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DEMOSPONGES AND HEXACTINELLID SPONGES FROM THE LOWER DEVONIAN ROSS FORMATION OF WEST-CENTRAL TENNESSEE

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ABSTRACT—A fauna of eight taxa of demosponges and hexactinellid sponges has been collected from the Lower Devonian (Lochkovian) Ross Formation, largely out of the upper Birdsong Shale Member in Benton, Decatur, and Perry Counties in west-central Tennessee. The Upper Birdsong Shale ("bryozoan zone") in which the sponges are most common appears to have been deposited below normal wave base in a quiet marine environment, and represents a terrigenous clastic sediment influx onto a carbonate shelf that had existed in the area from at least the middle Silurian. Benton Quarry in Benton County was the most productive locality for fossil sponges.

The new demosponge genera and species *Ginkgospongia foliata* and *Coniculospongia radiata* occur with the new species *Haplistion lobatum* and skeletal mats of fine spicules, along with moderately rare specimens of *Hindia sphaeroidalis* Duncan. The new hexactinellid genus and species *Stiodermiella amanita* and *Stiodermiella tetragona* are characterized by peculiar ornamented papillose, swollen spicules that produce a massive, armored layer on the upper part of the sponge. The latter are associated with the new hexactinellid species *Twenhofelella bulbulus,* which has relatively normal-appearing hexactines, and with an indeterminate hexactinellid genus, which has spinose hexactines in irregular orientation in a small, platelike fragment. Root tufts of probable hexactine origin also occur.

Swollen spicules in *Stiodermiella* are reminiscent of swollen spicules in the family Stiodermatidae Finks, largely from the Permian of western Texas, but elements of the family are also known from Lower Carboniferous to Permian rocks in Europe and North America.

INTRODUCTION

SPONGES WERE collected from the Lower Devonian (Lochkovian) Ross Formation in west-central Tennessee, from a north–south band of outcrops along the western margin of the Tennessee River Valley, in Benton, Decatur, and Perry Counties (Figure 1). These are the first sponges described from the formation. The sponges occur in the interbedded bioclastic limestones and fine-grained terrigenous rocks of the upper part of the formation, which also contains a diverse and abundant normal-marine fauna.

The Ross Formation is of early Lochkovian age (Figure 2), and it rests conformably on the Decatur Formation of Pridolian and earliest Lochkovian age (McComb and Broadhead, 1980). The Ross Formation is overlain by the cherty Camden Formation of late Lochkovian and early Pragian ages. Rocks in the interval are primarily limestone, with minor interbedded, fine-grained, terrigenous rocks. Birdsong beds are mainly terrigenous rocks (Figure 2). Dunbar (1918, 1919) and Wilson (1949) believed that unconformities separated the Decatur Limestone and overlying Ross Formation. Reid (1983) and McComb (1987) demonstrated that no unconformity exists between the Decatur and Ross beds.

The Ross Formation in the study area is composed of two units (Figure 3); the lower Rockhouse Limestone Member is 4–5 m thick, and the overlying Birdsong Shale Member ranges in thickness from 4.5 m to a maximum of 19.4 m in the area of concern (Dunbar, 1919; Wilson, 1949; Reid, 1983; Gibson, 1988). The Birdsong Member comprises alternating beds of argillaceous limestone and calcareous shale that contain abundant transported fossil debris. The member is divided into two informal units (Figure 3): a lower "brachiopod zone" (Dunbar, 1919), 2.5 m thick at Elkins' Quarry to 15 m thick at McClanahan's Quarry (Gibson, 1988); and an upper informal unit. The upper or "bryozoan zone," is composed of thin-bedded limestone and shale that contain abundant ramose bryozoans and echinoderm fragments. The "bryozoan zone" is 2 m thick at Elkins' Quarry and 4.75 m thick at Benton and Parsons Quarries (Gibson, 1988). The bryozoan-rich beds of this member yielded most of the sponges described here (Table 1).

Rocks of the Ross Formation were deposited on a shallow marine shelf, at about 25°S latitude (Barrett, 1985; Scotese et al., 1985; Gibson, 1988) between four large-scale structural features: the Illinois Basin, on the north, and the Black Warrior Basin, on the south, and between the Nashville Dome uplift, on the east, and the Ozark uplift, on the west. During most of Ross deposition, the shelf sloped gently toward the Illinois Basin, as suggested by transgression of the Ross Limestone Member toward the south (Broadhead et al., 1989). The Ross Formation appears to have been deposited on a shallow marine shelf, mostly at or below normal wave base, but above storm wave base (Reid, 1983; McComb, 1987; Cappaccioli, 1987; Gibson, 1988; Broadhead et al., 1989; Clement, 1989). The influx of terrigenous clastic sediments temporarily changed the character of the carbonate shelf that had persisted since the middle Silurian and was re-established by deposition of Camden beds.

Gibson (1988) showed that most beds in the "brachiopod zone" of the Birdsong Shale Member are graded and apparently were produced during storm events that winnowed the substrate and concentrated the skeletal material. The area experienced a major influx of terrigenous clastic debris during accumulation of the "brachiopod zone" beds.

The upper Birdsong Shale ("bryozoan zone") appears to have been deposited below normal wave base and in a marine setting that was generally quiet. Occurrence of several crinoid specimens that essentially disarticulated in place, without transport, suggests that the "bryozoan zone" beds accumulated in a quiet environment. During deposition of the upper Birdsong Shale, the shelf was also subject to rare episodic storm events, however, as indicated by graded beds containing oriented tentaculitids and interbedded layers that contain well-preserved echinoderms

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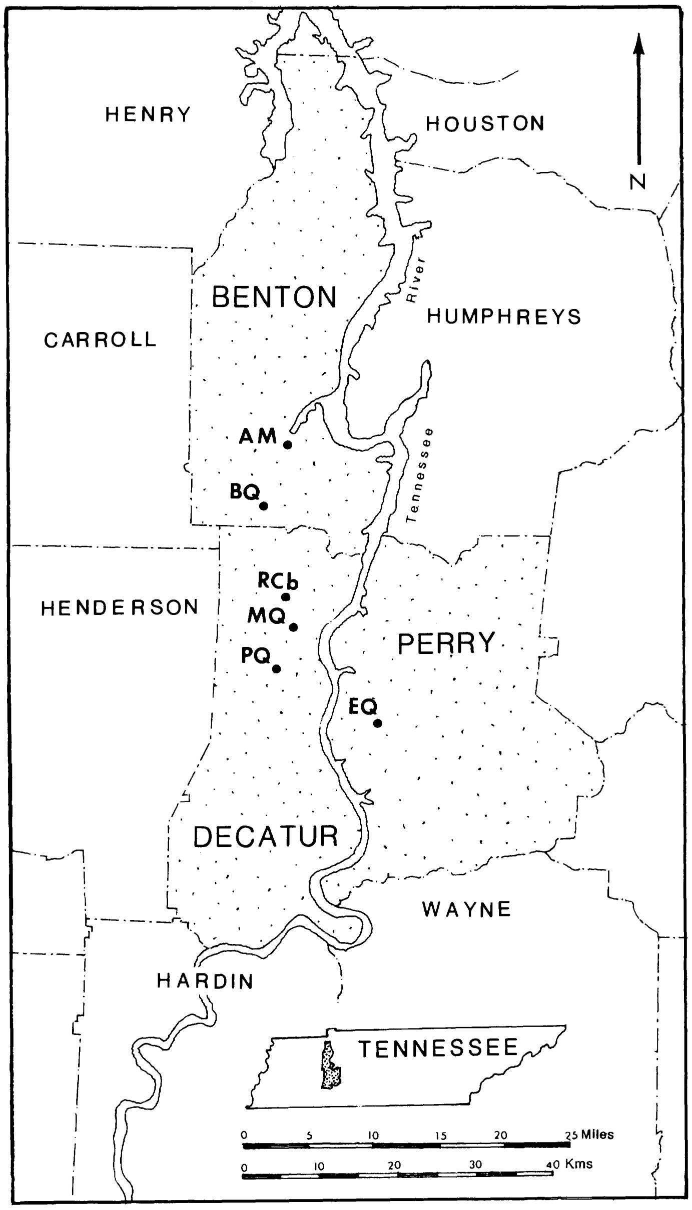


FIGURE 1—Index map to fossil sponge localities from west-central Tennessee. Allens Mill, AM; Benton Quarry, BQ; Elkins' Quarry, EQ; McClanahan's Quarry, MQ; Parsons Quarry, PQ; Road Cut b, RCb; all in Benton, Decatur, and Perry Counties of west-central Tennessee.

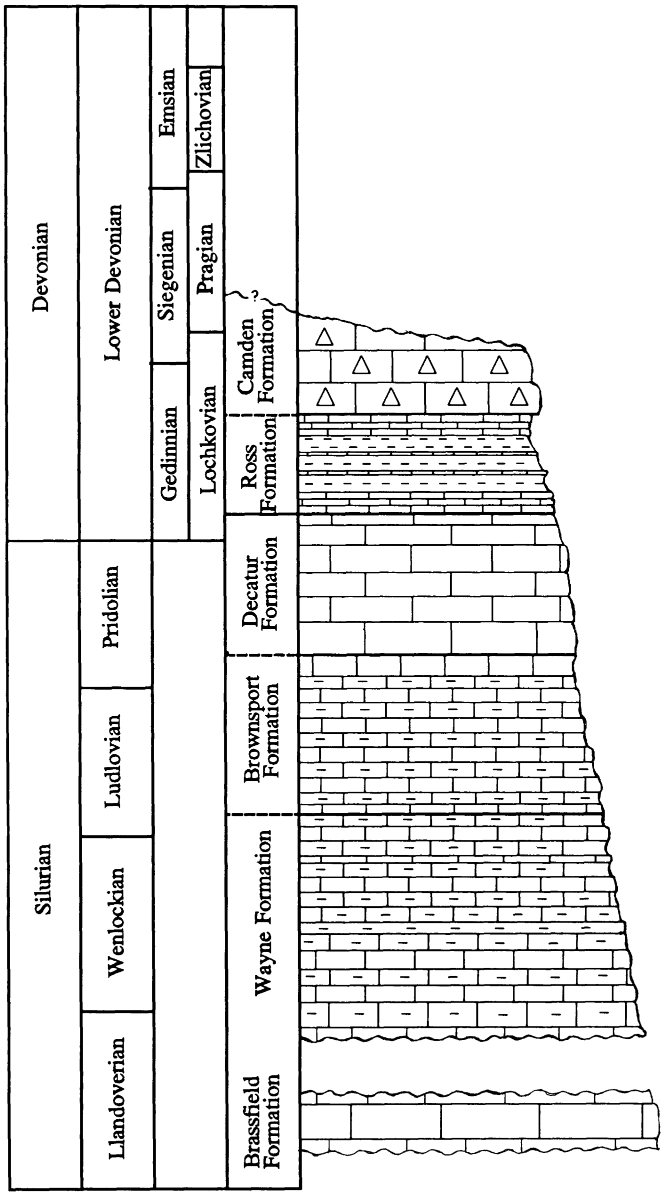


FIGURE 2—Generalized stratigraphic column of Silurian to Lower Devonian rocks of west-central Tennessee (Wayne Formation boundaries from Barrick, 1983).

(Gibson, 1988; Clement, 1989). Epibionts on some echinoderms indicate that the bottom was not a site of constant influx of terrigenous material, but that the echinoderms were exposed for a period long enough for epibiont settlement and growth. The well-preserved nature of the delicate sponges also suggests they accumulated under relatively quiet waters. The unfused, thin-walled demosponges appear to have been little disturbed, and the intact, somewhat more massive, unfused skeletons of the hexactinellids also suggest quiet conditions and lack of transport.

Fossils described here are deposited in paleobiology collections of the U.S. National Museum (USNM), in Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Class DEMOSPONGIA Sollas, 1875
Order MONAXONIDA Sollas, 1888
Family SOLLASELLIDAE(?) von Lendenfeld, 1887
Genus GINKGOSPONGIA n. gen.

Type species.—Ginkgospongia foliata n. sp.

Diagnosis.—Stalked, thin-walled, lobate or crenulate palmate to funnel-like sponge expands upward from stalk as lobes, each with upward-expanding brushlike arrangement of monaxons, probably oxeas, to produce leaflike form.

Discussion.—Discussion of forms with which the new genus might be confused is treated in discussion of the type species below.

Etymology.—Ginkgo, Chinese or Japanese word for maidenhair tree; *spongia,* sponge; in relationship to the ginkgo-leaflike appearance of the flattened sponge.

GINKGOSPONGIA FOLIATA n. sp.
Figure 4.1, 4.2

Diagnosis.—Stalked, thin-walled, lobate palmate or funnel-like sponges, with 4–5 major lobes or crenulations to 4–5 mm wide in upper part where spicules in brushlike fibrous structure. Skeleton dense, divergent upward from more or less columnar stalk to form moderately open-textured walls in upper parts of lobes. Skeleton made of oxeas(?) 1–2 mm long and 0.02–0.03 mm in maximum diameter. Sponge with lobed, leaflike flattened form.

Description.—Single, small, bladelike holotype of prominently stalked, thin-walled, lobate or crenulate palmate sponge. Basal stalk 5 mm across and high, with flattened thickness of approximately 1 mm. Fibrous appearing spicular structure expands upward from stalk to 4–5 major lobes or crenulations, each approximately 4–5 mm across in upper part of sponge. Entire specimen approximately 25 mm high, with maximum curved width of approximately 20 mm, and flattened thickness of approximately 3 mm.

Skeletal structure dense, spicules upward-divergent, packing particularly dense in stalk and lower part of sponge, but more loosely and widely spaced in upper part, particularly around more or less complete lobe tips, where some vertical gaps, 0.2–0.3 mm wide, probably represent subvertical radial canals. No evidence of canals or round pores normal to flattened sponge surface.

Spicules only moderately preserved in somewhat nodular, coarse, pyritic replacements. Where best preserved, oxeas(?) approximately 0.02–0.03 mm in maximum diameter and 1–2 mm long, but double taper not conclusively shown. Some coarse nodular spicule impressions range to 0.04 mm in diameter.

Some of wall appears flattened slightly diagonally and folded so that matrix locally incorporated or preserved between flattened lobes; lobes most distinctly separated in upper part, but separation only ill-defined in middle and lower part above stalk. No conclusive evidence of spongocoel, but sponge could have been very thin-walled, steeply obconical funnel-like form with crenulate walls, now flattened to produce lobate appearance, or palmate, single-layered sponge with lobate foliate appearance, but certainly sponge has irregular crenulate three-dimensional structure, even as flattened.

Discussion.—We know of no sponge with which this genus and species can be readily compared. It certainly belongs within the Monaxonida because of its simple spicule arrangement and makeup. It lacks any tetraxial spicules, such as characterize lithistids, and it lacks hexactines, so it cannot be placed within the Hexactinellida. Consequently, it is proposed here as a new genus and new species.

