

## Trace fossils from the Middle and Upper Eocene (Bartonian–Priabonian) molasse deposits of the Pamplona Basin (Navarre, western Pyrenees): palaeoenvironmental implications

HUMBERTO ASTIBIA<sup>1\*</sup>, FRANCISCO JAVIER RODRÍGUEZ-TOVAR<sup>2</sup>, IGNACIO DÍAZ-MARTÍNEZ<sup>3</sup>, AITOR PAYROS<sup>1</sup> and SILVIA ORTIZ<sup>4</sup>

<sup>1</sup>Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea (UPV/EHU), Bilbao, Basque Country, Spain

<sup>2</sup>Departamento de Estratigrafía y Paleontología, Facultad de Ciencias, Universidad de Granada, Campus Universitario de Fuentenueva s/n, Granada, Spain

<sup>3</sup>CONICET-Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, General Roca, Argentina

<sup>4</sup>PetroStrat Ltd, Tan-y-Graig, Parc Caer Seion, Conwy, Wales, UK

An ichnological study was carried out in the Middle–Upper Eocene sedimentary succession of the Pamplona Basin. This succession represents the molasse stage of the western part of the South Pyrenean peripheral foreland basin and extends from deep-marine turbiditic (Ezkaba Sandstone Formation) to deltaic (Pamplona Marl, Ardanatz Sandstone and Ilundain Marl formations) and marginal marine deposits (Liédena Sandstone Member, Gendulain Formation). The tectonosedimentary evolution of the basin can also be recognized by means of the ichnoassemblages preserved throughout the succession and by the ichnofacies analysis. A total of 23 ichnogenera and at least 28 ichnospecies have been identified. The assemblage of the Ezkaba Sandstone is characteristic of the deep-sea *Nereites* ichnofacies. The *Ophiomorpha rudis* and the *Paleodictyon* ichnosubfacies can be differentiated in this unit, which are typical of channel axis and off-axis environments. Trace fossils in the Ardanatz Sandstone and Ilundain Marl formations, with dominance of *Thalassinoides* and especially *Ophiomorpha*, could be related to the *Cruziana* ichnofacies, developed in relatively low-energy environments, in semicohesive muddy substrates with intercalated silt and sand. The ichnofauna of the Liédena Sandstone Member is composed of bird tracks, and invertebrate horizontal and vertical structures. Microbial mat impressions also occur. The evidence suggests that microbial mats acted as a taphonomic bias favouring the preservation of vertebrate tracks and conditioning the presence of other trace fossils. Consequently, the assignment of this ichnofauna to a specific ichnofacies is tentative, most likely a combination of the *Mermia* and *Scoyenia* ichnofacies. Copyright © 2016 John Wiley & Sons, Ltd.

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### 1. INTRODUCTION

The analysis of trace fossils, along with traditional sedimentological studies, is commonly used to interpret depositional systems and environmental changes from the geological record (see McIlroy, 2004; Knaust and Bromley, 2012). In the South Pyrenean area, significant ichnological contributions have resulted from the study of Lower–Middle Eocene flysch deposits (Heard and Pickering, 2008; Rodríguez-

Tovar *et al.*, 2010; Cummings and Hodgson, 2011; and references herein), but few ichnological descriptions have been carried out in the Middle–Upper Eocene molasse deposits; only some accounts of Late Eocene avian ichnofossils have been published to date (Mangin, 1962; Raaf *et al.*, 1965; Payros *et al.*, 2000; Astibia *et al.*, 2007). This scarcity may partly be due to the shallow marine and terrestrial molasse accumulations being commonly represented by amalgamated coarse-grained deposits, which are not ideal for trace fossil preservation.

In this work, we present an ichnological analysis carried out in a 1500 m-thick Middle–Upper Eocene (approximately 40–34 Ma) sedimentary succession accumulated in the western part of the South Pyrenean foreland basin, which

\*Correspondence to: H. Astibia, Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea (UPV/EHU), Apartado de Correos 644, 48080 Bilbao, Basque Country, Spain. E-mail: humberto.astibia@ehu.eus

shallows from deep-sea into intertidal conditions. This succession is represented by the Ezkaba Sandstone, Pamplona Marl, Ardanatz Sandstone, Ilundain Marl and Gendulain formations, and represents the molasse stage (see Astibia *et al.*, 2005). The objective of this study is to carry out a trace fossil analysis throughout the molasse succession in order to recognize changes in the ichnoassemblages and ichnofacies that can be related to the tectosedimentary evolution of the basin. The above-mentioned avian ichnofossils are also revisited, and other invertebrate ichnoassemblages first identified in the Pamplona Basin are presented.

## 2. GEOLOGICAL SETTING

The Pyrenees are a collision mountain belt created by the Santonian–Miocene convergence of the European and Iberian plates (Muñoz, 2002) (Fig. 1a). The oblique plate convergence led to the formation of a narrow marine gulf during late Cretaceous and Palaeocene times, opening northwestwards into the Bay of Biscay (Atlantic Ocean). The gulf was located at approximately 35°N latitude and had shallow carbonate ramps on its northern and southern margins (Pujalte *et al.*, 2002). Further plate convergence during the Eocene caused tectonic uplifting of the Pyrenees. The resulting deformation reached its maximum intensity during the Early and Middle Eocene, when peripheral foreland basins developed to the south and north of the rising Pyrenean orogen (Muñoz, 2002; Pujalte *et al.*, 2002). Due to the oblique convergence of the Iberian and European plates, the Pyrenean uplift was a diachronous westward extending process, which implies that tectonic activity and palaeogeographic changes progressively propagated to the west. The present study focuses on the western part of the South Pyrenean foreland basins, referred to here as the Pamplona Basin (Fig. 1a and b).

The Eocene succession of the Pamplona Basin clearly shows a typical foreland basin evolution. In Early–Middle Eocene (Ypresian–Lutetian) times (approximately 56–40 Ma), the South Pyrenean Basin corresponded to an underfilled deep-marine trough (Pujalte *et al.*, 2002). The foredeep was axially filled by siliciclastic turbidites (the so-called Hecho Group) (Figs. 1b and 2) sourced from the Pyrenean highlands, while it was flanked on the passive southern margin by extensive shallow-water carbonate ramps (Payros *et al.*, 1999, 2010). During this stage, the main denudation area was in the emergent eastern Pyrenees.

The denudation of the western Pyrenean orogen began in Middle Eocene (Bartonian) times (approximately 40 Ma). Rivers flowing from the newly uplifted areas delivered

increasing amounts of sediments to the remaining marine areas, causing progressive overfilling and shallowing. A 1500 m-thick Bartonian–Priabonian shallowing-upward succession accumulated in the Pamplona Basin, which represents the molasse stage of the western foreland basin.

The lower part of this succession is represented by the Ezkaba Sandstone Formation, a channel-levee, siliciclastic turbidite system fed directly from the uplifting orogen to the north (Payros *et al.*, 1997) (Figs. 1b–3a–c). Thus, it records the onset of the tectonically induced emergence and denudation of the western Pyrenean axial zone. The overlying Pamplona Marl, Ardanatz Sandstone and Ilundain Marl formations mainly represent prodelta, delta front and restricted platform environments, respectively (Astibia *et al.*, 2005, 2014) (Figs. 1b–3a and d–f). These units were related to the progradation of the deltaic Belsue–Atares Formation from the east (Puigdefàbregas, 1975). Finally, the Late Eocene (Priabonian) Gendulain Formation (approximately 34 Ma) (Puigdefàbregas, 1975) is composed of coastal deposits divided into three distinct members: the lower evaporite member, the middle sabkha marl member and the upper Liédena Sandstone Member (Figs. 1b–3g). The latter unit contains the youngest deposits with marine influence in the region, as the equivalent sediments to the east were accumulated by a fluvial system (Martes and Biban formations; Puigdefàbregas, 1975). The Liédena Sandstone Member also contains conglomerates with clasts made up of Lutetian turbidites, showing that the Hecho Group deposits were already unroofed, implying that the Pyrenean axial zone had been uplifted at least 1500 m by Priabonian times (Payros *et al.*, 2000). Furthermore, growth strata and lateral variations in facies and thickness in the Liédena Sandstone record the synsedimentary tectonic deformation of the Pamplona Basin in Priabonian times, probably related to the inception of east–west-trending blind thrust sheets. It has therefore been concluded that during the Late Eocene, in response to increasing tectonic activity, a sole thrust propagated beneath the South Pyrenean Basin, causing it to detach and convert into an emergent piggy-back basin. Consequently, a new foreland basin, the Ebro Basin, formed further to the south (Muñoz *et al.*, 2002).

## 3. METHODS AND MATERIALS

The trace fossils studied herein come mainly from the sandy units accumulated during the molasse stage of the Pamplona Basin: Ezkaba Sandstone Formation, Ardanatz Sandstone (and lower part of Ilundain Marl) Formation and Liédena Sandstone Member of the Gendulain Formation (Figs. 1b–3). The Pamplona Marl Formation was not

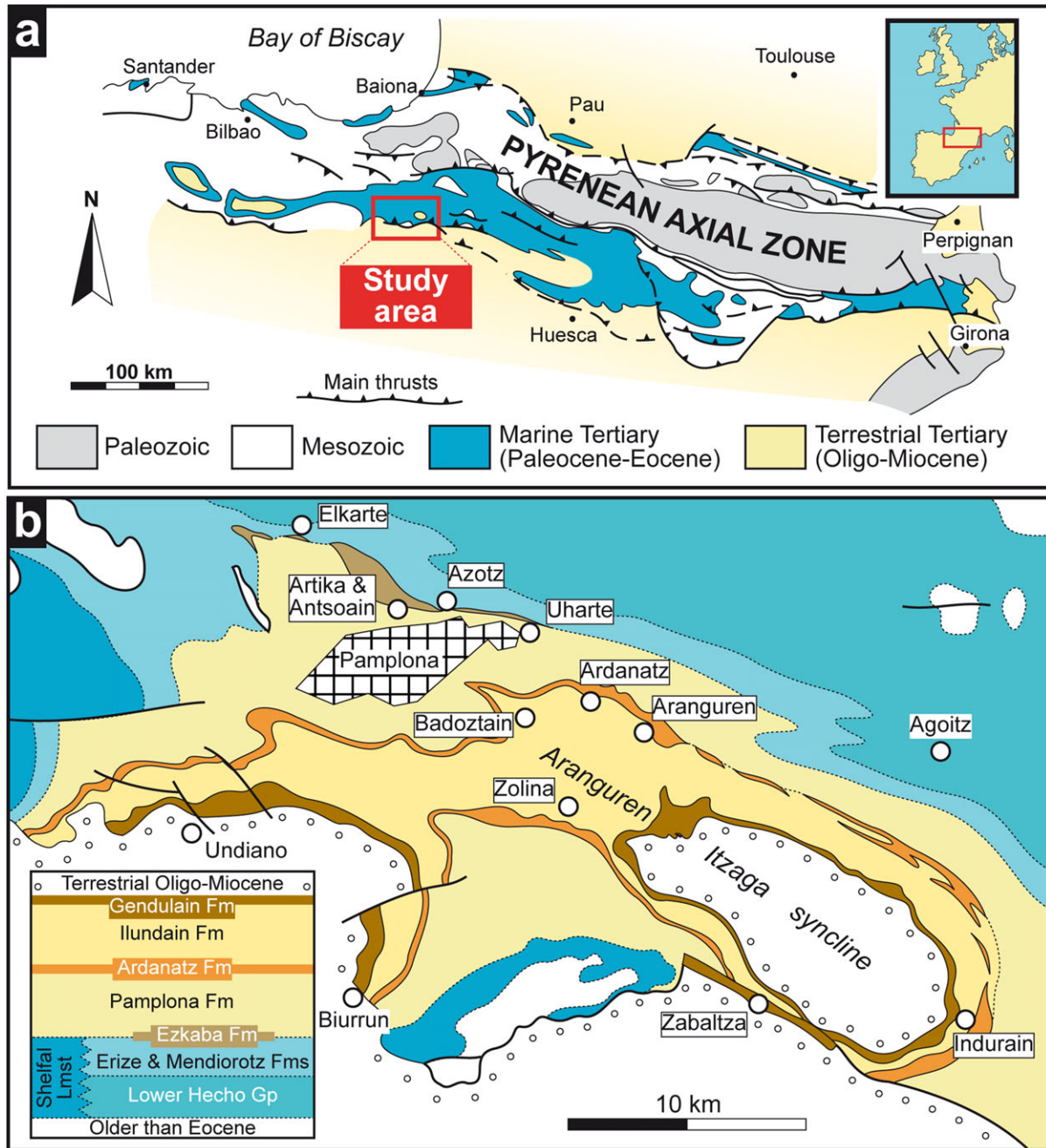


Figure 1. Simplified geological maps of the Pyrenees (a), with location of the study area in the western part of the South Pyrenean zone (SPZ), and of the Pamplona Basin and nearby areas (b). The studied formations are highlighted in boxes, and sites referred to in the text are indicated. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

analysed in this study, although field observations are included in the discussion. For the specific localities, see Figure 1b and Table 1. Precise locations are not given for the protection of the fossil sites in accordance with Natural and Cultural Heritage legislation. Those who want to know further details are asked to contact the corresponding author.

Trace fossils from the Ezkaba Formation have been arranged in morphological groups following Książkiewicz (1977), with modifications by Uchman (1995). For the toponomy of invertebrate trace fossils, we have followed the classification of Martinsson (1970). Avian footprints have been described and classified according to Payros *et al.* (2000), De Valais and Melchor (2008) and Díaz-Martínez *et al.* (2015).



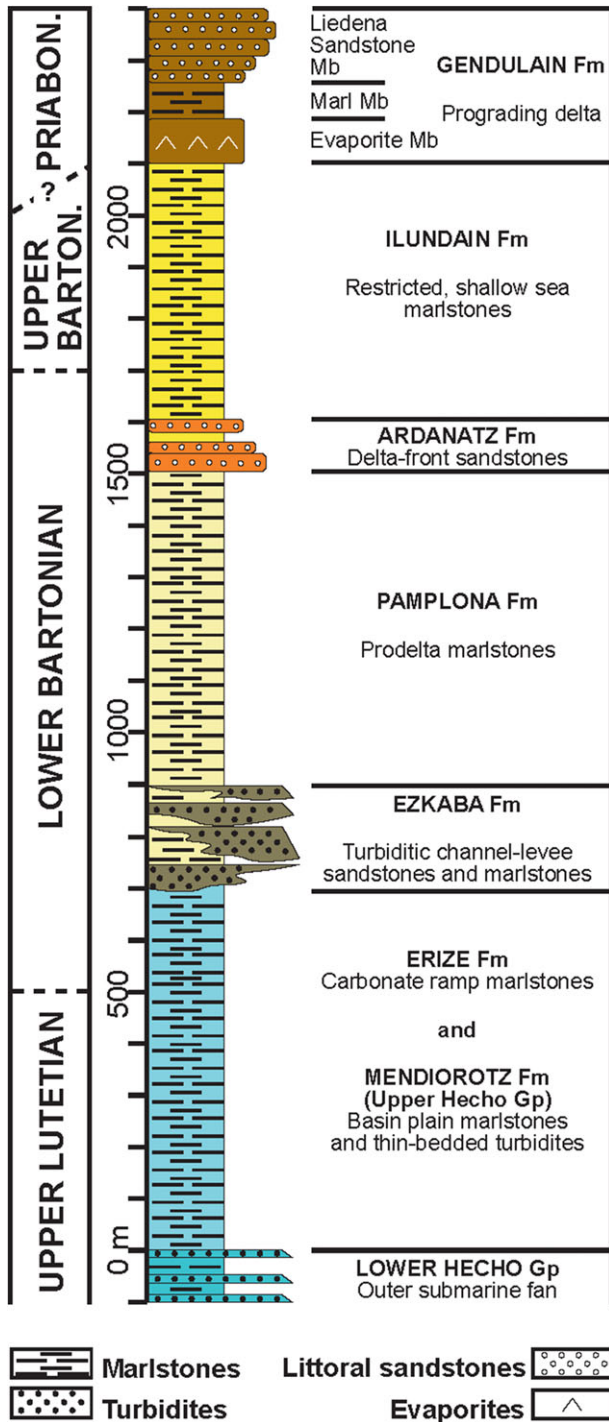


Figure 2. Representative columnar section of the Middle–Upper Eocene succession in the Pamplona Basin (Navarre), with its constituent lithostratigraphic units and the depositional environments so far proposed in the literature. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Most specimens were studied in the field. Some hand samples are provisionally deposited in the Department of Stratigraphy and Paleontology of the University of the Basque Country (Bilbao).

