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Protovirgularia dichotoma—Protovirgularia rugosa: An Example of a Compound Trace Fossil from the Lower Cretaceous (Agrio Formation) of the Neuquén Basin, Argentina

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This study focuses on the description of a compound trace fossil from the Cretaceous of the Neuquén Basin, Argentina. This structure comprises two discrete ichnotaxa: *Protovirgularia* cf. *dichotoma* M'Coy, 1850, and *Protovirgularia* cf. *rugosa* (Miller and Dyer, 1878). Open nomenclature is chosen due to some differences from the ichnospecies diagnoses. The compound trace as a whole is the product of locomotion and resting behaviors (repichnia and cubichnia); this is not questioned but discussed. The inferred producer is a deposit-feeding palaeotaxodont bivalve, which belongs to a taxonomic group almost unknown and not yet reported in the Neuquén Basin. The sample was taken from rocks interpreted as being deposited in a tide-influenced, marginal-marine setting, corresponding to the uppermost section of the Agrio Formation. This also represents one of the first cases of a compound trace fossil described for the Neuquén Basin.

Keywords Compound Trace Fossil, *Protovirgularia*, *Lockeia*, Cretaceous, Neuquén Basin, Agrio Formation, Ichnology, Argentina

INTRODUCTION

The concept of compound trace fossils is a relatively new concept in ichnology. Even though it had been described by several authors (e.g., Osgood, 1970; Bromley and Frey, 1974; Frey and Seilacher, 1980), it was not until Pickerill (1994) defined and differentiated "composite" and "compound" specimens that the concept formally was accepted by most ichnologists. Compound trace fossils arise from a behavioral change of a single trace producer (Pickerill, 1994). The structure as a whole will, therefore, comprise two or more ichnotaxa that grade directly one into another; these ichnotaxa usually occur as, and historically have been defined with respect to, discrete specimens (Pickerill, 1995).

As Bertling et al. (2006) have clearly stated, there are basically two types of behaviors that may lead to the formation of such structures: i) either the same individual behaves differently over time, or ii) it simultaneously behaves in two distinct ways. The former is the case of the ichnofossil treated herein.

The main aim of this article is to provide an example of a compound trace fossil involving two ichnotaxa (*Protovirgularia* cf. *dichotoma* and *P.* cf. *rugosa*) produced by a palaeotaxodont, a group of bivalves that has not yet been reported in the Neuquén Basin, Argentina. It is also one of the first records of compound trace fossils described in this basin (see Pazos et al., 2008; Pazos and Fernández, in press).

GEOLOGICAL SETTING

The Neuquén Basin (Fig. 1) is located in the west-central part of Argentina, between 34° and 41° S, spanning mainly over North Patagonia and Cuyo regions. The Mendoza Group (Neuquén Basin) crops out from the south of Mendoza to the south of Neuquén and comprises several units. Its terminal portion is represented by the Agrio Formation (Late Valanginian-Early Barremian), defined by Weaver (1931).

The invertebrate fauna documented from the Agua de la Mula Member (Late Hauterivian-Early Barremian), which is the upper member of this formation, is varied and abundant (see Aguirre-Urreta et al., 1999; Lazo, 2005; Lazo et al., 2005; Rodríguez, 2007) and includes bivalves and ammonites, among many other groups.

The sample was collected from outcrops of the uppermost part (see Fig. 2) of the Agua de la Mula Member (Leanza et al., 2001) of the Agrio Formation at the type locality of the unit (Bajada del Agrio section). This is located between 38° 23' and 38° 25' S, and 70° and 70° 03' W, 56 km north from

