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# Three-dimensionally integrated trace fossils from shallow-marine deposits in the Lower Cretaceous of the Neuquén Basin (Argentina): *Hillichnus agrioensis* isp. nov.

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ABSTRACT:

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A complex trace fossil that requires a three-dimensional (3D) reconstruction is described and interpreted. The specimens studied are assigned to a new ichnospecies (*Hillichnus agrioensis*) of *Hillichnus* Bromley *et al.*, 2003. Most of them are uncollectable and a compound iconotype was designed to characterise the new ichnospecies. The three-dimensional trace fossil has been recorded in marginal-marine deposits close to the top of the Agrio Formation (Lower Cretaceous of Neuquén Basin, Argentina). The new ichnospecies shows a different pattern of feeding than *H. lobosensis* Bromley *et al.*, 2003, and records defaecation downward in the deeper preservational level (level 4). Feather-like structures (level 2) that typify the ichnogenus also record the activity of an inhalant siphon and indicate a retractile movement. The vertical shafts (level 1) are scarcely recorded. Aligned double rings also document the infaunal habit of the tellinid bivalves that are considered the most likely producers of the trace. It is clear that when only level 2 is exposed, in some cases this form can be assigned to *Jamesonichnites heinbergi* Dam 1990a consequently, this ichnospecies is interconnected with more than one ichnogenus. Vertical projections recorded in branches differ from the type ichnospecies *H. lobosensis* Bromley *et al.*, 2003. The occurrence in marginal-marine facies is congruent with the record of *Jamesonichnites* but not common in the type species and similar to those more frequent in deep-sea deposits (e.g. *Polykampton alpinum* Ooster, 1869).

**Key words:** Compound trace fossil; *Hillichnus*; Lower Cretaceous; Neuquén Basin; Shallow marine; Ichnology.

## INTRODUCTION

Trace fossils are the records left behind by the activity of the animals in their daily business (Ekdale and Bromley 2001). As such, they may be simple, complex or the result of a combination of multiple activities (behaviours) at a point that requires special treatment for their naming (e.g. Bertling *et al.* 2006). At first sight, most ichnogenera are the result of single behaviours that fit in traditional categories like feeding, locomotion, resting, habitation, escape, refuge, gardening, swimming, and others. However, a tracemaker may present a combination of behaviours at the same time, or it can behave differently in a chronological order (e.g. Bertling *et al.* 2006); both cases belong to the category of compound trace fossils (cf. Pickerill 1994).

Three-dimensional exposures allow the entire morphology of the trace for reconstruction and thus permit interpretative work on the behaviour and the taphonomical controls that favoured or discouraged preservation of some part in a compound trace fossil. Suggestions for naming traces that involve several ichnogenera include compound ichnogenera (Bertling *et al.* 2006), giving the whole trace a new name (Pickerill 1994), or naming using every ichnogenus that conforms the entire structure (e.g. *Protovirgularia*, *Lockeia*, *Lophoctenium*) as was previously used in Ekdale and Bromley (2001); this may also be suggested for intergrading *Maculichna* and *Umfolozia* (Pazos 2000). The last example corresponds to arthropod trackways, which can be named as suggested by Minter *et al.* (2006): The senior name may not prevail and a combined nomenclature is suggested (i.e. *Umfolozia-Maculichna*).

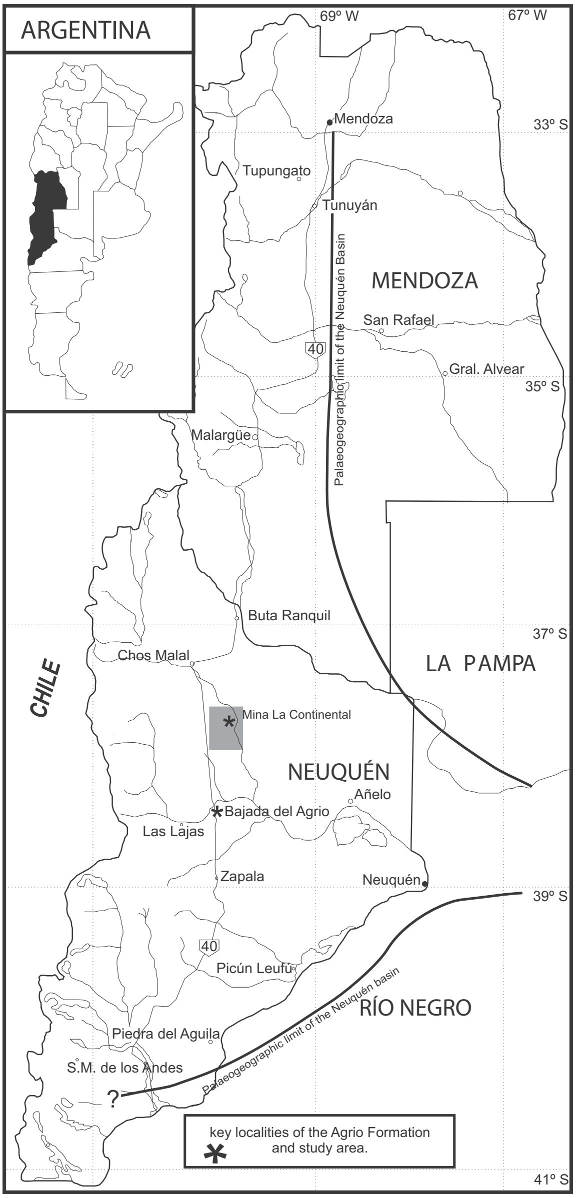
In the case of *Hillichnus lobosensis* Bromley *et al.*, 2003, the morphology is clearly the result of changes in behaviour rather than an answer to substrate differences. This ichnotaxon involves the alternation of locomotion, feeding, respiration, and defaecation (Bromley *et al.* 2003), which is a problem if we wish to follow very strict behavioural categories.

The main aim of our paper is to recognise a new ichnospecies of *Hillichnus* as well as to provide a description of these 3D trace fossils and highlight the occurrence and behavioural differences with the type ichnospecies. The material described herein derives from the Lower Cretaceous Hauterivian deposits of the Agrio Formation in the Neuquén Basin, Argentina (Text-fig. 1) and was mentioned briefly by Pazos *et al.* (2007, 2008a, b). As a result of our investigation, we propose the new ichnospecies *Hillichnus agrioensis,* originating from the material recently shown by Pazos *et al.* (2008a, b).