Etymology.—*Foliatus,* Latin, leafy, in reference to the leaflike appearance of the flattened sponge.

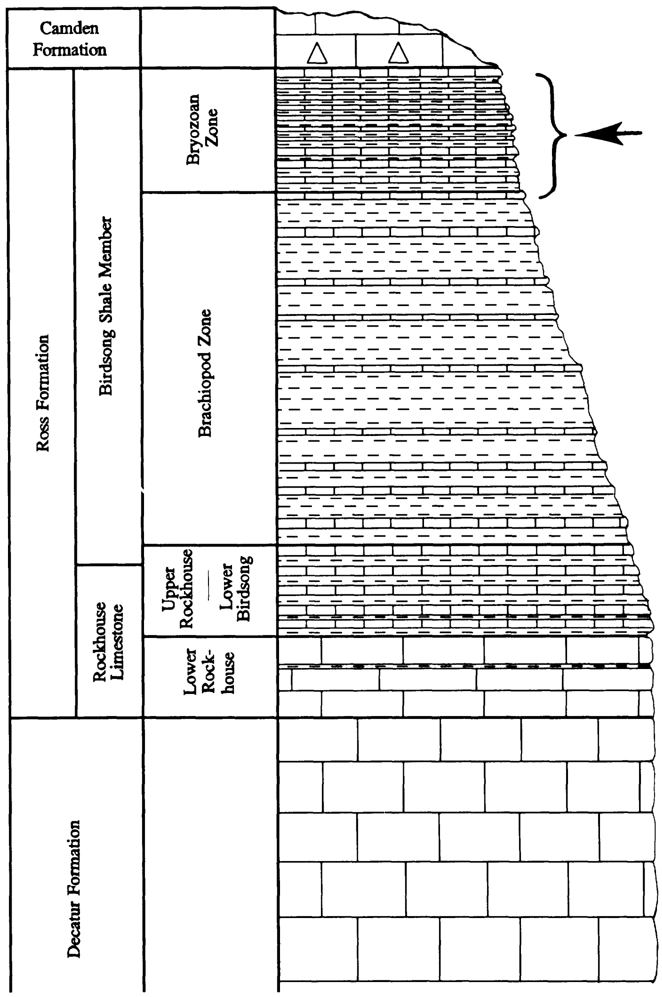
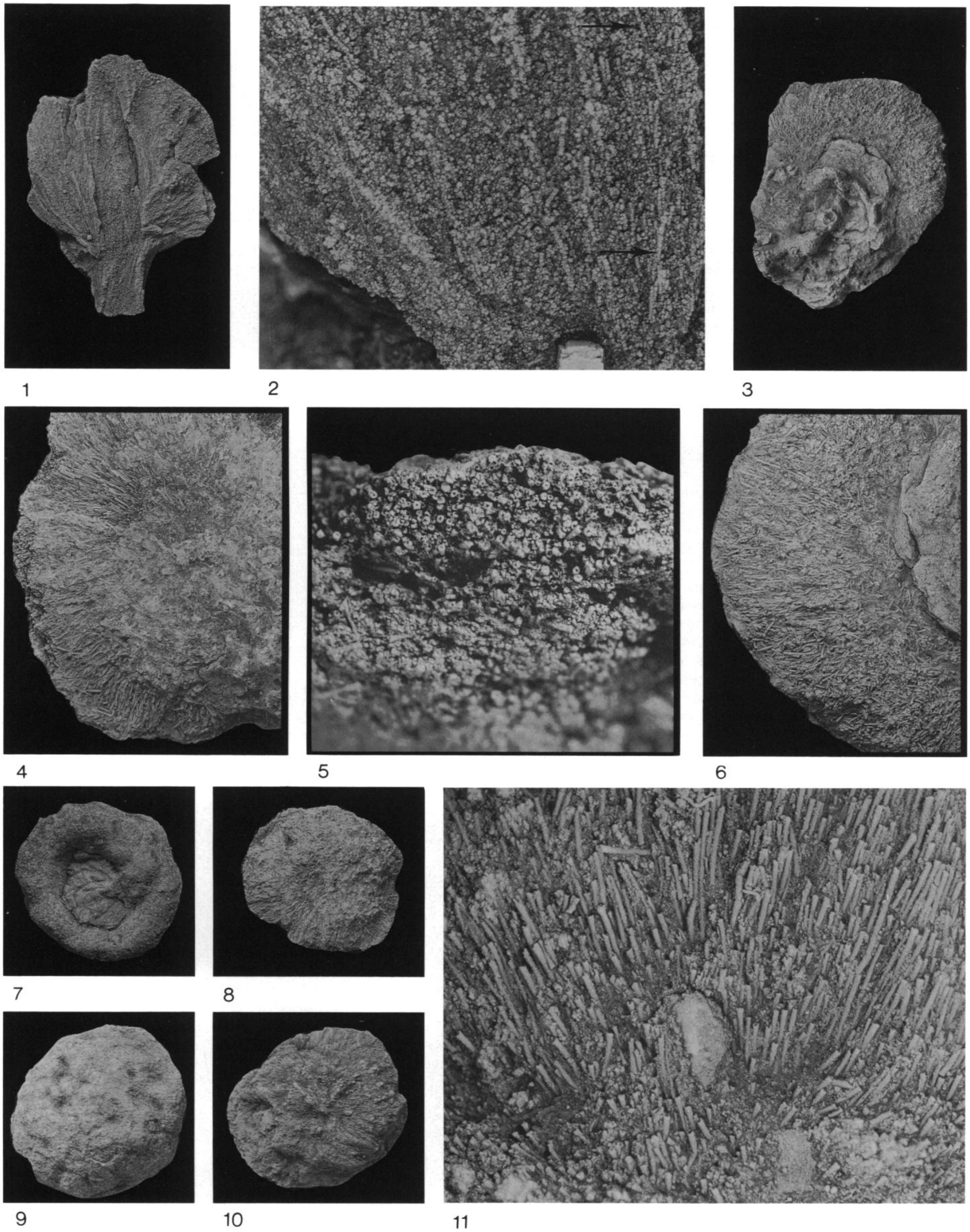


FIGURE *3*—Generalized stratigraphic column of Decatur and Ross Formations in west-central Tennessee (thicknesses are averages from Gibson, 1988, and McComb, 1987). Most of the sponges described here came from the "bryozoan zone" at the top of the Ross Formation (arrow), in upper beds of the Birdsong Shale Member.

TABLE *1*—Ross Formation sponge occurrences.

Genus and species	Localities AM	BQ	MQ	PQ	EQ	RCb
Ginkgospongia foliata n. sp.	R(2)	—	—	H, R	—	—
Coniculospongia radiata n. sp.	H	—	—	—	—	P, R
Mat short spicules	F(4)	—	—	—	—	—
Haplistion lobatum n. sp.	—	—	H	—	—	—
Hindia sphaeroidalis Duncan	F(2)	—	—	—	—	R(2)
Twenhofelella bulbulus n. sp.	—	—	—	H, R(2)	—	—
Hexactine indeterminant	R	F	—	—	—	—
Stiodermiella amanita n. sp.	—	H, P(3), R(2)	—	R	P	—
Stiodermiella tetragona n. sp.	—	H, P	—	—	—	—
Root tufts	—	F(4), R(5)	—	—	—	—
Hexactine spicule, isolated	—	—	—	—	R(2)	—

H = holotype; P = paratype; F = figured specimen; R = reference specimen; number of specimens in parentheses; AM = Allens Mills; BQ = Benton Quarry; MQ = McClanahan's Quarry; PQ = Parsons Quarry; EQ = Elkins Quarry; RCb = northern road cut on Tennessee Route 69.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Material and occurrence.—Holotype, USNM 436590, and a small fragmental reference specimen, from the Birdsong Shale, Ross Formation, Parsons Quarry; two larger reference specimens from Benton Quarry, one from the undifferentiated Ross Formation and the other from the "brachiopod zone" of the Birdsong Shale.

Genus Coniculospongia n. gen.

Type species.—*Coniculospongia radiata* n. sp.

Diagnosis.—Broadly flaring, funnel-like to discoidal or basinlike small sponges, with or without small stalks, skeletons composed of radiating smooth oxeas 0.5–2.0 mm long and 0.02–0.05 mm in maximum diameter. Spicules unclustered and generally parallel or subparallel, may be somewhat more loosely spaced on upper gastral surface. Lacks coronal spicules; spicules not interwoven but radially subparallel.

Discussion.—Comparisons of the genus with similar forms is treated in discussion of the type species below.

Etymology.—*Coniculus,* Greek, small cone; *spongia,* sponge, in relationship to the small, conical, funnel-like form of the genus.

Coniculospongia radiata n. sp.
Figure 4.3–4.11

Diagnosis.—Funnel-like to platterlike-discoidal, broadly flaring, and obconical small sponges, with or without stalk, composed of upward and outward, radially arranged, smooth oxeas range at least 0.5–2.0 mm long and 0.02–0.05 mm in diameter. Spicule packing moderately dense in lower but may be less dense in upper part, where uncommon radial gaps 0.1–0.2 mm wide occur irregularly.

Description.—Broadly flaring, low obconical, to funnel-like and platterlike sponges with or without small stalks, but thin, flaring sheetlike upper part. Holotype with small stalk, 3 mm high, expands gradually upward from rounded base to approximately 5 mm in diameter, but then flares abruptly, in almost horizontal sheetlike fashion, to maximum diameter of 18 × 23 mm, as presently preserved, with parts of edges broken. Entire sponge approximately 6 mm high, and upper sheetlike part 3 mm thick; composed of loose, divergent spicules in upper part, but side-by-side and moderately dense in lower or dermal part of sponge.

Spicules smooth oxeas, range at least 0.05–0.20 mm long and mostly 0.04–0.05 mm in maximum diameter, taper in both directions to sharp tips, but complete spicules not observed in pyritic replacement. Spicules steeply subparallel to outer margins of small conical stalk, but essentially parallel to upper and lower surfaces in stacked skeleton above. Locally small open gaps or possible canals, 0.1–0.2 mm across, occur in upper part as interruptions in skeleton. Upper surface curves downward in outer part to produce rounded to distinctly covergent margin.

Paratype 12 × 15 mm in upper maximum diameter, and approximately 4 mm high, lacks prominent stalk, but shows upward, radiating oxeas in central base, above which spicules diverge abruptly in upper flat part of sponge in side-by-side, close packing. Some gaps approximately 0.1 mm wide occur irregularly in upper part of skeleton. Oxeas with common mid-length maximum diameter of approximately 0.04 mm to 1–2 mm long, as straight to gently curved, closely stacked elements. Each spicule where broken on edge, shows prominent central axial canal, 0.010–0.015 mm in diameter.

Third, somewhat tentatively assigned, specimen somewhat more basin-shaped and thicker walled sponge, approximately 15 mm in diameter and 6 mm high, with walls approximately 3 mm thick. Lacks prominent stalk, but with radial skeletal structure in base, and somewhat more obscure skeleton than in other specimens assigned to species. Sponge with slightly smaller spicules, generally range 0.025–0.030 mm in maximum diameter.

Discussion.—The sponges are placed within the order Monaxonida because of their simple spiculation and radial skeletal structure. *Belemnospongia* (Miller, 1889, p. 155; Ulrich, 1889; 1890, p. 248; Rigby et al., 1979) is a rounded, low-conical or discoidal sponge. It generally has strongly bundled spicules with a vortex near the center of the flattened cone. It is more complex than the species described here, which has a very simple skeletal structure.

Belemnospongia parmula Rigby, Keyes, and Horowitz, 1979, from the Mississippian of Alabama, has a radiate architecture. Those sponges may be of approximately the size as the species here, but that Alabama species has a skeleton of more complexly interwoven spicules, each 0.10–0.16 mm in diameter and several millimeters long, which are considerably larger than spicules seen in the material here. The sponges here are certainly not collapsed spherical *Sphaeriella* Rigby and Bryant, 1979 (p. 1005–1009), but were originally broadly flaring, platterlike obconical forms. There is no previously described fossil genus to which these sponges can be clearly related.

Choia Walcott (1920, p. 292) is also a flattened conical genus, but it, too, has a more complex skeleton that includes major diactine spicules that extend far beyond the central skeletal disk (Rigby, 1986) and contrasts with the species described here. *Trichospongia sericea* Billings, 1865, from the Ordovician of the Mingan Islands, Quebec, is a larger hemispherical sponge with poorly known structure. Billings (1865, p. 357) noted that it may have a concentric structure and, thus, would be clearly distinct from the radially structured sponges described here. Most of the other described simple radiate fossil sponges tend

