ICHNOLOGY OF MARGINAL MARINE FACIES OF THE AGRIO FORMATION (LOWER CRETACEOUS, NEUQUÉN BASIN, ARGENTINA) AT ITS TYPE LOCALITY

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Abstract. This study includes a thorough systematic analysis of the ichnological record in the uppermost section of the Agua de la Mula Member of the Agrio Formation (Mendoza Group) in the Neuquén Basin (Argentina). The Bajada del Agrio section represents an environment evolving from marine to marginal-marine. Five main facies were defined: (1) an oolitic-skeletal bar; (2) transgressive pelites and coquinas (bioclastic conglomerates); (3) progradational coarsening-upward sandstones; (4) heterolithic deposits; and (5) heterolithic and carbonatic deposits. Fluctuating salinity and/or hypersalinity is inferred in the open tidal-flat deposits (facies 4). Sixteen ichnotaxa were identified and three types of trace fossils were described using open nomenclature because of the poor preservation of the material. Three ichnoassemblages are described. The section yielded trace fossils of callianasid decapods, palaeotaxodont bivalves, annelids and small tetrapods. Paleoenvironmental information drawn from trace fossils is coincident with sedimentologic evidence. It also highlights the current lack of accurate ichnological models for marginal marine hypersaline or fluctuating-saline environments, and suggests that sharp salinity changes in the environment not necessarily implie a decrease in ichnodiversity.

Key words. Ichnology. Salinity. Marginal marine environment. Cretaceous. Neuquén Basin. Argentina. Agrio Formation.

Resumen. ICNOLOGÍA DE FACIES MARINO MARGINALES DE LA FORMACIÓN AGRIO (CRETÁCICO INFERIOR, CUENCA NEUQUINA, ARGENTINA) EN SU LOCALIDAD TIPO. Esta contribución constituye el primer análisis sistemático exhaustivo del registro icnológico de la sección superior del Miembro Agua de la Mula de la Formación Agrio (Grupo Mendoza) de la Cuenca Neuquina (Argentina). La sección de Bajada del Agrio representa un ambiente que evolucionó de marino a marino marginal. Se definieron cinco facies: (1) barra oolítico-esqueletal; (2) pelitas y coquinas transgresivas (conglomerados bioclásticos); (3) areniscas grano y estratocrecientes progradacionales; (4) depósitos heterolíticos; y (5) depósitos heterolíticos y carbonáticos. En los depósitos de planicie de marea abierta (facies 4) se registran evidencias de hipersalinidad y/o salinidad fluctuante. Se identificaron dieciséis icnotaxa en total, y se describieron tres tipos de trazas fósiles con nomenclatura abierta; además, son descriptas tres icnoasociaciones. Se registra la presencia (para esta localidad) de decápodos callianásidos, bivalvos paleotaxodontos, anélidos y pequeños tetrápodos como parte de la fauna local. La información paleoambiental tomada de las trazas fósiles es coincidente con la obtenida por la línea de evidencia sedimentológica. Además, evidencia la actual ausencia de un modelo icnológico preciso para ambientes marino marginales con hipersalinidad y/o salinidad fluctuante. Sugiere también que estos ambientes no necesariamente muestran una disminución en la icnodiversidad.

Palabras clave. Icnología. Salinidad. Ambiente marino marginal. Cretácico. Cuenca Neuquina. Argentina. Formación Agrio.

TRACE fossil assemblages are particularly useful when studying transitional environments, because of the high variations in sedimentological parameters and the complex facies organization found in these settings. In such contexts, an ichnological analysis may be relevant in order to identify physicochemical variations in the depositional setting.

Abundant trace fossils occur in the normal marine Mesozoic successions of the Neuquén Basin (*e.g.*, Lazo *et al.*, 2005; Ballent *et al.*, 2006; Bressan and Palma, 2009; Kietzmann and Palma, 2010; Kietzmann *et al.*, 2010). Only a handful of studies refer to marginal marine environments (*e.g.*, McIlroy *et al.*, 2005; Schwarz *et al.*, 2006; Rodríguez *et al.*, 2007), but these are lacking in-depth systematic analyses.

The purpose of this study is to undertake the first thorough systematic analysis of the ichnological record in the uppermost section of the Agua de la Mula Member of the Agrio Formation (Mendoza Group) in the Neuquén Basin, Argentina (Figs. 1.1–1.2).

Contributions to the study of ichnofossils in this region have been published by Spalletti *et al.* (2001a), Pazos and Cirigliano (2006), Fernández and Pazos (2008), and Fernández *et al.* (2010).

GEOLOGICAL SETTING AND STUDY SITE

The Neuquén Basin (Fig. 1.1) is located in central-western Argentina between S34° and S41°, spreading over part of the provinces of Neuquén, Mendoza, Río Negro and La Pampa. It contains an at least seven kilometer thick Meso-

zoic–Cenozoic sedimentary succession (Vergani *et al.*, 1995; Legarreta and Uliana, 1999). During the Cretaceous —and coetaneously to the deposition of the Mendoza Group (Fig. 1.2)— the Neuquén Basin was undergoing an extensional stage in a back-arc compressive setting and was strongly affected by sea-level and tectonic fluctuations because of its narrow northwestern connection with the ocean (Zapata and Folguera, 2005). Most of the Jurassic and Lower Cretaceous deposits are represented by highly fossiliferous marine facies of varied nature associated with ingressions from the Pacific Ocean (Howell *et al.*, 2005). The Agrio Formation (early Valanginian–early Barremian?) was defined by Weaver (1931) and constitutes the terminal portion of the Mendoza Group; it lies exposed from central Mendoza to southern Neuquén. It reaches a maximum thickness of 1500 m and has been divided into three members: the lower Pilmatué Member, the middle Avilé Member, and the upper Agua de

la Mula Member (Leanza *et al.*, 2001). Rocks of the Agrio Formation below surface are interdigitated (Vergani *et al.*, 1995) with the prograding fluvial siliciclastics of the Centenario Formation, and at the studied locality they are unconformably overlain by the Huitrín Formation.

The fauna of the Agua de la Mula Member is late Hauterivian–early Barremian according to Aguirre-Urreta *et al.* (2007, 2008). It is varied and abundant (see Aguirre-Urreta, 2003; Lazo, 2005; Lazo *et al.*, 2005; Rodríguez, 2007; Aguirre-Urreta *et al.*, 2011), including bivalves, corals, ammonoids, gastropods, bryozoans, serpulids, sponges, echinoids, decapods, foraminifera and ostracods. Excellent preservation, biodiversity, and abundance of organisms allows a very precise ammonoid, bivalve, palynomorph and nannofossil biostratigraphy (Bown and Concheyro, 2004; Aguirre-Urreta *et al.*, 2005, 2007; Ballent *et al.*, 2006; Lazo *et al.*, 2009).
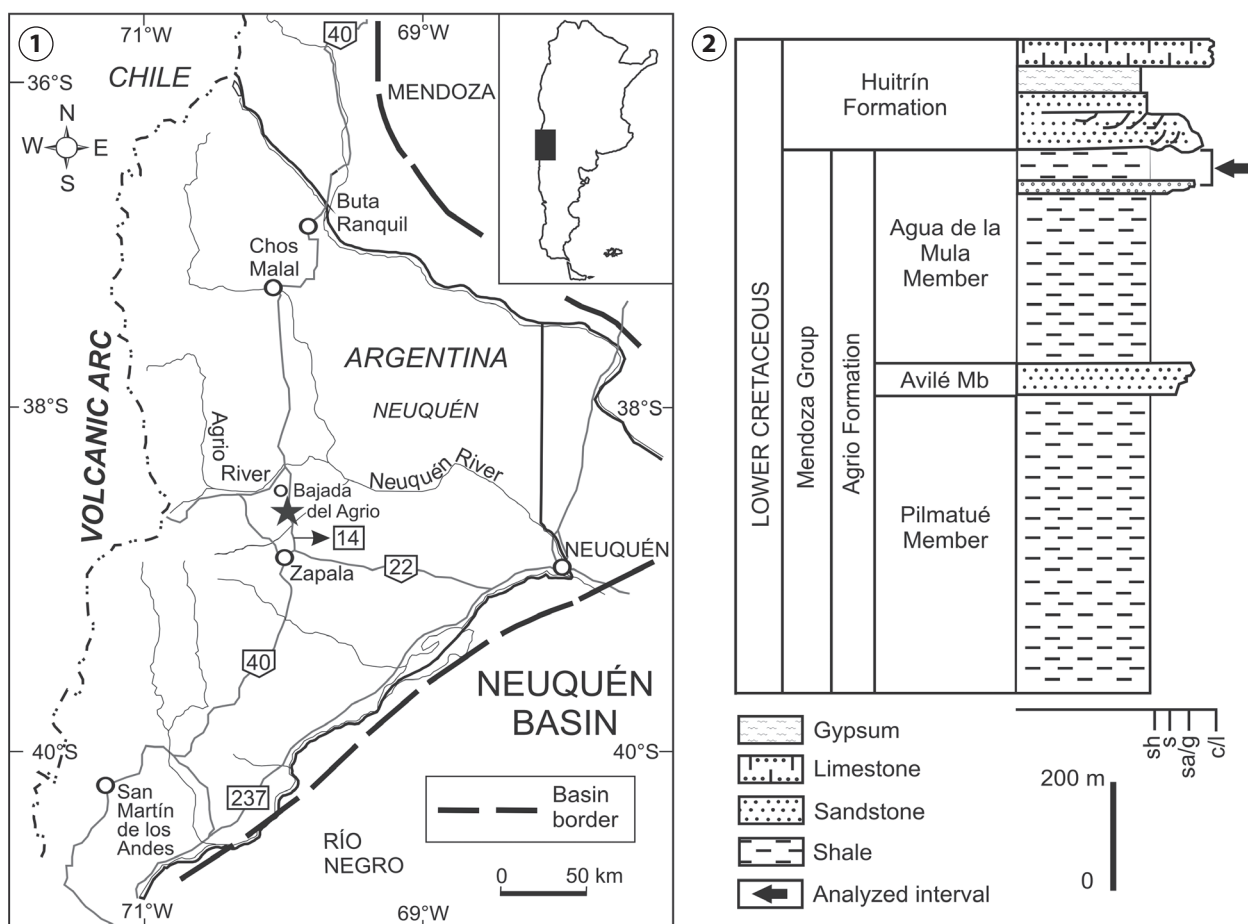