## 4. ICHNOLOGY

### 4.1. Trace fossils

The following list provides a brief description and discussion of the trace fossils found in Ezkaba Sandstone, Ardanatz Sandstone, Ilundain Marl and Gendulain (Liedena Sandstone Member) formations (Figs. 4–8 and Table 1). Ichnotaxa are listed alphabetically. Bird traces are described after the invertebrate traces.

#### 4.1.1. *Belorhappe* isp. (Fig. 5g)

**Remarks.** Poorly preserved single specimen, angular (zigzag) meandering string, rather straight, at least 166 mm long, with short prolongations at the apices of triangular meanders, string about 4 mm in diameter, filled with material lighter in colour than the surrounding sedimentary rock, meanders with ‘wavelengths’ of 21–26 mm, amplitudes (height) of triangles 11.5–13.0 mm, apical angle of 115° to 120°. The trace is assigned to *Belorhappe* Fuchs, 1895 (see emended diagnosis by Uchman 1998), by the typical angular zigzag second order meander, but a ichnospecies characterization is difficult, resembling specimens of *Belorhappe zickzack* (Heer, 1876) and *Belorhappe fabregae* (Azpeitia, 1933) in Książkiewicz (1977, fig. 39 and pl. 24), and of *Belorhappe zickzack* of Uchman *et al.* (2004). However, the studied specimen is larger and the apical angle is more open than in these cases; it is more similar in size to the ‘Zigzag cylinder’ of Uchman *et al.* (2004).

#### 4.1.2. *Chondrites* isp. (Fig. 4a)

**Remarks.** Endichnial branched thin (>1 mm diameter) tunnels; according to their size, they could be assigned to *Chondrites targioni* (Brongniart, 1823), but poor preservation precludes a conclusive classification. Tunnels are filled with either sediment lighter than the encasing sedimentary rock or a darker (altered) ferruginous material. *Chondrites* von Sternberg, 1833, is generally considered a deeper-tier trace fossil probably produced by chemosymbiotic organisms capable of living in dysaerobic conditions, but other interpretations have also been proposed (see Izumi, 2014; and references herein).

#### 4.1.3. *Cochlichnus* isp. (Fig. 8a and b)

**Remarks.** Hypichnial convex trace, resembling a sine curve, regularly meandering, smooth and non-branching burrow of uniform width and horizontal trail. Very thin, width is approximately 0.1 mm; maximum length recorded is 3 mm. *Cochlichnus* Hitchcock, 1858, is regarded as either a grazing trail (pascichnion) or, more likely, a locomotion trail (repichnion). Buatois and Mangano (1993)

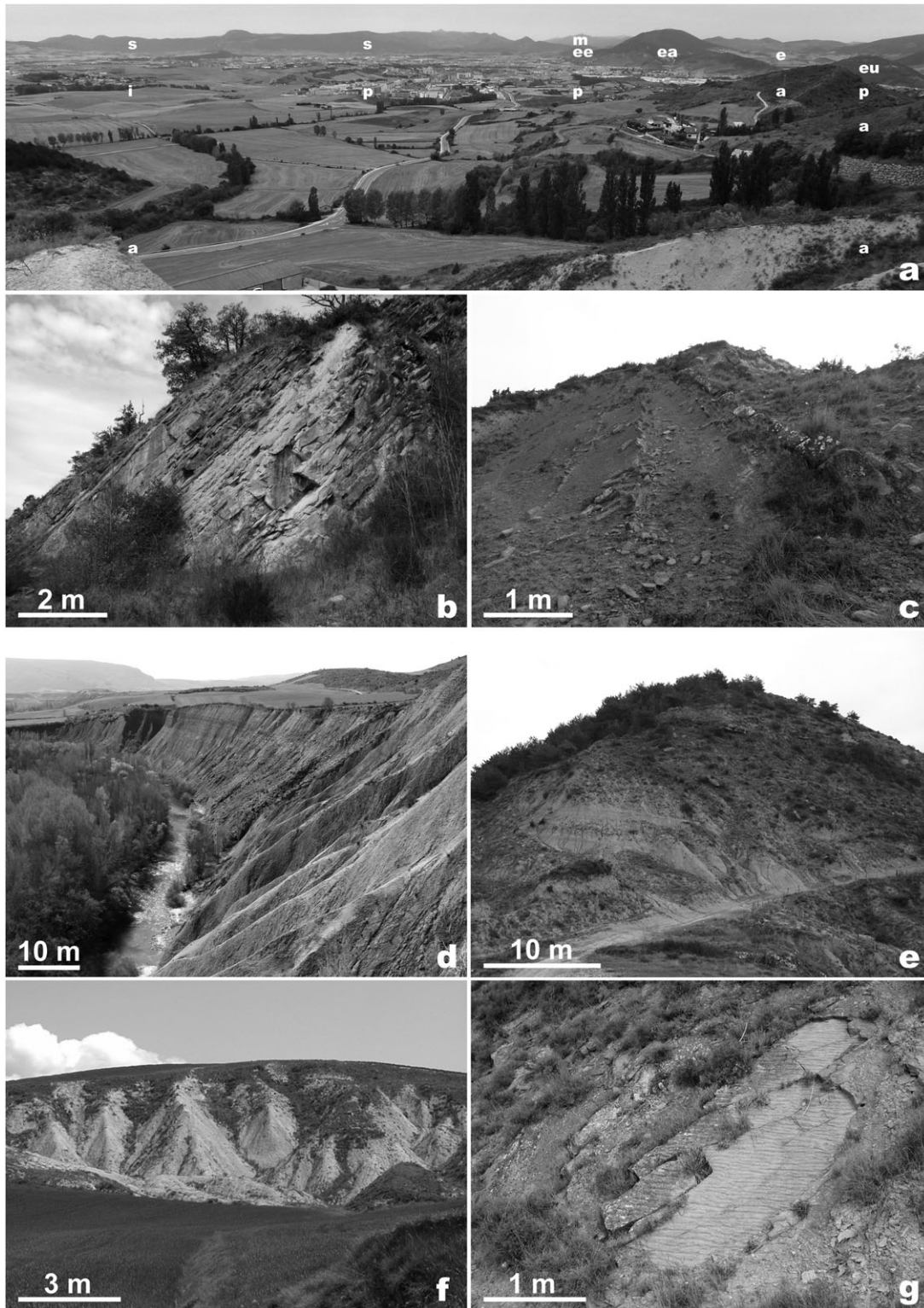


Figure 3. Field views of some of the outcrops of Middle–Upper Eocene (Bartonian) of the Pamplona Basin and surrounding areas (Navarre, Western Pyrenees). (a) General view of the Pamplona Basin from the Ardanatz outcrop. Foreground, Ardanatz Sandstone (a). Further left is the city of Pamplona-Iruñea and surrounding towns and the agricultural lands on the Pamplona Marl (p) and Ilundain Marl formations (i). To the right of the city, hills correspond to the Ezkaba Sandstone (Uhartre, eu, Artika-Antsoain, ea, and Elkarte, ee). In the more distant background is the Erize Marl Formation (e), Lutetian limestones of Sarbil (s) and Mesozoic of Aralar (m). (b) Uhartre outcrop (Ezkaba Formation). (c) Elkarte outcrop (Ezkaba Formation). (d) Grez outcrop (Pamplona Formation). (e) Ardanatz outcrop (Ardanatz Sandstone). (f) Badoztain outcrop (Ilundain Formation). (g) Idotzin outcrop (Gendulain Formation).

Table 1. Lithostratigraphic units of the Pamplona Basin (Navarre, Western Pyrenees) and vertical distribution of trace fossils

Lithostratigraphic units	Sedimentary environments	Localities	Trace fossil	Abundance	Ichnofacies (ichnosubfacies)						
Gendulain Formation (Liédena Sandstone Member)	Coastal deposits (mixed intertidal flat developed in a partially protected embayment or marginal lagoon) (Payros <i>et al.</i> , 2000)	Xabier, Indurain, others	<i>Cochlichnus</i> isp.	Common	Combination of <i>Scoyenia-Mermia</i>						
			<i>Gruipeda</i> isp.	Rare							
			<i>Koreanaornis</i> isp.	Abundant							
			cf. <i>Koreanaornis</i>	Common							
			<i>Leptoptilostipus pyrenaicus</i>	Abundant							
			cf. <i>Leptoptilostipus</i>	Rare							
			<i>Palaeophycus tabularis</i>	Common							
			Vertical tubes	Common							
			<i>Planolites</i> isp.	Common							
			<i>Halopoa imbricata</i>	Common							
Ilundain Marl Formation	Delta front and restricted shallow platform deposits (Astibia <i>et al.</i> , 2005)	Zolina, Badoztain	<i>Ophiomorpha</i> isp. 1	Abundant	<i>Cruziana</i> <i>Glossifungites</i> ?						
			<i>Spongiomorpha</i> cf. <i>oraviense</i>	Rare							
			<i>Spongiomorpha</i> cf. <i>sicula</i>	Rare							
			Indeterminate spreite burrow	Rare							
			Ardanatz Sandstone Formation			Ardanatz, Aranguren	<i>Halopoa imbricata</i>	Common			
							<i>Ophiomorpha nodosa</i>	Abundant			
							<i>Ophiomorpha</i> isp. 2	Common			
							<i>Spongiomorpha</i> cf. <i>oraviense</i>	Common			
							<i>Spongiomorpha</i> cf. <i>sicula</i>	Rare			
							<i>Thalassinoides</i> isp.	Common			
Pamplona Marl Formation		Not included in this work									
					Ezkaba Sandstone Formation		Laterally migrating channel-levee turbidite system (Payros <i>et al.</i> , 1997)	Antsoain, Artika	<i>Belorhaphé</i> isp.	Rare	<i>Nereites</i> ( <i>Ophiomorpha rudis</i> )
									<i>Ophiomorpha annulata</i>	Common	
									Elkarte	<i>Ophiomorpha rudis</i>	
			<i>Chondrites</i> isp.	Rare							
			<i>Helminthorhaphé flexuosa</i>	Common							
			<i>Multina minima</i>	Common							
			<i>Nereites irregularis</i>	Rare							
			<i>Ophiomorpha annulata</i>	Common							
			<i>Ophiomorpha rudis</i>	Common							
<i>Paleodictyon strozzii</i>	Abundant										
<i>Planolites</i> isp.	Common										
? <i>Squamodictyon</i> isp.	Rare										
Azotz			<i>Taenidium</i> cf. <i>crassum</i>	Rare	<i>Nereites</i> ( <i>Ophiomorpha rudis</i> )						
			<i>Phymatoderma</i> isp.	Rare							
			<i>Pilichnus dichotomus</i>	Rare							
			<i>Scolicia strozzii</i>	Common							
			Uharte				<i>Ophiomorpha annulata</i>	Common			
							<i>Ophiomorpha rudis</i>	Abundant			
							<i>Planolites</i> isp.	Common			
							<i>Scolicia strozzii</i>	Common			
							<i>Scolicia vertebralis</i>	Rare			

The table shows the lithostratigraphic units, the sedimentary environments of each unit, the trace fossils and their abundance, and the ichnofacies.



discussed briefly the ichnotaxonomy of the seven nominal ichnospecies of *Cochlichnus* and considered only three to be valid, *C. anguineus* Hitchcock, 1858, *C. antarcticus* Tasch, 1968 and *C. annulatus* Orłowski, 1989. Assignment to an ichnospecies in this case has to be either to *C. anguineus* or *C. antarcticus* since *C. annulatus* is characterized by its annulated outer walls (Orłowski, 1989), a feature not present in this material.

#### 4.1.4. *Helminthorhapse flexuosa* Uchman, 1995 (Fig. 5a)

*Remarks.* Hypichnial, 1.0–1.5 mm wide meandering strings. The meanders' depth ranges from 11 to 25 mm and is 0.5–3.5 mm wide. There are no distinct bulges at the meanders' bends. Only two *Helminthorhapse* specimens were identified, but the absence of bulges at the bends suggests, in principle, they do not correspond to the ichnospecies *Helminthorhapse japonica* (Tanaka, 1970). *Helminthorhapse* is a graphoglyptid structure, reflecting an agrichnia behaviour (see Uchman, 1995, 1998). Recent models on trails of *Helminthorhapse flexuosa* support their relationship with an efficient search for food (Sims *et al.*, 2014).

#### 4.1.5. *Halopoa imbricata* Torell, 1870 (Fig. 6b and c)

*Remarks.* Hypichnial convex, long, fairly straight to slightly curved and unbranched burrows, variable diameter along one burrow, surface with irregular longitudinal furrows and wrinkles. Burrow segments are 3.0–12.5 mm wide and 40 to >300 mm long. The characteristics are ichnotaxobases that fit well with those of *Halopoa imbricata* according to the emended diagnosis by Uchman (1998).

#### 4.1.6. *Indeterminate spreite burrow* (Fig. 6a)

*Remarks.* Slightly inclined to subhorizontal U- and/or V-shaped spreite burrows, the longest ones exceeding 160 mm, limbs (marginal tunnels) 6.0–8.5 mm wide with partially scratched surface. Bioglyphs are also observed in the spreite. The predominant horizontal orientation of the studied specimens could suggest a tentative assignation to the ichnogenus *Rhizocorallium* Zenker, 1836, which is distinct from the vertically orientated *Diplocraterion* Torell, 1870, but poor preservation makes a conclusive ichnotaxonomical assignation difficult. *Rhizocorallium*, mainly *R. jenense* Zenker, 1836, is commonly related to omission and erosion surfaces, associated with firm and compacted substrates, as revealed by the presence of bioglyphs; thus, this ichnogenus is useful in the interpretation of firmgrounds associated to several-orders of transgressive–

erosive surfaces (i.e., Rodríguez-Tovar and Pérez-Valera, 2008; and references herein).

#### 4.1.7. *Multina minima* (Uchman, 2001) (Fig. 5a)

*Remarks.* Very irregular hypichnial network preserved in full relief. Meshes are about 3 mm across. The string is about 0.7 mm wide. For discussion of *Multina minima*, see Uchman (2001).

#### 4.1.8. *Nereites irregularis* (Schafhäütl, 1851) (Fig. 5b)

*Remarks.* Endichnial, tightly meandering ribbon 2.0–2.5 mm wide. The ribbon is meniscate. The ribbon corresponds only to the central part (the faecal string) of the typical trail of *Nereites* MacLeay, 1839. This ichnogenus usually has side lobes or lateral zones (the envelope zone), but the absence of this envelope is common in *Nereites irregularis* (Uchman, 2007a; Rodríguez-Tovar *et al.*, 2010).

