

The oldest known well-preserved Radiolaria

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SUMMARY — *Radiolaria discovered in shallow-water calcite micrites from the lower Ordovician of Spitsbergen are the oldest known well-preserved representatives of their subclass. The varied Radiolaria assemblage lacks several groups characteristic of higher Palaeozoic rocks, but at least one totally new family is present. Nassellaria, Albaillellaria and Palaeoscenidium are absent. The Entactiniidae (Spumellaria) are represented by primitive shelled forms and also, apparently, by unshelled, spicular types. Non-entactiniid Spumellaria are tentatively recognized. All three basic Radiolaria architectures are present, though the lower Ordovician representatives are often apparently unrelated phylogenetically to later Palaeozoic and post-Palaeozoic taxa.*

RIASSUNTO — *Si illustrano i Radiolari scoperti entro calcari micritici di ambiente neritico, nell'Ordoviciano inferiore delle isole Spitzbergen. Si tratta dei più antichi rappresentanti ben conservati di questa sottoclasse. La associazione appare varia, malgrado manchino parecchi gruppi caratteristici di livelli paleozoici più recenti. Per contro, vi è rappresentata una famiglia del tutto nuova. Mancano i Nassellaria, Albaillellaria e Palaeoscenidium. Gli Entactiniidae (Spumellaria) sono rappresentati sia da forme a scheletro ben definito, di tipo primitivo, che da forme prive di scheletro definito, unicamente provviste di spicole. Alcuni esemplari vengono tentativamente riferiti a Spumellaria non entactiniidi. I tre tipi fondamentali di architettura dello scheletro, caratteristici dei Radiolari, sono presenti nella associazione studiata; tuttavia, queste forme dell'Ordoviciano inferiore appaiono spesso non correlabili filiticamente con i taxa più recenti, paleozoici e postpaleozoici.*

A. INTRODUCTION

Few major, long-ranging animal groups with an abundant fossil record have an early history so poorly understood as the Radiolaria. Almost entirely this is due to their usual very poor preservation as fossils in Palaeozoic rocks, most frequently in siliceous sediments where they can be studied only in thin sections. At best, thin section study has provided an incomplete knowledge of Radiolaria morphology in the Palaeozoic, and led to some highly misleading conclusions regarding the relationships between Palaeozoic and Modern forms (Riedel 1967).

Considerable advances in the understanding of upper Palaeozoic Radiolarians during the last twenty years — including the recognition of at least one exclusively Palaeozoic suborder — are due entirely to the discovery of rare faunas which can be totally or partially separated from their carbonate or phosphate matrices (Deflandre 1946, Foreman 1959, Holdsworth 1964). Separable lower Palaeozoic Radiolarians are scarcer still, and the discovery in 1970 of an excellently preserved fauna in acid-insoluble residues of lower Ordovician limestones of the Valhallfonna Formation (Vallance and Fortey 1968), Spitsbergen (upper-

most unit of the Oslobreen Group) is therefore of great taxonomic and evolutionary significance. Previously, the earliest faunas of comparable preservation known to the writers were those from calcareous, graptolitic concretions of the Cape Phillips Formation, Cornwallis Island, ranging in age from Llandovery to Ludlow (1).

B. LITHOLOGY, STRATIGRAPHY AND PALAEOENVIRONMENT OF THE RADIOLARIAN ROCKS

Practically all previously known, well preserved faunas come from concretions where skeletons are preserved, uncorroded as quartz (Deflandre 1946, Foreman 1959, Holdsworth *in press*) or where they have been very perfectly replaced by dolomite (Holdsworth 1967) or phosphate (Kling and Reif 1969). The Spitsbergen occurrence is unusual in that the quartz-preserved specimens occur in bedded, brown, calcite micrites. As yet the Radiolaria have been found at only three horizons in five metres of limestone, 180-185 metres from the base of the Valhallfonna Formation.

