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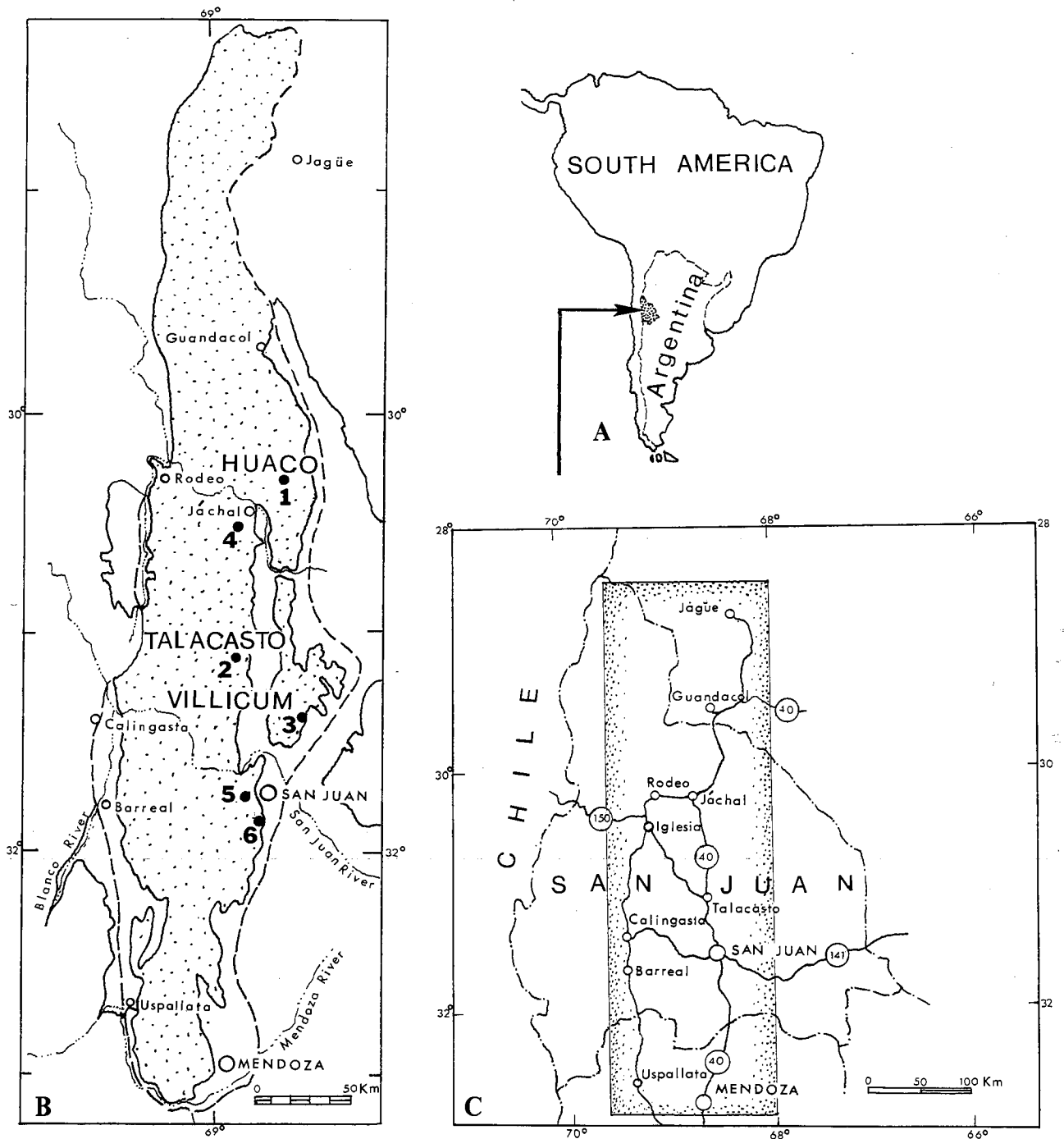


FIGURE 1.—Index map to Ordovician sponge localities in Argentina. A—South America showing the position of the province of San Juan within Argentina (arrow). B—Sponge localities within the Precordillera (stippled) of central San Juan Province. Major localities (1–3) include: 1, the Huaco locality along sulfurous Agua Hedionda Creek, 30 miles east of Jáchal City; 2, Talacasto Gulch section in the Precordillera Central, approximately 89 km northwest of San Juan City; 3, Don Braulio Gulch in the Villicúm Range, approximately 40 km northwest of San Juan City. Other minor localities (4–6) include: 4, Loma del Piojo at San Roque Hill; 5, Las Lajas Gulch, west of San Juan City; 6, La Flecha Gulch in the Chica de Zonda Range, south of San Juan City. C—Map of San Juan Province showing the position of map B in the central part of the province.

Hexactinellid Sponges from the Silurian-Devonian Roberts Mountains Formation in Nevada and Hypotheses of Hexactine-Stauractine Origin

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ABSTRACT

A moderately diverse fauna of hexactinellid sponges is described from the Devonian(?) upper part of the Silurian-Devonian Roberts Mountains Formation from a locality in Starvation Canyon in the Independence Mountains, Elko County, Nevada. *Diagoniella nevadensis* Rigby and Stuart, 1988, *Protospongia conica* Rigby and Harris 1979, *Protospongia spina* n. sp., *Protospongia* sp. 1, *Protospongia* sp. 2, and *Gabelia pedunculus* Rigby and Murphy, 1983, are present. These were apparently transported, size sorted, and buried by distal turbidity currents. Many samples have monospecific bedding plane "faunules," which suggest that localized and different original sponge "oases" were sources for the multiple turbidite-related accumulations. Stratigraphic and phylogenetic systematic evidences for increasing complexity versus simplification for the origins of hexactines and stauractines are summarized and discussed; hexactines as old as stauractines appear to have been the basic early spicule at about the beginning of the Cambrian, although evidence is still equivocal.

INTRODUCTION

A new hexactinellid sponge locality was discovered in Nevada during fieldwork in 1988 by S. R. Holmes and Larry Denison for the Freeport-McMoRan Gold Company, Elko, Nevada. They were collecting surface samples as part of a geochemical prospecting project when they discovered the locality in the upper Roberts Mountains Formation in Starvation Canyon (fig. 1), in the Water Pipe Canyon 7 $\frac{1}{2}$ -Minute Quadrangle in the Independence Mountains of Elko County.

The Roberts Mountains Formation is about 200 m thick in the area, and the sponges occur approximately 32 m below the Roberts Mountains thrust. The exact stratigraphic position of the locality within the Roberts Mountains Formation is unknown, except that it appears to be in the upper part of the preserved section. How much of the upper part of the formation is faulted out beneath the Roberts Mountains thrust is not known.

This study adds to the growing number of localities of hexactinellid sponges known from the Silurian-Devonian Roberts Mountains Formation in northeastern Nevada

and is the second discovered in the Independence Mountains. *Gabelia* was described from the formation from the Roberts Mountains, Nevada (Rigby and Murphy 1983). A more diverse assemblage was described from the formation from the Mahala Creek area in the Independence Mountains by Rigby and Stuart (1988) from a locality approximately 15 km northeast of the Starvation Canyon locality on the eastern flank of the Independence Mountains. Additional species of *Gabelia* were described from the formation from the Snake Mountains by Rigby, Maher, and Browne (1991).

Skeletons of the sponges were generally replaced by pyrite, now altered to limonite, and occur in various states of preservation and completeness. Such limonitic preservation is common in fossil sponges and apparently resulted from alteration of pyrite that initially replaced the opaline siliceous spicules during early diagenesis. Most of the fossils appear to be part of coarse debris laminae and were apparently transported into the basin of deposition, principally as fragments.

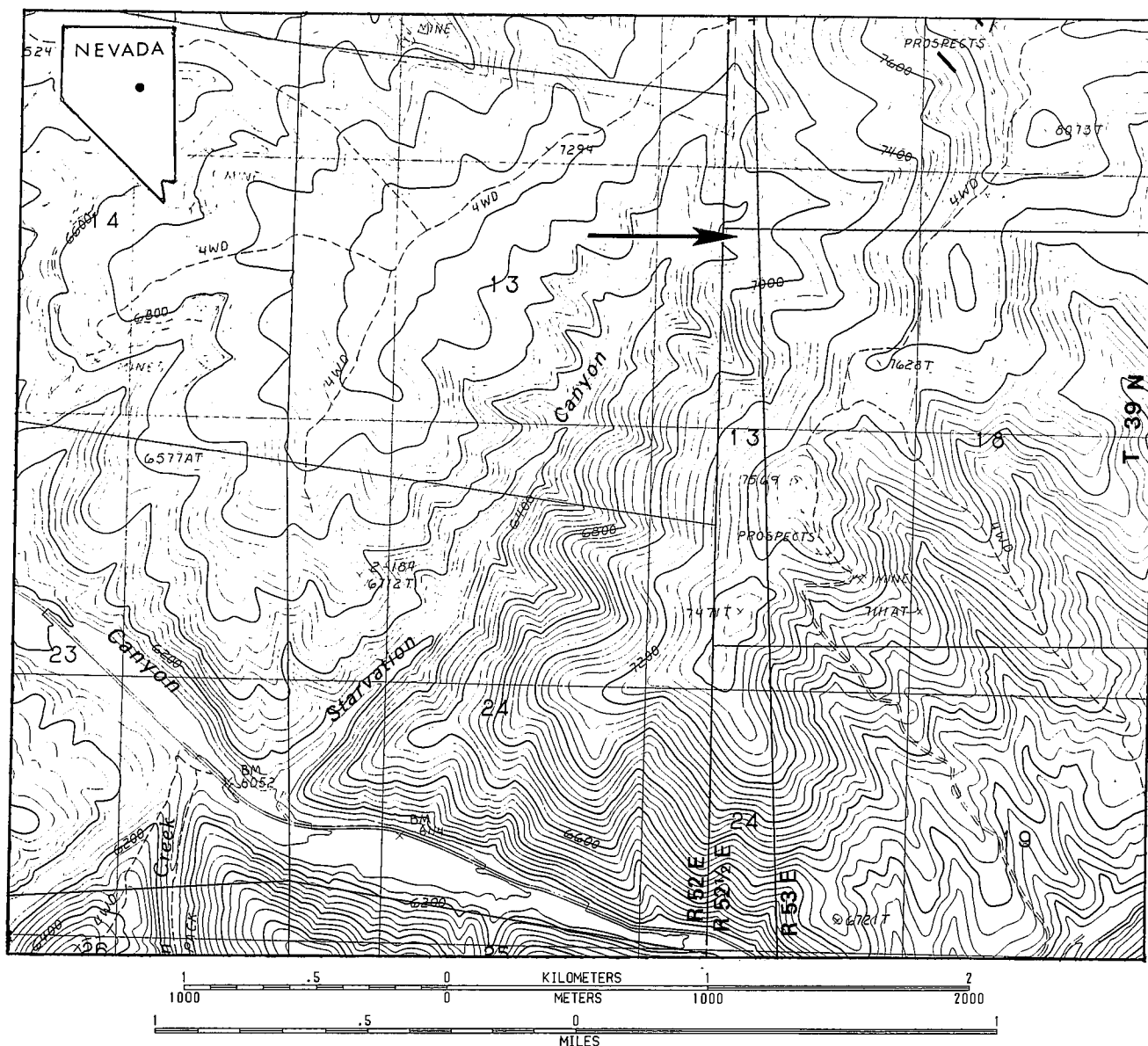


FIGURE 1.—Index map of the sponge locality in the headwaters of Starvation Canyon in section 13, T. 39 N, R. 52 $\frac{1}{2}$ E, in the Water Pipe Canyon 7 $\frac{1}{2}$ -Minute Quadrangle in the Independence Mountains of Elko County, Nevada. Base map from Water Pipe Canyon Quadrangle. North is toward top.

