TREMICHNUS: A NEW ICHNOGENUS OF CIRCULAR-PARABOLIC PITS IN FOSSIL ECHINODERMS

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ABSTRACT—The new ichnogenus *Tremichnus* is proposed to include simple circular-parabolic pits, with or without associated stereom swellings, on fossil echinoderms, primarily crinoids. *Tremichnus* is a common trace fossil that is largely confined to columns and calyces of Paleozoic crinoids; the ichnogenus ranges at least from Middle Ordovician to Permian, and perhaps into the Mesozoic. Four new ichnospecies are also defined: *T. paraboloides,* the type species, comprising deep circular-parabolic pits, 0.15–3.5 mm, without associated gall-like swellings; *T. cysticus,* similar, though smaller pits surrounded by cystose masses of stereomatic secretion; *T. minutus,* uniformly small, non-overlapping pits commonly surrounded by raised rims; and *T. puteolus,* very large, shallow pits generally with a concentric inner ring-like groove. A similarly large pit, *T.* sp. aff. *T. puteolus* occurs on diploporitan cystoids.

Review of mode of occurrence of these pits suggests that *Tremichnus* was the work of a sessile, host-selective epibiont, probably a parasite or a commensalistic filter feeder. The pits were apparently produced by a combination of embedment (i.e., inhibition of stereom growth) and some true boring (i.e., removal of stereom).

INTRODUCTION

A VARIETY of epizoans produced borings, embedment structures and deformations in the skeletons of Paleozoic crinoids. At least seven distinctive types of epibiont deformation have previously been recognized (Franzén, 1974; Brett, 1978a). To date, only one of these traces has been formally named as an ichnofossil, i.e., *Schizoproboscina* (Arendt, 1961); others have been informally ascribed to the activities of particular taxonomic groups, e.g., gall-like swellings produced by *Phosphannulus* (Welch, 1976) or barnacle borings (Branson, 1964). The most abundant type of trace fossil in crinoids consists of circular to parabolic pits, with or without associated deformation (Franzén, 1974; Brett, 1978a). I previously used the nontaxonomic and noncommittal term circular-parabolic pits or simply pits in referring to these structures (Brett, 1978a). However, the term "pits" is vague and "circular-parabolic pits" becomes an awkward and unaesthetic name for these common structures. It is necessary to carefully distinguish this type of trace from the several other forms of deformation that may occur in fossil crinoids; thus, a name is needed for the structures.

The pits under discussion constitute a widespread and readily recognized Paleozoic trace fossil. Furthermore, such informal terms as pits are omitted from ichnological listings (e.g., Volume W of the *Treatise on Invertebrate Paleontology*). Consequently, following Osgood's (1979) maxim "trace fossils must be named to survive," it is fitting that this category of parabolic pits be given formal ichnogeneric status.

Brett (1978a, p. 219) argued that the term *Myzostomites,* sometimes applied to this catence (BMS), the Royal Ontario Museum Häntzschel, 1975), is misleading and should be abandoned, since these pits are quite unlike myzostomid galls or cysts and were almost certainly produced by a wholly different type of organism. Misleading implications alone cannot be grounds for discarding particular ichnogeneric terms. Hence, a review of the history of the term *Myzostomites* is in order.

Clarke (1921, p. 58) was apparently the first author to use the term Myzostomites (not italicized) in reference to deformations in fossil crinoids. He did not propose a type species, or holotype specimen, nor is it clear that he intended Mysostomites to be a formal generic name. Moreover, the sense in which Clarke meant the term is ambiguous. In the text, he used Myzostomites as a synonym of myzostomid galls, implying reference to the traces. However, in the caption for fig. 46, on page 59, he described "a crinoid stem from the Carboniferous with deep pits over the surface which may be *due to the work of Myzosto-*

mites" (italics mine), implying the trace maker. Also, it is clear from his discussion that Clarke had reservations about applying the name Myzostomites to all pits (or pit-formers) in Paleozoic crinoids, including the specimen he figured. Thus, for example, he wrote (1921, p. 58): "On the columns of Paleozoic crinoids, small gall-like protuberances are occasionally found, with a central perforation, and several authors have ascribed these to the Myzostomum. These [supposed] Myzostomid galls (Myzostomites) have been recorded from rocks as early as the Upper Ordovician, but we must confess to knowing very little about them, and some of the pittings and depressions on crinoid columns which have been thought to be the inner cavities of Myzostomid cysts are doubtless of other origin."

