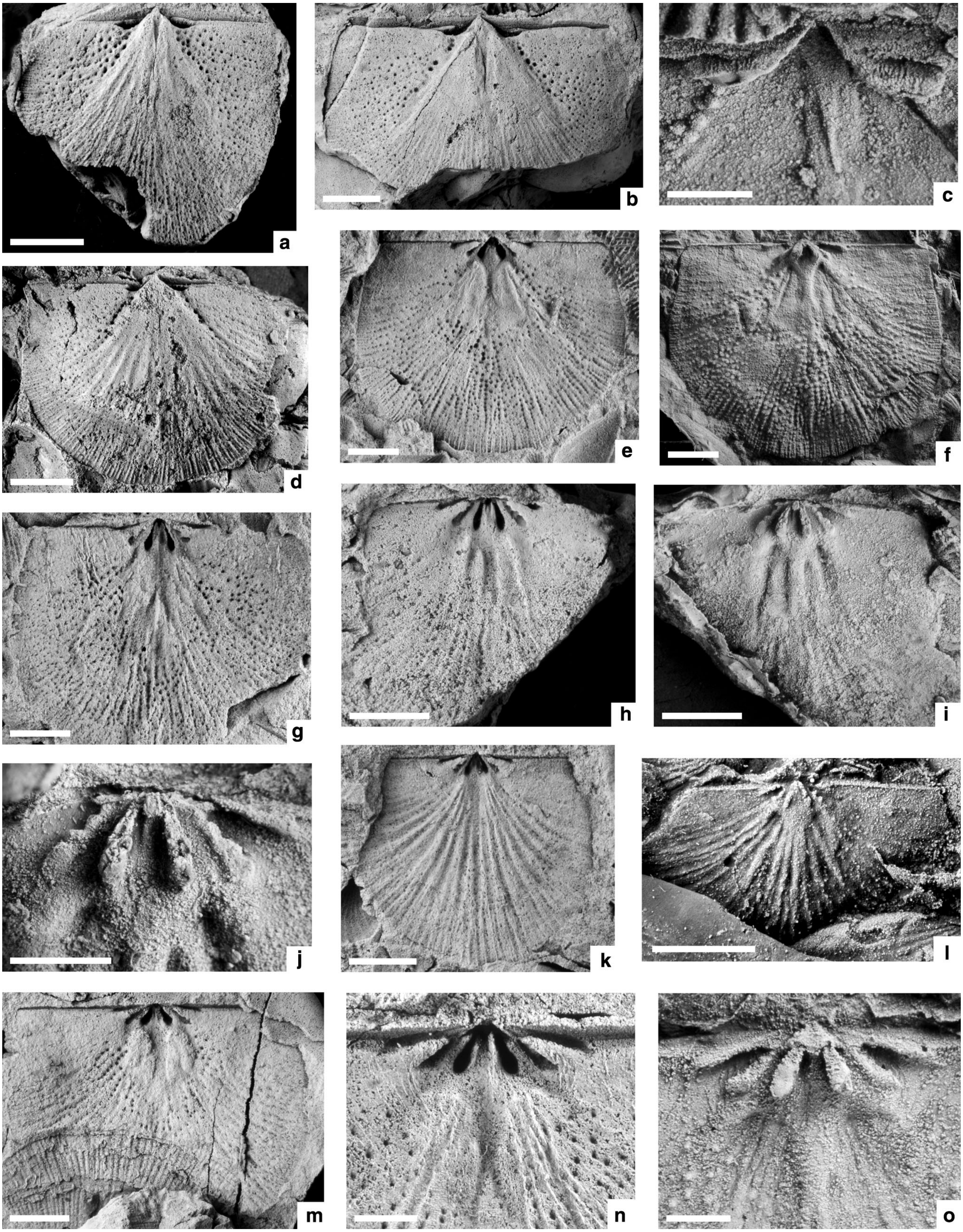

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Cocks (1994, p. 684). In fact, no other ridges are present behind the sockets. These ridges—named "accessory sockets" by Temple (1965, p. 410)—are accommodated in the ventral valve within a pair of elongate depressions excavated between the teeth and the posterior valve margin (Fig. 8n, o). The hypertrophy of these ridges in *C. fascifer* (as well as in its possible ancestor *Eostropheodonta chilcaensis*) is a substantial difference from *Palaeoleptostrophia*, in which the posterior pair of socket ridges is hardly developed [cf. illustration of cardinalia of the type species *P. jamesoni* (Reed) given by Rong and Cocks (1994), pl. 4, fig. 8]. Overall, the articulation system of *Castellaroina* fits within the third evolutionary stage of strophomenoids depicted by Cocks and Rong (2000), which is typically represented by *Eostropheodonta* and *Palaeoleptostrophia*. The posterior adductor scars are large, suboval, bounded posterolaterally by curved broad ridges; the anterior adductor scars are smaller and more weakly impressed than the posteriors, and often are divided by short faint trans-muscle septa. A broad, rounded median ridge merged with the front of the cardinal process dividing the dorsal muscle field is always present in both Precordilleran species. The muscle scars, bounding ridges, and dorsal median ridge of *C. fascifer* only differ from those seen in *Eostropheodonta* in being more prominent.

Castellaroina telimelensis Racheboeuf and Villeneuve, 1992, from Ludlow beds of Guinea, is quite similar to *C. fascifer* in size and ornament. In the African species, however, shells tend to be more transverse in outline and the profile of the ventral valve is less convex. Ornament of the two species is also similar, with costellae increasing by intercalation on the ventral valve and bifurcation on the dorsal. Unfortunately, the authors illustrate only two ventral exteriors corresponding to a juvenile and an adult specimen, but none of the distinctive dorsal valve. Internally, the ventral valves of the two species are nearly identical. The dorsal interior of *C. telimelensis* differs in having smaller cardinalia with proportionally shorter cardinal process lobes and the poorly impressed muscle field. The presence of crenulations or denticles on teeth and sockets is not mentioned, but probably they are not preserved because of the coarser grain of the moulds.

