Infaunal molting in Trilobita and escalatory responses against predation

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ABSTRACT

The outstanding fossil record of trilobites contrasts with our limited knowledge of their life-styles and strategies. Aspects such as infaunalism and behavioral defensive skills in this group have yet to be demonstrated conclusively. We report new insights based on a striking scler-ite configuration exhibited by three phacopid trilobite species, part of a late Silurian–Early Devonian *Paciphacops* (*Paciphacops*) Maksimova, 1972, lineage. An unusual molt pattern pro-vides compelling evidence of infaunal behavior, which accounts for a hiding, antipredatory adaptation. In addition, strengthening of the exoskeleton and acquisition of spines indicate an evolutionary trend toward morphological defensive strategies. Both trends in active and passive traits are considered escalatory in nature, thus providing unequivocal support for understanding the ecological role of trilobites as a main prey group in the context of the global diversification of predators recorded during middle Paleozoic time.

INTRODUCTION

Some intervals of geologic time were characterized by the intensification of escalated adaptive trends among marine prey groups, thought to be driven by the macroevolutionary impact of increasing predation pressure. In such scenarios, interpreted to represent paleoecological revolutions (Signor and Brett, 1984; Vermeij, 1977), the escalation hypothesis (Vermeij, 1987) strongly predicts, among other traits (Brett, 2003; Harper, 2003; Leighton, 2001; Vermeij, 1987, 2008), the evolution of active escape behavioral strategies in prey (Vermeij, 2008). Unraveling these evolutionary trends is a major challenge, since preserved attitudes are extremely rare in the fossil record (Benton, 2010). Trilobites are the main vagrant Paleozoic invertebrates, and therefore the ideal case to test these defensive skills. However, their role as participants in Paleozoic ecosystems through direct biotic interactions is still an unresolved paleobiological concern, due to the poorly known ethologic information in contrast with the wide array of morphological designs attained by the group (Fortey and Owens, 1997; Fortey and Owens, 1999). In particular, the apparent neutrality of this iconic Paleozoic fossil group is striking in the macroevolutionary context of the middle Paleozoic, interpreted to be a time of revolutionary intensification of predator-prey interactions (Baumiller and Gahn, 2004; Kowalewski et al., 2005; Nagel-Myers et al., 2009).

In this contribution we analyze a new trilobite molt pattern that provides compelling evidence of infaunal behavior based directly on body fossils. The new morphological and ethological evidence provided here confirms the evolutionary predictions of the escalation hypothesis in a late Silurian–Early Devonian phacopid lineage. The recognition of the middle Paleozoic marine revolution as a major bioevent, as independently suggested by concurrent data from other coeval fossil groups (Baumiller and Gahn, 2004; Nagel-Myers et al., 2009; Signor and Brett, 1984), is thus supported by trilobite evidence.

GEOLOGICAL SETTING AND OCCURRENCE OF FOSSILS

The fossils we studied are from Silurian–Devonian siliciclastic shelf successions of the Precordillera basin, western Argentina (Fig. 1; Figs. DR1 and DR2 in the GSA Data Repository[1]). The Los Espejos Formation (middle to late Silurian) is composed of a shaly succession at the base, with progressively more interbedded sandstones and tempestite beds toward the top. Trilobite fossils come from the upper part of the unit at the Loma de los Piojos section (7 km southwest of Jáchal), Cerro del Fuerte section (10 km southeast of Jáchal), and the La Chilca
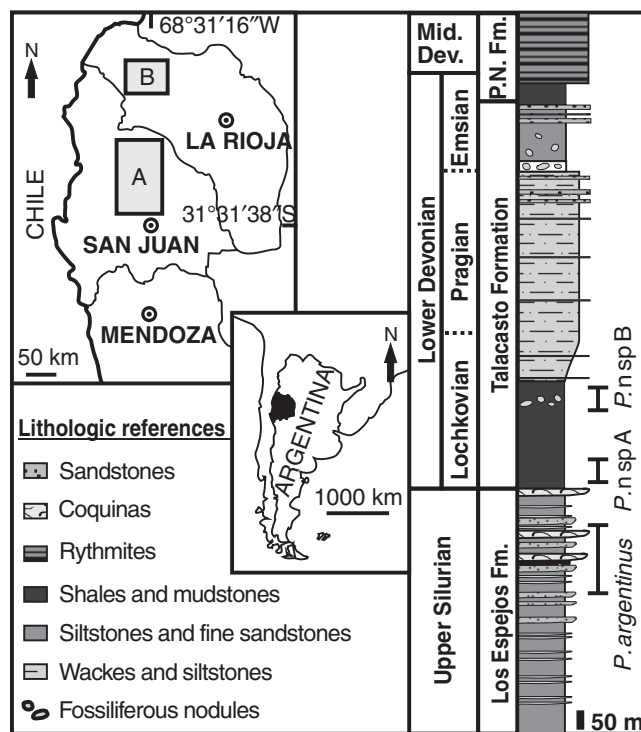

