

PALAEOECOLOGY OF SILURIAN CYCLOCRINITID ALGAE

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ABSTRACT. Cyclocrinitids are intriguing macrofossils, commonly considered calcareous green algae, which are locally abundant in certain Ordovician and Silurian deposits. Silurian cyclocrinitids were ecologically and morphologically similar to dasycladacean algae. Cyclocrinitids and dasyclads commonly coexisted, and showed similar patterns of radiation and decline in response to early Palaeozoic environmental changes. Locally, Silurian cyclocrinitids showed considerable variation in adult thallus size; populations in certain environments had significantly smaller thalli than neighbouring populations. This variation was probably due to differences in light intensity, which is an important control on the growth of Recent algae. Cyclocrinitids should, therefore, be useful locally as relative depth indicators: populations with small thalli should indicate deeper, darker waters. In all cases the relative depths indicated by cyclocrinitid size variation are the same as those indicated by the invertebrate communities. This supports the hypothesis that Lower Silurian invertebrates were largely zoned by factors related to water depth. Communities containing cyclocrinitids probably existed at depths of less than 100 m.

THE cyclocrinitids are a small group of problematical organisms which lived in shallow-marine environments from mid-Ordovician to early Silurian times. Although generally rare as fossils, they may be locally common in association with more familiar Palaeozoic forms such as brachiopods and corals. In a few places they reach such high densities that they outnumber all other fossils combined. Cyclocrinitids are useful guide fossils for a number of European and North American rock units, and several marker beds have been named for *Cyclocrinites* or a related genus.

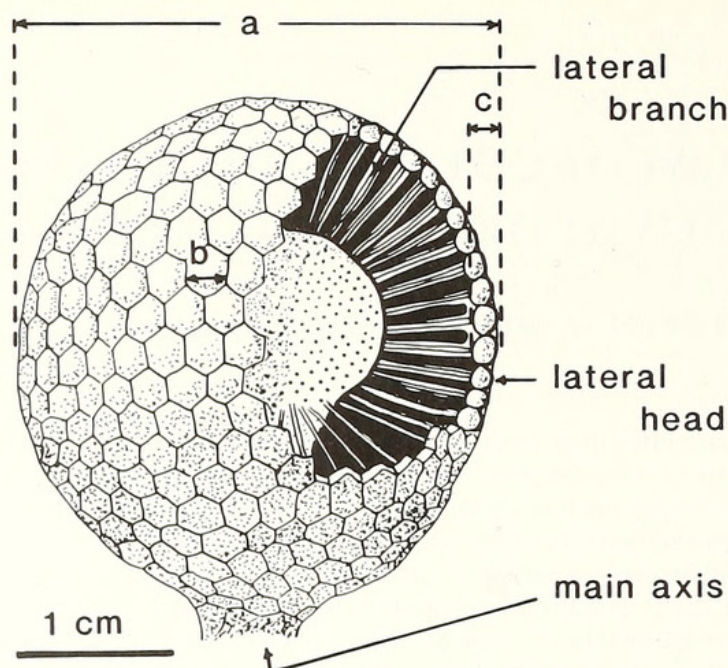
The systematic placement of cyclocrinitids is still debated today, nearly 150 years after they were first described. This study focuses instead on cyclocrinitid ecology, particularly on their responses to environmental change. Their distribution was affected by global environmental events, and they were also sensitive to local variations. This makes them useful as palaeoenvironmental indicators; specifically, they can be used to test the proposed palaeoenvironmental significance of the associated Silurian invertebrate communities.

MORPHOLOGY

Cyclocrinitids were essentially hollow organisms (text-fig. 1). They were attached to the substrate by a central axis, which supported lateral branches that radiated outwards in all directions. The branches expanded at their distal tips to form thick lateral heads, which were hexagonal in outline and packed tightly together in a honeycomb-like fashion. Thus an ovoid or spherical thallus was formed which completely enclosed the main axis and the lateral branches. Calcium carbonate encrusted various parts of the thallus.

All Silurian cyclocrinitids had generally spherical thalli which were calcified about the interior surface of the lateral heads. Consequently, only the lateral heads are usually preserved, but a few specimens with internal structures are known (text-fig. 2A-E; see also Elliott 1972; Nitecki and Johnson 1978). Silurian cyclocrinitids may be preserved in their original spherical shape, usually as internal moulds (text-fig. 2F-L), or they may be flattened to varying degrees after burial.

The size of intact spherical thalli can be measured in three different ways. The most direct method is to measure the thallus diameter (text-fig. 1a). Furthermore, individual lateral heads increase in size along with the total diameter, so that lateral head width (text-fig. 1b) or thickness (text-fig. 1c) can



TEXT-FIG. 1. Reconstructed morphology of *Cyclocrinites dactioloides*. Dimensions: a = thallus diameter; b = lateral head width; c = lateral head thickness. Modified after Nitecki (1972, fig. 12).

also be used as size indicators. It is usually impossible to reconstruct the original diameters of flattened thalli, but lateral head width can be used as a relative size indicator instead.