The leptostrophiid referred to as *Castellaroina* sp. from the Lipeón Formation of NW Argentina (Benedetto 1991) is represented by a single dorsal exterior and a ventral internal mould (Fig. 11u, v). No dorsal interiors have been found, and thus reliable specific identification cannot be made. The dorsal ornament is strongly fascicostellate with primary ribs initially simple, enlarged forwards and bifurcated at the first growth lamella and near the anterior third of the valve, generating a finely ribbed marginal area, as in *C. fascifer*. The Lipeón species differs from *C. fascifer* in its more transverse shell outline and the presence of a shallow median sinus on the dorsal valve, although post mortem deformation cannot be discarded. The ventral valve is similar to that of juvenile specimens of *C. fascifer* but differs in having short dental plates.

Fig. 9 **a–p** *Castellaroina fuertensis* nov. sp. **a** Ventral valve exterior, latex cast (CEGH-UNC 19249); **b** ventral valve external mould (CEGH-UNC 19250); **c** ventral valve external mould (CEGH-UNC 19262); **d** ventral valve exterior mould (CEGH-UNC 25689); **e** ventral valve latex cast (CEGH-UNC 25692); **f** ventral valve exterior latex cast (CEGH-UNC 19281); **g** ventral valve exterior mould (CEGH-UNC 19316); **h** dorsal valve internal mould (CEGH-UNC 25648); **i** ventral valve exterior mould (CEGH-UNC 19289); **j** dorsal valve exterior, latex cast (CEGH-UNC 19343); **k** ventral valve exterior, latex cast (CEGH-UNC 19304); **l** dorsal valve latex cast (CEGH-UNC 19279); **m** dorsal valve exterior latex cast (CEGH-UNC 19250); **n** ventral valve internal mould (CEGH-UNC 25691); **o** ventral valve internal mould (CEGH-UNC 25691); **p** ventral valve internal mould (CEGH-UNC 19307). **a–h**, **j–p** *scale bar* 5 mm; **i** *scale bar* 2 mm ▶

Castellaroina fuertensis **nov. sp.** (Figs. 9a–p, 10a–o)

Derivation of name. After Cerro del Fuerte, the type locality of the new species.

Holotype. An internal mould of a dorsal valve CEGH-UNC 19292 from the Cerro del Fuerte section.

Paratypes. Ventral valve CEGH-UNC 19262 from Talacasto (Quebrada Ancha section); internal mould of ventral valve CEGH-UNC 25662 from the Cerro del Fuerte section; internal mould of ventral valve CEGH-UNC 19237 from Talacasto (Salto Macho section); external mould of dorsal valve CEGH-UNC 19289 from Cerro del Fuerte; dorsal external and internal moulds CEGH-UNC 19252 from the Talacasto area (Salto Macho section).

Material. Talacasto area: Quebrada Ancha section CEGH-UNC 19339–19346, 19257–19270, 26648–26649; Salto Macho section CEGH-UNC 19231–19239, 19248–19251, 19254–19256; Cerro del Fuerte, CEGH-UNC 19284–19328, 25689–25691; Las Aguaditas section CEGH-UNC 19329–19333; Río de Las Casitas section CEGH-UNC 19223–19227; Quebrada Las Tunas section CEGH-UNC 19274–19280; Cerro La Chilca section, CEGH-UNC 25689.

Type locality and horizon. Cerro del Fuerte, Los Espejos Formation, approximately between 300 and 330 m above the contact with the La Chilca Formation.

Diagnosis. Gently concavoconvex shell with alate cardinal extremities. Ventral valve finely and uniformly parvicostellate, dorsal valve ramicostellate. Posterolateral rugae usually present. Teeth crenulated lacking denticles. Dental plates absent. Thick ventral process continuous with low blade-like myophragm. Ventral muscle field large, subtriangular, flabellate, bounded by ridges formed by coalescence of coarse pseudopunctae. Adductor scars deeply

