A new Ordovician tubular 'alga' from Norway

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Hoeegonites kringla, a new genus and species, is described from the Middle Ordovician Furuberg Formation in the Mjøsa Districts of the Oslo Region, Norway. Its morphology suggests that it is an alga; however, the interpretation of its biology makes any exact taxonomic assignment speculative. The nature of the little known or understood group of tubular 'algae' from the Silurian and Ordovician of Norway is equally problematic. Thus, the exact systematic position of *Hoeegonites* is problematic, and it is tentatively placed among the siphonous chlorophyte complex.

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Numerous Lower Paleozoic fossils, particularly the so-called Problematica, are traditionally assigned to various algal taxa. The interpretation of many of these organisms, especially the Ordovician and Silurian ones, as algae is questionable, and their exact placement among thallophytes is certainly in doubt. The general problems of the algal 'taxonomic wastebaskets' are discussed in detail by Riding & Voronova (1985 and references therein) and by Babcock (1986 and references therein).

It is surprising how many various Ordovician and Silurian 'algae' have been described, and at the same time how little biological information these descriptions provide. Therefore, the anatomy of these 'algae' must be better understood before any sophisticated schemes of classification can be proposed, and before any phylogenetic models are constructed.

It is on this simple goal of morphological understanding of individual taxa that the work on the Lower Paleozoic algae must concentrate.

The Norwegian Ordovician and Silurian 'algae'

If the stromatolites, oncolites, rhodoliths and other organosedimentary structures are excluded, then the following Ordovician and Silurian 'algae' can be recognized in Norway:

(1) the phytoplankton, e.g. acritarchs;
(2) the blue-greens, e.g. *Girvanella* (other supposed cyanobacterians, *Nuia* and *Renalcis*, have not been recognized in Norway);
(3) the reds, e.g. *Solenopora* (*Parachaetetes* is unknown in Norway);
(4) the spherical forms, e.g. cyclocrinitids and receptaculitids;
(5) those persistently assumed to have been good dasycladaceans: *Rhabdoporella, Vermiporella* (shown by Kozlowski and Kazmierczak (1968) to be of unknown affinities) and *Dasyporella* (*Intermurella, Novantiella, Callithamniopsis, Primicorallina, Inopinatella*, etc., have not been positively identified in Norway);
(6) the tubular supposed codiaceans, e.g. *Dimorphosiphon* and *Palaeoporella*;
(7) non-calcareous problematic, e.g. *Chaetocladus* and *Primicorallina* (the great many other problematic algae, e.g. *Aphroporella, Frutexites, Epiphyton, Rothpletzella, Ortonella*, are not identified in Norway).

There are other ways in which these could be arranged. Traditionally, however, most of those in groups 4–7 have been placed among Dasycladales or in related taxa (e.g. Korde 1973; Bassoullet et al. 1979), or more reasonably, as Riding & Voronova (1985) have done, are classified by their external and internal morphologies without regard to their supposed extant analogues. The published literature on these 'algae' is very large and the numerous opinions on their nature are frequently very definitive. But are these opinions correct? We believe that doubts cast by Babcock (1986) and Riding & Voronova (1985) on the assignment of many of these fossils to the extant algal taxa are serious enough to caution against a premature reconstruction of their phylogenetic relationship. All systems of classification are tentative, but particularly of fossils whose biology is poorly understood, as the biology of most of the Ordovician and Silurian algae certainly is.

Perhaps the paleoalgologists have a reluctance to assign their algae to Problematica and by so doing to admit ignorance. But these fossils, just because they do not have any living counterparts, need not be problematical any more than dinosaurs, graptolites or ammonoids are.

Tubular algae

The tubular algae are calcareous perforate tubes, and their classification has been based on the shape of the tube (whether straight or branched), on the ratio of the thickness of the calcareous sleeve to the tube, and on the arrangement and shapes of pores. But the interpretation of their nature as algae (like the interpretation of the spherical cyclocrinitids as dasyclads) was based on the assumption that the tube represents the thallus, that the inner hollow cavity is the siphon (or the central axis), that the calcified sleeve is the cortex, and that the pores represent the laterals. Generally these tubular fossils were placed as a family within Siphonales or within Dasycladales. However, there are three objections to these assignments.

