

Paleoecology of the foraminifer *Acruliammina longa* (Tappan, 1940) from the upper Hauterivian of the Neuquén Basin (northern Patagonia, Argentina)

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ARTICLE INFO

Article history:

Received 31 December 2023

Received in revised form

10 February 2024

Accepted in revised form 10 February 2024

Available online 15 February 2024

Keywords:

Benthic foraminifera

Lower Cretaceous

Agrio Formation

Paleoenvironment

Paleoecology

ABSTRACT

Herein the epibiont agglutinated placopsilinid foraminifer *Acruliammina longa* from the upper Hauterivian of the Neuquén Basin is discussed. This is the first record from South America of *A. longa*, already known from the upper Valanginian to lower Turonian of North America and Europe. The studied material consists of foraminiferal tests forming macroids and encrusting the valves of *Ptychomya koeneni*, coming from poorly lithified claystones/siltstones to marlstones forming high frequency (6th-order) depositional sequences within the upper Hauterivian Agua de la Mula Member of the Agrio Formation. This new record extends the paleobiogeographic distribution of *A. longa*, and allows us to investigate the paleoenvironmental and paleoecological significance of this species in a mixed carbonate and siliciclastic ramp. Energy dispersive spectroscopy and X-ray computed microtomography were used to evaluate taphonomic features of foraminiferal tests, highlighting differences between tests that encrust bivalves and those forming macroids, which also differ in their position within the 3rd-order sedimentary sequences. *A. longa* tests encrusting bivalves are less damaged, show coarser grain size, and occur throughout the 3rd-order regressive systems tracts, whereas tests forming macroids show higher breakage and finer grain size, occurring throughout the 3rd-order transgressive systems tracts. This distribution allows us to interpret changes in rates of terrigenous input at the time of encrustation, and also in energy conditions, highlighting the opportunistic behavior of *A. longa*. Low sedimentation rates represent the main paleoenvironmental condition that favored foraminiferal propagule settlement and the growth of *A. longa*, both on bivalve fragments exposed on the seafloor in the case of macroids, and on living *Ptychomya koeneni* shells.

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1. Introduction

Extant encrusting foraminifera colonize a variety of substrates above the sediment-water interface at diverse depths ranging from shallow to deep sea, inhabiting reef environments (e.g., Gischler and Ginsburg, 1996; Rasser and Piller, 1997; Bosellini and Papazzoni, 2003; Peryt and Peryt, 2021) up to abyssal ocean floors (e.g., Wendt, 1974; Gooday and Haynes, 1983; Richardson-White and

Walker, 2011). Encrusting foraminifera have been largely used in paleoecological and paleoenvironmental analysis (Martindale, 1992; Perrin, 1994; Jonasson and Schröder-Adams, 1996; Bosellini and Papazzoni, 2003; Shahat, 2017). They are an important component of marine encrusting communities, and they represent main components of carbonate nodules (Reid and Macintyre, 1988; Prager and Ginsburg, 1989; Bassi, 2005; Bassi et al., 2020; Caratelli et al., 2021), deep-sea manganese nodules and crusts (Wendt, 1969; Mullineaux, 1988), hardgrounds (Resig and Glenn, 1997), and live and dead skeletal substrates made up of mollusks (Mullineaux and DeLaca, 1984; Langer and Bagi, 1994; Jones and Hunter, 1995; Voight and Walker, 1995). In fossil and Recent shallow marine environments, encrusting foraminifera are common components of reef-building

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communities, forming skeletal buildups in association with corals, algae, and sponges (Perrin, 1992; Plaziat and Perrin, 1992; Schulte et al., 1993; Bassi et al., 2020). The paleoenvironmental significance of encrusting foraminifers has been repeatedly pointed out (e.g., Bosellini and Papazzoni, 2003; Richardson-White and Walker, 2011), although little is known about their paleoecology. Ancient and modern agglutinated encrusting foraminifers can inhabit cryptic microenvironments or live exposed on diverse organic and inorganic surfaces, preferring epibenthic microhabitat and passive suspension feeding strategies (Martindale, 1992; Matteucci, 1996; Bosellini and Papazzoni, 2003; Walker et al., 2011).

Among encrusting agglutinated foraminifers, the members of the family Placopsiliniidae Rhumbler, 1913 (suborder Lituolina Lankester, 1885) often dwell in neritic environments. This family includes multi-chambered, initially planispiral, later uncoiled agglutinated tests; the subfamily Placopsiliniinae Rhumbler, 1913 encompasses six genera (Loeblich and Tappan, 1987; Kaminski, 2014), including *Acruliammina* Loeblich and Tappan, 1946. *Acruliammina* encrusts both organic and inorganic substrates, commonly in association with serpulids, bryozoans, and sponges (Brönnimann and Jayet, 1967; Hercegová, 1988; Žitt and Nekvasilová, 1996; Žitt et al., 2006). Herein, we report the first occurrence of *Acruliammina longa* (Tappan, 1940) from the upper Hauterivian Agua de la Mula Member of the Agrio Formation (Neuquén Basin, Argentina). The occurrence of *A. longa* from this unit also represents the first report of the species from South America. *A. longa* is an encrusting agglutinated foraminifer, introduced by Tappan (1940) as *Placopsilina longa*, from the Grayson Formation (Albian) of the Washita Group (Texas). To date, the known stratigraphic distribution of *A. longa* ranges from the upper Valanginian to the lower Turonian? of several shallow marine successions in key localities of Europe and North America. It has been recorded from the Lower Cretaceous of Texas and Oklahoma (Loeblich and Tappan, 1946; Frizzell, 1954), the lower Hauterivian of Switzerland (Brönnimann and Jayet, 1967), the Cenomanian-lower Turonian? of the Bohemian Cretaceous Basin in the Bohemian Massif (Czech Republic) (Hercegová, 1988; Žitt and Nekvasilová, 1996; Žitt et al., 2006), and the Upper Cretaceous of France (Hercegová, 1988). The investigated specimens of *A. longa* were collected from high-frequency sedimentary couplets packages related to eustatic 6th-order Milankovitch precession-driven cycles, composing a highly fossiliferous, mixed carbonate and siliciclastic succession of late Hauterivian age (*Crioceratites schlagintweiti* and *Crioceratites diamantensis* zones; Aguirre-Urreta and Rawson, 1997). After characterizing the taphonomic features of specimens and positioning their stratigraphic occurrence within 3rd-order sedimentary sequences, we discuss the possible relationships between the inferred behaviors of *A. longa* (i.e., feeding habit, life position, selection of agglutinated material) and paleoenvironmental parameters (e.g., sedimentation rate and type(s) of available sediment). The specimens from the Agua de la Mula Member indicate that the paleobiogeographic distribution of *A. longa* is broader than previously indicated and shed light on the paleoenvironmental significance of this species in the context of a middle to outer, mixed carbonate and siliciclastic ramp in the central sector of the Neuquén Basin. Furthermore, *A. longa* is related to environments characterized by low sedimentation rates (Hercegová, 1988), so its record in the transgressive deposits of the Neuquén Basin represents a further clue that allows us to corroborate previous paleoenvironmental reconstructions for the study area.

2. Geological setting

The Agrio Formation (lower-upper Valanginian to lower Barremian) is widely exposed in the Neuquén Basin of west-central Argentina, reaching up to 1500 m thickness (Leanza et al., 2001;

Howell et al., 2005; Spalletti et al., 2011) (Fig. 1). It is the topmost unit of the Mendoza Group, conformably overlying the marine and continental Mulichinco Formation (Valanginian), and discordantly covered by the continental Huitrín Formation (Barremian) (Leanza et al., 2001; Spalletti et al., 2001; Howell et al., 2005) (Fig. 1). Weaver (1931) subdivided the unit into the Pilmatué, Avilé, and Agua de la Mula members (Leanza et al., 2001). The Pilmatué and Agua de la Mula members consist of thick, high-frequency cyclic successions of marine mixed carbonate and siliciclastic ramp deposits (i.e., mudrocks, marlstones, limestones, sandstones) (Legarreta and Uliana, 1991; Spalletti et al., 2001; Archuby and Fürsich, 2010; Archuby et al., 2011). The Avilé Member is a continental unit and represents a relative sea-level drop (Leanza et al., 2001; Veiga et al., 2002).

The Agua de la Mula Member consists of a highly fossiliferous succession bearing mainly ammonites, bivalves, and gastropods (Weaver, 1931; Aguirre-Urreta and Rawson, 1997; Aguirre-Urreta et al., 2005; Lazo et al., 2005; Archuby, 2009), and a microfossil content mostly made up of calcareous nannofossils, ostracods, and foraminifers (Musacchio, 1979; Bown and Concheyro, 2004; Ballent et al., 2006; Concheyro et al., 2009; Caramés, 2011; Caratelli and Archuby, 2023a, 2023b). Among foraminifers, benthic and rarely planktonic species occur, with polymorphinids and vaginulinids being the most abundant benthic taxa of the Agua de la Mula Member. The record of encrusting foraminifers is poor and limited to the calcareous taxon *Webbinella* sp. (Ballent et al., 2006), and to agglutinated specimens forming macroids (Caratelli et al., 2021) or referred to *Tolypammia vagans* Brady (Luci and Cichowolski, 2014). The agglutinated foraminifer analyzed in this study encrusts bivalves (*Ptychomya koeneni* Behrendsen, 1892) and forms macroids. The material was collected from two stratigraphic sections (Agua de la Mula and Bajada del Agrio, hereafter AM and BA, respectively) encompassing the marine succession of the Agua de la Mula Member in the central sector of the Neuquén Basin (northern Patagonia, Argentina) (Fig. 2). The two sections consist of mixed carbonate and siliciclastic deposits mostly made of thin bedded dark shales and shaly marlstones with subordinated shell-rich bioclastic carbonates and sandstones (Weaver, 1931; Spalletti et al., 2001; Archuby and Fürsich, 2010). High-frequency sedimentary couplets characterize the analyzed succession, alternating throughout 3rd-order transgressive/regressive sedimentary sequences (Archuby and Fürsich, 2010). These couplets packages are called starvation/dilution (S/D) sequences (*sensu* Archuby et al., 2011), and are interpreted as eustatic 6th-order Milankovitch precession-driven cycles (Archuby and Fürsich, 2010; Archuby et al., 2011). S/D sequences are made of mixed bioclastic sandstones, and pelitic and marly intervals, respectively. Bioclastic sandstones are characterized by i) an erosional base, ii) abrasion, breakage, and disarticulation of macrofauna dominated by mollusks at the lower part of package (base of starvation hemisequence), iii) high diversity and well-preserved macrofauna with bioerosion and encrustation occurring upward (top of starvation hemisequence), and iv) a deepening-upward trend (Archuby, 2009). When fully developed, it is possible to detect a horizon of maximum flooding approximately in the middle of the starvation hemisequence, implying that it includes the early part of the next 6th-order regression (i.e., starvation hemisequences encompass the transgression and the early part of the next regression; Archuby and Fürsich, 2010). In the study area, S/D sequences are usually thicker throughout 3rd-order regressive systems tracts and thinner throughout 3rd-order transgressive systems tracts. The agglutinated foraminifer *A. longa* forming macroids and encrusting bivalves occurs in marine deposits of middle to outer ramp, in the *Crioceratites diamantensis* Zone (upper Hauterivian) in both the AM and BA stratigraphic sections (Fig. 2). The collected material was