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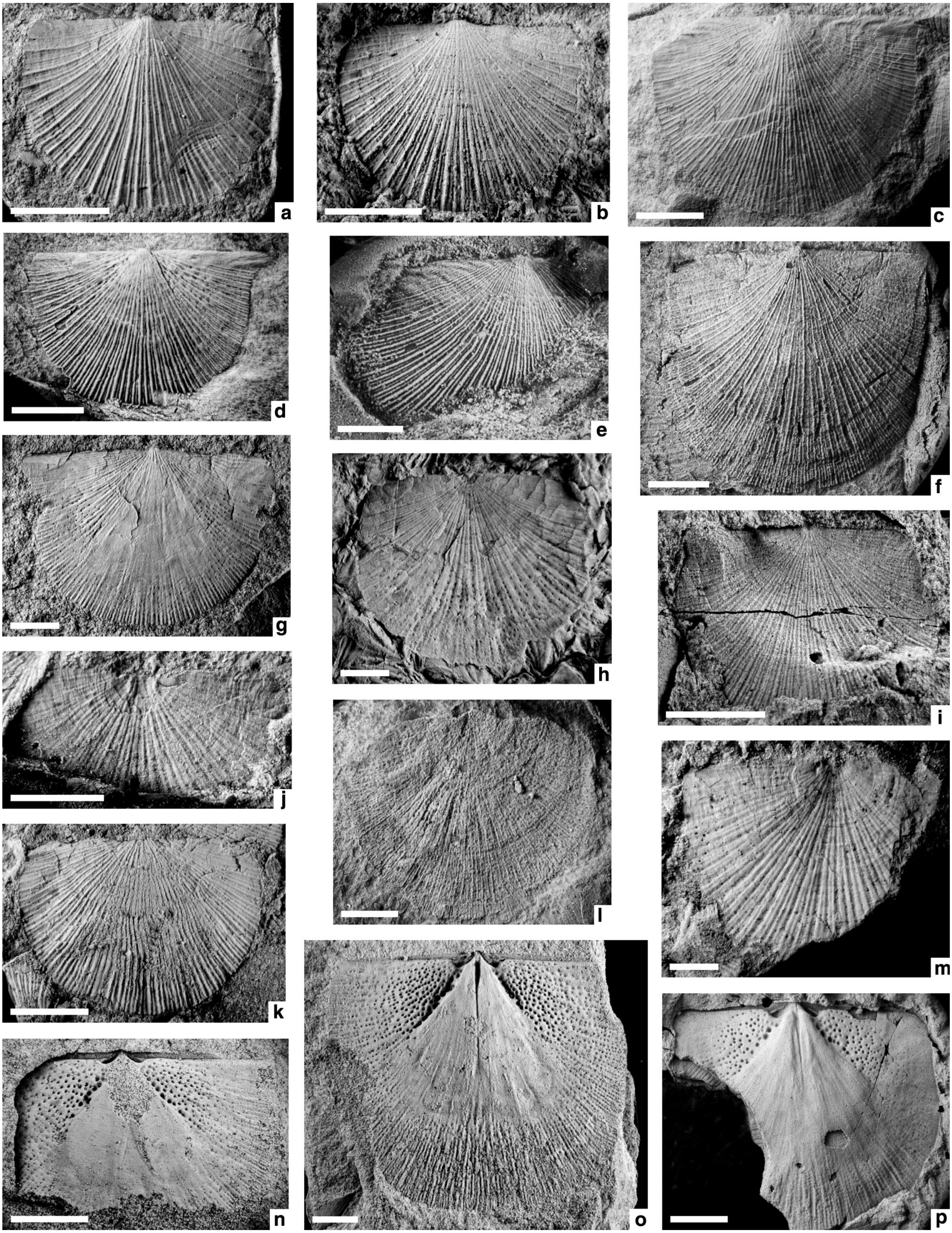

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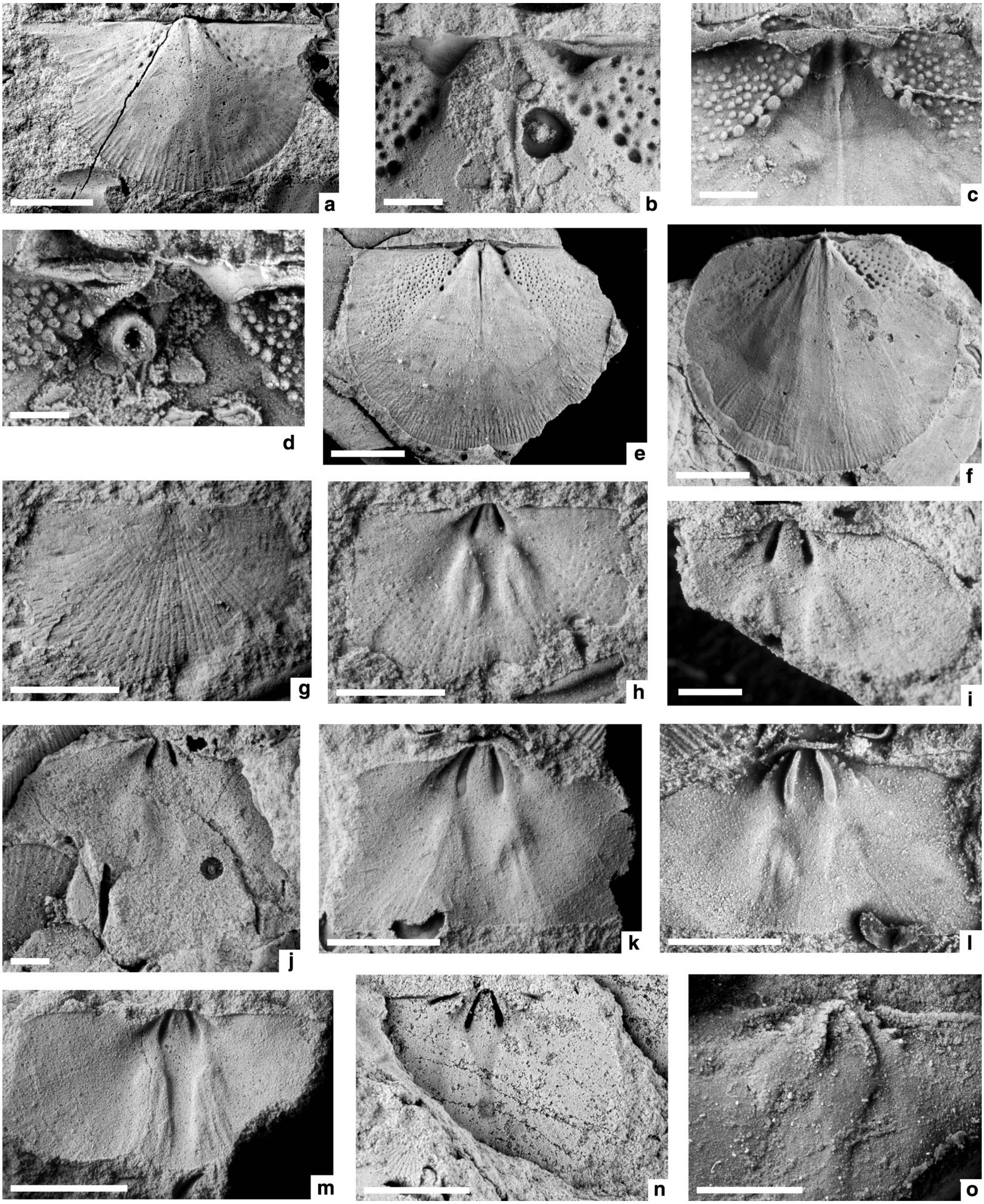

impressed posteriorly, their anterior margins varying from indistinct to fairly well defined. Cardinal process lobes slender, blade-like, slightly diverging and widely separated from one another. Inner pair of socket ridges with few spine-like crenulations; posterior socket ridges stronger than anterior, lacking crenulations and denticles.

