THE TRACE FOSSIL *Gyrochorte*: ETHOLOGY AND PALEOECOLOGY

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ABSTRACT

Specimens of the trace fossil *Gyrochorte* from the Ordovician, Jurassic and Cretaceous of Utah, and the Pliocene of Spain are described. These occurrences expand the stratigraphic range of the ichnogenus, and allow for a re-examination of this paleoenvironmentally sensitive and puzzling trace fossil. The recognition of the penetrative characteristic of the trace is essential for a correct identification, as some trace fossils have been erroneously ascribed to *Gyrochorte* in the past. The producer must have been a detritus-feeding worm-like animal, probably an annelid, that created a bilobed, vertically penetrating and sometimes plaited meandering trace. *Gyrochorte* typically occurs in sandy facies in moderately energetic nearshore and shallow marine paleoenvironments in association with other trace fossils, usually pascichnia and fodinichnia.

Keywords: Trace fossils, *Gyrochorte*, ethology.

RESUMEN

Se describen especímenes de la pista fósil *Gyrochorte* del Ordovícico, Jurásico y Cretácico de Utah (Estados Unidos) y del Plioceno de España. Estos hallazgos extienden el rango estrátigráfico del icnogénero y permiten reevaluar la interpretación de este icnofósil y su significado paleoambiental. El reconocimiento del carácter penetrativo característico de este icnofósil es esencial para su correcta identificación. El productor debió de ser un animal vermiforme detritívoro, probablemente un anélido. *Gyrochorte* aparece típicamente en facies arenosas depositadas en medios marinos someros de energía moderada asociado a otras pistas, normalmente pascichnia y fodinichnia.

Palabras clave: Pistas fósiles, *Gyrochorte*, etología.

INTRODUCTION

The trace fossil *Gyrochorte* Heer, 1865 is a frequently encountered ichnogenus in the fossil record, particularly in Mesozoic strata. However, some authors who have reported *Gyrochorte* did not consider its characteristic taphonomic and preservational features, resulting in some confusion and frequent misuse of the ichnotaxon. A complete *Gyrochorte* specimen commonly is preserved as a bilobate positive epirelief with a corresponding negative hyporelief. These two semireliefs represent the top and bottom features of a more complex wall-like burrow that is preserved only occasionally in full relief and only in very particular sediment types (e.g., mica-rich sand) does it clearly exhibit its internal structure.

Recent discoveries of *Gyrochorte* by the authors in strata of different ages (Ordovician, Jurassic, Cretaceous and Pliocene) in Utah and Spain allow us to re-examine the ichnogenus. The purposes of this paper are: 1) to describe the new material, 2) to re-examine the constructional features of the ichnogenus in order to discuss its ethological significance and to establish the most likely tracemaker, 3) to analyze its paleoenvironmental distribution, and 4) to interpret the paleoecology of the tracemaker.

SYSTEMATIC ICHNOLOGY

Gyrochorte Heer, 1865

Emended diagnosis

Wall-like burrow with a top part (positive epirelief) consisting of two convex lobes with a median furrow and

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a bottom part (negative hyporelief) consisting of two grooves and a median ridge (Fig. 1). The lobes on the top (and more rarely the grooves at the base) commonly exhibit transverse meniscus-like discontinuities and often obliquely aligned plaits. The internal structure (when recognizable) is constituted of repetitive biconvex-up modular units (spreiten). The burrow exhibits an irregular meandering or arcuate course, but more rarely it can be straight or gently curved. It is typically preserved as epichnial bilobate ridges associated with equivalent hypichnial bilobate grooves, both following the same path and corresponding to the same burrow. More rarely preserved as full reliefs (endichnia).

Gyrochorte comosa Heer, 1865

Figs. 1-7

Material and localities

The material is stored in the University of Utah Ichnology Collection (UUIC). Specimens from eight localities have been studied: Skull Rock Pass, Lower Ordovician, Utah (UUIC 1034-1037, 1073); Fossil Mountain, Lower Ordovician, Utah (UUIC 648-649); Nephi, Middle Jurassic, Utah (UUIC 984-1022, 1024); San Rafael Swell, Middle Jurassic, Utah (UUIC 961, 963, 965, 1056-1057); Gunlock, Middle Jurassic, Utah (UUIC 1025-1027); Hanna, Middle Jurassic, Utah (UUIC 1028); Spring Canyon, Upper Cretaceous, Utah (UUIC 1031-1033); Sant Onofre, Lower Pliocene, Spain (UUIC 1029-1030). A short description of the situation of this localities is given in Appendix 1.

Description

The studied *Gyrochorte* are between 1 and 4.5 mm wide and they are commonly preserved as epireliefs with their corresponding hyporeliefs in sandstone or grainstone layers between a few milimeters and 2 centimeters thick. The oblique spreiten that constitute the internal structure of the burrows have been recognized only in Ordovician specimens from Skull Rock Pass (Figs. 2.A-2.B). In these specimens the three main vertical planes of the burrow (the two lateral and the medial) have acted as preferential breakage and erosional discontinuities. In the rest of the material, the penetrative character of the structure can be recognized by observing bilobate semireliefs on intermediate laminae between the epireliefs and hyporeliefs of the same specimen (Fig. 7.A). The Ordovician *Gyrochorte* are usually straight or gently curved (Fig. 2), while the Mesozoic and Neogene specimens are irregularly sinuous and often form loops (Figs. 3-7). The epireliefs exhibit frequent sudden changes in direction that are absent or less pronounced in the corresponding hyporeliefs, which usually show less winding morphologies (Figs. 3.C-3.F, 4.E-4.F). Figure 5 shows the differences between the hyporeliefs and epireliefs of some Jurassic specimens. Crosscutting is common in all of the material. The lobes in most epireliefs show crude transverse meniscus-like striae, which are the external expression of the internal spreiten. A few specimens exhibit very well defined sets of double plaits bounded by chevron-like scars (Figs. 4.A, 4.B). The hyporeliefs occasionally show the meniscus-like structures (Figs. 4.D, 4.F), but they are more commonly smooth.

