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SPONGES FROM THE EARLY DEVONIAN GARRA FORMATION, NEW SOUTH WALES

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ABSTRACT—Thirteen species of fossil sponges from limestones of the Garra Formation of late Lochkovian–early Pragian age are described, and their distribution within the lower part of the limestone is recorded. The lithistid genera *Garraspongia* and *Brianispongia,* and the calcisponge *Radiothalamos* are described as new, together with the type species of these genera. The new species *Devonospongia garrae, Isispongia monilifera* and *Astylospongia tarda* are also described. The sponges throve during the deepest-water phase of limestone deposition.

INTRODUCTION

SPONGES were first recorded from the Garra Formation in the Wellington Caves area by Pickett in 1969. Since that time a study of the formation has begun (Johnson, 1975; Chatterton, Johnson and Campbell, 1979) which will comprise a detailed examination of the silicified invertebrates from the limestone and their ecology. Most of the sponges described here for the first time are based on material collected by Johnson in the course of his study. The first specimens of *Devonospongia garrae* n. sp. were collected by Rigby during a visit to the area in 1976.

The geology of the area has been described by Basnett and Colditz (1945), Strusz (1965) and Johnson (1975). A Devonian age for the Garra beds was first suggested by Hill and Jones (1940); a more refined dating was presented by Druce (1970), who reported the conodonts *Eognathodus sulcatus* Philip and *Pedavis pesavis* (Bischoff and Sannemann), and determined a mid-Siegenian age. According to Johnson (1975), *P. pesavis* occurs in samples from near the base of the formation (see also Chatterton, Johnson and Campbell, 1979).

The basal beds of the Garra Formation overlie passage beds from the andesitic Cuga Burga Volcanics, of very Early Devonian age (Lochkovian). The top of the Garra Formation is everywhere eroded and the next younger rocks in the area are orthoquarzites of the Catombal Group of Late Devonian age, which in places lie unconformably on the Garra Formation.

Johnson (1975, p. 113) divided the Garra Formation into a succession of 20 units covering 970 m of strata and summarized the history of the formation as follows: 1) Initial transgressive phase; reworking of volcanics, onset of carbonate deposition and appearance of marine biota (units 1–2). 2) Period of fluctuating, predominantly subtidal carbonate deposition on a shallow platform; variable terrigenous influx continues (units 3–9). 3) Period of gradual carbonate buildup; cessation of terrigenous influx; quiet environment with highly diverse fauna, shallowing and decreasing in diversity towards close (units 10–11). 4) Development of sabkha-style, tidal and desiccated supratidal flats (units 12–17). 5) Brief subtidal episode; quiet environment with diverse fauna (unit 18). 6) Further development of tidal and supratidal flats (units 19–20). 7) Cessation of deposition; uplift and erosion.

The sponge assemblages are for the most part associated with units 10 and 11 of Johnson's scheme and thus fall within the conodont zone of *Pedavis pesavis,* which probably ranges across the Lochkovian/Pragian boundary.

By far the commonest sponge species is *Attungaia wellingtonensis,* which occurs at most localities from which sponges have been recorded. Its compact and robust skeleton of well-fused desmas make it more likely to be preserved, as it would neither fall apart after death, nor be broken easily during minor disturbance, either through biologic action or water movement. *Garraspongia vannus* is

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TABLE *1*—Distribution of sponge species in the Garra Formation. Bed numbers up to G523 are unit 10, bed G524 is unit 11. *Isispongia monilifera* n. sp. is not included, as material of this species was collected prior to establishment of terminology for beds and units. For details of bed numbers see Chatterton, Johnson and Campbell (1979, text-fig. 2). + = common; O = not common; ? = tentative assignment.

Bed number	G501	G502	G504	G506	G509	G519	G517	G518	G520	G521	G523	G524
Coelocladiella sp.			O									
Devonospongia garrae			+	O			+	O		+		
Brianispongia quadratipora			O		O		O					
?Isispongia sp.			O			O					O	
Astylospongia tarda			O							O		
Attungaia wellingtonensis				+			+	+		+	O	O
Garraspongia vannus	O		?	O			O	?	?	O		
Varneycoelia favosa							O			O		
Haplistion sp.						O						
rhizomorine sponge indet.			O									O
?Columellaespongia sp.							?			O		
lyssakid unident.		O										
Radiothalamos uniramosus							O	O		O		O

equally robust but is much less common. The skeleton of *Devonospongia garrae* is thinner-walled and less robust than that of most other species, so that it invariably occurs as fragments, although it ranks second in terms of relative abundance. Most of the other species are relatively rare, and formed an insignificant proportion of the total fauna.

In the interval through which the sponges are abundant, Johnson (personal commun., 1981) recognizes two distinct brachiopod assemblages, the upper one beginning with horizon G516 (Table 1). Whatever ecological factors may have influenced the change in composition of the brachiopod assemblages do not appear to have affected the sponges, as most species occur in both of Johnson's brachiopod units (Table 1). Sponges are, however, more abundant in the upper unit, so that the factors may have affected abundance rather than composition of the assemblages. The sponge faunas are associated with that phase of the formation representing deposition in the deepest water. It may be that the brachiopods in this interval were more sensitive to depth changes than were the sponges.

With few exceptions our material comes from Johnson's section G, southeast of Wellington golf course. For details of the locality and its geology the reader is referred to Figure 1, here reproduced from Chatterton, Johnson and Campbell (1979).

Eleven specimens collected by Pickett from a small biostrome in unit 18 near the top of the formation in Johnson's section D, may be sponges. Specimens MMF 15039 to 15049 show a gross morphology similar to that of *Haplistion*; however, there is no trace of spicules, and the material is now entirely calcitic. Some of the skeletal tracts appear to have been hollow, which suggests an organism at least on the coelenterate level (Figure 2L), similar to *Syringoporella* Kettner 1934, but which appears to be devoid of tabulae.

ACCESSORY OR FOREIGN SPICULES

Specimens of at least five species, while having a parenchymal spiculation of a single desma type, include scattered spicules of other types, most commonly oxeas or elaborated oxeas. These accessory or foreign spicules are not cemented into the skeletal framework in the way that the desmas are, but are held in place by the packing of parenchymal spicules about them. Long axes of the accessory spicules are frequently aligned approximately parallel to canals within the sponge, and are most obvious where they project beyond the main skeletal framework, into the canals. Accessory spicules are known from the following species: ?*Coelocladiella* sp. (epipolasid or possibly rhizomorine lithistid), *Astylospongia tarda, Garraspongia vannus* (eutaxicladine lithistids), *Devonospongia garrae* (chiastoclonellid lithistid) and a fragmentary anthaspidellid which cannot be assigned with certainty. Such spicules are most abundant in the last two species, where they are regular features of the skeleton. They are known

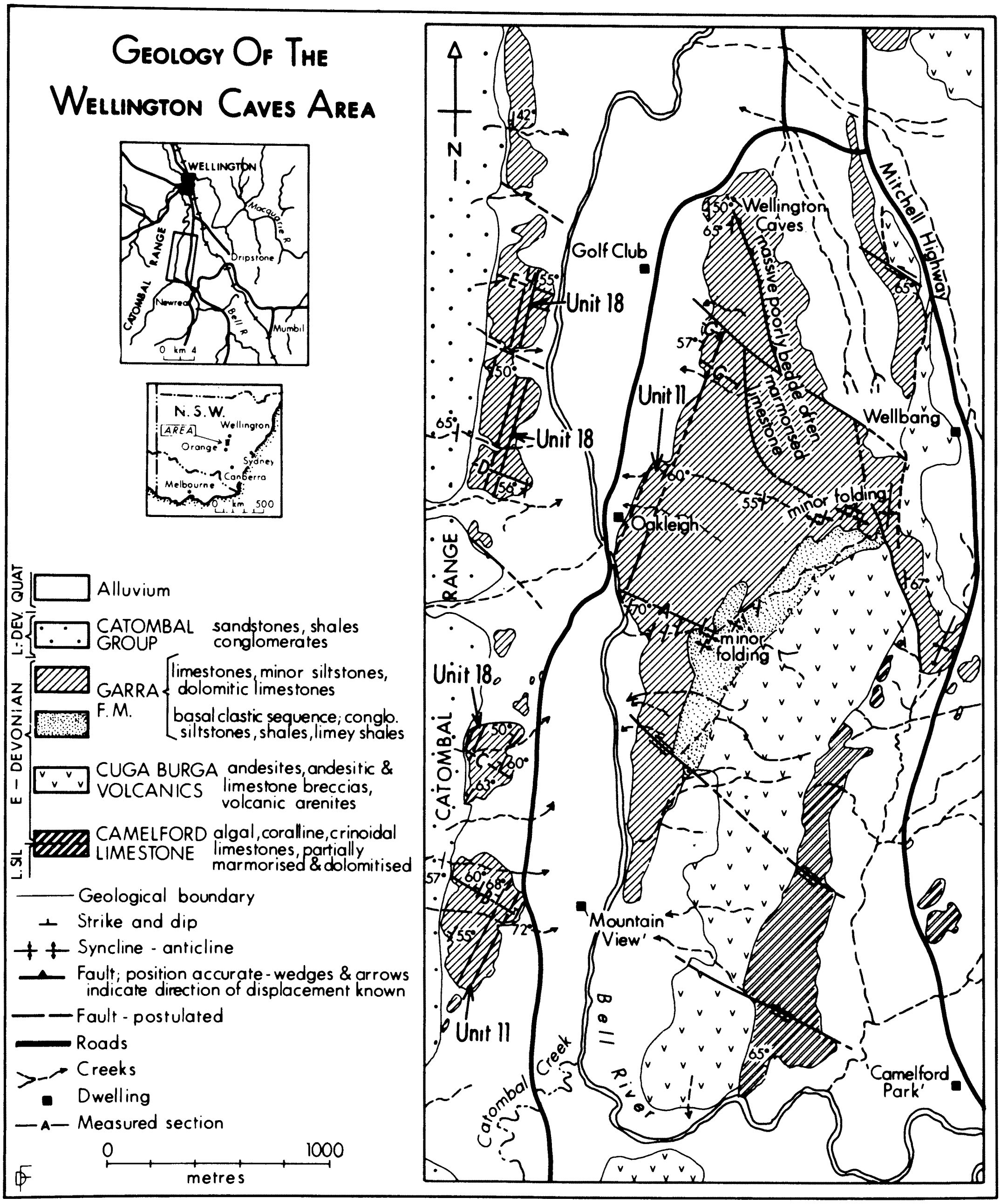


FIGURE *1*—Geological map showing the location of sections measured through the Garra Formation near Wellington Caves. On the legend L. = Late and E. = Early. From Chatterton, Johnson and Campbell, 1979; reproduced by permission.

among the eutaxicladines by only a few spicules (Figure 3). In the considerable material of *Attungaia wellingtonensis* in which spicules are beautifully preserved, no accessory spicules have been observed. There may, therefore, be some reason for considering the rare oxeas of *Garraspongia vannus* as accidental inclusions, either before or after the death of the sponge, though they appear to sit naturally enough in the spicular mesh.