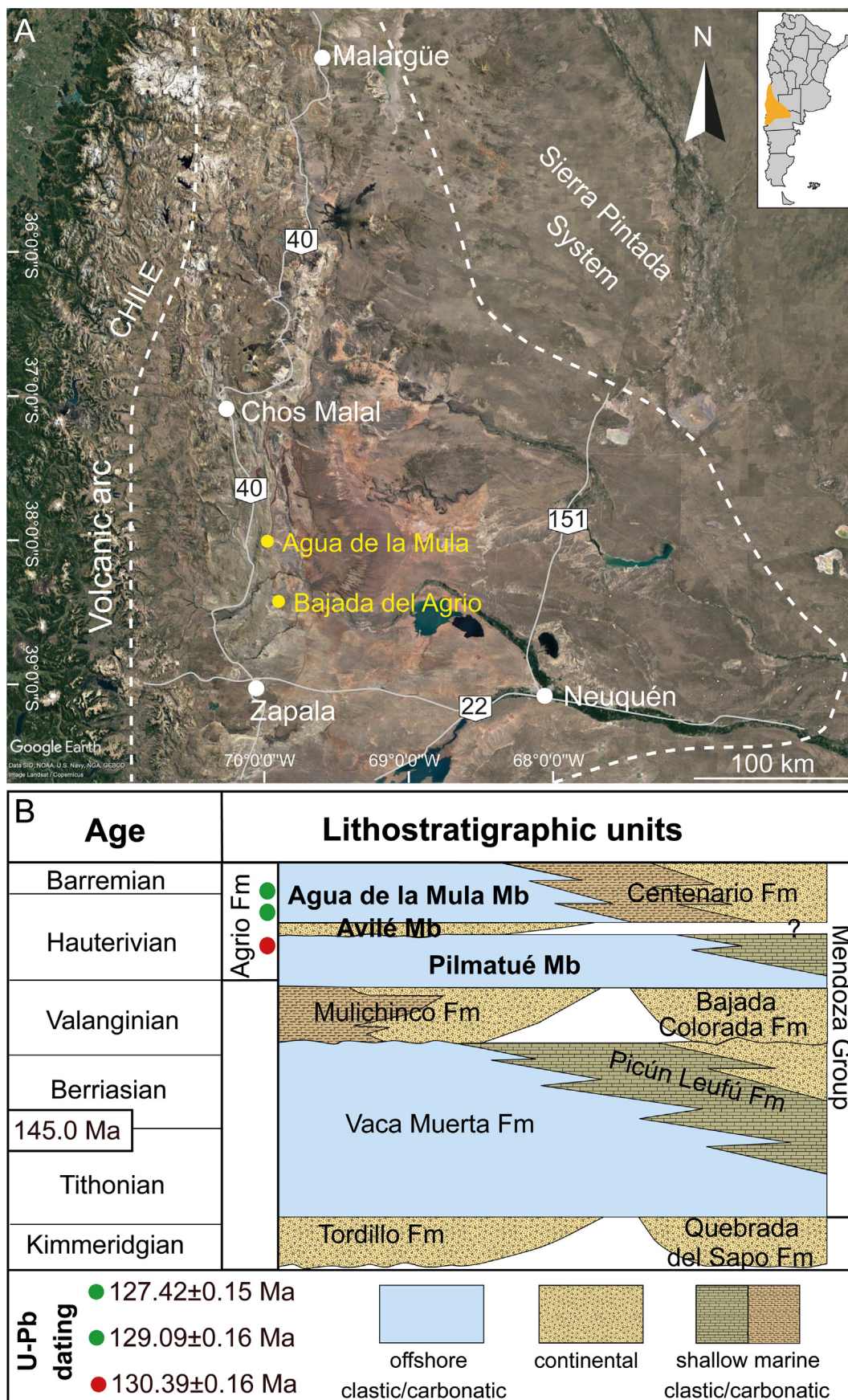
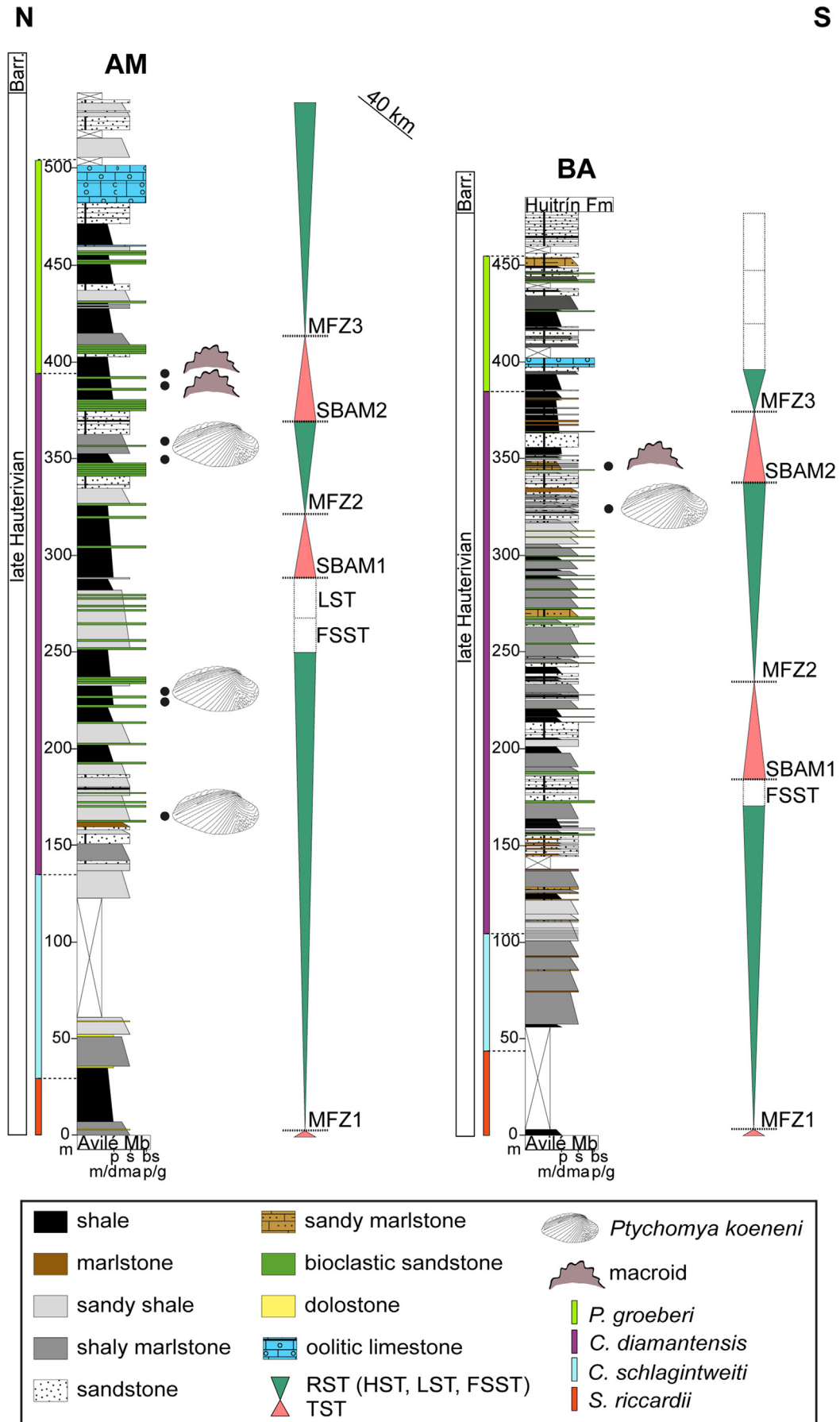


Fig. 1. (A) Google Earth satellite image showing the location and boundaries of the Neuquén Basin, and the two studied stratigraphic sections (modified from Archuby et al., 2009). White dotted line: Neuquén Basin boundary; thinner grey lines: National Routes. (B) Chronostratigraphic scheme of the Mendoza Group showing high-precision U–Pb dating referring to tuff layers embedded in the Pilmatué and Agua de la Mula members marked by red and green dots, respectively (after Howell et al., 2005). U–Pb zircon ages are from Aguirre-Urreta et al. (2015, 2017).



sampled at the top of starvation hemisequences, from poorly lithified claystones/siltstones to marlstones, which rest on top of mixed bioclastic sandstones. Regardless of the systems tract type sampled, both macroids and *Ptychomya koeneni* shells were collected from rather thin (ca. 2–3 m thick) S/D sequences. Moreover, macroids and bivalves encrusted by *A. longa* never occur together at the same 3rd-order depositional sequence. Indeed, *Ptychomya koeneni* characterizes the lower part of the *Crioceratites diamantensis* Zone, following within the first and second 3rd-order regressive systems tracts, whereas macroids mostly occur in the upper part of the *Crioceratites diamantensis* Zone, within the third 3rd-order transgressive systems tract.

