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ORDOVICIAN LITHISTID SPONGES OF THE GREAT BASIN

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This information should be considered preliminary.
It has not been edited or checked for completeness
or accuracy.

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Abstract

Fossiliferous strata with abundant lithistid demosponges were studied at several horizons and localities within the Lower and Middle Ordovician Pogonip Group of the Great Basin. Collections were made from sponge-bearing wackestones, mudstones, and shales that were deposited along the uppermost slope or outer shelf of a carbonate platform and occur at the boundary between the *Orthidiella* and *Anomalorthis* Zones of the Antelope Valley Limestone at Ikes Canyon in the Toquima Range of central Nevada. Other specimens were gathered from small sponge/algal reef mounds that formed along the margin of an intra-shelf basin and occur about 35 m below the top of the Shingle Limestone in the Egan Range of eastern Nevada. Lithistid sponges from the Fillmore Formation and Juab and Wah Wah Limestones in the Ibex area of western Utah were also studied.

The collection of over 700 excellently preserved lithistid sponges from these localities has allowed a much-needed description and revision of the suborder Orchocladina. The family Anthaspidellidae has been redefined to include only those orchoclads with a fairly regular canal disposition and a skeleton typically dominated by dendroclones that horizontally join adjacent trabs. A new family, the Streptosolenidae, has been erected to hold those genera that have a more irregular canal pattern and a skeleton in which polyclonid dendroclones usually connect to each other or to trabs of differing distances from the exterior.

The taxonomy of many of the previously described sponges in these units has been also been revised. Within the Anthaspidellidae, *Anthaspidella traini* Bassler and *Anthaspidella inyoensis* Pestana have been synonymized with *Anthaspidella clintoni* Bassler. *Archaeoscyphia annulata* Cullison has been synonymized with

Nevadocoelia pulchra Bassler, and both this species and *Nevadocoelia mazourkensis* Greife and Langenheim have been transferred to the genus *Archaeoscyphia* Hinde. *Nevadocoelia* cf. *N. pulchra* Greife and Langenheim has also been placed in *Archaeoscyphia*. However, de Frietas' (1988) reassignment of *Calycocoelia typicalis* Bassler to *Archaeoscyphia* is not justified. *Patellispongia clintoni* Bassler, *Patellispongia magnipora* Bassler, and *Patellispongia minutipora* Bassler have been synonymized with *Patellispongia oculata* Bassler. Finally, *Hesperocoelia undulata* Bassler has been synonymized with *Hesperocoelia typicalis* Bassler.

Four new genera and thirteen new species are described. New taxa within the Anthaspidellidae include: *Rugocoelia eganensis*, n. gen., n. sp., *Archaeoscyphia bassleri*, n. sp., *Archaeoscyphia eganensis* n. sp., *Archaeoscyphia pannosa*, n. sp., *Archaeoscyphia rossi*, n. sp., *Calycocoelia murella*, n. sp., *Colinispongia regularis*, n. gen., n. sp., *Egania typicalis*, n. gen., n. sp., and *Patellispongia brosiusae*, n. sp. New taxa within the Streptosolenidae include: *Streptosolen mccafferyi*, n. sp., *Streptosolen nodosus*, n. sp., *Lissocoelia cylindrica*, n. sp., and *Verpaspongia nodosa*, n. gen., n. sp.

Introduction

The Ordovician Period was a time of significant changes in marine shelf communities and overall global diversity. It was during this time that true reefs made a permanent appearance (Fagerstrom, 1987), hardgrounds began to be extensively colonized (Palmer, 1982; Brett, 1988; Wilson et al., 1992), bioturbation became common (Droser and Bottjer, 1989), and many modern groups of marine organisms made their debut (Jablonski et al., 1983; Sepkoski and Sheehan, 1983). The relatively low-diversity, trilobite-dominated communities of the Cambrian gave way to complex, suspension-feeding communities with abundant brachiopods, mollusks, bryozoans, and echinoderms (Palmer, 1982; Sepkoski and Sheehan, 1983; Fagerstrom, 1987). This characteristic "Paleozoic Evolutionary Fauna" then dominated marine shelf environments until the end of the Permian (Sepkoski and Sheehan, 1983).

One of the more important members of the Paleozoic Evolutionary Fauna, particularly during the Ordovician, was lithistid demosponges belonging to the suborder Orchocladina. These organisms first appeared in the Cambrian but underwent an explosive radiation during the first half of the Ordovician. With their rigid, siliceous skeletons composed of interlocking spicules, or dendroclones, they became the major reef-builders during the Early Ordovician. In fact, Alberstadt and Repetski (1989) have recognized an Early Ordovician sponge/algal facies that can be traced around Laurentia from Newfoundland to the Great Basin. The lithistids were largely displaced from these shallow-water reef environments by corals, stromatoporoids, soft-bodied demosponges, and bryozoans later in the Ordovician (James, 1983; Fagerstrom, 1987; Johns, 1993), but were important deep-

water reef-builders during the Jurassic and Cretaceous periods. Lithistid sponges are alive today, but are restricted to cryptic and deep-water environments.

The bioherms constructed by lithistid sponges and calcareous algae during the Early Ordovician represent some of the earliest Phanerozoic reefs. Unfortunately, this important stage in the evolution of reef biotas is not well-represented in the fossil record. The earliest part of the Middle Ordovician, the Whiterockian Stage, is represented by a major unconformity over most of the North American platform. It is only at the margins of the continent that fossiliferous rocks are preserved and one can see how marine communities evolved at this time.

This study deals with several sections of Early and Middle Ordovician age within the Pogonip Group of the Great Basin (Figures 1 and 2). The units of greatest interest are the Antelope Valley Limestone at Ikes Canyon in the Toquima Range of central Nevada and the Shingle Limestone located in the southern Egan Range near the community of Sunnyside about 90 km south of Ely in eastern Nevada. Both units consist of interbedded limestone and shale, but the Shingle Limestone is slightly older (Hintze et al., 1985; Ross et al., 1989). Nearly all of the Antelope Valley Limestone was apparently deposited during the Whiterockian Stage (Kay, 1962; Hintze et al., 1985; Ross et al., 1989; Ross and Ethington, 1991). Although part of the Shingle Limestone has been attributed to the lowermost zone of the Whiterockian Stage (Hintze et al., 1985; Ross et al., 1989), the trilobite, brachiopod, and conodont faunas (Ethington, 1979; Harris et al., 1979) suggest that it should instead be placed entirely within the uppermost Ibexian, as is done here.

The fossiliferous units within the Antelope Valley Limestone at Ikes Canyon occur as sponge beds, whereas those of the Shingle Limestone exposure consist of abundant sponge reef mounds 2 to 7 m across and 1 to 4 m high. The assemblages in

the two units are nevertheless quite similar, and both were probably deposited in open marine carbonate environments with some terrigenous input. The sponge beds at Ikes Canyon probably formed along the uppermost slope of a carbonate platform or along the outer shelf (Ross et al., 1989; Johns, 1993), whereas the sponge/algal reef mounds in the Egan Range probably developed along the margin of an intra-shelf basin in only 10 to 20 m of water (Johns, 1993). Both faunas are rich and diverse, with abundant lithistids, nautiloids, eocrinoids, rhombiferans, crinoids, orthid brachiopods, gastropods, pliomerid trilobites, and members of other groups.

Specimens were also collected from the Fillmore Formation and Juab and Wah Wah Limestones in the Ibex area of western Utah. The flat-pebble conglomerates and interbedded limestones and shales of the Ibex area occurred in more nearshore environments than either of the sponge assemblages examined in Nevada. The Fillmore Formation is Early Ordovician in age and contains occasional calathid mounds, whereas the younger Wah Wah and Juab Limestones both exhibit isolated sponge mounds of about the same dimensions as those seen at Sunnyside.

The Early Ordovician sponge mounds in the Fillmore Formation of western Utah were described by Church (1974) and Dattilo (1988). These mounds are 1 to 2 m high, 2 to 3 m wide, up to 30 m long, and, like the assemblages at Ikes Canyon and Sunnyside, are dominated by lithistid sponges with associated echinoderms, pliomerid trilobites, gastropods, nautiloids, and brachiopods. Church (1974) also delineated a possible community succession, with stromatolitic algae and sponges forming the climax community. Toomey (1970) described bioherms with a similar fauna from the Lower Ordovician El Paso Group in West Texas, but the climax community in these buildups was dominated by *Pulchrilamina*, a coelenterate-like organism of unknown affinities. Klappa and James (1980) analyzed similar, small

mounds in the Table Point Formation in Newfoundland, and concluded that palmate lithistid sponges formed the climax community there as well.

Middle Ordovician buildups dominated by lithistid sponges also occur in the upper Chickamauga group in Tennessee (Moore, 1977), the Table Point Formation in Newfoundland (Klappa and James, 1980), and in the upper 20 m of the Juab Limestone (Rigby, 1965; Ross et al., 1989) and upper Wah Wah Limestone (Wyatt, 1979) in the Ibex area of Utah. Moore interpreted the sponge buildups in Tennessee as lagoonal patch reefs that formed in relatively shallow water. Unfortunately, Rigby's description of the sponge mounds in the Juab is from a Geological Society of America abstract, and is, therefore, very limited in detail. However, Wyatt (1979) analyzed the sponge mounds occurring in the underlying Wah Wah Limestone and concluded that they were essentially mud mounds with associated sponges. Ross et al. (1989) briefly discussed the mounds in the Juab and Shingle Limestones, although they referred to them as calathid mounds with "possible sponges" (p. 171), and felt that they represented either isolated patch reefs on the shelf or an outer-shelf belt of scattered bioherms.

Although they are the primary constructors in these Ordovician reef mounds, Early Paleozoic lithistid sponges, particularly those belonging to the largest and most common group, the Orchocladina, are poorly understood. As part of this study, many previously described genera and species were redescribed, and four new genera and thirteen new lithistid species were named. A new family, the Streptosolenidae, was erected to include those sponges having a more irregular spiculature than taxa traditionally placed within the major orchoclad family, the Anthaspidellidae.

Geological Setting

Attempting to understand the stratigraphic relationships of the Ordovician units of the Great Basin has occupied geologists for decades. Most of these correlations have been based on the fossils within the units, and typically upon a single group of organisms. Groups that have been used include trilobites (Hintze, 1952; Kellogg, 1963; Whittington and Kindle, 1963; Ross, 1967, 1970; Demeter, 1973; Terrell, 1973; Young, 1973; Hintze, 1979; Ross and Ethington, 1991), brachiopods (Cooper, 1956; Kellogg, 1963; Jensen, 1967; Ross, 1970; Hintze, 1979; Ross and Ethington, 1991), graptolites (Kay, 1962; Kay and Crawford, 1964; Braithwaite, 1976; Mitchell, 1991; Ross and Ethington, 1991), conodonts (Hintze, 1979; Ethington, 1979; Harris et al., 1979; Ethington and Clark, 1981; Mitchell, 1991; Ross and Ethington, 1991), bryozoans (Kay and Crawford, 1964; Hintze, 1979; Ross and Ethington, 1991) and corals (Ross and Ethington, 1991).

Ross and others (Ross et al. ,1989; Ross and Ethington, 1991) have precisely defined the Whiterockian Stage and designated its stratotype at Whiterock Canyon. As so defined, the Whiterock Stage immediately precedes the Blackriverian or Mohawkian Stage and spans 12 million years. It is subdivided into four faunal zones, originally delimited by trilobites and brachiopods (Ross, 1951; Hintze, 1952; Cooper, 1956) but now modified to include other organisms as well (Ross and Ethington, 1991). A compilation of these faunal zones is shown in Table 1.

Although Cooper (1956) believed that the sponge beds were in the *Anomalorthis* Zone, some of the trilobites (Ross, 1970) and echinoderms (Sprinkle, 1971) suggest that they may actually be in the *Orthidiella* Zone. The collections of the entire fauna made in this study indicate that the most diverse sponge beds occur across the boundary between the *Orthidiella* and *Anomalorthis* Zones. The

ZONE O
Lichenaria-Oepikina Zone

Brachiopods: *Camerella nuda* Cooper, *Dactylogonia* sp., *Dorytreta* sp., *Leptellina occidentalis* Ulrich and Cooper, *Macrocoelia* sp., *Oepikina* sp., *Plectorthis perplexus* Ross, *Valcourea* spp.
Conodonts: *Pygodus serra* and *P. anserinus* Zone
Corals: *Eofletcheria* sp., *Lichenaria* spp.
Graptolites: *Hustedograptus teretiusculus* Zone at top

ZONE N
Upper *Anomalorthis* Subzone

Brachiopods: *Anomalorthis lonensis* (Walcott), *A. nevadensis* Ulrich and Cooper, *A. oklahomensis* Ulrich and Cooper, *Aporthophyla typa* Ulrich and Cooper, *Desmorthis costatus* Cooper, *D. nevadensis* Ulrich and Cooper, *Hesperomena leptellinoidea* Cooper, *Rhysostrophia nevadensis* Ulrich and Cooper, *R. occidentalis* Ulrich and Cooper, *Toquimia kirki* Ulrich and Cooper
Trilobites: *Basilicus mckeei* Ross, *Bathyurus extens* (Hall), *Pseudomera barrandei* (Billings), *Psedoolenoides acicaudus* Hintze, *Uromystrum* sp. Hintze

ZONE M
Lower *Anomalorthis* Subzone

Brachiopods: *Anomalorthis fascicostellatus* Ross, *A. lonensis* (Walcott), *A. nevadensis* Ulrich and Cooper, *A. oklahomensis* Ulrich and Cooper, *A. resoi* Ross, *A. utahensis* Ulrich and Cooper, *Asymphylotoechia nolani* Ross, *Desmorthis crassus* Ross
Trilobites: *Pseudomera barrandei* (Billings), *Psedoolenoides dilectus* Hintze

ZONE L
Orthidiella Zone

Brachiopods: *Anomalorthis lambda* Ross, *A. vermontensis* Cooper, *A. juabensis* Jensen, *Idiostrophia valdari* Ross, *Ingria cloudi* Ulrich and Cooper, *Liricamera* sp., *Orthambonites marshalli* Wilson, *Orthidiella* spp., *Orthidium* spp., *Trematorthis* sp.
Graptolites: *Isograptus victoriae* Zone at base
Trilobites: *Ectenotus westoni* (Billings), *Peraspis erugata* Ross

Table 1 — The zones and subzones of the Whiterockian Stage and their characteristic faunas (after Ross and Ethington, 1991).

Orthidiella Zone fauna is similar to that found in the Table Head Group of western Newfoundland, suggesting correlation to that unit (Cooper, 1956; Kay, 1962; and Whittington, 1965), as well as to the lower part of the Simpson Group in Oklahoma (Cooper, 1956; Lewis, 1982).

Cooper (1956) felt that the Pogonip Group in Nevada extended only to the top of the Whiterockian Stage, but studies of other groups suggested that it was at least partially deposited during later times. In fact, Nolan et al. (1956), using essentially the same data as Cooper, concluded that the Pogonip was entirely contained within the Chazyan Stage. This latter view was also shared by Kay (1962) and Kay and Crawford (1964), who based their interpretations on the graptolite facies. However, the Chazyan Stage has itself been subsumed into the uppermost Whiterockian, so the interpretations of Cooper and these later authors are compatible (Kay, 1962; Ross et al., 1982; Ross, 1984; Ross and Ethington, 1991; Sloan, 1991).

The distribution of the Pogonip Group across the Great Basin is shown in Figure 2. The Pogonip consists of interbedded limestones and shales and reaches a maximum thickness of about 1400 m in eastern Nevada (Kleinhampl and Ziony, 1985). It includes the Goodwin Limestone, the Stoneberger and Ninemile Shale, the Antelope Valley Limestone, the House and Shingle Limestones, the Fillmore Formation, the Perkins Canyon Formation, the Kanosh Shale, and the Wah Wah, Juab, and Lehman Limestones. Many of these units are stratigraphically equivalent but diachronous, as shown in Figure 2 (Ross and Ethington, 1991; and many others). Based on its fauna and facies relationships, the Pogonip Group is interpreted as ranging from the base of the Ordovician across the entire Whiterockian Stage into the lowermost Blackriverian (Hintze et al., 1985; Ross et al., 1989; Ross and Ethington, 1991).

The Antelope Valley Limestone constitutes a large proportion of the Pogonip in central Nevada, and apparently extends from just below the Whiterockian/ Ibexian boundary to just above the Whiterockian/Blackriverian boundary (Ross et al., 1989; Ross and Ethington, 1991). The Antelope Valley Limestone averages about 800 m thick where completely exposed, and has a variable composition, ranging from thin, interbedded limestones and shales in the lower part to oncolitic shoal grainstones and wackestones in the middle portion of the unit to silty, dominantly limestone facies near the top (Ross, 1970; Ross et al., 1989). A schematic section of the Antelope Valley Limestone at Ikes Canyon is shown in Figure 3 and a measured section through the sponge beds is provided in Appendix I.

The stratigraphy of the rocks in the Egan Range has received relatively little study. Kellogg (1963) studied the Paleozoic section here, and determined that the Shingle Limestone formed the middle part of the Pogonip Group. He believed the former was deposited during the Late Canadian and Early Chazyan Stages, although he had doubts about where to place the boundary. Ross et al. (1989) placed the mound-bearing portion of the Shingle Limestone within the *Orthidiella* Zone. Ethington (1979), however, looked at the conodonts in these units, and identified the same conodont successions in the Pogonip Group of the Egan Range as in the Ibex area of Utah. He interpreted the Juab and Wah Wah Limestones of Utah, which are probably equivalent to the Shingle Limestone in the Egan Range (Hintze et al., 1985; Ross et al., 1989), as uppermost Ibexian in age, rather than lowermost Whiterockian. Harris et al. (1979) compared the conodont biostratigraphy across Nevada, and correlated the Antelope Valley Limestone at Ikes Canyon with the Kanosh Shale and Lehman Formation in the Egan Range, making the sponge mounds in the Shingle Limestone slightly older than the sponge beds in central

Nevada. Ethington (1979) also correlated the Antelope Valley Limestone in the Toquima Range with the Kanosh Shale and Lehman Limestone in the Ibex area of Utah. Hintze (1979) analyzed all of the biostratigraphic information from the Ibex area from numerous workers and taxa, and compared zonations based on trilobites, brachiopods, graptolites, echinoderms, conodonts, pelecypods, ostracods, bryozoa, cephalopods, corals, gastropods, and sponges. He placed the Juab Limestone and Kanosh Shale in the Whiterockian Stage, and the Wah Wah and Fillmore Formations in the Ibexian Series. Because portions of the Shingle Limestone are equivalent to both the Wah Wah and Juab Limestones (Hintze et al., 1985; Ross et al., 1989), this would place the Shingle Limestone on the boundary between the Lower and Middle Ordovician.

The Shingle Limestone itself averages about 350 m in thickness and ranges from flat-pebble conglomerates near the base to interbedded silty limestones and shales near the top (Hintze, 1952; Kellogg, 1963; Ross et al., 1989). It is primarily limited to the rocks of the Egan Range and may eventually be synonymized with the units in western Utah (Taylor, pers. comm., 1/92). The sponge mounds occur in the uppermost part of the formation, about 35 m below the top. A section through the unit at Sunnyside is shown in Figure 4 and a measured section is provided in Appendix I.

Methods of Study

Over 700 specimens of lithistid sponges and hundreds of other species were studied from the the Antelope Valley Limestone at Ikes Canyon, from the Shingle Limestone in esatern Nevada, and from the Fillmore, Wah Wah, and Juab

Limestones in the Ibex area of Utah. These were primarily collected by the author and Anita Brosius of Cleveland, Ohio, during the summers of 1988-1990, but a great many additional specimens were collected by James Sprinkle of the University of Texas at Austin over the past twenty-one years. Other fossils were collected during the 1991 and 1993 field seasons by Colin Sumrall, also of the University of Texas at Austin, and from 1988-1993 by Thomas Guensburg of Rock Valley College in Rockford, Illinois.

To aid in their description and identification, some of the sponges were sectioned and polished. Some of the polished surfaces were then etched in concentrated hydrochloric acid to bring out the structures, and acetate peels were made. Thin-sections were also ground to examine details of the spiculature and canal disposition.

For the purposes of photography, many of the specimens were inked, then coated with ammonium chloride sublimate. To emphasize fine details of the canals and spiculature, many of the specimens were also photographed while immersed in water.

Lithistid Sponge Characters

Sponges are among the most common organisms in modern, shallow marine environments, particularly in the tropics. The most abundant poriferans in modern environments are the "soft" demosponges, in which the protein spongin is a primary skeletal component. Because spongin breaks down after death, such sponges have left a very poor fossil record (Rigby, 1987). Nevertheless, the remains of other groups of sponges are commonly found throughout the Phanerozoic

record. Their spicules are the primary constituent of some rocks, and large-scale collection from almost any fossiliferous, marine rock will typically turn up a few individuals. Their perceived rarity is probably more an artifact of most paleontologists' failure to recognize and identify the sponges than the absence of these versatile organisms. In fact, certain periods in time, including the Ordovician, have particularly rich sponge faunas.

There are several reasons why sponges have been ignored by so many paleontologists over the years. First, there is a general attitude that the most obvious sponge features, such as shape, are of little or no taxonomic value. Second, many paleontologists believe that the features that are taxonomically important, such as spicule type, are either destroyed by diagenesis or require extensive preparation of polished surfaces or petrographic sections. Finally, there is a feeling among many geologists that sponges are very rare as fossils, and are thus of only minor paleontological significance. Why go through the trouble of identifying something that isn't that important anyway?

Actually, all of these attitudes are incorrect. The shapes of sponges, and other features such as surface ornamentation, are more consistent than is commonly believed. Much of the research on the consistency of sponge shape under different environmental conditions has been conducted on keratose sponges such as *Hippiospongia* and other commercially important species (Storr, 1976). Members of this order tend to have a somewhat amorphous shape strongly influenced by nutrient levels and current strength (Storr, 1976). The same is true of many encrusting genera. In fact, a recent study of *Haliclona* and other members of the order Haplosclerida (Bond, 1992) has demonstrated that some demosponges with isolated spicules are able to rearrange their spicules, sometimes changing their canal

patterns and shape on an almost daily basis! However, a survey of the literature, the study of the faunas described herein, and my own extensive personal diving experience on tropical reefs has convinced me that this is not the case for many other poriferans. Although sponges have a more plastic morphology than most other organisms, overall shape and surface ornamentation are remarkably consistent even in somewhat different environments. Purple tube sponges (*Callyspongia vaginalis*) form long purple tubes whether they are in 1 or 100 m of water, strong or weak currents. Every *Euplectella* has the same complex interweaving of siliceous spicules. Even minor features, such as surface ridges, can exhibit amazing consistency of spacing and form among different individuals (e.g., the near constant ridge-spacing in *Rugocoelia*, n. gen., described herein). Thus, when employed with caution, overall shape and some forms of ornamentation can be useful and distinctive characters.

Nevertheless, form should never be used as the sole defining feature of a taxon. In fact, no single character should be used as the basis for defining any taxon, particularly among sponges. Rather, taxa should be diagnosed by the possession of a consistently shared, uniquely derived assemblage of characters. Obviously, the characters used will vary depending on the organisms and taxonomic levels that one is studying. Table 2 provides a list of characters often used to classify sponges. Unfortunately, features of larval development and soft anatomy, so widely used to classify living sponge taxa, are almost never available when working with fossil forms.

Instead, delineation of fossil species has to rest upon morphological characters. In fact, almost all species, both living and extinct, are defined on the basis of their morphology. A useful alternative to the traditional species concept was proposed by

Table 2 — Some of the characters that have been used in higher-level sponge classification and the respective citations. **1**= Rauff, 1893-1895; **2**= Bassler, 1927; **3**= Bassler, 1941; **4**= Lévi, 1953; **5**= de Laubenfels, 1955; **6**= Lévi, 1957; **7**= Finks, 1960; **8**= Reid, 1968; **9**= Lévi, 1973; **10**= Bergquist, 1978; **11**= Hartman, 1982; **12**= van Soest, 1987; **13**= de Freitas, 1988; **14**= Boury-Esnault et al., 1990. Complete citations are provided in the bibliography.

SKELETAL COMPOSITION = 5, 6, 9, 10, 11, 12

REPRODUCTIVE STRATEGIES = 9, 10

MEGASCLERE SHAPE AND SIZE = 1, 5, 6, 9, 10, 12, 13

SURFACE FEATURES = 6, 10

SHAPE = 2, 3, 6, 7, 9, 10, 11

SPICULE ARRANGEMENTS = 1, 9, 10, 12, 13

MICROSCLERE SHAPE AND SIZE = 6, 8, 9, 10, 12

DIVERSITY OF MICROSCLERES = 12

LARVAL STRATEGY = 4, 6, 9, 10, 11, 12

LARVAL MORPHOLOGY = 6, 9, 10, 11, 12

PRESENCE OF A CALCAREOUS BASAL MASS = 12

PRESENCE OF A DERMALIA = 12

CYTOLOGICAL FEATURES = 9, 10, 11, 12, 14

CHOANOCYTE CHAMBER SIZE AND SHAPE = 11, 12

GEMMULE FORMATION = 12

PROTEIN SYNTHESIS AND BIOCHEMISTRY = 9, 10, 11, 12

SKELETAL ARCHITECTURE = 6, 9, 10, 11, 12, 13

USE OF FOREIGN MATERIAL IN SKELETON = 12

CANAL AND PORE ARRANGEMENTS = 6, 7, 9, 10, 13

TEXTURE = 6, 9, 10

ECOLOGY = 6, 10

COLOR = 6, 9, 10, 11

CAUSES BIOEROSION = 12

Donoghue (1985), who suggested using shared, derived, morphological characters to delineate monophyletic "phylogenetic species". Because of the lack of information in the geological record regarding interbreeding, nearly all fossil species must be defined on the basis of their morphology or interpreted ecological niche. Although the stratigraphic and geographic occurrence of fossil populations has been used to distinguish separate species, geographic distance between populations may not be conclusive evidence that they did not interbreed. For example, Paleozoic species of articulate brachiopods, which are generally considered to be relatively endemic organisms with poor dispersal, may have had planktotrophic larvae capable of traveling great distances (Valentine and Jablonski, 1983). Using stratigraphic separation to help delineate species is probably legitimate, if the length of time between occurrences is on the order of tens of millions of years or more, and so long as it is not the only basis for their classification into two (or more) taxa. The geological record is not everywhere complete, and the absence of fossils in a certain area at a particular time does not demonstrate that the group did not exist at that time. There could have been a continuous, interbreeding population throughout the time that fossils were not preserved, and the point in time at which one would separate different populations into different species would be completely arbitrary. The phylogenetic species concept avoids all of these complications by defining species on the presence of shared, derived characters. Any groups of organisms that lack significant differences in their morphological characters can thus be considered to belong to the same phylogenetic species.

It would be ideal if the groups defined as species in the traditional or genetic sense and those defined as morphospecies were one and the same, but morphology is not necessarily indicative that two groups can or could interbreed. Nevertheless,

most species are defined on the basis of their morphology, and it is generally assumed that both species concepts define the same groups. Recent experiments with cheilostome bryozoans suggest that this is true (Jackson, 1989; Jackson and Cheetham, 1990), but whether this holds for other organisms remains to be tested. Given the absence of alternatives, we must assume that morphological similarity reflects the ability to interbreed, at least until provided with evidence to the contrary. Thus, the taxa described and defined herein are best considered as phylogenetic species. For the sake of brevity, phylogenetic species will hereafter be referred to simply as "species".

This study is primarily concerned with the classification of lithistid sponges within the suborder Orchocladina. Spicule type, both microscleres and megascleres, is usually an ordinal, subordinal, or familial level character (Reid, 1968). Members of the Orchocladina are currently separated into two families, the Anthaspidellidae and the Chiastoclonellidae, and a new family, the Streptosolenidae, is described herein. The Anthaspidellidae and Streptosolenidae are characterized by having well-developed radial architecture and monaxonic dendroclones, although these may take the form of amphiarborescent, triclonid, or quadraclonid spicules (Figure 5) (Reid, 1968; van Kempen, 1978; de Freitas, 1988). In contrast, the Chiastoclonellidae often lack radial architecture and their spiculature is dominated by chiastoclones (Figure 5) (Rigby, 1983). Nearly all demosponge taxa described herein possess radial architecture and monaxonic dendroclones, so these features are not useful for distinguishing between them. The features primarily used to separate taxa at the genus- and species-level in this study are outlined below. The glossary provides a list of morphological terms and their definitions.

Shape. The single most obvious feature of a sponge, the form or overall shape of the organism, can be useful when employed with caution. As discussed above, some demosponges exhibit extreme plasticity of shape, whereas others maintain a high degree of morphological regularity. For most of the taxa described herein, the shape varies somewhat, but stays within recognizable bounds. For example, *Calycocoelia* maintains a generally cylindrical shape, although individuals vary from cylindrical to obconical (Plates 4-6). *Streptosolen* is more variable, with some individuals nearly flat or even bowl-shaped, while others are tall and obconical (Plates 12-14). Similarly, specimens of *Lissocoelia ramosa* may have almost any number of branches, but the branching is always dichotomous. Shape and the consistency of shape can thus be used as distinctive characters at the generic level for these lithistids.

Skeletal Architecture. As noted by de Freitas (1988) and others and substantiated in this study, the arrangement of spicules within the skeleton is a key diagnostic feature for many orchoclads. These sponges have a radial architecture (*sensu* Lévi, 1973) in that the dendroclones are arranged radially and concentrically around the center of the sponge, with their digitate ends fusing together to form the main supportive elements, the trabs (Rigby and Bayer, 1971; de Freitas, 1988). Essentially, the vertical portions of the trabs can be viewed as the siderails of a ladder, with the dendroclones as the rungs (Rigby and Bayer, 1971) (Figure 6). The trabs angle outward and branch as they rise, eventually becoming more horizontal or even perpendicular to the outer surface. The gaps between the intraserial spicules connecting the trabs create the radial canals, with the trabs on either side separating adjacent canals. Often, one or more columns of parietal spicules are inserted between adjacent canals as well. In addition, the surface of trab pinnulation

is consistent at the specific, and in some cases generic, level. This skeletal arrangement is most regular in the anthaspidellids, but can also be seen in streptosolenids and chiastoclonellids.

The consistency, dimensions, and features of this skeletal net can be used to distinguish different species and genera. Some taxa have coarse spiculature, others very fine. The skeletal net can be very consistent, or it can be somewhat irregular. The number of trabs separating adjacent canals (and hence the number of parietal columns) is useful for distinction at the species-level (de Freitas, 1988, and herein); however, in combination with other features, it may also be useful for distinguishing genera. The number of trabs between adjacent columns of radial canals usually varies by only one or two among species within the same genus (Rigby, 1973; Johns, 1993). The size and spacing of the spicules and other skeletal features can vary within a species or even an individual, but are sufficiently consistent within most taxa to help in separating them from others.

Canal Disposition. Because the spacing between the spicules defines the canals, there is obviously a close correlation between skeletal architecture and the arrangement and character of canals within an individual. Although the canal patterns among some sponges are highly variable (Bond, 1992), the fused spiculature of the lithistids provides for more regularity. Some taxa show remarkable consistency between individuals, with average radial canal diameters and spacing varying by only a few tenths of a millimeter. Others, such as *Streptosolen*, have much greater variations in size and spacing within a single individual. Thus, not only is the actual size and spacing of the canals important, but the degree of variation of the canal patterns is as well. In addition, the extent and direction of

curvature of the radial canals and the distribution of vertical parietal canals can be important characters for classification.

The family Anthaspidellidae has been defined by the possession of vertically stacked radial canals, and many of the sponges described herein have such a canal arrangement. However, while the stacking of radial canals in some taxa is very regular, it is much more variable in others. This difference was first noted by Rigby (1983) and has been used here to help distinguish the Streptosolenidae, n. fam., from the more regular Anthaspidellidae. Even among the latter, however, the vertical spacing between radial canals can vary within individuals, making this feature less diagnostic than some have thought (e.g., de Freitas, 1988).

Ectosomal Layer. In most sponges, the spicules of the thin ectosome covering the external and internal surfaces are usually much finer than the endosomal spiculature. This is also true for many of the lithistids described here. The preservation and development of the ectosome can be highly variable. Recrystallization and silicification often alters the outer surface of many specimens, creating a weathered rind and destroying the dermalia (de Freitas, 1988; herein). Furthermore, the dermal layer is inconsistently developed among modern sponges, sometimes even within the same individual (Burton, 1963). The same was apparently true for many lithistids (Finks, 1960; de Freitas, 1988). A dermal layer is present in some specimens of *Steliella*, *Archaeoscyphia*, and *Calycocoelia*, but not in others (de Freitas, 1988). For *Archaeoscyphia minganensis*, *Rugocoelia eganensis* (gen. nov.), and other annulated species, the ectosome is typically well-developed on the crests of the ridges but only poorly developed in the troughs (de Freitas, 1988; herein). The tops of the ridges were the most exposed parts of the sponges and would thus have required the greatest armoring. However, they would also have

been the most abraded during burial and weathering. The fact that the dermal layer is still thicker on the crests of the annulations than in the troughs suggests that the differences in dermal layer between the crest and the troughs is a result of differential development rather than differential preservation. If true, then the consistent occurrence of a well-developed dermal layer can be used as a feature for distinguishing some taxa. Again, however, caution must be exercised, and the presence or development of dermal layer should probably not be used as the sole distinguishing characteristic of a taxon (e.g., *Patellispongia* versus *Psarodictyum*).

Besides being finer, the spiculature of the dermal layer is also much more irregular than that of the endosome. Openings within the dermal layer are generally less ordered than those in the endosomal structure, and frequently bear no spatial relationship to the underlying canals. Despite this variability, the size and spacing of these pores has been used to separate different taxa (Bassler, 1927, 1941). These distinctions are unjustified on current evidence, and several species, particularly within the genus *Patellispongia*, have thus been synonymized.

Lithistid Sponge Classification

Lithistid sponges are truly living fossils. They were important reef-builders during the Ordovician, Jurassic, and Cretaceous Periods, and they were an important part of typical marine faunas at other times, such as the Permian. With their fused, siliceous skeletons, they were easily preserved and represent one of the few sponge groups with a substantial fossil record.

Today, however, lithistid sponges are generally restricted to cryptic environments or water depths of 200 to 500 m (Brien, 1973). Because they are no

longer part of well-lit, shallow-water marine communities, lithistid sponges have been largely ignored by zoologists. Because few paleontologists actively study fossil sponges, lithistids have been largely ignored by the paleontological community as well. As a result, we know almost nothing about the ecology and biology of these organisms, despite their importance in paleocommunities and their potential for helping to resolve many questions regarding the phylogeny and classification of the Porifera.

It is widely accepted that the order Lithistida is polyphyletic (de Laubenfels, 1955; Finks, 1960; Bergquist, 1978; Hartman, 1980, 1982; Rigby, 1983). The group as a whole is defined by the possession of fused and complexly interwoven spicules called desmas that are formed by successive deposition of silica around a spicular core (Sollas, 1888; Lévi, 1991). This additional silicification also fuses the desma to its neighbors. Depending on the group, the desmas can be highly irregular or follow a basic plan, i.e., being monocrepid, tetracrepid, etc. Desmas apparently evolved independently on two or more occasions (Reid, 1970; van Soest, 1987), but all lithistids have traditionally been grouped together. This has been more a matter of practicality than anything else, because our knowledge of lithistid anatomy, ontogeny, and phylogeny has been too poor to allow any meaningful separation between the groups.

Because of the confusion regarding their origins, the classification of lithistid taxa has changed repeatedly. At times it seems as if the old adage about economists also holds true for sponge taxonomists: if you put two of them together in a room, you'll end up with three different opinions. Various classification schemes and the authors who proposed them are shown in Table 3. For the purposes of this study,

Table 3 — Various classification schemes that have been proposed for the lithistid sponges.

RAUFF, 1894
Class SILICEA
Order TETRACTINELLIDA
Suborder LITHISTIDA
Tribe TETRACLADINIDAE
Tribe ANOMACLADINIDAE
Subtribe ISOTAXININAE
Subtribe DITAXININAE
Tribe RHABDOMORINIDAE
Subtribe DIDYMORININAE
Tribe RHIZOMORINIDAE

DE LAUBENFELS, 1955; FINKS, 1960
Class DEMOSPONGEA
Order LITHISTIDA
Suborder ANOMACLADINA
Suborder RHIZOMORINA
Suborder MEGAMORINA
Suborder EUTAXICLADINA
Suborder TETRACLADINA

FINKS, 1967b
Class DEMOSPONGEA
Order LITHISTIDA
Suborder ANOMACLADINA
Suborder RHIZOMORINA
Suborder MEGAMORINA
Suborder EUTAXICLADINA
Suborder DICRANOCLADINA
Suborder ORCHOCLADINA
Suborder SPHAEROCLADINA

REID, 1968
Class DEMOSPONGIA
Order LITHISTIDA
Suborder TETRACLADINA
Suborder DIDYMMORINA
Suborder MEGAMORINA
Suborder DICRANOCLADINA
Suborder ORCHOCLADINA
Suborder SPHAEROCLADINA
Suborder TRICRANOCLADINA

LÉVI, 1973
Class DEMOSPONGIAE
Subclass TÉTRACTINOMORPHES
Order DESMOPHORIDA

HARTMAN, 1980,1982
(for living taxa only)
Class DEMOSPONGIAE
Subclass TETRACTINOMORPHA
Order LITHISTIDA
Suborder TRIAENOSINA = DESMOPHORIDA (Lévi)
Suborder RHABDOSINA
Suborder ANOPLINA

RIGBY, 1983
Class DEMOSPONGIA
Suborder TETRACLADINA
Suborder RHIZOMORINA
Suborder DIDYMMORINA
Suborder MEGAMORINA
Suborder DICRANOCLADINA
Suborder ORCHOCLADINA
Suborder SPHAEROCLADINA
Suborder TRICRANOCLADINA

LÉVI, 1991 (non-comprehensive)
Class DEMOSPONGIA
Order STREPTOSCLEROPHORIDA
Suborder TETRACLADINA
Suborder RHIZOMORINA
Suborder MEGAMORINA
Suborder DICRANOCLADINA

Rigby's (1983) classification will be used. This scheme is the most widely accepted in this country and the most applicable when dealing with Paleozoic forms.

It was not the purpose of this study to revise the classification of the Lithistida. Rather, this study only redescribed the lithistid taxa that dominated the Ordovician sponge communities of the Great Basin. Although some familial revision was necessary, the primary focus was at the generic and specific level.

The suborders of Lithistida can be broadly divided, with some reservations, into two groups. The Orchocladina, Sphaerocladina, Rhizomorina, and Didymmorina have anaxial or monaxial desmas and may represent one origination event, while the Dicranocladina, Megamorina, and Tetracladina represent another event (Reid, 1970). The Tricranocladina, which includes *Hindia*, might have originated independently of either group (Reid, 1970).
As suggested by Finks (1967a), the lithistid sponges probably arose from monaxonid ancestors. The oldest known lithistids are Middle Cambrian orchoclads from Australia, Canada, and Utah (Kruse, 1983; Rigby, 1991a). The monaxial spicules of these and other Early Paleozoic lithistids suggests that their ancestor was itself monaxial. The first lithistids with true tetraxial desmas do not appear until the Carboniferous (Finks, 1967a).

The taxa discussed below are all members of the Orchocladina. This suborder is currently divided into the families Anthaspidellidae and Chiastoclonellidae, distinguished on the basis of their spiculature. A new family, the Streptosolenidae, is proposed herein to include those former members of the Anthaspidellidae having a more irregular canal disposition, a less organized skeletal net, and in which the trabs and dendroclones are of approximately the same diameter.

Systematic Paleontology

R. S. Bassler (1927, 1941) named and described several species of lithistid sponges from the Antelope Valley Limestone at Ikes Canyon in central Nevada. Unfortunately, his descriptions lack many details now considered crucial to poriferan taxonomy. Furthermore, some of the characters on which he did distinguish his species, such as wall thickness or the size and spacing of openings in the ectosome, are now known to be too variable to serve for separation of distinct taxa.

On the basis of over 700 specimens from Ikes Canyon, from the Shingle Limestone in the Egan Range of eastern Nevada, and from contemporaneous localities in the Ibex area of western Utah, a complete revision of Bassler's species has been made, and several new taxa described. Several other workers have mentioned or described Ordovician sponges from the Great Basin since Bassler, and, where appropriate, these too have been revised.

The following species are considered valid and have been redescribed: *Anthaspidella clintoni* Bassler, *Hesperocoelia typicalis* Bassler, *Lissocoelia ramosa* Bassler, *Nevadocoelia grandis* Bassler, *N. traini* Bassler, *N. wistae* Bassler, *Patellispongia oculata* Bassler, and *Streptosolen occidentalis* Bassler. Large collections of *Calycocoelia typicalis* from its type locality indicate that it is distinct from *Archaeoscyphia* and should not be synonymized, as was done by de Freitas (1988). The following new taxa are described herein: *Archaeoscyphia bassleri*, n. sp., *Archaeoscyphia eganensis*, n. sp., *Archaeoscyphia rossi*, n. sp., *Calycocoelia murella*, n. sp., *Egania typicalis*, n. gen., n. sp., *Lissocoelia cylindrica*, n. sp., *Patellispongia brosiusae* , n. sp., *Colinispongia regularis*, n. gen., n. sp., *Rugocoelia eganensis*, n. gen., n. sp., *Streptosolen mccafferyi*, n. sp., *Streptosolen nodosus*, n. sp., and

Verpaspongia nodosa, n. gen., n. sp. In the absence of consistent distinguishing characteristics, the following species have been synonymized: *Anthaspidella traini* Bassler and *A. inyoensis* Pestana with *A. clintoni* Bassler, *Archaeoscyphia annulata* Cullison with *Archaeoscyphia pulchra* (Bassler), *Hesperocoelia undulata* Bassler with *H. typicalis* Bassler, and *Patellispongia clintoni* Bassler, *P. minutipora* Bassler, and *P. magnipora* Bassler with *P. oculata* Bassler. In addition, *Nevadocoelia mazourkensis* Greife and Langenheim, *N. pulchra* Bassler, and *N.* cf. *N. pulchra* Greife and Langenheim have been reassigned to *Archaeoscyphia*.