These horizons are of undoubtedly early Ordovician age, graptolites occurring some 40 metres below (Fortey 1971) being of *Isograptus* Zone age (Zone 8 of Berry (1960)), and rare graptolites of the same,

(1) Allusions to Silurian Radiolaria in this article are based entirely on work in progress on these Cornwallis Island faunas by B. K. H.

or possibly the succeeding zone being found slightly above the horizons. Trilobites in the radiolarian limestones are closely similar to those described by Whittington (1965) from the Middle Table Head Formation and from other North American localities (Ross 1967) of Whiterock age. Such an horizon may correlate with the *D. hirundo* or possibly *D. bifidus* Zone of the standard British sequence, and the radiolarian limestones are considered, therefore, as being late Arenig in age.

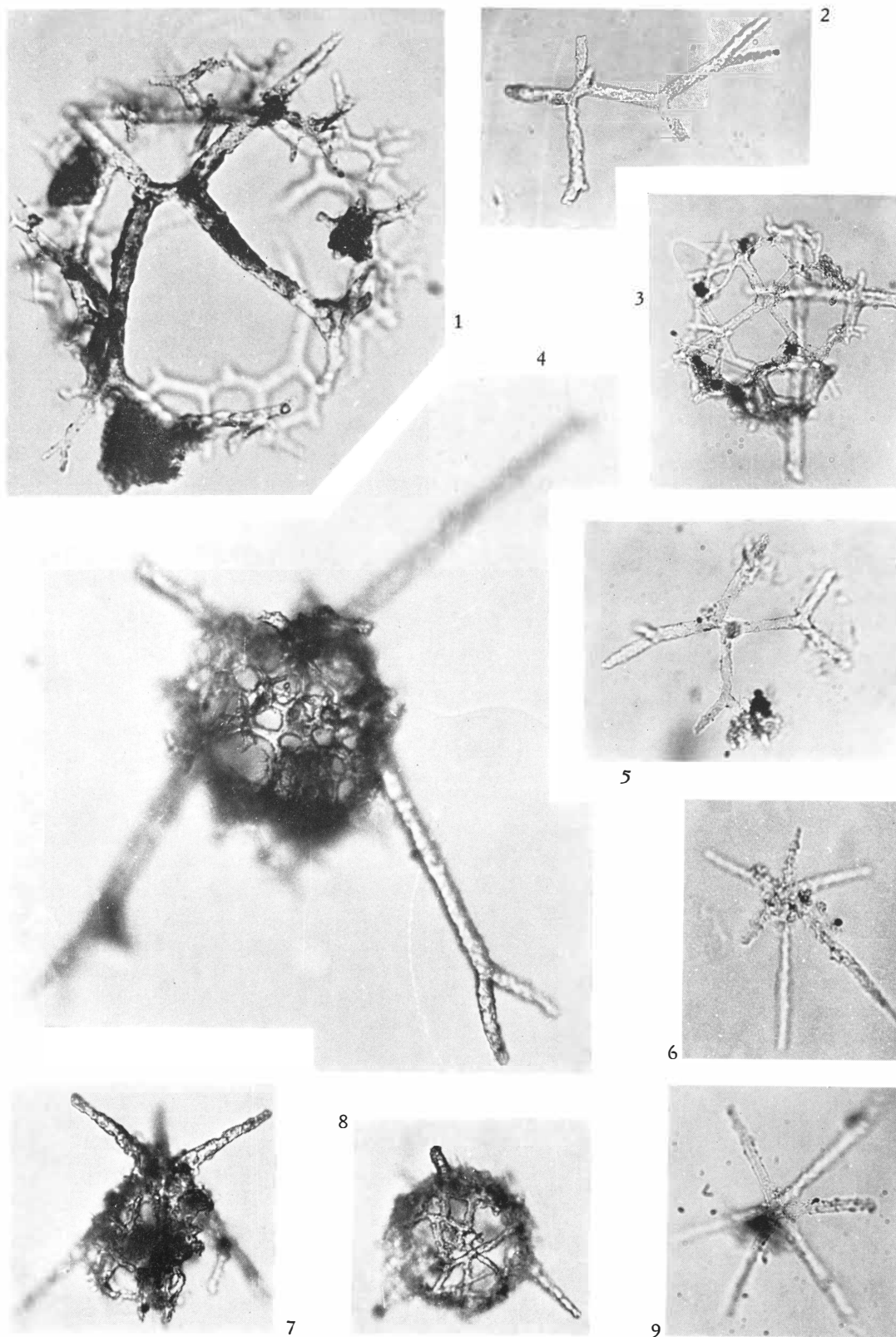
The associated fauna clearly indicates that the Radiolaria assemblage is derived from a comparatively shallow water column. The radiolarian micrites contain many trilobites, ostracodes, brachiopods, sponges, chitinozoa and fragmentary graptolites, and immediately overlie beds with algal oncoliths, *Girvanella*-type nodules and large, current-oriented orthoconic nautiloids. Presence of the Radiolaria at three levels only is unlikely to be due to ecological factors, as the radiolarian limestones differ little in other respects from the remainder of the upper part (ca. 50 metres) of the Formation. It is significant, however, that at all three levels sponge megascleres and siliceous spicules of unknown affinity are more than usually abundant, comprising up to thirty percent of the acid-insoluble residue. Where unusually large quantities of siliceous skeletal debris were incorporated into the accumulating calcareous sediment it is possible that silica saturation of interstitial water was achieved relatively rapidly during early diagenesis, protecting the Radiolaria assemblage from total solution. That some redistribution

