



Encrusting patterns and life habit of Mesozoic trigonoids: a case study of *Steinmanella quintucoensis* (Weaver) from the Early Cretaceous of Argentina

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LETHAIA



Luci, L. 2010: Encrusting patterns and life habit of Mesozoic trigonoids: a case study of *Steinmanella quintucoensis* (Weaver) from the Early Cretaceous of Argentina. *Lethaia*, Vol. 43, pp. 529–544.

Trigonoid bivalves of the genus *Steinmanella* Crickmay are abundant at the top of the Vaca Muerta Formation, Neuquén Basin of Argentina, of Early Valanginian age. The species *Steinmanella quintucoensis* (Weaver) is frequently encrusted by oysters, serpulids and mytilids. Oysters are the most conspicuous encruster, followed by serpulids and then mytilids. A taphonomic, palaeoecological and taxonomic analysis was performed on the encrusting fauna of *S. quintucoensis*. An analysis of encrusting preference was performed on the basis of differences in ornamentation of the host shell, which was divided in a strongly tubercled flank and a smoother ribbed corselet and escutcheon zone. A higher encrustation frequency was found for the corselet and escutcheon zone, over the larger flank. Possible explanations are differences in the sculpture of each part of the valve, closeness to the respiratory openings of the host, and relation to life position of the trigonoids. In this respect, a palaeoecological analysis of the life position of the genus *Steinmanella* was made on the basis of functional morphology, encrustation patterns and comparison with related fossil forms as well as living representatives, finding that the most suitable position to explain encrustation patterns and functional morphology is one with the flanks below the water–sediment interface, and the corselets exposed above the substrate. □ *Early Cretaceous, encrustation, Neuquén Basin, trigonoids.*

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The term epibiont includes all boring or attaching organisms that inhabit hard surfaces of organic origin, during the life of their host or after its death (Taylor & Wilson 2002). In particular, encrusters are those epibionts that can secrete hard parts and are cemented to another hard skeleton. Epibionts can establish complex communities on their hosts, with successive generations and faunas, and even symbiotic relationships among themselves and with their hosts (Giacobbe 2002). The study of epibiont faunas has proven to be a useful palaeoecological tool, allowing the interpretation of modes of life and interspecific interactions between the epibionts and the host, for both benthic and nektonic hosts (e.g. Seilacher 1960; Brande 1982; Baird *et al.* 1989).

Study of epibiont communities has certain advantages, given that their organisms are preserved *in situ* with high spatial fidelity (Rodland *et al.* 2004). Stenotopic epibionts may provide precise environmental information. Epibiont associations are more strongly controlled by the environment than by the host, although the latter can be important at the species level, and therefore they allow us to refine environmental inferences (Rodland *et al.* 2004). Among

bivalves, there are studies involving mytilids such as *Pinna* Linné (Kay & Keough 1981; Keough 1984; Corriero & Pronzato 1987; Giacobbe 2002), oysters (Mauna *et al.* 2005; Parras & Casadío 2006), scallops (Pitcher & Butler 1987; Pond 1992; Lescinsky 1993), mussels (Laudien & Wahl 1999), as well as other groups (e.g. Scanland 1979; Brande 1982). For trigonoids, epibiont communities were analysed by Villamil *et al.* (1998), and briefly commented by Stanley (1977), Francis & Hallam (2003) and Lazo (2003). The first and the latter focused on the genus *Steinmanella* Crickmay, a genus that is very common in the Early Cretaceous marine facies of Argentina. At the top of the Vaca Muerta Formation, the abundant species *Steinmanella quintucoensis* (Weaver 1931) is frequently encrusted, with shells sometimes displaying large encrusters, or shells sometimes almost completely covered by them.

The life habit of *Steinmanella* is currently under discussion, with several authors presenting different models with contrasting positions of the shell in relation to the sediment, varying from semi-infaunal to nearly epifaunal. Thus, the abundant *S. quintucoensis* recorded in the Vaca Muerta Formation provides a

good opportunity to test the preferences of encrusters on the shell. As long as the *post mortem* epibionts can be differentiated from those encrusted during the life of their host, their location on the shell will provide evidence of the portions of the shell that remained emerged from the substrate. Even the orientation of the epibionts can provide information on life orientation of their hosts (e.g. Seilacher 1960; Brande 1982). Therefore, the main goals of this study are: (1) to study the encrusting fauna of the species *S. quintucoensis*, involving its taxonomy, palaeoecology and taphonomy; (2) to perform a statistical analysis of encruster's distribution patterns on the host shell; (3) to analyse the location and orientation of epibionts with respect to the host's shell; and (4) to interpret the mode of life of the genus *Steinmanella* on the basis of encruster distribution on the shell, functional morphology and comparisons with Recent trigoniods and *Steinmanella*-related genera.

Geological setting

All the specimens examined in this study were collected at Cerrito de la Ventana, Huncal, west-central Neuquén ($38^{\circ}0.055' \text{ S} - 70^{\circ}14.810' \text{ W}$; Fig. 1); this area belongs to the outcrops of the Neuquén Basin or Embayment, a wide, triangular-shaped bay or gulf that extended to the east of a convergent oceanic-continental margin, representing an important marine ingression that contains a thick Mesozoic–Cenozoic sedimentary succession (Vergani *et al.* 1995). The Mesozoic section of the Neuquén Basin was affected by generalized extensional efforts given by the breakup of western Gondwana and the opening of the South Atlantic Ocean (Vergani *et al.* 1995).

The measured section belongs to the Vaca Muerta Formation, a marine unit with a thickness of between 200 and 1700 m (Gulisano *et al.* 1984), thinning to the east. In the studied area, it overlies the Tordillo Formation and is covered by the Mulichinco Formation, which records an episode of major retreat of the sea, and the base of which is a first-order sequence boundary (Schwarz 2003). The Vaca Muerta Formation consists of black shales and calcareous shales, with clays and calcareous clays rich in organic matter (Doyle *et al.* 2005). Several authors (Marchese 1971; Doyle *et al.* 2005; Leanza *et al.* 2006; among others) have suggested a restricted oxygenation for the Vaca Muerta shales, but oxygen levels cannot have dropped enough to prevent colonization of the bottom, as abundant, well-calcified benthic biota has been found in the black shales. Doyle *et al.* (2005) found that the dysoxic–anoxic condition changes towards the top of the unit, where oxygen levels would increase. The

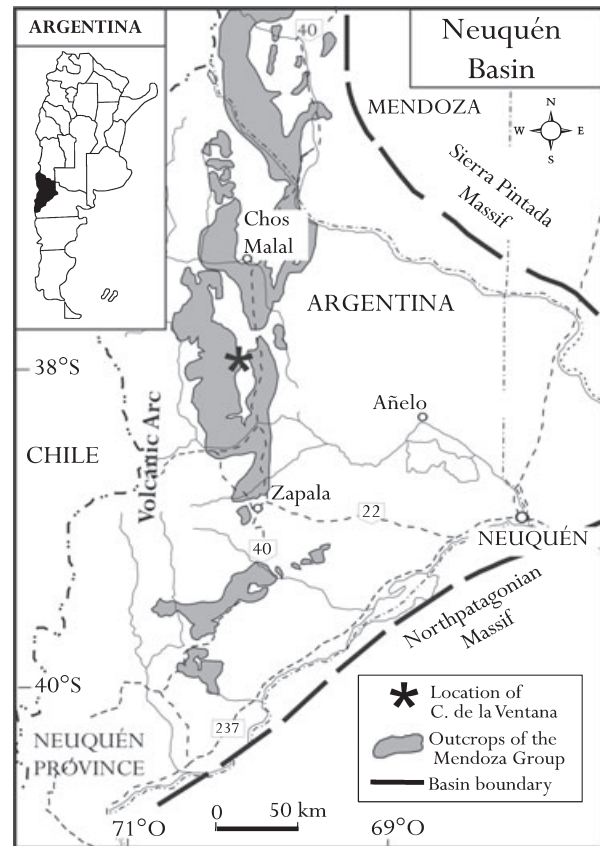


Fig. 1. Map showing the extension and limits of the Neuquén Basin, in mid-western Argentina; the location of the outcrops of the Mendoza Group in Neuquén Province, Cerrito de la Ventana and the measured section.

