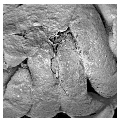
Phosphatized bromalites from the lower Paleozoic of NW Argentina

Gustavo G. Voldman, Fernando J. Zeballo, N. Emilio Vaccari,
Marcelo G. Carrera, Dirk Knaust & Adrian P. Hunt



Bromalites, the fossilized remains of material sourced from the digestive system of organisms, are often overlooked in micropaleontological samples, but offer valuable insights into the paleoecology of ancient ecosystems. This study focuses on Furongian (upper Cambrian) to Floian (Lower Ordovician) bromalites from the Central Andean Basin of the Eastern Cordillera, NW Argentina. In many samples, bromalites dominate as the primary organic residue after acid treatment. The recovered assemblage consists of 276 coprolites and cololites, including *Anfractuosocoprolithus aphelus* Bischoff, *A.* cf. *aphelus* Bischoff, *Coprulus oblongus* Mayer, *Hyperocoprolithus levigatus* Bischoff, *Isvilina kanygini* Schallreuter, *Rhizocorallites articularis* Müller, *Transmeristocoprus multifidus* Bischoff, *Transmeristocoprus*? isp., and three unidentified ichnospecies (A, B, and C). Furthermore, a new ichnogenus, *Helicobromites*, is established, with the description of a new ichnospecies, *H. andinus*. These ichnospecies may reflect the activity of mollusks as well as that of poorly documented organisms such as ascidian tunicates, polychaetes, holothurians, and perhaps nektonic vertebrates. In this way, the coprolites and cololites from the Eastern Cordillera significantly enhanced the reconstruction of lower Paleozoic ecosystems in the southwestern Gondwanan seas • Key words: feces, trace fossil, paleoecology, Cambrian, Ordovician.

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Gustavo G. Voldman (corresponding author) & Marcelo G. Carrera, CICTERRA (CONICET-Universidad Nacional de Córdoba), Facultad de Ciencias Exactas, Físicas y Naturales, Av. Vélez Sarsfield 1699, X5016GCA, Córdoba, Argentina; gvoldman@unc.edu.ar • Fernando J. Zeballo, Laboratorio de Análisis de Materiales por Espectrometría de Rayos X (CONICET-Universidad Nacional de Córdoba), Facultad de Matemática, Astronomía, Física y Computación, Av. Medina Allende s/n esq. Av. Haya de la Torre, X5016GCA, Córdoba, Argentina • N. Emilio Vaccari, CICTERRA (CONICET-Universidad Nacional de Córdoba), Universidad Nacional de La Rioja, Av. Luis M. de la Fuente s/n, F5300 La Rioja, Argentina • Dirk Knaust, Equinor ASA, 4035 Stavanger, Norway • Adrian P. Hunt, Flying Heritage and Combat Armor Museum, 3407 109th SW, Everett, WA 98204, USA

The significant rise in biodiversity and biomass during the Great Ordovician Biodiversification Event (GOBE) undoubtedly coincided with an increase in the production of animal waste products (*e.g.*, Knaust 2020a, fig. 12). Hunt (1992) introduced the term bromalite for all digestive products including egested regurgitalites, defecated coprolites and digestive tract infillings which are consumulites and include cololites (intestinal fillings). The terminology and fossil record of bromalites has been reviewed by Hunt & Lucas (2012, 2021) and Knaust (2020a) and they can offer alternative insights into otherwise inaccessible paleoecological aspects of the ancient ecosystems (*e.g.*, Devaere *et al*. 2014). Small-sized phosphatized bromalites are documented from several Cambrian–Ordovician fossil sites in different paleogeographic domains, such as Laurentia (Peel 2015, Hawkins *et al*. 2018), Baltoscandia (Toom *et al*. 2020, Olempska *et al*. 2023), South China (Shen *et al*. 2014), and the eastern and southern margins of Gondwana (Bischoff 1994, Aldridge *et al*. 2006). The relatively scarcity of studies on bromalites partly reflects taphonomic processes that biased its fossil record (*e.g.*, Peel 2015).

In the Eastern Cordillera of NW Argentina (Fig. 1), Central Andean Basin, a considerable number of late Cambrian to Lower Ordovician calcareous rock samples yielded phosphatic fossils after acid treatment for the recovery of conodonts. We interpret these fossils as bromalites principally on the basis of composition, biogenic morphology and similarity to described bromalites. Detailed justification for their identifications and origins is given later in this paper. In some stratigraphic intervals (*e.g.*, Lower Ordovician of the Zenta Range), bromalites

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constitute the main organic component of the acid residue, whereas in others (*e.g.*, Acoite Formation at La Ciénaga de Purmamarca), they remain as an important secondary component of the fossil assemblage. Due to their abundance, excellent preservation and morphological variety, our aim is to explore the diversity of bromalites from the lower Paleozoic of NW Argentina and use them to better reconstruct the ancient ecosystem for that time interval in the southwestern seas of Gondwana.

Geological background

The Lower Paleozoic stratigraphy of the eastern region of the Eastern Cordillera is assigned to the ~ 3,700 m thick siliciclastic Santa Victoria Group, which comprises the Santa Rosita Formation (Furongian Stage 10 to Tremadocian) and the Acoite Formation (Floian to lower Dapingian). Both formations are famous for their highly fossiliferous content, including acritarchs, brachiopods, bivalves, gastropods, cephalopods, trilobites, ostracods, echinoderms, graptolites, and conodonts. Deposition took place in a wave-dominated shallow-marine ramp setting punctuated by geographically restricted tide-dominated valley incisions and deltaic progradations (summarized in Astini 2003, 2008; Vaucher *et al.* 2020; Waisfeld *et al.* 2023).