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◀ **Fig. 10** **a**–**o** *Castellaroina fuertensis* nov. sp. **a** Ventral valve internal mould (CEGH-UNC 19237); **b**, **d** ventral valve internal mould, and latex cast showing cardinalia (CEGH-UNC 19297); **c** ventral valve interior, latex cast (CEGH-UNC 19307); **e** ventral valve internal mould (CEGH-UNC 19293); **f** ventral valve internal mould (CEGH-UNC 25690); **g**, **h** dorsal valve, internal and exterior mould (CEGH-UNC 19252); **i** dorsal valve internal mould (CEGH-UNC 19301); **j** dorsal valve internal mould (CEGH-UNC 19286); **k**, **l**, dorsal valve, internal mould and latex cast (Holotype CEGH-UNC 19292); **m** dorsal valve internal mould (CEGH-UNC 19321); **n**, **o** dorsal valve internal mould and latex cast, details of cardinalia (CEGH-UNC 19253). **a**, **e**–**h**, **k**–**n** *scale bar* 5 mm; **b**–**d**, **i**, **j**, **o** *scale bar* 2 mm

Description. Shell gently concavoconvex of semielliptical outline; small specimens wider than long (about 75 % as long as wide) becoming nearly as long as wide in largest individuals due to markedly allometric growth. Largest shells about 22 mm long and 25 mm wide; maximum width slightly anterior to hinge line; cardinal angles auriculate to mucronate, but in some large shells alae are shorter or poorly developed, the cardinal angles becoming nearly orthogonal. Ventral umbo low, dorsal umbo undifferentiated. Ventral interarea very low, apsacline, dorsal interarea lineal. Radial ornament in ventral valves of juvenile specimens unequally parvicostellate, with 1–4 smaller costellae between the stronger, rounded primary costellae; with growth, ornament becomes subequally and finely parvicostellate with 13–15 costellae per 3 mm measured on the anterior third of valve. Dorsal valve with several orders of costellae arising principally by bifurcation (ramicostellate pattern). Posterolateral rugae usually well defined in most specimens. Concentric ornament of fine, closely spaced growth lines.

Ventral interior with teeth relatively small, transversely elongated, flaring at up to 120°. Dental plates absent. Anteromedial faces of teeth with few deep subcircular pits which interlocked with spine-like denticles along the crest of the anterior socket ridges. Posterodorsal faces with a series of subvertical denticles (rarely preserved), which lack counterparts in the sockets. Pedicle callist present, transversely striated. Robust plate-like ventral process in continuity with myophragm. Ventral muscle field large, subtriangular, deeply impressed posteriorly, divided longitudinally by a variably developed, usually blade-like myophragm which dies out at about two-thirds of muscle field. Diductor scars large, flabellate, with anterior margin ranging from indistinct to gently impressed occupying about 60–65 % shell length. Adductor field narrow, elongate oval, raised on the valve floor, entirely enclosed by diductor scars. Vascular system preserved in some individuals as straight radial canals, which initiate a short distance anterior to the muscle field bifurcating near the margin. Extramuscular area with largest pseudopunctae on both sides of muscle field, weakly marked by external ornament with the exception of largest valves in which inner ribs are accentuated by small, aligned pseudopunctae. Slightly divergent proximal trunks of *vascula myaria* present in well-preserved interiors.

Dorsal interior with ventrally projected slender blade-like cardinal process lobes (10–15 % as wide as long), widely separated at their base, diverging at 20°–25° to one another. Minute ridge between the cardinal process lobes supporting posteriorly a reduced chilidium. Cardinalia raised on low notothyrial platform merged anteriorly with a wide flat median ridge tapering and terminating at anterior margin of the muscle field. Anterior socket ridges as slender as the cardinal process lobes, straight, diverging about 40° to the hinge line, bearing a series of 4–6 spine-like crenulations aligned on their tops; posterior (outer) socket ridges more prominent than anterior, almost parallel to the hinge (maximum divergence up to 10°). Dental sockets slightly concave to nearly planar in cross-section, their posterior wall lacking denticles. Adductor field slightly to moderately impressed in mature individuals, occupying about 30 % valve length; posterior adductor scars elongate suboval, larger than anterior, radially striated, separated from the small rounded anterior adductor scars by variably developed oblique ridges. Internal surface almost smooth or faintly marked by external ornament.

