Morphology, ethology and taxonomy of the ichnogenus *Schaubcylindrichnus*: Notes for clarification

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ABSTRACT

Two recent publications dealing with the trace fossil *Schaubcylindrichnus* (Frey and Howard, 1981) in Cenozoic outcrops have been published independently in the same year (Löwemark and Hong, 2006; Nara, 2006). The two studies came to similar conclusions regarding morphology, somewhat different conclusions with respect to the behavior of the trace maker, and diametrically opposed conclusions regarding the ichnotaxonomy. The two studies (Löwemark & Hong, 2006; Nara, 2006) were published in parallel without taking the other into consideration. During the 2nd International Ichnological Congress in Krakow 2008 the authors had the opportunity to compare their results (Löwemark and Nara, 2008). We therefore feel that a clarifying note is timely.

Morphologically, *S. coronus* is shown to typically consist of three distinct parts: a bundle of thickly lined, often crossing tubes that have been constructed after each other, a feeding funnel connected to one end of the burrow system, and a fecal mound connected to the other end (Nara, 2006). Löwemark & Hong (2006) introduced a new ichnospecies, *S. formosus*, based on the differences in morphology to the original description of *S. coronus* that outlined a congruent bundle as the typical form. However, subsequent comparison of *S. formosus* with Nara's (2006) descriptions of *S. coronus* showed that the former can be accommodated in the latter. *S. formosus* therefore should be considered as a junior synonym of *S. coronus* and be abandoned.

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1. Introduction

The trace fossil *Schaubcylindrichnus* was originally envisaged to consist of a congruent bundle of thickly lined tubes that represented the result of a deposit feeding activity by the gregarious producers (Frey and Howard, 1981; Frey and Pemberton, 1991). The trace fossil was first only observed in shoreface depositional settings in certain Cretaceous strata in North America (Frey and Howard, 1981; Frey and Pemberton, 1991). However, recent studies (Löwemark and Hong, 2006; Nara, 2006) show that the trace fossil now has been found on most continents in a large variety of settings ranging from near shore to continental slope, and in strata at least from the Carboniferous to the Pleistocene.

In 2006 two separate papers addressing the morphology, ethology and taxonomy of the ichnogenus were published (Löwemark and Hong, 2006; Nara, 2006). Löwemark and Hong (2006) described sheaves of diverging, thickly lined, downward-bending (bow-shaped) tubes from Miocene sandstones in NE Taiwan, which they interpreted to be the

result of a filter feeding producer. As the observed morphological features differed markedly from the original descriptions of *Schaubcylindrichnus* (Frey and Howard, 1981; Frey and Pemberton, 1991), they considered the described type to be a new ichnospecies of *Schaubcylindrichnus*, *S. formosus*.

Nara (2006) described similar traces from Japanese formations of Cenozoic age. His studies revealed that the bow-shaped converging sheaves were associated with a funnel in one end and a mound-like structure in the other end. This led Nara to come to a somewhat different ethological explanation; the producer was a funnel feeder. Such a complex morphology differs considerably from the original description by Frey and Howard (1981). Nara (2006) also made comparative studies with the type specimens of the previously established ichnospecies of *Schaubcylindrichnus* (*S. coronus* Frey and Howard, 1981, and *S. freyi* Miller, 1995), and concluded that all the specimens actually showed a complete morphological gradation between the congruent bundles of *S. coronus* and the loose sheaves of *S. freyi*. Hence, Nara (2006) included all the schaubcylindrichnian specimens into the type ichnospecies, *S. coronus*.

Although the two studies (Löwemark & Hong, 2006; Nara, 2006) were published in parallel without taking the other into consideration, subsequent joint work has led us to some convincing conclusions. The aim of this study is to clarify the present stand of

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knowledge regarding morphology, ethology, and taxonomy of the ichnogenus *Schaubcylindrichnus* and its ichnospecies.

2. Morphology and ethological interpretation

Löwemark and Hong (2006) studied specimens from the Miocene Taliao Formation in northeastern Taiwan. They described a sheaf of bow-shaped, sand-lined tubes that typically converge to a central point in the lower, horizontal part of the burrow system. Their observations clearly differed from the original description of a sheaf of congruent tubes (Frey and Howard, 1981). On the other hand, Nara (2006) studied a number of specimens from Neogene to Quaternary strata of Japan, and described a nearly complete specimen which consisted of a bundle of bow-shaped tubes attached to a funnel and a mound at their upper ends (Fig. 1A). Through the comparison of these specimens with type materials of the two previously established ichnospecies of *S. coronus* (Frey and Howard, 1981) and “*S. freyi*” (Miller, 1995), he concluded that all the schaubcylindrichnians clearly belonged to a same ichnospecies, and therefore should be included in *S. coronus*, having priority. The previously reconstructed morphology of schaubcylindrichnian trace fossils as a J-shaped, congruent bundle of tubes were based on partially eroded specimens (Nara, 2006). Furthermore, Nara (2006) found that congruent bundles of relatively smaller, tightly packed tubes, somewhat comparable to the original description of *S. coronus*, were products by tracemakers in an early developmental stage. The difference in arrangement of the tubes, i.e., tightly packed bundle vs. loosely gathered group, was explained due to an ethological change through the trace makers' growth (Nara, 2006).