AFFINITIES

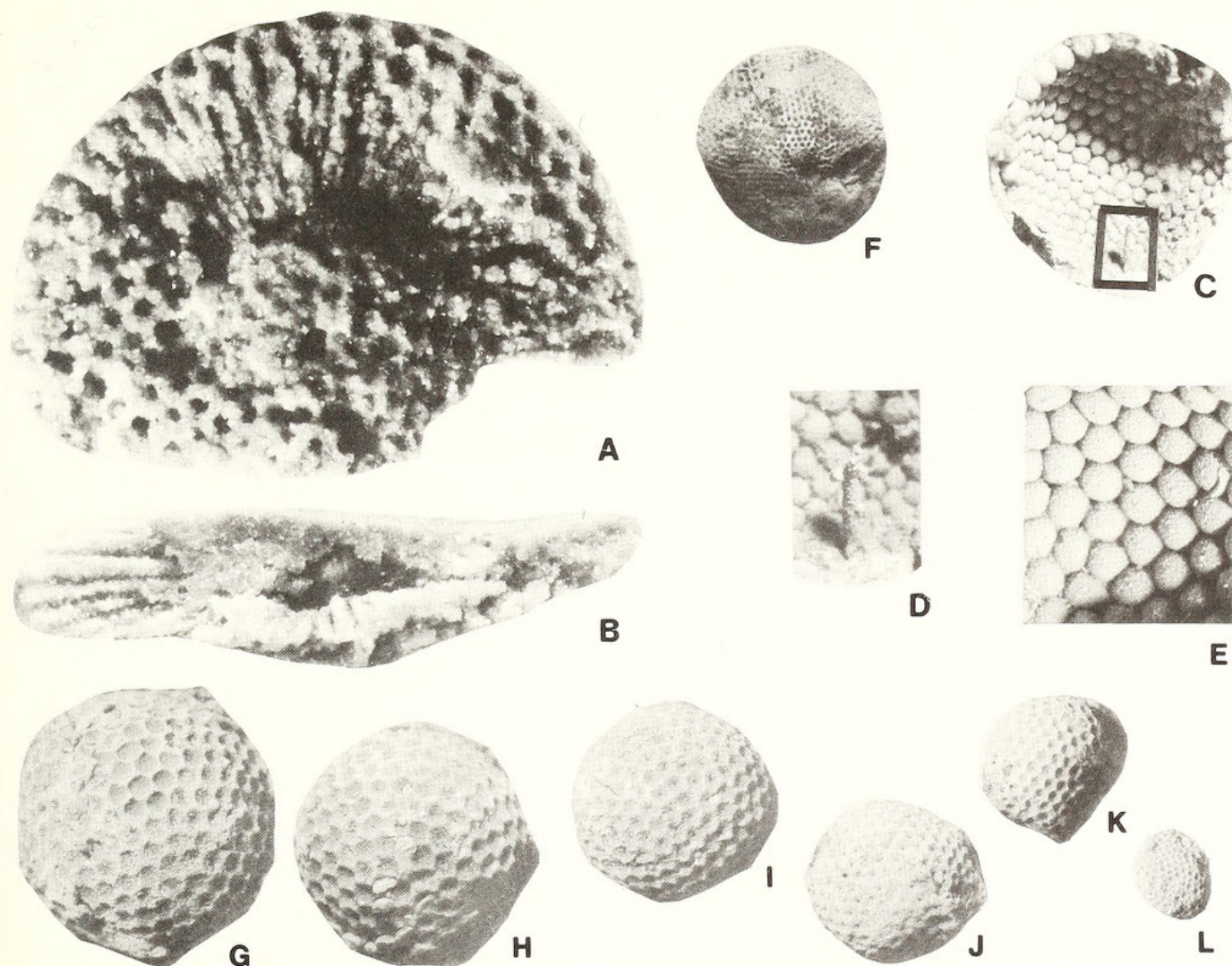
Cyclocrinitids were first described by nineteenth-century invertebrate palaeontologists, who variously considered them foraminiferans, sponges, corals, bryozoans, gastropod eggs, cystoids, or tunicates. Eventually it became clear that they actually resembled calcareous green algae, specifically dasyclads such as *Bornetella* and *Neomeris* (Nitecki 1970; Nitecki and Johnson 1978).

The Family Dasycladaceae is a distinctive clade of the Division Chlorophyta (green algae). Dasyclads are characterized by a central stem with primary branches radiating outwards in regular whorls (J. H. Johnson 1961a). In some forms, the branches dilate at the tips to form hexagonal heads, which are closely packed together to form a faceted outer cortex. Many Recent forms are encrusted by calcium carbonate (as aragonite). Cyclocrinitids shared this general morphology, and Pia (1927) placed them within the Dasycladaceae as the Tribe Cyclocriniteae (= Cyclocrineae). This view has since gained wide acceptance (Osgood and Fischer 1960; Riding 1977).

More recently, Nitecki (1970, 1972, 1976) has allied cyclocrinitids with the even more problematical receptaculitids. It is now thought that receptaculitids are calcareous algae of uncertain position (Rietschel 1969; Rietschel and Nitecki 1984). If cyclocrinitids are truly related to this group, then they too should be considered problematic calcareous algae (Fischer and Nitecki 1982). However, other receptaculitid workers believe that the two groups are unrelated (Campbell *et al.* 1974; Rietschel 1969, 1977). Recent studies of dasyclad evolution continue to place cyclocrinitids within the Dasycladaceae (Elliott 1972; Herak *et al.* 1977).

