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 soft-bodied 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 A 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

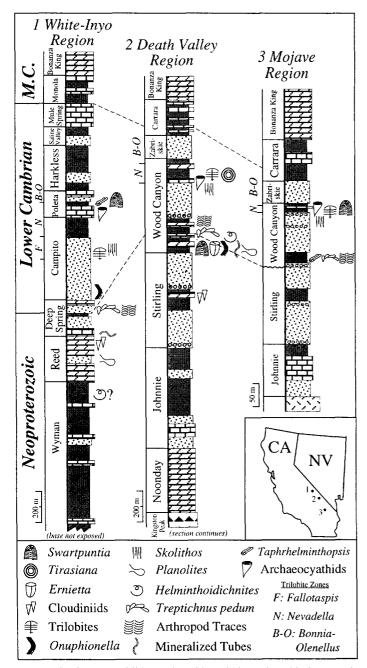


FIGURE 1—Generalized lithostratigraphic and biostratigraphic framework for fossils presented herein. Faunal symbols reflect confirmed first occurrences of body or trace fossils within each region, and are positioned to the right of their corresponding section (data from Langille, 1974; Alpert, 1974; 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 17146; 3, 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 fossil-bearing 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

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 \sim 4 mm wide, with low relief; inner zone \sim 3 mm wide with slightly higher relief; zones separated by a deep (\sim 0.5 mm) groove. Inner and outer zones each bear three to four rugose lineations \sim 0.5 mm thick. Central boss exhibits highest relief on specimen and is \sim 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.

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

specimen to *Tirasiana disciformis* on the basis of its close resemblance to figured specimens from Russia, but believe that exact assignment is not possible without additional specimens and thorough revision of "medusoid" taxonomy.

Genus cf. Swartpuntia Narbonne, Saylor, and Grotzinger, 1997

Figures 3, 4

Swartpuntia germsi NARBONNE, SAYLOR, AND GROTZINGER, 1997, p. 957, fig. 4; p. 960, fig. 6; p. 963, fig. 9; p. 964, fig. 10.

Description.—LACMIP 12726, Figure 3.1: Proximal fragment of multifoliate frond consisting of several petaloids and portion of central stalk. Specimen 62 × 51 mm. Two discrete petaloids visible in cross section along slab margin. Surface petaloid consists of a sheet of 22 parallel tubular segments preserved in convex epirelief that extend laterally from a central stalk. Tubular segments are up to 42 mm long and range from 1.0 to 1.7 mm in diameter; diameter constant over the length of the segments; segments follow vertical topography of slab surface. Segments form an approximately forty-five degree angle with central stalk; this angle increases distally to 55 degrees. Stalk 11 mm at widest point, preserved depressed relative to the neighboring topography by up to 8 mm; two raised projections and two faint lateral grooves visible on stalk.

UCMP 37450, Figure 3.2: Fragment of frondose petaloid; preserved in convex epirelief. Total surface area 10.8 cm x 9.3 cm. Petaloid segments semicircular in cross-sectional relief, but not clearly tubular, straight to arcuate in plan view, generally oriented parallel to one another. Two large areas of contiguous segments are 6.3×2.8 cm (e.g., right side of specimen in Fig. 3.2) and 9.0×5.3 cm (e.g., left side of specimen in Fig. 3.2). At least 30 segments are visible on right side of specimen, 29 visible on left side. Segments up to 4.2 cm long, 1–2 mm wide, 0.1–0.3 mm in relief; segments follow surface relief of up to 8.5 mm. On portion of slab surface, segments curve outward from center of slab and form sigmoidal pattern; two sets of segments present in this region, one on a ~ 1 -mm-thick upper layer overlying segments of the adjacent, underlying layer, indicating presence of two petaloids (Fig. 3.2, arrow).

Material examined.—One nearly complete specimen (UCMP 34750) from UCMP loc. B8026, one incomplete specimen (LACMIP 12726) and numerous fragments from LACMIP loc. 17108.

Occurrence.—Wood Canyon Formation, Kelso Mountains, California (LACMIP loc. 17108); Poleta Formation, White Mountains, California (UCMP loc. B8026).