Vaca Muerta environment has thus been interpreted as a poorly oxygenated offshore environment, which becomes shallower towards the top of the unit (Leanza *et al.* 2006).

This unit is not only rich in ammonoids and marine reptiles, but also microfossils (Leanza *et al.* 1977). Trigoniods only peak in abundance near the top of the unit. The age of the Vaca Muerta Formation spans from the Early Tithonian to the Early Valanginian (see Aguirre-Urreta & Rawson 1999; Leanza *et al.* 2006).

The measured section, in Cerrito de la Ventana, can be accessed through National Route 40 and then the gravel road to Coihueco, by crossing the Coihueco Creek. Only the top of the Vaca Muerta Formation was measured, resulting in a 50-m section (Fig. 2) composed mainly of black shales and silts interrupted by three packstone beds. These packstones can be followed laterally. They are composed mainly of oysters and trigoniods belonging to the genus *Steinmanella*. Other bivalves and ammonoids have also been found immersed in shales. The presence of *Lissonia riveroi* and *Neocomites wichmanni* Zones indicated an Early Valanginian age (Aguirre-Urreta & Rawson 1999).

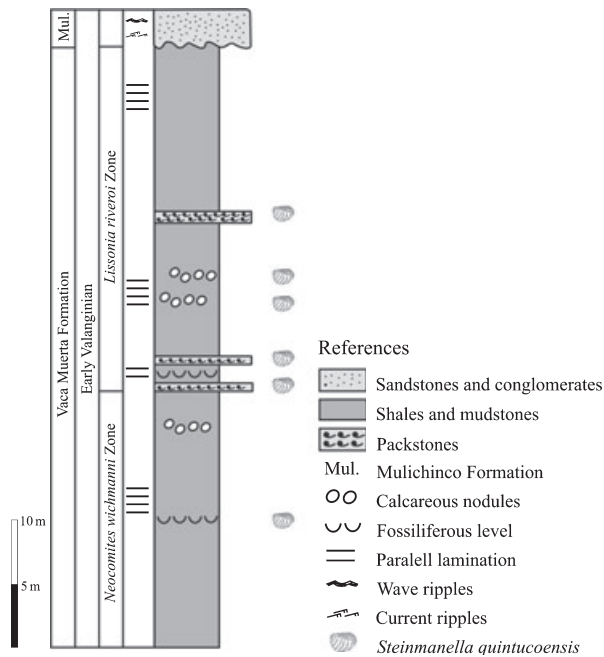


Fig. 2. Measured section at the top of the Vaca Muerta Formation in Cerrito de la Ventana; beds containing *Steinmanella quintucoensis* are indicated.

Materials and methods

A total of 175 specimens of *S. quintucoensis* were collected in Cerrito de la Ventana at the top of the Vaca Muerta Formation. They were collected *in situ* from the black shales and packstones (Fig. 2). None was found in life position. Sampling was random, without taking into consideration the degree of encrustation at the moment of collection. All specimens were later deposited in the repository of the Cátedra de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón 2, Buenos Aires, Argentina, under catalogue numbers CPBA 20300–20302.

In the laboratory, the specimens were examined for encrustation, and the following taphonomic indexes were taken for encrusters: (1) articulation, articulated when valves are preserved together, or disarticulated when valves are separated; (2) fragmentation, entire shell, shell little fragmented when small fragments are missing, shell moderately fragmented when 25–50% of the shell is missing, shell highly fragmented when more than 50% of shell surface is missing; (3) corrosion, absent, low when ornamentation is visible, moderate when ornamentation is blurred and high when nearly effaced; and (4) filling, shells empty or shells filled with sediment. The same indexes were scored for *S. quintucoensis* shells and two taphofacies were

recognized for them. Orientation in the field was also observed for trigonoids.

Each *Steinmanella* specimen was observed under a binocular microscope (with a maximum resolution of 40×) to locate and identify the epibionts. The location of each encruster on the shell was plotted on diagrams of each trigonoid. Then the distribution pattern of epibionts was tested statistically. Two distinct areas were defined in each valve: strongly tuberculated flank and smoothly ribbed corselet plus escutcheon. Following the criterion of Mauna *et al.* (2005), a differential weight was assigned to each section of the valve; as the flank comprises most of the valve surface, it was given a weight of two-thirds of the total valve surface, whereas the corselet and escutcheon section was given a weight of one-third of the valve surface. A chi-square test was performed to assess the differential encrustation of each sector of the valve, by counting the number of encrusted flanks and contrasting it against the number of encrusted (corselet and escutcheon). The escutcheon was considered as a similar surface to the corselet, as although it is slightly tuberculated, the tubercles are much smaller and less prominent than those on the flank. Considering valve surface alone, if no preferences were demonstrated among encrusters, the flank should be more frequently encrusted. The left and right valves were also compared, to test the existence of any preference by the encrusting fauna. To assess the encrusting pattern across facies, the samples of *S. quintucoensis* were separated by lithofacies (shales vs. packstones), and analysed separately to test the preference for flank or (corselet and escutcheon) of the encrusters in each facies. Finally, to compare the frequency of encrustation (number of encrusters per valve) between lithofacies, a Student's *t*-test for comparison of two means was performed for shales and packstones, using PAST software (Hammer *et al.* 2001).

Taphonomic analysis

A more detailed analysis of lithofacies and taphofacies can be found in Luci (2008), with a summary given here. As discussed above, two lithofacies were recognized in the measured section: packstones and black shales. The first is interpreted as storm beds, whereas the black shales are regarded as the deposition of fine material under quiet water conditions (see Luci 2008). Two taphofacies were recognized: reworked bivalves (Rb) and bivalves in black shales (Bb). Taphofacies Rb is always found within the packstones, whereas taphofacies Bb is found in the black shales lithofacies. The first one comprises cementing epifaunal, reclining and shallow infaunal reworked bivalves (oysters and

S. quintucoensis; see Luci 2008), with shells oriented sub-parallel to stratification plans. The filling of the shells is composed of silt, although some shells are preserved empty, with the valves crushed together. Oysters are mainly disarticulated. Fragmentation is high to moderate. In particular, trioniids show high corrosion and edge modification, whereas disarticulation is low and fragmentation is moderate to low; encrustation on the inner valve surface was observed only in two small shell fragments. For the oysters, stacking and nesting patterns were observed, and convex side-down orientation is common. This taphofacies is interpreted as reworking of shallow infaunal and epifaunal bivalves by storm waves and currents. The degree of fragmentation and edge modification reflects the high water energy during transport and redeposition (with this respect it should be noted that both the oysters and the trioniids found are very thick-shelled; additionally, the 'schizodont' dentition of trioniids made them particularly resistant to disarticulation). The taphonomic modification observed is mainly due to mechanical causes; as is shown by the cleanly broken tubercles, scratches on the shell surface and impact marks on the shells, which are frequent, and it is also common to observe the absence of the external layer of the shell, especially in the flank and umbo areas, bordered by a regular, smooth limited fracture. The degree of temporal mixing of this taphofacies is that of a within-habitat association (Kidwell 1998); the shell accumulations belong to successive generations of bivalves accumulated in the same environment, stable over time, that were eventually reworked, possibly along with alive trioniids removed from life position during storm events, and redeposited. All packstones are included in the same biozone (*Lissonia riveroi*).

Taphofacies Bb includes reclining, shallow and deep infaunal, semi-infaunal and epifaunal bivalves (see Luci 2008). Filling is shaley or calcareous, articulation is high (disarticulation is mostly found in epifaunal species, especially in oysters), fragmentation is low to moderate, corrosion and edge modification are moderate, and encrustation is moderate. Only the epifaunal and semi-infaunal bivalves have been encrusted. Overgrowth of bivalve shells by calcareous nodules is common. Preservation of internal moulds is also found, especially for thin-shelled bivalves. Preservation of the bivalve fauna is usually good, even pristine among the infaunal species, whereas semi-infaunal and epifaunal forms often show high to moderate corrosion. In particular, the trioniid shells are often dissolved, from moderately to a point in which the shell is preserved as patches of irregular size and shape; sometimes even internal moulds are also partially dissolved.

