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EARLY CAMBRIAN EDIACARAN-TYPE FOSSILS FROM CALIFORNIA

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ABSTRACT—Ediacara-type fossils are rare in the southwestern United States, and Cambrian occurrences of soft-bodied Ediacaran-type fossils are extremely rare. We report both discoidal and frondlike fossils comparable to Ediacaran taxa from the western edge of the Great Basin. We describe one specimen of a discoidal fossil, referred to the form species ?*Tirasiana disciformis*, from the upper member of the Lower Cambrian Wood Canyon Formation from the Salt Spring Hills, California. Two fragmentary specimens of frond-like softbodied fossils are described from the middle member of the Lower Cambrian Poleta Formation in the White Mountains, California, and the upper member of the Wood Canyon Formation in the southern Kelso Mountains, California. On the basis of similarities with fossils from the lower member of the Wood Canyon Formation and from the Spitzkopf Member of the Urusis Formation of Namibia, these specimens are interpreted as cf. *Swartpuntia*. All fossils were collected from strata containing diagnostic Early Cambrian body and trace fossils, and thus add to previous reports of complex Ediacaran forms in Cambrian marine environments. In this region, *Swartpuntia* persists through several hundred meters of section, spanning at least two trilobite zones.

INTRODUCTION

LTHOUGH THEIR systematics and paleoecology are still being evaluated, Ediacaran biotas are now known from most continents, and have been documented in a wide variety of depositional environments ranging from shallow subtidal settings to environments near storm wave base (see summaries in Glaessner, 1984; Narbonne, 1998; Dalrymple et al., 1999). In the past, the lack of modern biological or preservational analogues has led to quite varied interpretations of their paleobiologic affinity (e.g., Seilacher, 1989, 1992; Retallack, 1994; McMenamin, 1998). However, documentation of putative molluscs (Fedonkin and Waggoner, 1997), sponges (Gehling and Rigby, 1996; Brasier et al., 1997), echinoderms (Gehling, 1987), medusoid hydrozoans (Narbonne et al., 1991), cnidarians (Gehling, 1988), and other taxa with modern affinities (Runnegar and Fedonkin, 1992) has shifted attention away from controversy over their phylogenetic relationships and more towards their mode of occurrence.

At one time, the Precambrian-Cambrian boundary was thought to coincide with a mass extinction of all Ediacaran biotas, with subsequent replacement in the Lower Cambrian by bioturbating and skeletonized organisms (see summaries in Gehling, 1991; Runnegar and Fedonkin, 1992; Conway Morris, 1993; Hallam and Wignall, 1997). More recently, workers have begun to reinterpret assumptions about the temporal and stratigraphic distribution of Ediacaran biotas, largely through breakthroughs in understanding their unique mode of preservation (Gehling, 1986, 1996, 1999; but also see Wade, 1968) and through new occurrences of diagnostic Ediacaran fossils in Cambrian strata (Jensen et al., 1998).

Previous attempts to explain the preservation of Ediacaran fossils have relied on interpretations of unique paleobiology or on analogy (e.g., Seilacher, 1984, 1989, 1992; Retallack, 1994). More recently, Gehling (1986, 1996, 1999) used a variety of sedimentologic and taphonomic criteria to document a previously overlooked taphonomic factor: microbial mantling of Ediacaran organism carcasses. Preservation of these organisms in coarse siliciclastic sediments was facilitated by microbial mantling of sediments, with subsequent restriction of pore-water migration (Gehling, 1996, 1999). An increase in vertical bioturbation in the Early Cambrian, documented by increases in tiering depth and intensity of deep burrowing (Bottjer and Ausich, 1986; Droser and Bottjer, 1989), caused the disappearance of these mat surfaces in the Phanerozoic. Because preservation of Ediacaran biotas was dependent on the presence of microbial mats, the loss of these mats nearly eliminated the taphonomic conditions necessary for their preservation in subtidal sandy marine environments (Seilacher and Pflüger, 1994).