Sponges from the Roberts Mountains Formation in the Independence Mountains generally occur flattened on bedding planes of laminated, calcareous siltstone and interbedded silty limestone, whether from near the base of the formation (Rigby and Stuart 1988, p. 129) or from the upper part of the formation, as with those described here. These fossils were discovered in rocks exposed in a window beneath the upper thrust plate of the Roberts Mountains thrust fault, apparently composed of the Ordovician Snow Canyon Formation (Valmy) (see Ketner [1980] and Ross [1982] for regional relationships, and

Birak and Hawkins [1985] for geology of Jerritt Canyon gold district).

The locality is in the headwaters of Starvation Canyon (fig. 1), which is a northeast branch of major Taylor Canyon in the southwestern part of the Water Pipe Canyon 7 $\frac{1}{2}$ -Minute Quadrangle. The locality is 550 m south and 65 m east of the northeast corner of section 13, T. 39 N, R. 52 E, or 65 m east and 40 m south of the northwest corner of section 13, T. 39 N, R. 52 $\frac{1}{2}$ E; the sponges came from the latter section 13, which is a wedge-shaped, narrow correction section. The locality is at an elevation of ap-

proximately 6,840 feet in northern canyon exposures and talus, in the middle of the three upper branches at the head of Starvation Canyon, and is at 41° 16' 41" N latitude and 116° 03' 58" W longitude in the Independence Mountains, Elko County, Nevada, approximately 60 km north-west of the community of Elko.

The Roberts Mountains Formation was named by Merriam (1940, p. 11–12) to include the predominantly dark gray, well-bedded limestone that underlies the light gray Lone Mountain Dolomite and overlies the dark gray dolomite of the Ordovician Hanson Creek Formation in the type area in the Roberts Creek Mountain area, about 30 miles north of Eureka, Nevada. The formation in the type area is considered of Middle Silurian age. In eastern Nevada, however, the formation underlies the Rabbit Hill Limestone (Winterer and Murphy 1960, p. 134–36) with an apparently gradational and conformable contact. The latter formation contains a Helderbergian fauna and is considered to be Early Devonian. Because the sponges from Starvation Canyon come from the upper part of the formation, they are considered to be of likely Early Devonian age, but may be Late Silurian because we are uncertain of the stratigraphic position of the locality in the complex structure associated near the Roberts Mountains thrust fault.

Type material is deposited in collections of the U.S. National Museum of Natural History (USNM).

ACKNOWLEDGMENTS

We appreciate stratigraphic and locality information provided by Robert J. Stuart of Independence Mining Company, Inc., of Elko, Nevada. The fossils were collected under Stuart's direction when Holmes and others were employees of Freeport-McMoRan Gold Company, prior to that company becoming part of Independence Mining Company, Inc.

Mehl's research study trip to North America was supported by Deutsche Forschungsgemeinschaft (Ke 322/5-3) at the Institut für Paläontologie of the Freie Universität Berlin. L. T. Bird assisted in manuscript and illustration preparation, and J. R. Mortenson made the photographs from negatives prepared by Rigby in the Department of Geology, Brigham Young University. Brigham Young University covered much of the fossil preparations and manuscript and illustration costs as part of a grant to Rigby. W. E. Reif kindly allowed Mehl to restudy the types of the Carboniferous *Microhemidiscia ortmanni* Kling and Reif, 1969. H. Mostler also allowed Mehl to examine the Upper Cambrian "hemidiscs" in his collection from the Milo Formation of Iran. M. H. Nitecki and C. W. Stock provided detailed reviews of the manuscript. Their help is much appreciated.

SYSTEMATIC PALEONTOLOGY

Class HEXACTINELLIDA Schmidt, 1870

Order RETICULOSA Reid, 1958

Superfamily PROTOSPONGIOIDEA Hinde, 1887

Family PROTOSPONGIIDAE Hinde, 1887

Genus DIAGONIELLA Rauff, 1894

DIAGONIELLA NEVADENSIS Rigby and Stuart, 1988

figs. 2.4, 2.6–2.8, 3, 4.2, 4.3, 5, 6.1, 6.2,
6.7, 6.8, 7.6–7.8, 8

Diagoniella nevadensis RIGBY AND STUART, 1988, p. 132–34, figs. 3.7–3.9.

Emended diagnosis. *Diagoniella* with principal skeleton of ranked, diagonally arranged hexactines with up to four ranks clearly preserved in steeply obconical sponge. Prominent vertical bundles of greatly elongated vertical paratangential rays of hexactines form upward-expanding tracts in interior and converge to pointed base. First-order quadrules in upper part of the preserved sponge approximately 2 mm across. Sponges thin walled, surface lacks ornamentation; lacks marginalia.

Description. USNM 463495 is characteristic of thin-walled species; sponge is conico-cylindrical, 7 cm long, and with maximum flattened incomplete width near top of 10 mm (fig. 4.2), but osculum base and lateral margins not preserved; skeletal elements diverge upward from base and show corresponding increase in sizes of principal spicules.

Two vertical rows or tracts of bundled spicule rays are the most prominent skeletal features; these diverge upward from 1.8 mm apart near base to 4.8 mm near top; tracts separated by column of first-order hexactines with diagonally oriented paratangential rays; first-order rays range from approximately 3 mm, in basal region, to 10 mm long in upper part; ranges of dimensions of four spicule orders given in table 1. Skeletal fabric somewhat irregular in basal region with only two orders of spicules distinguishable. Third- and fourth-order spicules appear 4–5 cm above lowest preserved part of sponge. Quadrules between first-order hexactines subdivided by successively smaller second-, third-, and fourth-order spicules, all with diagonal arrangements. Quadrule sizes shown in table 2.

Spicules appear superficially as stauractines, but proximal and distal rays evident as central swellings and central canals of spicular rays present at ray junctions (figs. 5, 6.2, 7.6, 7.7). Under high magnification, small cylindrical holes frequently evident in nodes of axial cross areas (fig. 7.7); holes represent axial canals in distal or proximal rays normal to major tangential rays and conclusively prove principal spicules not stauractines but hexactines. Nodes projecting from spicule ray junctions represent rudimen-



tary or atrophied proximal-distal rays, but well-developed paratangential rays give rise to stauractinelike appearance of spicules. Whether true stauractines also present cannot be determined.

The two prominent vertical bundled tracts composed of up to 20 elongate rays of hexactines, which appear superficially as diactines. Some hexactines between tracts with ray junctions close to, directly on, or within ropelike tracts; many with one or two significantly elongated paratangential rays curved to join other parallel rays in tracts (fig. 2.6); ray junctions of hexactine spicules common, their rays combine to form vertical tracts; uncertain whether any diactines present. General widths of flattened spicular tracts approximately 0.5 mm, but thinner and less pronounced toward base and thicker toward osculum; basalmost preserved tracts consist of only one or two parallel rays, suggesting that tracts of prolonged spicular rays did not project far beyond sponge base as a root tuft. Sponges probably attached to substrate without root tuft or specialized anchorate spicules but perhaps fixed by external rays of marginal hexactines that projected only 1–2 mm beyond basal surface.

Specimen USNM 463496 with oscular margin (figs. 2.4, 6.1, 8) is flattened specimen 60 mm long and about 11 mm in maximum flattened width and preserves uppermost 6–7 mm of skeleton, including osculum and about upper one-third of body wall, but with base missing. Pyritic preservation shows many details, such as central canals that clearly document hexactine nature of spicules.

Skeletal organization generally corresponds to USNM 463495, but only one prominent, vertical, spicular tract nearly completely preserved. Hexactines with partially atrophied proximal-distal rays make up a thin, apparently single-layered wall between tracts, and four diagonally arranged ranks of spicules form reticulation with rays that interfinger with others in vertical spicular tract; dimensions of individual spicules given in table 1 and those of skeletal quadrules in table 2.

Osculum with flattened width of 4.75 mm, surrounded by wall 0.5 mm thick, measured along upper flattened margin. Spicular organization becomes irregular toward oscular margin, and orders of diagonally arranged spicules become obscure (figs. 2.4, 6.2); margin characterized by higher proportion and larger numbers of smaller, densely packed spicules with no distinct order; spicules oriented more nearly parallel to oscular margin than diagonally; ray lengths of spicules range 0.4–1.0 mm.

Specimen USNM 463497 with entire base and lateral margins fairly complete, but upper part not preserved. It is 4 cm long and 2.3 cm in maximum flattened width. Faint traces of six vertical spicule tracts diverge upward from near gently rounded base (fig. 2.8); distances between vertical tracts range 2.0–3.0 mm apart, 0.5 cm above base, and 4.7–7.8 mm apart, 1.8 cm above base. No projecting marginal prosthelia nor anchoring root spicules observed. Spicules limonitic weak outlines without details, such as central canals.