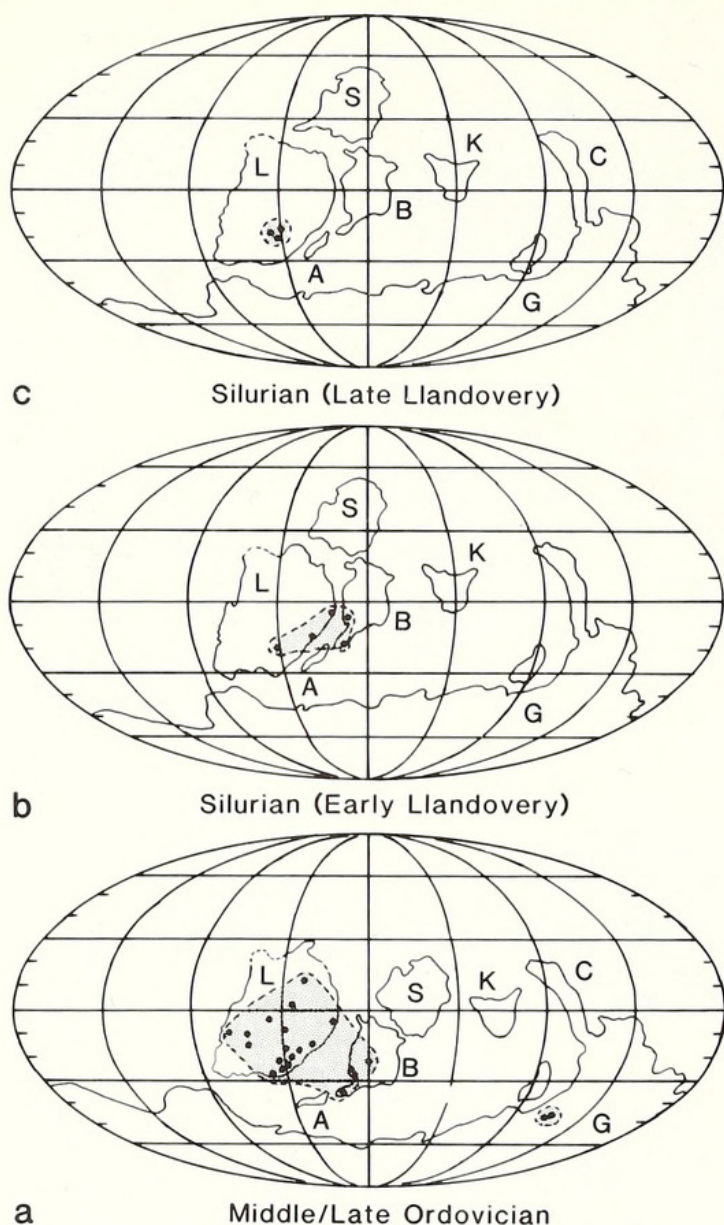
STRATIGRAPHIC RANGE

The earliest known cyclocrinitids are of middle Ordovician age. They apparently expanded rapidly, since middle and late Ordovician cyclocrinitids are widely distributed in North America,



TEXT-FIG. 2. Representative cyclocrinitid algae from the Lower Silurian of Iowa and Norway. A, B, *Cyclocrinites dactiolooides* Owen. Portion of a single specimen from near the top of the Farmers Creek Member of the Hopkinton Dolomite (loc. 79), FMNH UC 59064. See also Nitecki and Johnson 1978. A, apical view showing radial arrangement of lateral branches, $\times 3.25$. B, lateral view showing lateral branches, $\times 3.25$. C-E, *C. dactiolooides* Owen. Hollow cast of a single specimen from near the top of the Farmers Creek Member of the Hopkinton Dolomite (loc. 79), FMNH UC 59430. C, interior view of thallus, $\times 1$. D, enlarged view of main axis remnant (box in C), $\times 2$. E, enlarged view of lateral heads, showing the distal tips of the lateral branches (the rest of the branches are not preserved), $\times 2$. F, *C. favus* Salter. Internal mould of immature thallus (= *Mastopora* sp. of Kiaer 1908) from the upper part of the Leangen Member of the Solvik Formation in Asker, Norway, FMNH PP 34246, $\times 1$. G-I, *C. dactiolooides* Owen. Three thalli from the upper part of the Farmers Creek Member of the Hopkinton Dolomite (loc. 79), FMNH UC 59442, 59443, and 59458 respectively, $\times 1$. All belong to a pentamerid community dominated by *Harpidium maquoketa*. J-L, *C. dactiolooides* Owen. Three thalli from the lower part of the Farmers Creek Member of the Hopkinton Dolomite, FMNH UC 59237, 59293 (loc. 28), and 62733 (loc. 49) respectively, $\times 1$. All belong to a stricklandiid community dominated by *Stricklandia laevis* (= *S. lens ultima*).

northern Europe, and even the central Himalayas (text-fig. 3a). Three genera and at least eight species are currently recognized (J. H. Johnson 1961b; Nitecki 1970 and references therein). Present evidence suggests that the global range of cyclocrinitids began to shrink during the late Ordovician. By early Llandovery time, only two species, *Cyclocrinites favus* and *C. gregarius*, remained, and they had a much more restricted geographic distribution (text-fig. 3b). They were



TEXT-FIG. 3. Palaeogeographic distribution of cyclocrinids. Solid circles = fossil localities, dotted line = inferred range. A = Avalonia, B = Baltica, C = China, G = Gondwana, K = Kazakhstania, L = Laurentia, S = Siberia. *a*, Middle and Late Ordovician. Genera present include *Cyclocrinites* (= *Mastopora*, *Nidulites*, *Pasceolus*), *Coelosphaeridium*, and *Apidium*. North American localities from Nitecki (1970); European localities from Johnson (1961*b*) and Høeg (1961); Asian localities from Reed (1912). Ashgill base map from Scotese (1984, fig. 3). *b*, Early Llandovery (Rhuddanian-lower Aeronian). *Cyclocrinites favus* and *C. gregarius* are the only species present; they may be synonymous. See text-fig. 5 for locality references. Ludlow base map from Scotese (1984, fig. 4). *c*, Late Llandovery (upper Aeronian-Telychian). *C. dactiolooides* is the only species present. No later cyclocrinids are known. See text-fig. 5 for locality references. Ludlow base map from Scotese (1984, fig. 4).

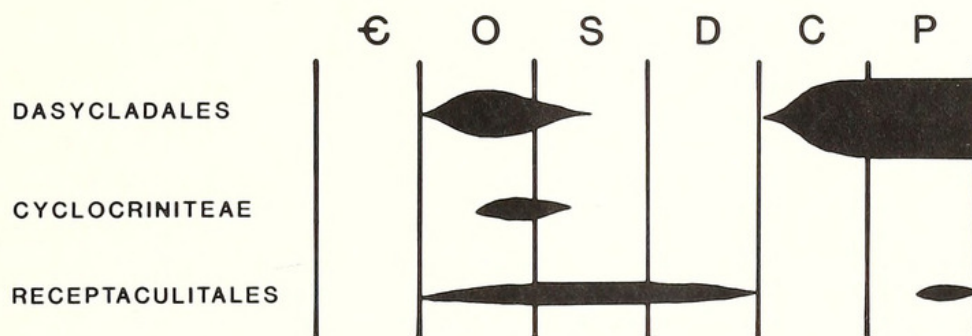
succeeded in the late Llandovery by *C. dactiolooides*, the last known cyclocrinid, which is found only in the American Midwest (text-fig. 3*c*). The group was apparently extinct by the start of Wenlock time.