3. Materials and methods

The analyzed material consists of several dozen of specimens of agglutinated foraminifers that were found encrusted on 20 specimens of *Ptychomya koeneni* (14 specimens from the AM section, 6 specimens from the BA section), as well as forming 50 macroids (38 from the AM section, 12 from the BA section) (collection numbers: MOZ-Pm 001-007, MOZ-Pm 061-123) (Fig. 3). These specimens were compared with those considered to represent the genus *Acruliammina*, as well as with material previously attributed to other genera whose descriptions and comparisons fit with the features of the test observed in our specimens. The specimens were analyzed by means of a Philips XL20 Scanning Electron Microscope (SEM) at the Instituto de Investigación en Paleobiología y Geología, General Roca, Río Negro Province, Argentina. Semiquantitative chemical analysis was performed using a voltage of 20 kV on thin sections of macroids. Energy dispersive spectroscopy (EDS) was used to carry out the analysis, performing chemical element mapping and obtaining X-ray spectra of the main elements composing the agglutinated tests walls. Scanning electron microscope (SEM) images were taken with a Zeiss EVO 15. X-ray computed microtomography was used in order to evaluate the distribution of agglutinated foraminifers encrusting macroids without destroying them. Computed tomography images were acquired using a ZEISS Xradia Context, and a total of 897 DICOM file format with 16-bit were obtained over a 360° sample rotation. X-ray images were visualized using the free open source software 3D Slicer. The studied material is deposited in the Juan A. Olsacher Museum of Zapala (Neuquén province), Paleomicroinvertebrates collection (acronym: MOZ-Pm).

4. Results

4.1. Systematic description

Order Lituolida Lankester, 1885

Suborder Lituolina Lankester, 1885

Family Placopsilinidae Rhumbler, 1913

Subfamily Placopsilinae Rhumbler, 1913

Genus *Acruliammina* Loeblich and Tappan, 1946

Type species: *Placopsilina longa* Tappan, 1940

Acruliammina longa (Tappan, 1940)

(Figs. 4–6)

1940 *Placopsilina longa* Tappan, p. 100, pl. 15, figs. 9a–10.

1946 *Acruliammina longa* (Tappan), Loeblich and Tappan, p. 252, pl. 36, figs. 20a–c.

1954 *Acruliammina longa* (Tappan), Frizzel, p. 80, pl. 7, figs. 28a–b.

1964 *Lituola ?fragilis* Kristan-Tollmann, p. 42–43, pl. 5, figs. 6–11.

1987 *Placopsilina cenomana* d'Orbigny, Loeblich and Tappan, p. 80, pl. 65, figs. 11–12.

1988 *Acruliammina longa* (Tappan), Hercegová, p. 151, text figs. 2–4.

Description. Test multi-chambered with simple chamber lumen, hollow, without secondary septa or labyrinth interior (Fig. 5E–F); wall agglutinated, attached at least initially for the enrolled early stage, later uncoiled, uniseriate, with cylindrical chambers, probably free of the attachment; aperture consists of a low slit against the attachment in the early stage, later terminal and double, and finally cribrate. Simple wall structure with no labyrinthic interior, and no secondary septa within chambers are the main differences between the members of the Placopsilinae Rhumbler, 1913 and those included into the Haddoniidae Saidova, 1981 and Coscinophragmatidae Thalmann, 1951 (Schmidt and Jäger, 1993).

Remarks. The tests consist of finely to coarsely agglutinated quartz grains and quartzitic cementing material. Quartz grains are 'roughly finished' (Loeblich and Tappan, 1987, p. 80) and their size varies (quartz grain size is in average from 0.01 to 0.04 mm). EDS analyses show that test wall composition is dominated by Si, representing detrital quartz, as well as subordinate Al, Na, and K, suggesting feldspar grains and clay particles as main components (Fig. 7A–E). Both outer and inner surfaces of all analyzed tests are insoluble in 10% hydrochloric acid (HCL) solution, confirming a dense package of siliciclastic grains forming test wall, and thus a rather homogeneous composition. EDS analyses also indicate calcite as the dominant filling mineral of the interior of the foraminiferal chambers, which in some cases is replaced by apatite (Fig. 7F–H). Scattered diagenetic pyrite framboids also occur filling the chambers and showing a wide size distribution ranging from 2.5 to 25 mm in diameter (Caratelli et al., 2021).

The study material is incomplete since many specimens are broken tests, and their terminal portion is likely missing since it often lacks the erected, free final stage of growth that characterizes this species. Size and shape of the tests are very irregular and variable in outline, probably reflecting the relief of the skeletal substrate that they encrust. Although the growth mode is not always well-defined, early chambers seem to be planispirally coiled and never trochospiral. Number and size of chambers in the coiled stage are variable, and in some specimens chambers appear subtriangular in outline (Fig. 8A–B). In contrast, the uniserial arrangement consists of convex chambers, wider than high, commonly with bending array (Fig. 8C–I). It is unclear whether chambers regularly grow in size as they are added. The uniserial stage consists of up to 23 chambers, or is shorter, with 5–10 chambers. Sutures are straight, slightly arched in the coiled stage, and more incised in the rectilinear stage (Fig. 8C–I). An accurate estimate of chamber dimensions (i.e., number, length, and height of chambers) is difficult, because of the impossibility to isolate specimens and detach them from encrusted surfaces without breaking them. However, a rough estimate of dimensions using computed microtomography is provided below. Also, specimens often overlap, hampering the recognition of which elements of the test belong to a single individual (Fig. 4). The chamber lumen is simple, without secondary septa, in agreement with the character of the genus *Acruliammina*.

Fig. 2. Stratigraphic sections of the Agua de la Mula Member of the Agrio Formation at Agua de la Mula (38°03'20.68"S and 70°01'57.11"W) and Bajada del Agrio (38°25'51.24"S and 70°00'40.17"W) localities. The sections report the location of macroids and *Ptychomya koeneni* encrusted by *Acruliammina longa* (black dots). Ammonite biozones follow Aguirre-Urreta and Rawson (1997) and Aguirre-Urreta et al. (2005). Sequence stratigraphy is from Archuby et al. (2011). LST: Lowstand systems tract; MFZ: Maximum flooding zone; HST: Highstand systems tract; FSST: Falling stage systems tract; SBAM: Sequence boundary within the Agua de la Mula Member; TST: Transgressive systems tract; RST: Regressive systems tract. p: pelite; s: sandstone; bs: bioclastic sandstone; m/d: mudstone/dolostone; ma: marlstone; p/g: packstone/grainstone.

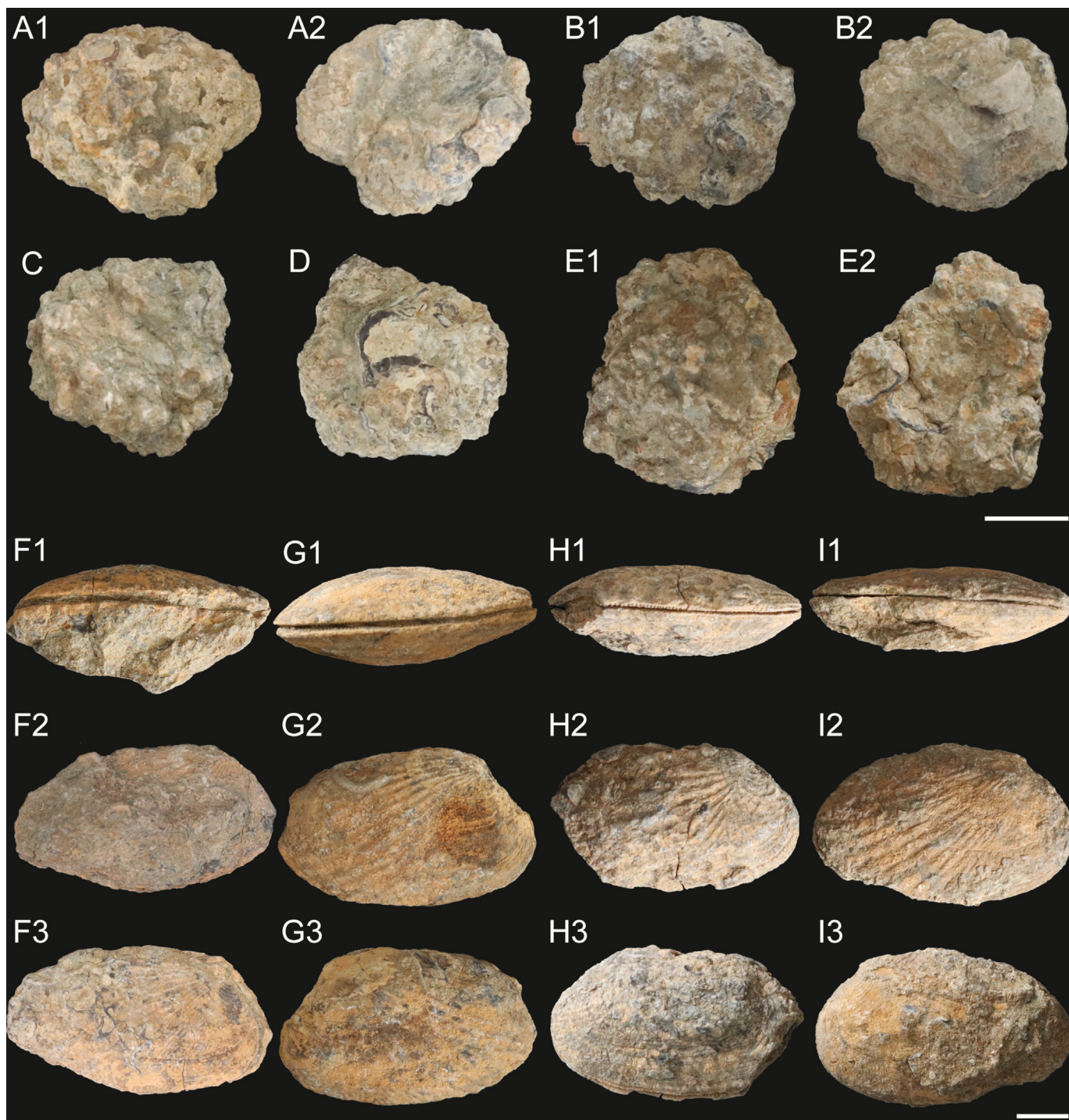


Fig. 3. Macroroids (A–E) and *Ptychomya koeneni* (F–I) from the AM and BA sections. Macroroids: A1, B1, C, E1, upper surface showing warty appearance of foraminifers; A2, B2, D, E2, lower side with concave area in the center. Both sides also show encrusting oysters and bryozoans. Scale bar equals 1 cm. Collection numbers: MOZ-Pm 061 (A); MOZ-Pm 062 (B); MOZ-Pm 063 (C); MOZ-Pm 064 (D); MOZ-Pm 065 (E). *Ptychomya koeneni*: F1, G1, H1, I1, ventral view of specimens of *P. koeneni* showing shell commissure; F2–I3, right valves (F2, G2, H2, I2 and F3) and left valves (G3, H3 and I3) of specimens of *P. koeneni* showing encrusting *A. longa*, oysters, and serpulids. Scale bar equals 1 cm. Collection numbers: MOZ-Pm 104 (F); MOZ-Pm 105 (G); MOZ-Pm 106 (H); MOZ-Pm 107 (I).

