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Behavioural variants of the trace fossil *Gyrochorte*

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Abstract

The trace fossil *Gyrochorte* is common in Upper Jurassic siliciclastic rocks of the Kachchh Basin, western India. In the Kimmeridgian Katrol Formation, *Gyrochorte comosa* Heer, 1865 is tied to storm-generated fine-grained sandstones and exhibits an internal structure composed of double arches in cross-section, confirming the three-dimensional nature of the trace fossil and its interpretation as produced by a deposit-feeder moving obliquely through the sediment. In the Tithonian to Lower Cretaceous Umia Formation, *Gyrochorte* occurring in thin-bedded, ripple-laminated medium-grained sandstones displays a range of morphological features connected with the sideway exploitation of the substrate (formation of fans) and variations in the degree to which the producer occupied an upright or forward inclined position within the sediment. The morphological expressions of these behavioural variants are subsumed in the new ichnospecies *Gyrochorte variabilis*.

Key words: trace fossils, ethology, Upper Jurassic, Lower Cretaceous, Kachchh Basin

Zusammenfassung

Das Spurenfossil *Gyrochorte* ist in oberjurassischen siliziklastischen Gesteinen des Kachchh-Beckens, westliches Indien, weit verbreitet. In der Katrol-Formation (Kimmeridge) tritt *Gyrochorte comosa* Heer, 1865 in feinkörnigen Sandsteinen auf, die durch Sturmereignisse abgelagert wurden. Die Internstruktur der Spur besteht im Querprofil aus nach oben gerichteten Doppelbögen. Sie untermauern die Interpretation der Spur als dreidimensionale, mauerartige Spur eines schräg durch das Sediment wandernden Sedimentfressers. In der Umia-Formation (Tithon bis Unterkreide) tritt *Gyrochorte* in dünnbankigen rippelgeschichteten mittelkörnigen Sandsteinen auf und zeigt eine Reihe morphologischer Merkmale, die teils auf seitliche Durcharbeitung des Substrats (Bildung von Fächern) zurückgehen, teils auf die unterschiedliche Position des Erzeugers im Sediment (senkrecht oder schräg nach vorne geneigt). Diese morphologischen Variationen werden im Spurenfossil *Gyrochorte variabilis* isp. nov. zusammengefasst.

Schlüsselwörter: Spurenfossilien, Ethologie, Oberjura, Unterkreide , Becken von Kachchh

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1. Introduction

Gyrochorte is an easily recognised, widespread trace fossil in Jurassic siliciclastic shallow-water environments (e.g., Häntzschel & Reineck 1968; Hallam 1970; Heinberg 1973; Karaszewski 1973; Fürsich 1974, 1998; Kulkarni & Ghare 1991; Schlirf 2000; Gibert & Benner, 2002; Seilacher 2007). The ribbon-shaped trace, separated by a median furrow and, when well preserved, with V-shaped ornamentation (plaits), most commonly occurs as positive epirelief on rippled surfaces and as negative hyporelief. In both cases the trails trace the morphology of the surface. Weiss (1940, 1941) assumed that *Gyrochorte* is a horizontal trail of a deposit-feeding worm-like organism, even though he recognised the distinct three-dimensional nature of the trace fossil and the upward displacement of sediment. The most likely explanation of the morphology (and thus of the behaviour) displayed by *Gyrochorte* was put forward by Heinberg (1973), who found specimens in the Jurassic of East Greenland that showed internal structures connecting the upper and lower surface expression of the trace fossil. He interpreted the three-dimensional structure as the expression of an organism moving obliquely through the sediment in search of food, whereby the producer displaced the sediment backwards and, at the same time, also a small distance upwards. *Gyrochorte* is characteristically preserved at internal surfaces of thin-bedded heterolithic sediments. Its distribution pattern may therefore be biased: occurrences in thicker sand- or siltstones as full relief stand no chance to be recognised, as the internal structures are generally not preserved.

Gyrochorte is abundant at some levels in Upper Jurassic strata of the Kachchh Basin of western India offering features that deserve to be documented. These are the three-dimensional preservation in the Kimmeridgian Katrol Formation and a behavioural variant that occurs in sandstones of the Tithonian to Lower Cretaceous Umia Formation. The latter is accommodated in a new ichnospecies, *Gyrochorte variabilis* isp. nov.

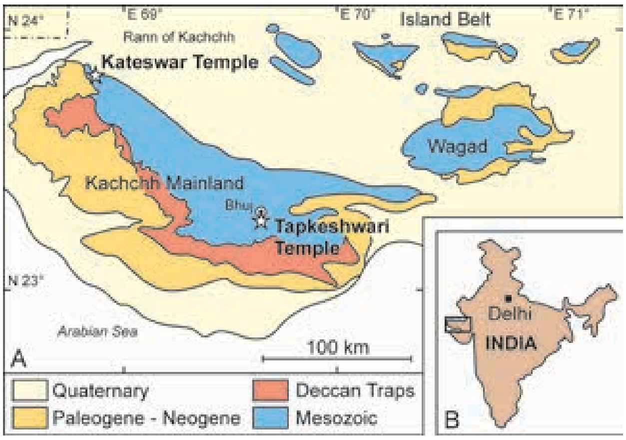

Figure 1: Localities of *Gyrochorte* discussed in this paper.

2. Material

Several slabs from the Katrol Formation from the ridge west of the Bhuj-Tapkeshwari Temple road, north of the Tapkeshwari Temple (co-ordinates: N23°10´57´´, E69°40´03´) and from the Umia Formation ESE of Kateswar Temple (N23°46´18.8´´, E68°53´35.1´´; Fig. 1). The material is partly stored in the collections of the Department of Geology, University of Rajasthan (RUC2016I Ka-1) and in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie, Munich (SNSB-BSPG 2016 I 22-24). In addition, numerous observations were made in the field.

