

# Functional morphology of the Ordovician plectambonitoid brachiopod *Inversella* (*Reinversella*) *arancibiai* Herrera & Benedetto from the San Juan Formation, Argentine Precordillera

JUAN L. BENEDETTO, LEONOR SORRENTINO, NORMA CECH AND TERESA M. SÁNCHEZ

BENEDETTO, J.L., SORRENTINO, L., CECH, N. & SÁNCHEZ, T.M., March 2008. Functional morphology of the Ordovician plectambonitoid brachiopod *Inversella* (*Reinversella*) *arancibiai* Herrera & Benedetto from the San Juan Formation, Argentine Precordillera. *Alcheringa* 32, 53-63. ISSN 0311-5518.

Juan L. Benedetto [jbenedetto@arnet.com.ar]; Norma Cech [ncech@com.uncor.edu]; Teresa M. Sánchez [tsanchez@com.uncor.edu] CONICET, Centro de Investigaciones Paleobiológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. Av. Vélez Sarsfield 299, X5000JJC Córdoba, Argentina. Leonor Sorrentino [leonor.sorrentino@sci.monash.edu.au] School of Geosciences, Monash University, PO Box 28E, Clayton, Victoria 3800, Australia. Received 29.6.2006; revised 24.10.2006.

New well-preserved material of the plectambonitoid brachiopod *Inversella* (*Reinversella*) *arancibiai* Herrera & Benedetto, 1987 collected from the San Juan Formation (Darriwilian, Middle Ordovician) of the Argentine Precordillera is described and illustrated, allowing a better understanding of its functional morphology. *Inversella* (*Reinversella*) is one of the earliest known brachiopods to develop a geniculate shell. Adult specimens of *I. (R.) arancibiai* have an open delthyrium indicating attachment throughout life. We infer that juvenile specimens lacking geniculation lived umbo-down and that development of geniculation could reflect a progressive change in mode of life from erect to reclined. The posterior thickening of valves indicates a life position with the umbonal region sunk in the substrate and the trail orientated in a subvertical position. Since open shelf settings inhabited by *I. (R.) arancibiai* have low sedimentation rates, it seems improbable that geniculation was an adaptation to counter shell burial. Its function was most probably to separate exhalant and inhalant currents. We hypothesize that the deep channel developed along the periphery of the ventral valve functioned as a collector of waste waters towards the posterolateral regions of the shell where exhalant currents were expelled.

Key words: Brachiopod, Ordovician, Argentina, Precordillera, functional morphology.

*REINVERSELLA* Bates, 1968 is a bizarre plectambonitoid brachiopod characterized by a double deflection of valve borders and a distinctive ornament of concentric rugae. In most internal and external features, it resembles the simple geniculate genus *Inversella* Öpik, 1933, leading Cocks & Rong (1989) to consider *Reinversella* as a subgenus within the former. The type species of

*Reinversella* is *R. monensis* Bates, 1968, from the upper Arenigian Treiorwerth Formation of Anglesey, Wales. The only other record of this subgenus is *Inversella* (*Reinversella*) *arancibiai* Herrera & Benedetto, 1987, from the San Juan Formation of the Argentine Precordillera. The Argentine species was defined on just two nearly complete ventral valves, one of which (holotype) was decalcified to show internal features. Subsequent intensive sampling from the upper part of the San Juan Formation at Cerro Viejo (the type

locality), Sierra de Villicum and Cerro la Chilca yielded numerous better-preserved specimens exhibiting hitherto unknown morphological features. The primary purpose of this paper is to redescribe and illustrate this new material of *I. (R.) arancibiai*. Second, we attempt to elucidate the functional significance of the doubly geniculate margin and its implications for life position.

### Stratigraphic occurrence

The Argentine Precordillera is characterized by widespread Cambro-Ordovician carbonate sequences recording deposition on a passive margin platform (Fig. 1). The topmost unit of this succession is the 300-

380 m thick San Juan Formation, which conformably overlies the restricted-platform dolostones and limestones of the La Silla Formation (Fig. 2). The basal contact is a flooding surface marking a rapid change to subtidal open-marine facies. A lower interval of microbial-sponge reefs is succeeded by a variety of lithofacies ranging from inner-ramp, wave-agitated shoal environments to deep-ramp settings (Cañas 1999, Cañas & Carrera 2003). Skeletal and intraclastic wackestones and packstones bearing rich marine faunas are the most typical and widely distributed lithologies of the San Juan Formation (Fig. 2). Cañas (1995, 1999) interpreted these rocks as mid-ramp deposits influenced by sporadic storm events and developed between the fair-weather and storm wave base. The deposits host sponge, bryozoan, brachiopod, gastropod, rostroconch, cephalopod, trilobite, receptaculitid, echinoderm and algal megafossils (see Benedetto 2003 and references therein for an updated compilation). The specimens of *Inversella (Reinversella) arancibiai* described here were collected from the uppermost 20 m of the San Juan Formation at Cerro Viejo, Cerro La Chilca and Sierra de Villicum localities (Fig. 1). In all three stratigraphic sections, but especially in the first, this interval consists mostly of richly fossiliferous nodular wackestones and mudstones deposited in mid- to outer-ramp, low-energy settings below the storm-wave base, with low sedimentation rates (Cañas 1999). A sharp contact separates these beds from the overlying marls and black shales of the Los Azules Formation.