Discussion.—It is difficult to pinpoint abiogenic mechanisms which could plausibly create a surface 1) characterized by series of up to 30 parallel surface striae which extend across an uneven sediment surface yet which penetrate the surface at the same depth; 2) in which the tubular elements are rounded in cross-sectional view; 3) in which striae arc in one direction and then in the other direction without crossing; 4) in which two layers of similarly sized but obliquely oriented striae occur on overlying sediment layers less than 0.5 mm thick; and 5) on which there are no other tool marks.

The slab surface topography appears to reflect original bedding plane features (although the transverse markings and surface striae appear to have draped this sedimentary surface, and together with the presence of the inferred stalk in LACMIP 12726, may have later modified this surface). In addition, well-preserved underlying trace fossils and sedimentary structures suggest that these features are not metamorphic, diagenetic, or structural features. Thus, the best candidates to produce the observed features might include a) a comblike object drifting across the sea bottom; b) an arthropod with 20–30 appendages

scratching surficial or underlying sediment surfaces; c) folding or shearing of microbially-bound sediment; or d) impression of a frond-like soft-bodied carcass.

Ridges consistently conform to the topography of both specimens, which have a variety of bumps and depressions comprising up to 8 mm of vertical relief. The ridge-trough depth (measured along individual continuous segments) does not vary more than 0.3 mm in any individual tubular segment. Comblike tool marks made by hard inorganic objects or skeletonized debris would not be expected to conform so precisely to surficial topography, but would rather exhibit variable impression depths as the structure's edges passed across the substrate surface. A shifting current could account for the sigmoidal pattern within the surface striae, but would not account for their consistent parallel orientation over a 150 cm² surface. The only known parallel tool and drag marks made by soft tissue (Haines, 1997) are unlike those observed on study specimens, and have not been documented on two successive sediment layers on the same specimen, as in UCMP 37450.

If these specimens were scratch marks made by arthropods, one would expect splaying of the impressions as appendages moved outward/inward from the torso, tapering of the scratches toward their distal tips, deep impressions (or prod marks) at one edge of the impressions, and/or variations in the depth of penetration of the sediment corresponding to variations in surface topography. None of these features is present. Furthermore, on both specimens the segments occur on two different layers, are oriented obliquely to one another, and are separated by less than a millimeter of sediment. If they represent arthropod undertracks, one would expect all of them to occur on the same surface, unless the lower set was excavated and cast by another sediment layer, which was then scratched (without penetrating into the underlying layer)—a scenario which seems improbable. Arthropod scratch marks from elsewhere in this region (including Monomorphichnus; Alpert, 1974, 1976a, 1976b; Langille, 1974) are morphologically quite different from these features, largely because in Monomorphichnus traces, the size of the scratches in an individual set varies. Lastly, most arthropod scratch marks preserved in sharp convex hyporelief are typically formed on the bottom of a bedding plane, through the casting of the scratch trough, unlike our samples which exhibit convex ridges on bed tops.

Bunching or shearing of a microbially-bound sediment surface would not preserve such sharp regular folds. Nor would bunching or shearing produce a central stalk perpendicular to the ridges and abutting them. Surface textures of suspect-microbial features from siliciclastic strata of this region are typically more polygonally wrinkled, pustulose, and irregularly shaped than observed here (Hagadorn and Bottjer, 1997). Elongate subparallel striae associated with deformation of suspect microbially-bound sediment are typically more widely spaced, radiate outward from the locus of deformation, taper distally, and are larger than structures figured here (McIlroy and Walter, 1997).

The difficulty reconciling inorganic, tool, trace, weathering, or deformational origins for these structures, together with their morphologic and preservational similarities to certain Ediacaran "frond" taxa, suggest that our specimens are body fossils of "fronds." Several Ediacaran genera are similar to our specimens, but closer comparisons rule out most of them. The figured specimens are much larger than published accounts of *Nasepia* (Germs, 1973). The presence of a central stalk, multiple petaloids, and reduced size of tubular segments reject the possibility that the study specimens are *Ernietta*, which is typically preserved in three dimensions, rather than splayed on a bedding plane (Pflug, 1972). The tubular segments are narrower, longer (relative to overall specimen width), and less regularly arching