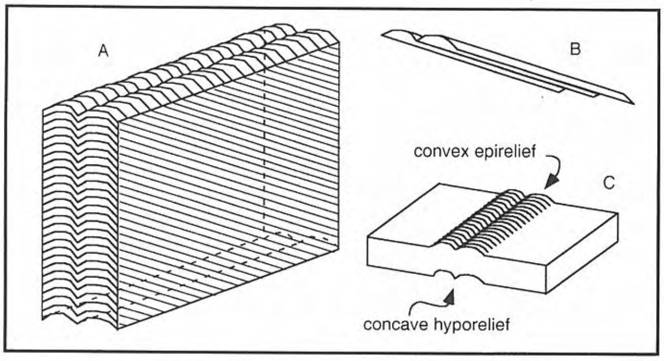

Figure 1. **A.** Constructional model of *Gyrochorte*. **B.** Morphology of an individual spreite. **C.** Typical preservation of *Gyrochorte*.

Discussion

The most important characteristic for a correct identification of *Gyrochorte* is the recognition of the vertical dimension of the burrow. This can be observed by finding associated convex epireliefs and their corresponding concave hyporeliefs in the same beds, or by the observation of the structure in full relief. *Aulichnites* Fenton and Fenton, 1937, is a convex bilobate epichnial trail, but it lacks the vertical dimension and the lobes are smooth. Several authors have designated bilobate epichnial positive trails as possible *Gyrochorte* (Hakes, 1976; Walter *et al.*, 1989), but the attribution is doubtful without the corresponding hyporeliefs. Several other trace fossils that are hypichnial bilobate ridges also have been assigned erroneously to *Gyrochorte*, and most of them probably correspond to the ichnogenus *Protovirgularia* (Macsotay, 1967; Ksiazkiewicz, 1970, 1977; Pickerill, 1980; Crimes *et al.*, 1981). Frey and Chowns' (1972) Silurian *Gyrochorte* from Georgia are not *Gyrochorte* but quadrilobate trilobite trails (A. Rindsberg and A. Martin, oral communication).

Several described ichnospecies of *Gyrochorte* do not belong to the ichnogenus. *"Gyrochorte" carbonaria* Seilacher,1954, common in continental settings (Pollard, 1988), is not real *Gyrochorte* (Seilacher, 1963; Häntzschel, 1975). *Gyrochorte robusta* Ghare and Kulkarni, 1986 was erected on the basis of its greater width when compared to *G. comosa*. However, size must be used cautiously as an ichnotaxobase, and if used, size criteria require some sort of statistical data to support them (Pickerill, 1994). On the other hand, the size range given by Ghare and Kulkarni (1986) for *G. robusta* (6-9 mm) falls in the range known for *G. comosa*. *G. burtani, G. imbricata* and *G. obliterata,* which were erected by Ksiazkiewicz (1977), are positive hyporeliefs attributed by Uchman (1998) to several ichnospecies of *Protovirgularia*. *Gyrochorte zigzag* Seilacher and Alidou, 1988 from the Silurian of Benin shares some characters with *G. comosa* (backfill, preservation as correlative