Apertures are terminal, rounded, and cribrate, with circular and quite regularly spaced foramina. Up to 5 foramina were observed on the apertural face (Fig. 5A–B). Foraminal diameter ranges from 0.06 to 0.1 mm. Generally, 1 to 2 foramina are present at basal position of chambers (Figs. 6, 8A). When foramina increase in number (3–5), they are either distributed next to each other in an intermediate

position on the apertural face, or circularly arranged (Fig. 5A–B). Moreover, supplementary openings are visible along chamber sutures on the dorsal side of tests (Figs. 6, 8). These openings consist of multiple, round to ovate pores, ranging from 0.02 to 0.07 mm in diameter. This distribution pattern of supplementary openings was observed on specimens encrusted both on macroroids and bivalves.

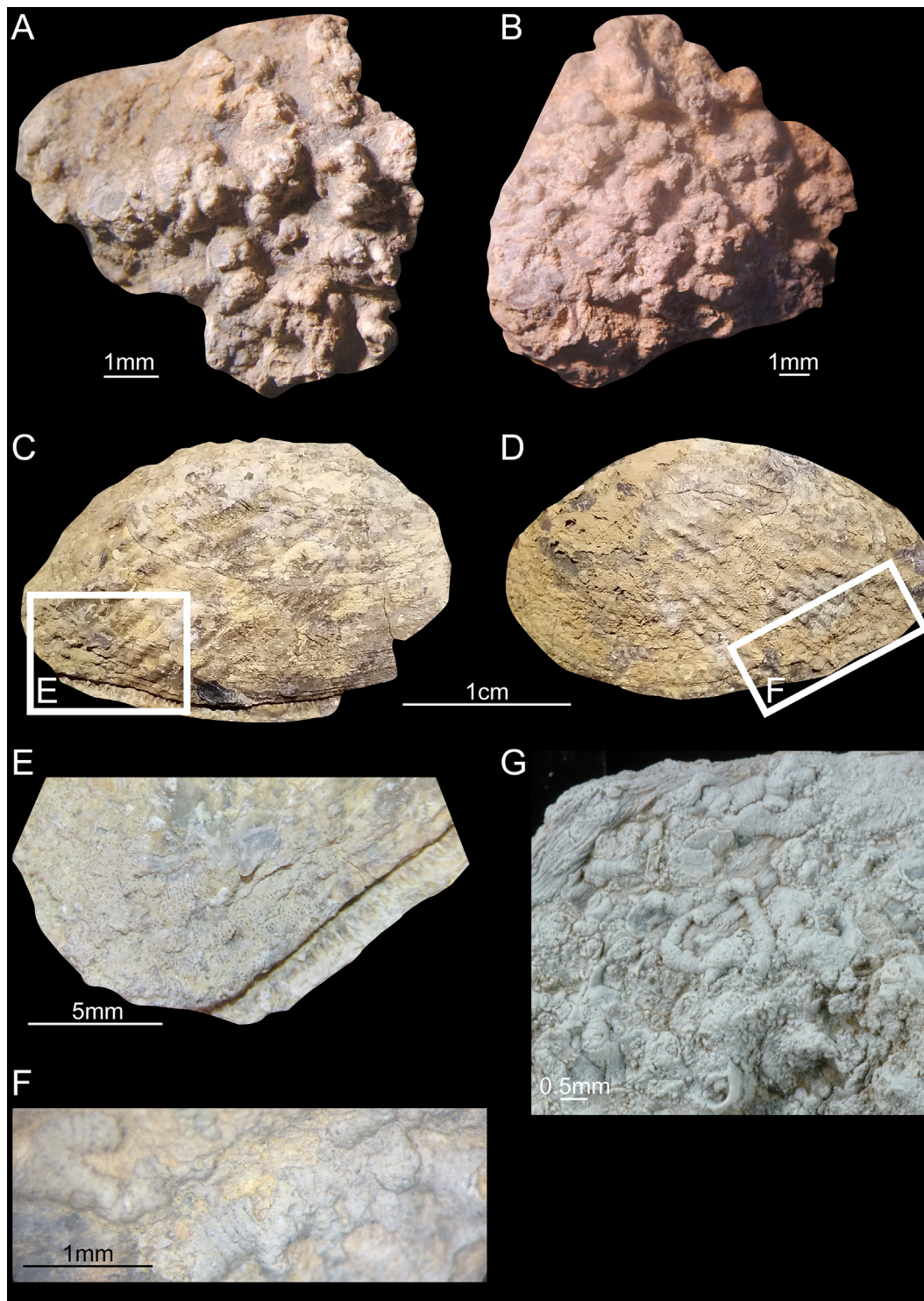


Fig. 4. Agglutinated foraminifer *AcruIAMmina longa* encrusted on macroids and *Ptychomya koeneni*. (A–B) View of two macroids with several encrusting specimens on the surface. Collection numbers: MOZ-Pm 066 (A); MOZ-Pm 067 (B). (C–D) *P. koeneni* encrusted by *A. longa* only on the posterior half of a right and left shell respectively. Collection numbers: MOZ-Pm 108 (C); MOZ-Pm 109 (D). (E–F) Detail of encrusting *A. longa* on the upper surface of *P. koeneni*. *AcruIAMmina* specimens overlap, hindering the recognition of each one. Note in E that the shell commissure is free of encrusting foraminifera. (G) Detail of *A. longa* specimens overlapping each other; a small initial coil and later rectilinear chambers are visible. Collection number: MOZ-Pm 110.

Dimensions:

Length of test: ranging from 2 to 7 mm.
 Diameter of coiled stage: ranging from 1 to 2.5 mm.
 Number of chambers in coiled stage: ranging from 5 to 8.

Number of chambers in uniserial stage: highly variable, ranging from 9 to 23.
 Height of chambers: ranging from 0.06 to 0.3 mm.
 Length of chambers: ranging from 0.08 to 0.5 mm.

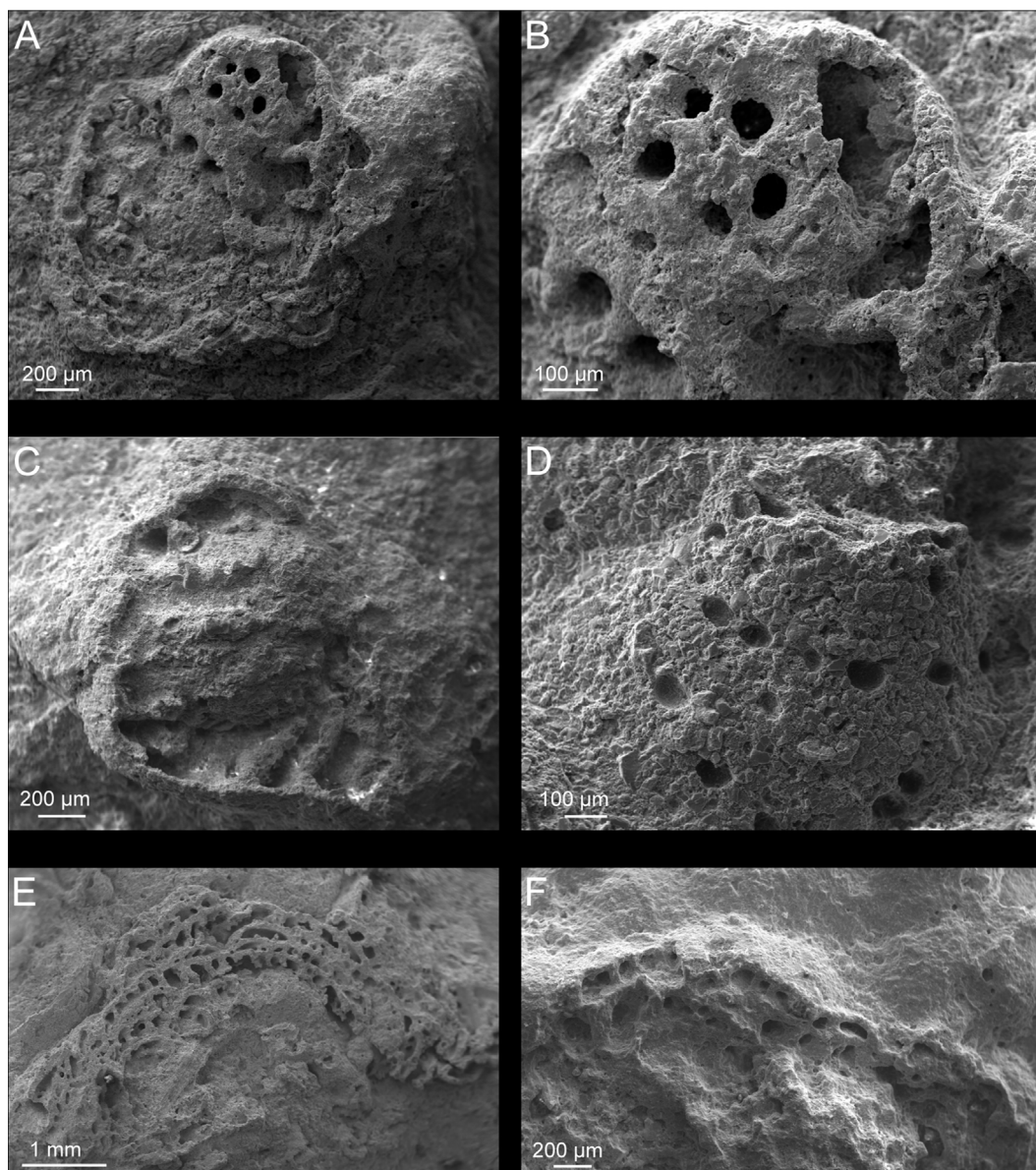


Fig. 5. Scanning electron photomicrographs of *AcruIAMmina longa*. (A–C) Specimens forming macroids. Collection number: MOZ-Pm 066. (D–F) Specimens encrusting *Ptychomya koeneni*. Collection numbers: MOZ-Pm 108 (D–E); MOZ-Pm 109 (F). (A) Broken specimen with cribrate aperture with up to five rounded foramina on the apertural face. (B) Detail of the foramina shown in figure A. (C) Dorsal view of a broken specimen showing uniserial chambers arrangement with bending array. (D) Detail of the agglutinated test wall with at least two rows of possibly supplementary openings in sutural position. Note that agglutinated grains are coarser than those shown in figure B. (E–F) Different rows of sub rectangular, uniserial chambers, with single apertural openings at basal position. Note the simple (non-alveolar-labyrinthic) agglutinated wall structure in both specimens.