Before the widespread recognition of the importance of microbial mantling of soft tissues, there were scattered reports of Lower, Middle, and Upper Cambrian "Ediacaran-style" fossils (Cloud and Nelson, 1966; Durham, 1971; Borovikov, 1976; Narbonne et al., 1991: Conway Morris, 1993: Crimes et al., 1995: Waggoner and Collins, 1995). Perhaps the most thoroughly documented Cambrian Ediacaran-type organisms are those from the Burgess Shale, including a frondlike form and several probable cnidarians (Conway Morris, 1993). Furthermore, recent reports of Ediacaran fossils mere meters beneath disconformably overlying Cambrian sediments (Grotzinger et al., 1995; Narbonne et al., 1997) cast doubt on the hypothesized disappearance of all Ediacaran biotas at the Precambrian-Cambrian boundary. Recently, Jensen et al. (1998) documented both frondlike and "medusoid" Ediacaran-style fossils from Lower Cambrian strata of Australia (also see Crimes and McIlroy, 1999). These observations suggest that the preservational conditions that favored preservation of Ediacaran biotas had been greatly reduced by the latest terminal Proterozoic, but may have shifted to deeper marine settings (Crimes and Fedonkin, 1996) or become restricted to narrow preservational intervals in Early Cambrian shallow subtidal environments (Seilacher and Pflüger, 1994; Hagadorn and Bottjer, 1999).

The Great Basin of the western United States is well known for its thick, well-exposed sections of Neoproterozoic and Cambrian strata, which represent a variety of alluvial and marine facies (e.g., Fedo and Cooper, 1990; Link et al., 1993). Although rocks in the study area (Fig. 1) have been locally subjected to regional tectonism and intrusion (e.g., Burchfiel and Davis, 1981; Wernicke et al., 1988), many sections are remarkably well preserved, and provide a rich source for paleobiologic and sedimentologic information. Even so, Ediacaran fossils have only recently been recognized in the Great Basin (Horodyski, 1991; Hagadorn and Waggoner, 2000). Coupled with reports of new Ediacaran biotas from Namibia (Narbonne et al., 1997), these discoveries led us to re-examine other occurrences of suspected Ediacaran fossils from the Great Basin-most of which were previously discounted because they were Cambrian in age, because they were fragmentary specimens, or because comparable bauplans were not known among existing Ediacaran taxa. We present a brief history and description of these fossils, their



FIGURE 1—Generalized lithostratigraphic and biostratigraphic framework for fossils presented herein. Faunal symbols reflect confirmed first occurrences of body or trace fossils within each region, and are positioned to the right of their corresponding section (data from Langille, 1974; Alpert, 1974; Hunt, 1990; Horodyski et al., 1994; Lipps and Fedonkin, 1988; Bahde et al., 1997; Hagadorn, 1998; Hagadorn and Waggoner, 2000). Dashed lines indicate approximate position of the terminal Proterozoic–Lower Cambrian and Lower–Middle Cambrian boundary in this region. For comparative purposes, the vertical scale for the Mojave region section has been exaggerated 3×. [White-Inyo and Death Valley lithostratigraphy modified from Nelson (1976)]. Inset, Sample locations within each of these three lithostratigraphic provinces, including: 1, UCMP Locality Number B8026; 2, LACMIP Locality Number 17108.

stratigraphic occurrence, and their relevance to the temporal distribution of Ediacaran biotas.

GEOLOGIC SETTING

The fossils described here are from three sites: the Salt Spring Hills in the southern Death Valley region of eastern California, the southern Kelso Mountains in the Mojave Desert region of southeastern California, and the White Mountains of eastern California. These localities represent strata deposited in the craton margin hinge zone (Kelso Mountains) and the more rapidly subsiding inner-to-outer miogeocline (Salt Spring Hills and White Mountains, respectively; Bahde et al., 1997). The regional stratigraphy, detailed stratigraphic context, sampling horizons, and study locations are illustrated in Figure 1. Although absolute age constraints are not available for the studied sections, consideration of available stratigraphic, paleontologic, and chemostratigraphic information (outlined below) allows us to firmly establish an Early Cambrian age for our fossils.

In the Salt Spring Hills (Death Valley region; Fig. 1.2), samples were collected from the upper member of the Wood Canyon Formation, at a site about 0.5 km NE of Amargosa Spring (LAC-MIP Locality Number 17146). In the southern Kelso Mountains (Mojave Desert region; Fig. 1.3), samples were collected in situ from the upper member of the Wood Canyon Formation, approximately 4.5 km NW from Kelso Station (LACMIP Locality Number 17108). At both localities, the upper Wood Canyon Formation contains nevadiid trilobites, helicoplacoid skeletal elements, and a number of typical lower Paleozoic trace fossils, including Rusophycus and Skolithos (Langille, 1974; Fedo and Cooper, 1990; Hunt, 1990; Mount et al., 1991; S. Hollingsworth, personal commun., 1998). Treptichnus pedum (Bahde et al., 1997) and Taphrhelminthopsis also occur in an interval several meters thick at the base of the middle member of the Wood Canvon Formation. The lower member of the Wood Canvon Formation, which crops out in miogeoclinal sections of the Death Valley region (such as the Salt Spring Hills), contains T. pedum, and, very close to the base, cloudiniid-like tubes and other Ediacaran fossils such as Ernietta and Swartpuntia (Horodyski, 1991; Horodyski et al., 1994; Runnegar et al., 1995; Hagadorn and Waggoner, 2000). Carbon isotopic studies of Wood Canyon Formation and Stirling Quartzite carbonates are consistent with an Early Cambrian age for rocks from the study localities (Corsetti, 1993, 1999; Runnegar et al., 1995; Runnegar, 1998; R. Ripperdan, personal commun., 1998).