Among Paleozoic eutaxicladine lithistids spicules other than desmas are reported in *Carpospongia* by Rauff (1893, p. 288, pl. 12, fig. 2). In this single specimen the monaxons are grouped into bundles that occur in the large radial canals (?prosochetes), and were supposed by Rauff to project beyond the surface. The proximal ends of these long spicules sometimes penetrate the parenchymal meshwork, but basically they are localized, not scattered throughout the mesh, as in the Garra material. (Rauff also mentions the presence of such spicules in "other astylospongiids," but does not elaborate). Oxeote spicules in *Hindia* and *Astylospongia* were considered by Finks (1970, 1971) to support a dermal membrane. *Scheiella* (Finks, 1971) includes a remarkable variety of spicule types. Finks (1960) reported the presence of smooth monaxons in *Haplistion* Young and Young and *Chaunactis* Finks; in the latter he documented a dermal layer of monaxons as well.

The fact that accessory spicules occur in a number of genera suggests that they may occur more frequently in Paleozoic sponges than supposed. They suggest the possibility of establishing closer phylogenies, but at present our knowledge of spiculation in Paleozoic lithistids is too sketchy to develop the idea.

SYSTEMATIC PALEONTOLOGY

Class DEMOSPONGEA Sollas, 1875
Order EPIPOLASIDA Sollas, 1888
Family HELIOSPONGIIDAE Finks, 1960
Genus COELOCLADIELLA Finks, 1960

Type species.—*Coelocladiella lissa* Finks, 1960.

?COELOCLADIELLA sp.
Figure 4J–N

Material.—A single specimen, MMF 23757 from horizon G504, unit 10, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet.

Description.—The specimen is the proximal fragment of a small conical sponge, 14 mm long, 8 mm in maximum diameter, reducing to 4.5 mm at the base. The proximal termination is not complete, but the spongocoel is 3 mm wide at its maximum and slightly oval. The exterior of the sponge is smooth and covered with evenly spaced prosopores up to 0.5 mm in diameter; apopores on the inner surface are only slightly larger, up to 0.7 mm.

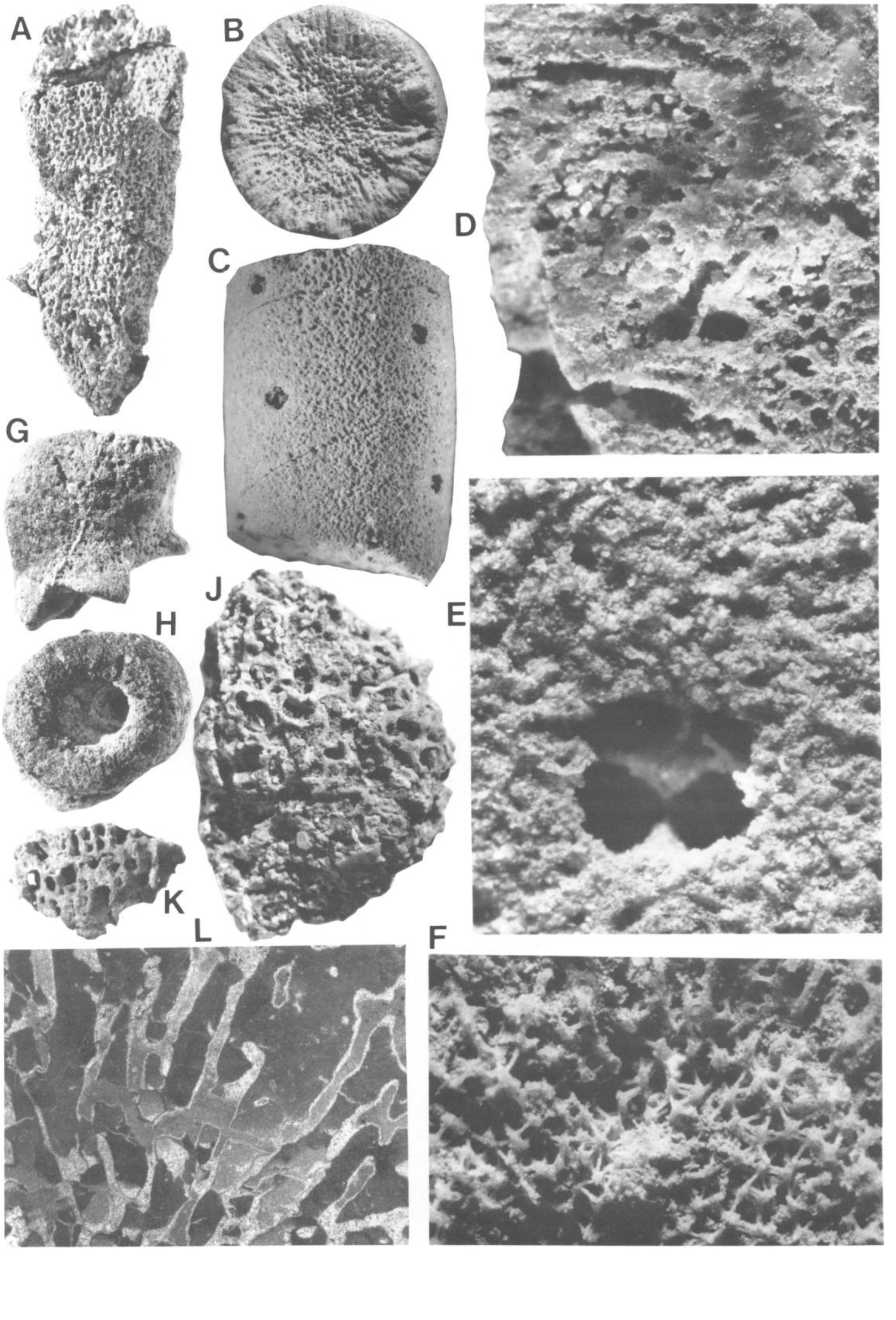
The skeleton is made up of monaxial rhizoclone spicules arranged in closely sub-parallel fashion in tracts which are about 0.2 mm thick in their least dimension, including 2–4 spicules in this thickness. The spicules are straight or slightly curved, about 0.02 mm thick, and reach at least 0.5 mm long. They are not smooth, but bear short processes, somewhat similar to those of rhizoclone desmas. No reticulation of these spicules has been observed. Such detail is obscured in the general silicification. Their general arrangement is similar to that of *Heliospongia excavata* figured by Finks (1960, p. 12, figs. 5, 6, 8). In addition to the parenchymal spicules, accessory spicules of basically monaxonic type are present. These are finely spinose, and may be oxeote or bear lateral branches, shorter and usually not as stout as the main shaft, and all deflected towards one end of the shaft. A small group of fused chiastoclones occurs adhering to the spongocoel wall but these are considered to have been washed in after the death of the sponge.

Remarks.—Affinities of the sponge described here are not unequivocal. It is referred to the Heliospongiidae because of a general similarity in structure with species described by Finks (1960). However, the processes on the parenchymal spicules and the presence of branched accessory spicules, albeit basically monaxonic, throw some doubt on the assignment. The possibility remains that the basic skeleton is composed of rhizoclones whose reticulate arrangement was not observed because of loss of detail due to silicification.

Order LITHISTIDA Schmidt, 1870
Suborder TETRACLADINA Zittel, 1978
Family CHIASTOCLONELLIDAE Rauff, 1895
Genus DEVONOSPONGIA Howell, 1957

Type species.—*Archaeocyathus*? *clarkei* de Koninck, 1876.

Diagnosis.—Cylindrical to vase-shaped, simply branching sponges in which the principally radially-arranged canals occur in vertical rows, thus dividing the skeleton into a series of roughly vertical parieties (term of



Pickett, 1969, p. 21) which anastomose to a slight extent, and are connected by crossbars usually less than the full thickness of the wall.

Remarks.—No comments on the affinities of the genus were ventured until it was referred to the family Attungaiidae by Pickett (1969). At that time, the only known specimens of the genus came from the type locality, and on these spiculation is vague. The skeleton was interpreted by Pickett as consisting of sphaeroclones. Preservation of the species at Wellington Caves is much superior to that at Taemas, the type locality of *D. clarkei*; the strong similarity of the grosser skeletal features of *D. garrae* and the type species prompted a critical re-examination of the material described in 1969. While it remains impossible to determine the nature of the spicules of *D. clarkei* with complete certainty, it appears probable that the structures interpreted by Pickett as sphaeroclone centra are the knots produced by the fusion of chiastoclone clads. In *D. garrae* the rhabds of adjacent spicules are not uncommonly fairly close and parallel to one another, producing a characteristic "double-barrelled" appearance. This feature can also be observed in sections of better preserved *D. clarkei*. Such sections also show longer spicules which may be equivalent to the necessary spicules of *D. garrae*. It thus seems probable that the two species are congeneric, and that the spiculation of *D. clarkei* is similar to that of the better-preserved *D. garrae*.