First, there are many living organisms other than Siphonales and Dasycladales whose skeletal anatomy consists of perforated tubes; it is equally easy to compare these tubular fossils with sponges and with archaeocyathids, whose central cavities and pores may or may not be regularly arranged. The archaeocyathid wall is generally more solid than the sponge wall, but sponges with solid walls are also known.

Second, there are many living organisms other than Siphonales and Dasycladales which consist of a central axis and a whorled or irregular arrangement of skeletal elements. For example, living red algae (e.g. Florideophyceae, Ceramiaceae and Corallinaceae) have thalli consisting of a central axis and regularly arranged branches; and in extant corals (e.g. octocorals) polyps are in regular verticils or are borne irregularly.

Third, those tubular Ordovician and Silurian forms assigned to living families of siphonous chlorophytes are assumed to have the morphological bauplan identical to that of their living counterparts, and thus unchanged since the Lower Paleozoic. However, these relatively common tubular fossils became extinct (just like cyclocrinitids) at the end of the Silurian, and are apparently without any descendants.

Among these tubular organisms there is a new undescribed Norwegian fossil, the *Hoeegonites*.

Systematic paleontology

Hoeegonites *gen. nov.*

Name: The name *Hoeegonites* is dedicated to the dean of Norwegian paleoalgologists, Ove Arbo Høeg.

Diagnosis: As that of the species.

Composition: One species only.

Hoeegonites kringla *sp. nov.*

Diagnosis: Body small, thin and rigid, uniaxial, cylindrical, very gently expanding, radially symmetrical, circular in cross section. Central axis pronounced with diameter of approximately one-half of thallus (typically 40–45%). Laterals from claviform to ovate but distinctly robust and globose. Primaries branch once to from four to possibly eight secondaries; branches tightly packed, probably in whorls; youngest (first formed) whorls of at least four, oldest (last formed) of at least twelve branches; calcification aragonitic, heavy and continuous between laterals and forming distinct perforated sleeve around axis.

Measurements: Diameter of thallus 1.2–2.0 mm. Length up to and possibly much over 16 mm; many fossils 15–16 mm long are observed. Primaries 0.25–0.31 mm long and 0.24–0.26 mm wide. Secondaries approximately 0.050–0.068 mm wide.

Morphology: While it is easy to think of *Hoeegonites* as an alga (of the siphonous chlorophyte complex), it is very difficult to demonstrate its algal nature. This is mostly due to the preservation of the fossils which are *not* actual remains or their replacement, but rather are a calcification of areas *between* the skeletal elements. This preservation produces perforated tubes. Therefore, our interpretation of *Hoeegonites* as a siphonous alga is tentative (Fig. 1).

The thalli of *Hoeegonites* are straight, cylindrical and unbranched. The ends are abruptly rounded to tapering, and it is possible that the upper end is rounded, while the lower end is tapering. We do not know whether the body was attached, and if so how. It is possible that *Hoeegonites* was segmented in a manner of recent *Halimeda*, or the contemporaneous *Dimorphosiphon* (occurring together with *Hoeegonites*) – however, this is presently pure conjecture.

The central axis at the equatorial region is approximately one-half of the diameter of the body (Fig. 2). At one end the axis is circular in cross section and distinctly narrowed (Fig. 2E), and presumably tapered at the opposite end.

In longitudinal and, to a lesser extent, horizontal sections, branches appear in whorls. The oldest and smallest parts appear to have had fewer laterals per whorl than the larger, younger parts. The number of primaries per whorl increases apically from at least four to probably no more

