Hyolith-dominated shell beds from the Lampazar Formation in NW Argentina: patterns and processes of origin in the Late Cambrian (Furongian) seas of western Gondwana

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Late Cambrian (Furongian) shell beds in the Salta Province of NW Argentina are unique because of the presence of abundant hyolith skeletal remains within them. Hyolith shell beds are located in the mid-upper part of the Lampazar Formation at the Angosto de La Quesera locality, and are the first recorded accumulations of this type in the lower Palaeozoic of the South American Andean Basin. The shell beds are of the order of several mm thick, and are laterally persistent within outcrop scale, with a few metres of lateral development. Two types of hyolith shell beds are recognised: Type 1 is a storm-dominated, event concentration, represented by dispersed to densely packed accumulations of well preserved hyolith and gastropod shells (*Strepsodiscus austrinus*). Hyolith conchs are current oriented with the long axes parallel to unidirectional flow on the sandstones surfaces. Type 2 shell beds are background, composite concentrations, of poorly preserved, comminuted debris of hyolith shells with associated gastropod and trilobite sclerites (dominated by *Parabolina*, *Beltella* and *Leiostegium*). The genesis of both shell beds was controlled primarily by physical processes, such as storms and current and/or wave agitation. The thickness, simple internal fabric and geometry shown by both accumulations are typical of Cambrian-style shell-beds.

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SHELL BEDS were recurrent features in the peri-Gondwanan shallow mid to high latitude Cambrian-Ordovician seas. These remarkable components of benthic ecosystems, provide important clues about the original environment and palaeoecology of shallow marine platforms (Brett & Baird 1986; Fürsich & Oschmann 1993; Zuschin *et al*. 2003). In fact, the Cambrian-Ordovician interval was a critical period not only in the history of life, but also to shell development and accumulation (see Li & Droser 1997, 1999). Skeletonised metazoans appeared during the early Cambrian, and subsequently radiated throughout the early Palaeozoic (Webby *et al*. 2004). This radiation significantly affected the composition, taphonomic features, physical dimension and abundance of shell beds forming during this time (Li & Droser 1999). The earliest shell beds appeared in the Cambrian, associated with the first skeletonised fossils. Subsequently, shell beds become more common, thicker and taxonomically more diverse throughout the Cambrian. Physical processes, such as storm events, were mainly responsible for production of these shell beds (Li & Droser 1997). Whilst Lower Ordovician (Ibexian) shell beds are primarily trilobite- and echinoderm-dominated they are taphonomically similar to Cambrian shell beds. In contrast, brachiopod, ostracod and gastropod shell beds tend to dominate Middle Ordovician (Whiterockian) strata (Li & Droser 1999).

Nearly all shell beds described from the early Palaeozoic peri-Gondwanan realm consist of monotaxic accumulations of bivalves, bryozoans and/or echinoderms; and polytaxic concentrations include brachiopod valves or trilobite sclerites and/or combined brachiopod-trilobite associations, with gastropod, bivalve, nautiloid and rostroconch shells. Although the first record of hyoliths (Cambrian-Permian) in the Argentine literature

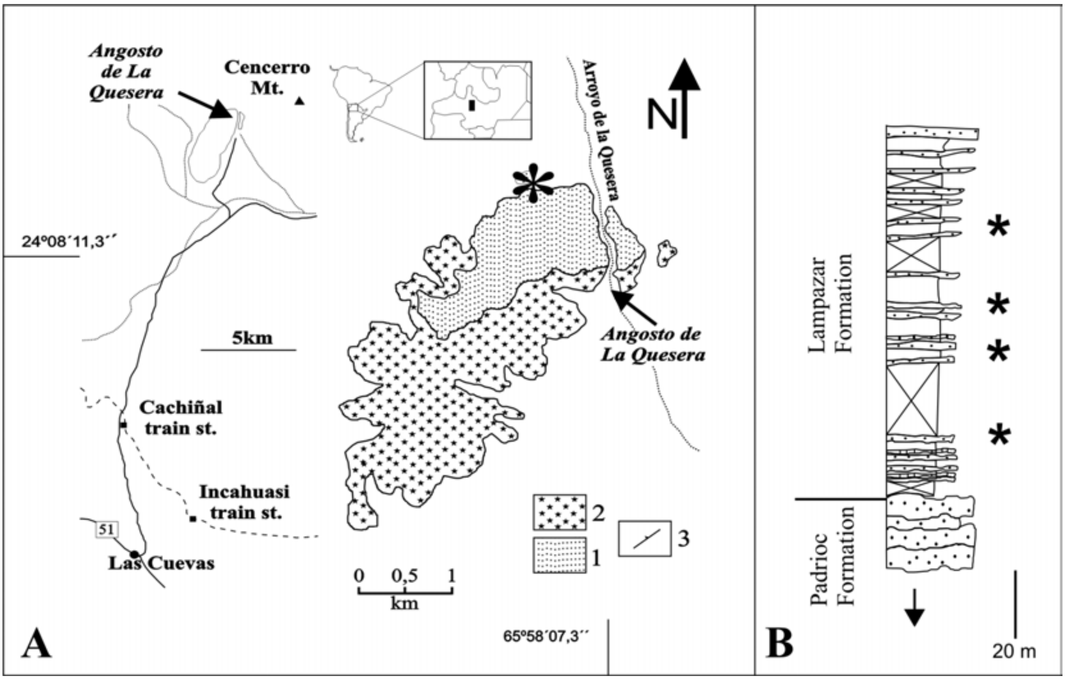

Fig. 1. **A**. Location of the studied site at the Angosto de la Quesera locality, Cordillera Oriental of Salta Province, NW Argentina. 1. - Cambro/Ordovician strata; 2. - La Quesera Granite; 3. - Strata depth and orientation. **B**. Stratigraphic sketch of the Lampazar Formation exposed at the locality, asterisk marks the position of the hyolith shell beds (Modified from Hongn *et al*. 2001)

belongs to Kayser (1876), these organisms have become one of the "forgotten groups" in the early Palaeozoic literature of South America. More importantly, with a few exceptions (see Luo *et al*. 1994; Hou *et al*. 2004) hyolith remains are rarely recorded as the dominant constituents of shell beds.

