

Lower Cambrian trace fossil evidence for predation on trilobites

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Predation upon trilobites previously has been inferred from large coprolites containing trilobite fragments, and from specimens of trilobites with healed wounds. The discovery of large burrows (*Dolopichnus gulosus*, n. ichnogen., n. ichnosp.) in micritic quartz arenite of the Lower Cambrian Poleta Formation in Esmeralda County, Nevada, suggests that sea anemones preyed upon trilobites. *Dolopichnus* n. ichnogen., vertical cylindrical burrows with a central cylindrical core, is interpreted as dwelling burrows of sea anemones. In the specimens studied, the core contains coarser-grained material, and in one series of burrows, is composed of trilobite fragments and micrite pellets, cemented with sparite. The central cylinder is interpreted to be a cast of the sea anemone's coelenteron, which in some specimens contains stomach contents.

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Lower Cambrian rocks of southern Esmeralda County, Nevada, contain large burrows that indicate sea anemones preyed upon trilobites. The locality (Locality 52 of Stewart 1970:173; UCLA Locality 6164) is in the NE 1/4 of sec. 33 and NW 1/4 of sec. 34, T. 6 S., R. 42 E. (unsurveyed), Mount Jackson, Nevada quadrangle (USGS 7.5 minute, 1968), about 4.5 miles S 9° E of the junction of State Routes 3 and 71, in the hills northeast of Mount Dunfee. The burrows are present in two quartz arenite beds of the quartzite unit of the Upper Member of the Poleta Formation (Middle Member of Stewart 1970:59), 55 feet and 110 feet below the base of the upper limestone unit. Trilobite fragments occur in the burrows of the upper bed.

Similar burrows were observed in the same unit of the Poleta Formation on the west side of Eureka Valley, Inyo County, California (Locality 3 of Stewart 1970:71), and are reported from the Upper Member of the Wood Canyon Formation (Lower Cambrian) in the Nopah Range, Death Valley area, California (Langille 1974).

The abundance of trilobites in the early Paleozoic is well established, but there is only

sparse evidence suggesting the presence of their predators. Large coprolites containing trilobite fragments have been reported in the Lower Cambrian of New Brunswick by Matthew (1891:154-155; summarized by Dawson 1894: 50-51). Matthew suggested that squids were responsible for the coprolites (and for other markings, now interpreted as inorganic) and that they preyed upon trilobites, which had spines for protection against such predators. Additional coprolites, 5 and 9 cm wide, have been reported by Durham (1971) in the Lower Cambrian Poleta Formation of the White-Inyo Mountains, California.

Predators may have inflicted wounds on trilobites, and several examples of trilobites with healed wounds are known (Harrington 1959:O107). An additional case has been found in the Lower Cambrian Latham Shale at Cadiz, California, where a specimen of *Paedeumias clarki* Resser (Fig. 1) lost a part of the left side of its cephalon; the wound healed, with the anterior margin inflected inward.

The large dwelling burrows described below indicate that Early Cambrian sea anemones were sessile predators of trilobites.

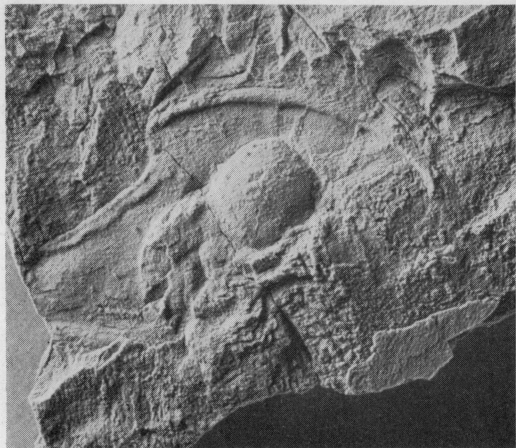


Fig. 1. *Paedeumias clarki* Resser, exhibiting healed wound on left side of cephalon. UCLA 49507. Collected by T. R. Fairchild from Latham Shale, Cadiz, California, UCLA Locality 3376. $\times 3$.

Dolopichnus gulosus n. ichnogen.,
n. ichnosp.

Figs. 2-6.

Holotype. – UCLA 49508, Figs. 3A, B.

Paratypes. – UCLA 49509-49511, Figs. 4-6.

Name. – From the Greek *dolopos*, ambusher, plus *ichnos*, and the Latin *gulosus*, greedy, gluttonous.