EXPLANATION OF PLATE 10

All figures x200. Numbers are those assigned to specimens in the authors' collection.

- Figs. 1, 4 - SP088, SP013. Aff. *Entactinia* Foreman spp.
 2, 5 - SP056c, SP051a. Bar centred, spicular entactiniid spp.
 3 - SP062c. Aff. *Stigmosphaera* Rust sp.
 6, 9 - SP091a, SP078c. Possible point-centred, spicular entactiniid spp.
 7, 8 - SP014, SP042. Entactiniid *genus novum*. 7 - lateral view; 8 - adapical view.

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of silica occurred is clear from the clots of secondary quartz which commonly plug the interiors of spherical Spumellarians.

C. MORPHOLOGY AND CLASSIFICATION OF THE RADIOLARIA

1. Introduction

The fauna can be classified under three broad headings: (A) Shelled and unshelled Spumellaria of the Family Entactiniidae; (B) « Sphaeroids » - multishelled and single shelled Spumellaria, apparently lacking an internal entactiniid spicule; (C) Spicular and conical-shelled forms which appear to constitute a previously unknown family.

All the unquestionable shelled entactiniid are of distinctly primitive type, including forms which exhibit two new basic spicule-shell patterns.

There is no trace of Nassellaria - not surprisingly, as unequivocal evidence for their existence in previously investigated Palaeozoic faunas is still lacking. More important, the exclusively Palaeozoic suborder Albaillellaria, first known at present from the Wenlock and important in Devonian and Carboniferous faunas, is also totally unrepresented. It would be rash to conclude from the evidence of a single fauna that the Albaillellaria are of post-Arenig origin, particularly as the group is quite frequently missing from entactiniid-rich assemblages of Namurian age (Holdsworth 1969). On the other hand, the overall range of radiolarian morphology in the Arenig assemblage is greater than that in albaillellariid-free Carboniferous faunas, and it is not unreasonable to expect that Albaillellaria would have been included had they existed in Arenig time. It is equally reasonable to believe, from the simple and almost certainly primitive Silurian albaillellariids, that the Wenlock representatives do not long post-date the origin of the suborder. Also absent from the Arenig fauna is *Palaeoscenidium* Deflandre, the earliest unquestionable species being Silurian.