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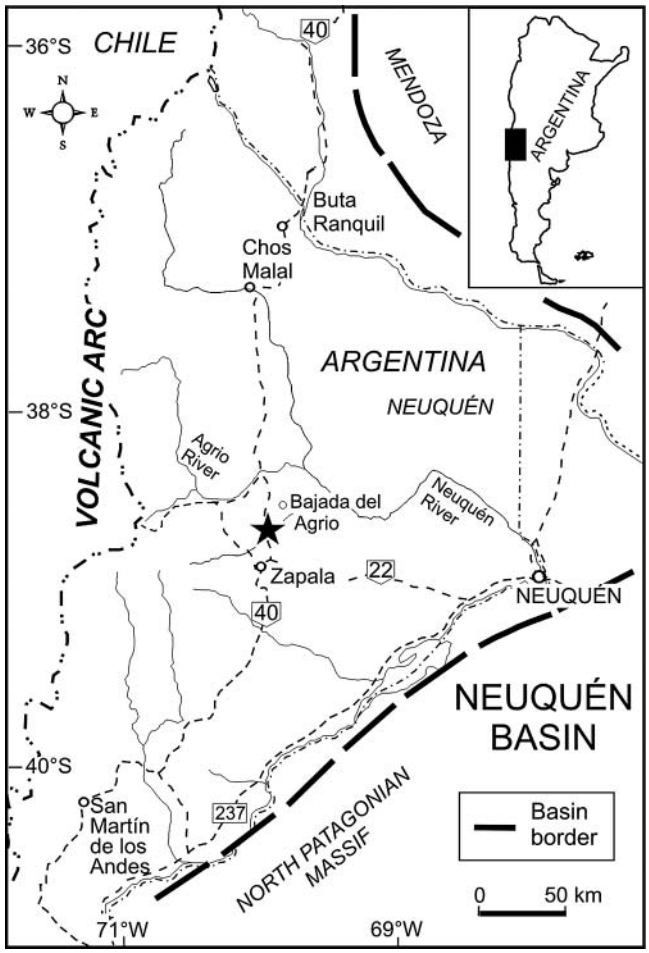

FIG. 1. Map of the Neuquén Basin and its position in Argentina. See location of the study site (near locality Bajada del Agrio) marked with a star, along with other main localities.

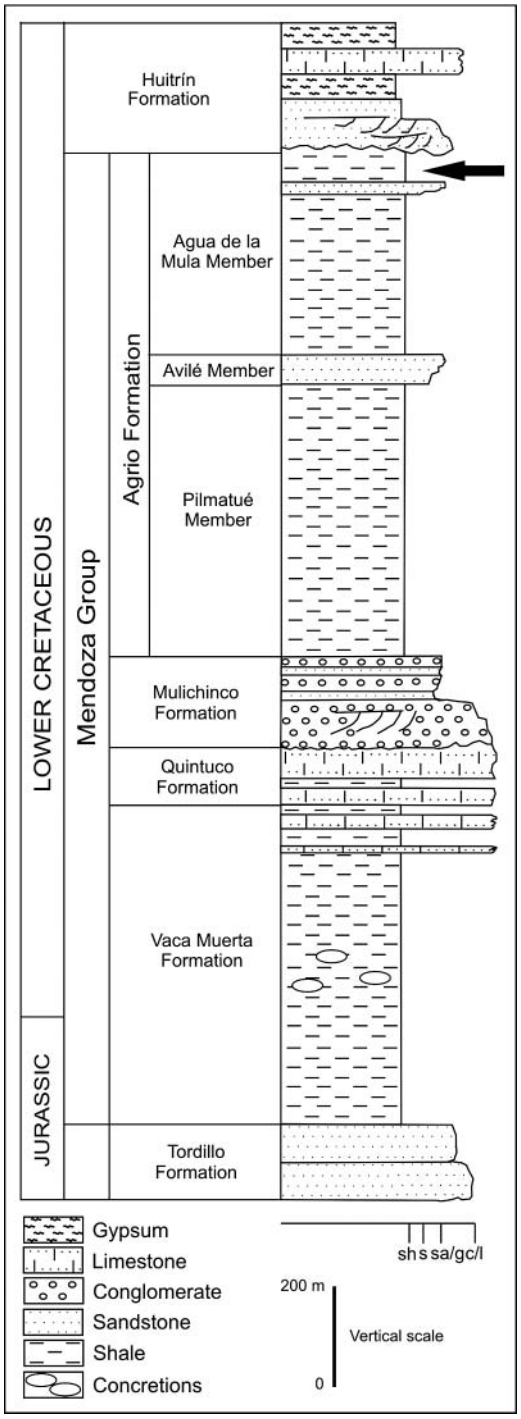

FIG. 2. Stratigraphic column of the Mendoza Group. The arrow marks the approximate position of the level bearer of the compound trace fossil.

the city of Zapala and 1.5 km south from the town of Bajada del Agrio.