Figure 1. 1, Map of the Neuquén Basin and its position in Argentina. See location of study site (near Bajada del Agrio) marked with a star/ *Mapa de la Cuenca Neuquina y su posición en Argentina. Ver ubicación del sitio de estudio (cercano a la localidad de Bajada del Agrio) señalada con una estrella.* **2,** Stratigraphic column of the Mendoza Group. The arrow marks the position of the studied interval/ *Perfil estratigráfico del Grupo Mendoza. La flecha señala la posición del intervalo estudiado.*
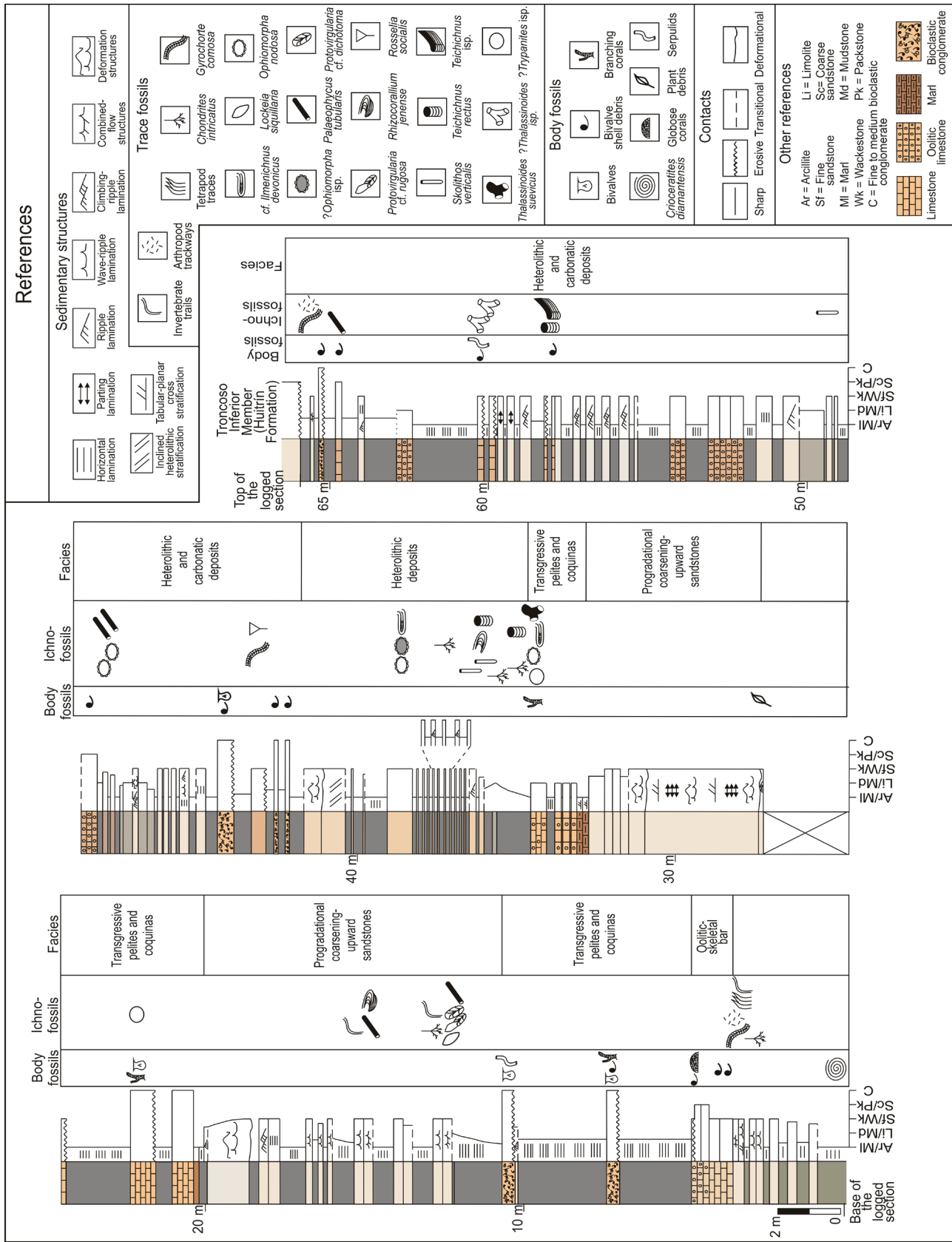
Figure 2. Logged section of the upper part of the Agua de la Mula Member at Bajada del Agrio / *Perfil columnar de la sección cuspidal del Miembro Agua de la Mula en Bajada del Agrio.*

Ammonites are extremely rare in the studied section; only a few fragmentary specimens of *Crioceratites diamantensis* (Gerth) were collected from the lower beds. However, based on lateral correlations we may assume that the studied interval partly overlaps the *Crioceratites diamantensis* and the *Paraspiticeras groeberi* biozones (Aguirre-Urreta *et al.*, 2007). The absence of *P. groeberi* Aguirre-Urreta and Rawson in the studied section could be a consequence of taphonomic bias, adverse paleoenvironmental conditions (see below), or simply years of fossil collecting at this well-known locality. Nevertheless, this absence has already been reported also for this interval at Mina La Continental (Tunik *et al.*, 2009).

The study area (Fig. 1.1) is located in the center of Neuquén Province, 56 km north from the city of Zapala and 160 km south from Chos Malal. This site is the type locality of the Agrio Formation, on the eastern limb of the Agrio anticlinal, 1.5 km south from Bajada del Agrio. The area is located between 38°23′S and 38°25′S, and 70°00′ and 70°03′W, where the uppermost section of the Agua de la Mula Member of the Agrio Formation lies well exposed on both sides of Provincial Highway 14. The intersection point between the highway and the outcrop is 38°25′12.81″S–70°00′56.99″W.

MATERIAL AND METHODS

The uppermost part of the Agua de la Mula Member (Figs. 1.2 and 2) was thoroughly analyzed. Emphasis was laid on the ichnological content; body fossils and sedimentological characteristics were examined too. Whenever possible, representative hand samples of the trace fossils were taken; these are housed in the collection of the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (**CPBA**). Facies analysis was undertaken alongside the ichnological study. It was considered convenient that these sources of information should not influence each other. Nevertheless, trace fossils were not ignored, but incorporated as data in lithofacies descriptions and interpretations. Thus, facies analysis is primarily sedimentologic. It can be divided into two parts: (1) the definition of lithofacies and their interpretation (Tab. 1, online); and (2) the combination of these into facies, and their posterior environmental interpretation (see Tab. 2, online, and the following section).

ICHNOLOGICAL AND PALEOENVIRONMENTAL BACKGROUND

Earlier studies on the depositional environment of the

Agua de la Mula Member of the Agrio Formation interpreted it as an open marine ramp (Spalletti *et al.*, 2001b; Ballent *et al.*, 2006). In particular, Spalletti *et al.* (2001a) interpreted the upper part of the Agrio Formation at Bajada del Agrio as shallow subtidal to proximal offshore sub-environments influenced by fair weather and storm waves.

Twenty-three lithofacies were distinguished in this study (see Tab. 1, online). Five main facies (Fig. 2; Tab. 2, online) were defined: (1) oolitic-skeletal bar; (2) transgressive pelites and coquinas (bioclastic conglomerates); (3) progradational coarsening-upward sandstones; (4) heterolithic deposits; (5) heterolithic and carbonatic deposits. Sub-environments represented by facies 3, 4 and 5 (see Tab. 2, online) contradict previous interpretations proposed for the top of the unit at Bajada del Agrio (*e.g.*, Spalletti *et al.*, 2001a). However, it is worth mentioning that even when these authors stated that the interval analyzed by them ends at the contact with the Huitrín Formation, the cuspidal part of the Agrio Formation is missing in their logged section (Spalletti *et al.*, 2001a, fig. 3). We consider that the last strata illustrated in their section actually correspond to our oolitic-skeletal bar, located 63 m below the contact with the Huitrín Formation. Therefore, it is possible that both studied intervals do not match completely.

Deposits at the base (first 3.2 m) of the interval represent the end of the previous depositional cycle. Therefore, they were neither interpreted as sub-environments nor included in the facies analysis, as their environmental description would be incomplete. These deposits constitute a coarsening-upward succession of tabular geometry representing a shallowing-upward marine succession. Even though they were not taken into account for facies analysis, they were included in the column because they are in contact with facies 1 and they provide ichnosystematic and water-depth information. This information is included in the systematic section but excluded from any environmental conclusion based on ichnological information.

A complete description and interpretation of the defined facies is included in Table 2 (online). In summary, the logged section represents an environment which evolved from marine to marginal-marine. It began with the last part of a shallowing-upward succession that ended in an oolitic bar. This bar was drowned by a first transgression evidenced by a ravinement surface (top of facies 1). The overlying pelites were deposited during fair weather periods, while the associated coquinas are the product of storm events (facies 2). There was eventual entry of hyperpycnal flows (facies 3) into a water-body, entailing rapid sedimentation (see Tab. 2, online, and Fig. 3.1). The system then evolved firstly into an open and later to a more restricted

tidal flat (crossed by meandering channels and heterolithic interchannel areas) with high and/or fluctuating salinity (facies 4 and 5). For further environmental information on the Agua de la Mula Member see Pazos and Cirigliano (2006), Pazos *et al.* (2007), Fernández and Pazos (2008), Lazo *et al.* (2008), Pazos *et al.* (2008a, 2008b), Concheyro *et al.* (2009), and Tunik *et al.* (2009).

Previous ichnological information for the Agrio Formation

Previous research reported the presence of trace fossils in the Agrio Formation. Lazo *et al.* (2005) found trace fossils in the Agua de la Mula Member that are typical of soft-firm muddy and sandy bottoms. In deposits interpreted as a mid-ramp setting, some of the observed traces were (1) "concretionary thalassinoid trace fossils" and (2) others assigned to *Cruziana* ichnofacies. In lithofacies interpreted as outer ramp deposits, "fine bioturbation and concretionary thalassinoid trace fossils" were also recorded. Ballent *et al.* (2006) studied the Cuesta del Chihuido section and described moderate to profuse indeterminate bioturbational structures in some levels and *Thalassinoides* Ehrenberg in others. Pazos *et al.* (2007) and Pazos (2009) reported abundant theropod trackways at the Mina La Continental section. At the same locality, Pazos and Fernández (2010) described compound trace fossils (a new ichnospecies, *Hillichnus agrioensis*) produced by tellinid bivalves.