*Inversella (R.) arancibiai* is confined to the *Ahtiella argentina* Zone (Herrera & Benedetto 1991, Benedetto 2002), from the upper part of the San Juan Formation (Fig. 2). The age of this biozone in the type locality of Cerro Viejo is early Darriwilian (*Lenodus variabilis* Zone; Ottone *et al.* 1999). This age is supported by the occurrence in

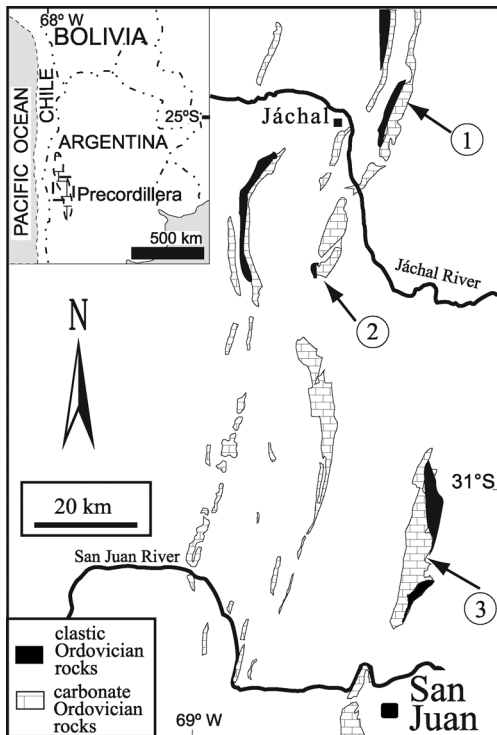


Fig. 1. Map of the Argentine Precordillera showing the distribution of Ordovician carbonate rocks and collection locations numbered: (1) Cerro Viejo (Quebrada Los Gatos), (2) Cerro la Chilca, (3) Sierra de Villicum (Quebrada Don Braulio).

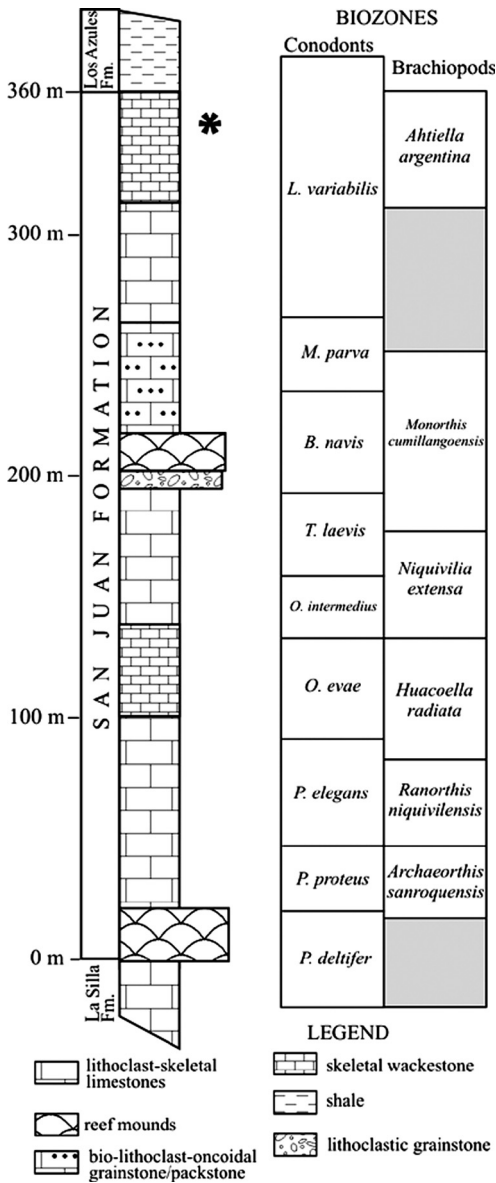


Fig. 2. Composite stratigraphic column of the San Juan Formation based on data from the Cerro Viejo and Cerro la Silla sections (modified from Cañas 1999 and Carrera *et al.* 1999), and biostratigraphic framework (after Albanesi & Ortega 2002 and Benedetto 2002). Asterisk marks the horizon bearing *Inversella* (*Reinversella*) *arancibiai*.

the overlying black shales of graptolites belonging to the *Undulograptus dentatus* Zone of Darriwilian (Da2) age, which

correlates with the uppermost Arenigian–lowermost Llanvirnian of the British Series (Brussa *et al.* 2003). In the Sierra de Villicum and Cerro La Chilca sections, the top of the San Juan Formation has been referred to the *Eoplacognathus suecicus* conodont Zone (Albanesi & Ortega 2002, and references therein), of Darriwilian (Da3) age.

### Systematic palaeontology

*Repositories.* Studied specimens are deposited in the palaeontological collection of Centro de Investigaciones Paleobiológicas (CIPAL), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina, under the prefix CEGH-UNC. Holotype material is housed in the Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina, prefix CORD-PZ.