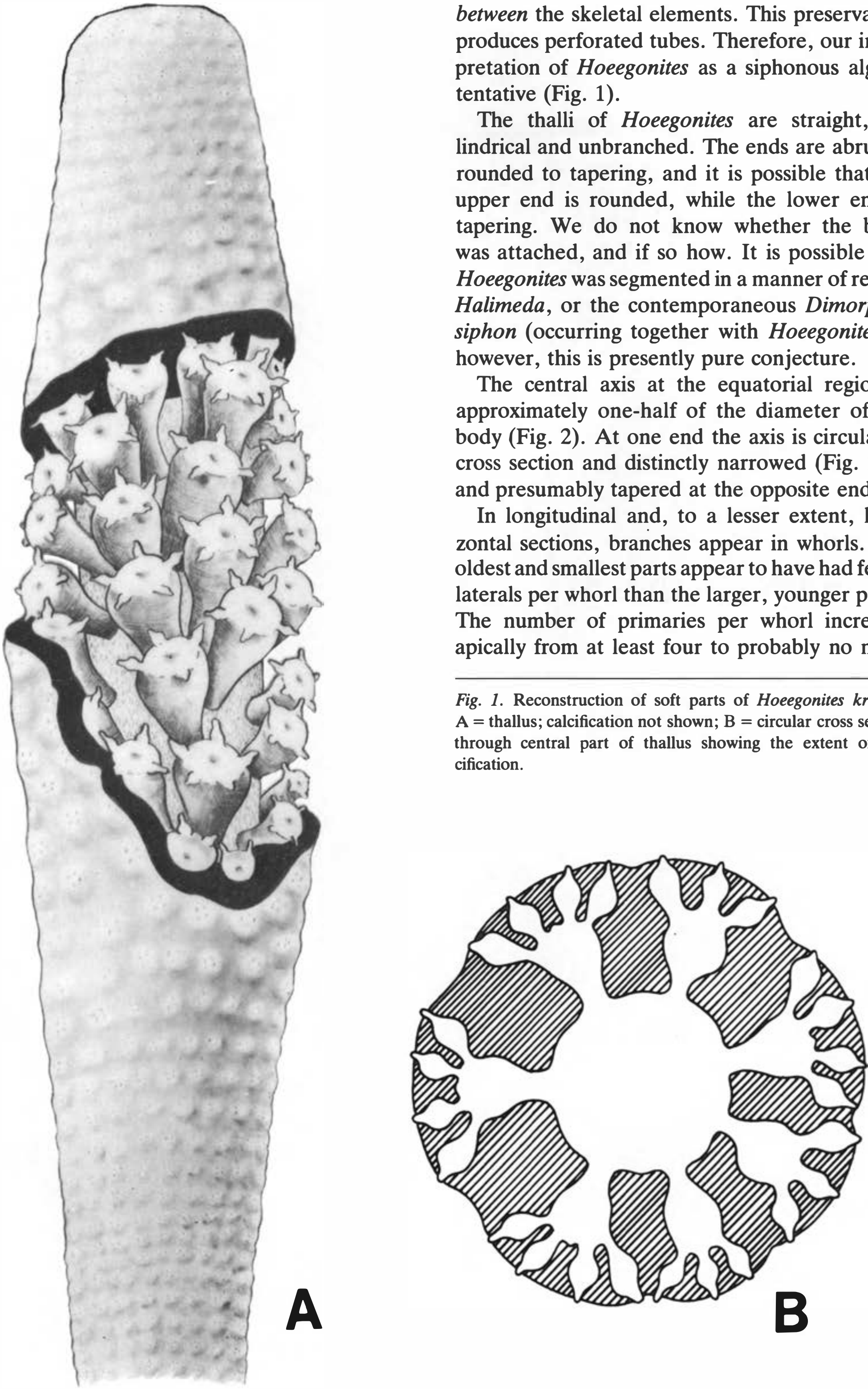