Spalletti *et al.* (2001a) recorded the following ichnogenera in the Agua de la Mula Member at Bajada del Agrio: *Arenicolites*, *Chondrites*, *Cochlichnus*, *Gordia*, *Gyrochorte*, *Helminthopsis*, *Monocraterion*, *Palaeophycus*, *Phycodes*, *Rhizocorallium*, *Scolicia*, *Taenidium*, *Teichichnus* and *Thalassinoides*. Pazos and Cirigliano (2006) reported *Gyrochorte* from the uppermost levels of this unit.

SYSTEMATIC PALEONTOLOGY

Ichnofossil nomenclature currently follows the rules and recommendations of the International Code of Zoological Nomenclature (ICNZ, 1999). This does not free ichnology from problems, one of the biggest and most persistent being the lack of an objective ichnotaxobases system. Ichnotaxobases are the characteristics deemed appropriate for ichnotaxonomic identification (Bromley, 1990). Several authors have contributed with data and proposals aiming to reach a solution (*e.g.*, Bromley, 1990; Goldring *et al.*, 1997; Genise, 2004), but it was not until 2006 that a probable consensus was achieved. Bertling *et al.* (2006) made explicit those attributes that should be considered ichnotaxobases, suggesting at the same time the systematic rank at which they

should be used (a concept first stated by Fürsich, 1974a). It is important to mention that in the diagnoses (but not necessarily in the descriptions) of ichnotaxa it would not be appropriate to use those characteristics that have already been disregarded as ichnotaxobases. However, there are cases in which no emended diagnosis exists yet taking into account these matters. As performing an ichnotaxonomic revision is beyond the scope of this work, we chose to use the most recent (emended or not) diagnoses of the analyzed ichnotaxa. At the same time, we point out– when necessary– the use or misuse of certain features that have been rejected as bases for ichnotaxonomic attribution (Bertling *et al.*, 2006). Future emendations of those diagnoses should correct these aspects.

Some ichnologists (*e.g.*, Lockley, 2007) believe there are two trends in icnotaxonomy, *i.e.*, that of invertebrate ichnologists, with an ethological approach, and that of vertebrate ichnologists, which approach the issue from the producer's point of view ("biotaxonomic" approach). Nevertheless, others (*e.g.*, Minter *et al.*, 2007) suggested that there is no such difference. In this work, the ichnotaxobases accepted as valid by Bertling *et al.* (2006) were taken as ground for the systematic arrangement. Therefore, the approach is merely morphological, and could only be considered indirectly ethologic if taking into account that trace morphology partly reflects the producer's behaviour. There is only one example of a trace attributed to a vertebrate (see **Tetrapod swimming traces**). Given that it is not possible to identify the producer with greater taxonomic certainty, it cannot be considered that the approach has been biotaxonomic.

Identified ichnotaxa. These include those traces assigned to a certain ichnotaxon; as a total, 13 ichnogenera and 16 ichnotaxa were identified. They are: *Chondrites intricatus* (Brongniart), *Gyrochorte comosa* Heer, cf. *Ilmenichnus devonicus* Hecker, *Lockeia siliquaria* James, *Ophiomorpha nodosa* Lundgren, ?*Ophiomorpha* isp., *Palaeophycus tubularis* Hall, *Protovirgularia* cf. *dichotoma* M'Coy, *Protovirgularia* cf. *rugosa* (Miller and Dyer), *Rhizocorallium jenense* Zenker, *Rosselia socialis* Dahmer, *Skolithos verticalis* Hall, *Teichichnus rectus* Seilacher, *Teichichnus* isp., *Thalassinoides suevicus* (Rieth),?*Thalassinoides* isp. and ?*Trypanites* isp.

Lockeia siliquaria, *Protovirgularia* cf. *dichotoma* and *P.* cf. *rugosa* were found in this section but are not described herein, since they were reported by Fernández *et al.* (2010).

Traces described using open nomenclature. These are three types of trace fossils that have not yet been assigned to ichnotaxa.

Ichnogenus **Chondrites** von Sternberg, 1833

Type ichnospecies. *Fucoides targionii* Brongniart, 1828; subsequent designation by Andrews, 1955.

Diagnosis. Regularly branching tunnel systems consisting of a small number of main galleries open to the surface, which ramify at depth to form a dendritic network (Fürsich, 1974b; Uchman, 1999).

Remarks. *Chondrites* is ethologically classified as a feeding trace (fodinichnia). It is generally assigned to depositivorous and/or suspensivorous annelids or sipunculids. Fu (1991) revised the ichnogenus distinguishing only four ichnospecies: *C. targionii* (Brongniart), *C. intricatus* Brongniart, *C. patulus* Fischer-Ooster and *C. recurvus* (Brongniart). Nevertheless, other ichnospecies such as *C. stellaris* Uchman or *C. caespitosus* (Fischer-Ooster) are also used.
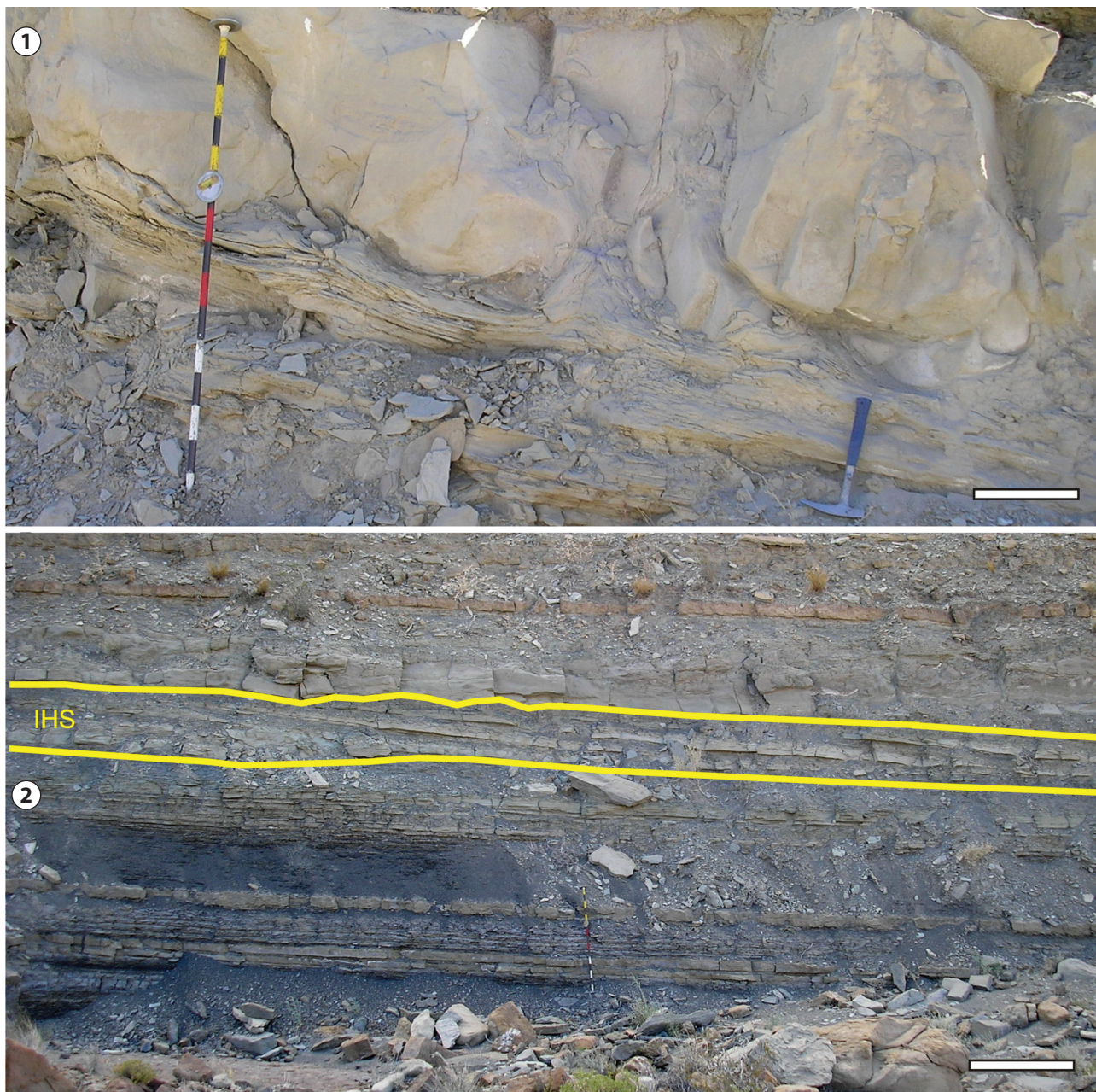

Figure 3. 1, Sandstones and siltstones with syn- to slightly post-depositional deformation structures/ *areniscas y limolitas con estructuras de deformación sin a ligeramente posdepositacionales.* Scale bar/ *escala gráfica* = 30 cm. **2,** Photo mosaic illustrating the level with inclined heterolithic stratification (IHS)/ *fotomosaico ilustrando el nivel con estratificación heterolítica inclinada (IHS).* Scale bar/ *escala gráfica* = 1,5 m.

Chondrites? *intricatus* (Brongniart, 1823)
Figures 4.1–2

Diagnosis. Small *Chondrites* composed of numerous downward radiating, mostly straight branches. The angle of branching is usually less than 45º. Branches less than 1 mm wide. Burrow system over 20 mm wide (partially emended by Uchman, 1999).

Description. The diameter of the tunnels is constant, being equal or less than 1 mm. It is preserved as: (1) endichnia, with only cross-sections of tunnels visible, filled with lighter-colored material than the host rock (both being pelitic material), and with no distinguishable ramifications; and (2) convex epireliefs (see Figs. 4.1–2) or concave hyporeliefs, with both transversal and longitudinal views available. Ramifications are observed; the angle of branching is always less than 45º and generally 20º–40º. No mastershaft open to surface was observed. Only one order of branching present.

Remarks. Because of the slight curvature of some branches and the incomplete preservation, the ichnospecific assignment remains tentative. Although Bertling *et al.* (2006) recommended not using size as an ichnospecific ichnotaxobase, we chose herein to use the diagnosis emended by Uchman (1999). While it includes diameter as a diagnostic character, it also comprises other characteristics appropriate as ichnotaxobases that allow comparison with the other three ichnospecies. It differs from *C. targionii* in the width of the branches, as in the latter these are several milimeters wide, but also commonly slightly curved (unlike the straight branches in *C. intricatus*). *C. intricatus* is also different from *C. recurvus* because in this species branching only occurs on one side of the main gallery, while in *C. intricatus* branching is more radial. In *C. patulus* the angles of branching are obtuse, while in the analyzed specimens angles are always acute. *C. caespitosus* shows rather winding branches, but they are mostly straight in *C. intricatus*. *C. stellaris* shows a width of tunnel/ width of burrow system ratio different from those in *C. intricatus* (Uchman, 1999).

