***Rhizocorallium* in Estuarine Ingersoll Shale (Upper Cretaceous Eutaw Formation, Eastern Alabama Coastal Plain)**

Charles E. Savrda^{a*}

P. Sean Bingham^{a,b}

Phillip A. Daymond^a

^a*Department of Geosciences, Auburn University, Auburn, AL 36849-5305, USA*

^b*Present address: Devon Energy, 20 N. Broadway Ave, Oklahoma City, OK 73102 USA*

*Corresponding author. Tel. +1 334 844 4887; fax +1 334 844 4486.

E-mail address: savrdce@auburn.edu (C.E. Savrda)

Keywords: *Rhizocorallium*, Cretaceous, Ingersoll shale, Estuarine, Ichnofossils

ABSTRACT

The ichnofossil *Rhizocorallium*—an oblique to horizontal U-shaped spreiten burrow—has been recognized in a broad range of Phanerozoic continental, marginal marine, and shallow to deep marine facies. Nonetheless, occurrences of this ichnotaxon in Cretaceous estuarine deposits are rarely described. Herein we document *Rhizocorallium* in the Ingersoll shale, a carbonaceous clay lens within an estuarine succession contained in the Upper Cretaceous (Santonian) Eutaw Formation exposed in the eastern U.S. Gulf coastal plain. The Ingersoll *Rhizocorallium* specimens, assigned to *R. commune* var. *irregulare* based on their basic morphology, horizontal disposition, dimensions, and actively filled spreiten, record a change in depositional conditions and substrate consistency linked to transgression. The Ingersoll shale accumulated rapidly in a restricted tidal channel in a bayhead delta setting and hosts an impoverished resident ichnofauna reflecting soupground conditions. In contrast, attributes of *Rhizocorallium* (e.g., burrow wall bioglyphs) and associated *Thalassinoides* in the upper part of the Ingersoll shale reflect firm substrates (i.e., *Glossifungites* ichnofacies). Firmground development and colonization reflect burial dewatering and subsequent exhumation by bay-shoreline ravinement of clays and the concomitant shift to estuarine central bay deposition. The biological affinity of the *Rhizocorallium* trace makers cannot be confidently established. However, based on relatively straight and seemingly current-aligned axes, passive burrow fills, lack of associated fecal pellets, and emplacement in firm clay, these structures were likely produced by suspension-feeding organisms—either crustaceans or worms—that took advantage of wave- or tide-induced currents in shallow areas near the estuary head.

1. Introduction

The ichnogenus *Rhizocorallium* refers to oblique to horizontal, U-shaped spreiten burrows. In an extensive literature review and assessment of *Rhizocorallium*, Knaust (2013) notes that biogenic structures assignable to this ichnotaxon: (1) have a very long geologic range, from Early Cambrian (e.g., Mazurek, 2014) through Recent (e.g., Hodgson, Gingras, &

Zonneveld, 2015); (2) formed in carbonate and siliciclastic softgrounds, as well as post-Paleozoic firmgrounds, in a wide spectrum of marginal and shallow marine environments but also in post-Paleozoic deeper marine and continental settings; and, (3) depending on age, depositional setting, substrate type, and specific morphologic attributes, have been attributed to the activities of deposit- or suspension-feeding worms, crustaceans, or insect larvae (see Table 3 in Knaust, 2013).

Notably, of the nearly two hundred literature sources reviewed by Knaust (2013), approximately thirty address Cretaceous occurrences of *Rhizocorallium*. Of these, only three speak to occurrences in purported estuarine deposits, all of which are hosted in sandstones within formations of the North American Western Interior (Basan and Scott, 1979; MacEachern, Pemberton, Gingras, & Bann, 2007; Boyd and Lillegraven, 2011). In the current contribution, we document a recently recognized collection of mud-hosted *Rhizocorallium* in the Ingersoll shale, an informally named estuarine deposit within the Upper Cretaceous (Santonian) Eutaw Formation exposed in the eastern United States Gulf Coastal Plain. Herein, we describe the morphology of the Ingersoll *Rhizocorallium*, leading to more detailed ichnotaxonomic assignment following the scheme of Knaust (2013). From this, we address our described specimens in the context of substrate consistency, paleoenvironment, and sequence stratigraphic setting, and discuss the potential biological affinity and ethology of the trace makers.

2. Ingersoll Shale

The Ingersoll shale is a thin (<1 m) clay lens best known for its well-preserved terrestrial fossil biota. It contains a diverse flora (Bingham, Savrda, Knight, & Lewis, 2008; Stults, Axsmith, Knight, & Bingham, 2012), amber with inclusions (Knight et al., 2010), and fossil feathers (Knight, Bingham, Lewis, & Savrda, 2011). This clay lens, part of a transgressive estuarine sequence comprising the Eutaw Formation (Savrda and Nanson, 2003; Bingham et al., 2008), is exposed on a hillslope near Phenix City, eastern Alabama (Fig. 1), approximately 2 m above the

unconformable contact with the underlying fluvial Tuscaloosa Formation. The stratigraphic context and lithologic character of the Ingersoll shale, described in detail previously (Bingham et al., 2008; Savrda, Bingham, Knight, & Lewis, 2009), are summarized below.