2. The Entactiniidae

The Entactiniidae is a major group of Palaeozoic Radiolaria, currently considered a family of the Spumellaria (Riedel 1967), characterized by an internal system of spicule rays (4-8 in number), usually, but not always, arising from a median bar and commonly communicating with the externally developed main spines. The unquestionable Arenig Entactiniidae are all of distinctly primitive form in relation to the most completely known spectrum of 5 genera and 53 species in the Upper Devonian Ohio Shale fauna (Foreman 1963). Spicules are either six-rayed, point-centred - a type not seen in the Ohio fauna but known in the Carboniferous Holdsworth 1966; Rust 1892(2) - four-rayed, point-centred (very rare) or six-rayed, bar-centred.

The primitive nature is displayed in the great strength of the internal spicule, the rays in many cases being as strong as the spines, and the spines being essentially unmodified extensions of the primary spicule rays. In upper Palaeozoic faunas, only *Haplentactinia* Foreman (Upper Devonian) approaches such simplicity. The great majority of upper Palaeozoic entactiniids have spicule rays considerably weaker than the spines — particularly where concentric shells are developed — and the spines themselves are often bladed. Equally significantly, the Arenig shells are either crude and spinular in construction or very irregularly latticed, and the spicule centre is invariably highly eccentric in relation to the shell centre.

Most extreme in this latter respect is Entactiniid *genus novum* (Plate 1, figs. 7,8) in which six spicule rays, not quite orthogonal in symmetry, meet at a point. The irregular, cobweb-like lattice, however, is developed from only three rays, the spicule centre thus lying in the thickness of the shell wall. Total symmetry is radial rather than

(2) It is not entirely certain from the figures that these species of Rust's - *Stigmatosphaera mira* and *Stigmatosphaerostylus notabilis* - do have truly point-centred spicule rays.

spherical, and the spicule centre can be considered as marking an « apical pole ». No such organization is known at higher Palaeozoic levels.

The remaining shelled entactiniids are more typical in that the spicule centre, though frequently highly eccentric, lies inside the shell capsule. Some specimens, however, show unique features.

The commonest of these forms may provisionally be referred to as « aff. *Entactinia* Foreman spp. », in which six primary rays arise from a comparatively long median bar (three from each end) which is positioned very eccentrically within a crude, spinular shell (Plate 1, figs. 1,4). In at least one species, all six primary rays continue externally as main spines (Plate 1, fig. 4) — a typically entactiniid feature — and the shell is generated from spinules arising from a single level on one or more of the rays. But some or all of the main spines show strong terminal bifurcations (Plate 1, fig. 4), a feature not previously known amongst members of the family.

Further, in at least one other species (Plate 1, fig. 1), four of the six rays do not continue externally as main spines, but generate the very loose shell by repeated terminal bifurcation and by single strong lateral branches from two of these rays. The two rays continuing as spines make no contribution to the shell. They are developed from opposite ends of the median bar, emerge immediately from the shell and give a distinct polarity to the entire skeleton. In a single specimen, provisionally referred to as « aff. *Tetrentactinia* Foreman sp. », (SP010a) only four, strong, point-centred rays appear to be present, all of which probably contribute to the highly irregular shell by repeated terminal bifurcation.

Specimens representing a fourth skeletal organization in the Arenig entactiniid assemblage are provisionally referred to as « aff. *Stigmatosphaera* Rust spp. » (Plate 1, fig. 3). There is a resemblance to *Haplentactinia*, except that the short median spicule bar of this Devonian genus is absent and the six, strong spicule rays of perfect ortho-

nal symmetry meet at a point. The shell arises from quadruplets of secondary rays, each set developed at a single point on each of the six primary rays, these points being at dissimilar distances from the primary spicule centre.

The prevalence of spicule bifurcation amongst the Valhallfonna shelled entactiniids leads to the conclusion that bar-centred spicules with bifurcating rays but no lattice (Plate 1, figs. 2,5), comparatively common in the fauna, represent totally unshelled Entactiniidae. Such forms have not previously been recognized. Six-rayed, point-centred spicules, not quite orthogonal in symmetry (Plate 1, figs 6,9) might, by analogy, be considered the unshelled counterparts of Entactiniid *genus novum*. The eccentricity of shell relative to spicule centre in the shelled genus may be mirrored in the unshelled spicules by the distribution of hairs which, in the majority of cases, are apparently either developed preferentially on three of the six rays or confined to three rays alone. Very rarely rays are all naked (Plate 1, fig. 9).