Nonetheless, in reviewing various fossil problematica, Howell (1962, p. 167) selected Clarke's figure 46, the pitted crinoid stem, as an informal "type" of "*Myzostomites clarkei*" Howell. He also used Clarke's caption definition of *Myzostomites,* for he gave the following diagnosis (Howell, 1962, p. 167): "*Formed* small, gall-like protuberances, with central perforations, on columns of crinoids" (italics mine). Howell thus implied that the term *Myzostomites* should refer to the trace maker. He did not formally designate a holotype specimen as, indeed, he could not since *Myzostomites,* by his definition, refers to a hypothetical, soft-bodied myzostomid worm. Häntzschel (1975) accepted Howell's *M. clarkei* as the type genus, but redefined *Myzostomites* as an ichnogenus referring to gall-like swelling on crinoid stems, each with a central perforation. Nonetheless, *Myzostomites clarkei* Howell is a *nomen nudum,* for three reasons: 1) it was never formally described, 2) no holotype was designated, and 3) it refers to a hypothetical organism. This leaves *Myzostomites* as an informal, undefined taxon. Ironically, even if, by fortuitous preservation, a fossil "worm" were to be found associated with the pits, which could then serve as a lectotype for *M. clarkei,* the term *Myzostomites* could not correctly be applied to the pits or gall traces in Häntzschel's sense. Bromley (1970, 1981) has recently emphasized that trace fossils must be given names independent of those of the known or supposed trace maker. For these reasons, and because of the ambiguity of Clarke's original definition, *Myzostomites* is best discarded as a formal term.

A new ichnogenus, *Tremichnus,* is proposed herein to accommodate circular-parabolic pits in crinoids. This taxon, therefore, includes traces of the type which Häntzschel (1975) included in *Myzostomites* and others which do not show associated deformation. The two types have previously been shown to be intergradational (Brett, 1978a).

REPOSITORIES

Specimens described in the present paper are reposited in the Buffalo Museum of Science (BMS), the Royal Ontario Museum (ROM), the University of Michigan Museum of Paleontology (UMMP) and the American Museum of Natural History (AMNH).

SYSTEMATIC PALEONTOLOGY

Ichnogenus TREMICHNUS n. gen.

Type species. — *Tremichnus paraboloides* n. ichnospecies.

Diagnosis. — Circular pits or embedment structures of varying diameter (about 0.1 to 4.0 mm) occurring on the plates of echinoderms, primarily crinoids, with or without associated thickening or gall-like deformation of the plates. Pits regularly parabolic in cross section, with diameter/depth ratios variable from about 0.1–1.0; no internal expansion or other ramifications. Holes always oriented perpendicularly to external plate surfaces, tapering inward; generally not penetrating through plates. Adjacent pits may overlap one another.

Remarks. — This diagnosis of *Tremichnus* differs from that of Häntzschel's (1975) "*Myzostomites*", primarily in emphasizing the parabolic pits rather than swellings of crinoid stereom. The swellings are a reaction of the host and are not invariably associated with the pits. In contrast, the pits occurring on a given host species are relatively consistent in morphology, whether or not they are associated with swellings. The diagnosis "gall-like protuberances on crinoid stems with a central perforation" (Häntzschel, 1975, p. 129) is best reserved for types of deformation (e.g., see Warn, 1974; Welch, 1976) other than *Tremichnus.*

Tremichnus is morphologically most similar to the newly defined ichnogenus *Oichnus* (Bromley, 1981). However, the latter is de-

fined as "circular to subcircular holes of bio-
genic origin bored into hard substrates."
Considerable evidence suggests that the pits
in crinoid plates, here designated *Tremich-
nus,* were formed largely, or entirely, by local
inhibition of stereom growth (Franzén, 1974).
This is particularly evident where the holes
are centered on gall-like swellings. Thus, they
are embedment structures, or more probably,
combined embedment-borings (see below),
rather than simple boreholes. Furthermore,
Oichnus is never associated with other de-
formation, the holes rarely overlap one
another, and they frequently penetrate
through the substrate. *Tremichnus* pits, on
the other hand, frequently overlap one
another, are often associated with deforma-
tions and rarely penetrate the substrate.
Rather, these traces appear to be uniquely
associated with the stereom of crinoids and
evidence for host specificity (Brett, 1978a)
suggests an obligatory relationship between
the producers of this trace and crinoids.
Tremichnus differs from *Schizoproboscina*
Arendt, the only other named ichnogenus of
crinoid pits, in that the latter consists of paired
holes connected by an internal U-shaped ca-
nal; *Schizoproboscina* also occurs exclusively
on the arms of (Carboniferous) crinoids.

Etymology.—Trema, pore or cavity, *ich-
nus,* trace.

TREMICHNUS PARABOLOIDES n. ichnosp.
Figures 1, 2

*Diagnosis.—*Pits, circular, regularly and
smoothly parabolic in cross section; about as
deep as wide (depth/diameter ratio: 0.9);
ranging in size from 0.1–3.6 mm in diameter
($\bar{x} = 0.95$ mm, SD $= 0.65$, N $= 529$ pits); up
to 100 pits of varying size may occur on a
single calyx. Pit apertures sharply demarcat-
ed, flush; never beveled or surrounded by a
raised rim or gall-like outgrowth, pits rarely
associated with vague swelling of the under-
lying stereom; pits frequently intersecting at
borders.

