

NON-MARINE INVERTEBRATE TRACE FOSSILS FROM THE TERTIARY CALATAYUD-TERUEL BASIN, NE SPAIN

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ABSTRACT

Relatively diverse trace fossils made by insects, other arthropods and oligochaete worms occur in the Miocene lacustrine and marginal lacustrine deposits of the Calatayud-Teruel basin (NE Spain). They include the ichnospecies *Celliforma* isp., *Celliforma* ? isp. A and B, *Celliforma* ? aff. *habari*, *Rosellichnus* cf. *arabicus*, *Spongiomorpha* isp., *Labyrinthichnus terrerensis* n. igen. et isp., *Taenidium barreti*, *Beaconites filiformis* n. isp. and *Polykladichnus aragonensis* n. isp. Their taxonomic and ethologic interpretations and cross-cutting relationships permit to envisage new lines of evidence for reconstructing transitions from dry-ground terrestrial to moist-ground and subaqueous environments, related to episodic floodings in lacustrine ponds. These environmental transitions (related to external controls) are characterized by benthic community replacements, evinced by vertical successions of *Termitichnus*, *Scoyenia* and *Mermia*-like ichnofacies.

Keywords: Trace fossils, ichnofacies, lacustrine deposits, Miocene, Spain.

RESUMEN

En los depósitos lacustres del Mioceno de la depresión de Calatayud-Teruel (NE España) se ha reconocido una amplia diversidad de icnofósiles realizados por insectos, otros artrópodos y gusanos poliquetos. Se han determinado las siguientes icnoespecies: *Celliforma* isp., *Celliforma* ? isp. A y B, cf. *Celliforma* ? aff. *habari*, *Rosellichnus* cf. *arabicus*, *Spongiomorpha* isp., *Labyrinthichnus terrerensis* n. igen. et isp., *Taenidium barreti*, *Beaconites filiformis* n. isp. y *Polykladichnus aragonensis* n. isp. Su afinidad taxonómica y etológica, junto a las relaciones geométricas que conservan entre ellos, permiten aportar nuevas informaciones sobre los procesos biogénicos registrados en los medios sedimentarios lacustres. Éstos se caracterizan por variaciones graduales relacionadas con las inundaciones episódicas del sustrato lacustre y su consecuente desecación: desde los medios claramente subacuáticos a los parcialmente encharcados que finalizan en exposiciones subaéreas. Dicha transición, influenciada por controles externos, se caracteriza por la presencia de reemplazamientos de comunidades bentónicas, reflejadas por la sucesión vertical de las icnofacies de tipo *Termitichnus*, *Scoyenia* y *Mermia*.

Palabras clave: Pistas fósiles, icnofacies, depósitos lacustres, Mioceno, España.

INTRODUCTION

Non-marine paleoichnology has experienced a quick development during the last decade. It became clear that trace fossils can be helpful to determine some environmental parameters in non-marine settings, similarly to the proposals envisaged in marine environments (Hasiotis and Bown, 1992; Donovan, 1994; Buatois and Mángano, 1995, 1998). Unfortunately, recognition of trace fossils and ichnofacies in non-marine depositional

systems is commonly very incomplete. For this reason, each contribution on this topic is a small step towards new reappraisals of the problem.

A relatively rich assemblage of trace fossils has been found in the Miocene non-marine, lacustrine deposits of the Calatayud-Teruel basin (NE Spain). The aim of this paper is the description and interpretation of the trace fossils and ichnofacies found at the locality of Terror (Fig. 1), as a tool for interpreting indicators of palaeoenvironmental changes.

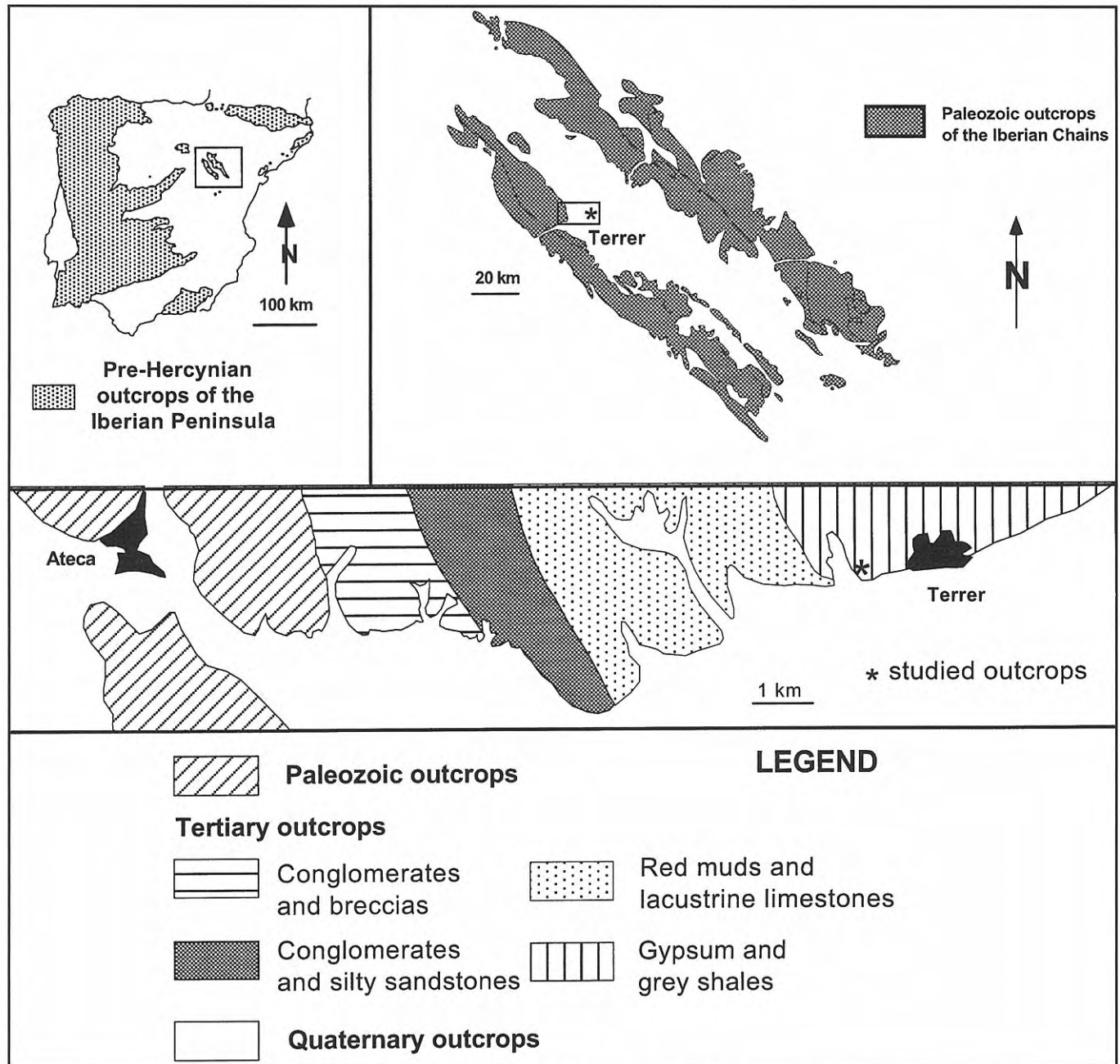


Figure 1. Geologic sketch of the Calatayud-Teruel basin in the NE of the Iberian Peninsula.

Ichnological research of Tertiary continental evaporite successions in Spain, including the Calatayud-Teruel basin, has been previously carried out by Rodríguez-Aranda (1992) and Rodríguez-Aranda and Calvo (1998). The latter authors recognized small and large rhizoliths, 'tangle-patterned small burrows', 'isolated large burrows', 'L-shaped traces' and vertebrate tracks.

GEOLOGIC SETTING AND STRATIGRAPHY

The Tertiary Calatayud-Teruel basin exhibits a NW-SE-trending pattern in NE Spain. It cuts longitudinally the Paleozoic and Mesozoic outcrops of the Iberian

Ranges, dividing them into the western and eastern Iberian chains. The basin consists of a mosaic of troughs with different tectonostratigraphic evolution. Our study is focused in the western margin of the Calatayud sub-basin, in the outcrops bounding the locality of Teruel (Fig. 1), which are equidistant from the Paleozoic rocks of the western Iberian chain and the Tertiary Calatayud depocenter. From a lithostratigraphic point of view, the fill of the Calatayud sub-basin shows a distinct lateral change, from conglomerates and breccias near the Paleozoic border to alternating gypsum and marls in its depocenter. In its middle part, a belt composed of brownish shales and gypsum crops out parallel to the Paleozoic margin. This lithostratigraphic unit, named "Gypsum and grey shales" by Olmo *et al.* (1983),

consists of brownish to grey shales (0.2 to 20 m thick) alternating with gypsum beds up to 0.5 m thick, and with isolated green, sandy marlstones at the bottom.

An upward increase of gypsum beds is recognized in this lithostratigraphic unit throughout the geomorphologic "mesetas" of the area; hence, the lower part of the formation records the better conditions to contain trace fossils. The age of these deposits is Aragonian to Vallesian (Miocene) based on the occurrence of vertebrate remains (Crusafont *et al.*, 1966). We have studied the western outcrops of the "Gypsum and grey shales" unit, located at the base of the westernmost "meseta" near Terrer. The "mesetas" exhibit successive sequences (3.5 to 12 m thick; Fig. 2) composed, from bottom to top, of (1) an irregular base overlying the previous sequence, (2) 2-5 m of reddish shales, partly cemented by carbonate, containing episodically greenish sandy marlstones (up to 0.8 m thick) with mm-thick parallel lamination, interbedded mudcracks, and isolated cm- to dm- thick irregular gypsum nodules (0.5-1 m thick), and (3) nodular gypsum (0.2-1 m thick) on the top of the sequences. The lowermost sequence contains a distinct sandy marlstone bed, the thinnest nodular gypsum bed of the whole sequences, and is very rich in trace fossils. Reddish shales can be subdivided into small-scale cycles (cm-thick), composed of grading siltstone-to-argillite units, rich in organic matter, and overlain by common mudcracks. Each sequence represents the partial filling of the sub-basin by episodic inundites, scarce episodes of lacustrine deposition and the final widespread subaerial exposure of the sub-basin under arid conditions leading to evaporite deposition.