The section of Eutaw Formation pertinent to this study encompasses units 5 through 8 of Bingham et al. (2008). Depicted in figure 2, these include, in ascending order: (1) *Ophiomorpha*-bearing, cross-stratified, coarse-grained sands deposited in tidal channels (unit 5); (2) planar-bedded sands and clays deposited in tidal flat settings (unit 6); (3) the Ingersoll shale lens, described further below, deposited in a restricted tidal channel (unit 7); and (4) highly bioturbated, fossiliferous muddy sands with remnant rippled sand and carbonaceous clay lenses (Fig. 3B) and *Teredolites*-bored logs (unit 8). Units 5 through 7 were deposited in a bayhead-delta system, whereas unit 8 accumulated in a proximal estuarine central bay setting. The base of the latter unit, which is sharp and variably truncates the tops of units 6 and 7 (Fig. 3A, C), formed in response to transgression and bay-shoreline ravinement.

The Ingersoll shale generally can be described as an unlithified, carbonaceous, pyritiferous clay. Bingham et al. (2008) previously divided the Ingersoll shale into three subunits (A, B, and C) based on gradational changes in texture and fabric (Fig. 2). Subunit A is characterized by thin, graded sand-clay couplets that record diurnal and neap-spring tidal cyclicity. Subunit B is dominated by faintly laminated to massive clay but locally contains thin (1 mm), continuous and discontinuous laminae of fine sand, silt, and plant detritus. As originally described, subunit C consists of seemingly massive clay with common subvertical slickensided joints and only rare fine sand or silt laminae. Our recent field studies, however, reveal an increase in frequency of fine sand laminae in the upper part of subunit C towards the previously unexcavated margin of the clay lens (Fig. 3C). Except in the oxidized lower part of subunit A, the Ingersoll is organic carbon-rich (average total organic carbon = 1.45%) and pyritiferous (average sulfide S = 2.8%). Inclusion-bearing amber clasts are concentrated in subunit A, whereas well-preserved plant remains and fossil feathers occur throughout the Ingersoll shale.

The Ingersoll shale generally is only weakly bioturbated and contains a sparse, low-diversity *resident* ichnofauna (Fig. 2). The sandier subunit A contains rare vertical, concentrically laminated burrows referred to as “*Rosselia*-like” structures (Bingham et al., 2008). However, mucus trails, now manifest as narrow, discontinuous, straight to meandering, rarely branched, virtually flat and mostly horizontal ribbons of pyrite, occur throughout the Ingersoll shale and are particularly abundant in clay-dominated subunits B and C. Pyritized mucus films are inferred to have been secreted by epibenthic or shallow endobenthic organisms, perhaps grazing gastropods and errant worms, as they moved along or at shallow depths within soupy, oxygen-deficient substrates (Savrda, Daymond, & Hespel, 2016).

The upper part of subunit C also hosts larger and more distinct ichnofossils that were emplaced after erosion of the top of the Ingersoll shale and thus emanate from the base of the overlying central bay sediments (unit 8). These include large diameter (1-7 cm), irregular, typically branched, sharp-walled, sand- or muddy sand-filled burrows allied with *Thalassinoides* (Fig. 3D), as well as the *Rhizocorallium* described herein.

3. Ingersoll *Rhizocorallium*

3.1. Materials

A total of 22 partial specimens of *Rhizocorallium* were examined in detail for this study. Nine of these were collected previously and archived in the sedimentology laboratory at Auburn University, whereas the remainder are specimens encountered during renewed field excavation of the Ingersoll shale. All specimens occur within the uppermost 8 cm of subunit C. Most specimens are isolated in pure clay host sediments (e.g., Fig. 4A, B, D, F). However, two pass obliquely through or follow along a thin interval of interlaminated clay and fine sand encountered along the newly excavated margin of the lens (Fig. 4C, E).

3.2. Preservation

All documented specimens are preserved in full relief. Most are expressed as horizontal to very slightly inclined U-tubes with spreiten. This preservational bias reflects the propensity for

the Ingersoll shale to split easily only along bedding-parallel surfaces. Vertical to steeply inclined proximal portions of *Rhizocorallium* U-tubes are recognized only where they coincide with subvertical slickensided joints in clays (Fig. 4D) and where they obliquely penetrate intervals with thin sand laminae (Fig. 4E).

Difficulties in uniformly splitting unconsolidated clays to expose thinly spaced, areally extensive bedding-parallel surfaces precluded confident evaluation of spatial densities of *Rhizocorallium*. Nonetheless, densities of *Rhizocorallium* appear to vary significantly within the upper part of the Ingersoll shale. Systematic excavation and splitting generally yielded only 1 to 3 isolated specimens per m², but locally two or more specimens were tightly clustered. In one archived sample, three specimens co-occur on a 200-cm² bedding-plane surface (Fig. 4A).

3.3. Trace Fossil Description

Most of the specimens are incomplete, representing short segments, some of which lack the distal U-bend of the burrow. Minimum lengths of U-tubes range from 4.2-21.0 cm (average = 8 cm). Axes of the u-tubes are typically straight, although the axis of the longest specimen is gently curved (Fig. 4C). U-tube widths vary among specimens from 17-33 mm with an average of 25 mm. Tube diameters range from 3-10 mm, averaging 6.5 mm, and generally covary with u-tube width (e.g., Fig. 5A). Limbs of the U-tubes are essentially parallel to one another. In longer specimens, both U-tube width and tube diameter gradually increase distally (Fig. 5A).

Burrow tubes exhibit circular to slightly elliptical cross sections and sharp walls. Tubes are typically filled with sediment derived from the overlying unit 8. This sediment consists of either light to medium brown, very fine- to fine-grained micaceous sands containing scattered very coarse quartz sand grains and granules, or darker and finer-grained sediment comparable to unit 8 remnant mud lenses. However, some tubes appear to be partially unfilled. Both sand and mud tube fills lack both macroscopic and microscopic evidence of pelleting or any other internal fabric and likely were passively emplaced. Exposed tubes walls (in specimens wherein

tubes remained unfilled or fills were washed out) and exteriors of mud-filled tubes are marked by well-defined, 3-10-mm-long, parallel to subparallel, longitudinal scratch marks (Fig. 4B, F).