Remarks. Externally, *C. fuertensis* differs from *C. fascifer* in the less convex ventral valve, the alate cardinal extremities and the well-developed posterolateral rugae. Ornament in *C. fuertensis* is finer and more uniform than in *C. fascifer*. Adult specimens of *C. fascifer* are clearly distinguishable by their primary costellae being far more prominent and less numerous, often lacking intercalations on the posterior third of the valve; with growth, however, rib density near the anterior margin becomes quite similar in the two species. The main difference in ornament lies in the dorsal valve: although in *C. fuertensis* costellae increase in number by branching, they are much finer than in *C. fascifer*, and their width is approximately uniform, generating a typical ramicostellate pattern. Ventral interiors of the two Precordilleran species are very similar, and as stated above, medium-sized to large specimens can only be differentiated on the basis of the stronger convexity in *C. fascifer*. The length and proportions of the ventral muscle scars, as well as the angle of divergence of bounding ridges, are quite variable in both species, but on average the diductor muscle scars are best delineated anteriorly in *C. fuertensis*. In addition, teeth in *C. fuertensis* are smaller and less elongated transversally than in *C. fascifer*, and denticles are stronger (and consequently better preserved) in the latter. Dorsal interiors of *C. fuertensis* can be distinguished from *C. fascifer* by the slender and proportionally more elongated cardinal process lobes, the less prominent anterior socket ridges bearing spine-like

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crenulations and the stronger dorsal muscle bounding ridges, especially in larger valves. *Castellaroina telimelensis* Racheboeuf and Villeneuve, from the Upper Silurian of Guinea, is similar to *C. fuertensis* except that it has short and thick dental plates—which confirms that, as in *Eostropheodonta*, development of dental plates in *Castellaroina* is variable—and the cardinal process lobes are less elongated.

Genus ***Eostropheodonta*** Bancroft, 1949

Type species. Orthis hirnantensis M'Coy, 1851. Late Ordovician (Hirnantian), Hirnant Formation, Wales.

Eostropheodonta chilcaensis chilcaensis (Benedetto, 1995) (Fig. 11 a–t)
1995 *Aphanomena chilcaensis*, Benedetto, 1995, p. 445, pl. 60, figs. 8–17

Material. Cerro La Chilca, CEGH-UNC 7226–7230, 7241–7249, 7344, 7351–7354; Agua de Felipe CEGH-UNC 7231–7240; El Refugio (c. 1.5 km south of Loma de Los Piojos) CEGH-UNC 7211–7225.

Emended diagnosis. Medium-sized, gently convex shell with unequally parvicostellate ornament in younger specimens and subuniform parvicostellate ornament in mature specimens. Costae increasing in number by intercalation on the ventral valve and by bifurcation and intercalation in the dorsal valve. Dental plates short and thick, occasionally absent. Ventral process strong. Cardinal process lobes plate-like, slightly divergent. Anterior socket ridges often crenulated; posterior socket ridges stronger than anterior, interlocking with deep ventral accessory fossettes located behind teeth.

Remarks. This material was referred originally to the genus *Aphanomena*, but following the arguments of Rong and Cocks (1994) it is reassigned here to *Eostropheodonta*. A key feature of *Eostropheodonta* is the presence of well-developed dental plates. In the type species *E. hirnantensis* (M'Coy) their length is rather variable, as can be seen, for example, in the specimens from the Hirnantian of Wales and Poland illustrated by Temple (1965), ranging from fairly long and relatively slender to short and thick (cf. pl. 19 figs. 1 and 3, and pl. 17 figs. 1 and 4). In the Precordilleran material short dental plates are usually present (Fig. 11j, k, n, o), although in juvenile specimens they are very short or even absent. *E. chilcaensis* also shares with the type species of *Eostropheodonta* the absence of denticles on the posterior margins of sockets and the prominence of the accessory sockets in the ventral valve interlocking with the posterior socket ridges. Other features of the Precordilleran species, such as crenulated teeth, elongated and posteroventrally directed cardinal process lobes, and large but anteriorly poorly delineated ventral muscle field, are all characters shared not only with *Eostropheodonta* but also with other basal leptostrophiids. The presence in *E. chilcaensis* of features distinctive of *Castellaroina* (e.g. morphology of socket plates, strong ventral process, incipient costellae bifurcation in the dorsal valve) leaves this species as its possible ancestor, as previous cladistic analysis shows. On balance, we refer this species to *Eostropheodonta* based on the presence of short dental plates. Although shell ornamentation is somewhat difficult to use as a taxonomic criterion, the parvicostellate ornament of the dorsal valve and the lack of defined bundles precludes the assignment of the La Chilca material to the genus *Castellaroina*.

Fig. 11 a–t *Eostropheodonta chilcaensis chilcaensis* (Benedetto). ▶ **a** Ventral valve exterior, latex cast (CEGH-UNC 7234a); **b** ventral valve exterior, latex cast (CEGH-UNC 7234b); **c** ventral valve exterior, latex cast (CEGH-UNC 7235); **d** ventral valve exterior, latex cast (CEGH-UNC 7217); **e** ventral valve exterior, latex cast (CEGH-UNC 7248); **f** ventral valve exterior, latex cast (CEGH-UNC 7239); **g** dorsal valve exterior (CEGH-UNC 7218); **h** dorsal valve, external mould (CEGH-UNC 7219); **i** ventral valve exterior, latex cast (CEGH-UNC 7245); **j**, **k** dorsal valve, internal mould, and latex cast (CEGH-UNC 7342); **l**, **p** dorsal valve internal mould, and latex cast (CEGH-UNC 7244); **m** dorsal valve internal mould (CEGH-UNC 7215); **n**, **o** ventral valve, internal mould and latex cast (CEGH-UNC 7229); **q**, **r** dorsal valve, internal mould and latex cast showing detail of cardinalia (CEGH-UNC 7215); **s** dorsal valve, internal mould (CEGH-UNC 7228); **t** ventral valve, internal mould (CEGH-UNC 7212); **u**, **v** *Castellaroina* sp. (Lipeón Formation). **u** Dorsal valve exterior, latex cast (CEGH-UNC 2659); **v** ventral valve, internal mould (CEGH-UNC 3660). **k**, **l**, **m**, **p**, **r** *scale bar* 2 mm; **a–j**, **n**, **o**, **q**, **s–v**, *scale bar* 5 mm

***Eostropheodonta chilcaensis parvula* nov. subsp.** (Fig. 12a–o)
1995 *Aphanomena* cf. *mullochensis* (Reed, 1917), Benedetto, 1995, p. 448, pl. 60, figs. 1–7.