Diameter of foramina: ranging from 0.06 to 0.1 mm.

Wall thickness: mainly from 0.05 to 0.02 mm.

Comparison. According to Kaminski (2014), the subfamily Placopsilininae Rhumbler, 1913 includes the genera *AcruIAMmina* Loeblich and Tappan, 1946, *Ammocibicides* Earland, 1934, *Ammocibicides* Saidova, 1975, *Lapillincola* Wilson, 1986, *Placopsilina* d'Orbigny, 1850 and *Subbdelloidina* Frenzen, 1944. *AcruIAMmina* differs from the genera of the families Haddoniidae (e.g., *Haddonia*) and Coscinophragmatidae (e.g., *Bdelloidina* and *Coscinophragma*) in having simple chambers (not labyrinthic) and wall composition made of quartzitic cement (Schmidt and Jäger, 1993). Among the Cretaceous members of the Placopsilininae, the main differences between *AcruIAMmina*, and *Subbdelloidina* and *Placopsilina* are the single aperture only and the overall lower number of chambers, which are features typically of the latter (Loeblich and Tappan, 1987). However, Schmidt and Jäger (1993) indicate for

Subbdelloidina a multiple aperture. *AcruIAMmina* differs from *Lapillincola* by the absence of an unattached, erect final portion of the test, and a cribrate aperture (Wilson, 1986).

All *AcruIAMmina longa* specimens from the Agua de la Mula Member are insoluble in HCL, and the only cementing material occurring between grains is quartzitic. This observation corresponds to Hercegová's (1988) for the wall composition of *A. longa* from the Bohemian Cretaceous Basin. However, the pseudochitinous layer observed in the specimens from the Czech Republic was not recognized in the study material. *A. longa* differs from *A. neocomiana* Bartenstein, 1962 in having a quartzitic cement and no supplementary structures (e.g., internal pillars) within the chambers (Frieg, 1980; Hercegová, 1988). Size, shape, and number of chambers are the main distinguishing features between *A. longa* and *A. neokasilovae* Hercegová, 1988. *A. longa* shares with *Lituola? fragilis* specimens size, number and shape of foramina, and wall structure.

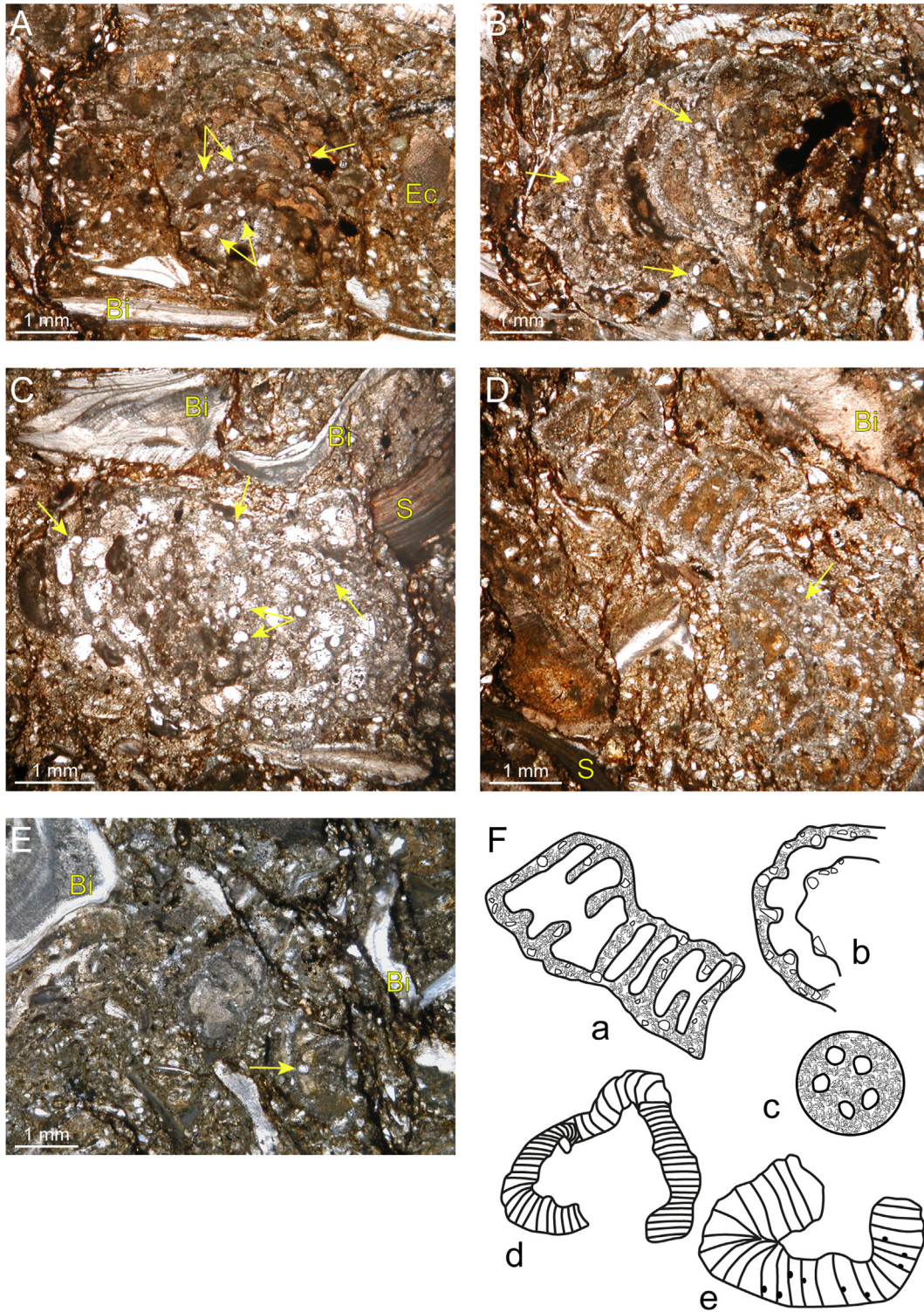


Fig. 6. Thin-section photomicrographs (A–E) and interpretative sketch (F) of *Acruiliammina longa*. (A–C). Longitudinal sections showing single foramina in basal position. Collection number: MOZ-Pm 001. (D–E) Longitudinal sections of two different specimens in each figure. Top left (D) and middle (E) show tests with rectilinear chambers array and single openings. Yellow labels into images, Bi: bivalve; Ec: echinoid; S: serpulid. Yellow arrows refer to possible supplementary openings in sutural position. Collection numbers: MOZ-Pm 002 (D); MOZ-Pm 003 (E). (F) Sketch showing different views of the study material: a-b) longitudinal sections of wall test with agglutinated granules and quartzitic cement; c) transversal section of the apertural face with rounded foramina; d) dorsal side of three overlapping specimens; e) dorsal side of uniserial, bent test, with supplementary openings in sutural position. Not to scale.

However, the material from the Upper Triassic Zlambach marl (Austria) is fragmentary, missing the early coiled portion of the test (Kristan-Tollmann, 1964), and thus any detailed comparison is hampered. Although the general external morphology of *A. longa*

tests described by Brönnimann and Jayet (1967) from Switzerland, as well as the shape, size, and arrangement of chambers, closely resemble the study material, the microtexture of test walls differs. Brönnimann and Jayet (1967) observed two different layers

composing the test wall: a thin outer layer made of dense quartz grains almost free from cement, and an inner (lower) layer composed of microgranular calcite cement. They recognized this subdivision of the test wall in transmitted light, describing an inner layer darker than the outer one due to microgranular calcite. Based on this difference, we agree with Hercegová (1988) in considering *A. longa* described by Brönnimann and Jayet (1967) as a different species. Another difference between our material and the specimens from the lower Hauterivian of Switzerland is in the number of openings in the coiled stage. A single terminal opening is described by Brönnimann and Jayet (1967), whereas our specimens show at least 2 openings at basal position (Fig. 8A–B). The distribution of the apertural foramina resembles that described for *A. longa* by both Hercegová (1988) and Brönnimann and Jayet (1967), where up to 2 foramina characterize the chambers of the early growth stages in a terminal and basal position, whereas multiple openings occur during test growth in the uncoiled, rectilinear stage.