Figure 1. Location map of studied areas in Precordillera basin, western Argentina. A: San Juan Province. B: La Rioja Province. Simplified column shows stratigraphic position of studied *Paciphacops* (*P.*) species in Silurian–Devonian sedimentary succession. See Figures DR1 and DR2 (see footnote 1) for more detailed maps of fossiliferous localities. Fm.—Formation, P.N.—Punta Negra, Mid. Dev.—Middle Devonian.

section (16 km west of Tucunuco), all from San Juan Province. The Los Espejos Formation yields *Paciphacops* (*Paciphacops*) *argentinus* (Thomas, 1906), mainly preserved in mudstones of the upper part.

The Talacasto Formation (Lower Devonian) overlies the los Espejos Formation. It is composed of shales and intensely bioturbated mudstones at the lower part, with more frequent sandy beds toward the top. The unit is interpreted to represent muddy shelf settings. Two new species of *Paciphacops* are recognized in the Talacasto Formation. The earliest, *Paciphacops* n. sp. A, occurs in the mudstones of the lowermost part of the unit (lower Lochkovian), at the Poblete Sur Creek (near Talacasto Creek, 70 km northwest of San Juan city), in San Juan Province. *Paciphacops* n. sp. B (late Lochkovian) includes most of the studied specimens and comes from two localities: the Las Aguaditas section, 10 km to the southwest of Jáchal, San Juan Province, and the Sierra de las Minitas section (Fig. DR2), 200 km to the north of Jáchal, in La Rioja Province. In both cases, *Paciphacops* n. sp. B derives from dark gray to black carbonate-rich nodules, included in an identical bioturbated shale-rich succession.

EVIDENCE OF INFAUNAL MOLTING IN TRILOBITES

More than 20 specimens have been found that show a recurrent distinctive arrangement of associated exoskeletal units, and are therefore interpreted to represent molt ensembles (Brandt, 1993; Henningsmoen, 1975; McNamara and Rudkin, 1984; Speyer, 1985).

The molt pattern of *Paciphacops* (Fig. 2; Figs. DR3 and DR4) departs from traditional arrangements so far known for Phacopida (Speyer, 1985, 1987) and for Trilobita as a whole. The thoracopygidium is preserved still perfectly articulated and outstretched, frequently with a gentle dorsal bending. The cephalon is in front of, but separated by sediment from, the first thoracic segment, and is perpendicularly oriented or gently rotated backward over the thorax. The hypostome, when preserved, is in its original life posture (without inversion or rotation), yet slightly displaced backward and located adjacent to and below the posterior part of cephalon and anterior thoracic segment (Fig. 2A; Figs. DR4A and DR4B). The position of the hypostome in the context of the molt ensemble defines a distinct three-dimensional molt arrangement, which accounts for a dorsal-up orientation. Thus, it differs from the Salterian pattern, which typically is in one plane, and from those described by Speyer (1985) that involve either bidimensional arrangements or dorsal-down orientations.

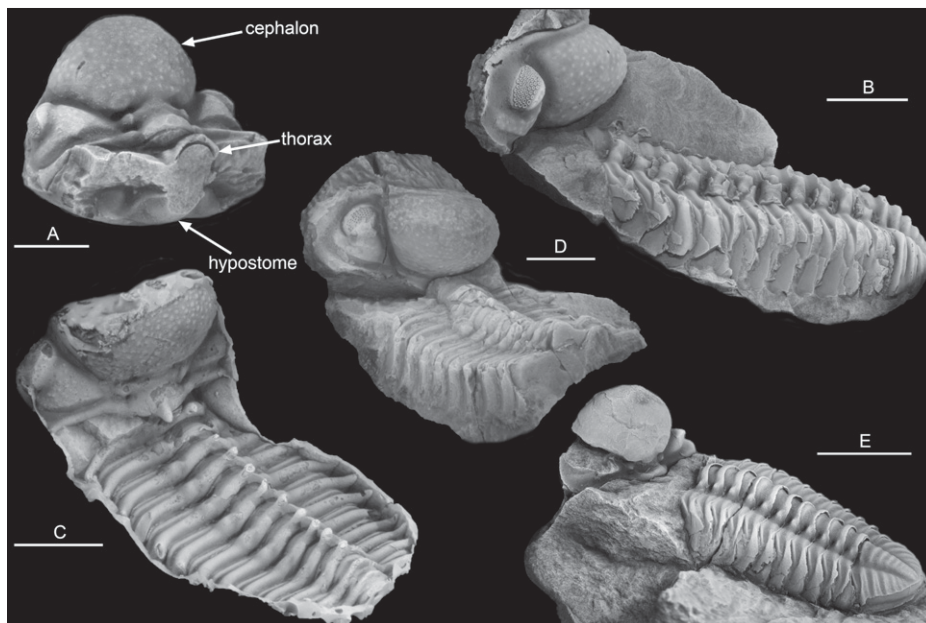Even under very low energy conditions, no physical processes or taphonomic agents could