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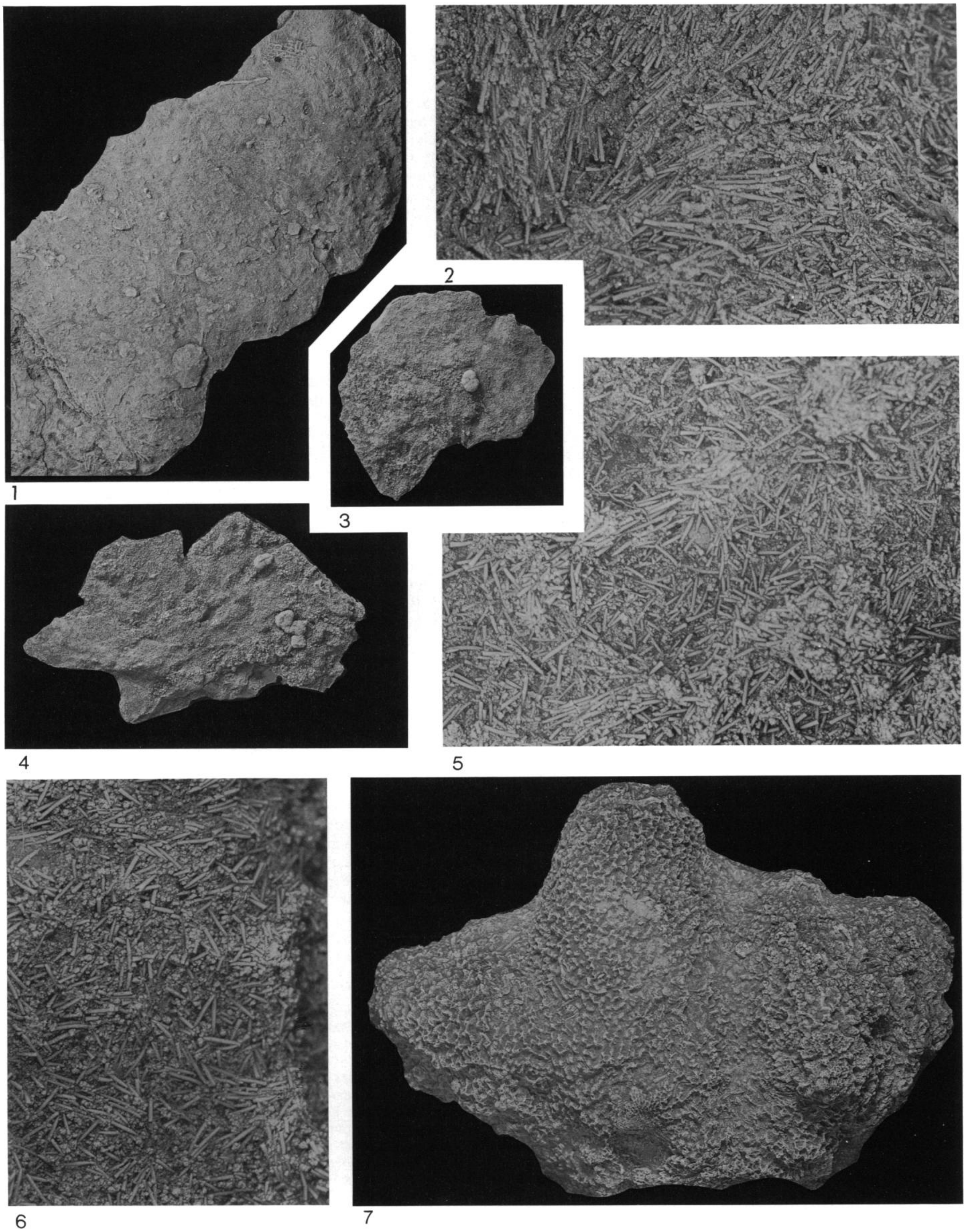
Figure 4—*Ginkgospongia* and *Coniculospongia* from the Birdsong Shale, Ross Formation of Tennessee. *1, 2, Ginkgospongia foliata* n. sp., holotype, USNM 463590, Parsons Quarry. *1,* side view showing leaflike, stalked, lobate to palmate sponge, with fine upward-expanding brushlike skeleton of oxeas, ×2; *2,* photomicrograph of fine, dense, vertically expanding brushlike skeleton of small oxeas (arrows), in somewhat irregular, nodular pyritic replacement, ×20. *3–11, Coniculospongia radiata* n. sp. *3, 6,* holotype, USNM 463591, Benton Quarry. *3,* view from above into the partially matrix-filled, broad, funnel-like sponge, with radial fine monaxial skeletal structure showing the best preserved upper part, where smooth oxeas produce radial thatch, ×2; *6,* photomicrograph shows detail of the radiating thatch of oxeas in upper rounded edge of the wall of the funnel-like sponge, ×5. *4, 5, 8, 10, 11,* paratype, USNM 463592, Road Cut b Locality. *4,* photomicrograph of platterlike, upper surface shows the characteristic radial skeletal thatch of oxeas, ×5; *5,* side view shows prominent axial canals of the pyritized spicules, ×20; *8,* lower surface of the small sponge shows general radiate nature of the skeleton in the flat pyritized specimen, ×2; *10,* upper surface shows upward expanding, radially arranged, monaxial spicules and the lack of a shallow depression, ×2; *11,* photomicrograph shows upward and outward divergent oxeas in the lower right center of the sponge, as shown in *10*; fragments of crinoidal debris have been included in the pyritized specimen, ×20. *7, 9,* reference specimen, USNM 463593, Road Cut b locality, ×2. *7,* view from above shows shallow, bowl-like, spongocoel depression in the moderately thick-walled, funnel-like sponge; *9,* view from below of the rounded, unstalked, small sponge.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to be globular or spherical, such as *Opetionella* von Zittel, 1878 (p. 4), or *Tethya* Lamarck 1814 (p. 69–80).

Ginkgospongia includes prominently stalked, bladed to palmate, possibly funnel-like sponges with thin walls that were crenulate or lobed. Each lobe has a more or less distinct, upward-divergent, skeletal structure. It contrasts to *Coniculospongia,* which is more bowl-shaped and has an unlobed, commonly discoidal, form.

Etymology.—*Radiatus,* Latin, rayed, beaming, shining, in reference to radial arrangement of spicules.

Material and occurrence.—Holotype, USNM 463591, Benton Quarry; and paratype, USNM 463592, Road Cut b; and an additional tentatively assigned figured specimen, USNM 463893, from the Road Cut b locality, all from the Birdsong Shale, Ross Formation.

Fine-textured spicule mat
Figure 5.1, 5.2

Description.—One moderately large piece with distinctive mat of spicules occurs in collection as bedding-plane fragment, approximately 11–12 cm long and 5 cm across, in thin plate approximately 3 mm thick. Specimen composed, in part, of areas of irregularly arranged spicules and, in part, of regular, subparallel, tresslike arrangement of oxeas 0.04 mm in diameter and 2–8 mm long, although most short. Most small, loglike fragments only approximately 2 mm long, and general rate of taper gentle, so most fragments appear with moderately uniformly cylindrical dimensions.

Whether specimen part of mat of root tuft spicules or part of thin sponge wall not apparent, but does include long, needlelike spicules of same general dimensions as in small associated root tufts. If only root tuft, appears as part of armored layer several centimeters across. Total dimensions not preserved in fragment available, and could have covered considerably larger area than represented by platy specimen.

Material and occurrence.—Figured specimen, USNM 463614, Birdsong Shale, Benton Quarry, and additional unnumbered reference specimen from the Birdsong Shale at Parsons Quarry.

Mat of fine short spicules
Figure 5.3–5.6

Description.—Several small fragments, 2–3 cm across, of mat of fine spicules occur in collection. Irregular, chiplike fragments composed of strewn to regularly packed, side-by-side, short, abruptly doubly tapering, but relatively robust-appearing, small oxeas. Spicules with maximum diameter at mid-length of 0.02–0.03 mm and generally 0.5–0.6 mm long; occur en echelon, in closely packed masses in layers only 1–2 mm thick. Spicules in some areas irregularly oriented, although all essentially in plane, and in other areas with decidedly tresslike parallel orientation. Fragments may be part of root tufts or part of simple, thin-walled demosponges.

Discussion.—These spicules are among the smallest oxeas in the collection. They are smaller than those in the plumose root tufts, described below, and also smaller and considerably shorter than spicules in the thin mat of fine spicules described above.

Material and occurrence.—Two figured specimens, USNM 463594 and 463595, plus two reference specimens, USNM 463496 and 463497, Benton Quarry, and figured specimen, USNM 463599, from Road Cut b locality, Birdsong Shale, Ross Formation.

Order Lithistida Schmidt, 1870
Suborder Rhizomorina von Zittel, 1878
Family Haplistiidae de Laubenfels, 1955
Genus Haplistion Young and Young, 1877
Haplistion lobatum n. sp.
Figures 5.7, 6.10, 6.11

Diagnosis.—Ovoid, lobate *Haplistion* with surface marked by nodes of tract tips of rectangular three-dimensional skeleton, with radial tracts 0.7–1.1 mm in diameter, mostly 1.0 mm across, cross-connected by horizontal or concentric tracts, 0.3–0.5 mm across, defining mesh spaces approximately 1.0–1.2 mm across. Tracts composed dominantly of moderately spaced rhizoclones, mostly 0.3–0.4 mm long and 0.03–0.04 mm in diameter, each with common, small zygomes to 0.02 mm in diameter and high along shaft. Oxeas may be present, 1–2 per section, as coring spicules but relatively rare.

Description.—Sponge ovoid, lobate, moderately large specimen to 108 mm across and 73 mm high and 40 mm thick, with three main lobes, each 25–30 mm across and high, with rounded distal summit. Surface of sponge marked by low, small nodes of tract tips projecting 1–2 mm above general surface.

Skeleton organized into rectangularly arranged, strong, radial tracts and less well developed horizontal or concentric tracts in an open, crudely rectangular, three-dimensional skeleton. Openings or mesh spaces between tracts range 0.6–1.8 mm across, with most approximately 1.0–1.2 mm in diameter, as round openings between rectangularly arranged skeletal tracts, spaced such that approximately 4 mesh spaces occur per 5 mm.

Radial tracts range 0.7–1.1 mm in diameter, with most approximately 1.0 mm across on and near surface, cross-connected by horizontal or concentric tracts, 0.3–0.5 mm across in narrow areas, but thicker where expanded to merge with other tracts. Both horizontal and vertical or radial tracts with ragged exteriors. Tracts composed of only moderately subparallel, fairly loosely packed rhizoclones and possibly other associated spicules. Each tract contains many spicules; 20–30 spicules exposed on surface of one-half circumference of even small, horizontal tracts; considerably more numerous subparallel spicules evident on surfaces of larger radial tracts. Many appear irregularly stacked like somewhat distally convergent poles, but without distinct regular pattern in tract tips. Spicules more nearly subparallel on surface of intervening horizontal tracts, and probably in seg-

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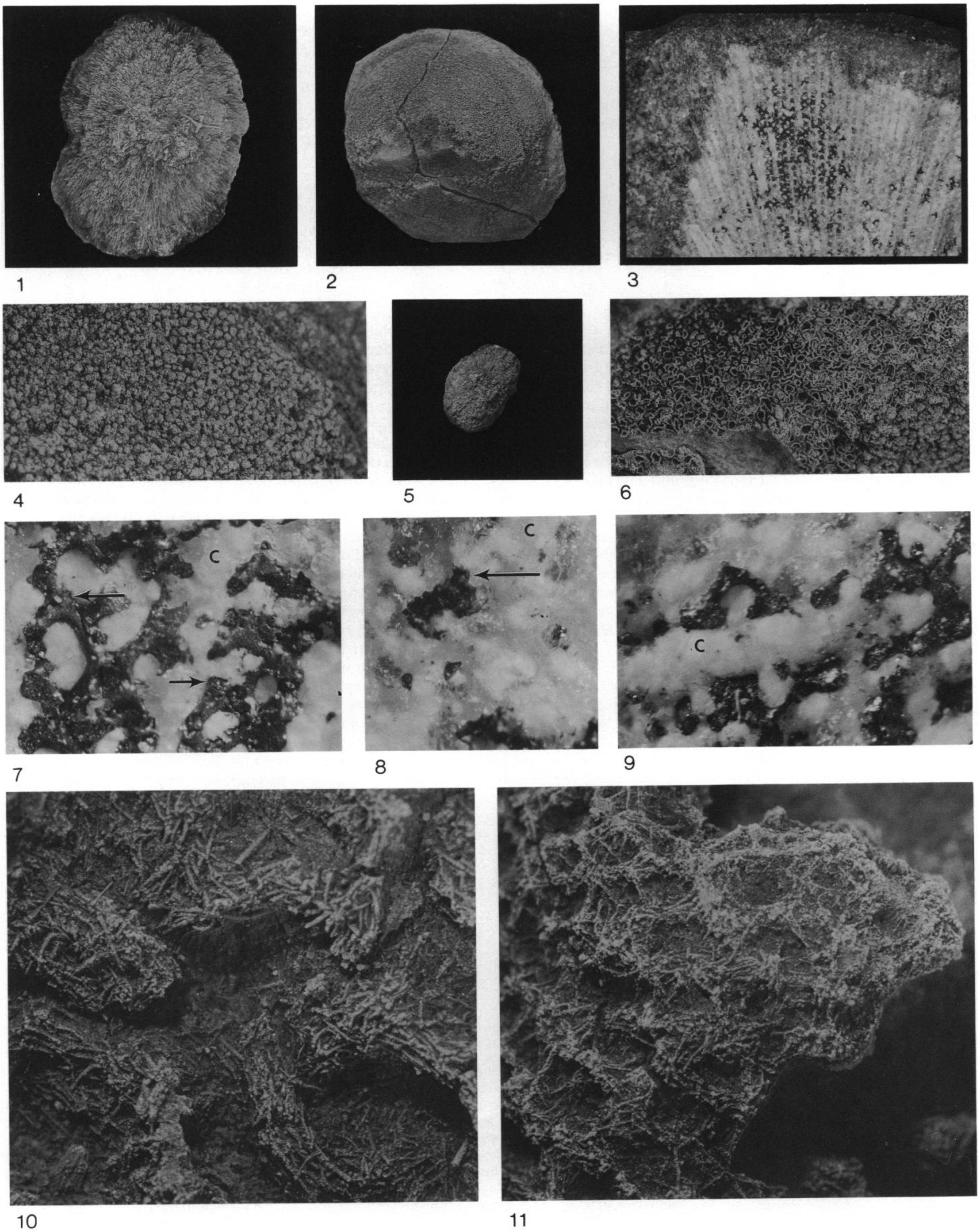
Figure 5—*Haplistion lobatum* n. sp. and mats of fine spicules from Birdsong Shale, Ross Formation. *1, 2,* fine-textured spicule mat, USNM 463614, Benton Quarry. *1,* moderately large, thin sheet of small spicules, part of armored layer several centimeters across; coarse crinoidal, brachiopod, and bryozoan debris have been incorporated into the mat, ×1; *2,* somewhat irregular part of the spicule mat, ×20. *3, 5,* mat of fine, short spicules, figured specimen, USNM 463594. *3,* general appearance of surface of part of the mat, mat 1–2 mm thick, ×2; *5,* photomicrograph shows general nature of small, robust-appearing, short oxeas characteristic of the mat, in moderately irregular orientation, ×20. *4, 6,* mat of fine, short spicules, USNM 463595, Benton Quarry. *4,* general view of the fragment that has incorporated some echinoderm debris within the thatch, ×2; *6,* photomicrograph shows nature of fine, pyritized, small oxeas with various orientations, some show only as subcircular cross sections where they rise steeply to the mat surface, ×20. *7, Haplistion lobatum* n. sp., side view shows characteristic lobate nature of the sponge and the surface marked by small node and tract tips in roughly rectangularly arranged skeleton; holotype, USNM 463598, "bryozoan zone" of Birdsong Shale, McClanahan's Quarry, ×1.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ments of mesh in interior of sponge, as well, although that not clearly demonstrated on weathered specimen available.

Spicules dominantly rhizoclones, range 0.2–0.6 mm long but most approximately 0.3–0.4 mm long, and range 0.03–0.04 in diameter, with most approximately 0.03 mm in diameter, as more or less doubly tapering shafts or axes of spicules. Surface of spicule shaft which faces exterior of tract, generally smooth, but other side ornamented with small zygomes, processes that range from tiny nodes to moderately long, fingerlike elements. These zygome processes range 0.02 mm and less in diameter, and range from small irregularities to somewhat longer digitate extensions, perhaps to 0.04 mm long, generally spaced 0.04–0.08 mm apart, with considerable irregularity along shaft. Most spicules gently curved C- or S-shaped, but some nearly straight, as well. Curvatures generally conform to surfaces of tracts, and spicules curve to make intermesh openings relatively smooth surfaced.

Small oxeas occur locally in skeleton, and range 0.2–1.0 mm long and 0.01–0.04 mm in diameter. These may occur as coring spicules, 1–2 per section, but relatively rare spicules in skeleton.

Spicules within tracts generally occupy one-half to two-thirds volume in areas where moderately open-textured, but more than that where spicules tend to lie more or less side-by-side instead of roughly parallel.