Class STROPHOMENATA Williams *et al.*, 1996  
 Order STROPHOMENIDA Öpik, 1934  
 Superfamily PLECTAMBONITOIDEA Jones, 1928  
 Family TAFFIIDAE Schuchert & Cooper, 1931  
 Subfamily AHTIELLINEAE Öpik, 1933

#### *Inversella* Öpik, 1933

*Type species.* *Inversella borealis* Öpik, 1933

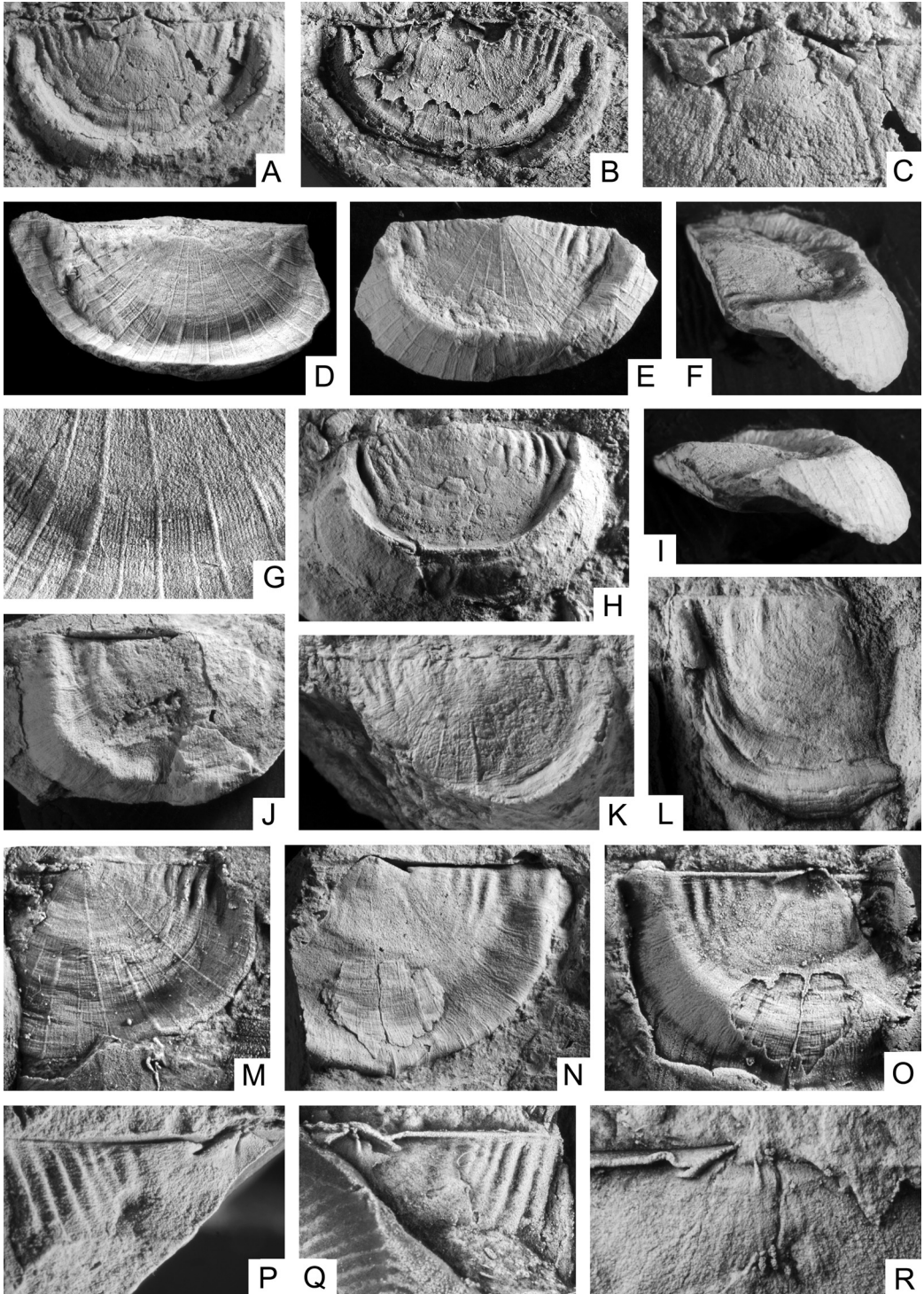
#### *Inversella* (*Reinversella*) Bates, 1968

*Type species.* *Reinversella monensis* Bates, 1968

#### *Inversella* (*Reinversella*) *arancibiai* Herrera & Benedetto, 1987 (Fig. 3)

*Material.* One conjoined specimen, CEGH-UNC 4456, from Quebrada Don Braulio,





Sierra de Villicum, uppermost San Juan Formation; two exteriors of ventral valve, CEGH-UNC 22409-22410, from Cerro la Chilca, uppermost San Juan Formation; five external moulds of ventral valve, one exterior of dorsal valve, two internal moulds of ventral valve and two internal moulds of dorsal valve, CEGH-UNC 4457, 4458, 10642, 21907a, 21907b, 21908a, 21908b, 21909, 21910, 22053, 22054, from Cerro Viejo (Quebrada Los Gatos), uppermost San Juan Formation, 3.4 m below the contact with the Los Azules Formation. All localities in San Juan province, Argentine Precordillera.