3. *Gyrochorte comosa* Heer, 1865 in the Kimmeridgian Katrol Formation

In many areas of the Kachchh Basin the Kimmeridgian Katrol Formation consists of a predominantly fine-grained (argillaceous-silty) bioturbated lower part, into which parallel-laminated and less commonly ripple-laminated fine-grained sandstones are intercalated up-section. Towards the top of the formation, sandstones dominate, in which hummocky-cross-stratification (HCS) becomes increasingly prominent. This top part of the formation is well exposed on the ridge NNE of the Tapkeshwari Temple (Fig. 2). It is in all three types of sandstones (parallel-laminated, with oscillation ripples and with HCS) that *Gyrochorte comosa* is common, forming curved bilobate ribbons on both upper surfaces (as positive epireliefs; Fig. 3A) and lower surfaces (as negative hyporeliefs; Fig. 3B). In contrast to the “classical” *Gyrochorte*, plaits are only rarely developed but fine striations forming a wide V are occasionally seen. As is generally the case in *Gyrochorte* the lower surface counterparts do not exactly mirror the upper surface expression indicating that the organism not only occupied an oblique position when moving forward but, at the same time, was also inclined to some extent sidewise.

At some levels, the sediment between the upper and lower expression of the trace fossil is clearly disturbed (Fig. 4A), a sign that this zone has been reworked by the organism producing the trace fossil. This slightly oblique zone is 12 mm wide and displays a double-arched internal structure, particularly well visible at internal partings. In thin-sections (Fig. 4B) these convex-upward directed double arches are closely packed and document an upward displacement of sediment for 2 mm. Similar double-arched structures are also seen in the neighbouring sediment (Fig. 4B). Thus, it appears that the producer of *Gyrochorte* also mined the surrounding sediment without producing the characteristic convex-up epirelief on the bedding plane.

4. *Gyrochorte* in the Tithonian to Lower Cretaceous Umia Formation

Gyrochorte occurs at some levels within the Umia Formation ESE of the Kateswar Temple. In this section, the Umia Formation starts with a highly ferruginous condensed unit called the Umia Ammonite Beds. They correspond to the maximum flooding zone of a third-order cycle. Near the top of the highstand systems tract of this cycle and in the transgressive systems tract and highstand systems tract of the following cycle, *Gyrochorte* is encountered in thin (4-7-cm-thick), maroon, poorly sorted, medium-grained sandstone with oscillation ripples (Fig. 5; see also Fürsich & Pandey 2003: fig. 8, there erroneously called *Syringomorpha*). Apart from the typical double ridge seen on upper bedding planes the producer applied a different programme to exploit the sediment for food which resulted in a different morphology, described in detail in the following.