SYSTEMATIC ICHNOLOGY

A part of the illustrated specimens are housed in the Zaragoza University (MPZ 17122 to MPZ 17132) and some of them in the Institute of Geological Sciences of the Jagiellonian University in Krakow (acronym 159P).

Celliforma GROUP

This is an informal group that includes trace fossils bearing small single or clustered, elongated cells, commonly produced by hymenopteran insects. The erection of this group is useful because the determination of its ichnogenera in poorly preserved specimens is sometimes difficult. The group includes the ichnogenera *Celliforma* Brown, *Uruguay* Roselli, *Palmiraichnus* Roselli and *Rosellichnus* Genise and Bown, among others.

Celliforma Brown, 1934

Diagnosis

Vasiform, globular or subcylindrical cells commonly preserved as internal moulds; distal end rounded, and

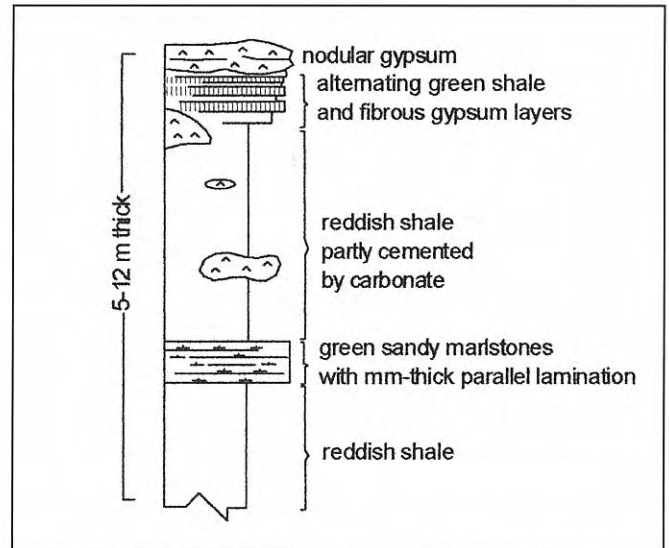


Figure 2. Stratigraphic section of the studied outcrops at Terrer.

proximal end either truncated irregularly or capped by a flat or conical closure, having spiral or concentric grooves on its inner surface; margins polished or smooth, so that internal moulds are easily separated from the rock matrix. The trace fossil lacks antechamber or wall (modified after Retallack, 1984, and using the criteria applied by Genise and Hazeldine, 1998).

Remarks

Traditionally, all the trace fossils defined by the first part of the above diagnosis have been recognized as *Celliforma* Brown. However, Genise and Hazeldine (1998) have separated the forms with antechamber and wall under the ichnogenus *Palmiraichnus* Roselli, 1987. In addition, the latter authors ascribed to *Celliforma* only solitary cells, while other authors include in *Celliforma* forms associated with galleries (Thackray, 1994; Elliot and Nations, 1998). The taxonomic affinity of *Celliforma* needs further discussion and revision (Retallack, 1984; Genise and Hazeldine, 1998), which is beyond the scope of this paper. *Celliforma* is generally regarded as bee cells (Brown, 1934; Elliot and Nations, 1998, with references).

Celliforma isp.

Fig. 3A-I, M, P

Material: About 70 specimens (159P1-11 and MPZ 17122-17124, 17127, 17131) and numerous observations in the field.

Description

Mostly oblique, rarely vertical (Figs. 3M, 3P), smooth vasiform cells, mostly up to 6-7 mm in diameter and 10-15 mm (exceptionally 18 mm) long. The maximum width of the cells occurs between 1/3 and 1/2 of the length from the distal termination. The cells are slightly ellipsoidal in cross section. Some specimens display a distinct constriction in

the proximal part (Fig. 3C). The distal end is rounded, whereas the proximal termination is irregularly truncated. One specimen (Fig. 3P) displays an inverted conical structure at the top, representing likely the remnant of the input-tunnel.

Remarks

It is not clear if all the identified forms belong to only one ichnospecies, because of the gradual transitions among different morphotypes, e.g. between those with constrictions and those more cylindrical. All of them are solitary and oriented in the same way. The described form is distinctly smaller than other solitary *Celliforma*. Moreover, *C. spirifer* Brown, 1934 displays a spiral closure (lid) of the cells. The absence of closures, however, can be related to the emergence of adults (Houston, 1987). *C. germanica* Brown, 1935 is characterized by a constriction at the middle part. Dimensions of the cylindrical, stout *C. nuda* Brown, 1935 are not known. *C. ficoides* Retallack, 1984 is typified by a long constriction in the proximal part, distinctly longer than in some of the described forms. In addition, it is larger and oriented subhorizontally in radial clusters. Other ichnospecies are clustered (*C. habari* Thackray, 1994, *C. rosellii* Genise and Bown, 1994, *C. dakotensis* Elliot and Nations, 1998) or display a distinct wall (*C. arvernensis* Ducreux, Billaud and Truc, 1988, *C. pinturensis* Genise and Bown, 1994, and *C. gomezii* Domínguez Alonso and Coca Abia, 1998). The latter two ichnospecies do not belong to *Celliforma* according to the above diagnosis, due to the presence of a distinct wall.

Celliforma ? isp. A

Fig. 3J-L

Material: 6 specimens (MPZ 17125-17126).

Description

Large, oblique, amphora-like cells resembling *Celliforma*, 12-17 mm in diameter and at least 35 mm long. Its cells are commonly intersected by subvertical shafts, which are about 5 mm in diameter. *Celliforma* ? isp. A is filled by poorly cemented brownish silt, which is easily removed during exploitation or by washing. For this reason, it is commonly preserved as cavities.

Remarks

Its not clear whether the described form displays a

planar termination, which is an important diagnostic character for *Celliforma* (Edwards *et al.*, 1997); therefore, we left it in an open nomenclature. The size of the found specimens corresponds to *Celliforma arvernensis* Ducreux, Billaud and Truc, 1988, from the Eocene of the Massif Central (France), but the latter form is walled, vertically oriented and more cylindrical in shape.

Celliforma ? isp. B

Fig. 3N

Material: 1 specimen (MPZ 17128).

Description

This specimen is composed of small cells arranged obliquely around the lower part of a vertical, slightly winding shaft. There are three, slightly oblique cells on one side and one poorly preserved cell on the other side of the shaft. Each cell is 8-9 mm long and up to 5 mm in diameter. The margin of the cells is very distinct in the distal part and badly preserved in the remaining part. The vertical shafts are at least 55 mm long and 4-5 mm in diameter.

Remarks

Cells attached to tunnels should be separated as a new ichnogenus (Genise, pers. commun., 1999) and, therefore, we described such forms in open nomenclature. *Celliforma* ? isp. B resembles *Celliforma ficoides* Retallack, 1984 due to the oblique arrangement of the cells around the vertical shafts, but the cells of the latter form are characterized by the presence of a long constriction in the proximal part and stumpy cells. The geometry of *Celliforma* ? isp. B resembles the burrows made up by the halictine bee *Lasioglossum (Dialictus) zephyrum* (Eickwort, 1969), whose cells display a distinct "neck" resembling *Celliforma ficoides* Retallack.