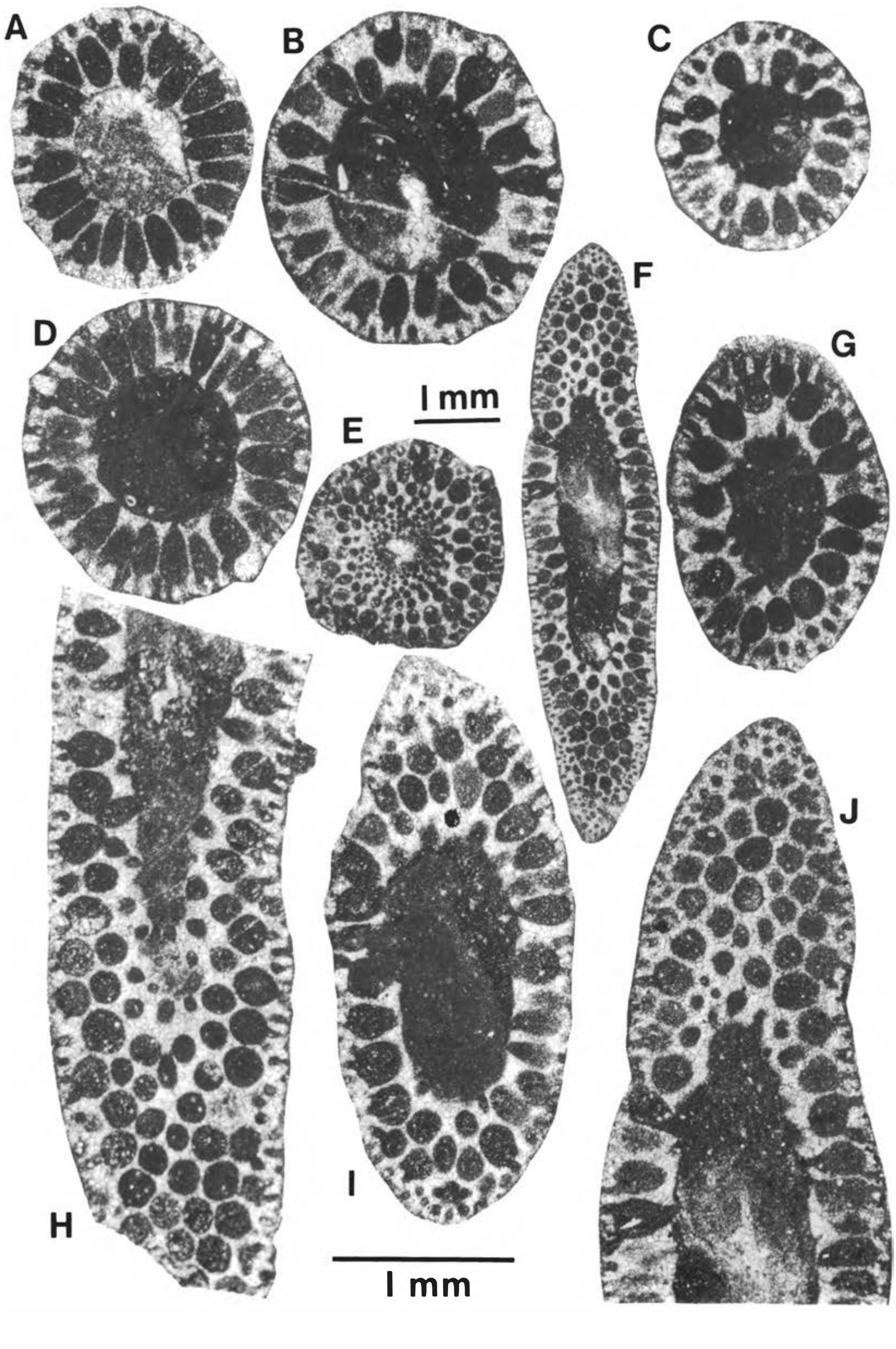