The preservation status of trionioids is variable, with nearly pristine shells that could have remained buried, with little displacement after death, mixed together in the same strata with specimens that have undergone extensive taphonomic modification. Encrustation of trionioids is, in this taphofacies, also variable, with some shells heavily encrusted on one valve only, whereas other specimens show only a few encrusters restricted to a small area of the shell. This taphofacies is interpreted as a within-habitat association (Kidwell 1998). The low degrees of fragmentation and disarticulation suggest minimum reworking and transport. The kind of corrosion typical of this taphofacies belongs mainly to the chemical type, with dissolution of shells and calcareous infills, and blurring of shell features, especially in trioniids, due to partial dissolution of recrystallized shells. The aragonitic composition of such valves could have been more prone to dissolution. The moderate encrustation reveals a certain period of exposition of shells on the substrate, as encrusters are found covering different areas of the shells of infaunal and semi-infaunal bivalves; the infaunal species, deep or shallow, show no sign of incrustation, so it is likely that they remained buried.

The increase in water energy observed in the packstones lithofacies in comparison with the black shales lithofacies is also reflected on the corresponding taphofacies. Taphofacies Rb is associated with the packstone lithofacies, with the typical features of high-energy environments; taphonomic modification is mainly caused by mechanical agents, related to reworking of shells. Taphofacies Bb is consistent with lower-energy environments, in which exposition above the substrate and chemical agents are the main causes of taphonomic modification.

The encrusting fauna

A total of 473 encrusting specimens were found on 175 shells of *S. quintucoensis*; the encrusting fauna is abundant, but diversity is low: the fauna is mainly composed of two groups of oysters (85%), followed by serpulids (13%) and mytilids (2%). The high abundance of serpulids is strongly biased by one heavily encrusted shell (Fig. 4E, F), which concentrates over 50 small serpulids covering most of the right valve. Therefore, this specimen was excluded from the statistical analysis. No bioerosion traces were found.

In general, there is only one generation of encrusters, overgrowth among them being rare. It is also noted that those encrusters that reached a large size are located on the corselet; the ones on the flank are smaller, their size and shape conditioned by the large tubercles covering the flank. Contact between

encrusters is frequent; oysters are commonly clustered together, and mytilids have been found in clusters of three to four individuals or instead solitary. It is interesting that when mytilids are present, no other encruster is found near them, or even in other parts of the same shell, and they are found only as encrusters. Serpulids are commonly solitary as well, surrounding tubercles on the flank, or following the ribs in the corselet; they have been found clustered only in the heavily encrusted specimen mentioned above.

The encrustation pattern observed in other species of *Steinmanella* found together with *S. quintucoensis* in Cerrito de la Ventana (*S. neuquensis* Burckhardt and *S. curacoensis* Weaver) is very similar; they were disregarded for the statistical analysis given the small sample size ($n = 6$ and $n = 7$ respectively). Of the non-trigonioid bivalves found in black shales, only the semi-infaunal and epifaunal ones showed encrustation. Shallow and deep infaunal bivalves completely lacked encrusters, suggesting that these shells remained buried after death. In addition, ammonoids were also heavily encrusted by oysters and serpulids.

None of the trigonoids was found in life position, and thus there was in all cases at least a minimum of reworking. Nevertheless, time-averaging is limited to that of a within-habitat association (no biostratigraphical condensation), which are assemblages accumulated over a period of environmental stability (Kidwell 1998). Only individuals from a single persistent community are mixed along successive generations. These associations range from decades to <100,000 years for shallow settings (see Kidwell 1998).

Analysis of the encrusting fauna

Oysters. – Two gryphaeid genera were identified: *Aetostreon* Bayle and *Amphidonte* (*Ceratostreon*) Bayle (Figs 3A, C, E, G; 4B, C, E, F). Several large, reclining *Aetostreon* have also been collected from black shales in the studied locality and they are one of the most abundant elements found in the packstones. *Aetostreon* has a robust, inequivalve, large shell (8–11 cm long), and the ornamentation is given by lamellar, sinuous growth lines. Fixation area is usually small, but is often conspicuous by means of xenomorphism. The right valve is slightly concave and thinner than the left valve. *Amphidonte* (*Ceratostreon*) has an inequivalve shell of medium size (3 cm in length), with a coma-shaped outline. The fixation area is usually large, occupying most of the left valve. The sub-genus is readily recognized by the presence of chomata. The left valve is convex, with prominent radial ribs. The right valve is flat, also ribbed; the ribs extend to the commissure, resulting in a crenulated ventral margin. Both groups are cementing at least during the

juvenile stage, but both may retain such habit for its entire lifetime.

There are three preservation modes for the oysters: hard parts, fixation marks and internal moulds. The first is the most common, with both *Aetostreon* and *Amphidonte* (*Ceratostreon*) cemented by the left valve, which can be whole or fragmented; the shells are usually disarticulated. Shell size varies from millimetres to a few centimetres, and some *Aetostreon* are rather large when compared with the host (Fig. 3A, C, E). Fragmentation is moderate and corrosion is low. The inner surface of the valves is often pristine, except in large oysters, when corrosion is moderate. Fixation marks are oval or sub-circular marks left by the cementation of the oyster. These marks, although they may not represent the true size the oyster might have reached, indicate the location of attachment of the encruster. The preservation of internal moulds is the less-common mode of preservation. When it occurs, the right valve is missing, and the left valve is broken and partially covered by a silty internal mould (Fig. 3G, H).

Serpulids. – Serpulids found attached to *S. quintucoensis* consisted of cylindrical tubes fixed completely to the substrate (Fig. 4E). The tubes are externally smooth and follow the host's ornamentation, or else slightly curl on themselves or along other serpulids. They are 1–5 cm long and 1–3 mm in diameter. They are solitary, with the exception of the bivalve mentioned above, with numerous small serpulids clustered together. The tubes are highly fragmented; the infill is silty, and corrosion is moderate. They were assigned to the genus *Parsimonia* Regenhardt (see Ware 1975), which is common in the Early Cretaceous of the Neuquén Basin (see Lazo *et al.* 2005). The observed serpulids are cementing (sessile) and suspension feeders; they remain attached to a hard surface throughout their lives. Extant serpulids are mostly marine, although they can inhabit a variety of environments, including estuaries and lagoons (ten Hove & van der Hurk 1993). It is likely that these serpulids were epifaunal, given that at least the open end of the tube needed to be above the sediment–water interface, given the filter-feeding habitat of these worms, in order for the tentacle crown to be extruded. In the Agrio Formation of the Neuquén Basin, several studies have reported encrusting *Parsimonia antiquata* (e.g. Lazo 2007) as epibionts on hard substrates, including bivalved and ammonite shells; he also reports mass aggregation of such worms, in which most specimens were epifaunal and cemented over other dead worms of the same species and over shell fragments. In addition, Cataldo (2008) has reported serpulid encrusters assigned to *Parsimonia* on epifaunal gastropods. Other