Ichnogenus *Gyrochorte* Heer, 1865

Type ichnospecies. *Gyrochorte comosa* Heer, 1865; subsequent designation by Häntzschel, 1975.

Diagnosis. Wall-like burrow with a top part (positive epirelief) consisting of two convex lobes with a median furrow and a bottom part (negative hyporelief) consisting of two grooves and a median ridge. The lobes on the top (and more rarely the grooves at the base) commonly exhibit transverse meniscus-like discontinuities and often obliquely aligned plaits. Internal structure (when recognizable) consists of repetitive biconvex-up modular units (*spreiten*). Burrows exhibit an irregular meandering or arcuate course, but more rarely they may be straight or gently curved (emended by Gibert and Benner, 2002).

Remarks. The producers are endobenthic organisms, possibly gastropods, crustaceans or worms. See Gibert and Benner (2002) for a discussion of their ethology. According to Heinberg (1973), *Gyrochorte* is produced by the oblique movement of an elongated organism within the substrate. Gibert and Benner (2002) considered that the most likely producer is an annelid. The ichnogenus has been associated with a wide range of salinities, supporting an opportunistic behaviour for the producers in a context of environmental stress related to high and/or fluctuating salinities. It is common in sandy facies from shallow marine deposits of high to moderate energy, including bars, beaches and embayments (Gibert and Benner, 2002).

A very similar ichnogenus is *Aulichnites* Fenton and Fenton, which appears as a bilobate convex epirelief. Some authors considered that the lobes of *Aulichnites* are ornamented by smooth striae perpendicular to the axis (Fürsich, 1998) to transversal chevron-like marks (Sequeira Fernandes *et al.*, 2002). Others (*e.g.*, Frey and Howard, 1990; Gibert and Benner, 2002) stated they have no ornamentation whatsoever. Even when not all of the specimens analyzed in this work have a definite ornamentation, they were all considered to belong in *Gyrochorte* rather than in *Aulichnites*, following Gibert and Benner (2002). Besides, we decided not to consider size-based criteria, as size should no longer be an acceptable ichnotaxobase (Bertling *et al.*, 2006), contrarily to the opinion of Sequeira Fernandes *et al.* (2002), who stated that these two ichnogenera differ in width (*Aulichnites* being wider than *Gyrochorte*).

Gyrochorte comosa Heer, 1865
Figure 4.4

Diagnosis. Same as for ichnogenus.

Description. Burrows of straight to slightly curved course. Studied specimens are 2–4 mm wide; most of them are preserved as convex epireliefs. Oblique *spreiten* constituting inner structure (Heinberg, 1973) is not visible. The lobe ribbons are well defined only in a few specimens.

Remarks. For this ichnospecies we chose to follow the diagnosis published by Gibert and Benner (2002) for the ichnogenus; it is more adequate than the one presented by Häntzschel (1975), especially when considering that *G.*

comosa is the type ichnospecies. A revision of this ichnogenus and its ichnospecies would be of great utility, given the scanty taxonomic bibliography on the subject.

Ichnogenus *Ilmenichnus* Hecker, 1980

Type ichnospecies. *Rhizocorallium devonicum* Hecker, 1930; original designation.

Diagnosis. Unlined, horizontal to slightly oblique burrows in sediment, made up of uni-lobed to multi-lobed U-shaped *spreite* structures; exterior with longitudinal to transverse grooves and ridges (emended by Schlirf, 2011).

Remarks. For a thorough comparison with other U-shaped burrows see Schlirf (2011).

cf. *Ilmenichnus devonicus* (Hecker, 1930)
Figures 5.4, 5.6

Diagnosis. *Ilmenichnus* with straight to sinuous or planispiral *spreite*-lamina without pustules (emended by Schlirf, 2011).

Description. Tongue-like *spreiten*-burrows. Most specimens are 3–14 cm long and 6 cm wide; width generally increasing distally. Specimens are parallel to the bedding; they appear as positive epireliefs (Fig. 5.6) or as mixed positive/negative epireliefs (Fig. 5.4).

Remarks. These specimens are here tentatively assigned to the ichnogenus *Ilmenichnus* for being horizontal, U-shaped structures and presenting single-*spreiten* laminae (*sensu* Schlirf, 2011). However, the exterior "with longitudinal
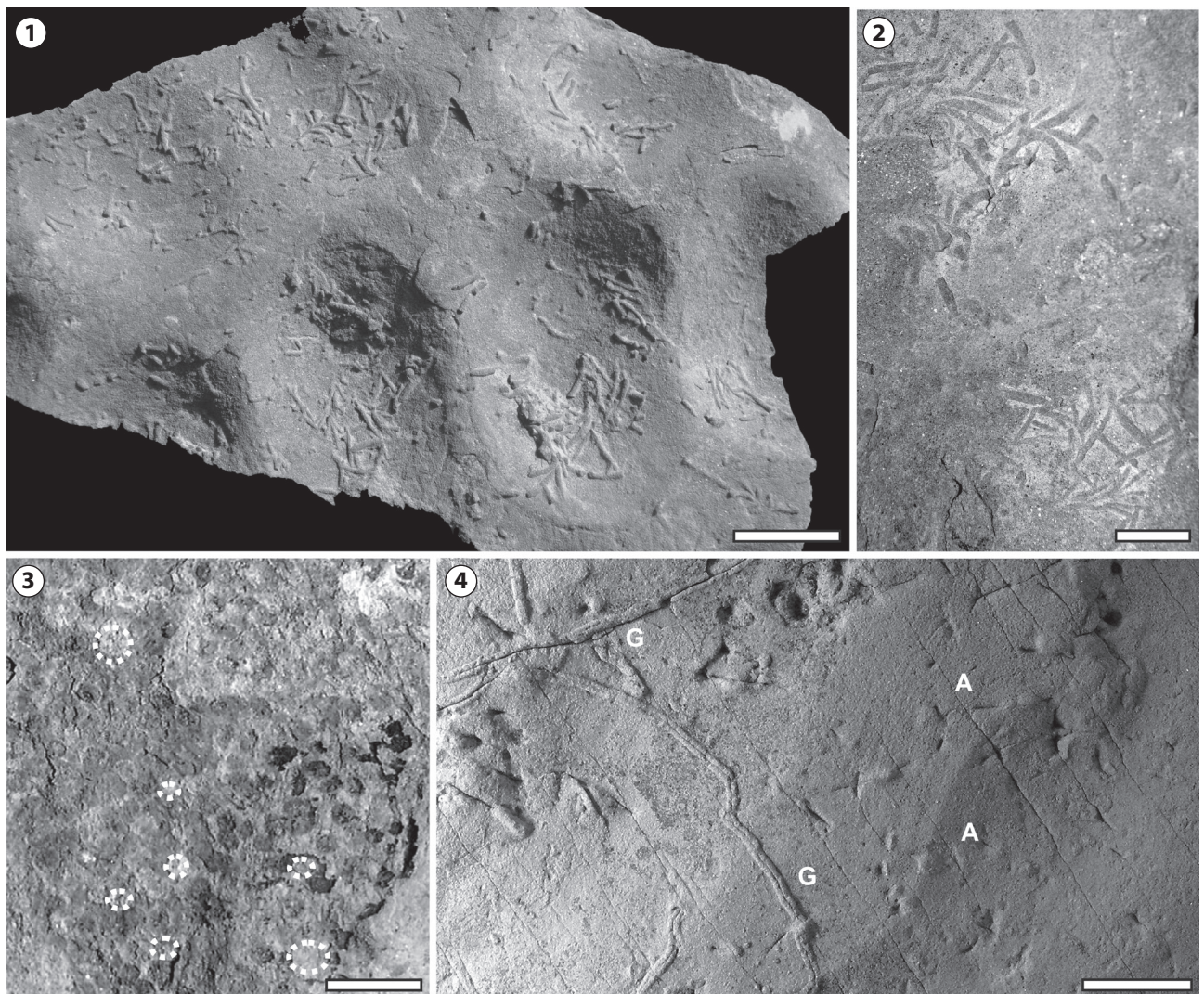

Figure 4. 1–2, *Chondrites intricatus* (Brongniart), CPBA 20433. **1,** preserved in sandstones with ripple crests as bedform/ *preservado en areniscas con crestas de óndulas como forma de lecho*; **2,** detail of CPBA 20433/ *detalle*. **3,** ?*Trypanites* isp., field photograph, on coral fragments, top view/ *sobre fragmentos de corales, vista en planta*. **4,** *Gyrochorte comosa* Heer, CPBA 20434 (G) and arthropod trackways/ *rastrilladas de artrópodos*, CPBA 20437 (A). Scale bar/ *escala gráfica* = 2 cm (1, 3–4), 1 cm (2).

transverse grooves and ridges" mentioned in the emended diagnosis (Schlirf, 2011) of this ichnotaxon is not observed. Nevertheless, this could be a preservational bias. Within *Ilmenichnus*, they fit the characteristics of the ichnospecies *I. devonicus*. Another possibility is that the specimens are in fact examples of *Rhizocorallium jenense* (see below); as they are preserved on a bedding plane, only a two-dimensional preservation is available, and the presence of double-spreite laminae (*sensu* Schlirf, 2011) cannot be confirmed.

The presence of mixed positive/negative epireliefs may indicate that –in some cases– the difference between positive or negative epirelief is not given by the sedimentologic characteristics or the preservation of the trace at the time of production. Instead it may be a result of differential preser-

vation or destruction of its elements, in particular, the marginal tunnel.

Ichnogenus *Ophiomorpha* Lundgren, 1891

Type ichnospecies. *Ophiomorpha nodosa* Lundgren, 1891; by monotypy.

Diagnosis. Simple to complex burrow systems lined at least partially with agglutinated pelletoidal sediment (Howard and Frey, 1984; modified by Uchman, 1999).