3. *Sphaeroids*

This second group of Spumellaria contrasts most strongly with the unquestionable entactiniids described above, and is considerably more abundant. Two concentric shells are most commonly present. Single shelled specimens are less frequent and three shells are very rare. Spines, invariably unbladed, vary in number from six to probably more than thirty, usually of similar or only slightly variable strength on a single specimen.

The shells are of reticulate structure and spherical in form — very different to the coarse, spinular shells of aff. *Entactinia*, aff. *Tetrentactinia* and aff. *Stigmatosphaera*. The shell reticulum is continuous with circlets of 4-6 small spinules borne on each spine or beam. Characteristically, roots of spinules in groups continuous with the outermost shell arise at very slightly different levels, leading to slight imperfections

in shell sphericity. Offsetting is most apparent in spicule circlets which ornament spines, and lateral fusion of spinules from adjacent spines and fusion with by-spines sometimes results in an incomplete «extra shell».

Low spine counts (6-7) are associated with the larger, more robust specimens (Plate 2, fig. 6). Often there is no trace of an inner shell. In other specimens, spines continue inwards as strong rods (beams) to terminate in remnants of an inner, very loose and delicate lattice. In no case is there evidence of inward continuation of beams beyond the second lattice. A few specimens showing no inner shell do preserve small fragments of considerably more delicate inward penetrating rods continuous with the main spines. Conceivably these could represent the distal ends of entactiniid spicule rays, but equally they could be fragments of weak beams.

Specimens with higher spine counts (approximately 10-20) (Plate 2, fig. 10) invariably show a second shell and are probably closely related to very rare three shelled specimens. All major spines penetrate as beams to the innermost lattice, but no trace has been found in any specimen of a ray continuing into the central cavity. It appears highly improbable that this group possessed an entactiniid-style central spicule.

The highest spine counts occur in small individuals (Plate 2, fig. 9) which invariably possess a second shell, though offsetting of spinules in both shells frequently blurs the concentric structure. All spines continue inwards as beams but have never been seen to penetrate beyond the inner shell.

Since the comparatively recent recognition of the importance of entactiniids amongst Palaeozoic faunas and subsequent growing awareness of the morphological diversity within the family, some doubt has existed as to the reality of Palaeozoic non-entactiniids (i.e. truly non-spiculate forms) previously described from indifferently preserved material prepared by thin sectioning. The Valhallfonna fauna suggests quite strongly that as early as lowest Ordovician two

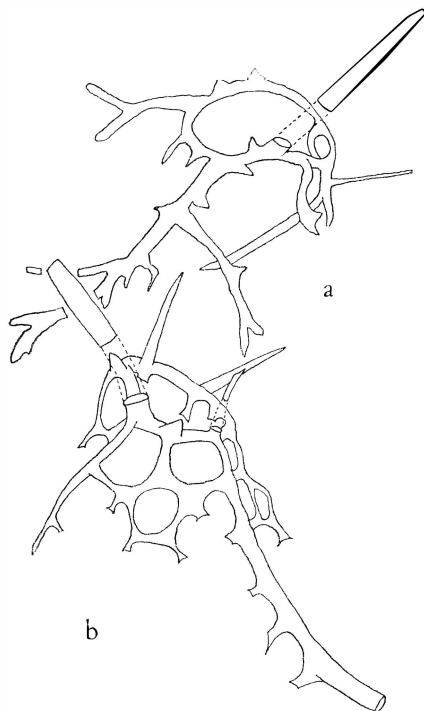
major spumellarian groups coexisted - entactiniid and non-entactiniid. There may, therefore, be less reason for suspicion regarding apparently non-entactiniid Palaeozoic spumellarian faunas such e.g. as that of the Devonian Caballos Novaculite (Aberdeen 1940; Riedel and Foreman 1961) described from thin sections, and many of Hinde's (1890) «Astrosphaeridae» from the southern Scottish mid-Ordovician are probably related to the Valhallfonna apparent non-spiculates.

