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BERGAUERIA PRANTL (CAMBRIAN AND ORDOVICIAN), A PROBABLE ACTINIAN TRACE FOSSIL

STEPHEN P. ALPERT

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STEPHEN P. ALPERT

Department of Geology, University of California, Los Angeles

ABSTRACT—New discoveries of *Bergaueria* Prantl, 1945, are reported from the Lower Cambrian Harkless and Poleta Formations of the White-Inyo Mountains and the Latham Shale of the Marble Mountains of California. A new species, *Bergaueria radiata*, is described from Cambrian rocks of Nevada and Lower Cambrian rocks of California. Burrows of *Bergaueria* have previously been reported from Cambrian and Ordovician rocks of Europe and North America. These trace fossils are probably casts of actinian (sea anemone) dwelling burrows. The genus is related to *Conostichus*, a trace fossil from the Pennsylvanian of the United States.

INTRODUCTION

T HE genus Bergaueria Prantl, 1945, was proposed for cylindrical protuberances on the underside of Ordovician sandstone beds of central Bohemia (Prantl, 1945, 1946). These structures were interpreted as casts of burrows made by sedentary organisms, probably analogous to the living anthozoans Cerianthus or Edwardsia. Subsequent workers, describing new specimens of Bergaueria or reviewing the genus, agree with Prantl's interpretation that the structures were made by coelenterates, owing to the radial symmetry, (Lessertisseur, 1955), or, more specifically, by anthozoans (Häntzschel, 1958; Howell and Hutchinson, 1958), and most probably by actinians (Seilacher, 1956; Häntzschel, 1962, 1965; Radwański and Roniewicz, 1963; Arai and Mc-Gugan, 1968). In comparison with the burrows made by living anthozoans (Frey, 1970), the fossils are similar to actinian burrows, and unlike the deep, vertical, cerianthid dwelling tubes.

A possible body fossil of an actinian (*Mac-kenzia*) is known from the Middle Cambrian Burgess Shale (Wells and Hill, 1956). Thus, the Lower Cambrian specimens of *Bergaueria* represent the earliest known occurrence of sea anemones in the fossil record.

Bergaueria represents a permanent or semipermanent dwelling burrow (Domichnia) of a soft-bodied organism, by Seilacher's (1964) ethological classification of trace fossils (for a summary of the various classifications of trace fossils, and other concepts in palichnology, see Osgood, 1970, or Frey, 1971). Relatively rapid influx of sand on a normally quiet muddy bottom in which the anemones lived probably caused burial and death of the organisms in place. As the bodies in the burrows decomposed, sand from the bed above slumped into the burrows, leading to the formation of casts on the bottom of the sandy bed (Prantl, 1946; Radwański and Roniewicz, 1963; Arai and Mc-Gugan, 1968). Evidence for this interpretation is the slump structures that occur in the sandy laminae both within and above the burrow casts (Pl. 1, fig. 9; Arai and McGugan, 1968, Pl. 36, figs. 5, 8, 11).

The casts are characterized by a cylindrical shape with a flat to hemispherical base having a central indentation, radial ridges, and concentric impressions. Some are preserved as hemispherical projections on the lower surface of sandy beds. Known specimens of *Bergaueria* range between 15 and 45 mm in diameter, with the length equal to or less than the diameter. Specimens occur singly and in clusters or colonies.

OCCURRENCES OF BERGAUERIA

Specimens of Bergaueria have been found in Lower Cambrian to Middle Ordovician rocks of Europe and North America. Bergaueria perata Prantl has been described, reported, or illustrated from the Middle Ordovician (Upper Llandeilian) of central Bohemia (Prantl, 1945, 1946), the Middle Cambrian of the Grand Canyon (McKee, 1945, Pl. 8, fig. d; Seilacher, 1956), the lower Paleozoic of the State of Washington (Howell and Hutchinson, 1958, as B. magna), the Upper Cambrian of the Holy Cross Mountains in Poland, and the Lower Cambrian of northern Spain (Radwański and Roniewicz, 1963), the Lower Cambrian of Alberta and western Newfoundland (Arai and McGugan, 1968), and the Lower Ordovician (Lower Arenigian) rocks of Wales



TEXT-FIG. 1—Map of California and Nevada. Bergaueria has been found near Goldfield, Westgard Pass, Andrews Mountain, and Cadiz.