Fig. 1. Reconstruction of soft parts of *Hoeegonites kringla*. A = thallus; calcification not shown; B = circular cross section through central part of thallus showing the extent of calcification.


A
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than twelve; we say 'at least' and 'probably' because specimens with both ends preserved have not been observed. The number of branches in the reconstruction (Fig. 1) *appears* to be different from the number of branches in Fig. 2. However, all thin sections are cut through branches belonging to more than one whorl, and thus Fig. 2 appears to have more branches than the reconstruction in Fig. 1. We assume that the nuclear area must have had four primaries. As the thickness of thallus increases, the number of laterals per whorl and, to a lesser degree, the size of individual laterals also increases. We have no exact information on the apical pole, but it appears that there was no apical lacuna. No septa are observed.

Primaries branch once. However, the number of secondaries is at least four, and five to possibly eight are occasionally present. The shapes of primaries and secondaries are approximately the same; that is, they are very robust, thick and ovate. The length of secondaries is generally less than one-half of that of the primaries. All branches within a single whorl are of the same size. Secondaries generally seem to continue in the same direction as the primaries and are thus on the same plane as the primaries.

No lids or cribellae of any nature are observed, nor is there any evidence of polygonal facets on the surface.

Calcification was distinctly in the form of a solid envelope around the thallus. The skeleton appears to have been aragonitic, as it consists of the mosaic of calcite crystals common in originally aragonitic skeletons. As the result of the heavy calcification the exterior of the body must have been smooth, with possibly small openings in the cortex representing the apices of the secondaries.

Biology of Hoeegonites: Before assigning problematic fossils to any algal group, two fundamental questions must be answered. First, where was the photosynthesis conducted, and second, where were the reproductive organs? Ideally, we would wish to know the actual position of photosynthetic and sexual organs, but in practice we would be satisfied with a model that could suggest their loci and that could at the same time prohibit their occurrence on other areas of the body. And here we have our great difficulty: in *Hoeegonites* (as in most other fossil 'algae') we cannot locate such centers, and we can only speculate on their possible sites.

There are two ways in which *Hoeegonites* could have assimilated, one through a photosynthetic hair, the other through pigments (plastids) within the body of the alga. The photosynthetic hair could have been terminal on the thallus, either in the form of a brush-like tuft or as a loose set of hair; or the hair could have been terminal at the ends of each or some of the second degree branches. The hair at the ends of the body, if present, may or may not have been more permanent than those at the ends of laterals, which may or may not have been deciduous. Thus, if the photosynthetic hair were indeed present, the hair could have been either at the ends of secondaries, or terminal and apical on the thallus. Their presence at the ends of the secondaries could explain the frequent lack of calcification of the apices of secondaries. Their presence at the end of the body, on the other hand, could explain the shape of the apical region.

Sex organs are equally difficult to place. If our fossils represent the fertile stage, then the large extent of calcification excludes all areas except the interiors of the central axis and the branches. If the gametangia (or other sexual organs) were within branches, then branches were fertile; or had both fertile and assimilative functions, with the primaries being fertile and the secondaries photosynthetic. Possibly the fertile laterals had an entirely different morphology and were produced at a different time in the development of the individual; or, if the gametangia were in the central axis, all laterals were sterile. We have no preference for any of these hypotheses.

There are more questions concerning the biology of *Hoeegonites* for which we have no answers: Why was the whole body so heavily calcified? How were gametangia discharged? Was the heavily calcified calcareous envelope ruptured? Did the whole body disintegrate? Obviously our knowledge of the paleobiology, and hence of the nature and the systematic posi-

Fig. 2. Photomicrographs of sections of *Hoeegonites kringla*. Shore section, Bergevika N., Helgøya, Mjøsa, Norway. Collected by N. Spjeldnaes in 1962. No. PMO 113184 in the collections of the Paleontological Museum of the University of Oslo. A–E, G = cross sections at right angle to the main axis; F, H–J = cross sections along the main axis. E = section through the rounded/tapering end of thallus. Note that the small scale applies to Fig. F only. The larger scale at the bottom applies to all other figures.

tion of *Hoeegonites*, will remain a highly speculative matter until the answers to these questions are forthcoming.

Comparison with living siphonous chlorophytes: All Paleozoic so-called dasycladaceans and codiaceans, or perhaps even all Lower Paleozoic chlorophytes, have certain features in common that set them apart from most other groups of fossils. These are the presence of the central cavity (interpreted as a central axis) from which canals (interpreted as branches) radiate generally in a regular manner, and which are embedded in the heavy calcification (interpreted as cortex-forming). Thus a fossil is morphologically a tube with a porous wall. These characters unite these Lower Palezoic 'chlorophytes' into an apparently coherent taxon.