The genus *Anthaspidella* Ulrich and Everett in Miller, 1889 is oversplit, and a complete revision of this taxon is needed. Such a revision was beyond the scope of this project, but the species described herein should be sufficiently distinct morphologically and stratigraphically to remain valid.

The systematic descriptions of the species are arranged taxonomically following Rigby's (1983) classification. Museum abbreviations for the studied specimens include: TX, Texas Archive for Geologic Research, University of Texas, Austin; UCMP, Museum of Paleontology, University of California, Berkeley, California; USNM, National Museum of Natural History, Washington, D. C.; and YPM, Peabody Museum, Yale University, New Haven, Connecticut. The localities given in the descriptions are shown in Figure 1.

The Great Basin sponge fauna represents the first reported occurrence of many different genera and species which later appeared in the eastern United States, Canada, Europe, or Australia. As many invertebrate lineages underwent radiations during the upper Ibexian and early Middle Ordovician, many of these lithistid taxa may have actually originated in the relatively shallow-water environments of the Great Basin. However, it is more probable that the sponge taxa discussed herein are

merely the earliest described representatives of their species, and that the record of their true originations has not yet been discovered.

Systematic Descriptions

Phylum PORIFERA Grant, 1872

Class DEMOSPONGIA Sollas, 1875

Discussion — Sollas (1875) erected this class to include siliceous sponges lacking sexiradiate spicules. The name he gave for this group was Demospongiae. This was later revised by Moore et al. (1952) to Demospongea, and Finks (1967b), in turn, introduced a spelling of Demospongia. The Code of Zoological Nomenclature has no official rules regarding the proper endings for taxa above the family level, other than requiring that they be latinized. All of the above names have perfectly acceptable latinized endings, although Sollas' name is feminine while de Laubenfels' and Reid's are neuter. In the absence of official guidelines, all three names have been used extensively in the literature (Table 4).

Table 4 — The three versions of the name for the class comprising the demosponges and selected citations in which they have been used.

Demospongiae — Sollas, 1875; Brien, 1973; Lévi, 1973, 1991; Bergquist, 1978; Hartman, 1980, 1982; de Vos et al., 1991; van Soest, 1991; West, 1992

Demospongea — Moore et al., 1952; de Laubenfels, 1955; Finks, 1960, 1967a, 1970; Rigby, 1977a, Lévi, 1978; van Kempen and ten Kate, 1980; Rigby, 1987; de Freitas, 1988

Demospongia — Finks, 1967b; Reid, 1968; Rigby, 1977c, 1980, 1983

Because it is more widely used in the paleontological literature and has no gender connotations, the name Demospongia is employed herein.

Subclass TETRACTINOMORPHA Lévi, 1953

Order LITHISTIDA Schmidt, 1870

Suborder ORCHOCLADINA Rauff, 1895

Family ANTHASPIDELLIDAE Ulrich in Miller, 1889

Description — Variously-shaped, from lamellar and palmate to cylindrical, branching, or funnel-shaped; highly organized canal system, with vertically stacked radial canals sometimes intertwining with vertical canals of comparable diameter; apopores emptying into cloaca or forming individual oscula, usually in clusters; horizontal dendroclones fused at tips to form trabs, latter often cored by oxeas; surficial ridges or nodes often present; ectosome variably developed, almost always finer than endosomal skeleton.

Discussion — This family was described by Ulrich (1890) to include the genera *Anthaspidella, Aulocopium, Climacospongia, Edriospongia, Streptosolen, Syringophyllum,* and *Zittelella,* but was first published by Miller (1889) who apparently had access to Ulrich's manuscript. Rauff (1894) erected the family Archaeoscyphidae for goblet- or bowl-shaped sponges having curved radial canals organized into vertical rows. However, the Archaeoscyphidae, the Aulocopiidae Rauff, 1895, and part of the Eospongiidae de Laubenfels, 1955, were later included within the Anthaspidellidae by Finks (1967c). He defined the family as including massive to bowl-shaped forms in which the dendroclones are both horizontal and oriented parallel to the outer surface; their tips unite to form vertical, ladder-like series that are arranged in spoke-like groups

radiating from the central axis. As noted by Rigby and Dixon (1979), some genera lack any ectosome, but many others have either a moderately to well-developed dermal layer.

Trabs, the large spicular structures forming the "siderails" of the ladder-like series, are a feature common all members of the Orchocladina (Figure 9). These were originally thought to be produced solely by the fusion of the dendroclone tips, but Finks (1967a) discovered that the trabs of *Climacospongia* were cored by fine oxeas which presumably guided their growth and provided structural strength. Since then oxeas have been found in the trabs of *Fibrocoelia* (van Kempen, 1978), *Somersetella* (Rigby and Dixon, 1979), *Hudsonospongia* (van Kempen and ten Kate, 1980), *Archaeoscyphia* (van Kempen and Hellingwerf, 1983; de Freitas, 1988), *Capsospongia* (Rigby, 1986a), *Playfordiella* (Rigby, 1986b), *Malongullospongia* (Rigby and Webby, 1988), *Patellispongia* (Rigby and Webby, 1988), *Yarrowigahia* (Rigby and Webby, 1988), *Calycocoelia* (de Freitas, 1988), *Protachilleum* (Beresi and Rigby, 1993) and *Talacastonia* (Beresi and Rigby, 1993). Thin-sections through the sponges described in this study show that such oxeas are also found in the trabs of *Egania, Anthaspidella, Hesperocoelia, Streptosolen,* and *Nevadocoelia,* and *Colinispongia,* suggesting that, in general, the trabs of orchoclads are cored by oxeas.

Rigby (1986a, p. 52) has suggested that two orchoclad lineages may have evolved in the Cambrian: one in which the trabs were cored by oxeas, and one in which they were not. The subsequent discoveries of monaxons in the trabs of many other orchoclad genera since then suggest that this is probably not the case. It is not clear whether coring spicules are present in *Rankenella,* the oldest known anthaspidellid, but they do occur in *Capsospongia,* a genus from the Middle Cambrian Burgess Shale (Rigby, 1986a). Cored trabs are also found in the

Streptosolenidae, although several well-preserved genera in the family show no sign of coring spicules. Thus, cored trabs are characteristic of most members of the Anthaspidellidae, including some of its earliest representatives, and are found in many members of the Streptosolenidae as well. The presence or absence of coring spicules thus appears to have little higher-level taxonomic importance. The occurrence of such spicules in most orchoclads, including some of the earliest representatives, suggests that this was the primitive condition, and that the coring oxeas have since been independently lost in several genera.

Of course, it is also possible that the lack of correlation between cored versus uncored trabs and familial classification is a result of inappropriate familial designations. Considering the still very basic nature of fossil sponge taxonomy, this might well turn out to be the case. However, in the absence of more definitive evidence, it is assumed that the family level classification herein is valid, and that the absence of cored trabs in different genera is the result of homeoplasy.

Genus ANTHASPIDELLA Ulrich and Everett in Miller, 1889

Synonymy —

Anthaspidella Miller, 1889, p. 153; Ulrich and Everett, 1890, pp. 256-267; Bassler, 1927, p. 394; Butts, 1940, pp. 142, 175; Bassler, 1941, pp. 99-100; Butts, 1941, p. 54; de Laubenfels, 1955, p. E64; Langenheim et al., 1956, p. 2093; Pestana, 1960, p. 864-865; Rigby, 1971a, pp. 50-51; Toomey and Nitecki, 1979, p. 165; Beresi and Rigby, 1993, pp. 52-56.

Type Species — *Anthaspidella mammulata* Ulrich and Everett in Miller, 1889. Ulrich and Everett (1890) named both *A. mammulata* and *A. florifera* as types, but Miller (1889) and de Laubenfels (1955) selected the former as the sole type species.

Description — Lamellar, saucer- to funnel-shaped, often with short, subcylindrical stem. Apopores form star-shaped clusters on upper surface, with 5 or more apopores per cluster; clusters sometimes swollen. Radial canals vertically stacked, anastomosing. Vertically oriented apochetes arising in mid-section of wall, becoming perpendicular to upper surface and coming together to form apopore clusters. Scalariform skeletal net, with at least one parietal series between radial canals, trabs cored by oxeas. Dermal and gastral layers sometimes well-developed, but much finer than endosome.

Occurrence — Eastern, central and southwestern United States, Manitoba, Argentina. Ibexian Series to Blackriverian Stages, Lower to Middle Ordovician.

Discussion — The name *Anthaspidella* first appeared in print in Miller's 1889 monograph on North American geology and paleontology. De Laubenfels (1955) cited Miller as the author of the genus, but Miller himself attributed the taxon to Ulrich and Everett, whose detailed descriptions of this genus and its species appeared the following year. Apparently, Miller had access to a preprint of Ulrich and Everett's work. This matter was discussed by Finks (1967c), and, as he notes, the Code of Zoological Nomenclature requires that the proper citation be Ulrich and Everett in Miller, 1889.

Anthaspidella is a relatively uncommon genus within the Antelope Valley Limestone, which marks its earliest stratigraphic occurrence. Pestana (1960) reported that it is common within the Blackriverian Johnson Spring Formation of California, and it is certainly abundant within the Platteville Formation of Illinois

of the same age (Ulrich and Everett, 1890; Shaver et al., 1985). Butts (1940, 1941) described an anthaspidellid sponge from the Whiterockian age sediments of the Lenoir and Ottosee Limestones in Virginia, but this may not *Anthaspidella*. De Laubenfels (1955) cited the stratigraphic range of this genus as Cambrian to Ordovician, and the geographic range as Illinois to East Asia. Unfortunately, there is no indication of what led de Laubenfels to believe that *Anthaspidella* occurred in either the Cambrian or East Asia. An extensive survey of the literature has failed to yield any citation for *Anthaspidella* from either one. Rigby (pers. comm., 2/93) has suggested that the anthaspidellid spicules from the Cambrian of Australia mentioned by Gatehouse (1968) and eventually described as *Rankenella* (Kruse, 1983) might have been known to de Laubenfels and led him to place *Anthaspidella* in the Cambrian, but, as Rigby notes, this doesn't explain the East Asian occurrence.

Anthaspidella is one of the few lamellate or palmate members of the Anthaspidellidae. It is readily distinguished from all other similarly shaped genera, including *Patellispongia, Psarodictyum, Hesperocoelia, Cockbainia, Rugocoelia,* and *Syringophyllum,* in having large, clustered apopores on the upper, gastral surface.

ANTHASPIDELLA CLINTONI Bassler, 1927

Plate 1, Figures 1-6, Plate 2, Figures 1-2

Synonymy —

Anthaspidella clintoni Bassler, 1927, p. 394; Bassler, 1941, p. 99-100.

Anthaspidella cf. *A. scutula* Langenheim et al., 1956, p. 2093.

Anthaspidella inyoensis Pestana, 1960, pp. 864-865.

Anthaspidella traini Bassler, 1927, p. 394; Bassler, 1941, p. 100.

Description — Lamellate, saucer- to funnel-shaped, often with short, subcylindrical stem; sponge wall 5 to 20 mm thick. Lower surface smooth, occasionally marked by irregular nodes. Apopores form star-shaped clusters on upper surface, with about 5 to 25 apopores per cluster; clusters sometimes swollen, distance of 3 to 25 mm from center to center.

Radial canals 0.6 to 1.4 mm in diameter, vertically stacked and separated by 0.2 to 1.6 mm. Radial canals slightly sinuous, with parietal separation of 0.2 to 1.1 mm. Vertically oriented apochetes arising in mid-section of wall, becoming perpendicular to upper surface and clumping together to form apopore clusters. Individual apochetes 0.7 to 1.9 mm in diameter, clusters between 2.5 and 12 mm across.

Scalariform skeletal net, with 2 to 4 trabs and at least one parietal series between radial canals. Trabs 0.1 to 0.13 mm in diameter, cored by 2 to 3 oxeas which are 0.01 to 0.02 mm across. Surface of trab pinnation in midwall, trabs diverge to intersect dermal and gastral surfaces between 30 and 60°, usually about 45°. Amphiarboreascent dendroclones dominate, connect adjacent trabs horizontally. Endosomal spicules 0.03 to 0.07 mm in diameter, 0.275 to 0.35 mm long, with cladome rays 0.25 mm across. Differentiated dermal and gastral layers sometimes well-developed, and having a higher proportion of polyclonid spicules, particularly triclonids. Ectosomal spicules average 0,025 mm in cross-section and 0.25 mm long.

Type Specimen — Holotype USNM 79643.

Measurements — Dimensions of the holotype are: height = unknown, diameter = 113^{+} mm, average wall thickness = 9.5 mm.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada, and the Johnson Spring Formation, Mazourka Canyon, Inyo

Mountains, California. The Ikes Canyon sediments are of Whiterockian age, while the Mazourka Canyon units are of Blackriverian age, Middle Ordovician.

Discussion — *Anthaspidella clintoni* is the only member of this genus found at Ikes Canyon. As with the other palmate taxa found here, specimens of *A. clintoni* are invariably broken and incomplete, preventing any interpretation of their attachment structures.

In his descriptions of the Ikes Canyon sponges, Bassler (1927, 1941) distinguished two species. He placed those individuals with smaller, more closely-spaced oscular clusters and thinner walls in *A. clintoni,* and put the bigger specimens with larger, more widely-spaced clusters and thicker walls in *A. traini.* However, the better collections available in this study demonstrate that there is no clear distinction between these two groups, and that the Nevada representatives of *Anthaspidella* form a continuum of cluster size, cluster spacing, and wall thickness (Figures 7 and 8).

The plot of cluster size versus cluster spacing is the most informative, but also needs some explanation. A best-fit line through the data is shown, but the 17 plotted specimens have a fair degree of scatter; apparently, not only are cluster size and spacing somewhat variable features, but the relationship between them is also relatively inconsistent. At first glance, the specimens appear to fall into two or perhaps three groups: those with clusters less than 5 mm in size spaced less than 6 mm apart, and those with clusters more than 5 mm in size spaced over 6 mm apart. The larger, thicker fragments with clusters over 8 mm in size and more than 100 mm apart appear to form a possible third group. However, the plotted values are averages only; the actual range of cluster size and spacing within individuals easily fills the apparent gaps. It is also interesting to note that the holotype of

Anthaspidella clintoni falls in almost the exact center of the total data set. The holotype of *A. traini* is very poor, with the uppermost surface being eroded and the lower surface completely covered by skeletal debris. The thickness of the sponge wall shows almost no correlation to size; although the largest fragments with the largest clusters are also the thickest, the two thinnest sponges are well within the central grouping.

Thus the specimens plotted in Figure 7 form a continuum from those with small, closely-spaced clusters to those with large, widely-spaced clusters. The differences between specimens may be ontogenetic, with older, larger sponges having larger, more widely-spaced clusters. In the absence of any consistent differences between specimens, *Anthaspidella clintoni* and *A. traini* are synonymized. The specimen of *A. inyoensis* described from California by Pestana (1960) has features that likewise fall within this range, so it too has been synonymized with *A. clintoni.* As mentioned earlier, the representatives of *Anthaspidella* from the Platteville Limestone have been oversplit and, until they are revised, meaningful distinctions between these specimens and those from the Great Basin cannot be made.

Beresi and Rigby (1993) have recently described several new species of *Anthaspidella* from the San Juan Formation in Argentina, but all differ in several important ways from *A. clintoni.* Specimens of *A. inornata* have significantly smaller pores and canals than the individuals from the Great Basin, and the skeleton is less regular. *A. annulata* has smaller pores and finer spiculature than *A. clintoni,* and is characterized by prominent annulations, a feature not seen in any of the individuals from Nevada. *A. alveola* lacks the lateral canals that feed into the apopore clusters of *A. clintoni* and has much larger trabs. in addition, all three of

the South American species are dominated by triclonid spicules, whereas *A. clintoni* is dominated by amphiarborescent dendroclones.

Genus ARCHAEOSCYPHIA Hinde, 1889a

Synonymy —

Archaeocyathus Billings, 1859, p. 346; Billings, 1861a, p. 5; Billings, 1861b, pp. 944-946; Billings, 1865, pp. 354-357; Dawson, 1865, p. 103; Nicholson, 1872, p. 68; Dawson, 1875, p. 152; Miller, 1877, p. 154; Nicholson, 1879, p. 139; Römer, 1880, p. 299; Zittel, 1876-1880, p. 728; Hinde, 1884, p. 835; Walcott, 1887, pp. 145-146; Hinde, 1888b, pp. 226-228; Hinde, 1889a, pp. 131-133; de Koninck, 1898, pp. 52-53; Chamberlain and Salisbury, 1907, p. 363; Okulitch, 1935, pp. 99-100.

Archaeoscyphia Hinde, 1889a, pp. 142-143; Miller, 1889, p. Rauff, 1894, pp. 238-239; Dana, 1895, p. 497; Schuchert and Twenhofel, 1910, p. 687; Boucart and Le Villain, 1931, p. 13; Schuchert and Dunbar, 1934, pp. 64, 68; Twenhofel, 1938, p. 34; Bassler, 1941, p. 93-94; Cullison, 1944, p. 48; de Laubenfels, 1955, p. E53-E54; Sando, 1957, pp. 110-111; Bolton, 1960, p. 8; Rigby and Nitecki, 1973, pp. 3-9; Shimer and Schrock, 1944, p. 51; van Kempen, 1978, pp. 311-318; Toomey and Nitecki, 1979; van Kempen, 1981, pp. 156-168; van Kempen and Hellingwerf, 1983, pp. 69-75; de Freitas, 1988, pp. 1868-1877; Rigby and Webby, 1988, pp. 29-31; Beresi and Rigby, 1993, pp. 11-20.

Calycocoelia Rigby, 1973, pp. 801-804.

Ethmophyllum Walcott, 1886, p. 75-89; Miller, 1889, pp. 159-160; Lesley, 1889-1890, pp. xxii, 225.

Nevadocoelia Langenheim et al., 1956, p. 2089; Greife and Langenheim, 1963, pp. 567-568.

Petraia Billings, 1859, p. 345.

Somersetella Rigby and Dixon, 1979, pp. 614-615.

Steliella Hinde, 1889b, pp. 395-396; Wilson, 1948, pp. 19-21; de Laubenfels, 1955, E61; Wilson, 1957, pl. 1, fig. 9-11.

Type Species — *Archaeoscyphia minganensis* (Billings), 1859.

Description — Obconical to cylindrical, occasionally branching or digitate, with moderately thick wall and spongocoel extending nearly to base. Surface often marked by variably developed annulations or ridges. Radial canals vertically stacked, upward-arching, peak of arch usually coincides with surface of trab pinnation. Vertical canals often present, concentrated in parietal spiculature near outer surface. Scalariform skeletal net, with 2 to 6 trabs between radial canals, trabs often cored by oxeas. Polyclonid or amphiarborescent dendroclones dominate, depending on species, and connect adjacent trabs horizontally. Dermal layer sometimes well-developed, but much finer than endosome.

Occurrence — Worldwide distribution, with major occurrences in the United States, Canada, Europe, Australia, and South America. The genus ranges from the Ibexian Series, Lower Ordovician, to the Wenlockian Series, Lower Silurian.

Discussion — *Archaeoscyphia* is probably the most famous Paleozoic lithistid, and, as a result, most poorly-preserved, cylindrical Ordovician sponges have been assigned to it. Unfortunately, Billings' original descriptions (1859, 1861a, b, 1865) were based on coarsely recrystallized material and his descriptions were relatively poor. Hinde (1889a) later redescribed the type material in great detail; nevertheless, the skeletal structures remained unclear, and for many years the genus was

recognized on its external morphology alone (de Freitas, 1988). Rigby and Nitecki's (1973) detailed description of *Archaeoscyphia boltoni* finally allowed recognition of specimens using the much more meaningful internal and skeletal structures.

In 1988, de Freitas extensively revised the genus, using new and larger collections of *Archaeoscyphia* and similar genera from the Canadian Arctic. After analyzing the variation in skeletal structure and canal arrangement within and between species in these collections, de Freitas synonymized *Calycocoelia* Bassler, 1927, *Rhopalocoelia* Raymond and Okulitch, 1940, *Somersetella* Rigby and Dixon, 1979, and *Steliella* Hinde, 1889b, with *Archaeoscyphia* Hinde, 1889a. He attempted to show that there was a continuum of variation in morphology, and that separation of species into these different genera was highly subjective.

De Freitas (1988) did an excellent job of demonstrating this continuum of variation among archaeoscyphid species. As he defines it, the genus as a whole exhibits weak to very pronounced annulation, apochete diameters of 0.2 to 1.5 mm, poor to well-developed dermal layer, straight to sinuous radial canals, etc. Species whose features fall within this range he places in *Archaeoscyphia*. Unfortunately, the range of variation de Freitas ascribes to *Archaeoscyphia* is such that, following his approach, practically any obconical or cylindrical anthaspidellid from the Early Paleozoic could be assigned to this genus.

Although recognizing the high degree of variation among archaeoscyphid species, de Freitas (1988) failed to recognize the importance of the ways in which the features vary with respect to each other. As he notes, the primary features of these species are canal diameter, character, and arrangement, the number of parietal trabs, overall form, and the strength of annulation. Taxa for which all or nearly all of these features are close to those of *A. minganensis*, the type species, should be placed in

Archaeoscyphia proper. Those in which several or most of these features are consistently quite different from *A. minganensis* are probably best placed in separate genera, particularly where these features are more extreme than seen in most other archaeoscyphid species. However, a detailed revision of de Freitas' *Archaeoscyphia* is beyond the scope of this work, especially since most of these taxa are from Silurian rocks in Canada. Therefore, despite some reservations and changes, de Freitas' (1988) classification is largely followed here.

Archaeoscyphia is a widespread genus abundant in many Ordovician and Silurian sediments. Specimens attributed to this genus are quite common in Lower Ordovician sponge-algal mounds in Texas and Oklahoma (Toomey and Nitecki, 1979). However, it is relatively uncommon within the Lower and Middle Ordovician rocks of the Great Basin. Representatives are found in the Ibexian age sediments of the Shingle Limestone, and in the Whiterockian rocks of the Antelope Valley Limestone, the Wah Wah Limestone, and the Mazourka Group. Some sponges from the Antelope Valley Limestone and the Mazourka Group were formerly assigned to *Nevadocoelia*, but are here placed within *Archaeoscyphia*.

Because of its variability, there is no one feature that serves to distinguish *Archaeoscyphia* from most other members of the family. Species that should probably be included in this genus generally have a fairly regular scalariform skeleton with at least two trabs separating series of radial canals, possess some polyclonid parietal spicules, some degree of annulation, and a dendroclone to trab diameter ratio of 0.3 to 0.75. The taxon is still in need of revision, however, and until this is done, further delineation of the genus is not possible.

ARCHAEOSCYPHIA BASSLERI, n. sp.

Plate 2, Figures 3-5

Etymology — The species is named for the late Raymond Bassler, who first described the Great Basin sponges.

Description — Cylindrical or tubular shape, with 3.5 to 14.5 mm thick wall and spongocoel extending nearly to base. Surface marked by well-developed annulations, 4 to 6 mm thick, about 1 to 3 mm high, and 6 to 10 mm apart. Diameter between ridges 1.5 to 3.5 cm, increasing upward, height 5.25 cm or more. Slightly serrated spongocoel comprising from 25 to 35% of diameter.

Radial canals vertically stacked with 1.5 mm between them, approximately 0.9 to 1.2 mm in diameter, very straight and unarched. Canals separated horizontally by 0.3 to 0.5 mm, with at least 1 parietal series between. Additional set of horizontal, concentrically arranged canals 0.75 mm in diameter with parietal separations of 0.75 mm and vertical spacing of 0.25 to 0.5 mm that produce a checkered pattern in sagittal sections. Vertical canals irregularly shaped, about 1.0 mm in diameter, and relatively few in number.

Scalariform skeletal net, with 2 trabs between radial canals, trabs 0.05 to 0.1 mm in diameter. Surface of trab pinnation near midpoint. Amphiarborescent dendroclones dominate, but triclonid and quadraclonid dendroclones are common. Endosomal spicules average 0.03 to 0.04 mm in diameter, 0.175 mm in length. No ectosomal layer preserved.

Type Specimen — Holotype 1784TX26; paratype 1784TX27.

Measurements — Dimensions of the holotype are: height = 33.7^{+} mm, diameter = 12.5 mm at base, 22.8 mm at top, wall thickness = 3.5 mm near base, 6.4 mm near top.

Occurrence — Shingle Limestone, southern Egan Range, Nevada. Upper Ibexian Series, Lower Ordovician.

Discussion — This is a very rare species of *Archaeoscyphia* from the Shingle Limestone. Only two specimens could be assigned to this taxon with confidence, yet they are sufficiently different from any other decribed form to warrant the erection of a new species. *A. bassleri* resembles most other members of this genus in having well-developed annulations, a very deep spongocoel, and a very regular scalariform skeletal net. It differs, however, in having particularly large radial canals with an average vertical separation of 1.5 mm. Species such as *A. scalaria*, *A. alternata*, or *A. minganensis* also have very large canals, but the canals are much closer together. *A. annulata*, *A. gislei*, and *A. attenuata* have large vertical separations of the canals, but the canals themselves are much smaller. The very straight and unarched nature of these canals serves to further distinguish *A. bassleri* from other *Archaeoscyphia*, most of which have sinuous or at least slightly arched canals.

ARCHAEOSCYPHIA EGANENSIS, n. sp.

Plate 3, Figures 1-3

Etymology — The specific name derives from the southern Egan Range in eastern Nevada where the species occurs.

Description — Cylindrical, with 4 to 6 mm thick wall; surface marked by more-or-less regular annulations, 2 to 4 mm thick, about 1 to 3 mm high, and 4 mm apart. Diameter between ridges about 2 cm, increasing upward, height greater than 4 cm. Spongocoel irregular near base, becoming rounded as it progresses upward, comprising from 30 to 55% of diameter.

Radial canals vertically stacked with about 0.2 to 0.9 mm between them, approximately 0.6 to 0.8 mm in diameter, angling downward towards spongocoel. Radial canals straight, separated by parietal distance of 0.2 to 0.7 mm, and cored by monaxons 0.15 to 0.2 mm in diameter. Vertical canals scattered through parietal spiculature, 0.25 mm across.

Scalariform skeletal net, with 5 to 7 trabs between radial canals, trabs 0.02 mm in diameter. Surface of trab pinnation about one-third of way through sponge wall from gastric margin, trabs diverge to intersect dermal and gastral surfaces at 30 to 40°. Endosomal spicules 0.01 mm in cross-section, 0.075 mm long. Dermal layer well-developed, 0.35 to 1.0 mm thick, with openings 0.4 to 0.7 mm across. Dermal spicules fine, 0.01 mm in diameter, 0.2 to 0.3 mm long, commonly polyclonid.

Type Specimens — Holotype 1784TX17; paratypes 1784TX18-23.

Measurements — Dimensions of the holotype are: height = 33.4^{+} mm, diameter = 22.2 mm, wall thickness = 4.1 mm at base, 5.9 mm near top.

Occurrence — Shingle Limestone, southern Egan Range, Nevada. Upper Ibexian Series, Lower Ordovician.

Discussion — In its vertically stacked canals, deep spongocoel, and annulations, *A. eganensis* is quite similar to other species of *Archaeoscyphia*. It differs, however, in the fineness of its spiculation: its trabs and dendroclones are only 10 to 50% as thick as those seen in any congeneric species. In addition, or perhaps because of this fine spiculation, *A. eganensis* has from 5 to 7 trabs between adjacent rows of radial canals, more than is found in any other species of *Archaeoscyphia*. The species is uncommon within the Shingle Limestone, but is most abundant within the sponge mound and associated facies.

ARCHAEOSCYPHIA MAZOURKENSIS (Greife and Langenheim), 1963

Plate 3, Figure 10

Synonymy —

Nevadocoelia mazourkensis Greife and Langenheim, 1963, p. 568.

Description — Cylindrical, with 7 to 14 mm thick wall and rounded spongocoel extending nearly to base. Surface marked by strong annulations, 7 to 8 mm thick, about 1 to 4 mm high, and 14 to 15 mm between crests. Diameter between ridges about 2 to 4 cm, height greater than 7.0 cm. Spongocoel comprising about 30% of diameter.

Radial canals vertically stacked with about 0.2 to 0.5 mm between them, approximately 0.2 to 0.5 mm in diameter. Canals separated horizontally by 0.4 to 1.4 mm, and are cored by monaxons 0.4 mm in diameter.

Scalariform skeletal net, with 2 trabs on average between radial canals, trabs 0.11 to 0.13 mm in cross-section. Quadroclonid and triclonid dendroclones present, but amphiarborescent spicules dominate. Endosomal spicules 0.05 to 0.1 mm in diameter. Dermal layer absent.

Type Specimen — Holotype UCMP 10317.

Measurements — Dimensions of the holotype are: height = 64.5^{+} mm, diameter between ridges = 21.8 mm at base, 37.9 mm near top, and wall thickness = 7.0 mm near base, 14.3 mm near top.

Occurrence — Mazourka Group, Mazourka Canyon, Inyo Mountains, California. Ibexian Series to Whiterockian Stage, Lower to Middle Ordovician.

Discussion — Greife and Langenheim (1963) erected the species *Nevadocoelia mazourkensis* on the basis of this specimen, but it is here assigned to *Archaeoscyphia*. Representatives of *Nevadocoelia* are characterized by distinctive

ornamentation, and usually have only 1 trab between adjacent rows of radial canals. Greife and Langenheim's type, however, possesses the annulations typical of *Archaeoscyphia* and usually has 2 rows of trabs between canals. In addition, it has a number of polyclonid dendroclones, whereas the skeletal net of *Nevadocoelia* has very few such spicules.

In its external features, *Archaeoscyphia mazourkensis* is very similar to most other anthaspidellids with annulations and a deep spongocoel. It lacks the vertical parietal canals seen in *A. gislei* but is otherwise indistiguishable from it. The ridges are much less pronounced than in *A. baltica*, but again, the two species are otherwise very similar. However, the greatest similarity is to *Archaeoscyphia annulata* (Rigby). The only apparent differences between the California specimen and those described from the Silurian of Quebec is that the latter species is more obconical and the ridges are larger with respect to the sponge as a whole. However, it must be noted that many of the internal characters could not be seen in Greife and Langenheim's (1963) specimen because it is so coarsely resilicified. As a result, it is probably best to leave *A. mazourkensis* as a separate taxon until better-preserved representatives are found.

ARCHAEOSCYPHIA PANNOSA, n. sp.

Plate 3, Figures 4-7, 9

Etymology — The species name comes from *pannos*, or ragged, and is in reference to the distinctive, serrated margin of the spongocoel.

Description — Obconical to tubular, with 3.5 to 10 mm thick wall and spongocoel extending nearly to base. Surface often marked by well-developed

annulations, 4 to 5 mm thick, about 4 mm high, and 6 to 10 mm apart. Diameter between ridges 0.6 to 3 cm, increasing upward, height 7.0 cm or more. Spongocoel with serrated appearance and comprising from 30 to 50% of diameter; serrations corresponding to apopores, approximately 0.5 mm deep.

Radial canals straight, roughly 0.4 mm in diameter, and penetrate sponge wall horizontally; canals vertically stacked with 1.1 to 1.8 mm between them, separated by parietal distance of about 0.4 mm. Vertical canals from 0.8 to 1.4 mm in diameter, but few in number and concentrated in outer portions of sponge wall.

Scalariform skeletal net with 2 trabs between radial canals; trabs approximately 0.05 mm in diameter. Endosomal spicules 0.02 mm in cross-section. Dermal layer poorly developed.

Type Specimens — Holotype 1784TX28; paratypes 1784TX29-30.

Measurements — Dimensions of the holotype are: height = 70^{+} mm, diameter = 6.7 mm near base, 29.8 mm near top, and average wall thickness = 9.0 mm.

Occurrence — Shingle Limestone, southern Egan Range, Nevada. Upper Ibexian Series of the Lower Ordovician.

Discussion — The margin of the spongocoel in *A. pannosa* is indented where the apochetes flow into it. Because the canals are vertically stacked, this produces longitudinal ribs down the interior of the cloaca. When transversely sectioned, these ribs create a serrated margin, a feature not reported in any other archaeoscyphid.

A. pannosa can also be distinguished from other *Archaeoscyphia* by the large vertical spacing between its radial canals. Most species in this genus have radial canals vertically separated by 0.5 to 1.0 mm, whereas those of *A. pannosa* are

consistently 1 to 2 mm apart. Of similar species with a comparable canal pattern, *A. attenuata* de Freitas has a digitate form and has 2 to 5 trabs between adjacent canals. *A. baltica* van Kempen has a substantially different form than *A. pannosa,* with more irregular annulations and a root-like peduncle. In addition, the former species has a well-developed dermal layer, whereas that in *A. pannosa* is poorly defined. *A. amplia* (Rigby and Chatterton) also differs from the Nevada species in having a well-developed dermal layer. Its lack of annulations, branching form, and relatively small spongocoel also serve to distinguish this species from *Archaeoscyphia pannosa.* The latter species has more closely spaced ridges and finer spiculation than *A, nana* from South America. Finally, *A. pannosa* can be separated from *A. bassleri,* n. sp., with which it is found, by the very large, unarched radial canals in the latter species.

ARCHAEOSCYPHIA PULCHRA (Bassler), 1927

Plate 4, Figures 1, 5; Plate 5, Figures 1, 3

Synonymy —

Nevadocoelia pulchra Bassler, 1927, p. 392; Bassler, 1941, pp. 95-96.

Archaeoscyphia annulata Cullison, 1944, p. 48.

Description — Cylindrical, with 4 to 9 mm thick wall and rounded spongocoel extending nearly to base. Surface marked by very strong annulations, 4.5 to 11 mm thick, about 15 to 25 mm high, and usually 11 to 26 mm apart, generally concave downward. Diameter between ridges 16 to 50 mm, increasing upward, original height 130 mm or more. Spongocoel comprising from 35 to 50% of diameter.

Radial canals 0.5 to 1.2 mm in diameter, vertically stacked, with about 1.0 to 1.3 mm between them. Canals arching upward towards spongocoel, with parietal separation of 0.3 to 1.5 mm. Additional set of horizontal, concentric canals apparently connect the radial canals and form a checkered arrangement of alternating rows. Concentric canals are approximately quadrate, 0.75 mm to 1.25 mm in long dimension perpendicular to sponge wall, 0.5 to 1.0 mm along short axis, with parietal separations of 0.4 mm to 0.6 mm and vertical spacing of 0.25 mm. Vertical canals up to 0.7 mm in diameter, but usually much smaller and very rare.

Scalariform skeletal net, with 2 to 4 trabs between radial canals, trabs 0.05 to 0.1 mm in diameter. Surface of trab pinnation poorly developed, but located near midpoint of sponge wall; trabs remain parallel to gastral margin, but intersect dermal surface at about 15 to 20°. Polyclonid spicules dominate, with amphiarborescent dendroclones also common. Endosomal spicules 0.02 to 0.04 mm in diameter, 0.5 to 0.9 mm in length. Dermal layer variably developed, composed of polyclonid spicules.

Type Specimen — Holotype USNM 79635.

Measurements — Dimensions of the holotype are: height = 129^{+} mm, diameter between ridges = 36.1 mm at base, 49.2 mm at top, and wall thickness between ridges = 6.4 mm at base, 6.7 mm at top.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada, and the Rich Fountain and lower Theodosia Formations, Ozark Uplift, Missouri. The localities in Missouri are from the Ibexian Series of the Lower Ordovician, and the Nevada occurrence is from the Whiterockian Stage, Middle Ordovician.

Discussion — *Archaeoscyphia pulchra* is easily recognized, for it has particularly large radial canals spaced a comparable vertical distance apart. In addition, its extremely pronounced ridges are larger and better developed than those of most archaeoscyphids. Finally, *A. pulchra* has only the slightest degree of trab pinnation. Unlike any other archaeoscyphid, the trabs remain nearly vertical across the entire sponge wall. As a result, they only intersect the dermal surface at a low angle except where the outer surface has bulged out to form the ridges.

A. pulchra is a rather rare species in the Great Basin. Sponges from Mazourka Canyon were tenatively assigned to this species by Langenheim et al. (1956) and Greife and Langenheim (1963), but these belong to a different taxon and are described herein as *Archaeoscyphia* sp. 1. *A. annulata* was described by Cullison (1944) from the Lower Ordovician sediments of the Ozark Uplift, but a reexamination of the type specimens for it and *A. pulchra* show that there are no significant differences between these two species. The ridges are on average more widely spaced and the trabs are slightly thicker in the Missouri specimens, but otherwise the two taxa are identical. The greater spacing of the ridges can be easily attributed to phenotypic variation, particularly considering the variability of ridge development in other species of *Archaeoscyphia*. The greater trab thickness is probably a result of the resilicification of the Missouri specimen. In the absence of any consistent, significant difference, *A. annulata* Cullison is herein synonymized with *A. pulchra* (Bassler). This also resolves a potential nomenclatural conflict with *Calycocoelia annulata* Rigby, which should probably be reassigned to *Archaeoscyphia*.

Toomey and Nitecki (1979) identified *A. annulata* as one of the major constituents of Lower Ordovician reef mounds in Texas and Oklahoma, and Sando

(1957) described similar specimens from the Rockdale Run Formation in Maryland. However, the specimens illustrated by these authors do not resemble *A. pulchra*, and almost certainly belong to another species.

ARCHAEOSCYPHIA ROSSI, n. sp.

Plate 2, Figures 6-9

Etymology — The species name is after Reuben J. Ross, Jr., who has devoted much of his career to the geology of the Great Basin.

Description — Tubular or cylindrical, with 2 to 4 mm thick wall and spongocoel extending nearly to base. Surface marked by regular annulations, 2 to 4 mm thick, 1 to 2 mm high, and 4 mm apart. Diameter between ridges 0.5 to 1.8 cm, increasing slightly upward, height 6.0 cm or more. Rounded spongocoel comprising about 30% of diameter.

Radial canals vertically stacked with 0.6 to 0.8 mm between them, approximately 0.3 mm in diameter; canals straight and nearly horizontal, slightly arched near midpoint, separated horizontally by 0.3 mm. Vertical canals rare, 0.4 mm across.

Scalariform skeletal net, with 2 to 4 trabs between radial canals, trabs 0.03 to 0.05 mm in diameter. Surface of trab pinnation about one-third to one-half of way through sponge wall from gastral margin, trabs parallel to gastral surface, diverge to intersect dermal surface at 45 to 55°. Polyclonid dendroclones dominate, but amphiarborescent ones also common. Endosomal spicules 0.01 to 0.02 mm in cross-section, 0.15 to 0.2 mm in length, cladome rays 0.03 in diameter. Dermal layer well-developed, ectosomal spicules 0.025 mm in diameter, 0.25 mm long.

Type Specimens — Holotype 1784TX36; paratypes 1783TX1, 1784TX37.

Measurements — Dimensions of the holotype are: height = 27.4^{+} mm, diameter = 18.2 mm in middle, and average wall thickness = 4.2 mm.

Occurrence — Shingle Limestone, southern Egan Range, Nevada, and Wah Wah Limestone, section H, Ibex area, Utah. The former locality is in the upper Ibexian Series of the Lower Ordovician, the latter in the Whiterockian Stage of the Middle Ordovician. Both units consist of interbedded limestones and shales.

Discussion — This small anthaspidellid occurs in association with the sponge reef mounds in both the Shingle and the Wah Wah Limestones. *A. rossi* is distinguished from other species primarily by its fine spiculature, relatively small, closely-spaced annulations, and thin walls. Taken together, these features warrant the erection of a new species.

A. rossi is associated with the sponge mounds in both the Shingle and the Wah Wah Limestones. It was probably a specialist adapted to the clear water and hard substrates associated with these buildups.

ARCHAEOSCYPHIA sp. 1 (Greife and Langenheim), 1963

Plate 3, Figure 8

Synonymy —

Nevadocoelia pulchra(?) Langenheim et al., 1956, p. 2089.

Nevadocoelia cf. *N. pulchra* Greife and Langenheim, 1963, p. 567.

Description — Cylindrical, with surface marked by very strong annulations, 1.5 mm thick, about 6 mm high, and 10 to 12 mm apart. Diameter between ridges about 2 cm, height greater than 4.5 cm. Radial canals approximately 0.2 to 0.3 mm in

diameter, but spacing obscured by recrystallization and silicification. Skeletal net scalariform, but other details destroyed.

Studied Specimen — UCMP 10316.

Measurements — Dimensions of the specimen are: height = 18.3^{+} mm, maximum diameter = 18.6 mm.

Occurrence — Mazourka Group, Mazourka Canyon, Inyo Mountains, California. Ibexian Series to Whiterockian Stage, Lower to Middle Ordovician.