*Description.* Shells up to 23.5 mm wide, transversely semi-elliptical to subquadrangular in outline, with maximum width at hinge line. Average length/width ratio 0.64. Cardinal extremities right-angled, rounded, in some cases expanded into small alae. Ventral valve with gently convex disc bordered by a doubly geniculate margin defining a prominent, subangular peripheral rim at two-thirds valve length (Fig. 3A, B, H, J-O). Angle of ventral geniculation of about 70°. Dorsal geniculation variable from 60° to 80° in profile. Trail always well developed, long, one-half to two-thirds of disc length (Fig. 3E, F, I). Dorsal disc nearly flat, with deep, rounded, marginal trough developed immediately before the sharp dorsal geniculation (Fig. 3D-F, I). Both ventral and dorsal discs with up to six concentric rugae confined to the posterolateral areas, becoming more prominent

and longer with growth; in one specimen (holotype) the two last formed rugae are weak but almost continuous through the ventral visceral disc (Fig. 3A, B). Ventral interarea planar, strongly apsacline, larger than the very low, anacline dorsal interarea. Delthyrium triangular, entirely open. Notothyrium open. Weak parvicostellate ornament (Fig. 3G) with 15–22 fine costellae at valve margin between each pair of which intercalate 4–8 parvicostellae.

Ventral interior (Fig. 3A, C, E, N, O) with small teeth supported by relatively short dental plates diverging at about 130°. Ventral muscle field wide and short, weakly impressed, with adductor and diductor subtriangular in outline, approximately equal in size. Ventral mantle canal system saccate, with narrow, straight, slightly diverging *vascula media* arising from anterolateral margins of diductor scars and with strongly bifurcated distal branches well impressed on the trail.

Dorsal interior (Fig. 3P, Q) with thin, rod-like brachiophores diverging anteriorly at about 115°, continuous with chilidial plates, which bound the notothyrium. Dental sockets deep, semiconical. Cardinal process simple, ridge-like (Fig. 3R). Notothyrial platform raised slightly above the valve floor, transversely triangular to subrhomboidal in outline. Dorsal median septum absent. Dorsal muscle field and vascular system not preserved.

*Remarks.* As noted by Herrera & Benedetto (1987) in the original description, the

←  
 Fig. 3. *Inversella* (*Reinversella*) *arancibiai* Herrera & Benedetto, 1987. A–C, CORD-PZ 8586 (holotype), internal mould of ventral valve (A), × 2, latex cast (B), × 2, and detail of ventral mould (C), × 3.5, Cerro Viejo (Quebrada Los Gatos). D–F, I, CEGH-UNC 4456, dorsal (D), ventral (E), oblique (F) and lateral (I) views of conjoined specimen, × 2.5, Sierra de Villicum (Quebrada Don Braulio). G. Detail of external ornament, specimen figured in D, × 6. H. CEGH-UNC 22410, exterior of ventral valve, × 2, Cerro La Chilca. J. CEGH-UNC 22054, internal mould of ventral valve, × 2, Cerro Viejo. K. CEGH-UNC 10642, exterior of ventral valve, × 2. L. CEGH-UNC 21909, exterior of ventral valve, × 2. M–O. CEGH-UNC 21907a, ventral valve, latex cast of exterior (M), internal mould (N) and latex cast of interior (O), all × 2.5, Cerro Viejo. P, Q. CEGH-UNC 22053, dorsal valve, internal mould (P) and latex cast of interior (Q), × 4, Cerro Viejo. R. CEGH-UNC 21907b, dorsal valve, detail of cardinalia, × 4.5, Cerro Viejo.

Argentine material of *Reinversella* differs externally from the type species *I. (R.) monensis* in being more transverse in outline, in its parvicostellate ornament and also in the discontinuous rugae confined to the posterolateral areas (the Welsh specimens have prominent concentric rugae over the entire surface of both discs). Internally, *I. (R.) arancibiai* differs in its more widely divergent dental plates and much shorter and nonbilobate ventral muscle field. Although no complete dorsal interiors are known from the San Juan Formation, the new specimens reveal that cardinalia of *I. (R.) arancibiai* are rather similar to those of the Welsh species, both having a ridge-like cardinal process on a low, subtriangular notothyrial platform.

The monospecific *Guttasella* Neuman, 1976, from the Darriwilian (lower Llanvirnian) Virgin Arm Tuffs of the Summerford Group, Newfoundland, also possesses a double geniculation and a well-defined submarginal dorsal trough, but differs from *Reinversella* in lacking concentric rugae. It should be noted, however, that although the internal mould figured by Neuman (1976, pl. 5, fig. 2) is smooth, the presence of rugae on posterolateral corners cannot be discarded due to the incompleteness of the valve. In shell outline and parvicostellate ornament *Guttasella gutta* Neuman, 1976 resembles *I. (R.) arancibiai*, but its cordate, proportionally longer ventral muscle field is most similar to that of *I. (Inversella) borealis* Öpik, 1933 and *I. (Reinversella) monensis*. The intergradations of many features in the three forms suggest close phylogenetic relationships between them.