Derivation of name. Latin (nominative, feminine, singular) *parvula*, little, small.

Holotype. Internal mould of dorsal valve CEGH-UNC 7266 from Río Escondido.

Paratypes. Ventral internal moulds CEGH-UNC 7250 and 25682, and a ventral exterior CEGH-UNC 7377 from Río Escondido; dorsal external mould CEGH-UNC 25681 from Cerro del Fuerte (western slope of Cerro La Silla).

Material. Cerro Cumillango CEGH-UNC 2034–2041; Río Escondido CEGH-UNC 7266–7288; Cerro del Fuerte (western slope of Cerro La Silla) CEGH-UNC 25683–25686.

Type locality and horizon. Lower part of the La Chilca Formation, Río Escondido section, approximately 10 km east of Jáchal City.

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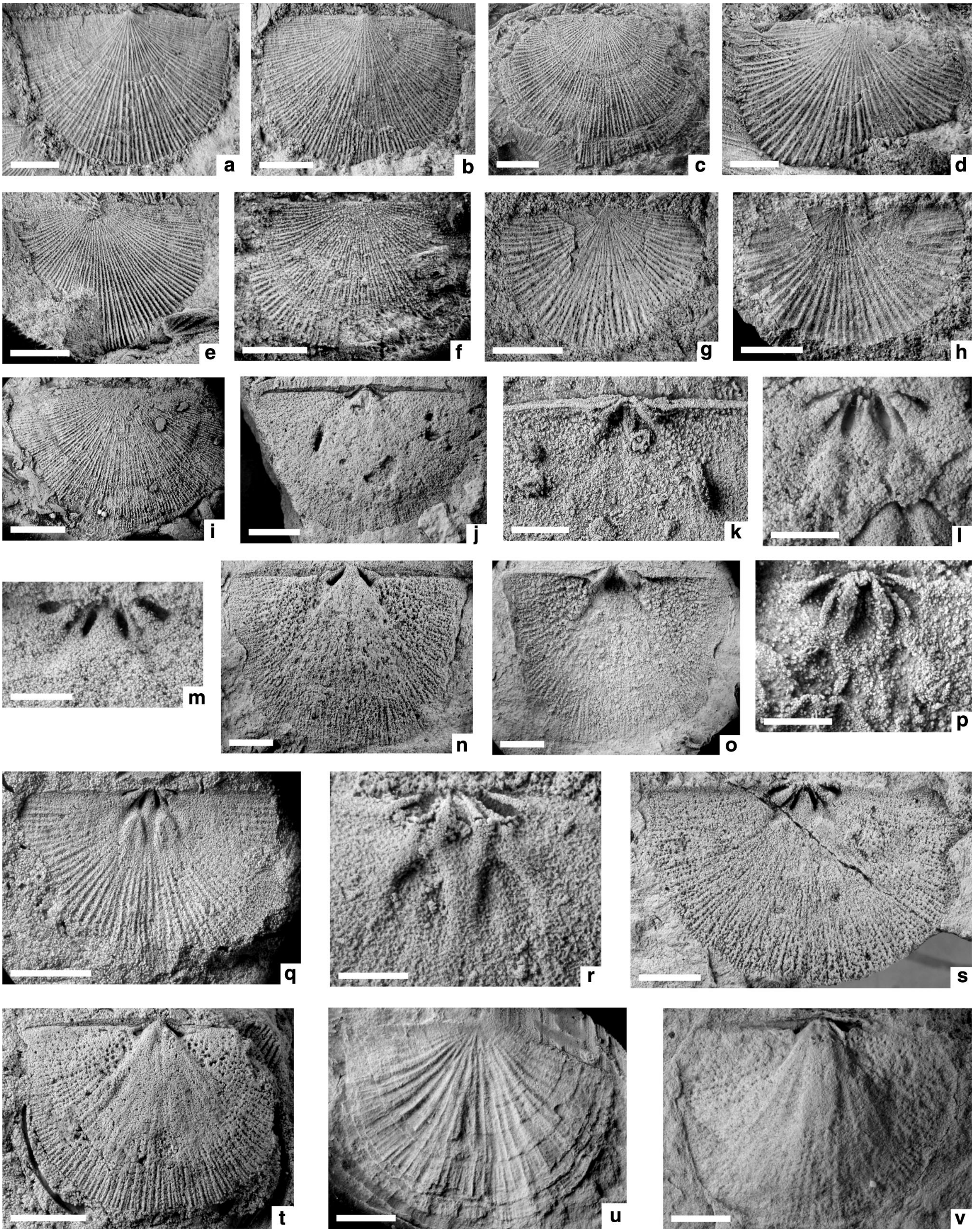