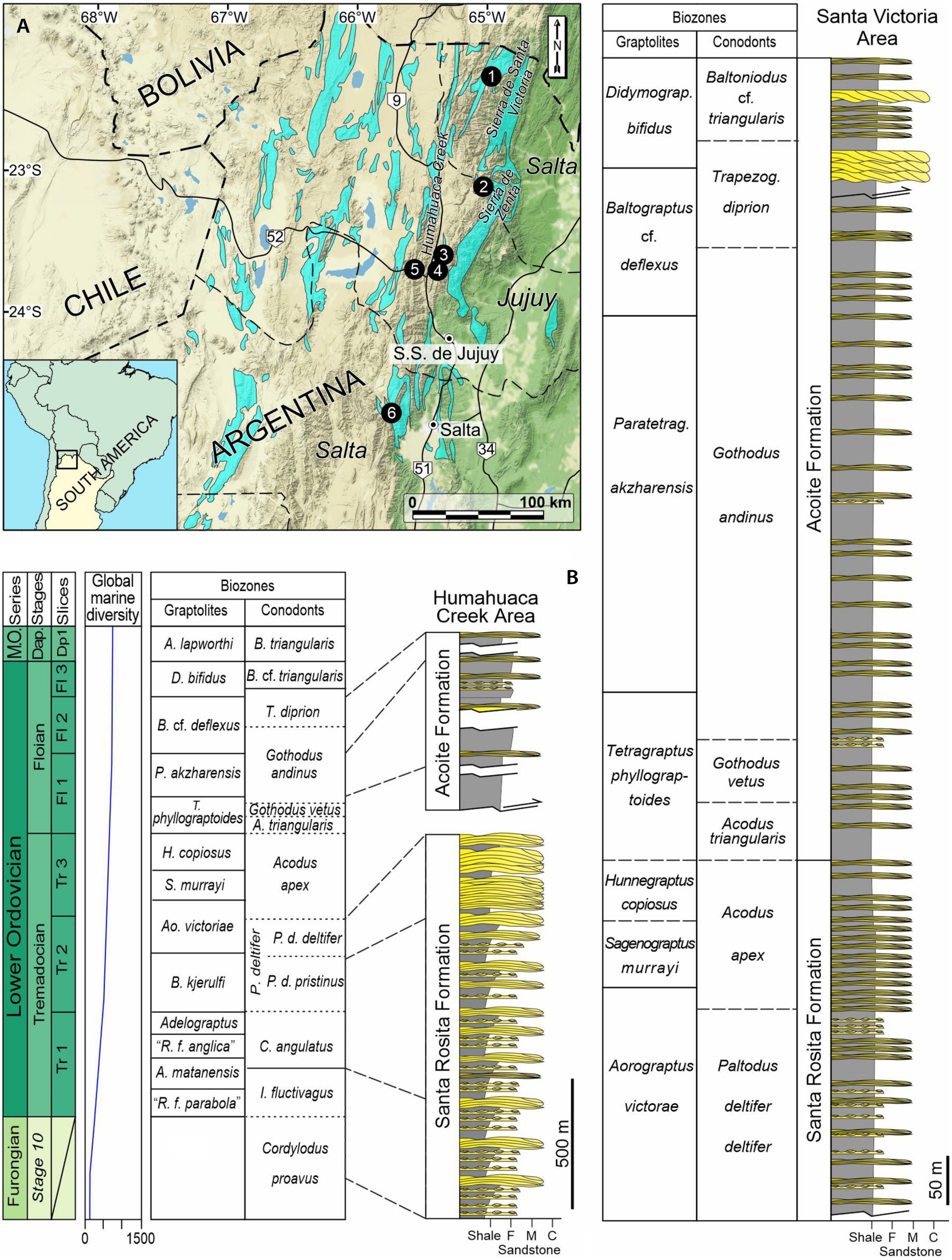
The Santa Rosita Formation reaches up to a maximum thickness of 2,300 m in its type area, in the extreme north of Argentina near the border with Bolivia, yet detailed stratigraphic studies of the succession in the Santa Victoria Range are lacking (Turner 1960). Conversely, the southern outcrops of the Santa Rosita Formation at Quebrada de Humahuaca are better known. There, the Santa Rosita Formation is characterized by wave-dominated, shallow marine environments ranging from shoreface to shelf settings and accounts for fallout deposition during fair-weather intervals punctuated by storm-related events. Upward coarsening and thickening parasequences record a largely progradational trend during highstands. These deposits alternate with spatially restricted, tide-dominated estuarine valleys and, locally, with fluvial-dominated delta front settings (*e.g.*, Astini 2003, Buatois *et al.* 2006, Vaucher *et al.* 2020). After a detailed stratigraphic and paleoenvironmental analysis, Buatois *et al.* (2006) distinguished six members in the Santa Rosita Formation of the Alfarcito area, namely the Tilcara, Casa Colorada, Pico de Halcón, Alfarcito, Rupasca and Humacha members, each of them representing transgressive-regressive cycles of different magnitude. Both the Tilcara and Pico de Halcón members deposited in fluvio-estuarine environments, whereas the remaining units reflect deposition in an open sea, shallow platform setting.

The Acoite Formation, the upper unit of the Santa Victoria Group, records the maximum flooding event at the basin scale (Astini 2003, Astini *et al.* 2004). It reflects deposition in outer to inner shelf environments affected by fair-weather and storm waves, though in more distal settings than the Santa Rosita Formation (Such *et al.* 2007).

In the Zenta Range, Lower Ordovician strata are superbly exposed, exhibiting rhythmic monotonous series of shaly intervals punctuated by clastic wedges, which correspond to prograding coastal systems dominated by wave activity and storms towards the top (Astini 2008). However, other sedimentary and paleontological features of this succession are less known, hampering its correlation to other sectors of the basin (Aráoz 2009, Zeballo *et al.* 2013). For instance, in the surroundings of the Santa Ana village, there are outcrops of gray-green shales and yellowish gray sandstones interbedded with sparse gray and lenticular layers of coquinas and subordinate calcarenites. A series of rocks samples from these levels yielded a conodont fauna referable to the *Acodus deltatus*–*Paroistodus proteus* Zone and the *Paltodus deltifer* Zone (*P. deltifer pristinus* Subzone). Alternatively, strata cropping out at the Laguna Verde Section comprise stratified sandstones interbedded with lenses of coquina and carbonate-cemented sandstones containing broken inarticulate brachiopods and conodonts referable to the upper Floian (Voldman *et al.* 2013a, *cf.* Carlorosi & Heredia 2013).

In the inner shelf deposits of the Santa Victoria Group, fragments of brachiopods (including lingulids), trilobite and crinoids, as well as conodonts occur in shell lags. Trilobites, articulated and semi-articulated, are locally common within the mudstone units (Waisfeld & Vaccari 2003). Furongian to lower Tremadocian inner shelf deposits are dominated by very shallow-tier structures produced by trilobites (e.g., *Cruziana*, *Rusophycus*) and

Figure 1. A – map showing the distribution of Ordovician sedimentary outcrops in NW Argentina (in cyan), along with the locations of key fossiliferous localities of the Eastern Cordillera analyzed in this study: 1 – Santa Victoria Area (Acoite, Chulpíos, and San Felipe creeks); 2 – Zenta Range – Valle Colorado; 3 – Huacalera Area (El Arenal, and Humacha creeks); 4 – Tilcara Range (Rupasca, San Gregorio, and Punta Corral creeks); 5 – Purmamarca Area (Chalala, Coquena, and La Ciénaga de Purmamarca sections); and 6 – Pascha-Incamayo Area • B – conodont-graptolite biostratigraphic chart with schematic stratigraphic columns of the Santa Victoria Group at the Santa Victoria Area (locality 1 of the map) and the Huamahuaca Creek Area (localities 3–5) (modified from Toro *et al.* 2015, Mángano *et al.* 2021, Waisfeld *et al.* 2023). The studied coprolite-bearing stratigraphic interval involves the initial stage of invertebrate marine radiation of the GOBE (normalized curve of marine genus-level diversity of invertebrates from Harper *et al.* 2020, and Servais *et al.* 2023).