Some hyolith accumulations probably originated as faecal clusters (e.g. Vannier & Chen 2005), with opercula preserved in disorganised association with conchs as a result of active predatory activity. These types of peculiar associations are seen as elliptical, elongated ribbon-like and concentric aggregates (Vannier & Chen 2005).

This contribution constitutes the first record of mass accumulations of hyoliths in Furongian strata of NW Argentina (Fig. 1), and in the western margin of the early Palaeozoic supercontinent of Gondwana

TERMINOLOGY AND CLASSIFICATION

In this study, we have employed the field description schemes of Kidwell (1991) and Kidwell & Holland (1991). Hence, our qualitative observations were made with special attention to shell bed thickness, lateral continuity, geometry, contacts, shell packing and taphonomic signatures of the shelly remains. For descriptive purposes only the term "well preserved" is used here when shells exhibit minimal or no damage, and "poorly preserved" if the shells are disarticulated or fragmented and abraded/corroded. Based on Kidwell (1991), the shell bed classification includes four types: 1. event-concentrations; 2. composite-concentrations; 3. hiatal/condensed concentrations, and 4. lag-concentrations.

The absence of well preserved opercula is a major impediment to identifying hyolith taxa confidently (see Marek 1963, 1967). The lack of opercula from the Lampazar Formation thus precluded detailed taxonomic analysis of the hyolith material. However, it should be noted that material from the Lampazar Formation does provide some taxonomically useful traits.

GEOLOGIC SETTING

Siliciclastic sequences dominate the Cambrian-Ordovician strata of the central Andean Basin, with more than 5000 metres of strata in certain areas such as Santa Victoria (Salta Province, Argentina) and Tarija (Bolivia). Sandstones, shales and minor limestones characterise a wide range of sedimentary environments that includes estuarine, wave-, storm-dominated and open marine conditions (Moya 1999; 2002; Moya *et al*. 2003a; Aceñolaza 2003, 2005).

The early Palaeozoic stratigraphy in NW

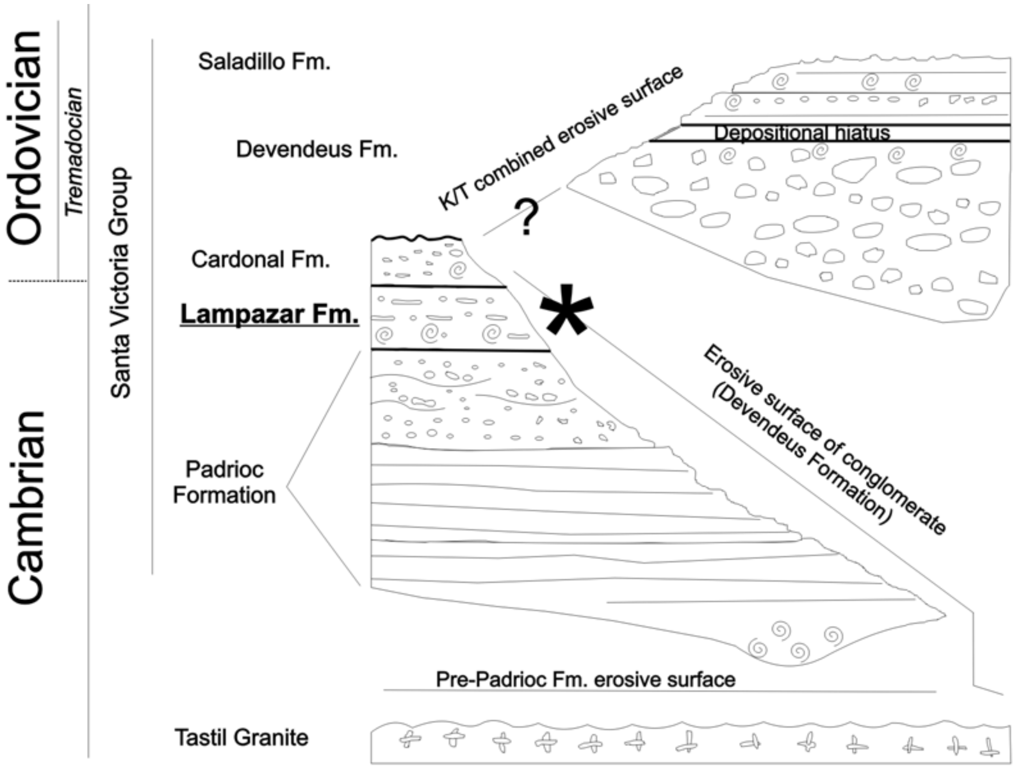

Fig. 2. Cambro-Ordovician stratigraphic scheme for the Angosto de la Quesera locality in the Salta Province. Owing to the particular arrangement of facies of the Devendeus Formation conglomerates, the Lampazar Formation crops out only in the NW sector of the area.