The specimen from the White Mountains was collected in situ from the lower 25 meters of the lower siltstone unit of the middle member of the Poleta Formation (J. Durham, personal commun., 1997; Fig. 1.1). In this region, a three-part (i.e., upper, middle, lower) subdivision of the Poleta Formation is used (McKee and Moiola, 1962; Stewart, 1970). The specimen was collected near Westgard Pass in the White Mountains (UCMP Locality Number B8026). The lower part of the lower siltstone unit of the middle member of the Poleta Formation contains brachiopods, helicoplacoids, and trilobites belonging to the Nevadella Zone (e.g., Durham and Caster, 1963; McKee and Gangloff, 1969; Nelson, 1976; Moore, 1976a). Underlying strata also contain abundant archaeocyathids, Skolithos, T. pedum, and Taphrhelminthopsis (Langille, 1974; Alpert, 1976a; Moore, 1976a; Hagadorn et al., 1994). Carbon isotope stratigraphy and trace fossil analyses of the White-Inyo sequence suggest the presence of a large hiatus at the base of the underlying Campito Formation (Runnegar, 1998), and reveal a negative isotopic excursion (Corsetti and Kaufman, 1994; Corsetti, 1999) and presence of T. pedum in the upper member of the Deep Spring Formation. Together, these observations suggest that the overlying strata, including the Poleta Formation, are Early Cambrian in age.



FIGURE 2—1, Sole of bed from upper member of the Wood Canyon Formation, Salt Spring Hills, CA (LACMIP 12740). Discoidal specimen ?*Tirasiana disciformis* is at center of slab, amidst a variety of trace fossils, including an obliquely dipping *Planolites* burrow that abuts the specimen at upper margin (arrow), ×1.5. 2, Close-up of ?*T. disciformis*, illustrating two regions of circular rings surrounding a quasi-polygonal-shaped pointed central region. Specimen is preserved in convex hyporelief on a surface that contains the casts of numerous trace fossils, ×4.

SEDIMENTOLOGY AND DEPOSITIONAL CONTEXT

The specimen from the Salt Spring Hills (Death Valley region) is preserved on the sole of a 1-cm-thick very fine-grained sand layer in a slab that is characterized by alternating mm- to cm-thick layers of very fine- to fine-grained quartz arenite and shale. The millimeter-thick silt/claystone which underlies the fossilbearing sand layer has been partially removed by surficial weathering, resulting in formation of "desert varnish" on the bed sole. Upper and lower surfaces of the slab are moderately well bioturbated (bii3 of Miller and Smail, 1997) and discrete trace fossils are preserved in convex hyporelief and full relief. The study sample and adjoining slabs include well-preserved forms such as *Cruziana, Diplichnites, Monocraterion, Palaeophycus, Planolites,* and *Skolithos,* as well as rare molds of trilobite skeletal elements.

The specimen from the Kelso Mountains (Mojave Desert region) is preserved on the top of a 2.5 cm-thick bed composed of very fine to fine grained quartz arenite. Grains are subrounded to rounded and distinct laminae or grading are not visible. Along the slab margins where petaloid structures are truncated, two indistinct layers of opaque and gray interbedded quartzitic sediment appear to underlie the specimen by 5-7 mm. These layers dip obliquely toward the inferred central stalk of the specimen. The base of the sampled bed has been moderately bioturbated (bii3), and small Planolites burrows are visible in convex hyporelief. The Kelso Mountains specimen figured herein is the largest fragment of a specimen extracted from steeply inclined strata exposed atop a small topographic saddle. Lack of bedding plane exposures and closely spaced fractures at this site made extraction of a complete specimen impossible. In addition to the large fragment illustrated here, a number of smaller fragments were also collected and will be deposited at the Los Angeles County Museum of Natural History (LACMIP). These fragments exhibit similar preservational features, including apparent petaloid ribbing. At this locality, the

upper member of the Wood Canyon Formation consists of interbeds of hummocky cross-stratified siltstone and fine sandstone. Interference ripple and wrinkle marks are locally present, as are *Skolithos* traces, and thin carbonate interbeds. These lithofacies are consistent with an interpretation of a mixed tidal and stormswept shallow-marine shelf.