Both authors clearly noted the striking difference from the very fundamental concept of the ichnogenus *Schaubcylindrichnus*; rather than being a bundle of congruent, non-branching or crossing tubes as described by Frey and Howard (1981), the typical arrangement was found to be a converging sheaf of tubes that not seldom cross-cut each other.

The composite nature of the trace fossil noted by Nara (2006) with a funnel and a mound was not originally described from the Taiwanese localities. However, subsequent additional studies at the

two localities resulted in the identification of several sedimentary features situated in connection with the termination of the tubes (Fig. 2). These features displayed downward arching laminae and chaotic structures interpreted to be a part of collapsed feeding funnels (Fig. 2).

In the Taiwanese localities, relatively smaller, congruent sheaves of tubes like an original description of *S. coronus* are present but not common (Löwemark and Hong, 2006). Judging from the fact that the trace-bearing strata commonly suffered from intense bioturbation and no primary structure was preserved (Löwemark and Hong, 2006), such smaller sheaves, probably formed in a shallower tier, as well as the fecal mound on the sediment surface, are also interpreted to have been obliterated by bioturbation, or scoured by erosional events.

Regarding feeding habits of the tracemaker, Löwemark and Hong (2006) interpreted it to be a filter feeder, based on the overall bow- or J-shape of the tubes suggesting an open connection to the surface, the thick lining indicating prolonged use, and the high-energy environment where the Taiwanese schaubcylindrichnians were found. The composite specimen of Nara (2006) (Fig. 2A), however, showed that the trace was neither the result of mere deposit feeding nor filter feeding, but clearly represents a funnel feeding behavior. Although not initially observed in the Taiwanese setting, subsequent detailed studies revealed the presence of a few funnels as noted above (Fig. 2). In his detailed studies of the topotype material of *S. coronus*, Nara (2006) also found evidence for the presence of a funnel. Thus, the ethological explanation proposed by Nara (2006), a funnel feeder, is the most plausible (Fig. 2B).

The observation of size gradation within single bundles together with the observed branching and cross-cutting of older tubes by younger ones (Fig. 3) led both Nara (2006) and Löwemark and Hong (2006) to conclude that the originally envisaged behavior, gregarious deposit feeding, was unlikely. The size gradation within single bundles suggests that the tubes were constructed in a sequence by a growing organism rather than by a number of cohabiting producers. Furthermore, converging and crossing tubes were also observed in topotype material of *S. coronus* (Nara, 2006). Such characteristics clearly show that the tubes cannot have been in use at the same time, a strong argument against the gregariousness.

Fig. 1. A) Complete specimen showing bow-shaped, thickly lined tubes connected to a feeding funnel in one end and a fecal mound in the other. Same specimen as Nara (2006; Fig. 7). B) Drawing showing conceptual model of *Schaubcylindrichnus coronus* and its three distinct parts; the feeding funnel, the fecal mound, and the bundle of superimposed tubes. The tracemaker, a probable enteropneust (Nara, 2006), produced a funnel in the sea floor at the end of the bow-shaped tube to trap organic matter. Feces were excreted at the other end in the form of a small mound on the sediment surface. As new tubes were constructed, likely as a response to disturbances or for subsurface deposit feeding, a bundle of converging, crossing tubes resulted.

Fig. 2. “*Schaubcylindrichnus formosus*” (= *S. coronus*) of the Miocene Taliao Formation. The coins, 26 mm in diameter, give scales. (A) A sheaf of tubes is connected to a funnel-like structure, displaying downward-tapering, alternating laminae of sand and mud arranged in a cone-in-cone pattern. The observed structures are very similar to the structures interpreted as a feeding funnel by Nara (2006). (B) A single tube is attached to a probable feeding-funnel.

Fig. 3. In the studied material a seamless transition between the “endmember” forms of the formerly described *Schaubcylindrichnus* (A: *S. coronus* sensu Frey and Howard; B: “*S. freyi*” sensu Miller, 1995; C: “*S. formosus*” sensu Löwemark and Hong, 2006) could be observed.