On the other hand, Valhallfonna two shelled forms with 10-20 spines can be compared quite closely with Foreman's (1963) Devonian «*Entactinosphaera? hapala*» in which there is some reason to believe that a spicule existed (see Foreman 1963, p. 280). The difficulty of detecting the often much reduced proximal portions of the spicule in concentrically shelled entactiniids cannot be overemphasized, and the whole problem of defining major lineages amongst the Palaeozoic Spumellaria is further complicated by the demonstration of secondary loss of spicules amongst lower Carboniferous pylomate entactiniids (Holdsworth *in press*).

4. *Radiolaria familia nova*

This new family is represented by conular, spongy shells bearing axial to sub-axial and lateral apical spines, together with flank-lateral spines (Plate 2, figs. 1, 3, 8). The density of the apex wall varies, the spongy structure sometimes extending to the shell tip (Plate 2, fig. 3), but more commonly the apical wall is of spicular construction (Plate 2, figs. 1, 4, 7, 8). This structure is highly variable in detail, but usually a single, prominent apical spine, axial to sub-axial in orientation, and set to one side of the «cephalis», provides a centre for three, usually sinuous rays — one or more of which supply the more apical of the flank spines (Text-figure 1b). Very commonly two of these rays are connected by a loop from which — as from the proximal portions of the primary rays — subsidiary

spines arise. Possibly also belonging to this family is a new, irregularly branching, tri-radiate spicular genus (Plate 2, figs. 2, 5) (Text-figure 1a). Detailed homologies have



Explanation of Text-figure 1 - Semi-diagrammatic drawings to illustrate similarity between Radiolaria *familia nova* sp. (spicular form) - a. (SP054) - and apical structure of Radiolaria *familia nova* sp. (conical form) - b. (SP003) - see also Plate 2, fig. 1).

not yet been established, but there is a marked general resemblance between the naked spicules and the apical rays of the

conical genus — sometimes extending to the presence of inter-ray loops (Text-figure 1).

The conical species differ radically from any previously known Radiolaria. The disposition of the apical spines is rather similar to that in *Popojskyellum* Deflandre (Tournaisian-Namurian), but cephalic structure, shell-wall and disposition of flank spines are all quite different in the Carboniferous genus. The sub-cephalic shell structure is somewhat similar to that in *Cyrtentactinia primotica* Foreman (Upper Devonian), but the Arenig cones completely lack the internal entactiniid spicule which, in *C. primotica*, is contained within a blunt, broad « cephalis ».