The taxonomic position of the genus however is still not entirely clear. Spicules of the skeletal framework lack the ordered arrangement of the Anthaspidellidae; their rhabds are neither parallel to the surface as in Anthaspidellidae nor normal to it as in Anthracosyconidae; true tetraclones typical of Jereidae appear to be absent. Among Paleozoic families this leaves the Chiastoclonellidae, with which the genus is tentatively grouped. Accessory spicules of the types described for *D. garrae* are so far unreported in orchoclad sponges; amongst tetracladine forms dermal spicules, usually of a basically triaene type, have been reported in several genera. Alone in bearing accessory spicules other than dermalia is *Eustrobilus* Schrammen, 1910 (Discodermiidae), from the Late Cretaceous, which bears rather short fusiform oxeas among the tetraclones of the rigid skeletal network. The variety of spicule types makes *Devonospongia* unique among Paleozoic lithistids.

DEVONOSPONGIA GARRAE n. sp.
Figures 5C–N; 6C

Holotype.—MMF 22569 from unit 10 (G504), Garra Formation, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet. Early Devonian (late Lochkovian–early Pragian).

Paratypes.—MMF 22568, MMF 22567, from unspecified levels within unit 10 near the type locality; MMF 21952 from unit 8, Garra Formation, Oakleigh Station, grid reference 18749620 Dubbo 1:250,000 sheet. Further specimens are MMF 23721–5 from horizons G504, G518, G521, G517, G521, respectively, near the type locality.

Diagnosis.—Relatively thin-walled *Devonospongia* in which knots formed by fusion of clad tips may reach 0.3 mm.

Description.—The specimens are all fragments of a cylindrical or slightly vasiform sponge, which may have reached a diameter of 60 mm, with a broad central spongocoel

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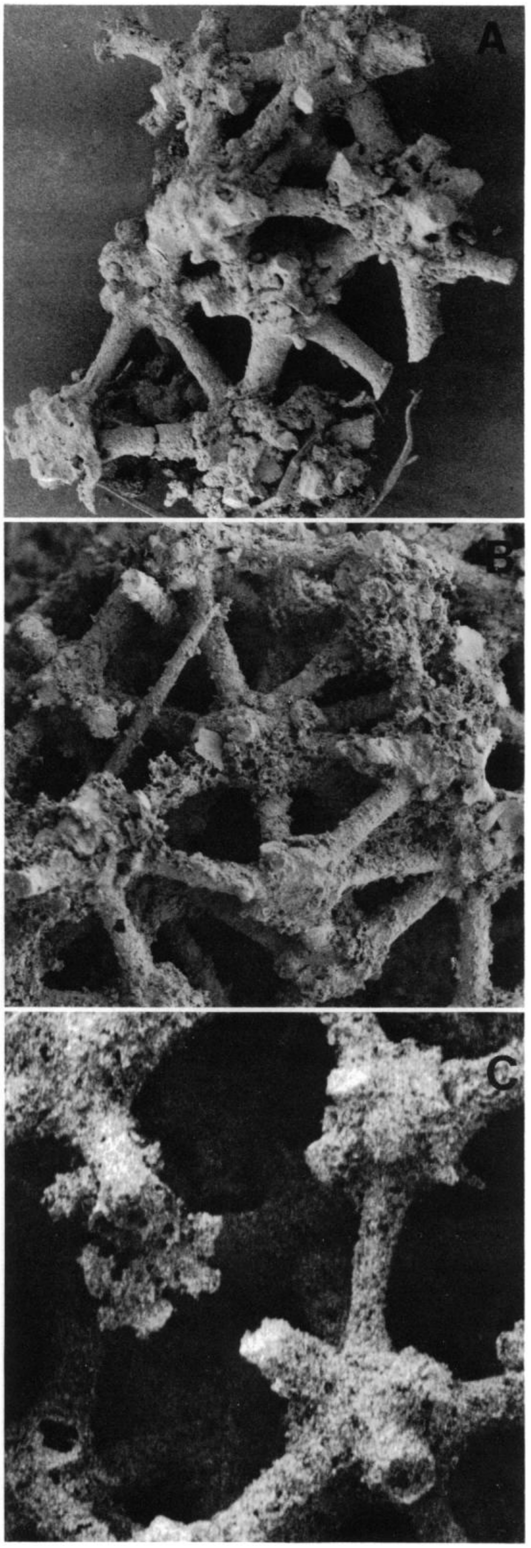
FIGURE 2—Sponges from the Garra Formation. Originals of *A–J* are from unit 10 and of *K* from unit 11, southeast of Wellington Golf Course, Wellington, N.S.W.; original of *L* from unit 18, western side of Bell River, 2.8 km south southwest of Wellington Caves. *A, Columellaespongia* sp., lateral view, MMF 23733, ×1. *B–F, Brianispongia quadratipora* n. gen., n. sp., holotype, MMF 22570. *B,* transverse fracture, showing absence of spongocoel, ×4. *C,* lateral view showing distribution of four-sided apopores, ×4. *D,* longitudinal fracture, showing canals and trabs, ×20. *E,* detail of surface with prosospores and single apopore, ×40. *F,* detail of *B,* showing anthaspidellid spiculation, ×20. *G, H, Attungaia wellingtonensis* Pickett. Lateral and oscular views of a small, complete specimen, showing holdfast and distal termination, ×1. *J, ?Haplistion* sp. indet., fragment, MMF 23732, ×3. *K,* family and genus indet., fragment MMF 23731, ×3. *L,* doubtful sponge, longitudinal thin section, MMF 15049, ×6.



running the full length of the sponge. Branching was not observed, unlikely in such fragmentary material. The walls, which are 7–8 mm thick, are formed of vertical, somewhat anastomosing spicule tracts called parieties, separated by stacked rows of canals that perforate the wall in radial planes. The canals bend and branch within the radial planes. The largest specimen measures 55 mm by 32 mm; it carries 9 parieties in 20 mm, as does the holotype specimen, which measures 19 mm by 15 mm. The stacks of canals are slightly narrower than the intervening parieties; in the holotype the parieties range from usually 1 mm or slightly more to 1.7 mm across, and the canal stacks are 0.5–0.7 mm across, while in specimen MMF 22567 the skeletal tracts reach 2.6 mm and the canal stacks 1.0 mm across.

The exterior of the sponge is more uneven than in the type species, particularly when the parieties are somewhat irregular. There is no difference between the incurrent and excurrent surfaces of the material at hand.

The continuous spicular framework consists of fused dendroclones and chiastoclones, united at their tips to form approximately spherical knots up to 0.3 m in diameter, but varying in size according to the number of spicules uniting at a point, which can be at least as many as twenty. Shafts of the spicules are delicately spinose and 0.2–0.3 mm long. It is difficult to determine the nature of the clads at their ends, but there is at least a bifurcation. The parieties bear from three to five knots of clads across their width. Not infrequently two rhabds lie parallel and quite close together—even closer than their width—producing a double-barrelled appearance. The knots produced by fusion of the clads show no sign of any regularity in their arrangement.

Larger spicules of various types are scattered throughout the main spicular frame-

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FIGURE *3*—Eutaxicladine skeletal frameworks, ×100. All from Garra Formation, southeast of Wellington Golf Course, New South Wales. *A, Astylospongia tarda,* MMF 23756. *B, Garraspongia vannus,* with oxeote spicule, MMF 23745. *C, Attungaia wellingtonensis,* MMF 22616. Note the much greater size of the spicules of this species.

work and not fused to it. These accessory or foreign spicules are smoother than the desmas, frequently quite smooth, and may be straight or curved oxeas, hexacts, or rather irregular triacts or tetraxons. Oxeas may exceed 3 mm in length. Some rays are usually broken and it is often difficult to be certain of the original form of the spicule. There is no indication that these spicules are restricted to particular parts of the skeleton. Their long rays may project into canals free of the structural desmas.

Remarks.—Poor knowledge of the grosser morphology of *D. garrae* restricts its distinction from *D. clarkei* to finer skeletal details. Walls of *D. garrae* are thicker than those of the type species. Knots produced by fusion of the clads are 0.12–0.16 mm across in *D. clarkei,* whereas they may reach 0.3 mm in diameter in *D. garrae.*

There is a possibility that the fine spines observed on the shafts of some chiastoclones (Figure 5G, J) could be secondary, as they do not appear to be present on all specimens (Figure 6C). However the associated possibly foreign spicules in those specimens showing spinules are entirely smooth, and the SEM study indicates no discontinuity between spicule shafts and spinules; therefore, we interpret the tiny spines as a primary feature.

Family ANTHASPIDELLIDAE Miller, 1889
BRIANISPONGIA n. gen.

Type species.—*Brianispongia quadratipora* n. sp.

Diagnosis.—Slender, branching, cylindrical sponges without either a spongocoel or major axial apochetes but bearing scattered apopores on the smooth surface. The skeleton is constructed of dendroclones in ladder-like arrangement, fused at their ends to form continuous trabs which are distally directed at the axis, but arch gradually upward and outward toward the exterior during growth.