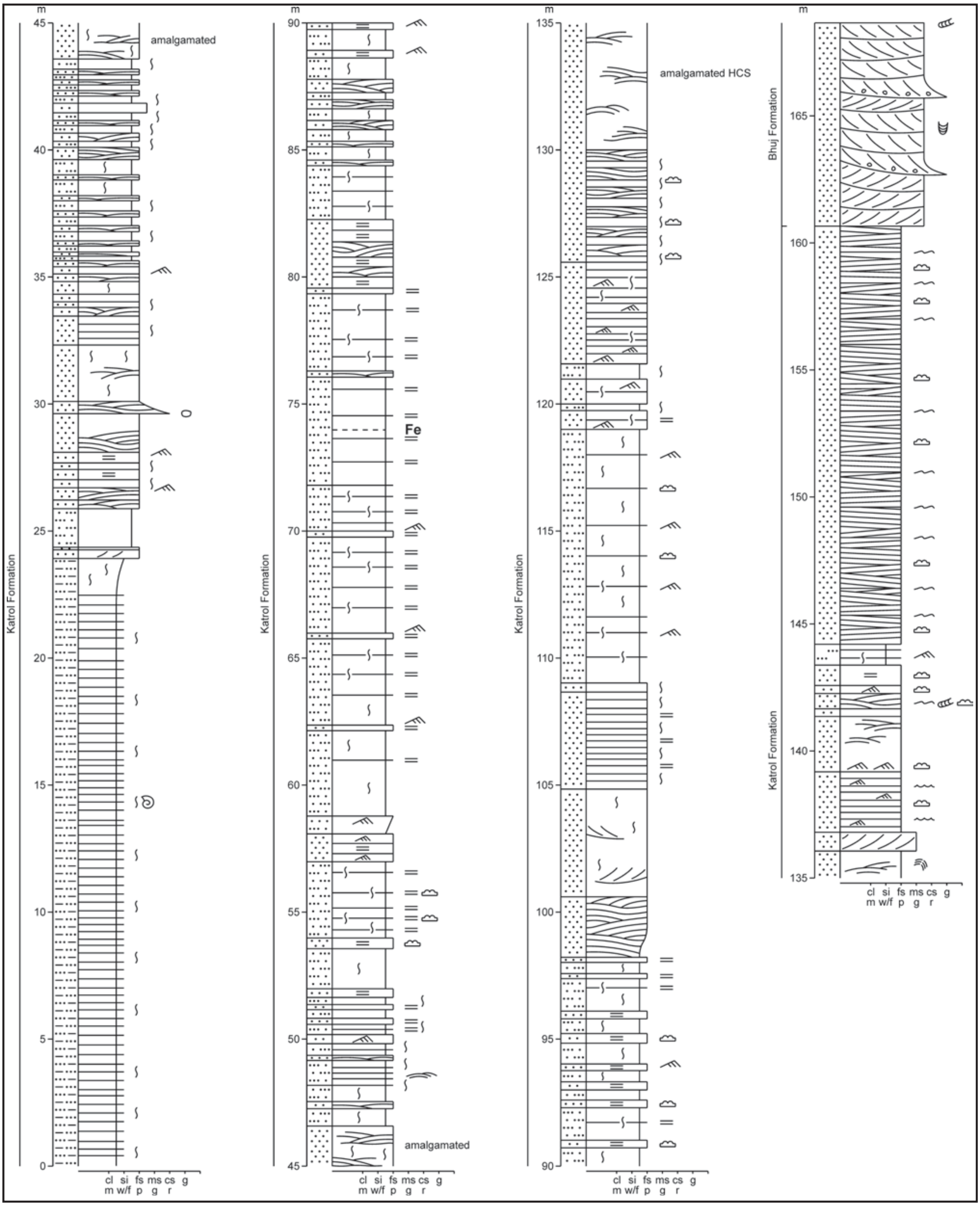

Figure 2: Section through the Katrol Formation north of the Tapkeshwari Temple. *Gyrochorte comosa* Heer, 1865 is particularly common in the upper, storm-dominated part of the succession. For key of symbols see Fig. 5.

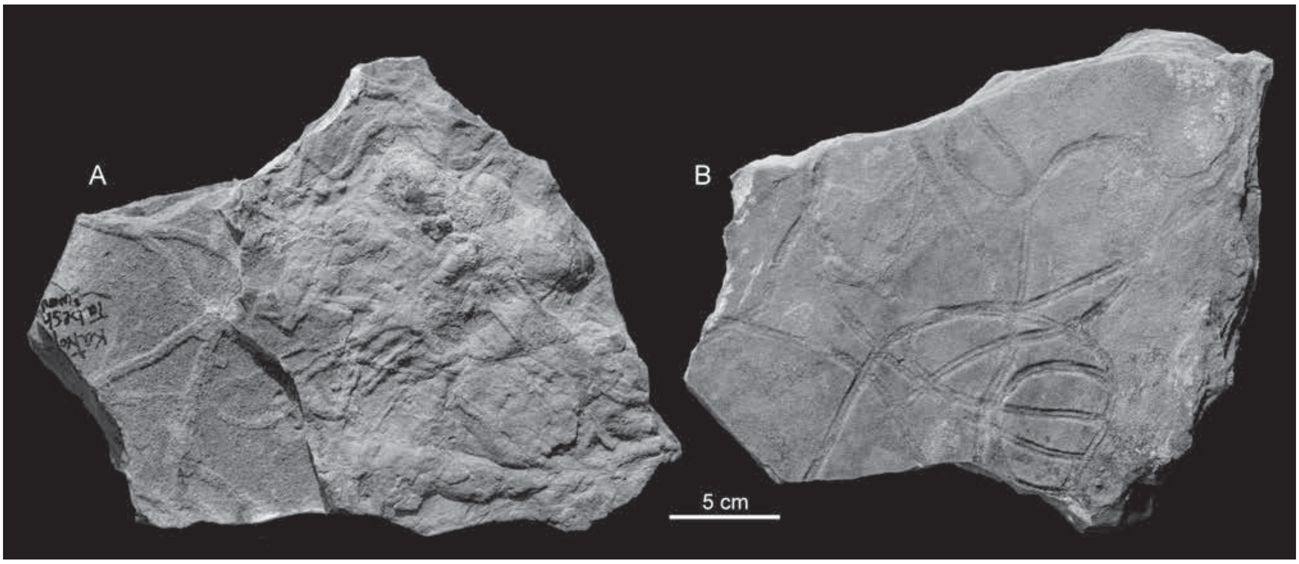

Figure 3: *Gyrochorte comosa* Heer, 1865 in fine-grained sandstone of the Katrol Formation; ridge north of the Tapkeshwari Temple. A. Upper surface view. B. Lower surface view.

4.1 Morphology

The largest slab available for study (Fig. 6) is 5 cm thick and roughly 35 x 45 cm in size. On its irregular lower surface, there are large flute casts, positive hyporeliefs of simple horizontal burrows, 7 mm in diameter (*Planolites* isp.) and indistinct positive hyporeliefs 15-17 mm in diameter, which possibly represent *Thalassinoides* networks. Seen are also negative bilobate reliefs of *Gyrochorte*, but in much lower abundance than on the upper surface. On the upper surface there are asymmetric ripple marks with a crest-to-crest distance of 15 cm.

On the upper surface different morphological expressions of *Gyrochorte* can be seen. The “classical”, curved to winding bilobate ribbon with either irregular plaits, fine transverse striations or smooth surface (=*Gyrochorte comosa* Heer) is comparatively rare (Type 1; Fig. 7A). The positive reliefs are 3.6 to 7.1 mm in width. This “classical” development can change into pairs of elongated oblique pads, which are serially arranged along the axis of the ribbon and separated by narrow depressions (Type 2; Fig. 7A, C). These depressions consist of darker, more fine-grained material which apparently weathered more easily. The “normal” bilobate ribbon may also change into a ribbon, in which the median depression is still visible, but the two parts consist of closely packed, aligned elongated pads, 1 mm in diameter. These pads are obliquely arranged with respect to the long axis of the ribbon, whereby no V-shaped arrangement is present but on both parts of the ribbon the pads point in the same direction (Type 3; Fig. 7C). Another variant is that the bilobate ribbon changes into obliquely arranged elongated rounded ridges, 2 mm in diameter, in which the bilobate arrangement gets gradually lost (Type 4; Fig. 7B). The ridges extend for about 15 mm and are separated from each other by thin interstices consisting of finer-grained material.