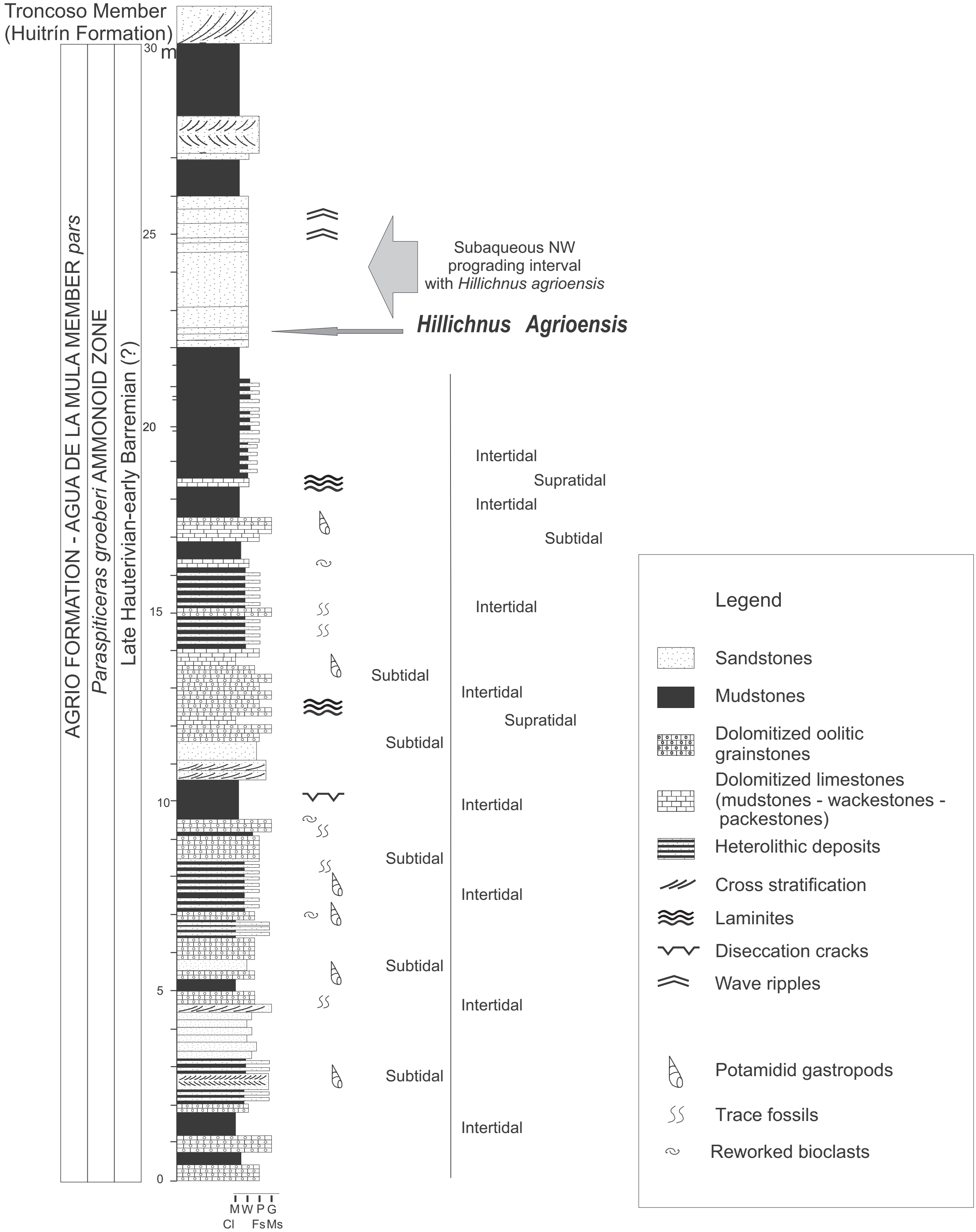
## GEOLOGICAL SETTING AND STUDY AREA

The Neuquén Basin (Text-fig. 1) is located in west-central Argentina between 34º and 41ºS. It contains more than 7000 m of marine and continental deposits of Late Triassic to Paleogene age (Vergani *et al.* 1995; Legarreta and Uliana 1999). Most of the Jurassic and Lower Cretaceous deposits are represented by highly fossiliferous marine facies of diverse nature associated with transgressions from the Pacific Ocean (Howell *et al.* 2005).

The Agrio Formation (upper Valanginian–lower Barremian) was defined by Weaver (1931) as highly fossiliferous marine strata and is divided into three members named by Leanza *et al.* (2001). In particular, the upper member (Agua de la Mula Member), which contains the trace fossils of this study (Text-fig. 2), was recently zircon dated and showed an age of upper Hauterivian 132 ± 1 Ma (Aguirre-Urreta *et al.* 2008). This constitutes the first absolute age of the Hauterivian stage and also demonstrates that biostratigraphic correlations between Tethyan and Gondwanan biozones are accurate. The upper member, composed of siliciclastic and carbonate cycles (Spalletti *et al.* 2001), is historically considered to be normal marine throughout. Recently, however, the uppermost part was assigned to a marginal-marine environment with




Text-fig. 1. Location of the studied locality in a palaeogeographic map of the Neuquén Basin




Text-fig. 2. Section showing the siliciclastic interval bearing *Hillichnus agrioensis* evidence supporting subaerial exposure (e.g. top-flat ripples, desiccation cracks, theropod tracks) and tidal influence, such as tidal channels with a flood-ebb palaeocurrent pattern but also laminites (Pazos and Cirigliano 2006; Pazos *et al.* 2007, 2008a; Tunik *et al.* 2008). The Agua de la Mula Member (late Hauterivian–early Barremian) has a rich invertebrate fauna, including benthic epifaunal and infaunal groups (e.g. Lazo 2005; Lazo *et al.* 2005; Rodríguez 2007), nektonic forms, ammonites and nannofossils. These fossils are the basis for the biostratigraphic zonations and correlations (Aguirre-Urreta and Rawson, 1997; Bown and Concheyro 2004; Aguirre-Urreta *et al.* 2005, 2007; Ballent *et al.* 2006).