Discussion — This species has only been identified from a single, coarsely silicified specimen from Mazourka Canyon, and is thus very poorly defined. Langenheim et al. (1956) and Greife and Langenheim (1963) assigned this sponge to *Nevadocoelia pulchra* because of its "flange-like ... transverse ridges, cloaca penetrating throughout, obconical or oval shape, and prosopores in closely spaced parallel rows" (Greife and Langenheim, 1963, p. 567). However, these features are characteristic of archaeoscyphids in general, and the ridges are much smaller and more widely spaced than those of *N. pulchra*. The specimen is buried in the rock, and the spongocoel cannot be seen. The radial canals of this specimen are also much smaller and closer together than in Bassler's species. Unfortunately, the specimen is too grossly silicified for any more detailed analysis, and is best left as an indeterminate species.

Genus CALYCOCOELIABassler, 1927

Synonymy —

Calycocoelia Bassler, 1927, p. 392; Bassler, 1941, pp. 96-97; de Laubenfels, 1955, p. E54; Langenheim et al., 1956, p. 2089; Greife and Langenheim, 1963, p. 569; Rigby, 1967b, pp. 767-769; Rigby, 1973, p. 804; Rigby and Chidsey, 1976, pp. 3-8; van Kempen, 1978, pp. 318-321; van Kempen, 1981, pp. 156-172; Beresi and Rigby, 1993, pp. 20-23.

probably *Rhopalocoelia* Raymond and Okulitch, 1940, pp. 210-212; de Laubenfels, 1955, p. E53; Rigby, 1967b, p. 769; Beresi and Rigby, pp. 23-29.

Type Species —*Calycocoelia typicalis* Bassler, 1927.

Description — Obconical, tubular, or pedunculate, with moderately thick wall and rounded or slightly irregular spongocoel extending nearly to base. Surface usually smooth, very rarely marked by poorly-developed, irregular annulations. Radial canals vertically stacked, upward-arching. Vertical canals sinuous, concentrated in parietal spiculature near outer surface. Scalariform skeletal net, with 1 to 3 trabs between radial canals. Trabs separated by 0.1 to 0.5 mm, and cored by oxeas with diameters of 0.07 mm. Amphiarborescent dendroclones dominate, very few polyclonid spicules; dendroclones attach adjacent trabs horizontally. Dermal layer sporadically developed, but much finer than endosome.

Occurrence — United States, Canada, South America and the Baltic area. Ibexian Series, Lower Ordovician, to Ludlow Series, Upper Silurian.

Discussion — Bassler erected the genus *Calycocoelia* for the unornamented archaeoscyphid-like sponges from the Antelope Valley Limestone at Ikes Canyon. In part, this resulted from uncertainty regarding the internal and skeletal structure of *Archaeoscyphia*. In his revision and redescription of the latter genus, de Freitas (1988) synonymized *Calycocoelia* with *Archaeoscyphia*. Although de Freitas' (1988)

classification is largely followed in this work, the 136 specimens of *Calycocoelia typicalis* collected in this study support the separation of at least this species from *Archaeoscyphia*. Although some species that probably should be placed in *Archaeoscyphia* lack annulation, most possess weak to pronounced ridges. However, very few of the specimens from Nevada have even poorly developed annulations. In addition, *C. typicalis* has only 1 to 2 parietal trabs, generally fewer than most other species de Freitas (1988) placed in *Archaeoscyphia*. Finally, those parietal series that do occur in *C. typicalis* are overwhelmingly dominated by amphiarborescent dendroclones. In contrast, the parietal series of many species of *Archaeoscyphia* have large percentages of triclonid and quadraclonid dendroclones (de Freitas, 1988). Finally, the trabs of *C. typicalis* are exceptionally thick with respect to the dendroclone diameters. Thus, the ratio between dendroclone and trab diameters is only about 0.25, somewhat less than that for most archaeoscyphids (Table 5). This relatively low DTD ratio is also found in *C. solenos* and *C. micropora*. In having weak annulation, 2 trabs between the radial canals, a fair number of triclonid spicules, and a DTD ratio of about 0.46, however, *C. annulata* Rigby shares more features with *Archaeoscyphia* than *Calycocoelia* and is therefore reassigned to the former genus. Because *C. typicalis*, *C. solenos*, and *C. micropora* and are all more similar to each other than to any other archaeoscyphid, *Calycocoelia* is here maintained as a separate and distinct genus with *C. typicalis* as the type species.

Calycocoelia is distinguished from *Nevadocoelia* in having a somewhat more irregular skeleton and in lacking any surface ornamentation other than the most rudimentary annulations. In addition, the upper surface of *Calycocoelia* is flat or slightly convex between the dermal surface and the spongocoel, whereas that of

Table 5 — Trab and minimum dendroclone diameters for species of *Archaeoscyphia* and related genera, and the ratio between them. Note that species of *Calycocoelia* and *Somersetella* tend to have lower DTD ratios than most species assigned to *Archaeoscyphia*. All values are in millimeters. Data compiled from Rigby, 1967b; Rigby and Nitecki, 1973; de Freitas, 1988; Rigby and Chatterton, 1989; and Beresi and Rigby, 1993.

SPECIES	Trab Diameter	Dendroclone Diameter	DTD RATIO
Archaeoscyphia alternata	0.11	0.06	0.55
A. annulata (Rigby)	0.065	0.03	0.46
A. aulocopiformis	0.13	0.10	0.77
A. bassleri	0.075	0.035	0.47
A. boltoni	0.25	0.035	0.14
A. eganensis	0.02	0.01	0.50
A. gislei	0.12	0.04	0.33
A. mazourkensis	0.065	0.03	0.46
A. minganensis	0.19	0.07	0.37
A. pannosa	0.05	0.02	0.40
A. pulchra	0.075	0.03	0.40
A. rossi	0.04	0.015	0.38
A. scalaria	0.20	0.065	0.32
Calycocoelia micropora	0.07	0.02	0.29
C, perforata	0.19	0.13	0.68
C. solenos	0.12	0.025	0.22
C. typicalis	0.20	0.05	0.25
Nevadocoelia grandis	0.09	0.04	0.44
N. traini	0.05	0.035	0.70
N. wistae	0.10	0.03	0.33
Rhopalocoelia clarki	0.19	0.05	0.26
R. rama	0.10	0.03	0.33
Somersetella amplia	0.14	0.035	0.26
S. conicula	0.16	0.045	0.28
S. digitata	0.12	0.018	0.15

Nevadocoelia usually has a slight lip around the osculum. The presence of a deep spongocoel, regular canal arrangement, and well-organized spiculation also distinguish *Calycocoelia* from superficially similar taxa such as *Streptosolen*. However, *Calycocoelia* is very similar to *Rhopalocoelia*. Both are smooth, cylindrical or club-shaped sponges with remarkably similar canal arrangements and spiculation. Beresi and Rigby (1993) have recently redescribed the type species of *Rhopalocoelia, R. clarkii,* from the Ordovician San Juan Formation in Argentina and noted that the genus may turn out to be a synonym of *Calycocoelia*. Comparing

their description with that of *C. typicalis* here reveals that there are almost no differences between the two species. Unfortunately, the type specimens of *Rhopalocoelia* were not available for this study, so a synonymization of these taxa here would not be appropriate. If *C. typicalis* and *R. clarkii* are eventually synonymized, then the name *Calycocoelia* would have priority. Other species currently included in *Rhopalocoelia* such as *R. regularis* or *R. rama*, have a branching habit (Beresi and Rigby, 1993) or large parietal gaps (Rigby, 1967b), and should probably be placed in another genus.

Within the Great Basin, *Calycocoelia* is represented by *C. typicalis*. It is found within the Whiterockian sponge beds of the Antelope Valley Limestone at Ikes Canyon and the Mazourka Group in Mazourka Canyon, California. At Ikes Canyon, *Calycocoelia* is one of the most common sponges. Representatives of the genus have also been found in Silurian rocks in Canada (Rigby, 1967b; Rigby and Chatterton, 1989) and the Ibexian of Argentina (Beresi and Rigby, 1993). *Calycocoelia* has also been reported from a glacial erratic in Holland by van Kempen (1978); he believed it originated from Ordovician sediments in the Baltic area, but determining a more precise age and location was not possible.

CALYCOCOELIA TYPICALIS Bassler, 1927

Plate 4, Figures 2-4; Plate 5, Figures 2, 4; Plate 6, Figure 1

Synonymy —

Calycocoelia typicalis Bassler, 1927, p. 392; Bassler, 1941, pp. 96-97; Langenheim et al., 1956, p. 2089; Greife and Langenheim, 1963, p. 569; Rigby and Chidsey, 1976, pp. 3-8.

Calycocoelia inyoensis Greife and Langenheim, 1963, p. 569.

not *Calycocoelia* cf. *C. typicalis* van Kempen, 1978, pp. 318-321.

Description — Obconical, tubular, or pedunculate, arising from a broad base, with 4 to 22 mm thick wall and spongocoel extending nearly to base. Surface usually smooth, very rarely marked by poorly-developed, irregular annulations. Diameter about 1.5 to 5 cm, increasing upward, height usually between 7.5 and 10 cm, but sometimes as great as 21 cm or more. Spongocoel rounded to slightly irregular, sometimes off-center, widening upward and comprising from 20 to 60% of diameter.

Radial canals vertically stacked with 0.3 to 2.0 mm between them, but usually only separated by 0.5 to 1.0 mm. Parietal distance between radial canals of 0.1 to 2.1 mm, but typically only 0.2 to 1.0 mm. Radial canals 0.4 to 1.2 mm in diameter, slightly upward-arching, peak of arch usually near midpoint of sponge wall. Larger radial canals often cored by monaxons typically 0.4 to 0.5 mm in diameter. Vertical parietal canals sinuous, 0.3 to 0.4 mm across, concentrated in parietal spiculature near outer surface.

Scalariform skeletal net, with 1 to 3 trabs between radial canals, trabs separated by 0.1 to 0.6 mm, 0.13 to 0.2 mm in diameter, and cored by 2 to 5 oxeas which are 0.025 mm across. Surface of trab pinnation along gastral margin to one-third of way through sponge wall, trabs diverge to intersect dermal surface at 30 to 45°. Amphiarborescent dendroclones overwhelmingly dominate. Endosomal spicules 0.05 mm in diameter, 0.2 to 0.6 mm in length, with cladome rays 0.05 mm across.

Dermal layer sporadically developed, up to 1 mm thick, but much finer than endosome, with minute openings 0.2 mm across.

Type Specimen — Holotype USNM 79637.

Measurements — Dimensions of the holotype are: height = 92^{+} mm, diameter = 10.8 mm at base, 21.3 mm at top, wall thickness = 14.8 mm at base, 23.5 mm at top.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada, the Mazourka Group, Mazourka Canyon, Inyo Mountains, California, and the Fort Peña Formation, Marathon area, Texas. The Mazourka Group ranges in age from the Ibexian Series to Whiterockian Stage, Lower to Middle Ordovician. The other two localities are Whiterockian in age.

Discussion —*Calycocoelia typicalis* is the most common species of this genus and is abundant where it occurs. Although its skeletal architecture is fairly constant, *C. typicalis* exhibits a wide range of variability in shape. Some specimens, such as the holotype, are extremely obconical and squat, whereas others are very slender and pedunculate. A complete continuum of intermediate morphologies between these extremes can be found. The shape and relative size of the spongocoel can likewise vary between individuals, although the diameter of the spongocoel consistently increases upward, matching the upward expansion of the sponge as a whole.

Bassler's original descriptions (1927, 1941), based on his small collections, did not recognize this variability and stated that the sponge was "cup-shaped" or "goblet-shaped", i.e., obconical. Given this description, Greife and Langenheim (1963) erected the species *C. inyoensis* for specimens of *Calycocoelia* from Mazourka Canyon that were instead cylindrical and had a somewhat irregularly-shaped cloaca. With the collection of over one hundred additional topotypes from Ikes Canyon, it is obvious that the morphology of *C. inyoensis* falls well within the range of variation of *C. typicalis*. Greife and Langenheim's (1963) holotype for *C. inyoensis* is very coarsely silicified, preventing any detailed study of the spiculature. The

structures that are preserved are indistinguishable from those of *C. typicalis*. For these reasons, *C. inyoensis* is synonymized with *C. typicalis*.

Another feature common to most specimens of *C. typicalis*, and, in fact, to many other anthaspidellid taxa, is the presence of large monaxons running down the approximate middle of the radial canals. Because the canals are often sinuous, these monaxons frequently intersect the canal wall, but nevertheless parallel the canal and occupy its approximate center. In *C. typicalis*, these spicules are usually 0.4 to 0.5 mm in diameter, much larger than either typical endosomal spicules or even trabs. When traced through the sponge body, these monaxons originate near the surface of trab pinnation and continue outward to the dermal surface. The coring of radial canals is a highly variable feature in *C. typicalis* and the other species in which it is found, and is not even consistently developed within an individual. The presence of such monaxons is therefore useless as a taxonomic character.

The presence of these large monaxons in the radial canals is probably a defensive strategy adopted by the sponge to minimize clogging of the prosopores by sediment and/or prevent the entry of parasitic organisms into the sponge body. Modern demosponges are plagued by parasites and have adopted a wide range of strategies to deal with them (Sarà and Vacelet, 1973). Paleozoic lithistids had similar problems, as the infestation of numerous Ikes Canyon sponges by a parasitic brachiopod amply demonstrates (Johns, 1990, 1993). By having the centers of the prosopores occupied by these monaxons, the cross-sectional area of the canal is reduced by 25%, while the effective canal diameter is reduced by twice as much. Thus, the sponge was able to substantially reduce the overall diameter of the canal while reducing the cross-sectional area by a much smaller amount (Figure 9). This would have prevented clogging by at least the larger sand grains, and would have

kept out all but the smallest parasites. In all of the sponges examined, the ends of the monaxons are worn off, indicating that they once extended out beyond the dermal surface of the sponge. This would have assisted in their presumed function and given the sponge a prickly surface.

Modern sponges reproduce both sexually and asexually, and Paleozoic lithistids presumably did the same. One specimen of *C. typicalis* from Ikes Canyon provides one of the best examples of asexual reproduction preserved in the fossil record (Plate 6, Figure 1). This specimen consists of two complete but fused individuals, the smaller apparently having budded off the larger, but remaining attached. However, the fact that only one such specimen was recovered among the several hundred collected suggests this was probably a rather rare means of reproduction.

In lacking annulations, having only 1 trab separating radial canals, possessing a low DTD ratio, and in the overwhelming dominance of amphiarborescent dendroclones, *C. typicalis* can be distinguished from most species of *Archaeoscyphia*. Other taxa which have been ascribed to *Calycocoelia* include *C. annulata* Rigby, *C. solenos* Rigby, *C. micropora* Rigby and Chatterton, *C. perforata* Beresi and Rigby, and *C. murella*, n. sp.. Because of its annulation, the number of trabs between radial canals, and its DTD ratio, *C. annulata* is herein assigned to *Archaeoscyphia*. It is thus quite unlike *C. typicalis*. *C. perforata* has exceptionally large pores and a very high DTD ratio and may belong to a new genus. Unfortunately, it is a rare sponge and is known only from fragments. Until better material can be found it is best left in *Calycocoelia*. Both *C. micropora* and *C. solenos* fit the definition of *Calycocoelia* as defined here, but differ from the Nevada specimens in their finer and more irregular spiculation. In addition, the spiculation changed from very regular to rather irregular in *C. micropora* as the sponge grew, an unusual feature not seen in

C. typicalis. *C. murella*, also from the Great Basin, is quite similar to *C. typicalis*, but the latter species has coarser spiculation, larger canals, and the spongocoel is usually not as great a percentage of the sponge's diameter.

A European specimen of *C. typicalis*. was described by van Kempen (1978), and, in gross morphology, it is very similar to the Nevada species. However, the radial canals are smaller than those in *C. typicalis* and slope downward, unlike those in the type species which arch upward. Given the difference in these important characters, as well as the great geographic separation, van Kempen's specimen is probably best placed in a distinct species.

C. typicalis is most similar to *Rhopalocoelia clarkii*, as mentioned above. The trabs are slightly coarser, the spicules slightly longer, and there are somewhat more triclonid spicules in the endosome of *R. clarkii*. The most significant apparent difference between the two taxa is that the trabs intersect the gastral and dermal surfaces at about 10 to 20° in *R. clarkii*, and at about 30 to 45° in *C. typicalis*. The two species are most likely synonyms, but officially synonymizing the two genera is best done after examination of the type specimens of *Rhopalocoelia*, which were not available for this study.

CALYCOCOELIA MURELLA, n. sp.

Plate 6, Figures 2-4

Etymology — The species name is Latin for "little wall", referring to the relatively thin walls of this taxon.

Description — Obconical or pedunculate with thin stem, with thin, 2.5 to 4 mm thick wall and rounded spongocoel extending nearly to base, comprising 50 to 60%

of diameter. Surface smooth, without annulations. Diameter ranging from 8.0 to 20.0 mm, increasing upward, height greater than 40 mm.

Straight radial canals 0.25 to 0.5 mm across, vertically stacked with 0.4 to 0.9 mm between them, parietal separation of 0.2 to 0.7 mm. Radial canals upward-arching, peak of arch usually coincides with surface of trab pinnation. Vertical canals 0.25 mm in diameter, concentrated near midpoint of sponge wall. Set of minor canals 0.03 to 0.05 mm in diameter parallel to trabs.

Scalariform skeletal net, with 1 to 2 trabs between radial canals. Trabs lack any sign of coring monaxons. Surface of trab pinnation one-third to halfway through sponge wall from gastric margin, trabs intersect dermal and gastral surface at 45° to 60°. Amphiarborescent dendroclones dominate, but triclonid spicules also common. Dermal layer up to 0.15 mm thick with minute openings 0.1 mm across. Ectosomal spicules 0.01 to 0.03 mm in diameter.

Type Specimens — Holotype 1784TX44; paratypes 1784TX45-46.

Measurements — Dimensions of the holotype are: height = 3.91^{+} mm, diameter = 15.6 mm at base, diameter = 19.7 mm at top, and wall thickness = 2.5 mm near top.

Occurrence — Shingle Limestone, southern Egan Range, Nevada. Upper Ibexian Series, Lower Ordovician.

Discussion —*Calycocoelia murella* is rare and only three specimens could be definitively assigned to this species. All were closely associated with the reef mounds themselves, suggesting that this species preferred attaching to the hard mound surface.

C. murella differs form its congeneric species in having finer spiculation and smaller radial canals. The Nevada species also has a very regular skeletal net, much

more regular than that found in either *C. solenos* or *C. micropora*. However, the most obvious difference between *C. murella* and the other taxa assigned to *Calycocoelia* is the relatively large spongocoel and thin walls found in the Shingle Limestone species. Although a few specimens of *C. typicalis* have very large spongocoels and thin walls, none are as small and delicate as *C. murella*.

Representatives of this species are also similar to *Rhopalocoelia clarkii*, which may itself be a synonym of *C. typicalis*. However, *C. murella* has finer spicules and smaller canals than *R. clarkii*, and its spongocoel is still relatively larger than that seen in the latter species.

COLINISPONGIA, n. gen.

Type Species — *Colinispongia regularis*, n. sp.

Etymology — The genus is named after Colin Sumrall, who discovered the holotype.

Description — Palmate shape, relatively thin wall; surface smooth or slightly undulose. Straight radial canals vertically stacked and often discontinuous with 1 to 3 trabs between radial canals. Apopores quadrate and remarkably regular, producing a checkered pattern. Scalariform skeletal net dominated by amphiarborescent dendroclones. Surface of trab pinnation from one-third to one-half of way through sponge wall from gastral surface. Ectosomal layers well-developed and completely covering external surfaces, but open and thin.

Occurrence — Western United States. Ibexian Series, Lower Ordovician.

Discussion — Although a palmate shape is found in several anthaspidellid genera, these specimens from the Great Basin are significantly different from every previously described taxon in having a very thin but well-developed ectosome and in the astonishing regular spacing of the large apopores. *Colinispongia* could easily be mistaken for a coral, but the spicular nature of the skeleton as seen under high magnification shows that it is clearly a sponge.

Colinispongia lacks the characteristic features of other palmate genera in the order. For example, it exhibits neither the clustered apopores of *Anthaspidella* or the regular ridges and fine spiculature of *Rugocoelia*. It does not have the irregular spiculature or longitudinal excurrent canals of *Hesperocoelia* or *Pseudopalmatohindia*. It also lacks the regular vertical canals and digitate protrusions of *Cockbainia*. *Colinispongia* is most similar to *Patellispongia* or *Psarodictyum*, but the very regular apopores are unlike those seen either of the latter genera. In addition, the structure of the thin ectosome is substantially different from that of *Patellispongia*, and its consistent development serves to distinguish it from *Psarodictyum*, which has no ectosome.

COLINISPONGIA REGULARIS, n. sp.

Plate 11, Figures 1, 4

Etymology — The species name is in reference to the regularity in size and spacing of the apopores.

Description — Palmate shape, originally 20 cm or more in diameter, but often found as broken fragments. Wall thickness ranging from 1.5 to 8 mm. Surface relatively smooth, slightly undulose.

Radial canals vertically stacked and very regular, with 1.0 to 1.7 mm vertical distance between, usually only separated by 1 or 2 intraserial dendroclones. Canals approximately 0.3 to 0.7 mm in diameter and nearly straight, slightly arched, often discontinuous, usually cored by monaxons 0.1 to 0.25 mm in diameter. Canal openings spaced 0.6 to 1.4 mm apart horizontally. Vertical canals, 1.4 mm across, rare and scattered through endosomal spiculature.

Scalariform skeletal net with 1 to 3 trabs between radial canals, trabs 0.075 to 0.1 mm across, cored by oxeas 0.01 mm in diameter. Surface of trab pinnation from one-third to one-half of way through sponge wall from gastral surface. Divergent trabs intersect gastral surface at approximately 35° and intersect the dermal surface between 60 and 90°. Amphiarborescent dendroclones dominate almost exclusively in parietal spiculature. Endosomal spicules 0.025 mm in diameter, approximately 0.275 to 0.5 mm long, cladome rays 0.02 to 0.05 mm in diameter.

Ectosomal layers well-developed, 0.2 to 0.3 mm thick on both sides, with both amphiarborescent and triclonid spicules 0.025 mm in diameter and about 0.3 mm in length that join to form nodes 0.15 to 0.25 mm across. Ectosome completely covers external surfaces, but open and thin, with openings in skeletal net 0.2 to 0.5 mm across.

Type Specimen — Holotype 1787TX1; paratypes 1784TX10, 1785TX1-3.

Measurements — Dimensions of the holotype are: diameter = 129^{+} mm, and average wall thickness = 3.8 mm.

Occurrence — Shingle Limestone, southern Egan Range, Nevada; Fillmore Formation, Ibex area, Utah. Both localities are from the Ibexian Series, Lower Ordovician.

Discussion — The thin, nodose character of the ectosome and large, regularly spaced apopores distinguish this species from any other taxon in *Patellispongia* or other palmate taxa and serve to define the genus. *Colinispongia regularis* is found not in the sponge mounds of the Shingle Limestone, but in the older *Calathium*/sponge beds at Sunnyside and in the Fillmore Formation. It is more common in these older units, and may have been more tolerant of the somewhat muddier waters and softer substrates associated with these units. However, one specimen was found in float with a matrix similar to that seen in the sponge mound horizon, suggesting that this species may have occurred in this facies as well.

Genus EGANIA, n. gen.

Type Species — *Egania typicalis*, n. sp.

Etymology — The name is in reference to the Egan Range, where the type specimens were found.

Description — Obconical to massive, usually with hemispherically rounded upper surface, often lacking even a shallow spongocoel. External surface unornamented and smooth. Sponge body penetrated by several large, vertical excurrent canals which are loosely clustered around axis. Radial canals subhorizontal, fairly straight, occurring in more-or-less vertical series. Mostly scalariform skeletal net, with surface of trab pinnation midway between dermal surface and axis. Polyclonid spicules dominate, often not in horizontal orientation, amphiarborescent dendroclones also common. Dermal layer variably developed.

Occurrence — Western United States. Ibexian Series, Lower Ordovician.

Discussion — Many orchoclad lithistids have a tubular to massive shape pierced by large, excurrent canals. In nearly all of these, however, any such axial apochetes are tightly clustered in the center of the sponge and frequently exit into a spongocoel. Some of the small, tubular sponges from the Shingle Limestone in eastern Nevada have an unusual architecture in which these vertical canals are only loosely clustered about the axis, with many of the vertical apochetes scattered throughout the body of the sponge.

There are three described genera that have a large proportion of the vertical excurrent canals scattered through the sponge wall rather than just axially clustered, and these are *Eospongia* Billings, *Canningella* Rigby, and *Fistulosospongia* Rigby. The sponges from the Egan Range, however, do not share the major characters of any of them. Not only does it have a fairly irregular spiculature, but *Eospongia* lacks any ordered radial canal structures. *Canningella* is unique among the anthaspidellids in having alternating bands of dense and open skeletal material (Rigby, 1986b). *Fistulosospongia* has well-developed radial canals and possesses a scalariform skeleton. but the vertical apochetes are completely scattered throughout the sponge body with no axial clustering at all. For these reasons, a new genus, *Egania*, has been erected to hold the sponges from the Shingle Limestone.

EGANIA TYPICALIS, n. sp.

Plate 14, Figures 2-3, 7; Plate 15, Figures 1-4

Etymology — The species name refers to the fact that this is the type species of the genus.

Description — Cylindrical to obconical shape, upper surface hemispherical and convex, no spongocoel present. As much as 65 mm or more in height; diameter at base from 2.5 mm in juveniles to 23.4 mm in larger specimens; diameter at top from 6.5 to 26.0 mm. Surface relatively smooth, with only poorly developed, irregularly spaced ridges less than 1 mm in any dimension.

Sponge body penetrated by 1 or more vertical canals which are 1.2 to 2.7 mm in diameter, increasing upward in size. Some vertical canals are clustered around axis, many others are scattered through sponge wall; depending on closeness of axial canals, shape may be prismatic or rounded. Radial canals ovoid, elongated parallel to axis, vertically stacked, with 0.2 to 0.4 mm between them in both vertical and horizontal directions. Radial canals approximately 0.2 to 0.6 mm in diameter, separated by 1 to 3 trabs, and angle upward at 45° from dermal surface; canals disappear into confused spiculature about midway towards axis of sponge.

Scalariform skeletal net with most dendroclones attaching to adjacent trabs; many dendroclones are not horizontal, producing some irregularities in spiculature. Trabs 0.03 to 0.08 mm in diameter and cored by 1 or 2 oxeas 0.01 to 0.025 mm across. Surface of trab pinnation midway between dermal surface and axis of sponge. Trabs diverge to intersect dermal surface at approximately 70 to 90°. Triclonid and quadraclonid spicules dominate, but amphiarborescent dendroclones common. Endosomal spicules, 0.02 to 0.03 mm in diameter and 0.3 to 0.5 mm long, cladome rays 0.01 to 0.03 mm across.

Type Specimens — Holotype 1784TX38; paratypes 1784TX39-43.

Measurements — Dimensions of the holotype are: height = 64.0^{+} mm, diameter = 3.5 mm at base, 6.7 mm at top.

Occurrence — Shingle Limestone, southern Egan Range, eastern Nevada. Upper Ibexian Series, Lower Ordovician.

Discussion — In lacking a spongocoel but having a fairly regular spiculature and radial canal arrangement, *Egania typicalis* is readily distinguished from any other sponge with which it occurs. In some specimens, the excurrent canals may be tightly clustered about the axis and have a prismatic shape like that seen in *Streptosolen* or juveniles of other species such as *Calycocoelia* or *Nevadocoelia*. However, the straight and regular radial canals and anthaspidellid skeleton of *E. typicalis* are quite unlike those of *Streptosolen* or any other member of its family. On the other hand, the scattering of many large vertical canals through the body of the sponge is also very different from the pattern seen in the juveniles of any other anthaspidellid. The small size of the trabs in *E, typicalis* is also unusual and helps to further distinguish this taxon.

This species was limited to the sponge mounds and associated facies, and is a rare species even in these units. This suggests that it was only able to survive in the clear, sunlit waters in which the reef mounds developed, and, unlike some of the other sponges, could not tolerate the muddier water or softer substrates associated with the other beds within the Shingle Limestone.

Genus NEVADOCOELIA Bassler, 1927

Synonymy —

Nevadocoelia Bassler, 1927, p. 392; Bassler, 1941, pp. 94-96; de Laubenfels, 1955, p. E54.

Type Species — *Nevadocoelia wistae* Bassler, 1927.

Description — Obconical, tubular, or pedunculate, with broad base and rounded spongocoel extending nearly to base, often with slightly raised lip around osculum. Some specimens reach very large sizes. Surface smooth or marked by fine anastomosing ridges or nodes, but ornamentation limited to sides of sponge. Radial canals vertically stacked and straight, occasionally arched. Vertical canals rare, concentrated in parietal spiculature near outer surface. Scalariform skeletal net, with 1 to 3 trabs between radial canals, trabs separated by 0.1 to 0.5 mm and cored by oxeas. Amphiarborescent dendroclones dominate. Dermal layer sporadically developed, but finer than endosome.

Occurrence — Western United States. Whiterockian Stage, Middle Ordovician.

Discussion — In his descriptions of the Ikes Canyon sponge fauna, Bassler placed the obconical archaeoscyphids without ornamentation in the genus *Calycocoelia*, and those with a more cylindrical shape and some form of surface ornament in *Nevadocoelia*. Much later, de Freitas (1988) synonymized *Calycocoelia* with *Archaeoscyphia*; not having any type material, he did not attempt any revision of *Nevadocoelia* With the much larger collections available in this study, *Calycocoelia* has been redefined and left as a distinct genus. Although *N. pulchra* Bassler and *N. mazourkensis* Greife and Langenheim should be included in *Archaeoscyphia*, the other species of *Nevadocoelia*, including the genotype, comprise a separate genus.

Nevadocoelia is readily distinguished from all other obconical to cylindrical anthaspidellids by its distinctive ornamentation. Whereas most species of *Archaeoscyphia* have weak to well-developed annulations, most specimens of *Nevadocoelia* have fine anastomosing ridges or pronounced nodes (Plate 6, Figures

8-9; Plate 7, Figures 2, 5), allowing identification of even very small fragments. The exception is *N. grandis*, the surface of which is sometimes smooth. Even in this species, however, there are typically widely spaced fine ridges or scattered nodes (Plate 7, Figure 1). The ornamentation in *Nevadocoelia* also contrasts with that of *Calycocoelia*, the surface of which is either smooth or very weakly annulate. In addition, most specimens of *Nevadocoelia* possess an oscular lip, a feature not seen in either *Calycocoelia* or *Archaeoscyphia*.

Of greater phylogenetic significance, the canal disposition and skeletal architecture possess features not found together in other genera. Like *Calycocoelia* and unlike *Archaeoscyphia*, *Nevadocoelia* has very few trabs between radial canals, and the parietal spiculature that is present is dominated by amphiarborescent dendroclones. However, the radial canals in *Nevadocoelia* are often straight and angle upward or even horizontally into the spongocoel. The arched canals seen in most other archaeoscyphids are found in some specimens of *N. traini*, but, together with other features, there is little likelihood of confusion.

Nevadocoelia has a relatively restricted geographic and stratigraphic range, and, to date, has only been found within the Whiterockian age sediments of the Great Basin. Within these rocks, though, it is common and is a major component of the fossil assemblages.

NEVADOCOELIA WISTAE Bassler, 1927

Plate 6, Figures 6-7; Plate 7, Figures 2, 4-6

Synonymy —

Nevadocoelia wistae Bassler, 1927, p. 392; Bassler, 1941, p. 94-95.

Description — Cylindrical, often pedunculate, with rounded spongocoel extending nearly to base. Surface ornamented by low, loosely anastomosing ridges, 0.7 mm high, 0.7 to 1.3 mm across and separated by no more than 3.5 mm; ridge size and spacing remaining nearly constant as sponge grows. Diameter usually between 1.5 and 3 cm, increasing upward, with height up to 11 cm. Osculum with pronounced lip, spongocoel widening upward and comprising from 25 to 45% of total diameter.

Radial canals typically 0.4 to 0.8 mm in diameter and vertically stacked but irregularly spaced, with 0.1 to 2.2 mm between them, parietal separation of 0.2 to 0.4 mm. Radial canals straight, perpendicular to dermal surface but flexing upward just before gastral surface to intersect spongocoel at about 45°. Canals cored by monaxons 0.25 to 0.38 mm in diameter. Rare vertical canals 0.4 mm in diameter, scattered in spiculature.

Scalariform skeletal net, with 1 to 3 trabs between radial canals, trabs separated by 0.1 to 0.5 mm. Trabs 0.3 to 0.4 mm in diameter, cored by 1 or 2 oxeas which are 0.25 mm across. Surface of trab pinnation varies from gastral surface to near midpoint of sponge wall, trabs parallel to gastral surface, but diverge to intersect dermal surface at about 60°. Amphiarborescent dendroclones dominate almost exclusively. Endosomal spicules 0.025 to 0.075 mm in cross-section, 0.15 to 0.5 mm long. Dermal layer sporadically developed.

Type Specimen — Lectotype USNM 79632c, designated herein. As with *N. traini*, Bassler had three cotypes from which he originally described these species. He illustrates one of these (Plate 19, Figures 6 and 7) in his 1941 publication and refers to it as "the type", implying that it was the one upon which he primarily based

his description. It is also the best-preserved of the three cotypes. For these reasons, it is chosen as the lectotype.

Measurements — Dimensions of the lectotype are: height = 58.7^{+} mm, diameter = 12.2 mm at base, 29.5 mm at top, wall thickness = 3.4 mm near base.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada. Whiterockian Stage, Middle Ordovician.

Discussion — Like *N. traini*, *Nevadocoelia wistae* is restricted to the sponge beds of the Antelope Valley Limestone at Ikes Canyon, but is a very common species there. It is readily separated from *N. traini* and *N. grandis* in having fine, closely-spaced, anastomosing ridges. In addition, its radial canals angle upward toward the spongocoel, whereas they are arched in *N. traini* and remain horizontal in *N. grandis*. Its fine ornamentation, oscular lip, and oddly shaped canals also serve to distinguish this species from most other cylindrical anthaspidellids. *Archaeoscyphia eganensis* also has fine ridges, but the large number of trabs between radial canals and the relatively thinner walls in this species prevent any confusion between it and *N. wistae*.

NEVADOCOELIA GRANDIS Bassler, 1927

Plate 7, Figure 1

Synonymy —

Nevadocoelia grandis Bassler, 1927, p. 392; Bassler, 1941, p. 95.

Description — Cylindrical, sometimes obconical, with 10.5 to 14 mm thick wall and rounded spongocoel extending nearly to base. Surface sometimes smooth, but commonly marked by low ridges or nodes. Ornamentation variable: ridges from 0.5

to 1.6 mm high, 0.2 to 20 mm across and separated by 6 to 20 mm, with ridge size and spacing increasing with size of sponge; surface occasionally marked by scattered nodes which are 1.8 to 2.7 mm across. Diameter between ridges about 3.5 to 7.5 cm, height greater than 10 cm, sometimes greater than 20 cm. Spongocoel rounded to oval, widening upward and comprising from 25 to 50% of total diameter.

Radial canals typically 0.6 to 1.6 mm in diameter and vertically stacked with 0.2 to 0.7 mm between them, having a parietal distance of 0.1 to 0.3 mm. Radial canals straight and horizontal, remaining perpendicular to both dermal and gastral surfaces. Radial canals often cored by monaxial spicules, 0.1 to 0.15 mm in diameter. No apparent vertical canals.

Scalariform skeletal net, with 1, sometimes 2, trabs between radial canals. Trabs 0.05 to 0.125 mm in diameter and cored by at least 2 oxeas. Surface of trab pinnation near midpoint of sponge wall, trabs parallel to gastral surface but diverge to intersect dermal surface at 20 to 30°. Amphiarborescent dendroclones dominate. Endosomal spicules 0.02 to 0.05 mm in cross-section, 0.125 to 0.225 in length, cladome rays 0.05 mm across. Dermal layer sporadically developed.

Type Specimen — Holotype USNM 79634.

Measurements — Dimensions of the holotype are: height = 152^{+} mm, diameter = 88.2 mm at base, 95.7 mm near top, and wall thickness = 27.1 mm near base.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada. Whiterockian Stage, Middle Ordovician.

Discussion — This is a very rare species. It is restricted to the sponge beds of the Antelope Valley Limestone at Ikes Canyon, and even here it is very uncommon.

Of the 258 specimens of *Nevadocoelia* collected in this study, only four could be confidently assigned to this species.

Bassler (1941) erected this species to hold two very large archaeoscyphids, both much larger than any other sponges from the Antelope Valley Limestone. He noted that the overall features of these two specimens were similar to those of the smaller *N. wistae,* and considered that they simply might be larger individuals of this species. However, the ridges of the two large specimens were broader and more widely spaced than in *N. wistae;* because one of his specimens was complete, the ornament did not seem to represent a later stage of that found in *N. wistae.* Hence, Bassler placed the two large specimens in their own species.

The more detailed study of the fauna made here supports Bassler's conclusions. Besides its large size and different ornamentation, *N. grandis* can be distinguished from its congeneric species by its larger radial canals which are straight and pierce the sponge wall horizontally rather than at an angle.

NEVADOCOELIA TRAINI Bassler, 1927

Plate 6, Figures 5, 8-9; Plate 7, Figure 3

Synonymy —

Nevadocoelia traini Bassler, 1927, p. 392; Bassler, 1941, p. 95.

Description — Cylindrical, sometimes obconical, with rounded spongocoel extending nearly to base. Surface ornamented by small nodes 2.0 to 2.5 mm across and usually separated 3 to 6 mm; nodes are generally arranged in vertical rows, but occasionally clump together to form low ridges. Nodes are limited to sides of sponge. Diameter usually between 8 and 70 mm, but averaging between 15 and 35

mm, increasing upward, with height up to 11 cm or more. Osculum with pronounced lip, spongocoel widening upward and comprising from 20 to 30% of total diameter.

Radial canals typically 0.5 to 0.9 mm in diameter and vertically stacked but irregularly spaced, with 0.1 to 1.2 mm between them vertically, 0.1 to 0.6 mm horizontally. Radial canals changed during ontogeny; earliest ones flex upward to enter spongocoel at a low angle, but later canals are nearly straight and horizontal. Radial canals near osculum are usually slightly arched with peak of arch coinciding with surface of trab pinnation. No apparent vertical canals.

Scalariform skeletal net, with 1 to 3, rarely 4, trabs between radial canals; trabs 0.025 to 0.08 mm in diameter and are cored by oxeas 0.01 mm across. Surface of trab pinnation parallel to and approximately one-third of way through sponge wall from gastral surface. Trabs diverge to intersect dermal surface at 20 to 40°. Amphiarborescent dendroclones dominate, but triclonid and quadraclonid dendroclones also found. Endosomal spicules 0.02 to 0.05 mm in diameter, 0.1 mm long, cladome rays about 0.05 mm across. Dermal layer sporadically developed, finely spiculate, forming an irregular meshwork with 0.3 to 0.7 mm pores.

Type Specimens — Lectotype USNM 79633c, designated herein. Bassler had three cotypes from which he originally described the species. He illustrated two of these (Plate 19, Figures 1 to 5) in his 1941 publication, of which 79633c is the better-preserved and has the most features. It is therefore chosen as the lectotype.

Measurements — Dimensions of the lectotype are: height = 92.8^{+} mm, diameter (crushed) = 18.6 mm at base, 24.1 mm at top, and wall thickness = 9.0 mm at base, 9.2 mm near top.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada. Whiterockian Stage, Middle Ordovician.

Discussion — Although it is only found within the sponge beds of the Antelope Valley Limestone at Ikes Canyon, *Nevadocoelia traini* is a common species there. It is readily distinguished from *N. wistae* and *N. grandis* in having many arched radial canals and in having prominent nodes arranged more-or-less in columns across its dermal surface. In addition, the surface of trab pinnation is consistently one-third of the way through the sponge wall from the gastral margin, whereas it is in the middle of the wall in *N. grandis* and varies from the gastral margin to the center of the wall in *N. wistae.*

N. traini is separated from superficially similar species with which it occurs by the regularity of its spiculature and ornamentation. *N. traini* can also be distinguished from *Streptosolen nodosus*, n. sp., by the more sinuous canals and shallow spongocoel in the latter species. Although hard to distinguish on the basis of external features, the two species are thus readily separated when either the upper surface or a longitudinal section is available. Another sponge from the Ikes Canyon locality, *Verpaspongia nodosa,* also bears a superficial resemblance to *N. traini.* However, the nodes in the latter species are much smaller, irregularly spaced, and cover the entire exterior of the sponge, including the upper surface. In addition, the dermal surface of *V. nodosa* is covered by a dense, finely spiculate layer which is much more extensive than the ectosome of *N. traini.*

Genus PATELLISPONGIA Bassler, 1927

Synonymy —

Patellispongia Bassler, 1927, p. 393; Bassler, 1941, pp. 97-98; de Laubenfels, 1955, p. E54; Langenheim et al., 1956, p. 2089; Greife and Langenheim, 1963, p. 569; Rigby, 1971a, pp. 49-50; Rigby and Webby, 1988, pp. 37-39; Rigby and Chatterton, 1989, pp. 25-27; Beresi and Rigby, pp. 48-51.