Remarks. It is mostly preserved as endichnia, and interpreted as a feeding and dwelling structure (fodinichnia and domichnia) produced mainly by callianasid decapods (Frey *et al.*, 1978). Pellets are considered to be of fecal origin. *Ophiomorpha* is usually associated with shallow marine envi-
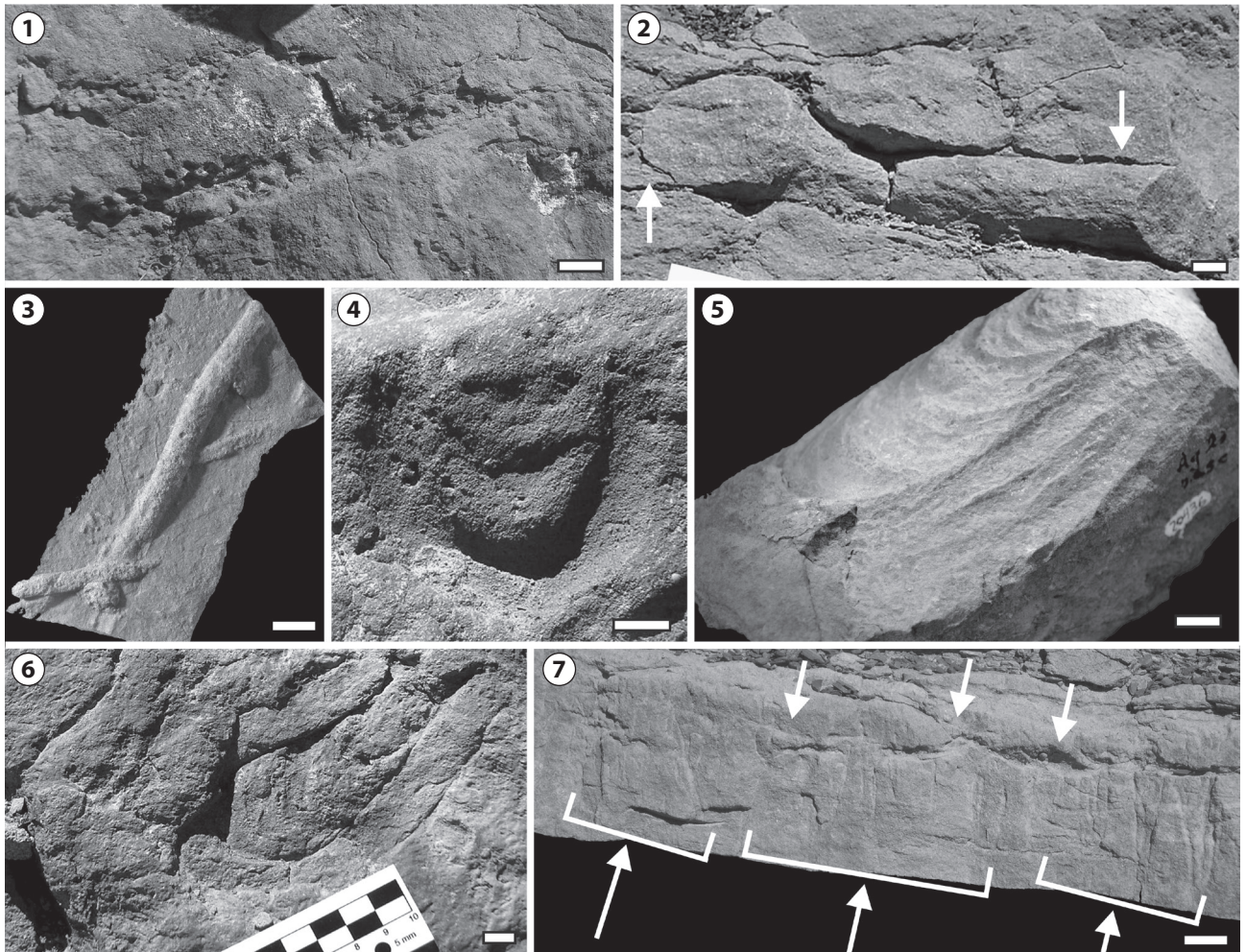

Figure 5. 1, ***Ophiomorpha nodosa*** Lundgren**,** field photograph, as endichnia in sandstones, view perpendicular to stratification/ *como endichnia en areniscas, vista en corte perpendicular a la estratificación.* **2,** ?***Ophiomorpha*** isp., field photograph, possible bifurcation point, as endichnia in sandstones, view perpendicular to stratification, the arrows mark the position of the mentioned crenulations/ *posible punto de bifurcación, vista en corte perpendicular a la estratificación, las flechas indican las crenulaciones mencionadas.* **3,** ***Palaeophycus tubularis*** Hall, CPBA 20435. **4, cf.** ***Ilmenichnus devonicus*** (Hecker)**,** field photograph. **5,** ***Rhizocorallium jenense*** (Zenker), CPBA 20436. **6, cf.** ***Ilmenichnus devonicus*** (Hecker) field photograph: two superimposed specimens/ *dos ejemplares sobreimpuestos.* **7,** ***Skolithos verticalis*** (Hall)**,** field photograph, specimens (lower arrows) and ripple lamination (upper arrows)/ *especímenes (flechas inferiores) y laminación ondulítica (flechas superiores).* Scale bar/ *escala gráfica* = 1 cm.

ronments. It can be found nowadays in all kinds of nearshore environments, including lagoons and estuary floors (Pollard *et al.*, 1993).

Ophiomorpha may be difficult to differentiate from *Thalassinoides* Ehrenberg, when specimens show poorly preserved pellets or imprints.

Ophiomorpha nodosa Lundgren, 1891
Figure 5.1

Diagnosis*. Ophiomorpha* with burrow walls consisting predominantly of dense, regularly distributed discoid, ovoid, or irregular polygonal pellets (Frey *et al.*, 1978).

Description*.* Traces oblique or horizontal to stratification. No branching is observed. Pellets are subcircular in outline and homogeneously distributed. In some weathered specimens preserved as endichnia, the external moulds of 2–3 mm diameter pellets that appear as depressions; galleries are 8–12 mm wide. In other cases, these traces are preserved as positive epireliefs, with an average diameter of 35 mm and worn pellets.

Remarks*.* As no branching was observed in the analyzed specimens, they cannot be considered "burrow systems". According to Merrill (1984), occurrence of isolated tunnels may be of significance, for instance, if the producer inhabited the substrate during a short period. But that does not seem to be the case in the specimens here analyzed. Lack of discernible branching is clearly due to the nature of the exposures of the host rock. They are missing possibly because of abrupt termination of the host stratum, or because of prolongation of the tubes into non-outcropping sectors of other beds.

Regarding the wearing observed on the outer surface of some specimens of *O. nodosa* (and the consequent loss of definition of the pellets) it is worth mentioning that —based on the study of modern beach environments— Weimer and Hoyt (1964) attributed similar characteristics in tunnels exposed to wave action. In the specimens studied herein wearing may also be attributed to this agent. However, exposure and postdiagenetic erosion or pellets originally poor in cohesion cannot be discarded.

As pointed out by most authors (*e.g.*, Anderson and Droser, 1998; Gibert *et al.*, 2006), the main diagnostic characteristics distinguishing ichnospecies of *Ophiomorpha* are the shape and arrangement of the pellets. This was the criterion followed in this paper. While in *O. nodosa* pellets are subcircular and relatively large, in *O. annulata* Książkiewicz they are elongated and arranged perpendicularly to the burrow axis; in *O. recta* Fischer-Ooster they are clayey and quite

small, in *O. irregulaire* Frey *et al.* they are oval to conical (Frey *et al.*, 1978), in *O. puerilis* Gibert *et al.* they are rodshaped with rounded ends, and in *O. borneensis Keij* they are bilobate.

?*Ophiomorpha* isp.
Figure 5.2

Description*.* Horizontal to oblique tubes of subcircular to oval outline, preserved as endichnia in cross-section or longitudinal view. The average diameter of the tubes is 3 cm, and their maximum observed lenght is 15 cm. Cross-section of specimens show subtle crenulations along the edges (Fig. 5.2).

Remarks*.* The crenulations, together with the association of these specimens with *O. nodosa*, allow us to assign them with reservation to *Ophiomorpha*. Crenulations are probably the marks left by pellets. In these cases, weathering (and consequent loss of definition of the pellets) must have taken place too. In any event, if they actually were unquestionably referable to *Ophiomorpha*, they differ from *O. nodosa* in size and preservation.

Ichnogenus *Palaeophycus* Hall, 1847

Type ichnospecies*. Palaeophycus tubularis* Hall, 1847; subsequent designation by Miller, 1889.

Diagnosis*.* Infrequently branched, distinctly lined, essentially cylindrical, predominantly horizontal to inclined burrows in which the sediment infilling is typically of the same lithology and texture as the host bed (Pemberton and Frey, 1982; modified by Frey and Howard, 1985).

Remarks*.* It is ethologically classified as a dwelling (domichnia) or feeding (fodinichnia) structure of mobile, suspensivorous or predatory worm-like organisms such as annelids (Fillion, 1989). Sediment fill is passive, gravity induced (for further detail on sediment fill see Fillion, 1989). The common type of preservation (epirelief or endichnia) suggests that the activity of the producer took place along sedimentologic interfaces (Pemberton and Frey, 1982).

A similar ichnogenus is *Planolites* Nicholson, and there has been a longtime debate about the criteria used to separate them (Aceñolaza and Yanev, 2001). Alpert (1975) proposed that the most useful criterion is the presence or absence of branching in *Palaeophycus* and *Planolites*, respectively. However, since the work of Pemberton and Frey (1982), this criterion has been disregarded (*e.g.*, Buatois, 1989; Fillion, 1989). According to Pemberton and Frey (1982), *Palaeophycus* differs from *Planolites* because of the presence of a wall. Such features may be of greater taxonomic value, as they reveal ethological aspects (Buatois, 1989).

Palaeophycus tubularis Hall, 1847
Figure 5.3

Diagnosis. Smooth-walled, unornamented, straight to sinuous cylindrical burrows, thinly but distinctly lined (Pemberton and Frey, 1982; modified by Frey and Howard, 1985).

Description. Slightly collapsed, unornamented, straight or sinuous, unbranched, hypichnial burrows. They are subcircular in outline, 3–20 mm (averaging 7 mm). The maximum observed length is approximately 14 cm. Lining is rare and less than 0.5 mm thick when present. The sediment fill is of the same lithology as that of host beds.

Remarks. Although lining is not observed in all specimens, the material was referred to this ichnotaxon because of the type of filling (passive), as reported in similar cases by other authors (*e.g.*, Buatois, 1989). Lining was possibly not preserved in some cases due to weathering (*e.g.*, Frey and Howard, 1985).