Figure 2. *Paciphacops* (*Paciphacops*) Maksimova, 1972, infaunal *molt* ensembles. Pattern is characterized by upright directed cephalon, articulated thoracopigydium, and hypostome beneath. Scale bars in A–E = 5 mm. A: *Paciphacops* (*Paciphacops*) new species B, CEGH-UNC f12.744 (Cátedra de Estratigrafía y Geología Histórica, Universidad Nacional de Córdoba), cephalon with associated first thoracic segment and hypostome in three-dimensional arrangement, posterolateral view. B: *Paciphacops* (*Paciphacops*) new species B, CEGH-UNC 24.088, lateral view; note cephalon almost inverted over thorax. C: *Paciphacops* (*Paciphacops*) new species B, CEGH-UNC 24.081, posterolateral view; note almost vertically oriented cephalon in unstable position over first thoracic segment, strong thickening of carapace, and big spines on cephalon and thorax. A–C are from late Lochkovian, Las Aguaditas Creek, Talacasto Formation, San Juan Province, Argentina. D: *Paciphacops* (*Paciphacops*) new species B, PULR 118 (Paleontología, Universidad de La Rioja), posterolateral dorsal view; note dorsal bending; late Lochkovian, Sierra de las Minitas, Talacasto Formation, La Rioja Province, Argentina. E: *Paciphacops* (*Paciphacops*) *argentinus*, CEGH-UNC 24.078, posterolateral dorsal view; note lack of spines, and small size; late Silurian, Loma de los Piojos section, Los Espejos Formation, San Juan Province, Argentina.

be invoked to preserve the described molt pattern above the seafloor (Speyer, 1987). The preservation of the intact three-dimensional arrangement, with the cephalon in such unstable vertical position, can only be envisaged as the result of a biologically driven mechanism, the trilobite being entirely buried and enclosed by soft sediment.

As illustrated in detail in Figure 3 and in Movie DR1 (in the Data Repository), an underground molting sequence of a phacopid trilobite, which has no functional facial sutures, satisfactorily explains the arrangement of the molt elements. At the end of the ecdysis process, the buried trilobite dragged and rotated the entire cephalon backward over the intact thoracopygidium, leaving the described molt signature. We envisaged that the trilobite remained buried until enough mineralization was accomplished in the new carapace so that the animal was ready to return to the seafloor to continue its habitual lifestyle (Fig. 4; Movie DR1). The sedimentary context and contrasting taphonomic signatures of *Paciphacops* exuviae and accompanying shelly remains are consis-

tent with these interpretations. *Paciphacops* is either the only or the most abundant articulated trilobite preserved; *Paciphacops*-bearing beds are bioturbated, and other trilobite species and co-occurring bivalved groups (e.g., brachiopods and bivalves) display a high degree of disarticulation. In addition, fragmentation and orientation to stable postures of hard parts are pervasive. Hence, the taphonomic signature of shelly remains associated with *Paciphacops* is indicative of background disturbance on the surface of the substrate, and consequently argues against sudden burial, an otherwise parsimonious explanation for frequent articulated occurrences of multielement organisms and/or hydrodynamically unstable attitudes.