Discussion.—The spicular skeleton of *Brianispongia* is so characteristically anthaspidellid that there is no doubt about its taxonomic position. None of the genera referred to the Anthaspidellidae by Finks (1960) has external morphology comparable with that of *Brianispongia.* Among other genera the most superficially similar form appears to be the calcareous sponge *Virgola* De Laubenfels, 1955 (nom. nov., pro *Virgula* Girty, 1909) from the Permian Capitan Formation, Guadalupe Mountains, although that genus is poorly understood. No external apopores have been described for the genus, which suggests that an axial excurrent system was present, in which case the genus is clearly demarcated from *Brianispongia.* The strongly annulated exterior of the Permian genus further distinguishes it from the smooth *Brianispongia.*

Derivation of name.—The genus is named for Brian Johnson, who recovered the material of the type species, and whose stratigraphic study of the Garra Formation forms the basis of the locality information.

BRIANISPONGIA QUADRATIPORA n. sp.
Figures 2B–F; 6A

Holotype.—MMF 22570 from unit 10 (G504), Garra Formation, southeast of Wellington golf course, grid reference 188196535 (yards), Dubbo 1:250,000 sheet.

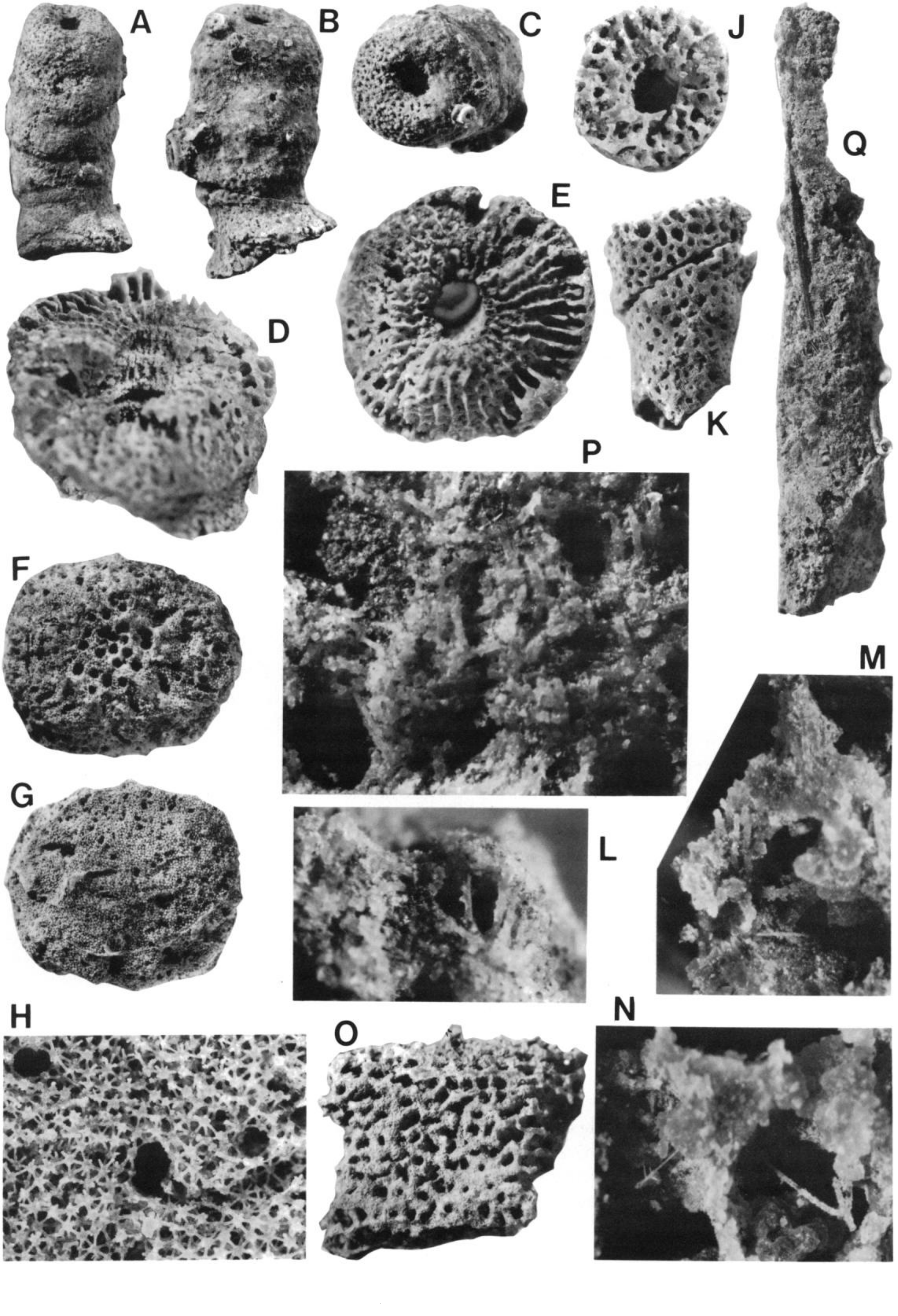
Paratypes.—MMF 23740–2 from unit 10 near the type locality, horizons G517, G506, G509, respectively.

Derivation of name.—*quadratiporus,* square-pored, referring to the common shape of the apopores.

Diagnosis.—*Brianispongia* with branches near 10 mm in diameter and distant, usually four-sided, apopores.

Description.—The species forms cylindrical branches 9–10 mm in diameter, without a spongocoel. The proximal and distal terminations are unknown. One specimen (MMF 23740) demonstrates branching; the branch is similar in diameter to the main axis. The surface is smooth, unmarked by ridges or annulations, but is perforated by fine incurrent pores ca. 0.1 mm in diameter and spaced up to 0.3 mm apart, though they are usually closer. Apopores are regularly spaced, 0.4–0.9 mm in diameter, and 5–7 mm apart. They tend to be square in outline, and are usually formed of four major apochetes. The apochetes form a radiating group, independent of the orientation of the "ladders" and trabs of fused clads that make up the bulk of the skeleton.

The spicular fabric is more open in the axial region of the holotype, showing the typical anthaspidellid ladder-like arrangement of dendroclones; the fused ends of the rays produce continuous trabs, which become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dominant near the surface, where the basic nature and arrangement of the spicules become obscure in the holotype, due to thickening during silicification. In the axial area the rhabds are 0.7–0.12 mm long, and the trabs are 0.12–0.15 mm in width. In unsilicified specimens dendroclones of axial and surficial parts are similar.

Genus ISISPONGIA Pickett, 1969

Type species.—*Isispongia paradoxa* Pickett, 1969.

Discussion.—The genus *Isispongia* was referred to the Anthaspidellidae by Pickett (1969), although none of the original material was sufficiently well preserved to show fine details of the spiculation. The structures interpreted as trabs are neither as robust as in other anthaspidellid forms, nor are the trabs as clearly continuous but are made of vertical series of knots. The type material of *I. paradoxa* has been re-examined, but no further evidence of the nature of the spicules could be gleaned. Dendroclones of the types are about 0.12 mm long and the trabs vary from 0.08–0.12 mm. This is quite within the range of the material here referred to *Isispongia.* It has not been possible to demonstrate the presence of oxeas in the type species and these spicules may be foreign in the new Garra species. Consequently there must remain some reservation in assignment of the material described below, especially considering the considerable difference in spiculation between *Isispongia monilifera* and the unassigned species described below, which may also be a species of *Isispongia,* in which case *I. monilifera* will need re-assignment, as the two species are not congeneric. Oxeote spicules occur in both species, but they are extremely rare in *I. monilifera,* and abundant in the unnamed species. In addition, the trabs of *I. monilifera* are robust compared to those of the other, and probably also of the type species, *I. paradoxa.*

ISISPONGIA (?)MONILIFERA n. sp.
Figure 7A–B

Holotype.—MMF 15105, probably from unit 10, Garra Formation, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet.

Derivation of name.—*moniliferus,* bead-bearing, alluding to the beaded appearance of the trabs.

Diagnosis.—*Isispongia* with a relatively even surface and stout trabs internally, showing a beaded appearance due to the large knots formed by the fusion of clads.

Description.—The holotype is a massive sponge 130 mm wide and 110 mm high, and is incomplete. The upper surface is preserved, but proved impossible to prepare except for small areas around the edge, as the margin consistently fritted away with continuing acid treatment. The upper surface is slightly undulating and without major projections. It bears rounded pores 0.8–1.0 mm in diameter scattered unevenly but not more than 3 mm apart over the surface. The skeleton is traversed by canals that are aligned normal to the surface, are 1.0–1.3 mm in diameter and are up to 3 mm apart. In the outermost 5–7 mm of the sponge the canals are smaller and do not display the continuity and straightness of those deeper in the body of the sponge. Horizontal canals are short, small, and inconspicuous.