A final variant of *Gyrochorte* shows a fan-like arrangement of elongated rounded bilobate ridges whereby individual ridges reach a length of several tens of mm (Type 5; Figs. 8, 9). In Fig. 8 the fan is bordered on one side by a shallow, rounded groove, 4 mm in width. Although the coarse nature of the sediment makes it difficult to recognise further details, the ridges and the groove between them appear to be composed of faintly visible oblique to transverse pads. In some specimens (e.g., Fig. 9) the grooves are rounded and of the same width (1.5-2 mm) as the equally rounded ridges. Due to the strict parallel arrangement of ridges and grooves, the bilobate nature is no longer apparent. Both ridges and grooves are crossed by faintly visible, obliquely arranged ridges.

As all variants of the trace fossil are present at different levels of the bedding plane (i.e. follow the contour), they must be interpreted as three-dimensional structures.

4.2 Taxonomic consequences

As the different morphological expressions seen on the bedding plane are all connected to classical *Gyrochorte*, it is quite clear that they should be attributed to this ichnogenus. The high morphological variability of the trace fossil, documenting behavioural variants deviating from that of *Gyrochorte comosa* Heer, 1864, requires, however, that the *Gyrochorte* specimens from the Umia Formation of Kateswar to be accommodated in a new ichnospecies. As these morphologies occur at several levels within the section, they are clearly not a “freak” occurrence but represent a characteristic, probably genetically fixed, behaviour pattern of the trace fossil producer.

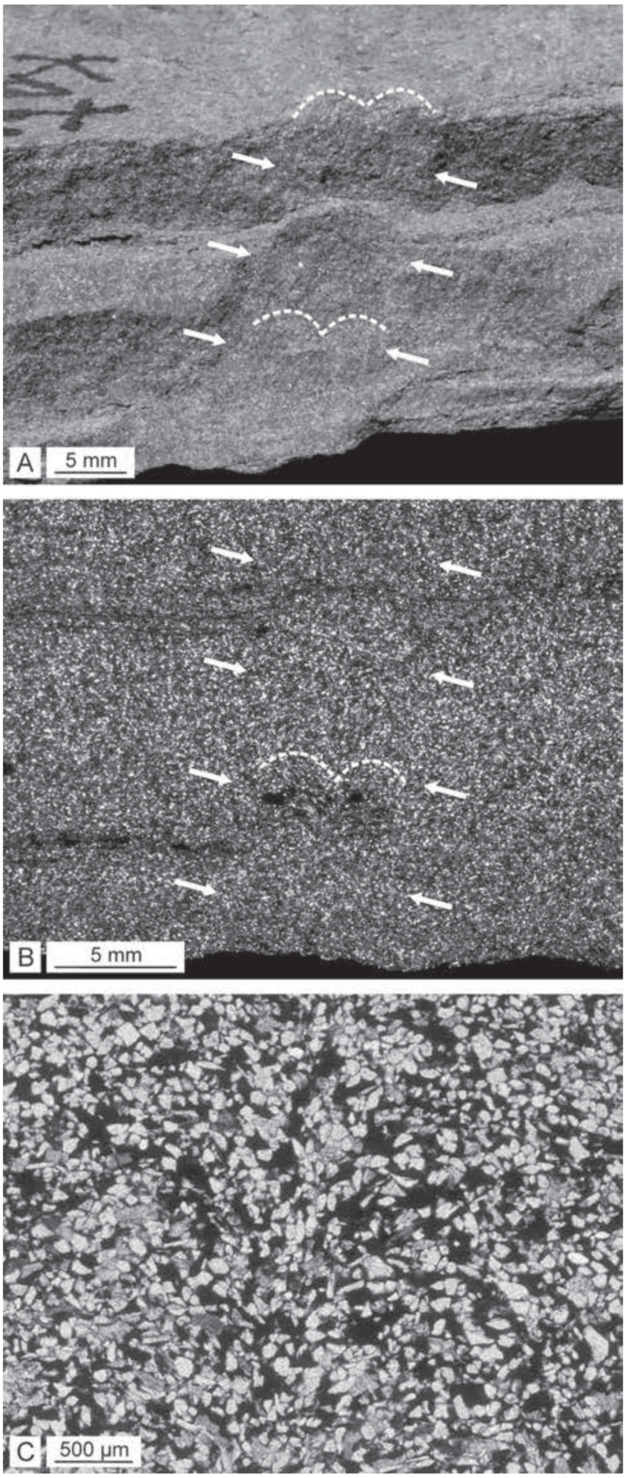

Figure 4: *Gyrochorte comosa* in fine-grained sandstone of the Katrol Formation at the Tapkeshwari Temple section. **(A)** Cross-section of the bioturbated area (arrowed) between upper surface (positive epirelief) and corresponding lower surface expression (negative hyporelief) clearly indicates that both are part of a single trace fossil. **(B)** Thin-section through the specimen in A exhibiting the double-arched internal structure (arrowed) of *Gyrochorte*. Note that such structures occur also in the neighbouring sediment, suggesting that bioturbation of the sandstone by the *Gyrochorte* producer was more pervasive than documented by the surface expressions of the trace. **(C)** Enlarged area of B shows the non-random arrangement of quartz grains.