Argentina is dominated by different cycles, subdivided into three major units: The Ediacaran-early Cambrian Puncoviscana Formation (Aceñolaza & Aceñolaza 2005 and references therein); the Cambrian Mesón Group (Moya 1998; Sánchez 1999; Sánchez & Salfity 1999); and the Cambrian-Ordovician Santa Victoria Group (Moya 1999; Aceñolaza 2003, 2005).

The Lampazar Formation is the first highly fossiliferous stratigraphic unit dominated by shales and sandstones in the Santa Victoria Group, partially representing a time equivalent unit to the widely distributed Santa Rosita Formation (Fig. 2; Aceñolaza *et al*. 1999). This unit is extensively distributed in the region, with outcrops to the north in the Angosto del Moreno, Los Colorados, Ronqui Angosto and Cajas and to the south in the type area at Incamayo-Parcha (Tortello & Rao 2000; Astini 2003).

The Angosto de la Quesera and Tres Cruces localities constitute classical areas in the early Palaeozoic literature of northern Argentina. Keidel (1943) described in impressive detail the sedimentary features of these strata, most of which were later confirmed by modern analysis (Hongn *et al*. 2001; Moya *et al*. 2003b; Aceñolaza *et al*. 2003; Pinilla *et al*. 2008).

Outcrops of the Lampazar Formation in this area are located in the NW sector of the Angosto de La Quesera and along the eastern flank of the road heading to the Abra de Palomares (Fig. 1A). The section is lithologically dominated by yellowish-green, fine to medium sandstones with lesser amounts of shale. Strata transitionally overlying this unit include the thick grey quartzites of the Padrioc Formation and are followed, transitionally as well, by a small and incomplete succession of yellowish sandstones and quartzites probably belonging to the Cardonal Formation. Hummocky cross stratification is prevalent in the lower section of the unit, while wave generated ripple, cross stratification with clear unidirectional cross-laminations are found in the mid-upper part of the section (Fig. 4). Grading parallel to cross-lamination associated with current rippled sandstone beds is also observed. Trace fossils and fossil debris in the lower part of the Lampazar Formation denote clear unidirectional and fairly strong currents in a shallow shoreface setting as represented by these strata (Fig.1B, 3A). Flute markings with clearly developed “heads” and downstream tails are developed over sandstones associated with trace fossils and bioclast sclerites.