## Functional morphology

The plectambonitoids *Inversella* and *Guttasella* are the earliest known brachiopods to have developed a geniculate shell. This architectural pattern was later acquired independently by *Leptaena* and related

forms, a diverse and successful group of strophomenoids characterized by a dorsally geniculate shell. The earliest Leptaeninae occur at the end of Darriwilian (Da4 = 'Llandeilian'), becoming abundant and widespread through the Late Ordovician, Silurian and Devonian, and persist until the Early Carboniferous, spanning a time interval of about 130 Myrs. The double geniculation of *Inversella* (*Reinversella*) and *Guttasella*, with the associated submarginal external 'gutter' on the dorsal valve, represents a further level of complexity of the geniculate shell pattern, which appears recurrently in some species of *Leptaena* (*Leptaena*) Dalman, 1828, *Leptaena* (*Ygdrasilomena*) Cocks, 2005 and *Limbimurina*, Cooper, 1956. This indicates that such a shell design was functionally successful among the strophomenides. It is noteworthy that development of geniculation is usually associated with more or less prominent rugae on the visceral areas, not only in the leptaenins but also in other strophomenoids such as *Luhaia* Rõðmusoks, 1956 (subfamily Furcitellinae), and *Kjaerina* Bancroft, 1929 and *Kjerulfina* Bancroft, 1929 (subfamily Rafinesquininae), suggesting a functional correlation between these features.

There are many hypotheses about the mode of life of the large, concavo-convex strophomenides. The traditional hypothesis, first proposed by Lamont (1934) and subsequently supported by Rudwick (1970), Richards (1972), and Bassett (1984), considers that after a short period of attachment to the substrate, individuals detached becoming capable of resting on soft bottoms with the convex valve (usually the ventral) downward, partially sunk into the sediment, and the geniculation directed upwards, elevating the commissure well above the water-sediment interface. Based on biomechanical experiments, Savarese (1994) and Leighton & Savarese (1996) concluded that geniculate morphotypes of *Rafinesquina* Hall & Clarke, 1892 lived convex-down,



floating in highly fluid mud. This recumbent attitude, however, is improbable in *Reinversella* because its ventrally directed second deflection would have submerged the commissure in the sediment.

A radically different convex-up shell orientation was proposed by Lescinsky (1995) using information from epibiont distribution on *Strophomena* shells, in which encrusting (mainly by trepostome bryozoans) is not random, being greater on the convex valves. This hypothesis has been refuted by the argument that in such a position, the commissure will tend to sink into the mud (Leighton & Savarese 1996), but perhaps the main objection is that the convex-up position is the most stable hydrodynamically for reworked shells, leading epibionts to colonize their surface post-mortem and before burial.

A different life strategy was inferred by Spjeldnaes (1984) based on the density of encrustation on *Leptaena* specimens from the Wenlock of Gotland, Sweden. He noted that the number of epifaunal organisms is greatest on the trail and peripheral ridge and on the ventral valve. However, encrusters are also present on the dorsal valve, leading him to infer that *Leptaena* lived attached in a subvertical position, umbo-down, with both valves free of the sediment. The finding of some specimens of *Leptaena depressa* (J. de C. Sowerby, 1824)

buried in a vertical position supports this interpretation of the mode of life in species having a functional pedicle in the adult, such as *Leptaena rhomboidalis* (Wahlenberg, 1818; Hoel 2005). Evidence from muscle attachments in this high-energy species led Hoel (2005) to postulate a reconstruction in which the trail is orientated away from the main water flow to avoid damaging the lophophore. Contraction of the pedicle adjustor muscle would then have produced a rotational movement of the shell, changing the orientation of the commissure with respect to the current, from approximately parallel to obliquely upwards, creating turbulence around the commissure that facilitated capture of food particles.

Adult specimens of *I. (Reinversella) arancibiai* have a large, entirely open delthyrium indicating that they lived attached throughout their life. However, the two-phase geniculation of this species (Fig. 4), first directed ventrally and then dorsally (the latter is responsible for the long trail), once again poses questions about this structure's function. For example, it may be important for separating inhalant and exhalant currents, preventing a rapid sinking of the animal into the substrate, generating eddies around the commissure, or anchoring partially buried shells in an inclined or vertical position, among other

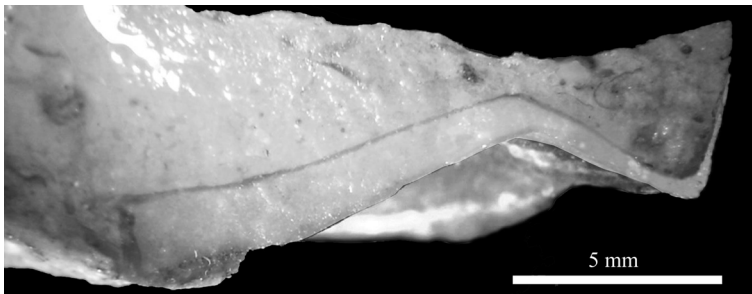


Fig. 4. Slightly oblique longitudinal section of ventral valve CEGH.UNC 4457 from Sierra de Villicum, showing progressive thinning of valve towards geniculation ( $\times 7.5$ ).