The living siphonous chlorophytes, on the other hand, have a relatively bushy thallus structured as a siphon and bearing branches in single or multiple whorls; or the branches are irregularly placed and the protoplasm is generally continuous, without septa or partitions.

Our tubular fossils fit well into some but not all criteria which define the living siphonous algae. As already stated, however, these characters are not the sole properties of siphonous chlorophytes but are shared with other groups of organisms. The presence or absence of septa becomes important, but since septa are seldom calcified, they are rarely observed in fossils. Consequently, *Hoeegonites* cannot be considered a member of Dasycladales or of Siphonales with any degree of certainty. However, if our interpretations of *Hoeegonites* as a calcareous cortex surrounding the primary and secondary laterals will prove correct (and by analogy the central canal as a central axis, and pores as laterals), and if we assume that septa were absent, then in effect we have in *Hoeegonites* an almost perfect primitive representative of siphonous chlorophytes. The size of the thallus of *Hoeegonites* and the sizes and ratios of branches and the central axis are consistent with the simplified morphology of living Siphonales and Dasycladales.

Thus the assignment of *Hoeegonites* to the siphonous complex of chlorophytes should be considered possible. It must be treated, however, with caution until more information on the apical and adapical regions of the thallus is available and after a reasonable level of confidence of their biology (particularly, the presence or absence of septa and/or locations of photosynthetic and sexual activities) is reached.

Comparison with cyclocrinitids: The best known among all the Ordovician and Silurian 'algae' are the cyclocrinitids. They consist of at least seven genera assigned to three families, and since the 1896 publication of Stolley they are considered to belong in Dasycladales. Recently, however, arguments have suggested that they represent a distinct extinct group of algae of an unknown division.

Hoeegonites differs from cyclocrinitids in the shape of the thallus, the anatomy of the branches, and in the calcification.

The cyclocrinitid thallus is always spherical, but *Hoeegonites* is always elongated and tubular. This difference may not be significant, should *Hoeegonites* prove to have an apically closed body. If *Hoeegonites* had an upper and/or lower opening, then its body plan would drastically differ from most cyclocrinitid taxa, in which the apical area is entirely surrounded by fused lateral heads. (Only one cyclocrinitid, the *Apidium*, may have had an apical lacuna.)

Branches in almost all cyclocrinitids consist of distinct shafts and globellae, and the globellae terminate with cribella. The globella, and particularly the porous, sieve-like cribellum, is so unique to cyclocrinitids that it sets them apart from all other known fossils (or living forms) and makes the relationship of *Hoeegonites* (with its globose primary and secondary laterals) to cyclocrinitids, at best, remote.

In cyclocrinitids the walls of globellae are calcified, while in *Hoeegonites* the calcification fills in the spaces between the branches. This difference in the nature, extent and thickness of calcification is fundamental. Among cyclocrinitids *Coelosphaeridium* is an exception. *Coelosphaeridium*'s laterals are generally without shafts, globellae and cribella, and its calcification is similar to that of *Hoeegonites*. Calcification of *Coelosphaeridium* is, however, calcitic, while *Hoeegonites* and other cyclocrinitids are aragonitic. In any case, *Coelosphaeridium* appears very different from all other known cyclocrinitids, and its position among cyclocrinitids is questionable.

Type locality: Along the northeastern shores of Lake Mjøsa, and along the strike of the northern limb of syncline in the lowest part of road at

Bergevika on Helgøya Island on Lake Mjøsa, Norway (Fig. 3).

Stratigraphy: *Hoeegonites* is found in the lowest part of the Furuberg Formation (Fig. 4). This part of the formation can be correlated with the base of the Caradocian and with the Estonian Idavere stage. In the type locality, and at Furuberget, the range of *Hoeegonites* just overlaps that of *Coelosphaeridium sphaericum* (zone of *C. sphaericum*). In the other localities it follows immediately over this zone.