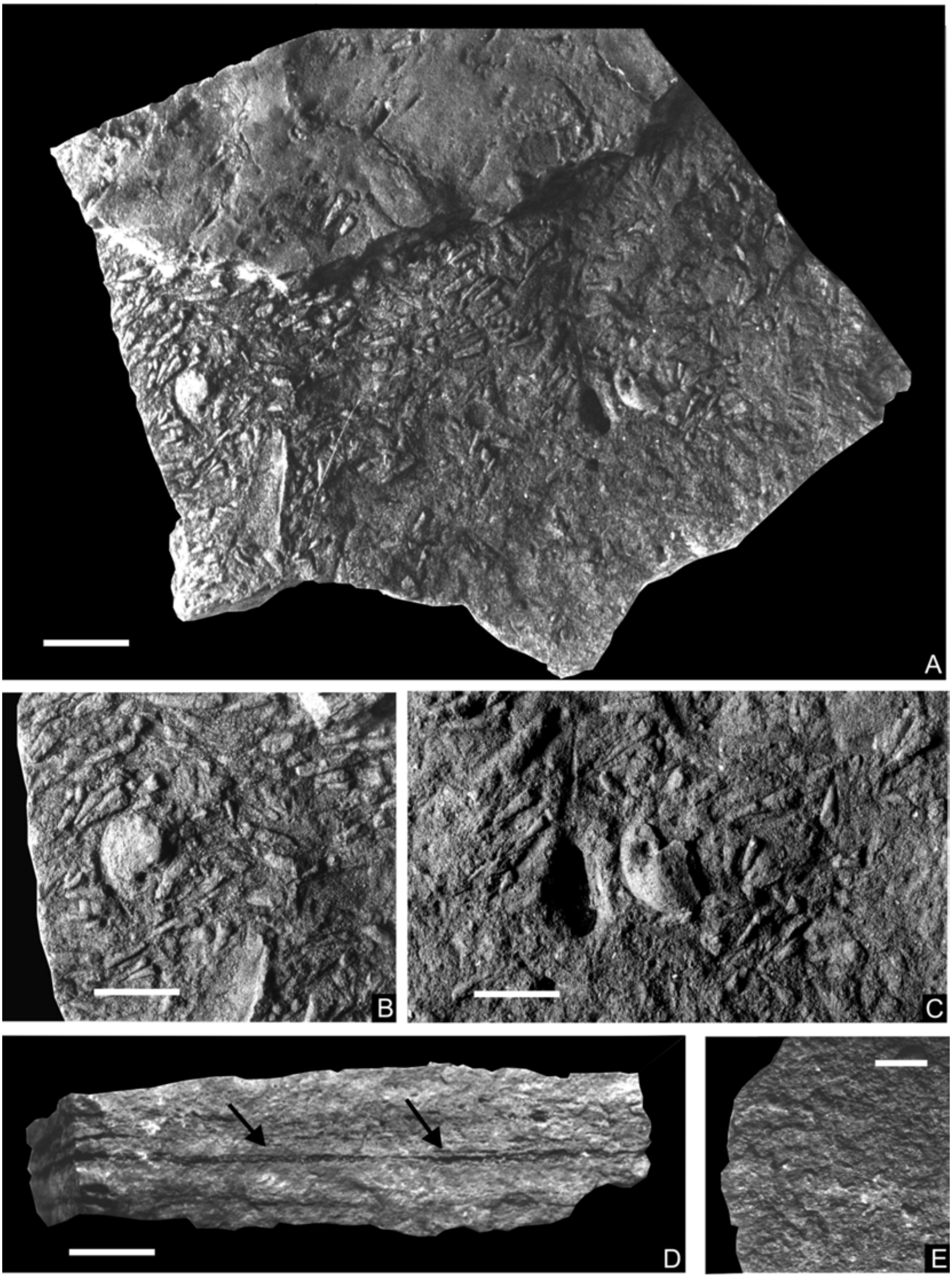

Fig. 3. Hyolith shell beds of the Lampazar Formation at the Angosto de La Quesera locality, Salta Province, NW Argentina. **A**. Large sample with current oriented shells (Type 1 shell bed). Notice the two gastropods in the left and right sector of sandstone (scale 3 cm). **B, C**. Close up of gastropods where orientation of hyoliths can be seen. Gastropods acted as large particles disrupting currents and orientation of other bioclasts downstream (scale 2 cm). **D**. Lateral view of a sandstone layer where hyolith shell bed is highlighted by darker-coloured levels (scale 3 cm). **E**. Type 2 shell bed with highly fragmented hyolith remains (scale 1 cm).

The middle and upper section of the unit displays gutter casts (Whitaker 1973) associated with hummocky cross stratification, a common signature in storm-dominated shelf environments (Walker & Plint 1992). Encased sandstone gutter casts protruding from the outcrop were also recorded in the strata. Single beds display limited lateral continuity, with some amalgamation of thicker sandstone layers.

The Lampazar Formation at the Angosto de La Quesera is a highly fossiliferous sequence containing trilobites, trace fossils, conodonts, brachiopods and molluscs that provide valuable biostratigraphical data which in turn permit accurate dating of strata as a Furongian succession (Pinilla *et al*. 2008).

NATURE OF THE SHELL BEDS

Following the pioneer studies of Kidwell (1990) and Kidwell & Brenchley (1994, 1996), several studies (e.g., Li & Droser 1997, 1999; Simões *et al*. 2000; Cherns *et al*. 2008; Sterren 2008) have consistently demonstrated that patterns of shell accumulations vary throughout the Phanerozoic. Changes are largely tied to the increase in the diversity and environmental distribution of shell-producers and in taphonomic feedback among the living organisms and skeletal remains (Kidwell & Brenchley 1994; Li & Droser 1997). Based on certain sedimentologic, stratigraphic and taphonomic features, such as the physical dimension, taxonomic composition and taphonomic signatures of the skeletal accumulations, Kidwell & Brenchley (1994, 1996) have recognised two main modes of shell concentrations, called the Archaic and Modern modes. Thin (bi-dimensional), dispersed, and internally simple, brachiopod-dominated concentrations characterise the Archaic mode of concentrations. This mode was predominant throughout the Palaeozoic and into the Triassic. Conversely, the Modern mode is mainly represented by densely packed, meter scale thick (three-dimensional), internally complex shell-beds, formed by more durable hard parts (mollusc-dominated), which are commonly found in Cretaceous and Cenozoic strata. However, Li & Droser (1997, 1999) have noticed that Cambrian and Early Ordovician shell concentrations are not taphonomically similar to those of Archaic and Modern modes. Hence, the authors refined Kidwell's modes of shell concentration by including a Cambrian mode. Usually, the fabric of the Cambrian and Lower Ordovician shell beds are internally simple (see Li & Droser 1997, 1999), while Late Ordovician and younger concentrations (especially in the Mesozoic and Cenozoic) are amalgamated or accretionary shell beds, generally exhibiting a complex internal fabric characterised by lateral and vertical variation in shell packing, orientation, and sorting.

The Cambrian is a critical period in the development of shell accumulations due to the diversification of shelly metazoans. In general, Cambrian shell beds are dominated by trilobites, brachiopods, gastropods, echinoderms and small tubular shells. These are relatively thin, simple fabric, storm-generated event concentrations that predominate in shelf and siliciclastic facies. Composite and condensed shell beds are common in platformal, carbonate dominated environments (Li & Droser 1997). The Furongian Lampazar Formation accumulations are the first record of hyolith-dominated shell beds from western Gondwana. As for other Cambrian concentrations (see Li & Droser 1997) their genesis was controlled primarily by physical processes, such as storm events and current and/or wave agitation. The Lampazar Formation accumulations are composed of skeletal remains typical of Sepkoski's (1981) Cambrian Evolutionary Fauna, and are good examples of the Cambrian mode of shell concentration *sensu* Li & Droser (1997). These shell beds are intercalated in sandstones, suggesting alternation of periods with faunal development and shell bed generation. Similar taphonomic, taxonomic and ecological conditions are unknown in lower parts of the unit in the area, and in the outcrops of the Lampazar Formation at Cajas, Incamayo or El Moreno regions of Argentina. The unique occurrence of this shell bed is interpreted to be the result of a particular suite of high energy local environmental conditions that characterise the sedimentary sequence, and the presence of more durable, "one-piece" skeletal remains of hyolith shells.

AFFINITIES OF HYOLITHA

The Class Hyolitha Marek, 1963 encompasses bilaterally symmetrical, calcareous, operculate, conical-shelled organisms (Malinky *et al*. 2004). There is no consensus on the affinities of the group, with some authors supporting a molluscan affinity (Marek & Yochelson 1964, 1976; Wills 1993; Yochelson 2000; Malinky & Yochelson 2007), whereas others consider them a separate phylum (Runnegar *et al*. 1975; Runnegar 1980; Pojeta 1987; Kouchinsky 2000).