Discussion.—*Haplistion frustrum* was described by Rigby and Chatterton (1989, p. 11–12) from the Cape Philips Formation of Baille Hamilton Island in the Arctic Islands of Canada. That species is discoidal to funnel-shaped and has relatively small vertical tracts with moderately open mesh-spaces. This contrasts sharply with the coarser textured, massive, Devonian species described here. Similarly, *Haplistion*(?) sp. described by them (1989, p. 10–11) also has skeletal tracts that are considerably smaller, only 0.30–0.35 mm in diameter, although individual rhizoclones in that species do have the general appearance of spicules like those in the Devonian sponge from Tennessee.

The somewhat older *Haplistion regulare* Rigby and Webby, 1988 (p. 16–18), from the Upper Ordovician Malongulli Formation of central New South Wales, has strongly subcylindrical vertical tracts that are cross-connected by horizontal tracts and common pinlike, single dendroclones in a skeletal structure distinctly different from the relatively massive tracts in the Devonian Tennessee species. Strong domination of skeletal structure by the distinct subcylindrical radiating tracts in *H. regulare* contrast to the structure in our sponge, although tract and spicule dimensions are not all that different in detail.

Finks (1960, p. 88) subdivided the then described species of *Haplistion* into two major groups, based on size of mesh spaces and relative dimensions of the radial and horizontal tracts. The first group is characterized by mesh spaces less than 1 mm across and with radial and horizontal tracts of approximately equal thickness. The second group of species has mesh spaces approximately 1 mm or more across and with horizontal tracts about half the diameter of the radial ones. It is with the second group that the species described here is related. Finks further subdivided that group into Subgroups A and B, based principally on dimensions of radial tracts, separating those forms with radial tracts generally less than 1 mm in diameter from those with radial tracts generally 1 mm or more in diameter. It is with those species with radial tracts generally 0.5–1.0 mm in diameter, Finks' Subgroup A, that the present species is related. He noted that within that general group, both smooth oxeas and strongyles occur in the tracts, along with the dominant rhizoclones, and that combination is probably a generic character. He noted that of the species in Group 2, Subgroup A, *Haplistion sphaericum* Finks, 1960, and *Haplistion arcticum* Dunikowski, 1884, include oxeas and strongyles in the tracts. He also observed that oxeas alone have been reported from *Haplistion gruenewaldti* (Stuckenberg, 1895) and *Haplistion orientale* (Tschernyschew, 1898), both of Permian age. Whether strongyles occur with the rare oxeas amid the dominant rhizoclones in the present species is not presently determined, because only the weathered surface of the sponge is available. Only oxeas have been clearly identified with their doubly tapering pointed tips, but some of what may appear to be broken fragments could be strongyles with rounded tips in an otherwise basically non-tapering spicule.

Of the species in the subgroup, perhaps *Haplistion sphaericum* Finks, 1960, is the most similar, although tract spacing is more distant in that species than in our specimen. *Haplistion gruenewaldti* (Stuckenberg, 1895) is a more branching, stemmed form than our moderately massive lobate species, and so they contrast in growth forms. *Haplistion vermiculatum* (Carter, 1878) is a small form, only a few millimeters across, and contrasts sharply to the large, massive structure shown here. In addition, spicules and fibers, as figured by Hinde (1887, Pl. 5, figs. 2, 2A), have different packing, orientation, and fabric than that in the species from Tennessee.

Haplistion timorense (Gerth, 1929) is a relatively coarsely textured spherical form with prominent radial tracts and consistently less prominent horizontal ones. Gerth noted that the radial tracts are not over 1 mm in diameter, and that the cross-connecting horizontal tracts are not over 0.5 mm, which is in the general range of elements in the Devonian form described here, but its strongly radiate spherical skeleton contrasts with

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FIGURE 6—*Hindia sphaeroidalis* Duncan, 1879, and *Haplistion lobatum* n. sp. from the Birdsong Shale, Ross Formation, Tennessee. *1–9, Hindia sphaeroidalis* Duncan, 1879. *1, 5,* figured specimen, USNM 463600, "bryozoan zone," upper Birdsong Shale, Benton Quarry. *1,* shows general radial arrangement of spicules in the skeletal structure; prominent hexactine in the right is foreign, ×5; *5,* ×2. *2–4, 6–9,* figured specimen, USNM 463600, bryozoan beds from the upper Birdsong Shale, Benton Quarry. *2,* fractured, large, figured specimen showing general spherical form, as viewed at right angles to matrix stratification indicated by slight flare, particularly prominent in the upper left and lower right; spherical shape is characteristic of the genus and species, ×1; *3,* photomicrograph of fractured interior surface shows dark, pyritized spicules that define prominent upward-and-outward divergent radial canals; spicules in light areas are preserved virtually as molds in carbonate replacement, ×5; *4,* characteristic weathered surface shows light canal fillings surrounded by dark, impressed, moldlike remnants of spicules, ×5; *6,* oddly silicified part of the skeleton, on the exterior, in which silica rinds surrounded the now dissolved pyritic skeletal structure, ×5; *7–9,* dark pyrite spicules in light calcareous matrix, with arched tricranoclones characteristically fused where digitate clonome rays articulate to sculptured surfaces that produce knobby, equally spaced, tripodal-like skeletal elements; short brachyome indicated by arrows in *7* and *8*; prominent canals (C) defined by radially stacked spicules, ×50. *10, 11, Haplistion lobatum* n. sp., holotype, USNM 463598, "bryozoan zone" of Birdsong Shale, McClanahan's Quarry. *10,* photomicrograph shows irregularly curved, moderately well defined, but open tangential tracts of moderately, loosely packed rhizoclones, generally with smooth surface of spicules oriented toward pores and exteriors of the tracts; loose spicules occur in the matrix filling some of the canals, particularly prominent in the lower right, ×20; *11,* skeleton on small lobe or node shows the uniformly spaced interskeletal openings defined by prominent tracts of light-gray, loosely packed, curved rhizoclones, characteristic of the genus and species, ×10.

the less regular structure in our species. Our sponge has the grossly lobate shape of *Haplistion verrucosum* (Dunikowski, 1884), described from the Permian of Spitzbergen, but it does not have the wartlike sculpture characteristic of that species.

Because of differences in skeletal structure, gross development, and sizes of particular skeletal elements, the species is considered here as new, particularly where its stratigraphic isolation within the Lower Devonian separates it far from the similar-appearing *Haplistion* species of the Upper Carboniferous and Permian.

Etymology.—*Lobos,* Greek, elongate projection or protuberance, in reference to the lobate form of the species.

Material and occurrence.—Holotype, USNM 463598, from the Birdsong Shale, "bryozoan zone," McClanahans's Quarry, Tennessee.

Suborder TRICRANOCLADINA Reid, 1968
Family HINDIIDAE Rauff, 1893
Genus HINDIA Duncan, 1879
HINDIA SPHAEROIDALIS Duncan, 1879
Figure 6.2–6.9

Hindia sphaeroidalis DUNCAN, 1879, p. 91, Pl. 9, figs. 1–6; RAUFF 1894, p. 335, Pl. 15, Pl. 16, Pl. 17, figs. 1–4; RIGBY AND WEBBY, 1988, p. 61–63, Pl 26, figs. 1–10, Pl. 27, figs. 1–3.
Hindia fibrosa HINDE, 1883, p. 57, Pl. 13, figs. 1, la–b.
(For a more complete synonymy see Rigby and Webby, 1988, p. 61.)

Discussion.—The large example in the collection is virtually identical with sponges of the species from the Ordovician, and particularly from the Ordovician of New South Wales, Australia (Rigby and Webby, 1988), where well-preserved silicified material shows well the characteristic internal structure of the skeleton and canal system. The specimen here is unusual in North American collections because of its relatively large size. The genus and species is one of the most widely distributed Paleozoic sponges, occurring from the Ordovician in North America and Australia up through the Devonian in many areas.

Material and occurrence.—Figured specimen, USNM 463600, from the upper Birdsong Shale, "bryozoan zone," Benton Quarry, plus two small reference specimens from the Road Cut b locality, Birdsong equivalent.

Class HEXACTINELLIDA Schmidt, 1870
Subclass AMPHIDISCOPHORA Schulze, 1887
Order AMPHIDISCOSA Schrammen, 1924
Family PELICASPONGIIDAE Rigby, 1970
Genus TWENHOFELELLA Rigby, 1974
TWENHOFELELLA BULBULUS n. sp.
Figure 7.1, 7.2, 7.4, 7.5, 7.7, 7.8

Diagnosis.—Steeply obconical to bulbous small sponges, stalked with expanded upper part; skeleton of normal hexactines of several orders with short proximal rays and long tangential rays; latter irregularly oriented. Coarsest or first-order spicules with tangential rays 2 mm long and 0.15 mm in basal ray diameter. Skeletal pores ill-defined in relatively massive-appearing skeleton. Spongocoel probably shallow but ill-defined in laterally flattened specimen, although sponge probably thin-walled.

Description.—Expanding steeply obconical to bulbous small sponge with lower stalked portion and upper globose expanded portion, flattened laterally during diagenesis. Holotype approximately 25 mm tall, with lower half in irregularly defined stalk, 6 × 13 mm at base, expands upward to 18 × 10 mm at top of stalk. Sponge expands to maximum diameter of approximately 24 × 12 mm in upper globose part, and rounds to upper flattened oscular margin, with osculum 2 × 7 mm in the flattened sponge.

Skeleton composed of normal hexactines with relatively short proximal and distal rays, but with tangential rays prominent in pyritized preservation. Tangential rays irregularly oriented so surface of skeleton appears as mat of spicules without rectangular or parallel development. Spicules of several orders present. First-order spicules with long, smooth rays, subcylindrical in inner one-third, but tapering to sharp pointed tips in outer part of rays to 2 mm long, with most approximately 0.15 mm long and 0.15 mm in basal ray diameter. Second-order spicules with rays approximately 1 mm long and 0.10 mm in basal diameter, occur interspersed and with rays intermeshed with first-order spicules. Third-order spicules with rays approximately 0.5 mm long and with basal ray diameters of 0.06 mm, somewhat less obvious than coarser spicules, but common. Numerous other smaller spicules also occur, but their structure generally not well preserved. Some with rays 0.3–0.4 mm long and 0.04 mm or less in basal diameter. Spicules of upper globose part of sponge somewhat coarser than those in stalklike area, but change in size appears gradational. No thickening of skeletal elements evident in outer part, and no development of armoring dermal layer. Pores in skeleton ill-defined, but some circular impressions, approximately 0.3–0.4 mm across, occur as interruptions between triangularly oriented and spaced rays.

Discussion.—The somewhat goblet-shaped brachiospongiid separated out here is characterized by relatively unspecialized, though moderately coarse, hexactines that make up at least a major part of the dermal and endosomal layers. They also appear to extend with some commoness into the interior of the thin-walled sponge. Within the Pelicaspongiidae, *Pelicaspongia sterea* Rigby, 1970, from the Frasnian Mt. Hawk Formation in Alberta, is a relatively thin-walled, bowl-shaped form, but with walls perforated by large, circular, parietal gaps. It has moderately enlarged hexactines on both the gastral and dermal surfaces, but with much of the interior made of irregularly oriented, considerably smaller hexactines. A stalk is not present in the

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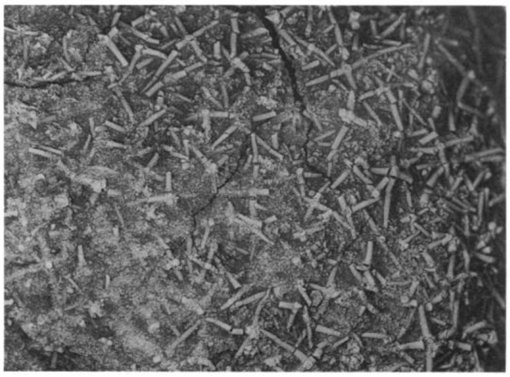
FIGURE 7—*Twenhofelella bulbulus* n. sp. and hexactinellid genus indeterminate from the Birdsong Shale, Ross Formation, Tennessee. *1, 2, 4, 5, 7, 8, Twenhofelella bulbulus* n. sp., Birdsong Shale, Ross Formation, Parson's Quarry. *1, 2, 4, 7,* holotype, USNM 463601, spoil pile, Parson's Quarry. *1, 2,* photomicrographs show characteristic irregular orientation of smooth, well defined hexactines of several orders, separated by dark argillaceous matrix; pyritized spicules show four prominent tangential rays and less well developed distal rays; rounded upper surface near spongocoel margin to the right, ×5; *4,* side view of holotype shows bulblike form with moderately well defined stalk at the base; skeleton made of irregularly oriented hexactines, ×2; *7,* photomicrograph shows fractured, but clearly recognizable hexactines of the principal skeleton as pyritized pseudomorphs of the originally siliceous spicules, ×20. *5, 8,* reference specimen, USNM 463615, Parson's Quarry. *5,* flattened fragment shows characteristic development of irregular, though somewhat smaller spicules than those in the holotype; orientation of the flattened fragment unknown, ×2; *8,* photomicrograph shows pyritized hexactine-based spicules; most are hexactines but some are modified to pentactines, in the surficial layer near the center, ×20. *3, 6,* hexactinellid genus indeterminate, figured specimen, USNM 463602, Benton Quarry. *3,* small, platelike irregular fragment contains the numerous nodose to spinose hexactines in irregular orientation, ×2; *6,* photomicrograph shows several spinose hexactines with prominent nodes or spines in braceletlike rosettes up to six radial rows of spines per ray; rays of several sizes of spicules are prominent in the weathered surface, ×20.