interpretations (Bassett 1984, Datillo 2004, Hoel 2005). First, it is significant that juvenile shells of *I.* (*Reinversella*), like the leptaenines, lack geniculation, being thin-shelled, plano-convex to gently biconvex, and that changes in growth direction start at about two-thirds of valve length, possibly at the onset of sexual maturity: see discussion of Timms & Brunton (1991) for productides. It seems likely that juveniles, lacking geniculation, lived umbo-down, and probably were able to adjust the shell position relative to the water currents (Fig. 5A). The question is: what does development of the geniculation imply for life position? Superficially, it could reflect a progressive change in mode of life, from erect to reclined. Among brachiopods, there are many examples of morphological trends during ontogeny related to drastic changes in the mode of life (e.g. Manceñido & Walley 1979). The first deflection of valve margin may be viewed as a hypertrophied concentric ruga, and one of its functions may have been, as we speculate below, to facilitate water circulation within the mantle cavity. The corresponding outermost ridge along the periphery of the ventral valve may in turn have played an important role in elevating the commissure above the sediment when individuals began to recline (Fig. 5C). Once the reclined position was achieved more or less permanently, the trail grew upwards without any restriction. In transverse sec-

tion (Fig. 4), valves are thicker posteriorly, and become progressively thinner towards the geniculation, the marginal ridge and the trail being particularly thin. In this respect, *Reinversella* clearly differs from *Leptaena*, in which the shell is thickest in the marginal ridge. This indicates a life position with the posterior third of the shell sunk in the substrate and the anterior commissure considerably more elevated. As a result, the trail becomes orientated in a subvertical position (Fig. 5D). Since the low-energy, open-shelf settings inhabited by *I.* (*R.*) *arancibiai* have low sedimentation rates, it seems improbable that geniculation had been an adaptation to mitigate rapid shell burial. At such a depth, the bottom is affected only by weak, sporadic, storm-induced currents, so that the most probable function of the trail was to separate exhalant and inhalant currents, being functionally analogous to the plicate commissure of other brachiopod groups (Hoel 2005).

The function of the pronounced channel along the periphery of the ventral valve, which corresponds to the external marginal ridge (Figs 3A, B), is difficult to assess. *Inversella* (*R.*) *arancibiai* probably possessed a ptycholophous or schizolophous lophophore similar to that inferred for the strophomenide *Leptaenoidea* and most plectambonitoids (Williams & Rowell 1965, Hurst 1975, Vogel 1986, Williams *et al.*

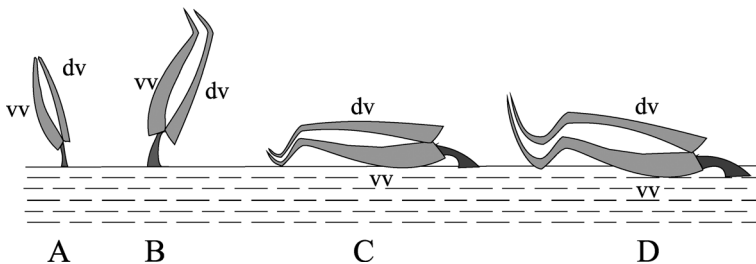


Fig. 5. Reconstruction of hypothesized mode of life of *Inversella* (*Reinversella*) *arancibiai*. A, juvenile stage; B, C, intermediate stages; D, adult stage. vv, ventral valve, dv, dorsal valve.



1997). If an analogy is established with the pattern of water circulation inferred by Hoel (2005) for *Leptaena depressa*, the inhalant current in *I. (R.) arancibiai* would have entered through the entire anterior commissure, well above the muddy substrate. Our interpretation of the marginal channel is that it may have helped to collect and conduct waste waters towards the posterolateral regions of the shell, where exhalant currents were expelled just above the water–sediment interface. As noted above, concentric rugae are confined to the posterolateral areas, becoming stronger as the shell grows, culminating a complete semicircular ruga, which precedes the first geniculation. We infer that development of rugae in *I. (R.) arancibiai* is unrelated to strengthening of the shell, but they play a role in conducting water out of the shell. Since juvenile individuals lack geniculation, and probably were capable of orientating the shell relative to the currents, this would make elimination of metabolic residues more efficient than in adults. We hypothesize that the function of the first complete ruga was essentially similar to that of the marginal channel developed subsequently, and marks the start of the change from an umbo-down subvertical to a reclined position. However, the permanent reclined mode of life, with the posterior part of the shell partially buried into the sediment, was probably not achieved until the second main geniculation and trail became fully developed.

## Acknowledgements

We are very grateful to Ian Percival and an anonymous reviewer whose comments helped us to improve this paper. This research was supported by grants from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PIP 5599) and Agencia Nacional de Promoción Científica y Técnica (FONCyT, PICT 21857).