Hyoliths were armoured with a four piece scleritome consisting of an elongate conch, generally oval-shaped operculum, and two spines of "helens" protruding from beneath the operculum, all of which readily separated after the death of the animal. Some hyoliths possess septae that divided the conch into closed chambers

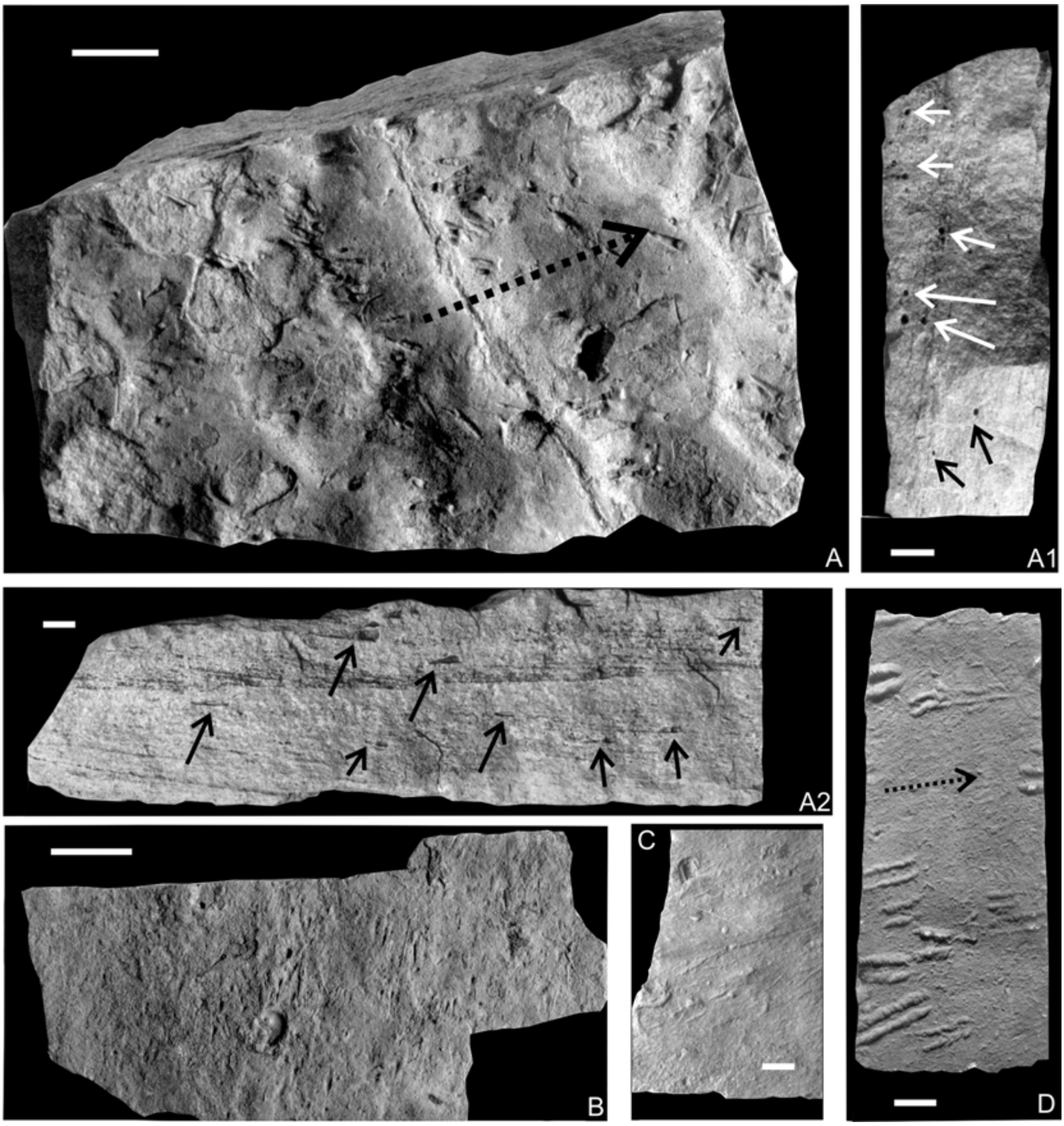

Fig. 4. Sandstone soles of the Lampazar Formation at the Angosto de La Quesera locality. **A**. Rippled sandstone layer (wave and combined ripples) with hyoliths preserved on the climbing surfaces of the ripples (scale 3 cm). **A1**. Frontal view of same piece with arrows pointing toward the cross sections of the hyoliths (scale 3 cm). **A2**. Lateral view of the same, with lateral views of hyoliths within the sandstone matrix (scale 3 cm). **B**. Sole of sandstone layer with tool marks, a gastropod and current-oriented hyoliths (scale 4.5 cm). **C**. Sandstone layer with an olenid trilobite cranidium acting as a complementary bioclast within the hyolith shell beds (scale 1 cm). **D**. Current-oriented trilobite trace fossils supporting the directional flow of water (Rusophycus isp. and cruzianiform traces) (scale 2.2 cm).

at the apex. The ventral surface of the conch has a flattened shape whereas the dorsum is variably inflated, creating a sub-triangular cross section; the shell aperture is covered by a sub-triangular, curved operculum. The helen-bearing hyoliths were probably mobile and the helens may have contributed both to locomotion and stabilisation of the shell.

The Class Hyolitha ranges from the early Cambrian to at least the Middle Permian (Fischer 1962), and are recorded from a varied spectrum of marine sedimentary strata. These organisms are considered to be a relict of the Cambrian Evolutionary Fauna (Sepkoski 1981). Hyoliths attain their greatest abundance and most widespread distribution in the Cambrian and decline thereafter until their Permian extinction. Post Cambrian occurrences are largely confined to stressed marine environment facies, where competition with other marine benthos would have presumably been diminished (Malinky *et al*. 2004).