A
68°W
67°W
66°W
65°W
-23°S
-24°S
N
BOLIVIA
CHILE
ARGENTINA
SOUTH AMERICA
Salta
Jujuy
Sierra de Santa Victoria
Sierra de Zenta
Humahuaca Creek
S.S. de Jujuy
Salta
9
52
34
51
1
2
3
4
5
6
0
100 km
B
Series
Stages
Slices
M.O.
Dap.
Dp1
Lower Ordovician
Floian
Fl 3
Fl 2
Fl 1
Tremadocian
Tr 3
Tr 2
Tr 1
Furongian
Stage 10
Global marine diversity
0
1500
Biozones
Graptolites
Conodonts
A. lapworthi
B. triangularis
D. bifidus
B. cf. triangularis
B. cf. deflexus
T. diprion
P. akzharensis
Gothodus andinus
T. phyllograptoides
Gothodus vetus
A. triangularis
H. copiosus
Acodus apex
S. murrayi
Ao. victoriae
P. d. deltifer
P. deltifer
B. kjerulfi
P. d. pristinus
Adelograptus
"R. f. anglica"
C. angulatus
A. matanensis
"R. f. parabola"
I. fluctivagus
Cordylodus proavus
Humahuaca Creek Area
Acoite Formation
Santa Rosita Formation
500 m
Shale F M C
Sandstone
Santa Victoria Area
Biozones
Graptolites
Conodonts
Didymograp. bifidus
Baltoniodus cf. triangularis
Baltograptus cf. deflexus
Trapezog. diprion
Paratetrag. akzharensis
Gothodus andinus
Tetragraptus phyllograp-toides
Gothodus vetus
Acodus triangularis
Hunnegraptus copiosus
Sagenograptus murrayi
Acodus apex
Aorograptus victorae
Paltodus deltifer deltifer
Acoite Formation
Santa Rosita Formation
50 m
Shale F M C
Sandstone

shallow-tier vermiform burrows (e.g., *Palaeophycus tubularis* Hall), while the upper Tremadocian-Dapingian inner shelf deposits are characterized by *Trichophycus venosus* Miller cross-cutting the more shallowly emplaced trilobite and trace fossils of worms (Mángano & Buatois 2011).

The bromalites described here are composed of carbonate-fluorapatite, indicating that their formation was associated with early phosphogenetic conditions necessary to preserve their delicate morphology. These remains have subsequently been removed and redeposited together with skeletal remains forming layers of coquinas

Table 1. Geographical information and biostratigraphic age of studied bromalite-bearing samples from the Eastern Cordillera, NW Argentina.

Sample	Locality	Lat. / Long.	Biozone	Stage	Reference
C3	Pascha/Incamayo	24.673° S/65.741° W	*P. d. deltifer*	Tremadocian	Zeballo (2011)
C31	Pascha/Incamayo	24.672° S/65.745° W	*P. d. deltifer*	Tremadocian	Zeballo (2011)
C32	Pascha/Incamayo	24.671° S/65.745° W	*P. d. deltifer*	Tremadocian	Zeballo (2011)
Chal1A	Chalala Creek	23.713° S/65.473° W	*P. d. pristinus*	Tremadocian	Zeballo (2011)
Chu8.5	Chulpíos Creek	22.267° S/64.999° W	*G. andinus*	Floian	Voldman *et al.* (2017)
Chu13	Chulpíos Creek	22.269° S/65.996° W	*G. vetus*	Floian	Voldman *et al.* (2017)
Chu14	Chulpíos Creek	22.270° S/64.993° W	*G. vetus*	Floian	Voldman *et al.* (2017)
Chu15	Chulpíos Creek	22.270° S/64.992° W	*A. triangularis*	Floian	Voldman *et al.* (2017)
Chu97	Chulpíos Creek	22.271° S/64.990° W	*A. triangularis*	Floian	Voldman *et al.* (2017)
La Ciénaga	La Ciénaga de Purmamarca	23.700° S/65.545° W	*G. andinus*	Floian	Voldman & Vaccari (2025)
ElAr1	El Arenal Creek	23.475° S/65.337° W	*C. angulatus*	Tremadocian	Zeballo & Albanesi (2013)
ElAr5	El Arenal Creek	23.471° S/65.335° W	*C. intermedius* (*H. simplex* Subzone)	Furongian	Zeballo & Albanesi (2013)
ElArB	El Arenal Creek	23.473° S/65.338° W	*C. angulatus*	Tremadocian	Zeballo & Albanesi (2013)
Hum0	Humacha Creek	23.475° S/65.344° W	*P. d. deltifer*	Tremadocian	Zeballo (2011)
Pascha Coq1	Pascha/Incamayo	24.545° S/65.736° W	*P. d. deltifer*	Tremadocian	Unpublished collection
QA.AC.x-1	Acoite Creek	22.280° S/64.999° W	–	Floian	Unpublished collection
QPB2	Santa Victoria Area	22.267° S/64.976° W	*P. d. deltifer*	Tremadocian	Voldman *et al.* (2013b)
SVH4	Santa Victoria Area	22.250° S/64.972° W	–	Floian	Unpublished collection
SG4	San Gregorio Creek	23.623° S/65.351° W	*C. angulatus*	Tremadocian	Zeballo (2011)
SG7B	San Gregorio Creek	23.622° S/65.352° W	*C. angulatus*	Tremadocian	Zeballo (2011)
SG8	San Gregorio Creek	23.621° S/65.352° W	*P. d. pristinus*	Tremadocian	Zeballo (2011)
ValleCol5	Valle Colorado	23.371° S/64.976° W	*A. deltatus–P. proteus*	Floian	Zeballo *et al.* (2013)
Zen2	Zenta Range	23.356° S/64.976° W	*A. deltatus–P. proteus*	Floian	Zeballo *et al.* (2013)
Zen3b	Zenta Range	23.355° S/64.976° W	*A. deltatus–P. proteus*	Floian	Zeballo *et al.* (2013)
Zen10b	Zenta Range	23.338° S/65.013° W	*A. deltatus–P. proteus*	Floian	Zeballo *et al.* (2013)
Zen11	Zenta Range	23.341° S/65.016° W	*A. deltatus–P. proteus*	Floian	Zeballo *et al.* (2013)
Zen17	Zenta Range	23.316° S/65.000° W	*G. andinus*	Floian	Voldman *et al.* (2013a)
Zen17.2	Zenta Range	23.316° S/64.999° W	*G. andinus*	Floian	Voldman *et al.* (2013a)
SAGAS2	Zenta Range	23.151° S/64.994° W	–	Floian	Voldman *et al.* (2013a)

(*cf.* Freeman *et al.* 2019). The presence of microconglomerate containing phosphatic bioclasts has been described in NW Argentina mainly from Middle to Upper Ordovician orthoquartzites (Centinela, Zanjón and Labrado formations) (*e.g.*, Mastandrea & Leanza 1975, Schalamuk *et al.* 1983, Aceñolaza *et al.* 2008). Duperron *et al.* (2018) observed that phosphatic rocks of the Santa Victoria Group at the Mojotoro Range reflect sedimentary reworking of biogenic particles and are not constrained to a phosphogenic interval *sensu stricto*.