Type Species — *Patellispongia oculata* Bassler, 1927.

Description — Palmate or discoidal, often becoming bowl- or funnel- shaped; with somewhat broadened attachment surface, rarely developed into a short stem. Surface usually smooth, occasionally undulose. Radial canals vertically stacked and sinuous, but penetrate the cortex at approximately right angles. Additional canal sets often present, but with varying degrees of development; skeletal pores usually large. Surface of trab pinnation between dermal surface and midwall.

Scalariform skeletal net, with 1 to 3 trabs between radial canals, trabs usually cored by monaxons. Amphiarborescent dendroclones dominate, but polyclonid spicules common, particularly in dermal and gastral layers. Dermal and gastral layers well-developed, up to 2 mm thick, spiculature somewhat finer than that of endosome. Incurrent openings in dermal layer generally small and mimic underlying pattern of radial canals, but excurrent openings larger and more irregularly spaced over surface.

Occurrence — Western United States, Canada, South America, and southeast Australia. Ibexian Series, Lower Ordovician, to Wenlockian Series, Lower Silurian.

Discussion — *Patellispongia* is easily distinguished from most other members of the Anthaspidellidae by its palmate shape and the absence of the characteristic features of other lamellate genera. For example, *Patellispongia* lacks the clustered

apopores of *Anthaspidella*, or the regular ridges and fine spiculature of *Rugocoelia*. The genus is distinguished from *Hesperocoelia* in not having large excurrent canals longitudinally piercing the sponge wall. It differs from *Cockbainia* in possessing neither regular vertical canals nor digitate protrusions, and does not have the regularly spaced quadrate pores of *Colinispongia*.

Patellispongia is very similar to *Psarodictyum* in shape and spiculature, but differs in having a well-developed ectosome (Rigby and Webby, 1988; Beresi and Rigby, 1993), a feature not seen in *Psarodictyum*. The original description of *Psarodictyum* was very short and uninformative, but Rigby and Webby (1988), Rigby and Chatterton (1989), and Beresi and Rigby (1993) have provided much more detailed descriptions of species from the Ordovician of Australia and South America and the Silurian of Canada. However, the presence of an ectosome can be highly variable among individuals within a species, and a detailed review of the type specimens of *Psarodictyum* may indicate that the two genera should be synonymized (Rigby and Webby, 1988; Rigby and Chatterton, 1989; Beresi and Rigby, 1993). Unfortunately, such a review is beyond the scope of this project, but is underway by Rigby (pers. comm., 3/93).

The skeletal structure of *Patellispongia* is more open than that of many other anthaspidellids. Radial canals are often vertically separated by only single dendroclones, and the distinction between radial canal openings and gaps between intraserial spicules is not always clear. In addition, some species of *Patellispongia* have multiple sets of canals. For example, *P. australis* possesses three main canal systems: in addition to the radial series, it has two tangential sets that also penetrate the sponge wall (Rigby and Webby, 1988). Species from the Great Basin also have additional canal series, but these are not as well-developed as those in *P. australis*.

Patellispongia is one of the more common sponges in the Antelope Valley and Shingle Limestones and has a global distribution. Rigby (1971a) identified a species of *Patellispongia* from the Ordovician of Manitoba, Rigby and Webby (1988) described *P. australis* from the Late Ordovician of Australia, and Beresi and Rigby (1993) recognized *P. robustus* from the Early Ordovician of Argentina. In addition, Klappa and James' (1980) discussion of sponge mounds in the Whiterockian sediments of the Table Head Formation in Newfoundland illustrates several palmate sponges occupying identical ecological roles as the *Patellispongia* at Sunnyside. The large, swollen "oscula" on these sponges observed by these authors (Figure 16, p. 436) appear identical to the swellings produced by the parasitic brachiopod that infests this genus at Ikes Canyon. Considering the high similarity of the Table Head and Pogonip trilobite and brachiopod faunas, one might expect that the sponges would be similar as well. Thus, *Patellispongia* was probably widespread across Laurentia and Gondwanaland by the beginning of the Whiterockian Stage.

PATELLISPONGIA OCULATA Bassler, 1927

Plate 8, Figures 1-5; Plate 9, Figures 1-5; Plate 10, Figure 1

Synonymy —

Patellispongia oculata Bassler, 1927, p. 393; Bassler, 1941, p. 97.

Patellispongia oculata(?) Langenheim et al., 1956, p. 2089.

Patellispongia cf. *oculata* Greife and Langenheim, 1963, p. 569.

Patellispongia clintoni Bassler, 1927, p. 393; Bassler, 1941, pp. 97-98.

Patellispongia magnipora Bassler, 1927, p. 393; Bassler, 1941, p. 98.

Patellispongia minutipora Bassler, 1927, p. 393; Bassler, 1941, p. 98.

Patellispongia sp. Rigby, 1971a, pp. 49-50.

Description — Lamellate, varying from palmate to funnel- or bowl-shaped, usually flaring at base, sometimes with a short stem. Often found as broken fragments, but original diameter probably as much as 40 cm or more. Wall thickness ranging from 1 to 13 mm, but usually only 4 to 8 mm. Surface relatively smooth, slightly undulose.

Radial canals vertically stacked but slightly irregular, with 0.1 to 2.0 mm vertical distance between, usually only separated by 1 or 2 intraserial dendroclones. Canals approximately 0.2 to 1.0 mm in diameter and sinuous, usually towards lower end of range, often cored by monaxons 0.2 to 0.5 mm in diameter. Canal openings usually spaced 0.1 to 0.7 mm apart horizontally, but sometimes as much as 1.2 mm apart. Poorly developed set of sinuous, horizontal, concentric canals also present, about 0.4 to 1.0 mm in diameter. Shallow tangential canals just beneath gastral surface empty into large ectosomal pores.

Scalariform skeletal net with 1 to 2 trabs between radial canals, trabs 0.1 to 0.3 mm across, cored by oxeas 0.05 to 0.08 mm in diameter. Surface of trab pinnation from one-third to one-half of thickness through wall from incurrent side. Amphiarborescent dendroclones dominate almost exclusively. Endosomal spicules 0.05 to 0.1 mm in diameter, 0.25 to 0.5 mm long, cladome rays 0.025 to 0.05 mm in diameter.

Ectosomal gastral layer well-developed and 0.7 to 1.8 mm thick; dermal layer present but much thinner and more patchy. Ectosome thin along rim of sponge, and underlying endosome is visible. Ectosomal pores highly variable in size and spacing. Openings on incurrent side 0.4 to 0.7 mm in diameter and spaced from 0.2 to 0.5 mm apart; openings on excurrent side 0.6 to 1.8 mm across and spaced 1.0 to 4.6 mm apart

from center to center. Incurrent dermal pores average about 50 to 75% of diameter of radial canals, and excurrent dermal pores average about 100 to 200% of radial canal diameter. Ectosomal layer openings on dermal surface mimic underlying endosomal canals fairly well and are arranged in checkered pattern; openings on gastral surface spaced almost randomly, each opening fed by very shallow tangential canals apparently draining endosomal canals. Ectosomal spicules mostly polyclonid, about 0.02 to 0.05 mm in diameter and 0.25 to 0.4 mm long.

Type Specimen — Holotype USNM 79638.

Measurements — Dimensions of the holotype are: diameter = 116.1^{+} mm, and average wall thickness = 8.2 mm.

Occurrence — Shingle Limestone, southern Egan Range, Nevada; Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada, Mazourka Group, Mazourka Canyon, Inyo Mountains, California, and the Red River Formation, Manitoba. The Shingle Limestone is from the upper Ibexian Series of the Lower Ordovician, the Antelope Valley Limestone at Ikes Canyon dates from the Whiterockian Stage of the Middle Ordovician, and the Mazourka Group ranges from the Ibexian Series to the Whiterockian Stage. The Red River Formation has an uncertain age, and can only be assigned to the Upper Ordovician.

Discussion — *Patellispongia oculata* is one of the most common sponges in both the Shingle and Antelope Valley Limestones. Lamellar fragments of this sponge are a major component of the Sunnyside sponge mounds, and completely cover the surface of some bedding planes at Ikes Canyon. Although fragmentation after death inflated its apparent abundance, this species is nevertheless the most common lithistid sponge at both localities.

In describing the Ikes Canyon fauna, Bassler (1927) originally placed the members of *Patellispongia* into four species, which he separated on the basis of wall thickness, pore size, and vertical spacing of the radial canals. However, the large collection of individuals made in this study show that there is no consistent relationship between any of these features, and the range of variation within an individual can be almost as great as that found within the species as a whole. The first feature Bassler (1927) used, wall thickness, should never be employed as a major character for distinguishing taxa. Because of their discoidal shape, individuals of *Patellispongia* are thickest near their base and become thinner near the rim. As the specimens usually occur as broken fragments, the apparent wall thickness is thus entirely dependent on from which part of the sponge the fragment came and has no taxonomic value. In addition, Bassler mistook ectosomal pores for true prosopores and apopores, and used the variation between these ectosomal structures as the basis for erecting different species. Considering the recrystallization of the Ikes Canyon specimens and the state of sponge taxonomy in the 1920's, such a mistake is understandable. Nevertheless, the ectosome of demosponges tends to be highly irregular and variable, and using details of its structure for distinguishing different species cannot be justified. Thus, even though individuals can differ in the size and spacing of their ectosomal pores, in the absence of any other consistent, distinguishing features, it is probably best to group all of Bassler's species together.

To illustrate the variability of ectosomal pore size and spacing in this species, plots of these measurements for some better-preserved individuals of *Patellispongia* are shown in Figures 10 through 14. As the graphs illustrate, there is no consistent association or clumping of these features among the specimens. Although one or two individuals show extreme values in each of the comparisons made, it was not

the same individuals for every plot. Separating distinct taxa solely on the basis of one or two specimens having extreme values for features as variable as canal diameter and pore spacing seems unjustified. These "oddities" are therefore attributed to individual variation.

Although average pore size and spacing tend to increase together, even this relationship was poorly correlated. In the absence of any other consistent, distinguishing features, *P. magnipora* Bassler, *P. minutipora* Bassler, and *P. clintoni* Bassler have thus been synonymized with *Patellispongia oculata* Bassler, the genotype. For the same reasons, *Patellispongia* sp. from the Ordovician Red River Formation of Manitoba should probably be placed in *P. oculata* as well.

Patellispongia oculata differs from *P. brosiusae*, also from the Great Basin, in having a less regular canal disposition and substantially coarser spiculation. In addition, the ectosome is better-developed on the gastral surface of *P. oculata* and on the dermal surface of *P. brosiusae*. *P. oculata* also lacks the alternating rows of long and short dendroclones found in *P. brosiusae*, a feature that also separates it from *P. alternata* from the Silurian of Canada. *P. oculata* can be distinguished from *P. australis* because it lacks the large, horizontal tangential canals found in the latter species. Furthermore, the surface of trab pinnation is along the gastral margin in *P. australis*, and between the midwall and the dermal surface in *P. oculata*.

The type species is quite similar to *P. robusta* from Argentina, but has several important differences. *P. oculata* has a thicker ectosome and lacks the well-developed stalk seen in the South American species. In addition, *P. oculata* is dominated almost exclusively by amphiarborescent dendroclones, whereas *P. robusta* is composed largely of triclonid dendroclones.

The only other taxon with which *P. oculata* might be confused is *Colinispongia regularis*, n. gen., n. sp. However, the latter species has very large and regularly-spaced dermal openings and radial canals, quite unlike those in *P. oculata*.

Patellispongia oculata is a widespread species and local population differences occur. For example, individuals from Sunnyside have more regularly and closely-spaced dermal openings than those from Ikes Canyon, and the surface is somewhat more undulose. Similarly, specimens from the Mazourka Group usually have only one parietal row between the radial canals, and the surface of trab pinnation is closer to the incurrent surface. Although consistent within these populations, neither of these differences seems sufficient to warrant the erection of a new species.

PATELLISPONGIA BROSIUSAE, n. sp.

Plate 10, Figures 2-3, 5, 7

Etymology — The species is named after Anita Brosius of Cleveland, Ohio, who helped collect many of the specimens described here and whose assistance in the field was greatly appreciated.

Description — Palmate shape, originally 12 cm or more in diameter, often found as broken fragments. Wall thickness ranging from about 3.0 to 7.0 mm. Surface relatively smooth, but with vague, poorly developed annulations 3.5 to 5.5 mm thick, about 1.5 mm high, and with 6.5 to 7.5 mm between adjacent crests.

Radial canals vertically stacked and remarkably regular, with 0.4 to 1.1 mm vertical distance between, usually separated by 12 or more intraserial dendroclones. Canals approximately 0.4 to 1.4 mm in diameter and arched, with peak of arch near center of sponge wall. Additional set of very fine canals parallel to trabs. Canals

often cored by monaxons 0.125 to 0.25 mm across. Radial canals spaced 0.25 to 0.5 mm horizontally. Vertical canals 0.2 mm in diameter sparsely scattered through sponge wall. Irregular, sinuous transverse canals 0.8 mm across are present but rare.

Scalariform skeletal net, with 2 to 3 trabs between radial canals, trabs 0.075 mm across, cored by up to 3 oxeas 0.01 mm in diameter. Two types of dendroclones present: both are 0.025 mm in diameter with cladome rays 0.01 to 0.02 mm in diameter, but interserial set is approximately 0.13 to 0.15 mm long, intraserial set about 0.15 to 0.25 mm long. Surface of trab pinnation parallel to gastral margin, but trabs diverge from midwall to intersect dermal surface at about 45°. Amphiarborescent dendroclones dominate, but triclonid and quadraclonid dendroclones also common.

Ectosomal layer well-developed, up to 0.6 mm thick, with both amphiarborescent and polyclonid spicules 0.01 mm in diameter and about 0.25 mm in length. Ectosome completely covers dermal surfaces, with openings 0.3 to 0.5 mm across, but is absent or patchy on excurrent side. Ectosomal spicules about 0.3 mm in diameter, generally 0.8 to 0.9 mm long.

Type Specimen — Holotype 1784TX16; paratypes 1784TX11-15.

Measurements — Dimensions of the holotype are: diameter = 104^{+} mm, and average wall thickness = 3.0 mm.

Occurrence — Shingle Limestone, southern Egan Range, Nevada. Upper Ibexian Series, Lower Ordovician.

Discussion — Because of its palmate shape and well-developed ectosome, this species is assigned to *Patellispongia*. It differs from all of its congeneric species, though, in a number of ways. To begin with, the canal disposition and skeletal features of *P. brosiusae* are far more consistent than those of either *P. oculata* or *P.*

australis, and are instead more like *P. alternata* from the Silurian of Canada. *P. brosiusae* differs from its congeneric species in other ways as well. It has a larger proportion of polyclonid dendroclones in the parietal spiculature than any member of the genus except *P. robustus*. In addition, the intraserial spiculature is quite dense, with at least 12 dendroclones vertically separating radial canals. *P. brosiusae* also has 2 to 3 trabs separating adjacent canals, rather than only 1 or 2 as is found in other species. Finally, the external annulations, though vague, are still better developed than those of *P. oculata*, *P. australis*, or *P. robustus*. The dermal layer of *P. brosiusae* is dense with large, scattered openings, and is thus quite different from that of *Colinispongia regularis*.

P. brosiusae is most similar to *P. alternata*, but can be distinguished by the differences in the shapes of their radial canals and the more gastral position of the surface of trab pinnation in *P. brosiusae*. Of greatest importance, however, the trabs of *P. brosiusae* are cored by up to three oxeas, whereas those of *P. alternata* show no good evidence of such structures. Thus, despite their similarities, the sponges from the Shingle Limestone and those from Canada should probably be placed in separate taxa.

Genus RUGOCOELIA, n. gen.

Type Species — *Rugocoelia eganensis*, n. sp.

Etymology — From *rugos*, meaning wrinkle, and *coelia*, meaning hollow, a common ending for sponge genera.

Description — Lamellate and funnel-shaped, somewhat broadened attachment surface, occasionally with a short stem. Surface marked by remarkably regular concentric ribbing. Radial canals straight and vertically stacked, penetrating the cortex at approximately right angles. Vertical canals present but rare. Surface of trab pinnation along gastral margin. Scalariform skeletal net, with 1 to 3 trabs between radial canals. Amphiarborescent dendroclones dominate, but finely spiculate. Dermal layer well-developed, particularly on ridges; gastral layer often present.

Occurrence — Shingle Limestone, southern Egan Range, Nevada. Ibexian Series, Lower Ordovician.

Discussion — *Rugocoelia* is a monotypic genus, and thus the generic and specific characters are the same. The spiculature is somewhat finer than most other anthaspidellids, but extremely regular. This regularity is best illustrated by the diagnostic ridges, which, in size and spacing, look remarkably like oscillation ripples in fine sandstone, and are quite unlike the surface ornament of any other anthaspidellid. These "ripples" rarely vary by more than 2 mm either within or between individuals. Although more closely spaced in younger specimens, the ridges are consistently 1 to 2.5 mm high, and 1 to 1.5 mm across. Such consistency suggests that the "ripples" had a genetic, rather than an environmental, basis. This implies that surface features such as ridges and nodes in other closely-related anthaspidellids also had a genetic origin, supporting the use of such features for taxonomic purposes.

To date, *Rugocoelia* has been found only within the Shingle Limestone of eastern Nevada. Nevertheless, fragments of it are one of the major constituents of the sponge mounds here. Its distinctive ridges allow *Rugocoelia* fragments to be readily identified in cross-sections through sponge mound rock.

RUGOCOELIA EGANENSIS, n. sp.

Plate 11, Figures 2-3, 5; Plate 12, Figure 1

Etymology — The species name derives from its occurrence in the Egan Range of eastern Nevada.

Description — Lamellate, funnel- or bowl-shaped, often with a short stem, with overall height reaching 6 cm or more. Typically found as broken fragments, but original radius as much as 9 cm from center to edge of sponge. Surface marked by very regular, ripple-like ridges 1 to 2.5 mm high, 1 to 1.5 mm across, with 5.5 to 15 mm between ridge crests, spacing typically increasing with sponge size. Wall thickness between ridges varying from 1.5 to 4 mm, rarely more.

Radial canals vertically stacked with 0.2 to 1.0 mm between them, separated by parietal distances of 0.3 to 1.1 mm. Canals straight, approximately 0.3 to 0.7 mm in diameter. Vertical canals 0.3 mm in diameter, but rare.

Scalariform skeletal net, with 1 to 3 trabs between radial canals, trabs 0.025 to 0.05 mm in diameter. Surface of trab pinnation along and parallel to gastral margin, trabs diverge to intersect dermal surface at 40 to 50°. Amphiarborescent dendroclones dominate. Endosomal spicules 0.015 to 0.025 in diameter and 0.35 mm long, with cladome rays 0.025 mm across.

Ectosomal dermal layer well-developed, about 0.4 mm thick, slightly thicker on ridges. Spiculature and pore pattern of ectosome reflects that of underlying endosome, with spicules linking to form nodes that overlie the trabs; spiculature particularly dense on crests. Dermal pores usually 0.2 to 1.0 mm across, generally spaced 0.4 to 0.6 mm apart in both vertical and parietal directions. Gastral layer variably developed, with pores 0.4 to 0.6 mm in diameter, spaced 0.3 to 0.7 mm apart vertically, 0.4 to 1.1 mm apart horizontally. Ectosome composed of monoclonid and

polyclonid dendroclones, with spicules having diameters of 0.02 mm and lengths of 0.12 to 0.13 mm.

Type Specimens — Holotype 1784TX1; paratypes 1784TX2-6.

Measurements — Dimensions of the holotype are: diameter = 59^{+} mm, and average wall thickness = 2.5 mm in troughs.

Occurrence — Shingle Limestone, southern Egan Range, Nevada. Upper Ibexian Series, Lower Ordovician.

Discussion — Being the only known species in the genus, the defining characteristics of the genus serve to distinguish *Rugocoelia eganensis* from other anthaspidellids. The relatively fine spiculature and regular skeletal framework are the most important phylogenetic features, but the regular "ripples" allow the species to be identified from even small fragments.

Rugocoelia eganensis is one of the most common species within the sponge mounds of the Shingle Limestone, second only to *Patellispongia oculata* in abundance. Its absence from any other units within the Shingle Limestone suggest that it was a specialist adapted to the relatively high-energy, clear, shallow-water environments in which the sponge mounds developed.

Family STREPTOSOLENIDAE, n. fam.

Type Genus — *Streptosolen* Ulrich and Everett in Miller, 1889.

Description — Variously-shaped, from discoidal and palmate to cylindrical, branching, or funnel-shaped. Fine, irregular spiculature composed of monoclonid and polyclonid dendroclones fused at tips to form trabs, latter often cored by oxeas; trabs and dendroclones usually of comparable diameter. Complex, intertwining canal systems typical; apopores emptying into cloaca or forming individual, but

clustered, oscula. Surface usually smooth, but surficial ridges or nodes sometimes present. Dermal and gastral layers variably developed; spicules of endosome and ectosome often of comparable size.

Discussion — Over the years, the family Anthaspidellidae has grown from seven to over fifty genera. Generally, any taxon possessing a skeleton largely composed of acrepid dendroclones has been placed into this family. As a result, the Anthaspidellidae now includes a wide variety of very different genera which probably bear little, if any, relationship to each other.

As noted by Rigby (1983, 1991a), there are two very distinctive groups within what are currently classified as anthaspidellid sponges. To use the example of Rigby and Bayer (1971), the first group has a relatively coarse skeleton with a ladder-like arrangement of the spicules in which large trabs serve as "siderails" to which dendroclone "rungs" attach. The spiculature thus has a two-dimensional aspect: with few exceptions, any two adjacent dendroclones will be approximately parallel, or at least in the same plane (Figure 6A). This scalariform skeleton results in a very regular, vertical stacking of the radial canals. Examples of genera with such a skeleton include *Anthaspidella* itself, *Archaeoscyphia*, and *Patellispongia*. The second group, represented by taxa such as *Streptosolen*, *Lissocoelia*, and *Hesperocoelia*, has a much more irregular, usually finer, skeleton. Although the radial canals may still appear vertically stacked, they are often sinuous and intertwining and frequently exit into vertical, axial apochetes. In addition, the endosomal spiculature contains a larger proportion of polyclonid dendroclones or even rhizoclones, and these will frequently attach to each other instead of the trabs. When they do connect two trabs, the dendroclones are often not horizontal. Furthermore, the trabs they connect may not be at the same depth, i.e., one trab may

be farther from the surface than the other. The result is a more complex, three-dimensional skeleton (Figure 6B). The trabs provide some regularity to the structure, but the endosomal skeleton of this second group is otherwise remarkably similar to the ectosomal dermal layer found in some species of *Archaeoscyphia* and closely related taxa. In fact, in some streptosolenid genera, such as *Lissocoelia*, there is no true ectosome; instead, the endosomal spiculature becomes denser near the surface.

Because of these differences, a new family, the Streptosolenidae, is erected to include those orchoclad sponges with less regular skeletons composed of dendroclones. The members of this family are distinguished from the Chiastoclonellidae in having an endosomal skeleton predominantly of dendroclones rather than chiastoclones, and in possessing well-developed radial architecture. They are separated from the Anthaspidellidae by the greater irregularity of their skeleton and the greater complexity of the canal systems that result. The higher proportion of polyclonid spicules and the poor development of a true dermal layer in many streptosolenids also serve to help distinguish the members of the two latter families. Demosponge genera with dendroclone skeletons and the families to which they are assigned here are shown in Table 6.

Table 6 — A compilation of recognizable lithistid sponge genera which have been placed in the Family Anthaspidellidae, and the families to which they are assigned here.

Family Anthaspidellidae, Ulrich in Miller, 1889
Amplasospongia Rigby and Webby, 1988
Anthaspidella Ulrich and Everett in Miller, 1889
Archaeoscyphia Hinde, 1889a
Brianispongia Pickett and Rigby, 1983
Calycocoelia Bassler, 1927
Canningella Rigby, 1986b
Capsospongia Rigby, 1986a
Cauliculospongia Rigby and Chatterton, 1989
Climacospongia Hinde, 1883
Cockbainia Rigby, 1986b
Colinispongia, n. gen.
Dunhillia Rigby and Webby, 1988
Egania, n. gen.
Fibrocoelia van Kempen, 1978
Finksella Rigby and Dixon, 1979
Fistulosospongia Rigby, 1986b
Gleesonia Rigby and Webby, 1988
Incrassospongia Rigby, 1977a
Isispongia Pickett, 1969
Malongullospongia Rigby and Webby, 1988
Multistella Finks, 1960
Nevadocoelia Bassler, 1927
Okulitchina Wilson, 1948
Patellispongia Bassler, 1927
Phacellopegma Gerth, 1927
Playfordiella Rigby, 1986b
Protachilleum Zittel, 1877
Psarodictyum Raymond and Okulitch, 1940
Rankenella Kruse, 1983
Rhopalocoelia Raymond and Okulitch, 1940
Rugocoelia, n. gen.
Somersetella Rigby and Dixon, 1979
Steliella Wilson, 1948
Syringophyllum Ulrich, 1889
Vandonia Rigby and Webby, 1988

Table 6 (cont.)

Family Streptosolenidae, n. fam.
Allosaccus Raymond and Okulitch, 1940
Antrospongia Rigby and Chatterton, 1989
Aulocopella Rauff, 1895
Aulocopium Oswald, 1847
Aulocopoides Howell, 1952
Camarocladia Ulrich and Everett in Miller, 1889
Dendroclonella Rauff, 1895
Edriospongia Ulrich and Everett in Miller, 1889
Eospongia Billings, 1861
Gallatinospongia Okulitch and Bell, 1955
Hesperocoelia Bassler, 1927
Hudsonospongia Raymond and Okulitch, 1940
Lissocoelia Bassler, 1927
Ozarkocoelia Cullison, 1944
Perissocoelia Rigby and Webby, 1988
Pseudopalmatohindia Rigby and Webby
Streptosolen Ulrich and Everett in Miller, 1889
Verpaspongia, n. gen.
Wilbernicyathus Wilson, 1950

Genus STREPTOSOLEN Ulrich and Everett in Miller, 1889

Synonymy —

Streptosolen Miller, 1889, p. 165; Ulrich and Everett, 1890, pp. 273-274; Bassler, 1927, p. 394; Bassler, 1941, p. 100; de Laubenfels, 1955, p. E64; Langenheim et al., 1956, p. 2089; Greife and Langenheim, 1963, p. 570.

Type Species — *Streptosolen obconicus*, Ulrich and Everett in Miller, 1889.

Description — Highly variable shape: cylindrical to obconical to almost discoidal. Surface generally smooth, but irregular swellings, vague annulations, or even nodose protrusions common. Canal system complex with multiple sets of intertwining, often branching, canals. Radial canals sinuous, but empty into vertical apochetes that extend from base to at least one shallow depression on summit. Complex skeletal net, dendroclones attach to each other or connect trabs of different

depths from surface. Polyclonid dendroclones common in endosome, often not in horizontal orientation. Skeletal net complex with multiple sets of intertwined canals. Surface of trab pinnation parallel to dermal surface, with trabs diverging to intersect gastral surface. Ectosome well-developed.

Occurrence — Western and central United States. Ibexian Series, Lower Ordovician, to Blackriverian Stage, Middle Ordovician.

Discussion — Like *Anthaspidella*, the name *Streptosolen* first appeared in Miller's 1889 monograph on North American geology and paleontology. As discussed by Finks (1967c), Miller apparently had a preprint of Ulrich and Everett's work and cited them as the authors of the name. Thus, the proper citation should be Ulrich and Everett in Miller, 1889.

Streptosolen is one of the most common sponges within the Shingle and Antelope Valley Limestones. A single, coarsely silicified individual has also been collected from the Mazourka Group of California (Langenheim et al., 1956; Greife and Langenheim, 1963). However, the only other reported occurrence of the genus was the original description from the Platteville Formation of Illinois by Ulrich and Everett (1890). It is possible that other occurrences of this taxon remain unreported, but, if not, *Streptosolen* has a relatively limited geographic and stratigraphic range.

Streptosolen is distinguished from most other taxa by its highly irregular spiculature and canal arrangement. *Archaeoscyphia* and related genera have similar shapes, but their deep spongocoel, vertically stacked canals, and relatively simple skeletons make confusion with *Streptosolen* unlikely. *Eospongia* and many other streptosolenids have vertical apochetes emptying into a shallow spongocoel, but these taxa lack the intertwining radial and concentric canals found in *Streptosolen*. The radial canals in some species of *Streptosolen* are so sinuous that

they appear as separate, elongate "windows" in sagittal section, rather than as whole, individual canals (Plate 13, Figure 3; Plate 14, Figures 4-5). Other taxa that have such complex, intertwining canals, such as *Edriospongia*, lack any sort of spongocoel. In size and structure, *Streptosolen* is most similar to *Hudsonospongia* and *Aulocopium*. However, both of these genera have more regular, S-shaped canals, and *Aulocopium* also lacks the prominent vertical apochetes of *Streptosolen*. Furthermore, the direction of trab pinnation in both *Hudsonospongia* and *Aulocopium* is primarily towards the dermal surface, whereas in *Streptosolen* the trabs instead diverge to intersect the gastral surface at a large angle.

STREPTOSOLEN MCCAFFERYI, n. sp.

Plate 12, Figures 3, 6-10

Etymology — After Mark McCaffery of Austin, Texas, whose advice regarding proper Latin and Greek endings and conjugations has proved invaluable in composing these systematic descriptions.

Description — Highly variable shape: cylindrical to obconical to almost discoidal, height ranges from 1 to almost 4.5 cm. Exterior generally smooth, but vague annulations common. Diameter increases upward, from 12 to 35 mm at base to usually 35 to 45 mm near top. Upper surface concave, but with shallow spongocoel into which 10 to over 35 vertical apochetes empty. Each spongocoel surrounded by many horizontal, sinuous canals which are often partly exposed so as to produce a starburst pattern of canals "radiating" away from the spongocoel. Spongocoel usually between 6.5 and 8.0 mm across, often depressed, 2 to 3 mm deep, and surrounded by elevated rim.

Canal system very complex with multiple sets of intertwined canals. Major, subhorizontal canals very sinuous, but empty into or become vertical apochetes that extend from base to shallow depression or spongocoel on summit. Major subhorizontal canals 0.4 to 1.0 mm in diameter, vertical apochetes about 0.7 to 2.0 mm in diameter, almost all vertical and horizontal canals cored by monaxons 0.4 to 0.7 mm across. Most vertical apochetes empty into spongocoel where they are separated by 0.1 to 0.5 mm, but such vertical excurrent canals are also scattered throughout sponge body. Major subhorizontal canals separated by 0.1 to 1.0 mm vertically, by 0.4 to 0.8 mm horizontally. Central canals longest and probably oldest, additional canals added to sides and spongocoel as sponge grew.

Complex skeletal net, dendroclones attach to each other or connect trabs of different depths from surface. Polyclonid dendroclones dominate, often not in horizontal orientation. Skeletal net complex, with generally 2 trabs between radial canals. Trabs very fine, 0.125 to 0.175 mm in diameter, spaced 0.25 to 0.75 mm apart, cored by oxeas 0.025 mm in cross-section. Surface of trab pinnation near midpoint of sponge wall; trabs parallel to dermal surface, diverge to intersect gastral surface at approximately 45°. Dendroclones 0.025 to 0.05 mm in diameter, about 0.25 mm long, and with cladome rays 0.025 m in cross-section. Ectosome of polyclonid spicules usually present, about 0.5 mm thick, with irregular openings 0.2 to 0.5 mm across.

Type Specimen — Holotype 1784TX47; paratypes 1784TX48-54.

Measurements — Dimensions of the holotype are: height = 21.5^{+} mm, one-half of original diameter at top = 35.0 mm.

Occurrence — Shingle Limestone, southern Egan Range, Nevada. Upper Ibexian Series, Lower Ordovician.

Discussion — Like the other known species of *Streptosolen*, *S. mccafferyi* is limited to a single unit at a single locality, in this case, the sponge mounds of the Shingle Limestone at Sunnyside. It is one of the more common species within these units, suggesting that it too was a specialist adapted to the shallow, well-lit waters and hard substrates of the reef mounds.

S. mccafferyi is most similar to *S. occidentalis*, but can be distinguished from that species by the former's smaller size and better developed spongocoel rim. *S. mccafferyi* also tends to have straighter canals, coarser, more regular spiculation, and a larger number of irregular annulations. Of greatest importance, though, *S. mccafferyi* has only 10 to 40 apochetes emptying into its spongocoel, whereas *S. occidentalis* rarely has fewer than 60. The number of apochetes per spongocoel also help to distinguish this species from *S. obconicus* which has only 5 or 6 apochetes per spongocoel, and *S. nodosus*, which usually has between 30 and 40. *S. mccafferyi* also lacks the nodular ornament of the latter species.

STREPTOSOLEN NODOSUS, n. sp.

Plate 13, Figures 1-5

Etymology — The species name is in reference to the distinctive nodular ornamentation of this species.

Description — Shape irregular and variable, but usually obconical or pedunculate; up to 7 cm or more in height with single shallow spongocoel depression at top having depth less than 15% of total height. Entire surface marked by small nodes, usually 0.7 to 1.2 mm in size, but up to 2.6 mm across. Nodes spaced more or less randomly, up to 5 mm apart from center to center. Rounded base with

no obvious attachment structures, becoming as much as 50 mm in diameter near top. Spongocoel rounded, comprising about 25 to 40% of total diameter.

Radial canals 0.5 to 1.5 mm in diameter and separated by 0.6 to 1.8 mm in the vertical direction, by 0.4 to 1.1 mm in the horizontal direction. Radial canals sinuous, producing elongate "windows" rather than continuous canals in cross-section, and empty into or form vertical apochetes that exit through spongocoel. Apochetes elongated perpendicular to sponge wall, 1.2 to 1.9 mm in diameter, about 30 to 40 clustered together in spongocoel. Other vertical canals in endosome are of similar size but more sinuous. Minute transverse canals 0.2 mm in diameter serve to link canal systems together. Nearly all major canals are cored by large monaxons 0.4 to 0.6 mm across.

Scalariform skeletal net with 2 to 5 trabs between radial canals, trabs 0.05 mm in diameter. Surface of trab pinnation about 4 to 5 mm in from dermal surface in approximate middle of sponge wall; trabs diverge to intersect dermal surface at 20 to 30°, but intersect gastral surface at about 80 to 90°. Polyclonid dendroclones dominate in endosome, but amphiarborescent spicules also common; dendroclones average 0.2 to 0.3 mm in diameter.

Ectosome well-developed, with amphiarborescent and polyclonid spicules. Dermal pores 0.4 to 1.0 mm in diameter, from 0.5 to 1.0 mm apart from center to center.

Type Specimen — Holotype 1766TX21; paratypes 1766TX22-27 and 1767TX9-15.

Measurements — Dimensions of the holotype are: height = 42^{+} mm, diameter at top = 39.8 mm.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada. Whiterockian Stage, Middle Ordovician.

Discussion — In its conical shape and nodular ornament, this species bears a superficial similarity to *Nevadocoelia traini*, with which it is associated. However, *Streptosolen nodosus* has a more obconical shape and the nodes are less regular. More importantly, the shallow spongocoel, irregular spiculature, and complex canal arrangement of *S. nodosus* make confusion between these two taxa unlikely. The nodular ornament is quite unlike that seen in any other streptosolenid, allowing this taxon to be easily distinguished from its congeneric species.

S. nodosus is much rarer than *S. occidentalis*, and is represented by only 36 specimens. Like the latter species, it was probably a specialist and may have settled only where the communities had had a chance to develop for many years before being buried.

STREPTOSOLEN OCCIDENTALIS, Bassler, 1927

Plate 12, Figure 5; Plate 13, Figures 6-7; Plate 14, Figures 1, 4-5, 8

Synonymy —

Streptosolen occidentalis Bassler, 1927, p. 394; Bassler, 1941, p. 100.

Description — Highly variable shape: cylindrical to obconical to almost discoidal, height ranges from 2 to over 14 cm. Diameter increases upward, from 9 to 46 mm at base to over 100 mm near top. Upper surface usually concave, but sometimes flat or even convex, with one, two, or more shallow spongocoels into which 60 to over 100 vertical apochetes empty, though as few as 25 apochetes occur in the spongocoels of young specimens. Each spongocoel surrounded by many horizontal, sinuous canals which are often partly exposed so as to produce a

starburst pattern of canals "radiating" away from the spongocoel. Each spongocoel usually between 10 and 20 mm across, but can reach sizes of up to 35 mm; spongocoels often depressed, 1.5 to 5.0 mm in depth, sometimes surrounded by elevated rim. Exterior generally smooth, but irregular swellings or vague annulations common.

Canal system complex with multiple sets of intertwining canals. Major, subhorizontal canals sinuous, but empty into or become vertical apochetes that extend from base to at least one shallow depression or spongocoel on summit. Major canals 0.5 to 1.6 mm in diameter, vertical apochetes 1.2 to 2.3 mm in diameter, almost all vertical and horizontal canals cored by monaxons 0.4 to 0.7 mm across. Most vertical apochetes empty into spongocoel where they are separated by only 0.1 to 0.5 mm, but such vertical excurrent canals are also located throughout sponge body. Subhorizontal and vertical canals also linked by large, transverse canals 1.2 to 1.8 mm across. Major subhorizontal canals separated by 0.2 to 3.5 mm vertically, by 0.1 to 1.5 mm in horizontal direction; almost entire range of specific variation in canal spacing and size found within any given individual. Irregular spiculature probably allowed some degree of water flow between all canal systems. Central canals longest and probably oldest, with additional canals added to sides and spongocoel as sponge grew.

Complex skeletal net, dendroclones attaching to each other or connecting trabs of different depths from surface. Polyclonid dendroclones common to dominant, often not in horizontal orientation. Skeletal net complex, with generally 2 trabs between radial canals. Trabs very fine, 0.05 mm in diameter, spaced 0.15 to 0.375 mm apart. Surface of trab pinnation along and parallel to dermal surface, trabs diverge out to intersect gastral surface at about 90°. Dendroclones 0.025 mm in

diameter, from 0.075 to 0.15 mm in length, and with cladome rays 0.01 mm in cross-section. Thin dermal layer of polyclonid spicules sometimes present, having irregular openings 0.1 to 0.5 mm across. Ectosomal spicules 0.025 to 0.05 mm in diameter.

Type Specimens — Lectotype USNM 79645b, designated herein, and cotype USNM 79645a. Bassler (1927, 1941) based this species upon two cotypes, which are figured by him in his later publication (Plate 23, Figures 1 and 2). The specimen in Figure 1 is better preserved and exhibits more of the features characteristic of this species, and is therefore designated as the lectotype.

Measurements — Dimensions of the lectotype are: height = 70.6^{+} mm, diameter = 23.2 mm at base, 64.6 mm x 42.2 mm at top.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada. Whiterockian Stage, Middle Ordovician.

Discussion — *Streptosolen occidentalis* is only found within the sponge beds of the Antelope valley Limestone at Ikes Canyon, but within these units it is one of the most common sponges. Of the 560 lithistid sponges collected from the sponge bed biofacies, almost 20% were *S. occidentalis*. This species was apparently a specialist that was well-adapted to the conditions in which the sponge beds were deposited, but was unable to tolerate the muddier waters in which adjacent units were presumably laid down.

S. occidentalis can be distinguished from its congeneric species by the very large number of apochetes that empty into its spongocoel(s). The smallest spongocoel on the smallest specimen on which the upper surface is exposed has 26 vertical apochetes in it, the largest spongocoel has over 110. Most individuals have between 60 and 90 apochetes emptying into each cluster. *S. obconicus*, the type species, has an

average of only 5 or 6 per spongocoel, *S. mccafferyi* has from 10 to about 35 per spongocoel, and *S. nodosus* has about 30 to 40 per spongocoel. The substantially smaller trabs and dendroclones of *S. occidentalis* also help to separate it from *S. mccafferyi*. The former species also tends to be larger and have a less well-developed rim around the spongocoel. *S. occidentalis* can be readily distinguished from *S. nodosus*. because it lacks the nodose ornamentation of the latter species.

The smaller, presumably younger, specimens of *Streptosolen occidentalis* had about two to three dozen vertical apochetes running through them and emptying into their main spongocoel, while larger, older individuals had 60, 80, or even 100 such apochetes emptying into their main spongocoel. The spicular material around the spongocoel would thus have had to have been rearranged or resorbed in order to make room for the new apochetes and radial canals. Although this ability is common among modern demosponges (Bond, 1992), it has never been reported for any lithistid, living or extinct.

Genus HESPEROCOELIA Bassler, 1927

Synonymy —

Hesperocoelia Bassler, 1927, p. 393; Bassler, 1941, pp. 98-99; Greife and Langenheim, 1963, p. 570; Rigby and Webby, 1988, p. 46.

Type Species — *Hesperocoelia typicalis* Bassler, 1927.

Description — Palmate and undulose, with multiple spongocoels repeatedly branching, usually in same plane. Spongocoels deep, extending nearly to base of

sponge and exiting along upper margin. Sponge wall thin, external surface unornamented and smooth. Radial canals straight, more or less perpendicular to dermal and gastral surfaces, occurring in alternating vertical series to produce checkered pattern. Canals usually separated by 3 trabs, trabs cored by oxeas. Complex skeletal net, dendroclones attach to each other or connect trabs of different depths from surface. Triclonid and quadraclonid dendroclones dominate, often not in horizontal orientation. No true ectosome, but spiculation becomes denser along exterior and interior surfaces.