Pemberton and Frey (1982) acknowledged five ichnospecies, and they differentiated them mainly by the lining and ornamentation of the walls. *P. heberti* Saporta and *P. tubularis* are characterized by the lack of ornamentation, a feature distinguishing then from *P. striatus* Hall, *P. sulcatus* (Miller and Dyer), and *P. alternatus* Pemberton and Frey, which present parallel, anastomosing, and alternating annulations and striae, respectively. *P. tubularis* shows thinner walls than *P. heberti*. Other ichnospecies described after 1982 include *P. ferrovittatus* Hoffman and *P. canalis* Elphinstone and Walter which, unlike *P. tubularis*, show submillimetric sculpture and prominent longitudinal grooves, respectively. *P. annulatus* Badve, *P. serratus* McCann and *P. crenulatus* Buckman present annulate ornament, while *P. tubularis* includes unornamented specimens.

Ichnogenus *Rhizocorallium* Zenker, 1836

Type ichnospecies. *Rhizocorallium jenense* Zenker, 1836; by monotypy.

Diagnosis. Wedge-shaped double-*spreite* burrows, built up of U-limbs, oblique to parallel towards bedding plane; width of U constant or distally increasing; limbs distinct (emended by Schlirf, 2011).

Remarks. See Schlirf (2011) for comparison with other U-shaped burrows.

Rhizocorallium jenense Zenker, 1836
Figure 5.5

Diagnosis. More-or-less straight to bent, short protrusive U-shaped double-*spreite* laminae structures, commonly oblique to bedding plane with a vertically retrusive component (limb-*spreite* lamina); ratio of limb to limb-spreite lamina >1:2; overall morphology of resulting structure is wedge-shaped; exterior may be short, parallel longitudinal or crisscrossing ridges and grooves (emended by Schlirf, 2011).

Description. Wedge-shaped burrows with double-*spreite* laminae. The whole structure is approximately 12 cm long and between 4.5–6.5 cm wide; width generally increases distally. Specimens are oblique to the bedding plane, as endichnia.

Remarks. They are interpreted as dwelling structures (domichnia) made by mixed deposit-suspension feeding organisms (Schlirf, 2011). Uchman and Gaździcki (2006) mentioned that the distal increase in width may be reflecting ontogenetic growth of the producer.

Ichnogenus *Rosselia* Dahmer, 1937

Type ichnospecies. *Rosselia socialis* Dahmer, 1937; by monotypy.

Diagnosis. Vertical to inclined, generally downwards-tapering single or rarely branched (in form of secondary successive branching), lined burrows, circular to irregularly oval in cross-section; burrow in part layered concentrically around a central to excentral tube (emended by Uchman and Krenmayr, 1995).

Remarks. It is classified as a feeding structure (fodinichnia) and/or a dwelling structure (domichnia) of annelids, crustaceans or sea anemones (Chamberlain, 1971; Chamberlain and Clark, 1973; Książkiewicz, 1977; Sequeira Fernandes *et al.*, 2002). The basal portion of *Rosselia* is similar to *Cylindrichnus concentricus* Howard; intergradation between both has been observed in isolated specimens (Sequeira Fernandes *et al.*, 2002). *Cylindrichnus* may constitute, at least in some cases, an erosional remnant of *Rosselia* (McCarthy, 1979). The intergradation and/or resemblance with specimens of *Asterosoma* von Otto have been also commonly reported (*e.g.*, Chamberlain, 1971; Cotter, 1973; Howard and Frey, 1984; Miller and Knox, 1985). According to Chamberlain (1971), the two represent the same type of behaviour of a worm-like organism, *Asterosoma* being the horizontal expression; the latter is interpreted by Bromley and Uchman (2003) as produced by a small deposit-feeding organism. According to these authors, *Asterosoma* and *Cylindrichnus* are both in need of taxonomic revision; this might also shed more light on their differences with *Rosselia*. *Rosselia* is distinguished from *Monocraterion* Torell because the base of the latter is a simple shaft, while the interior or *Rosselia* carries laminae (Frey and Howard, 1985). As the host bed is not laminated, we cannot make reference to any downward deflection of the laminae adjacent to the trace, typical of escape traces (Pienkowski, 1985) and collapse structures (Kamola, 1984). More impor-

tantly, the conical morphology of the structure observed as a whole and the cone-in-cone laminar inner configuration are both distinctive characters of *Rosselia* and are not present in escape or collapse structures.

Rosselia socialis Dahmer, 1937
Figure 6.1

Diagnosis. *Rosselia* displaying bulb-like swelling(s) in the proximal part of burrow (emended by Uchman and Krenmayr, 1995).

Description. Conical structure, sub-perpendicular to bedding, with a maximum diameter (2.3 cm) at the top and a minimum diameter (0.8 cm) at the base. The approximate length is 10 cm. Cone-in-cone laminae are observed internally. It is preserved as endichnia.

Remarks. *R. socialis* used to be distinguished from other ichnospecies of *Rosselia* by its inner structure and the shape of the upper part of the burrow. Uchman and Krenmayr (1995) revised this ichnogenus and synonymized *R. rotatus* McCarthy with *R. socialis*. They also pointed out that *R. chonoides* Howard and Frey could be either reworked *R. socialis* or something else, and should therefore be excluded from this ichnogenus. The general shape of the analyzed specimens is similar to the spindle-type morphology (Fig. 6.2) instead of the funnel-type one, both proposed by Nara (1995; 1997). According to Nara (1995), the producers could be terebellid polychaetes. Other options could be other annelids or sea anemones (*e.g.* Chamberlain, 1971; Schlirf, 2003). Frieling (2007) pointed out that *R. socialis* is typical of shallow marine siliciclastic environments. Uchman and Krenmayr (1995) stated that *R. socialis* reflects an inter- to sub-tidal environment in Miocene deposits.

Ichnogenus *Skolithos* Haldeman, 1840

Type ichnospecies. *Fucoides linearis* Haldeman, 1840; by monotypy.

Diagnosis. Single, vertical, unbranched burrows, cylindrical or subcylindrical, lined or unlined. Burrows perfectly straight to curved, sometimes inclined to the vertical. Diameter 1–15 mm; length from a few centimeters up to 1 m; diameter may vary slightly along lenght of burrow (from Alpert, 1974).

Remarks. Ethologically, this is a dwelling or feeding trace. In the cases where it is found in marine environments, the possible producers are polychaetes or phoronids (Alpert, 1974; also see Sequeira Fernandes *et al.*, 2002 and references therein). *Skolithos* appears in a variety of shallow marine environments; it has been documented from normal marine

settings to lagoons, bays, mouth-bars and fluvial channels (Uchman *et al.*, 2004).

Skolithos is usually differentiated from *Monocraterion* Torell because in the latter the aperture is funnel-shaped, while in *Skolithos* it is not expanded. First Hallam and Sweet (1966) and then Alpert (1974) mentioned the possibility that segments of *Monocraterion* lacking the conical expansion may be identified as *Skolithos*. He also pointed out that other vertical to sub-vertical burrows similar to *Skolithos*— such as *Diplocraterion* Torell and *Arenicolites* Salter— can be distinguished for being U-shaped. Bertling *et al.* (2006) stated that characteristics with a low preservation potential, such as tops of vertical burrows, are more likely to be eroded, and are therefore considered inappropiate as ichnotaxobases. In the case of the analyzed specimens, however, there is no evidence of erosion at the top of the *Skolithos*-bearing beds.

Skolithos verticalis (Hall, 1843)
Figure 5.7

Diagnosis. Burrows cylindrical to prismatic (when in contact), straight to curved, vertical to inclined. Diameter 1–4 mm; length 2–15 cm. Burrow wall smooth, rarely corrugated (from Alpert, 1974).

Description. Vertical to slightly curved, non-lined endichnia, 1 mm in diameter and up to 60 mm long, perpendicular or sub-perpendicular to bedding, filled with the same material as the host rock (fine-grained sandstone) but lighter in color. Some of the filling has been eroded, rendering the burrows an appearance of smooth grooves in vertical planes. The maximum length for approximately 50% of specimens appears to be controlled
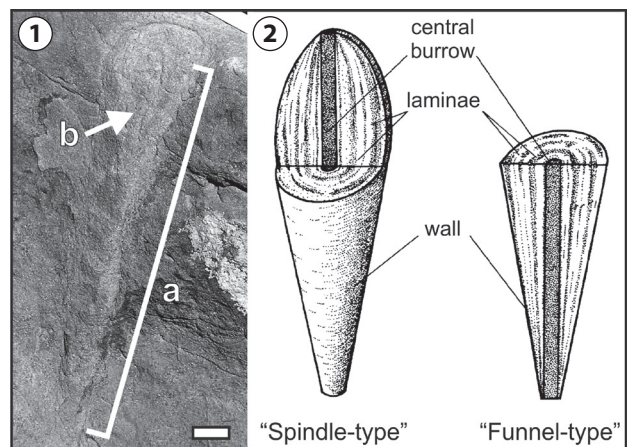

Figure 6. 1–2, *Rosselia socialis* Dahmer; **1,** field photograph, **a,** specimen, **b,** notice the central burrow/ *ver canal central (b)*; **2,** drawing of the morphology and internal structure of (from Nara, 1995)/ *esquema de la morfología y estructura interna (tomado de Nara, 1995)*. Scale bar/ *escala gráfica* = 1 cm.

by the maximum bed thickness. At the top of the beds, some of the tube openings can be seen, showing a circular outline.

Remarks. Alpert (1974) mentioned about 35 ichnospecies of *Skolithos* and related synonimized ichnogenera. However, he considered valid only five ichnospecies, *i.e.*, *S. verticalis* (Hall), *S. linearis* Haldeman, *S. magnus* Howell, *S. ingens* Howell and *S. annulatus* Howell. *S. verticalis* is distinguished from *S. linearis* and *S. magnus* because these last two show a greater diameter (3–7 mm and 6–12 mm, respectively) and also because of the wall characteristics and the nature of contacts (see Alpert, 1974). *Skolithos ingens* and *S. annulatus*, in addition to having a greater diameter, carry characteristically ornamented walls (protuberances in *S. ingens* and annulation in *S. annulatus*), which are absent in *S. verticalis*. Again, it should be stressed that size is not recommended as an ichnotaxobase at a specific level, despite the fact that it was used in the diagnosis of Alpert (1974) as he lacked modern systematic revisions of the ichnogenus dealing with this feature. *S. bulbus* Alpert, 1975, is distinguished from *S. verticalis* because of the presence of prominent bulbous expansions which are absent in the latter.