Often overlooked or under-reported, there are no studies of bromalites from the Santa Victoria Group, except in relation to pellet-filled burrows such as *Alcyonidiopsis pharmaceus* Richter & Richter and *Tomaculum problematicum* Groom. These ichnospecies were reported from black and green shales of the Santa Rosita Formation in several stratigraphic sections of the Humahuaca Creek (Aceñolaza 1996, Di Cunzolo *et al.* 2003).

Material and methods

The high abundance of bromalites in acid-insoluble residues of conodont samples from lower Paleozoic strata of the Eastern Cordillera encouraged the systematic search for different morphotypes in our repository collections. All of the rock samples were processed in 10% acetic acid or 7% buffered acetic acid following the standard laboratory procedures for recovering conodonts (Stone 1987, Jeppsson *et al.* 1999). The biostratigraphic age of the bromalites is constrained by the associated conodont, graptolite and trilobite fauna (*e.g.*, Voldman *et al.* 2013a, b, 2017; Zeballo 2011; Zeballo *et al.* 2013; Voldman & Vaccari 2025; Tab. 1). Many of the analyzed samples yielded phosphatized organic remains (*e.g.*, graptolites, echinoderms, orthoceratids, disarticulated trilobites, chitinozoans), with bromalites occurring in such a large number in some samples that picking all of them by hand was not feasible. For this reason, selected and morphologically representative specimens (those that were less fragmented or eroded, and varied in size) from different stratigraphic levels were collected for further analysis (Tab. 2). Fresh rock samples and the coarser fractions of the insoluble residue were also carefully examined during the analysis of the associated fauna, but no bromalites were recovered. Most of the specimens are gray-brown to black, though predominantly the latter. Images of the microfossils were captured using FE-SEM ZEISS Sigma at the Laboratorio de Análisis de Materiales por Espectrometría de Rayos X (LAMARX) of the Universidad Nacional de Córdoba, Argentina. All illustrated specimens are housed under the prefix CEGH-UNC in the Centro de Investigaciones en Ciencias de la Tierra (CICTERRA).

Description

The studied bromalites represent coprolites and evisceralites (cololites). Coprolites are fossilized, excreted food material and cololites are a type of consumulite that represents the infillings of intestines (Hunt & Lucas 2012, 2021). An evisceralite is a cololite that is a segment of infilled fossilized intestines preserved independent of,

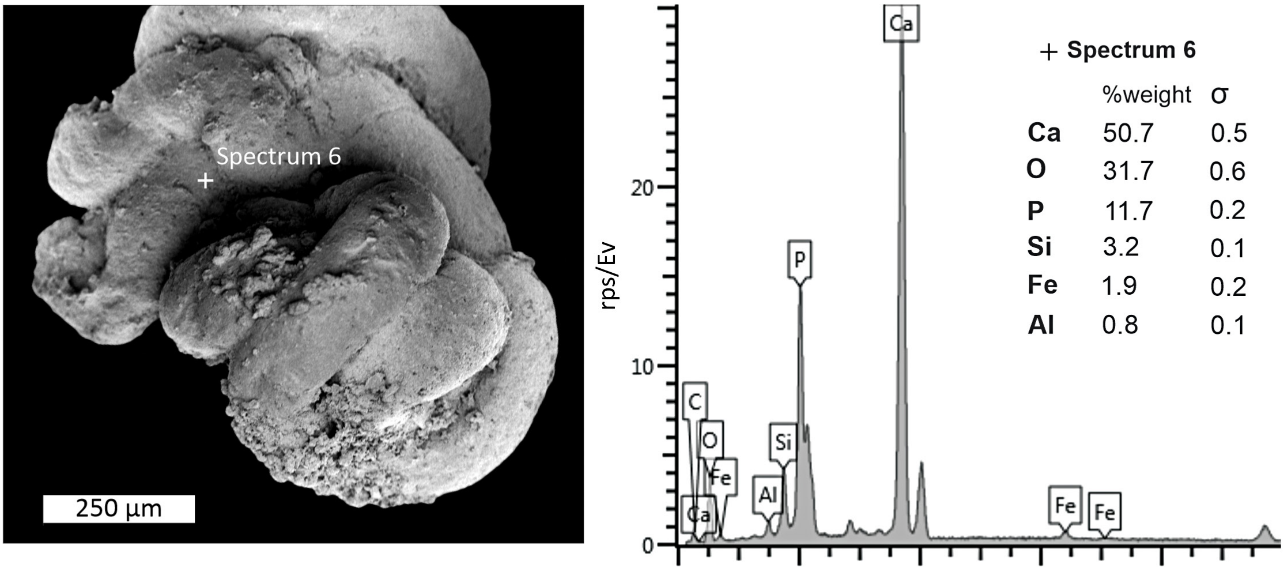


Figure 2. EDS spectrum of the specimen CEGH-UNC 27881 (Fig. 3Q) of *Anfractuosocoprolithus aphelus* Bischoff, 1994, showing a phosphatic composition.

Table 2. Bromalite contents of studied samples from the Eastern Cordillera, NW Argentina.

	Anfractuosuscoprolithus aphelus	*Anfractuosuscoprolithus* cf. *aphelus*	*Coprulus oblungus*	*Helicoprolithus andinus*	*Hyperocoprolithus levigatus*	*Isvilina kanygini*	*Rhizocorallites articularis*	*Transmeristocoprus multifidus*	*Transmeristocoprus* isp.	Ichnogenus *et* isp. A	Ichnogenus *et* isp. B	Ichnogenus *et* isp. C
C3	9	1										
C31	1											
C32		1										
Chal1A			2									
Chu8.5	1											
Chu13				1				3				
Chu14								1				
Chu15				1		1						
Chu97								9				
La Ciénaga	3	4	1	22		20	1	50			13	2
ElAr1		1										
ElAr5												2
ElArB	2											
Hum0	5	1		1								
Pascha Coq1	2		2			32					1	
QA.AC.x-1	3					1		18	3			
QPB2	1											1
SVH4								1				
SG4												1
SG7B											1	
SG8			1									
ValleCol5	1					5						
Zen2		1										
Zen3b	2					3				1		
Zen10b						1						
Zen11						1						
Zen17	16	1		1	2	1		2				
Zen17.2	8							2				
SAGAS2			1									
Total	54	10	7	26	2	65	1	86	3	1	15	6

or exterior to, a carcass (Hunt & Lucas 2012). Hunt & Lucas (2012, 2021) addressed the terminology used to describe the wide range of morphological characters of coprolites. Knaust (2020a) provided a comprehensive ichnotaxonomic review of invertebrate coprolites and cololites. Accordingly, the variable shape of the bromalites from the Eastern Cordillera are assigned into different categories of ichnotaxa, taking into account that size is not a decisive parameter, especially at the ichnogenus level (Bertling *et al*. 2022). Energy-dispersive X-ray (EDX) analysis of the specimens revealed a composition rich in P and Ca (Fig. 2).