Morphologic description

Large, vertical burrows are expressed as circular depressions randomly distributed on exposed bedding surfaces of quartz arenite of the Poleta Formation (Fig. 2). Two or more burrows are commonly in contact. The burrows are cylindrical to slightly conical, and 20-50 mm in diameter, most commonly 25 mm. The maximum height observed is 200 mm. Laminae in the quartz arenite bend downward around the burrows (Fig. 5A), and form concentric rings around the burrows on the upper bedding surface (Fig. 3B), making the burrows appear larger than their actual diameter.

The bottom of one large burrow (Fig. 3A) is a flattened hemisphere with concentric impressions and a shallow central depression, as in the genus *Bergaueria* Prantl (Alpert 1973).

A central, vertical, internal cylinder about 10 mm in diameter and up to 120 mm in height occurs in the burrows (Figs. 4A, B; 5 A, B; 6). The cylindrical core is distinct from the surrounding burrow, has a smooth wall, extends up to the top of the burrow, and may protrude as a small mound on weathered bedding surfaces (Figs. 2, 5B, 6). The central cylinder is bulbous or indistinct near the bottom of the burrow.

In the burrows of the upper bed, the central cylinders contain abundant trilobite fragments

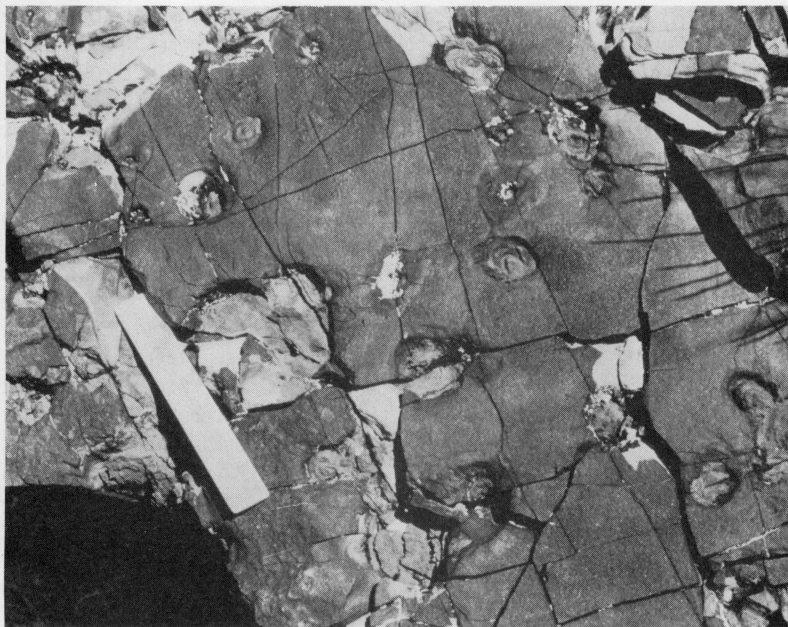
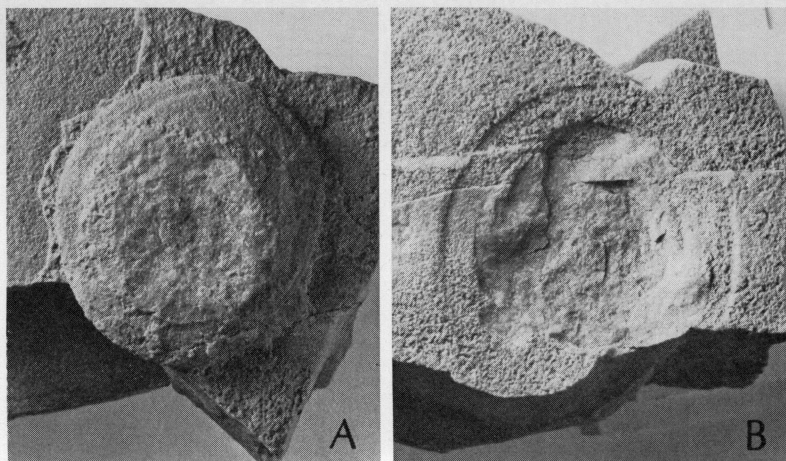


Fig. 2. Numerous burrows of *Dolopichnus gulosus* on upper bedding plane in quartzite (upper bed with burrows) of Poleta Formation. A cluster of burrows occurs to the right of the scale (scale is 15.5 cm long). Approx. $\times 0.2$.