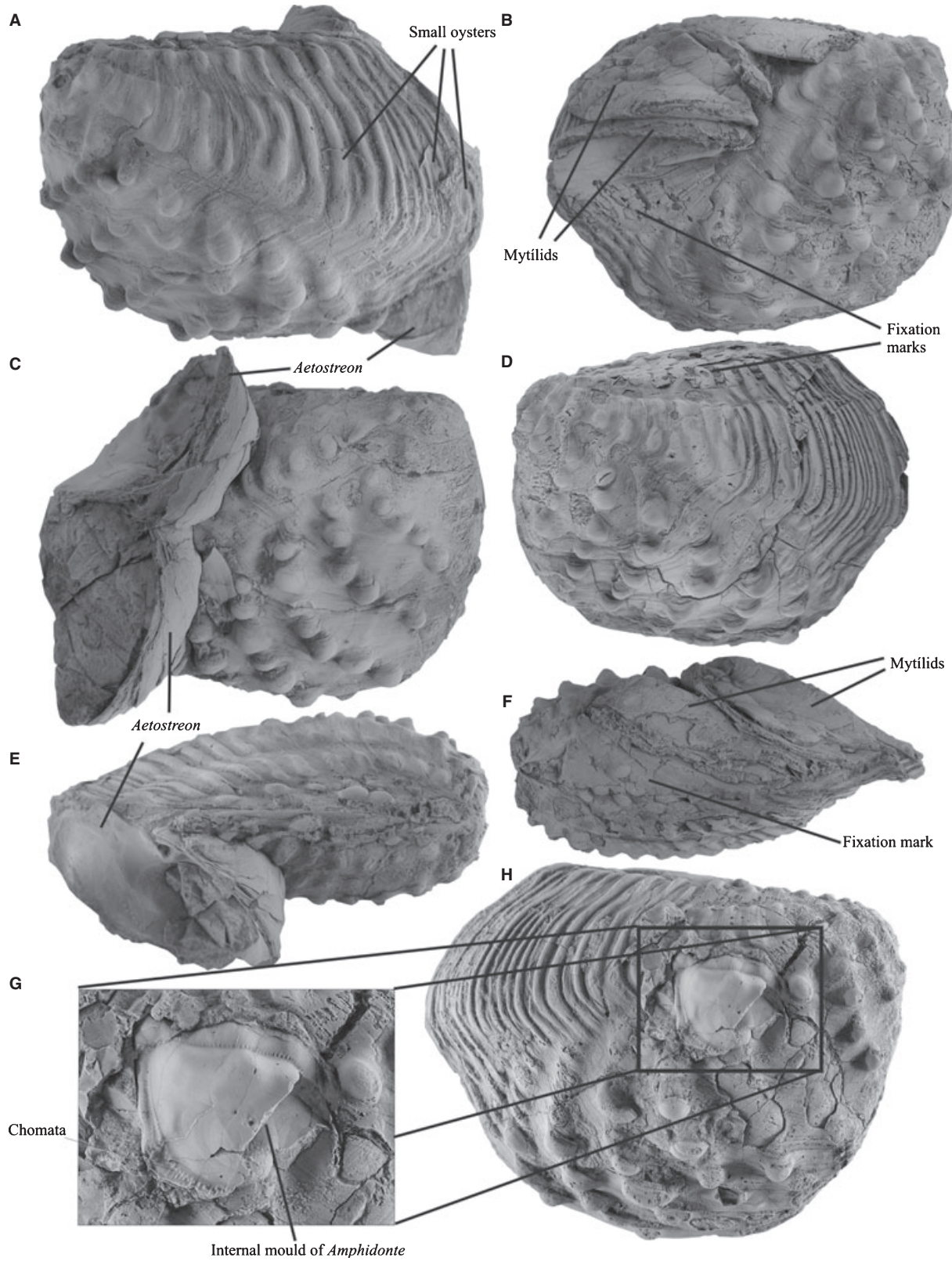


Fig. 3. Encrusted specimens. A, C, E, CPBA 20303: left, right and dorsal views. Trigoniid with two large *Aetostreon* sp. fixed side-by-side, and outgrowing the trigoniid's siphonal margin. Left corselet with three small oysters. B, D, F, CPBA 20300: right, left and dorsal views. Right valve encrusted by three mytilids and also with two mytilid fixation marks; left valve with one mytilid fixation mark. G, CPBA 20300: right view. An internal mould of *Amphidonte* (*Ceratostreon*) sp. can be seen on the antecarinal furrow and the upper flank. 7a, Detail (2×), showing chomata. Size 1:1

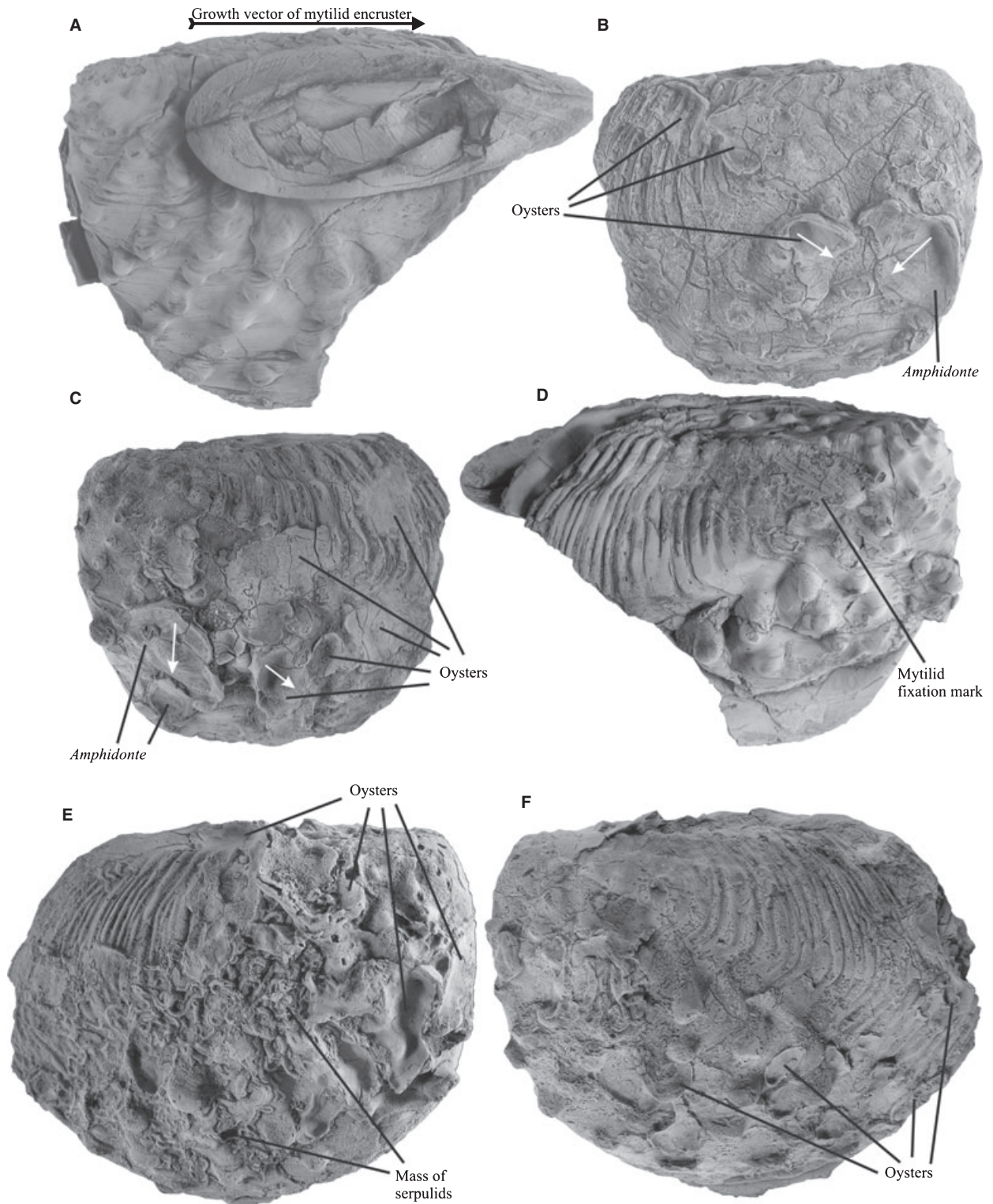


Fig. 4. Encrusted shells of *Steinmanella quintucoensis*. A, D, CPBA 20302: left and right views. Left valve with a large mytilid fixed by the dorsal margin, left valve with fixation mark of mytilid. B, C, CPBA 20300: right and left views. Valves encrusted by oysters covering both corselet and flank, from umbos to siphonal margin and dorsal to ventral margins. Oysters are disarticulated, and their orientations vary (white arrows showing growth vectors when possible). E, F, CPBA 20302: right and left views. Right valve with numerous small clustered serpulids (5–10 mm long). Both valves are also encrusted by oysters. Size 1:1

authors (see Seilacher *et al.* 2008) have also reported serpulids ‘piggybacking’ on modern *Nautilus* shells. On the contrary, most semi-infaunal serpulids inhabiting muddy substrate are mud-stickers or recliners that have various strategies to stabilize themselves, including the formation of colonial reeflets and glomerules. In general, the growth programmes of these forms are more organized, with helicoidal coiling patterns that act as anchors or ballast (see Seilacher *et al.* 2008).