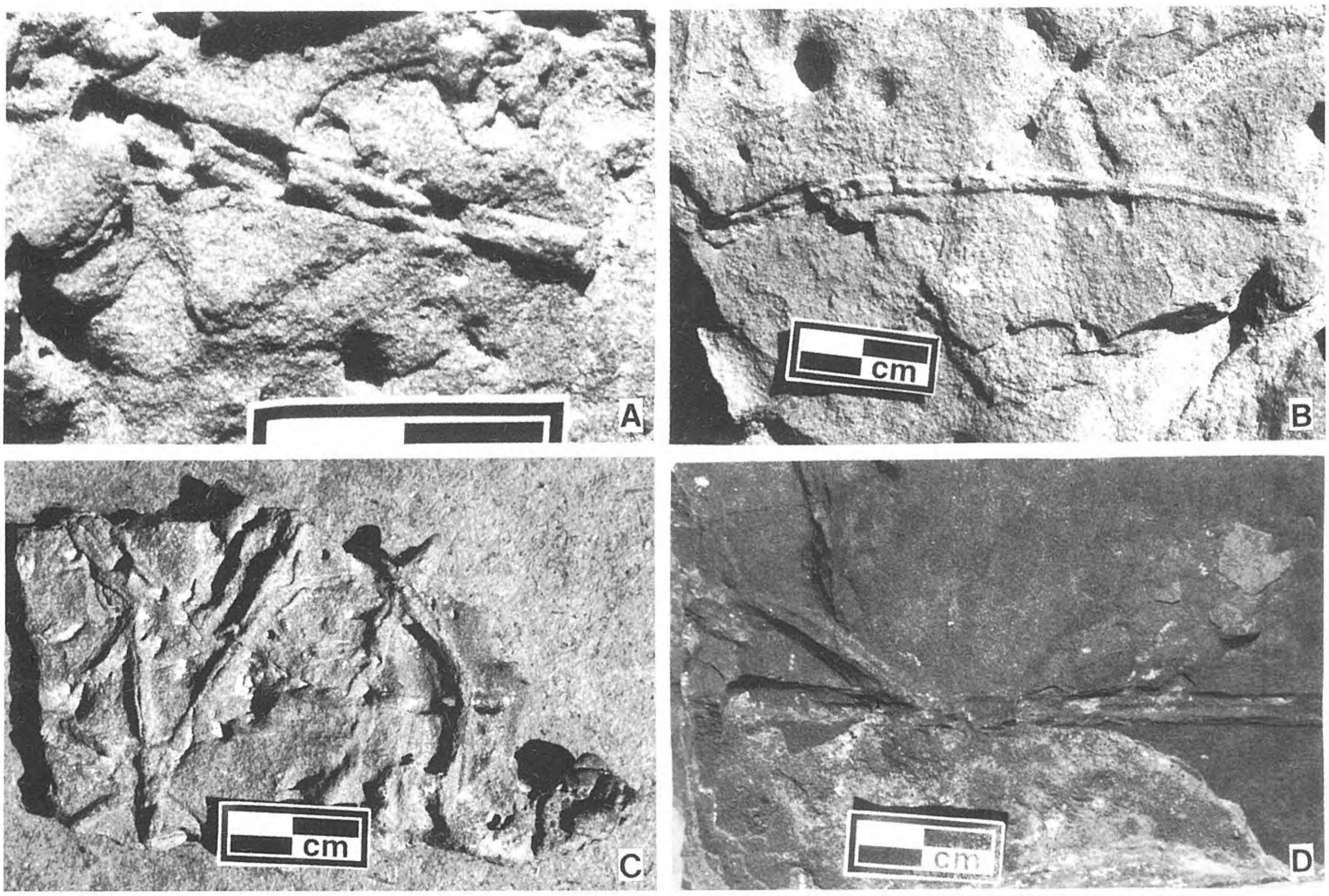

Figure 2. Ordovician *Gyrochorte*. **A.** Partly weathered specimen from Skull Rock Pass showing internal oblique discontinuities (UUIC 1037). **B.** Specimen from Skull Rock Pass displaying the double-arched oblique spreiten (UUIC 1073). **C.** Several crosscutting *Gyrochorte* from Skull Rock Pass (UUIC 1035). **D.** Specimen from Fossil Mountain exhibiting the typical very straight morphology of Ordovician *Gyrochorte* (UUIC 648).

positive epireliefs and negative hyporeliefs) but also important differences (no bilobate character). Seilacher and Alidou (1988) tentatively assigned the new ichnospecies to the ichnogenus *Gyrochorte*. We consider that the differences are important enough to assign this ichnospecies to a new and different ichnogenus.

The material described here from the Ordovician apparently exhibits straighter paths than the Mesozoic and Cenozoic specimens. New findings should help to determine if this difference is consistent enough to serve as an ichnotaxobase at the ichnospecific level.

Stratigraphic distribution: Lower Ordovician-Pliocene (see Table 1), being particularly abundant in the Jurassic and Cretaceous.

CONSTRUCTION, ETHOLOGY AND TRACEMAKER

Several authors have addressed the problem of the ethology and biology of *Gyrochorte*. Weiss (1941) and later Seilacher (1955) interpreted the trace as being produced by a worm-like organism burrowing obliquely through the sediment (see Seilacher, 1955, fig, 2b, p. 380). Fuchs (1895) pointed to the similarity of the epireliefs of *Gyrochorte* with collapsed tunnels created by modern amphipod crustaceans that had been described by Hancock (1858). Hallam (1970) points out that this interpretation cannot explain the vertical dimension of *Gyrochorte*. Heinberg (1973) described for first time the internal structure of the ichnofossil. The material described by Heinberg (1973) from the Lower Cretaceous of Greenland is found in extremely mica-rich sandstone, allowing the unusual preservation of the internal structure of the fossil trace. Heinberg's material revealed that *Gyrochorte* is constituted by oblique double-arched convex-up spreiten (what he called the "modular unit"). The spreiten repeat vertically and are responsible for the bilobate morphology of the epireliefs and hyporeliefs. In transverse section, *Gyrochorte* reveals the vertical stacking of the double ridge observed in the semireliefs (Fig. 1). These features had never been observed in other material, as the absence of flat grains did not allow their preservation. However, the Ordovician material from Skull Rock Pass described in this paper allows us to recognize some of the internal features of *Gyrochorte* and confirms Heinberg's observations (Figs. 2.A, 2.B).