Occurrence — Western United States. Ibexian Series, Lower Ordovician, to Whiterockian Stage, Middle Ordovician.

Discussion — Bassler (1927, 1941) recognized two species of *Hesperocoelia* within the Antelope Valley Limetone at Ikes Canyon. *H. typicalis* was characterized by elongate oscula and skeletal pores spaced an average of "4 per 3 mm" (p. 99). *H. undulata*, in contrast, had more circular oscula, was somewhat thicker and taller, and had "more delicate and closely spaced" pores (p. 99). An examination of Bassler's types and an additional 23 specimens collected for this study clearly demonstrates that the Ikes Canyon specimens all belong to a single species. The range of variation in thickness, height, and spiculature within a given individual easily includes the extremes that Bassler used to distinguish his two species. Furthermore, the apparent shape of the oscula seems more controlled by post-mortem compression and the plane through which the sponge is cut than any original, potentially genetic, differences between individuals. For these reasons, *H. undulata* has been synonymized with *H. typicalis*, the type species.

Hesperocoelia has a shape almost unique among the orchoclad sponges. It is palmate like *Anthaspidella* or *Patellispongia*, but unlike these genera, the sponge

wall in *Hesperocoelia* is penetrated by parallel, branching spongocoels that exit along the upper margin of the sponge. In the large size and arrangement of these vertical structures, *Hesperocoelia* can also be distinguished from *Cockbainia* from the Devonian of Australia. The only orchoclad with an architecture like that of *Hesperocoelia* is *Pseudopalmatohindia* from the Upper Ordovician Malongulli Formation of New South Wales. Rigby and Webby (1988) noted that *Hesperocoelia* and *Pseudopalmatohindia* might be synonyms; however, the former appeared to have radial canals, a feature lacking in the Australian specimens. Unfortunately, Bassler's original descriptions were inadequate for making any definitive judgment. The much larger collections made in this study show that *Hesperocoelia* does indeed possess horizontal radial canals, supporting Rigby and Webby's (1988) distinction of the two genera.

HESPEROCOELIA TYPICALIS, Bassler, 1927

Plate 16, Figures 1-6

Synonymy —

Hesperocoelia typicalis Bassler, 1927, p. 393; Bassler, 1941, pp. 98-99; Greife and Langenheim, 1963, p. 570.

Description — Palmate and undulose, with multiple, parallel spongocoels repeatedly branching, usually in midwall, and spaced about 1 to 1.5 mm apart. Spongocoels deep, extending nearly to base of sponge and exiting along upper margin; cloacas 2 to 4 mm in diameter, approximately circular or polygonal in cross-section, but becoming ovoid due to post-mortem compression or crowding by adjacent spongocoels and often narrowing slightly before reaching osculum. From 2

to 4 monaxons in each spongocoel, monaxons 0.4 to 1.6 mm in diameter. Sponge wall thin, 1 to 5 mm thick, external surface unornamented and smooth. Overall height up to 14 cm or more, but often broken into smaller fragments; total thickness of sponge from 3 to 14 mm, thickest at base and where undulations fold back on themselves. Total length as much as 23.5 cm.

External pores 0.2 to 0.5 mm in size, arranged in alternating, more-or-less vertical series so as to form a checkered pattern, with pores spaced 0.3 to 0.4 mm apart in all directions. Radial canals straight, 0.25 to 0.6 mm in diameter, and penetrate the sponge wall almost horizontally. Canals, on average, separated by 0.4 to 1.0 mm in vertical direction, 0.5 to 1.25 mm in horizontal direction. Usually 3 trabs between adjacent canals, trabs 0.05 to 0.1 mm in diameter, cored by oxeas 0.025 mm in diameter. Surface of trab pinnation along gastral margin, trabs diverge to intersect dermal surface at 70 to 80°.

Complex skeletal net, dendroclones attaching to each other or connecting trabs of different depths from surface. Triclonid and quadraclonid dendroclones dominate, often not in horizontal orientation. Endosomal spicules 0.025 to 0.075 mm in diameter, 0.075 to 0.25 mm in length, with cladome rays 0.025 mm across.

Dermal surface has layer of denser spiculation, 0.75 to 1.0 mm thick, but otherwise similar to underlying endosome. No such thickening developed along gastral surface.

Type Specimens — Lectotype USNM 79641, designated here. Bassler did not officially designate a holotype, but in 1941, he cited specimen USNM 79641 as a type with no other cotype mentioned. As this is the same specimen illustrated in his Plate 22, Figures 6 to 8, it seems best to designate this specimen as the lectotype.

Measurements — Dimensions of the lectotype are: height = 85.0^{+} mm, total thickness = 6.8 - 8.9 mm.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Nevada, and Mazourka Group, Mazourka Canyon, Inyo Mountains, California. The former locality is from the Whiterockian Stage, Middle Ordovician, the latter is from the Ibexian Series to Whiterockian Stage; Lower to Middle Ordovician.

Discussion — With its unique excurrent canal arrangement and complex spiculation, there is little difficulty in separating *Hesperocoelia* from any other orchoclad with which it occurs. *H. typicalis* from Nevada is distinguished from *Pseudopalmatohindia digitata* Rigby and Webby in having thinner trabs that intersect the outer surface at a greater angle and in having horizontal radial canals.

Hesperocoelia typicalis is one of the rarer sponges in the Antelope Valley Limestone, suggesting that it was a specialist and probably one of the later species to settle in the communities.

Genus LISSOCOELIA Bassler, 1927

Synonymy —

Lissocoelia Bassler, 1927, p. 392; Bassler, 1941, p 96; de Laubenfels, 1955, p. 54; Langenheim et al., 1956, p. 2089; Greife and Langenheim, 1963, pp. 568-569 ; van Kempen, 1969, pp. 101-108.

Type Species — *Lissocoelia ramosa* Bassler, 1927.

Description — Cylindrical, often branching, with branches maintaining same diameter; spongocoel penetrating center of all branches, extending nearly to base.

Sponge wall thin, external surface unornamented and smooth. Radial canals straight and horizontal, occurring in more or less vertical series. Canals separated by up to 3 trabs, trabs cored by minute oxeas. Complex skeletal net, dendroclones attached to each other or connecting trabs of different depths from surface. Polyclonid dendroclones common, often not in horizontal orientation. True ectosome absent, but spiculation becomes more dense along exterior and interior surfaces.

Occurrence — Western United States, Baltic area. Whiterockian Stage, Middle Ordovician to Carodocian Series, Upper Ordovician.

Discussion — *Lissocoelia* and similar small, tubular sponges are uncommon, but by no means rare, components of the Ordovician sponge faunas of the Great Basin. *Lissocoelia* proper occurs in the Antelope Valley Limestone, which marks its earliest occurrence. A representative of this genus has also been found in a glacial erratic from the Upper Ordovician sediments of the Baltic area (van Kempen, 1969). This suggests that the genus originated in Laurentia, but had spread across the Iapetus Ocean to Baltica by the end of the Ordovician.

Lissocoelia is distinguished from other members of the family by its tubular, branching shape and unornamented surface. Because the sponge wall is so thin, it also lacks the complex canal systems found in *Streptosolen* or *Hudsonospongia*. It differs from *Ozarkocoelia* Cullison in its smaller size and less regular spiculation.

LISSOCOELIA RAMOSA, Bassler, 1927

Plate 15, Figures 5-9

Synonymy —

Lissocoelia ramosa Bassler, 1927, p. 392; Bassler, 1941, p. 96; Langenheim et al., 1956, p. 2089; Greife and Langenheim, 1963, pp. 568-569.

not van Kempen, 1969, pp. 101-108.

Description — Cylindrical, with branching eventually producing arborescent shape; branching dichotomous but not necessarily in same plane, with spacing between branch points being highly variable. Spongocoel usually comprising 20 to 35% of diameter, but as much as 55% in some specimens. Spongocoel extending nearly to base, penetrating center of every branch, narrows slightly before osculum. Height from base to uppermost branch as much as 90 mm or more. Individual branches of more or less constant and equal diameter, but ranging from 7.0 to 16.5 mm across, with thickest portions immediately before branch points. Branches closely clustered, overall diameter of sponge about 10 cm or more. Surface remarkably smooth, devoid of any ornamentation. Wall thickness varies from 1.5 to 5.5 mm.

Radial canals arranged in alternating, more-or-less vertical series so as to form a checkered pattern, with 0.1 to 0.9 mm between them in both vertical and horizontal directions. Canals parallel to trabs, approximately 0.1 to 0.4 mm in diameter. Up to 3 trabs between radial canals, trabs 0.025 to 0.08 mm in diameter, trabs cored by monaxons 0.01 mm in diameter. Surface of trab pinnation between gastral margin and midpoint of sponge wall, trabs diverge to intersect dermal surface at approximately 90°.

Complex skeletal net, dendroclones attaching to each other or connecting trabs of different depths from surface. Triclonid and quadraclonid dendroclones common, often not in horizontal orientation. Endosomal spicules 0.05 in diameter and 0.1 mm long. Spiculation sometimes denser towards dermal surface, but no true ectosome developed.

Type Specimens — Lectotype USNM 79636b, designated herein. Bassler did not officially designate a holotype, but in 1941 cited specimen USNM 79636 as a cotype. There are actually two cotypes, USNM 79636a and 79636b. In his description of Plate 19, Figure 9 in this latter publication, he illustrates 79636b and cites this specimen as "the type", implying that this was the specimen on which he primarily based his description. Furthermore, the label accompanying this specimen now designates it as the holotype, although there is no indication of who changed the label. For all these reasons, USNM 79636b should be treated as the lectotype.

Measurements — Dimensions of the lectotype are: height = 66.3^{+} mm, diameter = 12.8 - 16.1 mm, and wall thickness = 3.4 - 6.8 mm.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada, and Mazourka Group, Mazourka Canyon, Inyo Mountains, California. The former locality is in the Whiterockian Stage, Middle Ordovician, while the Mazourka Group ranges from the Ibexian Series, Lower Ordovician to the Whiterockian Stage, Middle Ordovician.

Discussion — *Lissocoelia ramosa* is one of the more distinctive sponges of the Antelope Valley Limestone. Its small diameter and branching habit are unlike that of any other species from these beds and allow the identification of even poorly preserved specimens. The species does not occur in any of the other units examined in this study, but *L.* cf. *L. ramosa* has been described from a glacial erratic in Holland

that apparently originated in the Baltic craton (van Kempen, 1969). However, this specimen consists of a single tube 11 cm in length and thus lacks the dichotomous branching characteristic of *L. ramosa* proper. In addition, the Dutch representative has odd, "root-like" growths on one side of the sponge, and the dendroclones are two to three times as long as in the individuals from Nevada. For these reasons, the European specimens almost certainly belong to a different species. The "single, cylindrical body" (p. 101) described by van Kempen (p. 101) is in close association with another cylindrical body, and it is possible that the two single tubes are in fact different branches of the same individual.

The only other described species in this genus is *Lissocoelia cylindrica*, a new species from the sponge mounds in the Shingle Limestone. The two species can be distinguished by relatively smaller spongocoel, smooth exterior, and more extensive branching in *L. ramosa*. However, the two taxa are otherwise similar in spiculature and canal arrangement.

Lissocoelia ramosa is one of the few Toquima Range sponges that occurs in the Antelope Valley Limestone outside of the sponge beds. The species is also found in several units immediately below the sponge beds at Ikes Canyon, beds that were probably deposited in deeper water. This suggests that *L. ramosa* may have been better able to cope with the soft, muddy substrates associated with these units.

LISSOCOELIA CYLINDRICA, n. sp.

Plate 15, Figures 10-14

Etymology — The species name refers to the cylindrical shape of the sponge.

Description — Cylindrical or obconical, branching rare, possibly dichotomous. Rounded spongocoel usually comprising 35 to 60% of diameter, extending nearly to base, with undulose gastral surface. Up to 40 mm or more in height; total diameter from 7.5 to 20 mm, with wall thicknesses varying from 2.5 to 6.0 mm. Surface sometimes with poorly developed annulations about 6 mm across and 2 mm high; distance from crest of one annulation to another about 10 mm.

Radial canals in vertical series with 0.15 to 0.9 mm between them, separated by 0.2 to 0.3 mm horizontally. Canals straight, 0.3 to 0.8 mm in diameter, penetrating downward into sponge wall at approximately 45 to 60°. From 1 to 2 trabs between radial canals, trabs 0.02 to 0.05 mm in diameter and cored by monaxons 0.01 mm in diameter. Surface of trab pinnation near gastral margin about one-quarter of way into sponge wall; trabs diverge to intersect dermal surface at approximately 60 to 90°, usually at about 80°.

Complex skeletal net, dendroclones attaching to each other or connecting trabs of different depths from surface, often not in horizontal orientation. Triclonid and quadraclonid dendroclones dominate, but amphiarborescent dendroclones also common. Endosomal spicules 0.01 to 0.02 mm in diameter, 0.13 to 0.15 mm long, cladome rays 0.08 mm across.

Spiculation denser towards dermal surface, 0.3 to 0.4 mm thick. Dermal pores 0.3 to 0.5 mm in diameter, spaced about 0.2 to 0.8 mm apart in all directions.

Type Specimens — Holotype 1784TX32; paratypes 1784TX31, 1784TX33, 1784TX34, 1784TX35, 1784TX55, 1784TX58, 1784TX59, and 1788TX1.

Measurements — Dimensions of the holotype are: height = 39.6^{+} mm, average diameter = 17.5 mm, and average wall thickness = 4.5 mm.

Occurrence — Shingle Limestone, southern Egan Range, Nevada, and Fillmore Formation, section H, Ibex area, Utah. Ibexian Series, Lower Ordovician.

Discussion — This species has the irregular spiculation and poorly developed canal system characteristic of *Lissocoelia*, and is therefore assigned to this genus. It differs from *L. ramosa*, the type species, in having fewer branches, a relatively larger spongocoel, a tendency towards annulation, and a better developed radial canal system. Several specimens from the sponge mound horizon at Sunnyside have been assigned to this species; they range greatly in size, but there are specimens intermediate in size between the smallest and the largest. Some of the smaller individuals are similar to *L. ramosa*, but their relatively large spongocoel suggests that they are better placed in *L. cylindrica*, at least for now.

VERPASPONGIA, n. gen.

Type Species — *Verpaspongia nodosa*, n. sp.

Description — Cylindrical shape overall, constricted near middle. Height up to 7 cm or more. Spongocoel shallow and rounded, with apochetes emptying perpendicularly into it. Entire surface marked by small, scattered nodes. Radial canals absent, but large, concentric canals scattered randomly through sponge body. Apochetes straight, vertical in center, becoming subhorizontal towards edges. Complex polyclonid skeletal net. Spiculature becomes denser towards dermal surface.

Occurrence — Western United States. Whiterockian Stage, Middle Ordovician.

Discussion — Unfortunately, only one representative of this genus was found among the several hundred lithistids collected from the Antelope Valley Limestone. Although silicification has obscured some of the details of the spiculature and canal system, the specimen is sufficiently unique to warrant the erection of a new genus.

Because of its complex spiculature and irregular canal system, this genus is placed within the Streptosolenidae. *Verpaspongia* is most similar to *Allosaccus*, but lacks the radial canals of that taxon. The absence of radial canals and its highly irregular spiculature also serve to distinguish it from *Aulocopium*. *Verpaspongia* has some similarities to *Aulocopella* but does not have the radial structure or ribbing that characterize that genus.

VERPASPONGIA NODOSA, n. sp.

Plate 12, Figures 2, 4

Description — Cylindrical shape overall, but somewhat constricted in middle to produce two swollen halves. Diameter greatest near top, but ranging from 18 mm at base to about 35 mm near top, with diameter at maximum constriction only 11 mm. Height up to 7 cm or more. Spongocoel shallow and rounded, only 4 mm deep and approximately 8 mm across osculum, comprising about 20% of total diameter. Entire surface marked by small nodes, 0.8 to 1.2 mm in size, 1.5 to 2.5 mm apart from center to center, and scattered more-or-less randomly.

Radial canals apparently absent. Large, concentric canals penetrate sponge body, spaced from 0.2 to 0.7 mm apart; canals range from 0.5 to 1.3 mm in diameter,

but average only 0.7 to 0.8 mm in cross-section. Apochetes straight, 0.5 mm in diameter, and empty directly into spongocoel; relationship between apochetes and other canals unclear in specimen. Apochetes vertical in center, becoming subhorizontal towards edges.

Complex skeletal net dominated by triclonid spicules, but quadraclones and amphiarborescent dendroclones also common. Spicules attach to each other or to trabs of differing distances from surface. Trabs approximately 0.03 to 0.04 mm in diameter, spaced 1.0 to 1.5 mm apart. Dendroclones 0.02 to 0.03 mm across, shafts approximately 0.2 mm long. Spiculature becomes denser 0.5 to 2.0 mm from dermal surface; skeletal pores about 0.3 mm in diameter or less.

Type Specimen — Holotype 1767TX7.

Measurements — Dimensions of the specimen are: height = 69^{+} mm, diameter = 18.2 mm at base, 10.9 mm in middle, and 32.5 mm near top.

Occurrence — Antelope Valley Limestone sponge beds, Ikes Canyon, Toquima Range, Nevada. Whiterockian Stage, Middle Ordovician.

Discussion — *Verpaspongia nodosa* is represented by a single, very unusual, individual. In having a surface covered by small nodes, the members of this genus bear a superficial resemblance to *Nevadocoelia traini* or *Streptosolen nodosus*. However, the nodes in the specimen are smaller and more closely-spaced than in either of these genera, and they occur across the entire outside surface up to the oscular lip. The dense dermal spiculation is much thicker than in either *N. traini* or *S. nodosus*, and completely covers the exterior of the sponge. *V. nodosa* also has an unusual, almost dumbbell-shape, not seen in these other taxa. The central constriction is accentuated by post-mortem compression, but was probably prominent in life as well.

In its highly irregular dendroclone spiculature and lack of radial canals, *V. nodosa* differs from most other orchoclads. Apparently, water entered the sponge through the skeletal pores and eventually worked its way to the concentric canals. Because of resilicification, it is not clear if the concentric canals emptied directly into the apochetes.

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APPENDIX I: STRATIGRAPHIC SECTIONS

Measured Section 1:

Northside Section, Ikes Canyon

This is one of the best exposures of the portion of the Antelope Valley Limestone containing diverse fossil assemblages with sponges and other organisms. These beds cross the boundary of *Orthidiella* and *Anomalorthis* Zones, and the section measured here begins approximately 140 m below the top of the formation. The complete Antelope Valley Limestone section in Ikes Canyon is about 290 m thick and was measured by Ross (1970) beginning in the Roberts Mountain Formation and proceeding downsection through an unnamed formation into the Antelope Valley Limestone and down into the underlying Stoneberger Shale. The section described here is part of the Mill Canyon sequence (Kay and Crawford, 1964), and is located on the north side of the canyon about 1.0 km from its mouth in T. 14 N., R. 46 E., Nye County, Nevada, on the Diana's Punch Bowl 7.5 minute Quadrangle (Figure 15). Strike N. 9° W., dip 9° SW. The fossils mentioned occur primarily on bedding planes.

ORDOVICIAN SYSTEM **Thickness** (m)
POGONIP GROUP
ANTELOPE VALLEY LIMESTONE (total thickness 290 m (Ross, 1970))

Overlying Facies (includes beds not measured)
1.) Dark gray wackestone/packstone with occasional grainstone beds, thin- to medium-bedded with shaly partings; trilobites and brachiopods common, surface burrows on bedding planes .....**not measured**

Sponge Bed Facies

2.) Brownish-gray nodular wackestone/packstone interbedded with thinner yellowish shale beds, thin- to medium-bedded; sponges, trilobites, brachiopods, gastropods, and echinoderms common to abundant, becoming increasingly fossiliferous downsection **10.5**

3.) Dark gray wackestone/packstone interbedded with yellowish-orange shale beds, thin-bedded; sponges, echinoderms, trilobites, and gastropods common to abundant **2.4**

4.) covered interval **0.5**

5.) Dark gray wavy- to nodular-bedded pelletal wackestone/mudstone with occasional packstone beds, thin- to medium-bedded with shaly partings; trilobites, echinoderms, sponges, and brachiopods common to abundant **0.8**

6.) Medium gray wavy- to nodular-bedded pelletal packstone/wackestone interbedded with yellowish-shale beds, thin-bedded; trilobites and echinoderms common, uncommon sponges and brachiopods **0.7**

7.) Medium gray argillaceous pelletal wackestone/packstone, poorly exposed; trilobites and sponges common, uncommon bryozoans, brachiopods, and echinoderms, becoming increasingly fossiliferous downsection **0.3**

8.) Medium gray wavy- to nodular-bedded mudstone/wackestone interbedded with yellowish-shale beds, thin-bedded; sponges, trilobites, brachiopods, and echinoderms common **0.9**

9.) Medium gray slightly wavy-bedded mudstone with yellowish shaly partings, becoming increasingly shaly and nodular towards base; thin- to medium-bedded; burrowed, with trilobites, lingulids, echinoderms, and hexactinellid root tufts **2.7**

Upper Fossiliferous Facies

10.) Dark gray slightly wavy-bedded wackestone interbedded with pelletal packstone and yellowish shaly partings; thin- to medium-bedded; extensively burrowed, echinoderms and trilobites **0.6**

11.) Medium gray wavy- to nodular-bedded mudstone interbedded with yellow fissile shale; limestone thin- to medium-bedded, shale thin-bedded; extensively burrowed, some minor trilobite and echinoderm debris **2.3**

12.) Dark gray wavy- to slightly nodular-bedded wackestone/packstone with some thin, shaly partings; thin- to medium-bedded; burrowed, abundant trilobite and echinoderm debris, some sponges, hexactinellid root tufts , and snails, becoming less fossiliferous downsection **0.6**

13.) Dark gray wavy- to nodular-bedded mudstone with yellowish shaly partings; thin- to medium-bedded; trilobite and echinoderm debris common, some burrows **1.9**

Unfossiliferous Facies

14.) Dark gray wavy- to slightly nodular-bedded mudstone interbeddedwith yellow fissile shale; thin-bedded; rare trilobite and echinoderm debris **5.3**

15.) Medium gray nodular mudstone in yellowish-green fissile shale; thin-bedded; burrowed, trilobite and echinoderm debris **1.6**

Lower Fossiliferous Facies

16.) Dark gray wavy- to nodular-bedded silty wackestone interbedded with yellowish fissile shale; thin-bedded; trilobite and echinoderm debris, rare brachiopods and hexactinellid root tufts **4.3**

17.) Dark gray nodular mudstone/wackestone with occasional grainstone beds, interbedded with yellowish shale beds, thin-bedded; some burrows, trilobites and echinoderms common, brachiopods and sponges rare; hardground? **5.6**

18.) Dark gray mudstone/wackestone with thin yellowish shaly partings; medium-bedded; some burrows, trilobites, echinoderms, brachiopods, and snails common **1.3**

19.) Dark gray wavy- to nodular-bedded mudstone with occasional wackestone or packstone beds, interbedded with yellowish fissile shale; thin-bedded; some burrows, trilobites, brachiopods, and echinoderms common **1.2**

20.) Dark gray slightly wavy-bedded wackestone with thin yellowish shaly partings; medium-bedded; burrows, trilobites, echinoderms, and brachiopods common **0.5**

21.) Dark gray wavy- to nodular-bedded pelletal mudstone/ wackestone interbedded with yellowish fissile shale; thin-bedded; burrows, trilobites, brachiopods, and echinoderms common **4.9**

22.) Dark gray massive wackestone with thin yellowish shaly partings; snails, trilobites present **0.3**

Low-Oxygen Facies

23.) Dark gray slightly wavy-bedded mudstone/wackestone interbedded with yellowish fissile shale; thin- to medium-bedded; trilobites, brachiopods, and echinoderms rare **9.6**

24.) covered interval ..... **not measured**

Total measured thickness = 48.3 m

Measured Section 2:

Sunnyside Section, Egan Range

This section was measured through the Shingle Limestone of the Pogonip Group exposed in the southern Egan Range about 10 km west of the small community of Sunnyside in eastern Nevada. The beds described below contain a series of sponge mounds deposited during trilobite zone J of the Ibexian Series, making them slightly older than the sponge beds found in the Antelope Valley Limestone at Ikes Canyon. The section here begins a few meters below the top of the formation and the contact with the Kanosh Shale. The complete Sunnyside section is about 360 m thick and was measured by Kellogg in 1963. This exposure is located approximately 1.25 km northeast of Whipple Cave along the top of ridge 7726 in T. 8 N., R. 63 E., White Pine County, Nevada, on the Shingle Pass 7.5 minute Quadrangle (Figure 16). Strike N. 42° E., dip 38° SE. The fossils mentioned occur primarily on bedding planes.

ORDOVICIAN SYSTEM **Thickness** (m)
POGONIP GROUP
SHINGLE LIMESTONE (total thickness 350 m (Kellogg, 1963))

Uppermost Shingle Limestone

1.) Medium gray intramicrite with irregular dark gray grainstone intraclasts and occasional thin, wavy grainstone beds, medium-bedded, almost massive, with orangish shaly partings; fossiliferous with burrows, trilobites, echinoderms, brachiopods, and snails **12.9**

2.) Medium gray wavy to nodular-bedded *Nuia* grainstone with wackestone/packstone and micrite lenses and layers; medium-bedded grainstone and thin-bedded micrite with orangish shaly partings; chert nodules common; very fossiliferous with burrows, snails, trilobites, echinoderms, brachiopods, and algae **2.3**

3.) Dark gray wavy to nodular-bedded grainstone with algal boundstone; medium-bedded with yellowish shaly partings; chert nodules common; fossiliferous with trilobites, echinoderms, and some encrusting sponges, burrows common; forms top of cliff **2.8**

4.) Dark gray nodular grainstone and light gray wackestone/mudstone interbedded with orangish shale beds; thin-bedded; rare burrows **2.3**

5.) Dark gray nodular grainstone interbedded with light gray nodular wackestone/mudstone; thin-bedded with yellowish shaly partings; chert nodules common; very few fossils **0.5**

6.) Dark gray nodular grainstone and light gray wackestone/mudstone interbedded with orangish shale beds; thin-bedded; chert nodules uncommon; abundant fossil debris, including trilobites, echinoderms, and possibly algae **1.4**

7.) Medium gray wackestone with lenses or layers of dark gray grainstone; thin- to medium-bedded with yellowish shaly partings; echinoderms and snails **1.6**

8.) Medium gray wavy to nodular laminated wackestone interbedded with grayish fissile shale; thin-bedded; burrows and feeding trails, some trilobites and echinoderm debris **0.4**

9.) Light gray wackestone/mudstone with lenses of dark gray grainstone; thin- to medium-bedded with yellowish shaly partings; abundant sponge spicules, echinoderms, trilobites, and burrows; forms base of cliff **1.2**

10.) Brownish-gray, argillaceous grainstone, almost a coquina, with mudstone/wackestone intraclasts, interbedded with yellowish shale partings and beds; thin-bedded; abundant trilobites, echinoderms, nautiloids, and snails **0.7**

11.) Dark gray wavy to nodular grainstone with packstone/wackestone and yellowish shaly partings, becoming increasingly shaly and nodular downsection; thin- to medium-bedded; sponges, trilobites, snails, echinoderms, brachiopods, and burrows **7.0**

12.) Dark gray wavy to nodular grainstone/packstone/wackestone with light gray mudstone intraclasts and yellowish shaly partings; thin-bedded; sponges, trilobites, brachiopods, echinoderms, and burrows **0.1**

13.) Dark gray irregularly bedded *Nuia* grainstone with reddish-gray mudstone intraclasts and occasional yellowish shaly partings; medium-bedded; chert nodules; abraded fossil debris includes trilobites, brachiopods, snails, echinoderms, and nautiloids **0.2**

14.) Dark gray wavy grainstone with light gray mudstone intraclasts and yellowish shaly partings; thin-bedded; sponges, trilobites, snails, echinoderms, and nautiloids **0.03**

15.) Brownish-yellow , fissile silty pelletal shale; unfossiliferous; poorly exposed, weathering into slope **0.1**

Sponge Mound Horizon

16.) Light gray massive mud mounds composed of sponge-algal boundstone changing laterally and downward into dark gray echinoderm and *Nuia* grainstone with occasional flat mudstone pebbles; mounds average 1-2 m in height and 2-4 m in diameter, grainstones lenticular and thickly-bedded with cross-bedding; rare chert nodules; mound fossils are predominantly sponges with echinoderms, trilobites, and algae; grainstone fossils are almost entirely echinoderms and algae **2.9**

Interval Between *Calathium*/Sponge Biostromes and Sponge Mound Horizon

17.) Dark gray wavy to slightly nodular laminated algal boundstone and grainstone; thin-bedded **0.2**

18.) Dark gray grainstone and wackestone interbedded with thin, greenish-yellow fissile shale beds, becoming less shaly downsection; thin- to medium-bedded; chert nodules rare; sponges, trilobites, brachiopods, echinoderms, nautiloids, and burrows **1.6**

19.) Yellowish , fissile shale with occasional mudstone or wackestone lenses; thin-bedded; unfossiliferous shale, trilobite debris in limestones; poorly exposed, weathering into slope **0.2**

20.) Medium to dark gray slightly wavy mudstone/wackestone with grainstone megaripples and shaly partings, becoming more shaly and coarser-grained downsection; infrequent low mounds composed of algal boundstone; occasional light-gray, flat clasts of mudstone in shale; thin- to medium-bedded; turreted snails and burrows in wackestone, trilobites and echinoderms in grainstone **1.9**

21.) Dark gray grainstone and packstone interbedded with yellowish fissile shale beds and intermittent beds of light-gray flat clasts of mudstone; thin- to medium-bedded; snails, trilobites, echinoderms, and burrows in limestone **1.0**

22.) Dark gray slightly wavy packstone/grainstone with shaly partings; thin- to medium-bedded; trilobites and echinoderms common **0.2**

23.) Yellowish shale with gray nodular wackestone; poorly exposed; some trilobites **0.4**

24.) Light gray wackestone with yellowish shaly partings and thin shale beds; medium to thick-bedded; echinoderms and snails present **0.5**

25.) Covered interval, eroding into slope **1.4**

26.) Reddish-gray wavy grainstone with flat mudstone clasts interbedded with yellowish shale beds; thin- to thick-bedded; fossils include trilobites, echinoderms, and abraded *Calathium* **0.2**

27.) Medium gray *Nuia* grainstone interbedded with light gray algal boundstone with shaly partings and occasional flat clasts of wackestone/mudstone; thin-bedded, lenticular; snails and trilobites, echinoderms and brachiopods in grainstone **0.3**

28.) Reddish-gray slightly wavy grainstone with light gray mudstone intraclasts interbedded with yellowish, fissile shale; thin- to thick-bedded; trilobites and echinoderms in limestone **0.2**

29.) Yellowish shale, poorly exposed **0.4**

<u>*Calathium*/Sponge Biostromes</u>

30.) Medium-gray massive wackestone/packstone and algal boundstone and dark gray echinoderm grainstone interbedded with yellowish shale; thickly-bedded; sponges and *Calathium* common in limestone, with trilobites and echinoderms **1.5**

<u>Interval Between *Calathium* Mounds and *Calathium*/Sponge Biostromes</u>

31.) Yellowish shale, poorly exposed **0.1**

32.) Dark-gray wavy grainstone with flat clasts of mudstone interbedded with yellowish shale; thin- to medium-bedded; trilobites and echinoderms in limestone **0.2**

33.) Covered interval **2.1**

34.) Dark-gray wavy to nodular *Nuia* grainstone with flat clasts of mudstone and yellowish shaly partings; thin- to medium-bedded; trilobites, echinoderms, gastropods, brachiopods, sponges, nautiloids, algae, and burrows common, becoming increasingly fossiliferous downsection **2.0**

35.) Covered interval **2.2**

36.) Dark gray wavy to nodular grainstone interbedded with lenses of light gray mudstone/wackestone and yellowish shaly partings and beds; thin-bedded; trilobites, echinoderms, gastropods, and burrows present **0.9**

37.) Covered interval **1.0**

38.) Medium gray coquina-like grainstone with yellowish shaly layers; thin-bedded; trilobites, brachiopods, sponges, and encrusting bryozoans present **0.3**

39.) Dark gray grainstone with yellowish shaly layers; poorly exposed **0.4**

40.) Dark gray wavy grainstone with yellowish shaly layers and occasional mudstone intraclasts; thin- to medium-bedded; cross-bedded; trilobites and echinoderms in grainstone **0.2**

41.) Covered interval **0.4**

42.) Reddish-yellow slightly wavy, laminated siltstone with shaly partings; thin-bedded; some burrows and feeding trails **0.2**

43.) Covered interval **1.3**

44.) Dark gray wavy pelletal grainstone interbedded with lenses of light gray mudstone and siltstone; medium- to thick-bedded; some chert nodules; similar to flanking beds of mounds; echinoderms, trilobites, brachiopods, *Calathium*, and burrows present **0.2**

<u>*Calathium* Mound Horizons and Associated Facies</u>

45.) Medium gray mud mounds composed of sponge-algal boundstone changing laterally and vertically into dark gray echinoderm grainstone; mounds average 15 cm in height and less than 1 m in diameter, grainstone thick-bedded; *Calathium* and other algae common in mounds **0.3**

46.) Reddish-gray wavy to nodular grainstone interbedded with flat clasts of mudstone and lenses of light gray wackestone/ packstone and mudstone/wackestone, with yellowish shaly partings; thick-bedded; echinoderms, trilobites, and *Calathium* common **0.2**

47.) Dark gray nodular grainstone interbedded with light gray mudstone/ wackestone and yellowish, fissile shale; thin-bedded; echinoderms, trilobites, *Calathium* , and brachiopods common **0.2**

48.) Grayish-white mud mounds composed of algal boundstone changing laterally and vertically into dark gray echinoderm and pelletal grainstone with occasional mudstone pebbles; mounds average less than 0.5 m in height but more than 3 m in diameter; *Calathium* and other algae common in mounds, with trilobites and echinoderms **0.4**

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49.) Reddish-gray wavy to nodular wackestone/packstone with occasional layers of grainstone, flat clasts of mudstone, and yellowish shaly partings; echinoderms, trilobites, snails, and burrows common **4.2**

50.) Covered interval, beginning about halfway down slope and proceeding downsection into grainstone units and flat-pebble conglomerates ..... **not measured**

Total measured thickness = 61.3 m

GLOSSARY

APOCHETE — exhalent canal connecting apopyles to an apopore

APOPORE — exhalent opening from the apochete; may be equivalent to the oscula

APOPYLE — exhalent opening from the choanocyte chamber into an apochete

CHOANOCYTE — specialized, flagellated cell (collar cell) which generates water currents within the sponge and absorbs food particles

CHOANOCYTE CHAMBER — cavity within the sponge body occupied by choanocytes

DENDROCLONES — spicules within an anthaspidellid skeletal net that serve as crossbraces between adjacent trabs, i.e., they are the "rungs" in the scalariform spiculature; in some taxa, the trabs are composed solely of the fused tips of dendroclones.

DERMALIA — fine spicules that compose the ectosomal, or dermal, layer found in some sponges

DESMA — a siliceous spicule, often irregular in shape, that bears excrescences with which it fuses to other desmas

DTD RATIO — dendroclone to trab diameter ratio; a measure of the relative thicknesses of the dendroclones and trabs within a sponge

ECTOSOME — body region lacking choanocyte chambers; forms the external (dermal) or inner (gastral) surface of the sponge

ENDOSOME — inner part of the sponge, i.e., the main skeleton composed of megascleres

GASTRALIA — fine spicules that compose the interior, or gastral, layer found in some sponges

GASTRAL LAYER — ectosome found along the wall of the spongocoel

GASTRIC MARGIN — the wall of the spongocoel

MEGASCLERE — large, major supporting spicule

MICROSCLERE — very small, accessory spicule

MONAXON — spicule secreted along a single axis

OCTATINE SPICULE — spicule with 8 rays along 4 axes of growth

OSCULUM — major exhalent opening

OSTIUM — inhalent opening; equivalent to a prosopore

OXEA — monaxial spicule pointed at both ends

PARIETAL SERIES —vertical spicular columns in anthaspidellid sponges between those columns containing the radial canals

PLANE OF TRAB PINNATION — the vertical plane along which the trabs diverge, becoming more horizontal than vertical

PROSOCHETE — inhalent canal connecting prosopyles to a prosopore

PROSOPORE — inhalent opening into the prosochete; equivalent to an ostium

PROSOPYLE — inhalent opening into the choanocyte chamber from a prosochete

RADIAL CANAL — approximately horizontal canal through the sponge wall; equivalent to a prosochete, an apochete, or both

SKELETAL PORE — minor, irregular opening between spicules

SPONGIN — keratin-like protein of which the spicules of many "soft" demosponges are composed

SPONGOCOEL — central cavity of the sponge; equivalent to the cloaca of leucon-grade sponges

TRAB — rod formed by the union of dendroclone ray tips and often cored by oxeas; the skeletal net of anthaspidellids is organized like a row of vertical ladders, and the trabs serve as the siderails, helping to support the spicular "rungs"

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PLATE 1

ANTHASPIDELLA

Figure

1-6 *Anthaspidella clintoni* Bassler. 1, gastral view of specimen 1766TX29, X0.8; 2, gastral view of 1766TX49, X1; 3, sagittal view of 1766TX52, illustrating how canals come together and become perpendicular to the gastral surface to form apochete clusters, X1; 4, gastral view of holotype USNM 79643, X1; 5, gastral view of specimen 1766TX30, X1; 6, dermal view of 1766TX49, showing regular spiculature that characterizes the family, X1. Note how apochete cluster size and spacing varies dramatically within this species. Individuals with small, closely-spaced pores look very different from those with large, widely-spaced pores, and Bassler (1927, 1941) placed the former specimens in *A. clintoni*, the latter in *A. traini*. However, intermediate forms can be found between these extremes, and any division between these two groups would be arbitrary. For this reason, *A. traini* has been synonymized with *A. clintoni*.

PLATE 2

ANTHASPIDELLA, ARCHAEOSCYPHIA

Figure

1-2 *Anthaspidella clintoni* Bassler. 1, gastral view of USNM 79644, holotype of *A. traini*, X1; 2, close-up of gastral surface of 1766TX29, showing details of the apochete clusters, X3.

3-5 *Archaeoscyphia bassleri*, n. sp. 3, transverse section through holotype 1784TX26, showing exceptionally straight nature of radial canals, X2; 4, exterior view of holotype: vertically stacked canals can be seen on the weathered surface on the left side of the specimen, X2; 5, side view of paratype 1766TX56, showing annulation, X1.

6-9 *Archaeoscyphia rossi*, n. sp. 6-7, exterior views of paratype 1784TX37, showing annulations; the basal point is a result of breakage, X2 and X1, respectively; 8, top view of paratype 1784TX37, X2; 9, sagittal section through holotype 1784TX36, revealing shape of the radial canals, X2.

PLATE 3

ARCHAEOSCYPHIA

Figure

1-3 *Archaeoscyphia eganensis*, n. sp. 1, sagittal section of holotype 1784TX17, illustrating nature of radial canals, X1; 2, exterior view of holotype showing regular annulations and vertically stacked canals, X1; 3, transverse section of paratype 1784TX18, revealing the straight radial canals, X1.

4-7, 9 *Archaeoscyphia pannosa*, n. sp. 4, transverse section through holotype 1784TX28; X1.5; 5, sagittal and exterior views of holotype: the upper part of the specimen has been cut to reveal a sagittal section, while the lower part shows the weathered exterior surface, X1.5; 6-7, exterior views of paratype 1784TX29, showing the annulations which have been weathered away in the holotype, X1 and X2, respectively; 9, transverse section through holotype, showing serrated margin of spongocoel; the figure has been retouched to emphasize the margin which is otherwise obscured by color changes in the matrix and sponge material, X6.

8 *Archaeoscyphia* sp. 1 (Griefe and Langenheim). 8, exterior view of specimen UCMP 10316, X2. The coarse silicification of the skeleton prevents any more precise identification of this individual, and it is assigned to *Archaeoscyphia* primarily because of its annulations, an unreliable feature.

10 *Archaeoscyphia mazourkensis* (Griefe and Langenheim). 10, exterior view of holotype UCMP 10317, X1. Note the monaxons coring the radial canals.

PLATE 4

ARCHAEOSCYPHIA, CALYCOCOELIA

Figure

1, 5 *Archaeoscyphia pulchra* (Bassler). 1, exterior view of holotype USNM 79635: note the very well-developed annulations that help to distinguish the species, X1; 5, close-up of holotype showing the scalariform spiculature typical of *Archaeoscyphia*, X2.

2-4 *Calycocoelia typicalis* Bassler. 2, exterior view of 1766TX50, showing the almost pedunculate form of some individuals, X1; 3, top view of specimen 1766TX51, revealing the relatively small spongocoel and rounded osculum characteristic of this species; 4, close-up of 1766TX50, illustrating the regular, scalariform spiculature found in this genus, X4.

PLATE 5

ARCHAEOSCYPHIA, CALYCOCOELIA

Figure

1, 3 *Archaeoscyphia pulchra* (Bassler). 1, sagittal view of YPM 17135, holotype of *Archaeoscyphia annulata* Cullison; note the similarity in shape, size, and annulation to *A. pulchra* (Bassler); 3, close-up of YPM 17135, revealing the regular spiculature of the gastral surface; recrystallization and resilicification has enlarged the trabs; recrystallized masses may be the remains of gastralia, X4.