The uppermost deposits of this unit have been described as representing a marginal-marine depositional environment with evidence of subaerial exposure and tidal influence (Pazos and Cirigliano, 2006; Pazos et al., 2007, 2008; Tunik et al., 2009; Pazos, 2009). In Bajada del Agrio, where the sample was taken, the marginal-marine deposits consist of tidal flats with eventual subaqueous fluvial discharges (Fernández, 2008).

The Bajada del Agrio section recently has proved to be very rich in ichnofossils (Fernández, 2008; Fernández and Pazos, 2008). The level containing the compound trace presented herein is located 53 m below the contact between the Agrio Formation and the overlying Huitrín Formation (Fig. 2). The rocks containing the compound trace are fine-grained sandstones with combined-flow structures. The unit exhibits a tabular geometry and is lateral continuous. No body fossils were observed, and the only other trace fossil found at this level was *Palaeophycus tubularis* Hall, 1847.

MATERIAL AND METHODS

This compound trace fossil is housed in the collection of the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Buenos Aires, Argentina. The catalogue numbers are prefixed by CPBA-.

The procedural nomenclature adopted herein follows the one defined by Pickerill (1995): individual ichnotaxa that take part in a compound specimen should be assigned their appropriate names (binomial, following the ICZN of 1999). Thus, the compound structure as a whole will be named exactly as what it represents, that is, a certain ichnotaxon "with" or "intergrading with" at least another one (Pickerill, 1995). Open nomenclature is chosen due to some differences from the ichnospecies diagnoses.

SYSTEMATIC ICHNOLOGY

Discrete Ichnotaxa

The two discrete ichnotaxa are *Protovirgularia* cf. *dichotoma* and *P*. cf. *rugosa*. *Lockeia siliquaria* is associated and was described because of its importance in the inference of the producer. Diagnoses, remarks, etc., of the ichnogenera and ichnospecies involved are given below.

Ichnogenus *Protovirgularia* M'Coy 1850

Type ichnospecies: *Protovirgularia dichotoma* M'Coy, 1850

Diagnosis: Horizontal or subhorizontal cylindrical burrows, trapezoidal, almond-shaped, or triangular in cross-section, distinctly or indistinctly bilobated. Internal structure, if preserved, is formed by successive pads of sediment that may be expressed as ribs on the exterior. Ribs arranged in chevron-shaped, biserial pattern along external or internal dorsal part. Occasionally with smooth mantle covering the structure and/or oval mound-like terminations of the trace (after Uchman, 1998; Uchman and Gaździcki, 2006).

***Remarks*:** *Protovirgularia dichotoma* is interpreted as a burrow produced by bivalves (Han and Pickerill, 1994) through the rhythmic action of a muscular cleft-foot. Seilacher and Seilacher (1994) produced this trace in a series of neoichnological studies using modern specimens of the bivalve *Acila* Adams and Adams, 1858. As Bromley et al. (2003) summarize, this trace is usually associated with palaeotaxodont (Protobranchia) deposit feeders. It is usually ethologically classified as a locomotion trace (repichnia).

***Comparison*:** *Protovirgularia* is easily distinguished from biserial arthropod tracks by strict symmetry of impressions on both sides. For example, it is differentiated from *Cruziana* d'Orbigny, 1842 by its cross-section and the absence of scratch marks in the chevrons (Seilacher and Seilacher, 1994). See also difference with *Lockeia* below.

Protovirgularia cf. *dichotoma* M'Coy 1850

Figures 3, 4 A–B

***Diagnosis*:** Small, plaited, unbranched, keel-like trail, mostly straight or slightly curved, more rarely sinuous, consisting of a median line (ridge or furrow) with lateral, generally paired, bilaterally symmetrical, narrow wedge-shaped appendages (emended by Han and Pickerill, 1994).