The localities and grid references in which *Hoeegonites* has been definitively recorded are:

(1) type locality 095 362 (Bergevika, Helgøya, Hamar Nes District);
(2) Furuberget 094 444 (north side, Coelosphaeridium beds, and slightly higher), Hamar Nes District;
(3) southwest of Gjøvik 911 390 (old quarry, on side road to Vestre Totenvei, about 1.8 km southwest of Gjøvik) Toten District, with *Coelosphaeridium* and *Cyclocrinus porosus*;
(4) road section in road 4, at Eina 879 225, Toten District (together with *Cyclocrinus porosus*/ *C. spaskii* and *Mastopora* – highest recorded level. Also occurs with *Coelosphaeridium* lower in the same section). Toten District; and
(5) gravel pit at Sætra Farm, 864 185, south of Hågår railway station at Einavann, Toten District; probably same level as in (4).

Hoeegonites is very common and widespread in all these localities. In decalcified shales and 'rottenstones' it has possibly been overlooked, or regarded as crinoid stems, or other nondescript cylindrical fossils. It can, however, be easily identified by its characteristic pitting corresponding to the secondaries of branches.

Environmental interpretation: *Hoeegonites* occurs in dense, thin (3–8 cm) layers of limestone which alternate with equally thin layers of siltstone and relatively thick shaly units. Most of the associated bryozoans, brachiopods, trilobites and *Vermiporella, Dasyporella, Dimorphosiphon* and *Coelosphaeridium* appear more or less disarticulated. However, the presence of long unbroken fragments, and lack of micritization and transport wear suggests that *Hoeegonites* was not transported far.

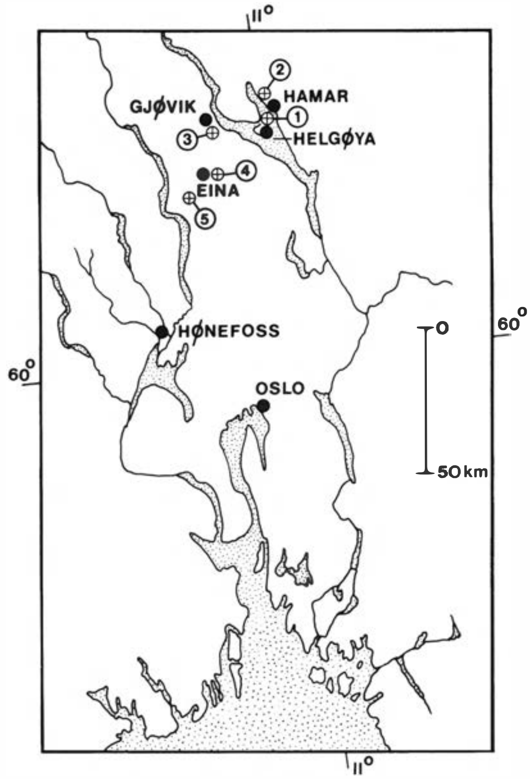

Fig. 3. Map of Oslo Region showing the distribution of *Hoeegonites kringla*. 1 = Helgøya (type locality), 2 = Furuberget, 3 = south of Gjøvik, 4 = Eina, 5 = Sætra, south of Hågår. The localities are marked with numbered circles with a cross. Black dots indicate geographical references introduced for orientation.

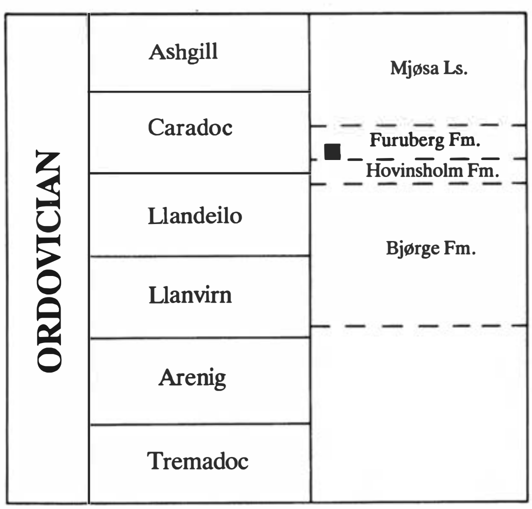

Fig. 4. Stratigraphic chart showing the distribution of *Hoeegonites kringla*.

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