Celliforma ? aff. *habari* Thackray, 1994

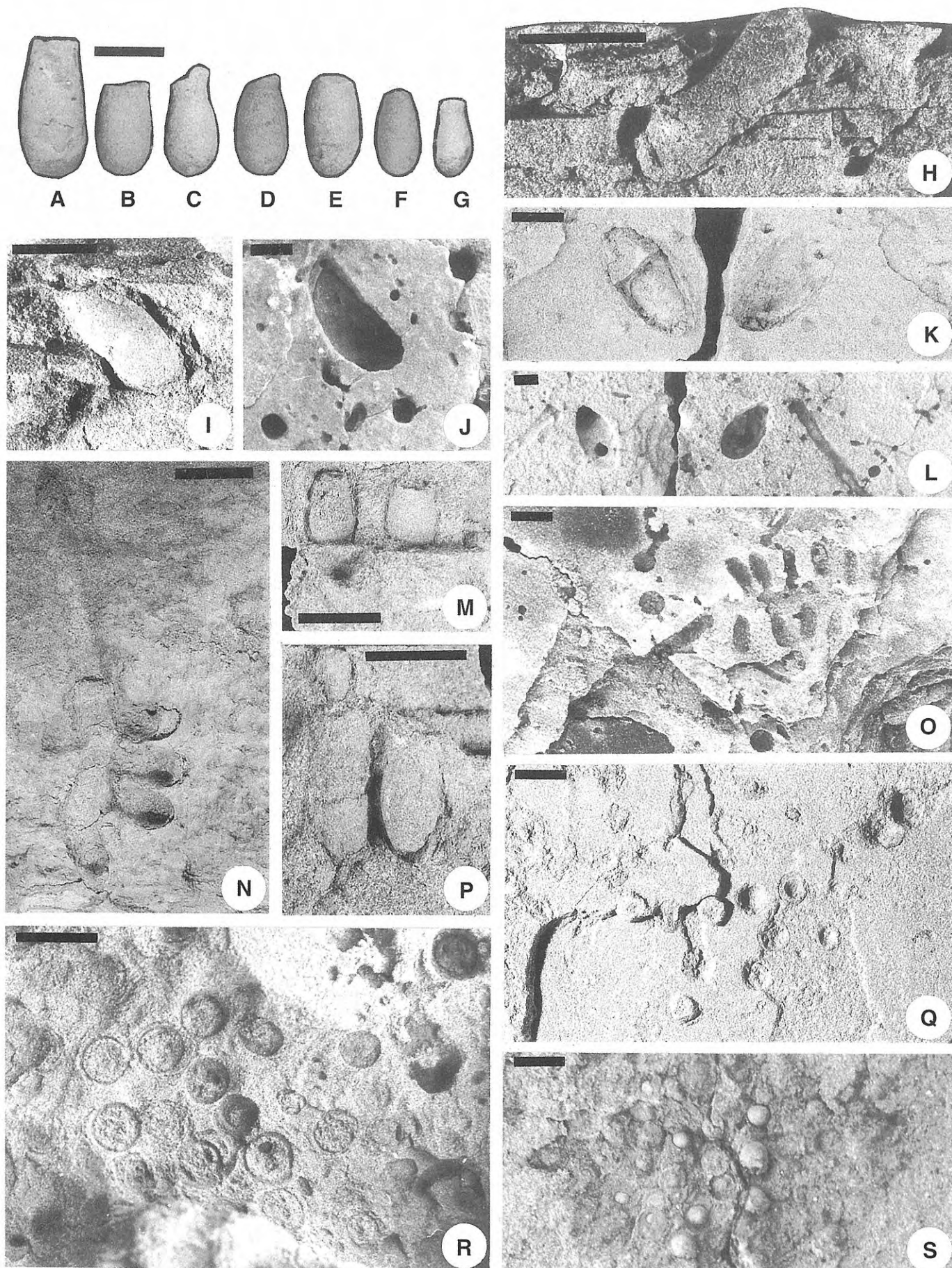
Fig. 3O

Material: 2 specimens (MPZ 17129-17130).

Diagnosis of *C. habari*

Subellipsoidal *Celliforma* cells, 6 mm long and 3.5 mm in diameter at the widest point; bluntly truncated at the proximal end, dorsal surface curved and ventral surface nearly flat; cell lining 0.5 mm thick, crudely

Figure 3. Trace fossils from the sandy marlstone bed. Scale bar: 1 cm for all figures. **A-G.** *Celliforma* isp. extracted from the host rock. A: 159P1, B: 159P2, C: 159P3, D: 159P4, E: 159P5, F: 159P6, G: 159P7. **H-I.** *Celliforma* isp. Original position in the host rock. H: 159P10, I: MPZ 17123-17124. **J.** *Celliforma* ? isp. A. Horizontal parting surface. Filling washed out during preparation (field photograph). **K-L.** *Celliforma* ? isp. A. Horizontal parting surfaces (upper and lower side). Filling washed out during preparation. K: MPZ 17125, L: MPZ 17126. **M.** *Celliforma* isp. Original position in the host rock. MPZ 17127. **N.** *Celliforma* ? isp. B. Original position in the host rock. MPZ 17128. **O.** *Celliforma* ? aff. *habari*. Horizontal parting surface. MPZ 17129. **P.** *Celliforma* isp. Original position in the host rock. MPZ 17131. **Q-R.** *Rosellichnus* cf. *arabicus*. Horizontal parting surface. Top view. Q: 159P12, R: MPZ 17132, detail of Fig. 6F. **S.** *Rosellichnus* cf. *arabicus*. Horizontal parting surface. Basal view. MPZ 17133.



laminated; cells arranged in paired, parallel rows with typical 0.5-2 mm spacing between adjacent cells; 5 mm space between paired rows with blunty truncate ends of cells oriented inward; paired rows paralleling the paleosol surface or at acute angles (30°), clustered in groups around vertical axes (modified after Thackray, 1994).

Description

It is recognized by their semicircular, horizontal to subhorizontal grooves, partly associated with paired rows of shallow elliptical depressions. The grooves are sectioned endichnial central tunnels, and the depressions are sectioned cells. They were originally filled with soft brownish mudstones, subsequently washed out during preparation. The cells are about 10 mm long and 5 mm in diameter in the widest point, which is located between one third and half distance from their rounded termination. Only 10 cells are visible, which are 1-6 mm apart. They were probably more abundant, but are not preserved. The central tunnel (5 mm in diameter) is almost straight in the place where the cells are located, and curved in the remaining part.

Remarks

According to Genise (pers. commun., 1999), cells attached to tunnels should be separated as a new ichnogenus, so that we described such forms in open nomenclature. *C. habari* from the Miocene of Kenya displays smaller and numerous cells bearing thin linings. They are more tear-shaped than the described form, and its central tunnel is not preserved. *C. dakotensis* Elliot and Nations, 1998, from the Upper Cretaceous of Arizona, is characterized by horizontal and vertical central tunnels, where the cells are bilaterally arranged around the horizontal tunnels and radially disposed around the vertical ones. In the described form, the cells are larger. It is not excluded that described form belongs to a new ichnospecies, but the material is insufficient for its erection. *Celliforma habari* should be excluded from the ichnotaxon *Celliforma* because its cells are clustered. Trace fossils similar to the described form are recently produced by the bee *Halictus sexcinctus* in middle Europe (Minkiewicz, 1934).

Rosellichnus Genise and Bown, 1996

Diagnosis

Groups of ovoid cells bearing distinct walls with smooth inner surfaces. The lower part of the cells are rounded, whereas their tops are flat and opened. The cells show parallel axes, and the upper part of their cluster is flat. The cells are arranged in a layer of several rows, whose bottoms and tops are at the same level forming a comb (after Genise and Bown, 1996, reduced).

Remarks

This ichnogenus may be produced by halictid bees forming underground nests (Genise and Bown, 1996). Halictid behaviour was described by Sakagami and Michener (1962) and Eickwort and Sakagami (1979). *Rosellichnus* differs from *Uruguay* in the upward convergence of the cells and the concave form of the upper part in *Uruguay* (after Genise and Bown, 1996).

Rosellichnus cf. *arabicus* Genise and Bown,
1996

Fig. 3Q-S

Material: about 30 specimens (159P12, MPZ 17132-17133).

Diagnosis of *R. arabicus*

Clusters of vertical cells arranged in 4-5 rows. It differs from *R. patagonicus* in having more rows of smaller cells. Cells are up to 8.5 mm in depth and show 6 mm as maximum diameter. Cell walls are thinner (about 1.0 mm) than in *R. patagonicus* (Genise and Bown, 1996).

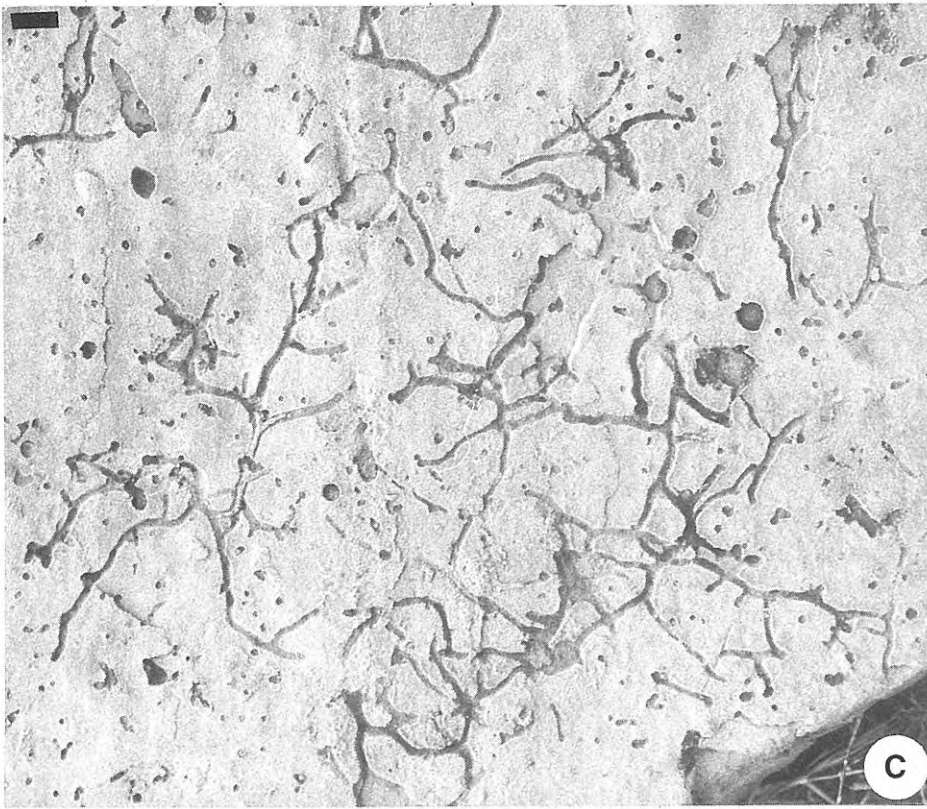
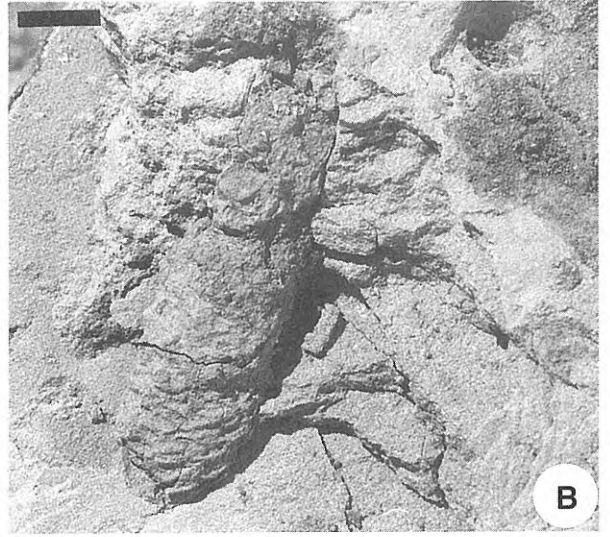
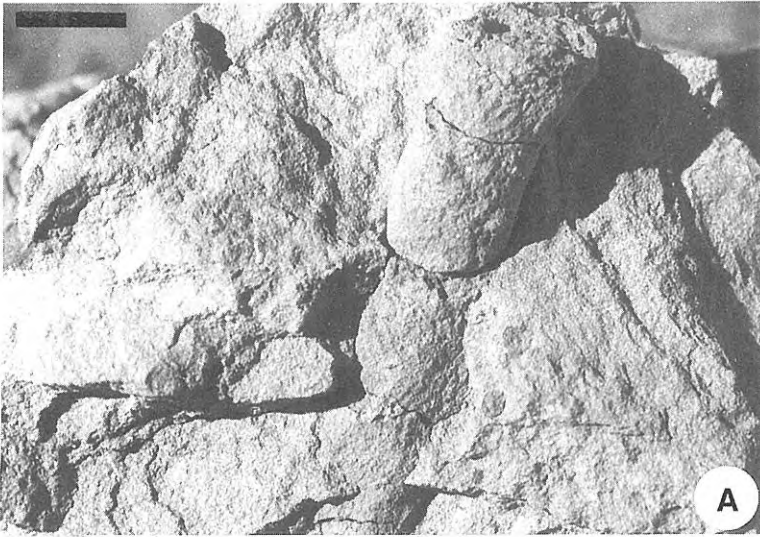
Description