## References

- ALBANESI, G.L. & ORTEGA, G., 2002. Advances on conodont-graptolite biostratigraphy of the Ordovician System of Argentina. In *Aspects of the Ordovician System in Argentina*, F.G. ACEÑOLAZA, ed., *INSUGEO, Serie Correlación Geológica* 16, 143-166.
- BANCROFT, B.B., 1929. Some new genera and species of Strophomenacea from the Upper Ordovician of Shropshire. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 73, 33-65.
- BASSETT, M.G., 1984. Life strategies in Silurian brachiopods. In *Autoecology of Silurian Organisms*, M.G. BASSETT & J.D. DOWSON, eds, *Special Papers in Palaeontology* 32, 237-264.
- BATES, D.E.B., 1968. The Lower Palaeozoic brachiopod and trilobite faunas from Anglesey. *Bulletin of the British Museum (Natural History)*, *Geology* 16, 127-199.
- BENEDETTO, J.L., 2002. The Ordovician brachiopod faunas of Argentina: Chronology and biostratigraphic succession. In *Aspects of the Ordovician System in Argentina*, F.G. ACEÑOLAZA, ed., *INSUGEO, Serie Correlación Geológica* 16, 87-106.
- BENEDETTO, J.L. (ed.), 2003. *Ordovician fossils of Argentina*. Secretaría de Ciencia y Técnica, Universidad Nacional de Córdoba, Córdoba, 560 pp.
- BRUSSA, E.D., MITCHELL, C.E., ORTEGA, G., MALETZ, J. & ASTINI, R.A., 2003. Middle Ordovician graptolite biostratigraphy from the Los Azules Formation at Los Gatos Creek, Central Precordillera, Argentina. In *Proceedings of the 7th International Graptolite Conference*, G. ORTEGA & G.F. ACEÑOLAZA, eds, *INSUGEO, Serie Correlación Geológica* 18, 21-25.
- CAÑAS, F.L., 1995. Early Ordovician carbonate platform facies of the Argentine Precordillera: restricted shelf to open platform evolution. In *Ordovician Odyssey*, J.D. COOPER, M.L. DROSER & S.C. FINNEY, eds, *The Pacific Section Society for Sedimentary Geology (SEPM)*, 221-224.
- CAÑAS, F.L., 1999. Facies sequences of Late Cambrian to Early Ordovician carbonates of the Argentine Precordillera: A physical stratigraphic comparison with Laurentian platforms. In *Laurentia–Gondwana Connections Before Pangea*, D. KEMP & V.A. RAMOS, eds, *Geological Society of America, Special Paper* 336, 43-62.
- CAÑAS, F.L. & CARRERA, M.G., 2003. Precordilleran reefs. In *Ordovician Fossils of Argentina*, J.L. BENEDETTO, ed., Secretaría de Ciencia y Técnica, Universidad Nacional de Córdoba, Córdoba, 131-153.
- CARRERA, M.G., SÁNCHEZ, T.M. & BENEDETTO, J.L., 1999. Paleoenvironmental controls on biofacies in the early Ordovician limestones of the Argentine Precordillera. In *Quo vadis Ordovician?*, P. KRAFT & O. FATKA, eds, *Acta Universitatis Carolinae, Geologica* 43, 475-478.