In specimens wholly contained in a clay host, spreiten are invariably comprised of the same clay. Spreite surfaces are marked by variably expressed, very low-relief (< 0.5 mm), concentric ridges and grooves. Where well-preserved, ridges and grooves occur in 3-4-mm-wide bundles; later-formed, more distal bundles truncate adjacent previously formed bundles (Fig. 4F). Spreiten contain no apparent pellets, and internal laminae are not manifest owing to uniform fine grain size. In the few specimens that traverse interlaminated sand and clay, spreiten appear more chaotic; longer packets comprising dark homogeneous clay irregularly alternate with shorter packets or patches of relatively clean, light gray sand derived from sand laminae in the host sediment (Fig. 4C). None of the spreiten exhibit evidence of vertical migration (retrosive movement) of the U-tube. In most specimens, the height of the spreite is slightly less than the vertical dimension of associated U-tubes, presumably reflecting differential compaction of clay-dominated spreiten.

Preferred axial orientation is suggested by general alignment of a set of clustered u-tubes in an archived sample (Fig. 4A). Reliable U-tube orientation data are available for only 11 specimens observed in the field. Bearings of U-tube axes, measured in the direction of the distal U-portion, show a significant spread to the northeast through northwest with a modal orientation of NNW (N8-10W) (Fig. 5B).

4. Discussion

4.1. Ichnospecies Assignment

The ichnotaxonomy of *Rhizocorallium* and associated U-shaped spreiten structures has been the subject of considerable discussion and debate (e.g., Fursich, 1974; Knaust, 2007, 2013; Rodríguez-Tovar, Buatois, Piñuela, Mángano, & García-Ramos, 2012; Schlirf, 2011). In the most recent and extensive review, Knaust (2013) argued based on morphologic attributes that there are only two valid ichnospecies of *Rhizocorallium*—*R. jenense* Zenker 1936 and *R.*

1
2
3
4 182 *commune* Schmid 1876—and that the latter can be divided into four subichnospecies or
5
6 183 varieties— ichnosubspecies *problematica* Gümbel 1861, ichnosubspecies *uliarensis* Firtion
7
8 184 1958, *R. commune* var. *irregulare* Mayer 1954, and *R. commune* var. *auriforme* Hall 1843. The
9
10 185 attributes of these forms are summarized in Figure 6. Following Knaust's (2013) scheme, the
11
12 186 Ingersoll *Rhizocorallium* are most allied with *R. commune* var. *irregulare* or *R. commune* var.
13
14 187 *auriforme* based on their predominantly horizontal disposition, presence of active fill in spreiten,
15
16 188 and lack of retrusive or trochospiral spreiten.
17

18
19
20 189 *R. commune* var. *irregulare* and *R. commune* var. *auriforme* have been distinguished, at
21
22 190 least in the German Triassic, on the basis of morphometrics (Knaust, 2013, fig. 27). Specimens
23
24 191 of *R. commune* var. *auriforme* are generally short (typically less than 7 cm long), narrow (mostly
25
26 192 less than 25 mm) and commonly slightly inclined (10-20°) to bedding. In contrast, although there
27
28 193 is overlap in size parameters, specimens of *R. commune* var. *irregulare* generally are larger,
29
30 194 typically greater than 10 cm long and 40 mm wide, and primarily horizontal. Measured lengths
31
32 195 and widths of the Ingersoll *Rhizocorallium* fall within the range of overlap between these two
33
34 196 forms. However, much of our length data derive from incomplete specimens. The more
35
36 197 complete Ingersoll specimens have minimal lengths ranging from 10 to 20 cm. Based on these
37
38 198 dimensions, as well the horizontal disposition of the U-tubes, the Ingersoll *Rhizocorallium* are
39
40 199 most appropriately assigned to *R. commune* var. *irregulare*.
41
42
43

44 200 **4.2. Substrate Consistency**

45
46 201 *Rhizocorallium* occurs in a variety of clastic and carbonate, soft and firm substrates and
47
48 202 thus is a common component of both *Cruziana* and *Glossifungites* ichnofacies (Fig. 6). The
49
50 203 affiliation of *R. jenense* with very firm substrates is clearly reflected by its morphologic
51
52 204 features—inclined disposition, pervasive networks of scratch marks, and generally structureless,
53
54 205 passive spreite fills that typically contrast markedly with host sediment. In contrast, variants of
55
56 206 *R. commune* may be associated with soft and firm substrates. All of these variants generally are
57
58 207 characterized by passive tube fills but actively filled spreiten (i.e., spreite sediment is composed
59
60
61
62
63
64
65

of biogenically reworked host sediment). However, soft- and firmground *R. commune* can be distinguished based on the absence or presence, respectively, of scratch marks on tube walls. The relatively uncompressed and locally unfilled U-tubes with well-developed burrow-wall bioglyphs in the Ingersoll shale specimens clearly indicate that they were emplaced in a dewatered, firm clay substrate. Thus, the Ingersoll *Rhizocorallium*, along with the associated sharp-walled *Thalassinoides*, represent the *Glossifungites* ichnofacies.