Fig. 3. *Dolopichnus gulosus*, holotype, UCLA 49508, from lower bed with burrows, UCLA Loc. 6164. Specimen uncoated; approx. $\times 0.8$.

□ A. Lower bedding plane with bottom of burrow preserved as a flattened hemisphere with concentric markings and a slight central depression. □ B. Upper bedding plane view. The central cylinder (10 mm in diameter) is visible on the specimen but not in the photograph.



up to 5 mm long (Fig. 4A). Trilobite fragments are sparse in the outer burrow and absent in the surrounding quartz arenite. Some short burrows lack a central cylinder and contain trilobite fragments throughout (Fig. 4C), and are probably the bottoms of tall burrows.

The outer walls of the burrows were observed in natural and sawed sections only, and appear to be without constrictions or ornamentation.

Microscopic description

In thin sections, the rock surrounding the burrows of the upper and lower beds is composed of very-fine to fine, well-sorted quartz grains (55–60 %) in a micrite matrix, with a small amount of limonite. About 2 % of the micrite has recrystallized to sparite, and locally irregular patches of sparite replace detrital quartz grains. The rock of the lower bed contains about 5 % plagioclase, and both beds contain minor secondary muscovite.

The composition of the rock in the burrows is different in the two beds. The central cylinder is indistinct in burrows of the lower bed, and prominent in burrows of the upper bed.

Burrows of the upper bed. – A distinct central cylinder containing abundant bioclastic fragments characterizes the burrows of the upper bed. Skeletal fragments and micrite pellets each compose 25–30 % of the central cylinder

(Fig. 4A), and are cemented with medium crystalline sparite (35–45 %). Detrital quartz comprises about 5 % of the central core. The bioclastic fragments are from 0.05 to 0.2 mm wide, up to 5 mm long, and generally are slightly curved to hook shaped in thin section. Poorly developed laminae parallel to the surface and an indistinct prismatic structure are present in some fragments. The morphology and internal structure of the fragments indicate that they are trilobite exoskeleton remains (Harrington 1959:O85–O87, Fig. 62; Horowitz & Potter 1971: 68–69, Pl. 47). In the central cylinder the trilobite fragments are subparallel to the bedding (Figs. 4A, 6).

The outer part of the burrow contains fewer detrital quartz grains (40–45 %) than the rock surrounding the burrows. Trilobite fragments comprise 5–10 % of the outer burrow. The grains are imbedded in a matrix of micrite, containing 20–30 % limonite and 5 % sparry calcite.

Burrows of the lower bed. – In thin section, the central cylinder is much less distinct and lacks trilobite fragments. The rock inside the burrow has nearly the same composition and texture as the surrounding micritic quartz arenite. However, limonite and carbonaceous material comprise about 20 % of the outer burrow and only 5 % of the surrounding rock and the central core. Grains in the central core are slightly coarser than those in the outer burrow and enclosing rock.

Diagnosis

Vertical, cylindrical burrows, 20–50 mm in diameter and up to 200 mm in height, containing a central cylindrical core, about 10 mm in diameter, of coarser grained material.

Dolopichnus gulosus differs from the specimens described by Philipp (1904, Pl. 3:1) as Problematicum in that the central core is

larger and the outer surface of the burrow does not have irregular constrictions. *D. gulosus* is larger and deeper than *D. mongraensis* (Verma, 1970) and is more cylindrical in shape.

Interpretation

Our interpretation of the above structures as dwelling burrows of sea anemones is supported by several lines of circumstantial evidence. The radial symmetry and cylindrical to conical shape are features possessed by other burrows generally attributed to sea anemones: *Conostichus* Lesquereux (Chamberlain 1971); *Bergaueria* Prantl (Alpert 1973); *Kulindrichnus* Hallam (1960); *Cylindrichnus* Toots (Chamberlain & Clark 1973:677, as *Anemonichnus*). In addition, the bottom of one burrow (Fig. 3A) is morphologically similar to *Bergaueria*, and some specimens of *Conostichus* possess a sub-cylindrical core (Chamberlain 1971:220). Finally, the burrows are similar in size and shape to living sea anemones, whose life habits can account for the features observed in the fossil burrows.