The skeleton is composed of dendroclones which are generally parallel to the surface of the sponge. Their ends are fused to form spherical knots which are aligned in rows normal to the surface; these rows are more pronounced in the deeper parts of the skeleton,

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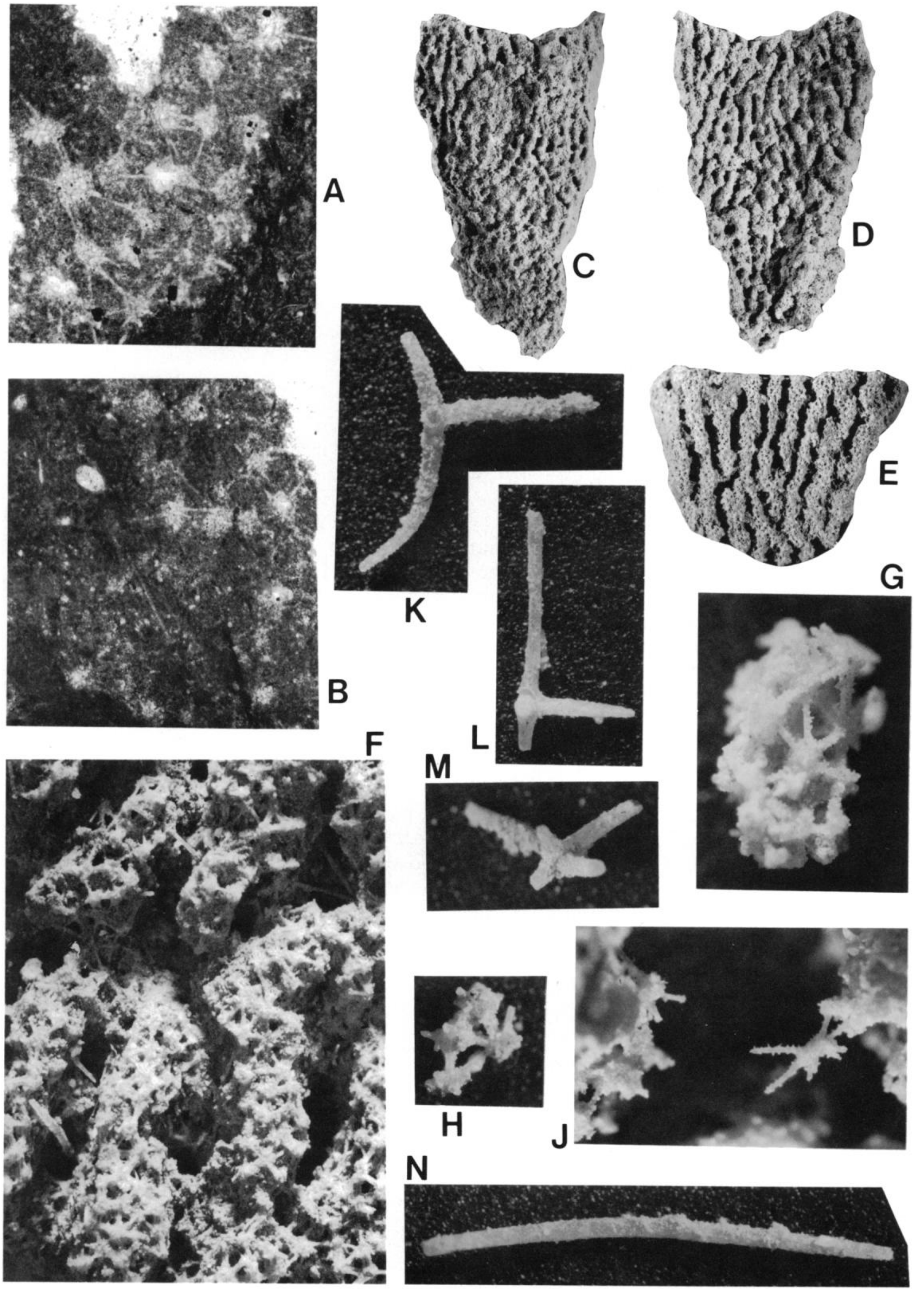
FIGURE 4—Sponges from the Garra Formation. All specimens from unit 10, southeast of Wellington Golf Course, N.S.W. *A–E, Radiothalamos uniramosus* n. gen., n. sp. *A,* lateral view of paratype, MMF 23739, ×2. *B, C,* lateral and oscular views of holotype, MMF 23738, ×2. *D,* oblique view of paratype, MMF 23737, showing detail of spongocoel wall, ×3. *E,* same specimen, oscular view, showing radial chambers and prosopores, ×2. *F–H, Astylospongia tarda* n. sp. *F, G,* upper and lower views of holotype, MMF 23756, ×2. *H,* detail of lower surface, showing spiculation, ×14. *J–N, ?Coelocladiella* sp. *J, K,* oscular and lateral views of only specimen, MMF 23757, ×3. *L–N,* details of spiculation, ×30. Note accessory spicules in *M* and *N. O, P,* family and genus indet. *O,* ?internal view of fragment, MMF 23730, ×3. *P,* detail of somatic spicules, ×30. *Q.* lyssakid, gen. et sp. indet. Lateral view, showing very large monaxon in upper half, MMF 23752, ×3.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and present a beaded appearance. The shafts of the dendroclones range from 0.27–0.37 mm and the diameter of the trabs from 0.3–0.4 mm. A few rare oxeote spicules occur in addition to the dendroclones.

Remarks.—This species has typically anthaspidellid spiculation. The surface shows neither the grooves of *Phacellopegma* nor the radial groups of pores of *Multistella.* Although a proper definition of the genus must await the discovery of material sufficiently well preserved to give details of the spiculation, the species is provisionally referred to *Isispongia* because of its simple morphology and obvious anthaspidellid affinities.

Genus and species indeterminate
Figures 6B; 7C–F

Material.—Specimens MMF 23726–23729 from unit 10, Garra Formation, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet, horizons G523, G504, G504 and G516, respectively; specimen MMF 15106 from an unspecified level within unit 10 at the same locality.

Remarks.—Specimens from three horizons within unit 10 showing somewhat different morphologies may belong to the same species, for their endosomal spiculation is closely similar. Fragments from near the surface of a sponge are bladed, ca. 7 mm thick, with a rounded growing edge. No dermal layer is preserved, and no conspicuous canals are developed. The rows of fused clads ("trabs" of Rigby and Bayer, 1971) are vertical, normal to the surface of the sponge, and are better developed a few millimeters below the surface. Subsurface fragments show vertical and horizontal canals, the latter 0.5–0.8 mm in diameter. The vertical canals are less well developed and less continuous. Fragments considered to be from a still deeper level within the sponge show strong vertical canals 1.5–2 mm in diameter, and many horizontal canals up to 0.8 mm in diameter.

In addition to the dendroclones which form the continuous framework of the skelton there are more or less abundant oxeote spicules which are enclosed within the mesh of desmas. Shafts of the dendroclones are 0.17–0.3 mm long, and the trabs range from 0.07–0.17 mm in diameter, thus being narrower than the canals between them. The oxeas reach at least 1.5 mm in length; they are generally incorporated among the fused clads, and are thus aligned normal to the surface of the sponge. The fragments described as subsurface fragments are from a different horizon and do not include oxeas, so they may not belong to the same species.

The sum of these morphologies suggests a basically massive sponge with high ridges on its exterior, and vertical canals of considerable diameter developed only in the central part.

The genus *Fibrocoelia* (van Kempen, 1978) has a spiculation very close to that of the present material. In *F. tubantiensis* van Kempen describes "dendroclones, irregular monocrepid desmas, rhizoclones and smooth styles; a few oxeas are probably present as well" (p. 321). Most of these types probably occur in the present material, though no rhizoclones have been positively identified, and it is not possible to distinguish between styles and oxeas. In addition, *F. tubantiensis* is a cylindrical sponge with a spongocoel. The fragmentary material of the present species shows no indication of either a cylindrical form or a spongocoel, so it is not referred to van Kempen's genus. However, the close similarity of the skeletal mesh implies the continuity of the lineage from the Ordovician at least into the Early Devonian.

The inclusion of oxeote spicules in the trabs

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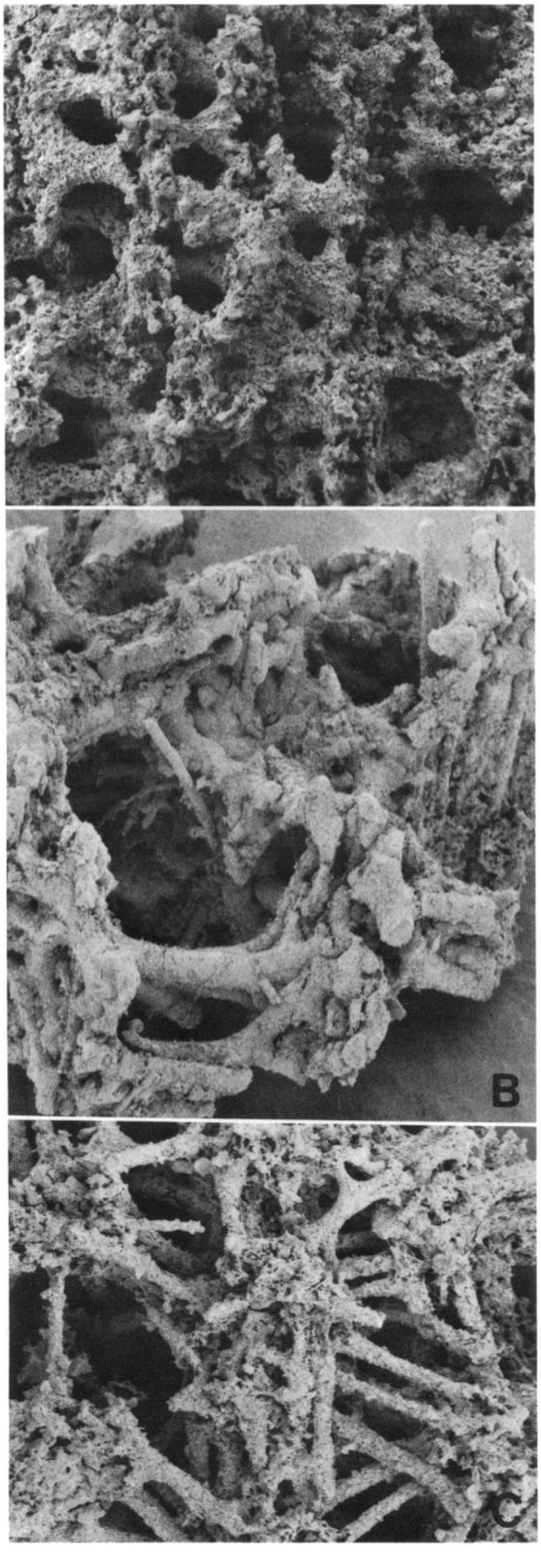
FIGURE 5—*Devonospongia* from New South Wales, *A, B, Devonospongia clarkei* (de Koninck), spicular fabric in thin section, specimen AM 4745, Zlichovian *Receptaculites*-limestone, Taemas, N.S.W., ×29. *A,* showing "double-barrelled" arrangement of rhabds. *B,* showing long ?oxeote spicule among spicular mesh. *C–N, Devonospongia garrae* n. sp., late Lochkovian–early Pragian Garra Formation, near Wellington Caves, N.S.W. *C, D,* exterior and interior views of paratype, MMF 22567, ×1. *E,* interior view of holotype, MMF 22569, ×2. *F,* portion of external surface of holotype, showing larger non-structural spicules set in a meshwork of fused chiastoclones, ×10. *G–J,* fragments of spicular meshwork of paratype, MMF 21952, showing fine spines on rhabds, ×25. *K–N,* a variety of non-structural spicule types separated from paratype, MMF 21952, ×25.



of this species calls to mind Finks' (1967, p. 1142) remarks on the similarity of the extant genus *Lithochela* Burton and the Silurian *Climacospongia* Hinde. Both Reid (1963) and Finks (1967) appear to consider *Climacospongia* a true lithistid sponge, but the monaxons of neither *Lithochela* nor *Climacospongia* are fused to a proper lithistid framework. Burton considered his genus a myxillid, and Hinde calls *Climacospongia* "a true Monactinellid sponge" (1884, p. 19). Nonetheless, the similarity of the structure of *Lithochela* and the present material is quite striking; some elaboration and intergrowth of the ends of desmas of *Lithochela* would produce a skeleton very close to that of the Devonian species.