2, 4 *Calycocoelia typicalis* Bassler. 2, sagittal view of 1766TX53, showing the deep penetration of the spongocoel and the pattern of trab pinnation; faint, slightly arched radial canals can also be seen, X1; 4, exterior view of holotype USNM 79637. Compare the shape of this individual to that of the other figured specimens. Members of this species can be found having shapes varying from pedunculate to obconical to cylindrical.

PLATE 6

CALYCOCOELIA, NEVADOCOELIA

Figure

1 *Calycocoelia typicalis* Bassler. 1, exterior view of 1767TX18, showing the budding of one individual off of another, X1.

2-4 *Calycocoelia murella*, n. sp. 2, 4, exterior views of holotype 1784TX44, illustrating the distinctive, tubular shape and regular spiculation of the sponge, X1 and X2, respectively; 3, transverse section through the holotype, revealing the relatively large spongocoel and thin walls that characterize this species, X2.

5, 8-9 *Nevadocoelia traini* Bassler. 5, sagittal section of 1766TX48, revealing the slightly arched radial canals and deep spongocoel found in this species, X1; 8, exterior view of 1766TX46, showing distibution of surficial nodes, X1; 9, exterior view of lectotype USNM 79633c, X1.

6-7 *Nevadocoelia wistae* Bassler. 6, top view of specimen 1767TX19, illustrating the straight to slightly sinuous canals seen in this species, X2; 7, close-up of lectotype USNM 79632c, showing the scalariform skeleton and dense spiculation composing the ridges, X4.

PLATE 7

NEVADOCOELIA

Figure

1 *Nevadocoelia grandis* Bassler. 1, exterior view of holotype USNM 79634; the surficial ornament on this specimen is similar to that of *N. wistae*, but other individuals have nodes like or *N. traini* or some combination of both, X1.

3 *Nevadocoelia traini* Bassler. 3, top view of 1760TX45, illustrating the relatively small osculum, X1.

2, 4-6 *Nevadocoelia wistae* Bassler. 2, exterior view of 1766TX59, showing the tubular to pedunculate shape and anastomosing ridges characteristic of the species; 4, top view of specimen 1766TX61, illustrating the oscular lip often found in members of this genus, X1; 5, exterior view of lectotype USNM 79632c, X1; 6, sagittal view of specimen 1766TX62, revealing nature of radial canals, X1.

PLATE 8

PATELLISPONGIA

Figure

1-5 *Patellispongia oculata* Bassler. 1, gastral view of USNM 79639, holotype for *Patellispongia clintoni* Bassler; note the large, scattered gastral pores characteristic of *P. oculata;* the circular object in the center of the specimen is a National Museum sticker, X1; 2, close-up of dermal surface of specimen 1766TX63, revealing the more regular arrangement of the dermal pores, X4; 3, gastral view of USNM 79638, holotype of *P. oculata,* the ectosomal pores on this specimen are unusually small and close together, but well within the range of variation seen in this species, X1; 4, dermal view of 1766TX37, showing the typical palmate shape of the species; 5, dermal view of specimen USNM 79640, holotype for *P. minutipora.* Only the dermal side is preserved on this specimen, and Bassler used the smaller pore size as the basis for separating this species. However, the dermal ectosomal pores are consistently smaller than the gastral ectosomal pores in all specimens of *Patellispongia* from Ikes Canyon, so distinguishing taxa on this basis is unjustified.

PLATE 9

PATELLISPONGIA

Figure

1-5 *Patellispongia oculata* Bassler. 1, close-up view of gastral surface of 1766TX33, showing the difference between surface covered by ectosome (bottom) and exposed endosome (top), X1.75; 2, sagittal view of specimen 1766TX42, showing nature of the radial canals, X2; 3, dermal view of USNM 99602, holotype for *P. magnipora;* although originally defined by the large gastral pore size, the ectosomal pore sizes on the incurrent side of the sponge are no larger than that of any other specimens of *Patellispongia* from Ikes Canyon; a well-preserved specimen of a craniopsid parasite is attached to the upper left region of the surface; 4, close-up of 1766TX36, revealing some of the shallow, tangential canals that empty into the gastral pores, X2; 5, gastral view of 1784TX7, a representative of *Patellispongia* cf. *P. oculata* from the Shingle Limestone, X1. The ectosomal pores on the gastral surfaces of specimens from Sunnyside are, on average, smaller and more closely-spaced than those from Ikes Canyon. The range of variation in size and spacing, however, falls well within that seen in the collections from the latter locality, so the erection of a new species on this basis alone is not justified. The slight differences in pore sizes and spacing between these two populations is probably a result of local variation.

PLATE 10

PATELLISPONGIA, RUGOCOELIA

Figure

1 *Patellispongia oculata* Bassler. 1, view of dermal surface of 1766TX32, showing the radiation of trabs away from the base. While many individuals are palmate, others, such as this, are more bowl-shaped, X1.5.

2-3, 5, 7 *Patellispongia brosiusae*, n. sp. 2, close-up of the dermal surface of paratype 1784TX16, illustrating the anthaspidellid spiculature, X3; 3, gastral view of holotype 1784TX12, showing the high degree of skeletal regularity found in this species; note the near absence of a gastral ectosome: this may be a result of abrasion, but all of the specimens assigned to this species lacked a well-developed gastral layer but had a reasonably thick dermal layer, indicating that the near absence of a gastal ectosome was original rather than taphonomic, X2; 5, gastral view of paratype 1784TX15, X1; 7, dermal view of holotype 1784TX12; note the well-developed ectosome and the slight annulations, X2.

4, 6, 8 *Rugocoelia eganensis*, n. gen., n. sp. 4, gastral view of part of the holotype, 1784TX1, showing the smooth gastral surface and scattered ectosomal pores, X2; 6, close-up of gastral surface of paratype 1784TX6, X4; 8, sagittal section of paratype 1784TX57, revealing the vertically-stacked radial canals and distinctive "rippled" profile; the light-colored sponge material is partly covered by darker matrix, X1.

PLATE 11

COLINISPONGIA, RUGOCOELIA

Figure

1, 4 *Colinispongia regularis*, n. gen., n. sp. 1, gastral view of holotype 1787TX1, showing the remarkably regular size and quadrate geometry of the ectosomal pore arrangement, X1; 4, sagittal view of holotype, illustrating horizontal radial canals and trab pinnation, X1.

2-3, 5 *Rugocoelia eganensis*, n. gen., n. sp. 2-3, dermal views of holotype 1784TX1, showing the distinctive, evenly-spaced ridges that characterize the genus, X1 and X1.5, respectively; 5, exterior view of paratype 1784TX2, showing the original bowl-like shape of the sponge, X1.

PLATE 12

RUGOCOELIA, STREPTOSOLEN, and *VERPASPONGIA*

Figure

1 *Rugocoelia eganensis,* n. gen., n. sp. 1, dermal view of holotype 1784TX1, showing the anthaspidellid spiculature and ectosomal thickening along the ridges, X2.

2, 4 *Verpaspongia nodosa,* n. gen., n. sp.. 2, exterior view of holotype 1767TX7, showing the overall shape of the sponge and the distribution of surficial nodes, X1; 4, top view of holotype illustrating the oscular lip; note that the nodes cover even the upper surface of the sponge, X2.

5 *Streptosolen occidentalis* Bassler. 5, exterior view of specimen 1784TX55, X1.

3, 6-10 *Streptosolen mccafferyi,* n. sp. 3, exterior view of paratype 1784TX56, X1; 6-7, exterior views of holotype 1784TX47, showing scattered dermal pores, X1, X2, respectively; compare the shape of this individual with that of the specimen in Figure 3: members of this species range from being almost flat to more erect and obconical; 8, transverse section through paratype 1784TX50, revealing the numerous vertical apochetes that run though the sponge, X1; 9, sagittal section through holotype 1784TX47, illustrating the vertical apochetes and fine, irregular spiculation, X2; 10, top view of paratype 1784TX53, showing the shallow spongocoel and the radiating canals that empty into it, X1.

PLATE 13

STREPTOSOLEN

Figure

1-5 *Streptosolen nodosus*, n. sp. 1, exterior view of holotype 1766TX21, showing the surficial nodes that characterize the species, X1; 2, exterior view of paratype 1766TX26, showing the more pedunculate shape of some individuals, X1; 3, sagittal section of paratype 1766TX22, illustrating the vertical apochetes that empty into the shallow spongocoel and the irregular arrangement of the radial and other canals, X1; 4-5, top view of holotype 1766TX21 and paratype 1766TX26, respectively; note the radiating canals and large apopores associated with the spongocoel, both X2.

6-7 *Streptosolen occidentalis* Bassler. 6, exterior view of lectotype USNM 79645b, illustrating the irregular spiculature and canal disposition characteristic of the genus, X1; 7, top view of 1766TX3, a specimen with two spongocoels, a not uncommon feature of this species; also note the sinuous, radiating canals, X1.

PLATE 14

EGANIA, STREPTOSOLEN

Figure

1, 4-5, 8 *Streptosolen occidentalis* Bassler. 1, exterior view of 1766TX54; compare the tall cylindrical shape of this specimen to that of the lectotype and other figured specimens: members of this species have a highly variable shape ranging from squat and widely obconical to almost tubular, X1; 4, sagittal view of specimen 1766TX56, illustrating the sinuous canals and and how they develop into vertical apochetes, X1; 5, sagittal view of 1767TX16, again revealing how the radial canals become vertical and empty into the shallow spongocoel; the canals are so sinuous that they appear discontinuous in cross-section; 7, top view of 1766TX57, showing the large number of apochetes that empty into the main spongocoel, a feature that serves to distinguish this species from its congeneric taxa; also note the second, smaller spongocoel in the lower left of the specimen, X1.

2-3, 7 *Egania typicalis*, n. gen., n. sp. 2-3, sagittal section through paratype 1784TX41, revealing the fine radial canals and scattered vertical canals, X1 and X2, respectively; 7, top view of paratype 1784TX42, X2;

6 *Streptosolen* sp. Griefe and Langenheim. 6, exterior view of badly weathered and resilicified specimen UCMP 30719, X2.

PLATE 15

EGANIA, LISSOCOELIA

Figure

1-4 *Egania typicalis*, n. gen. n. sp. 1, sagittal view of paratype 1784TX43, showing trab pinnation, X2; 2, exterior view of paratype 1784TX42, illustrating fine, irregular spiculature, X2; 3, transverse section of holotype 1784TX38, revealing the scattered vertical canals that characterize this genus, X1 and 2, respectively; 4, sagittal view of paratype 1784TX40, X2.

5-9 *Lissocoelia ramosa* Bassler. 5, exterior view of lectotype USNM 79636b, X1; 6-7, side views of specimen UCMP 10319 from the Mazourka Group; note the dichotomous branching that characterizes the species and the close association between adjacent branches, both X1; 8, same specimen as above, top view, X1; 9, close-up of specimen 1766TX34; the fine, polyclonid spiculature and scattered pores are typical of the family, but reminiscent of the ectosome of some anthaspidellids, X4.

10-14 *Lissocoelia cylindrica*, n. sp. 10, exterior view of holotype 1784TX32; X1, X2, respectively; 11, side view of paratype 1784TX34, showing how the stem widens as it branches; also note the fine, irregular spiculation characteristic of this genus, X2; 12, natural transverse section of 1784TX58, illustrating the radial canals and showing how much wider the sponge becomes as it branches, X2; 13, sagittal section of paratype 1784TX31, illustrating radial canals and trabs, X2; 14, exterior view of paratype 1784TX34, X2.

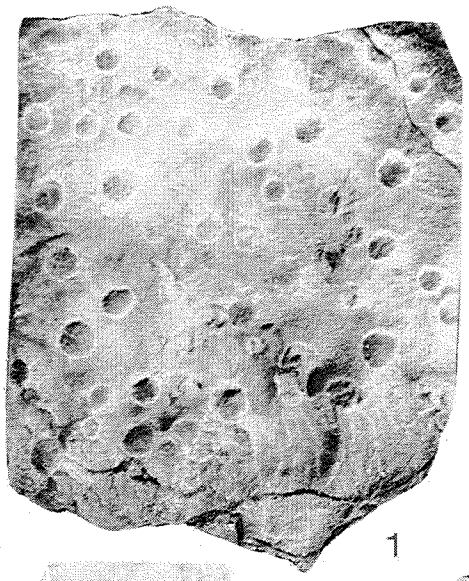
PLATE 16

HESPEROCOELIA

Figure

1-6 *Hesperocoelia typicalis* Bassler. 1, close-up cotype USNM 79642, revealing the multiple excurrent canals that characterize this genus and the radial canals that distinguish it from *Pseudopalmatohindia* Rigby and Webby; although Bassler separated *H. typicalis* and *H. undulata* primarily on the shape of their oscula, the excurrent openings in this specimen alone vary from nearly circular to highly ovoid, X4; 2, same specimen, natural size, X1; 3, sagittal view of 1766TX65, showing the radial canals, excurrent canals, and trab pinnation, X1; 4, exterior view of lectotype USNM 79641, X1; 5, close-up of same specimen, showing the fine, irregular, polyclonid spiculature typical of the family; 6, exterior view of USNM 79642, cotype for *H. undulata*, X1.

Plate 1



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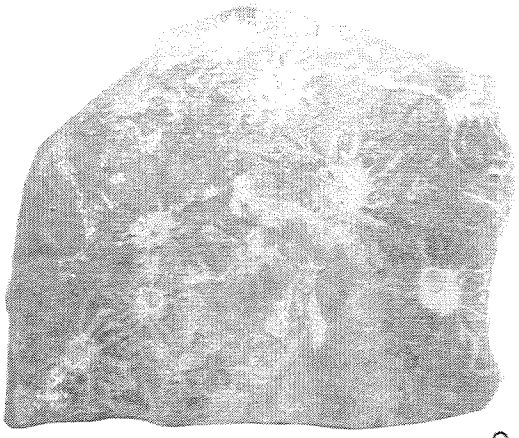

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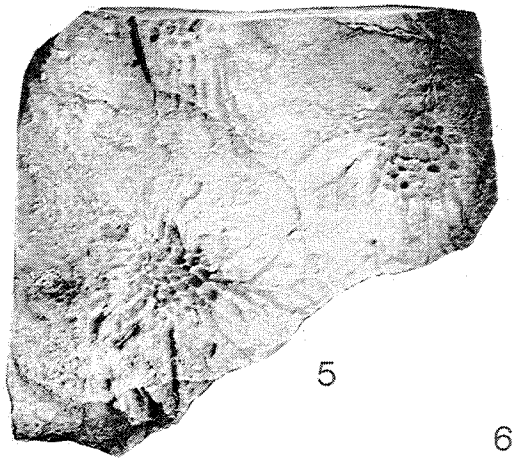

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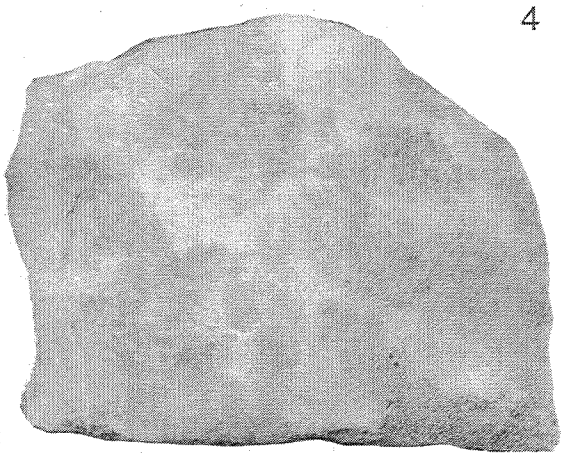

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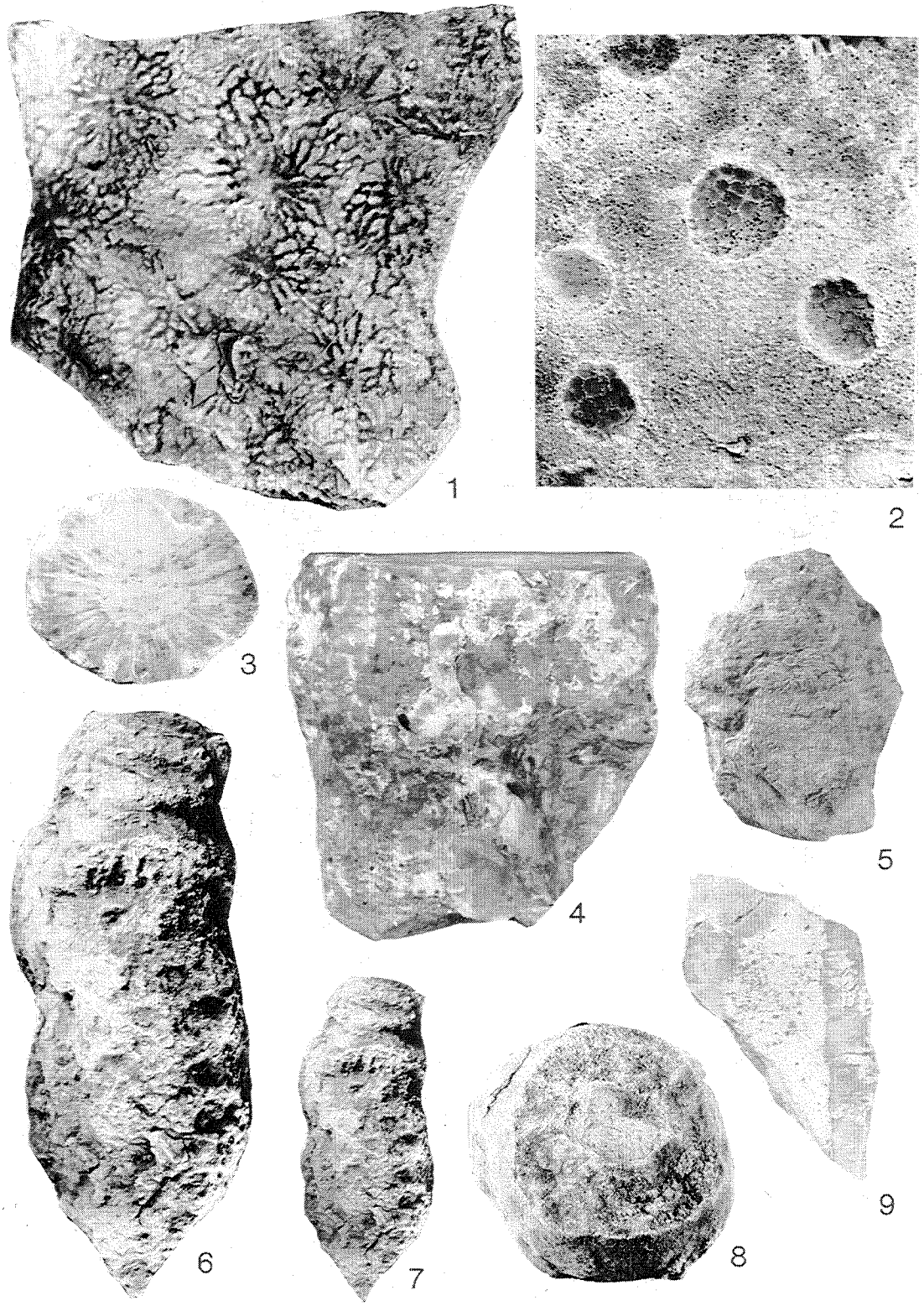

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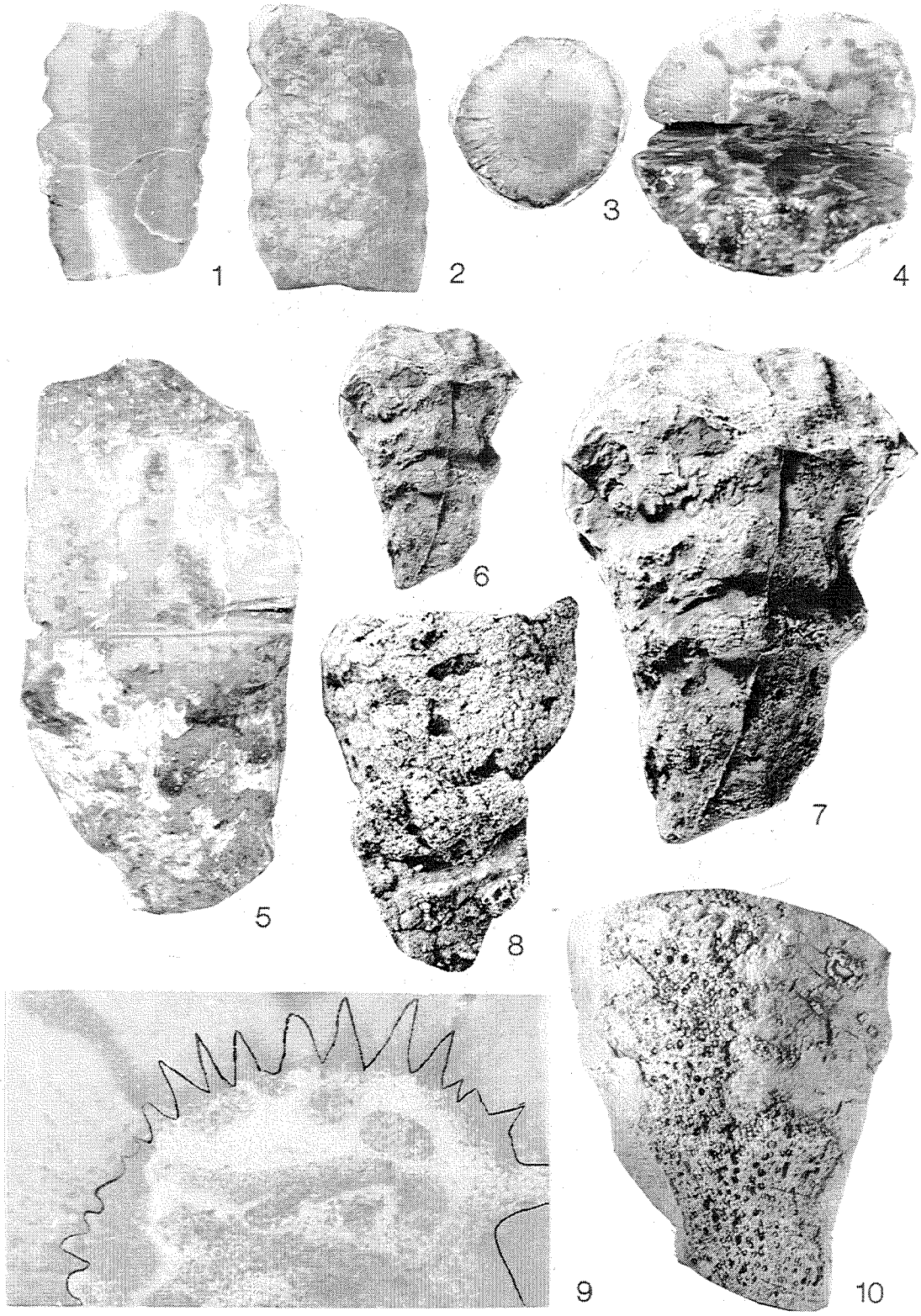

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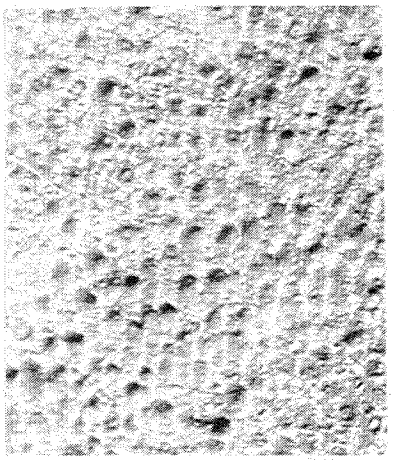

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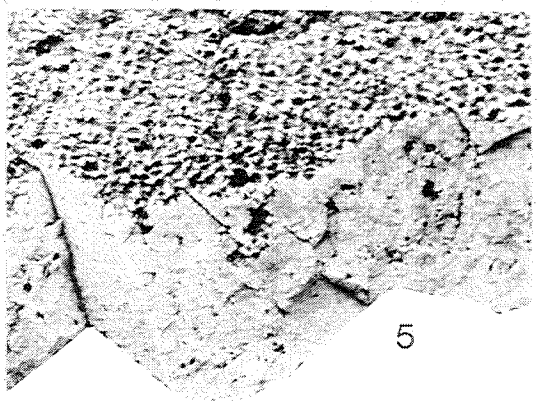

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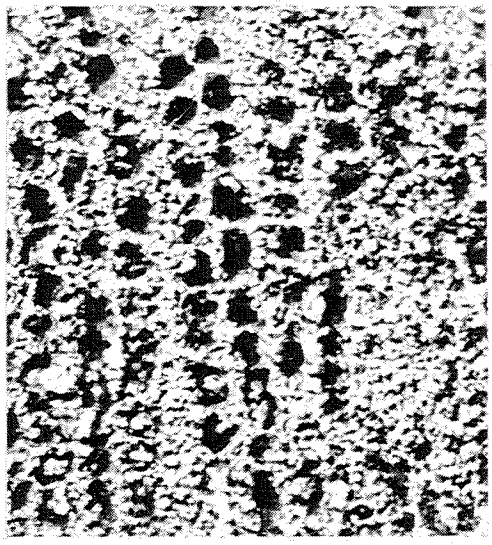

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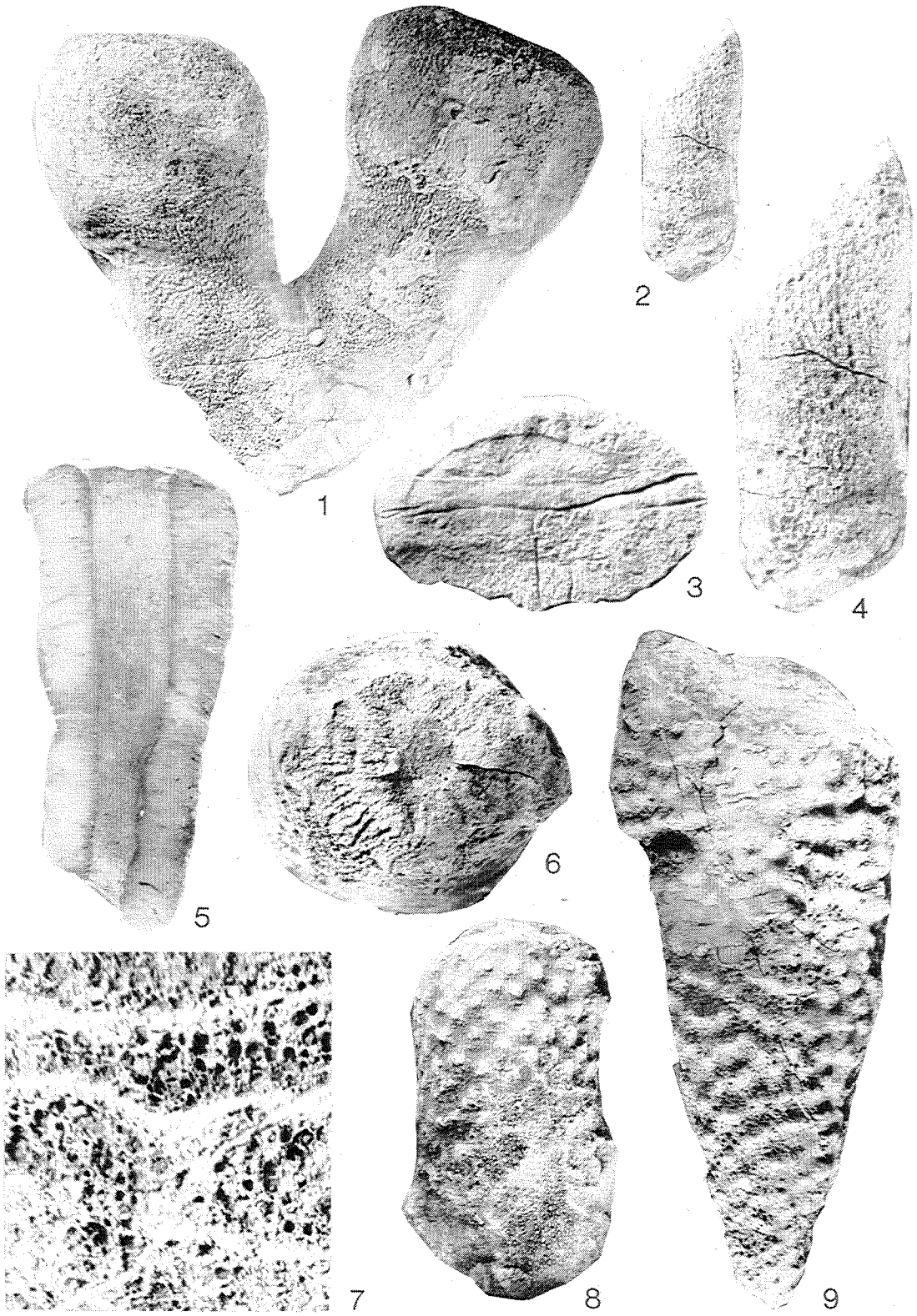

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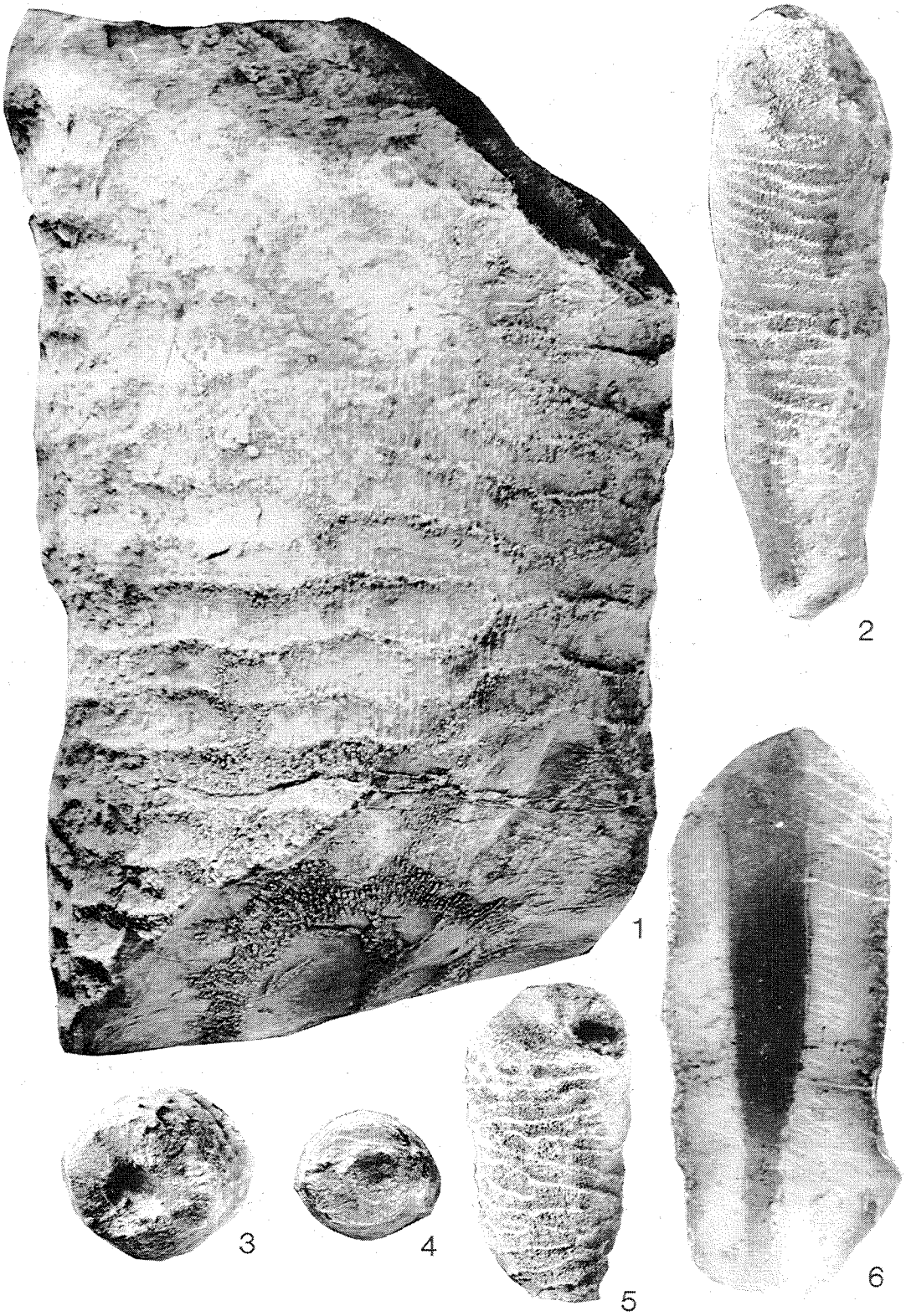

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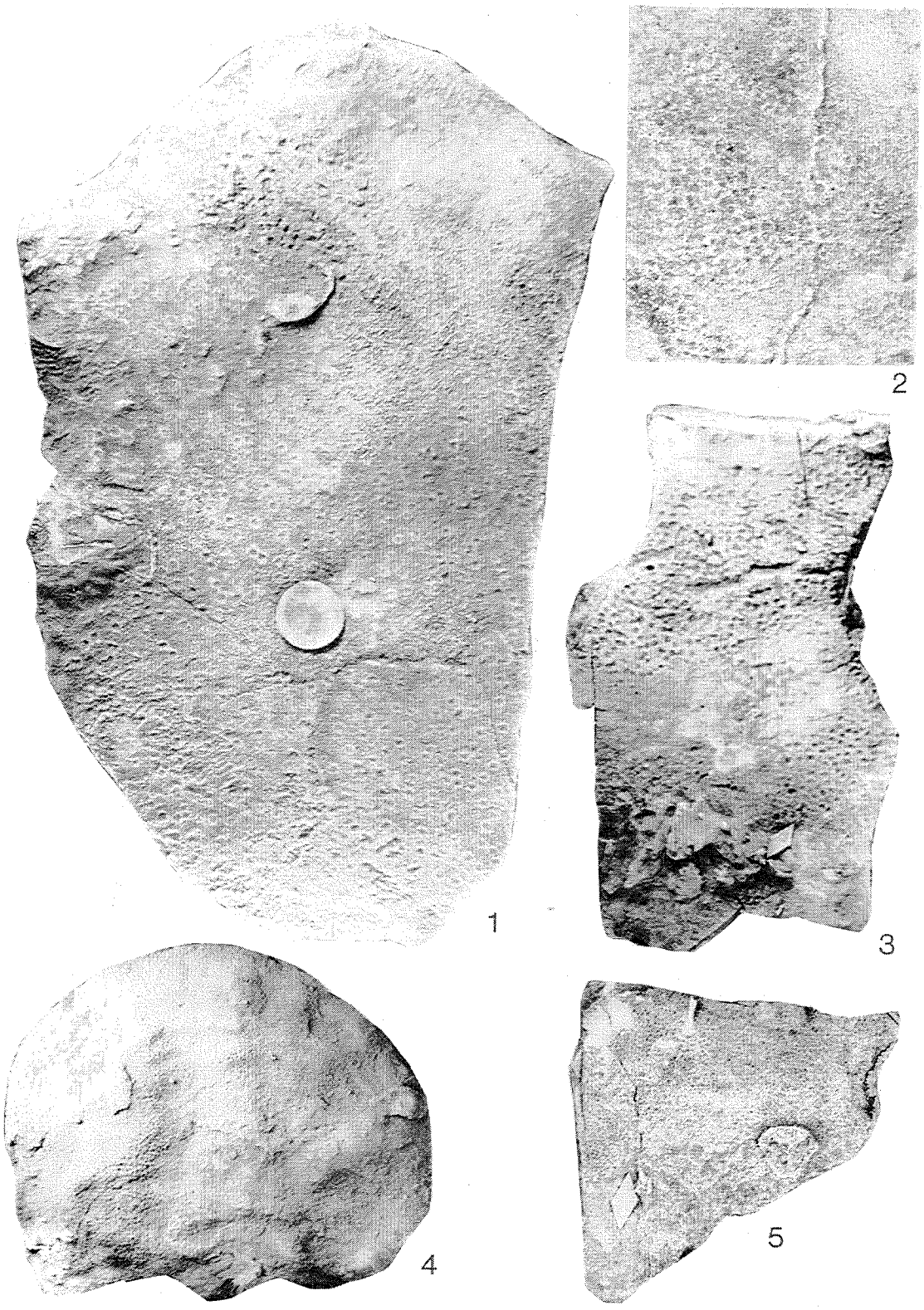

Plate 9

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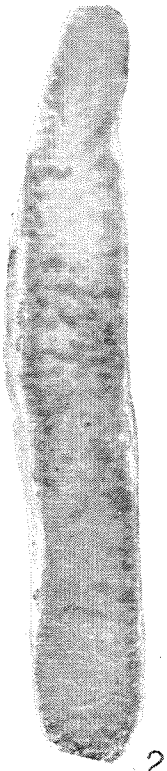

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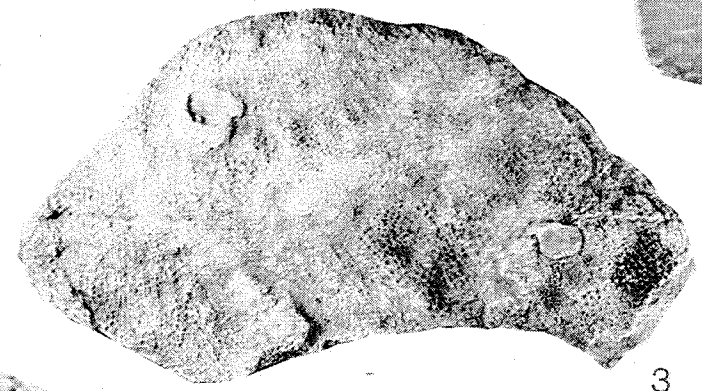

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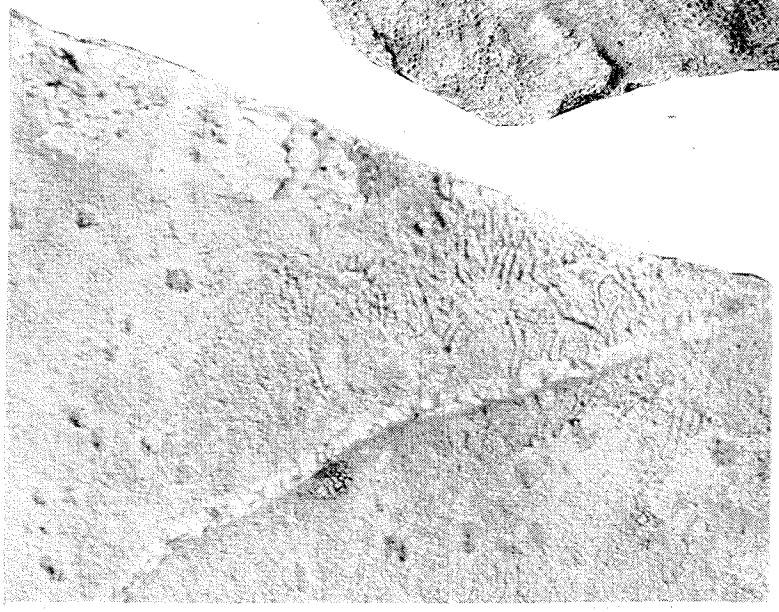

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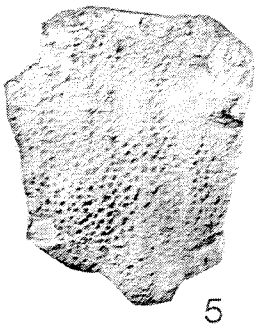