In a general sense, hyoliths are rare fossils, and are characteristically represented by low-diversity assemblages. Hyoliths has been recorded worldwide (Malinky *et al*. 2004, written communication), and Cambrian hyoliths are particularly well known from different localities of the world (Malinky & Berg-Madsen 1999).

In Argentina, hyoliths have received little attention. In a recent contribution, Pagani *et al*. (2005) presented a new species from the late Cambrian of NW Argentina (*Tajinella*? *iruyensis*), and provided an overview of the current status of Argentine material, but their study focused on the taxonomy of these organisms rather than on their environmental setting.

Earlier records of hyolith shell bed accumulations are restricted to the lower Cambrian hyolith shell beds of the Kunming, Jinming and Malong areas in Eastern Yunnan, China (Luo, *et al*. 1994), where well preserved *Allatheca xiaoluoguiensis* Jiang, occur as current orientated shell-beds deposited on a shallow carbonate shelf. In addition, Hou *et al*. (2004) figured more than one hundred specimens, some current aligned, on a bedding surface from the lower Cambrian at Ma´anshan, Chengjiang, China. European and American occurrences of shell beds have been mentioned by Holm (1893) and Marek & Yochelson (1976). The Swedish hyolith species comes from Cambrian strata, while the American material comes from late Cambrian sandstones of midwest USA. None of these shell beds have been studied in detail, and further studies could provide additional elements to understand the patterns and processes associated with the origin of these shell beds.

TAPHONOMY OF THE SHELL BEDS

The hyolith accumulations in the Lampazar Formation were formed in shallow water just at, or above, storm wave base. There is a clear distinction between the two recognised shell bed types. Type 1 are storm-generated event beds, and include parautochthonous skeletal remains. This type of shell bed ranges up to 6 cm thick and has an erosive base and ripple marks at the top. Hyolith shells in these beds were moved by currents, hydrodynamically oriented and deposited on the surface of sediments and on the slip-front of current ripples in the sandstones (Fig. 4A), with apertures pointing downstream. The associated gastropod remains are usually well preserved and also concordant to bedding.

Even though the Hyolithida have been recently interpreted as suspension-feeding organisms with the aperture oriented towards the oncoming currents (Marek *et al*. 1997), the lack of opercula associated with the studied shells is interpreted to be the result of the shells behaving like any other type of sedimentary particle as they were transported and deposited by currents. In fact, the hyolith and gastropod shells seem to have been rolling and sliding as part of the sedimentary bed load. Because impact tool marks are also observed, these fossils may also have been transported by saltation and suspension. However, prior to final burial, the hyolith and gastropod shells do not appear to have been exposed to much erosion or abrasion at the Taphonomic Active Zone (TAZ). There are no signs of bioerosion or encrustation on the surfaces of shells or moulds. Hence, taphonomic features indicate a lack of post-mortem infestation and encrustation by successive biota on the shells, supporting the notion of rapid burial. In addition, despite their association with current generated sedimentary structures, breakage of hyoliths is rare, highlighting in particular the "one piece integrity" of the shell layers. Finally, the hyoliths in the Type 1 shell beds are all of similar size. There are no signs of extensive shell reworking or winnowing in the concentrations. This suggests that episodic events generated mass concentrations by burying single rather than multiple populations of hyoliths.

Type 2 shell beds occur as polytaxic accumulations of poorly preserved, comminuted debris of hyolith shells with associated gastropod and rare trilobite sclerites. Shell fragments are dispersed to densely packed and are chaotically oriented in the matrix. Type 2 shell beds occur as background (composite) concentrations formed by accumulation of parautochthonous to allochthonous skeletal remains. The remains are highly fragmented, slightly rounded and appear to be of similar size. The absence of mud-blanketing layers and the lack of wholly intact skeletal remains (hyoliths with associated operculum and complete trilobites) suggests an early death with long residence time at the TAZ prior the final burial in shallow water, near shore conditions under low net rates of sedimentation.

The hyolith shell beds are common in the mid-upper part of the Lampazar Formation at the Angosto de La Quesera locality. Hyoliths are the dominant bioclasts in these bioaccumulations, although trilobite and brachiopod remains are also common at the upper levels of the sedimentary succession. Associated trace fossils are restricted to arthropods and soft bottom dwellers. Arthropods left cruzianiform and rusophycid traces (furrowing and resting traces) while the soft bottom dwellers left horizontal single and branched burrows, and vertical tubes (eg., *Palaeophycus* and *Skolithos*).

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REFERENCES

Aceñolaza, F. & Aceñolaza, G., 2005. La Formación Puncoviscana y unidades estratigráficas vinculadas en el Neoproterozoico – Cámbrico Temprano del Noroeste Argentino. *Latin American Journal of Sedimentology and Basin Analysis 12*, 67-91.

Aceñolaza, G.F., 2003. The Cambrian System in Northwestern Argentina: Stratigraphical and palaeontological framework. *Geologica Acta 1*, 23-39.

Aceñolaza, G.F., 2005. The Cambrian System in Northwestern Argentina: stratigraphical and palaeontological framework. Reply. *Geologica Acta 3*, 73-77.

Aceñolaza, G.F., Emig, C. & Gutiérrez-Marcos, J.C., 2003. Lingulid shell beds from the Ordovician of Argentina, with notes on other peri-Gondwanan occurrences. *INSUGEO, Serie Correlación Geológica 17*, 237-244.