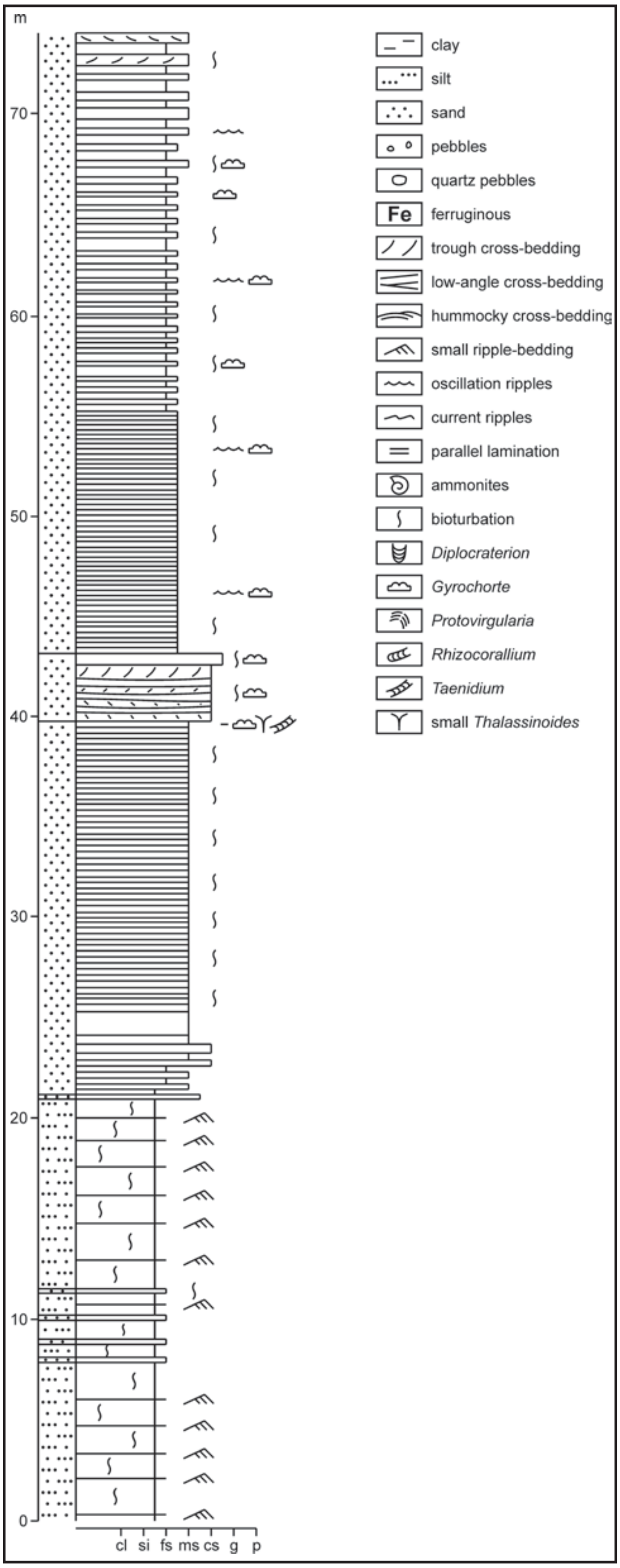

Figure 5: Lithology through the middle part of the Umia Formation ESE of the Kateswar Temple with horizons of *Gyrochorte variabilis* isp. nov.