The presence of concentrated trilobite skeletal fragments within the burrows leads us to believe that the sea anemones preyed upon trilobites. The central core within the burrow is interpreted to be a cast of the stomach or coelenteron, which in some specimens contains preserved stomach contents.

It is postulated that sea anemones ingested small trilobites, and digestive enzymes dissolved the soft parts of the trilobites; the exoskeletons were thus disarticulated, and possibly broken into smaller fragments by muscular action. The undigestible skeletal fragments were probably agglutinated by mucus, prior to expulsion through the mouth. Ejecting the material as a cohesive mass would have prevented the waste from dispersing and settling back down

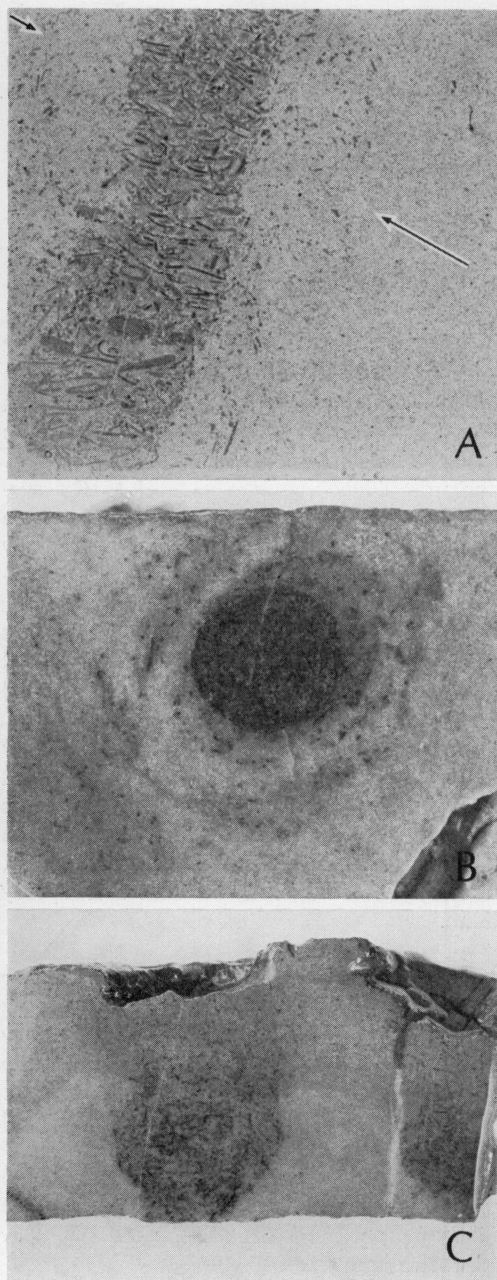


Fig. 4. *Dolopichnus gulosus*. □ A. Photograph of longitudinal thin section through central cylinder of paratype (UCLA 49509), upper bed with burrows. Position of section in burrow shown in Fig. 6. Central cylinder is delineated by abundant bioclastic material. Outer wall of burrow is indicated by absence of dark fragments (arrows). $\times 2.6$. □ B. Transverse section through paratype (UCLA 49509) (position shown in Fig. 6), showing distinct central cylinder of bioclastic fragments. $\times 1.9$. □ C. Vertical sections through short burrows filled with trilobite fragments. These are probably the bottoms of tall burrows. Paratype, UCLA 49511, upper bed with burrows. $\times 1$.