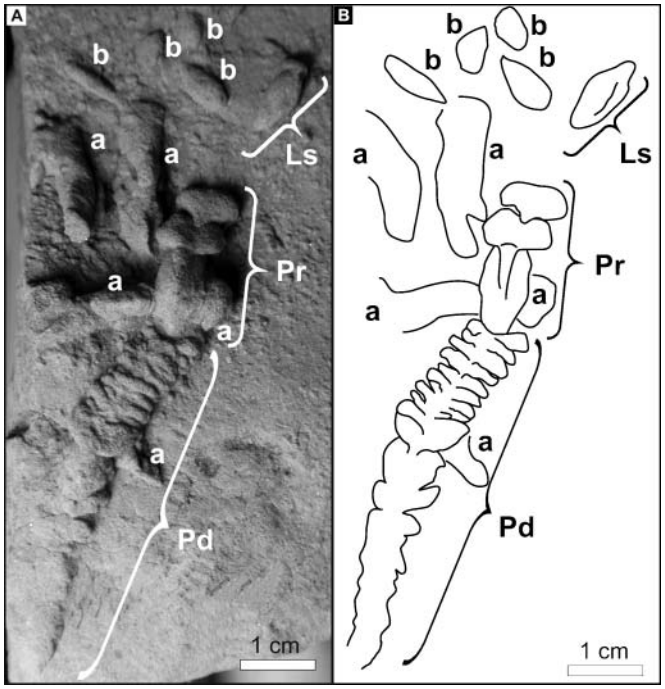

FIG. 3. Illustrations of the treated ichnotaxa. **A.** Compound trace fossil containing *Protovirgularia* cf. *dichotoma* (Pd; CPBA 20431) intergrading with *Protovirgularia* cf. *rugosa* (Pr; CPBA 20432) and with *Lockeia siliquaria* (Ls; CPBA 20430); a: unidentified trace fossils, probably weathered *Protovirgularia*; b: other *Lockeia* specimens. **B.** Outline of the compound trace fossil and associated traces.

***Description*:** Elongated and slighty curved trace, 33 mm long and 6 mm wide, preserved as a positive hyporelief. Chevron-like lamellar ornamentation is developed, which is reduced towards one of the extremes. It shows, on average, one lamella per millimeter.

***Remarks*:** *P*. cf. *dichotoma* is interpreted as a repichnia in Seilacher and Seilacher (1994). It represents the straightforward movement of the animal as it advances horizontally through the substrate by using its elongated cleft-foot as an anchor, applying the push-and-pull or double anchor technique. Even though this trace is usually attributed to the locomotion of bivalves, Seilacher and Seilacher (1994) have stated that scaphopods may produce similar traces. However, those scaphopods are discounted in this case because of the association of *P*. cf. *dichotoma* with specimens of *Lockeia siliquaria*.

***Comparison*:** *P. dichotoma* is differentiated from *P. rugosa* because it does not end in a *Lockeia*-like body. It is distinguished from *P. triangularis* MacSotay, 1967 as the latter presents a carinated cross-section; from *P. tuberculata* (Williamson, 1887) because *P. tuberculata* shows a clearly defined medial furrow; and from *P. longespicata* (de Stefani, 1885) as *P. longespicata* exhibits papillate chevrons, which may represent a palmate food-searching system (*P. longespicata* is classified as a feeding structure) with spreite-like backfill (Seilacher and Seilacher,