Vertical, small, smooth, walled cells, 4-6 mm in diameter, grouped into clusters. The wall is 0.7-1.2 mm thick in the lower part of the cells. It is composed of three layers, visible using hand lens. The cells are circular or sub-circular in cross-section, which are 0-3 mm apart. In one specimen, the upper part of a cluster of about 20 cells is visible in horizontal section. Some cells partially overlap each other, while others display slight lateral shifting. Preservation of the cells is very diverse, from relatively well preserved, with distinct contours, to completely indistinct. The cells within the clusters are poorly ordered, however single central rows can be distinguished. Their lower termination is rounded and located on slightly different levels.

Remarks

Rosellichnus arabicus, from the Miocene and Pleistocene of the United Arab Emirates (Genise and Bown, 1996), to which the described material is compared, occurs in combs with terminations of cells at the same level. Despite the differences, the similarities are strong enough to suppose that the described form was produced by halictid? bees (the behaviour of solitary bees has been described by Batra, 1984). The differences in preservation of individual cells and the overlapping features in the described material suggest that the bees reoccupied the cells several times.

Figure 4. Trace fossils from the sandy marlstone bed at Terrer. Scale bar: 1 cm for all figures. **A-B.** *Spongeliomorpha* isp. Oblique parting surface. A: MPZ 17134, B: MPZ 17135. **C-E.** *Labyrinthichnus terrerensis*. Base of the bed. Holotype in E. C-D: field photographs, E: MPZ 17136.



OTHER TRACE FOSSILS

Spongiomorpha Saporta, 1887

Diagnosis

Sparsely developed burrow systems, with vertical to horizontal components characterized by sets of longitudinal to oblique, fine, elongate striae on the exterior of the burrow casts (Fürsich *et al.*, 1981; Frey *et al.*, 1984).

Remarks

The marine *Spongiomorpha* was produced by crustaceans in firm substrates. Its origin and nomenclatural problems have been discussed by Fürsich (1973), Bromley and Frey (1974), Frey *et al.* (1984) and others. Non-marine *Spongiomorpha* has been reported by Bromley and Asgaard (1979) and Metz (1990). Similarly to the marine forms, the non-marine *Spongiomorpha* indicates also firm-ground substrates (Ekdale *et al.*, 1984).

Spongiomorpha isp.
Fig. 4A-B

Material: 2 specimens (MPZ 17134-17135).

Description

Oblique to straight, unlined cylindrical, isolated trace fossils, covered with oblique wrinkles, which are about 5 mm long and less than 1 mm wide. The wrinkles occur in bundles, forming a chevron pattern. They are interpreted as casts of scratch marks. The cylinders are 11-12 mm in diameter.

Remarks

The Late Triassic *Spongiomorpha milfordensis* Metz, 1993, from lake-margin deposits, displays a similar pattern of scratch marks, but it is predominantly horizontal, branched, and less than 5 mm in diameter. Mole crickets (Orthoptera: Gryllotalpidae) produce similar oblique scratches in their holes, but their tunnels are smaller (Metz, 1990). The Upper Triassic *Spongiomorpha carlsbergi* Bromley and Asgaard, 1979 (Ekdale *et al.*, 1984) shows comparable size, but it is dominantly horizontal and displays perpendicular to sub-perpendicular striae. The scratches of the striated oblique burrows (Bromley and Asgaard, 1979) are similar, but they are denser, cross-cutting themselves and longer. The forms described by Bromley and Asgaard (1979) belong to the "terrestrial suite" associated with lacustrine sediments.

Labyrinthichnus n. igen.

Derivation of name: from labyrinthine burrow system.

Type ichnospecies: *Labyrinthichnus terrerensis* n. isp.

Diagnosis

Cylindrical trace fossils composed of irregular nets, in which some cylinders can be disconnected on different levels. Vertical or oblique shafts can be present. Filling is passive.

Discussion

Labyrinthichnus displays some similarities to *Megagraption* Książkiewicz, 1968, *Multina* Orłowski, 1968, *Pseudopaleodictyon* Pfeiffer, 1968, *Olenichnus* Fedonkin, 1985, and *Vagorichnus* Buatois, Mángano, Wu and Zhang, 1995. *Megagraption* (see Uchman, 1998), similarly to *Labyrinthichnus* (see discussion below), is referred to open burrow systems, but its net is more regular and occurs on the same plane. Generally, the tunnels do not disappear on different levels. *Multina* (see Orłowski and Żylińska, 1996), and its junior synonyms *Olenichnus* and *Vagorichnus*, display active filling; probably, the same can be said of *Pseudopaleodictyon* Pfeiffer. The passive filling indicates an open burrow system. Its separation from similar but actively filled burrows is very significant, as discussed in the case of *Palaeophycus* and *Planolites* (Pemberton and Frey, 1982).

Labyrinthichnus terrerensis n. isp.
Fig. 4C-E, Fig. 5A-C

Derivation of name: from the village of Terrer (Spain), where the trace fossil was found.

Holotype: MPZ 17136 (Fig. 5D).

Type locality: Terrer (Zaragoza).

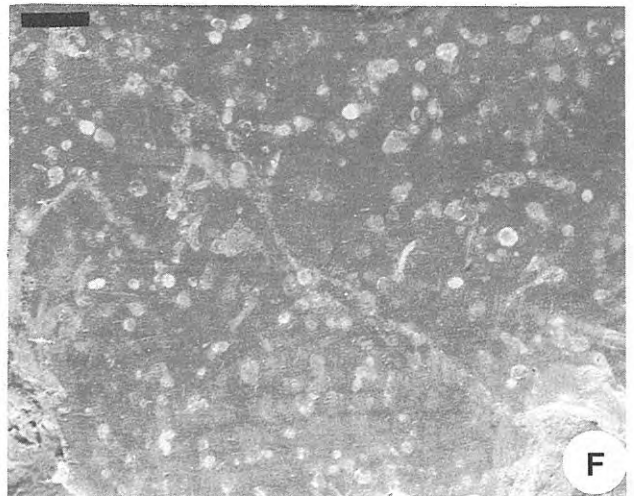
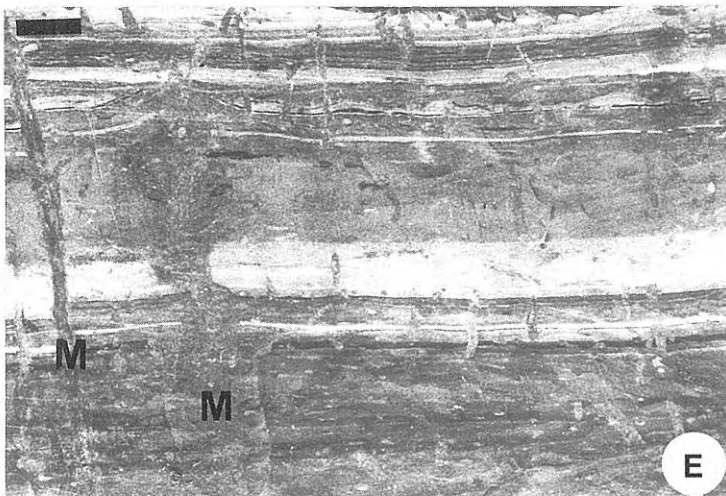
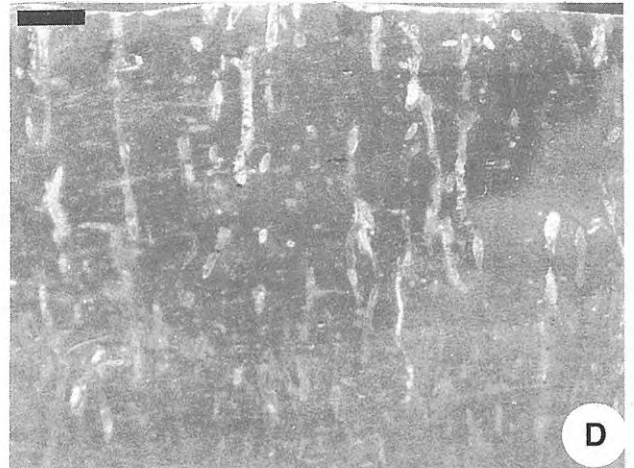
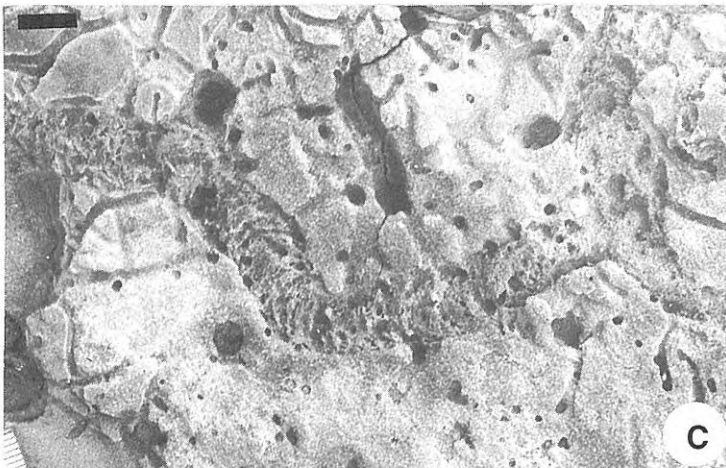
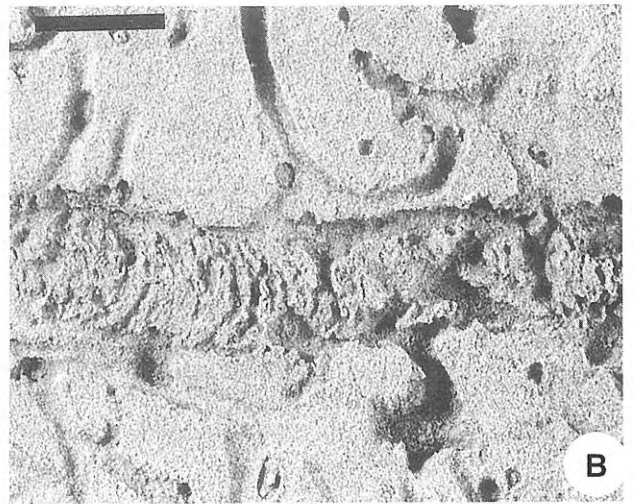
Dimensions of the holotype: a plate of 10 x 8 cm bearing an irregular net with burrows less than 1 cm wide.