Suborder EUTAXICLADINA Rauff, 1893
Family ASTYLOSPONGIIDAE Zittel, 1877
Genus ASTYLOSPONGIA Roemer, 1860

Type species.—*Siphonia praemorsa* Goldfuss, 1826.

ASTYLOSPONGIA TARDA n. sp.
Figures 3A; 4F–H

Holotype.—MMF 23756 from horizon G504, unit 10, Garra Formation, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet.

Paratype.—MMF 25078 from horizon G521 at the type locality.

Derivation of name.—*tardus,* late, this being the latest described member of the genus.

Description.—The holotype is a somewhat eroded, depressed globular sponge 10 mm high and 18.7 mm by 16.6 mm in its maximum and minimum horizontal dimensions. The upper surface shows a series of radially diverging apochetes 0.6–1.0 mm in diameter. Prosochetes 0.2–0.4 mm in diameter are revealed on the eroded sides of the sponge. They

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FIGURE 6—Skeletal frameworks of dominant dendroclones, ×100, all from Garra Formation, southeast of Wellington Golf Course, N.S.W. *A, Brianispongia quadratipora,* MMF 23742. *B,* gen. et sp. indet., showing abundant oxeote spicules, MMF 23727. *C, Devonospongia garrae,* dendroclones and a single chiastoclone. In contrast to *A* and *B*, the spicules unite to form knots and not trabs. Note spinules on the shafts of some spicules, MMF 25055.

are approximately horizontal. Outermost parts of the sponge are missing. The smaller paratype is even less complete and rather coarsely silicified.

Endosomal spicules are sphaeroclones, with rays 0.1–0.15 mm long. The centra are close to 0.1 mm in diameter. Rare oxeas up to 1 mm long are also present, and generally are associated with the canals.

Remarks.—The genus *Astylospongia* has been previously reported only from Ordovician and Silurian strata, making *A. tarda* the youngest representative of the genus.

Family Attungaiidae Pickett, 1969
Genus Attungaia Pickett, 1969

Type species.—*Attungaia cloacata* Pickett, 1969.

Remarks.—The genus *Devonoscyphia* Rietschel (1968) is very close in general morphology to *Attungaia*. The hollow cylindrical form and the skeleton of sphaeroclones are typical of both genera. However, the external surface of both species of *Attungaia* distinctly shows the open ends of many prosochetes, whereas Rietschel's description and illustration (pl. 2, fig. 4) indicate that the incurrent apertures "... nicht als deutliche Poren in Erscheinung treten" (p. 101). On the other hand, shallow depressions on the best-preserved specimens of *A. wellingtonensis* show that the openings of the prosochetes were screened by a dermal layer one spicule thick, which is missing in all but exceptional specimens. The possibility that *Attungaia* is a junior synonym of *Devonoscyphia* thus remains; a careful comparison of material of all three species is desirable.

Attungaia wellingtonensis
Pickett, 1969
Figures 2G–H; 3C

Remarks.—Much more material has been collected since this species was first described, and some of the specimens show very fine preservation of the spicular framework. Pickett (1969, pl. 10, fig. 1), interpreted the spicules as sphaeroclones. The appearance of the spicular mesh in *Attungaia, Garraspongia* and *Astylospongia* is virtually identical, differences being restricted to variations in proportions of shaft length, diameter of centra, and the number of rays fusing at a point. For this reason the family Attungaiidae was referred to the suborder Eutaxicladina.

Scanning electron microscope studies of spicules from the Garra Formation indicate that branching of the desmas of anthaspidellid species can usually be quite clearly observed in the trabs (Figure 6). On the other hand fusion of rays of desmas of astylospongiids and attungaiids is much more complete (Figure 3), and it is impossible to identify individual spicule boundaries.

Garraspongia, n. gen.

Type species.—*Garraspongia vannus* n. sp.

Diagnosis.—Flabelliform sponges with differentiated incurrent and excurrent surface; prosochetes and apochetes are normal to the surface; on the excurrent surface an additional system of apochetes parallel to the surface and immediately underying the dermal layer is developed; a differentiated dermal layer is present; spicular framework of sphaeroclones encloses occasional accessory oxeas.

Remarks.—The bladed form is unusual among Paleozoic sponges described so far, and clearly distinguishes it from all other Paleozoic eutaxicladines.

Garraspongia vannus n. sp.
Figures 3B; 8A–F

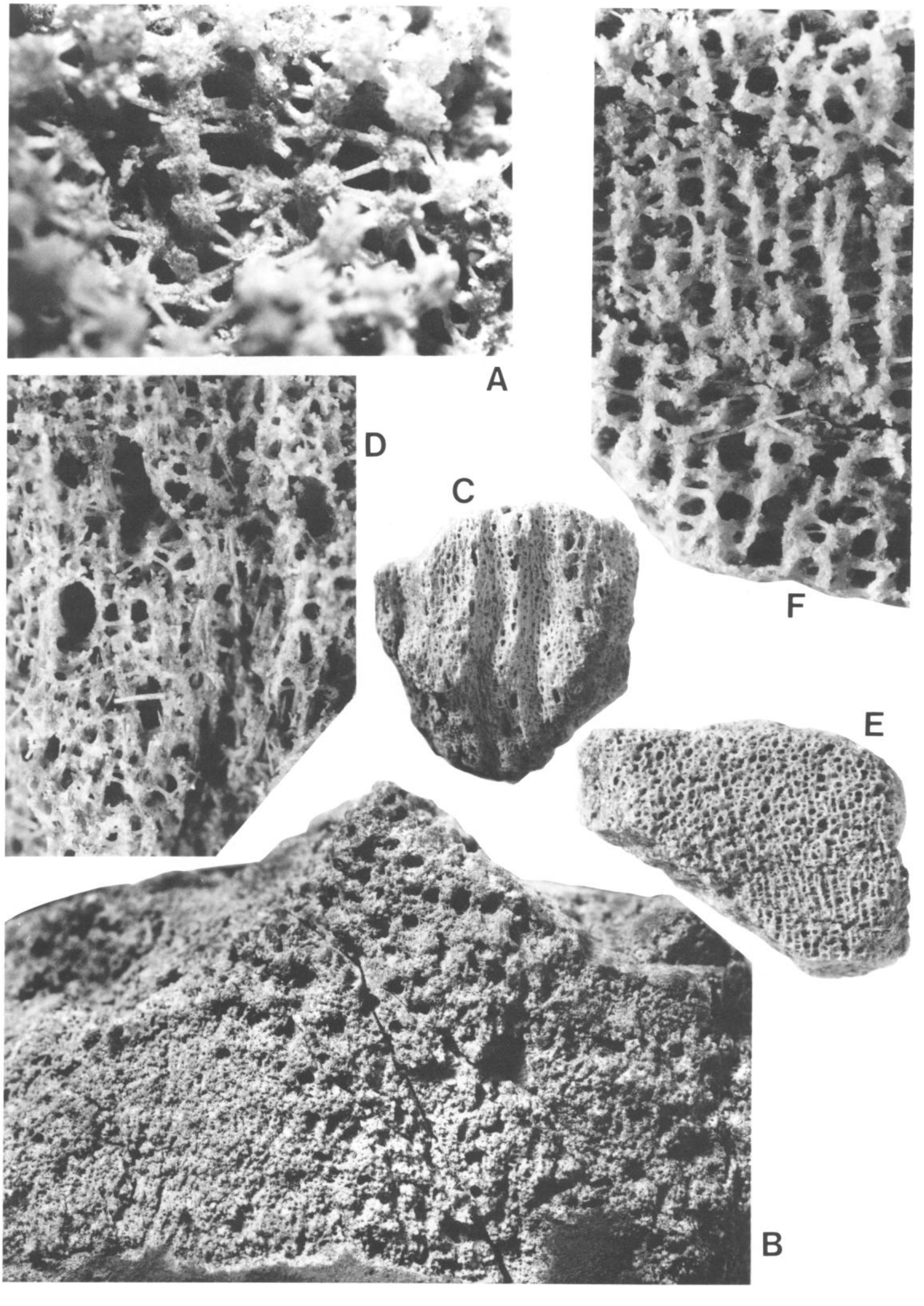
Holotype.—MMF 23743 from unit 10 (G517), Garra Formation, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet. Early Devonian (late Lochkovian–early Pragian). An almost complete specimen.

