

Chaniella, a new lower Tremadocian (Ordovician) brachiopod from northwestern Argentina and its phylogenetic relationships within basal rhynchonelliforms

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Abstract The new rhynchonelliform brachiopod *Chaniella pascuali* n. gen. n. sp. is described from the lower Tremadocian Guayoc Chico Group of northwestern Argentina. Cladistic analysis shows that *Chaniella* is closest to the billingsellides *Protambonites* and *Korinevskia*. The particular combination of features of the new genus, in particular the presence of narrow lateral deltidial plates instead of a complete pseudodeltidium, led to the designation of the new monotypic family Chaniellidae. Parsimony analysis supports the separation of clitambonitidines and billingsellidines as monophyletic clades within the order Billingsellida and places the protorthide *Arctohedra* and the orthides *Jivinella* and *Bohemiella* close to the ancestry of the billingsellides.

Keywords Ordovician · Brachiopods · Argentina · Phylogeny

Zusammenfassung Aus der Guayoc Chico-Gruppe des unteren Tremadociums in Nordwest-Argentinien wird der neue rhynchonelliforme Brachiopode *Chaniella pascuali* n. gen. n. sp. beschrieben. Eine kladistische Analyse zeigt, dass *Chaniella* den billingselliden Brachiopoden *Protambonites* und *Korinevskia* am nächsten steht. Die spezielle Kombination von Merkmalen dieser neuen Gattung, insbesondere der schmalen lateralen Deltialplatten anstelle eines vollständigen Pseudodeltidiums, führt zur Aufstellung der neuen monotypischen Familie Chaniellidae.

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Parsimony-Analysen bestätigen die Aufspaltung von Clitambonitiden und Billingsellidinen als monophyletische Kladen innerhalb der Ordnung Billingsellida und plazieren den Protorthiden *Arctohedra* und die Orthiden *Jivinella* und *Bohemiella* nahe des Ursprungs der Billingselliden.

Schlüsselwörter Ordovizium · Brachiopoda · Argentinien · Phylogenie

Introduction

Although rhynchonelliform (“articulated”) brachiopods had already achieved considerable morphological diversification during the Cambrian, their major radiation pulse did not occur until the Darriwilian, when most of the typical Paleozoic higher taxa appeared (Harper et al. 2004). Such a diversification postdates the extinction of several distinctive Early and Middle Cambrian brachiopods such as chileids, obolellids, naukatids, kutorginids, bohemiellids, and protorthoideans. In this context, discovery of new Late Cambrian-early Tremadocian brachiopods is critical to fill the gap between these two radiation phases and to search for the origin of clades involved in the Ordovician radiation.

By the Late Cambrian, the distinctive order Billingsellida started to diversify and spread geographically from low to high latitudes originating in the Early Ordovician the Baltic clitambonitoidean lineage and the more cosmopolitan polytoechoioidean lineage. Classified among the orthides until recently—with which they share numerous features—the Billingsellida were reassigned by Williams et al. (1996) to the class Strophomenata mainly on the basis of the presence of a delthyrium cover (pseudodeltidium/deltidium), a chilidium, and especially the possession of a

laminar secondary shell layer. In the revised *Treatise* classification (Williams and Harper 2000a, b), both clitambonitoideans and polytoechioideans were grouped into the suborder Billingsellidina, but subsequently Popov et al. (2001), in reassessing the phylogeny of tritoechiids and related genera, considered unlikely that billingsellidines are polyphyletic. On the other hand, they presented evidence supporting that tritoechiids and billingsellidines form a monophyletic clade.

The new genus *Chaniella* described in this paper is interesting as it displays some features (e.g., laterally disposed deltidial plates) that so far have been recorded in some of the earliest representatives of the superfamily Clitambonitoidea, such as *Atelelasma* Cooper, 1956 and *Apomatella* Schuchert and Cooper, 1931, combined with a well-developed pseudospondylium in the ventral valve like that seen in the tritoechiids, and a cardinalia closely comparable to that of *Protambonites* Havlíček (in Havlíček and Jospait 1972). The finding of this peculiar brachiopod in the lower Tremadocian of the Andean Gondwana shed light on the complex and still not well-resolved phylogenetic relationships among billingsellidines and basal rhynchonelliform taxa.

Fossiliferous locality, stratigraphy, and age

The thick, continuous, and richly fossiliferous Upper Cambrian-Lower Ordovician clastic shelf deposits of northwestern Argentina provide an excellent basis for studying the early stages of brachiopod diversification in temperate to cold waters of Gondwana (Benedetto 1998, 2007; Benedetto and Sánchez 2003; Sánchez and Benedetto 2004). These deposits, over 3,500 m thick, have been referred to as the Santa Victoria Group (Turner 1960). Formational nomenclature, however, differs geographically because of marked lateral and vertical lithofacial changes within the basin. The Upper Cambrian-Tremadocian succession unconformably overlies the Cambrian Meson Group, which consists of *Skolithos*-rich reddish sandstones and siltstones deposited in tide-dominated environments (Mángano and Buatois 1999).

The fossiliferous locality is located on the westernmost slope of the Cordillera Oriental, near its boundary with the Puna high plateau. The stratigraphic section is exposed about 7 km southeast of El Moreno village, at El Angosto locality (Fig. 1). Details of the stratigraphy, lithofacies and environments of this section were given by Buatois et al. (2003), and a biostratigraphic survey was given by Moya et al. (2003). Astini (2003) referred the lower part of the Cambrian-Tremadocian succession to the Padrioc and Lampazar Formations and the upper part with the Guayoc