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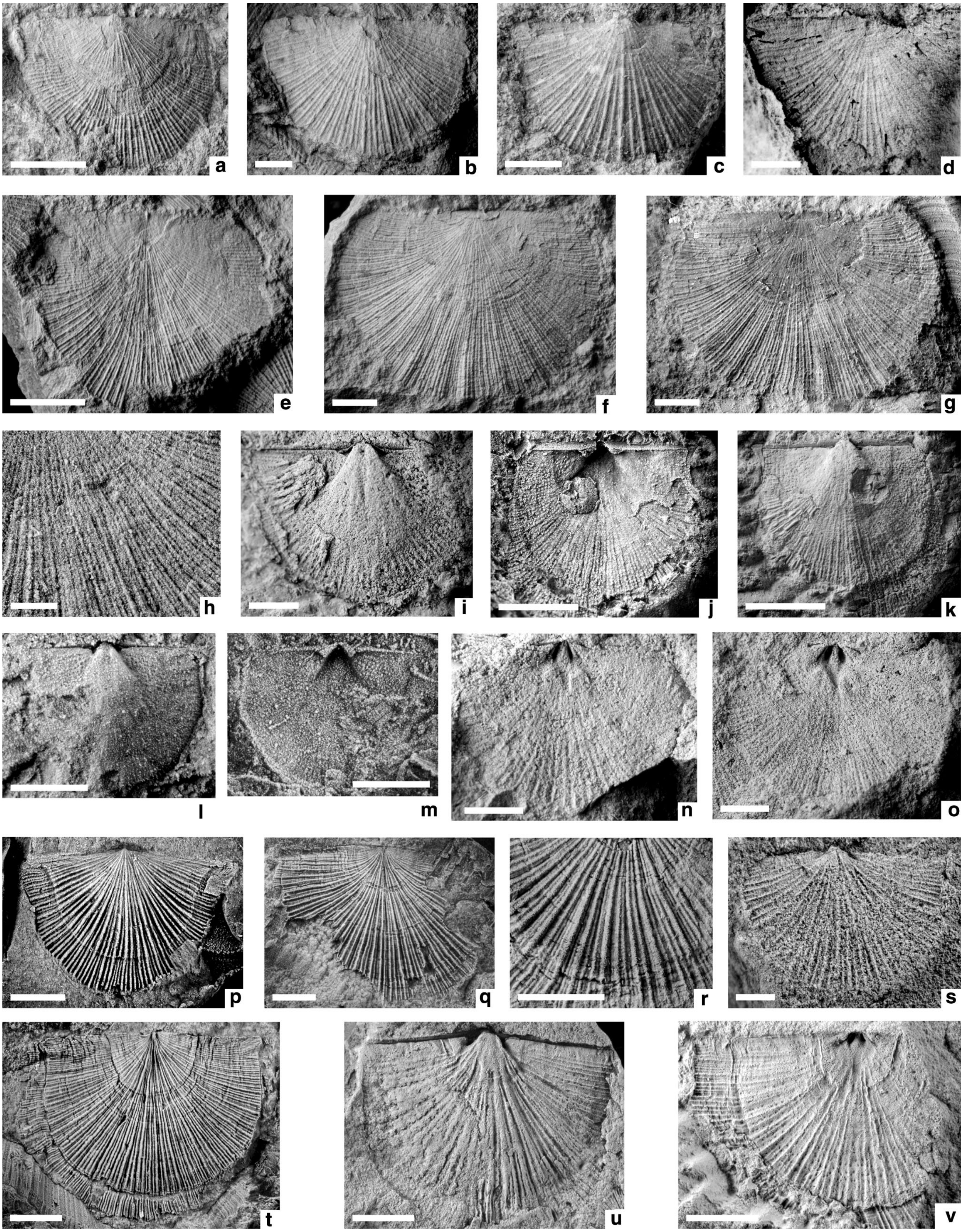

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◀ **Fig. 12** **a**–**o** *Eostropheodonta chilcaensis parvula* nov. subsp. **a** Ventral valve external mould (CEGH-UNC 25681); **b** ventral valve exterior (CEGH-UNC 7277); **c** ventral valve exterior, latex cast (CEGH-UNC 7279); **d** dorsal valve exterior, latex cast (CEGH-UNC 25686); **e** dorsal valve exterior, latex cast (CEGH-UNC 25682); **f**–**h** dorsal valve, external mould, latex cast, and detail of ornament (CEGH-UNC 25683); **i** ventral valve, internal mould (CEGH-UNC 7270); **j**, **k** ventral valve internal mould and latex cast (holotype CEGH-UNC 7266); **l**, **m** ventral valve internal mould and latex cast (CEGH-UNC 25685); **n** dorsal valve internal mould (CEGH-UNC 25684); **o** dorsal valve, internal mould (CEGH-UNC 2035); **p**–**v** *Eostropheodonta hirnantensis*. **p** Ventral valve exterior, latex cast (CEGH-UNC 21121); **q**, **r** dorsal valve exterior, latex cast, and detail of ornament (CEGH-UNC 25667); **s** internal mould of juvenile ventral valve (CEGH-UNC 25669); **t** dorsal valve exterior, latex cast (CEGH-UNC 25666); **u** ventral valve, internal mould (CORPZ-8272); **v** dorsal valve internal mould (CEGH-UNC 25668). **b**–**d**, **h**, **i**, **o**, **r**, **s** *scale bar* 2 mm; **a**, **e**–**g**, **j**–**n**, **p**, **q**, **t**–**v** *scale bar* 5 mm

Diagnosis. Shell small, semielliptical, gently concavoconvex with finely parvicostellate or multicostellate radial ornament. Dental plates varying from short and thin to vestigial. Ventral and dorsal muscle fields faintly impressed. Socket ridges blade-like.