Benthic calcareous algae generally reached peak diversities in the early to mid-Ordovician and subsequently declined through the late Ordovician and early Silurian (Riding 1984). This may have been due to glacio-eustatic sea-level changes or climatic deterioration. At any rate, both cyclocrinids and dasyclads conform closely to this general pattern (text-fig. 4). The appearance of cyclocrinids in the mid-Ordovician coincided with a major dasyclad radiation (Chuvashov and Riding 1984, text-fig. 7). These early dasyclads (Chuvashov and Riding's Assemblage I) subsequently declined, and they disappeared from the fossil record at about the same time as the cyclocrinids. Calcareous dasyclads reappeared in the Carboniferous and rediversified (Chuvashov and Riding's Assemblage II). Some of the late Palaeozoic dasyclads have been placed within the Cyclocriniteae (Pia 1927; Wood 1942), but such an assignment is probably incorrect.

The history of the receptaculitids is quite different. They appeared in the early Ordovician and showed little change in abundance until late Devonian time (Chuvashov and Riding 1984, text-fig. 3).

PALAEOECOLOGY

Cyclocrinittids were associated with typical Palaeozoic marine faunas, both along continental margins and in epicontinental seas. Palaeogeographic reconstructions indicate that most of them lived within 20° north and south of the equator (text-fig. 3); a few exceptions occur as far south as 45°. Palaeozoic reconstructions are still tentative, but the generally equatorial distribution is clear. Cyclocrinittids were encrusted by calcium carbonate, and presumably produced carbonate sediment after death. They were not restricted to carbonate environments, however, and they are abundant in certain siltstones and shales as well as in limestones and dolostones.



TEXT-FIG. 4. Comparative stratigraphic ranges of the Dasycladales, Cyclocriniteae, and Receptaculitales in the Palaeozoic (after Chuvashov and Riding 1984, text-figs. 3 and 7).

The main constraints on the local distribution of cyclocrinittids were probably light intensity and water energy. Cyclocrinittids were probably calcareous algae, and as such they would have required at least a certain minimum photon flux density for net photosynthesis. However, the intensity of submarine daylight is attenuated rapidly in even the clearest oceanic water; the attenuation is still more pronounced if there is any turbidity (Lüning 1981). This factor must have prevented them from occupying waters below a critical depth. Silurian cyclocrinittids were probably quite sensitive to water energy as well. Their thalli were hollow, weakly calcified, and almost certainly rather fragile. They were commonly flattened during burial, and it seems unlikely that they could have withstood persistent turbulence. Furthermore, cyclocrinittids on soft substrates probably attached themselves to small solid objects such as pebbles, coral fragments or shells, much as modern dasyclads do. Any movement or resuspension of the substrate would have been potentially disastrous for the attached thallus. Therefore, Silurian cyclocrinittids probably avoided shallow, unprotected waters. Their fossils occur primarily in quiet-water deposits that formed below normal wave base.

Storm-generated currents occasionally penetrate into deeper, normally quiet waters. The Silurian rocks of Iowa and Norway show the vulnerability of cyclocrinittids to such currents. Some beds contain large aggregations of well-sorted, spherical cyclocrinittid thalli, often packed tightly together in a single layer (Nitecki and Johnson 1978, fig. 4; Mørk and Worsley 1980, fig. 5). These thalli were apparently detached, rolled about, and swept together by currents. However, post-mortem transport of cyclocrinittids was probably uncommon, since their thalli were relatively large and remained intact after death. Most calcareous green algae disintegrate after death, and the resulting fragments may be transported widely (Riding 1975).

Cyclocrinittids were ecologically very similar to modern and ancient dasyclad algae. Dasyclads are also primarily equatorial, although *Dasycladus* and *Acetabularia* occur in the Gulf of Trieste at over 45° N. (Cinelli 1979). Recent dasyclads are usually, but not exclusively, associated with marine carbonate environments; dasyclad floras presently flourish on terrigenous sediments throughout the Mediterranean and along the main islands of Japan (Cinelli 1979; Arasaki and Shihira-Ishikawa 1979). Furthermore, Recent dasyclads also avoid rough water, and are usually found only below

wave base or in protected pools and lagoons (Wray 1977). A detailed study of fossil dasyclads by Elliott (1968) noted that they were extremely rare or absent in reef and shoal environments, but abundant in calm lagoons or coastal bays. Early dasyclads such as *Vermiporella*, *Rhabdoporella*, and *Dasyporella* are commonly associated with cyclocrinids in Ordovician and Silurian limestones (Kiaer 1920; Høeg 1961; J. H. Johnson 1961b; Gauthier-Coulloudon and Mamet 1981).

The receptaculitids were ecologically rather different. They were significant Palaeozoic reef-builders, and some may have been resistant to high water energies (Rietschel 1969; Nitecki 1972). Cyclocrinids and receptaculitids rarely co-occur.

CYCLOCRINITIDS AS DEPTH INDICATORS

Cyclocrinids were morphologically and ecologically very similar to Recent dasyclads, which suggests that they probably occupied similar depths. Great caution must be used in this approach (Riding 1975). It has often been assumed that Recent dasyclads are restricted to shallow water of less than 10–12 m depth (J. H. Johnson 1961a; Konishi and Epis 1962), but in fact many have much greater ranges. In the Mediterranean, *Dasycladus* ranges down to 90 m (Edelstein 1964) and *Acetabularia* occurs at 30–40 m (Funk 1955). In the Caribbean, *Acicularia* has been dredged from 73 m, *Dasycladus* from 55 m, and *Neomeris* from 50 m (Taylor 1960). Divers have found *Acetabularia* and *Neomeris* on fore-reef slopes in Jamaica at depths over 30 m (Goreau and Goreau 1973, figs. 21 and 22). However, all of these forms are most abundant in much shallower water. These records suggest that any palaeocommunity containing cyclocrinids most likely existed at depths no greater than 100 m, and probably less. Other studies of such late Ordovician and early Silurian communities have produced similar figures (Cocks and McKerrow 1984).