Ichnogenus *Teichichnus* Seilacher, 1955

Type ichnospecies. *Teichichnus rectus* Seilacher, 1955; by monotypy.
Diagnosis. Blade-like to gently curved, rarely branched *spreiten* structures consisting of several closely concentric, horizontal or inclined, longitudinally nested burrows inosculating to simple, singular tunnels. Burrows within a given *spreite* displaced upward (retrusive) or downward (protrusive), and oriented at various angles with respect to bedding (from Frey and Howard, 1985).
Remarks. An ethological interpretation places this trace in the groups of feeding or combined dwelling/feeding structures. They are usually attributed to annelids and other members of worm-like phyla, or even arthropods moving upward or downward. The *spreiten* probably represent an equilibrium response by the organism in an attempt to maintain the base of its burrow at a certain adequate depth within the substrate. They are generally preserved as full relief.

Teichichnus rectus Seilacher, 1955
Figure 7.1

Diagnosis. *Teichichnus* with more or less straight *spreite* lying in a vertical plane; longitudinal axes of *spreiten* oriented at various angles with respect to bedding (from Frey and Howard, 1985).
Description. All specimens are long, straight endichnia with retrusive *spreiten* and parallel to the bedding. The burrow is 1.2–1.5 cm wide and up to at least 10 cm long.

Teichichnus isp.
Figure 7.2

Description. Endichnia filled with the same material as the host rock. They present a sinuous axis, which is at least 20–25 cm long. The structure as a whole, as well as each *spreiten* lamina, is concave-upwards. It is 1 cm wide.
Remarks. It is differentiated from *Teichichnus rectus* by the oblique inclination of the plane containing the *spreiten* with respect to the bedding.

Ichnogenus *Thalassinoides* Ehrenberg, 1944

Type ichnospecies. *Thalassinoides callianassae* Ehrenberg, 1944; original designation.
Diagnosis. Large burrow-systems consisting of smooth-walled, essentially cylindrical components. Branches Y- to T-shaped and typically enlarged at bifurcation points. Burrow dimensions variable within a given system (from Frey and Howard, 1985).
Remarks. This ichnogenus is generally classified as a combination of dwelling and feeding structures, usually attributed to infaunal crustacean decapods —probably callianasids or similar arthropods.

Thalassinoides differs from *Ophiomorpha* by the lack of pellets on its walls. However, intergradations between the two genera are known to occur (*e.g.*, Frey *et al.*, 1978), and they constitute a typical example of compound traces (Bertling *et al.*, 2006).

Thalassinoides suevicus Rieth, 1932
Figure 7.3

Diagnosis. Predominantly horizontal, more or less regularly branched, essentially cylindrical components forming large burrow systems; dichotomous bifurcations more common than T-shaped branches (from Frey and Howard, 1985).
Description. Horizontal galleries with Y-shaped bifurcations and smooth margin, at least 10 cm long. Specimens consist of segments containing the bifurcation point; the three corresponding branches are not always observed.
Remarks. *Thalassinoides suevicus* differs from *T. paradoxicus* Woodward because the latter is less regularly branched, because it may be oriented at different angles from the bedding plane (horizontal examples are not predominant), and because T-shaped intersections are more common that Y-shaped bifurcations (Howard and Frey, 1984). *Thalassinoides suevicus* is also distinguished from *T. bacae* Ekdale and Bromley because the latter carries numerous and prominent vertical burrows associated with the horizontal ones. *T. horizontalis* Myrow presents a thick lining, absent in *T. suevicus*.

?*Thalassinoides* isp.

Figure 7.5

Description. Horizontal burrow-systems, more or less regu-larly branched, preserved as epichnia. Numerous bifurca-tions are observed, at an average of 18 cm apart. Galleries are 4–8 cm wide. The filling is mainly bioclastic (different
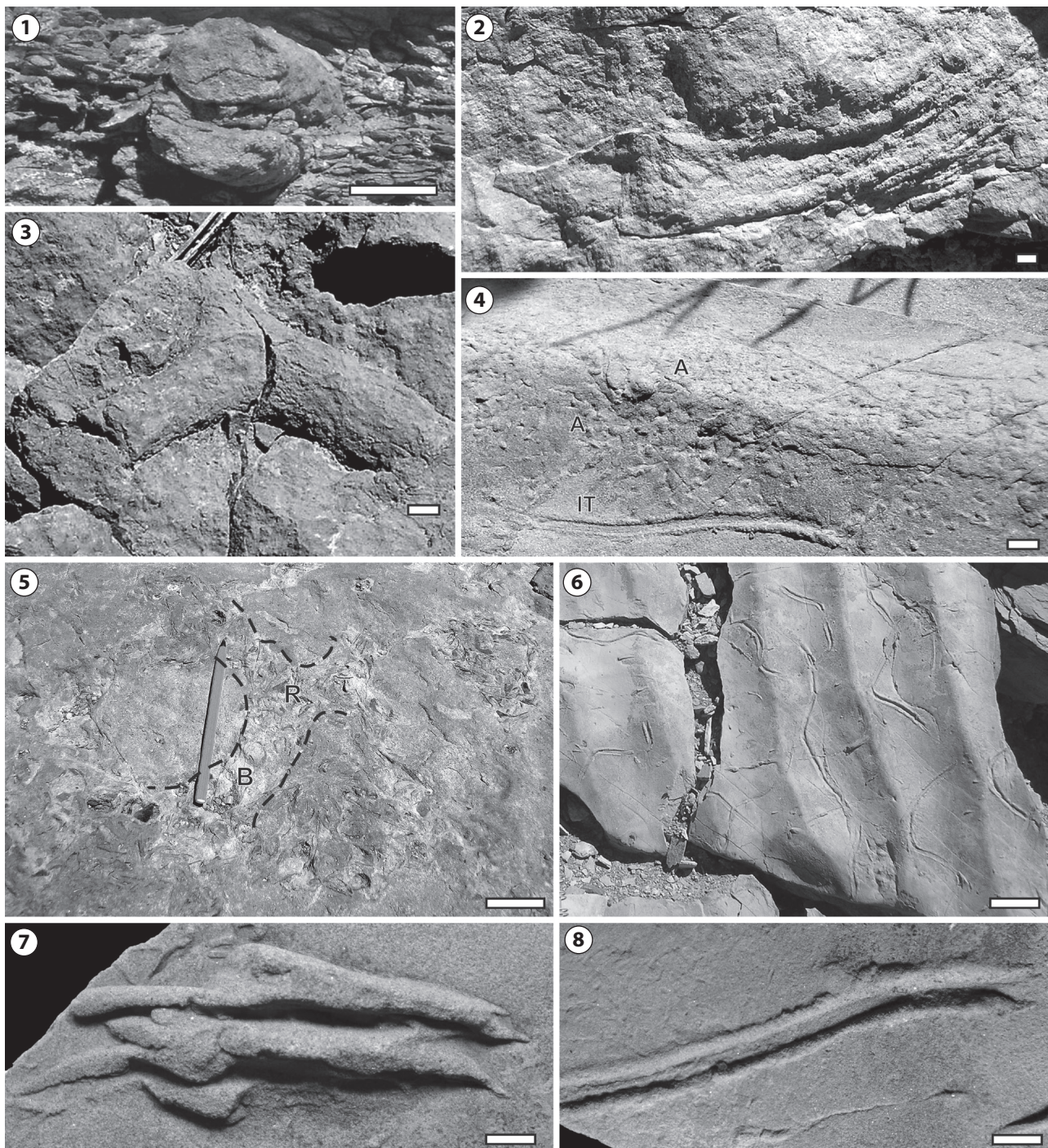

Figure 7. 1, *Teichichnus rectus* Seilacher; field photograph, in pelites/ *en pelitas*. **2,** *Teichichnus* isp., field photograph, view perpendicular to stratification/ *vista en corte perpendicular a la estratificación*. **3,** *Thalassinoides suevicus* Rieth, field photograph, "Y" ramification point/ *punto de ramificación en "Y"*. **4,** Field photograph: Invertebrate trails (IT) and arthropod trackways (A)/ *pistas de invertebrados (IT) y rastrilladas de artrópodos (A)*. **5,** ?*Thalassinoides* isp., field photograph, notice the bioclastic filling (B) of the galleries and "Y" ramification point (R)/ *notar el relleno bioclástico (B) de las galerías y el punto de ramificación en "Y" (R)*. **6,** Invertebrate trails and wave ripples, field photograph/ *pistas de invertebrados y ondulitas de oleaje*. **7,** Tetrapod swimming trace, CPBA 20438/ *traza de natación de tetrápodo*. **8,** Invertebrate trail, CPBA 20440/ *pista de invertebrado*. Scale bar/ *escala gráfica* = 1 cm (1 –4), 5 cm (5–6), 5 mm (7–8).

from the host rock), homogeneous, with bioclasts that are approximately 2 cm long.

Remarks. The homogeneity of the bioclastic fill suggests it was probably passive.

Ichnogenus *Trypanites* Mägdefrau, 1932

Type ichnospecies. *Trypanites weisei* Mägdefrau, 1932; by monotypy.

Diagnosis. Single-entrance, cylindrical, unbranched borings in lithic substrates, having circular cross-sections throughout length. The axes of the borgins may be straight, curved or irregular (Neumann *et al.*, 2008; modified after emended diagnosis in Bromley and D'Alessandro, 1987).

Remarks. Lithic substrates include all types of rocks, as well as hard skeletons such as coral, shell and bone (Kelly and Bromley, 1984). This ichnogenus is ethologically classifed as a dwelling trace (domichnia) and can be produced by different tracemarkers such as polychaetes, sipunculids, crustaceans and echinoids (Bromley, 1992; Asgaard and Bromley, 2008). *Trypanites* differs from *Gastrochaenolites* Leymerie because the latter presents a constriction (neck) in the apertural region and a lower diameter/length ratio (Bromley and D'Alessandro, 1987).

?*Trypanites* isp.
Figure 4.3

Description. Borings perpendicular to stratification produced on silicified *in situ* corals. The only parts of the borings exposed are their more external circular cross-sections, with a diameter of 2–4 mm. They are filled with fine-grained material and their preservation is not very good.

Remarks. Given the type of preservation (only cross sections on the surface of corals), it is not possible to determine with certainty if these are in fact *Trypanites*: the length of the borings is not observable. Although no constrictions have been found, the possibility of these borings representing examples of *Gastrochaenolites* can not be disregarded.

Open nomenclature traces

ARTHROPOD TRACKWAYS
Figures 4.4, 7.4

Description. Trackways preserved as negative epirelief. Each track (discrete mark) a relatively deep, straight to slightly curved groove, 4–7 mm long and approximately 1 mm wide. Only in some cases a series (see Minter *et al.*, 2007) can be individualized; orientation mostly chaotic.