The study area, named Mina La Continental, is located at the central part of the Neuquén Basin (see Text-fig. 1), in an area dominated by a succession of synclines and anticlines that are part of the fold-belt of the basin (Ramos and Folguera 2005). From a palaeogeographic point of view, it is located in the "basinal facies" situation (e.g. Legarreta 2002), which contrasts with the previously mentioned evidence of shallow water and subaerial exposure. Specifically, the area is part of the Mina La Continental anticline, which exposes the upper part of the Agrio Formation (Text-fig. 2) and the overlying Huitrín Formation. The logged section (Text-fig. 2) is situated at 35°54′23″S, 69°33′56″W and corresponds to the uppermost part of the Agrio Formation, where *Hillichnus* appears to be restricted to a siliciclastic sandstone package (Text-figs 3A, B) that also contains other ichnogenera that have no physical connection with *Hillichnus,* including *Ophiomorpha* ?*nodosa* (Text-fig. 5G; Lundgren 1891). The material from the logged section is currently under study.

## UPPERMOST AGRIO FORMATION SOUTH FROM 35° LATITUDE: SEDIMENTOLOGY AND PALAEOGEOGRAPHY

Spalletti *et al.* (2001) studied the type locality of the Agrio Formation by the Agrio river. This unit is composed of a succession of stacked siliciclastic-carbonate cycles interpreted as having been deposited in a middle to inner ramp (Spalletti *et al.* 2001). There, Fernández (2008) and Fernández and Pazos (2008) recently studied the uppermost 63 m of the unit, which contains some evidence of tidal influence, such as opposing palaeocurrents recorded in low-angle climbing ripples, and Inclined Heterolithic Stratification (IHS) conforming with tide-influenced point bars (e.g. Gingras *et al.* 2000; McIlroy *et al.* 2005). Robust evidence that the normal marine environment changed to a marginal marine one with hypersaline conditions toward the top was documented by Fernández (2008). Further north, in the area of the Mina La Continental, new observations in an approximately 30-m-thick succession have confirmed tidal influence, as evidenced by cross-bedding stratification with reactivation surfaces, mud drapes, desiccation cracks, laminites, and wave ripples (Text-fig. 3C) with short wavelength and combined-flow ripples (Pazos *et al.* 2009). However, the main tidal indicator is composed of a bidirectional palaeocurrent pattern in a heterolithic interval containing abundant ripples, where the flood tide dominated the palaeocurrents. Petrographically, the logged section underlying the siliciclastic package containing *Hillichnus* also contains oolitic limestones showing different dolomitization types. This evidence confirms diagenesis in the vadose zone as a result of marine and fresh water interaction (Tunik *et al.* 2009). Another locality between the type locality of the unit (Bajada del Agrio) and Mina La Continental, the Agua de la Mula section, repeats the record of siliciclastic-carbonate cycles recording mainly transgressive-highstand system tracts (Lazo *et al.* 2005) but without any evidence of subaerial exposure, nor tidal influence as clearly as detected in the logged section (Text-fig. 2). This point is crucial because it indicates that Mina La Continental does not have evidence of a progressive basin deepening attached to a basin axis of SE-NW orientation, as was previously suggested for the unit (Legarreta and Gulisano 1989); instead, it accurately points out the presence of a sediment source from the eastern border of the basin. All these palaeoenvironmental indicators invite reformulation of facies schemes (Pazos 2009) and palaeogeographic maps for this unit in the Neuquén embayment and fold-belt, which should modify hystorical oil exploration and models (e.g. Legarreta 2002). The new studies, compared with the classic ones (e.g. Spalletti *et al.* 2001; Lazo *et al.* 2005), showed not only facies differences but also a more diverse and abundant trace fossil content other than those with the typical elements assigned to *Cruziana* ichnofacies in prior works (e.g. Spalletti *et al.* 2001; Lazo *et al.* 2005; Lazo 2007) in several parts of the basin. For instance, there are few examples of dinosaur tracks, *Hillichnus* and *Lophoctenium*-like traces in marginal-marine settings (see some exceptions: Lockley *et al.* 2006; Rindsberg and Martin 2007;), and they are almost unaccounted for in marginal-marine trace fossil models affected by fluctuation in physical parameters and fundamental substrate and salinity changes (e.g. Pemberton *et al.* 2001; MacEachern and Gingras 2007; Letlley *et al.* 2007).

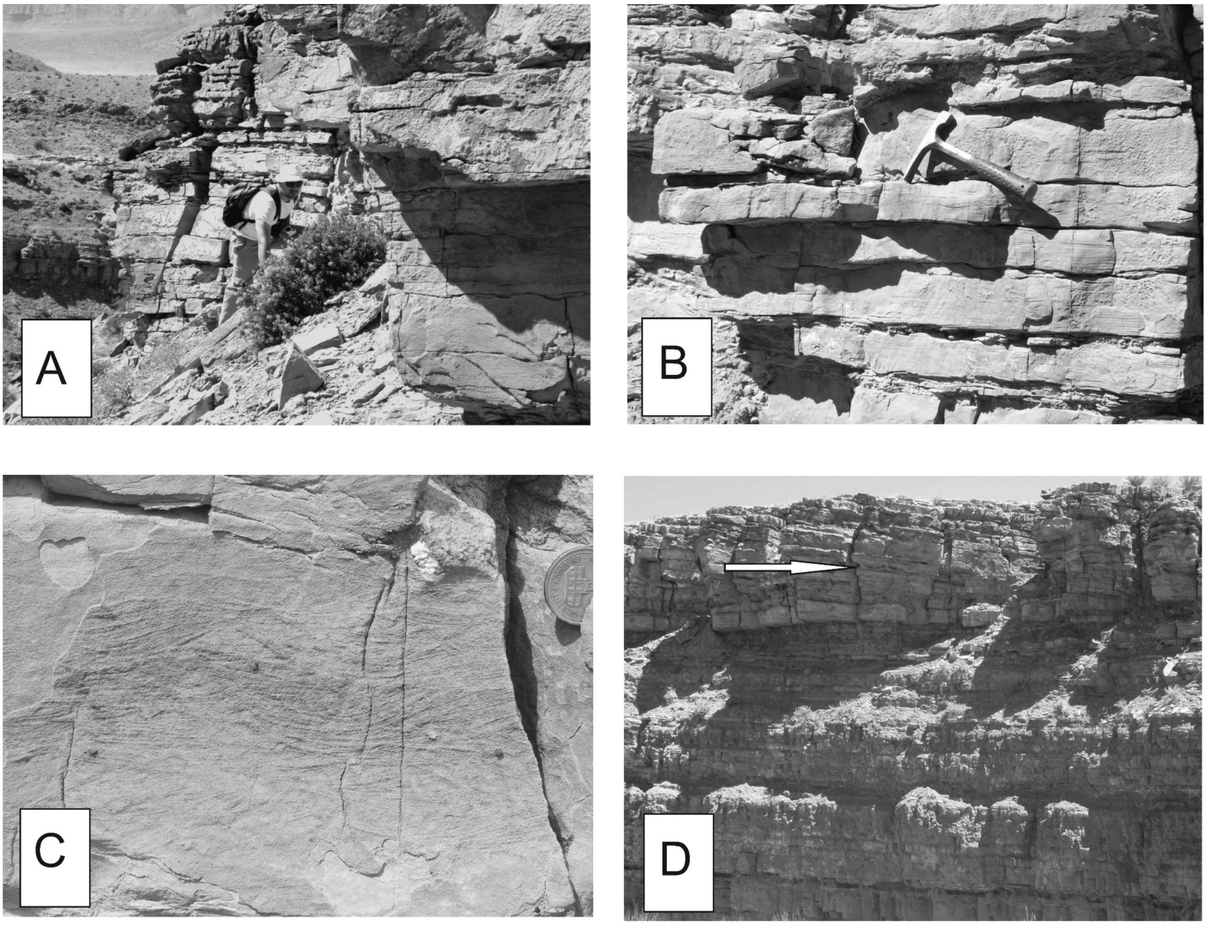
These trace fossils are also difficult to fit because of deviations from the archetypal ichnofacies models (e.g. MacEachern *et al.* 2007), which predict that subtidal settings have a mixture of the *Cruziana* and *Skolithos* ichnofacies, with *Cruziana* and *Scoyenia* ichnofacies in the upper part of tidal flats (Mángano and Buatois 2005). Conversely, *Lophotecnium*-like forms are frequent in deep-marine facies (e.g. Fu 1991).