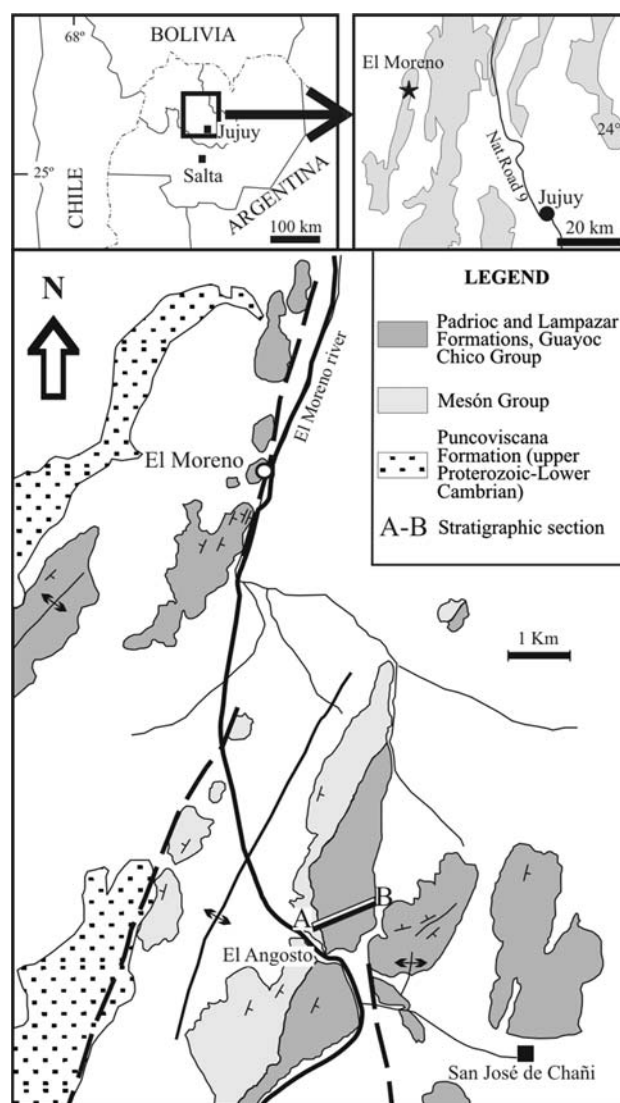


Fig. 1 General location of the studied area (*upper left*), distribution of Cambro-Ordovician rocks (*gray*) in the central Cordillera Oriental (*upper right*), and geologic sketch of the El Moreno area (modified from Moya et al. 2003) showing location of measured stratigraphic section and fossiliferous levels (*asterisk*)

Chico Group, which was subdivided into five informal lithostratigraphic units (“members”) (Fig. 2). The Guayoc Chico Group, about 280 m thick, rests conformably on the dark-gray offshore mudstones of the Lampazar Formation of Late Cambrian (Furongian) age according to the occurrence of the trilobite *Parabolina* (*Neoparabolina*) *frequens argentina* and conodonts of the *Cordylodus proavus* Biozone (*H. hirsutus* Subzone) recovered from the uppermost levels of this formation (Moya et al. 2003). The lower third of the Guayoc Chico Group is a sandstone-dominated interval representing shoreface deposition followed by prograding deltaic deposits. The overlying Green Shale Member reflects a renewed transgression. This fine-grained interval mostly corresponds to offshore and

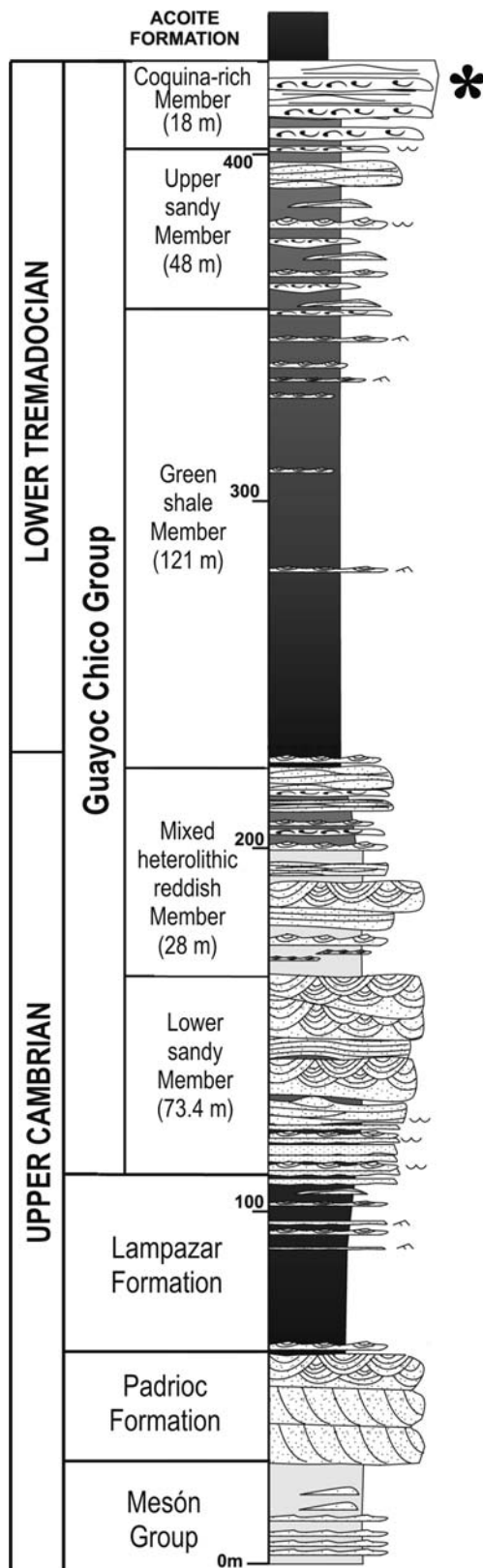


Fig. 2 Stratigraphic column of Upper Cambrian and Lower Ordovician strata of El Moreno area (modified from Buatois et al. 2003 and Astini 2003) showing the horizon from which *Chaniella pascuali* n. gen. n. sp. was collected (asterisk)

prodelta deposits (Buatois et al. 2003). The Guayoc Chico Group culminates with a regressive cycle represented by a succession of thin-bedded fine-grained sandstones passing up into cross-stratified sandstones and coquinas bearing *Chaniella pascuali* n. gen. n. sp. and *Nanorthis calderensis alternata* Benedetto, 2007 (Fig. 2). *Nanorthis calderensis* Benedetto is a widespread species confined to the upper part of the lower Tremadocian strata of the Central Andean Basin (Benedetto 2007). The Cambrian-Tremadocian boundary has been tentatively placed immediately above the base of the Green Shale Member, where *Anisograptus matanensis* first occurs, but it possibly lies some meters below this horizon. Associated forms are *Rhabdinopora flabelliformis* ssp. and *Callograptus (Pseudocallograptus) salteri* (Moya et al. 2003). The uppermost coquinas have yielded the lower Tremadocian conodont *Cordylodus angulatus* and the trilobite *Kainella meridionalis*.

Brachiopods occur as irregular, densely packed shell concentrations within cross-bedded sandstones; both taxonomic composition and preservational features are more or less uniform throughout the bed thickness. Shell beds are characterized by a high disarticulation ratio and a low degree of fragmentation. Small and large specimens coexist in the same bed, indicating a relatively poor hydraulic sorting. All these features suggest that specimens have been reworked to some degree but not transported far from their original life habitat. Sandstone beds are amalgamated and internal erosion surfaces separating hummocky cross-stratified beds are present. These beds occasionally pass upwards into fine-grained trough cross-stratified sandstones suggesting deposition in a storm-dominated lower to middle shoreface environment, which is consistent with taphonomic evidence.

Systematic paleontology

Studied specimens are deposited in the paleontological collection of Centro de Investigaciones Paleobiológicas (CIPAL), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina, under the prefix CEGH-UNC.

Order Billingsellida Schuchert, 1893

Superfamily Billingselloidea Schuchert, 1893

Family Chaniellidae nov.