An alternative approach is to use cyclocrinids as indicators of relative (not absolute) depth. As noted earlier, light intensity is attenuated rapidly with increasing water depth, and its spectral composition changes as well. The morphologies of photosynthetic organisms often vary in response to the ambient light conditions. Such ecophenotypic variation is particularly well known in colonial reef corals, which normally require photosynthetic algae as symbionts (Graus and Macintyre 1976). In general, most algal growth is reduced or arrested at low photon flux densities, resulting in small, stunted adult plants (review in Norton *et al.* 1981). Recent calcareous green algae, both udoteaceans and dasycladaceans, are no exceptions. Udoteaceans such as *Udotea* and *Halimeda* often show abnormal, reduced growth when cultured under fluorescent lights; such lights are approximately equal in intensity to tropical waters of 40–50 m depth (Colinvaux *et al.* 1965; Hillis-Colinvaux 1980, pp. 164–165). Among dasyclads, only *Acetabularia* has been studied in detail. Its growth and morphogenesis are largely controlled by the intensity and wavelength of the ambient light (review in Puiseux-Dao 1970). Deep-water specimens of *A. acetabulum* from the Mediterranean have whorls of unusually small diameter (Cinelli 1979).

Silurian cyclocrinids are associated with a variety of substrates, sedimentary features, and invertebrate faunas; they apparently ranged throughout many distinct environments. However, neighbouring populations from different environments generally show marked differences in thallus size. The close resemblances between cyclocrinids and dasyclad algae suggest that this size variation was probably due to differences in ambient light intensity. Therefore, cyclocrinid size variation should be useful locally as a relative depth indicator. Populations with smaller thalli should indicate deeper, darker waters, while those with larger thalli should indicate shallower, brighter waters.

CYCLOCRINITIDS FROM THE LLANDOVERY SERIES

Early attempts to classify cyclocrinids led to a profusion of genera and species, often based on preservational differences. The resulting confusion has been largely dispelled by Nitecki's (1970, 1972) revision of the North American forms. The present study confirms Nitecki's view that there were only two or three species of cyclocrinids present during the Silurian; these are restricted to the Llandovery Series (text-fig. 5).

LOWER SILURIAN										System Series Stage Position	Wales	Scotland	Norway	Anticosti Is.	NW Illinois	N Michigan	E Iowa	NE Illinois	Species
LLANDOVERY										WENLOCK									<i>Cyclocrinites favus</i> (Europe) <i>Cyclocrinites gregarius</i> (N. America) <i>Cyclocrinites dactyloides</i> (N. America)
Rhuddanian					Aeronian					Telychian									
A ₂	A ₃	A ₄	B ₁	B ₂	B ₃	C ₁	C ₂	C ₃	C ₄	C ₅	C ₆								
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TEXT-FIG. 5. The stratigraphic distribution of Silurian *Cyclocrinites*. Hatched bars = common occurrence, dotted bars = rare occurrence. Llandovery Stages after Holland (1985).

Wales: 1 = Gasworks Mudstone, Haverford 'Stage'. Localities: Strahan *et al.* (1914). Correlation: Ziegler *et al.* (1974).

Scotland: 2 = Mulloch Hill Formation. 3 = Glenwells Shale. 4 = Newlands Formation. Localities: Peach and Horne (1899), Cocks and Toghil (1973). Correlation: Ziegler *et al.* (1974).

Norway: 5 = Solvik Formation. 6 = Rytteråker Formation. Localities: Kiaer (1908), Mørk and Worsley (1980), Baarli (pers. comm.). Correlation: Baarli (1985).

Anticosti Island: 7 = Becscie Formation. 8 = Gun River Formation. Localities: Billings (1866), Twenhofel (1928). Correlation: Johnson *et al.* (1981).

North-west Illinois: 9 = Kankakee Formation (= Blanding Formation). 10 = Farmers Creek Member, Hopkinton Dolomite. Localities: Nitecki (1970, 1972). Correlation: M. E. Johnson (1983).

Northern Michigan: 11 = Lower Laminated Beds, Schoolcraft Formation. Locality and Correlation: Johnson and Campbell (1980).

Eastern Iowa: 12 = Farmers Creek Member, Hopkinton Dolomite. Localities and Correlation: M. E. Johnson (1983).

North-east Illinois-South-east Wisconsin: 13 = Waukesha or Racine Formations. Localities: Whitfield (1882), Nitecki (1970). Correlation: Willman (1973), M. E. Johnson (1983).

Two species of Llandovery cyclocrinids are now recognized in North America: *Cyclocrinites gregarius* in the lower Llandovery, and *C. dactiolooides* in the upper Llandovery. The two may also be distinguished by the relative width of the lateral heads; their thalli reached similar dimensions, but the lateral heads of *C. gregarius* are considerably smaller. The North American species *C. gregarius* may be a junior synonym of the contemporary European species *C. favus* (Kiaer 1908; Nitecki 1970, p. 100). The thalli of *C. favus* also had relatively small lateral heads (compare text-fig. 2f and 2i).

All Llandovery cyclocrinids are associated with diverse invertebrate faunas, usually dominated by brachiopods. Several distinct Llandovery communities have been recognized, and their palaeo-environmental significance has been studied in detail (Ziegler 1965; Ziegler *et al.* 1968; Cocks and McKerrow 1984). These communities were zoned in bands parallel to the shoreline, and so it is thought that their distribution was controlled by factors related to water depth. The original model (for Wales) placed the *Lingula* community in the shallowest water, followed by the *Eocoelia*, *Pentamerus*, *Stricklandia*, and *Clorinda* communities with increasing depth and distance from shore. In other areas, different communities may substitute for these, particularly in shallow water (Berry and Boucot 1970; Ziegler *et al.* 1974; M. E. Johnson 1977).

Llandovery invertebrate communities are commonly used to indicate relative water depths. Cyclocrinid size variation provides an independent measure of relative depth and can be used to test the value of this approach. Llandovery cyclocrinids are common in Iowa, Anticosti Island,

TABLE 1. Size variation in Llandovery cyclocrinid populations

a, *C. dactiolooides*. Farmers Creek Member, Hopkinton Dolomite, eastern Iowa

Index	Lower (n)	Upper (n)	Change
Thallus diameter (cm)	1.94(24)	2.78(36)	+43.3%*
Lateral head width (cm)	0.18(24)	0.26(36)	+44.4%*
Lateral head thickness (cm)	0.14(11)	0.24(15)	+71.4%*

b, *C. gregarius* (syntypes and hypotype). Becscie and Gun River Formations, Anticosti Island. Data from Bolton (1966), Nitecki (1970, table 4)

Index	Becscie (n)	Gun River (n)	Change
Thallus diameter (cm)	1.90(21)	2.86(8)	+50.5%*

c, *C. favus*. Leangen Member, Solvik Formation, Bjørkøya

Index	Lower (n)	Upper (n)	Change
Lateral head width (cm)	0.19(61)	0.21(402)	+10.5%*

d, *C. favus*. Leangen Member, Solvik Formation, Malmøya

Index	Shales (n)	Siltstones (n)	Change
Lateral head width (cm)	0.22(67)	0.24(39)	+9.1%†

Means compared with one-tailed *t*-test.