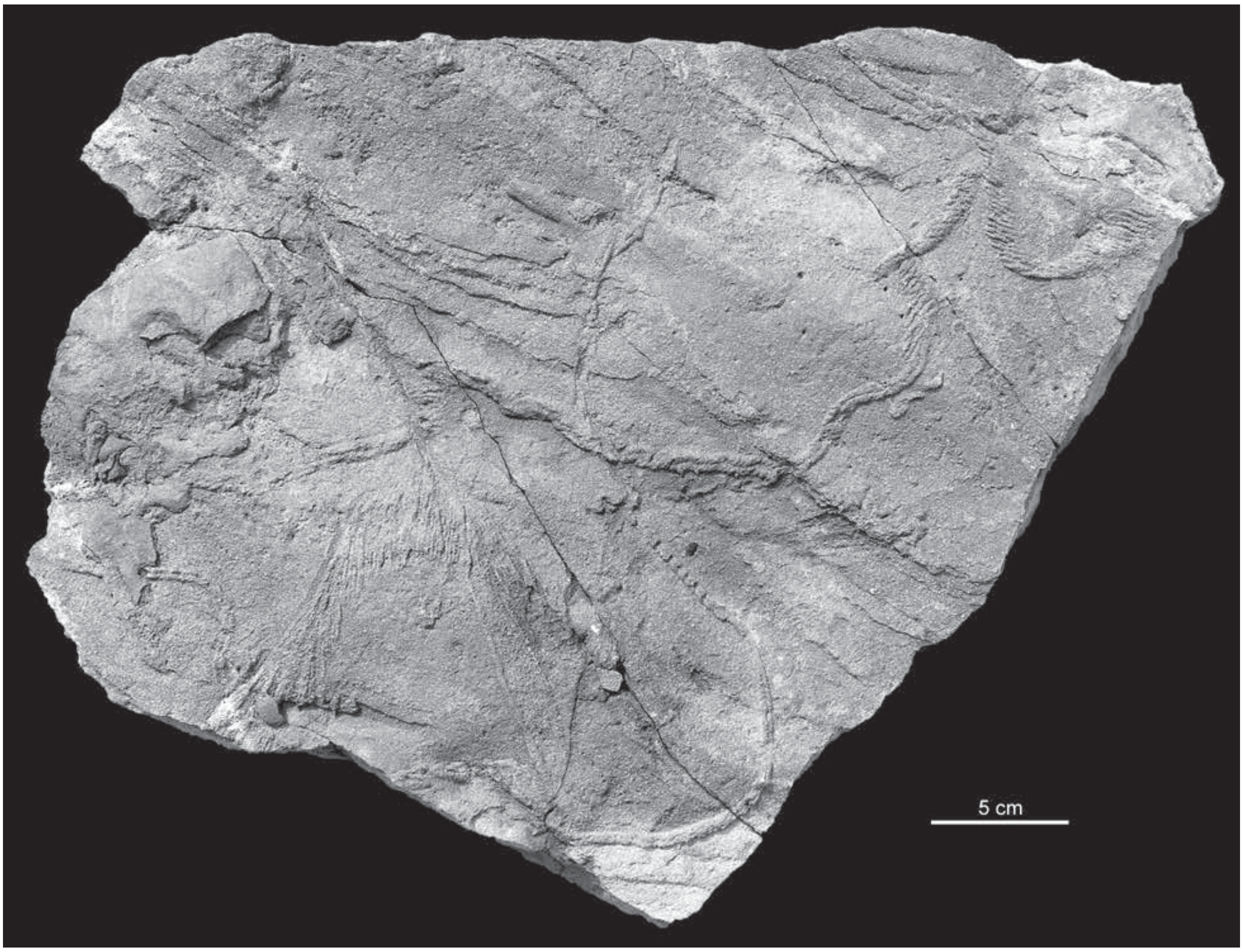

Figure 6: Different morphological expressions of *Gyrochorte variabilis* isp. nov. Holotype RUC2016I Ka-1, upper surface view; Umia Formation ESE of the Kateswar Temple.

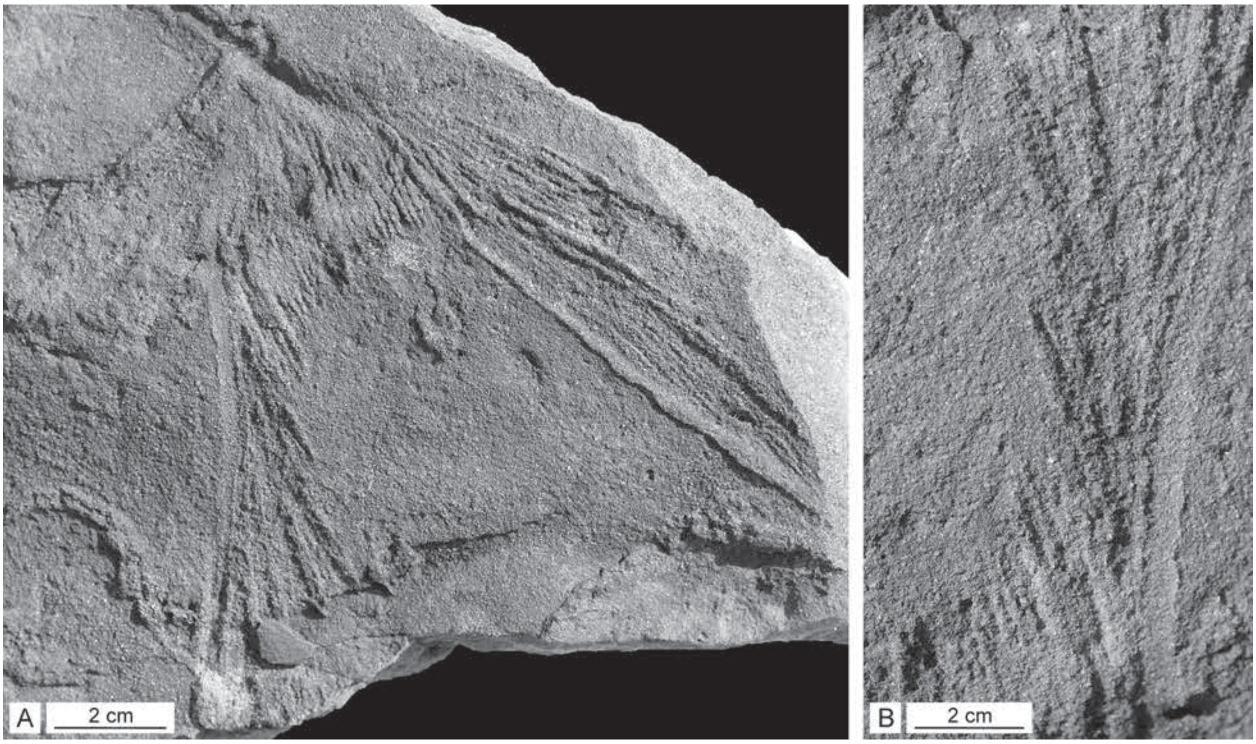

Figure 8: Fan-like expression of *Gyrochorte variabilis* isp. nov. on the upper bedding plane. Umia Formation, ESE of the Kateswar Temple (details of the holotype). A. The fan consists of bilobate ridges. The rounded groove, which forms the latest part of the fan, possibly was created when the organisms withdrew its body before constructing a new ray. B. Detail of A, showing indistinct bilobate ribbons crossed by faint transverse to oblique ridges.