FIGURE 2.—Hexactinellid sponges from the Silurian-Devonian Roberts Mountains Formation, Starvation Canyon locality. 1, *Protospongia* sp. 2 shows the moderately large first-order quadrules subdivided into four additional orders by stauractines, USNM 463511, X2. 2, *Protospongia conica* Rigby and Harris, 1979, delicate quadrately arranged skeleton has been partially pyritized and appears brown in a tan matrix, with low contrast: (a) USNM 463503, (b) USNM 463505, (c) USNM 463506, X2. 3, *Gabelia pedunculus* Rigby and Murphy, 1983, shows the general nature of the quadrately arranged, stauractine-based skeleton with long vertical rays compared with the shorter horizontal ones; only stalks of the species are preserved: (a) USNM 463513, (b) USNM 463512, X2. 4, 6, 7, 8, *Diagoniella nevadensis* Rigby and Stuart, 1988. 4, Essentially complete margin and oscular rim show prominent diagonal orientation of the hexactines and two moderately well preserved vertical tracts composed of modified long rays of hexactines, pyritized in part; irregular spiculation of moderately dense oscular margin shown near the top; conico-cylindrical form is incomplete at the base, USNM 463496, X2. 6, Large modified hexactine with long rays (arrows) are part of vertical tract; less modified hexactine with short distal ray, in lower left, top to right, USNM 463495, X15. 7, Moderately complete upper part of the conico-cylindrical specimen with two prominent vertical tracts of bundled vertical rays of modified hexactines, characteristic of the species; complete oscular margin shows moderately complex fine spicules of the upper end of the sponge, USNM 463498, X2. 8, Somewhat goblet- to bowl-shaped lower part of the moderately large obconical representative of the species, with moderately complete lateral margins and rounded base, but oscular margin not preserved; six vertical tracts or spicule rows diverge upward from near the rounded base; the diagonal orientation of tangential rays of the intervening hexactines are characteristic of the species and genus, USNM 463497, X2. 5, *Protospongia spina* n. sp., holotype shows prominent reticulated quadrules of the stauractine-based skeleton with presumably nearly complete, curved, bottom left part of the margin and with prominent long-rayed hexactines forming marginal spines along the left margin; these are the longest rayed spicules in the skeleton; oscular margin is not preserved, USNM 463510, X2.

Table 1.—Dimensions of spicules in *Diagoniella nevadensis* Rigby and Stuart, 1988, in millimeters.

	First Order		Second Order		Third Order		Fourth Order	
USNM Number	Ray Length	Basal Diameter	Ray Length	Basal Diameter	Ray Length	Basal Diameter	Ray Length	Basal Diameter
463495	2.5–3.0	0.12	0.9–1.3	0.11	0.30–0.45	0.10	0.12–0.25	0.08
463496	1.5–2.5	0.12	0.7–2.0	0.10	0.40–0.50	0.08	0.25–0.35	0.05
463497	3.0–4.2	0.18	1.1–1.5	0.10	0.40–0.85	0.05	0.15–0.30	0.035
Average	2.3–3.3	0.14	0.9–1.6	0.10	0.37–0.60	0.08	0.17–0.30	0.055

Organization, placement, and size ranges of the diagonally arranged spicules generally similar to other specimens of species; size ranges of four orders of spicules shown in table 1; spicules appear more delicate than in other specimens of the species, but this perhaps due to deep weathering.

Discussion. *Diagoniella nevadensis* Rigby and Stuart, 1988, was described based on a single specimen from the Silurian-Devonian Roberts Mountains Formation in the Mahala Creek area of the Independence Mountains of northern Nevada. They compared it with similar and

related sponges. The present collection contains 11 specimens of this species, a few of which are well preserved, and two additional specimens that are questionably referred to the species. This new material provides considerable additional morphologic data on skeletal architecture and, thus, allows new evaluations of phylogenetic implications. For example, spicules of *Diagoniella nevadensis*, originally interpreted as stauractines and diactines, are shown to be hexactines, in part, if not totally.

Diagoniella was erected by Rauff (1894, p. 248) as a subgenus of *Protospongia* Salter, 1864, to separate two Ordovician species with diagonal orientations of their spicules, *Protospongia coronata* Dawson, 1889, and *P. cyathiformis* Dawson, 1889, from other species with vertical and horizontal spicule rays. *Diagoniella* was raised to generic rank by Walcott (1920, p. 309), who designated *Protospongia coronata* Dawson, 1889, as the type species.

The Protospongiidae Hinde, 1887, includes, with other genera, both *Protospongia* Salter, 1864, and *Diagoniella* Rauff, 1894, and the latter have been characterized by skeletons of stauractines in thin, single-layered skeletal walls. The presence of definite hexactines in *Diagoniella nevadensis* Rigby and Stuart, 1988, and in *Diagoniella tubulara* Rigby and Harris, 1979, questions whether these species should remain within *Diagoniella* or whether they should be assigned to a new genus. This question will be answered by a thorough reexamination of the type species of *Diagoniella*.

Additional information is difficult to obtain, even after reexamination of Dawson's *Protospongia* type material by Mehl at the Redpath Museum of McGill University, Montreal. Dawson painted the spicules white to better document them in figures, because the pyritized spicules have so little contrast on the dark gray shale. Furthermore, Dawson added "spicules" to missing parts of the incompletely preserved sponges (e.g., oscular margin of *Protospongia tetranema*). These "improvements" on the holotype of *Diagoniella coronata* (Dawson, 1889) obscured the nature of its spicules. However, the holotype of *Protospongia cyathiformis* consists of part and counterpart, of which, fortunately, only one was painted while

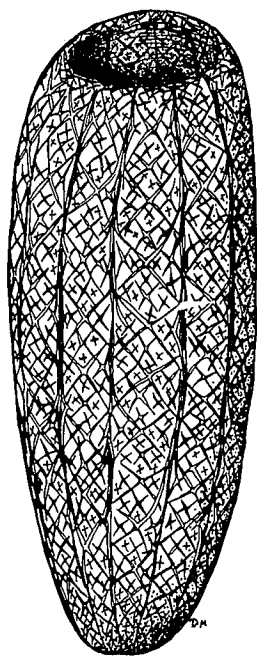


FIGURE 3.—Reconstruction of a *Diagoniella nevadensis* Rigby and Stuart, 1988. The diagonally arranged hexactines have moderate uniform rays in the regions between the prominent vertical tracts, which are formed of markedly elongated rays of modified hexactines in a pattern distinctive of the species. Paratangential rays of hexactines are prominent, but proximal and distal rays are generally reduced to small nodes in the thin-layered wall.

Table 2.—Dimensions of quadrule orders in *Diagoniella nevadensis* Rigby and Stuart, 1988, in millimeters.

USNM Number	First Order	Second Order	Third Order	Fourth Order
463495	2.3–2.6 × 3.0–3.3 (lower) to 2.3–2.6 × 4.0–4.5 (upper)	1.0–1.6 × 1.5–2.2	w 0.6–0.7	—
463496	1.6–1.8 × 2.0–2.3	0.5–0.7 × 0.9–1.8	0.3 × 0.5	—
463497	w 1.6–2.2	w 0.9–1.2	w 0.2–0.6 (irregular)	—
463498	2.2–2.8 × 3.5–4.0	1.0–2.0 × 2.0–2.5	0.6–0.7 × 1.0–2.0 (variable)	0.3 × 0.5
463499	w 2.0	w 1.0	w 0.5	w 0.2–0.3

w, width; e.g., 2.3–2.6 × 3.0–3.3, width × height.

the other shows enough detail to judge its spicule nature. Some of the preserved pyritized spicules have central swellings, and some spicule impressions exhibit circular holes in nodes of axial crosses. Such structures clearly indicate, at least in this species, the hexactine origin of some, if not all, “stauractines” within the protospongiid skeleton. Whether or not this is also true of the type species, *Diagoniella coronata*, cannot be determined, unless the white paint could be carefully removed to exhibit the true character of this and other holotypes, a step we strongly recommend.

New collections from the type locality might be the only way to solve the problem. Such recollection was attempted some years ago by Rigby, but unfortunately without producing significant new material.

Diagoniella, as defined by Rigby and Harris (1979), is a hexactine-bearing protosponge, although the principal spicules of the *D. tubulare* are diagonally oriented stauracts. The Devonian-Silurian *Gabelia* Rigby and Murphy, 1983, and *Asthenospongia* Rigby, King, and Gunther, 1981, are also protosponges with hexactines as main spicules. The Middle Cambrian *Pleodioria* Öpik, 1961, from Queensland, Australia, also has at least pentactine spicules. The somewhat more complexly spiculed *Cyathophycus* Walcott (1879a,b; 1881a,b) from the Ordovician of New York also has pentactine spicules, as noted by Dawson (1889). Mehl (1991) claimed that hexactines may have been the basic spicule type of the Hexactinellida and that stauractines were derived from hexactines by ray reduction (see Mehl 1992).

Even if the type species, *Diagoniella coronata* (Dawson, 1889), were shown to possess exclusively four-rayed spicules, one could still conclude that both *D. coronata* and the closely related *D. nevadensis* (for which a new genus would then be needed) arose from a common stem species that possessed hexactine spicules. If *Diagoniella* and *Protospongia* make up a single evolutionary lineage, which we see no reason to doubt, they both could have

arisen from the same hexactine-bearing stem species. The *Protospongia/Diagoniella* monophyletic group could then have evolved by the reduction of hexactines into stauractine principal spicules. The stem species of this group would actually have been closer in terms of spicular symmetry to *D. nevadensis*, with hexactines, rather than to the other exclusively stauractine-bearing genera of the Protospongiidae.

Another interesting aspect of phylogenetic significance is the presence of hexactines forming the prominent spicule tracts in *Diagoniella nevadensis*. The vertical tracts or rows are built by one or two paratangential rays, from several spicules, that are significantly elongated and actually function like diactines (to which they also show great similarity). This might suggest that vertical and horizontal rows of diactines of the groups originated, phylogenetically, from hexactines directly by elongation of one or two paratangential rays and reduction of others near the spicule center. Such a conclusion may suggest a common ancestor for the Protospongiidae and Dictyospongiidae, which would then most probably be considered as sister groups, particularly because some of the Dictyospongiidae (e.g., *Griphodictya* Hall and Clarke, 1899), do possess hexactines.

Paleoecological implications. One specimen (USNM 463497) with an apparently complete base, but without marginalia or prostalia, provides important paleoecological information concerning the species. We conclude that these sponges were only loosely attached to the substrate without any specialized basal spicules. They were apparently held upright with their bases partially buried in the sediment, without any root tufts, and thus, they probably lived in a quiet, nonturbulent environment. This further implies low sedimentation rates, because rapid deposition would have buried the small sponges, or at least clogged their canal systems, because they had no stalks to keep them well above the sediment.