The White Mountains specimen is preserved on the top of a thin (3 cm) bed of very fine grained sandy siltstone. The sample was collected from an outcrop characterized by thinly interbedded (1–10 cm thick) fine to very fine sandstones and siltstones/ shales (Moore, 1976a). In the figured specimen, underlying sediments are not bioturbated and faint submillimetric laminae are visible. A thin (0.3–1.0 mm) layer of concentrated helicoplacoid and trilobite debris occurs 3-4 mm beneath the specimen surface. The swaley surface topography of the sample likely reflects the shallow trough and crests of a ripple and is consistent with inferred deposition in a shallow subtidal environment adjacent to a carbonate-sandbar complex (Moore, 1976a,b).

SYSTEMATIC PALEONTOLOGY 12645

Figured specimens from the Kelso Mountains/(type number 12726) and Salt Spring Hills (type number 12740) are deposited with the LACMIP. The specimen from the White Mountains is deposited with the University of California Museum of Paleontology (UCMP) and is catalogued as type number 37450.

Genus ?TIRASIANA Palij, 1976 ? TIRASIANA DISCIFORMIS Palij, 1976 Figure 2

Tirasiana disciformis PALIJ, 1976, p. 71, pl. 22, fig. 4, pl. 23, figs. 1,2.

Description.—Discoidal form preserved in convex hyporelief, consisting of roughly circular concentric rings deformed into a quasi-polygonal shape; diameter 17 mm; vertical relief 0.5 mm. Discoid consists of three distinct zones: outer and inner bands

of rings, which surround a raised central boss. Outer zone ~ 4 mm wide, with low relief; inner zone ~ 3 mm wide with slightly higher relief; zones separated by a deep (~ 0.5 mm) groove. Inner and outer zones each bear three to four rugose lineations ~ 0.5 mm thick. Central boss exhibits highest relief on specimen and is ~ 4 mm in diameter; faint ring-like structures present along outer edge; boss in center. Outermost margin sharp, except where obscured by a *Planolites* burrow (Fig. 2.1, arrow) which appears to obliquely cross and undercut ring margin. 12645.

Material examined.—One specimen (LACMIP type 12740; Fig. 2) from LACMIP locality 17146. Additional specimens on base of large uncollectable bedding plane at LACMIP loc. 17146.

Occurrence.—Wood Canyon Formation, Salt Spring Hills, California (LACMIP loc. 17146).

Discussion.-Discoidal structures are common features of terminal Proterozoic and Lower Cambrian bed surfaces, and can reflect a variety of abiogenic and biogenic processes. An interpretation as a dewatering or sediment fluidization structure can be rejected because the specimen is preserved on a bed sole in convex hyporelief, which is unusual for fluid-escape structures. Such structures are typically preserved on bed surfaces, in convex epirelief (see summary in Reineck and Singh, 1980). Unlike our specimen, in modern muddy environments, rings in such structures overlap one another and in sandy settings pits form at the top of the mounded sediment (e.g., Ricci Lucchi, 1970). Furthermore, escape of fluidized sediment is commonly visible in overlying layers, and does not form fine contiguous rings after collapse. The specimen is also unlike degassing or collapse features observed from modern marine environments (see reviews in Cloud, 1960; Ricci Lucchi, 1970; Sun, 1986). Striae associated with deformation of suspect microbially-bound sediment are typically larger, more widely spaced, and are associated with radial lineations extending from the locus of deformation (McIlroy and Walter, 1997). The specimen could be a discoidal flute cast or a swirl structure produced by a partially exposed tube/strand, but the rings are contiguous despite deformation of the specimen, which would not be expected in a grooved structure created by a current. Although discoidal flute marks or "tether rings" have been previously described as fossils (cf. Bunyerichnus; Glaessner, 1969; Jenkins et al., 1981), the figured discoid is unlike such structures (Osgood, 1970).