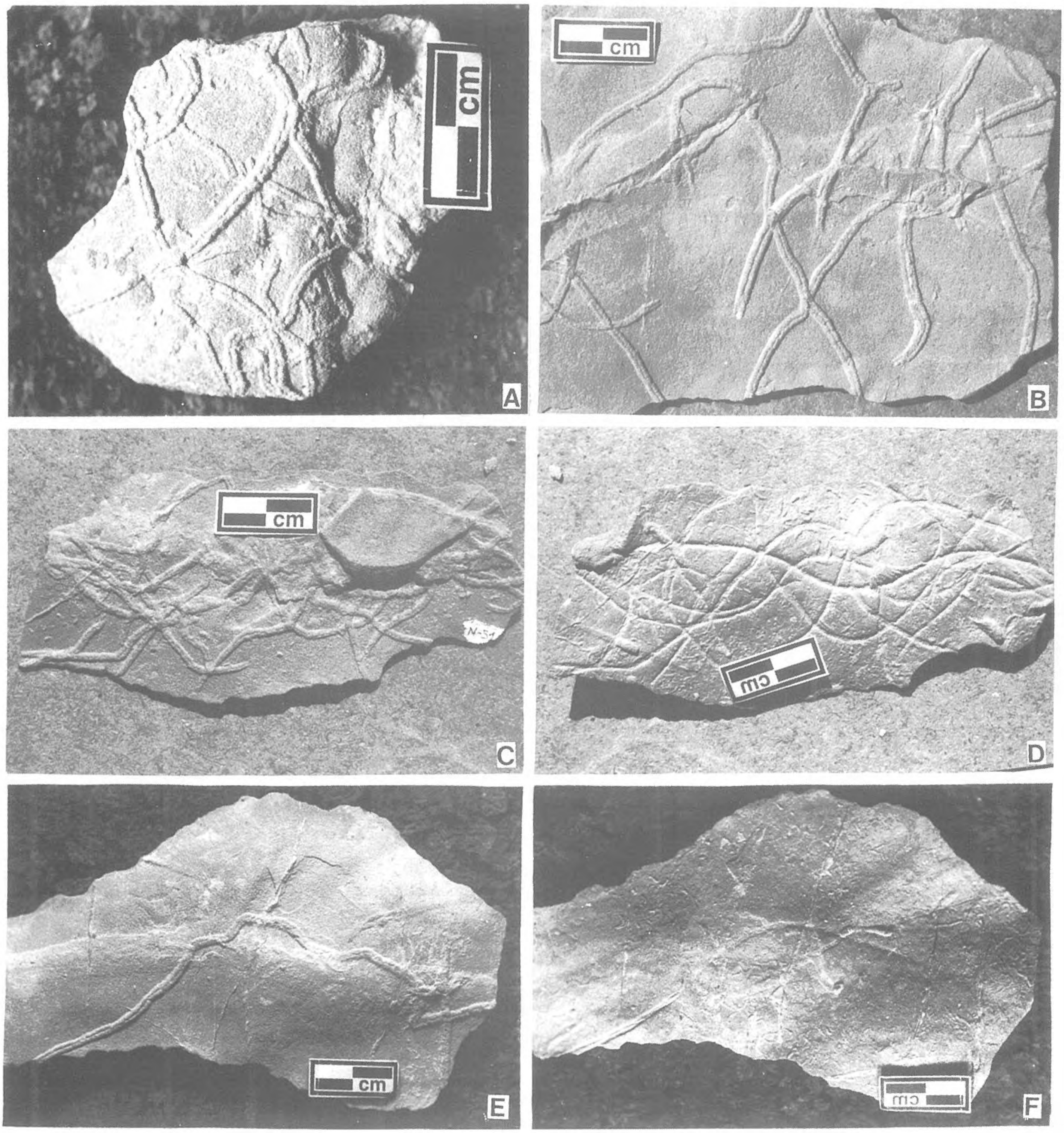

Figure 3. *Gyrochorte* from the Middle Jurassic Arapien Shale in Nephi. **A-B.** Crowded occurrences with numerous crosscutting burrows (epireliefs) (UUIC 940 and 1022). **C-D.** positive epireliefs (C) and corresponding negative hyporeliefs (D) of specimen UUIC 986. **E-F.** sharply bent positive epirelief (E) and corresponding smoothly curved hyporelief (F) (UUIC 988). D and F were printed in reverse to orient them in the same manner as C and E.

The spreiten can only be explained by active digging of the sediment and movement of the grains around the body of the producer. The double-arch morphology resulted from the displacement of the grains from the frontal and lower part of the body to the back along the sides. This digging activity resulted in forward movement of the animal but oblique to the axis of its body (Fig. 8). The greater irregular pattern of the epireliefs compared to the corresponding hyporeliefs observed in the Jurassic material of Utah, also pointed out by other authors (e.g.,

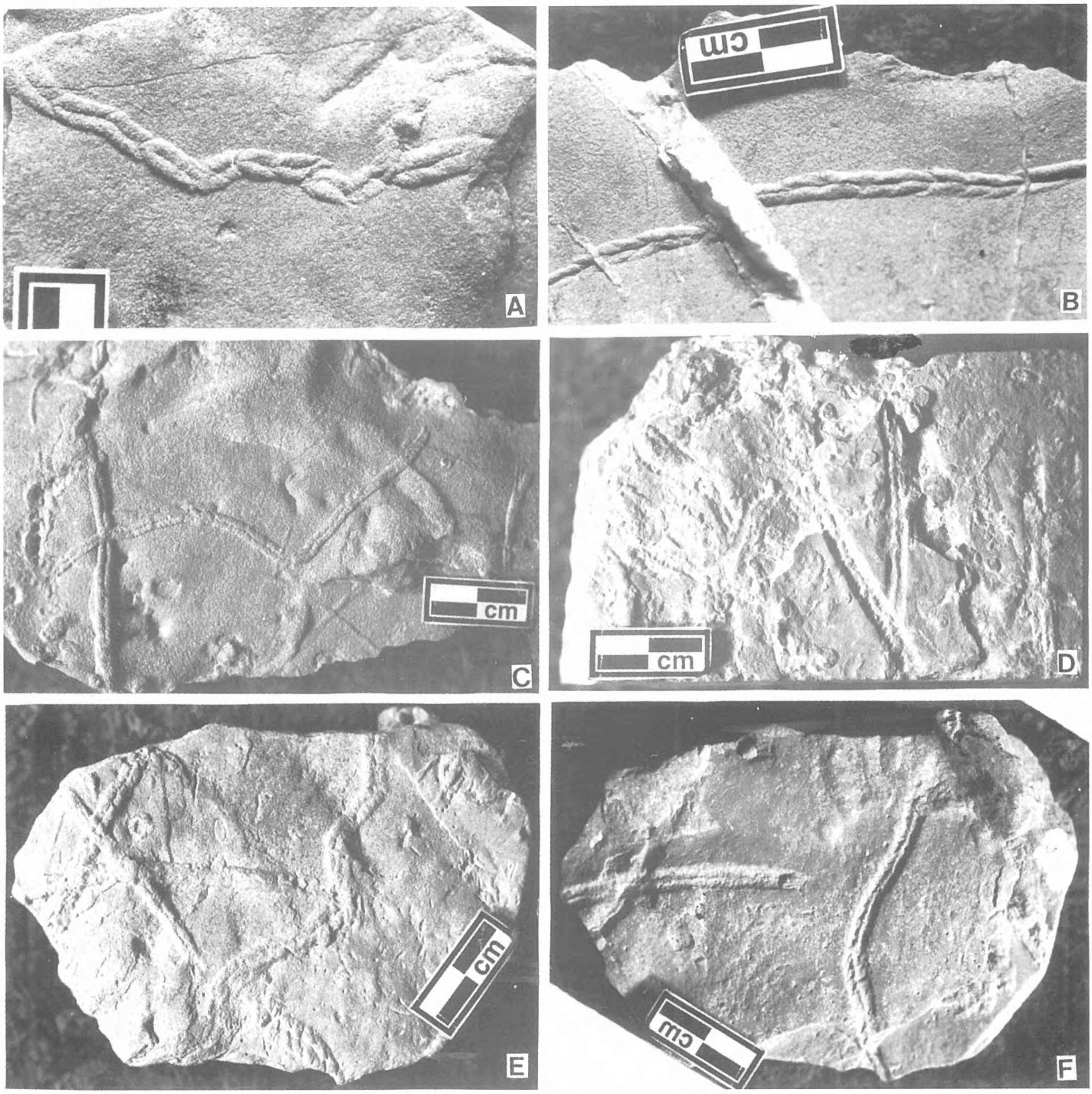

Figure 4. *Gyrochorte* from the Middle Jurassic of Utah. **A-B.** Epireliefs from Nephi displaying well-preserved plaited structure (UUIC 987 and 1021). **C.** Epirelief from Nephi showing well defined meniscus-like marks (UUIC 989). **D.** Hyporeliefs with well-defined lobes and transverse marks from the Carmel Formation in the San Rafael Swell (UUIC 965). **E-F.** Epirelief (E) and hyporelief (F) of specimen UUIC 1025 showing the less irregular path of the second. F was printed in reverse to orient the sample in the same manner as E.