4.3. Environment of Deposition

Rhizocorallium can be considered a facies-breaking ichnogenus. *R. jenensis* has been recognized in firmgrounds that developed in a variety of continental, marginal marine, and shallow to deep marine deposits (e.g., Fürsich & Mayr, 1981; Hayward, 1976; Knaust, 2013; Rodríguez-Tovar et al., 2012). Structures more allied with *R. commune* (as defined by Knaust, 2013) are common in Phanerozoic deposits representing various marginal marine (e.g., Buatois et al., 2005; Farrow, 1966; Greb & Chestnut, 1992; Hodgson et al., 2015; Jaglarz & Uchman, 2010; Joeckel & Korus, 2012; Rossetti & Santos, 2003), deltaic (e.g., Dafoe, Gingras, & Pemberton, 2010; Leren, Howell, Enge, & Martinus, 2010), and shallow, commonly storm-influenced shelf settings (e.g., Basan & Scott, 1979; Bhattacharya, Bhattacharya, Chakraborty, & Chakraborty, 2004; Buatois, Mángano, Alissa, & Carr, 2002; Chryastek, 2013; Kietzmann, Palma, Riccardi, Martín-Chivelet, & López-Gómez, 2014; Knaust, 2007; Kowal-Linka & Bodzioch, 2011; Loughlin & Hillier, 2010; Rodríguez-Tovar & Pérez-Valera, 2008; Schlirf, 2003; Worsley & Mork, 2001; Zonneveld, Gingras, & Beatty, 2010). However, they also have been recognized in deeper basin-floor and fan deposits of Cretaceous and younger age (e.g., Kotlarczyk & Uchman, 2012; Poursoltani, Moussavi-Harami, & Gibling, 2007; Uchman, 1992). Notably, *R. jenense* and firmground morphotypes of *R. commune* are typically associated with pelagic omission surfaces (e.g., Gaillard & Olivero, 2009) and various erosion surfaces tied to transgression (e.g., transgressive surfaces of erosion, TSE, and other marine flooding surfaces;

Fürsich, Kennedy, & Palmer, 1981; Noudar & Challai, 2002; Rodríguez-Tovar, Pérez-Valera, & Perez-Lopez, 2007; Rodríguez-Tovar & Pérez-Valera, 2008; Schlirf, 2003; Seilacher, 2007).

The Ingersoll *Rhizocorallium* were emplaced across a transgressive surface of erosion (TSE; Fig. 2) —i.e., the bay shoreline-ravinement surface that separates the restricted tidal channel clays of the Ingersoll shale from overlying proximal central bay deposits (unit 8; see Bingham et al., 2008). Originally highly fluid host clays of the Ingersoll shale were buried and dewatered, and then subsequently exhumed during cutting of the TSE by waves or tidal currents (Bingham et al., 2008). Colonization of the newly formed firmground likely occurred in a moderately energetic intertidal to shallow subtidal regime and, based on the variability of passive U-tube fills (sand versus mud) and progenitor growth manifest in dimensions of longer specimens, continued for a period of time after initiation of deposition of heterolithic central-bay sediments. However, the firmground likely was abandoned after significant bay sediment accretion.

Preferential orientation of *Rhizocorallium* spreiten has been noted previously and may reflect the prevalence of wave or tidal currents (e.g., Farrow, 1966; Fürsich, 1974; Worsley & Mork, 2001; Mork & Bromley, 2008; Rodríguez-Tovar & Pérez-Valera, 2008; but see Fürsich, 1975). Although the *Rhizocorallium*-orientation dataset for the Ingersoll shale is too small to draw confident conclusions, the NNW modal orientation (see Fig. 5B) generally corresponds to the inferred axis of the estuary and may reflect an organismal response to prevailing wave- or tide-induced currents near the head of the Eutaw estuary.

4.4. Trace Producers and Ethology

Rhizocorallium and similar U- or pouch-shaped structures (e.g., *Fuersichnus*, *Asthenopodichnium*) produced in continental firmgrounds and various other nonmarine substrates (wood, bone, etc.) have been attributed to the activities of mayfly or midge larvae (e.g., Bromley & Asgaard, 1979; Chamberlain, 1975; De, 2002; Fürsich & Mayr, 1981; Moran et al., 2010; Savrda, in press; Thenius, 1988; Uchman, Gaigalas, Meslesyte, & Kazakauskas,

2007), and possibly fungi (Genise et al., 2013). In contrast, as clearly evident in the review by Knaust (2013; table 3), *Rhizocorallium* in marine and marginal marine soft and firm substrates most commonly have been ascribed to deposit- or suspension-feeding crustaceans and/or worms (annelids, priapulids, etc.). Common attribution to crustaceans is based on the presence of scratch marks and other morphological irregularities (e.g., spine-shaped tubes protuberances; see Rodriquez-Tovar et al., 2012) presumed to be formed by chelae during burrow excavation. However, Knaust (2013) emphasized that such bioglyphs also could be formed by the stiff chitinous bristles characteristic of some worms. Recognizing possible exceptions for *R. jenense* in post-Paleozoic firmgrounds, Knaust (2013) favors polychaete progenitors based on the long-ranging occurrence of *Rhizocorallium* (Cambrian to Holocene), elliptical as opposed to cylindrical shape of commonly associated fecal pellets, rare *in situ* soft-body remains, and comparison with analogous structures produced by extant worms.

Fecal pellets and body fossils that might provide clues regarding the affinity of the trace makers are notably absent within the *Rhizocorallium* examined in the current study. The occurrence of *Rhizocorallium* with crustacean burrows—i.e., *Thalassinoides*—in the Ingersoll shale *Glossifungites* assemblage could hint at a comparable progenitor. However, associated *Thalassinoides* burrows have significantly larger diameters (1 to 7 cm) and they lack any physical connection to the *Rhizocorallium* specimens. Hence, while it is apparent that the *Rhizocorallium* organisms shared the firmground substrate with crustaceans, no definitive conclusions can be drawn about their biological affinity.