Aceñolaza, G.F., Gutiérrez-Marco, J.C., Rábano, I. & Díaz Martínez, E., 1999. Las lumaquelas de la Formación Sella (Ordovícico de la Cordillera Oriental boliviana) y su interés paleobiogeográfico. *XIV Congreso Geológico Argentino 1*, 355-358.

Aceñolaza, G.F., Milana, J.P., Heredia, S. & Simoes, M., 2003. Stratigraphical framework of the Angosto de la Quesera conglomerate complex (Cordillera Oriental of Salta): an incised valley system in the Tremadocian of NW Argentina. *INSUGEO, Serie Correlación Geológica 17*, 365-380.

Aceñolaza, G.F. & Nieva, S.M., 2001. Sobre algunas acumulaciones fosilíferas en el Ordovícico Inferior de la Cordillera Oriental Argentina. *Boletin Geológico y Minero 112*, 35-42.

Astini, R., 2003. The Ordovician Proto-andean basins. 1-74 in Benedetto, J.L. (ed.), *Ordovician Fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, .

Brett, C.E., & Baird, G.C., 1986. Comparative taphonomy: A key to paleoenvironmental interpretation based on fossil preservation. *Palaios 1*, 207-227.

Cherns, L., Wheeley, J.R., & Wright, V.P., 2008. Taphonomic windows and molluscan preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology 270*, 220-229.

Fischer, D.W., 1962. Small conoidal shells of uncertain affinities. 98-143 in Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology. Part W, Miscellanea*. Geological Society of America, New York and University of Kansas Press, Lawrence.

Fürsich, F.T. & Oschmann, W., 1993. Shell beds as tools in basin analysis. The Jurasic of Kachh, western India. *Journal of the Geological Society, London 150*, 169-185.

Holm, G. 1893. Sveriges Kambrisk-Siluriska Hyolithidæ och Conularidæ. *Sveriges Geologiska Undersökning, Afhandlingaroch uppsatser C 112*, 1–172.

Hongn, F., Tubia, J.M., Aranguren, A., Mon, R. & Battaglia, R., 2001. Intrusión del granito rojo de Tastil en areniscas eopaleozoicas en el Angosto de la Quesera, Cordillera Oriental, Salta. *Revista de la Asociación Geológica Argentina 56 (2)*, 349-352.

Hou Xian-Guang, Aldridge, R.J., Bergström, J., Siveter, D., Siveter, D.J, & Xiang-Hong, F., 2004. *The Cambrian Fossils of Chengjiang, China. The Flowering of Early Animal Life*. Blackwell Publishing, Oxford, 233 p.

Kayser, E., 1876. Uber primordiale und untersilyurische fossilien aus der Argentinischen Republik. *Actas de la Academia Nacional de Ciencias 8*, 297-332.

Keidel, J., 1943. El Ordovícico Inferior de los Andes del Norte Argentino y sus depósitos marino-glaciares. *Boletín de la Academia Nacional de Ciencias de Córdoba 36*, 140-229.

Kidwell S.M., 1990. Phanerozoic evolution of macroinvertebrate shell accumulations: preliminary data from the Jurassic of Great Britain. 309-327 in Miller, W.W. (ed.), *Paleocommunity Temporal Dynamics*. Paleontological Society, Special Publication 5.

Kidwell, S.M., 1991. The stratigraphy of shell concentration. 211-290 in Allison, P.A. & Briggs, D.E.G. (eds.), *Taphonomy: releasing the data locked in the fossil record*. Plenum Press, New York.

Kidwell S.M. & Brenchley P.J., 1994. Patterns in bioclastic accumulations through the Phanerozoic: Changes in input or in destruction? *Geology 22*, 1139-1143.

Kidwell S. M. & Brenchley P.J., 1996. Evolution of the fossil record: thickness trends in marine skeletal accumulations and their implications. 290-336 in Jablonsky D.H., Erwin D.H., Lipps J. H. & Brenchley P.J. (eds.), *Evolutionary Paleobiology*. University of Chicago Press, Chicago.

Kidwell S.M. & Holland S.M., 1991. Field description of coarse bioclastic fabrics. *Palaios 6*, 426-434.

Kouchinsky, A.V., 2000. Skeletal microstructures of hyoliths from the Early Cambrian of Siberia. *Alcheringa 24*, 65-81.

Li, X. & Droser M.L., 1997. Nature and distribution of Cambrian shell concentrations: evidence from the Basin and Range province of western United States (California, Nevada and Utah). *Palaios 12*, 111-126.

Li, X. & Droser M.L., 1999. Lower and Middle Ordovician Shell Beds from the Basin and Range Province of the Western United States (California, Nevada, and Utah). *Palaios 14*, 215-233.

Luo, H., Jiang, Z. & Tang, L., 1994. *Stratotype section for the Lower Cambrian stages in China*. Yunnan Science and Technology Press. Kunming, 183 p.

Malinky, J.M., 2002. A revision of Early to Middle Ordovician hyoliths from Sweden. *Palaeontology 45*, 511-555.

Malinky, J.M. & Berg-Madsen, V., 1999. A revision of Holm´s Early and Middle Cambrian hyoliths of Sweden. *Palaeontology 42*, 25-65.

Malinky, J.M., Wilson, M.A., Holmer, L.E. & Lardeux, H., 2004. Tube-shaped incertae sedis. 214-222 in Webby, B.D., Paris, F., Droser, M.L. & Percival, I.G. (eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York.

Malinky, J.M. & Yochelson, E.L., 2007. On the sytematic position of the Hyolitha (Kingdom Animalia). *Memoirs of the Association of Australasian Palaeontologists 34*, 521-536.