Diagnosis

Delthyrium open limited by narrow lateral plates. Chilidial plates present. Pseudospondylium well developed in adult specimens. Ventral mantle canal system strongly impressed, with gonocoels enclosed anteriorly by lateral branches of vascula myaria and posterolaterally by arcuate

projections of gonadal areas. Cardinal process ridgelike. Dorsal muscle field large, quadripartite. Dorsal mantle canal system pinnate.

***Chaniella* n. gen.**

Etymology

Refers to the San José de Chañi locality near El Angosto outcrops.

Type species

Chaniella pascuali new species.

Diagnosis

Convexiplane shell profile. Ventral interarea moderately high, transversely striated. Delthyrium bordered by narrow lateral plates. Notothyrium partially closed by chilidial plates. Ornament unequally parvicostellate. Valve margins often thickened by superposition of growth lamellae. Dental plates converging to valve floor to form in later growth stages a pseudospondylium merged anteriorly with a broad median ridge. Ventral diductor scars large, subtriangular; adductor field slightly longer than diductor scars, in some specimens confined to the anteromedian portion of muscle field. Ventral mantle canals strongly impressed with broad vascula myaria bounding gonocoels anteriorly and anterolaterally but not posterolaterally. Gonocoel areas with trunks variably projected to the margin. Cardinal process ridgelike. Dental sockets bounded by strong ridges subparallel to the hinge line. Dorsal muscle field large, quadripartite with posterior scars larger than anterior. Dorsal mantle canal system pinnate.

Discussion

At first glance, the new genus *Chaniella* resembles the eorthoïd *Jivinella incola* (Barrande, 1879) from the Upper Cambrian of Bohemia (Havlíček 1977). Internally, both genera display a well-developed pseudospondylium prolonged anteriorly by a median ridge and share a relatively similar pattern of a ventral vascular system. In *Jivinella* Havlíček 1949, however, it is saccate, while in *Chaniella* it seems to be intermediate between the saccate and pinnate patterns defined by Williams (1956). *Chaniella* clearly differs from *Jivinella* in some key features, such as the presence of narrow lateral deltidial plates and well-defined chilidial plates, suggesting closest affinities with the order Billingsellida as the cladistic

analysis presented below indicates. The only genera having lateral deltidial plates are the clitambonitidines *Atelelasma* and *Apomatella*, which differ from *Chaniella* by having a true spondylium. On the basis of cladistic analysis, it appears that this structure evolved convergently in the two lineages.

Chaniella shares with *Finkelburgia* Walcott, 1905 a pseudospondylium prolonged anteriorly by a median ridge and recessive dental plates. The new Argentine genus, however, differs in having chilidial and deltidial plates, a different pattern of mantle canals, and long socket ridges subparallel to the hingeline. Furthermore, the “spondylium” in finkelburgiids is spoon-like with its anterior margin strongly elevated above the valve floor and supported by a short ridge, like the spondylium of many syntrophidine pentamerids. In addition, the shell profile of finkelburgiids tends to be biconvex, whereas in *Chaniella* the ventral valve is almost planar. As is shown below, parsimony analysis indicates that finkelburgiids, anomalorthoïds (alimbellids), and basal porambonitoideans form a separate lineage.

The new genus *Chaniella* shows a certain degree of similarity with *Saccogonum* Havlíček, 1971, from the Upper Cambrian of Morocco (Havlíček 1971), particularly in its convexo-plane shell profile, proportionally high and striated ventral interarea, and ventral muscle field morphology. *Saccogonum* differs in having a short pseudodeltidium and a different ventral vascular system pattern.

Similarities between *Chaniella* and *Protambonites* are particularly strong in the dorsal valve. In both genera the notothyrial platform is high and prolonged anteriorly by a thin ridge bisecting a large quadripartite muscle field. In the well-known Spanish species *P. primigenius* Havlíček (in Havlíček and Josopait 1972), the dorsal adductor scars are very similar in outline and spatial arrangement, the posterior ones being the largest (cf. Villas et al. 1995, pl. 2, figs. 6–9). Another closely comparable feature is the pinnate dorsal vascular system with deeply impressed vascular trunks separated by long radial ridges, the marginal region of the valve forming a thickened peripheral rim. The relatively long socket ridges almost parallel to the hinge line are also similar. The chilidium is complete in *P. lermontovae* Andreeva, 1960 (Popov et al. 2001) but it is absent in *P. primigenius*, while in *Chaniella* the notothyrium is partially closed by narrow chilidial plates. *Korinevskia* Popov, Vinn & Nikitina, 2001 is also comparable to *Chaniella* in its convexiplane shell profile, short dental plates, and ventral muscle field with adductor scars extended well beyond the diductor pair. *Chaniella* clearly differs from both *Protambonites* and *Korinevskia* in lacking a pseudodeltidium.

***Chaniella pasquali* n. gen. n. sp.**

Etymology

This species is named for the Argentine paleontologist Prof. Dr. Rosendo Pascual.

Type material

Holotype An internal mould of ventral valve, CEGH-UNC 22961 (Figs. 3a–o). **Paratypes:** Two exteriors of ventral valve CEGH-UNC 22991 and 22992; four external moulds of ventral valve CEGH-UNC 22967a, 22993b, 22993c, 22994a; two external moulds of dorsal valve 22963b, 22994a; eight internal moulds of ventral valve CEGH-UNC 22962, 22963a, 22963c, 22965, 22968, 22983, 22990, and 22993; eight internal moulds of dorsal valve CEGH-UNC 22963c, 22964, 22972, 22977, 22978, 22979, 22985, and 22987a.

Type locality and type horizon

El Angosto section, approximately 7 km southeast El Moreno village, western flank of the Cordillera Oriental, Jujuy Province, Argentina. Upper part of the Guayoc Chico Group, lower Tremadocian (*Cordylodus angulatus* Biozone).

Diagnosis

As for the genus by monotypy.