Interpretation of the behavior of the trace makers is less problematic. Firmground *R. jenense* (as defined by Knaust, 2013) are likely dominichnia produced by suspension feeders (see also Fürsich, 1974). In contrast, depending in part on variety or ichnosubspecies, *R. commune* can be interpreted to reflect suspension feeding, deposit feeding, or a combination thereof (Fig. 6; Knaust, 2013). Based on their emplacement in stiff clays, their relatively short, straight and possibly current aligned axes, passive U-tube fills, and lack of fecal pellets in tubes

and spreiten, the Ingersoll *Rhizocorallium* most likely represent the work of suspension feeders that took advantage of wave- or tide-induced currents.

5. Summary

The Ingersoll shale provides a rare example of *Rhizocorallium* in a Cretaceous, mud-dominated estuarine deposit. The Ingersoll *Rhizocorallium* specimens, assignable to *R. commune* var. *irregulare* based on their simple morphology, horizontal disposition, dimensions, and actively filled spreiten, occur in variable densities as full-relief structures in the upper part of a clay lens formed in a restricted tidal channel in a bayhead-delta setting. Based on tube-wall bioglyphs, these structures were emplaced in a firm substrate. Colonization of this firmground by *Rhizocorallium* and associated *Thalassinoides* trace makers occurred following erosional exhumation of dewatered Ingersoll clays and the subsequent transition to estuarine central bay deposition in response to transgression. Evidence to discriminate among potential trace makers is lacking. However, based on relatively straight and possibly current aligned axes, passive burrow fills, lack of associated fecal pellets, and emplacement in semi-consolidated clay, the Ingersoll *Rhizocorallium* were likely produced by suspension-feeding crustaceans or worms that benefited from wave- or tide-induced currents in shallow waters near the head of the estuary.

ACKNOWLEDGEMENTS

This study was supported by NSF grant EAR-0633839. Michael Ingersoll graciously provided continued access to his property. Comments and suggested provided by Greg Baniak and an unidentified reviewer helped improve the manuscript.

References

Basan, P. B., & Scott, R. W. (1979). Morphology of *Rhizocorallium* and associated traces from the Lower Cretaceous Purgatoire Formation, Colorado. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 28, 5-23.

- Bhattacharya, H. N., Bhattacharya, B., Chakraborty, I., & Chakraborty, A. (2004). Sole marks in storm event beds in the Permo-Carboniferous Talchir Formation, Raniganj Basin, India. *Sedimentary Geology*, 166, 209-222.
- Bingham, P. S., Savrda, C. E., Knight, T. K., & Lewis, R. D. (2008). Character and genesis of the Ingersoll shale, a compact terrestrial fossil-lagerstätte, Upper Cretaceous Eutaw Formation, eastern Alabama. *Palaaios*, 23, 391-401.
- Boyd, D. W., & Lillegraven, J. A. (2011). Persistence of the Western Interior Seaway: historical background and significance of the ichnogenus *Rhizocorallium* in Paleocene strata, south-central Wyoming. *Rocky Mountain Geology*, 46, 43-69.
- Bromley, R. G., & Asgaard, U. (1979). Triassic freshwater ichnocoenoses from Carlsberg Fjord, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 28, 39-80.
- Buatois, L. A., Mangano, M. G., Alissa, A., & Carr, T. R. (2002). Sequence stratigraphic and sedimentologic significance of biogenic structures from a late Paleozoic marginal- to open-marine reservoir, Morrow Sandstone, subsurface of southwest Kansas, USA. *Sedimentary Geology*, 152, 99-132.
- Buatois, L. A., Gingras, M. K., MacEachern, J., Mangano, M. G., Zonneveld, J-P., Pemberton, S. G., Netto, R. G., & Martin, A. (2005) Colonization of brackish-water systems through time: Evidence from the trace fossil record. *Palaaios*, 20, 321-347.
- Chamberlain, C. K. (1975). Recent lebensspuren in nonmarine aquatic environments. In R. W. Frey (Ed.), *The Study of Trace Fossils* (pp. 432-458). New York: Springer Verlag.
- Chryastek, A. (2013). Trace fossils from the Lower Muschelkalk of Raciborowice Górne (North Sudetic Synclinorium, SW Poland) and their palaeoenvironmental interpretation. *Acta Geologic Polonica*, 63, 315-353.
- Dafoe, L. T., Gingras, M. K., & Pemberton, S. G. (2010). Wave-influence deltaic sandstone bodies and offshore deposits in the Viking Formation, Hamilton Lake area, south-central Alberta, Canada. *Bulletin of Canadian Geology*, 58, 173-201.