Weiss, 1941), is consistent with this constructional model and not with the "collapsed tunnel" model described by Hallam (1970). The lower part of the burrower's body followed a more regular course, and the upper part of the body, while closer to the surface where the sediment would have been looser and easier to burrow, could have followed a more irregular path. The plaited structure that is observed occasionally (Figs. 4.A, 4.B), often is associated with sudden changes of direction, and it probably corresponds to moments when the animal stopped its advance through the sediment. Hence, the internal and external features of *Gyrochorte* are consistent with the interpretation of Weiss (1941) and Seilacher (1955). The obliquely-burrowing worm interpretation has been followed by most later authors (e.g., Pemberton and Frey, 1984; Dam, 1990; Powell, 1992).

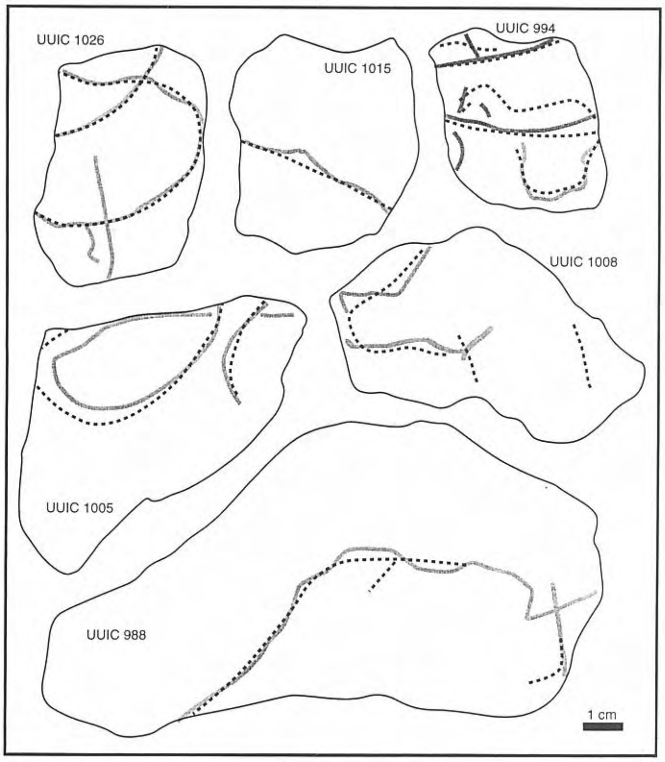

Figure 5. Superposition of epireliefs (gray lines) and hyporeliefs (discontinuous lines) of several specimens from Nephi, showing the more irregular pattern of the epireliefs.

There is no known modern equivalent of a behavior similar to that exhibited by *Gyrochorte*. Some organisms, such as the tube-bearing polychaete *Pectinaria* and some scaphopod mollusks, are known to burrow with the main axis of their bodies perpendicular or steeply oblique to the direction of movement, producing a wall-like area of disturbed sediment (Dinamani, 1964; Schäfer, 1972; Ronan, 1977; Bromley, 1996). However, the resulting biogenic structure is produced by plowing the tube or the shell through the sediment, and although this behavior could create a double ridge feature on the surface and a median discontinuity plane, it is unlikely that it could create an internally organized spreiten structure with sharp outer boundaries like those of *Gyrochorte*. Heinberg and Birkelund (1984) have suggested a caudofoveate aplacophoran as a possible producer for *Gyrochorte*. However, little is known about the burrowing behavior of these mollusks to support this interpretation. The only burrowing activity described for this group is the construction of vertical burrows (Barnes *et al.*, 1993). The *Gyrochorte* tracemaker must have been a worm-shaped animal with bilateral symmetry and bearing some sort of organs along the body that enabled it to manipulate and move the sediment. An annelid is a good candidate supported by several authors (Weiss, 1941; Heinberg, 1973; Karaszewski, 1973), as most other worms lack any external anatomical elements that could be used to move grains around their bodies. The vermiform morphology of the burrower is supported by the description by Stanley and Pickerill (1998) of Ordovician *Gyrochorte* that is intergradational with *Planolites* (see also figure 1.3, p. 24 in Pickerill, 1994).

If the assignment of a possible tracemaker for *Gyrochorte* is not an easy task, then the interpretation of its behavioral significance is, at least, equally difficult. The oblique burrowing behavior deduced from the internal structure of *Gyrochorte* is very unusual. It implies considerable effort, suggesting that the animal was not simply moving but also obtaining some sort of benefit from this behavior. The irregularly meandering path suggests that the animal was actively searching for food. Heinberg (1973) suggested that the peculiar behavior of the *Gyrochorte* producer was to bring the animal into contact with as much food as possible while using as little energy as possible, and so, he interpreted the trace as produced by a deposit feeder.

PALEOECOLOGY AND PALEOENVIRONMENT

ORDOVICIAN

The section in Skull Rock Pass (Utah) is part of the Filmore Formation (Hintze, 1951, 1973). These strata consist of shallow subtidal to intertidal storm-deposited and fair-weather sediments (Dattilo, 1993). Study of bioturbation structures (Benner, 2000) shows that they are abundant and diverse through the section, including *Thalassinoides*, *Planolites*, *Teichichnus*, *Chondrites*, *Phycodes* and *Gyrochorte*. *Gyrochorte comosa* occurs in the facies designated by Dattilo (1993) as "calcisiltite and calciarenite". This facies is generally fine-grained, thinly bedded, internally thinly laminated (planar, hummocky and more rarely ripples), and it is interbedded with shales or wavy-laminated mudstones. Dattilo (1993) interpreted this facies as deposited by short-term events, probably storms, in the lower shoreface.

The other Ordovician *Gyrochorte* studied in this paper come from the Kanosh Shale in Fossil Mountain, Utah. This formation is a mixed clastic and carbonate sequence deposited on a shallow marine shelf (Hintze, 1973; McDowell, 1988). The facies containing *Gyrochorte* are fine-grained, few centimeter thick, laminated sandstones interpreted as event beds, probably deposited by storms.

JURASSIC

Gyrochorte from the Middle Jurassic localities of Utah were produced in a shallow epicontinental sea that occupied most of central Utah during the Middle Jurassic (Imlay, 1980).