4.2. Taphonomic features

4.2.1. *AcruIAMmina longa* tests encrusting macroids

Macroids are sub-spheroidal to sub-discoidal in shape, 2–3 cm in diameter and 1–2 cm in height, and are characterized by an encrusting community made of agglutinated foraminifers, serpulids, bryozoan colonies, oysters, and undetermined bivalve bioclasts. Agglutinated foraminifers participating in the formation of macroids are almost exclusively represented by *AcruIAMmina longa*; the only exception being a few specimens referred to ?*Tolypamma* (see Caratelli et al., 2021). Fine-grained siliciclastic matrix fills bivalve bioclasts, which form the nuclei of each macroid and around which foraminifers encrust. As shown in X-ray CT scanning images (Fig. 9), the inner structure of macroids consists of bivalve valves or fragments colonized on both the upper and the lower side by encrusting agglutinated foraminifers. The irregular and variable chamber arrangement of encrusting foraminifers may reflect the morphology and distribution of the biogenic substrate they encrust, i.e., bivalve shells, in such a way that the growth pattern of the attached ventral side of foraminifers is strongly related to the shape of substrate. Foraminifers were not encrusted by other organisms, such as oysters, bryozoan colonies, and solitary serpulids that encrust the external surface of macroids (Caratelli et al., 2021). In many *A. longa* specimens associated to macroids the dorsal side of the test is broken or worn, and the latest erected and free chambers are missing. Damages affecting tests are irregular in shape and are interpreted as the result of hydrodynamic breakage. No borings or etchings, i.e., ecological interactions due to other organisms (e.g., predation, parasitism) were observed. Breakage of tests allowed us direct observation of the internal surfaces and structures. All agglutinated grains are irregular in shape, randomly oriented, and mainly composed of detrital quartz, feldspars, and clay particles. Quartz grain size ranges from 0.002 to 0.03 mm.

4.2.2. *AcruIAMmina longa* tests encrusting *Ptychomya koeneni* shells

Ptychomya koeneni shells are anteroposteriorly elongated, 6–8 cm long, and characterized by rows of crenulations and compound ribs on both valves (Archuby, 2009; Milla Carmona et al., 2017). The shells are very well preserved and almost all articulated. On *P. koeneni*, *AcruIAMmina longa* is found encrusting only the posterior half of shells, which in life is oriented towards the sediment-water interface, generally leaving the shell commissure free (Figs. 3, 8D). Specimens of *A. longa* are less damaged than those encrusting macroids. Tests are very close to each other on bivalves, up to mutual overgrowing, and form in some cases tangled masses that prevent a reliable identification of the growth mode of

individuals. Composition and shape of agglutinated grains are similar to the previous case. However, quartz grain size is coarser than that observed on tests associated to macroids and it ranges from 0.02 to 0.06 mm.

5. Discussion

5.1. Paleoeological significance of *AcruIAMmina longa*

AcruIAMmina longa is the dominant agglutinated foraminifer composing the Agua de la Mula encrusting fauna, together with *Placopsilina* sp. and *Tolypamma* sp. (Archuby, 2009; Caratelli et al., 2021). The paleoecology of this species has not been widely evaluated and little is known about its feeding habit. The investigated specimens form macroids, or encrust specimens of *Ptychomya koeneni* with articulated valves. In the case of macroids, colonization of *A. longa* specimens suggests that encrustation occurred after the death of the bivalves (both the internal and the outer surfaces of shells are encrusted) and prior to burial, indicating that dead shells were exposed on the seafloor, thereby favoring the breakage of foraminiferal tests. In contrast, colonization of *A. longa* on *P. koeneni* suggests a possible interaction in life between foraminifers and bivalves. The distribution of foraminifers only on the outer surface of the posterior end of bivalves and the growth cessation of foraminiferal encrustations at the shell commissure may indicate that both *A. longa* and bivalves were alive at the same time. According to Taylor (1979) and McKinney (1995), cessation of growth at margins of contact (i.e., shell commissure in our study) represents evidence of ecological interactions and a reliable evidence to interpret that both organisms involved were alive at the time of overgrowth. Thus, whereas a single macroid encrusted by *A. longa* may involve some degree of time-averaging, this phenomenon is absent in the case of the *A. longa*-*P. koeneni* association. The specimens included in this work were sampled from within-habitat time-averaging assemblages (Caratelli and Archuby, 2023a) obtained from 6th-order S/D sequences (Archuby et al., 2011). The distribution of *A. longa* is limited to the posterior half of bivalves, revealing clues for paleoecological strategies of both encrusting foraminifers and host. In particular, the *A. longa* distribution strongly suggests a true epibenthic microhabitat, with passive suspension feeding strategy, as is the rule for encrusters living above the sediment-water surface. On the other hand, a semi-infaunal lifestyle for *P. koeneni* has been confirmed by Archuby (2009).

5.2. Paleoenvironmental significance of foraminiferal encrustation on macroids and *Ptychomya koeneni*

Generally, the paleobiogeographic distribution of *AcruIAMmina longa* seems controlled by paleoenvironmental parameters influencing the sedimentary environment, e.g., organic carbon flux, oxygen level, sedimentation rate, and substrates suitable for propagule settlement. Although such parameters vary locally, within each sedimentary basin, *A. longa* has always been found encrusted on rock fragments and skeletal substrates, and associated with bryozoans, mollusks, echinoderms, and serpulids in the different sedimentary successions. Moreover, this species is often related to transgressive deposits (e.g., Cretaceous Bohemian Basin – Hercegová, 1988). The same distribution is also observed in the Neuquén Basin, where *A. longa*-dominated macroids occurs at third 3rd-order transgressive systems tract deposits encrusting skeletal substrates. *A. longa* occurs in both mixed shelves (e.g., in the Bohemian Cretaceous Basin, Czech Republic – and the Neuquén Basin, Patagonia, Argentina) and shallow-water carbonate environments (e.g., the Washita Group, Texas and Oklahoma, – and the Vaudois Jura, Switzerland) (Fig. 10). The paleogeographic distribution of

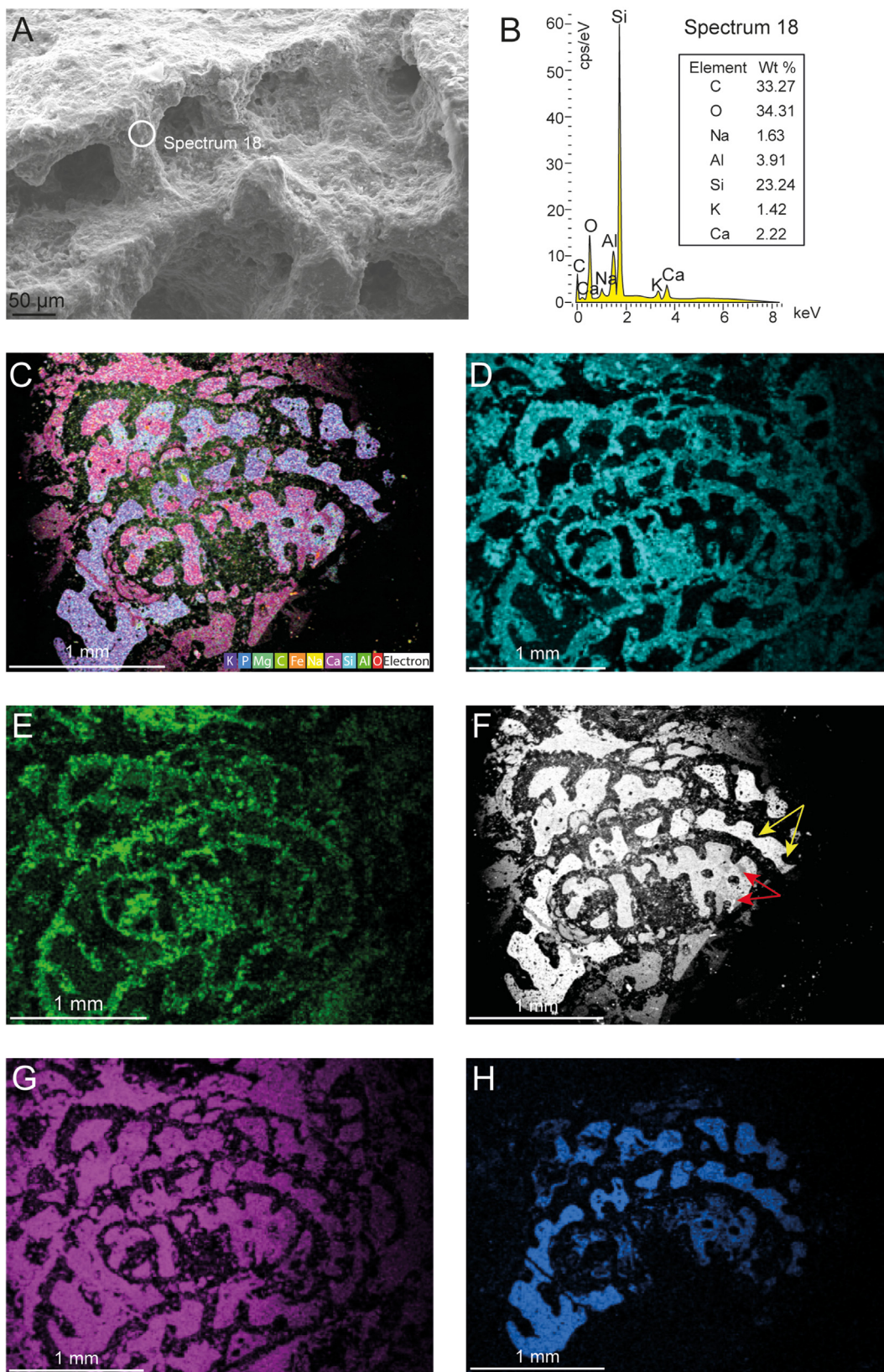


Fig. 7. (A) Scanning electron photomicrograph showing two rows of chambers with uniserial array and sub-rectangular shape. Collection number: MOZ-Pm 108. (B) EDS spectrum referring to the foraminiferal test shown in A. Si, Al, and Na are the main elements composing the foraminiferal test. (C) EDS map performed on two specimens showing both the main constituents of the foraminiferal test (Si, Al, Na) and the principal components of the chamber fill (Ca, P). (D–E) Element mapping images showing foraminiferal test composition, with Si (D) and Al (E) as the most abundant elements composing the test. (F) Scanning electron photomicrograph of an encrusting agglutinated foraminifer shown in longitudinal section. Yellow arrows mark single apertural foramina at basal position. Red arrows indicate up to 2 apertural foramina in the uniserial stage. (G–H) Element mapping images illustrate that Ca (G) and P (H) are the main elements filling the chambers, and suggest calcite and apatite as dominant minerals. Collection number: MOZ-Pm 002 (C–H).