Marek, L., 1963. New knowledge on the morphology of Hyolithes. *Sborník geologických Ved, Paleontologie 1*, 53-72.

Marek, L. & Yochelson, E.L., 1976. Aspects of the biology of Hyolitha (Mollusca). *Lethaia 9*, 65-81.

Marek, L., Parsley, R.L. & Galle, A., 1997. Functional morphology of hyoliths based on flume studies. *Vestník Ceského geologického ústavu 72*, 351-358.

Moya, M.C., 1998. El Paleozoico inferior de la Sierra de Mojotoro, Salta-Jujuy. *Revista de la Asociación Geológica Argentina 53*, 219-238.

Moya, M.C., 1999. El Ordovícico en los Andes del Norte Argentino. 134-152 in González Bonorino, G., Omarini, R. & Viramonte, J. (eds.), *Relatorio XIV Congreso Geológico Argentino, Geología del Noroeste Argentino 1*, ????PUBL, CITY???.

Moya, M.C., 2002. The Ordovician Basin of Northern Argentina. 23-31 in Aceñolaza, F.G. (ed.), *Aspects of the Ordovician System in Argentina*. INSUGEO, Serie Correlación Geológica 16.

Moya, M.C., Malanca, S. & Monteros, J.A., 2003a. The Cambrian-Tremadocian units of the Santa Victoria Group (northwestern Argentina): a new correlation Scheme. 105-112 in Albanesi, G.L., Beresi, M.S. & Peralta, S.H. (eds.), *Ordovician from the Andes, Proceedings of the 9th Internacional Symposium on the Ordovician System*. INSUGEO, Serie Corelación Geológica 17.

Moya, M.C., Monteros, J.A., Malanca, S., Ortega, G. & Albanesi, G.L., 2003b. Quebrada del Toro and Angosto de La Quesera, Eastern Cordillera, Salta Province. *INSUGEO, Miscelánea 11*, 47-49.

Pagani, M.A., Sabattini, N. & Tortello, M.F., 2005. A new species of hyolitha from the Late Cambrian of Northwestern Argentina. *INSUGEO, Serie Correlación Geológica 19*, 169-176.

Pinilla, M.K., Sabattini, N.M., Tortello, M.F. & Aceñolaza, G.F., 2008. A new species of *Strepsodiscus* Knight (Gastropoda, Bellerophontoidea) from the Upper Cambrian of northwestern Argentina. Neues *Jahrbuch fur Geologie und Palaontologie, Abhandlungen 248 (2)*, 217-223.

Pojeta, J., 1987. Phylum Hyolitha. 436-444 in Boardman, R., Cheetham, A. & Rowell, A.J. (eds.), *Fossil Invertebrates*. Blackwell Scientific Publications, Palo Alto.

Runnegar, B., 1980. Hyolitha: status of the phylum. *Lethaia 13*, 21-25.

Runnegar, B., Pojeta, J., Morris, N., Taylor, J.D. & Mcclung, G., 1975. Biology of Hyolitha. *Lethaia 8*, 181-192.

Sánchez, M.C., 1999. Sedimentología y paleogeografía del Grupo Mesón (Cámbrico) 126-133 in González Bonorino, G., Omarini, R. & Viramonte, J. (eds.), *Relatorio XIV Congreso Geológico Argentino, Geología del Noroeste Argentino 1*, ????PUBL, CITY???.

Sánchez, M.C. & Salfity, J.A., 1999. La cuenca cámbrica del Grupo Mesón en el Noroeste Argentino: Desarrollo estratigráfico y paleogeográfico. *Acta Geológica Hispanica 34*, 123-139.

Sepkoski, J.J., 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology 7*, 36-53.

Simões, M.G., Kowalewski M., Torello F.F., Ghilardi R.R. & Melo L.H.C., 2000. Early onset of modern-style shell in the Permian sequences of the Paraná basin: implications for the Phanerozoic trend in bioclastic accumulations. *Revista Brasileira de Geociências 30*, 495-499.

Sterren, A.F., 2008. Carboniferous and lower Permian shell beds in precordillera Argentina. Temporal variations and relationships with the trends proposed from the Phanerozoic. *Ameghiniana 45*, 303-320.

Tortello, M.F. & Rao, R.I., 2000. Trilobites y conodontes del Ordovícico temprano del Angosto de Lampazar (Provincia de Salta, Argentina). *Boletín Geológico y Minero 111*, 61-68.

Vannier, J. & Chen, J., 2005. Early Cambrian food chain: New evidence from fossil aggregates in the Maotianshan Shale biota, SW China. *Palaios 20*, 3-26.

Walker, R.G. & Plint, A.G., 1992. Wave- and storm-dominated shallow marine systems. 219-238 in Walker, R. & James, N. (eds.), *Facies Models*. Special Publication Geological Association of Canada.

Webby, B.D., Paris, F., Droser, M.L., & Percival, I.G.

(eds), 2004. *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, 484 p.

Wills, M.A., 1993. Mollusca incertae sedis. 265-270 in Benton, M.J. (ed.), *The Fossil Record 2*. Chapman and Hall, London.

Whitaker, J.H.McD., 1973. "Gutter casts", a new name for scour-and-fill structures: with examples from the Llandoverian of Ringerike and Malmoya, southern Norway. *Norsk Geologisk Tidsskrift 53*, 403–417.

Yochelson, E.L., 2000. Concerning the concept of extinct classes of Mollusca: or what may/may not be a class of mollusks. *American Malacological Bulletin 15*, 195-202.

Zuschin, M., Stachowitsch, M. & Stanton, R., 2003. Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth-Science Reviews 63*, 33-82.