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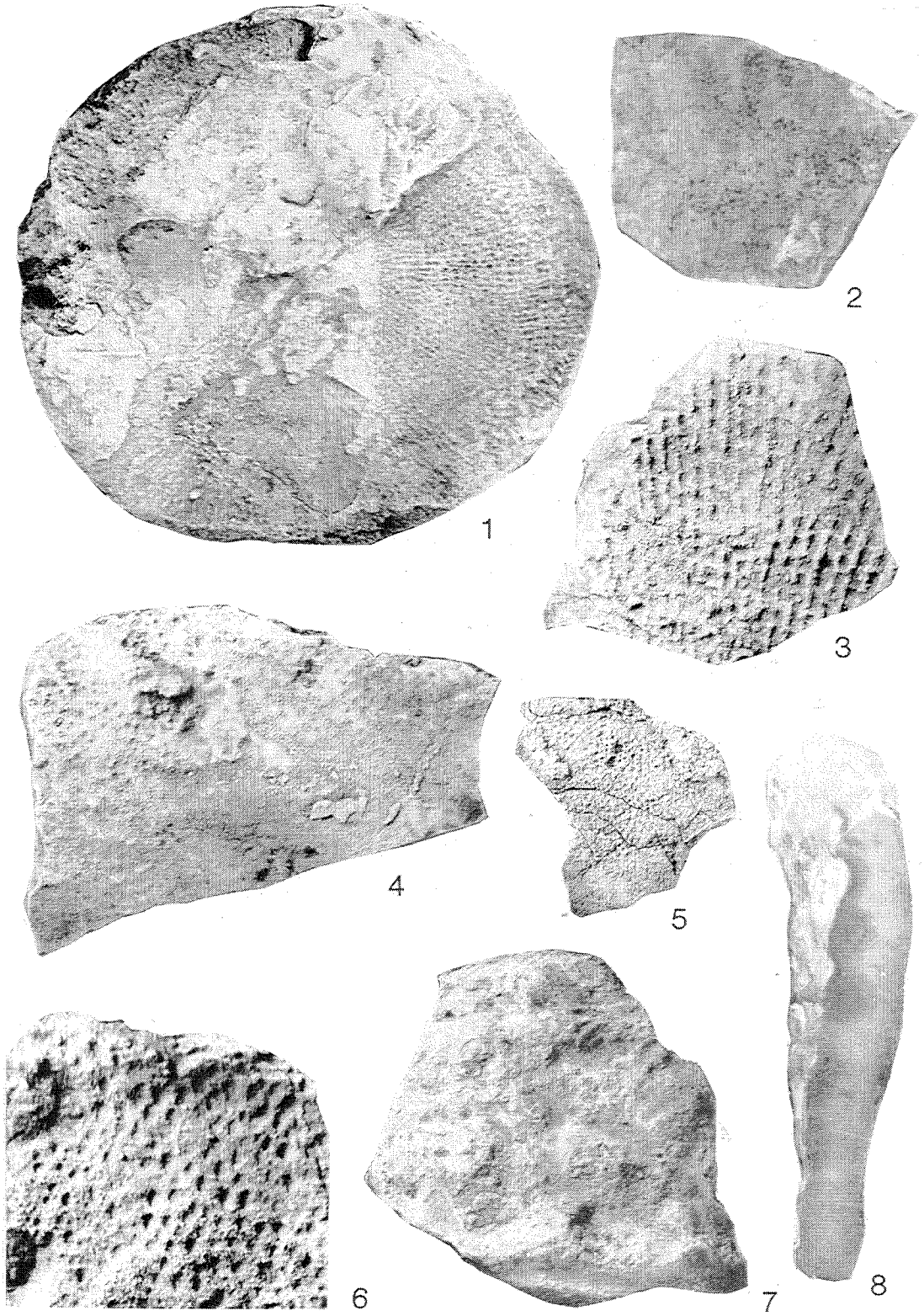

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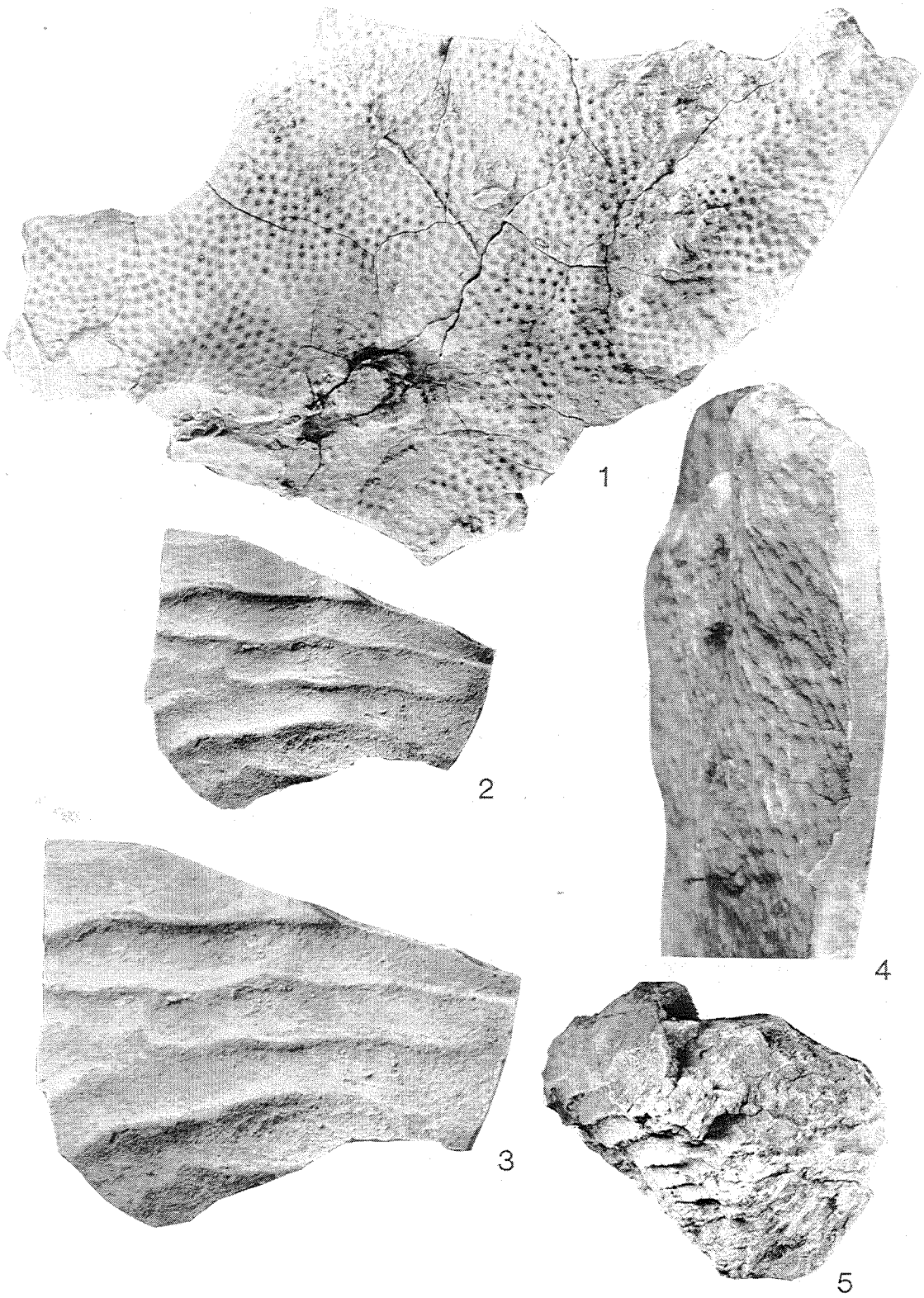

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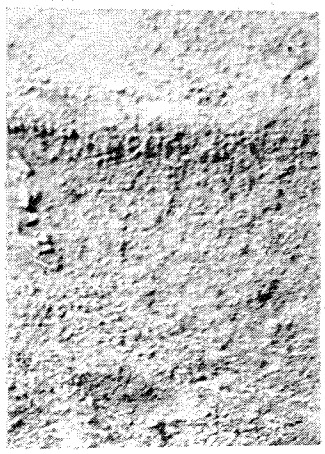
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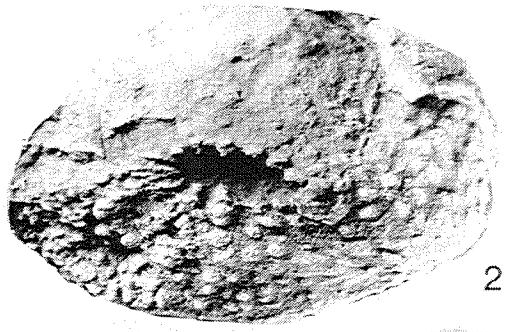
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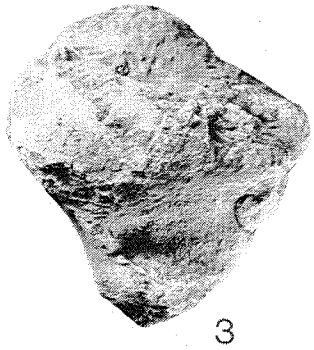
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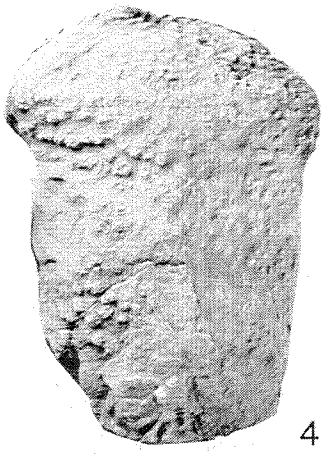
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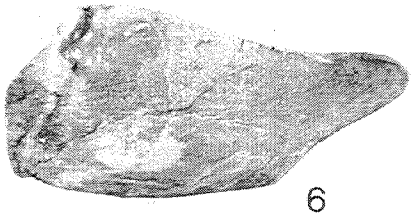
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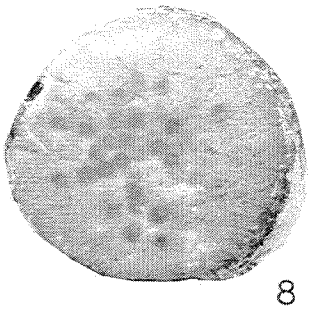
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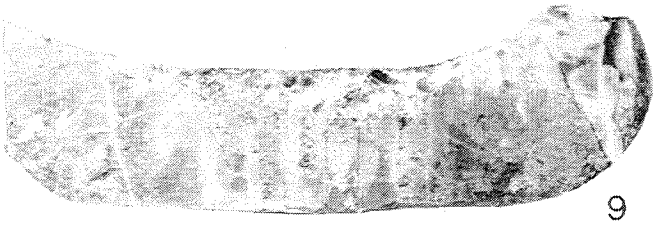
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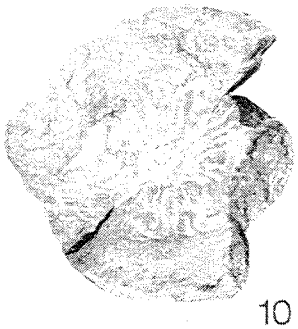
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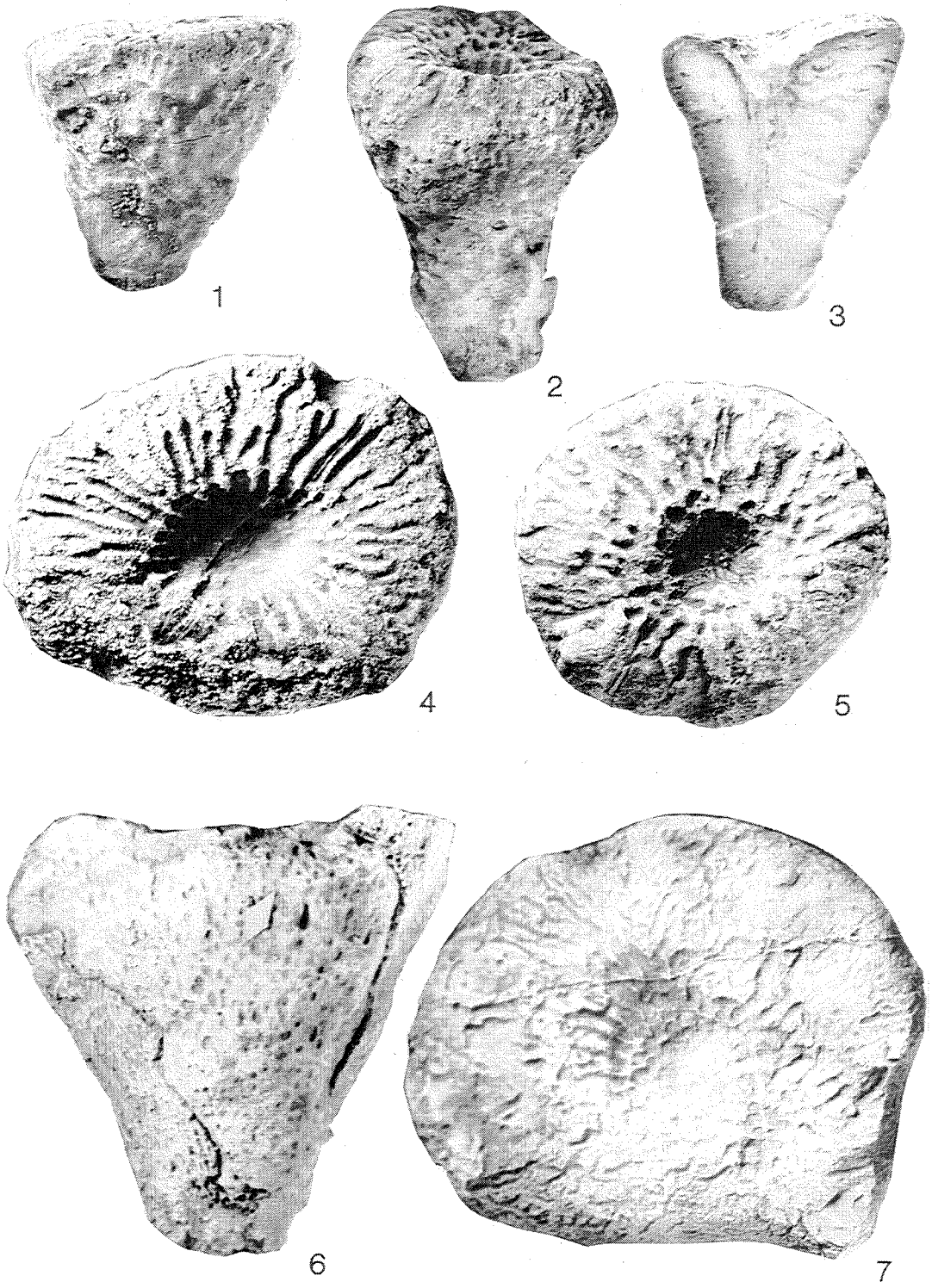

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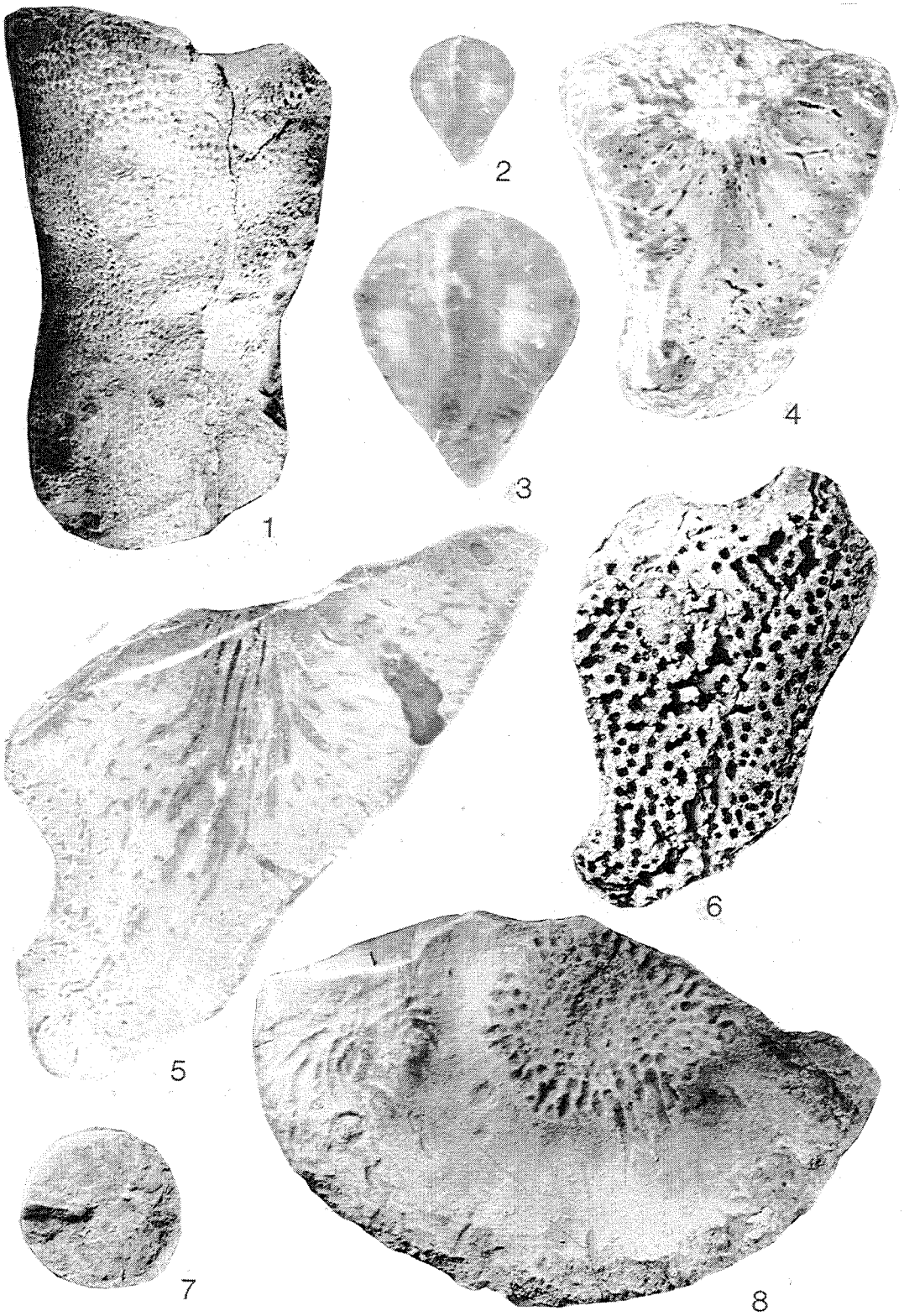

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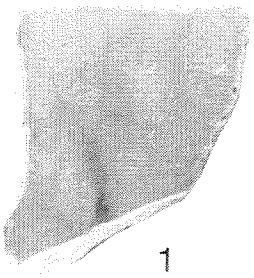
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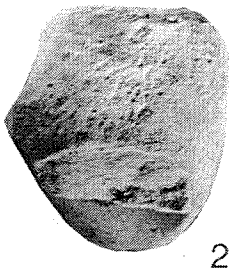
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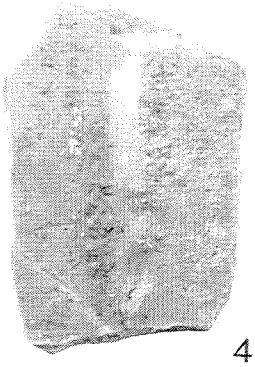
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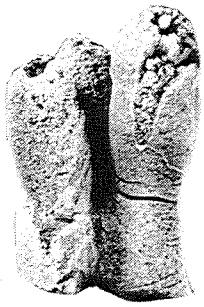
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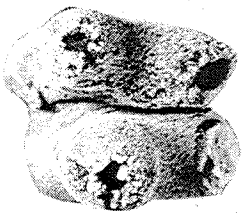
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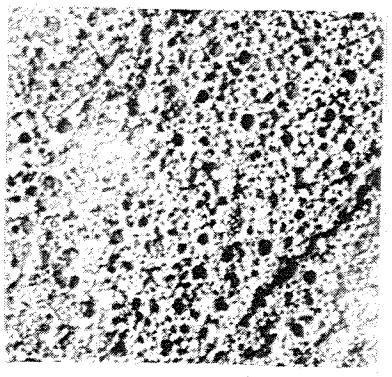
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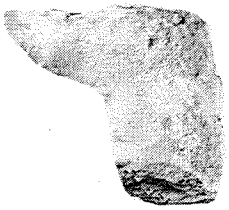
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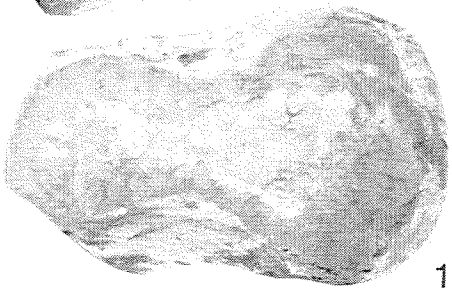
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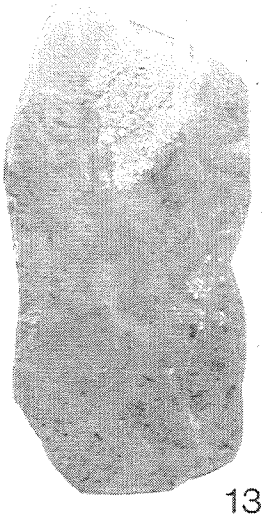
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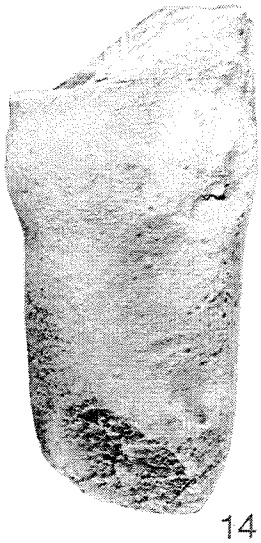
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Plate 16

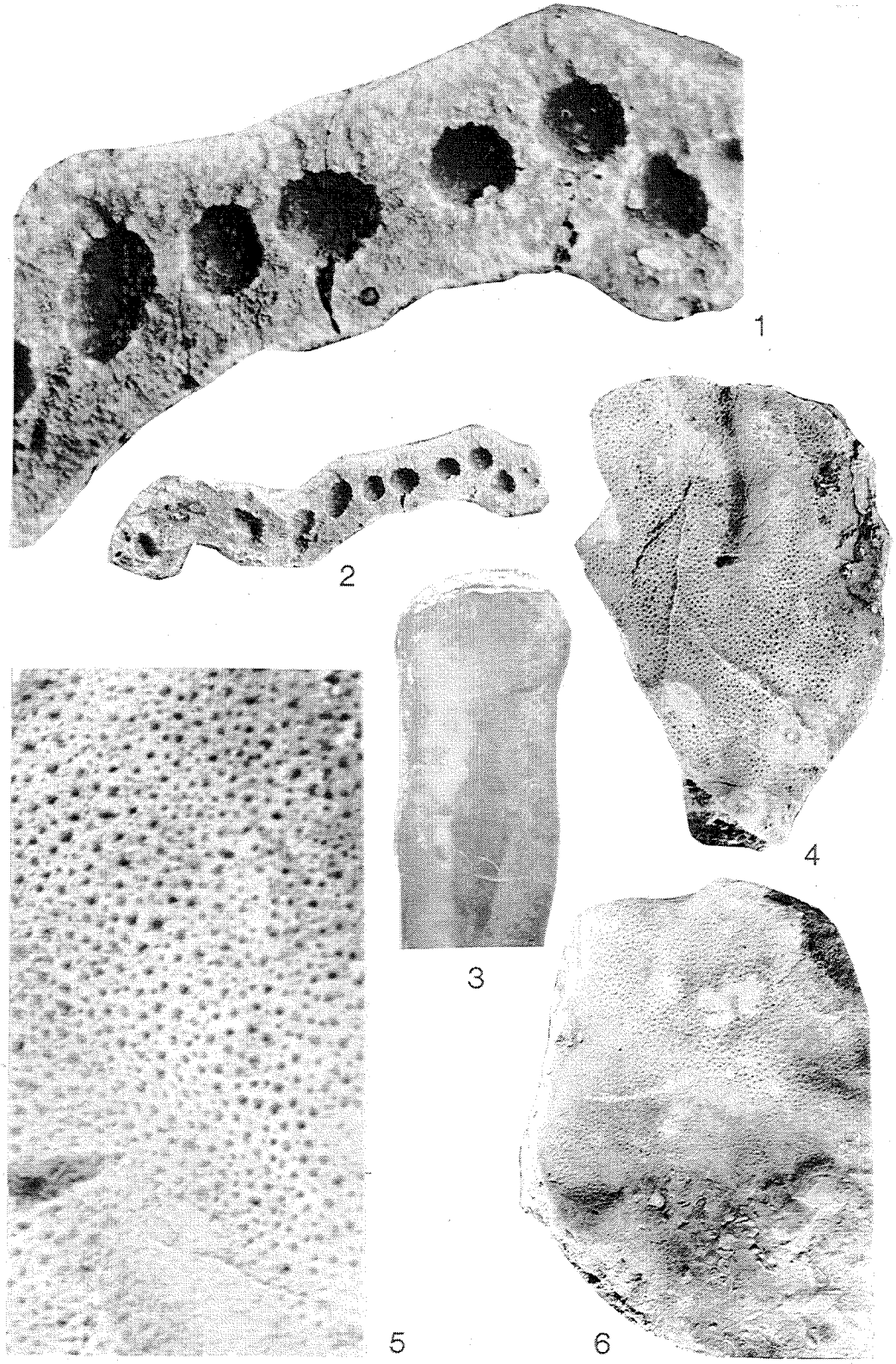


Figure 1 — Map of the Great Basin showing localities mentioned in the text: 1.) Ikes Canyon, 2.) Sunnyside, and 3.) Ibex area of western Utah. Ikes Canyon in the Toquima Range and the Sunnyside locality in the Egan Range were the principle collecting sites.

Figure 2 — Map of localities (**A**) and diagram (**B**) tracing the distribution of the Pogonip Group and its constituents across the Great Basin. The localities shown in **A** are: 1.) Death Valley; 2.) Meiklejohn Peak; 3.) the Hot Creek Range; 4.) Ikes Canyon; 5.) Whiterock Canyon; 6.) Mount Hamilton; 7.) Sunnyside; 8.) the Snake Range; 9.) the Ibex area of Utah; 10.) Fish Springs; and 11.) the Pavant Range. Note that many of the units are diachronous. The biostratigraphic zones are based on trilobites, brachiopods and other fossils. The lowermost zones are: 1.) *Saukiella junia* Zone, 2.) *Saukiella serotina* Zone, 3.) *Corbinia apopsis* Zone, and 4.) *Missisquoia* Zone. Data compiled from Hintze (1952), Kellogg (1963); Ross (1964); Lowell (1965); Ross (1970), Hintze (1979), Miller et al. (1982); Hintze et al. (1985); Ziony and Kleinhampl (1985); Palmer and Rowland (1989); Taylor et al. (1989); Ross and Etheridge (1991), and unpublished field trip notes by Ross. CP = Crystal Peak Dolomite, WR = Watson Ranch Quartzite. The boundaries and even identities of the Notch Peak Formation, House Limestone, and Whipple Cave Formation in eastern Nevada and western Utah are still a matter of debate and will probably be changed in the near future (Taylor, pers. comm., 1/92). The diachronous and gradational nature of the contacts in the Hot Creek Range make these formation boundaries questionable as well. Note that the diagram shows the stratigraphic ranges of units; their relative thicknesses may be different from those shown.

Figure 3 — Stratigraphic section through the Antelope Valley Limestone at Ikes Canyon, showing lithologies and major biofacies discussed in the text. **OF** = overlying facies, **SBF** = sponge bed facies, **UFF** = upper fossiliferous facies, **UF** = unfossiliferous facies, **LFF** = lower fossiliferus facies, and **LOF** = low-oxygen facies. Note that the sponge beds occur at the boundary between the *Orthidiella* and *Anomalorthis* Zones.

Figure 4 — Stratigraphic section through the Shingle Limestone at Sunnyside, showing lithologies and major biofacies discussed in the text. **USL** = uppermost Shingle Limestone units overlying the sponge mound horizon, **SMH** = lithistid sponge mound horizon, including both mounds and adjacent beds, **CMH** = *Calathium* mound horizon, and **IFC** = intraformational conglomerate underlying the mound horizons. The sponge and calathid mounds occur within a short stratigraphic distance of each other, and previous authors have mistaken the sponge bioherms for calathid buildups. Based in part on Kellogg (1963).

Figure 5 — Diagram illustrating some of the types of spicules discussed in the text. The dendroclones are the dominant spicules in the lithistid sponges described here. After Rigby (1983a).

Figure 6 — Comparison of anthaspidellid (**A**) and streptosolenid (**B**) skeletons. Note that the dendroclones are typically amphiarborescent, horizontal, and connect adjacent trabs in A, whereas they are usually polyclonid and connect trabs of different distances from the surface in B. As a result, the skeleton of anthaspidellids is much more regular than that of streptosolenids. Both figures are at approximately x40.

Figure 7 — Oscular cluster size versus distance between clusters in *Anthaspidella* from the Antelope Valley Limestone at Ikes Canyon. The distances are measured between the centers of clusters, and all values are averages. The actual range of sizes and distances in an individual usually varies at least a millimeter from the average within a given individual.

Figure 8 — Average wall thicknesses among specimens of *Anthaspidella* from the Antelope Valley Limestone at Ikes Canyon. The specimens are arranged in order of increasing wall thickness to illustrate the continuum of variation in this feature between individuals.

Figure 9 — Diagram illustrating the value of monaxons coring canals. Such a monaxon reduces the overall cross-section of the canal by only 25%, while reducing the largest opening by 75%. Such spicules would have helped to prevent parasites or sedimentary particles form entering the canal, while probably not significantly impairing the flow of water through the sponge.

Figure 10 — Plot of minimum versus maximum pore size in the gastral ectosome of *Patellispongia* from the Antelope Valley Limestone at Ikes Canyon. As the graph shows, the pore sizes are highly variable and separating species on this basis cannot be justified. In this and the following diagrams, the values are rounded to the nearest 0.1 mm.

Figure 11 — Plot of minimum versus maximum distances between neighboring pores in the gastral ectosome of *Patellispongia* from the Antelope Valley Limestone at Ikes Canyon. As the graph shows, the distances between pores are highly variable and separating species on this basis cannot be justified.

Figure 12— Plot of minimum versus maximum pore size in the dermal ectosome of *Patellispongia* from the Antelope Valley Limestone at Ikes Canyon. As the graph shows, the pore sizes are highly variable and separating species on this basis cannot be justified.

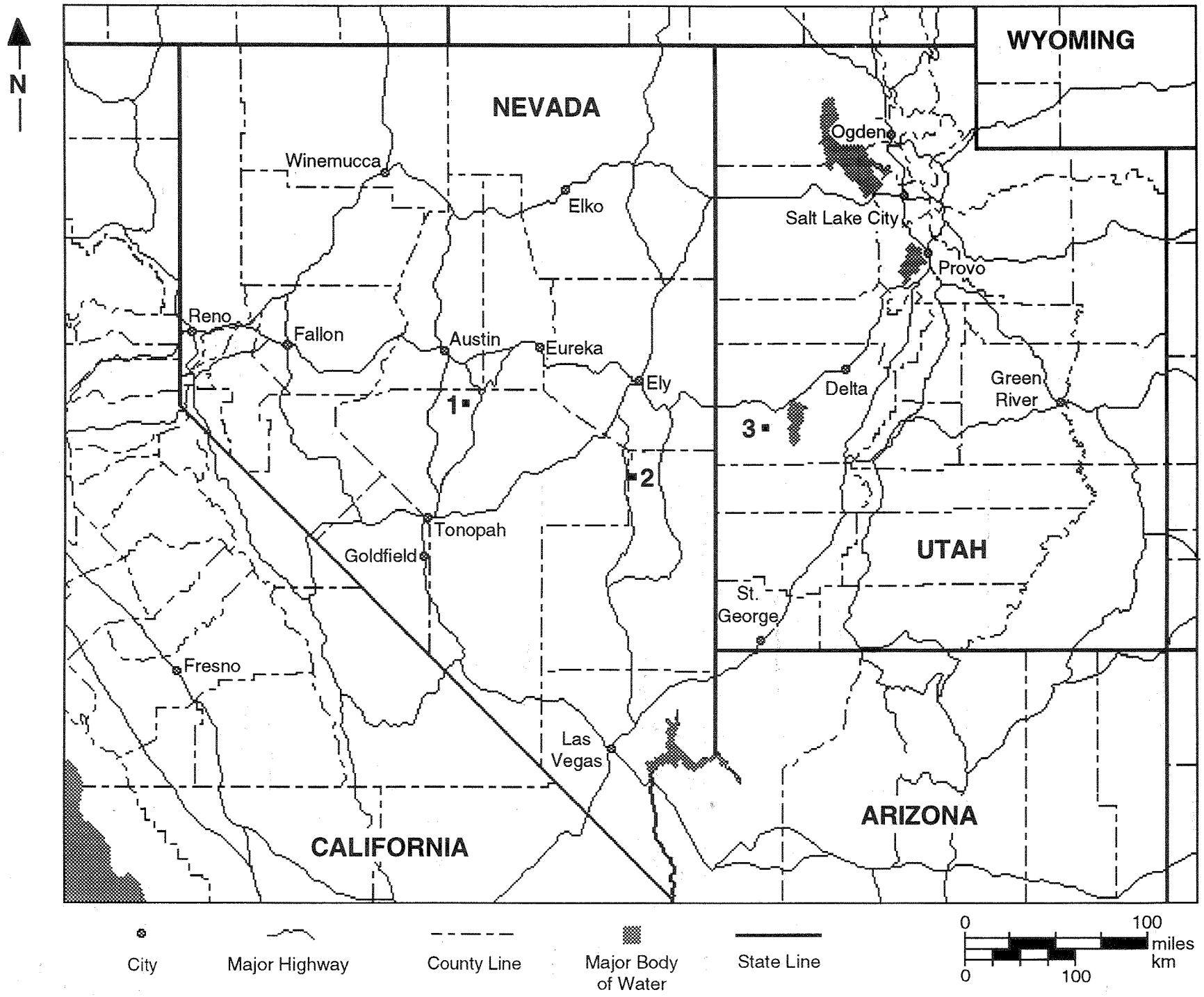
Figure 13 — Plot of minimum versus maximum distances between neighboring pores in the dermal ectosome of *Patellispongia* from the Antelope Valley Limestone at Ikes Canyon. As the graph shows, the distances between pores are highly variable and separating species on this basis cannot be justified.

Figure 14 — Plot of average size versus average distance between neighboring pores in the gastral (excurrent) and dermal (incurrent) ectosome of *Patellispongia* from the Antelope Valley Limestone at Ikes Canyon. Although the dermal pores are almost always smaller than the gastral pores, there is a great deal of variation in ectosomal pore size and spacing. Using such features to distinguish between different species is therefore unjustified.

Figure 15 — Close-up map of Ikes Canyon showing the line of the measured section. The specimens were primarily collected on the north side of the canyon along the flanks of peak 8474, and on the south side of the canyon in the side valley just north of peak 8317. More general locality information is shown in Figure 1.

Figure 16 — Close-up map of the Sunnyside exposure showing the line of the measured section through the Shingle Limestone. The specimens were primarily collected along the west side of peak 7726. More general locality information is shown in Figure 1.

Figure 1


N
NEVADA
WYOMING
UTAH
ARIZONA
CALIFORNIA
Winemucca
Elko
Ogden
Salt Lake City
Provo
Reno
Fallon
Austin
Eureka
Ely
Delta
Green River
1
2
3
Tonopah
Goldfield
St. George
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Las Vegas
City
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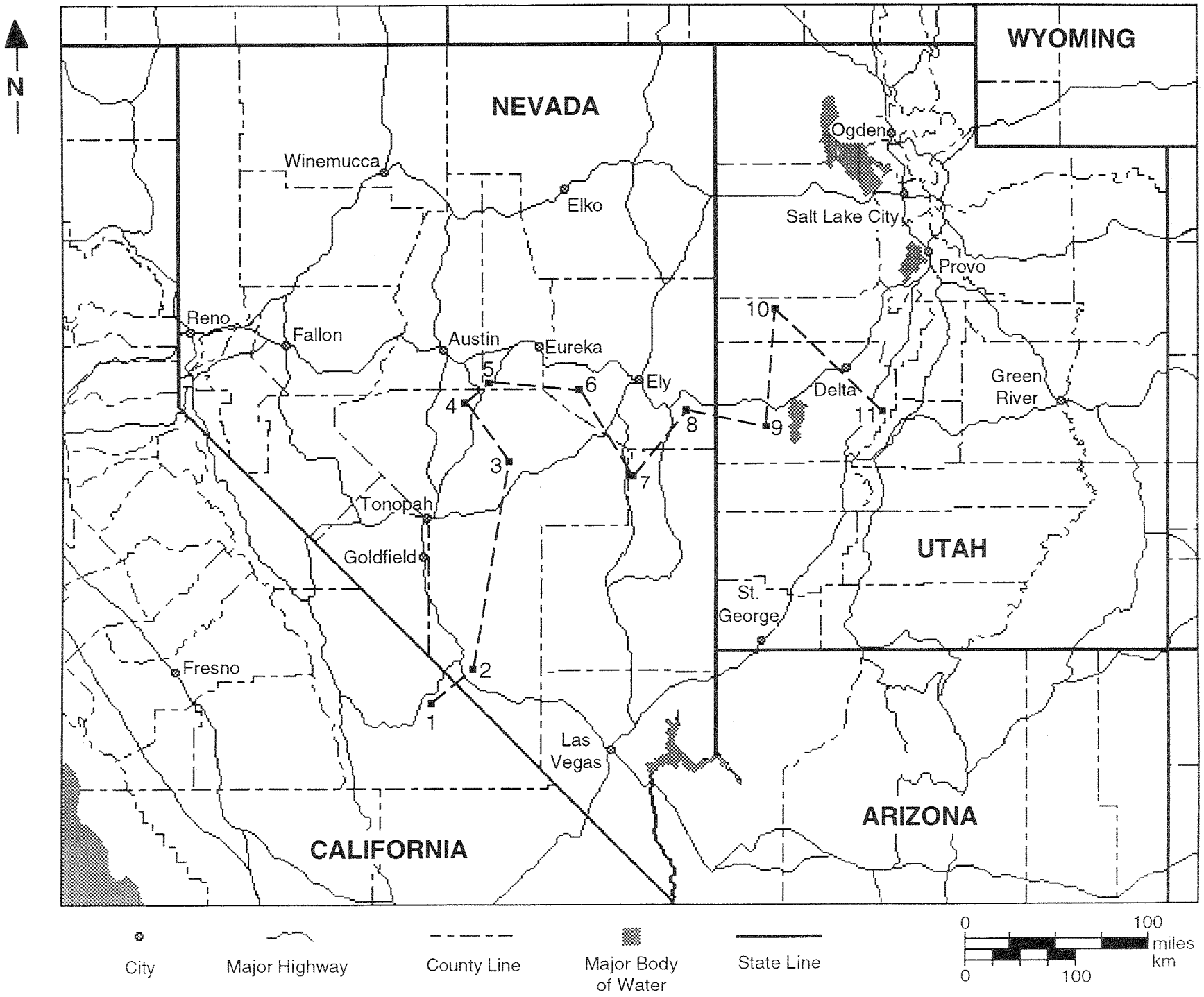
A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Goldfield
Fresno
Las Vegas
Ogden
Salt Lake City
Provo
Delta
Green River
St. George
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2
3
4
5
6
7
8
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10
11
City
Major Highway
County Line
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miles
km

Figure 2A

Figure 2B

B

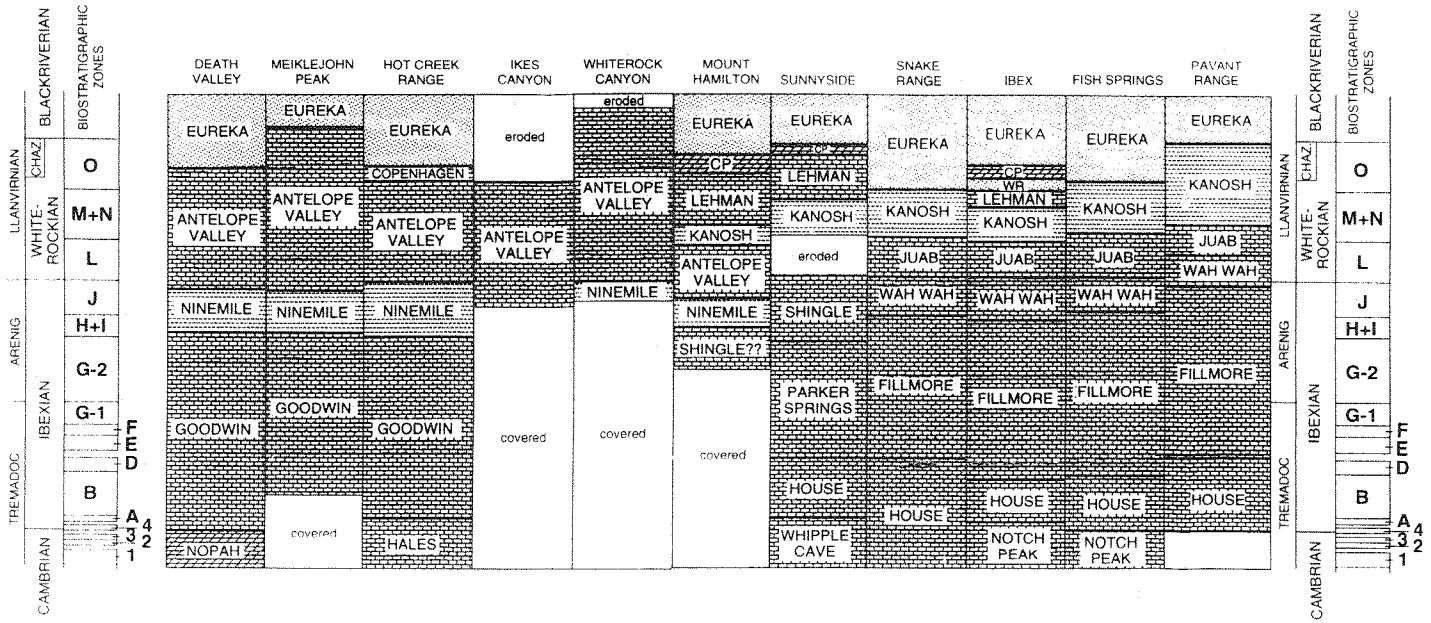

BLACKRIVERIAN
CHAZ
LLANVIRNIAN
WHITE-ROCKIAN
ARENIG
IBEXIAN
TREMADOC
CAMBRIAN
BIOSTRATIGRAPHIC ZONES
O
M+N
L
J
H+I
G-2
G-1
F
E
D
B
A
4
3
2
1
DEATH VALLEY
MEIKLEJOHN PEAK
HOT CREEK RANGE
IKES CANYON
WHITEROCK CANYON
MOUNT HAMILTON
SUNNYSIDE
SNAKE RANGE
IBEX
FISH SPRINGS
PAVANT RANGE
EUREKA
ANTELOPE VALLEY
NINEMILE
GOODWIN
NOPAH
COPENHAGEN
HALES
covered
eroded
CP
LEHMAN
KANOSH
SHINGLE??
SHINGLE
PARKER SPRINGS
HOUSE
WHIPPLE CAVE
JUAB
WAH WAH
FILLMORE
WR
NOTCH PEAK