It is also possible that this specimen represents an organism's resting trace. The most comparable discoidal trace fossils in this region are Bergaueria and the tops of Skolithos and Monocraterion. Helicoplacoid echinoderms preserved in situ are associated with resting traces that are also superficially similar to our fossil (F. Corsetti, personal commun., 1999). The fine concentric rings in this specimen are unlike Bergaueria, Skolithos, or Monocraterion. If the specimen was a type of Bergaueria (which in this region is nearly two to three times the size of the figured specimen, and is usually 0.5 to 1.5 cm deep), one would expect to see radial lineations or striations along the margins. Thus, the interpretation as the top of an infaunal cylindrical trace or the base of an anemone resting trace can be rejected. We compared our specimen to over a hundred helicoplacoid specimens, including several in situ helicoplacoids and helicoplacoid resting traces, collected by S. Dornbos (USC) and J. Wyatt Durham (UCMP). Despite the grainy surface topography and its occurrence in an interval known to have helicoplacoids, a helicoplacoid resting trace can be rejected because a) the specimen does not have the characteristic coiling diagnostic of such traces but, instead, consists of concentric rings; b) it is preserved in a coarser lithology than the vast majority of documented articulated or partially articulated helicoplacoids (which typically occur in shales); c) it is nearly twice the size of other observed helicoplacoid resting traces; d) rugose patterns along discoid margins are significantly smaller, less ornamented, and lack the characteristic rectangular shape of comparable molds of helicoplacoid plates from this region; and e) no evidence of a splayed helicoplacoid skeleton is observed (typically, helicoplacoid resting traces exhibit splaying of the upper skeleton, skeletal debris along one margin of specimen, or impressions of such debris; S. Dornbos, personal commun., 1999).

The placement that is most consistent with all observed data is that the fossil described here is an Ediacaran-type "medusoid" organism. Its preservation on the sole of a sandstone bed is very similar to that seen in the Ediacara Hills and other sites (cf. Wade, 1970). There are several described genera of annulated discoidal fossils that resemble our specimen. Unfortunately, the taxonomy of the simpler Ediacaran "medusoids" is in serious disarray; existing taxonomy is probably highly oversplit, and many, if not most, proposed "medusoid" genera probably represent preservational variants of identical organisms (Jenkins, 1992; Narbonne and Gehling, 1998). A number of "medusoid" genera are simply not well characterized and remain incertae sedis (Runnegar, 1992). Further complicating the situation is the fact that some "medusoids" are probably the holdfasts of certain Ediacaran frondlike taxa (Jenkins and Gehling, 1978). Resolving these problems is far beyond the scope of this paper. For comparative purposes, in making comparisons with previously described material, we have used established genera in the sense of form taxa.

The figured specimen is similar to the annularly chambered central portion of *Spriggia annulata*, although it lacks the marginal tentacles and delicate wrinkles in the outer band of the holotype. However, in *S. annulata* the major zones are not as well marked, and the finer concentric banding is much more extensive (Sun, 1986; note that Jenkins [1992] considered *S. annulata* to intergrade with species of *Cyclomedusa* and *Ediacaria*). In contrast, the specimen has more concentric zones and finer ornamentation than simple "medusoids" such as *Medusinites, Nemiana, Nimbia,* and *Paliella.* The lack of regularly spaced concentric furrows and thicker ring radii distinguish the figured specimen from *Kaisalia* and *Kullingia*.

The fossil is extremely similar to specimens described as *Tirasiana* (Palij, 1976), which lack radial ornamentation but show two, three, four, or five concentric zones around a central tubercle. In fact, the fossil described here has proportions virtually identical to medusoids described as *T. disciformis* from the Vendian-age Sylvitsa series of the central Ural Mountains (Bekker, 1990, pl. 27 fig. 1). The fossil falls within the range of morphologies given by Fedonkin (1990) for specimens from other Russian localities such as the White Sea. *Tirasiana*, like this fossil, may also show faint finer concentric ornament within the main zones, although this is variable.

Runnegar (1992) considered *T. disciformis* to be a valid taxon. However, Fedonkin (1990) found that at least some specimens of *Tirasiana* intergrade with specimens assigned to the species *Ediacaria flindersi*. The lack of any radial striae and small number of concentric zones distinguishes this specimen from typical specimens of *Cyclomedusa* and *Ediacaria*, although some smaller specimens assigned to these genera also lack radial ornament and have few zones. *Ediacaria* supposedly has marginal tentacles not found in *Tirasiana*, but these cannot be seen in many of the specimens assigned to *Ediacaria* (Fedonkin, 1990). It has even been argued that most specimens assigned to *Ediacaria* do not match the type material; in this case, most specimens of "*Ediacaria*" should perhaps be placed in *Tirasiana*. We cannot resolve this problem here. We have tentatively assigned this