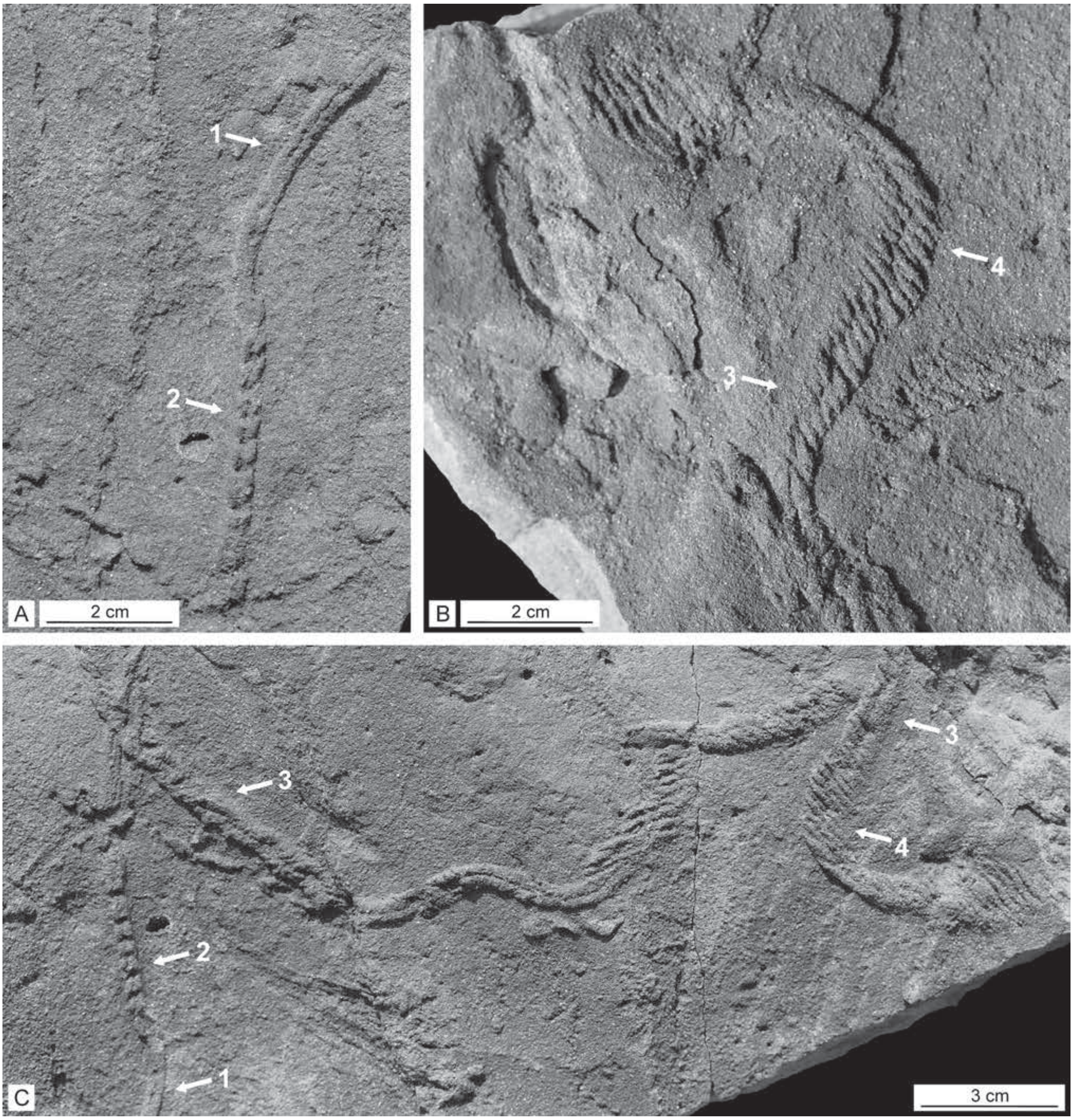

Figure 7: Morphological expressions of *Gyrochorte variabilis* isp. nov. from the Umia Formation of the Kateswar Temple section. Details of the holotype, upper surface view. **(A)** Transversely striated bilobate ribbon (Type 1) grading into paired, slightly elongated pads (Type 2). **(B)** Biserially arranged, elongate oblique pads (Type 3) gradually increase in length with the median furrow becoming very indistinct and irregular (Type 4). **(C)** Morphological expressions of types (1) to (4).

Figure 9: Part of a fan-like expression of *Gyrochorte variabilis* isp. nov. on the upper bedding plane. Umia Formation, ESE of the Kateswar Temple. The rounded ridges and grooves are of equal width and are crossed by faint, thin, oblique ridges (SNSB-BSPG 2016 I 22).

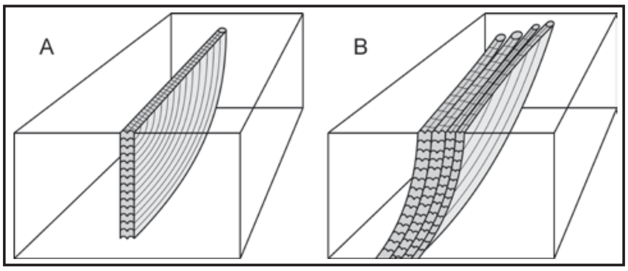

Figure 10: Sketch of the orientation of the three-dimensional wall-like *Gyrochorte*. A. *Gyrochorte comosa* Heer, 1865. B. Fan-like *Gyrochorte variabilis* isp. nov.

Gyrochorte variabilis isp. nov.
Figs. 6-11

Material: Six slabs of variable sizes from the Umia Formation ESE of the Kateswar Temple. Holotype: Slab RUC2016I Ka-1, displaying most of the behavioural patterns of the new ichnospecies. Paratype: Slab SNSB-BSPG 2016 I 22.

Etymology: Variabilis (Latin), variable. Named after the high morphological variability of the ichnospecies.

Diagnosis: *Gyrochorte* in which the bilobate ribbon, preserved as positive epirelief, changes into several different morphological expressions. These include (a) pairs of elongated oblique bulges, which are serially arranged along the axis of the ribbon and separated by narrow depressions, (b) short, obliquely arranged elongated bulges with respect to the long axis of the ribbon, (c) elongated, parallel ridges, arranged obliquely with respect to the long axis of the ribbon and with or without median groove, and (d) fan-like arranged rounded ridges, which are closely aligned, separated by grooves, or split into pairs. Ridges display an arcuate internal structure.