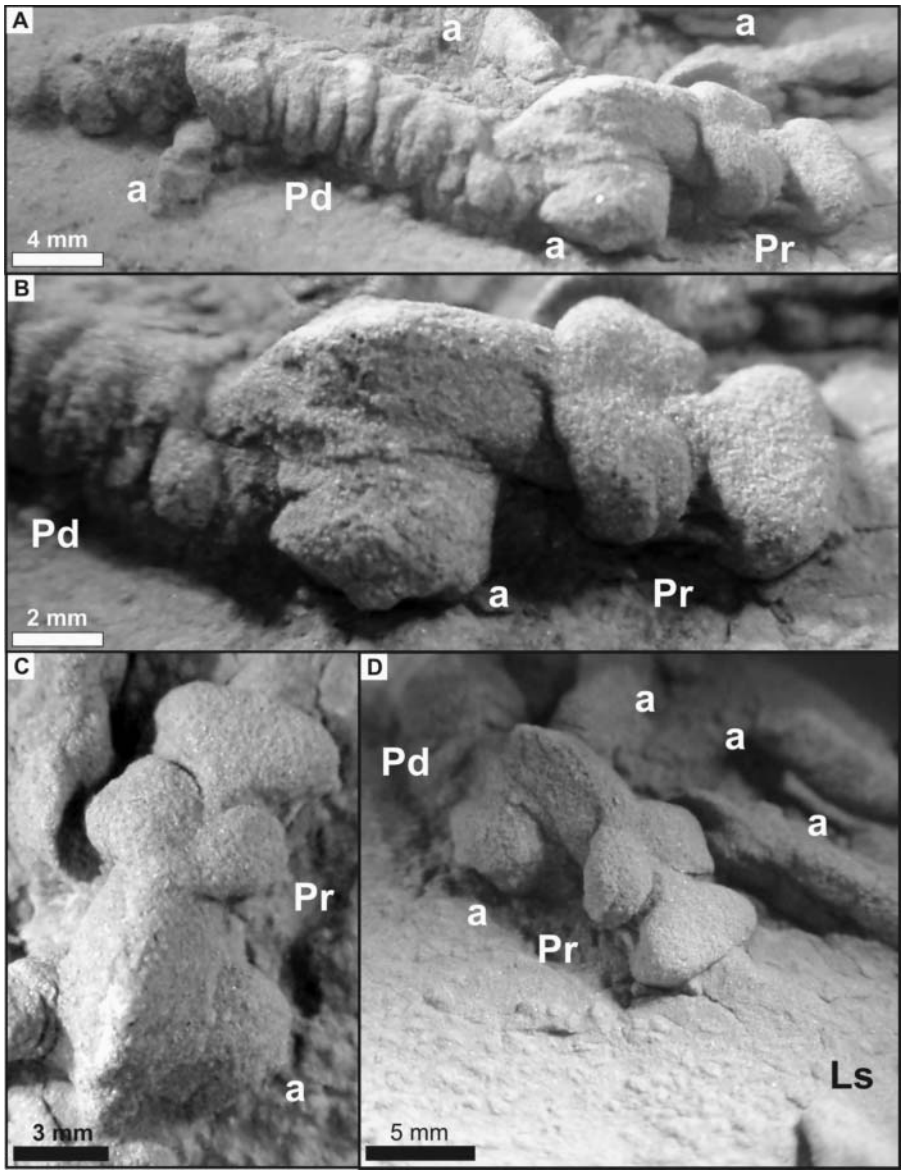

FIG. 4. Different perspectives and details of the specimen. **A.** *Protovirgularia* cf. *dichotoma* (Pd; CPBA 20431) intergrading with *Protovirgularia* cf. *rugosa* (Pr; CPBA 20432) in lateral view and associated traces (a: unidentified trace fossils, probably weathered *Protovirgularia*). **B.** Detail of 4 A with focus made on *Protovirgularia* cf. *rugosa*. **C.** Detail of Fig. 3 with focus made on *Protovirgularia* cf. *rugosa*. **D.** Different perspective showing *Protovirgularia* cf. *dichotoma* intergrading with *Protovirgularia* cf. *rugosa*, and a portion of the associated *Lockeia siliquaria* (Ls; CPBA 20430).

1994). In addition, *P. dichotoma* differs from *P. bidirectionalis* (Mángano et al., 2002) in that *P. dichotoma* exhibits sets of "V"-shaped marks or chevrons in opposite directions, which gather at the same central point.