The section in Nephi consists of evaporites, micritic carbonates and mixed carbonate-clastic grainstones of the Arapien Shale. Picard and Uygur (1982) and Lord (1985) interpreted the formation as having formed in a shallow storm-dominated shelf. *Gyrochorte* is very abundant in the grainstones that typically are a few centimeters thick and exhibit ripple lamination and more rarely parallel cross-lamination. These beds are interpreted as tempestites (Lord, 1985). Other trace fossils that occur in

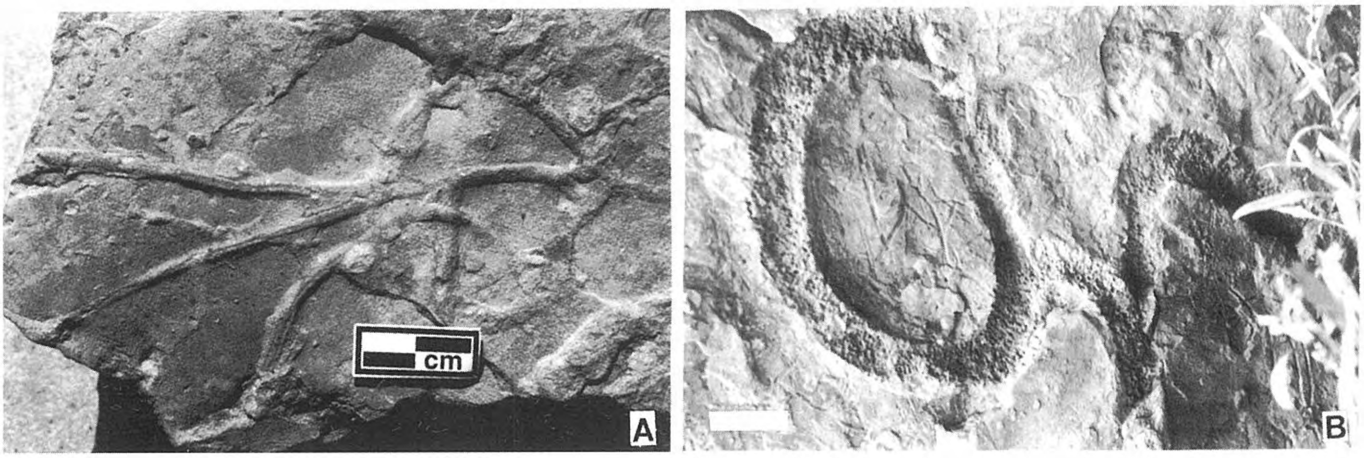

Figure 6. *Gyrochorte* from the Cretaceous of Spring Canyon. **A.** Detail of three specimens (epireliefs) (UUIC 1033). **B.** Abundant *Gyrochorte* associated with *Ophiomorpha irregulaire* (field specimen). Scale bar=5 cm.

this facies are *Planolites, Lockeia, Palaeophycus, Nereites,* and *Asteriacites* (Gibert and Ekdale, in press).

The presence of *Gyrochorte* in the Carmel Formation in the San Rafael Swell was recorded by Gibert and Ekdale (1999) in a section constituted by subtidal to supratidal carbonates, siliciclastics and evaporites. *Gyrochorte* is locally abundant in few-centimeter thick, cross-laminated to rippled sandstone and grainstone beds interpreted as deposited by storms. Gibert and Ekdale (1999) suggested hypersaline environments for the Carmel Formation from the characteristics (size, diversity, intensity of bioturbation) of the trace fossil assemblages. *Gyrochorte* occurs associated with other trace fossils, such as *Chondrites, Planolites, Lockeia, Protovirgularia,* and *Teichichnus.*

Smail and Wilson (1993), Wilson (1997) and Kilbourne *et al.* (1998) recorded *Gyrochorte* from another Carmel Formation locality, Gunlock, in southern Utah. The ichnogenus is very abundant in the grainstones of Member D of Nielson (1990). This member is interpreted as having been deposited in shoal and lagoonal settings. Trace fossils are abundant in the peloid and ooid-rich lagoonal siltstones and grainstones. Together with *Gyrochorte*, other trace fossils present are *Nereites, Asteriacites, Chondrites, Palaeophycus, Monocraterion* and *Teichichnus.*

Gyrochorte has also been found in the Twin Creek Formation near Hanna in northern Utah. Preliminary studies of the locality show that *Gyrochorte* is rare and occurs in association with *Chondrites, Planolites* and *Phycodes.*

CRETACEOUS

Gyrochorte from Spring Canyon, Utah, belong to the Storrs Member of the Star Point Formation. These deposits represent a deltaic progradational sequence. *Gyrochorte* occurs in fine to medium-grained sandstone beds on top of mouth bar deposits. These beds may represent sediment reworking on top of the bars. *Gyrochorte* is very abundant in these beds, and is associated with *Planolites, Ophiomorpha irregulaire, Chondrites,* and *Cylindrichnus.* Howard and Frey (1984) studied the ichnology of the Star Point Formation, but they did not mention the presence of *Gyrochorte.* However, Maberry (1971) reported the presence of the ichnogenus in the overlying Blackhawk Formation.

PLIOCENE

The Spanish Pliocene *Gyrochorte* come from the Campredó Blue Clay Unit (informal unit of Arasa, 1990) which records the filling of a small marginal marine bay (Arasa, 1990; Gibert and Martinell, 1996). The Campredó Unit is composed of clays and sandstones deposited in the central and marginal areas of the bay. The body fossil assemblages (mainly mollusk fauna) suggest that salinity conditions were low and were greatly influenced by freshwater input into the bay (Martinell and Domènech, 1984). *Gyrochorte* occurs in centimeter-thick sandstone beds intercalated with clays. These beds exhibit low-angle cross-stratification and ripples. They are most likely storm beds or storm-induced turbidites (Arasa, 1990). The occurrences are scarce although *Gyrochorte* is locally abudant in certain beds. *Gyrochorte* is found in association with *Teichichnus, Sinusichnus,* and more rarely *Nereites* and *Scolicia* (Gibert and Martinell, 1996).