Paratypes.—All are fragments, MMF 23744–51 from unit 10 near the type locality, horizons G519, G504, G501, G521, G520, G518, G506, G518, respectively.

Derivation of name.—*vannus* (Latin), a winnowing fan.

Diagnosis.—As for genus.

Description.—The holotype is a flabelliform sponge 106 mm wide, 84 mm high and averaging 6 mm thick. The margin is rounded and smooth, and continues around the lower surface of the sponge towards the attachment area, which is not preserved. Other specimens are incomplete fragments. Prosochetes on the decorticated incurrent surface are 0.2–0.3 mm in diameter. In those areas where the


A
D
C
F
E
B

dermal layer is present it is difficult to determine the structure of the prosopores. They appear to be very small (0.1–0.2 mm in diameter), and separated less than 1 mm from one another. Macroscopically such areas appear smooth and without obvious pores. On the decorticated excurrent surface apochetes are 0.3–0.4 mm in diameter and 0.6–2 mm apart. A system of somewhat radial canals occurs parallel to the surface below the dermal layer. These show up well in Figure 8D. In the holotype there is no indication of prosochetes parallel to the surface on the incurrent side; however, the specimen with the best-preserved spiculation, MMF 23746, suggests that shallow canals were developed normal to the growing edge of the sponge. The exhalant surface bears apopores 0.2–0.4 mm in diameter that are situated, usually singly, though not uncommonly two together, on the tops of small raised areas that are 1.5–2 mm in diameter, ca. 1 mm high and 3.6 mm apart. When well preserved the dermal layer appears minutely dimpled, with contiguous polygonal fields less than 1 mm in diameter.

The main skeletal framework consists of sphaeroclone desmas, whose rhabds are 0.13–0.17 mm long, and with centra 0.17–0.25 mm in diameter. In the holotype individual spicules are less easily recognizable and the skeleton has a frothy appearance. No individual dermal spicules can be recognized. On paratype MMF 23746 the desmas are entirely smooth on the outside, and the "frothy" layer of the holotype is not developed; instead, normal sphaeroclones continue to the surface where they form a continuous, scarcely porous dermal layer less than one spicule thick (Figure 8F). The accessory and perhaps foreign oxeas are slightly curved and 0.04–0.66 mm in diameter; they are long, but invariably broken or partly concealed. No polyactinal accessory spicules have been observed. Accessory spicules are distantly scattered through the main skeleton.

Suborder RHIZOMORINA Zittel, 1878
Family HAPLISTIIDAE De Laubenfels, 1955
Genus HAPLISTION Young and Young, 1877

Type species.—*Haplistion armstrongi* Young and Young, 1977.

HAPLISTION? sp. indeterminate
Figure 2J

Material.—MMF 23732 from horizon G516, unit 10, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet and one unnumbered fragment.

Remarks.—Two small fragments are tentatively referred here. Both are pieces of the interior of a sponge, showing the arrangement of spicule tracts characteristic of *Haplistion,* and a skeleton of rhizoclone desmas, which are all but obscured by silicification.

Family ?SCYTALIIDAE De Laubenfels, 1955
Genus VARNEYCOELIA Pickett, 1969

Type species.—*Varneycoelia favosa* Pickett, 1969.

VARNEYCOELIA FAVOSA Pickett, 1969
Figure 9

Material.—All specimens are fragments; MMF 23734, MMF 23735, MMF 25054 from horizon G521, MMF 23755 from horizon G517, unit 10, Garra Formation, southeast of Wellington golf course, grid reference 18819635 (yards) Dubbo 1:250,000 sheet.

Remarks.—None of the material recovered during the present study is as complete as the type material, although it comes from the presumed type locality. The scanning electron microscope has revealed the structure of the spicules better than could be observed at the time of the original description (Figure

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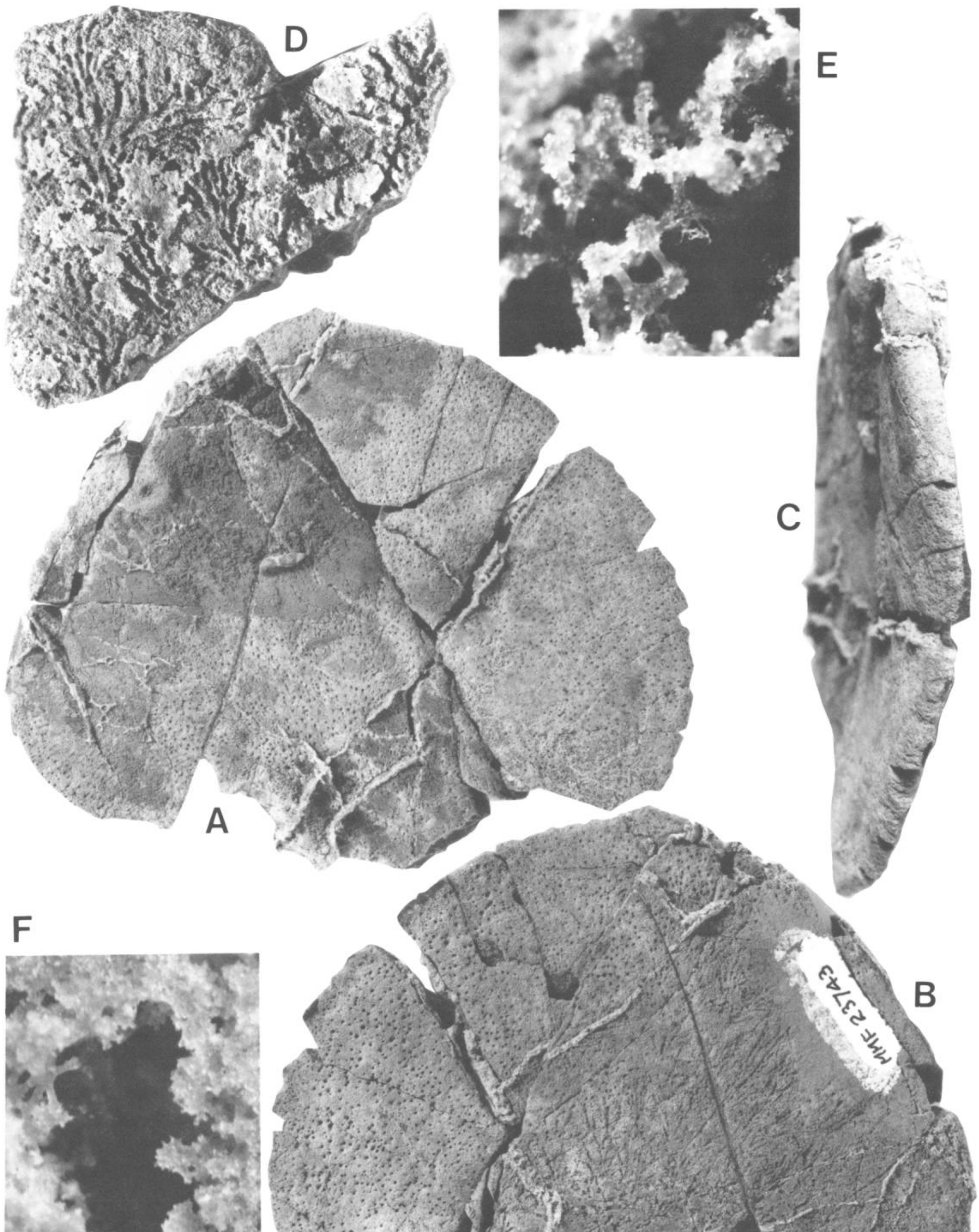
FIGURE 7—Sponges from the Garra Formation. All specimens from unit 10, immediately southeast of Wellington Golf Course, N.S.W. *A, B, Isispongia monilifera* n. sp., holotype, MMF 15105. *A,* detail of spiculation, ×20. *B,* view of eroded surface showing vertical canals (?apochetes), ×2. *C–F,* gen. et sp. indet. *C, D,* fragment from deeper portion of sponge, showing vertical and horizontal canals and spiculation, MMF 23728, ×3, ×15. *E, F,* fragment from closer to surface, MMF 23727, ×3, ×15.


D
E
C
A
MMF 23743
F
B

9). The species represents a minor component of the sponge fauna.

Family and genus indeterminate
Figures 2K; 4O–P

Material.—Three small fragments, one showing an inhalant surface. MMF 23730 (two fragments) from horizon G504, unit 10, and MMF 23731 from horizon G524, unit 11, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet.

Remarks.—The shape of the complete sponge is unknown; the exterior is smooth and curved. The internal skeletal structure is a series of densely spiculed layers parallel to the surface, separated by layers with a radiating alveolar structure. The parallel layers (previous external surfaces?) are ca. 1 mm apart, and are perforated by pores of irregular size and shape, but approximately 0.5 mm in diameter. The general structure is rather like a *Haplistion* with strongly developed horizontal layers. The spicule tracts are made up of rhizoclones ca. 0.05 mm in diameter. In addition there are many accessory spicules, chiefly monaxons, reaching a diameter of 0.25 mm and lengths in excess of 3 mm, and occasional simple foreign hexacts.

Family COLUMELLAESPONGIIDAE
Pickett, 1969
Genus COLUMELLAESPONGIA Pickett, 1969

Type species.—*Columellaespongia woolomolensis* Pickett, 1969.

COLUMELLAESPONGIA sp.
Figure 2A

Material.—A single specimen, MMF 23733, from southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet, unit 10, horizon G521.

Remarks.—Silicification makes it impossible to be certain that the desmas are rhizoclones. It is clear, however, that the skeleton is made up of elongated spicules which are aligned in parallel fashion in spicule tracts. These have an arrangement similar to that of *C. woolomolensis,* although there is a greater degree of anastomosis of the columellae than in the type species. The specimen is decorticated, somewhat conical, 80 mm long, 28 mm in maximum diameter and 17 mm wide at the base, which is the proximal part of the sponge just above the holdfast. The spongocoel reaches a maximum diameter of 20 mm.