Absence of marginal prostalia suggests that the sponges

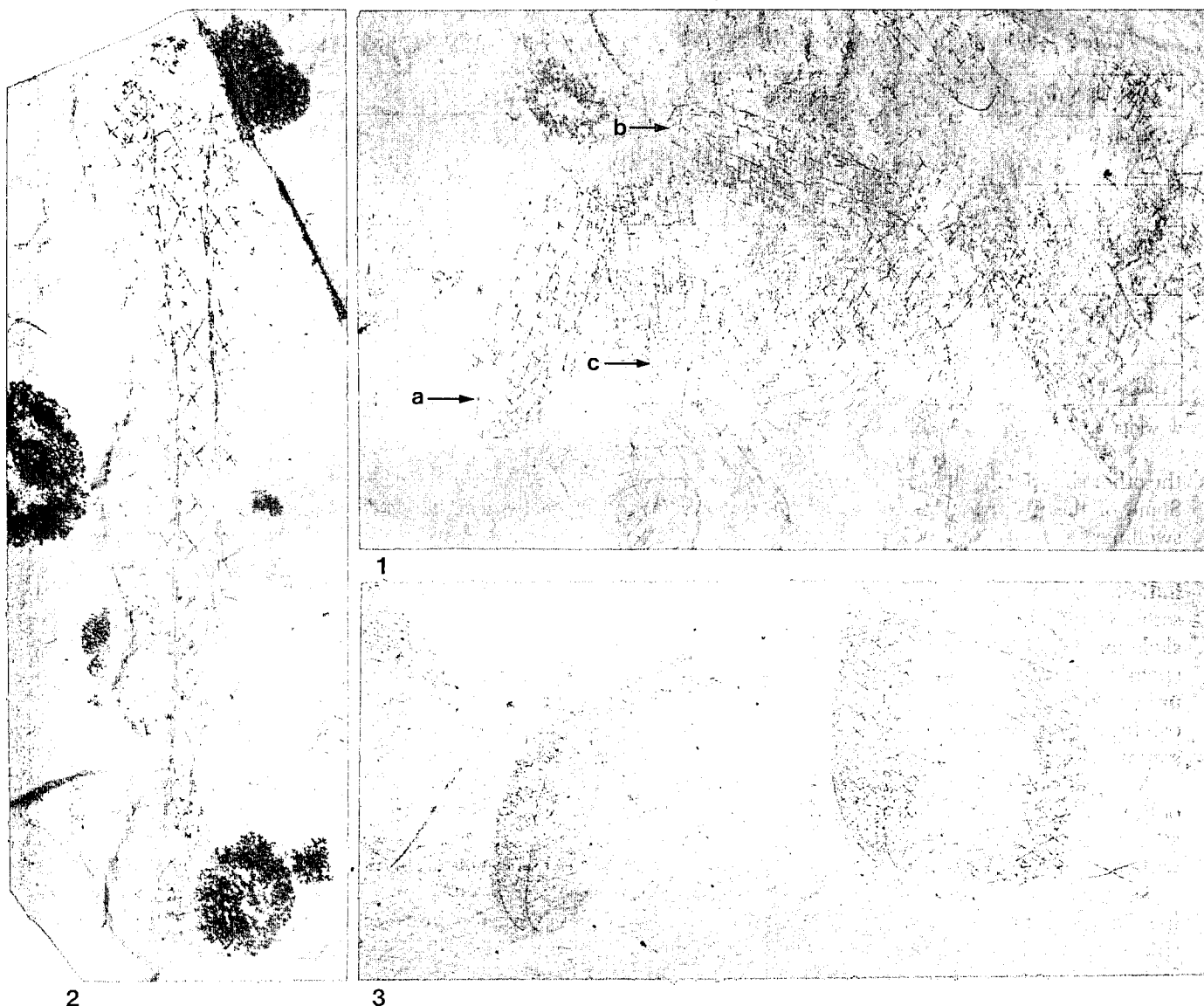


FIGURE 4.—*Diagoniella nevadensis* Rigby and Stuart, 1988, *Protospongia* sp. 1, and *Gabelia pedunculus* Rigby and Murphy, 1983. 1, Cluster of intermixed *Protospongia* and *Gabelia pedunculus* Rigby and Murphy, 1983, shows general uniform size of fragments, or the nearly complete lower parts of the small sponges on a single bedding plane; specimens preserved as faint limonite ghosts in a tan, silty limestone: (a) USNM 463507, (b) USNM 463508, (c) USNM 463509, X2. 2, 3, *Diagoniella nevadensis* Rigby and Stuart, 1988. 2, Well-preserved tracts and diagonal hexactines in subcylindrical specimen, USNM 463495, X2. 3, Two specimens preserved as faint limonite traceries on a single bedding plane; specimen on left shows a characteristic rounded base and at least two prominent tracts of vertical rays of modified hexactines, like that characteristic of the species; the other specimen, perhaps fragmented, shows the prominent diagonal relationships of the ordered hexactines of the skeleton, between the vertical tracts, but does not show the tracts as prominently, USNM 463499, X2.

may have settled on stable substrates, because marginal stabilization and balancing apparently was not necessary. If the sponges were attached to rather firm substrates, perhaps collagen fiber strands accumulated in their rounded basal regions. Although Recent hexactinellids are generally poor in collagen, they, nevertheless, do have some. It is possible that Paleozoic hexactinellids had more collagen fibers than the Recent ones. Early Paleo-

zoic hexactinellids (e.g., Protospongiidae) are commonly found with their spicules in place, although without fusion of spicules by siliceous organic cement, as is common in Mesozoic and Cenozoic Hexactinellida. Collagen may have held the spicules in place and may have been, in part, responsible for the common pyritic replacement of the spicules by providing the additional associated organic materials.

Spicules were preserved as pyrite, now weathered into limonite. The pyritization, however, was not as coarse as is normal in most fossils. Because only very delicate pyritization occurred, spicule pseudomorphs still show many fine structural details, such as central canals. Such exceptional preservation allows detailed study of the skeletal architecture.

Material. Figured specimens, USNM 463496–463499, and reference specimens, USNM 463500–463502, all from the Roberts Mountains Formation, Starvation Canyon locality.

Genus *PROTOSPONGIA* Salter, 1864

PROTOSPONGIA CONICA Rigby and Harris, 1979

figs. 2.2, 4.1, 6.3, 6.4, 7.4–7.5, 9–10

Protospongia conica RIGBY AND HARRIS, 1979, p. 974–76, pl. 1, fig. 1, pl. 2, figs. 1, 5, text figs. 2, 3.

Description. Largest specimen, USNM 463506, of four pyritized sponges on a single bedding surface appears to be nearly complete (fig. 2.2). Sponge body conico-cylindrical, 17.0 mm long and 6.5 mm in maximum width; distinctly obconical in lower part with pointed base and a few root-tuft spicules, the longest of which reaches 15.0 mm beyond base of sponge; osculum not visible.

Principal spicules stauractines, some with atrophied distal rays, generally arranged in regular vertical-horizontal pattern; parallel rays of neighboring spicules commonly reach to near ray junctions and sometimes beyond axial cross. Network of quadrate, often rectangular meshes formed principally by first- and second-order spicules; meshes coarsen upward approximately 6 mm across near base to 10–17 mm across in middle height of sponge.

Three orders of stauractines differentiated in sponge wall; dimensions are given in table 3. Rays of marginal first-order spicules project up to 5–7 mm beyond outer wall. A few second- and third-order spicules more or less diagonally arranged, but this orientation may be the result of disturbances prior to or during burial.

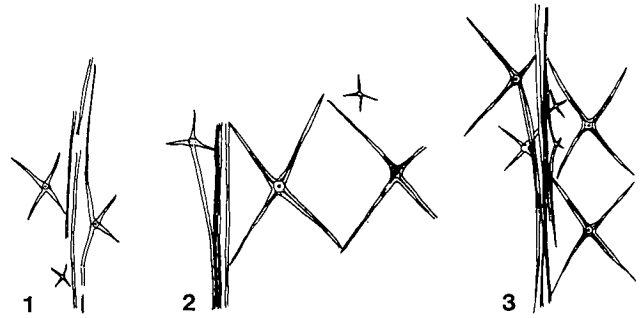


FIGURE 5.—*Camera lucida* sketches of spiculation of *Diagoniella nevadensis* Rigby and Stuart, 1988, showing the swollen nodalike ray junctions in which the reduced distal ray has a central axial canal; elongated vertical paratangential rays of the hexactines combine to produce the multirayed vertical tracts characteristic of the species, USNM 463495.

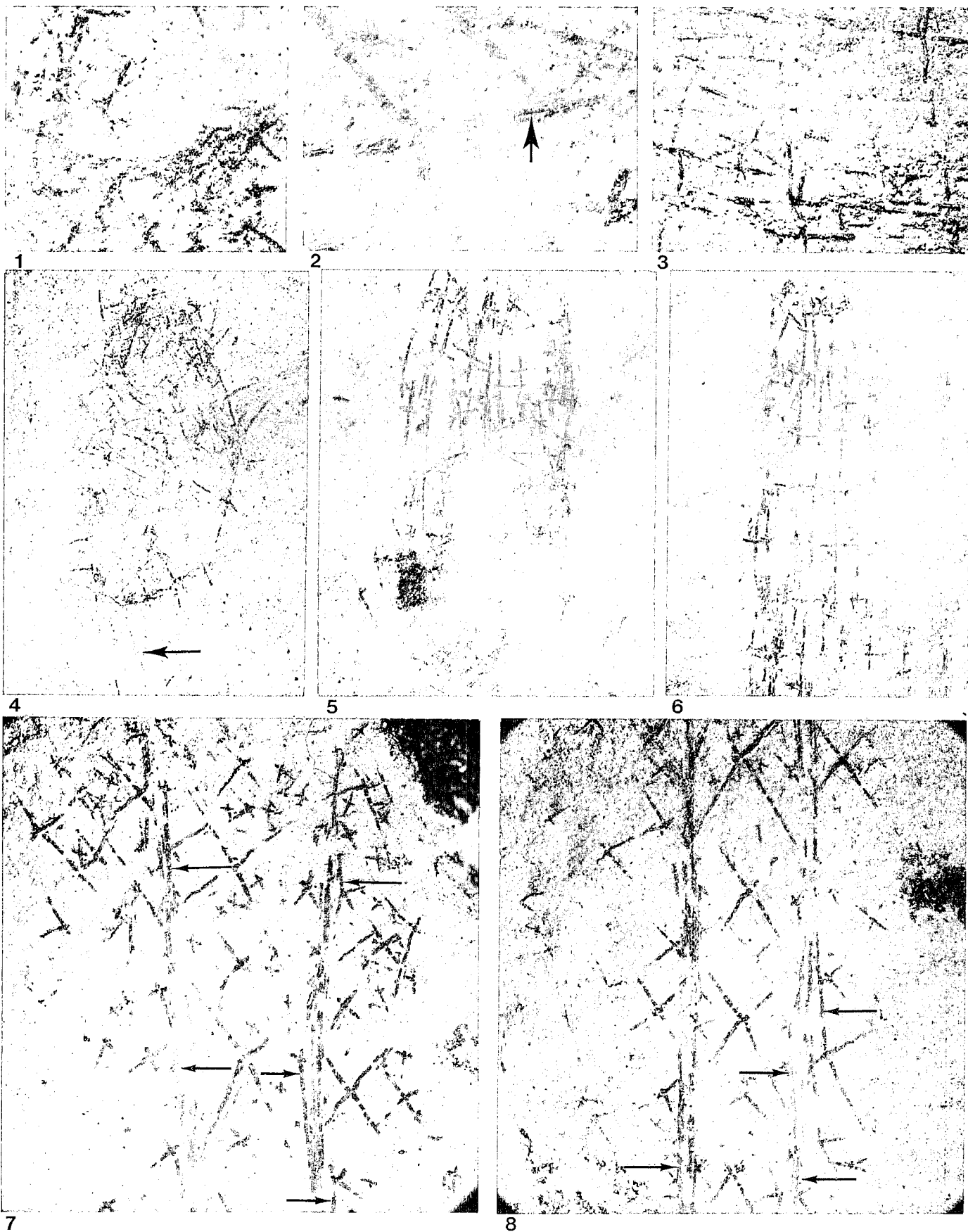
Six long, apparently anchoring spicules project beyond base of sponge, but uncertain whether all belong to this sponge; five assigned to sponge body without much doubt because of their orientation; all apparently stauractines with ray junctions located at margin of sponge body with one greatly prolonged ray pointing distally.