Protovirgularia cf. *rugosa* (Miller and Dyer, 1878)

Figures 3, 4

***Diagnosis*:** Commonly short *Protovirgularia* terminated by a smooth *Lockeia*-like body. Chevron markings are strong (Uchman, 1998; modified after Seilacher and Seilacher, 1994).

***Description*:** Trace fossil preserved as a positive hyporelief, 15 mm long and 4–6 mm wide. It contains chevron-like ornamentation, but only two chevrons are observed. *P*. cf. *rugosa* ends with a *Lockeia siquillaria* trace.

***Remarks*:** *P*. *rugosa* is ethologically classified as a resting trace (cubichnia). Chevrons are built by the cleft-foot of the bivalve when anchoring to the sediment (Seilacher and Seilacher, 1994).

***Comparison*:** It differs from the other ichnospecies of *Protovirgularia* for having a *Lockeia*-like body at one of the extremes.

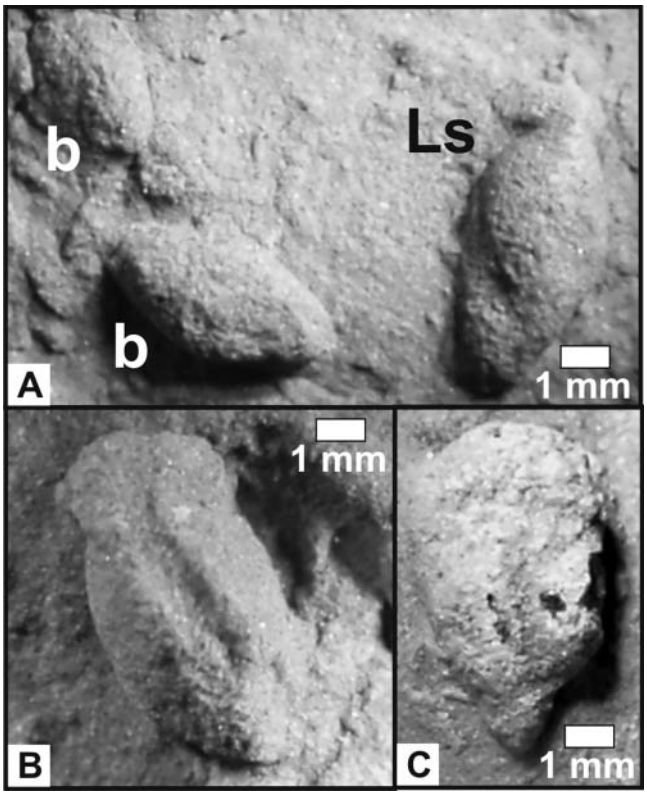

FIG. 5. Traces that accompany the compound specimen. **A.** *Lockeia siliquaria* (LS) and *Lockeia* sp. (b). **B.** and **C.** *Lockeia*-like bodies.

Compound Specimen

Protovirgularia cf. *dichotoma* intergrading with *Protovirgularia* cf. *rugosa*

Figures 3, 4 A–B

***General description*:** The order in which the names of the discrete ichnotaxa are given in the compound form is not due to a particular predominance of one of these ichnotaxa over another. Instead, the order is chosen because it reflects their relative spatial distribution (see Fig. 3).

From bottom left to top right (Fig. 3): *Protovirgularia* cf. *dichotoma* (Fig. 3, Pd) directly intergrades with *P*. cf. *rugosa* (Fig. 3, Pr). Both discrete ichnotaxa are assigned to the same individual producer (see Ethology). These traces are accompanied by others (Fig. 3): some of them are probably weathered *Protovirgularia* examples (Figs. 3, 4), others are *Lockeia* sp. specimens (Figs. 3, 5 A), and at least one of them is *Lockeia siliquaria* (Figs. 3, 4 D, 5 A). On the bottom left (Fig. 3), the compound structure loses ornamentation and relief.