Remarks. This material has been described in a separate paper (Benedetto 1995) and need not be repeated here. However, new material collected subsequently allows us to make some comments related mainly to its ontogeny. This small form is the first leptostrophiid that appears in the La Chilca Formation. Originally it was referred to as *Aphanomena* cf. *mullochensis* (Reed) by Benedetto (1995), but according to the synonymy proposed by Rong and Cocks (1994) it should be transferred to *Eostropheodonta*. However, generic assignment of these specimens is debatable since the dental plates range from vestigial to short and thin. As stated above, the dental plates in *Eostropheodonta* show a relatively high intraspecific variability even among specimens from the same beds, their length and thickness varying not only among species but also through ontogeny. In the sample of *E. hirnantensis* from the Don Braulio Formation, for instance, adult specimens display long and robust dental plates but they are short and thin in the juvenile shells (Fig. 12s). We consider that reduction of dental plates in our material is insufficient to separate it as a new genus, especially considering that in most other features it is indistinguishable from *Eostropheodonta* and closely comparable to *E. chilcaensis*. Mature shells of *E. chilcaensis parvula* are virtually identical to the juveniles of *Eostropheodonta chilcaensis* (Benedetto) from higher levels of the same formation, and the two forms have been found to be gradational in many characters. The wide overlap existing between the extreme morphologic variants of the two forms precludes their separation as different species. On the basis of a comparison of mature specimens, our material is considered here as a subspecies of *E. chilcaensis* from which it can be differentiated in its combination of smaller average size, thinner and often vestigial dental plates, poorly defined muscle fields, and more delicate cardinalia with posterior socket ridges of approximately equal thickness as anterior. As stated above, we interpret this subspecies as evolved by paedomorphosis from *E. hirnantensis*, and that reduction of dental plates could be explained in this way. *E. chilcaensis parvula* nov. subsp. is comparable to *Eostropheodonta whittingtoni* Lamont [(=*Eostropheodonta* cf. *mullochensis* (Reed)] described by Williams (1951) from the lower Llandovery of Wales, in its parvicostellate ornament, abbreviated dental plates, and slender cardinal process lobes. It can be differentiated from the Welsh species in lacking concentric rugae and cardinal alae. *E.* cf. *mullochensis* (Reed) from Llandovery beds of the El Horno Formation of Venezuela (Boucot et al. 1972) is very similar in size, outline, ornament and cardinalia, but differs in having longer and more slender dental plates. It is interesting to note that, in a juvenile Venezuelan specimen illustrated by the authors (p. 687, pl. 24, fig. 9), the dental plates are much shorter than in mature specimens.

Conclusions

Castellaroina fascifer is confined to the upper third of the Los Espejos Formation and the uppermost levels of the Tambolar Formation of the Precordillera basin. According to the graptolites, conodonts and palynomorphs, its age is essentially Ludlow, but the possibility that it extends into the Pridolian cannot be discarded. *C. fuertensis* nov. sp. has been reported from lower Ludlow strata of the Los Espejos Formation.

Castellaroina is closely allied with *Eostropheodonta* from which it can be differentiated on the basis of its peculiar dorsal ornament and absence of dental plates. Parsimony analysis shows that *Eostropheodonta hirnantensis* is closest to the outgroup and ancestral to the entire leptostrophiid clade. After the late Hirnantian biotic crisis, leptostrophiids in the Afro–South American Realm underwent a radiation, as is shown by the rich material from the Precordillera basin. It is inferred that the end-Ordovician *E. hirnantensis* is the basal form of the lineage, leading to *Castellaroina* through a series of gradual changes documented in the Llandovery subspecies of *Eostropheodonta chilcaensis*. We postulate that evolutionary trends along this lineage were directed mainly by heterochronic processes. The small size and the juvenile features exhibited by adults of *Eostropheodonta chilcaensis parvula*, of Rhuddanian age, suggest a paedomorphic origin of the Precordilleran leptostrophiid stock. Subsequently, peramorphic processes seem to have been dominant.

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Appendix

List of coded characters and character states used in cladistic analysis:

1. SHELL CONVEXITY. 0: biplanate or gently concavoconvex; 1: moderately concavoconvex; 2: strongly concavoconvex
2. ORNAMENT. 0: parvicostellate both valves; 1: fascicostellate both valves; 2: parvicostellate ventral valve, fascicostellate/ramicostellate dorsal valve; 3: "nervostrophiid" type
3. CONCENTRIC RUGAE. 0: absent; 1: present on the posterolateral areas; 2: present on the entire surface
4. VENTRAL MUSCLE FIELD BOUNDING RIDGES. 0: absent or very faint; 1: formed by prominent pseudopunctae; 2: continuous ridges
5. VENTRAL MUSCLE FIELD OUTLINE. 0: short, triangular or subcircular, poorly defined; 1: large flabellate, open anteriorly; 2: bilobate or kidney-shaped
6. VENTRAL MUSCLE FIELD SURFACE. 0: smooth; 1: partitioned by radial ridges
7. DENTAL PLATES. 0: present, well developed; 1: short or vestigial; 2: absent (teeth unsupported); 3: absent (teeth absent)
8. TEETH. 0: noncrenulate; 1: with crenulations only; 2: with crenulations and denticles (denticular plates); 3: absent
9. HINGE. 0: nondenticulate; 1: partially denticulate (one-third to one-half hinge length); 2: almost entirely denticulate
10. SOCKET RIDGES. 0: anterior and posterior ridges present; 1: anterior socket ridges only, located close to the cardinal process lobes; 2: both absent
11. VENTRAL PROCESS. 0: absent; 1: present
12. DELTHYRIAL CHAMBER. 0: absent; 1: present
13. VENTRAL SOCKETS BEHIND TEETH. 0: absent; 1: present
14. PROCESS PITS. 0: absent; 1: present
15. DORSAL MUSCLE FIELD. 0: not impressed or faintly impressed; 1: deeply impressed
16. DORSAL MUSCLE BOUNDING RIDGES. 0: absent or faint; 1: strong
17. DORSAL MEDIAN RIDGE. 0: low, short; 1: broad ridge; 2: blade-like
18. POSTERIOR DORSAL SOCKET RIDGE. 0: low; 1: strong; 2: absent
19. CARDINAL PROCESS LOBES. 0: elongate or plate-like, ventrally directed; 1: robust, almost equidimensional, ventrally directed; 3: posteriorly directed

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