Three small associated specimens (USNM 463503–463505) also may be assigned to this species (figs. 2.2, 6.4, 7.5, 10). Body heights range 5.0–8.5 mm, not including tiny anchoring spicules that may project additional 12 mm from bases.

Specimen USNM 463503 nearly complete, conico-cylindrical, 8.4 mm high and 5.9 mm in maximum flattened width; associated anchoring spicules to 13 mm long; wall composed of only two somewhat indistinct orders of spicules with four paratangential rays and some apparently atrophied distal rays; preserved spicule dimensions given in table 3, and quadrule dimensions given in table 4. It is uncertain whether diactines are also present. Some spicules with rays diagonal to major dimensions of sponge, but most with vertical rays parallel to flattened length of sponge. Some rays project laterally, like mar-

Table 3.—*Dimensions of spicules of Protospongia conica* Rigby and Harris, 1979, in millimeters.

USNM Number	First-Order Spicules		Second-Order Spicules		Anchoring Spicules	
	Ray Length	Basal Diameter	Ray Length	Basal Diameter	Max. Length	Basal Diameter
463503	0.75–1.40	0.07	0.22–0.50	0.03	13.0	0.04
463504	0.5–1.0	0.04	0.3–0.6	0.03	6.3	0.05
463505	0.9–1.3	0.04	0.2–0.5	0.03	12.0	0.06–0.2
Average	0.75–1.20	0.05	0.24–0.54	0.03	10.4	0.06–0.2



ginalia, and probably also from oscular margin, although latter not directly observed.

Five anchoring spicules project from base; most complete is 13 mm long to short lateral rays that project almost perpendicularly from long axis; axis continued beyond junction can be interpreted as four rayed or possibly six rayed, with two rays greatly elongated in direction of growth axis and, thus, functionally a diactine. Ray development different than in root-tuft spicules of modern lyssacine hexactinellids, which have one long ray and five other shorter rays modified to form anchor.

Specimen USNM 463504, located at edge of plate, consists of only lowermost two-thirds of sponge, now about 6 mm high with maximum width of 4 mm. Four-rayed body spicules in two indistinct orders; spicule dimensions given in table 3 and quadrule dimensions in table 4. Most spicules with horizontal-vertical orientations, particularly in upper part, but some with disturbed diagonal arrangement. Most complete of six visible anchoring spicules 6.3 mm long.

Specimen USNM 463505 consists of only basal fragment associated with seven radially projecting anchoring spicules; it is uncertain, however, whether all belong to a single sponge. Preserved base only 3.5 mm high and 1.2 mm wide, with at least two distinct orders of four-rayed spicules, dimensions of which given in table 3. Some apparently hexactine-based spicules with projecting rudiments of atrophied distal rays or axial ray holes indicating a proximal ray; most of these have disturbed diagonal orientations. Root-tuft spicules project to 12 mm beyond

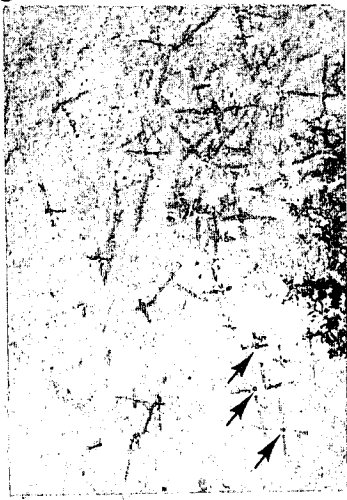
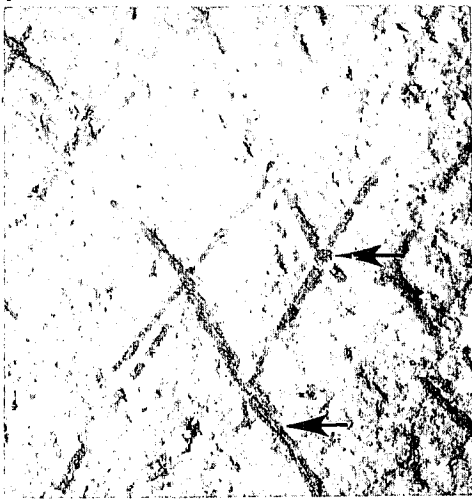
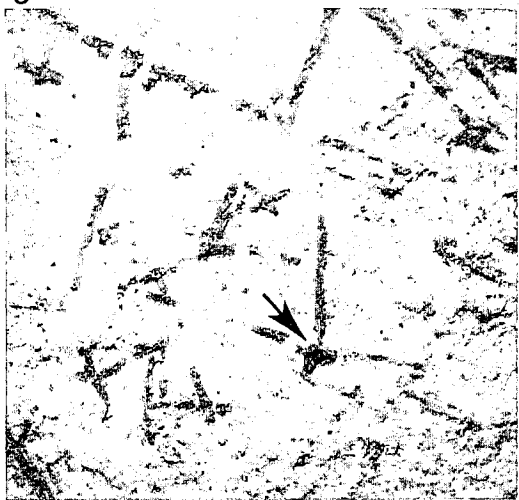
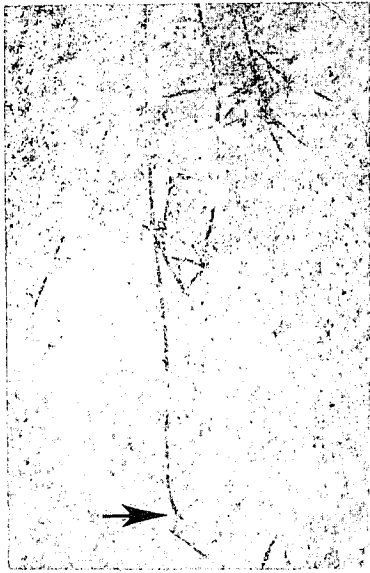
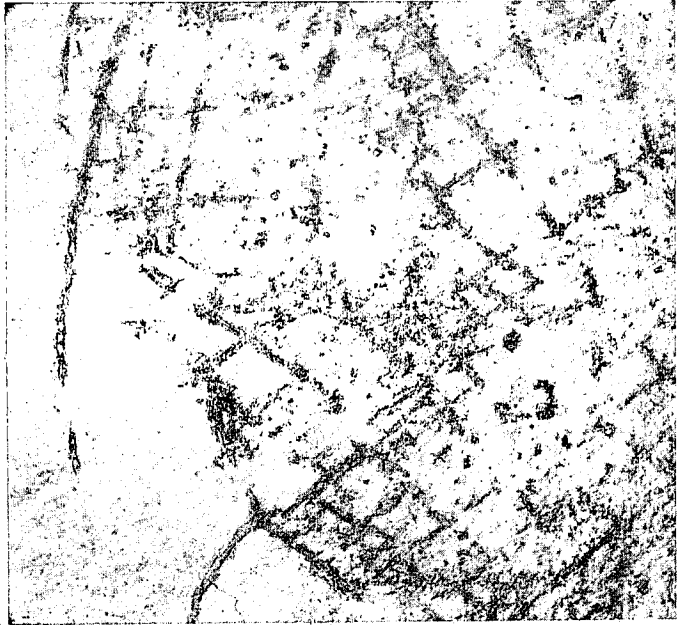
base; some of these clearly project from anisoactine stauracts with axial crosses approximately midway between two long rays.

All four sponges in sample show approximately same orientation with root tufts or bases pointing in similar directions. That orientation might be accidental or more likely a response to current influence. All specimens preserved as limonitic replacements.

Discussion. Comparisons with similar and related species were made by Rigby and Harris (1979, p. 975–76). Only three orders of spicules can be clearly distinguished, and even these are rather indistinct in two of the specimens. According to Rigby and Harris (1979, p. 975), the holotype of *Protospongia conica* has only two preserved orders of spicules in its body wall. The limited range of spicule sizes in these more completely preserved sponges and sizes of the whole sponges suggest that specimens USNM 463503–463505 might be juveniles, or that perhaps only two orders were actually present in the first place.

The apparent diactine nature of some root spicules in the described specimens may indicate a distinct root-tuft character for the species. Such spicules show remarkable contrast to those of Recent and Mesozoic root-tuft-bearing hexactinellids (which comprise most of the forms with a lyssacine spicular organization, sensu Ijima 1927 and Reid 1958–64, regardless of their systematic position). Such modern lyssacine Hexactinellida have anchoring spicules with only one greatly elongated proximal ray, with the five distal rays forming an anchor.

FIGURE 6.—Photomicrographs of *Diagoniella*, *Gabelia*, and *Protospongia* from the Silurian-Devonian Roberts Mountains Formation from the Starvation Canyon locality. 1, 2, 7, 8, *Diagoniella nevadensis* Rigby and Stuart, 1988. 1, Densely spiculed oscular margin in which essentially horizontal rays rim the circular opening, only part of which is shown, USNM 463496, X15. 2, Coarse first-order and second-order hexactines preserved as limonite replacements of the opaline siliceous spicules; a central axial canal is preserved in these delicately replaced rays (arrow) in the right center and at the left margin; a possible node of a distal ray shows above the ray intersection of the large spicule and may have a light filling of the circular axial canal, USNM 463495, X20. 7, 8, Two prominent vertical tracts of elongate hexactine rays (arrows) are separated by less modified regular hexactines in the intervening thin part of the skeletal wall (7, near top; 8, in middle of sponge), USNM 463495, X7. 3, 4, *Protospongia conica* Rigby and Harris, 1979. 3, Skeleton composed largely of delicately preserved stauractines in a light tan matrix; coarse first-order quadrules are divided into second- and third-order quadrules by spicules of reduced size; top is toward the left, USNM 463506, X15. 4, Small, diagonally flattened specimen with delicate skeleton made of stauractines; more or less complete oscular margin is at the top, and a few root-tuft spicules (arrow) extend below the base; rays of first- and second-order spicules project as marginalia into the light tan matrix; spicules replaced by limonite, USNM 463503, X7. 5, 6, *Gabelia pedunculus* Rigby and Murphy, 1983, shows the relatively open-textured, stauractine-based skeleton of the lower fingerlike stalk of the sponge; the only part of the complete gobletlike sponges preserved in this fauna; stauracts have long vertical rays and short horizontal ones and outline rectangular quadrules that are much higher than wide; brown limonite produces low contrast elements in a background of light tan matrix. 5, Partially preserved rounded base and lower stalk, upper margin not preserved, USNM 463513, X7. 6, Fragment incomplete at upper end, shows slightly upward convergence of the skeletal structure and small, equal-rayed, diagonal stauractines, perhaps of basal part of upper "cup" transition, USNM 463512, X7.