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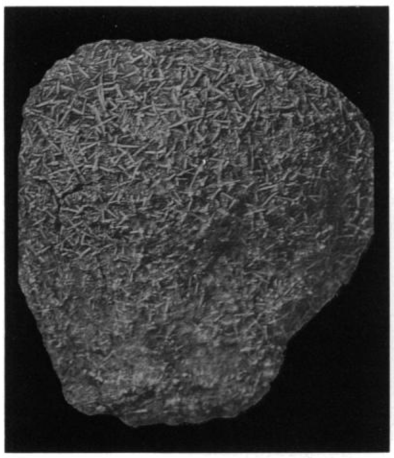

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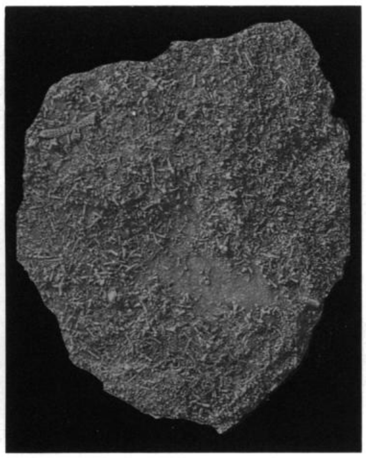

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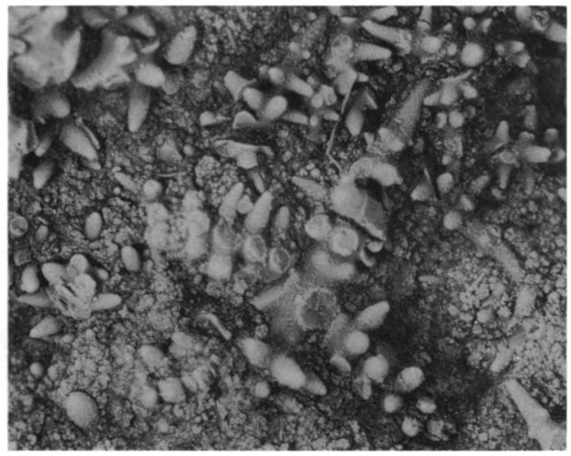

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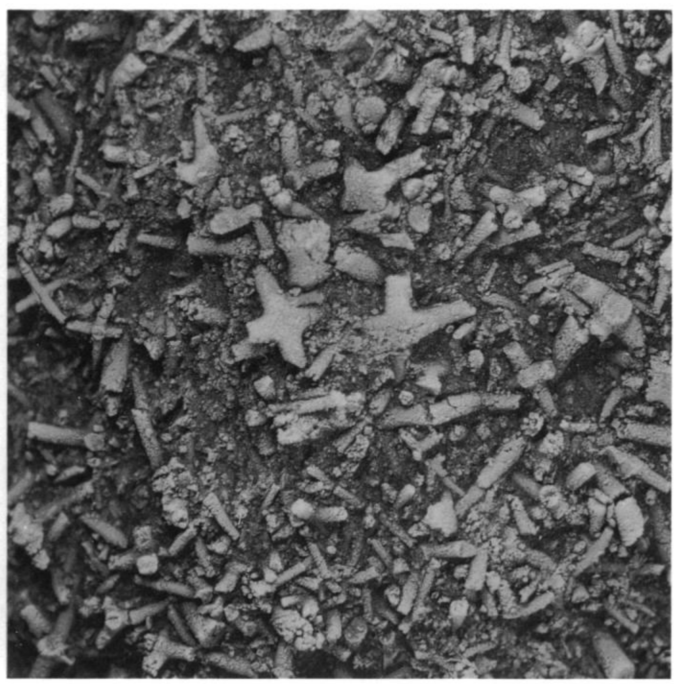

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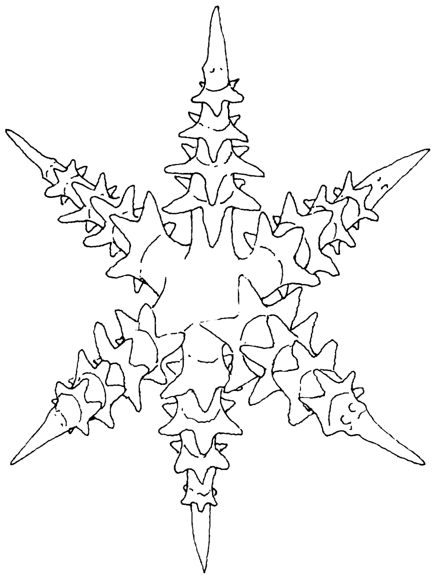

FIGURE 8—Sketch of a single spicule of the indeterminate hexactinellid, USNM 463602, from Benton Quarry, approximately ×10.

type species, and it is distinguished from the Early Devonian form, described here, in that respect. In addition, large parietal gaps are not evident in the species described here.

In many respects the species from Tennessee appears most similar to *Twenhofelella anticostiana* (Twenhofel, 1928), as redescribed by Rigby (1974), from the middle Niagaran Silurian Jupiter Formation of Anticosti Island in Quebec. That Silurian species is bowl-shaped, but it has a moderately thick wall, lacks a root tuft, and has moderately well developed parietal gaps through the wall, although they are not particularly evident on the exterior. Its walls seem to be armored with a layer of enlarged hexactines and pentactines(?), much as in the Devonian species from Tennessee. However, *Twenhofelella anticostiana* is a distinctly thick-walled form, with a prominent, but shallow, spongocoel.

Malumispongium (Rigby, 1967, p. 770), from the Silurian of the Gaspe Penninsula of Quebec, is also a bowl-shaped to vasiform sponge, with a skeleton made of irregularly oriented and variously sized hexactines, but it lacks coarse hexactines in a dermal layer, like those present in the form from Tennessee. In addition, *Malumispongium* is a very large sponge for the Paleozoic and has very thick walls perforated by very coarse parietal gaps. It may be a related form, but is easily separated from the moderately thin-walled sponge described here.

Etymology.—*Bulbulus,* Latin, a swelling, in reference to the bulb-shaped form, like a small electric light bulb.

Material and occurrence.—Holotype, USNM 463601, Parsons Quarry spoil pile, Birdsong Shale, plus one reference specimen, USNM 463615, from the Birdsong Shale at Parsons Quarry.

Hexactinellid genus indeterminate
Figures 7.3, 7.6, 8

Description.—Small platelike rectangular fragments up to 13 mm high and 24 mm wide, composed of spinose hexactines in irregular orientation and spacing, all rays of spicules sculptured by prominent nodes or spines arranged in transverse braceletlike rosettes, with nodes aligned in six radial rows of spines per ray (Figure 8). Basic spicules with relatively robust rays, 1.5–1.8 mm long and with basal diameters of 0.2–0.3 mm.

Characteristic ray with four "bracelets" or rosettes of spines, or nodes, relatively uniformly spaced approximately 0.2 mm apart, along ray, and each composed of six radiating spines, arranged uniformly about 60° apart around circumference of ray. Spines also in six radial rows, generally with size decreasing distally, although in some, first rosette may be represented only by nodes or lower spines. Spines of proximal rosettes generally 0.20–0.35 mm long and with basal diameters of 0.14–0.25 mm; each spine smoothly tapers to moderately sharp point. Intermediate rosette generally composed of spines 0.14–0.18 mm long and 0.12–0.16 mm in basal diameter. Outer or fourth rosette commonly with spines 0.10–0.12 mm long with basal diameters of 0.08–0.10 mm, continuous moderately uniform decrease in size of the spines distally. Generally spines oriented normal to axis of rays, but few may be pointed somewhat distally at angles of 50°–70° in middle parts of rays.

Distal 0.25–0.30 mm of each hexactine ray smooth, without spines, or with only small nodes, of possible fifth series, but generally distal tips taper smoothly and uniformly to sharp points. Outer smooth parts of large spicules approximately 0.08 mm in diameter near outer rosette, and from that diameter taper smoothly and uniformly to ray tip. Most secondary spines with circular cross sections, but some may be slightly elliptical, with long axis normal to axis of ray.

Spicules arranged in tracts 1–2 mm wide or wider that separate elliptical openings 2–3 mm long and 1.0–1.5 mm wide, on very irregular basis. Nature of entire skeleton and shape of sponge unknown.

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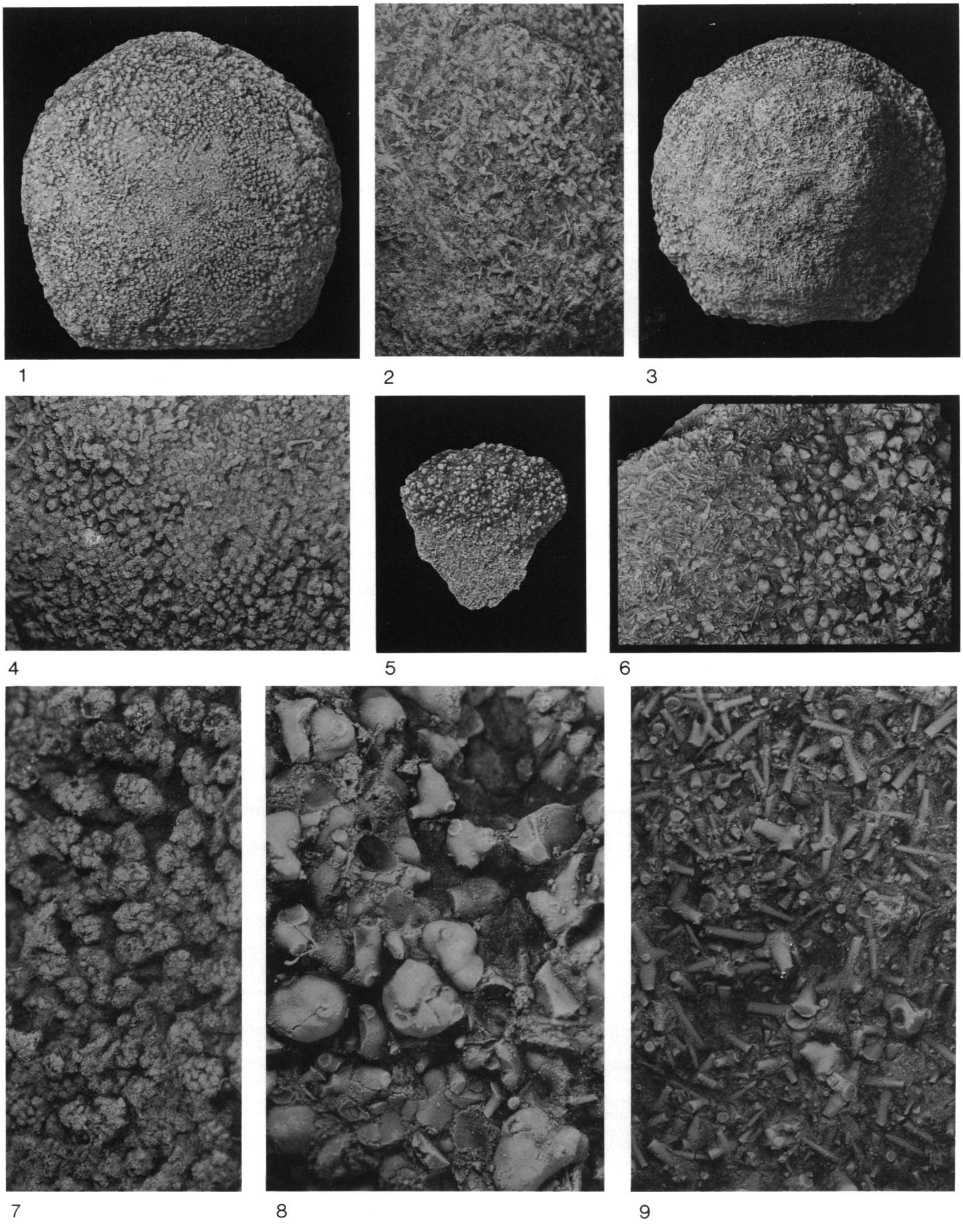
FIGURE 9—*Stiodermiella amanita* n. sp., Birdsong Shale, Ross Formation, Tennessee. *1–4, 7,* holotype, USNM 463603, Benton Quarry. *1,* arched, massive upper surface of low, mushroomlike sponge shows characteristic nodose dense cap with distal rays of spicules virtually side-by-side, with many somewhat papillose; tangential rays obscured, ×2; *2,* photomicrograph of central part of the base shows irregular hexactines in felted irregular network characteristic of the species, ×5; *3,* base with weak, irregular, massive stalk and overhanging, caplike part of the sponge, produced mushroomlike structure; irregular spicules of the central part of the base show in the center, and more regularly arranged hexactines particularly well shown in the upper left, ×2; *4,* photomicrograph of the upper armored layer, with cylindrical distal rays capped by papillae; hexactines of basic internal skeleton show in the upper left, ×5; *7,* photomicrograph shows papillose terminations of cylindrical distal rays of hexactines in the armored upper layer of the holotype, ×20. *5, 6, 8, 9,* paratype, USNM 463605, spoil pile undifferentiated Ross Formation, Benton Quarry. *5,* side view shows prominent stalk and massive spicules of the upper bulblike principal part of the sponge, ×2; *6,* photomicrograph shows upper part of the stalk, on the left, and lower part of the grossly enlarged hexactine spicules of the principal part of the skeleton, on the right, where all rays have been enlarged on some spicules, and only selected rays on others; degree of enlargement generally increases from the relatively unmodified spicules of the stalk up into the massive, armored layer, top of the specimen toward the right, ×5; *8,* photomicrograph of massive, overgrown spicules, in the upper part of the paratype, showing some grossly enlarged rays and others somewhat more nipple-shaped, where they have been fractured; fine matrix still separates most of the spicules, even in this massive layer; spicules have been replaced by pyrite, ×20; *9,* relatively unmodified hexactines of the stalk area of the paratype are irregularly oriented; some enlarged spicules in the middle and lower part of the figure represent the intermediate part of the sponge, top of the sponge is toward the bottom, ×20.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Discussion.—Somewhat similar spicules were described in the sponge *Oncosella catinum* Rauff, 1894 (p. 264, Pl. 7, figs. 5–11), from the Silurian Wenlock Limestone of Dudley, England. However, spicules in *Oncosella* are much more irregularly spinose, instead of four consistently spaced "bracelets" of uniformly spaced spines, as in our specimen. In addition, the spines figured by Rauff appear as irregularly curving and relatively delicate elements, rather than the moderately robust, straight, uniformly tapering spines seen in the specimen here.

Hinde (1888, Pl. 9, figs. 13, 13A) figured some irregular spinose "flesh spicules" of an unnamed hexactinellid, which are also irregularly spinose. They were recovered from chert beds of the Yoredale Series at Richmond, Yorkshire, and from a chert pebble out of the glacial drift at York, England. These spicules have considerable irregularity in spine size and spacing, and consequently contrast sharply to the very regular structure shown in the species here.

Under some preservations, spicules of *Spiractinella wrightii* (Carter, 1880), as figured by Hinde (1887, Pl. 8, figs. 1, 1A–H), which have a spiral orientation like threads on a screw, could appear similar if they were crudely preserved and seen only laterally. In detail, however, they certainly would not be confused.

Isolated spicules included in the genus and species *Rhakistella alba* by Weller (1930, p. 243) are somewhat similar to the spicules recognized here from the Birdsong Shale. Material included in Weller's species, however, have all the surfaces of each ray thickly set with small, equal-sized and equally spaced spines that occur completely along the length of the rays. This contrasts with the spicules here that have the nodes only in the proximal part of the rays and the outer parts are smooth. In addition, distal tips of some of the rays in Weller's species bifurcate at about mid-length into two prongs, and form spicules decidedly different from those present here, in addition to having different sculpture on the rays.

Acanthactinella benniei Hinde, 1888, was established for a series of relatively large, aberrant hexactine-based spicules with large spines that appear to be irregularly spaced. More distinctively they have rays that bifurcate and produce irregularly spinose processes, which produce highly irregular spicules, in a structure quite distinct from the regular predictable pattern seen in these Devonian spicules from Tennessee.