Stratigraphic setting: 1.5 m above the bottom of the westernmost Tertiary meseta near Terrer, along the old road N-II.

Material: 8 specimens (MPZ 17136, 159P13).

Diagnosis: the same as for the ichnogenus.

Figure 5. Trace fossils from the sandy marlstone bed (A-C) and from the lacustrine mudstones (D-G). Scale bar: 1 cm for all figures. **A-B.** *Taenidium barreti*, morphotype A. Parting surface close to the base of the bed. B is a detail of A. *Labyrinthichnus terrerensis* in background. MPZ 17137. **C.** *Taenidium barreti*, morphotype B. Parting surface close to the base of the bed. *Labyrinthichnus terrerensis* in background. MPZ 17138. **D-G.** *Beaconites filiformis*. Polished surfaces. D: holotype, MPZ 17139. D, E, G: vertical cross-section. F: horizontal section. M in E indicates cross-sections of mudcracks. E: MPZ 17140, F: MPZ 17139, G: MPZ 17141.



Description

Horizontal, irregular net composed of branched, slightly winding cylinders, which are 1-3 mm in diameter (the majority about 2 mm). Locally, they are thinly lined. The cylinders can overlap themselves. Some of them belong to different systems produced at different time. In a few specimens (Fig. 4D-E), the burrow system is collapsed. Tunnels display a distinct lining; in some cases, the tunnels can be disconnected on slightly different levels.

Locally, a master-like tunnel with lateral, somewhat short branches is visible; however, the tendency to form an irregular net still occurs. The net is associated with vertical to sub-vertical shafts of similar diameter. Some tunnels change slightly their width; however, this can be an effect of the intersection of the bed surface with the tunnels that are slightly winding in the vertical plane. Locally, the tunnels are slightly enlarged at the point of branching. The filling material, composed of red mudstones, was easily removed by washing, but in some nets it is still preserved within the tunnels.

Discussion

The lining, enlargements in the point of branching, and filling from overlying beds indicate that this trace fossil was an open burrow system composed of a horizontal labyrinth with vertical and oblique shafts, which could have been produced by beetles or their larvae. Similar burrow systems are produced by ground beetles (Carabidae) and variegated mud-losing beetles (Heteroceridae). The latter ones produce, however, shallow burrows below the ground surface (Ratcliffe and Fagerstrom, 1980). The tunnels of *L. terrerensis* were produced mostly at the boundary of sandy marlstones with underlying mudstones. Such a place can help to keep the proper moisture and/or temperature for trace-makers or their juveniles.

Taenidium Heer, 1877

Diagnosis

Variably oriented, straight, winding, curved or sinuous, essentially cylindrical, meniscate backfilled trace fossils. Secondary successive branching may occur, but true branching is absent (after Keighley and Pickerill, 1994).

Remarks

Ichnotaxonomic problems of *Taenidium*, related meniscate backfilled burrows and their formation were discussed in detail by D'Alessandro and Bromley (1987), Keighley and Pickerill (1994) and Uchman (1995). *Taenidium* occurs from the Lower Cambrian (Crimes *et al.*, 1992) to the Quaternary? (Wetzel, 1983; synonymized by D'Alessandro and Bromley, 1987).

Taenidium barreti (Bradshaw, 1981)

Fig. 5A-C

Material: 2 specimens (MPZ 17137-17138).

Diagnosis

Straight to variably meandering, unbranched, unwallled, meniscate backfilled burrow. Menisci are commonly hemispherical or deeply arcuate, tightly packed or stacked, forming non-systematic backfill or thin meniscate burrows (after Keighley and Pickerill, 1994).

Description

Morphotype A (Fig. 5A-B). Horizontal, slightly winding, cylindrical trace fossils (9-10 mm wide) with meniscate filling. Menisci are relatively shallow grouped into 10 units per cm. Some tunnels of *L. terrerensis*, located along the margin, mimic a wall; however, the latter structure is not present, as can be clearly seen in the remaining parts of the trace fossil.

Morphotype B (Fig. 5C). Horizontal, strongly winding cylindrical, unwallled trace fossils with meniscate filling. The cylinders are 10-12 mm wide and contain about 5 menisci per cm. Some groups of menisci are wider, and hence the burrow margin is slightly undulate.

Remarks

T. barreti occurs in Lower Ordovician to Pleistocene non-marine environments (Keighley and Pickerill, 1994). Squires and Advocate (1984) described this ichnospecies (as *Muensteria?* isp.) from a Miocene section in California related to mixed environments in which a braided river entered a lake. These authors interpreted the meniscate burrows as traces of infaunal deposit-feeders, probably aquatic oligochaetes.

Beaconites Vialov, 1962

Diagnosis

Small, cylindrical, unbranched, walled, meniscate burrows. They are straight to sinuous, horizontal or moderately inclined to vertical. They display weakly to strongly arcuate meniscate packets or segments enclosed by distinct, smooth burrow linings (Keighley and Pickerill, 1994) without external ornamentation.

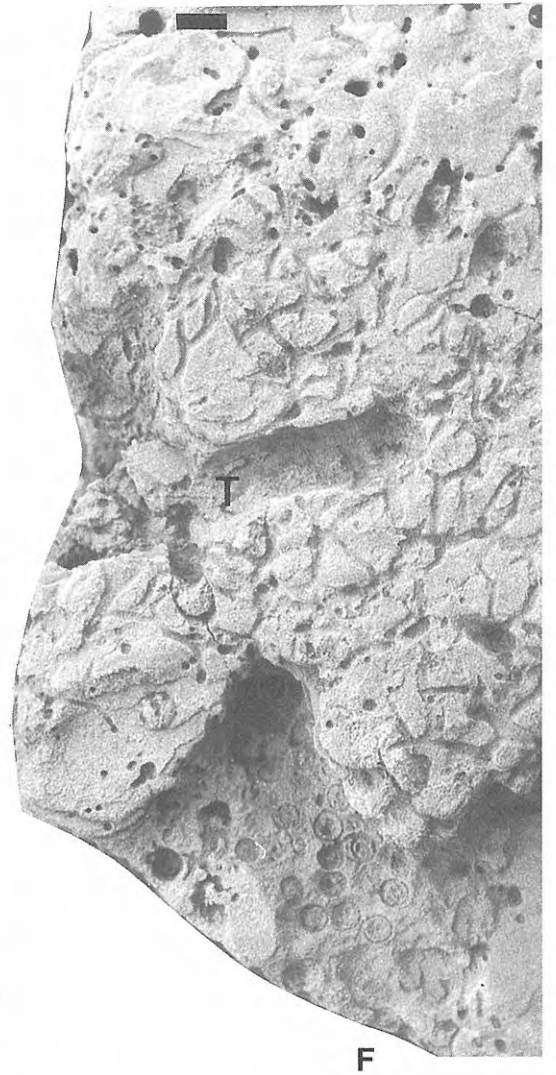
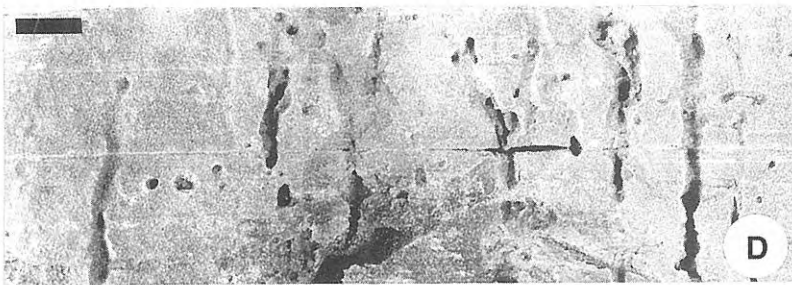
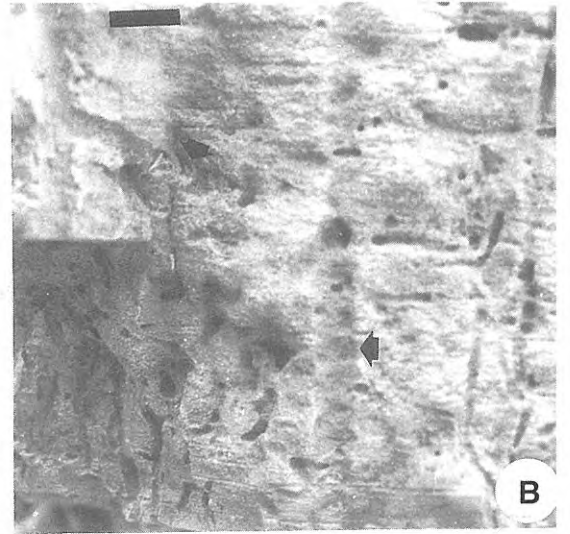
Beaconites filiformis n. isp.