6

7

8

The fact that all four specimens on this block are of approximately the same size and orientation may indicate their sorting and alignment are a result of preburial transport.

Material. One block with four, more or less complete specimens of *Protospongia conica* Rigby and Harris, 1979, including USNM 463503–463506, from the upper part of the preserved Roberts Mountains Formation, from the Starvation Canyon locality, Pipe Springs Canyon 7½-Minute Quadrangle, Elko County, Nevada.

PROTOSPONGIA SPINA n. sp.

figs. 2.5, 7.1, 7.2

Diagnosis. Coarse protospongiid with wall principally of stauracts in quadrule arrangements of at least five orders; first-order quadrules 4.0–4.5 mm wide and 3.8–4.2 mm high; some rays grouped to form loose bundles by overlap and with ray junctions on rays of larger orders; prominent hooklike distal rays of coarse first-order spicules distinctive.

Description. Holotype, USNM 463510, fragment 2.7 × 5.7 mm of large coarse-textured sponge; skeletal wall consists of stauractines with overlapping rays parallel to those of neighboring spicules along entire lengths. Some spicules with ray junctions centered in middle of quadrules of larger orders, but others with ray junctions on rays of larger orders produce a complex, bundled-appearing skeleton. At least five distinctive sizes of stauractines occur, all in regular quadrupled pattern characteristic of genus. Quadrule dimensions given in table 4, and spicule dimensions of holotype given in table 5. Spicules of network somewhat oblique because angles between rays not at right angles, but with angles over 90° in one

direction; angular relationships, however, appear as a result of postdepositional deformation rather than original structure.

Curved rays of marginal first- and second-order spicules project beyond sponge wall (fig. 2.5) as distinctive hooklike marginalia, which are rare within the Protospongiidae.

Discussion. *Asthenospongia acantha* Rigby, King, and Gunther, 1981, is a large protospongiid that appears similar to *Protospongia spina* n. sp. *Asthenospongia* has large hexactines with bent rays that are irregularly oriented in an otherwise moderately regularly quadrupled stauractine- and hexactine-constructed skeleton. The large spicules are spaced 2–3 first-order quadrules apart in a diamond spacing and have a projecting long distal ray that extends 7–11 mm beyond the sponge surface in thornlike fashion. However, *A. acantha* does not have the somewhat bundled parallel rays seen in the new Nevada species and has a much less regularly quadrupled basic skeleton. Although the holotype is only a fragment, we conclude that it is a new coarse-textured species of *Protospongia* characterized by the prominent, marginally projecting, curved distal rays and a regular coarse skeleton. Additional collecting may produce more completely preserved specimens.

Protospongia sp. 2, described below, is also a fragment of a coarse form. It might be considered as a fragment of *Protospongia spina*, but it lacks the coarse distal rays typical of the latter species and is, therefore, separated here.

Material. Holotype fragment, USNM 463510, from the Roberts Mountains Formation at the Starvation Canyon locality in the Independence Mountains, Nevada.

Etymology. *Spina*, L., thorn, in reference to coarse

FIGURE 7.—Photomicrographs of *Protospongia*, *Gabelia*, and *Diagoniella*. 1, 2, *Protospongia spina* n. sp., holotype shows regular, quadrule-based skeleton of somewhat bundled, parallel rays and coarse curved marginalia along the left margin of the sponge impression; marginalia have rays that curve outward and downward; these large spicules are distinctive of the species, USNM 463510, X7. 3, *Gabelia pedunculus* Rigby and Murphy, 1983, basal part of the stalk shows curved base lacking root-tuft spicules; skeletal structure somewhat distorted, presumably because of diagonal flattening; characteristic long vertical rays and short horizontal rays show throughout the skeleton, USNM 463514, X7. 4, 5, *Protospongia conica* Rigby and Harris, 1979. 4, Well-preserved conical base shows characteristic quadrupled structure and pointed tip with root-tuft spicules, some of which have down-flexed marginalia and lateral rays, but which are considerably smaller than in the coarse new species *Protospongia spina*, USNM 463506, X7. 5, Anchorlike root-tuft spicules associated with small incomplete specimen, the base of which is shown above; spicule appears to be a modified hexactine or pentactine associated with the flattened small specimen, USNM 463505, X7. 6–8, *Diagoniella nevadensis* Rigby and Stuart, 1988. 6, Hexactine spicules with prominent paratangential rays and less prominent nodes of distal rays in uniform hexactines, USNM 463495, X20. 7, Well-preserved spicule with prominent distal ray (upper arrow) and with well-defined axial canal and tangential ray (lower arrow), USNM 463496, X20. 8, Lowermost spicules of torn base show prominent swollen nodes of distal rays surrounded by light matrix and associated four paratangential rays; dark stain on the right is from a lichen, USNM 463595, X7.

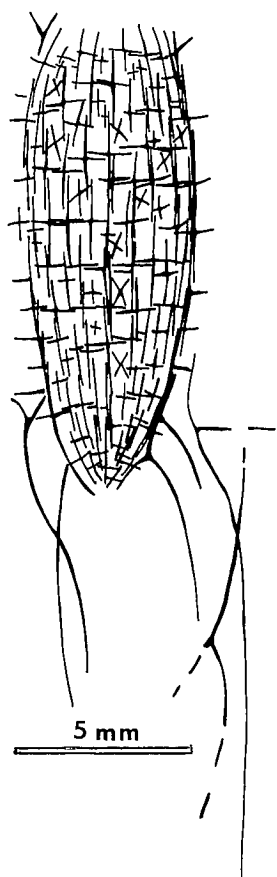


FIGURE 9.—Sketch of laterally flattened *Protospongia conica* showing relationship of the quadrulated skeletal structure and the small projecting root tufts at the pointed base. The specimen appears to be essentially complete, USNM 463506. Magnification is indicated by the bar scale.

Material. Figured specimens, USNM 463507–463509, and several other specimens, all on one slab, are from the Starvation Canyon locality in the Roberts Mountains Formation in the Independence Mountains of northern Nevada.

PROTOSPONGIA sp. 2

fig. 2.1

Description. Fragmentary specimen, USNM 463511, approximately 2×4 cm, of coarsely spiculated sponge wall without original margins. Spicules preserved as limonite, only stauractines occur and these oriented with rays parallel to those of neighboring stauractines for entire ray lengths; at least five orders of stauractines present and organized into regular pattern of ranked quadrules, in fashion typical of genus; quadrules may be somewhat rhombic for angles between spicular rays rarely at 90° , which may be the result of burial and compaction defor-

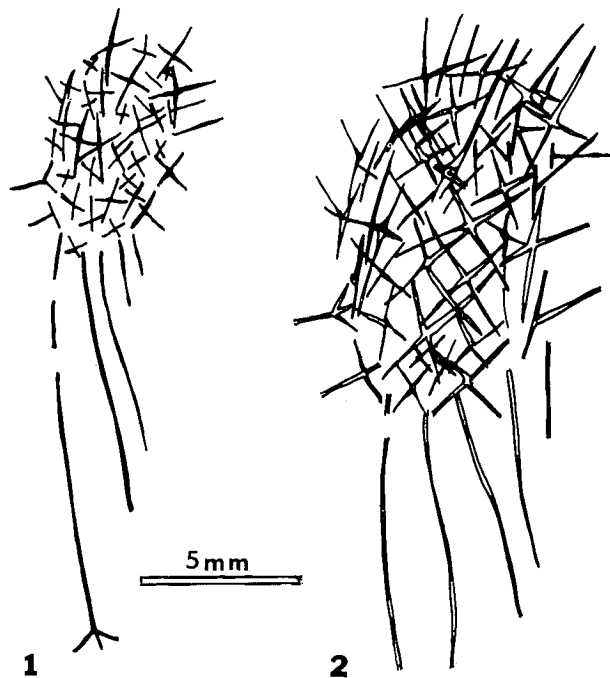


FIGURE 10.—*Protospongia conica* Rigby and Harris, 1979. Sketches of two small, possibly juvenile sponges with irregular spiculation, perhaps produced by diagonal flattening. Prominent root-tuft spicules extend below bases of the small sponges. Magnification is indicated by the bar scale.

mation. Quadrule dimensions are given in table 4, and spicule dimensions are given in table 5.

Discussion. The general organization of the spicular net and coarse spicule dimensions correspond, to a great extent, with those of *Protospongia spina* n. sp. (USNM 463510). Both specimens might well belong to the same large species of *Protospongia*, but this fragment (USNM 463411) lacks the coarse thornlike marginalia so characteristic of *P. spina* n. sp., and if they are from the same species, the fragments came from distinctly different parts of the sponge. Specific taxonomic position of this fragment cannot be determined because margins are not preserved.

Material. One fragment, USNM 463511, from the Roberts Mountains Formation at the Starvation Canyon locality in the Independence Mountains of Nevada.

Genus GABELIA Rigby and Murphy, 1983
GABELIA PEDUNCULUS Rigby and Murphy, 1983
figs. 2.3, 4.1, 6.5, 6.6, 7.3

Gabelia pedunculus RIGBY AND MURPHY, 1983, p. 799–802, figs. 2–5; RIGBY, MAHER, AND BROWNE, 1991, p. 709–10, figs. 2.3, 2.5, 3.3.

Description. Three fragments assigned to the species represent parts of basal stalks; two of fragments essen-

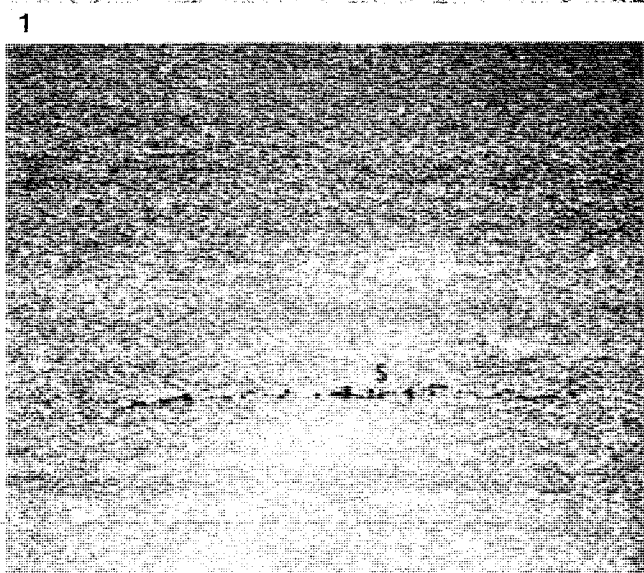


FIGURE 11.—Photomicrographs of thin sections from sample SRH-5V-1 showing textures and relationships to flattened sponges, X10. 1, Dark section of sponge spicules (S) in micro-cross-bedded (C) silty limestone; micro-convoluted bedding (B) occurs in the upper layers. 2, Flattened pyritized sponge (S) is opaque impression in laminated silty limestone.

tially complete; all three specimens now preserved as limonite replacements.