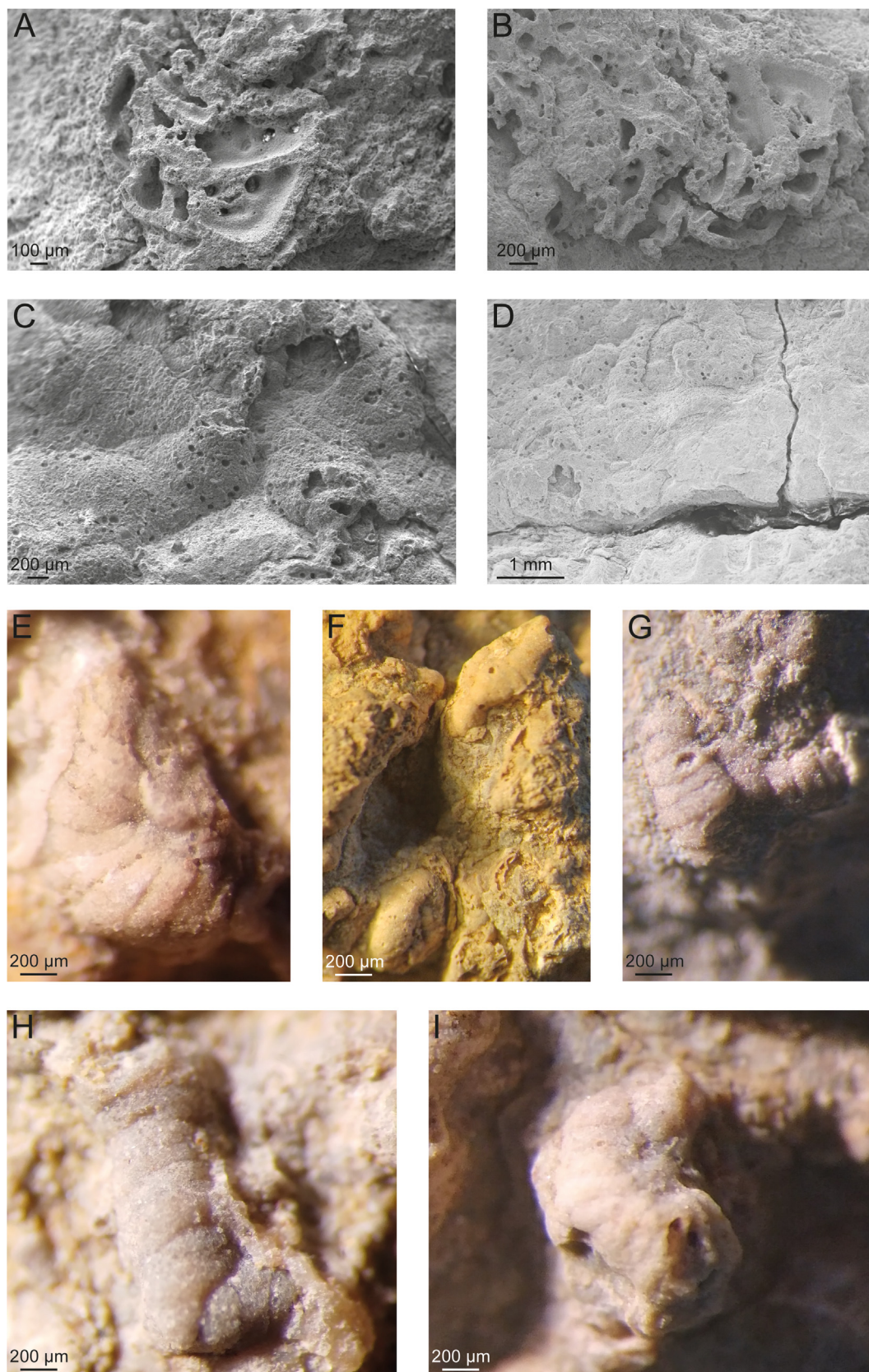


Fig. 8. (A–B) Spiral side of *A. longa* test made of up to 5 chambers with rows of apertural foramina at the base of the chambers. The simple (non-alveolar-labyrinthic) agglutinated wall structure is also visible. Collection number: MOZ-Pm 066. (C) Different specimens overlapped, bended, and with well visible rows of secondary apertures. (D) Multiple foraminiferal specimens encrusting *Ptychomya koeneni*. Note that shell commissure is free of encrusting foraminifera. Collection number: MOZ-Pm 108 (C–D). (E–I) Different specimens showing unrolled stage of the test with variable numbers of chambers. Specimens of figures E to F show at least 11 chambers; two overlapped specimens are shown in figure G; specimens in figures H and I show at least 8–9 chambers. Collection numbers: MOZ-Pm 066 (E–G); MOZ-Pm 067 (H–I).

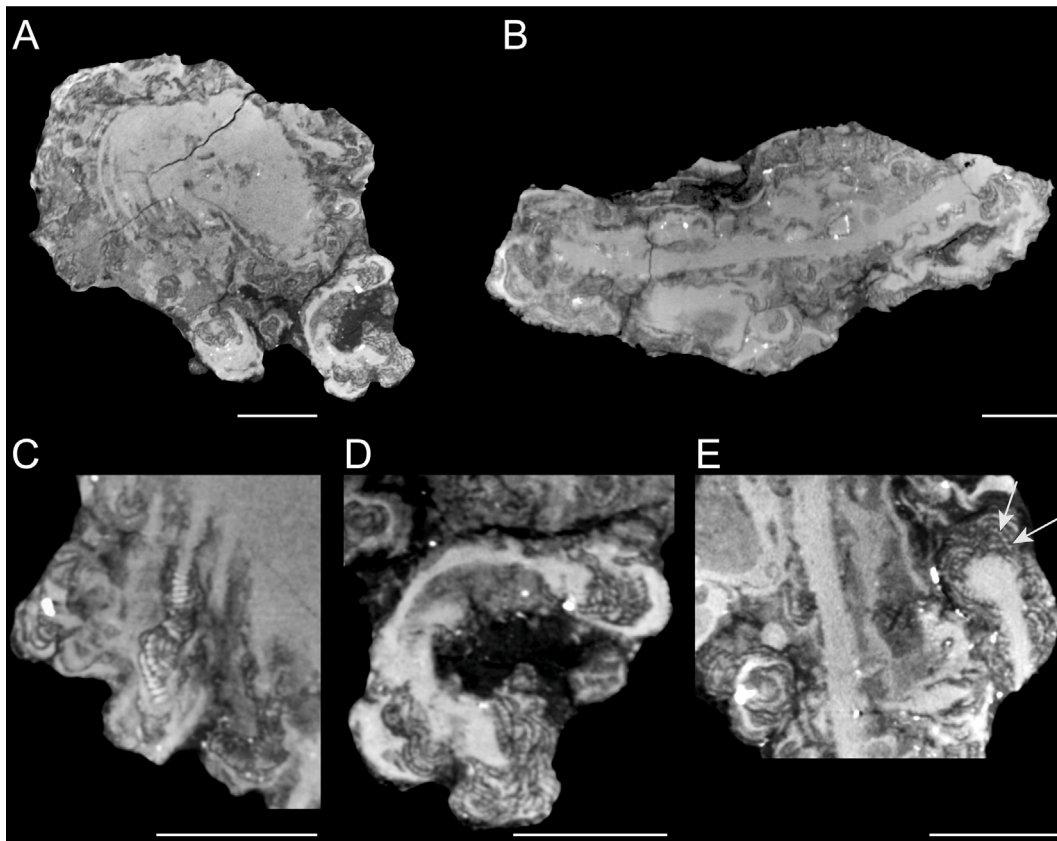


Fig. 9. X-ray CT image of a macroid showing the interior of a nodule made of bivalve bioclasts encrusted by *A. longa*. (A) Sagittal and (B) axial sections of the macroid, where epibiotic foraminifers cover both the outer and inner surface of bivalve bioclasts, suggesting different times of exposure of the encrusted surfaces. (C) Close-up of *A. longa* tests in sagittal view. Tests show uniserial chamber arrangement and bending array. (D–E) Close-up of *A. longa* specimens in sagittal (D) and axial (E) view, growing around bivalve bioclasts. In figure E note single apertures in basal position for specimen shown in the top left side (yellow arrows). Light grey color refers to bivalve bioclasts; dark grey color refers to siliciclastic sediment, which occurs both as matrix filling macroid voids and composing foraminiferal tests. Scale bars = 5 mm. Collection number: MOZ-Pm 068.

A. longa encompasses different latitudes at or above 30° N and S, thus thriving under suitable conditions likely limited to high paleolatitudes. Current data, far from establishing where *A. longa* originated, provide some information on the topic. The oldest stratigraphic occurrence of *A. longa* is an upper Valanginian-lower Hauterivian record from Switzerland (Brönnimann and Jayet, 1967). *A. longa* occurs in the Hauterivian of Texas and Oklahoma (Loeblich and Tappan, 1987) and in the upper Hauterivian of the Neuquén Basin (this paper). Later records are from the Cenomanian-lower Turonian? deposits of the Cretaceous Bohemian Basin (Czech Republic) (Hercegová, 1988; Žítt and Nekvasilová, 1996; Žítt et al., 2006) and generic Upper Cretaceous deposits of France (Hercegová, 1988). Although *A. longa* resembles the Upper Triassic *Lituola ?fragilis*, the fragmentary nature of the material described by Kristan-Tollmann (1964) does not allow us to confidently extend its stratigraphic distribution to the Triassic. A possible route of *A. longa* could have originated from the Tethys during the early Hauterivian and dispersed westward across the North Atlantic Ocean, reaching the coasts of both the USA and South America (dispersal route A in Fig. 10). However, arrivals in the Neuquén Basin across the Tethys Ocean, thus circumnavigating the continent of Gondwana, cannot be ruled out (dispersal route B in Fig. 10). Whatever the origin and dispersal route, its reconstruction requires a greater dataset. The absence of *A. longa* from Upper Cretaceous deposits of the Neuquén Basin could be due to changes in the paleogeography associated with the closure of the connection between the Neuquén Basin and the Pacific Ocean, and the onset of dominant continental sedimentation (Howell et al., 2005).