## Sedimentology of the *Hillichnus* interval

The interval containing *Hillichnus* is siliciclastic and was recently petrographically analysed by Tunik *et al.* (2009). It is composed of lithic arenites containing volcanic grains and old basement components. The interval is easily recognizable in the field because of its pale grey colour and sharp basal contact with the underlying heterolithic deposits (Text-figs 3B, D) and downward termination pattern (Text-fig. 3D). It is approximately 2.6 m thick and contains evidence of wave and current interaction (Text-figs 3B, C); most ripples show a quasi-symmetrical profile with an onshore direction, offshooting, and a complex internal geometry, all features considered as archetypal of combined-flow ripples (Myrow and Southard 1991). Very thin layers containing abundant organic matter and mica indicate settling from suspension or at least severe reduction in water energy. Conversely, some thin layers contain parting lineations, suggesting a short-lived upper-flow regime and confirming rapid energy fluctuation.

## The ichnogenus *Hillichnus*

Bromley *et al.* (2003) created a new ichnogenus for a trace fossil that had, up to that moment, a controversial history. It was described previously as fossilised impressions of seaweeds until Hill (1981) suggested an ichnological origin. Bromley *et al.*




Text-fig. 3. Selection of sedimentary features. A – View of the interval rich in *Hillichnus agrioensis*. B – Detail of stratification with downlap progradation. C – Wave and combined-flow ripples. D – Detail of the outcrops showing (arrow) the prograding interval analysed and the downward heterolithic strata. Note the sharp basal contact of the studied package. Scale =2.3 cm

(2003) identified this ichnotaxon in three different outcrops of Palaeocene turbidites deposits of the Carmelo Formation (Palaeocene) at Point Lobos, California. Their conclusion was that such peculiar traces warranted a new ichnogenus and ichnospecies: *Hillichnus lobosensis*. They established five morphological levels for this structure (a to e, based on different levels of exposure), stated that it belongs to a lower middle or deep tier, and proposed tellinacean bivalves as the most likely producers. Tellinaceans are vagile deposit-feeders, characterised by unpaired siphons whose precise functional activities differentiate them from the palaeotaxodont bivalves. These possible tracemakers produced complex and compound trace fossils but with a cleft foot whose action was recorded during locomotion (*Protovirgularia dichotoma* M'Coy 1850), almond-shaped forms (*Lockeia siliquaria* James 1879), and feeding activity recorded as "mopping" structures produced by the labial palps probing the substrate horizontally (*Lophoctenium*-like forms; see Ekdale and Bromley 2001, fig. 3). This new and peculiar ichnogenus is interpreted as the result of the activity of tellinid or semelid bivalves, based on comparisons with the type of bioturbation produced by the feeding activities of modern counterparts. Living tellinaceans, however, differ in that they usually feed on the sea floor rather than within the sediment.

The work of Bromley *et al.* (2003) confirms that certain trace fossils are of such a complex morphological structure that a three-dimensional study and description is needed. Those authors' constitution of different "levels" helped to explain variations in morphology that, in some cases, record ethological changes. Additionally, they compared the new ichnogenus with other feather-like traces, such as *Polykampton* and *Jamesonichnites,* and discussed the main reason for assigning the producer to tellinacean bivalves, namely, by comparison with bioturbation of living forms and observations in aquaria (see Bromley *et al.* 2003). Regrettably, traces similar to *Hillichnus* were also mistaken as "sea plants" in Japan according to the stories and illustrations included as "ikebana" by Seilacher (2008) in his book *Fossil Art*.

Unfortunately, the type specimen of *Hillichnus lobosensis* has a tragic destiny because of the impossibility of its being sampled and its exposure to continuous battle with the erosion and abrasion of Pacific Coast waves, tides and storms. Moreover, this is a challenging trace fossil for ichnologists because it is a conjoined biogenic structure based on a series of observations at different planes that required a 3D reconstruction for the interpretation to be precise (Bromley *et al.* 2003, fig. 16).

## OCURRENCE AT MINA LA CONTINENTAL

As previously pointed out, traces are included in a siliciclastic interval that comprises fine-grained greyish sandstones that highly contrast with the underlying (heterolithic) and overlying (green shale) beds (Text-fig. 2). Trace fossils are recorded in almost *in situ* blocks, and they would be practically invisible if oxidation of iron minerals had not taken place. The traces are disseminated through an area of about 2400 $m^2$. An examination of the succession of sedimentary structures leads to the conclusion that the trace fossils occur in the lower part of the siliciclastic package, close to the interface with the underlying deposits.