Mytilids. – The mytilids observed are mytiloid in shape, with thin growth lines (Figs 3B, D, F; 4A, D). Umbos are anteriorly situated, terminal and rounded. The shell is triangular in transversal view, with the maximum width over the ventral margin; the dorsal margin is convex. All specimens are oriented with their anteroposterior axis parallel or slightly oblique to the dorsal margin of the trigonioids, and all have similar size (4–5 cm). When clustered together, mytilids are longitudinally aligned, their beaks pointing in the same direction. Respiratory margins are in most cases oriented towards and perpendicular to the siphonal margin of the host. Villamil *et al.* (1998, Fig. 4) have described one specimen of *S. quintucoensis* found in the Valanginian of the Neuquén Basin, with mytilids attached to both valves. They assigned them to the genus *Lycettia* Cox without further explanations. Although they closely resemble the ones studied in this work, and may belong to the same group, preservation does not allow a more precise identification as taxonomy is strongly based on the hinge morphology (see Freneix 1980).

Some mytilids are articulated, almost intact, whereas others are crushed and fractured, although still attached to the shell by a layer of sediment adhered to the valve of the host. Other mytilids were detached from their hosts, and only a mark of their shell remained, printed on the sediment trapped between both bivalves, host and encruster. These marks preserve an impression of the growth lines of mytilids, and their general outline. Some mytilids are filled with silt, both the filling and the shell being partially dissolved, and some of them are empty.

The studied mytilids are byssate epifaunal (epibyssate) bivalves that are frequently attached to hard substrates; the triangular transverse outline, with the maximum width on the ventral margin, provides a larger surface for attachment (see Stanley 1970). The attachment must have occurred while the shells of *S. quintucoensis* were exposed over the sea floor after their death, or on the parts of the shell exposed above the water–sediment interface, during the life of the trigonioids.

Results – encruster preferences

A total of 175 specimens of *S. quintucoensis* were examined: 96 of them were encrusted (54.9%). Considering that some of the bivalves were preserved with both valves articulated, and others were disarticulated valves, a total of 338 valves were counted, of which 186 were encrusted (94 left valves, 92 right valves; see Table 1). Of the 338 valves collected, a total of 57 valves proceed from the black shales, 22 of which were encrusted (35.6%, 109 encrusters; see Table 2). A total of 159 valves were collected from the packstones, 55 of which were encrusted (34.6%, 140 encrusters). The remaining 122 valves were not collected *in situ*.

The chi-square tests resulted as follows (critical value is 3.841 for all cases). No differences were found between encrustation on left vs. right valves ($\chi^2 = 0.02$, $P = 0.05$). Both right and left valves showed a greater frequency of encrustation for the (corselet + escutcheon) than for the flank ($\chi^2 = 28.94$, $P = 0.05$ for left valves, and $\chi^2 = 15.66$, $P = 0.05$ for right valves). Specimens collected from the packstones were found to have a greater encrustation frequency for the corselet and escutcheon of both left and right valves ($\chi^2 = 8.29$ and $\chi^2 = 6.45$ respectively; $P = 0.05$ for each). On the contrary, the samples from the black shales had a greater encrustation frequency for the corselet and escutcheon than for the flank only in the left valve ($\chi^2 = 4.45$, $P = 0.05$ for left valves, $\chi^2 = 0.29$, $P = 0.05$ for right valves). The comparison between samples from each lithofacies resulted in a greater number of mean encrusters per valve for the black shales (4.95 encrusters per valve) than for the packstones (2.55 encrusters per valve; $t = 2.91$, $P = 0.0047$).

Table 1. Number of encrusted right and left valves of *Steinmanella quintucoensis*

Encrustation status	Right valves	Left valves	Total
Encrusted valves	92	94	186
Not encrusted valves	75	77	152

Table 2. Number of encrusted valves and total number of encrusters per facies

Facies	Encrusted valves	Percentage	Total valves	Number of encrusters
Black shales	22	35,6	57	109
Tabular packstones	55	34,6	159	140

Discussion

Distribution patterns of encrusters

No differences were found between encrustation of left and right valves, indicating that both were equally appealing for the encrusters to attach. This is in agreement with the equivalve condition of *S. quintucoensis*, and probably with its life habit as well; both result in equal advantages and disadvantages for encrusters attached at equivalent places of either valve. Strong differences in encrustation patterns between valves usually appear in bivalves that are strongly inequivalve, as is the case with oysters (Parras & Casadío 2006), or with scallops (Lescinsky 1993), in which position of the valves, ornamentation and shape vary between left and right valves.

Despite the fact that it occupies a smaller portion of the valve surface, the corselet and escutcheon were more frequently encrusted than the flank. Several reasons may explain the preference of encrusters for this site; a strong one is given by the smoother ornamentation displayed by the corselet, with thin, continuous ribs, which are a flatter surface than the flank. Encrusters would be able to attach, and particularly to grow, more easily on this kind of surface rather than on the strongly tuberculated flank. It has been reported that ornamentation can favour the fixation of epibionts as it increases the area available for fixation (Rodland *et al.* 2004); but in this case, the tubercles of the flank are too prominent, and too rounded, to be overgrown by epibionts cemented among them.

Another issue to be considered when explaining the preference for the corselet is the proximity to the respiratory openings. The encrusting fauna of *S. quintucoensis* is entirely composed of suspension feeding organisms, which could have taken advantage, during their host's life, of the inhalant and exhalant currents of the trigonoid. The samples collected often have encrusters located near the respiratory margin, but this is not always the case. Particularly in the oysters, it is also difficult to establish if their respiratory margin pointed towards that of their hosts; they are often fragmented and disarticulated and the umbo cannot be identified.

Furthermore, the preference for the corselet could be related to the position of the shell during the lifetime of the trigonoid; epibionts would only be able to attach in the parts of the shell that emerged from the substrate, while the host was alive; this would have been the case of the corselet, as has been proposed by several authors (Stanley 1977; Tashiro & Matsuda 1988; see below), whereas the flank remained buried and unavailable for attachment of

larvae unless the shell was removed from its original position. For this matter, it is essential to differentiate between encrusters attached during life, and those attached post-mortem. The difference is often subtle and hard to establish. Some useful criteria are the presence of encrusters on the inner side of the valves (Rodland *et al.* 2004), or attachment of encrusters in places where the host could not have survived, such as the commissure or the ligament. The specimens studied here were in most cases reworked (i.e. not in life position), further obscuring the original encrustation pattern.

The lack of overgrowth between encrusters indicates that the available space for fixation of larvae was not a limiting factor. Competition for space can force epibionts that attach late to take forced or uncomfortable positions on the host's surface, or else to attach to another encruster, thus establishing several generations of encrusters. This can reveal a certain time-averaging of the shells, as superposition of encrusters can respond either to an increment in competition for space, or to a prolonged time of exposition of the shell on the sea bottom (Lescinsky 1993). Space is a limiting factor for a community of encrusters only if the available surface is exposed for long enough to cause competition (Jackson 1977). In an oxygen-deprived environment, as is the case studied here, the lack of overgrowth is not necessarily signalling the absence of time-averaging, for the shells could lay exposed on the substrate for a while, and be encrusted on several occasions, without the abundance of larvae reaching a point when overgrowths were inevitable.

Comparison between encrustation patterns in black shales vs. packstones

Sample size of shells collected from packstones doubles that of shells from the shales; however, encrusters were more abundant in the latter. Taphonomy of trigonoid shells can provide evidence of the main processes affecting each facies, and explain the higher abundance of encrusters in the shales.

The shells of *S. quintucoensis* collected from the packstones were remobilized and redeposited, and were usually found oriented parallel to bedding. Analysis showed that they were more encrusted on the corselet and escutcheon than on the flank. Encrustation is frequent, but not extensive; there are no shells heavily covered by encrusters. Shells were probably remobilized shortly after death, or maybe even during life. A part of these shells have been highly reworked as some shell fragments have been encrusted on the inner side.