*Types.—*Pits in *Icthyocrinus laevis* Conrad;
lower Rochester Shale; Niagara Gorge at
Lewiston, New York. Holotype: BMS
E23971; paratypes: BMS E23968-23970.

*Remarks.—*Traces herein assigned to
Tremichnus paraboloides n. ichnosp., com-
prising types 1 and 2 of Brett (1978a), are
known to occur only in the calyces of cri-
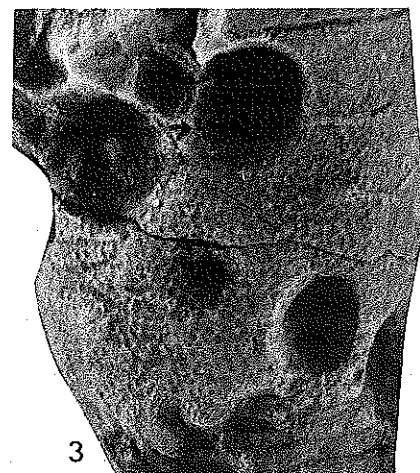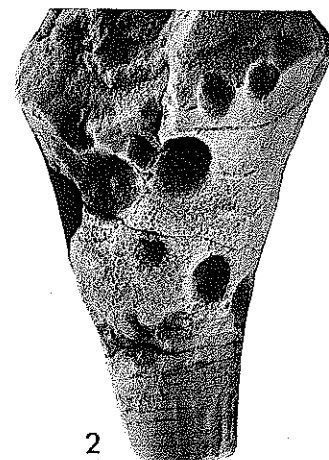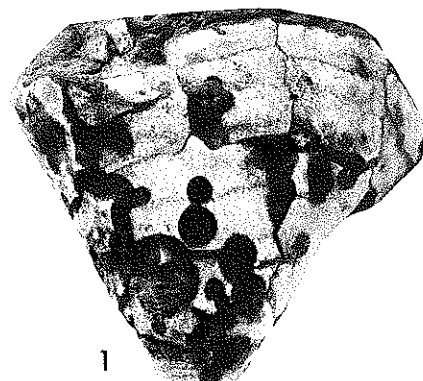noids. Thus far they have been reported in

FIGURE *1—Tremichnus paraboloides* n. ichnosp.,
circular-parabolic embedment pits in *Icthyocri-
nus laevis* Conrad, Rochester Shale, Lewiston,
Niagara County, New York. *1,* BMS E23970,
note varying sizes of pits and overlap between
adjacent holes, ×3. *2, 3,* BMS E23971, holo-
type, pits on calyx and proxistele, note slight
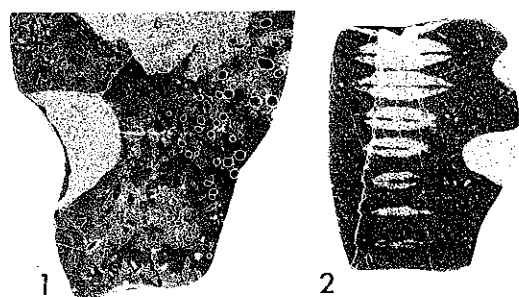swelling of stereom in vicinity of pits, ×3, ×6.

FIGURE 2—Longitudinal (axial) sections of *Trem-ichnus* pits in Silurian crinoids, illustrating pro-file appearance of pits, prints made from acetate peels. *1,* BMS E23972, *Tremichnus parabo-loides* n. ichnosp., large pit (3.2 mm maximum diameter) near base of a calyx of *Icthyocrinus laevis* Conrad; note smoothly parabolic outline, pit does not intercept crinoid thecal cavity, Rochester Shale, Niagara Gorge, Lewiston, Ni-agara County, New York, ×5. *2, T. cysticus* n. ichnosp., BMS E25006; sections of two pits of typical size (2.1, 1.7 mm maximum diameter) on a deformed crinoid column; note that pits are located in a gall-like swelling of the colum-nals, section of upper pit is not axial, Rochester Shale, Thrall Road cut Cambria, Niagara Coun-ty, New York, ×4.

Icthyocrinus (Silurian), *Synaptocrinus* (Mid-dle Devonian) and various calceocrinids (Paul, 1971, p. 41; Brett, 1978a).

Pits tentatively identified as *T.* cf. *para-boloides* occur in calyx plates and arms of *Carabocrinus* from the Middle Ordovician (Caradocian) Bromide Formation (Lewis, 1982, Pl. 3, figs. 18–20). Simple parabolic pits also occur in certain Silurian and Devonian cladid inadunates, e.g., *Gissocrinus* (Bather, 1893, Pl. 10, fig. 353) and *Cupressocrinites* (Sieverts, 1934; Sieverts-Dorek, 1963). Sim-ilar pits have been observed on several Mis-sissippian crinoids, notably platycrinitids (Brett, personal observ.).