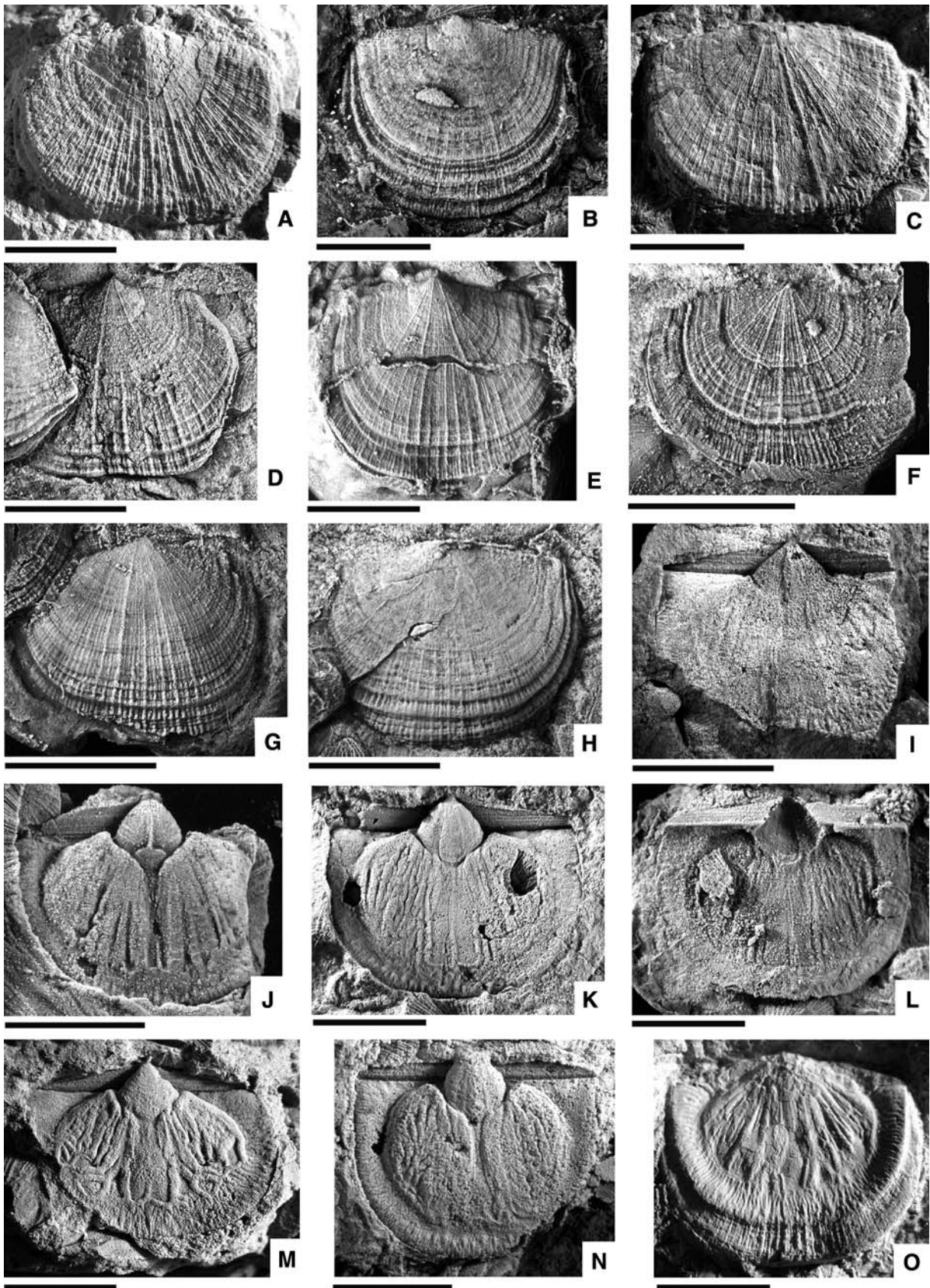
Description

Shell medium sized, up to 26 mm wide, convexiplane in lateral profile; outline semielliptical with slightly obtuse cardinal angles. Maximum shell width located between posterior third and midlength. Length about 75% of width. Ventral valve gently convex in posterior third becoming flat or slightly concave anteriorly. Ventral interarea planar to gently curved, proportionally high, 15–25% as high as wide, with striae parallel to hingeline, apsacline. Delthyrium triangular, open, slightly higher than wide, bordered by narrow lateral plates preserved in few specimens. Dorsal valve moderately and evenly convex; larger specimens with faint sulcus on the anterior half. Dorsal interarea planar, anacline, about one-third height of ventral interarea. Notothyrium partially closed by narrow chilidial plates fused near notothyrium apex. Ornament finely and unequally parvicostellate with six to eight accentuated rounded costellae at the umbo and two generations of accentuated costellae intercalated at about midlength and two-thirds valve length, respectively. At valve margin, accentuated costellae separated by intervals ranging from 0.6 to 1 mm wide, with two to four

parvicostellae within the interspaces. Conspicuous, more or less uniformly spaced growth lamellae best defined over the anterior half of both valves, more closely crowded at anterior margin, which in large specimens becomes strongly thickened by superposition of growth lamellae.

Ventral valve with small, transverse teeth. Ventral muscle field broad, subrhomboidal to pyriform, slightly wider than long in juvenile specimens but more or less equidimensional or longer than wide in adults, extending forward for about 30% of valve length. Dental plates well developed, converging to valve floor; in small to medium-sized specimens, dental plates elevate the muscle field only laterally, but in later growth stages it becomes raised both laterally and anteriorly in the form of a pseudospondylium (Figs. 4b, e). Diductor scars large, subtriangular, raised above level of the adductor field. Adductor field often subtriangular, elongated anteroposteriorly, slightly longer than diductor scars; in some specimens it is confined to the anteromedian portion of the muscle field, the diductor scars becoming adjacent but separated medially by a thin ridge (Fig. 3j). Pedicle callist generally well developed. Median ridge varying from a low thin ridge to a flat broad ridge originating in front of the adductor field. Ventral mantle canals strongly impressed showing a rather variable pattern consisting of broad, subparallel or slightly divergent vascula myaria which bifurcate at valve midlength into two principal branches, the lateral one bounding gonocoels anteriorly and anterolaterally but not posterolaterally. Gonocoel areas covered by irregular ridges and projected to the margin by variably developed trunks, the posterior of which are more prominent and arcuate, almost joining the lateral branch of vascula myaria (Fig. 3m). In other specimens, however, the pattern seems to be definitely pinnate (Figs. 3j, o).

Dorsal valve with high, subtriangular notothyrial platform surmounted by a ridgelike cardinal process slightly thickened anteriorly. Median ridge variably developed and merged at the front of the notothyrial platform, commonly extending anteriorly up to valve midlength or slightly beyond, in most specimens becoming undistinguishable from those ridges separating vascular trunks. Dental sockets transversely elongated, semiconical, bounded by strong socket ridges subparallel to the hingeline. Dorsal muscle field large, quadripartite, slightly wider than long, extended anteriorly for about 40% of valve length. Posterior adductor scars subtriangular, of digitate posterior margin; anterior adductor scars smaller than posterior ones, subovate to subrhomboidal, separated from posterior pair by an oblique ridge. Dorsal mantle canal system pinnate, consisting of 8–10 radial canals that bifurcate at the anterior third of valve and separated by thin radial ridges which traverse both posterior and anterior adductor scars, particularly in large specimens.