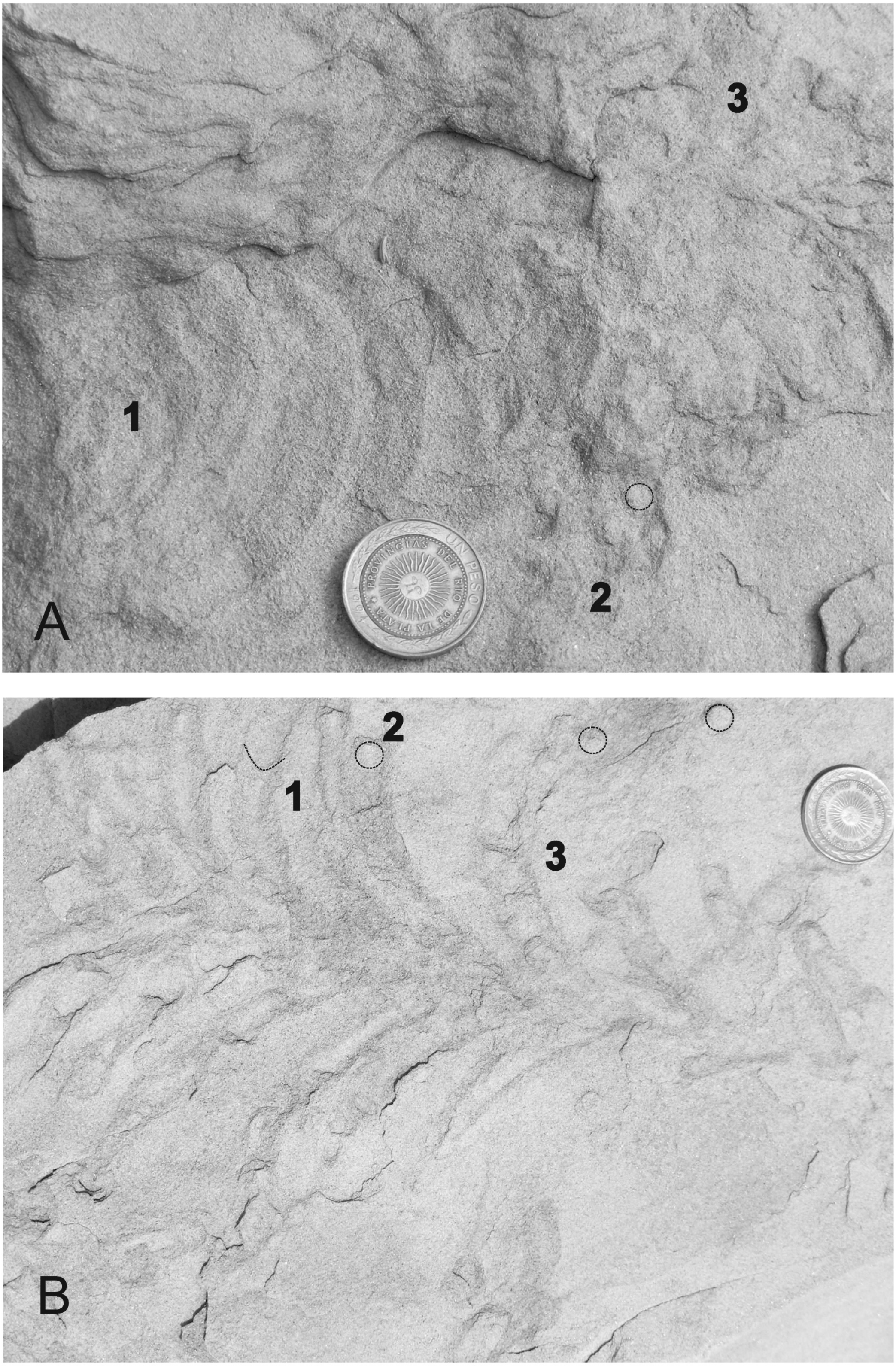
Unfortunately, sample collection is almost impossible without proper machinery, which will probably be done in the future. Nonetheless, the relative abundance of these "feathered" forms, favourable (arid) climatic conditions, and location far away from high hills or sea, guarantee that the traces will be preserved for centuries, unlike the type material of *Hillichnus lobosensis*. In fact, these trace fossils are only recognizable as a result of selective weathering and oxidation of iron minerals, which supplied an orange tint that enhances some features. This is very useful in forms that present a very subtle contrast compared with the surrounding lithology.