#### 4.1.9. *Ophiomorpha annulata* (Książkiewicz, 1977) (Figs. 4b and 5a)

*Remarks.* Hypichnial convex and concave burrows, straight or slightly curved, mainly solitary, only sporadically branched, with pelleted walls or, more commonly, with smooth margins; tunnel diameters about 3–7 mm wide. Burrows lined with agglutinated pelletoidal sediment are characteristic of the ichnogenus *Ophiomorpha* Lundgren, 1891 (Howard and Frey, 1984; Uchman, 1998). *Ophiomorpha* and *Thalassinoides* Ehrenberg, 1944 (see below), are substrate-controlled ichnogenera produced by the same tracemakers. The distinction between *Ophiomorpha* ichnospecies is based on the geometry of the burrow systems and the characteristics of the burrow linings (see Uchman, 2009). *Ophiomorpha annulata* is characterized by small-sized and elongated wall granules arranged perpendicular to the axis of the burrow (Uchman, 1998).

#### 4.1.10. *Ophiomorpha nodosa* Lundgren, 1891 (Fig. 6d–g)

*Remarks.* Endichnial and hypichnial convex and concave >burrows, mainly straight or slightly curved, occasionally branched with Y-shaped bifurcations, thick tunnels 15–31 mm wide, well-pelleted walls with dense and regularly distributed rounded, ovoid pellets, 2–5 mm in diameter. The presence of dense and regularly distributed rounded pellets allows the assignment of these to *Ophiomorpha nodosa*. Similar species are *Ophiomorpha borneensis* Keij, 1965, and *Ophiomorpha irregulaire* Frey *et al.*, 1978. However, *Ophiomorpha borneensis* is characterized by bilobate pellets (Uchman, 2009), whereas in *Ophiomorpha irregulaire*, pelletization is irregular and scarce, with flame-like and

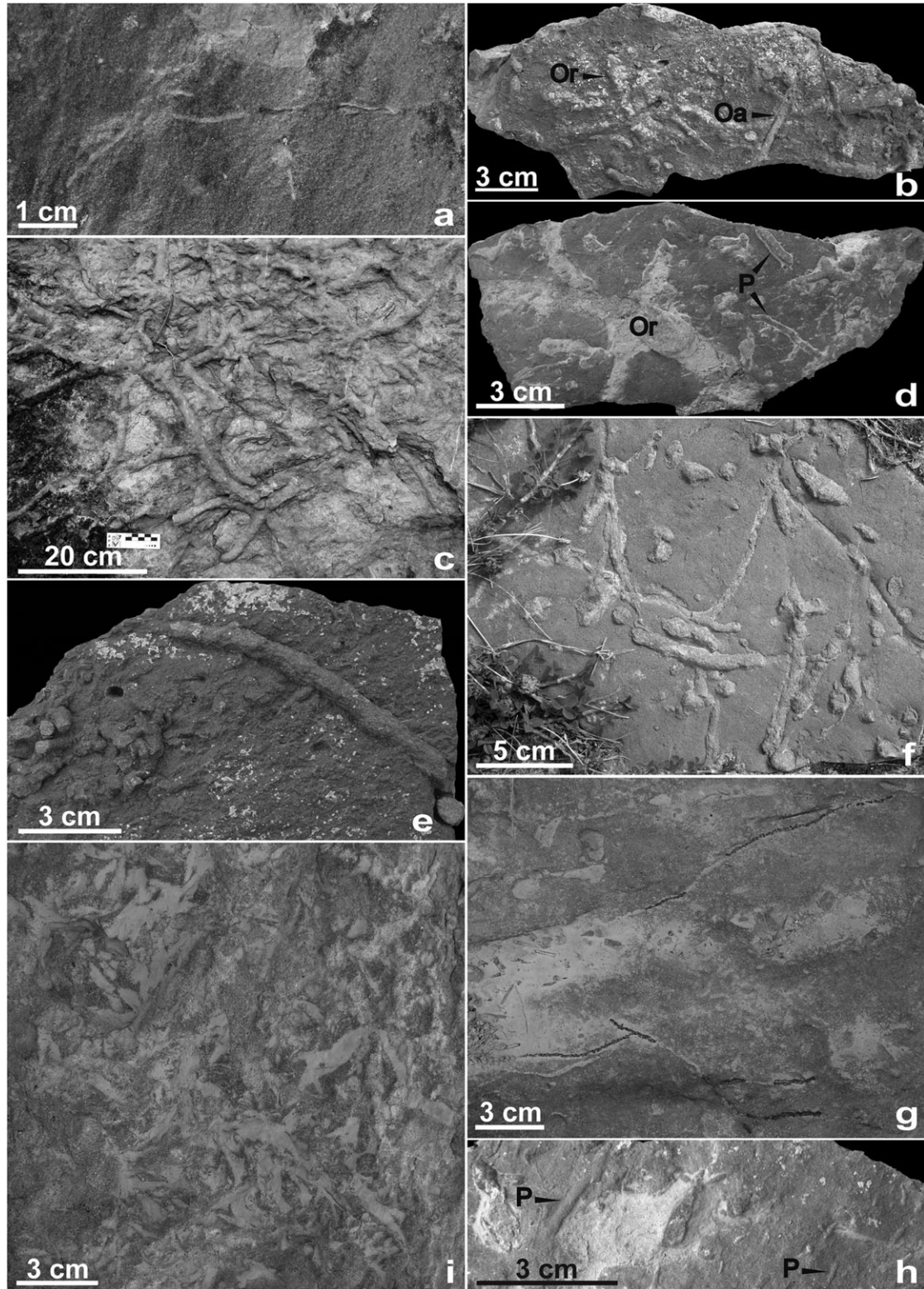


Figure 4. Trace fossils from the Middle Eocene (Bartonian) Ezkaba Formation. (a) *Chondrites* isp., endichnion (Elkarte). (b) *Ophiomorpha annulata* (Oa) and *Ophiomorpha* cf. *rudis* (Or) (Elkarte). (c) *Ophiomorpha rudis*, epichnia (Artika). (d) Meniscate form of *Ophiomorpha rudis* (Or) and *Planolites* isp. (P), hypichnia (Elkarte). (e) Crowded specimens of *Ophiomorpha rudis* covered with casts of scratch-marks (*Spongeliomorpha*-like) (Elkarte). (f) Horizontal and vertical forms of *Ophiomorpha rudis* (Uharte). (g) *Pilichnus dichotomus*, endichnion (Azotz). (h) *Planolites* isp. (P), hypichnia (Uharte). (i) *Phymatoderma* isp., endichnion (Azotz). All the traces are preserved in sandstone beds.



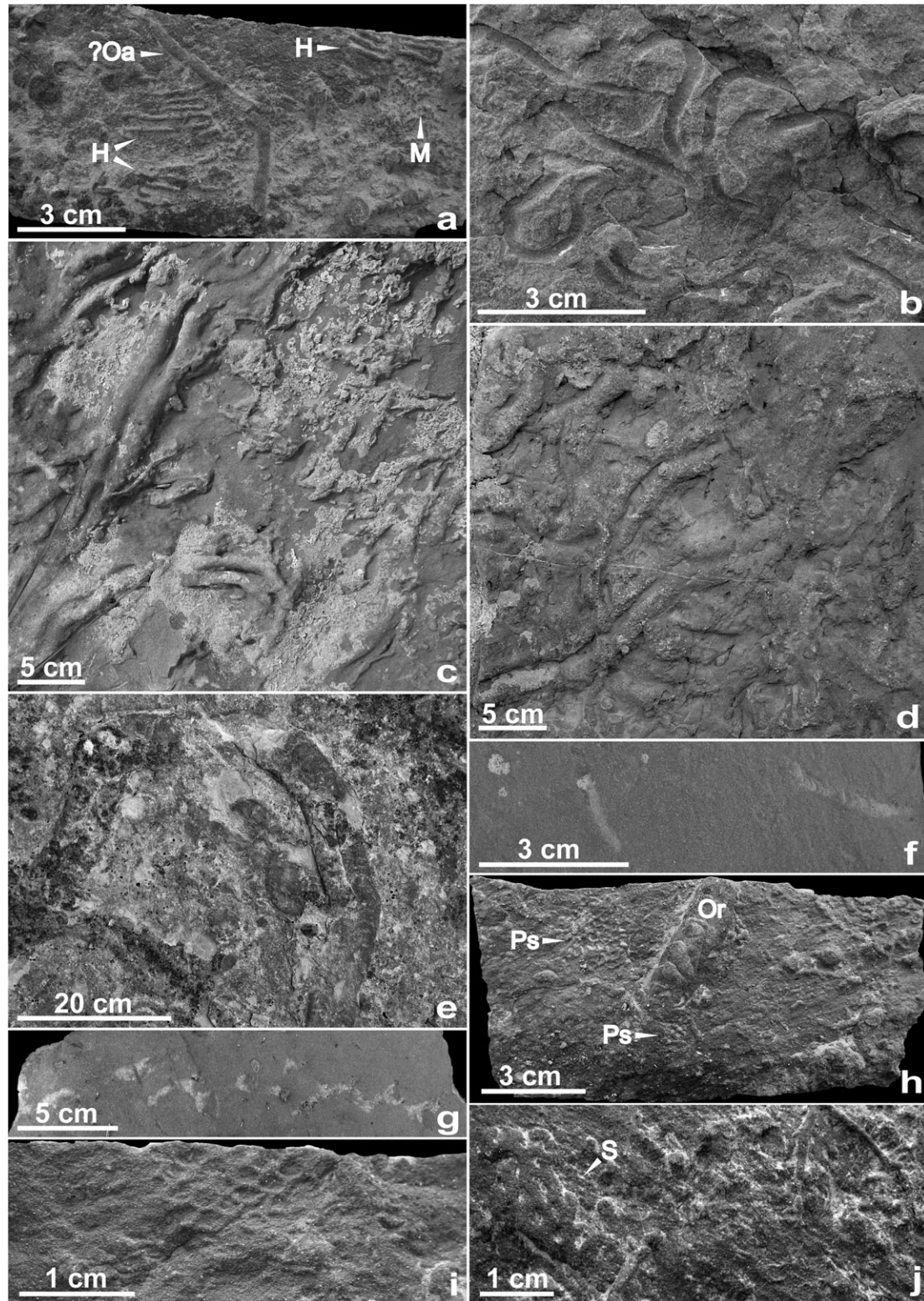


Figure 5. Trace fossils from the Middle Eocene (Bartonian) Ezkaba Formation. (a) *Helminthorhaphe flexuosa* (H), *Multina minima* (M), and *Ophiomorpha annulata* (Oa), hypichnia (Sample E1, Elkarte). (b) *Nereites irregularis*, endichnion (Elkarte). (c) *Scolicia strozzii*, hypichnion (Uharte). (d) *Scolicia strozzii*, hypichnion (Azotz). (e) *Scolicia vertebralis*, epichnion (Uharte). (f) *Taenidium* cf. *crassum*, endichnion (Elkarte). (g) *Belorhaphe* isp. (Antsoain). (h) *Paleodictyon strozzii* (Ps), and *Ophiomorpha rudis* (Or), hypichnia (Sample E2, Elkarte). (i) *Paleodictyon strozzii*, hypichnion (Elkarte). (j) *?Squamodictyon* isp. (S), hypichnia (Elkarte). All the traces are preserved in sandstone beds.



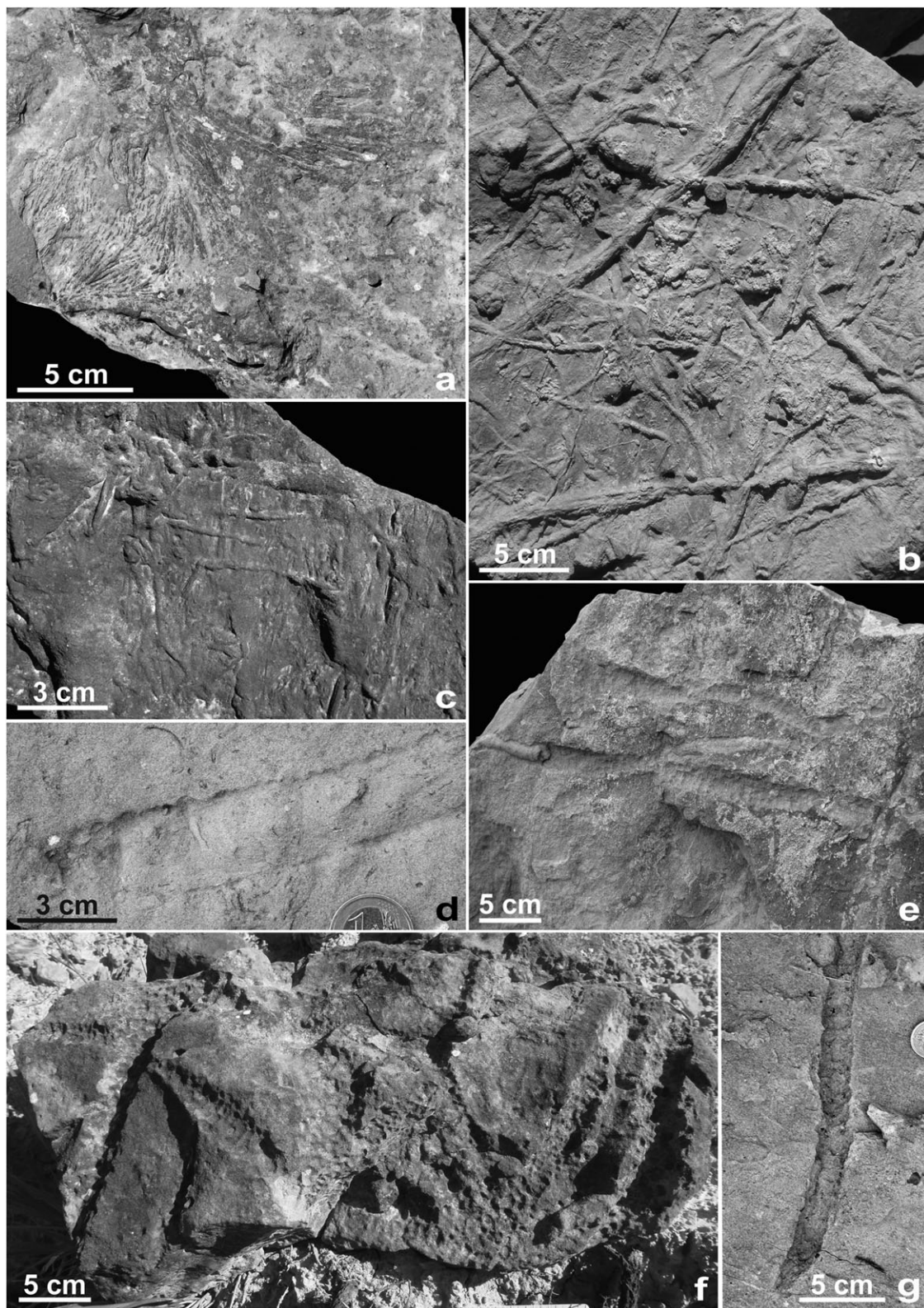


Figure 6. Trace fossils from the Middle Eocene (Bartonian) Ardanatz Sandstone–Ilundain Marl formations. (a) Indeterminate spreite burrow, endichnion (Zolina). (b) *Holapoa imbricata*, hypichnia (Zolina). (c) *Holapoa imbricata*, hypichnia (Ardanatz). (d) *Ophiomorpha nodosa*, longitudinal section of an endichnion (Ardanatz). (e) *Ophiomorpha nodosa*, concave shafts (Ardanatz). (f) *Ophiomorpha nodosa*, horizontal irregular maze (Ardanatz). (g) *Ophiomorpha nodosa* (Ardanatz). All the traces are preserved in sandstone beds.