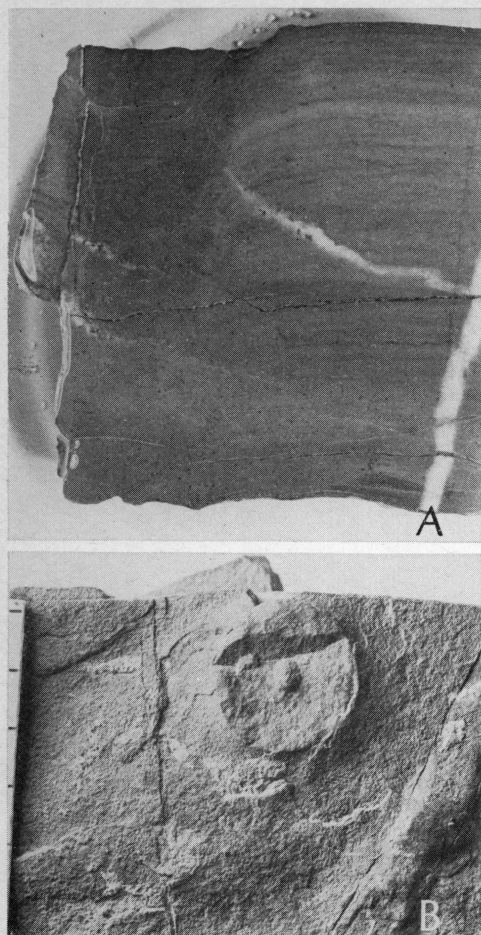


Fig. 5. *Dolopichnus gulosus*, lower bed with burrows. Paratype, UCLA 49510. $\times 0.75$. □ A. Vertical section; laminations bend downward around burrow. Central core discernible near bottom. □ B. Lower bedding plane view of same specimen. Central core is expressed as a raised mound.

on the anemone. Rapid sedimentation facilitated the preservation of the coelenteron and stomach contents of the anemone.

This interpretation is supported by the feeding habits of living sea anemones. Modern anemones are known to be voracious, and eat almost anything they can catch and swallow (Stephenson 1928:87). Common prey of anemones are crustaceans, such as crabs. Anemones will ingest live or dead individuals, and even molted exoskeletons (Mariscal 1970:11). The Early Cambrian anemones probably caught live trilobites small enough to ingest.

After ingesting food, modern anemones nor-

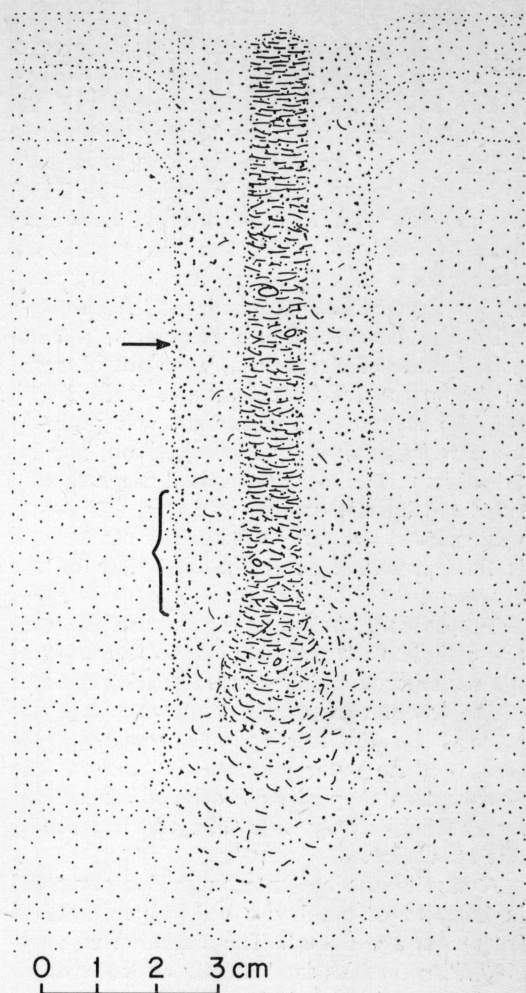


Fig. 6. Vertical section through center of paratype (UCLA 49509) of *Dolopichnus gulosus*, showing distinct central cylinder with indistinct bulbous base. Laminations were not observed in the upper bed with burrows, but are shown in the figure. The positions of the sections shown in Fig. 4A and B are indicated by the bracket and arrow, respectively.

mally expand to their widest extent (Stephenson 1928:89). About 6.5 hours are required for digestion (Mariscal 1970:11). Material expelled from the digestive cavity of sea anemones is coated with mucus (Hyman 1940:596) or enclosed in mucous sacs (Schäfer 1972:420-421) which float upward or are removed by currents. The expanded state during digestion may mold the mucus-coated undigestible material into a smooth cylinder, to prevent damage from sharp shell fragments during expulsion.

The long digestive period of sea anemones could explain the presence of stomach contents in many of the burrows.

The burrow-dwelling sea anemones of the early Paleozoic were apparently unable to migrate upward to keep pace with rapid sedimentation (Alpert 1973). A sudden burial of the anemones by a thick layer of sand may have caused their death, and can explain the preservation of the coelentera and burrows. As the anemone decomposed, sand from above filled the burrow. Slump structures, a common feature of *Bergaueria*, were not observed in the burrows. The coelenteron, if filled with trilobite fragments and mucus, was probably more resistant to early decomposition, and retained its vertical orientation and shape as sand filled the burrow around it. Later, the mucus was replaced by sparry calcite. The coelenteron is thus preserved as the central core of the burrow.