ANTIPREDATORY STRATEGIES IN THE MIDDLE PALEOZOIC MACROEVOLUTIONARY CONTEXT

Although based on indirect sources, previous information suggesting infaunalism among trilobites is provided by a great body of evidence, such as assumptions based on trace fossil production (Osgood, 1970; Seilacher,
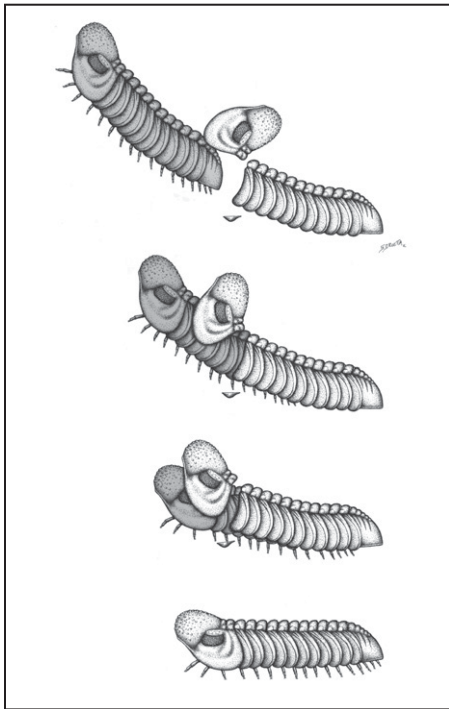
Figure 3. Infaunal molting process (exuviation) in *Paciphacops* (*Paciphacops*). Temporal sequence is from bottom to top. Trilobite, once entirely buried in soft sediment, shed old carapace moving forward and upward, slightly curving body upward, releasing hypostome, and simultaneously breaking cephalo-thoracic joint. It then discarded old cephalon (facial sutures were not functional in adult phacopids), dragging and rotating it while new body (dark gray) continued emerging from old carapace (light gray). As a result of this process, old cephalon, hypostome, and thoracopygidium rested in described configuration pattern (see text and Movie DR1; see footnote 1).
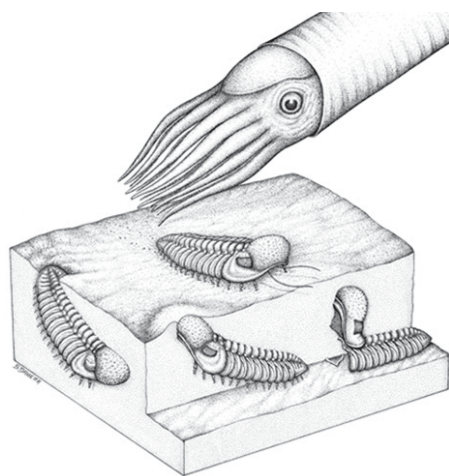

Figure 4. Hypothetical reconstruction of seafloor during middle Paleozoic time. Increasing predation pressure is represented by orthoconic nautiloid. *Paciphacops* (*Paciphacops*) *argentinus*, habitually vagile member of epibenthic fauna, is molting infaunally as antipredatory cryptic strategy.

2007), alleged function of morphological structures (Eldredge, 1970; Hammann, 1985; Thomas and Lane, 1984), or the record of trilobites inside burrows of uncertain authorship and/or origin (Cherns et al., 2006). A different body of evidence accounts for cryptic strategies during ecdysis. Trilobites hidden inside brachiopods (Brett, 1977), burrows (Chatterton et al., 2003; Chatterton and Fortey, 2008; Cherns et al., 2006), nautiloids (Davis et al., 2001), gastropods (Brandt, 1993), or reef cavities (Chatterton et al., 2003) have been extensively reported for different trilobite groups and geological periods. Most of these examples largely represent opportunistic skills for protection during molting, as a result of taking advantage of occasional shelter or refugia. In contrast to these examples, *Paciphacops* did not utilize random shelters. Burrowing in soft sediments for infaunal molting is understood as an evolutionary driven ethological acquisition, which can be conceived as an extreme case of cryptic behavior (Fig. 4). It is interpreted as a specific predator-deterrent behavior, because it is exclusively related to the most vulnerable period (exuviation) of the trilobite adult life. A modern analogue regarding such an infaunal antipredatory behavior might be represented by the snow crab *Chionoecetes opilio* (Fabricius, 1788), reported by Watson (1971).

Predation, as typical enemy-related biological interaction, has profound effects in the evolution of prey groups, which develop a wide array of adaptive responses, starting an arms race in the way predicted by the "escalation" hypothesis (Vermeij, 1987). Trends documented within phylogenetically independent clades in different ages, such as strengthening and thickening of skeletons, production of defensive spines, cryptic behaviors, and changes to more energy-demanding life habits and physiology, are interpreted as defensive strategies against predators and are overall viewed as typical escalatory responses (Brett, 2003; Vermeij, 2008).