## ICHNOTAXONOMY

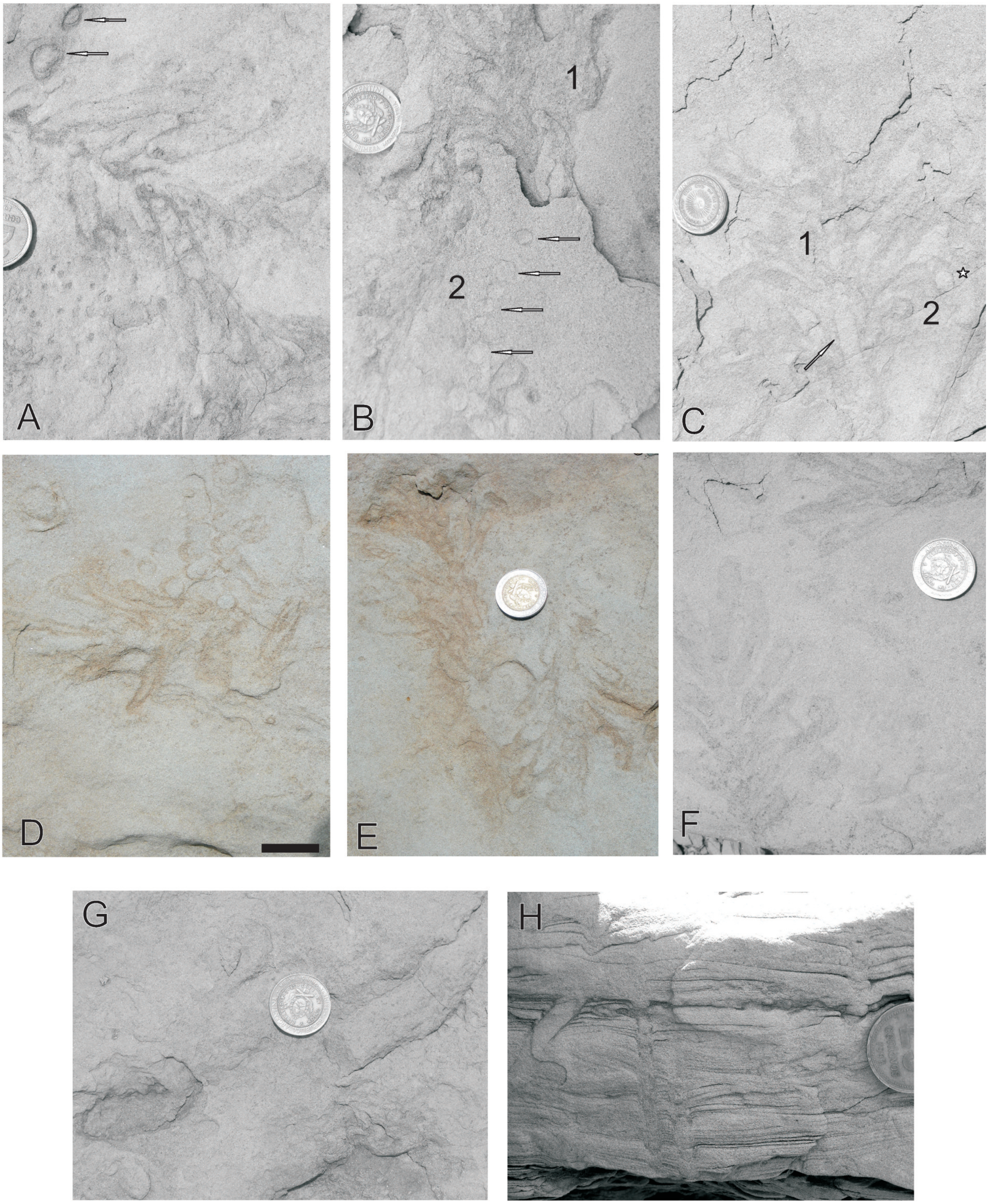
**Ichnogenus *Hillichnus* Bromley *et al.*, 2003**
***Hillichnus agrioensis* isp. nov.**

DIAGNOSIS: *Hillichnus* composed of 4 levels of exposure (Text-fig. 6). Feather/branch-like, almost flat structures (Text-figs 4A, B; 5A, C, F; 6: level 2), with a central tube (Text-fig. 5C, arrow) only visible at level 2 (Text-fig. 6); lateral branches arranged at an angle to each side (Text-fig. 4B). Branches straight to gently curved (Text-figs 3A, B) or palmate (Text-fig. 5F), variable within specimens (Text-figs 5A, C). In level 3, series of tubes mark the course of the branches in a deeper level (Text-fig. 6: level 3); in level 2, these series may be isolated at the end of each branch segment (Text-fig. 4B: 2). Level 4 (Text-fig. 6) comprises lobes with disturbed dark sediment (Text-figs 4 A: 3; 5B:1) and shows a vertical connection with level 2. Level 1, bearing vertical shafts, is not always present.

DESCRIPTION: This ichnospecies, as the type ichnospecies, is the result of a three-dimensional reconstruction. It was achieved by taking into account at




Text-fig. 4. Iconotypes of *Hillichnus agrioensis*. A – Branches (1) preserved as hyporrelief (almost flat) and convex in the frontal lobe (3) with bilateral geometry. Vertical projections (2) or small tubes. B – Feather-like branches showing spreiten (1) and lining and vertical projection (2) at the external part. The inner part (3) showing more tubes than spreiten. Black bar for scale = 2.3 cm




Text-fig. 5. A – Levels 2 and 3 showing branches, tubes with double ring (arrowed), and bunches of tubes. B – Two levels showing aligned tubes (2) pointed with arrows and a lower part (1) with lobes and sediment remobilization preserved as epirelief. C – Specimen showing a central tube with lining (arrow), a branch with changes in morphology (2) and tubes (*). Almost flat relief. D – *Jamesonichnites*-like forms with a double ring to top left. Black bar for scale = 2.3 cm. E. Similar to D, but with a clear retractile movement making spreiten with orange oxidation. F – Palmate branches. Almost flat relief. G – *Ophiomorpha* isp. Section showing pellets of one specimen cross-cutting the strata (lateral view). H – Vertical shafts corresponding to level 1 (Text-fig. 6). The thick, inclined tube is not clearly connected with the traces. Black bar for scale = 2.3 cm least 15 specimens, most of them corresponding to level 2, some to level 3 and 4, and only one to level 1. Level 4 is diagnostic of this new ichnospecies and the variable morphology observed in the branches of level 2 is absent in the type ichnospecies. In the latter, each stem shows the lammellar record with a series of feather-like fine impressions. In this new ichnospecies, rather than typical feather-like lamellar structures, spreiten documenting the lateral and downward movement of the siphons is recognised. Levels composed of the central tube in isolation were not observed in this new ichnospecies, but this may be a taphonomical artifact.

Preservation is almost always hypichnial. In level 2, material into each branch of the stem contrasts with the surrounding rock and contains fine-grained particles, particularly lining the borders. Isolated, grouped or aligned tubes (Text-fig 5B: 2, arrowed) are observable. Vertical shafts of level 1 (Text-fig. 5H), are not necessarily present, but sometimes appear as isolated double rings exposed on surface (Text-figs 5A, D: top left) or poorly preserved in level 3 (Text-fig. 6). Structures of level 4 resembling *Lophoctenium*-like traces are subtly preserved (Text-figs 4A. 3, 5B. 1).

One poorly preserved specimen from level 2 was collected and housed in the palaeontological repository of the FCEN-UBA (TC 21 244). Definitely, the best preserved part of this ichnospecies is the feather/branch-like form with a central (basal?) wall-lined tube up to 0.7 cm in diameter (Text-figs 4B, 5A, C; not always visible). The width of each branch is similar to that of the central tube, but a rounded form with an increase in width was observed on the external part in some specimens (Text-fig. 5F). The maximum length of each feathered form is 15 cm (Text-fig. 4B) but is most commonly 10 to 12 cm; the maximum whole width is approximately 8 cm (e.g. Text-fig. 4B). Only curved branches are constant in width (Text-fig. 4A. 1).