Systematic ichnology

Ichnofamily Bactrylliidae Knaust, 2020a

Ichnogenus *Transmeristocoprus* Bischoff, 1994

Type ichnospecies. – *Transmeristocoprus multifidus* Bischoff, 1994.

***Transmeristocoprus multifidus* Bischoff, 1994**
Figures 3A–F

1994 *Transmeristocoprus multifidus* n. ichnosp.; Bischoff, p. 281, pl. 3, figs 26–40.

Material. – Eighty-six specimens (samples Chu13, Chu14, Chu97, La Ciénaga, SVH4, QA.AC.x-1, Zen17, Zen17.2).

Remarks. – Bischoff (1994) provided a detailed description of this ichnospecies, consisting of phosphatic, more or less flattened microcoprolites with a transverse segmentation. In our material, this segmentation is inconsistently preserved, likely reflecting original biological variability rather than purely taphonomic processes. Bischoff (1994) suggested that they could correspond to feces of bivalves or gastropods, while Knaust (2020a) did not dismiss them from being cololites. Broken specimens from NW Argentina reveal a hollow structure, a feature not described by Bischoff (1994) and thus they may represent a different ichnospecies.

Occurrence. – Bischoff (1994) documented *T. multifidus* in the median portion of the Horn Valley Siltstone, Amadeus Basin, central Australia (lower Floian *Prioniodus amadeus* Zone, equivalent to the *P. elegans* Zone; Zhen 2019) and the median part of the Emanuel Formation, Canning Basin, NW Australia (lower Floian, late *P. proteus* Biozone to possibly earliest *P. elegans* Zone; Zhen & Nicoll 2009). Upon further biostratigraphic refinement, this ichnospecies appears as a potential index fossil for the lower-middle Floian.

***Transmeristocoprus* isp.**
Figures 3G, H

1994 *Transmeristocoprus* sp. Bischoff, pp. 281, 282, pl. 4, figs 50–52.

Material. – Three specimens (sample QA.AC-x1).

Remarks. – We conservatively follow Bischoff (1994) in distinguishing *Transmeristocoprus* isp. from the type species, based on its subcircular to subquadrate outline, smaller length/width ratio, and the smaller number of fecal segments. However, Bischoff (1994) did not exclude the possibility that both forms share the same producer. As in the type material from Australia, the specimens at hand occur in samples that contain *T. multifidus*. However, the Argentinean specimens have weaker developed fecal segments and a more ovoid shape, with a length/width ratio of ~ 1.5–2.

Ichnofamily Coprulidae Knaust, 2008

Ichnogenus *Isvilina* Schallreuter, 2003

Type ichnospecies. – *Isvilina kanygini* Schallreuter, 2003.

***Isvilina kanygini* Schallreuter, 2003**
Figures 3I–L

2003 *Isvilina kanygini* sp. n.; Schallreuter, p. 235, pls 1, 2, tab. 1.

Material. – Sixty-five specimens (samples Chu15, La Ciénaga, Pascha Coq1, QA.AC-x1, ValleCol5, Zen3b, Zen10b, Zen11, Zen17).

Remarks. – The size and shape of the material at hand closely resembles that of the type material from the Middle Ordovician of Siberia, although all analyzed specimens lack a broad groove on one side, often observed in the type specimens. Similar fecal pellets are produced by ascidian tunicates (Arakawa 1971, Knaust 2020a).

Occurrence. – Kirenskian–Kudrinian stages (Upper Ordovician) of the Siberian platform (Schallreuter 2003).

Ichnogenus *Coprulus* Mayer, 1952

Type ichnospecies. – *Coprulus oblongus* Mayer, 1952.

***Coprulus oblongus* Mayer, 1952**
Figures 3R, S, U

For synonymy, see Knaust (2020a).

Material. – Seven specimens (samples Chal1A, La Ciénaga, Pascha Coq1, SAGAS2, SG8).

Remarks. – Small clusters of elliptical coprolites with rounded ends, mostly oriented with their long axes parallel, and with a length/width ratio of ~ 2, were recovered from the Santa Rosita Formation at Chalala Creek. Additionally, isolated pellets with a similar shape were obtained from the Zenta Range. These tiny coprolites are readily assigned to the common ichnotaxon *Coprulus* *oblongus*, discussed by Knaust (2008, 2020a) and Lucas & Foley (2023). Although *C. oblongus* could be produced by different organisms, including bivalves and gastropods, it was more likely produced by annelid worms, particularly polychaetes (Knaust 2020a). For instance, *Tomaculum*-type fecal pellets have been described from the guts of palaeoscolecids from the lower Cambrian Sirius Passet of Greenland and the Lower Ordovician Fezouata of Morocco (Martin *et al*. 2016), and the lower Cambrian priapulid *Selkirkia* from Chengjiang (Lan *et al*. 2015).

Occurrence. – *Coprulus oblongus* has a broad temporal (lower Cambrian–Cenozoic) and geographic distribution (global).

Ichnogenus *Hyperocoprolithus* Bischoff, 1990

Type ichnospecies. – *Hyperocoprolithus constrictus* Bischoff, 1990.

Hyperocoprolithus levigatus Bischoff, 1990

Figures 3T, V

1990 *Hyperocoprolithus levigatus* n. sp.; Bischoff, pp. 218, 219, pl. 1, figs 13–22.

Material. – Two specimens (sample Zen17).

Remarks. – The investigated specimens agree well with the description and illustrations of Bischoff (1990), *i.e.*, they are pestle-shaped and have a smooth surface and rounded morphology. However, it is not discarded that they may belong to more than one ichnospecies. Bischoff (1990) regarded *H. levigatus* as feces of mollusks, probably gastropods, based on its striking similarity to fecal pellets of modern mollusks (Bandel 1974).

Occurrence. – Lower Llandovery–Wenlock, Orange-Cudal-Cobblers Creek area, central New South Wales.

Ichnofamily Lumbricariidae Schweigert, 2001

Ichnogenus *Anfractuosocoprolithus* Bischoff, 1994

Type ichnospecies. – *Anfractuosocoprolithus aphelus* Bischoff, 1994.