- De, C. (2002). Continental mayfly burrows within relict-ground in inter-tidal beach profile of Bay of Bengal coast: A new ichnological evidence of Holocene transgression. *Current Science*, 83, 64-67.
- Farrow, G. E. (1966). Bathymetric zonation of Jurassic trace fossils from the coast of Yorkshire, England. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2, 103-151.
- Firion, F. (1958). Sur la présence d'ichnites dans le Portlandien de l'île d'Oléron (Charente maritime). *Annales Universitatis Saravienis (Naturw.)*, 7, 107-112.
- Fürsich, F. T. (1974). Ichnogenus *Rhizocorallium*. *Palaontologische Zeitschrift*, 48, 16-28.
- Fürsich, F. T. (1975). Trace fossils as environmental indicators in the Corallian of England and Normandy. *Lethaia*, 8, 151-172.
- Fürsich, F. T., & Mayr, H. (1981). Non-marine *Rhizocorallium* (trace fossil) from the Upper Freshwater Molasses (Upper Miocene) of southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 6, 321-333.
- Fürsich, F. T., Kennedy, W. J., & Palmer, T. J. (1981). Trace fossils at a regional discontinuity surface: the Austin/Taylor (Upper Cretaceous) contact in central Texas. *Journal of Paleontology*, 55, 573-551.
- Gaillard, C., & Olivero, D. (2009). The ichnofossils *Halimedes* in Cretaceous pelagic deposits from the Alps: Environmental and ethologic significance. *Palaios*, 24, 257-270.
- Genise, J. F., Garrouste, R., Nel, P., Grandcolas, P., Maurizot, P., Cluzel, D., Cornette, R., Fabre, A-C., & Nel, A. (2012). *Asthenopodichnium* in fossil wood: Different trace makers as indicators of different terrestrial paleoenvironments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 365-366, 184-191.
- Greb, S. F., & Chesnut, D. R., Jr. (1992). Transgressive channel filling in the Breathitt Formation (Upper Carboniferous), eastern Kentucky coal field, USA. *Sedimentary Geology*, 75, 209-221.

- Gümbel, C. W. (1861). Geognostische Beschreibung des bayerischen Alpengebirges und seines Vorlandes (950 pp.). Gotha: Justus Perthes.
- Hall, J. (1843). Geology of New York. Part 4. Comprising the Survey of the Fourth Geological District (525 pp.). Albany: Carroll and Cook.
- Hayward, B. W. (1976). Lower Miocene bathyal and submarine canyon ichnocoenoses from Northland, New Zealand. *Lethaia*, 9, 149-162.
- Hodgson, C. A., Gingras, M. L., & Zonneveld, J-P. (2015). Spatial, temporal and palaeoecological significance of exhumed firmgrounds and other associated substrate types in Netarts Bay, Oregon, USA. *Lethaia*, 48, 436-455.
- Jaglarz, P., & Uchman, A. (2010). A hypersaline ichnoassemblage from the middle Triassic carbonate ramp of the Traticum domain in the Tatra Mountains, southern Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292, 71-81.
- Joeckel, R. M., & Korus, J. T. (2012). Bayhead delta interpretation of an Upper Pennsylvanian sheetlike sandbody and the broader understanding of transgressive deposits in cyclothems. *Sedimentary Geology*, 275-276, 22-37.
- Kietzmann, D. A., Palma, R. M., Riccardi, A. C., Martín-Chivelet, J., & López-Gómez, J. (2014). Sedimentology and sequence stratigraphy of a Tithonian-Valangian carbonate ramp (Vaca Muerta Formation): a misunderstood exceptional source rock in the southern Mendoza area of the Neuquén Basin, Argentina. *Sedimentary Geology*, 302, 64-86.
- Knaust, D. (2007). Invertebrate trace fossils and ichnodiversity in shallow-marine carbonates of the German Middle Triassic (Muschelkalk). In R. G. Bromley, L. A. Buatois, G. Mángano, J. F. Genise, & R. N. Melchor (Eds.), *SEPM Special Publication 88: Sediment-Organism Interactions: A Multifaceted Ichnology* (pp. 223-240), Tulsa, Society of Sedimentary Geology.
- Knaust, D. (2013). The ichnogenus *Rhizocorallium*: Classification, trace makers, palaeoenvironments and evolution. *Earth-Science Reviews*, 126, 1-47.

- Knight, T. K., Bingham, P. S., Grimaldi, D., Anderson, K., Lewis, R. D., & Savrda, C. E. (2010).
A new Upper Cretaceous (Santonian) amber deposit from the Eutaw Formation of
eastern Alabama, USA. *Cretaceous Research*, 35, 85-93.
- Knight, T. K., Bingham, P. S., Lewis, R. D., & Savrda, C. E. (2011). Feathers of the Ingersoll
shale, Eutaw Formation (Upper Cretaceous), eastern Alabama: the largest collection of
feathers from North American Mesozoic rocks. *Palaios*, 26, 364-376.
- Kotlarczyk, J., & Uchman, A. (2012). Integrated ichnology and ichthyology of the Oligocene
Menilite Formation, Skole and Subsilesian nappes, Polish Carpathians: a proxy to
oxygenation history. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 331-332,
104-118.
- Kowal-Linka, M., & Bodzioch, A. (2011). Sedimentological implications of an unusual form of the
trace fossil *Rhizocorallium* from the Lower Muschelkalk (Middle Triassic), S. Poland.
Facies, 57, 695-703.
- Leren B. L. S., Howell, J., Enge, H., & Martinius, A. W. (2010). Controls on stratigraphic
architecture in contemporaneous delta systems from the Eocene Roda Sandstone,
Trem-Graus Basin, northern Spain. *Sedimentary Geology*, 229, 9-40.
- Loughlin, N. J. D., & Hillier, R. D. (2010). Early Cambrian *Teichichnus*-dominated ichnofabrics
and palaeoenvironmental analysis of the Caerfai Group, southwest Wales, UK.
Palaeogeography, Palaeoclimatology, Palaeoecology, 297, 239-251.
- MacEachern, J. A., Pemberton, S. G., Gingras, M. K., & Bann, K. L. (2007). The ichnofacies
paradigm: a fifty-year retrospective. In W. Miller III (Ed.), *Trace Fossils: Concepts,
Problems, Prospects* (pp. 52-77), Amsterdam, Elsevier.
- Mayer, G. (1954). Eine neues *Rhizocorallium* asu dem Mittleren Hauptmuschelkalk von
Bruchsal. *Beiträge zur naturkundlichen Forschung in Südwestdeutschland*, 13, 80-83.
- Mazurek, D. (2014). The Tommotian phase of the Early Cambrian agronomic revolution in the
carbonate mud environment of Siberia. *Lethaia*, 47, 133-150.