Shells from the black shales showed a greater encrustation on the corselet and escutcheon of the left

valve only; the right one showed no difference between both parts of the valve. It must be considered that the number of encrusted valves was 15 left and 15 right, which is a rather small number for statistical analysis, and therefore results can be somewhat unreliable. However, the pattern of encrustation differs from what was observed in the shells collected from the packstones. Among the specimens collected from the shales, some are barely encrusted, whereas others have only one valve almost completely covered by encrusters. In this case, the encrusters can be revealing on which valve the trigonoid lied in the sea bottom; as only one of the shells has been encrusted, and both shells would be equally exposed while the bivalve was alive (all proposed life habits result in identical situation of valves with respect to the sediment; see below), the other would have been unavailable for encrustation. Most of the shells of this lithofacies completely lacked encrusters, and some of these are almost pristine, meaning that they could have remained buried after death. Other shells are strongly altered, with high corrosion, and yet they show no sign of encrusters; these could have lied exposed on the sediment for a considerable time, yet they were not colonized by encrusters. The greater mean of encrusters per valve found in the shales can be explained by the greater calm and stability of the environment, and possibly due to a more prolonged exposure of some shells over the sea bottom. Taphonomic modification could also alter encrusting patterns by removal of the most weakly attached encrusters in the case of trigonoid shells retrieved from the packstones, or by erasing other marks left by epibionts on the shell.

Oysters and serpulids have been found encrusting shells of *S. quintucoensis* collected from both shales and packstones, but mytilids have been found only in the shales. This could be due to a habitat preference, or to their detachment during remobilization of the *S. quintucoensis* shells deposited in the packstones. Storm processes could have had a greater impact on mytilids, which are thin-shelled and attached by a byssus, than on oysters and serpulids, which are cemented to the host by a large proportion of their shells and tubes respectively.

Analysis of orientation of encrusters with respect to orientation of the host

Some of the samples examined provide interesting examples of how the position of the encrusters on the host's shell can yield contrasting life habits for the trigonoids. One sample (CPBA 20300; Figs 3B, D, F, 5A) has the right corselet covered by at least three mytilids attached behind the umbo near the middle part of the corselet. A fourth mytilid that was not preserved, but

whose mark remains, was attached over the right marginal carina. The left valve has only one encruster, another mytilid attached behind the umbo, over the escutcheon, which is not preserved but has left a mark. All mytilids are close together, and they occupy only the right corselet and the left escutcheon; the left corselet and both flanks are free of encrusters. If these encrusters had attached in the exposed parts of the shell during life of the trigonoid, there are three possible life positions: one that exposes only the escutcheon and the right corselet; one that exposes both corselets; and one that exposes both corselets and part of the flanks, with the anterior margin of the shell buried up to behind the umbos. The first one is disregarded because it is highly inoperative: the trigonoid could hardly bury in such position, although it does expose exactly those areas of the shell that were colonized by encrusters. It is possible that the trigonoid attained such position after some perturbation, but it would probably accommodate its position soon; given the size of the epibiont bivalves, it is unlikely that their complete growth and development took place along the time spent by the host lying askew in the sediment.

The other two possible positions, although they are more compatible with burrowing mechanics and survival, raise the question as to why were not the left corselet in one case, and the left corselet and both flanks in the other (being byssate, mytilids could have attached to the flank; only one has been observed attached to such surface among the samples collected) occupied by other encrusters? It seems more likely that encrusters settled on the host's shell and grew after its death, when it was partially buried in the sea bottom. The size of the encrusters is considerable when compared with the size of the host, and some are attached over the dorsal margin; survival of the host was surely compromised with the aperture of the valves obstructed in such a way (some mytilids cross the dorsal commissure) as not to mention the unbalance issues caused by the mytilids, the extra weight, etc.

One small shell of *S. quintucoensis* (CPBA 20300) has the right posterior third of the shell covered by two large oysters, cemented next to one another, which completely cover the corselet and two ribs of the flank (Figs 3A, C, E, 5C). It is unlikely that the trigonoid could have survived with encrusters of such size that the host's shell would be easily taken out of balance. Furthermore, the margins of the oysters partially cover the trigonoid's respiratory margin. The left corselet is encrusted by three small (5–10 mm long) oysters, attached nearby the siphonal margin. The limited development of these encrusters is contrasting to that of the ones attached to

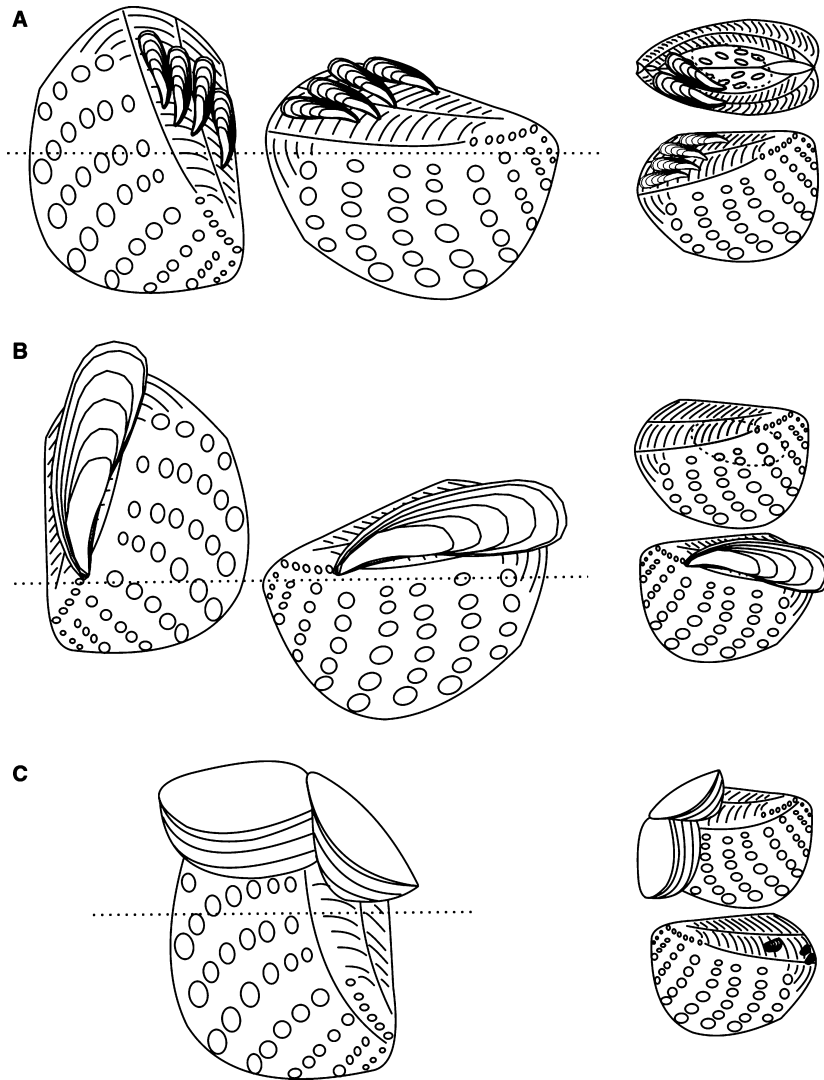


Fig. 5. *Steinmanella quintucoensis* shells encrusted by mytilids and oysters that reached exceptional size. Small diagrams at the right show general encrustation patterns of the shell, as can be seen in the pictures of Figs 4, 5. Shaded grey areas signal location of mytilid's fixation marks. All examples are made under the supposition that encrusting happened during life of the host. A, CPBA 20303, encrusted by mytilids. The diagram shows the two functionally plausible orientations permitted by the encrustation pattern. In this case, palaeoecology of the encruster can determine which orientation is correct: the first preferential attachment illustrated is for mytilids with a preference for horizontal attachment, whereas the second would be the case when mytilids preferentially attached in a vertical orientation. The same is true for B, CPBA 20302, but in this case the great size of the mytilid results in increased instability; and in addition, the fixation mark on the right valve diminishes the shell's surface that could have been buried in the sediment. C, CPBA 20303, encrusted by two large oysters that occupy a large proportion of the posterior half of the shell, leaving only one possible position, which is highly unstable.

the right valve: if oysters on both sides of the shell attached at the same time, under the same conditions, they all would have greatly developed, as the ones on the right side did. If these oysters attached at different times, the ones on the left had their development interrupted shortly after their settlement, whereas the ones on the right had more time to grow. Even if it is considered that all encrusters attached during life of the host, only one life habit is possible, with the anterior two-thirds of the shell buried and the posterior-most third exposed above the sediment–water interface. However, it is hard to

imagine a shell maintaining such position with the two large oysters attached on the same side, and it does not solve the issue of the remarkable growth differences between oysters on either valve. A similar example is given by the specimen CPBA 20302 from black shales, with the ventral–posterior margin missing, which is encrusted on the left corselet by a very large mytilid that extends along the dorsal margin and surpasses the siphonal margin; there is a second mytilid attached on the right valve below the umbo, oriented obliquely towards the dorsal margin (it is missing; only the mark was preserved; Figs 4A, D,

5B). Both encrusters could have attached at different times, and both would have resulted in an unstable position of the host's shell.