(Crimes, 1970). Bergaueria sp. has been described from Cambrian rocks near Goldfield, Nevada (Arai and McGugan, 1969).

Bergaueria is reported here, for the first time, from the Lower Cambrian of the White-Inyo Mountains and Marble Mountains of California. The White-Inyo Mountains localities are about 60 miles southwest of the Goldfield, Nevada area (Text-fig. 1).

In the White-Inyo Mountains, Bergaueria occurs in green shale, siltstone, and quartzite of the lower part of the Harkless Formation (Text-fig. 2) at several localities near the Westgard Pass area in the Blanco Mountain quadrangle, and also at a locality near Andrews Mountain in the Waucoba Mountain quadrangle. Two poorly preserved hemispherical structures resembling Bergaueria (Pl. 1, fig. 14) were found in the upper Poleta Formation below the Harkless Formation near Westgard Pass. The specimens measure 40 \times 47 mm across the base of the hemisphere, and are 16 mm high. All specimens collected were found as float on the outcrops, and most are poorly preserved.

In the Poleta and Harkless Formations, Bergaueria is associated with other trace fossils that suggest a shallow water environment.



TEXT-FIG. 2—Columnar section of the Poleta Formation and lower half of the Harkless Formation, Lower Cambrian, White-Inyo Mountains, California (Expanded from Nelson and Durham, 1966, fig. 1).

Bergaueria has been included as a representative member of the Cruziana or Skolithos trace fossil assemblages (Crimes, 1970), both characteristic of shallow waters. The Bergaueria of the Harkless Formation occurs in the same stratigraphic interval as trilobite traces (Rusophycus and Cruziana), but only rarely do they occur adjacent to each other (Pl. 1, fig. 11). The questionable Bergaueria found in the Poleta Formation occurs in a quartzite unit that contains abundant Skolithos. The only other trace fossils that are now known to occur with Bergaueria on the underside of beds are Diplocraterion (Radwański and Roniewicz, 1963, Pl. 9, fig. 1), and among Harkless specimens, small (1 to 5 mm wide), smooth, unbranched burrows parallel to the bedding, which are referrable to *Planolites* (Pl. 1, fig. 10). Diplocraterion and Bergaueria are adjacent on one of the Goldfield, Nevada specimens.

No trilobites are known to occur in the beds containing *Bergaueria* in the Poleta and Harkless Formations. However, the occurrences of trilobites lower in the Poleta Formation (*Fremontia*, *Olenellus*, *Paedeumias*) and higher in the Harkless Formation (*Paedeumias*, *Bonnia*) (Text-fig. 2) indicate that *Bergaueria* is within the *Bonnia-Olenellus* Zone in the White-Inyo Mountains (Nelson and Durham, 1966; Fritz, 1972).

The specimen of *Bergaueria* from the Marble Mountains (Pl. 1, fig. 3) was collected along with trilobites and trace fossils from the Lower Cambrian Latham Shale, by Takeo Susuki.

COMPARISON WITH CONOSTICHUS

The trace fossil most closely similar to *Bergaueria* is *Conostichus* Lesquereux (Pl. 1, figs. 12, 13), from Pennsylvanian rocks of the United States, also believed to be the casts of actinian burrows (Chamberlain, 1971). *Conostichus* differs from *Bergaueria* in that *Conostichus* is larger (average size about 65 mm in height and 45 mm in diameter), more conical than cylindrical or hemispherical in shape, and possesses more sculpturing (Branson, 1959, 1960, 1961, 1962; Chamberlain, 1971).