Anfractuosocoprolithus aphelus Bischoff, 1994

Figures 2, 3M–Q

1994 *Anfractuosocoprolithus aphelus* n. ichnosp.; Bischoff, pp. 276, 277, pl. 1, figs 1–5.

2015 *Lumbricaria multiforme*. – Buchholz, pp. 16, 17, pl. 4, figs a–q.

Material. – Fifty-four specimens (samples C3, C31, Chu8.5, La Ciénaga, ElArB, Hum0, Pascha Coq1, QA.AC.X-1, QPB2, ValleCol5, Zen3b, Zen17, Zen17.2).

Remarks. – The specimens from the Eastern Cordillera compare well to the rope-shaped type material from Australia. Bischoff (1994) considered that it may represent the excrements of worms, while Knaust (2020a) interpreted them as more probably cololites (evisceralites). The studied specimens appear to correspond in shape to the surface feces of annelid worms, such as those produced by *Arenicola marina* Linneaus.

Occurrence. – Lower–middle Cambrian erractics from NE Germany (Buchholz 2015); median portion of the Horn Valley Siltstone (lower Floian *Prioniodus amadeus* Zone, equivalent to the *P. elegans* Zone – Zhen 2019), Amadeus Basin, central Australia (Bischoff 1994).

Anfractuosocoprolithus cf. *aphelus* Bischoff, 1994

Figure 4L

Material. – Ten specimens (samples C3, C32, La Ciénaga, ElAr1, Hum0, Zen17).

Remarks. – Some specimens differ from *Anfractuosocoprolithus aphelus* in that the fecal string forms elongated, tightly braided rods, and not subrounded agglomerates with frequent superposition of the strings. When fragmented, these specimens may resemble *Volutacoprolithus conservatus* Bischoff, 1994, though it lacks diagnostic phosphatic spheres on its surface. Apparently, they could represent extreme shapes in the range of variability of *A. aphelus.*

Ichnogenus *Helicobromites* igen. nov.

Type ichnospecies. – *Helicobromites andinus* isp. nov.

Etymology. – From its helical shape.

Diagnosis. – Bromalite with a rod-like shape, consisting of a tight helical fecal string with subcircular to oval cross section.

Remarks. – *Helicobromites* igen. nov. differs from *Anfractuosocoprolithus* Bischoff, 1990, by the helical winding of the fecal string, a trait that would support its separation as a new ichnogenus. Its morphology is helical instead of scroll spiral, as the latter is characteristic of certain type of fish with spiral intestinal valve (*e.g.*, Gilmore 1992, Argyriou *et al*. 2016). It may resemble *Tubulaspira iecta* (Schallreuter 1977) from the Middle to Upper Ordovician