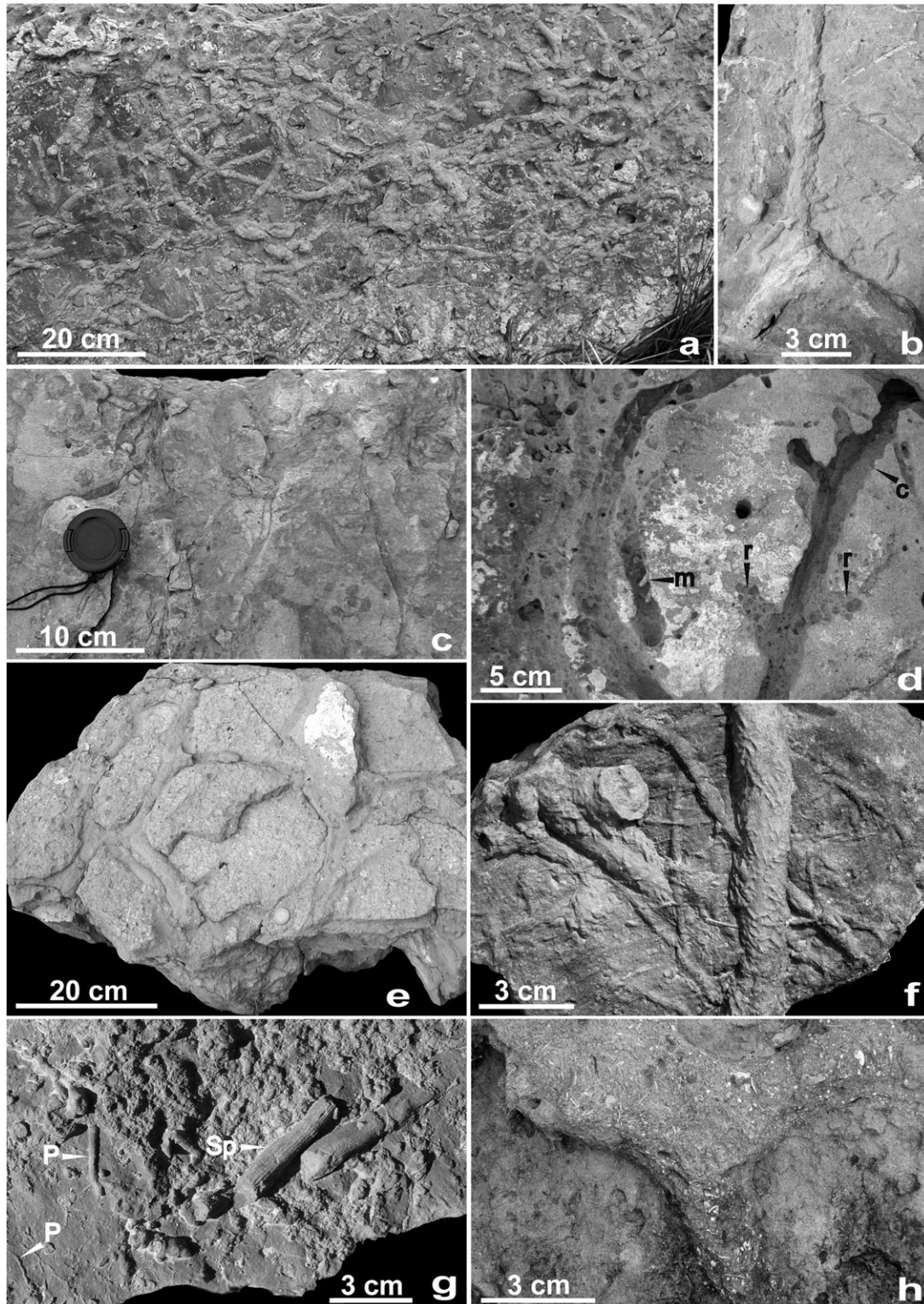


Figure 7. Trace fossils from the Middle Eocene (Bartonian) Ardanatz Sandstone–Ilundain Marl formations. (a) *Ophiomorpha* isp. 1, dense irregular maze, hypichnia (Zolina). (b) *Ophiomorpha* isp. 1, hypichnion (Zolina). (c) *Ophiomorpha* isp. 1, sand-filled subvertical cylinders (Zolina). (d) *Ophiomorpha* isp. 1, hypichnial concave burrows, meniscate filling remains (m), and rounded (r) and conical (?) (c) casts of wall granules (Badoztain). (e) *Ophiomorpha* isp. 2, horizontal regular maze (Ardanatz). (f) *Spongiomorpha* cf. *oraviense*, hypichnia (Aranguren). (g) *Spongiomorpha* cf. *sicula* (Sp) and *Planolites* isp. (P), hypichnia (Badoztain). (h) *Thalassinoides* isp., horizontal and oblique burrows filled with a bioclast rich (Nummulitidae, Pectinidae and others) sandy sediment (Ardanatz). All the traces are preserved in sandstone beds.



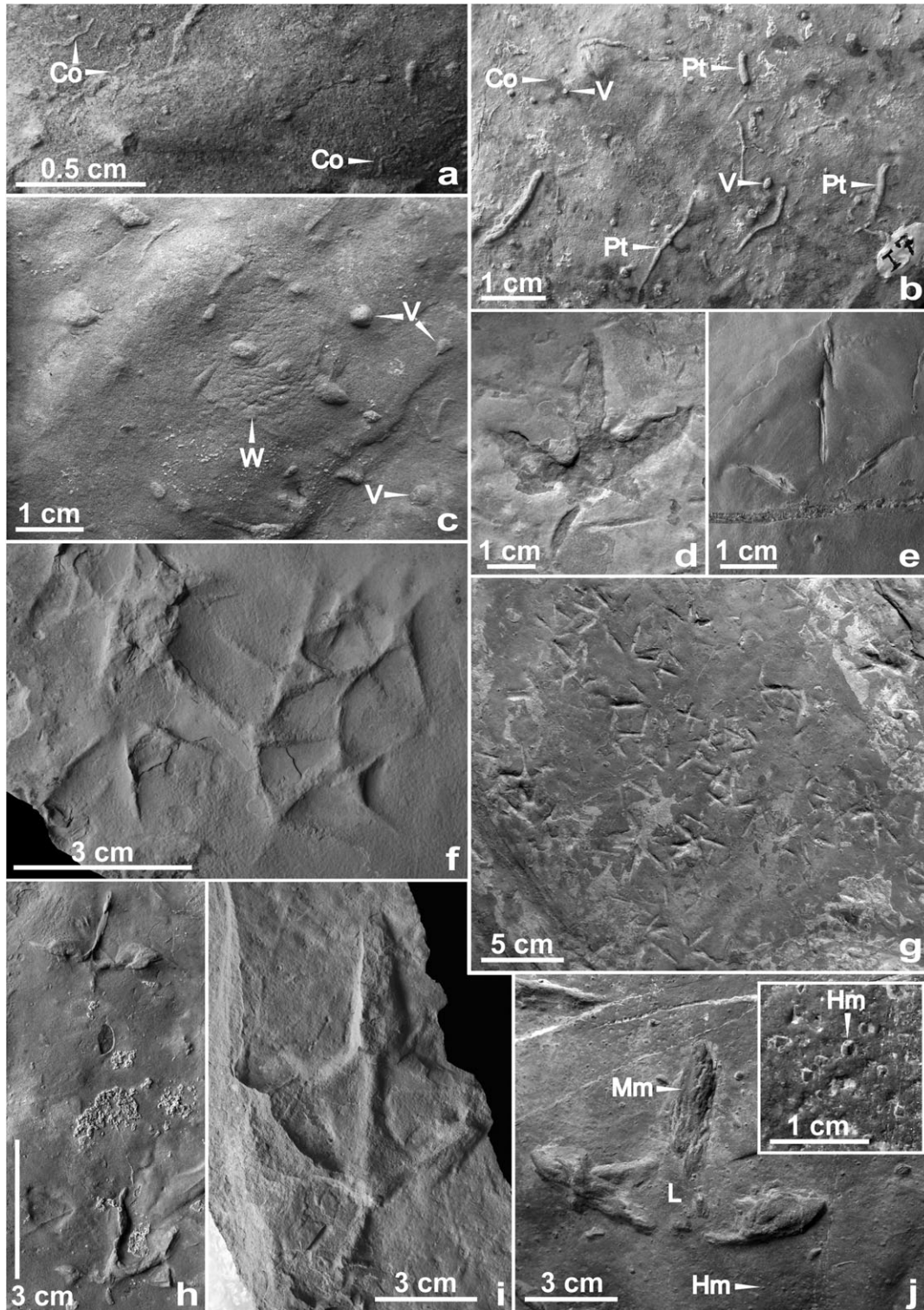


Figure 8. Trace fossils from the Upper Eocene (Priabonian) Liédena Sandstone (Gendulain Formation). (a) *Cochlichmus* isp. (Co), hypichnia (Sample I7, Indurain). (b) *Cochlichmus* isp. (Co), *Palaeophycus tubularis* (Pt) and vertical tubes (V), hypichnia (Sample I7, Indurain). (c) Vertical tubes (V) and wrinkle marks (W), hypichnia (Sample I8, Indurain). (d) *Gruipea* isp., hypichnion (Sample J2, Javier-Xabier). (e) *Koreanaornis* isp., epichnion (Javier-Xabier). (f) *Koreanaornis* isp., hypichnia (Sample LH2, Liédena-Ledeá). (g) *Koreanaornis* isp., epichnia (Sample Z1, Zabaltza-Ibargoiti). (h) cf. *Koreanaornis* isp., hypichnia (Sample I1, Indurain). (i) *Leptoptilostipus pyrenaicus* hypichnion (Sample J1, Javier-Xabier). (j) cf. *Leptoptilostipus* (L), microbial mat (?) (Mm) and halite moulds (Hm), hypichnia (Sample LI8, Liédena-Ledeá). The specimens in figs. d–j were reproduced from Payros *et al.* (2000). All the traces are preserved in sandstone beds.

conical pellets, showing horizontal meander maze galleries (López Cabrera and Olivero, 2014; Leaman *et al.*, 2015; and references herein).

#### 4.1.11. *Ophiomorpha rudis* (Książkiewicz, 1977) (Fig. 4b–f)

*Remarks.* Epichnial and hypichnial convex and concave tunnels, slightly curved and commonly branched, with Y-shaped (mainly) and T-shaped bifurcations forming meandering irregular mazes; coarse-grained lined walls, with irregular granules (agglutinated pelletoidal sediment) or more smooth margins or scratched walls; tunnel diameters between 6 and 35 mm. These traces correspond well with the ichnospecies *Ophiomorpha rudis*, as described by Uchman (2009). Burrows with smooth margins resemble *Thalassinoides*. Other similar traces, but with a bioglyph sculpture consisting of slightly scratched walls, could be allocated to *Spongiomorpha* de Saporta, 1887 (Fig. 4e). However, according to Uchman (2009), the smooth form is the most common morphology in the horizontal parts of *Ophiomorpha rudis* and the scratched form can also be included within the variability of the same ichnospecies; the occurrence of smooth burrows without walls, tunnels with irregular muddy sand granules or tunnels ornamented with scratches are all related with the consistency of sediment.

#### 4.1.12. *Ophiomorpha* isp. 1 (Fig. 7a–d)

*Remarks.* Endichnial and hypichnial convex and concave burrows, slightly curved, occasionally branched with Y-shaped bifurcations, forming high density, horizontal, irregular mazes; vertical shafts are common, tunnels 7–20 mm wide, knobby, densely granulated walls, but commonly segments with slightly rough, smoother walls, pellet shape variable from commonly ovoid-elongated to subspherical or slightly conical, 2–4.5 mm in diameter. The common, more granulated walls differentiate these traces from *Ophiomorpha rudis* (Książkiewicz, 1977), which has longer, smooth segments (see Uchman, 2009). As in *Ophiomorpha nodosa* Lundgren, 1891, the walls of these specimens are densely pelleted, but unlike this ichnospecies, other segments are smoother and finely rough. These smoother parts might correspond to the inner surface of the lining. The horizontal galleries form irregular mazes and not meander mazes as in *Ophiomorpha irregulaire*, and vertical shafts are absent or rare (see López Cabrera and Olivero, 2014; Leaman *et al.*, 2015, for distinctive features of *O. irregulaire*). By contrast, in the specimens described herein, the vertical shafts are deep and abundant (Fig. 7c). According to this, assignation of our specimens to *Ophiomorpha nodosa* and/or *Ophiomorpha irregulaire* is uncertain, even more so taking

into account the possible co-occurrence in the studied outcrops of both ichnospecies.

#### 4.1.13. *Ophiomorpha* isp. 2 (Fig. 7e)

*Remarks.* Vertical and horizontal tunnels, horizontal burrows forming regular mazes (polygonal structures). The burrows are as thick as in the *Ophiomorpha nodosa* specimens described above, but the walls are less rough. The differences between *Ophiomorpha* isp. 1 and 2 may have been caused by either lithological changes or may be due to the fact that only the interior surface of the lining has been preserved (smooth in both *Ophiomorpha nodosa* Lundgren, 1891, and *Ophiomorpha irregulaire* Frey *et al.*, 1978) and/or may be a response to other fossil-diagenetic modifications.

#### 4.1.14. *Palaeophycus tubularis* Hall, 1847 (Fig. 8b)

*Remarks.* Hypichnial convex, simple, unbranched, unornamented, straight to curved, very thinly lined, horizontal, inclined to vertical and shallow burrows with an identical infill to the host rock. Diameter is 0.5–1.5 mm; maximum length recorded is 20 mm. Pemberton and Frey (1982) studied the ichnotaxonomy of *Palaeophycus* Hall, 1847, and concluded that only five of the 54 proposed ichnospecies are valid (Keighley and Pickerill, 1997). Only one of them, *Palaeophycus tubularis*, presents unornamented walls like the traces described here.

#### 4.1.15. *Paleodictyon strozzii* Meneghini in Savi and Meneghini, 1850 (Fig. 5h and i)

*Remarks.* Hypichnial, small hexagonal net, mesh size 2.3–3.5 mm and strings about 0.8 mm wide. Following the scheme proposed by Uchman (1995), a number of ichnospecies have been differentiated based on the maximum mesh size and thickness of string. In *Paleodictyon strozzi*, mesh size is larger than in *Paleodictyon minimum* (Sacco, 1888) but less than in other ichnospecies such as *Paleodictyon maximum* (Eichwald, 1868) or *Paleodictyon majus* Meneghini in Peruzzi, 1880.

#### 4.1.16. ?*Phymatoderma* isp. (Fig. 4i)

*Remarks.* High density of endichnial curved bands, up to 8 mm wide and 30 mm long. Bands or ribbons feather-shaped, extending as asymmetrical bunches (feather duster-like), contours 'dentate' and poor defined, unlined. Infill lighter and more clay-rich than the host sedimentary rock, but no pelletal texture is observed. However, in *Phymatoderma* Brongniart, 1849, the lobes are commonly filled with pellets arranged perpendicularly to the longer



axes of the lobes (Fu, 1991). *Phymatoderma* has been interpreted as a product of an endobenthonic deposit-feeding animal. For discussion, see Izumi (2013, 2015).