One of fairly complete stalks, USNM 463512, occurs with more fragmentary one, USNM 463513, on same bedding plane and with same orientation (figs. 2.3, 6.5, 6.6). Quadrule dimensions and spicule dimensions for three specimens given in table 6.

Stalk USNM 463512 essentially complete from pointed-rounded base to base of cup margin(?), except where buried by matrix 3–10 mm above the base; total stalk 25 mm long and at least 6 mm wide at midheight,

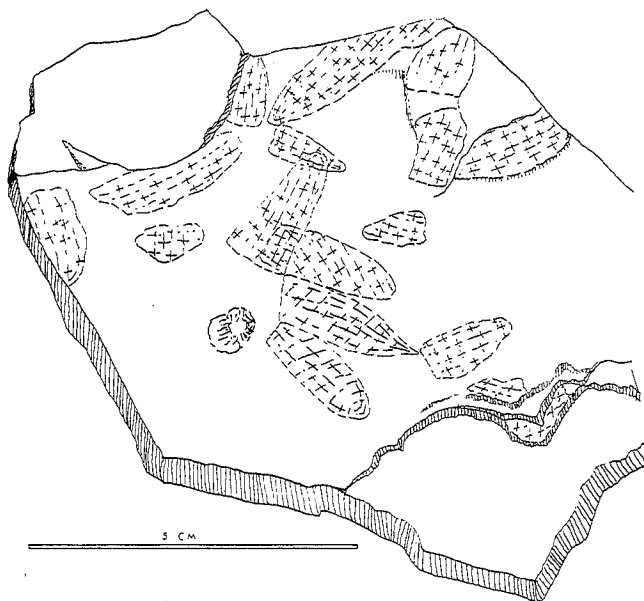


FIGURE 12.—Sketch shows positions of various specimens of *Protospongia* sp. 1 and *Gabelia pedunculus*, all flattened on two bedding plane surfaces. Sorting is thought to have been a function of transport by distal turbidity currents. Compare with figure 4.1.

basalmost 2 mm and upper 15 mm well exposed. Stauractines typically with long vertical rays and shorter horizontal rays form relatively high and narrow quadrules subdivided into smaller quadrules by at least second- and third-order spicules. Dimensions of first- and second-order spicules and quadrules given in table 6. Top of stalk narrows, and small equal-rayed stauractines in diagonal orientation between rays of main stalk stauracts may be basalmost part of cup(?).

Stalk of USNM 463513 11 mm long and 5.5 mm in maximum width, upper cup and part of rounded base missing; stalk consists of at least three orders of stauractines in horizontal-vertical orientation with vertical rays considerably longer than horizontal ones. First-order spicules with long vertical rays, parallel to growth direction, that overlap each other for approximately two-thirds of ray length, thus forming long vertical rows as quadrule margins (fig. 6.6). Such rows are semiparallel but do diverge and increase in number upward from rounded hemispherical base.

A few small, equal-rayed, diagonally oriented stauractines also present; such spicules especially common in upper part of stalk in what may be transition to upper cup region.

Gabelia stalk USNM 463514 fairly complete, 16 mm long and 8 mm in maximum width, with rows of stauractines arranged in general pattern of species (table 6); spicular network regular. Eight vertical rows of spicules

Table 6.—Stalks of *Gabelia pedunculus* Rigby and Murphy, 1983, quadrule and spicule dimensions in millimeters.

USNM Specimen	Quadrule Dimensions		First-Order Stauracts		Second-Order Stauracts	
	First-Order Top	Second Order	Ray Lengths	Basal Diameter	Ray Lengths	Basal Diameter
463512	0.7–1.20 × 2.8–3.1	0.4–0.7 × 1.0–1.6	V 2.0–2.6 H 0.45–0.80	0.11	V 0.8–1.2 H 0.30–0.45	0.05
463513	0.8–1.2 × 2.0–3.0	0.5–0.8 × 1.5–1.6	V 2.4–2.6 H 0.6–0.8	0.08	V 1.0–1.4 H 0.3–0.5	0.05
463514	0.9–1.2 × 2.2–2.5 mixed 1 and 2 orders	0.3–0.9 × 1.0–1.3	V 2.2–3.2 H 0.5–1.0	0.09	V 0.70–0.85 H 0.25–0.65	0.04

V, vertical heights or lengths; H, horizontal widths or lengths.

clearly identified near top of fragment and 10 rows at base; at least two orders of spicules present in wall; additional small to medium-sized, equal-rayed spicules with diagonal or irregular orientations also present.

Discussion. These stalks are interpreted to belong to *Gabelia pedunculus* Rigby and Murphy, 1983, in spite of their fragmentary preservation. Ranges of spicule and quadrule sizes in the material described here fall close to stalks of *G. pedunculus*, although horizontal rays in the holotype of the type species are somewhat longer, but this could be only ontogenetic differences. For comparisons of *Gabelia pedunculus*, *G. gigantea*, and *G. fascicula*, see table 7.

The small sizes of spicules on the fragments described here exclude them from the species *Gabelia gigantea* Rigby, Maher, and Browne, 1991. However, inclusion in both *Gabelia pedunculus* Rigby and Murphy, 1983, and *Gabelia fascicula* Rigby, Maher, and Browne, 1991, must be taken into consideration. The sponge fragments described here cannot be certainly related to *G. fascicula*, however, because that species was described from isolated cups, and its stalk is largely unknown.

The stalks are all fairly small fragments with lengths that range 11–25 mm. They may have been sorted during transport, prior to deposition and burial. These and other sponges in the collections were probably swept into the basin by turbidity currents.

Material. Three figured specimens, USNM 463512–463514, and three reference specimens on the slab with the protosponge cluster (USNM 463507–463509), all from the upper part of the Roberts Mountains Formation, Starvation Canyon locality, Water Pipe Canyon 7½-Minute Quadrangle, Elko County, Nevada.

PHYLOGENETIC ORIGIN OF HEXACTINE AND STAURACTINE SPICULES: INCREASING COMPLEXITY VERSUS SIMPLIFICATION

The first scientists to discuss phylogeny of sponge

spicules were neontologists (Ijima 1927; Kirkpatrick 1909; Schulze 1887a,b, 1893) and naturalists that worked on Recent and fossil materials (e.g., Sollas 1880). They concluded that hexactine spicules with a regular triaxial symmetry represent a basic feature within the poriferan group called Hexactinellida by Schmidt (1870). They also concluded that hexactines have been reduced to spicules of more simple symmetry, such as stauractines, diactines, and monactines within many hexactinellid groups (Schulze 1893). Thomson (1868) was the first to point out that diactines in some of his "Vitrea" show a rudimentary axial cross somewhere on the axial canal. He also concluded that "hexaradiate" spicules are not found within any other sponge groups. Later, the presence of axial crosses, which represent atrophied rays, were found to be widely distributed within the Hexactinellida. This feature was observed, for example, within the anchors of basal prostalia within the widely occurring barbed diactines called uncinates, as well as in most dermal monactines such as scopules and clavules (Ijima 1927; Schulze 1887b, 1899).

Spicules that line dermal and gastral surfaces in hexactinellid sponges generally tend to become reduced. They preferentially lose distal and/or proximal rays, so five-rayed pentactines and four-rayed stauractines are commonly found to be peripheral spicules with rays tangential to the outer surfaces. Because of this, Sollas (1880) suggested that the apparently exclusively stauractine skeletons of the Protospongiidae are composed of dermal spicules derived from parenchymal hexactines. This viewpoint was later supported by paleontologists, i.e., Reid (1958).

The hypothesis of increasing complexity of sponge morphology and skeletal structure in the course of early evolution was introduced by Haeckel (1866). The shift from single ascon to sycon and to complex leucon organization has become widely accepted. Only recently have the methods of phylogenetic or systematic analyses been

applied to high taxonomic levels in poriferan research (e.g., Mehl 1992, Reitner 1992, Reitner and Mehl 1993, van Soest 1991). Character compatibility and outgroup comparison sometimes indicate reversed polarity—that is, simplification or reduction of characters.

The Middle Cambrian Protospongiidae were long considered to be the oldest hexactinellids within the fossil record. Because these sponges were small, probably thin walled, and possessed only stauractine spicules, Finks (1960, 1970, 1983) proposed that they may have had an asconoid structure. He further argued that the first spicules developed in hexactinellid “embryos” (actually larvae) are stauractines, not hexactines, based on data presented by Okada (1928). This conclusion that the protosponges are primitive among the Hexactinellida was supported by Bergquist (1978) and Rigby (1986, p. 11), based again, in part, on Okada’s (1928) observation of larval spiculation in the extant *Farrea sollaris* Schulze, 1887b, and on the then known stratigraphic distribution of protosponges and stauractine spicules. Recently, Tabachnick (1991) proposed, again, the idea of an ontogenetic recapitulation of stauractine spiculation within larvae of *Farrea sollaris*. The widely cited publication by Okada (1928) is, so far, the only detailed study of hexactinellid ontogenesis based on regular periodic collection of living sponges throughout the year. Mehl (1991), however, argued that because of the presence of triaxial spicules within all living and most fossil hexactinellids, as well as their absence within the outgroup (*Demospongia*/Calcarea), hexactines can be considered as a constituent character of the Hexactinellida.

Stratigraphic considerations. The fragmentary record from the Early Cambrian shows that both types of hexactinellid spicules, stauractines and hexactines, were present shortly after the end of the Proterozoic. According to findings by Rigby (1986), stauractines occur much more abundantly than hexactines in Lower and Middle Cambrian sediments. However, samples from the Sinian-Vendian boundary layers of China are reported to contain only isolated hexactines and pentactines (Ding and Qian 1988). According to Mostler (1986, and personal communication 1992), hexactines have been present since the earliest Cambrian. It thus seems difficult, if not impossible, to definitely state whether hexactines or stauractines are the more primitive spicules based only on the fossil record. Indeed, this origin appears lost in the poor Precambrian record.