D. CONCLUSIONS

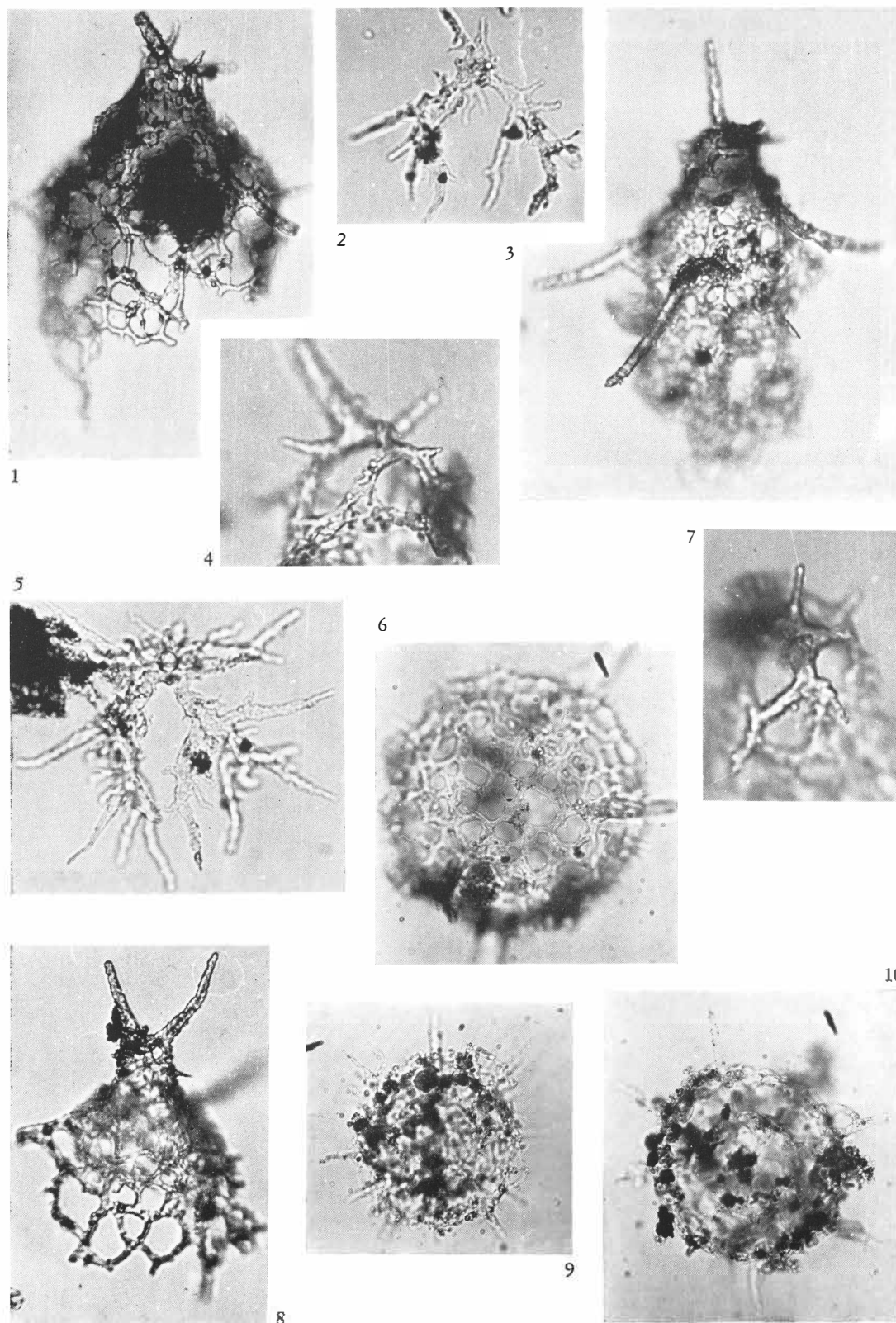
The Valhallfonna fauna shows that by earliest Ordovician time the three very basic skeletal types found amongst the Radiolaria — the unshelled spicule, closed sphere and cone — had been achieved. They were achieved, however, amongst groups which, to judge by the finer details of their architecture, are for the most part not merely unrelated to post-Palaeozoic taxa of analogous form, but which can also be considered to differ at generic and even familial level from later Palaeozoic species. The view of the Radiolaria as a group highly conservative in evolutionary terms, a view implicit in all taxonomic treatment of Palaeozoic forms prior to Deflandre (1952) and very completely reflected in Campbell (1954), is essentially mythical.

EXPLANATION OF PLATE 11

All figures x200, except 4 and 7, x415.

- Figs. 1, 3, 8 - SP003, SP016, SP022. Radiolaria *familia nova* spp., conical form.
 2, 5 - SP069d, SP070c. Radiolaria *familia nova* spp., spicular form.
 4, 7 - SP004. Radiolaria *familia nova* sp., conical form, showing apical structure.
 6, 9, 10 - SP010d, SP029d, SP045d, SP045b. Sphaeroids - apparently non-spiculate spumellarians.