Figure 3

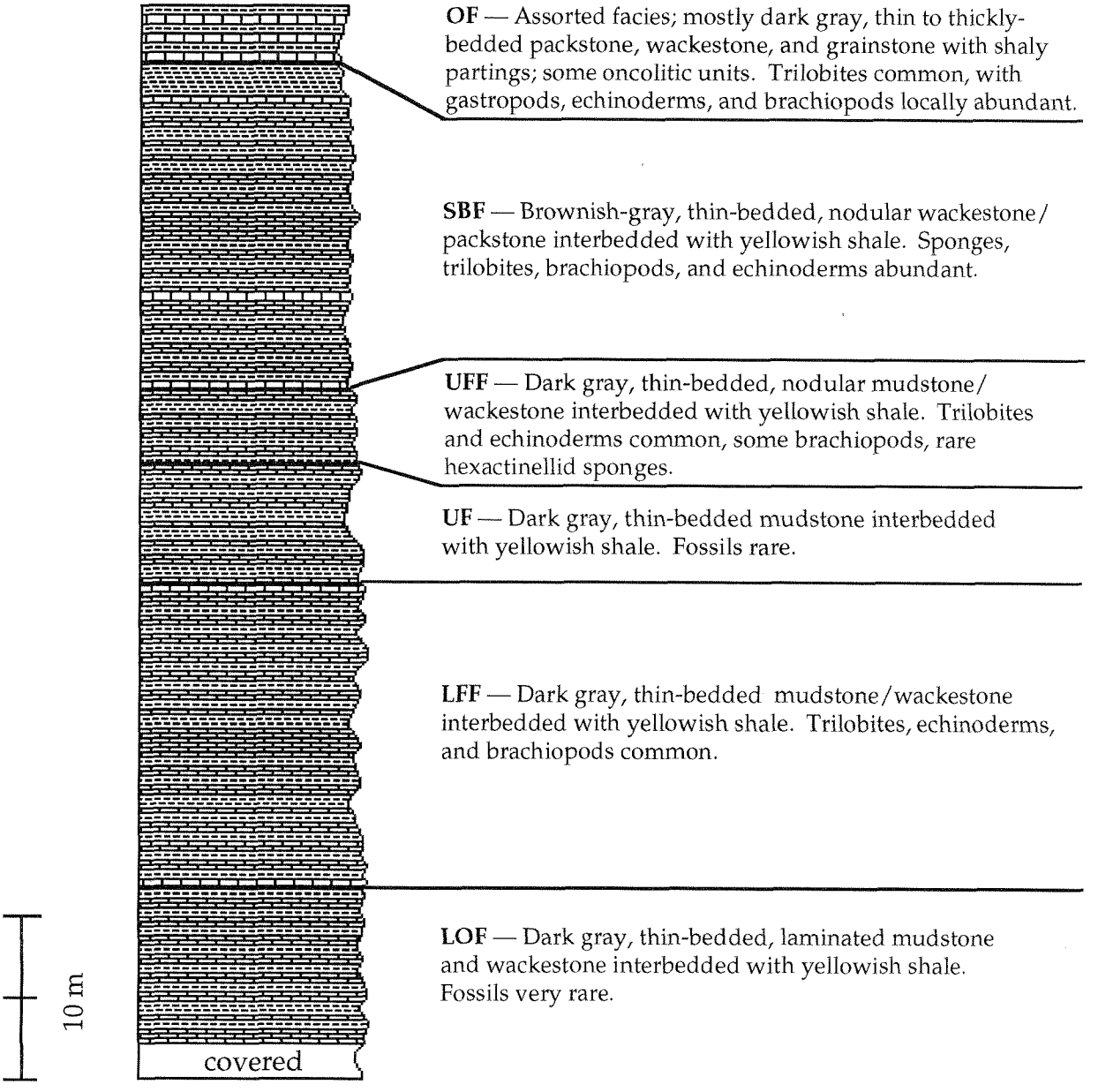

OF — Assorted facies; mostly dark gray, thin to thickly-bedded packstone, wackestone, and grainstone with shaly partings; some oncolitic units. Trilobites common, with gastropods, echinoderms, and brachiopods locally abundant.
SBF — Brownish-gray, thin-bedded, nodular wackestone/packstone interbedded with yellowish shale. Sponges, trilobites, brachiopods, and echinoderms abundant.
UFF — Dark gray, thin-bedded, nodular mudstone/wackestone interbedded with yellowish shale. Trilobites and echinoderms common, some brachiopods, rare hexactinellid sponges.
UF — Dark gray, thin-bedded mudstone interbedded with yellowish shale. Fossils rare.
LFF — Dark gray, thin-bedded mudstone/wackestone interbedded with yellowish shale. Trilobites, echinoderms, and brachiopods common.
LOF — Dark gray, thin-bedded, laminated mudstone and wackestone interbedded with yellowish shale. Fossils very rare.
10 m
covered

Figure 4

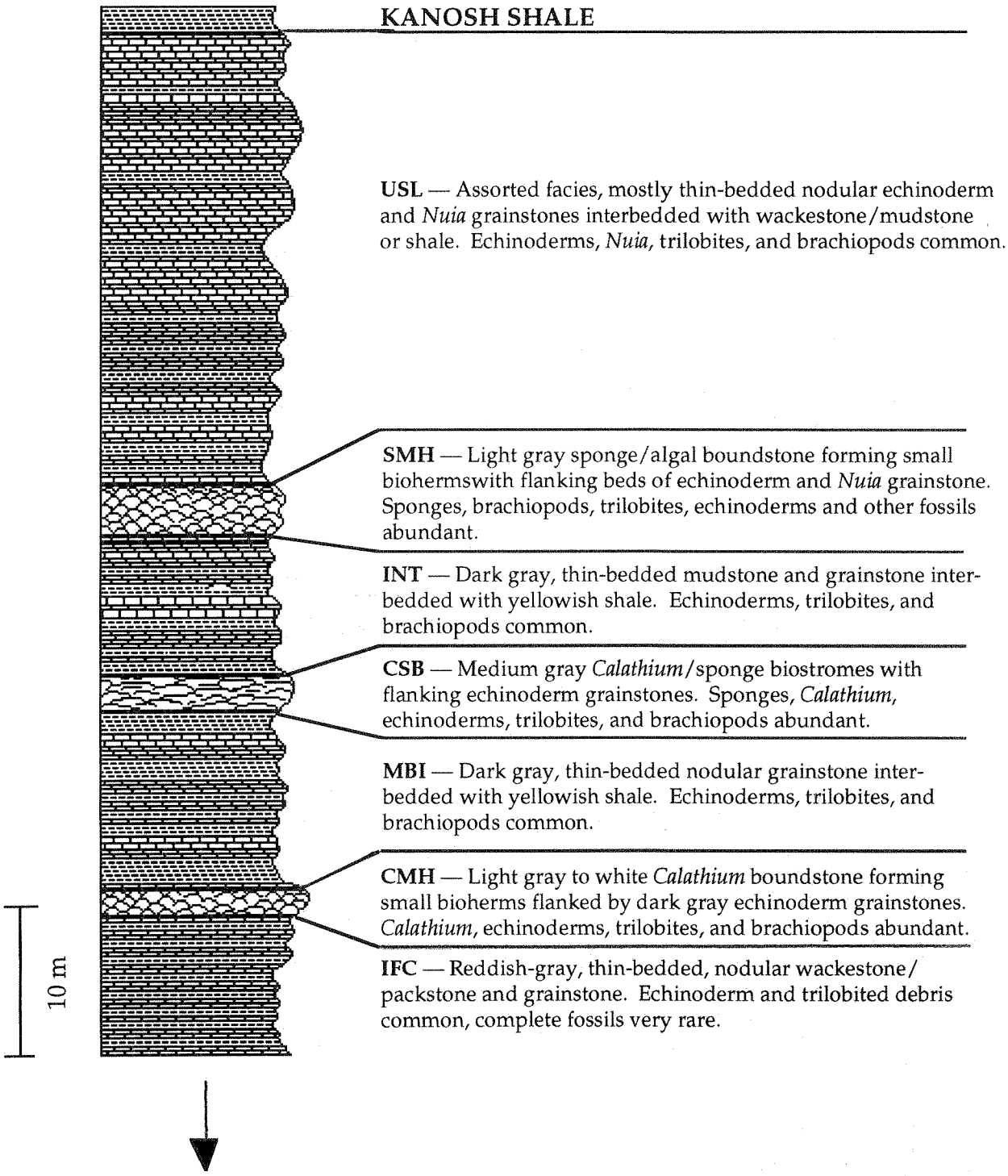

KANOSH SHALE
USL — Assorted facies, mostly thin-bedded nodular echinoderm and *Nuia* grainstones interbedded with wackestone/mudstone or shale. Echinoderms, *Nuia*, trilobites, and brachiopods common.
SMH — Light gray sponge/algal boundstone forming small biohermswith flanking beds of echinoderm and *Nuia* grainstone. Sponges, brachiopods, trilobites, echinoderms and other fossils abundant.
INT — Dark gray, thin-bedded mudstone and grainstone interbedded with yellowish shale. Echinoderms, trilobites, and brachiopods common.
CSB — Medium gray *Calathium*/sponge biostromes with flanking echinoderm grainstones. Sponges, *Calathium*, echinoderms, trilobites, and brachiopods abundant.
MBI — Dark gray, thin-bedded nodular grainstone interbedded with yellowish shale. Echinoderms, trilobites, and brachiopods common.
CMH — Light gray to white *Calathium* boundstone forming small bioherms flanked by dark gray echinoderm grainstones. *Calathium*, echinoderms, trilobites, and brachiopods abundant.
IFC — Reddish-gray, thin-bedded, nodular wackestone/packstone and grainstone. Echinoderm and trilobited debris common, complete fossils very rare.
10 m

Figure 5

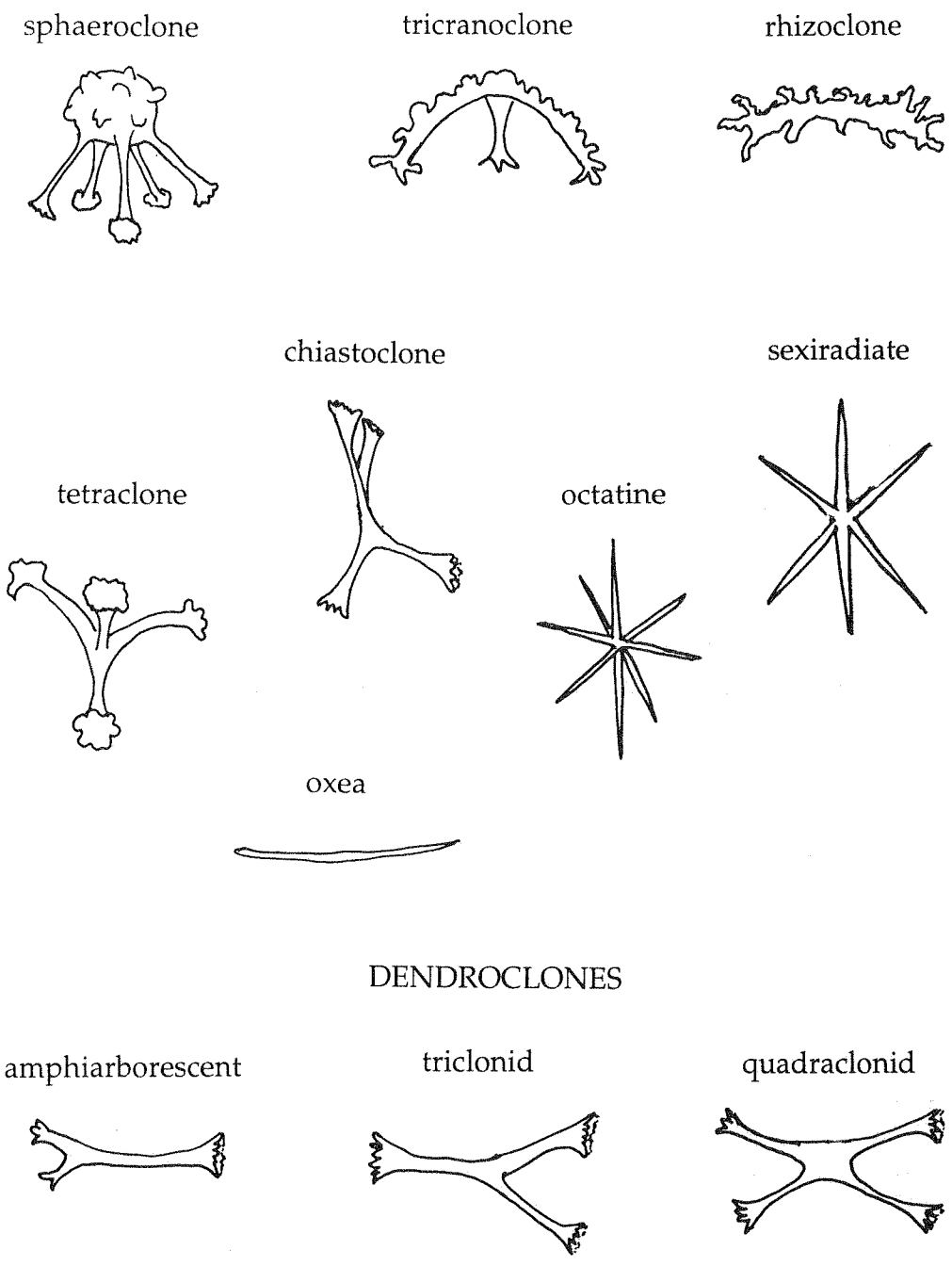
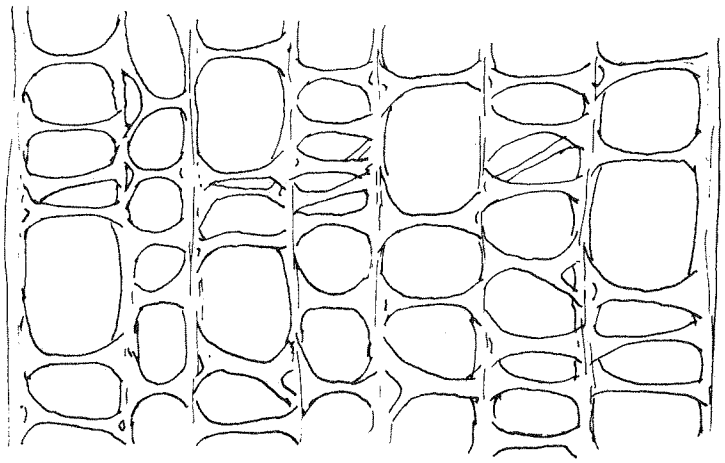

sphaeroclone
tricranoclone
rhizoclone
chiastoclone
sexiradiate
tetraclone
octatine
oxea
DENDROCLONES
amphiarborescent
triclonid
quadraclonid

Figure 6

A



B

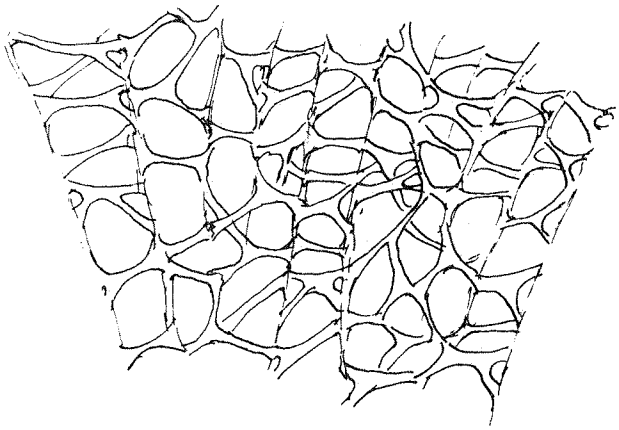


Figure 7

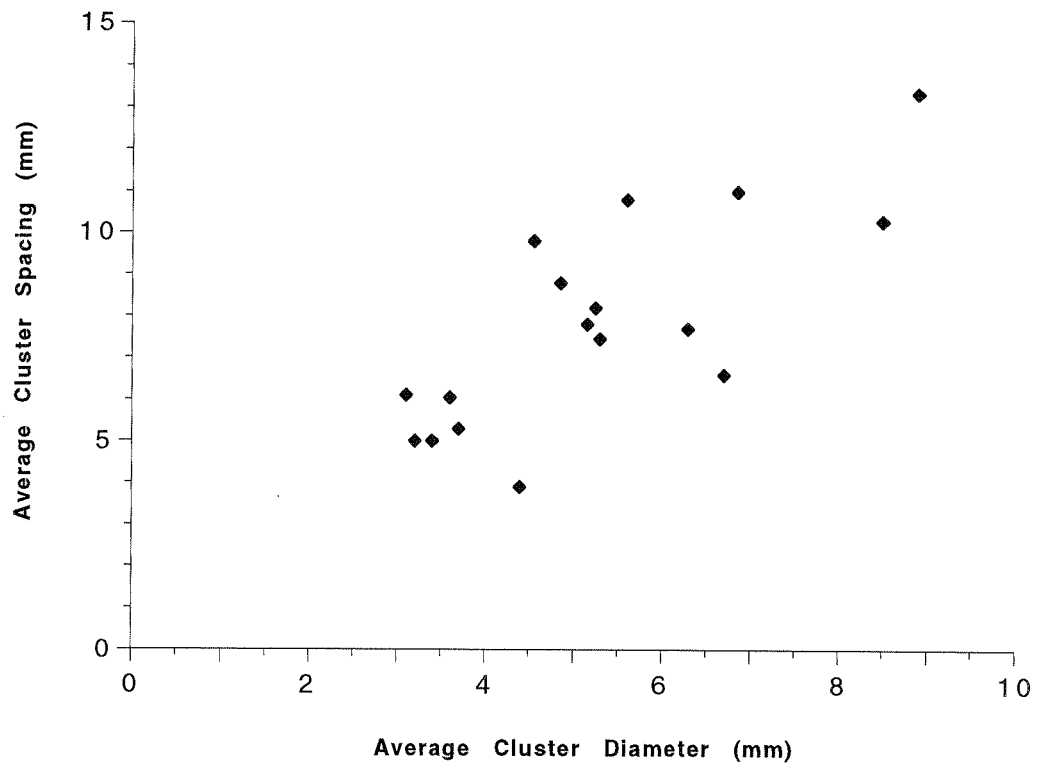

15
10
5
0
Average Cluster Spacing (mm)
0
2
4
6
8
10
Average Cluster Diameter (mm)

Figure 8

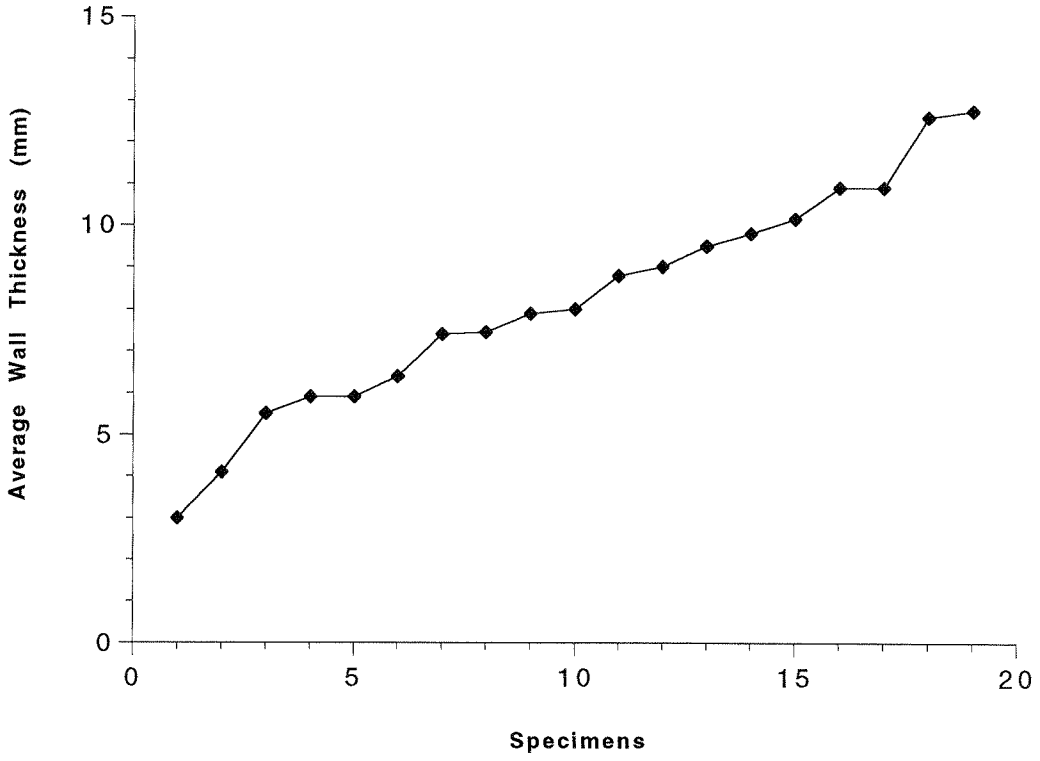
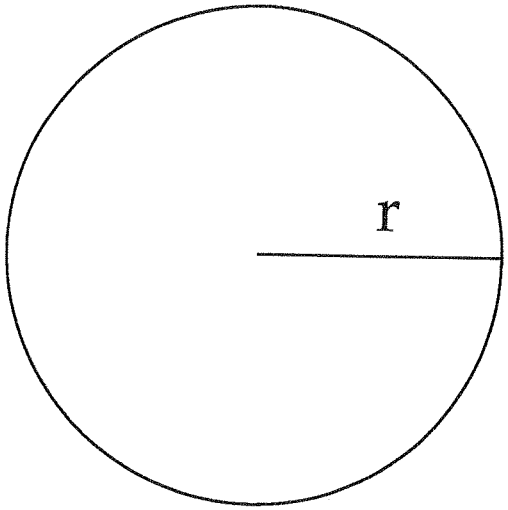
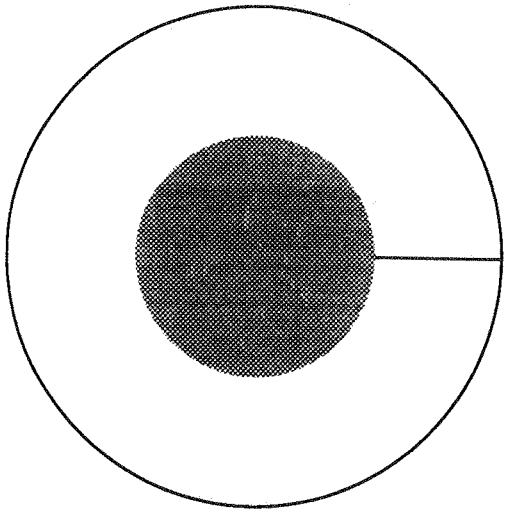


Figure 9



largest opening = 2r

cross-sectional area = πr^2



largest opening = r/2

cross-sectional area = $\pi r^2 - \pi r^2/4 = 3\pi r^2/4$

Figure 10

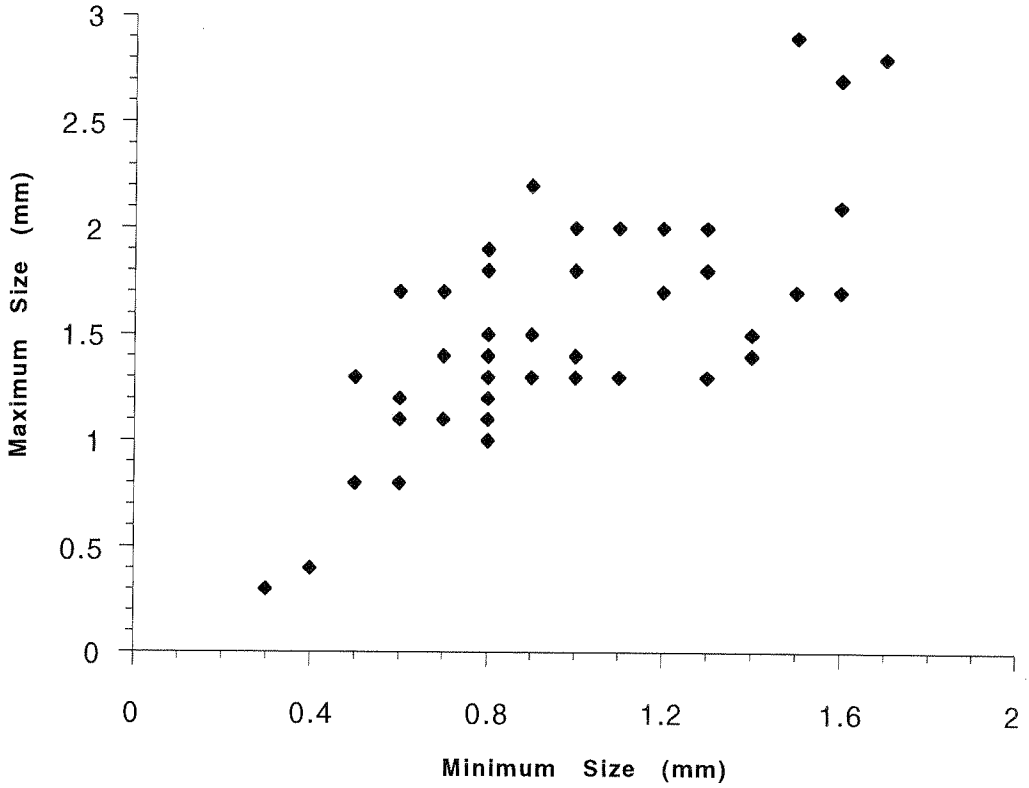


Figure 11

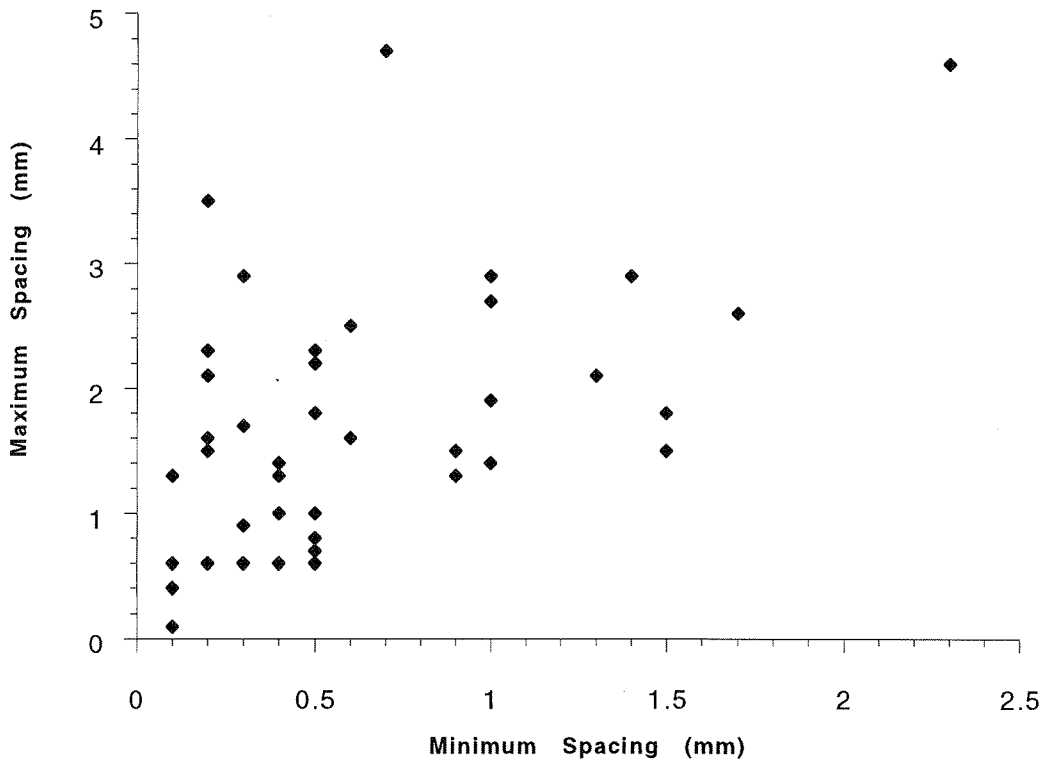


Figure 12

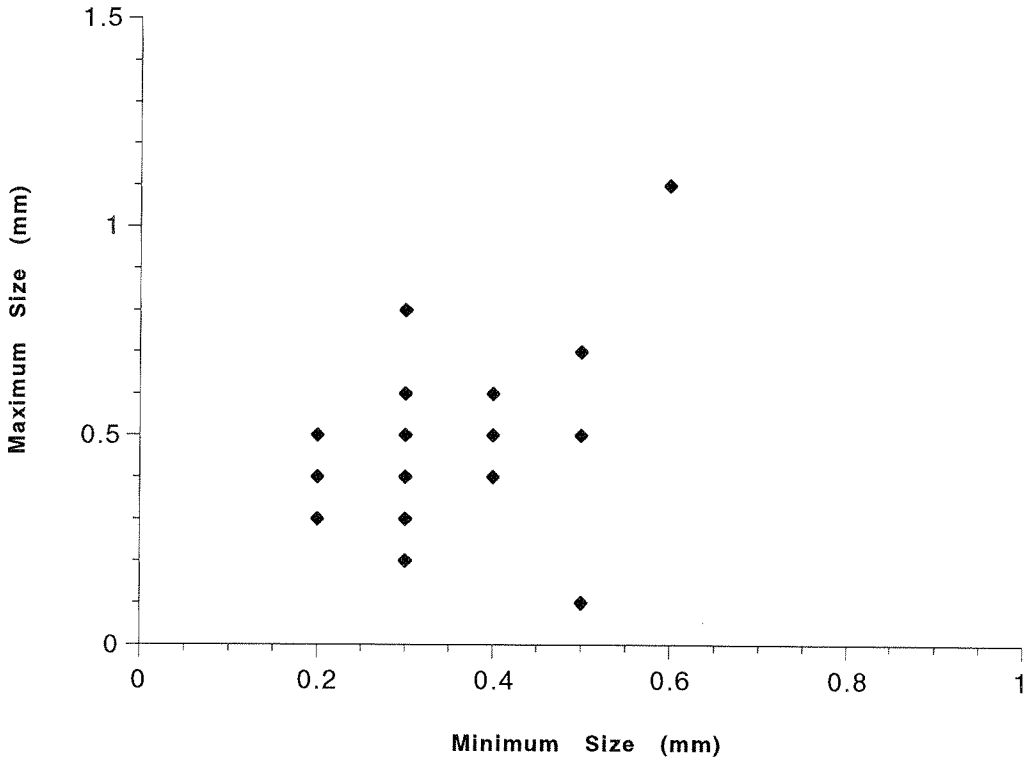


Figure 13

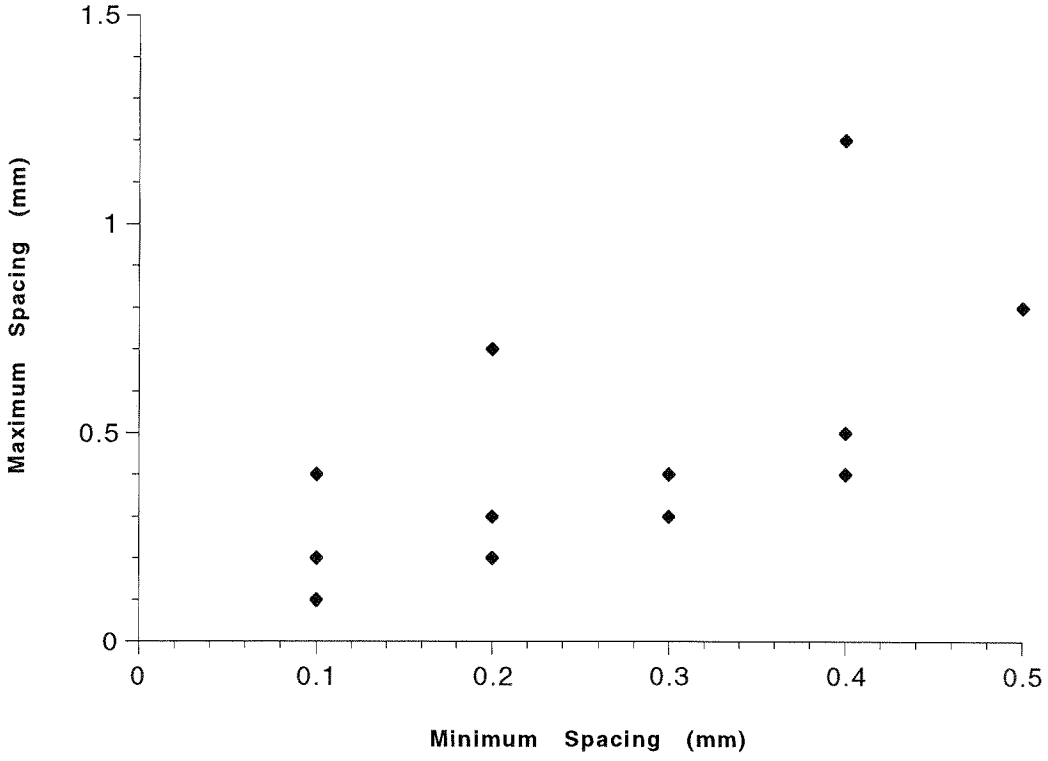


Figure 14

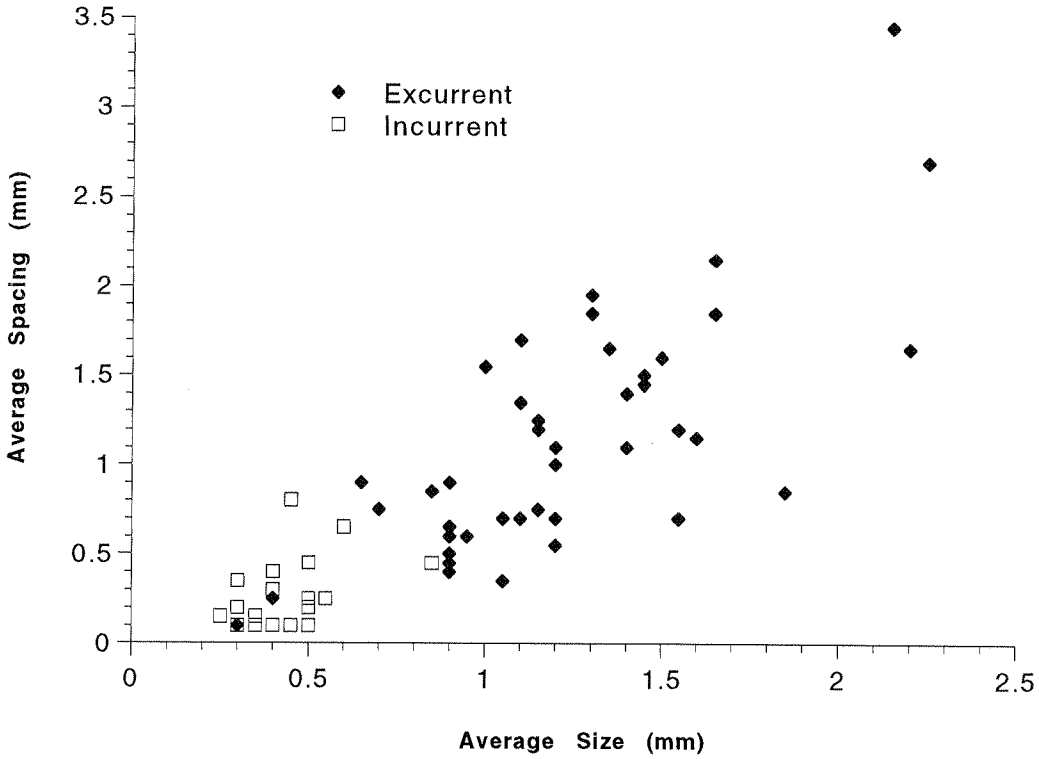
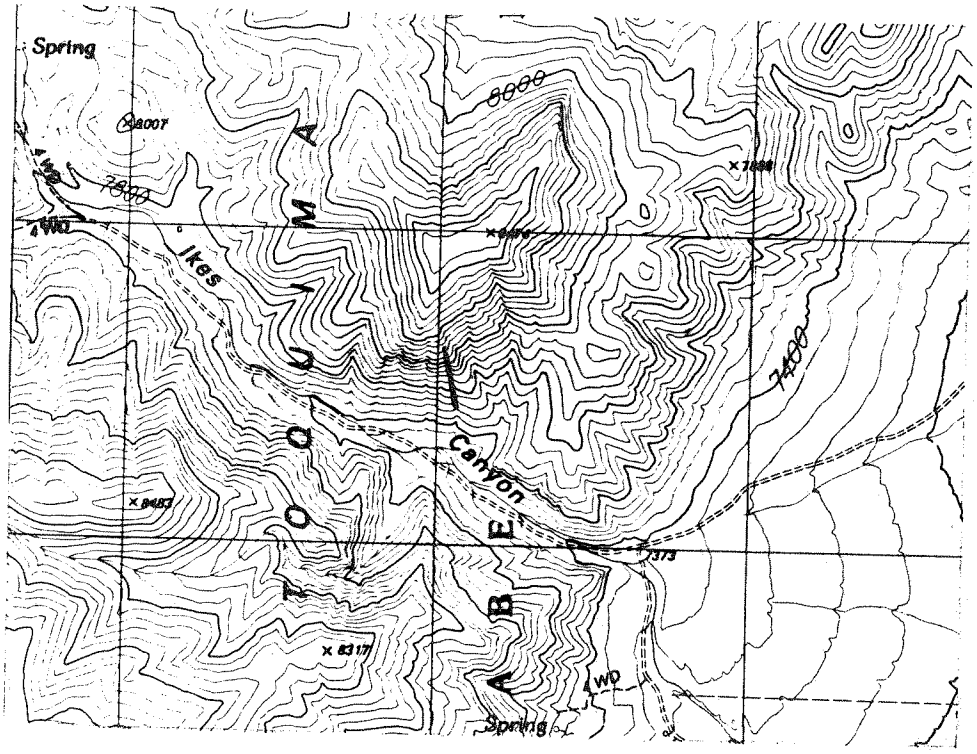
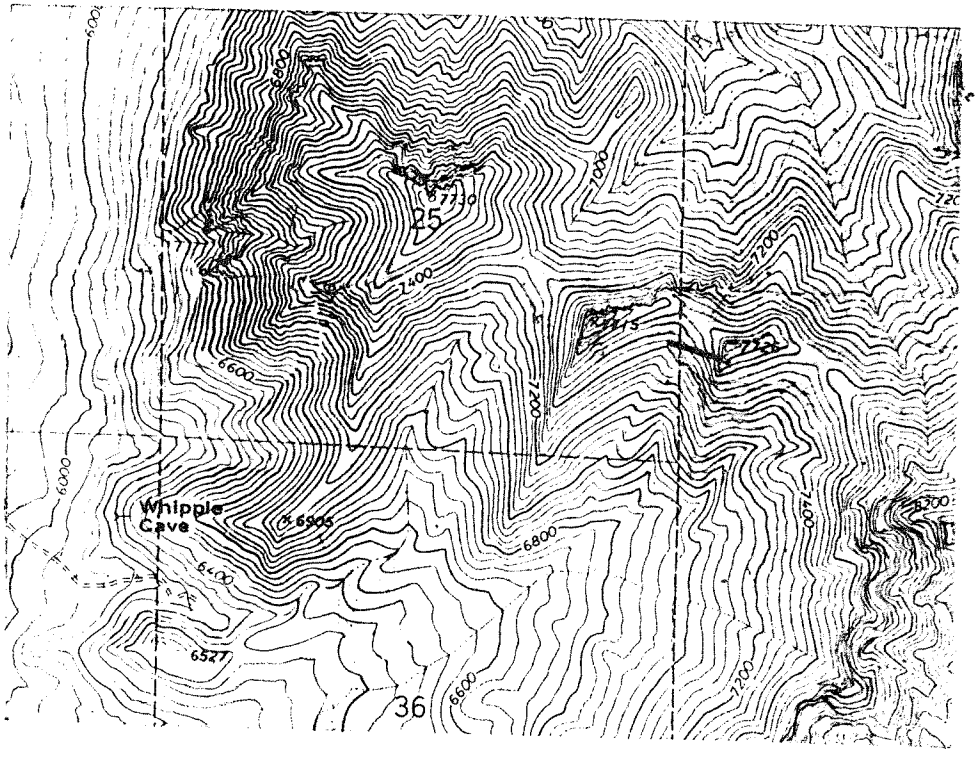

Excurrent
Incurrent
Average Spacing (mm)
Average Size (mm)
0
0.5
1
1.5
2
2.5
3
3.5

Figure 15


Spring
8007
7800
8000
7400
Ikes
Canyon
TOYABE
8317
WD
Spring

16


Whipple Cave
6905
6527
7730
7215
25
36
7000
7200
7400
7600
7800
6800
6600
6400
6000