Consequently, in all relevant aspects the trace fossils including Taiwanese specimens are nearly identical and clearly show the same morphological traits, as demonstrated in Table 1. It can therefore be concluded that all the schaubcylindrichnian trace fossils are composite burrow systems, each of which consists of a feeding funnel, an arched set of tubes, and a fecal mound attached to the opposite end of the tubes, and was probably formed by a solitary funnel feeder (Fig. 2).

3. Taxonomy

Löwemark and Hong (2006) introduced a new ichnospecies based on the differences in morphology from the description of the original ichnogenus (Frey and Howard, 1981; Frey and Pemberton, 1991). However, as demonstrated by Nara's (2006) comparison of the Japanese material with type material, together with additional observations of the specimens ranging from Mississippian to Pleistocene in ages, the typical form of *Schaubcylindrichnus* is not a congruent bundle, but a converging sheaf connected with a funnel and a mound. In the light of this revised morphological description, the *Schaubcylindrichnus* specimens observed in Taiwan can easily be accommodated within the ichnospecies of *S. coronus*, as discussed above. Furthermore, the complex composite

morphology of *Schaubcylindrichnus* shows a considerable morphological range with a seamless gradation between the endmember forms (Fig. 4). It therefore seems unnecessary and unjustified to subdivide the trace fossil into further ichnospecies as all the observed variability is found in the holo- and topotype material. A further subdivision based on the total morphology would also be of limited value as the trace typically only can be observed as eroded partial remains and a full reconstruction of the morphology requires study of thousands of specimens.

4. Conclusions

Based on an evaluation of the results from the two articles, three main conclusions can be drawn:

1. The morphology of *Schaubcylindrichnus* is characterized by three distinct parts: a funnel, a sheaf of converging thickly lined tubes, and a fecal mound.
2. Earlier ethological interpretations such as gregarious deposit feeding or filter feeding, can be ruled out in favor of a funnel feeding behavior.
3. Detailed morphological studies of the known schaubcylindrichnian specimens, including Taiwanese material, show that all *Schaubcylindrichnus* can be accommodated within the ichnospecies *S. coronus*. Consequently, *S. formosus* should be considered as a junior synonym and therefore be abandoned.

However, this comparison also raises a few questions that can only be answered through continued studies on detailed morphological features and their relation to different facies ranges.

Do the morphologic endmembers of *Schaubcylindrichnus* correspond to certain facies or they are developed as a response to particular environmental conditions? If so, a subdivision into different groups could prove to become a powerful tool for facies reconstructions. In such cases, subdivision at the ichnosubspecific level would be necessary.

Do the variations in the average number of tubes per sheaf reflect how often the structure had to be reconstructed after erosional events? And thus, could the number of tubes per sheaf be developed into a quantitative proxy for variability in wave or current action? The intergradation observed from single isolated tubes to looser or tighter sheaves does suggest that the forms could be a behavioral adaptation to differing environmental conditions.

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Table 1
Comparison of characteristics between *Schaubcylindrichnus coronus* reported by Nara (2006) and “*S. formosus*” Löwemark and Hong (2006).

	<i>S. coronus</i> after Nara (2006)	“ <i>S. formosus</i> ” after Löwemark and Hong (2006)
Tube diameter	1–12 mm ^a	10.5 mm
Lining thickness	0.5–8 mm	0.7–4 mm
Two-fold lining	X	X
Bow shape	X	X
Attached funnel	X	X ^b
Attached mound	X	–
Branching of tube	X	X
Cross-cutting of tubes in a single bundle	X	X

^a Internal diameter.

^b See, text and Fig. 2.

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Appendix A. Systematic ichnology

Ichnogenus *Schaubcylichtrichnus* Frey and Howard, 1981

1981 *Schaubcylichtrichnus coronus* n. ichnog. and ichnosp. –Frey and Howard, 801–803, figs. 1, 3.

1995 *Schaubcylichtrichnus freyi* n. ichnosp. –Miller, 142–145, figs. 4, 5.

2008 *Schaubcylichtrichnus formosus* n. ichnosp. –Löwemark and Hong, 4–8, figs. 4, 5, 6, 7, 11.

Diagnosis.—Substantially cylindrical, isolated or clustered tubes with thick, twofold, linings (after Nara, 2006).

Ichnospecies *Schaubcylichtrichnus coronus* Frey and Howard 1981 Figs. 1, 2.

Diagnosis.—*Schaubcylichtrichnus* showing bow-shape, mostly occurring as a cluster of tubes. A sediment-filled funnel or a sediment

mound may be associated with the upper extremities (after Nara, 2006).

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