- COCKS, L.R.M., 2005. Strophomenate brachiopods from the Late Ordovician Boda Limestone of Sweden: their systematics and implications for palaeogeography. *Journal of Systematic Palaeontology* 3, 243-282.
- COCKS, L.R.M. & RONG, JIA-YU, 1989. Classification and review of the brachiopod superfamily Plectambonitacea. *Bulletin of the British Museum (Natural History), Geology* 45, 77-163.
- COOPER, G.A., 1956. Chazyan and related brachiopods. *Smithsonian Miscellaneous Collections* 127, 1-1245.
- DALMAN, J.W., 1828. Uppställning och Beskrifning af de i Sverige funne. Terebratuliter. *Kongliga Svenska Vetenskapsakademiens Handlingar för År 1827*, 3, 85-155.
- DATILLO, B.F., 2004. A new angle on strophomenid paleoecology: Trace-fossil evidence of an escape response for the plectambonitoid brachiopod *Sowerbyella rugosa* from a tempestite in the Upper Ordovician Kope Formation (Edenian) of northern Kentucky. *Palaiois* 19, 332-348.
- HALL, J. & CLARKE, J.M., 1892. *An Introduction to the Study of the Genera of Palaeozoic Brachiopoda*, Natural History of New York, Palaeontology 8 (1). New York Geological Survey, van Benthuyssen & Sons, New York, 367 pp.
- HERRERA, Z.A. & BENEDETTO, J.L., 1987. El género *Reinversella* (Brachiopoda) en el Ordovícico temprano de la Precordillera Argentina. *Actas 10º Congreso Geológico Argentino* 3, 77-80.
- HERRERA, Z.A. & BENEDETTO, J.L., 1991. Early Ordovician brachiopod faunas from the Precordillera basin, Western Argentina: biostratigraphy and paleobiogeographical affinities. In *Brachiopods Through Time*, D.I. MACKINNON, D.E. LEE & J.D. CAMPBELL, eds. Balkema, Rotterdam, 283-301.
- HOEL, O.A., 2005. *Diversity and life habits of Silurian Strophomenide brachiopods of Gotland*. Doctoral thesis, Uppsala University, Department of Earth Sciences, 47 pp.
- HURST, J.M., 1975. The function of the brachial valve septa in plectambonitacean brachiopods. *Lethaia* 8, 63-67.
- JONES, O.T., 1928. *Plectambonites* and some allied genera. *Memoirs of the Geological Survey of Great Britain, Palaeontology* 1, 367-527.
- LAMONT, A., 1934. Lower Palaeozoic brachiopods of the Girvan District, with suggestions on morphology in relation to environment. *Annals Magazine Natural History* 10, 161-184.
- LEIGHTON, L. & SAVARESE, M., 1996. Functional and taphonomic implications of Ordovician strophomenide brachiopod valve morphology. In *Brachiopods*, P. COPPER & J. JIN, eds, Balkema, Rotterdam, 161-168.
- LESCINSKY, H.L., 1995. The life orientation of concavoconvex brachiopods: overturning the paradigm. *Paleobiology* 21, 520-551.
- MANCEÑIDO, M.O. & WALLEY, C.D., 1979. Functional morphology and ontogenetic variation in the Callovian brachiopod *Septirhynchia* from Tunisia. *Palaentology* 22, 317-337.
- NEUMAN, R.B., 1976. Early Ordovician (late Arenig) brachiopods from Virgin Arm, New World Island, Newfoundland. *Bulletin Geological Survey of Canada* 261, 11-61.
- ÖPIK, A.A., 1933. Über Plectamboniten. *Acta et Commentationes Universitatis Tartuensis* 24, 1-79.
- ÖPIK, A.A., 1934. Über Klitamboniten. *Acta et Commentationes Universitatis Tartuensis* 26, 1-239.
- OTTONE, E.G., ALBANESI, G.L., ORTEGA, G. & HOLFELTZ, G.D., 1999. Palynomorphs, conodonts and associated graptolites from the Ordovician Los Azules Formation, Central Precordillera, Argentina. *Micropaleontology* 45, 225-250.
- RICHARDS, R.P., 1972. Autoecology of Richmondian brachiopods (Late Ordovician of Indiana and Ohio). *Journal of Paleontology* 46, 389-405.
- RÖÖMUSOKS, A.K., 1956. *Luhaia*, novyi red strofomend iz verkhego ordovika Estonskoi SSR. *Akademia Nauk SSSR* 106, 1091-1092. [Russian].
- RUDWICK, M.J.S., 1970. *Living and fossil brachiopods*. Hutchinson, London, 199 pp.
- SAVARESE, M., 1994. Taphonomic and paleoecologic implications of flow-induced forces on concavoconvex articulate brachiopods: an experimental approach. *Lethaia* 27, 301-312.
- SCHUCHERT, C. & COOPER, G.A., 1931. Synopsis of the brachiopod genera of the suborders Orthoidea and Pentamerioidea, with notes on the Telotremata. *American Journal of Science (series 5)* 22, 241-255.
- SOWERBY, J. de C., 1824. *The Mineral Conchology of Great Britain; on coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the Earth*, 7 vols. (1812-1822, pl. 1-383; 1823-1846, pl. 384-648), London.
- SPIJELDNAES, N., 1984. Epifauna as a tool in autecological analysis of Silurian brachiopods. In *Autoecology of Silurian organisms*, M.G. BASSETT & J.D. DOWSON, eds, *Special Papers in Palaeontology* 32, 225-235.
- TIMMS, A.E. & BRUNTON, C.H.C., 1991. Growth rates and periodicity in *Antiquatonia* and *Plicatifer*, Lower Carboniferous Productacean brachiopods. In *Brachiopods Through Time*, D.I. MACKINNON, D.E. LEE & J.D. CAMPBELL, eds, Balkema, Rotterdam, 41-47.
- VOGEL, K., 1986. Origin and diversification of brachiopod shells: viewpoint of constructional morphology. In *Les Brachiopodes Fossiles et Actuels*, P.R. RACHEBOEUF & C. EMIG, eds, *Biostratigraphie du Paléozoïque* 4, 399-408.
- WAHLENBERG, G., 1818. *Petricata Telluris Svecanae*. *Acta Societatis Regiae Scientiarum Uppsalaensis* 8, 1-116.

- WILLIAMS, A. & ROWELL, A.J., 1965. Brachiopod anatomy. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda*, MOORE, R.C., ed., Geological Society of America, New York and University of Kansas Press, Lawrence, 6-57.
- WILLIAMS, A., CARLSON, S.J., BRUNTON, C.H.C., HOLMER, L.E. & POPOV, L.E., 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London (Series B)* 351, 1171-1193.
- WILLIAMS, A., BRUNTON, C.H.C. & MACKINNON, D.I., 1997. Morphology. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised)*, R.L. KAESLER, ed., Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 321-440.