The bulbous, indistinct bottoms of the central cylinders are probably due to rupturing of the coelenteron and downward settling of some of the trilobite fragments. Rupturing may also account for the few trilobite fragments observed in the outer part of the burrow. The near-horizontal preferred orientation of the larger trilobite fragments (Fig. 4A) is probably due to settling.

A cast of the coelenteron is also preserved in burrows of the lower bed, where trilobite fragments are absent. The coelenteron probably filled up with sand shortly after the death of the organism, and the lining was later replaced by sparry calcite.

Olenellid trilobites are abundant in the Upper Member of the Poleta Formation. Small and large specimens of *Fremontia*, *Paedemias*, and *Olenellus* are present, and the fragments in the burrows are probably of these genera. The tests of olenellid trilobites are very thin (Raw 1937:578), and could have been easily broken by the muscular action of the sea anemones.

Similar structures, from the Werfener Schichten (Triassic) of northern Italy, consisting of vertical, cylindrical burrows, 1–5 cm wide, with a 2 mm wide central core, were described by Philipp (1904:58–59, Pl. 3:1–5) under the heading Problematicum. The burrows occur in laminated calcareous sandstone. The central cylinder contains angular quartz and calcite grains, and is surrounded by a thin layer

of calcite. Philipp interpreted the structures to be soft-bodied organisms, such as sponges or ascidians, with a hollow central tube, possibly gastrovascular, that filled up with quartz and calcite grains shortly after the death of the organism, before decay of the surrounding body.

Taxonomy

Wurm (1912:127–129) proposed the genus *Cyclozoon* for Philipp's specimens and additional specimens from the Triassic of Spain, and named the species *C. philippi*. Other specimens of this nature were illustrated and described by Schmidt (1934), who interpreted them to be inorganic. The first report of this type of fossil was by Quenstedt (1879), who interpreted it as a coral, which he named *Laevicyclus* (no species erected). Häntzschel (1962; 1965) placed *Cyclozoon* in synonymy with *Laevicyclus*, but did not designate a type species for *Laevicyclus*.

Two distinct forms, of different origin, are presently in the genus *Laevicyclus*: Form A – large, cylindrical, vertical burrows with a small central cylinder (Problematicum of Philipp, and species from Nevada described herein), and Form B – vertical burrows with concentric scrapemarks on the upper bedding surface. Both forms have a similar appearance in bedding-plane view.

Quenstedt's (1879, Pl. 164:35) specimen is insufficiently described to determine if it is Form A or Form B. Philipp's (1904) specimens are Form A. Wurm's (1912) specimens are probably Form B, with a vertical repetition of the concentric markings around the burrow on successive bedding surfaces. Both forms are described by Schmidt (1934). Seilacher's (1953: 430; 1955:389–390) interpretation of *Laevicyclus*, a vertical dwelling burrow of a worm, with tentacle swirlmarks around the top of the burrow, is based on Form B, and is the current general concept of *Laevicyclus*. We presently propose that *Laevicyclus* be restricted to Form B, and that Form A be removed from *Laevicyclus* and named *Dolopichnus*:

Dolopichnus n. ichnogen.

Synonymy. – □ Problematicum of Philipp 1904:58–60, Pl. 3:1–5. □ *Cyclozoon* Wurm

1912:127–129 (*partim*, Problematicum of Philipp only, *non* Pl. 7:11); Schmidt 1934 (*partim*). □ *Laevicyclus* Quenstedt, Häntzschel 1962 (*partim*): W201, Fig. 123:3a (*non* 3b); Häntzschel 1965:51 (*partim*).

Diagnosis. – Vertical, cylindrical burrows, containing a narrower, vertical, central cylindrical core.

Interpretation. – Dwelling burrows of sea anemones, with a cast of the coelenteron preserved in the center of the burrow.

Type species. – *Dolopichnus gulosus* n. ichnosp.

Other species in genus. – The specimens described by Philipp (1904:58–60, Pl. 3:1–5) as Problematicum apparently belong in *Dolopichnus*.