Material and occurrence.—Figured specimen, USNM 463602, Birdsong Shale of the Ross Formation, Benton Quarry, and unnumbered silicified reference specimen from the Ross Formation at the Allen's Mill locality.

Genus Stiodermiella n. gen.

Type species.—*Stiodermiella amanita* n. sp.

Diagnosis.—Stalked, mushroomlike, or inverted cup-shaped sponges with stalk, if present, of normal-appearing hexactines, but upward-expanded cap with dense, gastral armor of spicules with expanded ray junctions, or centra, which may be papillose and combine to produce dense cortex. Internal spicules in nonparallel arrangement. Cortex, if present, covers canals.

Discussion.—Comparisons with various similar hexactinellids are treated in discussion of the type species below.

Etymology.—*Stion,* Greek, pebble; *derma,* skin or hide; *ella,* dimunitive, referring to the small armored tilelike or pebblelike armor of the small sponges; also named because of at least the superficial similarity to *Stioderma* from the Permian of West Texas (Finks, 1960, p. 132).

Stiodermiella amanita n. sp.
Figures 9, 10.1, 10.3

Diagnosis.—Small, stalked, mushroomlike sponge with expanded upper cap or armored crest, lacks osculum or spongocoel. Stalk of normal-appearing hexactines, and upper cap with similar spicules, plus armoring upper layer of spicules with expanded centers as massive nodes 0.3–0.8 mm in diameter. Nodes smooth to papillose, tangential rays generally small, short, and spinelike. Canal structure not evident.

Description.—Specimens range from stalked, mushroomlike, small forms to moderately high, mushroomlike sponge. Small, immature specimen approximately 15 mm high and 6 mm across clearly shows two skeletal zones, lower stalk approximately 8 mm high and upper, armored, massive crest approximately 7 mm high, expands upward to maximum diameter of 16 mm in upper, arcuate, massive cap. Stalk expands upward from broken base to maximum diameter of 11 mm, below abrupt flare into upper cap.

Somewhat larger, more nearly complete holotype, about 16 mm high, with somewhat eccentric stalk, somewhat laterally distorted, approximately 5 mm high. Sponge with maximum diameter of 30 × 32 mm in massive, armored crest, which expands abruptly upward from maximum stalk diameter of 20 × 24 mm. Upper massive crest approximately 10 mm thick with characteristic, armored, dense layer of expanded spicules characteristic of species.

Stalk composed of normal-appearing hexactines with small smooth rays 0.05–0.10 mm in diameter in lower and middle part. Some spicules with thickened rays in upper and outer part

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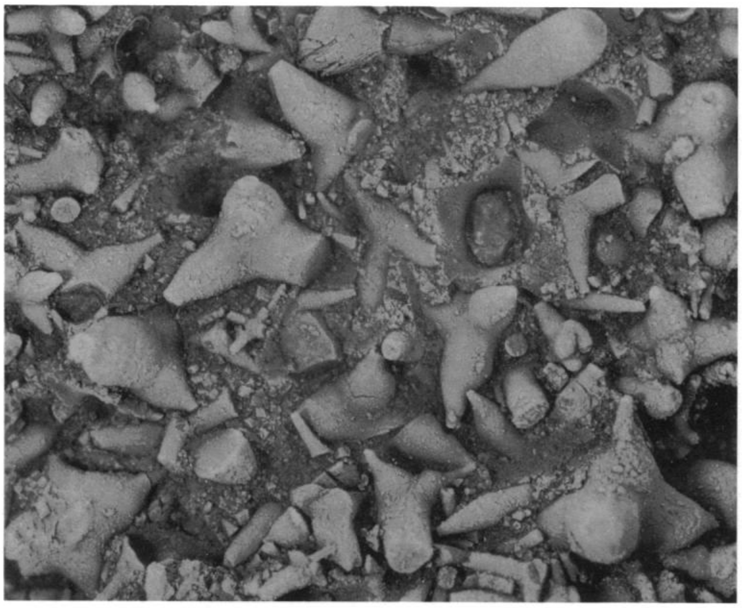
FIGURE *10*—*Stiodermiella amanita* n. sp. and *Stiodermiella tetragona* n. sp. from the Birdsong Shale, Ross Formation, Tennessee. *1, 3, Stiodermiella amanita* n. sp., paratype, USNM 463604, Benton Quarry. *1,* photomicrograph shows grossly enlarged spicules of the upper part of the sponge, and some regular, smaller hexactines, separated by pyritized matrix, ×20; *3,* fragment shows relatively unmodified hexactines, on the left, in what was probably the lower part of the sponge and the armored, thickly overgrown spicules characteristic of the upper part of the sponge on the right, ×2. *2, 4–7, Stiodermiella tetragona* n. sp., holotype, USNM 463608, Benton Quarry. *2,* photomicrograph of the upper part of the armored layer of the sponge, as shown in *6,* with prominent cortex, characteristic of the species, of strongly swollen and developed papillae that form almost arborescent or petalloid terminations to the distal rays, ×20; *4,* photomicrograph of part of the lower lateral surface shows the prominent rectangular, reticular arrangement of the distal rays, each capped by papillae that help form a prominent cortex; cortex covered relatively delicately spiculed, more interior layer in the lower part of the sponge, between the cortex and the massive, enlarged spicules of the dominant, swollen skeleton; a few swollen spicules are shown in the extreme lower right, in the three-layered skeletal structure, ×5; *5,* photomicrograph of tilted margin shows prominent, reticular, linear development of distal papillose rays in the lower and more massive part, with somewhat irregular papillose rays in the upper part; the massive irregular part is exposed on the tilted edge, where the undersurface has been partially eroded, ×5; *6,* top view shows the massive swollen spicules of the principal part of the skeleton, in the interior, but with papillose distal rays most prominent around the upper and left margins; bryozoans occur as ramose elements in the lower part and as fenestrate elements in the lower right, ×2; *7,* bottom of the sponge shows the massive, swollen spicules in the interior of the caplike part of the sponge; a finely spiculed layer is intermediate between the interior massive spicules and the reticulated cortex of papillae that forms the outer one-quarter to one-third of the sponge; crinoidal and bryozoan debris have been incorporated into the skeleton; rotated from orientation in *6,* ×2.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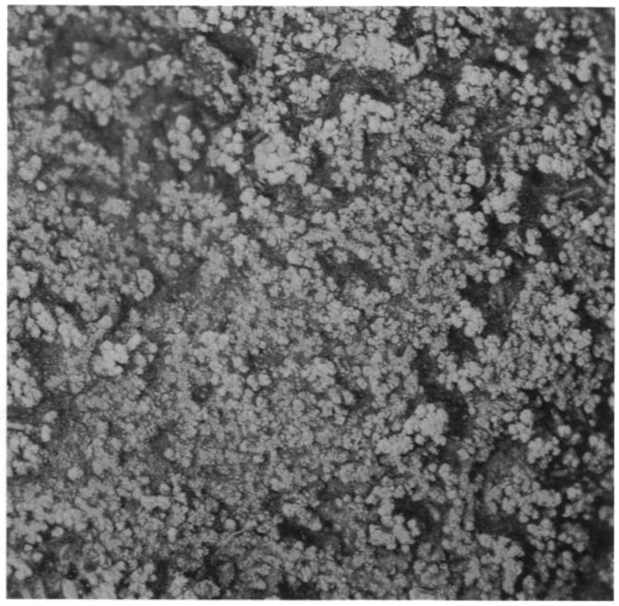
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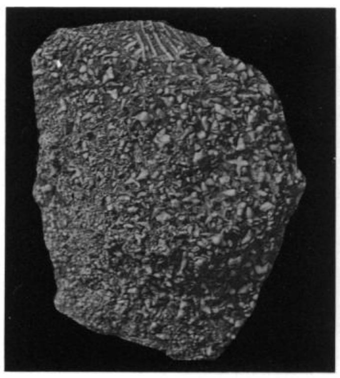
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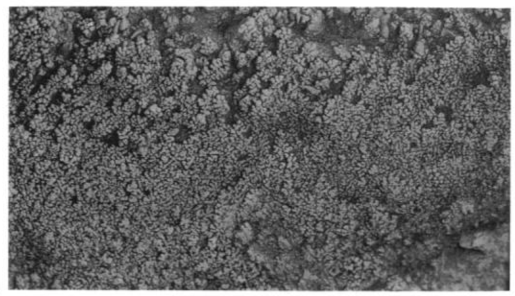
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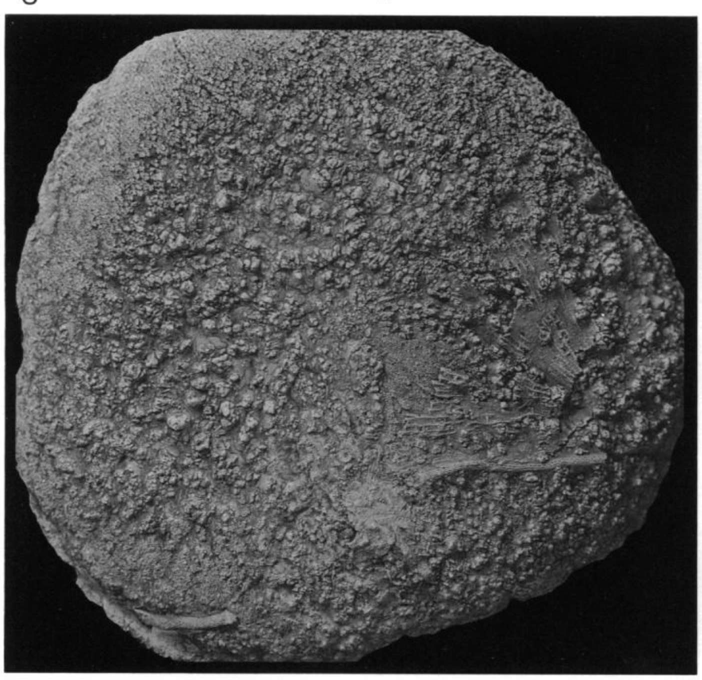
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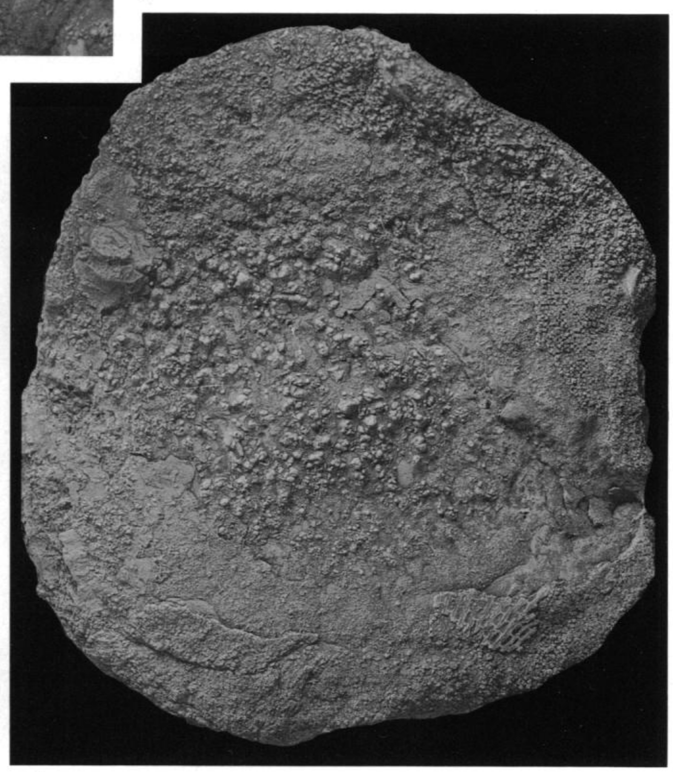
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of skeleton, but most of stalk composed of normal-rayed hexactines.

Upward gradation into overlying massive cap abrupt; through only 1–2 mm. Vertical fabric dominates in stalk, with vertical rays more prominent and 1–2 mm long; locally produce almost brushlike appearance where stalk flattened somewhat laterally. Other rays of hexactines, however, irregularly oriented, and certainly no rectangular nor regular fabric at right angles to elongate, vertical rays.

Upper 2–3 mm of dense gastral cap with spicules virtually side-by-side, but spicules less closely spaced in underlying 8–10 mm down to top of stalk. Armor spicules with expanded centers 0.5–0.8 mm apart, generally irregularly spaced, but locally in linear series, though not in rectangular pattern. Massive nodes range 0.3–0.8 mm in diameter, as hemispherical, central ray junction expansions, from which small rays 0.2 mm in diameter and 0.4–0.5 mm long radiate as somewhat tangential spines in some areas. Latter usually taper in somewhat curving fashion, so bases expanded but outer tips needlelike. Some such rays only 0.08–0.12 mm in diameter and 0.3–0.4 mm long in upper part of skeleton, so virtually entire surface of sponge represented by skeletal materials, without measurable pores.

Central domes of individual spicules range from smooth to nodose or papillose. Papillae generally small, irregular, hemispherical mounds, 0.04–0.08 mm in diameter and 10–20 per dome. Most domes on upper crest papillose, but papillae most characteristically developed on lower flanks of arched armor layer.

Upward-expanded part of sponge, thus densely spiculed, and massive, armored, almost like tile. Structure beneath armored layer, however, considerably more irregular and small spicules occur intermixed with ones with swollen ray junctions.

Stalk in small, immature form dominantly composed of normal, thin-rayed, smooth hexactines, but upper part of small specimen largely composed of spicules with globose ray junction area. These domes range 0.6–1.0 mm in diameter, with most approximately 0.8 mm across; from which extend small, almost spinelike rays, 0.06–0.10 mm in diameter that extend 0.2–0.3 mm along normal axes of hexactines. In most such spicules proximal ray somewhat swollen, but distal ray not well developed. In small sponge, most domes smooth, without papillae such as developed on larger sponges.

Small, intermediate fragment shows mix of swollen and normal rays, but in addition to swollen central region, numerous spicules with grotesquely swollen tangential rays, as well as proximal rays. Spicules characteristic of species, thus, range from those with swollen ray junction area, with almost spinose remnants of tangential rays, to those with proximal parts of tangential rays grotesquely swollen and only small tips that extend distally. Such swollen spicules typically develop in upper massive cap of sponge.

Discussion.—Small, mushroomlike sponges included in the species have smooth to slightly papillose swollen spicules that make up the massive, armored layer of the upper part of the mushroom-shaped sponge. Stalks are composed of irregularly oriented, smooth, long-rayed smaller hexactines. This structure contrasts to the inverted bowl-like specimens of the associated species, in which stalks are ill-defined, although a zone of mixing of fine and coarse spicules does occur in the central part of the concave lower part of the sponge. The upper, massive, armored layer of the bowl-like species has uniformly papillose spicules, papillose to the point where their microsculptured surfaces merge laterally to produce a dense irregular layer on the upper surface, where the swollen hexactines of the skeleton do not show. The latter species is also characterized by having an additional layer of very fine, normal hexactines, developed as a layer on the lower side, a layer developed between the regular skeleton, and an outer reticulate cortex. That produces a distinctly rectangular pattern as a separate layer on the undersurface.