◀ **Fig. 3** *Chaniella pascuali* n. gen. n. sp. **a** CEGH-UNC 22992; exterior of ventral valve. **b** CEGH-UNC 22993c; exterior of ventral valve (latex cast). **c** CEGH-UNC 22991; exterior of ventral valve. **d** CEGH-UNC 22994a; exterior of ventral valve (latex cast). **f** CEGH-UNC 22967a; exterior of ventral valve (latex cast). **g** CEGH-UNC 22963b; exterior of dorsal valve (latex cast). **h** CEGH-UNC 22994a; exterior of dorsal valve (latex cast). **i** CEGH-UNC 22983; internal mould of ventral valve, juvenile specimen. **j** CEGH-UNC 22963a; internal mould of ventral valve. **k–l** CEGH-UNC 22993c. **k** Internal mould of ventral valve, **l** latex cast. **m** Holotype CEGH-UNC 22961; internal mould of ventral valve. **n** CEGH-UNC 22968; internal mould of ventral valve. **o** CEGH-UNC 22990; internal mould of ventral valve. Scale bar 10 mm

Phylogenetic relationships of *Chaniella pascuali* n. gen. n. sp.

Cladistic analysis of the data matrix in Table 1 was performed using TNT (Tree Analysis Using New Technology) version 1.0 (Goloboff et al. 2003) selecting the heuristic search option with multiple random addition sequences plus “tree bisection reconnection” (TBR) branch-swapping algorithm, holding 10 trees in each addition sequence. The protorthide *Glyptoria* Cooper, 1976 was chosen as outgroup for rooting phylogenetic trees. To assess the phylogenetic position of *Chaniella pascuali* n. gen. et sp., 13 Cambrian and Tremadocian basal rhynchonelliform genera (Kutorginata, Protorthida, Orthida), 16 genera belonging to the order Billingsellida, and 2 porambonitoid genera (order Pentamerida) have been included in the analysis.

The 27-character matrix was analyzed for 31 taxa (Table 2). Parsimony analysis, in which all characters were unordered and unweighted, produced 50 minimal length trees, 126 steps long. The 50 and 75% majority rule consensus (MRC) trees are shown in Figs. 5 and 6, respectively. Phylogenetic relationships of 50% MRC tree are redrawn in Fig. 7, but branch length is calibrated to the age of the first appearance of taxa.

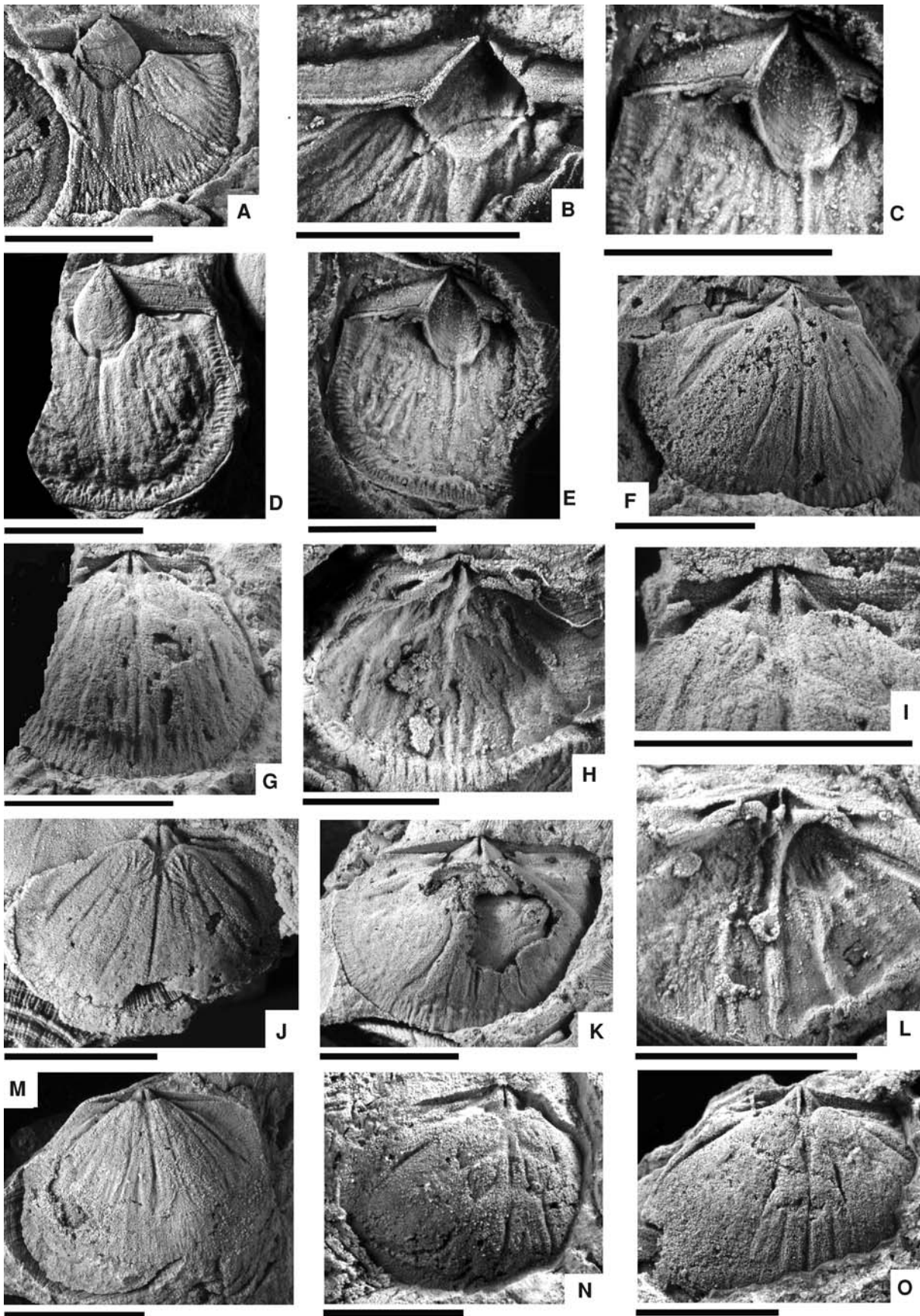
One important result of the 50% MRC tree is that *Chaniella* appears closely related to both *Protambonites* and *Korinevskia*. Similarities among these genera have been discussed above in the comparison of the new genus *Chaniella*. The genus *Saccogonum* Havlíček, 1971 lies close to the ancestry of the [*Chaniella* + *Protambonites* + *Korinevskia*] clade. In fact, *Saccogonum saccatum* Havlíček, 1971 displays some “primitive” features, such as short pseudodeltidium and absence of dental plates and a pseudospondylium. A striking feature shared by *Saccogonum* and *Chaniella* is the suboval, anteriorly located adductor muscle field (cf. Havlíček 1971, pl. 1 fig. 16 and Fig. 3j). Such an arrangement, however, is present in some basal rhynchonelliforms, such as the bohemiellids *Wimanelia* Walcott, 1908 and *Cymbricia* Roberts and Jell, 1990, and also in the Middle Ordovician clitambonitoid *Clinambon* Schuchert and Cooper, 1932, so this feature is

probably homoplastic. The genera *Billingsella* Hall and Clarke, 1892 and *Kozhuchinella* Severgina, 1967 are sister taxa that occupy the most basal position in this ingroup clade (family Billingsellidae), which is supported by two apomorphies: ventral vascular system saccate and lack of dental plates. In the 75% MRC tree (Fig. 6), both *Saccogonum* and *Chaniella* appear as basal members of all other taxa currently referred to the suborder Billingsellidina.