A comparison based on size of grains agglutinated by specimens of *A. longa* forming macroids (finer grain size) and encrusting *P. koeneni* shells (coarser grain size) provides clues about energy conditions of paleoenvironments. As known, agglutinated foraminifers are capable to select grains of different sizes and shapes, picking them up from the surrounding environment (e.g., Allen et al., 1999; Makled and Langer, 2010; Armynot du Châtelet et al., 2013). Studies on living benthic foraminifers have shown a possible relationship between agglutinated grain size and firmness of tests (e.g., Allen et al., 1998; Armynot du Châtelet et al., 2008, 2013). This relationship could provide implications in reconstructing the dynamic of the environment, since foraminifers with tests made of coarser grains are more suitable to live in lower energy environments, whereas finer tests can thrive in higher energy environments (Allen et al., 1998; Armynot du Châtelet et al., 2008, 2013). According to these studies, the coarser grain size characterizing tests of *A. longa* encrusted on *P. koeneni* may suggest relatively lower energy environments, whereas the finer grain size composing tests forming macroids may be associated with relatively higher energy environments. The absence of free chambers and breakage of the dorsal side of many *A. longa* tests associated to macroids can also be interpreted as related to higher energy conditions.

It is worth noting that both macroids and *P. koeneni* occur, in both sections, always at the top of starvation hemisequences and at relatively thinner S/D sequences with the 3rd-order sedimentary sequences. *A. longa* with tests made of finer agglutinated grains occurs in the basal and middle part of 3rd-order

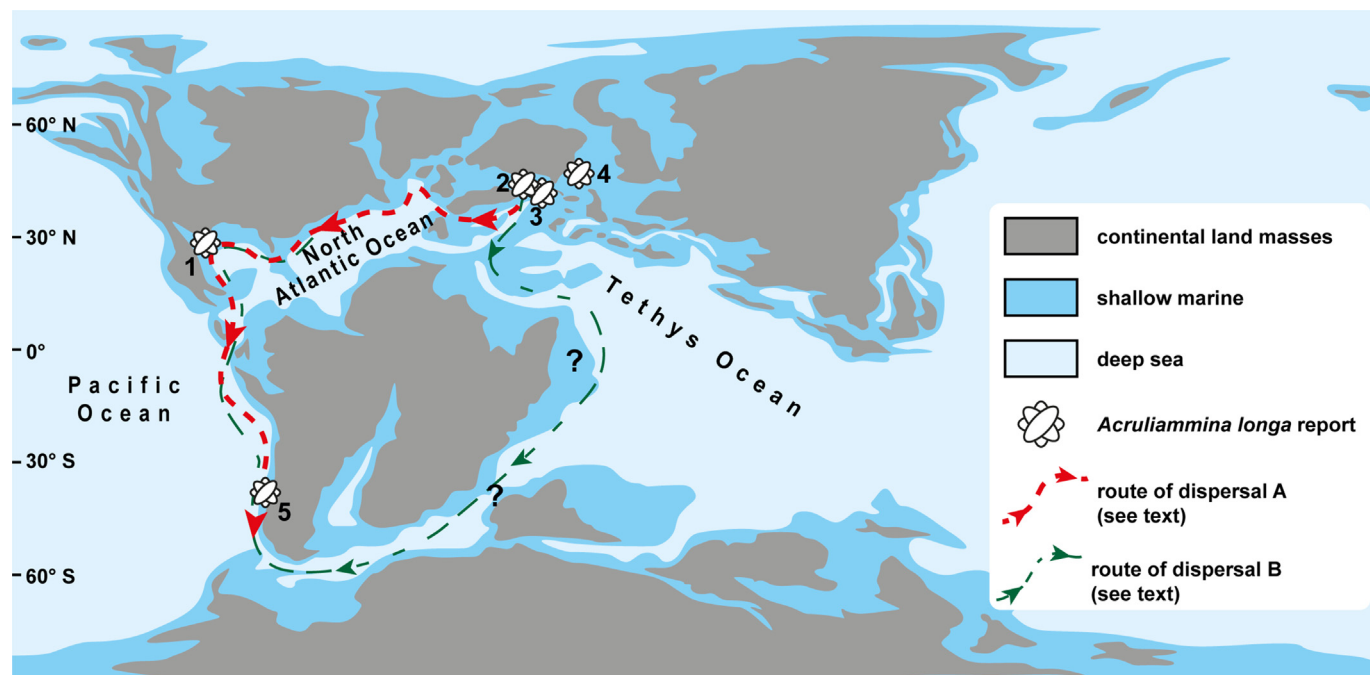


Fig. 10. Simplified paleobiogeographic map for the Cretaceous showing records of *AcruIAMmina longa* and its possible dispersal pathways (retrieved from <http://jan.ucc.nau.edu/rcb7>). 1 (Lower Cretaceous Washita Group, Texas and Oklahoma – Loeblich and Tappan, 1946); 2 (Upper Cretaceous of France – Hercegová, 1988); 3 (lower Hauterivian of Switzerland – Brönnimann and Jayet, 1967); 4 (Cenomanian-lower Turonian? of the Bohemian Cretaceous Basin, Czech Republic - Hercegová, 1988); 5 (upper Hauterivian of the Neuquén Basin, Argentina).

transgressive systems tracts, commonly characterized by lower sedimentation rates, whereas tests with coarser grains size occur throughout the 3rd-order regressive systems tract where higher sedimentation rates dominate. As to the occurrence of other foraminifers, the early regressive deposits at the third 3rd-order transgressive systems tract of the Agua de la Mula Member of the Agrio Formation is commonly barren or characterized by foraminifer-poor assemblages, often dominated by epifaunal species (e.g., *Reinholdella hofkeri*-dominated assemblages) (Caratelli and Archuby, 2023a, 2023b). In contrast, shallow infaunal associations occur at dilution hemisequences developed throughout 3rd-order regressive systems tracts, since higher organic matter is available in sediments below the sediment-water interface within a context of relatively high terrigenous input (Caratelli and Archuby, 2023a). Such infaunal-dominated associations are characterized by elongated and planispiral flattened morphogroups (C3 to C6, and A1 morphogroups in Caratelli and Archuby, 2023b). Changes in the composition of foraminiferal associations (infaunal-to epifaunal-dominated associations) throughout dilution hemisequences suggest that the latter did not develop under uniform paleoenvironmental conditions. Indeed, although dilution hemisequences developed under higher sedimentation rates than starvation hemisequences, the occurrence of encrusting *A. longa* on macroids and *P. koeneni* in the early regressive deposits provides further clues of likely shifting sedimentation rates, indeed suggesting a reduction in rates. *A. longa* was able to colonize skeletal substrates that, at least at the high hierarchy 3rd-order sedimentary sequences, were developed under different paleoenvironmental conditions, thus revealing its opportunistic behavior. Such habit is also suggested by the difference in agglutinated grain sizes within the tests, which might be related to changes in energy conditions as well as to the overall availability of any grains convenient to be agglutinated. However, if we look at the high-frequency (6th-order) S/D sequences, *A. longa* likely encrusted skeletal substrates under overall low

sedimentation rates that characterized the top of starvation hemisequences throughout both transgressive and regressive 3rd-order sequences.

6. Conclusions

Encrusting agglutinated foraminiferal specimens referred to the placopsilinid species *AcruIAMmina longa* (Tappan, 1940) are described from upper Hauterivian marine sediments of the Agua de la Mula Member of the Agrio Formation (Neuquén Basin, Argentina). The record is the first from South America and extends to the Southern Hemisphere the paleogeographical distribution of the species. Indeed, the new finding suggests that *AcruIAMmina longa* was a ubiquitous species inhabiting shallow-water environments at high latitudes. The current paleogeographic distribution of *A. longa* ranges from the Tethys to South America during the Cretaceous. Further records of *A. longa* from the Southern Hemisphere (i.e., northern South America, South Africa, and Australia) would shed light on paleobiogeographic models during the Cretaceous, thus helping to explain possible oceanic pathways. *A. longa* was found encrusted on *Ptychomya koeneni* shells or forming macroids, occurring at the top of starvation hemisequences of the high-frequency (6th-order) S/D sequences at both 3rd-order transgressive and regressive systems tracts along two stratigraphic sections. Foraminiferal specimens observed on bivalves and macroids show different taphonomic features, as well as changes in agglutinated grain size, providing further clues in interpreting rate of terrigenous input and energy conditions. *A. longa* tests encrusting *P. koeneni* are less damaged than those encrusting macroids and are made up of coarser sized grains, suggesting that they were more suitable to live in lower energy environments. Additionally, considering that the *P. koeneni* specimens were invariably articulated, the encrusting foraminifers were exposed no longer than the bivalve life span and, hence, little time exposed. Foraminiferal tests forming macroids show higher breakage and finer grain size,

leading to the inference that they could grow in higher energy conditions and/or were exposed more time on the sea floor. Even though the study material was collected from high frequency, early regressive beds at different 3rd-order depositional sequences, overall lower sedimentation rates allowed *A. longa* to colonize skeletal substrates throughout both 3rd-order regressive and transgressive systems tracts. Finally, low sedimentation rates seem to have played a pivotal role in controlling the distribution of *A. longa* in the Neuquén Basin, similarly to what has been previously described for shallow marine environments in both carbonate and mixed depositional settings.

CRediT authorship contribution statement

M. Caratelli: Writing – review & editing, Writing – original draft, Funding acquisition, Data curation, Conceptualization. **P. Citton:** Writing – review & editing, Writing – original draft, Data curation, Conceptualization. **F. Archuby:** Writing – review & editing, Writing – original draft, Funding acquisition. **J. Pignatti:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

The research was supported by Universidad Nacional de Río Negro – Argentina (PI UNRN 2017 40-A-612 project to A.F.); the Angelina Messina Grant (former Grant-in-Aid) from The Micropalaeontological Society to M.C.; the J.A. Cushman Award for Student Research from the Cushman Foundation for Foraminiferal Research to M.C. Martin Arce, Martin Parada, and Luciano Castro are thanked for their assistance during lab activities. The Editor-in-Chief Maria Rose Petrizzo and the reviewers Felix Schlagintweit and Lorenzo Consorti are acknowledged for their constructive comments and suggestions that contributed to improve the manuscript.

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