#### 4.1.17. *Pilichnus dichotomus* Uchman, 1999 (Fig. 4g)

*Remarks.* Endichnial, horizontal, winding and dichotomous Y-shaped strings, without walls. Strings are 0.8–2.5 mm wide and about 110 mm long, with a dark ferruginous fill composed of small cubic crystals of altered pyrite. Strings are surrounded by a white halo or bleaching zone. Bleaching can be a practically synsedimentary process, produced by reducing fluids (perhaps as consequence of biodegradation processes) that reduce the hematite ( $\text{Fe}^{3+} \rightarrow \text{Fe}^{2+}$ ) and may also reduce sulphate to sulphide and precipitate some of the iron as pyrite (see Chan *et al.*, 2005; Santander *et al.*, 2007). Bleaching was also previously observed in specimens of *Pilichnus dichotomus* (see Uchman, 2007b). The association of *Pilichnus* cf. *P. dichotomus*, along with *Oldhamia alata*, with matgrounds has recently been interpreted as revealing systematic undermat mining, reflecting an efficient exploitation of the organic matter preserved below the microbial mat (Buatois and Mángano, 2012). *Pilichnus* was originally recorded from Cretaceous turbidites (Uchman, 1999; Leszczyński, 2003), but its stratigraphic and palaeoenvironmental ranges have more recently been expanded, now including Cambrian and Ordovician shallow-marine deposits, Carboniferous turbidites (see Buatois and Mángano, 2012, for review) and Middle Jurassic mixed siliciclastic–carbonate sedimentary rocks (Joseph *et al.*, 2012). The specimen reported herein, from Eocene sedimentary rocks, represents the youngest record of this ichnotaxon.

#### 4.1.18. *Planolites* isp. (Figs. 4d and h, and 7g)

*Remarks.* Hypichnial burrows 0.9 to <5.0 mm wide, oriented more or less parallel to bedding, straight to gently curved, unlined, smooth to irregularly walled or annulated, unbranched. *Planolites* Nicholson, 1873, is probably produced by worm-like deposit feeders. For discussion, see Pemberton and Frey (1982) and Keighley and Pickerill (1995).

#### 4.1.19. *Scolicia strozzii* (Savi and Meneghini, 1850) (Fig. 5c and d)

*Remarks.* Meandering, smooth, hypichnial semi-relief, about 20–35 mm wide, bilobate meanders closely spaced, axial furrow narrow, 2–10 mm wide. *Scolicia* is a pascichnial (locomotion and feeding behaviour) trace fossil produced by spatangoid irregular echinoids (heart urchins), from shallow to deep-sea environments (Smith and Crimes, 1983). This trace is associated with silty to fine-grained sandy sedimentary rocks (Fu and Werner, 2000). Unlike other

examples of *Scolicia strozzii* described in the literature (Uchman *et al.*, 2004; Rodríguez-Tovar *et al.*, 2010), the axial furrow is narrower and does not take up most of the ridge width. *Scolicia strozzii* was described as *Taphrhelminthopsis* Sacco, 1888, or *Taphrhelminthoida* Książkiewicz, 1977, but they are now considered just preservational variants of *Scolicia* de Quatrefages, 1849. For discussion of *Scolicia* and its toponomic variants, see Uchman (1995) and Bertling *et al.* (2006).

#### 4.1.20. *Scolicia vertebralis* Książkiewicz, 1977 (Fig. 5e)

*Remarks.* Low epichnial, straight to curved, winding-meandering bilobate structure, 67–72 mm wide, with a central narrow furrow or groove with oblique ribs. In the central part of each lobe, a delicate and narrow groove is outlined, parallel to the axial groove. In general, the specimens of *Scolicia vertebralis* studied herein are wider than the typical specimens reported in the literature (e.g., Uchman *et al.*, 2004; Rodríguez-Tovar *et al.*, 2010).

#### 4.1.21. *Spongeliomorpha* cf. *oraviense* (Książkiewicz, 1977) (Fig. 7f)

*Remarks.* Hypichnial branched circular or elliptical burrows, 18–20 mm wide, surface partially covered by bioglyphs consisting of casts of incised scratches that form Y-shaped ridges. Ridges oriented mainly oblique to the axis of the burrow. When the ridges are in contact with each other, the bioglyph sculptures form a sub-rhomboidal irregular pattern(?). *Spongeliomorpha* Saporta, 1887, is recognized by its surface covered by bioglyphs, which are absent in *Thalassinoides* Ehrenberg, 1944 (smooth surface), and *Ophiomorpha* Lundgren, 1891 (pelleted lining). *Spongeliomorpha*, *Thalassinoides* and *Ophiomorpha* can be part of compound structures produced by malacostracan crustaceans (see Bertling *et al.*, 2006, fig. 15). Bioglyphs provide significant palaeoethologic information of the tracemaker (Ekdale and de Gibert, 2010). Thus, the characteristics of the bioglyph sculpture have been used as an ichnotaxobase (Bertling *et al.*, 2006) at the ichnospecific level of *Spongeliomorpha* (see Muñiz and Mayoral, 2001, for a review of the ichnospecies). The oblique arrangement of the scratches (ridges) in the studied specimens could be related to either the ichnospecies *Spongeliomorpha oraviense* or *Spongeliomorpha iberica* Saporta 1887 (Ekdale and de Gibert, 2010). We tentatively assigned the studied specimens to *S. oraviense* due to the poorly developed sub-rhomboidal irregular pattern, dissimilar to the well-developed rhomboidal pattern typical of *S. iberica* (Ekdale and de Gibert, 2010). *Spongeliomorpha* is usually associated to firmground conditions, as indicated by the presence of bioglyphs,



therefore being related to the *Glossifungites* ichnofacies and to stratigraphically significant surfaces (see de Gibert and Robles, 2005, for the record of high frequency marine flooding surfaces).

#### 4.1.22. *Spongiomorpha* cf. *sicula* D'Alessandro and Bromley, 1995 (Fig. 7g)

*Remarks.* Hypichnial, unbranched (?) burrows, 10–12 mm wide, surface partially covered by a strong bioglyph of longitudinal ridges that apparently do not cross each other. The longitudinal ornamentation links these ichnofossils to ichnospecies as *Spongiomorpha? annulatum* Kennedy, 1967, or *Spongiomorpha sicula*. However, a higher regularity and continuity of the ridges with respect to the main axis (see Muñiz and Mayoral, 2001) allows a tentative assignation to *S. sicula*.

#### 4.1.23. *?Squamodictyon* isp. (Fig. 5j)

*Remarks.* Poorly preserved net, hypichnial, small, scale-shaped meshes, about 3.5–4.5 mm long, strings 1.0–1.5 mm wide. Poor preservation hinders a conclusive classification. *Squamodictyon* is a typical graphoglyptid trace of the *Nereites* ichnofacies in flysch deposits, produced by an unknown farming animal (see Uchman and Wetzel, 2012). Seilacher (2007) considered *Squamodictyon* Vialov, Vyalov and Golev, 1960, as an ichnosubgenus of *Paleodictyon* Meneghini, 1850.

#### 4.1.24. *Taenidium* cf. *crassum* Bromley, Ekdale and Richter, 1999 (Fig. 5f)

*Remarks.* Endichnial, thinly lined(?), unbranched, straight or slightly curved cylindrical trace fossil, at least 19–32 mm long, 1.7–3.5 mm wide, meniscate fill composed of deep, paraboloid, asymmetrical and offset packets. Packets are differently coloured and accumulate more or less as an alternating pattern of light and dark bands. According to the diagnosis of Bromley *et al.* (1999) for *Taenidium crassum*, the asymmetrical meniscate backfill of our specimens allows assignation to this ichnospecies. However, it cannot be discarded that the apparent asymmetry could actually be a consequence of the section observed. The sharp outline of *T. crassum* specimens, together with their co-occurrence with *Thalassinoides*, was interpreted as indicative of firm substrates (Knaust and Costamagna, 2012). The presence of isolated tubular meniscate structures, with not repeated occurrence, allows its differentiation from *Zoophycos* (Rodríguez-Tovar and Dorador, 2014).

#### 4.1.25. *Thalassinoides* isp. (Fig. 7h)

*Remarks.* Gallery systems with vertical and horizontal components, horizontal burrows with Y-shaped bifurcations forming regular mazes of hexagonal structures, diameters of burrows between 8 and 35 mm, smooth walls. In some cases, the filling of *Thalassinoides* Ehrenberg, 1944, includes abundant bioclasts, mainly tests of larger foraminifers (Nummulitidae and others) and bivalve shell fragments (mainly Pectinidae) (Fig. 7h).

#### 4.1.26. Vertical tubes (Fig. 8b and c)

*Remarks.* Hypichnial convex (endichnial?), single, vertical, unbranched burrows, cylindrical or subcylindrical, lined or unlined and perpendicular to the bedding plane. Burrow fill predominantly massive and identical with overlying sedimentary rock. The dimensions of the burrows vary in different burrow populations; maximum observed diameters vary from 1 to 4 mm. The trace fossils are preserved as cylindrical or subcylindrical structures perpendicular to the bedding plane. In the slabs where they are present, there is no evidence of these vertical tubes in the perpendicular cross-sections. These traces could be related with *Skolithos* Haldeman, 1840, if each tube is an independent trace, or *Arenicolites* Salter, 1857, if the trace is U-shaped.

#### 4.1.27. *Gruipeda* isp. (Fig. 8d)

*Remarks.* Hypichnial convex bird tracks. They are anisodactyl, slightly asymmetric and tetradactyl, with three digit impressions directed forward and one directed backward. The footprints are small to medium in size from 48 to 50 mm and approximately as long as wide. Digit III (central) impression is the longest. Digit IV impression is slightly larger than digit II. Digit I is the smallest. The divarication between digits II and IV is about 100°. Webbing absent.

The three tracks classified as *Gruipeda* isp. are part of a trackway (repichnia). The tracks are not well preserved and present some variability among them. The digit impressions are more robust than *Koreanaornis*-like tracks. According with the diagnosis of *Gruipeda* (*sensu* De Valais and Melchor, 2008), these tracks could be classified within this ichnogenus. *Gruipeda* includes 12 nominal ichnospecies (see De Valais and Melchor, 2008) which differ among each other mainly by the size and divarication. As we have suggested above, the shape of the tracks studied here are variable, and they are not well enough preserved for a confident determination of the ichnospecies.

#### 4.1.28. *Koreanaornis* isp. (Fig. 8e–g)

*Remarks.* Hypichnial convex and epichnial concave repichnia bird tracks. They are anisodactyl, slightly

asymmetric and tridactyl or tetradactyl, with three slender digit impressions directed forward and, when impressed, one directed backward. The footprints are diminutive to small from 19 to 25 mm and approximately as long as wide. Digit III (central) impression is the longest. Digit IV impression is larger than digit II. When it is impressed, digit I is the smallest. Digit impressions are not connected proximally. The divarication between digits II and IV is very variable and ranges between 70° and 125° approximately. Claw marks are sometimes visible and metatarsal pad impression is absent. These tracks were considered by Payros *et al.* (2000) as part of type 5 *Charadriipeda* ichnosp. 1 in Panin and Avram (1962) and type 6 *Charadriipeda* ichnosp. 2. Díaz-Martínez *et al.* (2015) classified these tracks as *Koreanaornis* isp. (see discussion in this article).

#### 4.1.29. cf. *Koreanaornis* (Fig. 8h)

*Remarks.* Hypichnial convex and epichnial concave repichnia bird tracks. They are anisodactyl, slightly asymmetric and tetradactyl, with three slender digit impressions directed forward and one directed backward. The footprints are small from 33 to 40 mm and approximately as long as wide. Digit III (central) impression is the longest. Digit IV impression is larger than digit II. Digit I is the smallest. Digit impressions are connected proximally. A small proximal structure is present between toes III and IV in some samples, but is absent in the rest. The divarication between digits II and IV is very variable and ranges between about 70° and 125°. Claw marks are sometimes visible. Metatarsal pad impression is absent. These tracks were considered by Payros *et al.* (2000) as type 4 and part of type 5 *Charadriipeda* ichnosp. They are similar to the tracks classified here as *Koreanaornis* isp. but are less well preserved. The tracks are tetradactyl and the digit impressions are always connected proximally. Both features differ these tracks from *Koreanaornis* isp. tracks. Although these tracks do not share all the features of *Koreanaornis* isp., we classify them with open nomenclature as cf. *Koreanaornis*.

#### 4.1.30. *Leptoostipus pyrenaicus* Payros *et al.*, 2000 (Fig. 8i)

*Remarks.* Hypichnial convex and epichnial concave repichnia bird tracks. Anisodactyl, semi-palmate and slightly asymmetric tracks with three digit impressions directed forward and one directed backward. The tracks are large to very large (approximately between 80 and 120 mm) and approximately as long as wide. Digit III (central) impression is the longest. Digit II impression is smaller than digit IV impression, and both are slightly curved inward. Digit I impression is the smallest and incumbent. The divarication between digits II and IV is about 120°. Claw marks are

sometimes visible. An interdigital mesial web extends from the tips of the digit II and IV impressions to the middle part of the digit III impression. Payros *et al.* (2000) defined the ichnotaxon *Leptoostipus pyrenaicus* with webbed bird tracks published before by Mangin (1962) and Raaf *et al.* (1965). This ichnotaxon differs from other tracks of web-footed track makers (*Anatipeda* Panin and Avram, 1962, *Charadriipeda* Panin and Avram, 1962, *Phoenicopterichnum* Aramayo and Manera de Bianco, 1987, *Presbyornithiformipes* Yang *et al.*, 1995, *Uhangriichnus* Yang *et al.*, 1995, and *Roepichnus* Doyle *et al.*, 2000) mainly in the position of web mark.

#### 4.1.31. cf. *Leptoostipus* (Fig. 8j)

*Remarks.* Hypichnial convex repichnia bird tracks. Anisodactyl and slightly asymmetric tracks with three digit impressions directed forward and uncommonly one directed backward. The tracks are large (approximately between 80 mm) and slightly wider than long. Digit III (central) impression is the longest. Digit II impression is smaller than digit IV impression, and both are slightly curved inward. Digit I, when impressed, is the smallest. The interdigital divarication between digits II and IV is about 140°. A not well-impressed interdigital mesial web is present in some tracks from the tips of the digit II and IV impressions to the middle part of the digit III impression.

These bird tracks were classified by Payros *et al.* (2000) as intermediate type 1-2 and type 2. They are similar to *Leptoostipus pyrenaicus* but not so well preserved. The web mark and digit I impression are slightly impressed in some tracks and absent in others. In addition, the divarication between digits II and IV are larger in these tracks than in *Leptoostipus*. Nevertheless, the size, the inward curvature of digits II and IV and the outline are all similar to *Leptoostipus*. We consider that the differences between both morphotypes are due to changes in the mud behaviour where the track makers walked and show the variability of the *Leptoostipus* shape. As these last tracks do not present the precise features of the diagnosis of *Leptoostipus*, we have left them in open nomenclature.

## 4.2. Trace fossil distribution and associated lithostratigraphic units

The trace fossil assemblage of the Ezkaba Formation consists of 13 ichnogenera and 15 ichnospecies, which can be grouped according to their pre- and post-depositional origin. Thus, pre-depositional structures are *Belorhaphé* isp., *Helminthorhaphé flexuosa*, *Paleodictyon strozzii*, *Scolicia strozzii* and *?Squamodictyon* isp., while post-depositional structures consists of *Chondrites* isp., *Multina minima*,

*Nereites irregularis*, *Ophiomorpha annulata*, *Ophiomorpha rudis*, *?Phymatoderma* isp., *Pilichnus dichotomus*, *Planolites* isp., *Scolicia vertebralis* and *Taenidium crassum*. The most abundant trace fossils in this unit are *Ophiomorpha rudis* and *Paleodictyon strozzii*.

The trace fossil assemblage of the Ardanatz Sandstone and Ilundain Formations consists of five ichnogenera and eight ichnospecies: *Halopoa imbricata*, *Ophiomorpha nodosa*, *Ophiomorpha* isp. 1 and 2, *Planolites* isp., *Spongiomorpha* cf. *oraviense*, *Spongiomorpha* cf. *sicula* and *Thalassinoides* isp., together with spreite burrows (*?Rhizocorallium*). *Ophiomorpha nodosa* and *Ophiomorpha* isp. 1 are the most abundant traces.