Range. — Middle Ordovician?; Silurian (Wenlockian)–Middle Devonian (Givetian); Mississippian?.

Etymology.—Paraboloides, in reference to the regularly parabolic cross section.

TREMICHNUS CYSTICUS n. ichnosp.
Myzostomites clarkei Howell
Figures 3, 4

Diagnosis. — Circular parabolic pits resem-bling *T. paraboloides* but exhibiting a nar-
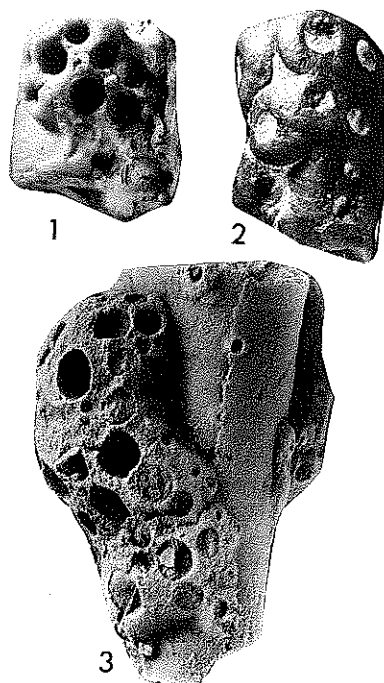

FIGURE 3—*Tremichnus cysticus* n. ichnosp., embedment pits surrounded by gall-like stere-om outgrowths. *1,* BMS E25004, crinoid col-umn from Gasport Limestone (Lockport Group), Craine Street quarry, Lockport, Niagara Coun-ty, New York, ×2.0. *2,* BMS E25005; highly deformed pluricolumnal, Rochester Shale, Ni-agara Gorge, Lewiston, Niagara County, New York, ×2.0. *3,* UMMP 63784, holotype, pen-tameric column, probably belonging to *Dendro-crinus,* with gall-like swelling surrounding cir-cular pits, Rochester Shale, Thrall Road cut, Cambria, Niagara County, New York, ×4.

rower range of diameters, 0.3–2.4 mm ($\bar{x} =$ 1.21, SD = 0.50, N = 110 pits), and occur-ring centered on gall-like swellings of crinoid stereom. Pits rarely overlap.

Types. — Pits in crinoid columns; Silurian Rochester Shale and Gasport Limestone. Ho-lotype, BMS E29375; paratypes, BMS E25004 and 25005.

Remarks. — This morphotype is equivalent to "*Myzostomites clarkei*" and matches the diagnosis of *Myzostomites.* It is quite possi-bly a local variant of the trace *T. paraboloides* and rarely appears to be gradational with the latter. The gall-like swellings clearly reflect a behavioral response of the crinoid host rather than a behavioral feature of the trace-maker.

T. cysticus is most common on certain types of crinoid columns, particularly the pentameric stems of *Dendrocrinus* spp. (Brett, 1978b). It has also been observed on the calyces of *Dendrocrinus* (two examples), and a single example, assignable to this ichnospecies, has been noted on *Eucalyptocrinites* (Brett, 1978a, p. 236, fig. 8). Pits with gall-like swellings in crinoid columns probably referable to *T. cysticus* have been reported from the Silurian (Wenlockian) of Gotland and the Devonian of Morocco (Franzén, 1974, figs. 1A, 1B, 5–14); from the Carboniferous of Great Britain (Etheridge, 1933) and from the Pennsylvanian of the North American mid-continent (Girty, 1915; Branson, 1964).

The taxon "*Cystocrinus tennesseensis* Roemer" reported from the Silurian Brownsport Formation (see Roemer, 1860) consists of crinoid pluricolumnals that are deformed by gall-like swellings and pits referable to *Tremichnus cysticus.*

Range.—Silurian (Wenlockian)–Carboniferous.

Etymology.—*Cysticus,* emphasizes the association with cyst-like stereom swellings.

FIGURE *4*—*Tremichnus minutus* n. ichnosp., minute, subequal-sized pits in *Eucalyptocrinites caelatus* (Hall), BMS E23974, holotype, pits on tegminal partition plates, Rochester Shale, Middleport, Niagara County, New York, ×2.0.

TREMICHNUS MINUTUS n. ichnosp.
Figures 4, 5

Diagnosis.—Small, shallow pits, typically aligned along crinoid sutures; pits generally uniform in size, ranging from 0.5–1.0 mm ($\bar{x} = 0.69$, SD $= 0.16$, N $= 124$; 80–100 pits per calyx, maximum); holes rarely, if ever, overlap one another; apertures sharp to slightly rounded; may be surrounded by low rims (Figure 5).

Types.—Pits on *Eucalyptocrinites caelatus*; Silurian (Wenlockian) Rochester Shale; Middleport, New York. Holotype, BMS E23974; paratype, AMNH 1721.