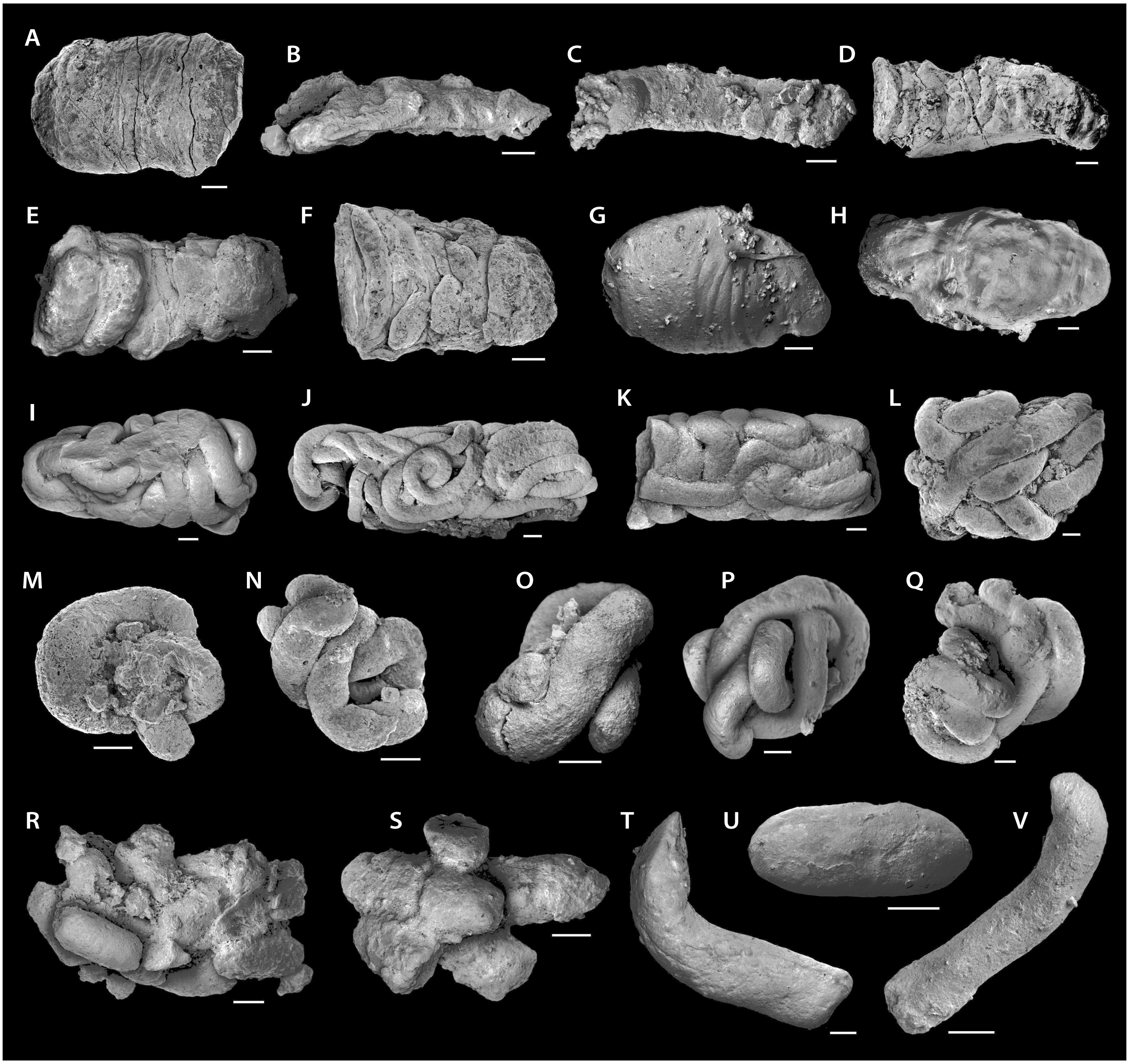


Figure 3. A–F – *Transmeristocoprus multifidus* Bischoff, 1994; A – CEGH-UNC 27765, sample Chu13; B – CEGH-UNC 27766, sample Zen17.2; C – CEGH-UNC 27767, sample SVH4; D – CEGH-UNC 27768, sample QA.AC.x-1; E – CEGH-UNC 27769, sample CHU97; F – CEGH-UNC 27770, sample CHU97 • G, H – *Transmeristocoprus* isp., sample QA.AC.x-1; G – CEGH-UNC 27771; H – CEGH-UNC 27772 • I–L – *Isvilina kanygini* Schallreuter, 2003; I – CEGH-UNC 27773, sample Chu15; J – CEGH-UNC 27774, sample Zen10b; K – CEGH-UNC 27775, sample Zen3b; L – CEGH-UNC 27776, sample Zen17 • M–Q – *Anfractuosocoprolithus aphelus* Bischoff, 1994; M – CEH-UNC 27777, sample C31; N – CGH-UNC 27778, sample Chu8.5; O – CEGH-UNC 27779, sample Zen3b; P – CEGH-UNC 27780, sample Zen17.2; Q – CEGH-UNC 27781, sample QA.AC.X-1 • R, S, U – *Coprulus oblongus* Mayer, 1952; R – CEGH-UNC 27782, sample Chal1A; S – CEGH-UNC 27783, sample Chal1A; U – CEGH-UNC 27784, sample SAGAS2 • T, V – *Hyperocoprolithus levigatus* Bischoff, 1990; T – CEGH-UNC 27785, sample Zen17; V – CEGH-UNC 27786, sample Zen17. All scale bars are 100 µm.

of Germany, yet the latter is thinner, hollow, and conical spiral. Aldridge *et al*. (2006) described coiled coprolites from bedding planes of the Upper Ordovician Soom Shale Lagerstätte, though these are also hollow and composed of clay minerals. The spatial arrangement of the string may represent fragments of a small coil-shaped burrow, such as in *Helicodromites* (*e.g*., Uchman & Rattazzi 2023) or *Gyrolithes* (Mángano *et al*. 2005). Holothurians (sea-cucumbers, Echinodermata) and ascidian (e.g., *Molgula manhattensis*, commonly known as "sea grapes") are also potential producers of helical fecal strings. Alternatively, 'Nemathelminthes' may present coiled guts, as described from the Lower Cambrian Chinese Maotianshan-Shale (Maas *et al*. 2007).

Helicobromites andinus **isp. nov.**
Figures 4A-G

Types. – Holotype (CEGH-UNC 27793, Fig. 4G), paratypes (CEGH-UNC 27787-27792, Fig. 4A–F).

Type horizon and locality. – Sample Chu13, Acoite Formation, Chulpíos Creek, Santa Victoria area, Jujuy Province, NW Argentina, Floian (Voldman *et al.* 2017).

Material. – Twenty-six specimens (samples Chu13, Chu15, La Ciénaga, Hum0, Zen17).

Etymology. – After the Andean Cordillera.

Diagnosis. – As for ichnogenus.

Description. – Microbromalite, rod-like subcircular, sculpture tight helical, cross-section subcircular, smooth surface, color light-brown to black.

Occurrence. – Floian, Santa Victoria Group, NW Argentina.

Ichnogenus *Rhizocorallites* Müller, 1955

Type ichnospecies. – Rhizocorallites articularis Müller, 1955.

Rhizocorallites articularis **Müller, 1955**
Figure 4P

For synonymy, see Knaust (2020b).

Material. – One specimen (sample La Ciénaga).

Remarks. – Knaust (2020b) discussed the ichnotaxonomy of *Rhizocorallites*, including its synonyms. Originally interpreted as a burrow (Müller 1955), it more likely represents mud-filled intestines as for instance of sea cucumbers (holothurians; Knaust 2020b).

Ichnofamily *Incertae sedis*

Form A
Figure 4H

Material. – One specimen (sample Zen3b).

Description. – Elongated, segmented intertwined coprolite with braided aspect.

Remarks. – There is a set of parallel lineation that runs sinuously and obliquely to the segments of the coprolite. The fact that the lineation runs the same direction across amalgamated segments, indicates extrusion during a single defecation event. Additionally, the presence of small holes may correspond to gas escape structures after decomposition decay, or microborings due to endobiont activity. Coiling occurs in some vertebrate coprolites, but none are similar to this specimen.

Form B
Figures 4M, N, Q, R

Material. – Fifteen specimens (samples La Ciénaga, Pascha Coq1, SG7b).

Description. – Elongated coprolites characterized by a coarse, fibrous texture and variable shape, including curved, cylindrical forms, while others are more bent or tightly helical twisted.

Remarks. – The external shape of this form resembles rolled and twisted sheets of paper. No inner biological structures are discerned under the petrographic microscope.

Form C
Figures 4I–K, O

Material. – Six specimens (samples ElAr5, La Ciénaga, SG4, QPB2).

Description. – Sinuously folded muddy strings with a high degree of morphological variation, ranging from loosely to tightly curved folds, and subcircular cross-section.

Remarks. – Olempska *et al.* (2023) described comparable specimens from the Furongian Słowińska Formation in Poland. They interpreted the coprolites as being produced by a small, benthic organism (not infaunal worms) only a few millimeters long, likely during defecation while moving forward and swinging the rear of its body from side to side. Some specimens from NW Argentina present circular holes (Fig. 4K). These may either reflect gas escape structures or microborings due to endobiont activity.

Discussion

Given the small size of the studied specimens (ranging from hundreds of microns to few millimeters), alternative interpretations beyond micro-bromalites were also considered. For example, steinkerns (typically internal casts of mollusks released after shell dissolution) may produce superficially similar structures. Among such cases, Datillo *et al.* (2016) described phosphatic microsteinkerns of

Figure 4. A–G – *Helicobromites andinus* isp. nov.; A – CEGH-UNC 27787, paratype, sample La Ciénaga; B – CEGH-UNC 27788, paratype, sample La Ciénaga; C – CEGH-UNC 27789, paratype, sample La Ciénaga; D – CEGH-UNC 27790, paratype, sample La Ciénaga; E – CEGH-UNC 27791, paratype, sample La Ciénaga; F – CEGH-UNC 27792, paratype, sample Chu13; G – CEGH-UNC 27793, holotype, sample Zen17 • H – Form A, CEGH-UNC 27794, sample Zen3b • I–K, O – Form C; I – CEGH-UNC 27795, sample SG4; J – CEGH-UNC 27796, sample QPB2; K – CEGH-UNC 27797, sample ElAr5; O – CEGH-UNC 27798, sample La Ciénaga • L – *Anfractuosocoprolithus* cf. *aphelus* Bischoff, 1994, CEGH-UNC 27799, sample Zen17 • M, N, Q, R – Form B; M – CEGH-UNC 27800, sample La Ciénaga; N – CEGH-UNC 27801, sample La Ciénaga; Q, R – CEGH-UNC 27802, sample La Ciénaga • P – *Rhizocorallites articularis* Müller, 1955, CEGH-UNC 27803, sample La Ciénaga. All scale bars are 100 μm.

gastropods from Ordovician limestones of the Cincinnatian Series, some of which also exhibit regular segmentation (Figs 4F, 9L). However, these forms display a relatively uniform, elliptical shape that tapers toward the apex, with a subcircular cross-section, a meniscate distal termination, and an absence of longitudinal grooves or ridges.