Fig. 5D-G

Derivation of name: after *filus* (Latin) - thread.

Holotype: MPZ 17139 (Fig. 6D).

Figure 6. Trace fossils from the sandy marlstone bed. Scale bar: 1 cm for all figures. **A-E** *Polykladichnus aragonensis*. Vertical parting surfaces. The holotype (P) in A. The vertical branched shafts in A-C (arrows). A: MPZ 17137, B: MPZ 17142, C: MPZ 17142, D-E: field photographs. **F.** *Rosellichnus* cf. *arabicus* (in the lower part, detail in Fig. 3R), *Labyrinthichnus terrerensis*, and ?washed out *Taenidium barreti* (T). Base of the bed. MPZ 17132.



Type locality: Terror (Zaragoza).

Dimensions of the holotype: a sample of about 20 x 10 cm, bearing a swarm of burrows at least 8 cm long.

Stratigraphic setting: 1 m above the bottom of the westernmost Tertiary meseta near Terror, along the old road N-II.

Material: more than 30 specimens (MPZ 17139-17141, 159P14-16).

Diagnosis

Predominantly vertically oriented, slightly winding, thinly lined *Beaconites*, whose diameter is less than 5 mm.

Description

Slightly winding, mostly vertical, but locally oblique, thinly lined, cylindrical trace fossils in which filling is locally meniscate. Their filling differs in colour and commonly in grain-size from the host rock. The trace fossils are 0.8-3.5 mm in diameter and at least 80 mm long. In some layers, they are very dense, up to 10 burrows per square cm of horizontal section. The trace fossil does not display true branches *sensu* D'Alessandro and Bromley (1987), but false and secondary successive branches.

Remarks

B. filiformis can be ascribed to *Beaconites* because of the meniscate filling and distinct lining. This ichnospecies differs from other *Beaconites* ichnospecies (see Keighley and Pickerill, 1994 for review) by its vertical orientation, small size and thin lining. *B. filiformis* was produced probably by larvae of Chironomidae. The same interpretation was given to a little larger and more variable oriented "type 3, tangle-patterned small burrows" from the Miocene hypersaline lake sediments of Spain (Rodríguez-Aranda, 1992). Larvae of Chironomidae are mostly organic detritus feeders and can occur in very dense populations (Oliver, 1971). They construct different types of lined tubes (McCall and Tevesz, 1982). According to Chamberlain (1975), their tubes are 0.5 to 3 mm across and up to 15 cm deep.

Polykladichnus Fürsich, 1981

Diagnosis

Lined or unlined, vertical tubes with Y- or U-shaped bifurcations with slight enlargements at points of bifurcation, usually connected to the bedding surface (after Schlirf *et al.*, in press).

Remarks

Polykladichnus is typified by *P. irregularis* Fürsich, 1981 from Jurassic, marginal marine deposits of Portugal. It is described as a small burrow with a lined tube, 2-5 mm in diameter, and Y-shaped bifurcations. The herein described *P. aragonensis* is unlined and displays U-

shaped bifurcations. However, the upward directed, Y- or U-shaped bifurcations are regarded as the most significant diagnostic features in this ichnogenus. For this reason, the former diagnosis of Fürsich (1981) is emended (Schlirf *et al.*, in press). *Arborichnus* Ekdale and Lewis, 1991 from the Quaternary fan delta deposits of New Zealand, can be included in *Polykladichnus* according to the proposed diagnosis.

Polykladichnus aragonensis n. isp.

Fig. 6A-E

Derivation of name: from the Aragón Region (Spain).

Holotype: MPZ 17137 (Fig. 6A, specimen indicated by P).

Type locality: Terror (Zaragoza).

Dimensions of the holotype: a slab up to 8 cm thick, bearing a swarm of burrows up to 9 cm long.

Stratigraphic setting: 1.5 m above the bottom of the westernmost Tertiary meseta near Terror, along the old road N-II.

Material: about 30 specimens (MPZ 17137-17142).

Diagnosis

Unlined *Polykladichnus* bearing slightly winding tubes, which display Y- bifurcations or U-shaped elements.

Description

Vertical to inclined cylindrical shafts, straight or slightly winding, single (?) or bearing Y-shaped branchings or curved U-shaped bifurcations. They are 1-2 mm in diameter and at least 90 mm long. Some tubes display several orders of bifurcations.

Remarks

Arenicolites isp. described by Bromley and Asgaard (1979) in the Upper Triassic lacustrine deposits of the Fleming Fjord Formation (East Greenland) is very similar. It was interpreted as a burrow of tubificid oligochaetes but, according to Chamberlain (1975), oligochaetes construct branched, radiating downwards tubes, similar to *Chondrites*. McCall and Tevesz (1982) illustrated oligochaete burrows from the Lake Erie, which form dense, three-dimensional, labyrinthine burrows. This type of branching is not observed in the described material. Burrows with upward bifurcations are produced by staphylinid beetles of the genus *Bledius*, described by Larsen (1936) in the Recent sandy beaches and dunes of Denmark. Walshe (1951) and Chamberlain (1975) mentioned U-shaped burrows of chironomids, but *Chironomus plumosus* produces shallow U-tubes without shafts (McCall and Tevesz, 1982). The mayfly *Hexagonia limbata* produces burrows composed of U-shaped elements with occasional blind shafts

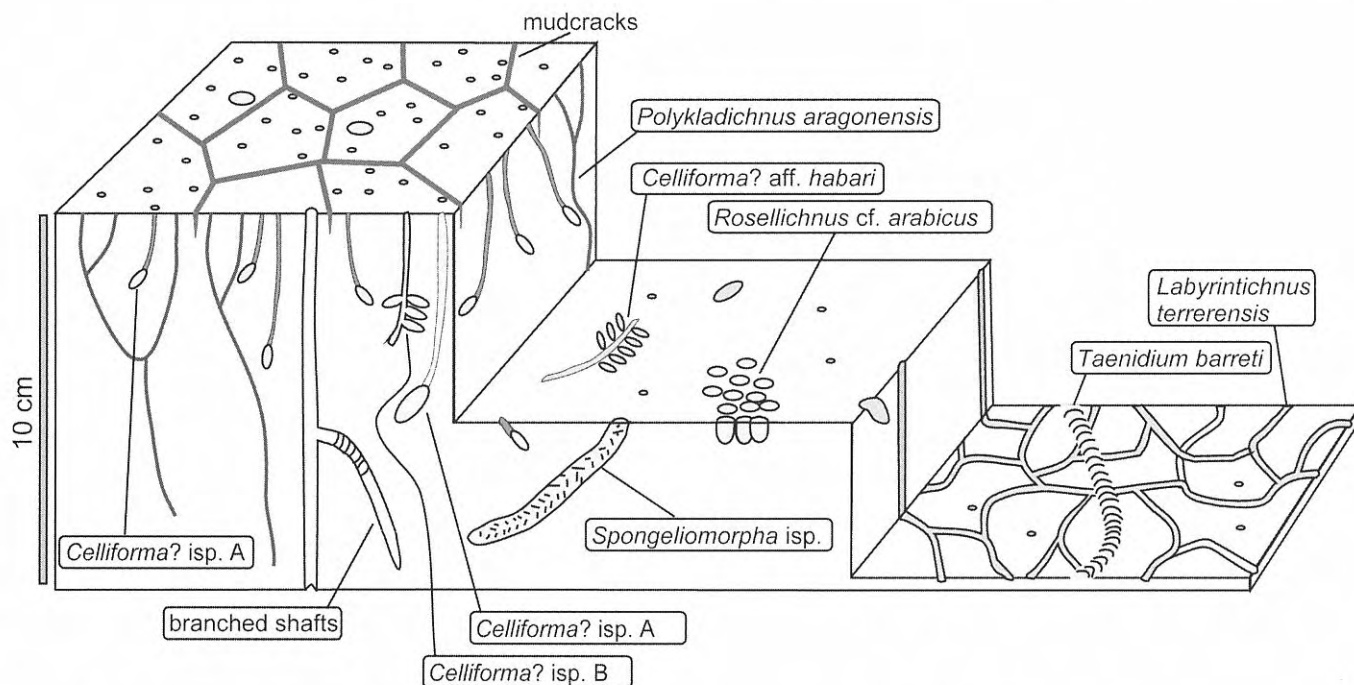


Figure 7. Distribution of trace fossils in the sandy marlstone bed. Trace fossils not at scale.