Another interesting example is that of a rather small shell of *S. quintucoensis* (CPBA 20300, 65 mm length), which has both flanks and corselets heavily encrusted by oysters (Fig. 4B, C). This seems to be a case of post-mortem encrustation, as all parts of the shell have been available for colonization. It is possible that the host was encrusted during life, but the post-mortem encrusters obscured the original pattern. The taphonomic features of the encrusting oysters could reveal the sequence of encrustation, as some oysters are more heavily worn than others.

In summary, these examples illustrate that the taphonomy of both shells and encrusters is fundamental to establish whether the shell was in life position or not, or if it is even possible to make such distinction. Epibiont analysis is a useful tool for investigating host's life habits, but it must be regarded carefully, and in consideration with other sources of information, as several possible solutions may arise from the encrustation pattern of one or a few specimens.

Implications for life habits of 'knobbly' trigonioids

Ecology of Neotrigonia Cossman

The morphology and behaviour of the only extant genus of the trigonioids was studied by Tevesz (1975) and Stanley (1977), among others. It has been characterized by both authors as a moderately fast burrower; the latter has stated that *Neotrigonia* is the fastest extant non-siphonate burrower. Tevesz (1975) described the burrowing mechanics of *Neotrigonia margaritacea* (Lamarck) and *Neotrigonia gemma* Iredale. They burrowed by extruding the large, muscular foot, and firmly setting its tip on the sediment. Sharp movements of the foot placed the shell in burrowing position and with oscillatory movements pushed and dragged the shell diagonally into the substrate. The shell attained its final position, retreating the foot and shutting the valves closed, at a depth within the sediment where the respiratory margin was at the sediment-water interface. *Neotrigonia margaritacea* had a similar behaviour, but the existence of encrusters in the posterior third of the shell showed that its final depth within the sea bottom is shallower than that of *N. gemma*. Tevesz (1975) highlighted the swiftness of the burrowing process despite the prominent, radial ornamentation of the valves, and the general outline of the shell, which is rather more robust and less

elongated than other shallow burrowers due to the size and strength of the foot.

The small *Neotrigonia* can be found in tidal channels filled with poorly sorted sand, but it is most common in the continental platform at greater depth (Stanley 1977). The establishment of this genus in tidal channels reveals the success of the burrowing mechanism, as in such an environment the shells are frequently removed from life position, needing to re-burrow quite often. This is in agreement with Mesozoic trigonioids, which have been commonly found in unstable and shifting substrates (Stanley 1977).

Palaeoecological models of Yaadia Crickmay

Yaadia is a Cretaceous genus from the North Pacific, found in inner platform facies, commonly in fine sand with crossed stratification, or finer facies, but it has been found in coarser facies also (Saul 1978). Life habits for this genus have been proposed by Stanley (1977), Saul (1978) and Tashiro & Matsuda (1988). The latter placed the shell by the sediment-water interface, with the corselet exposed and the flanks buried, on the basis of the general outline of the shell, which is triangular to sub-quadrate, with barely ornamented corselets that are frequently encrusted by oysters. They depicted several species of *Yaadia*, with little variation of this general position according to the shape of each form. On a general basis, the more elongated shells would have kept a larger proportion of the corselet below the sediment-water interface, whereas more rounded to triangular shells would expose the entire corselet and the upper part of the umbo.

Saul's (1978) model is very different. She evaluated the musculature of *Yaadia*, and concluded that it was similar to that of *Neotrigonia*, and thus the foot and burrowing capacity were also similar; but *Yaadia*'s blunt anterior margin and strongly tuberculated ribs would have prevented the shell from performing the oscillatory movements that other burrowers make. Therefore, based on the general outline of the shell, Saul (1978) proposed a semi-infaunal habit for *Yaadia*, with the shell perpendicular to the sediment-water interface, buried only up to the umbos, or else a similar habit with the shell buried up to the half of the flank, with the posterior half of the flank, and the corselet, exposed on the sea bottom. If this position was lost due to hydraulic removal, the valves could be kept shut until the foot could be extruded to reposition the shell. The cited author performed experiments in an aquarium where water currents revealed that such position was the most stable one; the ribs on the flank diminished the currents running parallel to

the commissure, whereas the turbulence at the water–sediment interface was diverted; these currents would also help to carry the food towards the siphonal margin, and it would also drive the excretion products away. Saul (1978) proposed that the schizodont hinge evolved parallel to the prominent sculpture of the flank, both features combining to lessen the turbulence around the shell and keep the valves shut in case of loss of life position.

Stanley (1977) proposed a similar model to that of Tashiro & Matsuda (1988). *Yaadia*'s flank sculpture worked as an anchor, which would be particularly effective on fine sediment, and which could facilitate the entrance of the shell into the substrate by tramping sediment between tubercles, which would then function as ribs. Ornamentation would compensate for the lack of a prosogyrous shell, in which the flat anterior margin provides anchoring (Stanley 1977). Many *Steinmanella* species do have a flat anterior margin; the ortogyrous to opistogyrous condition of trigonoids would have originated in the first representatives of the group, and was maintained due to the need of a spacious umbonal cavity, which could contain the robust teeth and the anterior adductor muscle. Several robotic models with and without ornamentation proved that sculpture favours burrowing, as the robot with tubercled flanks buried deeper with the same number of oscillatory movements (Stanley 1977). Trigonoids with pyramidal corselet would then have their flanks buried, their corselet exposed, and the siphonal margin over the water–sediment interface; the larger the corselet, the greater the reduction of turbulence around it (Stanley 1977).

Considering the life habit models proposed for *Yaadia*, which is, of the two genera considered, the most similar to *Steinmanella*, both Stanley (1977) and Tashiro & Matsuda (1988) concluded that the most plausible habit would be that of a shallow infaunal bivalve, with the siphonal margin level to or exposed above the sediment, the exposed proportion of the corselet varying with species. On the contrary, Saul (1978) proposed a semi-infaunal life habit, in which the large, muscular foot would provide the ability to quickly reburrow when life position is lost. The proposed orientation has several problems. One of them is the size and robustness of the shell; a vertical position would result in high instability, in particular with currents perpendicular to the saggital plane of the shell. Epifaunal thick-shelled bivalves are in general recliners or cementant, and inhabit high-energy environments (Stanley 1970). The thickness of *Yaadia*'s valves, the size of the shell and the prominent ornamentation seem unapt for a nearly epifaunal life habit. A vertical position of such shells would

result in a recurrent loss of life position, and the shell would be constantly dragged by currents, or even removed by the activities of other benthic organisms. In quieter environments, as the black shales of this study, such a position seems more plausible, yet in such context the deflection of vortices and currents loses strength given the greater stability of the environment. Furthermore, such life habit would result in even encrustation of both shells, for both flanks and corselets, as since the encrusters attached to the corselet are larger, the flank is often encrusted by smaller organisms when available. Another inconvenience of this position is a higher exposition to predation, for though the valves are thick, around the margins they are thin enough to be punctured by carnivore snails or attacked by other predators.

Palaeoecological models of Steinmanella

Villamil *et al.* (1998) analysed the encrusters of one specimen of *S. quintucoensis* that had 80% of the shell's length covered by several mytilids. They interpreted that the epibionts had attached during the life of the trigonoid shell, and thus proposed a life habit in which *S. quintucoensis* had the anterior half buried in the sediment, with the anteroposterior axis perpendicular to the sea bottom. Juveniles would have had a minor proportion of the shell buried into the substrate. Their analysis of the encrusters of one specimen of *S. steinmanni* (Phillipi) resulted in a similar life habit, with the anterior third of the shell buried in the sediment, and the rest of the shell projected to the water column.