Finally, the trace fossil assemblage at the Liédena Sandstone consists of seven ichnotaxa. Three are invertebrate ichnotaxa: *Cochlichnus* isp., *Palaeophycus tubularis* and vertical tubes. The other five correspond to bird footprints and are as follows: *Gruipeda* isp., *Koreanaornis* isp., cf. *Koreanaornis*, *Leptoptilostipus pyrenaicus* and cf. *Leptoptilostipus*. The most abundant traces are the bird tracks *Koreanaornis* isp. and *Leptoptilostipus pyrenaicus*. For a more specific view of the distribution and abundance in each locality and lithostratigraphic unit, see Table 1.

## 5. DISCUSSION

### 5.1. Ichnofacies and palaeoenvironmental inferences

The trace fossil assemblages show clear differences between the studied formations, allowing characterization of several ichnofacies/ichnosubfacies. The Ezkaba Sandstone and the Ardanatz Sandstone–Ilundain Marl formations show only two common ichnogenera, the facies-crossing *Planolites* and *Ophiomorpha*, in the latter case with different ichnospecies. The Gendulain Formation does not share any ichnogenus with other formations.

#### 5.1.1. Ezkaba Sandstone Formation

The trace fossil assemblage of the Ezkaba Sandstone Formation is characteristic of the deep-sea (more than 2000 m depth) *Nereites* ichnofacies, as revealed by the presence of graphoglyptids (e.g., Uchman, 2009; Uchman and Wetzel, 2011). The *Nereites* ichnofacies is associated to the different parts of a turbidite system, and it can be divided into three ichnosubfacies (Uchman, 2009). Firstly, the *Ophiomorpha rudis* ichnosubfacies, typical of thick-bedded turbidites from channels or proximal lobes or of thick-bedded fans of deep-sea clastic ramps, mainly consists of *Ophiomorpha*, *Scolicia* and, occasionally, *Nereites* and *Chondrites* (Uchman, 2001, 2009; Heard and Pickering, 2008). Secondly, the *Paleodictyon* ichnosubfacies from medium- to thin-bedded sandy flysch deposits features the presence of graphoglyptids (Seilacher,

1974; Uchman and Wetzel, 2011). Finally, the *Nereites* ichnosubfacies represents the most distal part of the turbidite system, with muddy distal flysch deposits and the presence of structures such as *Nereites*, *Phycosiphon* or *Zoophycos* (Seilacher, 1974; Heard and Pickering, 2008; Uchman, 2009). Mixed *Paleodictyon*–*Ophiomorpha rudis* ichnosubfacies would be characteristic of proximal off-axis environments (Heard and Pickering, 2008). Variations in the three ichnosubfacies, including transitions, have been registered in unique successions, where the ichnosubfacies have been related to varying bathymetric and hydrodynamic conditions (Bayet-Goll *et al.*, 2014). However, in such cases, the sedimentological data must be thoroughly analysed for the ichnological discrimination between sub-environments within submarine fans (Cummings and Hodgson, 2011).

According to the distribution and abundance of the trace fossil assemblage registered in the Ezkaba Sandstone Formation, the *Ophiomorpha rudis* and the *Paleodictyon* ichnosubfacies can be differentiated. In the Uharte, Azotz, Antsoain and Artika outcrops (Table 1), the ichnoassemblages show low diversity and are characterized by the dominance of *Ophiomorpha* (*O. rudis* and *O. annulata*) and the presence of *Scolicia* (*S. strozzii* and *S. vertebralis*) supporting the *Ophiomorpha rudis* ichnosubfacies. In Elkarte (Table 1), the presence of graphoglyptids (e.g., *Paleodictyon strozzii*, cf. *Squamodictyon* isp. and *Helminthorhapha flexuosa*) suggests the *Paleodictyon* ichnosubfacies. The record of *Ophiomorpha* (*O. rudis* and *O. annulata*) could be related to a mixed *Paleodictyon*–*Ophiomorpha rudis* ichnosubfacies ichnoassemblage.

Therefore, the ichnosubfacies distinguished in the Ezkaba Sandstone Formation could be mainly related to the variations in hydrodynamic energy and substrate (grain size) that occur in different parts of turbiditic depositional settings. Other important controlling factors of the deep-sea environment, such as oxygenation or organic matter content, may have had a variable incidence. The trace fossil assemblage is indicative of good oxygen (aerobic) conditions for the macrobenthic tracemaker community. In fact, trace fossils usually associated with decreasing oxygenation (dysaerobic conditions), such as *Chondrites* and *Zoophycos* (e.g., Rodríguez-Tovar and Dorador, 2014; and references herein), are very scarce or even absent. The general light colour of the sedimentary rocks supports such an interpretation. The presence of pre-depositional forms, mainly graphoglyptids, representing a K-selected equilibrium strategy (Ekdale, 1985; Uchman, 1995), is indicative of relatively stable, oligotrophic conditions during interturbidite deposition (Rodríguez-Tovar *et al.*, 2010, 2015).

#### 5.1.2. Ardanatz Sandstone–Ilundain Marl formations

The trace fossil assemblage of the Ardanatz Sandstone and Ilundain Marl formations, with dominance of *Thalassinoides*



and *Ophiomorpha*, can be related to the *Cruziana* ichnofacies, developed in relatively low-energy environments, in semicohesive muddy substrates with intercalated silt and sand. The archetypal *Cruziana* ichnofacies occurs from slightly above the fair-weather wave-base to the storm wave-base, from the lower shoreface to the lower offshore, under moderate- to low-energy conditions (e.g., MacEachern *et al.*, 2007; and references herein).

Such a wide lateral distribution of the *Cruziana* ichnofacies includes a wide range of depositional areas, which involves variations in environmental conditions and hence in the ichnological assemblage. This fact allows subdivision of the archetypal *Cruziana* ichnofacies (MacEachern *et al.*, 2007; Buatois and Mángano, 2011). Thus, a distal expression of the *Cruziana* ichnofacies is recognized at the transition between the archetypal *Cruziana* ichnofacies, towards more proximal positions, and the archetypal *Zoophycos* ichnofacies (or the *Nereites* ichnofacies) in a basinward direction, usually from the lower offshore towards the inner shelf, and associated with muddy siltstone and silty mudstone substrates (MacEachern *et al.*, 2007; Buatois and Mángano, 2011). With regard to *Thalassinoides* and *Ophiomorpha*, the distal expression of the *Cruziana* ichnofacies shows an increase in *Thalassinoides*, compared to the archetypal expression of the *Cruziana* ichnofacies where *Ophiomorpha* are comparatively more abundant (MacEachern *et al.*, 2007; Buatois and Mángano, 2011).

Accordingly, the stratigraphic variations registered in the relationship between *Thalassinoides* and *Ophiomorpha* in the Pamplona Basin are highly significant. Both ichnotaxa are continuously represented in the succession, but variations occur in their relative abundances. At the base of the Pamplona Marl Formation (not included in this analysis), both ichnotaxa are registered (field observations of *Thalassinoides suevicus* and *Ophiomorpha* *isp.*), but in the overlying Ardanatz Sandstone and especially in the Ilundain Marl formations, the abundance of *Ophiomorpha* shows a significant increase. According to this, a stratigraphic trend from the distal to proximal expressions of the archetypal *Cruziana* ichnofacies can be envisaged. This trend could be associated with the type of substrate as a major controlling factor. *Ophiomorpha*, as an externally pellet-lined burrow, is emplaced in sandy substrates, in which burrows are stabilized by reinforcing their walls, while *Thalassinoides*, with burrow margins dominantly smooth, commonly occurs in fine-grained substrates in which sediment linings are unnecessary.

The structures characterized by the presence of more or less well-developed bioglyphs (i.e., spreite burrows ?*Rhizocorallium*, *Spongeliomorpha* *cf. oraviense* and *S. cf. sicula*) might also be significant in terms of substrate

firmness. Their occurrence might be indicative of firmground conditions and the associated *Glossifungites* ichnofacies, although the presence of bioglyphs does not necessarily indicate a firmground (Seike and Nara, 2007).

### 5.1.3. Liédena Sandstone Member (Gendulain Formation)

The Liédena Sandstone ichnofauna presents low ichnodiversity, being just composed by vertebrate tracks (*Leptoilostipus*, *Koreanaornis* and *Gruipeda*), horizontal trails and burrows (*Cochlichnus*, *Palaeophycus*) and vertical tubes. While *Palaeophycus* and the vertical tubes occur in many settings (continental, coastal and marine), both the vertebrate tracks and *Cochlichnus* have been related to more specific environmental conditions and depositional environments. The typical environments where vertebrate tracks are commonly preserved are beaches, shorelines, estuaries, tidal lagoons, floodplains, deltas, lakes, water-holes and deserts (Thulborn, 1990). Vertebrate tracks have been cited in the continental ichnofacies *Scoyenia*, which is typical of transitional alluvial-lake zones, floodplains, ephemeral lakes, ponds and wet interdunes (Buatois and Mángano, 1995); in the *Octopodichnus*–*Entradichnus* ichnofacies, defined in aeolian dunes (Hunt and Lucas, 2007); and in the ichnofacies *Psilonichnus*, typical of backshore areas, washover fans, coastal dunes and supratidal flats environments (see Pemberton *et al.*, 1992). Desjardins *et al.* (2012) also suggested that vertebrate trackways may be present in the *Cruziana* ichnofacies of intertidal flats, lagoons and estuaries (Pemberton and Wightman, 1992; Mángano and Buatois, 1999).

In this study, the vertebrate tracks were produced in a nearly water saturated substrate, soft enough to allow the formation of the tracks and their subsequent preservation (de Gibert and Saez, 2009; Falkingham, 2014), thus indicating shallow-water conditions or subaerial exposure (Thulborn, 1990). Furthermore, the Liédena Sandstone vertebrate tracks are exclusively composed of bird ichnotaxa and two of them, *Koreanaornis* and *Leptoilostipus*, have been related to shorebird track makers (Lockley and Harris, 2010). Lockley *et al.* (1994) proposed the shorebird ichnofacies, which comprises ichnocoenoses of shorebirds attributable to Charadriiformes (waders and gulls), Anseriiformes (ducks and geese) and Ciconiiformes (storks and herons), and has definitely been interpreted as a lacustrine ichnofacies, although potentially associated with beaches, marine influenced lagoons or other lake types (Doyle *et al.*, 2000; de Gibert and Saez, 2009) considered the shorebird ichnofacies a subset of the *Scoyenia* ichnofacies (an ichnosubfacies *sensu* Melchor *et al.*, 2006) that characterizes the subaerial part of low-energy shore areas.

On the other hand, the presence of *Cochlichnus* in non-marine settings is typical of the *Mermia* ichnofacies and suggests perennial freshwater conditions from a low-energy environment (Buatois and Mángano, 2002; Hasiotis, 2002).

However, *Cochlichnus* isp. has also been recorded in subaerial conditions in wet mud (Hasiotis, 2002). Buatois and Mángano (1998) cited the presence of *Cochlichnus* in the *Scoyenia* ichnofacies, and Mikuláš *et al.* (2013) identified it in the *Cruziana* ichnofacies in tidal environments.

In summary, the Liédena Sandstone Member ichnofauna consists of ichnotaxa commonly, though not exclusively, recorded from continental-coastal settings. No ichnotaxa indicative of clear marine influence has been detected. The occurrence of ichnotaxa characteristic of more than one ichnofacies (bird tracks of *Scoyenia* ichnofacies and *Cochlichnus* of *Mermia* ichnofacies) in a single ichnofauna could be interpreted as a consequence of the trace fossil producers being environmentally tolerant animals that could inhabit and behave similarly in either setting. Alternatively, the host sediment body could have been subject to changes in environmental conditions while still at the surface (Keighley and Pickerill, 2003). In the latter case, the ichnofauna could be regarded as examples of composite ichnofacies that are taphonomic successors of combinations of the *Mermia* and *Scoyenia* ichnofacies (Keighley and Pickerill, 2003).

Microbial mat impressions have also been identified as wrinkle marks preserved in ripple troughs and as retracted zones in the digit impressions of some tracks. Microbial mats can greatly enhance the preservation of vertebrate and invertebrate surface tracks (e.g., Marty *et al.*, 2009; Carmona *et al.*, 2012). Carmona *et al.* (2012) found that thin microbial mats (0.5 cm thick) preserve trackways better than thick mats (1.5 cm thick). Hence, the variable preservation of the Liédena Sandstone Member tracks could likely be a consequence of different thicknesses of the microbial mats. The reducing chemical conditions beneath the microbial mats may have contributed to the formation of 'anoxic' minerals, such as pyrite (Schieber, 1999), which has also been observed in the surface of some slabs. Carmona *et al.* (2012) suggested that the cementation and highly reducing conditions below the microbial mat preclude colonization by typical endofauna in tidal-flats, thus preventing the obliteration of shallow imprinted vertebrate tracks. This could explain the abundance of bird tracks in the Liédena Sandstone Member, and the scarcity and low diversity of invertebrate traces. Therefore, the microbial mats acted as taphonomic bias favouring the preservation of vertebrate tracks and determining the presence of endofauna, which implies that the assignation of the ichnofauna to a particular ichnofacies is merely tentative (most likely a combination of the *Mermia* and *Scoyenia* ichnofacies).

## 5.2. Trace fossil analysis and the tectonosedimentary evolution of the Pamplona Basin

The Eocene succession of the Pamplona Basin shows a typical foreland basin evolution. Whereas denudation of the

Eastern Pyrennes occurred in the Early–Middle Eocene (Ypresian–Lutetian; approximately 56–40 Ma), the orogenic uplift began in Middle Eocene (Bartonian) times (approximately 40 Ma) in the western Pyrenean (Pujalte *et al.*, 2002). It is well known that peripheral foreland basins evolve from an underfilled to an overfilled depositional state (DeCelles, 2012). In ancient settings, the transition between these states (i.e., the degree of filling of the basin) is commonly approximated from the long-term trends in the sedimentary facies found in the basin. This is shown by the facies changes from deep-marine turbiditic deposits that accumulated in the foredeep during the underfilled stage (classically termed 'flysch' stage) to shallow-marine and continental deposits that accumulated during the overfilled 'molasse' stage. The flysch-to-molasse transition is commonly caused by both a reduction in the rate of thrust wedge advance or an increase in the rate of uplift, exhumation and sediment production in the thrust wedge (Sinclair, 1997a, b).

In the Ezkaba Sandstone Formation, graphoglyptid traces have been related to the *Nereites* ichnofacies (Uchman and Wetzel, 2011). This ichnofacies is typical of depths below 2000 m (Uchman, 2009). Besides, the presence of the *Ophiomorpha rudis* ichnosubfacies, interpreted as turbidite successions from channels, and *Paleodictyon* ichnosubfacies, related to flysch deposits, is also significant (Uchman, 2009). The lateral co-occurrence of both ichnosubfacies is controlled by changes in turbidite thickness and sand content from the channel axes to proximal off-axis areas. Therefore, the trace fossil analysis agrees with the sedimentological interpretation of the Ezkaba Sandstone Formation, which was attributed to as a northerly sourced, westwards migrating channel-levee turbidite system (Payros *et al.*, 1997).