A recent experiment by Shinn (1968) demonstrated the burrowing activity of a living coneshaped anemone, and its ability to migrate upward through sediment after being rapidly buried. The organism responsible for Conostichus was also able to move upward in its burrow to keep pace with sedimentation, as some specimens, when sectioned, show the bulbous basal structure high up in the burrow (Chamberlain, 1971). In addition, some specimens of Conostichus occur superimposed upon each other (cone in cone), indicating upward migration (Branson, 1959; Pfefferkorn, 1971). Analogous upward migration structures have not been found in Bergaueria, where rapid sedimentation supposedly resulted in the death of the organism. This may indicate that the ability for burrowing sea anemones to migrate upward in the sediment, to keep pace with relatively rapid sedimentation, evolved sometime between the Ordovician and Pennsylvanian periods.

Recently described fossil "tadpole nests" (Bhargava, 1972) resemble *Bergaueria* in shape and mode of preservation but not in origin. These casts are small mounds, 7 to 11 mm in diameter, found on the underside of orthoquartzite beds in the Upper Jurassic of India. Recent examples of tadpole nests are known both in fresh water and brackish marine environments (Bhargava, 1972), but their chances of preservation are slim (Cameron and Estes, 1971).

SYSTEMATIC PALEONTOLOGY

Variation within the species of *Bergaueria* is due primarily to the final state of contraction or dilation of muscles of the aboral end of the organism, which resulted in differences in the pattern of radial and concentric impressions on the bottom of the burrow and subsequent cast (Arai and McGugan, 1969), and secondarily to the mode and state of preservation. Commonly the lower ends of specimens of *Bergaueria* are poorly preserved, partially or completely broken off, or highly weathered, such that most or all of the details of the central depression, radial ridges, and concentric impressions are missing.

Genus Bergaueria Prantl, 1945

Bergaueria Prantl, 1945; 1946, p. 50–52; Lessertisseur, 1955, p. 68–69; Seilacher, 1956, p. 164, 165; Häntzschel, 1958, p. 85; 1962, p. W186; 1965, p. 15; Arai and McGugan, 1968, p. 205– 209; 1969, p. 93–94.

"Natural casts of small circular depressions," Mc-Kee, 1945, Pl. 8, fig. d.

Type species.—Bergaueria perata Prantl, 1945; 1946, p. 52–53, Pl. 1, text-figures 1, 2.

Description.—Cylindrical to hemispherical burrows, usually projecting from the underside of beds. Height equal to or less than diameter (15 to 45 mm). Base with shallow central depression, which in many specimens is surrounded by faint to strong radial ridges and concentric impressions (breaks in slope from bottom to side). Sides of cast smooth.

Concentric markings or a bowl-shaped depression owing to the subsequent internal filling by slump structure may be visible on the broken upper end of the burrow cast (Pl. 1, figs. 6, 8). Specimens occur in clusters or individually; those in large clusters are colonies are usually crowded but do not intersect.

BERGAUERIA RADIATA n. sp.

Pl. 1, figs. 1-4, Text-fig. 3

Bergaueria sp., Arai and McGugan, 1969, p. 93-94, Pl. 18, figs. 1-7.

Type specimens.—Holotype: Los Angeles County Museum of Natural History (LACM) holotype 1233, from near Goldfield, Nevada; exact locality and Cambrian formation unknown (Bergaueria sp., Arai and McGugan, 1969, Pl. 18, figs. 2, 7). Paratypes: LACM paratypes 1232, 1234, and 1236 respectively (Bergaueria