PALEOENVIRONMENTAL AND PALEOECOLOGICAL IMPLICATIONS

Other published occurrences of *Gyrochorte* are listed in Table 1, including the paleoenvironment interpreted for each one of them. All the occurrences of actual *Gyrochorte* are in nearshore and shallow marine deposits. The characteristic setting for the trace is moderate to moderately high energy environments, including bars, shorefaces of beach complexes, storm-dominated shelves and embayment areas. *Gyrochorte* typically is absent in permanently high energy settings, low energy outer shelves and deep-water environments. In most of the occurrences, *Gyrochorte* is dominant when it is present and the assemblages commonly exhibit low to moderate diversity. These assemblages are usually composed of shallow-tier traces, mostly pascichnia (such as *Planolites, Nereites* or *Curvolithus*), but also fodinichnia (such as *Teichichnus, Chondrites* or *Phycodes*) and cubichnia

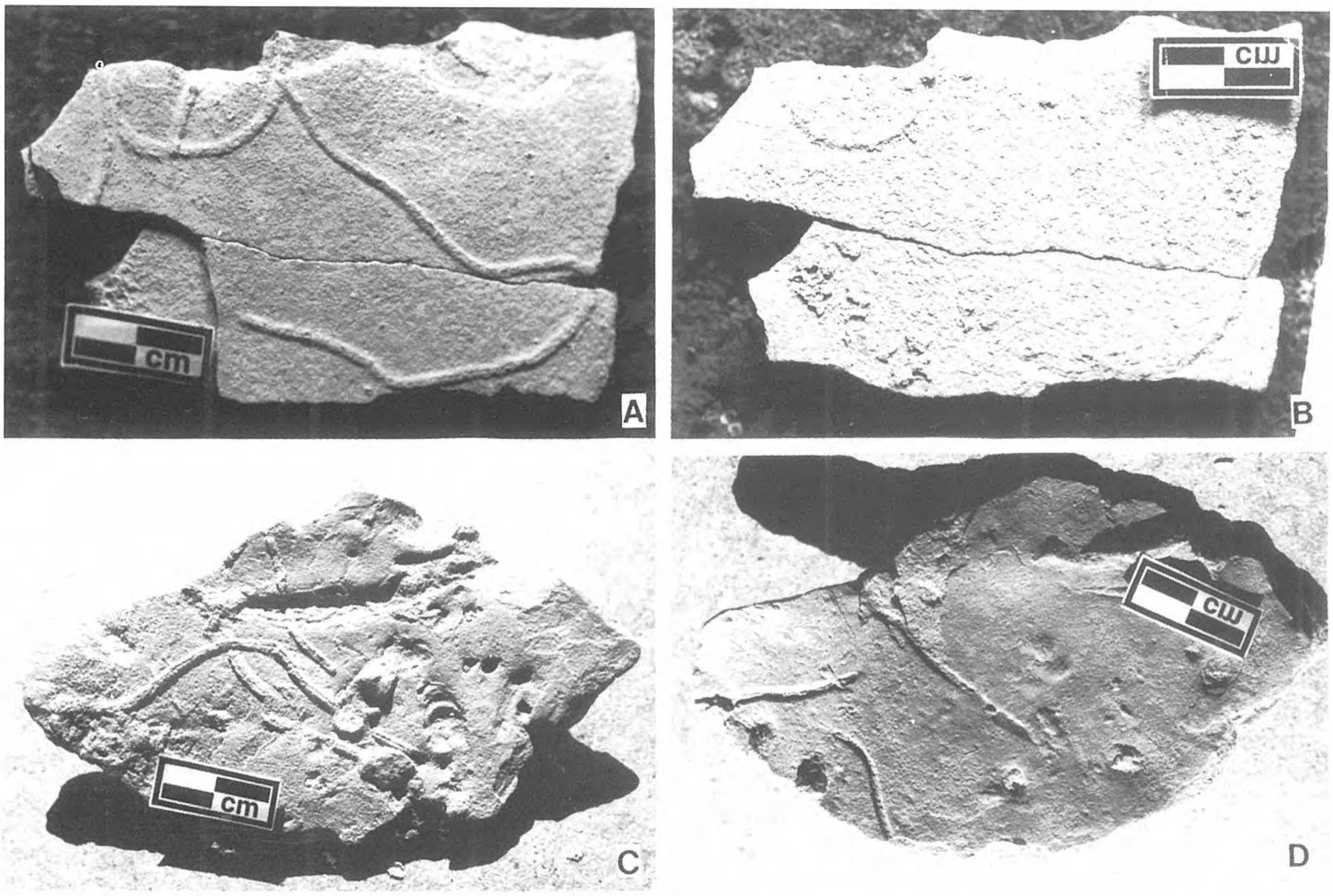

Figure 7. *Gyrochorte* from the Pliocene of Spain. **A-B.** Epirelief (A) and corresponding hyporelief (B) (UUIC 1029). **C-D.** Epirelief (C) and corresponding hyporelief (D). (UUIC 1030) B and D were printed in reverse to orient them in the same manner as A and C.

(*Asteriacites* or *Lockeia*). After the Late Jurassic, crustacean burrow networks (such as *Thalassinoides, Ophiomorpha* or *Sinusichnus*) were more commonly associated with *Gyrochorte*, although in some examples from the literature, it is not clear whether they occur in the same beds. The assemblages containing *Gyrochorte* are typical of the *Cruziana* ichnofacies. Hence, although individual trace fossils have to be used cautiously as paleoenvironmental indicators, *Gyrochorte* assemblages, where this trace fossil is common, can be very good indicators of nearshore and shallow marine environments, especially when considered together with the sedimentology and the associated trace fossils.

Gyrochorte is typically a post-event burrow, suggesting that its producer colonized sandy bottoms during quiet periods between high-energy events (most commonly storms). Powell (1992) suggested that *Gyrochorte* was a trace produced by an opportunistic animal. Ekdale (1985) indicated that opportunistic ichnotaxa show three main characteristics: 1) they are facies breaking, 2) their occurrences are highly localized (often in high-density isolated occurrences), and 3) the associated assemblages commonly show low diversity. These three points must be considered for *Gyrochorte*: 1) within its typical setting, *Gyrochorte* apparently has a great range of tolerance to environmental conditions, including hypersaline (Gibert and Ekdale, 1999) to hyposaline (Hallam, 1970; Gibert and Martinell, 1996) waters; 2) *Gyrochorte* occurrences usually display high density of the trace fossil; although this could be the result of a single very active animal moving through the sediment, the common occurrence of burrows of different sizes together (e.g., Fig. 3.A) suggests that this was not the case; 3) the assemblages containing *Gyrochorte* range from monospecific (e.g., Powell, 1992) to diverse (e.g., Dam, 1990). Thus, *Gyrochorte* partly complies with the three conditions pointed out by Ekdale (1985), and it can be considered to be the trace fossil of an opportunistic animal. The common presence of *Gyrochorte* in association with storm beds also supports the hypothesis that its producer was an opportunistic species adapted to the colonization of newly deposited sandy substrates after high energy depositional events.

