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 estratigráfico 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 detrítívoro, 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 semirelief 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 trace-maker, 3) to analyze its paleoenvironmental distribution, and 4) to interpret the paleoecology of the trace-maker.

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
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 curve, but more rarely it can be straight or gently curved. It is typically preserved as ephichnial 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 Ichthyology Collection (UUIUC). Specimens from eight localities have been studied: Skull Rock Pass, Lower Ordovician, Utah (UUIUC 1034-1037, 1073); Fossil Mountain, Lower Ordovician, Utah (UUIUC 648-649); Nephi, Middle Jurassic, Utah (UUIUC 984-1022, 1024); San Rafael Swell, Middle Jurassic, Utah (UUIUC 961, 963, 965, 1056-1057); Gunlock, Middle Jurassic, Utah (UUIUC 1025-1027); Hanna, Middle Jurassic, Utah (UUIUC 1028); Spring Canyon, Upper Cretaceous, Utah (UUIUC 1031-1033); Sant Onofre, Lower Pliocene, Spain (UUIUC 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 epirelief with their corresponding hyporelief in sandstone or grainstone layers between a few millimeters 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. 2A-2B). 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 semirelief on intermediate laminae between the epirelief and hyporelief of the same specimen (Fig. 7A). 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 epirelief exhibit frequent sudden changes in direction that are absent or less pronounced in the corresponding hyporelief, which usually show less winding morphologies (Figs. 3C-3F, 4E-4F). Figure 5 shows the differences between the hyporelief and epirelief of some Jurassic specimens. Crosscutting is common in all of the material. The lobes in most epirelief 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. 4A, 4B). The hyporelief occasionally show the meniscus-like structures (Figs. 4D, 4F), but they are more commonly smooth.

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 epirelief and their corresponding concave hyporelief 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 hyporelief. 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 (Mascotay, 1967; Ksiazkiewicz, 1970, 1977; Pickrell, 1980; Crimes et al., 1981). Frey and Chowny’s (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; Hantzschel, 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 ichnotaxonbase, and if used, size criteria require some sort of statistical data to support them (Pickrell, 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 hyporelief 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...
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 ichnotaxonbase 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. 2A, 2B).
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 epirelief compared to the corresponding hyporelief 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 oblique-burrowing worm interpretation has been followed by most later authors (e.g., Pemberton and Frey, 1984; Dam, 1990; Powell, 1992).
Ordovician *Gyrochorte* that is intergradational with *Planolites* (see also figure 1.3, p. 24 in Pickerill, 1994).

If the assignment of a possible trace maker 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 *Thalassinoidea, Planolites, Teichichnus, Chondrites, Phylocodes* and *Gyrochorte*. *Gyrochorte comosa* occurs in the facies designated by Dattilo (1993) as “calciisiltite and calcilutite”. 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 (Inlay, 1980).

The section in Nephi consists of evaporites, micritic carbonates and mixed carbonate-clastic grainstones of the Arapien Shale. Picard and Uygar (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
this facies are Planolites, Lockeia, Palaeophycus, Nerites, 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, Protovaginula, and Teichichnus.

Small 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 Nielsen (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 Nerites, 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 mound 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 irregulare, Chondrites, and Cylindricalichnus. 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 Domènec, 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 abundant in certain beds. Gyrochorte is found in association with Teichichnus, Sinusichnus, and more rarely Nerites and Scolecia (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, Nerites or Curvolutus), but also fodinichnia (such as Teichichnus, Chondrites or Phycodes) and cubichnia
(Asteriacites or Lockeia). After the Late Jurassic, crustacean burrow networks (such as Thalassinooides, 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
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.

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 1-70 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 Tarragona (province of Tarragona, Spain). *Gyrochorte* was found in the informal Campredó Blue Clay Unit of Arasa (1990) (Zanclean, Lower Pliocene).