Shell borings can create cavities that may subsequently serve as sites for the precipitation of authigenic apatite (*e.g.*, Henderson & McNamara 1985, Donovan *et al.* 2018). The morphology of the phosphatic infillings is thus inherently constrained by the geometry and orientation of the host shell, typically resulting in irregular, branched, cavity-conforming forms rather than discrete, consistently shaped bodies exhibiting segmentation. If such infillings were released by acid digestion, a wide range of morphologies would be expected, reflecting the diversity of host substrates and boring patterns—unlike the recurrent and discrete ichnotaxa (e.g., *Hyperocoprolithus levigatus*) identified in our assemblage.

Furthermore, no evidence of feeding traces or dwelling burrows has been yet documented in the Cambrian–Ordovician shell fossil collections from the Eastern Cordillera curated at CICTERRA. This absence aligns with the extremely sparse Paleozoic record of biogenic penetration in bivalve shells by predatory or parasitic organisms, a phenomenon that is far more common in post-Paleozoic assemblages (*e.g.*, Cosma & Baumiller 2005). Taken together, the abundance, consistency, and diversity of the analyzed structures strongly support a biological origin associated with digestive or excretory activity, rather than passive diagenetic mineral infill.

On the other hand, authigenic apatite nodules formed through secondary phosphatization—such as those nucleated around elongate bioclasts like trilobite sclerites or bryozoan fragments—typically exhibit irregular, cavity-conforming morphologies that mirror the heterogeneity of their substrates. In contrast, *Transmeristocoprus* displays a notably consistent diameter and overall shape, features that are more parsimoniously interpreted as the result of biological processes, such as defecation, rather than nodule nucleation around a bioclast.

Ultimately, fossil cyanobacteria may, in some cases, be mistaken for bromalites. For example, Castellani *et al.* (2018) described unbranched, uniseriate filamentous cyanobacteria from insoluble residues of 'Orsten' nodules, which may superficially resemble *Rhizocorallites* (Knaust 2020a, b). However, this segmented bromalite typically shows, when not disarticulated, a tightly curved and packed geometry that is more consistent with a cololite origin. Although the possibility of misidentifying *Rhizocorallites* cannot be entirely ruled out, the available morphological and paleontological evidence does not support a microbial interpretation in this case.

Potential tracemakers

The confident attribution of bromalites to their producers is typically only possible when they are discovered in direct association with the likely tracemakers (*e.g.*, Hawkins *et al.* 2018). In most cases, bromalites can only be assigned to crown-group taxa or broader taxonomic categories (*e.g.*, Hunt & Lucas 2021). Those recovered from the Santa Victoria Group were likely produced by a variety of invertebrate and possibly vertebrate organisms, each occupying distinct ecological niches. Even when bromalite ichnotaxa cannot be confidently linked to specific higher taxa, these records provide a valuable proxy for tracking paleoecological diversity through time.

Potential producers among sessile invertebrates include bivalves or gastropods (*Transmeristocoprus multifidus*, *Hyperocoprolithus levigatus*), ascidian tunicates (*Isvilina kanygini*), annelid worms (*Coprulus oblongus*, *Anfractuosocoprolithus aphelus*), sessile ascidians or 'Nemathelminthes' (*Helicobromites andinus*), holothurians (*Rhizocorallites articularis*), and other benthic organisms (Form C). Accordingly, the recovered bromalite specimens suggest that the holothurian record would extend back to the middle Tremadocian, predating the previously known Darriwilian occurrence of isolated ossicles (Reich 2001).

The braided (coiled) morphology of Form A might resemble that of certain vertebrate coprolites such as *Castrocopros* from the Pleistocene (Hunt & Lucas 2018). The twisted sheet morphology of Form B is reminiscent of coprolites produced by animals with a spiral intestine, including early fishes (Gilmore 1992) and possibly some eurypterids (Waterson *et al.* 1985, Sumner 1993), although no whorls are visible in transverse section. Alternatively, large shelly coprolites composed of trilobite, gastropod, bivalve, or crinoid fragments have been attributed to nonbiomineralised arthropods—such as phyllocarids and eurypterids—or other durophagous organisms, including trilobites and cephalopods (*e.g.*, Bicknell *et al.* 2023, 2024).

Non-conodont vertebrates are sparsely represented in the Ordovician record of the Central Andean Basin, limited to rare articulated specimens of *Sacabambaspis* from the Anzaldo Formation (?Sandbian) in central Bolivia and related microremains from the "Sepulturas Formation" (Darriwilian) of the Eastern Cordillera in Argentina (*e.g.*, Davies & Sansom 2009). In contrast, conodonts are well-documented in the Santa Victoria Group, although there is no evidence that they possessed a spiral intestine (Aldridge *et al.* 2006). To date, the only putative example of vertebrate coprolites from the Lower Ordovician is known from central Kazakhstan, consisting of clusters of conodont elements interpreted as fecal accumulations produced by an unidentified predator (Tolmacheva & Purnell 2002, Hunt & Lucas 2021). Within this limited context, the tentative identification of vertebrate coprolites in Tremadocian and Floian samples from the Eastern Cordillera remains uncertain. Nevertheless, while further investigation is needed to confirm their origin and paleobiological significance, these findings underscore the potential of the ichnological record to complement body fossil data in reconstructing early Paleozoic ecosystems.

Conclusions

While the Cambrian 'Explosion' marks the appearance of almost all animal phyla, the subsequent GOBE involved numerous and complex radiations that fundamentally reshaped global marine faunas. This includes major diversification among chitinozoans, conodonts, gastropods, graptolites, trilobites, cephalopods, brachiopods and reef-builders, among others taxa (*e.g.*, Servais *et al.* 2023). As illustrated by Knaust (2020a, fig. 12), invertebrate bromalites exhibit significantly greater diversity in the Ordovician than in the Cambrian. The bromalite ichnofauna analyzed in this study, consisting of seven ichnogenera and seven ichnospecies, along with three ichnospecies left in open nomenclature, further supports that this biodiversification had already begun by the Early Ordovician.

Moreover, the studied bromalites potentially evidence the activity of mollusks, such as bivalves or gastropods, as well as that of poorly documented organisms in the Santa Victoria Group, including their potential producers such as ascidian tunicates, polychaetes, holothurians, and possibly even nektonic vertebrates. These findings shed light on the hidden biodiversity of southwestern Gondwana, and may help fill significant gaps in its fossil record. This collection is paleobiologically important and we encourage further examination of micropaleontological samples for bromalites.

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