This occurrence is somewhat older than that of previously described specimens, which are Medial Devonian (Eifelian) in age.

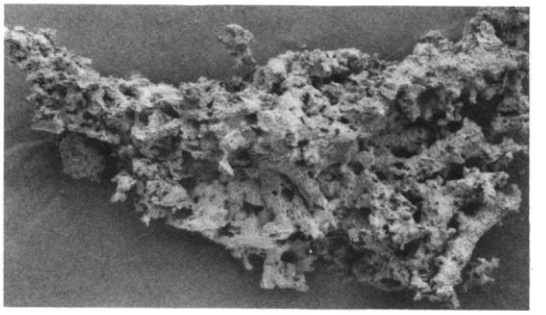


FIGURE 9—Rhizoclone spicules of *Varneycoelia favosa,* MMF 23755, Garra Formation, southeast of Wellington Golf Course, Wellington, N.S.W.

Class HEXACTINELLIDA Schmidt, 1870
Order LYSSAKIDA Zittel, 1877
Genus and species indeterminate
Figure 4Q

Material.—A single specimen, MMF 23752, from horizon G506, unit 10, southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet.

Description.—The preserved fragment is cylindrical, though slightly flattened, probably during lithification. It is 33 mm long and 6.2 by 5.0 mm in diameter. There is no indication of the presence of a spongocoel. The

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FIGURE 8—*Garraspongia vannus* n. gen., n. sp. Specimens from unit 10, Garra Formation, immediately southeast of Wellington Golf Course, Wellington, N.S.W. *A–C,* views of incurrent, excurrent and upper surfaces of holotype, MMF 23743, all ×1. *D,* excurrent surface of paratype, MMF 23746, showing plumose pattern of subdermal apochetes and remains of dermal layer, ×2. *E, F,* same specimen, showing detail of somatic and dermal spicules, respectively, both ×30.

surface was apparently smooth, and is overgrown by a small *Aulopora*.

The spicular framework consists principally of monaxons (probably mostly very long oxeas) of greatly varying size. The largest is 0.5 mm in diameter and probably as long as or longer than the length of the specimen; others are 0.03 mm in diameter and probably 1–2 mm long. No complete oxeas could be measured. Much rarer are associated simple hexacts. One almost complete spicule has a length of 0.7 mm. The only other identifiable hexact is stouter, but the rays are broken. There is no consistent orientation of the spicules, except that the long ones are necessarily aligned more or less parallel to the length of the sponge. Apart from the spicules the sponge is heavily silicified. The growth of *Aulopora* on the smooth outer surface suggests that there may have been some kind of dermal layer, but no spicules belonging to such a structure can be identified. Some oxeas occur either at the surface or very close to it. Some of the material defining the shape of the sponge is porous silica that shows no suggestion of regularity of structure and is interpreted as a result of imperfect silicification.

Remarks.—The form does not seem related to any of the lyssakid families which have known fossil representatives. In its cylindrical form and the dominance of oxeas it shows some similarity to the Leptomitidae, but these were simpler in structure and thin-walled tubular. The irregularly distributed hexacts also speak against such an assignment. It may represent a new group within the superfamily Protospongioidea Finks, 1960. The specimen may also be merely a root tuft of a larger hexactinellid, though it has a much more defined form than is usual in such structures.

Class CALCAREA Bowerbank, 1864
Order SPHINCTOZOA Steinmann, 1882
Suborder PORATA Seilacher, 1962

Remarks.—Seilacher (1962) proposed a division of the Sphinctozoa into two superfamilies which he named Porata and Aporata in direct reference to the nature of their external wall. The continuity of lineages within these two groups over geologic time and their usefulness as a taxonomic concept suggest a true phylogenetic basis for their separation. However, Article 35 (b) of the International Code of Zoological Nomenclature requires names of taxa of the family group to be based on type genera, and Seilacher's names are not in conformity with this rule. The Code includes no provisions for the formation of ordinal names. Therefore, to be able to continue using Seilacher's useful and informative names, we have raised the taxa to the level of suborder.

Family PHRAGMOCOELIIDAE Ott, 1974

Type genus.—*Phragmocoelia* Ott, 1974.

Diagnosis.—Retrosiphonate porate sphinctozoans with chambers divided internally by radial septa.

RADIOTHALAMOS n. gen.

Type species.—*Radiothalamos uniramosus* n. sp.

Diagnosis.—Unbranched thalamid sponges with a central tubular spongocoel and chambers divided internally by numerous radial partitions which may be porous, and which increase in number towards the periphery by intercalation.

Derivation of name.—Greek *radion,* ray and *thalamos* (masc.), chamber, alluding to the radial divisions within each successive chamber.

Remarks.—Apart from the new genus *Radiothalamos,* the Triassic *Phragmocoelia* Ott 1974 is the only genus in the order Sphinctozoa in which radial partitions are developed. There is no other skeletal development within the chambers, just as in *Radiothalamos.* The greatest difference between the two genera is the nature of the spongocoel wall. In *Phragmocoelia* this is a straight-sided cylinder bearing horizontal rows of apopores. In *Radiothalamos* it is constricted at the level of each chamber wall, and instead of true pores there are elongated openings between the ends of the "septa," somewhat constricted by crossbars and short projections which do not extend the full width; in fact, it is much less a recognizable structure than the spongocoel wall of *Phragmocoelia.*

Radiothalamos is the oldest sphinctozoan described so far, and its morphology is of consequence in a discussion of the phylogeny of the group. By the Carboniferous the group was already well differentiated, and both Ott (1967) and Finks (1970) recognize three lineages at that time. *Radiothalamos* is clearly related to the porate, retrosiphonate *Amblysiphonella*-lineage, but whether the new genus represents a primitive type close to the main evolutionary lineage or a side-branch specialized through development of radial divisions will only be established by discovery of more Devonian (and older) material.

The exciting recent discovery of living sphinctozoans (Vacelet, 1977) has proved that sphinctozoans are true sponges. *Neocoelia* Vacelet is close to *Stylothalamia* Ott (Cryptocoeliidae), and can be regarded as a living representative of the same porate, retrosiphonate lineage of which *Radiothalamos* is the oldest known form.

De Laubenfels (1955) suggested that the oscula on the chambers of *Girtyocoelia* implied that the central open tube was an inhalant siphon. At least for *Radiothalamos* this suggestion is insupportable. The exterior of the sponge is covered with small pores; the upper surface bears radial rows of somewhat larger pores surrounding the large central opening. If the central opening is an incurrent canal, the sponge was likely to have contaminated the strong inhalant stream by close proximity to the smaller exhalant canals of the upper surface; the alternate possibility seems much more probable, and is the usual condition of extant tubular sponges. None of the more recent work (Seilacher, 1962; Ott, 1967; Vacelet, 1977) offers any support for De Laubenfels' interpretation.

RADIOTHALAMOS UNIRAMOSUS n. sp.
Figure 4A–E

Holotype.—Specimen MMF 23738 from unit 10, horizon G517.

Paratypes.—MMF 23737, 23739 from unit 10, horizon G521, G518, respectively; MMF 23736 from unit 11, horizon G524. All specimens from southeast of Wellington golf course, grid reference 18819635 (yards), Dubbo 1:250,000 sheet.

Derivation of name.—*uniramosus,* single-branched, referring to the unbranched habit.

Diagnosis.—*Radiothalamos* with skeleton of a vertical linear unbranched series of chambers.

Description.—The skeleton of the sponge is made of a vertical uniserial row of chambers, traversed by a central opening which extends to the base of the sponge. Each chamber is subdivided by a series of intercalated, radial, septum-like partitions.

The three most complete specimens are 20 mm, 23 mm and 32 mm (incomplete) high. The base of the sponge is a flattened holdfast, indicating attachment to a substrate not preserved with any of the specimens. The slightly narrower juvenile portion of the sponge is 6.5–7.5 mm in minimum diameter and the sponge increases rapidly to a mature diameter of 10–13 mm. At maturity the sponge is more or less cylindrical, with slight and somewhat irregular annulations produced by constrictions between successive chambers. The osculum occurs at the base of a shallow apical depression. The osculum is oval or round, 1.5–2.5 mm in diameter and leads directly into the central tube or spongocoel.

Prosopores are generally most apparent on the upper surface, where they are in radial rows, corresponding to interspaces between the "septa." Side walls on the two complete specimens show no structures that can reliably be interpreted as prosopores (these are probably obscured by silicification). However the third, less complete specimen (MMF 23737) shows many prosopores ca. 0.2 mm in diameter and 0.5 mm apart, in which a vertical linear arrangement is only moderately defined. In places there is at least an equal suggestion of a horizontal arrangement.

Walls of the sponge are 0.2–0.3 mm thick and the "septa" are about 0.2 mm thick. The "septa" are pierced by pores which are larger and more irregular than the prosopores, and which sometimes are almost as high as the "septum" but are no wider than 0.4 mm.

The spongocoel is strongly annulated, for ends of the upper surfaces of the chamber walls project into it. These annulations are thus ca. 1.5 mm apart. The remainder of the wall of the spongocoel is formed by ends of the "septa," by crossbars that connect them, and by projections that do not extend the full interseptal distance. These projections and crossbars do not occur elsewhere on the "septa," but are restricted to the central tube wall.

The nature of the spiculation remains obscure. The skeletons have been thoroughly silicified. In the central tube of MMF 23737 there is some indication of straight-shafted spicules in a skeleton made up dominantly of rather irregular spicules with many processes. We do not know, at the present time, to what extent these structures represent original spicules. It seems more probable that the skeleton was solid, as in *Neocoelia.*

ACKNOWLEDGMENTS

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