(Charbonneau and Hare, 1998). These similarities allow us to suppose that *P. aragonensis* was produced by insects or their larvae.

Branched shafts

Fig. 6A-C

Material: about 10 specimens (MPZ 17142).

Description

Vertical to oblique, straight to slightly curved, unwalled cylindrical tunnels (3-4 mm in diameter), rarely branched. The branches, going obliquely downwards, are locally indistinctly meniscated. Rare, second-order branches occur.

Remarks

Tiger-beetles (Cicindelidae), which are common on moist areas of stream and lake shores, construct similar shelter burrows (Chamberlain, 1975). The modal diameter of burrows in Recent fluvial plains of Nebraska ranges between 3 and 4 mm (Stanley and Fagerstrom, 1974). Chamberlain (1975) mentioned that some cicindelid beetles pack the sediment behind during burrowing. This can suggest occurrence of a meniscate filling, present locally in the described form.

DISTRIBUTION OF TRACE FOSSILS AND COMMUNITY REPLACEMENTS

Almost all the trace fossils described above occur in one sandy marlstone bed of the Terrer section. The red lacustrine mudstones contain mainly *Beaconites filiformis*. *Labyrinthichnus terrerensis* occurs at the basal part of the sandy marlstone bed (Fig. 7). It is cross cut by

Taenidium barreti, whereas vice versa examples are rare. *Celliforma* isp., *Celliforma* ? ispp., and *Rosellichnus* cf. *arabicus* occur in the middle and upper parts of the marlstone bed. They are cross cut by branched shafts. Finally, all the previous trace fossils of the marlstone bed are cross cut by *Polykladichnus aragonensis*. The cross cutting relationships reflect a benthic community replacement in the colonisation of the substrate, which is controlled by external factors, such as the moist ground features of the substrate.

The density of the trace fossils is diverse. *Celliforma* isp., *Labyrinthichnus terrerensis*, *Beaconites filiformis*, *Polykladichnus aragonensis* and the branched shafts are very common. The other forms are less common, and *Rosellichnus* cf. *arabicus* is rare.

The trace fossils produced by the activities of insects, other arthropods and oligochaete worms described above can be grouped into three broad categories or ichnofacies, which represent three phases of community replacement:

1. *Celliforma* isp., *Celliforma* ? ispp. and *Rosellichnus* cf. *arabicus* (produced by Hymenoptera) represent the *Termitichnus* ichnofacies (Buatois and Mángano, 1995), which indicates a terrestrial environment. Hymenoptera insects installed their nests in non-inundated, preferentially dry, commonly well-insolated grounds. The open burrow system of *Labyrinthichnus terrerensis* was likely produced also in relatively dry grounds.

2. The meniscate *Taenidium barreti* and the branched shafts were produced rather in moist grounds. They are typical representatives of the *Scoyenia* ichnofacies (Buatois and Mángano, 1995, 1998). *Spongeliomorpha* isp. was produced in a cohesive, slightly firm ground. According to the latter authors, the *Scoyenia* ichnofacies is indicative of a transitional zone between terrestrial and subaqueous settings. According to Bromley and Asgaard (1979), the above trace fossils belong to the "terrestrial

suite". However, it is not clear which kind of substrate was colonized by *Polykladichnus aragonensis*. Other similar traces, such as *Arenicolites* sp., were ascribed to the "aquatic suite" by Bromley and Asgaard (1979). However, *P. aragonensis* can be produced by beetles in terrestrial environments (see discussion of the ichnotaxon). According to the scheme of non-marine ichnofacies of Buatois and Mángano (1995, 1998), the vertical trace fossils belong to the *Scoyenia* ichnofacies.

3. *Beaconites filiformis* is also a vertical trace fossil, but was produced in subaqueous environments, probably by chironomids. In the lower part of the described sedimentary sequences, this trace fossil occurs in beds affected by desiccation cracks, which are indicative of periodically drying out, shallow lacustrine deposits. However, in the upper part of the sequences, *B. filiformis* occurs in full subaqueous deposits, where the *Mermia* ichnofacies should occur. The latter ichnofacies contains different, small, horizontal, mostly grazing traces (Buatois and Mángano, 1995, 1998). The absence of this kind of traces can be caused by hypersaline conditions (indicated by precipitation of evaporitic remains), which eliminated most of typical animals in fresh-water lacustrine environments. Chironomid larvae can live in highly saline lakes (Rodríguez-Aranda and Calvo, 1998).

The cross-cutting relationships of trace fossils in the basal sandy marlstone indicate that the *Termitichnus* ichnofacies is replaced by the *Scoyenia* ichnofacies; the overlying beds contain only the subaqueous *Beaconites filiformis*. All the succession indicates a transition from dry-ground terrestrial to moist-ground environments, finally replaced by subaqueous conditions. The red lacustrine mudstones fill the open-burrow systems of the *Termitichnus* and *Scoyenia* ichnofacies. The Miocene lacustrine cycles of the Calatayud-Teruel basin seemingly display at least three community replacements in trace fossil distribution, indicating similar palaeoenvironmental changes. This enhances ichnological methods in investigations of lacustrine sedimentation processes.

CONCLUSIONS

A new ichnogenus (*Labyrinthichnus*) and three new ichnospecies (*Labyrinthichnus terrerensis*, *Polykladichnus aragonensis* and *Beaconites filiformis*) are erected in the Miocene lacustrine deposits of the Calatayud-Teruel basin (NE Spain). The whole ichnoassemblage includes, in the locality of Terrer, representatives of the *Termitichnus* ichnofacies (*Celliforma* sp., *Celliforma* ? isp. A and B, *Celliforma* ? aff. *habari*, *Rosellichnus* cf. *arabicus*, *Labyrinthichnus terrerensis*), the *Scoyenia* ichnofacies (*Taenidium barreti*, *Spongeliomorpha* sp., vertical shafts and probably *Polykladichnus aragonensis*), and an equivalent of the *Mermia* ichnofacies (*Beaconites filiformis*). The trace fossils were produced by burrowing insects, other arthropods and oligochaetes.

The vertical succession of the *Termitichnus* ichnofacies, *Scoyenia* ichnofacies and the equivalent of the *Mermia* ichnofacies indicates a gradual transition from dry-ground

terrestrial to moist ground environments, finally replaced by subaqueous conditions. These community replacements are related to episodic floodings of the lacustrine Calatayud sub-basin and subsequent evaporation leading to the development of dry grounds colonized by a wide diversity of soft-bodied animals.

The occurrence of a monospecific ichnoassemblage, composed of vertical *Beaconites filiformis* (produced probably by chironomid larvae) in the lacustrine sediments, is probably caused by hypersaline conditions (evinced by precipitation of evaporites), which eliminated typical fresh-water trace-makers responsible for the production of the horizontal traces indicative of the *Mermia* ichnofacies.

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REFERENCES

- Batra, S. W. T. 1984. Solitary bees. *Scientific American*, **250** (February), 86-93.
- Bradshaw, M. 1981. Paleoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (Lower Beacon Supergroup), Antarctica. *New Zealand Journal of Geology and Geophysics*, **24**, 61-652.
- Bromley, R. G. and Asgaard, U. 1979. Triassic fresh water ichnocoenosis from Carlsberg Fjord, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **28**, 39-80.
- Bromley, R. G. and Frey, R. W. 1974. Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*. *Bulletin of the Geological Society of Denmark*, **23**, 311-335.
- Brown, R.W. 1934. *Celliforma spirifer*, the fossil larval chambers of mining bees. *Journal of the Washington Academy of Sciences*, **24**, 532-539.
- Brown, R.W. 1935. Further notes on fossil larval chambers of mining bees. *Journal of the Washington Academy of Sciences*, **25**, 526-528.
- Buatois, L. A. and 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. and Mángano, M.G. 1998. Trace fossil analysis of lacustrine facies and basins. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **140**, 367-382.
- Buatois, L.A., Mángano, M.G., Wu Xiantao and Zhang Guocheng. 1995. *Vagorichnus*, a new ichnogenus for