This hypothesis can be tested in the three Argentinian phacopid species, all of which exhibit the molt pattern described herein. These species comprise a *Paciphacops* (*Paciphacops*) Maksimova, 1972 lineage, spanning ~10 m.y., from the late Silurian (Ludlow) to the Early Devonian (late Lochkovian). The earliest, *Paciphacops argentinus*, displays small size and a thin exoskeleton without spines (Fig. 2E; Figs. DR3A–DR3F). The earliest Devonian *Paciphacops* n. sp. A (Figs. DR3G–DR3J) is larger, the exoskeleton is thicker, and it has a spiny tubercle on the occipital ring (see Figs. DR3H and DR3I). The youngest (late Lochkovian) *Paciphacops* n. sp. B (Figs. 2A–2D; Fig. DR4) is the largest, with a much thicker exoskeleton, and prominent axial and abaxial spines on the cephalon and thorax (Fig. 2C; Figs. DR4D–DR4G). Hence, an evo-

lutionary trend toward the thickening of the carapace, the development of spinosity, and the increase in size is documented in this succession of species. Taking into account the nature of the infaunal molting process, the size increase necessarily implies a trend toward a greater burrowing depth, so that the late Silurian *Paciphacops argentinus* was perhaps the pioneer in acquiring the infaunal molting behavior, and *Paciphacops* sp. B the most specialized. Thus, twofold escalatory diagnostic defenses are recognized despite the fossil nature of our case study: morphological (passive) traits and ethological (active) ones.

In a recent global test based on diversity and abundance data of predators versus infaunal taxa throughout the Phanerozoic, Madin et al. (2006) found that escalatory trends between those groups were not driven by direct ecological interactions, being statistically insignificant or of coincidental correspondence. However, Dietl and Vermeij (2006) and Vermeij (2008) argued that heterogeneous global signals ignore processes operating at ecological scales, stating that escalation should be tested constrained to discrete temporal and spatial scales. Our study meets these requirements because it is conducted at a regional to local scale, within a single lineage limited to an evolutionary meaningful time interval, and occurring in comparable environmental settings within a single basin. Although the global diversity trajectory in Trilobita shows inconsistent evidence for escalatory long-term macroevolutionary trends (Madin et al., 2006), the trend exhibited by this *Paciphacops* lineage can be seen as a paradigmatic example of escalation, involving novel defenses, alternative means of exploiting space resources, and increasing metabolic performance to explore previously unoccupied ecospace and morphospace (Vermeij, 2008).

This escalatory trend is in concert with the evolutionary-ecological marine context proposed for late Silurian–Devonian time. There were significant changes in biotic interactions in middle Paleozoic seas, known as the middle Paleozoic marine revolution (Brett, 2003; Nagel-Myers et al., 2009; Signor and Brett, 1984; but see Huntley and Kowalewski, 2007). Several groups of durophagous predators such as arthropods, cephalopods, and fishes underwent an evolutionary burst that extensively intensified predation pressure in marine ecosystems (Brett, 2003; Nagel-Myers et al., 2009; Signor and Brett, 1984). Correspondingly, coeval evidence of increasing predation has been recognized in a number of prey groups, mainly crinoids (Baumiller and Gahn, 2004), bivalves (Nagel-Myers et al., 2009), hyolithids (Baumiller et al., 2010), and brachiopods (Kowalewski et al., 2005; Leighton, 2001). All these prey groups had limited motility or sessile life habits, and provide a good

record of both direct predator-prey interactions and morphological defenses. In contrast, the records from the vagrant benthos are restricted to very rare evidences of unsuccessful predation and structures interpreted ambiguously as defensive. Hence, in the context of this major bioevent, no conclusive signals of the incidence of predation pressure have been so far recognized among trilobites, except for a wide array of spines reported in several Devonian trilobites from Morocco (Brett, 2003; Chatterton and Gibb, 2010).

Aside from the escalatory antipredatory trend of the *Paciphacops* lineage, novel and more complex ecological roles can now be speculated for trilobites as active infaunal members during middle Paleozoic time (Fig. 3; Movie DR1). In this sense, they can be compared to irregular echinoids, which show analogous evolutionary trends during the Mesozoic marine revolution (Harper, 2003). According to our study, trilobites were intensely preyed upon, and their ecological role as participants in predator-prey interactions in the scenario of the middle Paleozoic marine revolution was significant and causally related with distinct macroevolutionary consequences.

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