The ichnoassemblage of the Ardanatz Sandstone and Ilundain Marl formations has been related to the *Cruziana* ichnofacies, which occurs from slightly above the fair-weather wave-base to storm wave-base (i.e., from the lower shoreface to the lower offshore) under moderate- to low-energy conditions (e.g., MacEachern *et al.*, 2007; and references herein). Finally, in the Gendulain Formation (Liédena Sandstone Member), the ichnoassemblage could be regarded as an example of composite ichnofacies that are taphonomic successors of combinations of the *Mermia* and *Scoyenia* ichnofacies (Keighley and Pickerill, 2003). The palaeohydrological and palaeoenvironmental scenario deduced from the bioturbation and organic structures (microbial mats), in addition to other sedimentary structures (halite moulds, desiccation cracks, raindrops marks, synaeresis cracks, flat-topped wave ripples with ladder-back ripples etc.; Payros *et al.*, 2000) is consistent with a tidal flat developed in a partially protected embayment or marginal lagoon behind a wave-dominated delta (Payros



*et al.*, 2000). Such an environment would have been extremely sensitive to water level oscillations, causing cyclic exposure and submersion of large areas, and to variations in salinity throughout the tidal cycle.

## 6. CONCLUSIONS

The sedimentary evolution recorded by the 1500 m-thick Middle–Upper Eocene succession of the Pamplona Basin suggests a progressive, long-term (approximately 40–34 Ma) shallowing from deep-sea into intertidal conditions. In addition to the influence of some tectonic uplift during the latest stages, such evolution was mainly driven by the progressive filling of the South Pyrenean foreland basin with sediments derived from the denuding orogen. Consequently, the succession can be readily ascribed to the overfilled, ‘molasse’ stage of foreland basin evolution (DeCelles, 2012). The shallowing-up evolution can also be recognized by means of the trace fossils preserved throughout the succession. Thus, the Middle Eocene Ezkaba Sandstone Formation contains trace fossils assigned to the *Ophiomorpha rudis* and *Paleodictyon* ichnosubfacies of the *Nereites* ichnofacies, which agrees with the sedimentological interpretation that related the unit to a laterally migrating channel-levee turbidite system (Payros *et al.*, 1997).

The Ardanatz Sandstone and Ilundain Marl formations contain trace fossils included in the *Cruziana* ichnofacies, which are representative of relatively low-energy environments with semicohesive muddy substrates containing intercalated silt and sand. According to the relationship between *Thalassinoides* and *Ophiomorpha*, a stratigraphic trend from the distal to proximal expressions of the archetypical *Cruziana* ichnofacies can be envisaged, the latter units accumulated between the fair-weather wave-base and storm wave-base.

The Liédena Sandstone Member of the Gendulain Formation, part of which accumulated in a partially protected embayment or marginal lagoon behind a wave-dominated barrier beach (Payros *et al.*, 2000), contains invertebrate trace fossils and vertebrate tracks. The evidence suggests that microbial mats acted as taphonomic bias favouring the preservation of vertebrate tracks and conditioning the presence of other trace fossils. Reducing chemical conditions beneath the microbial mats may have precluded colonization by typical endofauna in tidal-flats, thus preventing the obliteration of shallow imprinted vertebrate tracks and other sedimentary structures. Due to taphonomy, attribution of this ichnofauna to a specific ichnofacies is tentative (most likely a combination of the *Mermia* and *Scoyenia* ichnofacies).

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## REFERENCES

- Aramayo, S.A., Manera de Bianco, T. 1987. Hallazgo de una icnofauna continental (Pleistoceno tardío) en la localidad de Pehuen-Co (Partido de Coronel Rosales) Provincia de Buenos Aires, Argentina. Parte I: Edentata, Litopterna, Proboscidea. Parte II: Carnívora, Artiodactyla y Aves. *IV Congreso Latinoamericano de Paleontología Actas* 1, 516–547.
- Astibia, H., Elorza, J., Písera, A., Álvarez-Pérez, G., Payros, A., Ortíz, S. 2014. Sponges and corals from the Middle Eocene (Bartonian) marly formations of the Pamplona Basin (Navarre, western Pyrenees): taphonomic, systematic and paleoenvironmental approaches. *Facies* 60, 91–110.
- Astibia, H., Payros, A., Pereda Suberbiola, X., Elorza, J., Berreteaga, A., Etxebarria, N., Badiola, A., Tosquella, J. 2005. Sedimentology and taphonomy of sirenian remains from the Middle Eocene of the Pamplona Basin (Navarre, western Pyrenees). *Facies* 50, 463–475. la Cuenca de Pamplona (Navarra). *Revista Española de Paleontología* 21, 79–91.
- Astibia, H., Pereda Suberbiola, X., Payros, A., Murelaga, X., Berreteaga, A., Baceta, J.I., Badiola, A. 2007. Bird and mammal footprints from the Tertiary of Navarre (western Pyrenees). *Ichnos* 14, 175–184.
- Azpeitia, F. 1933. Datos sobre el estudio paleontológico del Flysch de la costa cantábrica y de algunos otros puntos de España. *Boletín del Instituto Geológico y Minero de España* 53, 1–65.
- Bayet-Goll, A., Neto De Carvalho, C., Moussavi-Harami, R., Mahboubi, A., Nasiri, Y. 2014. Depositional environments and ichnology of the deep-marine succession of the Amiran Formation (upper Maastrichtian–Paleocene), Lurestan Province, Zagros Fold-Thrust Belt, Iran. *Palaeogeography, Palaeoclimatology, Palaeoecology* 401, 13–42.
- Bertling, M., Braddy, S.J., Bromley, R.G., Demathieu, G.R., Genise, J., Mikuláš, R., Nielsen, J.K., Nielsen, K.S.S., Rindsberg, A.K., Schlirf, M., Uchman, A. 2006. Names for trace fossils: a uniform approach. *Lethaia* 39, 265–286.
- Bromley, R.G., Ekdale, A.A., Richter, B. 1999. New *Taenidium* (trace fossil) in the Upper Cretaceous chalk of northwestern Europe. *Bulletin of the Geological Society of Denmark* 46, 47–51.

- Brongniart, A.T. 1823.** Observations sur les Fucoïdes. *Société d'Histoire Naturelle de Paris, Mémoire* 1, 301–320.
- Brongniart, A.T. 1849.** Tableau des genres de végétaux fossiles considérés sous le point de vue de leur classification botanique et de leur distribution géologique. *Dictionnaire Universel Histoire Naturelle* 13, 1–27 (152–176).
- Buatois, L.A., Mángano, M.G. 1993.** Trace fossils from a Carboniferous turbiditic lake: implications for the recognition of additional nonmarine ichnofacies. *Ichnos* 2, 237–258.
- Buatois, L.A., Mángano, M.G. 1995.** The paleoenvironmental and paleoecological significance of the lacustrine *Mermia* ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage. *Ichnos* 4, 151–161.
- Buatois, L.A., Mángano, M.G. 1998.** Trace fossil analysis of lacustrine facies and basins. *Palaeogeography, Palaeoclimatology, Palaeoecology* 140, 367–382.
- Buatois, L.A., Mángano, M.G. 2002.** Trace fossils from Carboniferous floodplain deposits in western Argentina: implications for ichnofacies models of continental environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 183, 71–86.
- Buatois, L., Mángano, M.G. 2011.** *Ichnology: Organism–Substrate Interactions in Space and Time*. Cambridge University Press: Cambridge.
- Buatois, L., Mángano, M.G. 2012.** An Early Cambrian shallow-marine ichnofauna from the Puncoviscana Formation of Northwest Argentina: the interplay between sophisticated feeding behaviors, matgrounds and sea-level changes. *Journal of Paleontology* 86, 7–18.
- Carmona, N.B., Ponce, J.J., Wetzel, A., Bourno, C.N., Cuadrado, D.G. 2012.** Microbially induced sedimentary structures in Neogene tidal flats from Argentina: paleoenvironmental, stratigraphic and taphonomic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 353, 1–9.
- Chan, M.A., Bowen, B.B., Parry, W.T., Ormó, J., Komatsu, G. 2005.** Active hematite concretion formation in modern acid saline lake sediments, Lake Brown, Western Australia. *GSA Today* 15, 4–10.
- Cummings, J.P., Hodgson, D.M. 2011.** Assessing controls on the distribution of ichnotaxa in submarine fan environments, the Basque Basin, Northern Spain. *Sedimentary Geology* 239, 162–187.
- D'Alessandro, A., Bromley, R.G. 1995.** A new ichnospecies of *Spongeliomorpha* from the Pleistocene of Sicily. *Journal of Paleontology* 8, 71–84.
- DeCelles, P.G. 2012.** Foreland basin systems revisited: variations in response to tectonic settings. In: *Tectonics of Sedimentary Basins: Recent Advances*, Busby, C., Azor Pérez, A. (eds). Blackwell Publishing Ltd.: Hoboken; 405–426.
- Desjardins, P.R., Buatois, L.A., Mángano, M.G. 2012.** Tidal flats and subtidal sand bodies. In: *Trace Fossils as Indicators of Sedimentary Environments*, Knaust, D., Bromley, R.G. (eds). Elsevier: Amsterdam; 529–561.
- De Valais, S., Melchor, R.N. 2008.** Ichnotaxonomy of bird-like footprints: an example from the Late Triassic–Early Jurassic of northwest Argentina. *Journal of Vertebrate Paleontology* 28, 145–159.
- Díaz-Martínez, I., Suárez-Hernando, O., Martínez-García, B., Hernández, J.M., García Fernández, S., Pérez-Lorente, F., Murelaga, X. 2015.** Lower Miocene shorebird-like footprints from the Ebro Basin, La Rioja, Spain: paleoecological and paleoenvironmental significance. *Palaios* 30, 424–431.
- Doyle, P., Wood, J.L., George, G.T. 2000.** The shorebird ichnofacies: an example from the Miocene of southern Spain. *Geological Magazine* 137, 517–536.
- Ehrenberg, K. 1944.** Ergänzende Bemerkungen zu den seinerzeit aus dem Miozän von Burgschleinitz beschriebenen Gangkernen und Bauten dekapoder Krebse. *Paläontologische Zeitschrift* 23, 345–359.
- Eichwald, E. 1868.** *Lethaea rossica ou paléontologie de la Russie. Décrite et figurée*, Atlas. E. Schweizerbart: Stuttgart.
- Ekdale, A.A. 1985.** Paleoecology of the marine endobenthos. *Palaeogeography, Palaeoclimatology, Palaeoecology* 50, 63–81.
- Ekdale, A.A., de Gibert, J.M. 2010.** Paleoethologic significance of bioglyphs: fingerprints of the subterraneans. *Palaios* 25, 540–545.
- Falkingham, P.L. 2014.** Interpreting ecology and behaviour from the vertebrate fossil track record. *Journal of Zoology* 292, 222–228.
- Frey, R.W., Howard, J.D., Pryor, W.A. 1978.** Ophiomorpha: its morphologic, taxonomic, and environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 23, 199–223.
- Fu, S. 1991.** Funktion, Verhalten und Einteilung fucoider und lophoctenoider Lebensspuren. *Courier Forschungsinstitut Senckenberg* 135, 1–79.
- Fu, S., Werner, F. 2000.** Distribution, ecology and taphonomy of the organism trace, *Scolicia*, in northeast Atlantic deep-sea sediments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 156, 289–300.
- Fuchs, T. 1895.** Studien über Fucoiden und Hieroglyphen. *Akademie der Wissenschaften zu Wien, mathematisch-naturwissenschaftliche Klasse, Denkschriften* 62, 369–448.
- de Gibert, J.M., Robles, J.M. 2005.** Firmground ichnofacies recording high frequency marine flooding events (Langhian transgression, Vallès-Penedès Basin, Spain). *Geologica Acta* 3, 295–305.
- de Gibert, J.M., Saez, A. 2009.** Paleohydrological significance of trace fossil distribution in Oligocene fluvial-fan-to-lacustrine systems of the Ebro Basin, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 272, 162–175.
- Haldeman, S.S. 1840.** *Supplement to number one of 'A monograph of the Limniades, and other freshwater bivalve shells of the apparently new animals in different classes, and names and characters of the subgenera in Paludina and Anculosa'*. J. Dobson: Philadelphia.
- Hall, J. 1847.** *Palaeontology of New York* 1, C. Van Benthuysen: Albany.
- Hasiotis, S.T. 2002.** *Continental Trace Fossils*, Short Course Notes 51. SEPM Society for Sedimentary Geology: Tulsa.
- Heard, T.G., Pickering, K.T. 2008.** Trace fossils as diagnostic indicators of deep-marine environments, middle Eocene Ainsa-Jaca basin, Spanish Pyrenees. *Sedimentology* 55, 809–844.
- Heer, O. 1876–1877.** *Flora Fossilis Helvetiae. Die vorweltliche Flora der Schweiz*. J. Würster and Co.: Zürich.
- Hitchcock, E. 1858.** *Ichnology of New England. A report on the sandstone of the Connecticut Valley, especially its fossil footmarks*. W. White: Boston.
- Howard, J.D., Frey, R.W. 1984.** Characteristic trace fossils in nearshore to offshore sequences, Upper Cretaceous of east-central Utah. *Canadian Journal of Earth Sciences* 21, 200–219.
- Hunt, A.P., Lucas, S.G. 2007.** Tetrapod ichnofacies: a new paradigm. *Ichnos* 14, 59–68.
- Izumi, K. 2013.** Geochemical composition of faecal pellets as an indicator of deposit feeding strategies in the trace fossil *Phymatoderma*. *Lethaia* 46, 496–507.
- Izumi, K. 2014.** Isotopic and mineralogical variations in the infill of *Chondrites* from organic-rich black shale (Posidonia Shale, Germany) for assessing the mode of colonization. *Spanish Journal of Paleontology* 29, 107–116.
- Izumi, K. 2015.** Deposit feeding by the Pliocene deep-sea macrobenthos, synchronized with phytodetritus input: micropaleontological and geochemical evidence in the trace fossil *Phymatoderma*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 431, 15–25.
- Joseph, J.K., Patel, S.J., Bhatt, N.Y. 2012.** Trace fossil assemblages in mixed siliciclastic–carbonate sediments of the Kaladongar Formation (Middle Jurassic) Patcham Island, Kachchh, Western India. *Journal Geological Society of India* 80, 189–214.
- Keighley, D.G., Pickerill, R.K. 1995.** The ichnotaxa *Palaeophycus* and *Planolites*: historical perspectives and recommendations. *Ichnos* 3, 301–309.
- Keighley, D.G., Pickerill, R.K. 1997.** Systematic ichnology of the Mabou and Cumberland groups (Carboniferous) of western Cape Breton Island, eastern Canada, 1: burrows, pits, trails, and coprolites. *Atlantic Geology* 33, 181–215.
- Keighley, D.G., Pickerill, R.K. 2003.** Ichnocoenoses from the Carboniferous of eastern Canada and their implications for the recognition of ichnofacies in nonmarine strata. *Atlantic Geology* 39, 1–21.
- Keij, A.J. 1965.** Miocene trace fossils from Borneo. *Paläontologische Zeitschrift* 39, 220–228.
- Kennedy, W.J. 1967.** Burrows and surface traces from the Lower Chalk of Southern England. *Bulletin of the British Museum (Natural History), Geology* 15, 125–167.
- Knaust, D., Bromley, R.G. (eds). 2012.** *Trace Fossils as Indicators of Sedimentary Environments*. Developments in Sedimentology 64. Elsevier: Amsterdam.