Specimen	Diameter	Diameter of central area bordered by concentric impression	Height
LACM 1233 (A and M, Pl. 18, figs. 2, 7) (holotype)	28	17	13
LACM 1232 (A and M, Pl. 18, fig. 1) (paratype)	271/2	17	19
LACM 1234 (A and M, Pl. 18, figs. 3, 6) (paratype)	26	$14\frac{1}{2} \times 15\frac{1}{2}$	16
LACM 1235 (A and M, Pl. 18, fig. 4) (hypotype)	23×26	16×20	20
LACM 1236 (A and M, Pl. 18, fig. 5) (paratype)	22	16×17	$9\frac{1}{2}$
UCLA 48594 (Pl. 1, fig. 2) (paratype)	23×30	19×21	$10\frac{1}{2}$
UCLA 48595 (Pl. 1, fig. 1) (paratype)	32×35	25×26	12
UCLA 48596 (Pl. 1, fig. 4) (paratype)	26	not preserved	18
UCLA 48605 (Pl. 1, fig. 3) (paratype)	19×22	15×17	91/2

TABLE 1-Measurements (in mm) of the type specimens of Bergaueria radiata n. sp. A and M refers to Arai and McGugan, 1969.

sp., Arai and McGugan, 1969, Pl. 18, Figs. 1, 3 and 6, 5), same locality as above, UCLA 48594, 48595, 48596 (Pl. 1, figs. 1, 2, 4), from the lower Harkless Formation near Andrews Mountain in the Inyo Mountains, California, and UCLA 48605 from Latham Shale, Marble Mountains, California. Measurements of type specimens are given in Table 1.

Description.—Lower end with distinct to prominent radial ridges around central depression. Wide radial ridges, where present, may bear several secondary ridges (Text-fig. 3). Radial ridges bordered by a single strong concentric impression. Central depression may be elongate or slit-like, creating a faint biradial symmetry. Height about ½ of, to slightly less than the diameter.



TEXT-FIG. 3—Bergaueria radiata n. sp. Holotype, LACM 1233, showing radial ridges with secondary ridges. Basal view.

The large radial ridges (about 8 to 10) are $1\frac{1}{2}$ to 4 mm wide, expand outward from the central depression, and each contains about 3 secondary ridges. Some specimens have numerous narrow radial ridges only (Pl. 1, fig. 3). The radial ridges may be curved, and may extend beyond the concentric impression.

Remarks.—Bergaueria perata lacks or has faint radial ridges around the central depression. The concentric impressions of most specimens are weak and may be numerous. The height and diameter are nearly equal.

Bergaueria radiata differs from B. perata in that B. radiata 1) has distinct radial ridges, 2) has one strong concentric impression, 3) is smaller, 4) is generally not as high as it is wide, and 5) may have biradial symmetry.

Occurrences.—Cambrian, near Goldfield, Nevada; Lower Cambrian, northern Inyo Mountains, California (Harkless Formation); Lower Cambrian, southern Marble Mountains, north of Cadiz, California (Latham Shale).

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trace fossils from the White-Invo Mountains, California.

LOCALITIES OF FIGURED SPECIMENS

UCLA Locality numbers

- 4390-2400 feet north and 2200 feet east of SW corner sec. 21, T. 6 N., R. E., Cadiz quadrangle
- (1956), San Bernardino Co., California.
 (047-2500 feet west and 50 feet south of NE corner sec. 35, T. 7 S., R. 35 E., Blanco Mountain quadrangle (1951), Inyo Co., California.
- 6048-East edge of Cedar Flat, south side of hill 7401; 2500 feet west and 2000 feet south of NE corner sec. 4, T. 8 S., R. 35 E., Blanco Mountain quadrangle, Inyo Co., California.
- 6049—East edge of Cedar Flat, on ridge and saddle, east half of NE¼, sec. 4, T. 8 S., R. 35 E., Blanco Mountain quadrangle, Inyo Co., California.
- 6050—Near streambed, 2500 feet east and 900 feet north of SW corner sec. 35, T. 7 S., R. 35 E., Blanco Mountain quadrangle, Inyo Co., California.
- 6051-Near top of northeast facing slope, 11/2 miles N 80 W of Andrews Mountain (which is in sec. 18, T. 10 S., R. 36 E.), Waucoba Mountain quadrangle (1951), Inyo Co., California.
 6052—2400 feet east and 700 feet north of SW corner sec. 26, T. 7 S., R. 35 E, Blanco Mountain quadrangle, Inyo Co., California.