Remarks. These traces were classified in open nomenclature because the morphological data available at present is insufficient to assign them to an ichnotaxon. Besides, it may be

possible that they were actually undertracks (Goldring and Seilacher, 1971), which would difficult even more an ichnotaxonomic assignation because of the impossibility of comparing them with other examples of the same trace but with a different type of preservation (see Bertling *et al.*, 2006; Minter *et al.*, 2007). Tracks preserved as deep grooves are to be expected in aquatic arthropods, since they carry sharp appendages which penetrate into the sediment (Seilacher, 2007).

INVERTEBRATE TRAILS
Figures 7.4, 7.6 and 7.8

Description. Elongated, sinuous horizontal epichnia, composed of grooves and paired lateral elevations in fine-grained sandstones. Each groove is 2 mm wide; the structure as a whole (including paired elevations) is 7–8 mm wide. Some specimens contain a thin, median longitudinal crest, which is about 1 mm wide.

Remarks. The paired lateral elevations provide information about the substrate at the time of production of the traces. The substrate (fine and sandy) must have been slightly soupy or soft (Goldring, 1995). Regarding the producers, we can only assume that they were macroinvertebrates.

TETRAPOD SWIMMING TRACES
Figure 7.7

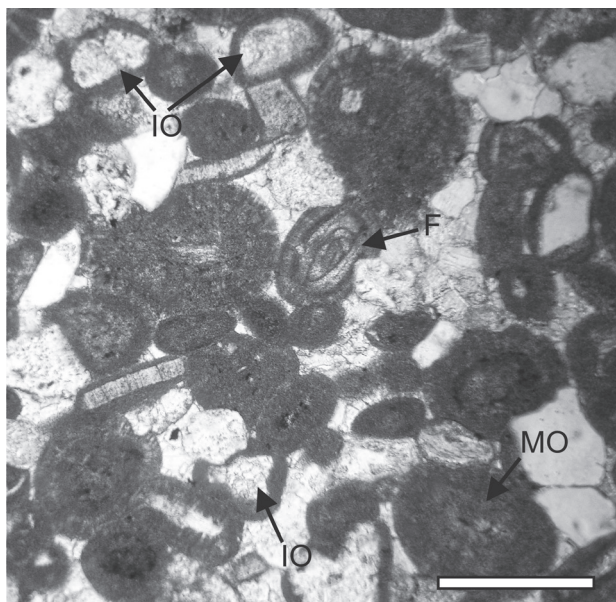**Description.** Tridactyl hypichnial mark composed of elon-

Figure 8. Thin section from deposits of the open to restricted tidal-flat facies/ *Corte petrográfico de muestra de la facies de planicie de marea abierta a restringida*. Scale bar/ *escala*: 1 mm. **References. F:** foraminifer as nucleus within an ooid/ *foraminífero como núcleo en ooide*; **MO:** micritized ooids/ *ooide micritizado*, **IO:** initial ooids/ *oolitas iniciales*.

gated, slightly curved crests. Two of them show what are possibly small, terminal, claw marks. Trace as a whole 28–48 mm long and 8–17 mm wide. The distal portion of the third crest is not preserved.

Remarks. Inclusion within an existing ichnogenus was not possible. In the description, the terms "distal" and "terminal" are used analogously to their usage in reference to anatomic parts of Tetrapoda. This trace is a three-digit impression reflecting behaviour of a swimming or wading small-sized tetrapod. These marks are remarkably similar to hypichnia in sandstones reported by Walter (1982, fig. 3 and plate 2) as swimming tetrapod traces. This author mentioned the impossibility of establishing with certainty if they are genuinely swimming traces or they reflect another related behaviour, such as a search for food in the substrate by aquatic or semiaquatic tetrapods. As inferred by Swanson and Carlson (2002, fig. 7) — who reported very similar marks—, it is probable that the producer used the substrate for forward propulsion while swimming, although it may also be evidence of a mere dragging of claws while wading in shallow waters. Similar traces from the Mulichinco Formation (early Valanginian, Mendoza Group; Neuquén Basin) were described by Pazos (2009).

Analysis of tetrapod traces considers morphological together with extramorphological characters resulting from variations in the gait and speed of the animal, the type of substrate and its consistency. However, this kind of approach can be pursued when there are enough samples to observe a wide range of variation of each of these parameters (Melchor and Sarjeant, 2004). In the case analyzed here, it is not possible to speculate with traits such as speed of the producer, or whether the mark was left by an anterior or posterior limb. However, preservational characteristics indicate that the substrate was semi-saturated with water but firm enough to permit the preservation of discrete marks (Swanson and Carlson, 2002). They also indicate that they were produced in very shallow water by a small-sized producer.

DISCUSSION

Ichnodiversity and environmental factors

The ichnodiversity of the entire section is moderate, but higher in the tidal-flat deposits (facies 4 and 5). These traces also show some of the features described by Mángano and Buatois (2004) for open-marine tidal-flat ichnofaunas. As this is an analysis of one section only, further conclusions in this matter would be premature. At this particular locality it is possible that the higher diversity in the tidal-flat deposits

may be caused by changing energetic conditions, presence of nutrients, or other factors. The presence of miliolids — which may indicate hypersalinity— in the open to restricted tidal-flat deposits agrees with data obtained by Lazo *et al.* (2008), reporting euhaline to hyperhaline conditions for the upper part of the Agua de la Mula Member. The possibility of abnormal salinity has also been pointed out by Taylor *et al.* (2009). Thus hypersalinity or fluctuating salinity as a factor cannot be disregarded. A relatively higher ichnodiversity is not to be expected in such a setting (Gibert and Ekdale, 1999), and it should be associated with euryhaline producer organisms. Ichnological studies in environments with fluctuating salinities usually report the presence of brackish-water conditions (*e.g.*, Kamola, 1984; Pemberton and Wightman, 1992; Gingras *et al.*, 1999; Rebata *et al.*, 2006), and only rarely hypersalinity (see Jaglarz and Uchman, 2010 and references therein). The relatively lower ichnodiversity found in the facies attributed to hyperpycnal flows may be explained by their rapid sedimentation and high energy, which produced surfaces unsuitable for colonization. Furthermore, the entry of these flows could also account for fluctuating salinity. Future studies of tide-influenced marginal-marine settings with hypersaline conditions could shed some light on the subject.

Some of the ichnotaxa reported by us (*Chondrites*, *Gyrochorte*, *Palaeophycus*, *Rhizocorallium*, *Teichichnus* and *Thalassinoides*) concur with findings reported by Spalletti *et al.* (2001a). Further discussion about the other ichnotaxa mentioned in their work is not possible since they were not illustrated and because of the discrepancies between the facies described in their text and their logged section (see **Ichnological and paleoenvironmental background**). They stated that ichnodiversity in this section is higher in post-storm deposits. As mentioned earlier, our analysis indicates that it is higher in tidal-flat deposits. Spalletti *et al.* (2001a) did not interpret the presence of such environment in this section; thus closer comparison becomes unlikely.

Environmental data provided by trace fossils, ichnoassemblages and producers

Only some of the ichnotaxa studied herein provide direct environmental information (see **Remarks** in the systematic section), but this information agrees with the one obtained by sedimentologic evidence. Summarizing:

1. *Gyrochorte* is produced after a certain stressing episode (such as storm events) in a shallow marine context; it is found in facies 1 (oolitic-skeletal bar) and 5 (interpreted as an open to restricted tidal-flat).

2. *Ophiomorpha* is also related to a shallow marine context;

in this section it is found in facies 4 (interpreted as an open tidal-flat) and 5 (interpreted as an open to restricted tidal-flat).

3. *Rosselia socialis* is typical of shallow marine deposits, and has been previously associated with tidal environments; it is here found in facies 5 (interpreted as an open to restricted tidal-flat).

4. *Skolithos* appears in a variety of shallow marine environments (including marginal marine ones); here it is found in facies 4 (interpreted as an open tidal-flat).

Not all the traces fossils described here can be grouped into ichnoassemblages. Nevertheless, three trace fossil assemblages can be recognized:

1. *Chondrites-Teichichnus-Skolithos* assemblage. This is the most diverse assemblage of the section. It is dominated by *Chondrites* found mainly in claystones of the open tidal-flat deposits (facies 4).

2. *Rhizocorallium assemblage.* This assemblage is dominated by *Rhizocorallium jenense*; it can be found in association with *Ophiomorpha nodosa*, *Ophiomorpha* isp. and *Thalassinoides* isp. It occurs primarily at the tops of coquinas or massive sandstones in open and open to restricted tidal-flat deposits (facies 4 and 5).

3. *Gyrochorte-arthropod trackways assemblage.* It contains *Gyrochorte comosa* and arthropod trackways. It is associated with very shallow-water deposits in open to restricted tidal-flat deposits (facies 5). No *Gyrochorte* specimen is cross-cut by arthropod trackways, so it is likely that in all cases *Gyrochorte* was produced after them. This is the only cross-cutting relationship that could be established, as in the other assemblages —though found in the same beds— different ichnotaxa do not appear together in the same area. Regarding the inferred trace-producers, we report the presence in this section of callianasid decapods, palaeotaxodont bivalves (Fernández *et al.*, 2010), annelids and small tetrapods as part of the local fauna. Other groups remain doubtful, *i.e.*, sea anemones, sipunculids, gastropods, phoronids, and crustaceans in general.

CONCLUSIONS

The studied section represents an environment evolving from marine to marginal-marine. It began with the last part of a shallowing-upward succession that ended in an oolitic bar. This bar was drowned by a first transgression evidenced by a ravinement surface. The overlying pelites were deposited during fair weather periods, while the associated coquinas are product of storm-events which transported material from the bar or nearby areas. Eventual hyperpycnal flows entered the body of water, evidenced by rapid sedimentation. The system then evolved firstly into an open and later into a more restricted tidal flat (heterolithic interchannel areas crossed by meandering channels) with high and/or fluctuating salinity.

Thirteen ichnogenera and sixteen ichnotaxa were identified. Three other types of trace fossils were described using open nomenclature. Three ichnoassemblages were distinguished.

The rather unusual presence of the ichnogenus *Chondrites* is reported in facies interpreted as tidal-flat deposits.

Callianasid decapods, palaeotaxodont bivalves, annelids and small tetrapods are some of the inferred producers of the traces and reported as part of the local fauna.

Although scarce, paleoenvironmental information drawn from trace fossils agrees with that obtained by sedimentologic evidence. Besides, it suggests the current absence of precise ichnological models for marginal marine environments with hypersalinity and/or fluctuating salinity. It also suggests that environments with marked salinity changes may not necessarily show a drop in ichnodiversity.

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