Tritoechiids form an undoubtedly monophyletic clade (node 6) linked by the following apomorphies: strongly convex, often hemipyramidal ventral valve, well-defined dental plates, and notothyrial platform supported by a short median septum. Because the search for phylogenetic relationships among this group is beyond the scope of this work, only some typical genera were included in the present analysis. It should be noted that *Antigonambonites* Öpik, 1934, which possesses a pseudospondylium instead of a true spondylium (Vinn and Rubel 2000), clusters within this clade, as in the tree constructed by Popov et al. (2001). In our parsimony analysis, this clade does not include *Protambonites* and *Korinevskia*, considered by Rubel and Wright (2000) as members of the family Polytoechiidae (redefined as family Tritoechiidae by Popov et al. 2001).

The clitambonitidines appear as a monophyletic sister group of the Billingsellidina in both the 50 and 75% MRC trees (node 3). *Apomatella* and *Atelelasma*—characterized by narrow deltidial plates—are a sister group of the lineage formed by genera having a complete deltidium, such as *Clitambonites* Pander, 1830, *Estlandia* Schuchert and Cooper, 1931, and related forms. It can be speculated that deltidial plates in *Chaniella*, which are morphologically comparable but not necessarily homologous to those of atelelasmates, are an ancestral feature with respect to the complete pseudodeltidium of billingsellides. In the 50% MRC tree, however, *Chaniella* is shown as having evolved its separate deltidial plates from an ancestral complete delthyrial cover. In contrast, the 75% MRC tree topology indicates that deltidial plates may be a primary feature originated from the open delthyrium of basal orthides (cf. Wright 1996), such as *Jivinella* or *Bohemiella*.

Placement of the protorthid *Arctohedra* Cooper, 1936 as a basal member of the Billingsellida (Fig. 5, node 2) supports the suggestion by Vinn and Rubel (2000) who considered the free ventral plate of *Arctohedra pyramidalis* Aksarina, 1975 as an ancestral stage of the clitambonitidine spondylium. In the phylogenetic tree constructed by Popov et al. (2001), *Arctohedra* forms a separate clade together with *Apomatella* and *Clitambonites*. Whether or not *Arctohedra* should belong to the billingsellides depends on which node (1 or 2) is designed to define the order Billingsellida.



◀ **Fig. 4** *Chaniella pascuali* n. gen. n. sp. **a, b** CEGH-UNC 22963c. **a** Internal mould of ventral valve. **b** Latex cast showing deltidial plates. **c–e** CEGH-UNC 22965. **e, c** Latex cast and detail of deltidial plates. **d** Internal mould of ventral valve. **f** CEGH-UNC 22979; internal mould of dorsal valve. **g–i** CEGH-UNC 22972. **g** Internal mould of dorsal valve. **h** Latex cast. **i** Detail of cardinalia. **j** CEGH-UNC 22963c; internal mould of dorsal valve. **k** CEGH-UNC 22977a; internal mould of dorsal valve. **l** CEGH-UNC 22985; interior of dorsal valve, latex cast. **m** CEGH-UNC 22964; internal mold of dorsal valve. **n** CEGH-UNC 22978; internal mould of dorsal valve. **o** CEGH-UNC 22987a; internal mould of dorsal valve. Scale bar 10 mm

Our results indicate that the orthides *Finkelburgia*, *Medessia* Andreeva, 1960, and *Astraborthis* Williams, 1974 and the Cambrian pentamerides *Radkeina* Laurie, 1997 and *Plectotrophia* Ulrich and Cooper, 1936, are all closely related forms, and that this lineage branches off at

the base of the rhynchonelliform differentiation. This view supports the relationships inferred by Carlson (1996) who stated that the earliest syntrophidines tend to cluster among the basal orthides. The association of these genera is not surprising owing to the close morphological similarities between anomalorthids (= alimbellids), the “plectorthoidean” *Astraborthis* and certain basal syntrophidines.

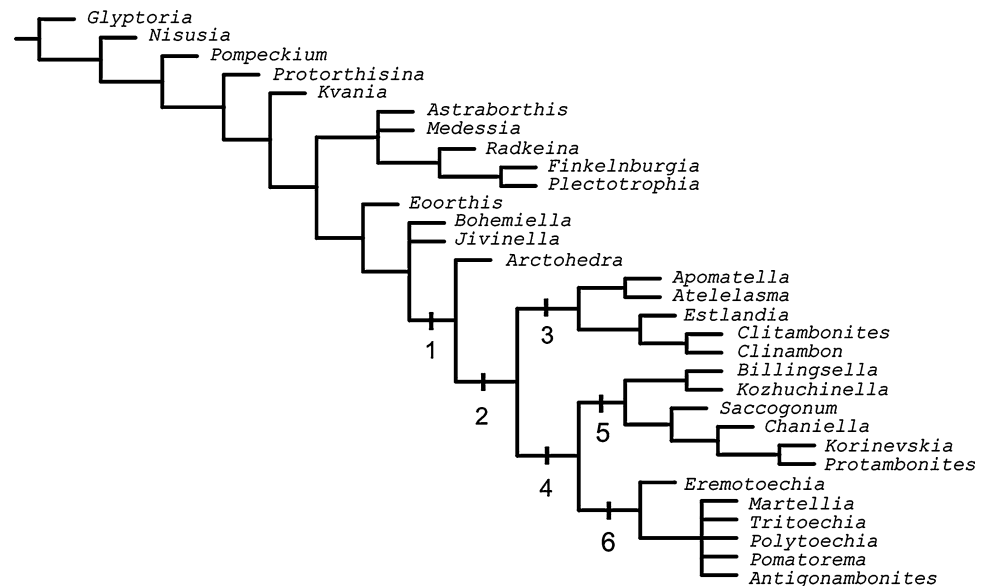
The Middle Cambrian eoorthid *Jivinella* is perhaps the orthide morphologically closest to both the billingsellide and the [*Astraborthis* + *Finkelburgia* + *Medessia* + basal porambonitoids] lineage. It appears that *Jivinella* and related basal orthides, in particular the bohemiellid *Bohemiella*, were the ancestors of more than one lineage of rhynchonelliform brachiopods. A more extensive search on the morphology of eoorthids, bohemiellids, protorthids and