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REFERENCES

- ABERDEEN, E., 1940, Radiolarian fauna of the Caballos formation, Marathon Basin, Texas: Jour. Paleont., 14, 127-139, pls. 20-21.
- BERRY, W. B. N., 1960, Graptolites of the Marathon region, West Texas: Univ. of Texas Bureau of Economic Geology, Pub. no. 6005, 179 pp. pl. 20.
- CAMPBELL, A. S., 1954, Radiolaria: in Cambell, A. S. and Moore, R. C., Protista 3, Treatise on Invertebrate Paleontology Part D, Geol. Soc. America and Kansas Univ. Press, 195 pp.
- DEFLANDRE, G., 1946, Radiolaires et hystrichosphaeridés du Carbonifère de la Montagne Noire: Comptes Rendus Acad. Sci. Paris, 223, 515-517.
- , 1952, *Albaillella* nov. gen., Radiolaire fossile du Carbonifère inférieur, type d'une lignée aberrante éteinte: Comptes Rendus Acad. Sci. Paris, 234, 872-874.
- FOREMAN, H. P., 1959, A new occurrence of Devonian Radiolaria in calcareous concretions of the Huron member of the Ohio Shale: Jour. Paleont., 33, 76-80, pl. 15.
- , 1963, Upper Devonian Radiolaria from the Huron Member of the Ohio Shale: Micropaleontology, 9, 267-304, pls. 1-9.
- FORTEY, R. A., 1971, *Tristichograptus*, a triserial graptolite from the lower Ordovician of Spitsbergen: Palaeontology, 14, 188-199, pls. 26-29.
- HINDE, G. J., 1890, Notes on Radiolaria from the lower Palaeozoic rocks (Llandeilo-Caradoc) of the South of Scotland: Annals Mag. Nat. Hist., 6, 40-59, pls. 3-4.
- HOLDSWORTH, B. K., 1964, Radiolarian nature of the thicker-shelled goniatite fauna phase in some Namurian limestone «bullions»: Nature, London, 201, 697-699.
- , 1966, A preliminary study of the palaeontology and palaeoenvironment of some Namurian limestone «bullions»: Mercian Geologist, 1, 315-337, pls. 18-20.
- , 1967, Dolomitization of siliceous microfossils in Namurian concretionary limestones: Geol. Mag., 104, 148-154, pl. 7.
- , 1969, Namurian Radiolaria of the genus *Ceratoliscum* from Staffordshire and Derbyshire, England: Micropaleontology, 15, 221-229, pl. 1.
- , in press, The Radiolaria of the Baltamani Formation, Lower Carboniferous: MTA Bull., Ankara.
- KLING, S. A., and Reif, W.-E., 1969, The Paleozoic history of amphidisc and hemidisc sponges: new evidence from the Carboniferous of Uruguay: Jour. Paleont., 43, 1429-1434, pl. 176.
- RIEDEL, W. R., 1967, Some new families of Radiolaria: Proc. Geol. Soc. London., 1640, 148-149.
- , and Foreman, H. P., 1961, Type specimens of North American Paleozoic Radiolaria: Jour. Paleont., 35, 628-632.
- ROSS, R. J., 1967, Some Middle Ordovician Brachiopods and Trilobites from the Basin Ranges, Western United States: Prof. Paper U. S. Geol. Survey 523-D, 1-43, pls. 1-10.
- RUST, D., 1892, Beiträge zur Kenntniss der Fossilen Radiolarien aus Gesteinen der Trias und der palaeozoischen Schichten: Palaeontographica, 38, 107-192, pls. 6-30.
- VALANCE, G. and FORTEY, R. A., 1968, Ordovician succession in North Spitsbergen: Proc. Geol. Soc. London., 1648, 91-7.
- WHITTINGTON, H. B., 1965, Trilobites of the Ordovician Table Head Formation, western Newfoundland: Bull. Mus. comp. Zool. Harv., 132, 275-442, pls. 1-68.