Remarks.—Pits of the *T. minutus* morphotype have been observed on crinoids of the Eucalyptocrinitidae. This ichnospecies differs from *T. paraboloides* in the absence of overlap between adjacent pits, the frequent presence of raised rims, and, when observed in groups, the uniformly small size of the holes.

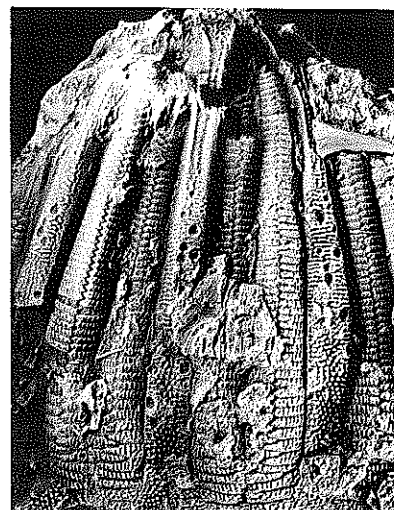Pits of the *T. minutus* type have been illustrated from spines of *Calliocrinus* and an unidentified camerate from the Silurian of Gotland (Franzén, 1974; figs. 1C, 4) and from the Devonian inadunate *Nuxocrinus* (McIntosh, 1983; fig. 3K, L). Bromley (1981, Pl. 1, figs. 1, 2) illustrated the test of a Cretaceous echinoid (*Echinocorys*) that is riddled with some 760 parabolic pits of slightly varying small size (about 0.4–1.0 mm diameter). These structures may represent embedment-borings comparable to *Tremichnus* and they are of approximately the same size range as *T. minutus,* but, in contrast to this ichnospecies, many pits on the Cretaceous echinoid overlap one another. However, assignment of these pits to either *Oichnus* or *Tremichnus* is deferred at present, pending closer examination of this and other pitted echinoid material.

Range.—Silurian (Wenlockian)–Middle Devonian (Givetian).

Etymology.—*Minutus,* in allusion to the uniformly small size of the pits.

TREMICHNUS PUTEOLUS n. ichnosp.
Figure 6

Diagnosis.—Moderate to large compared with *T. paraboloides, T. cysticus* or *T. minutus,* 0.5–4.0 mm diameter, ($\bar{x} = 1.61$, SD $= 0.99$, N $= 22$); few (maximum 7) pits per calyx; shallow pits (depth/diameter ratio
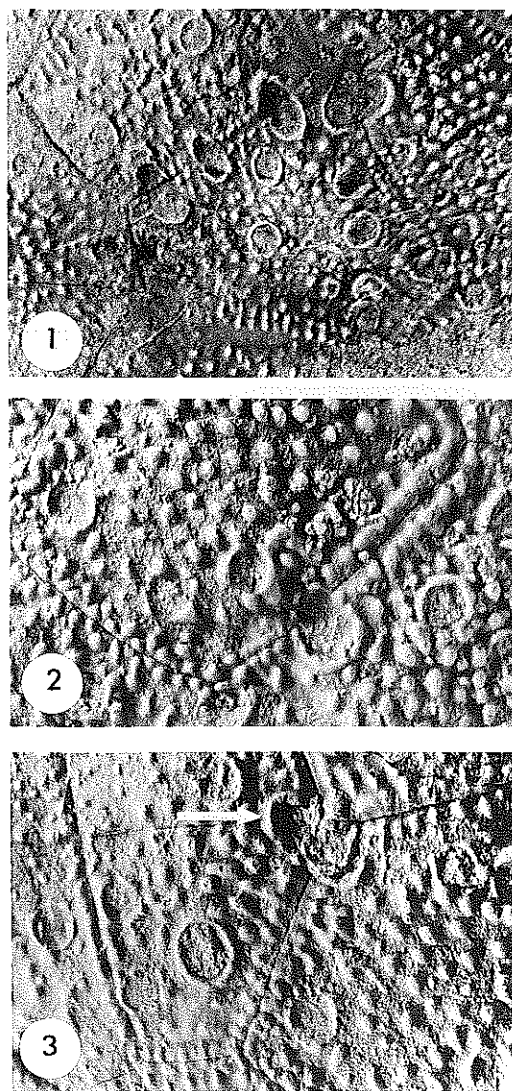
FIGURE 5—*Tremichnus minutus*, pits surrounded by circular rims of secondary stereom, on *Eucalyptocrinites caelatus* (Hall) (specimen is holotype of *Eucalyptocrinus papulosus* Hall), Rochester Shale, Salmon Creek, Sweden, Monroe County, New York, AMNH 1721. *1*, view showing contrast between circular pits centered on plates, and elliptical shaped pits located along plate sutures, distortion of *T. minutus* outlines produced by accretionary growth of plates, ×6. *2*, enlargement, showing details of pit rims, note that rims in certain cases blend laterally into tubercular ornamentation, indicating similar origin by secondary stereomic secretion, ×8. *3*, detail of rimmed *T. minutus* pits, note disruption of pit outline along triple junction of three plates (arrow), ×8. Figure *1* reprinted from Brett, 1978a, by permission of Lethaia.