Table 1 Characters state matrix used in TNT cladistic 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	20	21	22	23	24	25	26	27
<i>Glyptoria</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	0	3	0	0	0	2	?	0	0	0	0	0	0	0
<i>Billingsella</i>	1	0	2	0	1	1	0	0	1	2	0	0	1	0	0	0	0	2	1	2	2	0	1	1	1	2	0
<i>Saccogonum</i>	1	0	1	1	1	1	0	0	0	2	0	0	1	0	0	0	1	2	1	?	2	0	1	1	1	1	0
<i>Kozhuchinella</i>	3	0	1	0	1	1	0	0	2	2	0	0	1	0	0	0	0	1	1	2	2	0	1	1	1	1	1
<i>Clitambonites</i>	4	0	2	2	1	0	1	0	2	1	1	1	1	0	1	0	3	2	2	1	2	0	1	1	1	1	1
<i>Apomatella</i>	4	0	2	2	1	0	0	1	1	1	0	1	1	0	1	0	3	1	1	?	2	0	1	1	1	0	0
<i>Atelelasma</i>	0	0	1	1	1	0	0	1	1	2	0	1	1	0	1	0	3	1	1	1	2	0	1	1	1	1	0
<i>Clinambon</i>	4	0	2	2	1	0	1	0	2	2	1	1	1	0	1	0	3	2	?	1	2	0	1	1	2	1	1
<i>Estlandia</i>	1	0	1	1	1	0	1	0	2	2	1	1	1	0	2	0	3	1	1	1	2	0	1	1	2	1	1
<i>Protambonites</i>	1	0	2	0	1	1	0	0	2	4	0	0	1	1	0	0	1	2	2	1	2	0	1	2	1	1	0
<i>Korinevskia</i>	1	0	2	0	1	1	0	0	2	4	0	0	1	1	0	0	1	2	1	1	2	0	1	2	2	1	0
<i>Martellia</i>	4	0	2	0	1	1	0	0	2	2	0	0	1	2	0	1	1	1	1	1	2	0	1	2	4	2	1
<i>Tritoechia</i>	4	0	2	1	1	1	0	0	1	2	0	0	1	2	0	1	1	1	1	1	2	0	1	2	4	2	0
<i>Chaniella</i>	1	0	1	1	1	0	0	1	1	3	0	0	1	1	0	1	1	2	1,2	1	2	0	1	2	1	1	1
<i>Bohemiella</i>	0,3	0	1	1	0	0	0	0	0	2	0	0	1	0	0	0	0	1	1	1	1	0	1	1	0	1	0
<i>Eoorthis</i>	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	?	1	0	1	1	1	0	0
<i>Jivinella</i>	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	1	1	2	1	?	2	0	1	1	0	1	0
<i>Protorthisina</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	?	?	4	1	0	1	3	0	0
<i>Kvania</i>	0	0	0	1	0	0	0	0	0	1	0	0	1	2	0	0	0	1	?	?	3	0	0	1	1	1	0
<i>Polytoechia</i>	4	0	2	1	1	1	0	0	1	2	0	0	1	2	0	1	3	1	?	?	2	0	1	2	4	2	0
<i>Nisusia</i>	4	0	2	2	1	1	0	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0
<i>Pompeckium</i>	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	3	?	0	0	1	0	0	0	0
<i>Astraborthis</i>	0	1	0	1	0	0	0	0	0	1	0	0	1	2	0	1	1	1	?	?	2	0	1	1	1	1	0
<i>Pomatotrema</i>	4	0	2	1	1	1	0	0	2	2	0	1	1	2	0	1	2	1	1	1	2	0	1	2	4	2	1
<i>Arctohedra</i>	4	0	2	2	0	0	0	0	0	1	0	0	1	0	3	0	0	0	1	?	2	0	1	1	1	1	0
<i>Eremotoechia</i>	2	0	1	1	1	1	0	0	2	2	0	0	1	2	0	1	0	1	?	?	2	0	2	2	0	2	0
<i>Antigonambonites</i>	4	0	2	1	1	1	0	0	1	2	0	0	1	2	0	1	0	1	2	1	2	0	1	2	4	2	1
<i>Medessia</i>	0	1	0	1	0	0	0	0	0	2	0	0	1	2	0	1	0	1	3	?	2	0	1	1	1	1	0
<i>Radkeina</i>	0	1	0	1	0	0	0	0	0	1	0	0	1	2	0	1	1	1	?	?	2	0	1	1	1	2	0
<i>Finkelburgia</i>	0	0	0	1	0	0	0	0	0	2	0	0	1	2	0	1	1	1	3	3	3	0	0,1	1	0	2	0
<i>Plectotrophia</i>	0	1	0	1	0	0	0	0	0	2	0	0	1	1	0	1	1	1	?	?	2	0	1	1	1	2	0

Table 2 List of species used to construct genus-level character states (in alphabetic order)

Genus	Species
<i>Antigonambonites</i>	<i>A. planus</i> Öpik, 1934
<i>Apomatella</i>	<i>A. ingraca</i> (Pahlen, 1877) (Rubel and Popov 1994)
<i>Arctohedra</i>	<i>A. pyramidalis</i> Aksarina, 1975
<i>Astraborthis</i>	<i>A. uniplicata</i> Williams, 1974
<i>Atelelasma</i>	<i>A. perfectum</i> Cooper, 1956
<i>Billingsella</i>	<i>B. perfecta</i> Ulrich & Cooper, 1938
<i>Bohemiella</i>	<i>B. romingeri</i> Barrande, 1879
<i>Chaniella</i>	<i>Chaniella pascuali</i> n. gen. n. sp. (this paper)
<i>Clitambon</i>	<i>C. anomalus postumus</i> Öpik, 1934
<i>Clitambonites</i>	<i>C. adscendens</i> (Pander, 1830); <i>C. schmidti</i> (Pahlen, 1877)
<i>Eoorthis</i>	<i>E. remnicha</i> (Winchell, 1885)
<i>Eremotoechia</i>	<i>E. cloudi</i> Cooper, 1956; <i>E. inchoata</i> Popov, Vinn & Nikitina, 2001
<i>Estlandia</i>	<i>E. marginata</i> (Pahlen, 1877)
<i>Finkelburgia</i>	<i>F. butsi</i> Ulrich & Cooper, 1936
<i>Glyptoria</i>	<i>G. glypta</i> Cooper, 1976; <i>G. gulchensis</i> Popov & Tikhonov, 1993
<i>Jivinella</i>	<i>J. incola</i> (Barrande, 1879)
<i>Korinevskia</i>	<i>K. akbulakensis</i> (Andreeva, 1960)
<i>Kozhuchinella</i>	<i>K. mariinica</i> Severgina, 1967; <i>K. cf. mariinica</i> Severgina, 1967 (Laurie, 1997)
<i>Kvania</i>	<i>K. azulpampensis</i> Benedetto, 2007; <i>K. kvanica</i> (Havlíček, 1984); <i>K. mergli</i> Benedetto, 2007
<i>Martellia</i>	<i>M. mesocosta</i> (Benedetto, 1987); <i>M. reliqua</i> Popov, Vinn & Nikitina, 2001
<i>Medessia</i>	<i>M. uralica</i> Andreeva, 1960
<i>Nisusia</i>	<i>N. alaica</i> (Popov & Tikhonov, 1990)
<i>Plectotrophia</i>	<i>P. bridgei</i> Ulrich & Cooper, 1936
<i>Polytoechia</i>	<i>P. apicalis</i> (Whitfield, 1886)
<i>Pomatotrema</i>	<i>P. murale</i> Ulrich & Cooper, 1932; <i>P. fecunda</i> Popov, Vinn & Nikitina, 2001
<i>Pompeckium</i>	<i>P. kuthani</i> (Pompeckj, 1896)
<i>Protambonites</i>	<i>P. lermontovae</i> (Andreeva, 1960); <i>P. primigenius</i> Havlíček, 1972 (in Havlíček and Josopait, 1972; Villas et al. 1995)
<i>Protorthisina</i>	<i>P. simplex</i> Benedetto, 2007
<i>Radkeina</i>	<i>R. taylori</i> Laurie, 1997
<i>Saccogonum</i>	<i>S. saccatum</i> Havlíček, 1971
<i>Tritoechia</i>	<i>T. azulensis</i> Benedetto, 1987; <i>T. typica</i> Schuchert and Cooper, 1936