* Increase significant at 99% confidence level.

† Increase significant at 95% confidence level.

Great Britain, and Norway (text-fig. 5); the following sections examine the evidence in each of these areas.

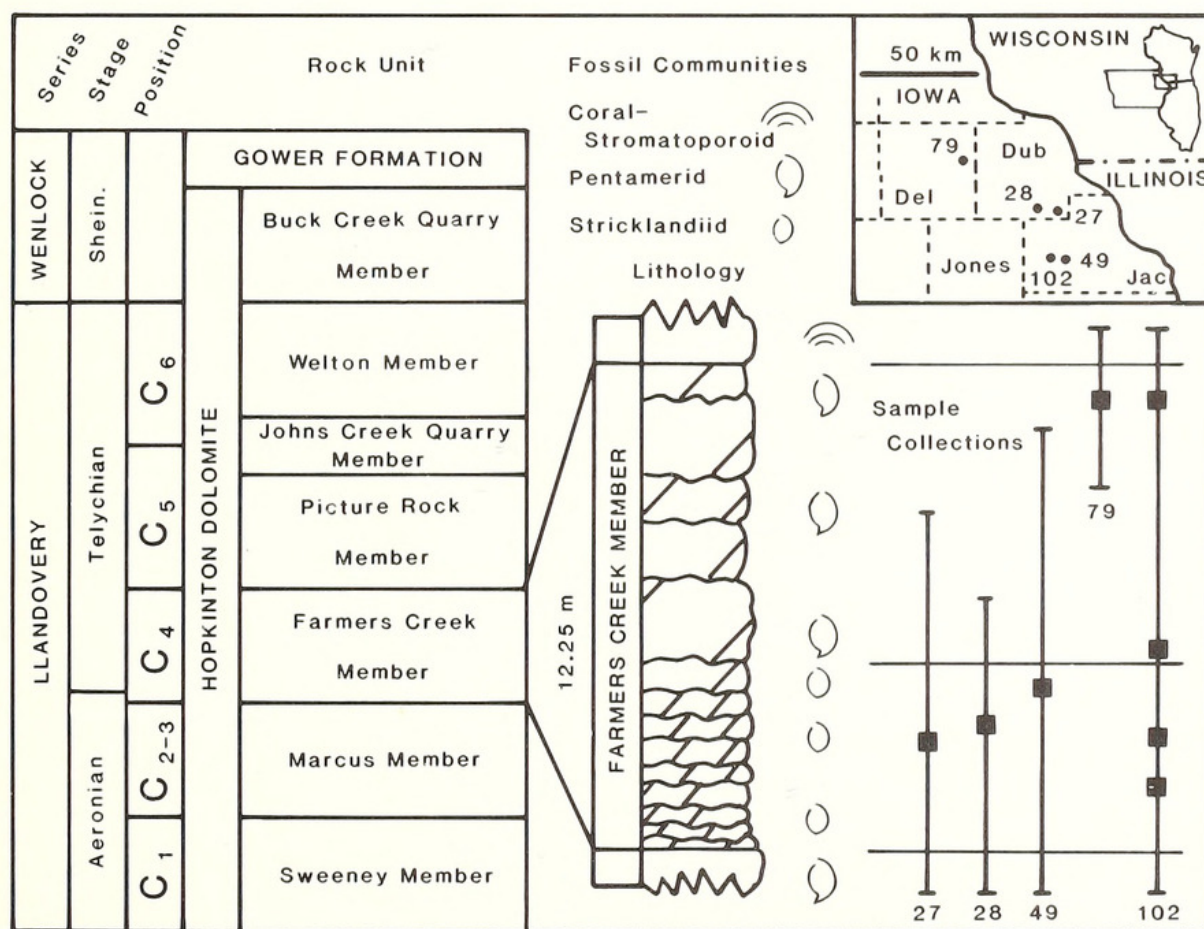
Data base. The Iowan data came from sixty exceptionally well-preserved thalli of *Cyclocrinites dactiolooides* which were collected from the Farmers Creek Member of the Hopkinton Dolomite in eastern Iowa (text-fig. 6). They are deposited at the Field Museum of Natural History in Chicago, Illinois.

The Norwegian data came from field measurements of 463 thalli of *C. favus* in the Leangen Member of the Solvik Formation on Bjørkøya, and from 106 thalli in the Padda Member of the Solvik on Malmøya (text-fig. 8). Thirteen immature *C. favus* thalli (= *Mastopora* sp. of Kiaer 1908) were collected from the upper Leangen Member in Asker, and deposited at the Field Museum.

The data on *C. gregarius* from Anticosti Island and *C. favus* from Great Britain came from previously published species descriptions. All numerical data for this study have been deposited with the British Library, Boston Spa, Wetherby, Yorkshire LS23 7BQ, UK, as a supplementary publication No. SUP 14025 (24 pages). The data are summarized in Table 1.

Iowa. The Farmers Creek Member of the Hopkinton Dolomite crops out in eastern Iowa and northwestern Illinois (text-fig. 6). It contains *C. (= Cerionites) dactiolooides* in such abundance that it was formerly called the 'Cyclocrinites Beds' (M. E. Johnson 1983). The unit contains well-preserved dolomitized fossils, but sedimentary structures are generally absent.

The lower third of the Farmers Creek is dominated by the deep-water brachiopod *Stricklandia laevis* (= *S. lens ultima*). Fragile fossils such as retreporiform bryozoans and crinoid calyxes are often preserved intact, suggesting low-energy, deep-water conditions. The upper Farmers Creek, however, contains a very different fossil assemblage, dominated by the shallower water brachiopod *Harpidium maquoketa*, a close relative of *Pentamerus*. There is evidence of occasional current activity, probably storm-generated: the brachiopods are



TEXT-FIG. 6. Stratigraphic and geographic distribution of *Cyclocrinites dactiolooides* populations in eastern Iowa. Llandovery Stages after Holland (1985).