1:6); typically with flattened, slightly irregular floors. Pits exhibit a faint and often incomplete ring (circular groove), concentric with outer borders; generally 0.2–0.5 mm inward from main border, but may occur outside outer border; pits frequently intersect.

Types.—Pits occurring in *Asaphocrinus ornatus* (Hall) and *Lecanocrinus macropetalus* Hall; Rochester Shale, St. Catharines, Ontario. Holotype, ROM 35801; paratype, USNM S1613.

Remarks.—At larger sizes this is a very distinctive morphotype, readily distinguished from all other *Tremichnus* by its shallow, broad profile and by the frequent presence of a concentric ring. However, it may be indistinguishable from *T. paraboloides* at smaller sizes (<1.0 mm). This unique trace has been recognized only on two species of Silurian crinoids, *Asaphocrinus ornatus* (Hall) and *Lecanocrinus macropetalus* Hall (one specimen).

However, comparably large, shallow pits apparently lacking concentric rings are present in certain other crinoid species, including *Icthyocrinus pyriformis* and *I. gothlandicus* (Springer, 1920, Pl. 32, figs. 116, 12a, b) in the Silurian and several late Paleozoic forms, such as the inadunate *Delocrinus* (Moore and Plummer, 1940), the flexible crinoid *Amphicrinus* (Brett, 1978a) and the blastoid *Pentremites robustus* (J. A. Waters, personal commun.). Ichnogeneric assignment of these traces requires further morphological study.

Range.—Silurian (Wenlockian); (possibly Silurian–Carboniferous).

Etymology.—*Puteolus*, Greek; a pit or shallow excavation.

TREMICHNUS sp. aff. T. PUTEOLUS

Diagnosis.—Large, shallow, hemispherical pits (diameter 3.5–4.0 mm; maximum depth about 2 mm); resembling pits of *T. puteolus*, but lacking concentric ring, more uniform in size and sometimes surrounded by raised rims.

Types.—Pits occurring on *Holocystites scutellatus* Hall; holotype, FMNH 5998; paratype, FMNH 8764; see Paul (1971, figs. 38A, 37A) for illustrations.

Remarks.—This large form of *Tremichnus* is found in numerous specimens of holocystitid diploporitans, especially from the Osgood Shale of Indiana. Virtually identical pits
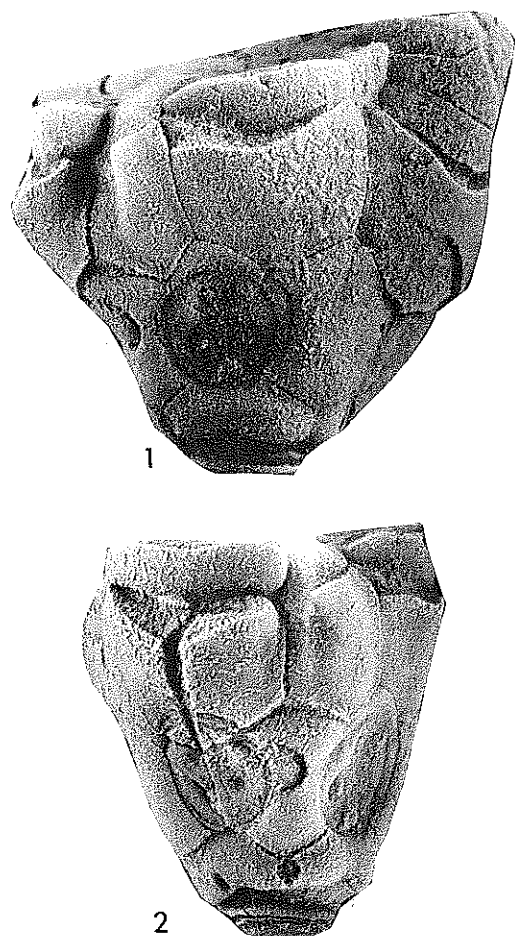
FIGURE 6—*Tremichnus puteolus* n. ichnosp., shallow embedment pits in *Asaphocrinus ornatus* Hall, note concentric ring. *1, 2,* ROM 35801, holotype, Rochester Shale, DeCew Falls, St. Catharines, Ontario, both views ×5. Figure reprinted from Brett, 1978a, by permission of Lethaia.

occur on species of *Holocystites* (*H. abnormis* Hall, *H. scutellatus* Hall), *Pentacystis simplex* Paul, *Trematocystis rotundus* Miller, *T. wetherbyi* Miller and *Pustulocytis ornatissimus* Miller. The pits may exhibit a selective distribution on one side of the cystoid thecae. These cases are currently the only known examples of *Tremichnus* pits on blastozoans. (See Paul, 1971, and Frest et al., 1977, for thorough accounts of these forms.)