Fig. 5 Fifty-percent majority rule consensus tree of 50 most parsimonious cladograms depicting relationships among the taxa discussed in the text and nodes

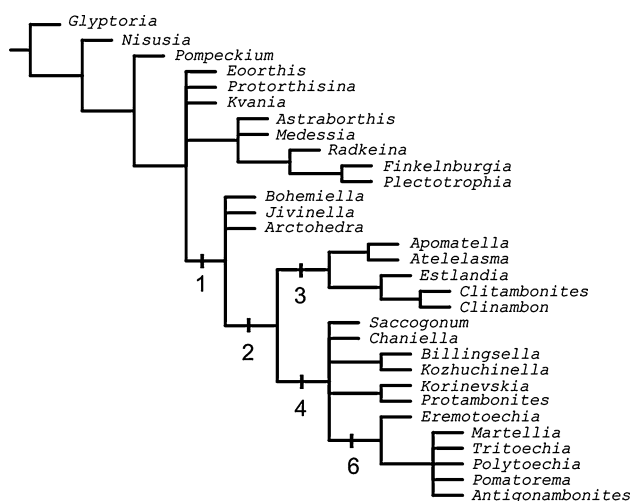


Fig. 6 Seventy-five-percent majority rule consensus tree of 50 shortest trees depicting relationships between the taxa discussed in the text and nodes



Fig. 7 Fifty-percent majority rule consensus tree depicting relationships between the taxa discussed in the text calibrated to chronostratigraphic scale. Black rectangles indicate the earliest documented appearance

other Cambrian orthides, as well as a careful cladistic analysis of these groups is needed to resolve this issue.

In the light of cladistic analysis conducted herein, *Chaniella* is placed in the suborder Billingsellidina (node 4) within the order Billingsellida (node 2). The

clitambonitidines, in agreement with Popov et al. (2001), should be classified as a separate suborder (node 3). Recognition of lower taxonomic ranks within the billingsellidines is more difficult. The results suggest that at least four, perhaps five, families could be recognized: (1) Billingsellidae, including *Billingsella*, *Kozhuchinella*, and related forms. (2) Protambonitidae, containing *Protambonites* and *Korinevskia*. Both genera also appear associated in the cladogram constructed by Popov et al. (2001). (3) Chaniellidae. According to the phylogenetic analysis conducted herein, *Chaniella* is assigned to the monogeneric family Chaniellidae characterized by separate deltidial plates instead of a complete pseudodeltidium. It should be noted that on the basis of classic morphological criteria this genus cannot be assigned consistently to any other family within the suborder Billingsellidina. (4) Tritoechiidae (= Polytoechiidae) is the better supported clade within the billingsellidines. (5) *Saccogonum* requires further investigation in order to clarify its systematic placement within the suborder Billingsellidina.

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Appendix

List of coded characters and character states used in cladistic analysis

1. Shell profile: subequally biconvex or ventribiconvex 0; convexiplane to dorsibiconvex 1; strongly dorsibiconvex 2; concavoconvex to planoconvex 3; ventral valve subpyramidal 4
2. Fold and sulcus: absent: 0; present: 1
3. Ventral interarea (height): low 0; medium 1; very high 2
4. Ventral interarea (inclination): strongly apsacline to orthocline 0; apsacline 1; procline to catacline 2
5. Delthyrium: entirely open, unmodified 0; modified 1
6. Pseudodeltidium: absent 0; present 1
7. Deltidium: Absent 0; present 1
8. Deltidial plates: absent 0; present 1
9. Notothyrium: open 0; separated chilidial plates 1; chilidium complete 2
10. Ornament: costate 0; coarsely costellate or fascicostellate 1; multicostellate 2; parvicostellate 3; rami-costellate 4
11. Pseudopuncta: Absent 0; present 1

12. Aditicles: absent 0; present 1
13. Deltidodont teeth: absent 0; present 1
14. Dental plates: absent or rudimentary 0; short recessive 1; well developed 2
15. Spondylium: absent 0; supported by one septum 1; supported by three septa 2; free anteriorly 3
16. Pseudospondylium: Absent 0; present 1
17. Ventral median septum: absent 0; short 1; extended beyond the muscle field 2; supporting spondylium 3
18. Ventral muscle field: indistinct 0; adductor scars as long as diductors 1; adductors longer than diductors 2
19. Ventral mantle canals: indistinct 0; saccate 1; pinnate 2; digitate 3
20. Dorsal mantle canals: indistinct 0; pinnate 1; digitate 2
21. Notothyrial platform: underlined by a transverse plate 0; absent or rudimentary 1; well developed 2; notothyrial chamber 3; brachiophore plates converging to form septalium 4
22. Septalium: absent 0; small 1; large, supported by a septum 2
23. Cardinal process: absent or rudimentary 0; simple, ridgelike 1; simple with enlarged myophore 2
24. Sockets/socket ridges: sockets absent or rudimentary, built on primary shell 0; sockets well developed, bounded by short socket ridges 1; socket ridges long, subparallel to hinge 2
25. Dorsal septum: absent or rudimentary 0; short, broad 1; long, blade-like 2; supporting septalium 3; short, supporting notothyrial platform 4
26. Dorsal muscle field: indistinct 0; quadripartite 1; muscle scars arranged radially 2
27. Dorsal peripheral rim: absent 0; present 1.

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