FIGURE 3—1, cf. Swartpuntia sp. from upper bedding plane surface of the upper member of the Wood Canyon Formation, Kelso Mountains, CA (LACMIP 12726). Note infolding and termination of parallel striae (right) at central stalk. Also note faint lineations on and perpendicular to the central stalk axis at left. 2, cf. Swartpuntia sp. from upper bedding plane surface of the middle member of the Poleta Formation, White Mountains, CA (UCMP 37450). Note presence of two thin (~0.5 mm) layers of parallel striae, visible at upper left of specimen where upper level of petaloid frond is preserved over lower level and striae appear to intersect one another (arrow). Although specimen has been chipped in center, striae on right side of specimen are from same layer as striae from middle left.

than many specimens of *Pteridinium* (Jenkins, 1992) and more regular than the transverse striae of *Dickinsonia* (Sprigg, 1947). The figured specimens are most similar to the multifoliate fronds described by Narbonne et al. (1997) as *Swartpuntia*.

Swartpuntia has been described from terminal Proterozoic strata of Namibia (Grotzinger et al., 1995; Narbonne et al., 1997), and from the terminal Proterozoic lower Wood Canyon Formation

of the southern Great Basin (Hagadorn and Waggoner, 2000). Similar, unnamed frond-like fossils, from the Lower Cambrian of southern Australia, have been documented by Jensen et al. (1998). Like the specimens described here, all of these fossils exhibit similar modes of preservation (including occurrence on bedding-plane surfaces and apparent sand casting of petaloid segments) and are associated with similar suites of sedimentary structures,

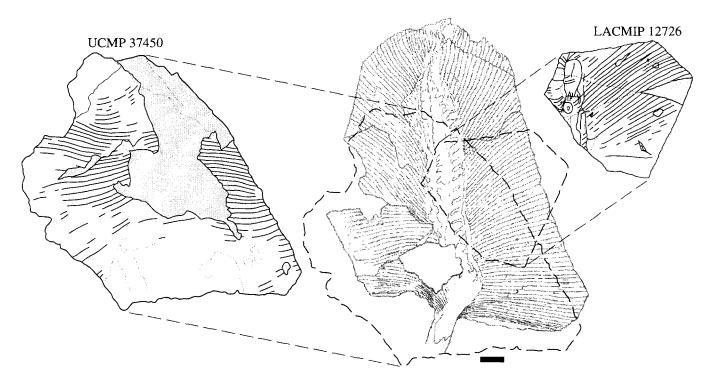


FIGURE 4—Camera lucida drawings and comparison of cf. Swartpuntia sp. from this study (upper right, LACMIP 12726; upper left, UCMP 37450) with similar drawing (center) of Swartpuntia germsi (modified from Narbonne et al., 1997). Dashed regions indicate inferred fragment locations relative to specimen from Narbonne et al. (1997). Note that specimen at left preserves two petaloid layers, as does specimen at center, and note striae size and spacing similarity in all three specimens. All camera lucida drawings are at the same scale; scale bar is 1 cm.

trace fossils, and "medusoid" body fossils (Jensen et al., 1998). The fronds figured in this study are similar in size and proportions to these previously described fossils, and share morphologic features including presence of a central stalk, multiple petaloid layers, and tubular petaloid segments in a sigmoidal to straight arrangement. Our fronds are roughly the same age as *Swartpuntia*-like fronds illustrated from Australia (Jensen et al., 1998). The intersection of tubular segments with the central stalk in LACMIP 12726 suggests that the raised stalk projections are equivalent to the V-shaped stalk ridges illustrated in Narbonne et al. (1997). Despite their low (≤1 mm) relief, the tubular segments maintain this relief relative to cm-scale variations in slab surface topography, both in distal regions of the petaloid, and in concave depressions at or near the central stalk.

LACMIP 12726 is most similar to the central stalk and proximal petaloid region of *Swartpuntia*, whereas UCMP 37450 is similar to the petaloid region (Fig. 4). Unfortunately, the petaloid margins and most of the stems are not preserved in our specimens, the dorsal-ventral orientation of our specimens is uncertain, and the petaloid:stalk proportions cannot be calculated. We cannot make a confident species-level identification, but assign the fossils as *?Swartpuntia* pending collection of more complete specimens.