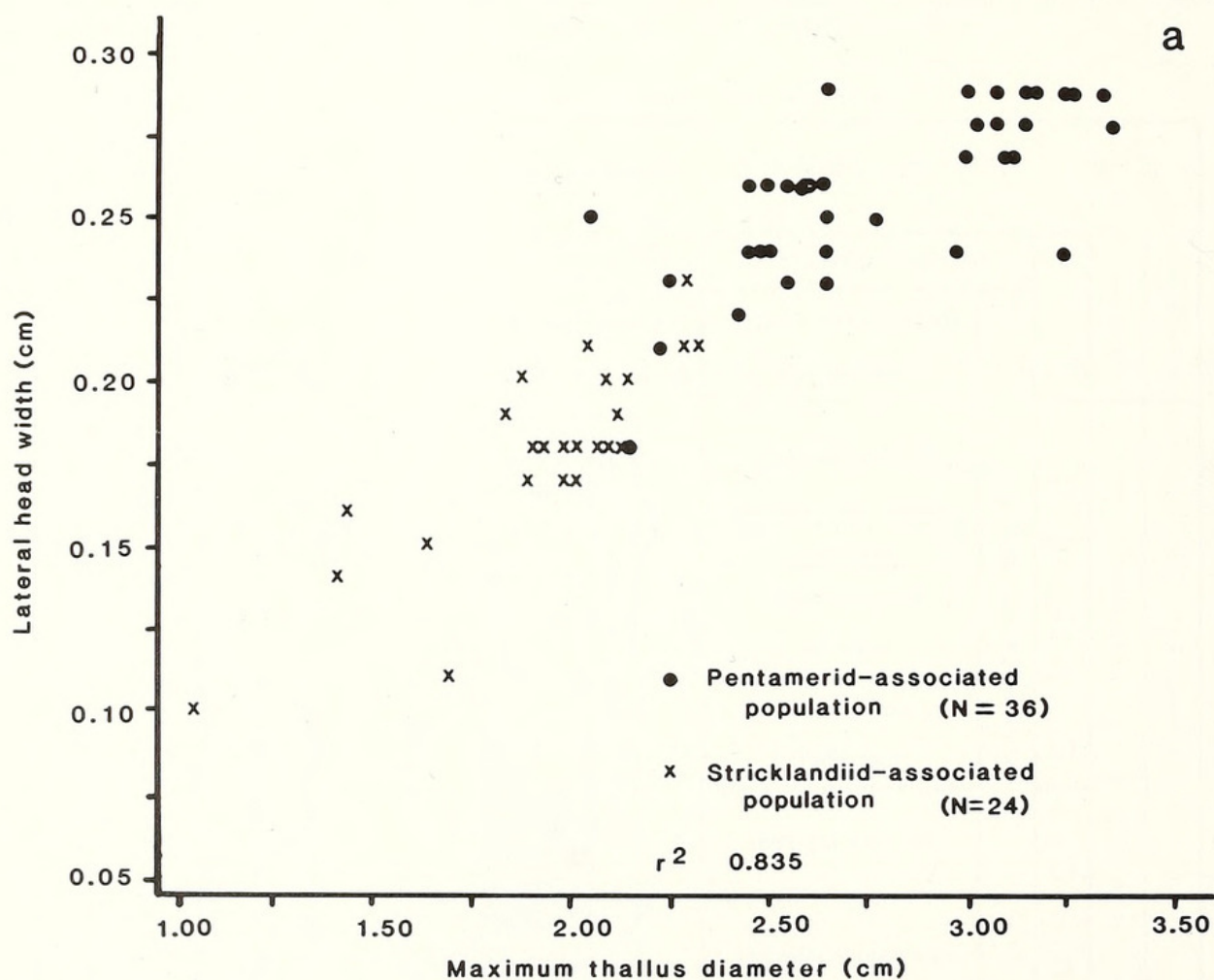
sometimes truncated by erosional surfaces, and the cyclocrinoids may be preserved in large, swept-together assemblages (Nitecki and Johnson 1978; M. E. Johnson 1977, 1980). The faunal evidence indicates that the upper Farmers Creek was deposited in significantly shallower water than the lower.

The cyclocrinoids are generally preserved as internal moulds, and many have some complete lateral heads as well. The specimens from the upper Farmers Creek are much larger than those from the lower, by all size measures (Table 1a). The size ranges of the two populations are generally distinct, with little overlap (text-fig. 7). Some representative thalli from the two populations are illustrated (compare text-fig. 2G-I with 2J-L).

The overlying Picture Rock Member of the Hopkinton Dolomite contains a very shallow coral-stromatoporoid community (thought to be the depth equivalent of the *Eocoelia* community). The tabulate corals and stromatoporoids here are usually flattened or lenticular, presumably in response to persistently high water energies. Until recently we believed that *C. dactioides* was excluded from this community; however, Brian Witzke (pers. comm. 1984) has found three thalli in a drill core through an apparent coral community from the Picture Rock or the top of the Farmers Creek. The largest had an estimated diameter of 4.8–5.2 cm, which is larger than any of the thalli examined in this study or by Nitecki (1970, table 5). The discovery of such an unusually large thallus is consistent with its location in unusually shallow water.

Anticosti Island. Cyclocrinoids are common in the Becscie and Gun River Formations of Anticosti Island, Quebec. These units consist predominantly of unaltered limestones with thin shaly partings, and the fossils and sedimentary structures are generally well preserved.