- feeding burrow systems and its occurrence as discrete and compound ichnotaxa in Jurassic lacustrine turbidites of Central China. *Ichnos*, **3**, 265-272.
- Chamberlain, C.K. 1975. Recent lebensspuren in non-marine environments. In: *The Study of Trace Fossils* (Ed. R.W. Frey). Springer Verlag, New York, 431-458.
- Charbonneau, P. and Hare, L. 1998. Burrowing behaviour and biogenic structures of mud dwelling-insects. *Journal of the North American Benthological Society*, **17**, 239-249.
- Crimes, T. P., García Hidalgo, J. F. and Poire, D. G. 1992. Trace fossils from Arenig flysch sediments of Eire and their bearing on the early colonisation of deep seas. *Ichnos*, **2**, 61-77.
- Crusafont, M., Villatta, J.F. y Julivert, M. 1966. Notas sobre la estratigrafía y paleontología de la Cuenca de Calatayud-Teruel. *Notas y Comunicaciones IGME*, **19**, 53-76.
- D'Alessandro, A. and Bromley, R. G. 1987. Meniscate trace fossils and the *Muensteria-Taenidium* problem. *Palaeontology*, **30**, 743-763.
- Domínguez Alonso, P. y Coca Abia, M.M. 1998. Nidos de avispa minadoras en el Mioceno de Tegucigalpa (Honduras, América Central). *Coloquios de Paleontología*, **49**, 93-114.
- Donovan, S. K. 1994. Insects and arthropods as trace-makers in non-marine environments and palaeoenvironments. In: *The Palaeobiology of Trace Fossils* (Ed. S. K. Donovan). John Wiley & Sons, Chichester, 200-220.
- Ducieux, J.L., Billaud, Y. et Truc, G. 1988. Traces fossiles d'insectes dans les paleosols rouges de l'Eocene supérieur du nord-est du Massif Central français: *Celliforma arvernensis* ichnosp. nov. *Bulletin de la Société géologique de France*, **4**, 167-175.
- Edwards, N., Jarzembowski, E. A., Pain, T. and Daley, B. 1997. Coccon-like trace fossils from the lacustrine-palustrine Bembridge Limestone Formation (Late Eocene), Southern England. *Proceedings of the Geologists' Association*, **109**, 25-32.
- Eickwort, G.C. 1969. Tribal positions of western hemisphere green seat bees, with comments on their nest architecture (Hymenoptera: Halictidae). *Annals of the Entomological Society of America*, **62**, 652-661.
- Eickwort, G.C. and Sakagami, S.F. 1979. A classification of nest architecture of bees of the tribe Augochlorini (Hymenoptera, Halictidae) with the description of a Brazilian nest of *Rhinocorynura inflaticeps*. *Biotropica*, **11**, 28-37.
- Ekdale, A. A. and Lewis, D. W. 1991. Trace fossils and paleoenvironmental control of ichnofacies in a late Quaternary gravel and loess fan delta complex, New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **81**, 253-279.
- Ekdale, A. A., Bromley, R. G. and Pemberton, G. S. 1984. Ichnology: the use of trace fossils in sedimentology and stratigraphy. *Society of Economic Paleontologists and Mineralogists, Short Course*, **15**, 1-317.
- Elliott, D. K. and Nations, J. D. 1998. Bee burrows in the Late Cretaceous (late Cenomanian) Dakota Formation, northeastern Arizona. *Ichnos*, **5**, 243-253.
- Fedonkin, M. 1985. Paleikhnologiya vendskich Metazoa [Paleoichnology of the Vendian Metazoa]. In: *Vendskaya Sistema I. Paleontologiya* (Eds. B.S. Sokolov and A.B. Iwanowskij). Nauka, Moscow, 112-117.
- Frey, R. W., Curran, A. H. and Pemberton, G. S. 1984. Tracemaking activities of crabs and their environmental significance: the ichnogenus *Psilonichnus*. *Journal of Paleontology*, **58**, 511-528.
- Fürsich, F. T. 1973. A revision of the trace fossils *Spongiomorpha*, *Ophiomorpha* and *Thalassinoides*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1972**, 719-735.
- Fürsich, F.T. 1981. Invertebrate trace fossils from the Upper Jurassic of Portugal. *Comunicações dos Serviços Geológicos de Portugal*, **67**, 153-168.
- Fürsich, F. T., Kennedy, W. J. and Palmer, T. J. 1981. Trace fossils at a regional discontinuity surface: the Austin/Taylor (Upper Cretaceous) contact in central Texas. *Journal of Paleontology*, **55**, 537-551.
- Genise J.F. and Bown T.M. 1994. New Miocene scarabeid and hymenopterous nests and Early Miocene (Santacrucian) paleoenvironments, Patagonian Argentina. *Ichnos*, **3**, 107-117.
- Genise, J.F. and Bown, T.M. 1996. *Uruguay Roselli* 1938 and *Rosellichnus* n. ichnogenus: two ichnogenes for clusters of fossil bee cells. *Ichnos*, **4**, 199-217.
- Genise, J.F. and Hazeldine, P.L. 1998. The ichnogenus *Palmiraichnus* Roselli for fossil bee cells. *Ichnos*, **6**, 151-166.
- Hasiotis S.T. and Bown T.M. 1992. Invertebrate trace fossils: the backbone of continental ichnology. In: *Trace Fossils* (Eds. C.G. Maples and R.R. West). *Short Courses in Paleontology*, **5**, 64-104. Paleontological Society, Knoxville, Tennessee.
- Heer, O. 1877. *Flora Fossilis Helvetiae. Vorweltliche Flora der Schweiz*. J. Wurster and Comp. Zürich, 182 pp.
- Houston, T.F. 1987. Fossil brood cells of Stenotritid bees (Hymenoptera, Apoidea) from the Pleistocene of South Australia. *Transactions of the Royal Society of South Australia*, **111**, 93-97.
- Keighley, D. G. and Pickerill, R. 1994. The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. *Palaeontology*, **37**, 305-337.
- Książkiewicz, M. 1968. O niektórych problematykach z fliszu Karpat polskich (część III) [On some problematic organic traces from the Flysch of the Polish Carpathians (part III)]. *Rocznik Polskiego Towarzystwa Geologicznego*, **38**, 3-17.
- Larsen, E.B. 1936. Biologische Studien über die tunnelgrabenden Kafer auf Skallingen. *Videnskabilige Meddelelser fra Dansk Naturhistorisk Forening*, **100**, 1-232.
- McCall, P.L. and Tevesz, M.J.S. 1982. The effect of benthos on physical properties of fresh water sediments. In: *Animal-Sediment Relations* (Eds. P.L. McCall and M.J.S. Tevesz). Plenum Press, New York, 105-176.
- Metz, R. 1990. Tunnels formed by mole cricket (Orthoptera: Gryllotalpidae): paleoecological implications. *Ichnos*, **1**, 139-141.
- Metz, R. 1993. A new ichnospecies of *Spongiomorpha* from the Late Triassic of New Jersey. *Ichnos*, **2**, 259-262.

- Minkiewicz, R. 1934. Les Pampilides à nide fixe et ceux à nidmomentené (Etude d'éthologie comparée). *Polskie Pismo Entomologiczne*, **13**, 43-60.
- Oliver, D.R. 1971. Life history of the Chironomidae. *Annual Review of Entomology*, **16**, 211-230.
- Olmo, P. del, Hernández, A. y Aragonés, E. 1983. *Mapa geológico de España. Escala 1:50000. Explicación de la hoja n. 437(25-17), Ateca*. IGME ed., 67 pp.
- Orłowski, S. 1968. Kambr antykiliny Łysogórskiej Gór Świętokrzyskich (Cambrian of Łysogóry Anticline in the Holy Cross Mountains). *Biuletyn Geologiczny*, **10**, 195-221.
- Orłowski, S. and Żylińska, A. 1996. Non-arthropod burrows from the Middle and Late Cambrian of the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, **41**, 385-409.
- Pemberton, G. S. and Frey, R. W. 1982. Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. *Journal of Paleontology*, **56**, 843-881.
- Pfeiffer, H. 1968. Die Spurenfossilien des Kulms (Dinant) und Devons der Frankenwalder Querzone (Thuringen). *Jahrbuch der Geologie*, **2**, 651-717.
- Ratcliffe B.C. and Fagerstrom J.A. 1980. Invertebrate lebenspuren of Holocene flood plains: their morphology, origin and paleoecological significance. *Journal of Paleontology*, **54**, 614-630.
- Retallack G.J. 1984. Trace fossils of burrowing beetles and bees in an Oligocene paleosol, Badlands National Park, South Dakota. *Journal of Paleontology*, **58**, 571-592.
- Rodríguez-Aranda, J.P. 1992. Significado de bioturbaciones en un medio evaporítico continental (Mioceno de la Cuenca de Madrid). *Geogaceta*, **12**, 113-115.
- Rodríguez-Aranda, J.P. and Calvo, J.P. 1998. Trace fossils and rhizoliths as a tool for sedimentological and palaeoenvironmental analysis of ancient continental evaporite successions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **140**, 383-399.
- Roselli, F.L. 1987. Paleocinología. Nidos de insectos fósiles de la cobertura Mesozoica del Uruguay. *Publicaciones del Museo Municipal de Nueva Palmira*, **1**, 1-56.
- Sakagami, S.F. and Michener, C.D. 1962. *The Nest Architecture of the Sweat Bees (Halictinae)*. The University of Kansas Press, Knoxville, 135 pp.
- Saporta, G. de. 1887. Nouveaux documents relatifs aux organismes problématiques des anciennes mers. *Bulletin de la Société géologique de France* (série 3), **15**, 286-302.
- Schlirf, M., Uchman, A. and Kümmel, M. (in press). Upper Triassic (Keuper) non-marine trace fossils from the Haßberge region (Franconia, southern Germany). *Paläontologische Zeitschrift*.
- Stanley, K.O. and Fagerstrom, J.A. 1974. Miocene invertebrate trace fossils from a braided river environment, western Nebraska, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **15**, 63-82.
- Squires, R.L. and Advocate, M.D. 1984. Meniscate burrows from Miocene lacustrine-fluvial deposits, Diligencia Formation, Orocoopia Mountains, southern California. *Journal of Paleontology*, **58**, 593-597.
- Thackray, G. D. 1994. Fossil nests of sweat bees (Halictinae) from a Miocene paleosol, Rusinga Island, western Kenya. *Journal of Paleontology*, **68**, 795-800.
- Uchman, A. 1995. Taxonomy and palaeoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria*, **15**, 1-115.
- 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.
- Vialov, O. S. 1962. Problematica of the Beacon Sandstone at Beacon Height West, Antarctica. *New Zealand Journal of Geology and Geophysics*, **5**, 718-732.
- Walshe, B.M. 1951. The feeding habits of certain chironomid larvae (subfamily Tendipedinae). *Proceedings of the Zoological Society of London*, **121**, 63-89.
- Wetzel, A. 1983. Biogenic structures in modern slope to deep-sea sediments in the Sulu Sea Basin (Philippines). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **42**, 285-304.

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