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Note added to proof:

While this paper was in press, I discovered that Bergaueria structures from Alberta were illustrated and described by T. G. Bonney in 1903 (Notes on specimens collected by Professor Collie, F.R.S., in the Canadian Rocky Mountains. Geological Magazine, Decade 4, 10:289–297; p. 291–293, pl. 17, fig. 3). Bonney mentions but rejects a coelenterate cast interpretation, in favor of casts of pits made by annelids. Additional field collecting has revealed the presence of *Bergaueria radiata* and *B*, sp. over

3000 feet lower in the section in the White-Invo Mountains. The occurrence is in the Andrews Mountain Member of the Campito Formation, approximately 1.000 feet stratigraphically below the the Montenegro Member (which contains abundant Fallotaspis), a half mile from the east end of Payson Canyon, near Westgard Pass. Various other trace fossils are found at this horizon, which is earliest Cambrian in age, as one specimen of the trilobite Fallotaspis has been found slightly lower in the section.

EXPLANATION OF PLATE 1

Specimens illustrated are deposited in the type collection of the Department of Geology, University of California. Los Angeles (UCLA).

- FIGS. 1,2,4-Bergaueria radiata n. sp., from the Lower Cambrian Harkless Formation, Inyo Mountains, California. 1,2, Paratypes, basal view. Specimens uncoated; color differences enhance detail. UCLA 48595 and 48594. 4, Side view of specimen half exposed from surrounding rock. UCLA 48596. Paratype. UCLA Loc. 6051. $\times 1$. 3-Bergaueria radiata n. sp., from the Lower Cambrian Latham Shale, Marble Mountains, Cali
 - fornia. UCLA Loc. 4390. Paratype. UCLA 48605. ×1.
 - 5,6—Two specimens of Bergauera sp. 5, Bottom view. 6, Top view of same slab, showing corresponding concentric markings, probably formed by slumping of sediment into burrows as dead actinians decomposed. Lower Cambrian, Harkless Formation, White-Invo Mountains, California, UCLA Loc. 6048, UCLA 48598, ×0.75.
 - 7,8-Bergauria sp. 7, Bottom surface. 8, Top view, showing concave surface, of same specimen. UCLA 48597. Lower Cambrian, Harkless Formation, White-Inyo Mountains, California. UCLA Loc. 6048. ×1.
 - 9-Bergaueria sp., cross section view, surface cut perpendicular to bedding. Burrows preserved by thin sandy layer, with shale above and below. Burrows in sharp contact with laminated shale below sandy layer. UCLA 48599. Lower Cambrian, Harkless Formation, White-Inyo Mountains, California, UCLA Loc. 6052. ×0.75.
 - 10-Several specimens of Bergaueria sp. (UCLA 48604) on bottom of bed, among unbranched cylindrical burrows parallel to bedding (Planolites, UCLA 48607). Lower Cambrian, Harkless Formation, White-Inyo Mountains, California, UCLA Loc. 6047. ×0.75.
 - 11-Several specimens of Bergaueria sp. (UCLA 48603) on bottom of bed, near Cruziana (UCLA 48606), a trilobite trail (at left, partially obliterated by later stubby burrows). Lower Cambrian, Harkless Formation, White-Inyo Mountains, California, UCLA Loc. 6049. ×1.
 - 12,13-Specimen of Conostichus, shown for comparison with Bergaueria. 12, Side, and 13, bottom view of conical specimen. UCLA 48608. Pennsylvanian (Missourian), Coffeyville Shale, Tulsa, Oklahoma. $\times 1$.
 - 14-Bergaueria(?) sp., Lower Cambrian, Poleta Formation, White-Inyo Mountains, California, UCLA Loc. 6050. UCLA 48601. ×0.75.

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Alpert