Sponges preserved as body fossils are well known from a few Middle Cambrian localities (e.g., Burgess Shale, British Columbia [Rigby 1986, Walcott 1920]; and Wheeler Shale and Marjum Formation, Utah [Rigby 1978, 1983; Rigby and Gutschick 1976; and Walcott 1920]). From the Lower Cambrian, however, hardly any essentially complete hexactinellid sponge fossils have

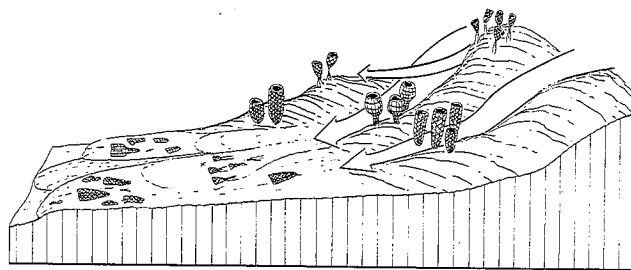


FIGURE 13.—Generalized reconstruction of possible distribution of sponges in discrete biocoenoses (“oases”) on a moderately barren bottom. Arrows show selective transport of these distinct assemblages and burial by turbidity currents to produce the essentially monospecific bedding plane occurrences characteristic of the Starvation Canyon locality. These differentiated thanatocoenoses are shown at the left. Not to scale.

been documented so far. Rigby (1987) published a description and figure of a fragmentary *Protospongia hicksi* Hinde, 1887, from the Lower Cambrian Parker Slate at Georgia, Vermont. The oldest known hexactinellid microscleres of hexaster- and amphidisc-type have been documented from sediments of Early Ordovician and Late Silurian age by Mostler (1986). The relatively large so-called “hemidiscs” described and figured by Mostler and Mosleh-Yazdi (1976) from the Upper Cambrian of Iran are probably not homologous with amphidiscs or with true hemidiscs. Paleozoic hemidiscosans have been described as *Microhemidiscia ortmanni* Kling and Reif, 1969, from the Late Carboniferous of Uruguay. These specimens were kindly sent to Mehl for restudy, by Reif, in 1991. Isolated hemidiscosan spicules have been reported from the Late Cretaceous as well (Ortmann 1912, Schrammen 1924). Mehl (1991–1992) examined the Upper Cambrian “hemidiscs” from the Mila Formation of Iran in the collection of Mostler. These spicules are megascleres, about 1 mm long, and are smooth with a clavulate “umbel” at one end and with just a tuberculated swelling at the other end. Comparisons of the Upper Cambrian “hemidiscs” with hemidiscs from the holotype of *Microhemidiscia ortmanni* and with hemidiscs of Upper Cretaceous sediments suggest that the Cambrian spicules may be clavules with swollen proximal tips. Neither these nor the Paleozoic paraclavules have close amphidisc or hemidisc affinities. We do not doubt the phylogenetic significance of hexactinellid microscleres (as was done by Finks [1970] and Bergquist [1978]) just because oxyhexasters and paraclavules occur together in the Carboniferous *Griphodictya epiphanes* Hall and Clarke, 1899, from Indiana.

Phylogenetic-systematic consideration. The Hexactinellida are monophyletic and are probably the monophylum best established within the Porifera, as indicated by results of studies by Mehl (1992). They represent a

Table 7.—Comparisons of skeletal dimensions in species of *Gabelia* in millimeters.

		First-Order Quadrules		First-Order Spicule Lengths				
Species	USNM Number	Stalks	Cups	Stalks		Cups		Source
				H	V	H	V	
<i>G. pedunculus</i>	340059	1.0–1.2 × 3.0–3.4	2.0–2.5	H 1.6–1.8	V 3.8–3.3	H 2.7–2.9	V 3.0–3.3	RM
<i>G. pedunculus</i>	427644	2.0–2.6 × 4.0–4.8	—	1.5	—	—	—	RMB
<i>G. fascicula</i>	427637	—	0.5–0.8 × 0.8–1.0	—	—	1.0–1.5	1.0–1.5	RMB
<i>G. gigantea</i>	427638	7 × 8–12	—	2.0–2.5	to 2.5	—	—	RMB

1.0–1.2 × 3.0–3.4, horizontal × vertical dimensions; RM, Rigby and Murphy 1983; RMB Rigby, Maher, and Browne 1991; H, horizontal; V, vertical.

very conservative group of sponges, as indicated by two observations. The major sister groups of Amphidiscophora and Hexasterophora have existed since the Early Paleozoic. These major hexactinellid groups apparently underwent little significant evolutionary changes in basic structure since their origination. Soft parts anatomy also shows little variation in living hexactinellid sponges, according to the few scattered studies done so far (e.g., Mackie and Singla 1983; Reiswig 1979, 1991; Reiswig and Mehl 1991). If such is true, that uniformity implies that hexactinellids have not evolved far away from their basic pattern, the characteristic pattern of the stem group of all Hexactinellida.

Hexactines built on triaxial-based spicules are certainly found within all Recent and most fossil representatives of the Hexactinellida. Hexactines are absent, however, within the outgroup Pinacophora (Calcarea/Demospongiae). Because of this distribution, siliceous triaxial spicules, or hexactines, are considered part of the hexactinellid basic pattern.

Stauractine dermalia are found within several groups of Recent Amphidiscophora, and they are also common within many Recent lyssacine groups of Hexasterophora. The dictyonine Hexactinosa (Hexasterophora) normally possess hexactine or pentactine dermal spicules only. In the Recent *Chonelasma calyx* Schulze, 1887b, however, all spicular transitions are found between hexactines and stauractines, some of which show slight distal swellings in the ray junction area (see Mehl 1992, pl. 9, fig. 1). The Upper Jurassic *Cribrospongia reticulata* Goldfuss, 1833, had stauractine dermalia exclusively (Salomon 1990). Most probably stauractine dermal spicules were developed convergently by ray reduction of hexactines within most major hexactinellid groups.

Ontogenetic recapitulation of phylogenetic processes. The recapitulation of spicule structure in sponges was based on the only thorough study on hexactinellid embryogenesis on the Recent hexactinellid sponge *Farrea sollasii* Schulze, 1887b, published by Okada (1928). Okada found that spicules first developed by the hexactinellid parenchymellar larvae are six, four-rayed larval spicules. This initial spiculation was observed and documented earlier by Ijima (1903, 1904) from larvae found in several different hexactinellids (e.g., *Leucopsacus orthodocus* Ijima, 1903, and *Vitrollula fertilis* Ijima, 1901). We still do not know, however, whether later produced hexactines ontogenetically develop from stauractines or if these larval spicules and adult hexactines originate from different somatic layers of these sponges. Okada (1928, p. 12) explicitly warned against making any phylogenetic conclusions concerning the evolution of spicules based on his ontogenetic findings.

PALEOECOLOGY AND TAPHONOMY

Most of the sponges in our collection were apparently only loosely attached to the substrate without anchoring spicules. For example, *Diagoniella nevadensis* Rigby and Stuart, 1988, and *Gabelia pedunculus* Rigby and Murphy, 1983, probably settled with their bases partly buried in sediment, for they did not have root tufts. This implies quiet, nonturbulent environments, stable soft substrates, and low rates of background sedimentation (see discussion of *Diagoniella nevadensis* above). A few forms, such as *Protospongia conica* Rigby and Harris, 1979, do have anchoring spicules.

Our sponges are not found in living positions and probably were not buried in situ. The fragmentary preservation of most specimens, as well as their apparent taxonomic sorting and the orientation of *Protospongia conica* and of *Gabelia pedunculus* stalks, point toward preburial transport. Size sorting is also strongly indicated by the cluster of at least 12 specimens of uniformly sized *Protospongia*, *Diagoniella*, and *Gabelia* fragments on one or two bedding planes on sample LD-5V-E. Thin section analyses confirm impressions of total flattening of the sponges on single bedding planes (fig. 11.2). Thin sections also show small-scale, low-angle cross-bedding and microconvoluted bedding (fig. 11.1) in graded silty limestone and calcareous siltstone. These are sedimentary features that strongly indicate transportation and burial by distal turbidite deposits. We conclude that these sponges were gently transported by mud-loaded turbidity currents prior to their final deposition and burial, probably in a continental shelf margin or in a basinal environment.

Sponges of the same genus and species commonly occur closely spaced on the same bedding plane (e.g., four *Protospongia conica* specimens on sample SRH-5V-3; at least five *Protospongia* specimens on sample LD-5V-3 [fig. 12]; and two *Gabelia pedunculus* stalks on sample LD-5V-4), which suggests that each species had a preferred lateral zonation and perhaps distinct distribution and that from these "oases" of occupation they were apparently carried away and buried by different turbidity currents (fig. 13). Because all the sponges and fragments in the present collection, independent of their taxonomic classification, have limited size range, approximately 1–6 cm, their original distribution in discrete "oases" or clusters seems to be the only reasonable explanation for their taxonomic separation into various taphocoenoses.

Such discrete occurrences of sponges may not necessarily represent true lateral biozonation but might be a result of clustering because of asexual reproduction (budding) or a short planktic larval phase. For example, Recent hexactinellid larvae can sometimes settle on dead

parts of the dictyonal skeleton of the "mother" sponge. In most cases, however, local environmental factors, such as nutrient-carrying currents, can cause accumulation of sponges in certain places. Such was the cause of discrete settlement of larvae of the modern sponge, *Pheronema carpenteri* (Thomson, 1869), found by Rice and others (1990) in the Arctic Ocean.

With reference to sponges described here, we may infer slightly different environmental requirements for forms with anchoring spicules, as compared with those without specialized basal spicules. The anchored tuft-attached sponges can be assumed to have been more tolerant of water currents with respect to both turbulence and suspended sediment load. Variations in current velocities sometimes seem to favor localized settlement of hexactinellid sponges (e.g., in the Arctic Ocean and in British Columbia; Reiswig personal communication 1990, Rice and others 1990). According to Rice and others (1990), topographic breaks often cause secondary reinforcement in velocities of bottom currents. The fragile hexactinellid sponge, *Pheronema carpenteri* (Thomson, 1869), was found settling preferentially not within the area of increased currents directly, but in close proximity to such areas. It was able to take advantage of increased load of suspended organic molecular components in the sea water. A hypothetical reconstruction suggesting localized communities and sorting, deposition, and burial by turbidity currents is shown diagrammatically in figure 13. We are not able to determine preferred directions of transport because the sponges were largely collected from loose talus, but it is presumed to have been off the shelf and onto the slope to the west.

CONCLUSIONS

New evidence of skeletal organization in well-preserved specimens of *Diagoniella nevadensis* Rigby and Stuart, 1988, documents the hexactine nature of the four-rayed principal spicules within this species. Some of these triaxon-based spicules are morphologically altered by elongation of prominent vertical tangential rays into functional diactines. The latter development might be a paradigm for the evolution of diactine parenchymal spicules in other hexactinellid groups, e.g., the Dictyospongiidae. Most hexactinellid sponges of this fauna were attached to the substrates without specialized basal spicules. *Diagoniella nevadensis* Rigby and Stuart, 1988, and *Gabelia pedunculus* Rigby and Murphy, 1983, especially, were probably restricted to very quiet environments with low sedimentation rates. Transport and deposition burial of these allochthonous sponge assemblages took place within distal turbidity currents. The taxonomic sorting of sponges on different layers suggests that they actually lived in various discrete biocoenoses.

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