Laevicyclus mongraensis Verma (1970:38, Pl. 1:6; Chiplonkar & Badwe 1970:9, Pl. 3:4, 4a) apparently belongs in *Dolopichnus*. The burrows are 14 mm in diameter on the upper bedding surface, taper downward, are about 20 mm tall, and have a central core about 4 to 5 mm in diameter.

Laevicyclus Quenstedt, 1879

Synonymy. □ *Laevicyclus* Quenstedt 1879:577, Pl. 164:35; Seilacher 1953:430, Fig. 5; Seilacher 1955:389–390, Pl. 18:1, Fig. 5:54; Lessertisseur 1955:12, 53, Fig. 2A; Seilacher 1956:165, Fig. 1:11; Henbest 1960, Fig. 177:1E; Häntzschel 1962 (*partim*):W201, Fig. 123:3b (*non* 3a); Häntzschel 1965:51 (*partim*); Kemper 1968:79–80, Pl. 2:3, Pl. 9:7; Frey 1970:15–16, Pl. 4:2, 3, Fig. 3F; Frey & Howard 1970:160, Fig. 2F. □ *Cyclozoon* Wurm 1912 (*partim*, *non* Problematicum of Philipp):127–129, Pl. 7:11; Schmidt 1934 (*partim*); Häntzschel 1965:28. □ ?*Palaeoscia* Caster 1942:26–29, Pl. 5:1–4; Osgood 1970:395–397, Pl. 71:3, Pl. 82:1–6.

Diagnosis. – Vertical, cylindrical burrows with concentric markings or circular structure on upper bedding surface.

Interpretation. – Dwelling burrows of worms, with tentacle swirlmarks on bedding surface.

Type species. – *Cyclozoon philippi* Wurm 1912 (*partim*, *non* Problematicum of Philipp):127–

129, Pl. 7:11 (the larger of the two specimens of Pl. 7:11 is here selected as lectotype of *C. philippi*).

Other species in genus. – *Palaeoscia floweri* Caster 1942:26–28, is here questionably transferred to *Laevicyclus*.

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REFERENCES

- Alpert, S. P. 1973: *Bergaueria* Prantl (Cambrian and Ordovician), a probable actinian trace fossil. *Jour. Paleontol.* 47, 919–924.
- Caster, K. E. 1942: Two siphonophores from the Paleozoic. *Palaeontogr. Americana* 3:14. 30 pp., 2 Pl.
- Chamberlain, C. K. 1971: Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma. *Jour. Paleontol.* 45, 212–246.
- Chamberlain, C. K. & Clark, D. L. 1973: Trace fossils and conodonts as evidence for deep-water deposits in the Oquirrh Basin of central Utah. *Jour. Paleontol.* 47, 663–682.
- Chiplonkar, G. W. & Badwe, R. M. 1970: Trace fossils from the Bagh Beds. *Palaeontol. Soc. India Jour.* 14 (1969), 1–10.
- Dawson, J. W. 1894: *Some Salient Points in the Science of the Earth*. 499 pp. Harper & Brothers, New York.
- Durham, J. W. 1971: Some Late Precambrian and Early Cambrian fossils from the White-Inyo Mountains of California. *Geol. Soc. Amer. Abstracts with Programs* 3:2, 114–115.
- Frey, R. W. 1970: Trace fossils of Fort Hays Limestone Member of Niobrara Chalk (Upper Cretaceous), west-central Kansas. *Univ. Kans. Paleontol. Inst. Contrib. Art.* 53, *Cretaceous* 2, 41 pp.
- Frey, R. W. & Howard, J. D. 1970: Comparison of Upper Cretaceous ichnofaunas from siliceous sandstones and chalk, western interior region, U.S.A. In T. P. Crimes & J. C. Harper (eds.): *Trace Fossils. Geol. Jour. Special Iss.* 3, 141–166.
- Häntzschel, W. 1962: Trace fossils and problematica. In R. C. Moore (ed.): *Treatise on Invertebrate Paleontology, Part W: Miscellaneous*, W177–W245. Univ. Kansas Press and Geol. Soc. Amer.
- Häntzschel, W. 1965: *Vestigia invertebratorum et problematica. Fossilium Catalogus, I. Animalia, Part 108*. 142 pp.
- Hallam, A. 1960: *Kulindrichnus langi*, a new trace-fossil from the Lias. *Palaeontology* 3, 64–68.
- Harrington, H. J. 1959: General description of Trilobita. In R. C. Moore (ed.): *Treatise on Inverte-*