The ichnotaxa involved also provide morphological details of the bivalve's shell and foot. *P*. cf. *dichotoma* and *P*. cf. *rugosa* show the characteristics of the bivalve's foot: it is a cleft-foot with a bifid tip of approximately 7 mm wide. *P*. cf. *rugosa* and the associated *L. siliquaria* specimens suggest that the shell of the bivalve was almond-shaped, unornamented, and about 7 mm long and 4 mm wide.

Toponomy: The compound specimen is preserved as a positive hyporelief in fine-grained sandstone, at an interface between claystone and sandstone.

The reduction of ornamentation towards one of the ends of the *P*. cf. *dichotoma* specimen is probably due to a descent of the organism within the sediment. Other than that, all components are developed at the same level in the substrate.

Ethology: It is most likely that more than one individual has produced all of the discrete traces seen in Figure 3 A. However, the compound structure is the one that involves the specimens that can be followed in a certain direction, are in contact with each other, and coincide in size.

L. siliquaria (Figs. 3, 4 D, 5 A), other small *Lockeia* specimens (Figs. 3, 5 A), and probably other weathered *Protovirgularia* examples (Figs. 3, 4) accompany the compound form. In those cases, the most likely producers are also bivalves, possibly the same individual or other individuals of the same taxonomic group. The spatial closeness, direction, and size of the *L. siliquaria* specimen probably indicate that its producer and the producer of the compound trace are the same individual. In the extremely well-preserved example of a compound trace fossil presented by Ekdale and Bromley (2001), there is not a strict physical connection between two of the discrete ichnotaxa (see fig. 1 in Ekdale and Bromley, 2001). In our specimen, spatial closeness may not be as good an argument as it was in the former case. Since there is no direct contact (Bertling et al., 2006) between *L. siliquaria* and the compound specimen, we prefer to keep this ichnotaxon as associated only with the compound trace. Other examples of *Lockeia*-like bodies (see Figs. 5 B–C) were found in the same level but as closely associated.

The producer of the compound specimen, almost undoubtedly a palaeotaxodont (Protobranchia) deposit-feeder bivalve (given the association with *Lockeia*), moved horizontally by rhythmically anchoring its cleft-foot to the sediment (producing *P*. cf. *dichotoma*), then turned a bit to its right (keep in mind it is a positive hyporelief), and slowed down almost stopping (*P*. cf. *rugosa*). The cleft-foot of these bivalves has a bifid tip, which allows them to use the "double anchor" technique, and is responsible for the chevrons in the trace.

The record of protobranchs for the Agrio Formation as well as for the entire Neuquén Basin is scarce. The few records known are yet to be described (Lazo, pers. comm., 2009).

Comparison: The most similar case (considering ichnotaxa involved and inferred producer) of a compound trace fossil is the one reported by Ekdale and Bromley (2001): a beautifully preserved example of *Protovirgularia dichotoma—Lockeia siquillaria—Lophoctenium*. In that case, the ethological categories are repichnia, cubichnia, and fodinichnia (feeding), since *Lophoctenium* "represents the repetitive lateral probing of the sediment around the bivalve for organic matter, using its labial palpal tentacles" (Ekdale and Bromley, 2001, p. 122).

In the Neuquén Basin there is, for the moment, only one known case of a compound trace fossil, *Hillichnus* Bromley et al., 2003. *Hillichnus* was reported by Pazos et al. (2008), also

from the Agua de la Mula Member of the Agrio Formation; this example has been recently described as a new ichnospecies, *Hillichnus agrioensis* by Pazos and Fernández (in press). This ichnotaxon is attributed to bivalves as well. However, it represents the other case that may lead to the formation of a compound trace fossil: the one formed when several behavioral activities of the same individual take place simultaneously (as opposed to a chronological order).

Ichnogenus *Lockeia* James, 1879

Type ichnospecies: *Lockeia siliquaria* James, 1879

***Diagnosis*:** Elongated, bilaterally symmetrical trace. Commonly almond-shaped, rarely triangular or heart shaped, with a smooth margin. Generally preserved as a hyporelief, usually with a distinct median crest. Vertical spreite can be present (modified by Schlirf et al., 2001).