Description: See section 4.

Discussion: The behaviour of *Gyrochorte comosa* Heer, 1865 i.e., oblique movements of an elongated organism through the sediment thereby displacing sediment backward and upward, has been undoubtedly documented by Heinberg (1973) in material from the Upper Jurassic of East Greenland (Fig. 10A). There, the orientation of mica flakes revealed double-arch structures that connect the negative hyporelief with the positive epirelief and confirmed the interpretation of Weiss (1940, 1941). *Gyrochorte variabilis* isp. nov. also shows this morphology but more commonly displays distinct modifications of the original feeding behaviour (Figs. 7-9, 11). Such behavioural variants have been noticed also earlier on by some authors. For example, Weiss (1940: pl. 14, figs. 1, 3) figured short lateral displacements of the ribbon, which he called "brushes". Seilacher (2007: 100, pl. 35) called such behaviour "fanning". In both cases, the fans are much smaller than the structures seen in Fig. 8.

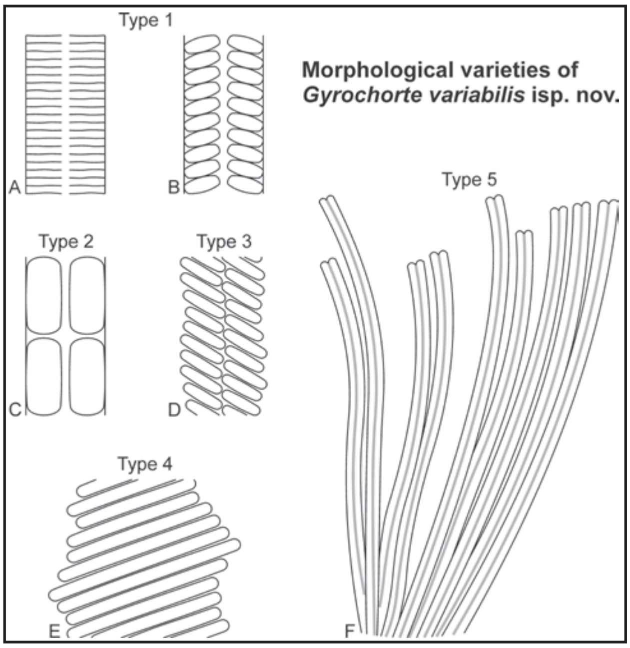

Figure 11: Sketch of the different morphological bedding-plane expressions of *Gyrochorte variabilis* isp. nov. Type 1: predominantly transverse ridges and biserially arranged pads. Type 2: biserially arranged pads, elongated in the direction of the ribbon and oblique with respect to the horizontal plane. Type 3: biserially arranged elongated pads, long axis of pads forming an angle with the direction of the ribbon. Type 4: Elongated pads forming an oblique angle with the direction of the ribbon (Fig. 7C). A biserial arrangement is no longer visible. Type 5: fan-like arrangement of bilobate rays. Types 3 to 5 are stages of a morphological continuum.

The fans appear to have been produced by the lateral movement of at least the front part of the elongated producer, most likely a worm-like organism or arthropod (see below). This probably resulted in the oblique to curved arrangement of the wall-like bioturbated zone (Fig. 10B). The shallow, rounded groove, 3 mm in width, which forms the last expression of the fan in Fig. 8 and which exhibits faint transverse striations, might represent the impression of the terminal part of the body due to the shift of the producer to a higher level (for an alternative, more likely explanation, see below). The features of the fan suggest that the organisms mined the sediment for food for some distance and then withdrew its body to construct a new ray of the fan. This withdrawal must have occurred at a lower level than the present bedding plane as otherwise the rays would not preserve features of the forward movement of the producer. In contrast, the shallow, rounded groove preserved at the end of the fan might, in fact, be the trace of such a withdrawal of the body at the level of the bedding plane.

The reason for the construction of fans may be the preferred exploitation of areas within the sediment particularly rich in organic detritus, which resulted in the different behaviour pattern displayed by *Gyrochorte variabilis*. The elongated pads obliquely arranged with respect to the long axis of the ribbon, in which the biserial arrangement is still visible (Type 3; Fig. 7B, C), probably are the initial step of the development of such fans.

Other, minor modifications of the behaviour pattern seen in the material from the Umia Formation (Fig. 11) are related to the position of the producer within the sediment, i.e. whether more or less vertical or forward inclined, which apparently varied considerably in the investigated material.

There is a general agreement that the producer of *Gyrochorte* was a worm-like organism, most likely an annelid (e.g., Weiss 1941; Heinberg 1973; Gibert & Benner 2002), whereas Heinberg & Birkelund (1984) suggested a caudofoveate aplacophoran. Seilacher (2007) identified the producer of *Gyrochorte* as a polychaete which used its parapodia to sort the sediment for food. This interpretation is followed here. The width of the shallow groove in Fig. 8 (3 mm) most likely corresponds to the diameter of the worm-like body.

5. Conclusions

(1) Specimens of *Gyrochorte comosa* Heer, 1865 from the Kimmeridgian Katrol Formation support the three-dimensional nature of the trace fossil by a double-arched internal structure, seen in cross-section, connecting bedding plane expressions (negative hyporelief and positive epirelief).

(2) *Gyrochorte variabilis* isp. nov. from the Tithonian Umia Formation exhibits a wide range of morphological features which are the expression of a behaviour pattern in which exploitation of the sediment for food occurred not only in one direction (forward) producing a ribbon-like structure, but also sideways, i.e. at an angle with the general direction of movement of the producer. This results in fan-like structures. The latter behaviour documents the systematic mining of a three-dimensional sediment body.

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