The life habit interpretation by Villamil *et al.* (1998) is based solely in the area covered by encrusters in one specimen only, and does not consider important aspects of functionality and hydrodynamics of the host, not to mention bibliographic references supporting the geotropic or phototropic orientation displayed by the encrusters. Moreover, in the samples examined for this study, serpulids are often controlled by ornamentation and their orientation varies greatly between samples; a similar situation is that of oysters. Mytilids are often oriented with the respiratory margin pointing in the same direction, but few epibyssate families prefer to adopt a vertical position (Stanley 1970). Villamil *et al.* (1998) suggested that the mytilids attached earlier would be partially covered by sediment as the trigonoid grew, yet without reaching a complete coverage as the clogging of the respiratory openings would result in the death of the encruster. However, the morphology of the epibiont mytilids signals them as epibyssate, which attach to a clean substrate, in contrast to endobyssate, which partially

burrow (Stanley 1972). Furthermore, the specimen of *S. quintuocoensis* examined by the cited authors was heavily encrusted only on the right valve, the left one being almost completely vacant. If competition for space had taken place, as was suggested by the authors, both valves would have been heavily colonized.

In addition, a vertical position with nearly 80% of the shell above the sea bottom would result in no shells with the nearly pristine preservation found in the shales, as after the death of the bivalve the shells would lie exposed without intervention of processes that unburied and exposed the shells. The existence of pristine shells in a low sedimentation rate environment suggests that these organisms were already buried at the time of their death.

Lazo (2003) analysed the palaeoecology of *Steinmanella pehuenuensis* (Leanza) and *Steinmanella transitoria* (Steinmann) from the Late Valanginian–Early Hauterivian. He signalled that the life position proposed by Villamil *et al.* (1998) is impossible to attain considering the angle of extrusion of the foot. He also pointed that the species of the genus *Steinmanella* are frequently large-sized, and a vertical position of the shell would result in great instability, the organism being subjected to recurrent reworking by currents. As a result, he proposed a shallow infaunal habit, with the siphonal margin at or slightly above the water–sediment interface. The specimens described by Lazo (2003, 2004) were collected from facies similar to the ones studied in this contribution; muddy and low-energy sea bottoms, and also storm deposits with abundant shell debris, originated in a higher-energy environment; these organisms seem to have preferred fine sediment, though not one conforming a soupy bottom, and they could tolerate different degrees of water energy and oxygenation.

Life habit proposed for Steinmanella in this study

The models proposed by Saul (1978) and Villamil *et al.* (1998) are at odds with burrowing mechanics, for the final position is incongruent with the angle of extrusion of the foot. In *Neotrigonia*, the foot is extruded through the anteroventral margin, opposite to the hinge; in more elongated genera as *Yaadia* and *Steinmanella*, it would be extruded by the ventral margin, the long anterior teeth (which can extend to the whole upper third of the anterior margin) preventing its extrusion through the anterior margin, where it should be extruded to burrow if the shell were to adopt a vertical position. Lazo (2003) referred to this difficulty, pointing that a vertical orientation would be impossible to attain given that the foot would be

extruded at the intersection of the anterior and ventral margins, or at the latter.

In addition, considering the location of the adductors, being the anterior one below the umbos, and the posterior one beneath the posterior third of the escutcheon, the pull resulting from the alternate contraction of these muscles would cause the shell to oscillate in an anteroposterior direction, dragging the shell downwards and forward by the ventral or anterior–ventral margin.

Considering all these inconveniences, the models presented by Stanley (1977) and Tashiro & Matsuda (1988) seem better adjusted to burrowing mechanics and the general features of knobby trigonioids. It is therefore proposed in this study that the genus *Steinmanella* adopted a position within the sediment similar to those envisioned by the authors cited above; the representatives of the genus *Steinmanella* would have burrowed up to the marginal carina, with the siphonal margin and the corselet above the water–sediment interface (Fig. 6). Along with Stanley (1977), ornamentation is considered here to have an anchoring role, which besides acting as a sediment trap would give the trigonioid greater stability once the final position within the sediment was obtained; the powerful muscular foot dragged the shell diagonally in a ventral–anterior direction, until reaching the required depth. The change of ornamentation that takes place in the corselet would serve hydrodynamic purposes, minimizing and deflecting small and moderate currents. Species of strongly ribbed trigonioids could have sustained their position within the sediment for considerable time, being removed only by waves or currents of considerable strength (Kelly 1995). Stanley

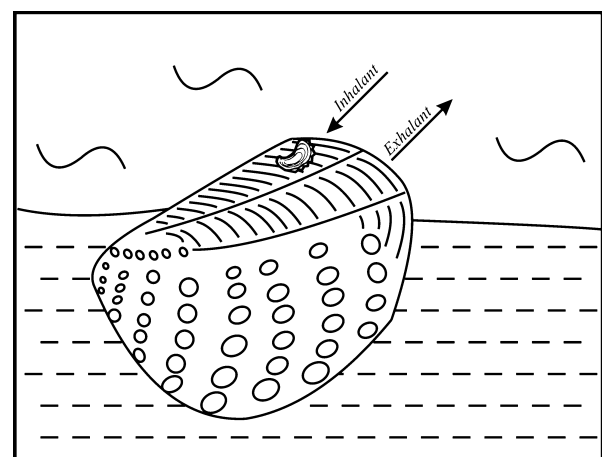


Fig. 6. Proposed life habit for *Steinmanella*, showing the angle of foot extrusion, and the corselet exposed above the water–sediment interface with an encrusting *Amphidonte* (*Ceratostreon*) in its posterior part, cemented near the trigonioid's respiratory currents. This is the most stable position and provides an available surface for colonization.

(1977) suggested that those species that display small tubercles in the corselet would be able to capture sediment particles with which they could camouflage; yet the studied *Steinmanella* species have ribbed corselets that must have remained clean, as encrusters are common, and at least in the case of oysters, larvae require a surface free of sediment or viscosity to attach (Stenzel 1971).

Conclusions

1. Encrustation is a valid and valuable tool to make inferences on life habit, but for them to be accurate, preservational history, palaeoecological requirements and functional morphology of both encrusters and hosts must be taken into consideration.
2. The encrusting fauna of *S. quintucoensis* is composed of oysters, mytilids and sepulids, with a strong dominance of the oysters, followed by sepulids and finally by mytilids.
3. Distribution of encrusters is biased towards the corselet and escutcheon, which could reflect a preference of the encrusters, or be related to the exposition of such surface during the life of the trigonoid. It is likely that both factors combined, the exposition of the corselet and escutcheon during life of the trigonoids, resulted in a longer time of exposition, and more frequent encrustation, while the flanks could only be encrusted if the shell was removed from its original position.
4. Specimens from the black shales have a greater number of encrusters per valve than specimens from the packstones, which could be due to a longer time of exposition.
5. The main features of the extant representatives of the Order Trigonioidea (genus *Neotrigonia*) are atypical when compared with other shallow burrowers; however, they are swift burrowers with the capacity to inhabit unstable substrates and quickly reburrow. The similarity of internal features of *Neotrigonia* and the Mesozoic representatives of the Order Trigonioidea, as well as the genus analysed in this study, would have resulted in the latter having a similar burrowing capacity, which allowed them to colonize a great variety of environments.
6. Proposals of vertical to sub-vertical orientation of *Steinmanella* and related taxa would result in great instability of the shell, and seem difficult to obtain considering the burrowing mechanics of the genus.
7. Considering the external features of *Steinmanella* shells, the powerful foot of extant *Neotrigonia*, and

burrowing mechanics, a semi-infaunal habit is proposed for *Steinmanella*, with valves buried up to the marginal carina and the corselets exposed above the substrate.

Acknowledgements. – I thank all who have contributed to this contribution. Darío G. Lazo (University of Buenos Aires) is thanked for his support and guidance during the development of this investigation. M. Beatriz Aguirre-Urreta (University of Buenos Aires) provided both a work place and helpful advice. Dr Marcela Cichowolski (University of Buenos Aires) and Dr Ana Parras (University of La Pampa) have read and commented on the manuscript, making helpful remarks. The author wishes to thank Lic. Diana E. Fernandez (University of Buenos Aires) for her help during fieldwork. I would also like to thank both anonymous reviewers for taking time to read and comment the manuscript, and I believe their comments and contributions have improved it; I would also like to thank Prof. Doyle's assistance in answering doubts and questions. This work was supported by ANPCyT – PICT 189 and UBACyT – X001Grants to M. Beatriz Aguirre-Urreta.

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