***Remarks*:** *Lockeia* is considered to be a resting trace (cubichnia) made by bivalves (Seilacher and Seilacher, 1994). Bromley and Asgaard (1979) pointed out that small crustaceans may also be potential producers.

***Comparison*:** *Lockeia* is distinguished from *Protovirgularia* as the two represent different behaviors (see Uchman and Gaździcki, 2006). *Lockeia* indicates size, shape, and ornamentation of the shell of the bivalve, and *Protovirgularia* indicates size and shape of the foot of the animal (Ekdale and Bromley, 2001).

Lockeia siliquaria James, 1879

Figures 3, 4 D, 5 A

***Diagnosis*:** Thin, elongated to stout, generally high-standing and almond-shaped trace. Walls are smooth and the trace exhibits strong arcuate to almost obtuse terminations. Occasionally vertical spreiten are present (Schlirf et al., 2001).

***Description*:** Almond-shaped trace with smooth walls, preserved as a positive hyporelief, 5–7 mm long and 3–4 mm wide. It does not show spreite. A median crest is observed.

***Remarks*:** *L. siliquaria* represents the place where the bivalve temporarily stopped for feeding (Ekdale and Bromley, 2001). *Lockeia siliquaria* (Fig. 3, Ls) is about 7 mm away from *P*. cf. *rugosa.*

***Comparison*:** *L. siliquaria* could be mistaken for *Lockeia ornata* (Mángano et al., 1998), but it differs in the absence of ornamentation on the walls.

DISCUSSION

According to Seilacher and Seilacher (1994), *P. rugosa* should be classified as a resting trace (a "cubichnial version of *Protovirgularia*"). If so, there is no doubt that the example presented herein is a compound trace fossil, since it clearly represents the intergradation of two ichnofossils that reflect two different behavioral categories. This is what we have chosen to do here. Nevertheless, we believe some issues regarding this matter are worthy of attention:

1. *Protovirgularia* and *Lockeia,* as ichnogenera, have been referred to (e.g., Uchman and Gaździcki, 2006) as the repichnia and cubichnia version of a bivalve's trace fossil, respectively. If so, the inclusion of *P. rugosa* in the cubichnia ethological category could be doubtful. After all, the characteristic chevrons are built by the foot when anchoring to the sediment, which is an action typically carried out during locomotion.
2. If what is stated in point 1) is considered to be accurate, a question regarding this compound structure as a whole arises; that is, could it represent the evidence of different locomotion styles or velocity rates, *P*. cf. *dichotoma* being the "faster" one and *P*. cf. *rugosa* being the "slower" one? Does this represent a behavioral change, even though we could include both traces within the same currently valid ethological category? *Running* is not the same as *walking*, *strolling*, or *wandering*.

Even after the work of Bertling et al. (2006), there are still matters regarding ichnotaxonomy that need to be discussed. For instance, within the realm of compound trace fossils, what exactly represents a change in behavior? Are the ethological categories historically used in ichnology sufficient to define whether or not two different traces could be considered a compound trace fossil? Or is it possible that two different conducts may fall into only one of these categories and yet represent a significant change in behavior that is worth describing? Is the *intention* of the producer the only thing to be taken into account when differentiating two similar yet distinct behaviors? If so, what happens when those intentions are unclear? We believe future ethological studies, with a more biological perspective, may allow the elucidation of these matters.

CONCLUSIONS

Protovirgularia cf. *dichotoma* intergrading with *P*. cf. *rugosa* represents an example of a particular kind of compound structure: the one formed by a chronological change in behavior of an individual. In this case, it appears to record locomotion followed by resting (repichnia and cubichnia).

The ichnotaxa involved and the associated specimens provided morphological details of the bivalve's shell and its foot, which cannot be inferred from body fossils. This allows for the interpretation of the producer as a particular group of infaunal bivalves: the palaeotaxodonts. Therefore, this compound trace also represents one of the very few records known of the existence of this group of bivalves in the Cretaceous of the Neuquén Basin. It is also one of the few cases of a compound trace fossil described from the Neuquén Basin and from Argentina.

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