- 412 Moran, K., Hilbert-Wolf, H. L., Golder, K., Malenda, H. F., Smith, C. J., Storm, L. P., Simpson, E.
413 L., Wizevich, M. C., & Tindall, S. E. (2010). Attributes of the wood-boring trace fossil
414 *Asthenopodichnium* in the Late Cretaceous Wahwaep Formation, Utah, USA.
415 Palaeogeography, Palaeoclimatology, Palaeoecology, 297, 662-669.
- 416 Mork, A., & Bromley, R.G. (2008). Ichnology of a marine regressive systems tract: the Middle
417 Triassic of Svalbard. Polar Research, 27, 339-359.
- 418 Noudar, M., & Challai, E. H. (2002). Facies and sequence stratigraphy of a Late Barremian
419 wave-dominated deltaic deposit, Agadit Basin, Morocco. Sedimentary Geology, 150,
420 375-384.
- 421 Poursoltani, M. R., Moussavi-Harami, R., & Gibling, M. R. (2007). Jurassic deep-water fans in
422 the Neo-Tethys Ocean: the Kashfrud Formation of the Kopet-Dagh Basin, Iran.
423 Sedimentary Geology, 198, 53-74.
- 424 Rodríguez-Tovar, F. J., & Pérez-Valera, F. (2008). Trace fossil *Rhizocorallium* from the Middle
425 Triassic of the Betic Cordillera, southern Spain: Characterization and environmental
426 implications. Palaios, 23, 78-86.
- 427 Rodríguez-Tovar, F. J., Pérez-Valera, F., & Perez-Lopez, A. (2007). Ichnological analysis in
428 high-resolution sequence stratigraphy: The *Glossifungites* ichnofacies in Triassic
429 successions from the Betic Cordillera (southern Spain). Sedimentary Geology, 198, 293-
430 307.
- 431 Rodríguez-Tovar, F. J., Buatois, L. A., Piñuela, L., Mángano, M. G., & García-Ramos, J.C.
432 (2012). Palaeoenvironmental and functional interpretation of *Rhizocorallium jenese*
433 *spinosus* (ichnosubsp. Nov.) from the lower Jurassic of Asturias, northern Spain.
434 Palaeogeography, Palaeoclimatology, Palaeoecology, 339-341, 114-120.
- 435 Rossetti, D. F., & Santos, A. E., Jr. (2003). Events of sediment deformation and mass failure in
436 Upper Cretaceous estuarine deposits (Cametá Basin, northern Brazil) as evidence for
437 seismic activity. Sedimentary Geology, 161, 107-130.

- 438 Savrda, C. E. (in press). Composite ichnofabrics: Categorization based on number of
439 ichnocoenoses and their temporal incongruence. *Palaios*.
- 440 Savrda, C. E., & Nanson, L. (2003). Ichnology of fair-weather and storm deposits in an Upper
441 Cretaceous passive-margin estuary (Eutaw Formation, western Georgia, USA).
442 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 202, 67-93.
- 443 Savrda, C. E., Bingham, P. S., Knight, T. K., & Lewis, R. D. (2009). The prospect of compact
444 estuarine lagerstätten. *Sedimentary Record*, 7, 4-8.
- 445 Savrda, C. E., Daymond, P. A., & Hespel, A-M. (2016). Preservation of mucus trails by early
446 pyritization in Cretaceous Ingersoll shale (Eutaw Formation, eastern Alabama, U.S.A.).
447 *Palaios*, 31, 25-34.
- 448 Schlirf, M. (2003). Palaeoecologic significance of Late Jurassic trace fossils from the
449 Boulonnais, N France. *Acta Geologica Polonica*, 53, 123-142.
- 450 Schlirf, M. (2011). A new classification concept for U-shaped spreite trace fossils: Neues
451 Jahrbuch für Geologie und Paläontologie Abhandlungen, 260, 33-54.
- 452 Schmid, E. E. (1876) *Der Muschelkalk des östlichen Thüringen* (20 pp.). Jena: Fromann.
- 453 Seilacher, A. (2007). *Trace Fossil Analysis* (226 pp). Berlin: Springer.
- 454 Stults, D. Z., Axsmith, B. J., Knight, T. K., & Bingham, P. S. (2012). The conifer *Araucaria*
455 *bladenensis* and associated large pollen and ovulate cones from the Upper Cretaceous
456 Ingersoll shale (Eutaw Formation) of Alabama. *Cretaceous Research*, 34, 142-148.
- 457 Thenius, E. (1988). Lebensspuren von aquatischen Insektenlarven aus dem Jungtertiär
458 Niederösterreichs. Trace fossils from nymphs of aquatic insects from the Neogene of
459 Lower Austria. *Beiträge zur Paläontologie Österreich*, 14, 1-17.
- 460 Uchman, A. (1992). Ichnogenus *Rhizocorallium* in the Paleogene flysch (outer western
461 Carpathians, Poland). *Geologica Carpathica*, 43, 57-60.