Range.—Silurian (Wenlockian).

MODE OF FORMATION OF *TREMICHNUS* PITS AND PALEOECOLOGY OF THEIR PRODUCERS

Borings and embedment structures, like other types of trace fossils, may provide considerable indirect evidence of the ethology, ecology, and evolution of their producers (Bromley, 1970; Frey, 1975). In the case of ichnofossils in echinoderms, the distribution and morphology of the holes may ultimately reflect not only the life-modes of the tracemakers but also the behavior of their substrates—living mesodermal tissue.

Parabolic holes of the *Tremichnus*-type could conceivably have been formed by either of two mechanisms, or a combination thereof. Bromley (1970) distinguished between borings, which are chemical or mechanical excavations produced by organisms, and embedment structures, which are formed by the secretion of skeletal material of a live host around an epizoan (see Cameron, 1969, for discussion).

The endoskeletal plates of echinoderms are dynamic structures containing calcigenic stromal cells that are capable of reacting to injuries or infestations by other organisms. Thus, it is possible that if an epizoan settled on a crinoid and possessed a chemical secretion that inhibited stereom growth, it could form a pit by simply occupying a site during normal or secondary growth of the crinoid plates.

On the other hand, pits could have been produced by the etching or mechanical rasping action of boring organisms such as gastropods (Carriker and Yochelson, 1968) or certain annelids, sponges, bryozoans, and barnacles. Such pits, examples of true borings, could occur in echinoderms as well as in exoskeletons of various other invertebrates, and might be expected to occasionally penetrate the calcite walls. Finally, it is possible that pits observed in crinozoans were produced by a combination of true boring by the epizoans and growth of the host's stereom, thus, embedment. This would result from rather gradual rates of etching by the boring organism, as opposed to the relatively rapid boring of gastropods (Carriker and Yochelson, 1968, report that holes are drilled by snails in a matter of hours). Unfortunately, no data are available on the rates of primary or secondary secretion in crinoids, although

some idea of the relative rates of secretion and penetration can be inferred from fossil material at hand.

Nearly all of the large pits occur in particularly thick areas of the crinoid skeleton such that they do not penetrate through the plates. Indeed, some occur centered on galls of secondary stereom. This is probably not coincidental, but strongly suggests that the pits were produced largely by embedment, through growth of stereom around the epizoan.

Further evidence for embedment is provided by specimens in which small pits fall on the sutures between calyx plates. This is well illustrated in specimens of *Eucalyptocrinites* with *Tremichnus minutus*. Such pits have elliptical outlines, in contrast to pits occurring away from the plate margins that are perfectly circular (Figure 5). The pits in these specimens are surrounded by low rims of stereom. These walls diminish in height toward plate sutures. Two examples of pits located on junctions among three plates are known (Figure 5.3). Here, the pit outlines are not merely elongated but have a three-part configuration. These specimens demonstrate occupation of the pit sites by epizoans during plate growth. Accretion of new calcite along the plate margins had the effect of stretching the area occupied by the epizoan, which was normally circular (as demonstrated by specimens not on sutures), to an elliptical shape. Concommitent distortion of the body of the epizoan may have taken place. However, in at least one case, the presence of an inner rim within the deformed elliptical outline of the old pit suggests that the epizoan remained in place during rifting of its former occupation site. Here again, the crinoid apparently reacted to the epizoan by secreting a new rim about it. This example illustrates that, in part, pits result from inhibition of growth of new stereom by the epizoan. Significantly, here increase in radius of the parabolic pit proceeded at a rate slower than or equal to the growth of the plate margins, therefore producing an elliptical shape.

Nevertheless, this is the exception rather than the rule. Most pits occurring on sutures of crinoids, including many *Eucalyptocrinites,* are circular in outline. This implies that the hole-forming process (whatever it was) out-completed skeletal accretion along the

plate boundaries. This, in turn, requires the removal of previously secreted stereom, and thus implies some true boring activity.

True boring is also indicated by another line of evidence. Two specimens of *Icthyocrinus* that were sectioned show a single large pit actually penetrating through the plates. This phenomenon cannot be accounted for by simple embedment processes.

Finally, Paul (1971) argued that pits on diploporitans (herein referred to as *Tremichnus* sp. aff. *T. puteolus*) represent boring or etching, in part. Paul concluded that the pits were produced by parasitic(?) organisms in living hosts, as evidenced by their preferential distribution on the cystoid thecae and by reorientation of humatipores beneath pits. However, he noted that "clearly plate material has been dissolved or scraped away from the sites of the pits," based on truncation of thecal pore structures (Paul, 1971, p. 39). On the other hand, common presence of rims around many of these pits and the fact that they never penetrate plates are, again, suggestive of embedment, in part.

These varying lines of evidence suggest that epizoans of roughly circular outline produced pits in crinoids by a complex process involving both local inhibition of stereom formation (embedment) and some actual removal of preexisting stereom.