The Docodermatidae Finks, 1960, are brachiospongioid sponges in which the dermalia are enlarged and in many cases have distal excrescences and extra tangential rays. In this respect, the Tennessee Devonian material appears similar to *Docoderma* Finks, 1960, but the skeletal structure in the dococdermatiids is organized into layers with a superdermal layer of fine, quadrate mesh above a dermal layer of very large pentactines or hexactines, which may have various outgrowths on their distal surfaces. The interior spiculation in the dococdermatiids is organized into crisscrossing bundles parallel to the surface, in a structure not evident in any of the specimens here. The similarity is somewhat superficial in relationship to development of the papillose, coarse hexactines in the outer dermal layer, and their combining to produce an irregular, complex layer, but the internal skeletons are different.

The Stiodermatidae Finks, 1960, also include hexactinellid sponges in which tangential rays of the hexactines may be locally swollen, but with distal rays of the dermalia more commonly swollen to simple spherical or club-shaped extensions. These are much larger than the other main rays of those spicules. The type species, *Stioderma coscinum* Finks, 1960, has numerous large parietal gaps that perforate the thin-walled, cuplike sponge, and dermalia of two general sizes. Smaller spicules are exterior to the larger ones and radially arranged around them, but fused to the larger elements to form a continuous rigid net. Such spicules and the fused net are not developed in the sponges from Tennessee. *S. coscinum* and the new sponge described here are comparable in the sense of having a relatively rigid, platelike dermal layer, but significant details of the spiculation are different, for papillose ray-junction expansions, such as characterize the Devonian Tennessee form, are not developed in the more or less smooth, knoblike distal rays of even the larger dermal spicules in *Stioderma coscinum.*

Etymology.—*Amanita,* Greek, like a kind of mushroom, in relation to the growth form of the species.

Material and occurrence.—Holotype, USNM 463603, Benton Quarry; small paratype, USNM 463604, Benton Quarry; small paratype, USNM 463605, Benton Quarry, Ross Formation (undifferentiated) spoil pile; paratype, USNM 463606, Benton Quarry; paratype, USNM 463607, bryozoan zone, Elkins Quarry, all from in situ in the Birdsong Shale of the Ross Formation, except USNM 463605. Collection includes one additional reference specimen from the Benton Quarry and another tentatively assigned reference specimen from the Birdsong Shale at Parsons Quary.

Stiodermiella tetragona n. sp.
Figures 10.2, 10.4–10.7, 11

Diagnosis.—Inverted, broad, bowl-shaped sponges, with principal skeleton mixture of irregularly oriented normal hexactines but with armored lower and upper layers of swollen hexactines with swollen ray-junctions on which papillae strongly developed; armor produces irregular cortex on dermal surface that lacks regularly rectangular pattern in similar cortex layer on the other side, where papillose centers produce rectangularly arranged sculpture in outer layer over inner cortex layer of tiny normal hexactines, on at least the outer two-thirds of the undersurface, as layer 0.2–0.5 mm thick beneath papillose cortex layer 0.2–0.3 mm thick.

Description.—Two inverted, bowl-like sponges occur in collection. Holotype subpentagonal, 42–48 mm across, and 6–8 mm thick, with gently invaginated base and gently arched upper distal surface. Principal skeleton on undersurface a mixture of normal, smooth, simply tapering hexactines intermixed with ones with swollen central ray junctions. Spicules on lower surface with swollen junctions to 1.0 mm, but most approximately 0.6–0.8 mm across, from which extend short tangential rays to approximately 1 mm long, but commonly much shorter. Latter rays, 0.2–0.3 mm across at base, taper abruptly and moderately smoothly to sharp tips.

Finer, intermixed, normal hexactines range to spicules with rays 1.0–1.5 mm long and 0.10–0.15 mm in diameter. These grade to tiny spicules that make up inner layer of fine-spiculed cortex on undersurface of sponge, where these spicules generally with rays less than 0.5 mm long. Cortex covers only outer two-thirds of undersurface of sponge but may have extended farther, and now removed from central, most concave part of base. Cortex fine, dense layer ranges 0.2–0.5 mm thick and consists mostly of spicules with rays 0.4–0.5 mm long and 0.02–0.03 mm in basal diameter, although some rare spicules with rays to 1.0 mm long and 0.04 mm in diameter occur. Spicules in matlike layer, with individual spicules oriented irregularly, no reticulate organization, and no clearly defined vertical or proximal–distal relationship of spicules.

Irregular layer overlain by papillose cortex well exposed on both outer part of base of sponge, as well as on upper surface. That papillose cortex layer on undersurface ranges 0.2–0.3 mm thick and composed of moderately rectangularly arranged and spaced spicules whose distal rays become distinctly papillose and produce reticulate pattern. Papillose centers range 7–8 per 2 mm, measured somewhat diagonal orientation of reticulation. These centers 0.15–0.20 mm in diameter and each with 10–15 papillae on somewhat expanded summits. Individual papillae 0.04–0.06 mm in diameter in cluster, generally hemispherical, and produce nodose crests in structures, that where expanded tend to form reticulate or minutely and regularly quadrate appearance of layer. Beneath outermost prominent surface, stalk-like bases of papillose rays separated by circular pore 0.2 mm in diameter that occur in centers of rectangular structure. Papillae appear to rise from ray junction of somewhat rectangularly spaced hexactines, each with normal, smooth, tangential rays, but with papillose distal rays.

Upper surface with finely papillose cortex, as well, but lacks regular reticulation of cortex on underside, but consists of moderately irregular, distinctly spherical papillae 0.06–0.10 mm in diameter, with most approximately 0.08 mm across. Papillae occur side-by-side, and produce armored layer interrupted only in a few places by circular pores, 0.15–0.20 mm in diameter and spaced approximately 0.5 mm apart, without any particular geometric predictability, in that part of cortex layer where best preserved. Elsewhere, even these small openings obscured in dense but thin cortex layer.

Reticulate nature of cortex on undersurface shows better on paratype as distinct rectangular pattern, with elements 7–8 per mm, arranged in somewhat diagonal pattern to complete periphery of sponge. Underlying fine feltlike spicule layer present but not as well preserved as on holotype. Swollen principal spicules of main skeleton show clearly on concave surface, mixed with more or less normal hexactines, with smooth, simply tapering rays. Most spicules, even larger ones, with rays only 1.0–1.5 mm long and swollen bases 0.2–0.3 mm across taper abruptly, but taper relatively uniform and simple in smaller, more nearly normal intermixed hexactines.

Discussion.—These forms with a well-developed cortex appear to be derived from the structurally somewhat simpler new species, *Stiodermiella amanita,* described above. That species may have papillose surfaces on spicules in the armoring layer,

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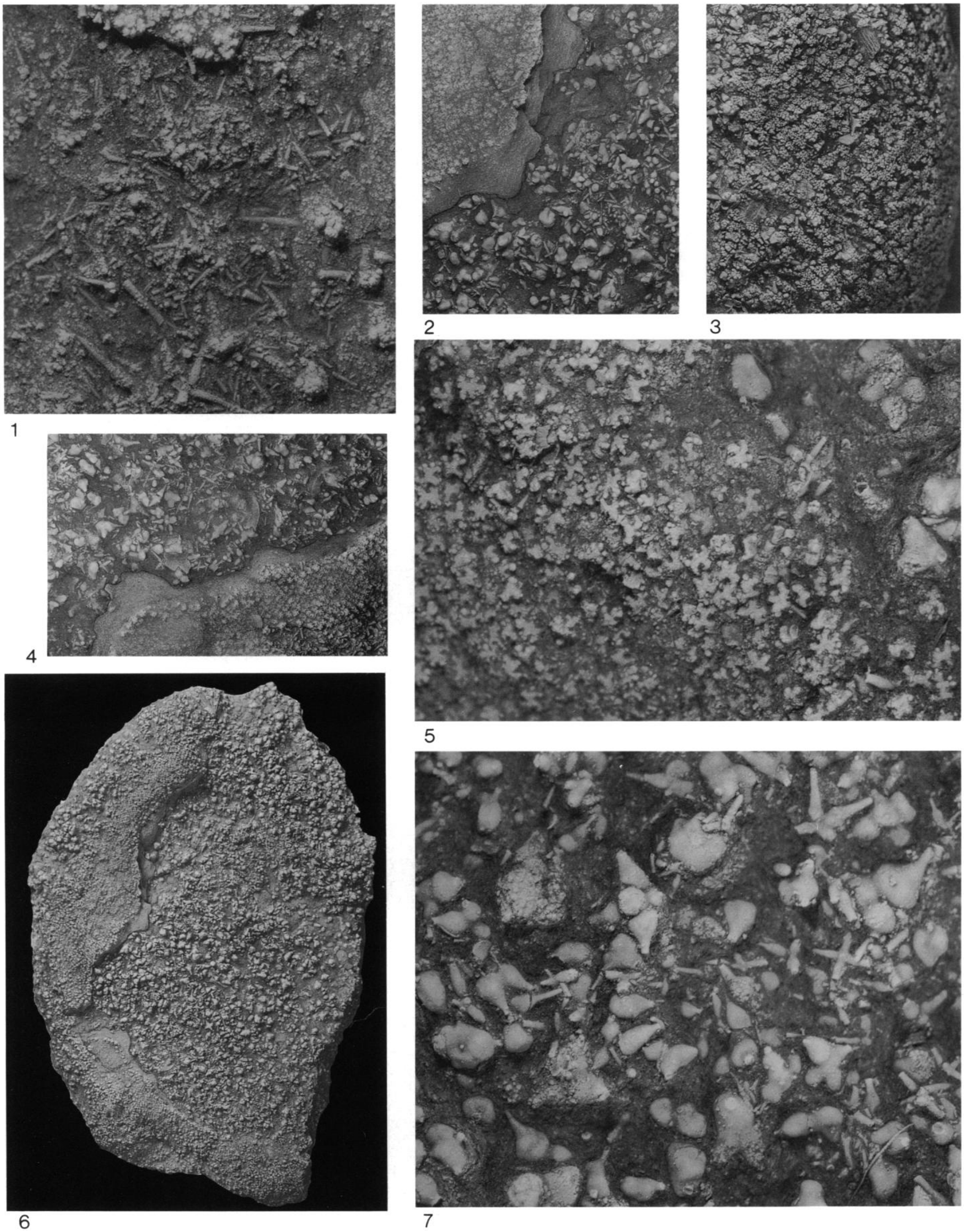
FIGURE *11*—*Stiodermiella tetragona* n. sp. from the Birdsong Shale, Ross Formation, Benton Quarry, Tennessee. *1, 3,* holotype, USNM 463608. *1,* photomicrograph of the irregular, finely spiculated layer exposed on the bottom of the sponge, with coarse papillae showing in the slightly raised layer at the top; hexactines of several ranks show in the irregularly oriented structure, ×20; *3,* upper edge shows the moderately coarse petalloid-looking papillae of the cortex layer, at the curved margin of the sponge, ×5. *2, 4–7,* paratype, USNM 463609. *2,* photomicrograph showing three distinct layers in the lower part of the skeleton, on the underside of the sponge; massive, gross spicules of the principal part of the skeleton occur in the center and lower right, overlain by a layer of fine spicules, almost matrix-appearing, intermediate between the coarse principal skeleton and the outer, somewhat rectangularly arranged cortex, ×5; *4,* photomicrograph showing the three-layered nature of the skeleton, somewhat like that in *2,* with the regular, distal rays of the massive outer cortex shown in the lower right; the finely spiculed, dense, intermediate layer shows well in the middle and upper part between the cortex and the massive spicules of the principal part of the skeleton, ×5; *5,* photomicrograph of the cortex layer and massive spicules of the principal part of the skeleton near the periphery of the sponge, with the cortex weathered and removed from the massive spicules on the right, ×20; *6,* lower part of the sponge fragment, essentially complete along the left, but broken on the right, in what was probably an early discoid sponge; principal massive skeleton shows well in the central part and the rectangularly arranged, papillose, cortex layer shows moderately well in the lower and upper left, above the finely spiculed dense layer, but resting directly on the massive layer near the outer margin, ×2; *7,* photomicrograph of the massive, spiculed interior of the sponge, where weathered on the lower surface, spicules irregularly oriented and overgrown to varying degrees, so that some appear nipplelike, others as bulbous forms, and others still less modified, as is characteristic of the genus and species; spicules are pyritized in pyritic clay matrix, ×20.