- brate Paleontology, Part O: Arthropoda I, 38-117. Univ. Kansas Press and Geol. Soc. Amer.
- Henbest, L. G. 1960: Fossil spoor and their environmental significance in Morrow and Atoka Series, Pennsylvanian, Washington County, Arkansas. *U. S. Geol. Surv. Prof. Paper 400B*, 383-385.
- Horowitz, A. S., & Potter, P. E. 1971: *Introductory Petrology of Fossils*. 302 pp. Springer-Verlag, New York.
- Hyman, L. H. 1940: *The Invertebrates. Vol. 1, Protozoa through Ctenophora*. 726 pp. McGraw-Hill, New York.
- Kemper, E. 1968: Einige Bemerkungen über die Sedimentationsverhältnisse und die fossilen Lebensspuren des Bentheimer Sandsteins (Valanginium). *Geol. Jb.* 86, 49-106, Pl. 2-9.
- Langille, G. B. 1974: *Earliest Cambrian-Latest Proterozoic Ichnofossils and Problematic Fossils from Inyo County, California*. Unpub. PhD Dissertation, State Univ. of New York, Binghamton.
- Lessertisseur, J. 1955: Trace fossile d'activité animale et leur signification paléobiologique. *Soc. géol. France Mém.* 74, n. sér. 150 pp., 11 Pl.
- Mariscal, R. N. 1970: A field and laboratory study of the symbiotic behavior of fishes and sea anemones from tropical Indo-Pacific. *Univ. Calif. Publ. in Zool.*, Vol. 91. 33 pp., 4 Pl.
- Matthew, G. F. 1891: Illustrations of the fauna of the St. John Group, No. V. *Royal Soc. Canada, Proc. Trans. Vol. 8 (1890), section 4*, 123-166, Pl. 11-16.
- Osgood, R. G., Jr. 1970: Trace fossils of the Cincinnati area. *Palaeontogr. Americana* 6:41, 281-444, Pl. 57-83.
- Philipp, H. 1904: Paläontologische-geologische Untersuchungen aus dem Gebiet von Predazzo. *Deutsch. Geol. Gesell. Zeit.* 56, 1-98, 6 Pl.
- Quenstedt, F. A. 1879: *Petrefactenkunde Deutschlands. I. Abth., Bd. 6, Korallen (Röhren- und Sternkorallen)*. Fues's Verlag, Leipzig. (Lief. 7-9, 1879; Volume dated 1881.)
- Raw, F. 1937: Systematic position of the Olenellidae (Mesonacidae). *Jour. Paleontol.* 11, 575-597.
- Schäfer, W. 1972: *Ecology and Palaeoecology of Marine Environments*. 568 pp., 39 Pl. Univ. Chicago Press.
- Schmidt, M. 1934: *Cyclozoon philippi* und verwandte Gebilde. *Sitz. Heidelberger Akad. Wiss., Math. Nat. Kl.* 1934, Abh. 6, 31 pp., 4 Pl.
- Seilacher, A. 1953: Studien zur Palichnologie. I. Über die Methoden der Palichnologie. *Neues Jb. Geol. Paläontol., Abh.* 96, 421-452.
- Seilacher, A. 1955: Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan). V. Spuren und Fazies im Unterkambrium. *Akad. Wiss. Lit. Mainz, Math. Nat. Kl., Abh.* 10, 1955, 373-399.
- Seilacher, A. 1956: Der Beginn des Kambriums als biologische Wende. *Neues Jb. Geol. Paläontol., Abh.* 103, 155-180, Pl. 8, 9.
- Stephenson, T. A. 1928: The British sea anemones. Vol. 1. *Ray Society, Vol. 113*. 184 pp., 14 Pl.
- Stewart, J. H. 1970: Upper Precambrian and Lower Cambrian strata in the southern Great Basin, California and Nevada. *U. S. Geol. Surv. Prof. Paper* 620. 206 pp.
- Verma, K. K. 1970: Occurrence of trace fossils in the Bagh Beds of Amba Dongar Area, Gujarat State. *Indian Geoscience Assoc. Jour.* 12, 37-40.
- Wurm, A. 1912: Untersuchungen über den geologischen Bau und die Trias von Aragonien. *Deutsch. Geol. Gesell. Zeit.* 63(1911), 38-174, Pl. 5-7.