- Uchman, A., Gaigalas, A., Meslesyte, & Kazakauskas, V. (2007). The trace fossil *Asthenopodichnium lithuanicum* isp. Nov. from Late Neogene brown-coal deposits, Lithuania. *Geological Quarterly*, 51, 329-336.
- Worsley, D., & Mork, A. (2001). The environmental significance of the trace fossil *Rhizocorallium jenense* in the Lower Triassic of western Spitsbergen. *Polar Research*, 20, 37-48.
- Zenker, J. C. (1936). *Historisch-topographisches Taschenbuch von Jena und seiner Umgebung* (338 pp.). Friedrich Frommann, Jens.
- Zonneveld, J-P., Gingras, M. K., & Beatty, T. W. (2010). Diverse ichnofossil assemblages following the P-T extinction, Lower Triassic, Alberta and British Columbia, Canada: Evidence for shallow marine refugia on the northwestern coast of Pangaea. *Palaios*, 25, 368-392.

Figure Captions

Fig. 1. Map of eastern U.S. Gulf coastal plain region showing outcrop belt of the Cretaceous system (gray), including the Eutaw Formation (black), and the location of the Ingersoll shale in eastern Alabama (small white square). The Ingersoll shale exposure is on private property at latitude 32°26'58.23"N, longitude 85°00'45.77"W.

Fig. 2. Stratigraphic context and lithologic character of the Ingersoll shale. Generalized columns showing the position of the Ingersoll shale (unit 7) in the lower part of the Eutaw Formation (left) and its internal stratigraphy (subunits A, B, and C; right). *Op*, *Rh*, *Ro*, *Ro?*, *Te*, *Th*, and *Pmf* = *Ophiomorpha*, *Rhizocorallium*, *Rosselia*, *Rosselia*-like structures, *Teichichnus*, *Thalassinoides*, and pyritized mucus films, respectively. The *Rhizocorallium* described herein are restricted to the upper part of subunit C, below the transgressive surface of erosion (TSE).

Fig. 3. Photographs of the Ingersoll shale and overlying muddy sands (unit 8). (A) Sharp contact (dashed) between the clay-dominated upper part of Ingersoll shale (subunit C) and unit 8. Note subvertical, slickensided fracture surface in the clay. Markings on face of unit 8 are tool marks

produced during excavation (bar scale = 10 cm). (B) Highly bioturbated, fossiliferous muddy sand in unit 8. Arrows indicate examples of common bivalve molds (scale in cm). (C) Oblique view of the top of the Ingersoll shale. Contact with unit 8 indicated by dash line. Note presence of discontinuous, locally rippled fine sand laminae (arrows) in upper part of Ingersoll shale (scale is in 10-cm increments). (D) Sharp-walled, gravelly sand-filled *Thalassinoides* penetrating top of Ingersoll shale (bar scale = 1 cm).

Fig. 4. Photographs of *Rhizocorallium* in the Ingersoll shale (all bar scales = 1 cm long). (A) Cluster of three subparallel specimens on bedding-parallel surface within clay. Clay and siltier mud comprise the spreite and burrow fill, respectively. (B) Clay-hosted specimen with scratch marks (bioglyphs) expressed on the exterior of spreite and on walls of empty U-burrow. (C) Elongate, gently curved and slightly bedding-oblique specimen cutting through fine sand laminae within clay. U-burrow is filled with sandy mud from unit 8. Poorly preserved spreite is composed of host clay and, locally, fine sand derived from adjacent laminae. (D) Proximal, subvertical part of U-burrow manifest in clay along a slickensided joint surface. Arrows indicate limbs of the U-tube. (E) Bedding-parallel expression of oblique segment of *Rhizocorallium* passing through fine sand laminae. Spreite (bounded by dashed lines) in this segment of the structure includes alternating clay and fine sand packets. (F) Close-up of specimen in clay showing scratch marks on U-tube and bundled ridges and grooves on spreite exterior.

Fig. 5. Dimensions and orientations of *Rhizocorallium* in Ingersoll shale. (A) Tube diameter versus U-tube width for the 22 specimens examined. In the two longest specimens (open circles and squares), both parameters increase distally, indicating progressive growth of the tracemakers. (B) Limited data on the bearing of specimens (n = 11), measured in the direction of the distal U-bend. Bearings show a significant spread to the northeast through northwest with a modal orientation of north-northwest (N8-10W).

Fig. 6. Summary of major morphotypes of *Rhizocorallium* and their potential progenitors, substrate associations, and ichnofacies affiliations based on Knaust (2013). The Ingersoll

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

514 specimens, best ascribed to *R. commune* var. *irregulare*, represent the firmground

515 *Glossifungites* ichnofacies.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

	A	B	C	D	E
Ichno-taxonomy	<i>R. jenense</i> ¹	<i>R. commune</i> var. <i>irregulare</i> ¹ (= <i>R. irregulare</i> ²)	<i>R. commune</i> var. <i>auriforme</i> ¹	<i>R. commune</i> var. <i>problematica</i> ¹	<i>R. commune</i> var. <i>uliansensis</i> ¹ (= <i>R. uliansensis</i> ²)
General Spreite Form	Short, variably inclined	Long, straight to winding, horizontal to slightly inclined	Short, typically slightly inclined	Horizontal to slightly inclined, vertically retrusive	Trochospiral
Fill	Passive, no pellets	Typically active fill; may or may not be pelleted			
Bioglyphs	Closely-spaced, net-like scratches	If present, scratch marks are more or less parallel and widely spaced			
Producers	Suspension-feeding polychaetes, crustaceans, insects	Deposit- and/or suspension-feeding polychaetes or crustaceans			
Substrate	Firmground	Softground to firmground			
Ichnofacies	<i>Glossifungites</i>	<i>Cruziana</i> or <i>Glossifungites</i>			

¹Knaust (2013), ²Fürsich (1974)