Vertical traces made by siphons are as much as 6 cm long but may have been longer before erosion. One specimen (Text-fig. 4A) with curved branches has connecting tubes (Text-fig. 4A. 2) oriented downwards and a *Lophoctenium*-like area occupying the lower level of the compound trace (Text-fig. 4A. 3), forming a lobed area with remobilised material, but also where a subtle bilateral disposition is distinguishable. It is considered the most interesting specimen, which, together with the trace illustrated in Text-fig. 4B, forms the core of the iconotype (i.e. drawing or photograph of a type specimen, used when a holotype cannot be formally established).

Structures in level 2 (Text-fig. 6), with their repetitive displacement, staggered and alternate symmetry, confirm that siphons were paired, as is typical of tellinaceans lacking mantled siphons (Bromley *et al.* 2003). Level 4 may be due to the release of faeces by downward movement of tentacles, although it is not clear if feeding was also involved. Level 1 records the central tube containing the siphons directed toward the surface. Planes containing clustered tubes aligned with the branches are not found in our material, but short courses of central and lateral tubes were observed (level 3).

DERIVATION OF NAME: From the Agrio Formation (see type horizon, Text-fig. 2).

ICONOTYPE: Text-figs 4A, B, 5C. The holotype is uncollectable given the exposure of the rock that bears the best preserved and most complete example of this trace fossil, including the central tube, branches of different shapes, isolated tubes emerging laterally, and deeper levels.

TYPE HORIZON: Siliciclastic package previously described and illustrated in Text-fig. 2.

TYPE LOCALITY: Mina La Continental, 9 km away from the National Road Nº 40, east of Las Lajas locality.

ETHOLOGICAL CHARACTERISTICS: This trace fossil is ethologically significant because it records variations in behaviour both within the same plane and also at different levels of exposure (Text-fig. 6). Level 1, the uppermost level, contains the superficial expression of the central tube used for respiration, and in lateral view the rising tubes produced by the movement of the siphons. Level 2 contains the impressive branch/feather-like forms, which record a combination of locomotion and (mainly) deposit-feeding, produced by probing with the retractile inhalant siphon, working alternately to each side. Feeding and digestion may have produced changes in the detrital minerals, as was shown in degradation, authigenesis, and destruction of some clay mineral like chlorite by *Arenicola marina* Linnaeus 1758 in experiments (McIlroy *et al.* 2003) that as a result became more susceptible to weathering and oxidation. A slightly decorticated plane (level 3) contains the trace of the downward movement of the siphon, while level 4 is considered to be the record of defaecation or feeding. Feeding structures, which so far are the most common, indicate the probing of the substrate (e.g. Bender and Davis 1984) with palpal tentacles. One of the features that Bromley *et al.* (2003) did not have a chance to analyse was vertical upward or downward movement of faeces. Studies by Chattopadhyaya *et al.* (2003) on tellinaceans living among mangroves indicate that faeces are usually deposited downward in the sediment; this behaviour also seems likely in our material (Text-fig. 4A. 3).

## COMPARISON WITH FEATHER-LIKE TRACES

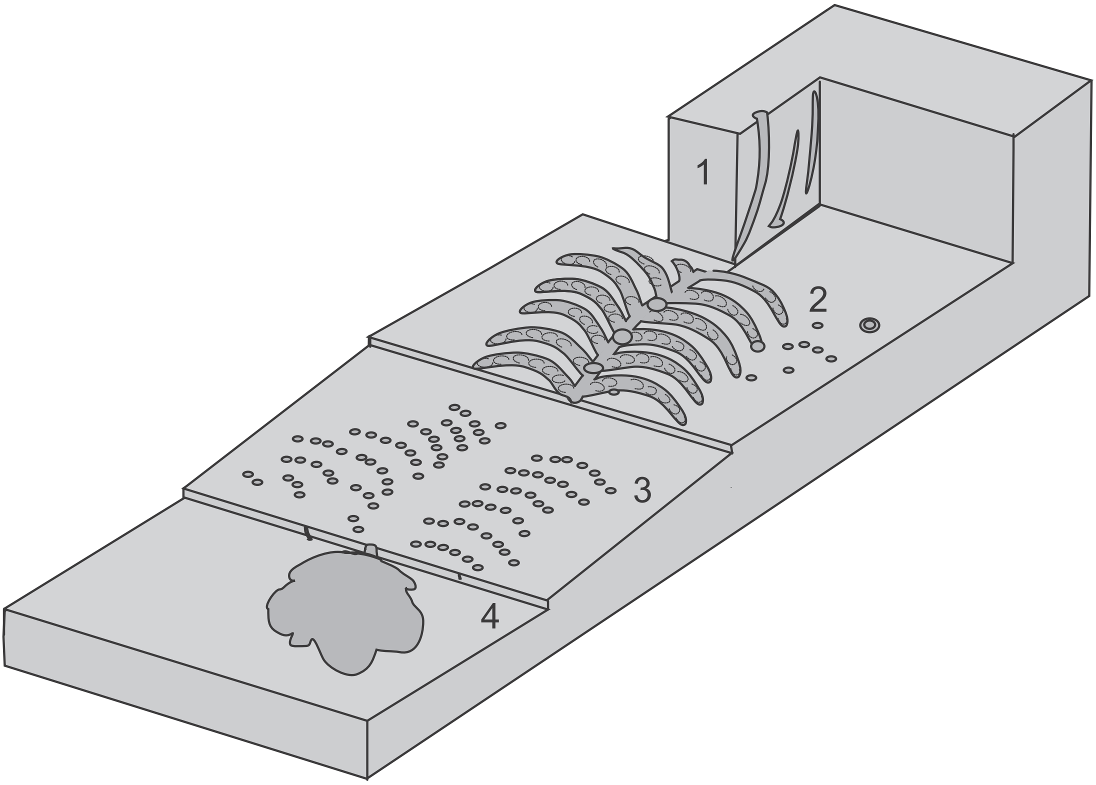
The traces assigned to this new ichnogenus contain the main diagnostic features of *Hillichnus* Bromley *et al.* (2003). However, the new ichnospecies suggests vertical movement of siphons not only for respiration but also for defaecation or deposit-feeding, which in fact was observed in living tellinaceans. We consider, however, that a deeper-tier position of the bivalve is more likely than in Palaeocene *Hillichnus lobosensis*.