FIGURE *12*—Root tufts from the Birdsong Shale, Ross Formation, Benton Quarry, Tennessee. *1, 12,* figured specimen, USNM 463613. *1,* photomicrograph of relatively fine spicules in the moderately, regularly arranged thatch, in the upper part of *12,* ×20; *12,* thin, platelike cluster composed essentially of irregularly plumose to thatched spicules, but also includes other debris, ×2. *2, 8, 9,* figured specimen, USNM 463612. *2,* photomicrograph showing general dimensions and subparallel arrangement of part of the spicule net, in some places with spicules obscured in the relatively massive pyritization, ×20; *8,* platelike tuft, approximately 2 mm thick, composed of a thatch of moderately uniformly sized monaxial spicules, ×2; *9,* layered thatch of distinct, small oxeas in several clusters of sweeping spicules, showing the nature of the upper left part of the tuft as shown in *8,* ×5. *3, 5, 7, 10,* figured root tuft, USNM 463610. *3, 5,* opposite surfaces of the somewhat twiglike tuft, showing the plumose spicules, particularly well shown in *5,* ×2; *7,* photomicrograph of the central part of the surface shown in *5,* but inverted, with a subparallel axial cluster of spicules and the upwardly and outwardly divergent to pinnate orientation of other spicules in the tuft, ×20; *10,* photomicrograph of the middle part of the root tuft, inverted from *5,* showing the general overall plumose pattern of the spicules characteristic of the tufts, ×5. *4, 6, 11,* figured specimen, USNM 463611. *4,* flattened surface of twiglike root tuft cluster of monaxial spicules; crinoidal debris and other fossil fragments have been incorporated within the tuft, particularly in the middle part, reverse side of tuft from *6,* and *11,* ×2; *6,* photomicrograph showing the densely packed, subparallel spicules, with an upwardly and outwardly plumose arrangement in the pyritized tuft, ×20; *11,* photomicrograph showing the entire width of the preserved tuft, with vertically clustered axial spicules shifting to upwardly and outwardly inclined, to distinctly outward along the right margin, in the middle part of the sponge, ×5.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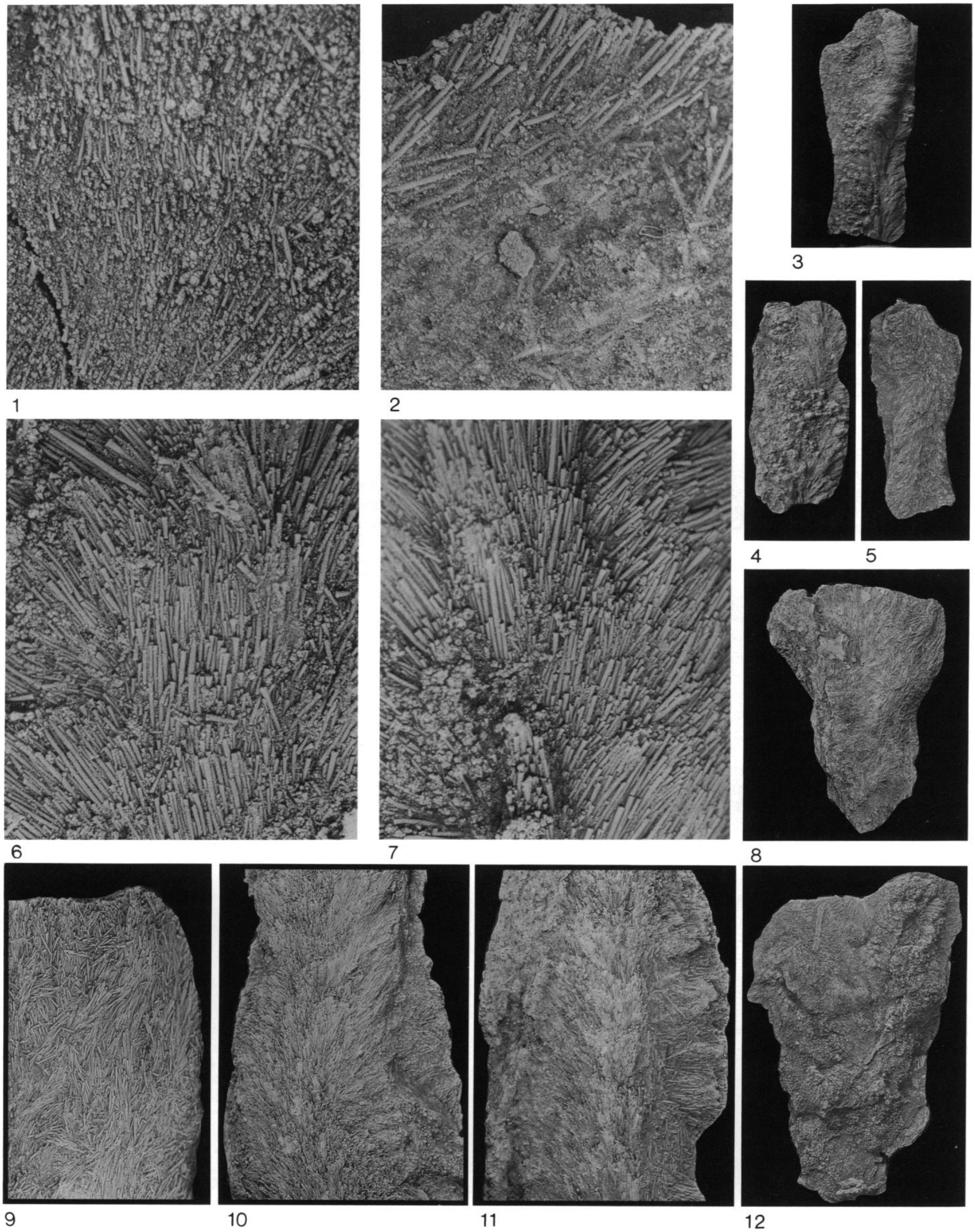
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at the crest of the sponge, but lacks the prominent cortex present in the sponges described here.

Comparisons with similar sponges have been treated in discussion of the genus, and comparison with the type species, *Stiodermiella amanita,* has been treated under discussions of that form.

Etymology.—*Tetragonus,* Greek, four-angled or square, in reference to the rectangular appearance of the finely papillose cortex on the underside of the sponge.

Material and occurrence.—Holotype, USNM 463608, and paratype, USNM 463609, both from the Benton Quarry, Birdsong Shale, Ross Formation.

Subclass uncertain
Root tufts
Figure 12

Description.—Several fragments of root tufts occur in collection, and generally one of two forms, either as more or less elongate, relatively narrow, plumose clusters or as somewhat flatter, thin sheets. Fragments of plumose clusters generally stemlike and 8–9 cm across and up to 20 mm long, and 2–3 mm thick in lens-shaped cross sections. Oxeas, 0.03–0.05 mm in diameter, with most approximately 0.04 mm in maximum diameter at mid-length. Most preserved as cylindrical fragments, but some show enough of full length to document double taper. Some sharp spinelike tips also occur in en echelon stacking of side-by-side spicules in clusters. Spicules range to several millimeters long, fragments to 2–3 mm long common. Clusters characteristically with central section of subparallel spicules from which spicules diverge in upward and outward smooth curving rays, so that sides of twiglike specimens have spicules essentially normal to margins. Three with peculiar structure where sense of upward-and-outward divergence reversed on opposite sides, so initial proximal and distal directions uncertain.

More platterlike or curved, thin, sheetlike forms with divergent spicule patterns more consistent from one side to other, but not strongly upward and outward divergent arrangement. Thin, curved, platelike, irregular fragments of probable thin-walled palmate or funnel-like forms. One of better preserved fragments triangular, approximately 25 mm tall and 22 mm wide, like gently curved fragment of funnel-like species with uniform wall approximately 2 mm thick. Other somewhat more ragged larger fragment, about 30 mm tall and 25 mm across, also gently curved with thickness of approximately 2 mm. Smaller fragment, approximately 1 cm tall, shows same general spicule pattern and wall thickness.

Spicule structure in fragments essentially subparallel, somewhat swirled to plumose, of irregular oxeas more or less side-by-side, but in a few places in crossing tractlike structures. No canals or pores evident in even irregular part of structure. Smooth, doubly tapering oxeas preserved as broken, cylindrical fragments 0.04–0.06 mm in maximum diameter; appear en echelon and essentially tangential to presumed outer convex and inner concave surfaces, with strong vertical component. Broken transverse section shows spicules essentially massively replaced, small pyritic rods, without evidence of central canal in the coarse replacement.

Discussion.—Relatively thin, curved, platelike fragments are probably parts of thin-walled, funnel-like, steeply obconical sponges, but whether some represent bits of undulating sheets of root tufts is impossible to tell from the material available. Because of their relatively consistent, uniform thicknesses from fragment to fragment, and within each fragment, they are tentatively considered as parts of funnel-like or palmate, thin-walled demosponges. They occur, however, with the fragments of plumosely arranged spicules that appear similar to root tufts described elsewhere.

Change in plumose orientation within a single cluster is reminiscent of the skeletal structure of *Wapkia* (Walcott, 1920). Rigby (1986, p. 29) observed that the skeleton of *Wapkia* is composed of elongate, oval or flattened fronds with oxeas in flaring and plumose patterns that in some places interfere and cross, or give the appearance of flaring in opposite directions, because of the irregular direction of flattening. As in the root tufts, here, the three-dimensional relationships of the original skeletal elements in *Wapkia* are somewhat problematic because of flattening of their original three-dimensional structure. *Wapkia,* however, has a considerably more complex skeletal arrangement, with canals and clustered spicules, and with an outer layer, in a decidedly different structure than any evident here in the root tufts or the thin, platelike fragments. It is one of the few Paleozoic sponges, however, that does have apparently opposed directions of flaring and plumose spicule orientation.

Material and occurrence.—Figured specimens, USNM 463610–463613, and four additional reference specimens, all from the "bryozoan zone" of the Birdsong Shale, Benton Quarry.

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We appreciate the supervision of T. W. Broadhead, while Clement was a graduate student under his direction at the University of Tennessee. Clement collected the sponges during a study of the echinoderm faunas of the Decatur Limestone and Ross Formation in west-central Tennessee, as part of a doctoral dissertation at the University of Tennessee. Clement was often accompanied in the field by M. A. Gibson, who was concurrently working on the Birdsong Shale, with an emphasis on epibionts (Gibson, 1988). Discussions with him were particularly helpful. Preparation, illustration, and description of the sponges were done by Rigby, as part of a major study of fossil Paleozoic sponges of North America, at the Department of Geology, Brigham Young University. L. T. Bird of Brigham Young University helped with figure construction and manuscript preparation. We appreciate the support of our institutions and those who have contributed to the study. T. de Frietas and J. W. Pickett provided helpful and critical reviews of the manuscript.

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APPENDIX

LOCALITIES

Allens Mill (AM), Benton County, 35°55′45″N, 88°05′15″W.

Two small, abandoned quarries on the north side of Birdsong Creek, the larger exposing approximately 10 m of Decatur Limestone, 6 m of Rockhouse Limestone, and 3 m of Birdsong Shale (Reid, 1983). The smaller quarry exposes about 3 m of Decatur Limestone, 5 m of Rockhouse Limestone, and 2 m of Birdsong Shale. Most specimens were collected from a bench 87 cm above the Decatur–Rockhouse contact.

Benton Quarry (BQ), Benton County, 35°52′30″N, 88°07′15″W.

Large Vulcan Materials Company quarry on Tennessee Route 192 at Holladay, Tennessee, exposing approximately 20 m of Decatur Limestone, 4.1 m of Rockhouse Limestone, and 16.3 m of Birdsong Shale (Reid, 1983). This is a complete section with bedded Camden Chert above the Ross Formation.

Elkins Quarry (EQ), Perry County, 35°37′15″N, 87°59′00″W.
Small, recently opened, quarry in western Perry County on north side of Tennessee Route 20/100, exposing approximately 10 m of Decatur Limestone, 4.3 m of Rockhouse Limestone, 4.5 m of Birdsong Shale (Gibson, 1988).

McClanahan's Quarry (MQ), Decatur County, 35°43′30″N, 88°04′30″W.
Active quarry, on the south side of Brodies Landing Road, exposing 15–20 m of Decatur Limestone, 6 m of Rockhouse Limestone, and 19.4 m of Birdsong Shale (Gibson, 1988). The top of the Birdsong is truncated, with unbedded chert rubble of the Camden Formation, above.

Parsons Quarry (PQ), Decatur County, 35°41′15″N, 88°06′15″W.
Large Vulcan Materials Company quarry on Tennessee Route 69 north of Parsons, Tennessee, exposing 34.5 m of Decatur Limestone (McComb, 1987), 5.1 m of Rockhouse Limestone, and 13.2 m of Birdsong Shale (Reid, 1983). The top of the Birdsong is an erosional surface, overlain by unbedded chert rubble of the Camden Formation.

Southern roadcut, (RCa), Decatur County, 35°43′30″N, 88°04′30″W.
Large roadcut on Tennessee Route 69, north of Parsons Quarry, exposing 12 m of Decatur Limestone, 1 m of Rockhouse Limestone.

Northern roadcut, (RCb), Decatur County, 35°46′30″N, 88°05′00″W.
Northern roadcut on Tennessee Route 69, exposing 5 m of Decatur Limestone, 3 m of Rockhouse Limestone, and 2 m of Birdsong Shale.

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UPPER PERMIAN SILICIFIED SPONGES FROM CENTRAL GUANGXI AND WESTERN HUBEI, SOUTH CHINA

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ABSTRACT—Well-preserved silicified sponges have been recovered from the Upper Permian Changxing Formation at Huangnitang in western Hubei province. The new species *Cystauletes grossa* and *Cystothalamia irregulara* are associated with *Cystothalamia* sp., *Colospongia salinaria irregularis* Zhang, 1983, *Sollasia ostiolata* Steinmann, 1882, *Virgola*? *osiensis* (de Gregorio, 1930), a questionable inozoan species, and a form questionably referred to the genus *Hikorodium*? sp. These sponges were detrital fragments that accumulated at the toe of the forereef, at the margin of slope facies and basin facies, at Huangnitang. *Amblysiphonella vesiculosa minima* Zhang, 1983, is represented in the collections from the Upper Permian Heshan Formation at the village of Guwu, near Heshan City in central Guangxi. Heshan beds that produced the silicified sponges are of Wujiapingian age and accumulated on a normal-marine, shallow-water carbonate platform, or in skeletal shoals within the carbonate platform, and represent a level-bottom community.

INTRODUCTION

WELL-PRESERVED SILICIFIED sponges have been recovered in Upper Permian rocks at several localities in South China (Figure 1). The fossils reported here came from near Heshan City, in central Guangxi (Locality 6, Figure 1), and from near Lichuan County, in western Hubei (Locality 2, Figure 1).

The Guangxi locality is immediately east of the village of Guwu (Figure 2), on the west bank of the Hongsui River, opposite the power station of Heshan City. The gray and dark-gray, medium- to thick-bedded, micritic limestone and skeletal limestone of the Upper Permian Heshan Formation are exposed there and yield abundant sponges, brachiopods, echinoderms, and other fossils (Jiang et al., 1982; Jiang and Qian, 1986; Liao, 1987). All of these fossils have been extensively silicified. Silicified sponges from the locality are usually large, and range up to 10 cm or more high (Zhou and Han, 1990). At nearby localities, the brachiopods *Kiangsiella* sp., *Squamularia grandis* Chao, *Leptodus* sp., *Matanoleptodus punctatus* Liao, *Megaderbyia* sp., and *Punctospirifer multiplicatus* (Sowerby), the gastropods *Ceraunocochlis* sp. and *Magnicapitatus*, and the sponges *Amblysiphonella vesiculosa*, *Colospongia* sp., *Subascosymplegma* sp., and *Coelocladiella* sp. were found in laterally equivalent rocks of the same part of the formation (Deng, 1981; Liao, 1987). The sponges occur in rocks that can be correlated with those of the Upper Permian Wujiapingian Stage in South China (Sheng et al., 1985; Zhang et al., 1988).

Lower, Middle, and Upper Permian rocks are well exposed in the Heshan district of central Guangxi Province (Figure 2). Lower Permian beds (P_1) are composed mainly of light-gray, medium- to thick-bedded, dense limestone intercalated with units of bioclastic limestone. Lower beds include some light-gray, thick-bedded dolomite. The main fossils in the unit are the fusulinids *Triticites* and *Pseudoschwagerina*. Lower Permian beds range from 400 to 530 m thick in the general region.

Middle Permian rocks in the Heshan area are divided into two formations, the Qixia Formation, below, and the Maokou Formation, above. The Qixia Formation (P_2Q) is mainly light-gray to dark-gray, medium- to thick-bedded limestone that contains abundant chert nodules. It has a thickness ranging from 120 to 400 m. The Maokou Formation (P_2M) is light-gray to medium-gray, thick-bedded limestone and cherty limestone. Some thin-bedded siliceous rocks and dolomite units occur in middle and upper parts of the formation. Most common fossils reported from the formation are fusulinids, such as *Neoschwagerina*, *Verbeekina*, and *Nankinella*, and the coral *Waagenophyllum*. Maokou beds range from 450 to 900 m thick in central Guangxi Province.

Upper Permian rocks in the Heshan area (Figure 3) consist