- Knaust, D., Costamagna, L.G. 2012.** Ichnology and sedimentology of the Triassic carbonates of North-west Sardinia, Italy. *Sedimentology* **59**, 1190–1207.
- Książkiewicz, M. 1977.** Trace fossils in the Flysch of the Polish Carpathians. *Palaeontologia Polonica* **36**, 1–208.
- Leaman, M., McIlroy, D., Herringshaw, L.G., Boyd, C., Callow, R.H.T. 2015.** What does *Ophiomorpha irregulaire* really look like? *Palaeogeography, Palaeoclimatology, Palaeoecology* **439**, 38–49.
- Leszczyński, S. 2003.** Bioturbation structures in the Holovnia siliceous marls (Turonian–lower Santonian) in Rybotycze (Polish Carpathians). *Annales. Societatis Geologorum Poloniae* **73**, 103–122.
- Lockley, M.G., Harris, J. 2010.** On the trail of early birds: a review of the fossil footprint records of avian morphological and behavioral evolution. In: *Trends in Ornithology Research*, Ulrich, P.K., Willett, J.H. (eds). Nova Science Publishers: Hauppauge; 1–63.
- Lockley, M., Hunt, A., Meyer, C. 1994.** Vertebrate tracks and the ichnofacies concept: implications for palaeoecology and palichnostratigraphy. In: *The Paleobiology of Trace Fossils*, Donovan, S.K. (ed). John Wiley and Sons: Chichester; 241–268.
- López Cabrera, M.L., Olivero, E.B. 2014.** *Ophiomorpha irregulare* and associated trace fossils from the Upper Cretaceous of Patagonia, Argentina: palaeogeographical and ethological significance. *Spanish Journal of Palaeontology* **29**, 33–44.
- Lundgren, B. 1891.** Studier öfver fossiliförande lösa block. *Geologiska Föreningen I Stockholm Förhandlingar* **13**, 111–121.
- MacEachern, J.A., Bann, K.L., Pemberton, S.G., Gingras, M.K. 2007.** The Ichnofacies paradigm: high-resolution paleoenvironmental interpretation of the rock record. In: *Applied Ichnology*, MacEachern, J.A., Bann, K.L., Gingras, M.K., Pemberton, S.G. (eds). SEPM Society for Sedimentary Geology, Tulsa, Short Course Notes **52**; 27–64.
- MacLeay, W.S. 1839.** Note on the Annelida. In: *The Silurian System. Part II: Organic Remains*. Murchison, R.I. (ed). Murray: London; 111–121.
- Mángano, M.G., Buatois, L.A. 1999.** Ichnofacies models in Early Paleozoic tide-dominated quartzites: onshore-offshore gradients and the classic Seilacherian paradigm. *Acta Universitatis Carolinae. Geologica* **43**, 151–154.
- Mangin, J.P. 1962.** Traces de pattes d'oiseaux et flutes-casts associés dans un "faciès flysch" du Tertiaire Pyréenée. *Sedimentology* **1**, 163–166.
- Martinsson, A. 1970.** Toponomy of trace fossils. In: *Trace Fossils*, Crimes, T.P., Harper, J.C. (eds). Seel House Press: Liverpool, Geological Journal, Special Issue **3**, 323–330.
- Marty, D., Strasser, A., Meyer, C.A. 2009.** Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. *Ichnos* **16**, 127–142.
- McIlroy, D. (Ed). 2004.** *The Application of Ichnology to Palaeo-environmental and Stratigraphic Analysis*. Geological Society, London, Special Publications, 228.
- Melchor, R.N., Bedatou, E., de Valais, S., Genise, J.F. 2006.** Lithofacies distribution of invertebrate and vertebrate trace-fossil assemblages in an Early Mesozoic ephemeral fluvio-lacustrine system from Argentina: implications for the *Scoyenia* ichnofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology* **239**, 253–285.
- Meneghini, G. 1850.** *Observazione stratigrafiche e paleontologiche concernenti la Geologia della Toscana e dei paesi limitrofi. In appendice alla memoria sulla struttura geologica delle Alpi, degli Apennini e dei Carpazi di Sir Roderick Murchison*. Firenze.
- Mikuláš, R., Meškis, S., Ivanov, A., Lukševičs, E., Zupiņš, I., Stinkulis, G. 2013.** A rich ichnofossil assemblage from the Frasnian (Upper Devonian) deposits at Andoma Hill, Omega Lake, Russia. *Bulletin of Geosciences* **88**, 389–400.
- Muñiz, F., Mayoral, E. 2001.** El icnogénero *Spongeliomorpha* en el Neógeno superior de la cuenca del Guadalquivir (área de Lepe-Ayamonte, Huelva, España). *Revista Española de Paleontología* **16**, 115–130.
- Muñoz, J.A. 2002.** Alpine tectonics I: the Alpine system north of the Betic Cordillera: the Pyrenees. In: *The Geology of Spain*, Gibbons, W., Moreno, T. (eds). Geological Society, London, 370–385.
- Muñoz, A., Arenas, C., González, A., Luzón, A., Pardo, G., Pérez, A., Villena, J. 2002.** Tertiary basins: Ebro Basin (Northeastern Spain). In: *The Geology of Spain*, Gibbons, W., Moreno, T. (eds). Geological Society, London, 301–309.
- Nicholson, H.A. 1873.** Contributions to the study of the errant annelids of the older Paleozoic rock. *Proceedings of the Royal Society of London* **21**, 288–290.
- Orłowski, S. 1989.** Trace fossils in the Lower Cambrian sequence in the Świętokrzyskie Mountains, central Poland. *Acta Palaeontologica Polonica* **34**, 211–231.
- Panin, N., Avram, E. 1962.** Noe urme de pas de vertebrate in Miocenul Subcarpatilor Ruminestkya. *Studie si Cercetari de Géologie, Géophysica, si Géografie, Serie de Géologie* **7**, 455–484.
- Payros, A., Astibia, H., Cearreta, A., Pereda-Suberbiola, X., Murelaga, X., Badiola, A. 2000.** The Upper Eocene South Pyrenean coastal deposits (Liédena Sandstone, Navarre): sedimentary facies, benthic foraminifera and avian ichnology. *Facies* **42**, 107–132.
- Payros, A., Pujalte, V., Orue-Etxebarria, X. 1999.** The South Pyrenean Eocene carbonate megabreccias revisited: new interpretation based on evidence from the Pamplona Basin. *Sedimentary Geology* **125**, 165–194.
- Payros, A., Pujalte, V., Orue-Etxebarria, X., Baceta, J.I. 1997.** Un sistema turbidítico Bartonense de tipo "channel-levee" en la Cuenca de Pamplona: implicaciones tectónicas y paleogeográficas. *Geogaceta* **22**, 145–148.
- Payros, A., Pujalte, V., Tosquella, J., Orue-Etxebarria, X. 2010.** The Eocene storm-dominated foralgal ramp of the western Pyrenees (Urbasa-Andia Formation): an analogue of future shallow-marine carbonate systems? *Sedimentary Geology* **228**, 184–204.
- Pemberton, S.G., Frey, R.W. 1982.** Trace fossil nomenclature and the *Planolites*–*Palaeophycus* dilemma. *Journal of Paleontology* **56**, 843–881.
- Pemberton, S.G., Ranger, M.J., MacEachern, J.A. 1992.** The conceptual framework of ichnology. In: *Applications of Ichnology to Petroleum Exploration, a Core Workshop*, Pemberton, S.G. (ed). SEPM Society of Sedimentary Geology, Tulsa, Core Workshop Notes **17**; 1–32.
- Pemberton, S.G., Wightman, D.M. 1992.** Ichnological characteristics of brackish water deposits. In: *Applications of Ichnology to Petroleum Exploration, a Core Workshop*, Pemberton, S.G. (ed). SEPM Society of Sedimentary Geology, Tulsa, Core Workshop Notes **17**, 141–167.
- Peruzzi, D.G. 1880.** Osservazioni sui generi *Paleodictyon* e *Paleomeandron* dei terreni cretacei ed eocenici dell'Appennino sett. e centrale. *Atti della Società Toscana di Scienze Naturali Residente in Pisa* **5**, 3–8.
- Puigdefàbregas, C. 1975.** La sedimentación molásica de la cuenca de Jaca. *Pirineos* **104**, 1–118.
- Pujalte, V., Baceta, J.I., Payros, A. 2002.** Tertiary: western Pyrenees and Basque-Cantabrian region. In: *The Geology of Spain*, Gibbons, W., Moreno, T. (eds). Geological Society, London, 293–301.
- de Quatrefages, M.A. 1849.** Note sur la *Scolicia prisca* (A. De Q.) annélide fossile de la craie. *Annales des Sciences Naturelles, Zoologie* **3**(12), 265–266.
- de Raaf, J.F.M., Beets, C., Kortenbout van der Sluijs, G. 1965.** Lower Oligocene bird-tracks from northern Spain. *Nature* **207**, 146–148.
- Rodríguez-Tovar, F.J., Dorador, J. 2014.** Ichnological analysis of Pleistocene sediments from the IODP Site U1385 "Shackleton Site" on the Iberian margin: approaching paleoenvironmental conditions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **409**, 24–32.
- Rodríguez-Tovar, F.J., Pérez-Valera, F. 2008.** Trace fossil *Rhizocorallium* from the Middle Triassic of the Betic Cordillera, Southern Spain: characterization and environmental implications. *Palaos* **23**, 78–86.
- Rodríguez-Tovar, F.J., Piñuela, L., García-Ramos, J.C. 2015.** Trace fossils assemblages from the Cenozoic "flysch units" of the Campo de Gibraltar Complex (southern Spain). *Ichnos*, doi: 10.1080/10420940.2015.1130708.
- Rodríguez-Tovar, F.J., Uchman, A., Payros, A., Orue-Etxebarria, X., Apellaniz, E., Molina, E. 2010.** Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* **285**, 50–65.
- Sacco, F. 1888.** Note di Paleocinologia Italiana. *Atti della Società Toscana di Scienze Naturali* **31**, 151–192.
- Salter, J.W. 1857.** On Annelide-burrows and surface-markings from the Cambrian Rocks of the Longmynd. No. 2. *Quarterly Journal of the Geological Society* **13**, 199–206.
- Santander, J., Soplana, A., Ramírez-Rodríguez, J.A., García-Peregrina, I., Castaños, J., Díez-López, A., Perdígón, O., Elorza, J. 2007.** Contenidos

- de CaCO<sub>3</sub> en los pares marga-caliza del Maastrichtiense y Daniense en Sopelana, Arco Vasco: facies grises frente a facies rojas. *Geogaceta* **43**, 95–98.
- de Saporta, G. 1887.** Nouveaux documents relatifs aux organismes problématiques des anciennes mers. *Bulletin de la Societe Geologique de France* **15**(3), 286–302.
- Savi, P., Meneghini, G.G. 1850.** Osservazioni stratigrafiche e paleontologiche concernati la geologia della Toscana e dei paesi limitrofi. In: *Memoria sulla struttura geologica delle Alpi, degli Apennini e dei Carpazi*. Murchinson, R.I. (ed). Nella Stamperia Granducale: Firenze, Appendix 246–528.
- Schafhäütl, K.E. 1851.** *Geognostische untersuchungen des südbayerischen Alpengebirges*. Literarisch-artistische Anstalt: München.
- Schieber, J. 1999.** Microbial mats in terrigenous clastics: the challenge of identification in the rock record. *Palaios* **14**, 3–12.
- Seike, K., Nara, M. 2007.** Occurrence of bioglyphs on Ocylope crab burrows in a modern sandy beach and its palaeoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **252**, 458–463.
- Seilacher, A. 1974.** Flysch trace fossils: evolution of behavioural diversity in the deep-sea. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **1974**, 223–245.
- Seilacher, A. 2007.** *Trace Fossil Analysis*. Springer: Berlin, Heidelberg.
- Sims, D.W., Reynolds, A.M., Humphries, N.E., Southall, E.J., Wearmouth, V.J., Metcalfe, B., Twitchett, R.J. 2014.** Hierarchical random walks in trace fossils and the origin of optimal search behavior. *Proceedings of the National Academy of Sciences of United States of America PNAS* **111**, 11073–11078.
- Sinclair, H.D. 1997a.** Flysch to molasse transition in peripheral foreland basins: the role of the passive margin versus slab breakoff. *Geology* **25**, 1123–1126.
- Sinclair, H.D. 1997b.** Tectono-stratigraphic model for underfilled peripheral foreland basins: an Alpine perspective. *Geological Society of America Bulletin* **109**, 324–346.
- Smith, A.B., Crimes, T.P. 1983.** Trace fossils formed by heart urchins — a study of *Scolicia* and related traces. *Lethaia* **16**, 79–92.
- von Sternberg, G.K. 1833.** *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt*. IV Heft. C.E. Brenck: Regensburg.
- Tanaka, K. 1970.** Trace fossils from the Cretaceous flysch of the Ikushumbetesu Area, Hokkaido, Japan. *Geological Survey of Japan, Report* **236**, 1–102.
- Tasch, P. 1968.** A Permian trace fossil from the Antarctic Ohio Range. *Transactions of the Kansas Academy of Science* **1903**, 33–37.
- Thulborn, T. 1990.** *Dinosaur Tracks*. Chapman and Hall: London.
- Torell, O.M. 1870.** Petrifacta suecana formationis Cambricae. *Lunds Universitet, Årsskrift* **6**, 1–14.
- Uchman, A. 1995.** Taxonomy and palaeoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria* **15**, 3–115.
- Uchman, A. 1998.** Taxonomy and ethology of flysch trace fossils: a revision of the Marian Książkiewicz collection and studies of complementary material. *Annales. Societatis Geologorum Poloniae* **68**, 105–218.
- Uchman, A. 1999.** Ichnology of the Rhenodanubian Flysch (Lower Cretaceous–Eocene) in Austria and Germany. *Beringeria* **25**, 65–171.
- Uchman, A. 2001.** Eocene flysch trace fossils from the Hecho Group of the Pyrenees, northern Spain. *Beringeria* **28**, 3–41.
- Uchman, A. 2007a.** Deep-sea ichnology: development of major concepts. In: *Trace Fossils: Concepts, Problems, Prospects*, Miller, W. (ed). Elsevier: Amsterdam; 248–267.
- Uchman, A. 2007b.** Deep-sea trace fossils from the mixed carbonate-siliciclastic flysch of the Monte Antola Formation (Late Campanian–Maastrichtian), North Apennines, Italy. *Cretaceous Research* **28**, 980–1004.
- Uchman, A. 2009.** The *Ophiomorpha rudis* ichnosubfacies of the Nereites ichnofacies: characteristics and constraints. *Palaeogeography, Palaeoclimatology, Palaeoecology* **276**, 107–119.
- Uchman, A., Janbu, N.E., Nemeč, W. 2004.** Trace fossils in the Cretaceous–Eocene flysch of the Sinop–Boyabat Basin, Central Pontides, Turkey. *Annales. Societatis Geologorum Poloniae* **74**, 197–235.
- Uchman, A., Wetzel, A. 2011.** Deep-sea ichnology: the relationships between depositional environment and endobenthic organisms. In: *Deep-sea Sediments*, Hüneke, H., Mulder, T. (eds.), *Developments in Sedimentology* **63**, 517–556.
- Uchman, A., Wetzel, A. 2012.** Deep-sea fans. In: *Trace Fossils as Indicators of Sedimentary Environments*, Knaust, D., Bromley, R. G. (eds.), *Developments in Sedimentology* **64**, 643–671.
- Vialov (Vyalov), O.S., Golev, B.T. 1960.** K. sistematike *Paleodictyon*. *Doklady Akademii Nauk SSSR (Proceedings of the USSR Academy of Sciences)* **134**, 175–178.
- Yang, S.Y., Lockley, M.G., Greben, R., Erickson, B.R., Lim, S.K. 1995.** Flamingo and duck-like bird tracks from the Late Cretaceous and Early Tertiary: evidence and implication. *Ichnos* **4**, 21–34.
- Zenker, J.C. 1836.** *Historisch-topographisches Taschenbuch von Jena und seiner Umgebung besonders in naturwissenschaftlicher und medicinischer Beziehung*. Jena.