Discussion.—The history of these specimens is relevant to understanding their importance and the credit due their collectors. The UCMP specimen was originally collected by J. Wyatt Durham in 1970, and noted in a talk given at the 1971 Cordilleran section GSA meeting (Durham, 1971). On the basis of his experience with Lower Cambrian biotas, Durham suggested that it was not a typical Cambrian faunal element and tentatively suggested it might be Dickinsonia. Conway Morris (1993) later figured the specimen in his comprehensive treatment of Ediacaran holdover taxa. Conway Morris thought that an assignment to Dickinsonia was plausible, but the apparent convergence

of the elongated segments on the upper portion of the specimen was not known from *Dickinsonia*. The LACMIP specimen (Fig. 3.1) was collected in 1992 by C. Fedo and J. Cooper (CSU Fullerton), and was interpreted as a soft-bodied impression, but was not formally described as an Ediacaran taxon because of the known Cambrian age. At that time, Cambrian occurrences of Ediacaran fossils were poorly known and *Swartpuntia* had not yet been discovered.

DISCUSSION

Collectively, the morphologic and sedimentologic characteristics of these specimens suggest that they are fossilized Ediacaran organisms. Although less spectacularly preserved than comparable specimens from Namibia and Australia, these fossils are nonetheless important because they help elucidate the temporal range and distribution of post-Vendian Ediacaran forms. Although simple discoidal "medusoids" have been noted in a variety of Cambrian strata (Narbonne et al., 1991; Crimes et al., 1995), more complex forms such as *Swartpuntia* are rare in the Cambrian. Furthermore, association with skeletonized Early Cambrian body fossils confirms the observations of Jensen et al. (1998) that complex Ediacaran fossils occur in Cambrian marine environments, but perhaps are only preserved under unique circumstances.

Of the two Early Cambrian forms described from this region, the cf. Swartpuntia specimens are of primary interest because they may be an example of a relatively long-ranging Ediacaran holdover taxon characteristic of shallow-marine environments. Regional stratigraphic comparison of the White Mountains and Mojave sections suggests that the lower member of the Wood Canyon correlates with the Deep Spring Formation (which underlies the Campito and Poleta Formations; Runnegar, 1998). Based on this correlation, and based on occurrences in the lower member of the Wood Canyon (Hagadorn and Waggoner, 2000),

Swartpuntia spans the pre-trilobite, Fallotaspis, and Nevadella Zones within the western Great Basin. Based on correlation of these sections with chronostratigraphically constrained sections from elsewhere (Landing et al., 1998), Swartpuntia may have a stratigraphic range ≥ 25 Ma.

Swartpuntia's long range and wide but scattered global distribution confirms that these fossils were likely only preserved where unique taphonomic windows existed. Although these fossils do not exhibit any diagnostic morphologic evidence to suggest microbial mantling of soft tissue (sensu Gehling, 1996, 1999), all three of the occurrences described here are from stratigraphic intervals characterized by suspect-microbial structures (Hagadorn and Bottjer, 1997, 1999). In both Australia and the Great Basin, Cambrian Swartpuntia-like fossils are also associated with soft-bodied "medusoids." These occurrences suggest limited persistence of Proterozoic-style soft-bodied preservation, thought to be made possible by microbial blanketing of sediments. Alternatively, it may indicate local modification of typical Phanerozoic-style burial processes, by decreased oxygen, restriction of vertically oriented bioturbation, early diagenetic mineralization, and/or rapid burial. Although occurrences of these fossils in the Great Basin are too rare and too scattered to make up a konservat-lagerstätten, such unusual burial processes are thought to account for many, if not most post-Proterozoic occurrences of soft-bodied preservation, such as the Burgess Shale (Seilacher, 1970; Seilacher et al., 1985; see also overview in Allison and Briggs, 1991; Seilacher and Pflüger, 1994). Our findings suggest that siliciclastic Cambrian strata that contain suspect-microbial structures should be examined carefully for further occurrences of Ediacara-type fossils.

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