Of particular interest to the interpretation of life modes of the epizoans is the question of whether they were sessile or vagrant. Most active boring organisms are parasites or predators that produce holes to obtain food. Such organisms generally produce only one or at most a very few holes in their prey (or host) organisms (Carriker and Yochelson, 1968). Melanellid gastropods parasitic on Recent crinoids are semi-sessile, moving occasionally from place to place on the calyces and arms of their hosts and boring through the plates to derive food from the host's body fluids and tissues (A. H. Clark, 1921; Vaney, 1913; Fishelson, 1974). These gastropods produce only a relatively small number of roughly equal-sized holes that penetrate the plates. In certain instances, the gastropods do remain sessile long enough to allow the crinoid host to produce a stereom swelling around the borehole (see Frest et al., 1977, p. 106).

Although it is possible that some boring

organisms might produce a few trial pits in locating favorable drilling sites, it is quite unlikely that they would expend large amounts of energy to produce numerous small pits instead of a single large hole. Some specimens of *Icthyocrinus* may have as many as 80 minute holes. Furthermore, large and small holes frequently occur on the same plates—usually in the thickest areas of the calyx. Thus, the hypothesis of trial-and-error boring for producing the observed patterns is rejected.

Moreover, since some *T. minutus* pits on *Eucalyptocrinites* have been distorted by growth of the crinoid plates containing them, it is implicit that these holes were occupied and their borders maintained for considerable time periods relative to the life of the crinoids. Evidence for sessility in the *Tremichnus*-formers on *Icthyocrinus* and other species is less conclusive; however, a sedentary mode of existence is suggested by several other observations. Thickening and distortion of crinoid plates in the vicinity of pits has been observed in several specimens of *Icthyocrinus*. This and other evidence of embedment of pit-formers in the stereom suggests that the latter organisms remained fixed during plate growth. The sharply defined outer boundaries of most pits on *Icthyocrinus* and other crinoids provide a second line of evidence for a sessile habit in the epizoans. Exceptional cases in which holes have been partially refilled by new stereom growth (Figure 1.3) indicate that crinoids were capable of healing the pits if they were not maintained by the epizoans. Thus, there is circumstantial evidence that most pits were occupied by their producers up to the time of death of the host.

A possible argument against this interpretation is the occurrence of overlap between pits on many crinoids. In general, modern organisms that produce borings as living sites tend to avoid interference with adjacent individuals (Prell, 1926; Evans, 1969). However, the author has observed numerous examples of overlap between *Trypanites* borings on hardground surfaces. These borings were clearly domichnia, not feeding traces of active organisms. There are two possible explanations for such overlap. Either 1) one of the pits was unoccupied by its former inhabitant prior to overlap; or 2) pits that were initially separated converged as the inhabit-

ants increased in size and produced correspondingly larger and deeper holes. Both members of an overlapped pair of *Tremichnus* pits on crinoid plates are usually sharply defined holes indicating that both were occupied by epizoans. Thus, the first alternative seems doubtful. Overlap generally involves at least one moderately large hole. The minute pits rarely touch one another. This suggests that during initial settlement the epizoans were spaced such that they did not interfere with one another. As noted previously, areas of overlap in larger pits are usually rather small, such that mutual interference was probably slight. These lines of evidence favor the second explanation.

The overall size-frequency distribution of pits from a roughly contemporaneous group of *Icthyocrinus* (see Brett, 1978a, fig. 4) is strikingly similar to right-skewed distributions characteristic of many marine invertebrates with high infant mortality. Observed cases of bimodality in the size distribution of pits on single calyces of *Asaphocrinus, Icthyocrinus* and calceocrinids may reflect two generations of pit-formers. Largest holes presumably represent occupation sites of large (mature) individuals while smaller pits may have been produced by a second generation of later settling epizoans. Notably, such bimodal distributions have only been observed on large crinoid calyces. Smaller specimens typically bear only a few relatively large holes, indicating the presence of only a single generation.

The probable mode of life of the producers of *Tremichnus* pits on crinoids can be summarized as follows: they were populations of relatively sedentary organisms, which lived selectively on the surfaces of certain echinoderm species. Paul (1971) and Brett (1978a) argued that these organisms were host-specific epizoans. *Tremichnus* were evidently harmful to their hosts, at times. In a trophic sense, these organisms may have been truly parasitic; by analogy with Recent gastropods parasitic in crinoids, Paul (1971, p. 40) and Frest et al. (1977, p. 106) suggested that the organisms may have derived some nourishment from the hosts' stromal tissues. Conversely, the epibionts may have been merely commensalistic forms, perhaps filter feeders (Brett, 1978a).

Finally, the possibility remains that differ-

ent ichnospecies reflect organisms with slightly different life modes; broad shallow pits might represent parasitic forms and more deeply conical *Tremichnus* were strictly commensals. In any case, both kinds were strongly host-specific and coevolved with their hosts.

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