CONCLUSIONS

1. The record of Lower Ordovician and Lower Pliocene *Gyrochorte* extends its known stratigraphic range at both ends. However, its stratigraphic record is

AUTHORS	AGE AND LOCATION	PALEOENVIRONMENT
Gibert & Martinell 1996, this paper	Lower Pliocene, Spain	bay (low salinity)
This paper	Upper Cretaceous, Utah	delta mouth bar
Pemberton & Frey 1984	Upper Cretaceous, Alberta	storm-influenced shelf
Zhou 1997	Lower Cretaceous, Tibet	shallow marine
Heinberg 1973	Lower Cretaceous, Greeland	shallow marine
Badve 1987	Lower Cretaceous, India	shallow sublittoral
Shringarpure 1984	Jurassic-Cretaceous, India	
Howard & Singh 1985	Upper Jurassic-Lower Cretaceous, India	nearshore, lagoonal and shallow shelf
Poiré 2001	L. Jurassic-L. Cretaceous, Argentina	storm deposits
Schlirf 2000	Upper Jurassic, France	mid to outer ramp
García-Ramos & Valenzuela 1979	Upper Jurassic, Spain	coastal to shallow marine
Fürsich 1974, 1975	Upper Jurassic, England and France	shallow marine
Kumar 1979	Upper Jurassic, India	shallow marine
Kulkarni & Ghare 1991	Middle-Upper Jurassic, India	shallow marine
This paper	Middle Jurassic, Utah	shallow marine (hypersaline?)
Hallam 1970	Middle Jurassic, England	marginal marine (low salinity)
Fürsich 1998	Middle Jurassic, India	low to intermediate energy ramp
Heinberg & Birkelund 1984	Middle Jurassic, Greenland	upper offshore
Powell 1992	Middle Jurassic, England	shoreface
Karaszewski 1973	Middle Jurassic, Poland	shallow marine
Weiss 1941	Middle Jurassic, Germany	
Dam 1990	Lower Jurassic, Greenland	storm-dominated shelf
Häntzschel & Reineck 1968	Lower Jurassic, Germany	shallow marine
Mayer 1980	Middle Triassic, Germany	
Stanley 1994, Stanley & Pickerill 1998	Late Ordovician, Ontario	storm-dominated shelf
This paper	Lower Ordovician, Utah	storm- dominated subtidal

Table 1. Reported occurrences of *Gyrochorte*.

very discontinuous. No *Gyrochorte* are known between the Ordovician and the Triassic, nor between the Cretaceous and the Pliocene.

2. The identity of the trace maker remains unknown, although it was most likely an annelid.

3. The paleoenvironmental record of *Gyrochorte* is restricted to moderate energy nearshore and shallow marine environments.

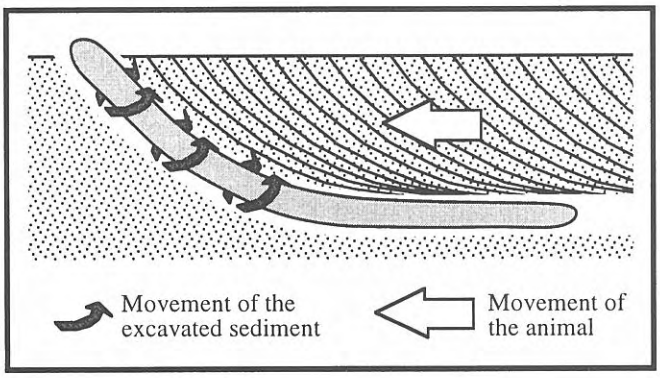

Figure 8. Model for the construction of *Gyrochorte* by a worm-like animal.

4. *Gyrochorte* probably was produced by an opportunistic animal colonizing sandy bottoms after high energy event deposition.

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APPENDIX 1: LOCALITIES

Skull Rock Pass

This site is located in the southern part of the House Range, approximately about 70 km southwest of the town of Delta, in western Utah. The section corresponds to the informal "light-gray ledge forming member" (Hintze, 1951, 1973) of the Lower Ordovician Fillmore Formation (Ibexian, equivalent to the Upper Tremadoc-Lower Arenig following Hintze, 1988).

Fossil Mountain

Fossil Mountain is located in the southeastern part of the Confusion Range, about 24 km southwest of Skull Rock Pass in western Utah. *Gyrochorte* was found in the Lower Ordovician Kanosh Shale Formation (lower Whiterockian, equivalent to the Upper Arenig following Hintze, 1988).

Nephi

Gyrochorte occurs in the Middle Jurassic Arapien Shale (Bathonian-Callovian) in Salt Creek Canyon, which is located west of the town of Nephi in central Utah.

San Rafael Swell

The specimens were obtained from the Middle Jurassic Carmel Formation (Bajocian-Bathonian) on the western side of the San Rafael Swell in central Utah. The studied outcrops are located in the intersection between Highway I-70 and a small dirt road known as the Moore road.

Gunlock

A few specimens were collected from the Carmel Formation (Bajocian-Bathonian, Middle Jurassic) in the Beaver Dam Mountains west of Gunlock in southern Utah.

Hanna

The section of the Twin Creek Limestone (Bajocian-Bathonian, Middle Jurassic) in the town of Hanna in the southern Uintah Mountains, northern Utah, also provided a few specimens of *Gyrochorte*.

Spring Canyon

The Storrs Member of the Star Point Formation (Campanian, Upper Cretaceous) has yielded abundant specimens of *Gyrochorte* in Spring Canyon, west of Helper in central Utah.

Sant Onofre

The locality of Sant Onofre is located in a clay quarry about 15 km south of Tortosa (province of Tarragona, Spain). *Gyrochorte* was found in the informal Campredó Blue Clay Unit of Arasa (1990) (Zanclean, Lower Pliocene).