The material studied here has been compared with the iconotype of *Hillichnus lobosensis.* The specimen regarded as holotype by Bromley *et al.* (2003) was not directly analysed. Nevertheless, the presence of different (vertical) expressions of lamellar movements permits herein the establishment of the iconotype for *H. agrioensis*. We consider that vertical movement for feeding or defaecation is a valid ichnotaxobase at the ichnospecies rank because it indicates differences in behaviour, although the diagnostic features of the ichnogenus remain identifiable. In addition, *Hillichnus lobosensis* presents a more meandering pattern, a more regular shape of each branch and stem, and a greater length (at our level 2) than *Hillichnus agrioensis*.

Despite the differences, it is possible to introduce an analogy between levels 1 to 4 (Text-fig. 6) proposed in this paper with levels A to E established by Bromley *et al.* (2003, fig. 4). Level 1 is equivalent to level E proposed by those authors, while levels 2 and 3 correspond to their C and D levels. Level 4 has no analogue in the material described by Bromley *et al.* (2003). Conversely, analogues of levels A and B are not present in our material.

*Hillichnus agrioensis* somewhat resembles a trace, also reported in very shallow marine deposits, from the Jurassic of Greenland by Dam (1990a, b), *Jamesonichnites heinbergi,* which according to Bromley *et al.* (2003) is included in the "family of *Hillichnus*". However, we can now conclude that *J. heinbergi* is a variant of expression of our level 2. The lack of evidence for vertical exploration of siphons for respiration or defaecation may have led Bromley *et al.* (2003) to be cautious with suggesting synonymy between both ichnogenera.

Recently, Lazo *et al.* (2008b, fig. 2, 8) reported *Jamesonichnites heibergi* from the Oxfordian carbonate




Text-fig. 6. Reconstruction of *Hillichnus agrioensis*. Level 1 is the expression of the vertical shafts. Level 2 contains branches and isolated or series of tubes. Level 3 is a slightly decorticated level 2 (partially observed). Level 4 is the deepest level and includes lobate forms that are in part similar to *Lophothecnium*. Scales change with level (idealized) beds of the La Manga Formation in the Neuquén basin. In that case, the material figured by Lazo *et al.* (2008) consists of longer feather-like forms, similar to those in level 2 of *Hillichnus lobosensis* (Bromley *et al.* 2003, fig. 4: level C). This occurrence is from shoreface deposits, rather than turbidites as in the record of the type ichnospecies. We suggest that this material should be included in *Hillichnus*. However, deciding whether it is an example of *H. lobosensis* or *H. agrioensis* would be premature, and more sections for 3D reconstructions are necessary to elucidate such uncertainty. Buatois *et al.* (2001) referred to *Polykampton* "flower-branched" traces from flysch of the Tarcau basin, Romania; these traces resemble *Polykampton* more than *Hillichnus*. Finally, the "ikebana" forms illustrated by Seilacher (2008), and now under study by Nara (pers. comm. 2008), are similar to *Polykampton* and not comparable in shape, size or occurrence with *Hillichnus agrioensis*. The oldest record of *Hillichnus* is from the Mississippian of Georgia (Rindsberg and Martin 2007), where the palaeonvironmental context (a brackish-water setting) is more similar to the one presented here.

## DISCUSSION

*Hillichnus lobosensis* and *H. agrioensis* alike represent examples of compound trace fossils, which arise from a behavioural change of a single tracemaker (Pickerill 1994; Rindsberg and Martin 2003). As Bertling *et al.* (2006) stated, there are basically two kinds of behaviour that may lead to the formation of such structures: either the same individual behaves differently in a chronological order, or it simultaneously behaves in two distinct ways. The latter is the case in *Hillichnus* (Bromley *et al.* 2003). No distinguishable variations in the substrate control the morphology of this ichnogenus.

One of the uncertainties documented by Bromley *et al.* (2003) when comparing *Hillichnus* with modern living tellinaceans is the doubt whether the tubes moved up or down, and how this may have related to defaecation. Based on our material, we conclude that the tubes moved down into the substrate while branches record deposit-feeding and locomotion, probably with the valves in vertical position as suggested by Bromley *et al.* (2003). No interaction with *Ophiomorpha* is indicated.

At first sight, the interval with branched forms (level 2) is restricted to a couple of centimetres, close to the interface with heterolithic deposits. No cross-cutting of specimens is observed with the exception of some rings, the expression of vertical tubes that may cut level 2 specimens. The relationship between the feeding activity and the layer containing a very thin accumulation of organic matter and mica probably suggests that the animal moved close to such levels, probing them beneath the surface. The vertical expression of the tubes is very unusual and should be considered as a minor ichnotaxobase, bearing in mind that modern tellinaceans can feed on the sea-floor (Bromley *et al.* 2003). No trace related to *Protovirgularia dichotoma* or almond-shaped *Lockeia* was found connected to our material, but combined *Lockeia-Lophoctenium*, as reported by Ekdale and Bromley (2001), are under study and tellinaceans remain the most probable trace-makers.

As previously suggested by Bromley *et al.* (2003), *Hillichnus* does not fit the usual ethological categories. In the case of *H. agrioensis* this situation is reinforced. Trace fossils such as these, that require 3D reconstructions, are almost impossible to identify in cores. Considering the low preservation potential of the vertical tubes in *Scolicia* de Quatrefages 1849, many ichnogenera have been based on the horizontal expression of different levels of *Scolicia* but representing decorticated or eroded levels (Uchman 2001). This was documented as different ichnogenera that artificially magnify the ichnodiversity. This could also be the case with *Hillichnus*.

## CONCLUSIONS

- *Hillichnus agrioensis* ichnosp. nov. is erected from material coming from the upper section of the Agrio Formation, upper Hauterivian–?Barremian (Upper Cretaceous), at Mina La Continental.
- *H. agrioensis* records deposit-feeding (fodinichnia), horizontal displacement (repichnia), respiration, and defaecation in at least 4 levels of exposure. Defaecation in the deepest level (4) concords with modern tellinacean behaviour.
- The material here described occurs in marginal-marine facies instead of turbidites as in the case of the type species *Hillichnus lobosensis.*
- Associated but not physically connected traces are *Ophiomorpha*.
- Traces produced by tellinaceans in the Agrio Formation are the only evidence of this group of bivalves in the unit and in the entire Upper Cretaceous of the basin.
- This contribution suggests that the ichnology of marginal-marine facies of the Agrio Formation needs further study, which is underway. Preliminary results indicate higher complexity than that shown by studies and models based on cores, in which biogenic structures like *Hillichnus* are almost undetectable.

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