The Becscie fauna is dominated by the pentamerid *Virgiana*, often in life position. The deeper water brachiopods *Stricklandia* and *Clorinda* occur rarely. More common are corals and stromatoporoids, especially

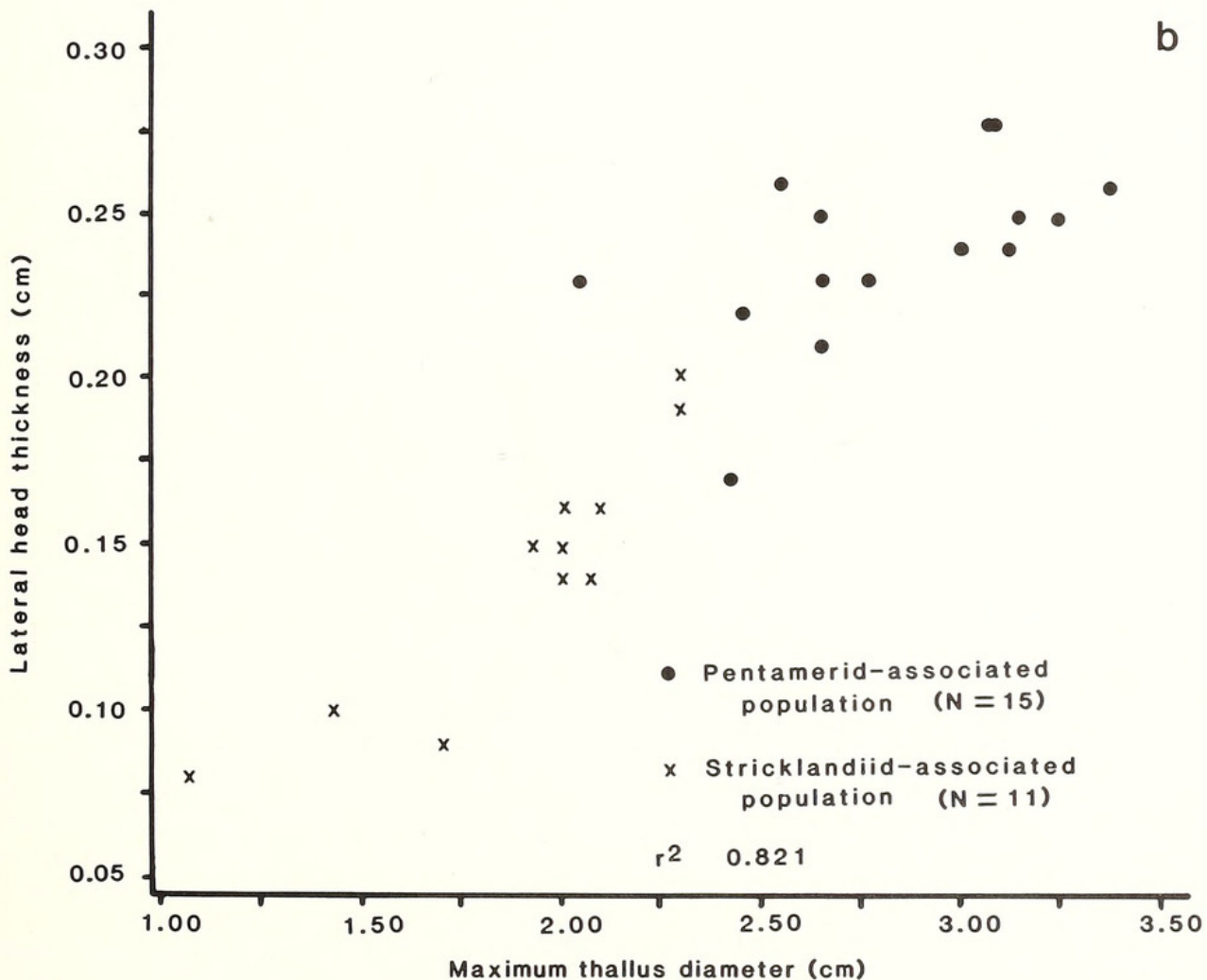


TEXT-FIG. 7a, b. Size variation in *Cyclocrinites dactioides* populations from eastern Iowa. The pentamerid-associated population is from the upper Farmers Creek Member, while the stricklandiid-associated population is from the lower Farmers Creek Member. Text-fig. 7b is on facing page.

at the top of the unit where they may form small bioherms, although brachiopods are still more abundant (Twenhofel 1928; Bolton 1981; Petryk 1981). Ripple marks are common, but larger bedforms are absent. Intraclasts of granule to pebble size are reported as well; these are mostly flat and may be imbricated (Petryk 1981).

Gun River deposition was initiated by a transgression, which Johnson *et al.* (1981) place at approximately an A_3 position. Deep-water conditions apparently continued in eastern Anticosti, but in the west shallowing soon resumed, and in general the Gun River in this area resembles the underlying Becscie. However, differences in the fauna and the sedimentary structures suggest significantly shallower water conditions. Pentamerids are much less conspicuous: *Virgiana* occurs only rarely in the lower Gun River, and is replaced by stunted *Pentamerus oblongus* (variety 'juvenalis'). The deep-water brachiopods *Stricklandia* and *Clorinda* are completely absent, but the generally shallow-water *Brachyprion* is abundant (Twenhofel 1928; Bolton 1972). Corals are also abundant, more so than in the Becscie, and locally they form common bioherms and biostromes (Twenhofel 1928; Petryk 1981). Ripple marking is common, including interference ripple marks. The upper Gun River also contains megaripples with wavelengths of 3.5–6.0 m and amplitudes of 15–20 cm. Channel-fill deposits 1 m wide and 10–15 cm are known as well. Intraclasts are larger than in the Becscie, up to large cobble size (Barnes *et al.* 1981; Petryk 1981).

Anticosti cyclocrinids usually occur as complete, but often deformed, internal moulds. The size variation between the Becscie and Gun River populations is so great that they were long considered separate species. They were first described by Billings (1866) as *Pasceolus gregarius* and *P. intermedius* respectively, but Twenhofel (1928) reassigned them to *Cyclocrinites* (their descriptions are reprinted in Nitecki 1970). The only morphological differences are thallus size and lateral head width; *C. intermedius* is larger in both respects. Nitecki's measurements of the type fossils (1970, table 4) show that the mean thallus diameter of the *C. intermedius* specimens is much greater than that of the *C. gregarius* specimens, and the size ranges do not even



overlap (Table 1b). Lateral head width apparently grew at a relatively slow rate, and their size variation in this regard is not as great.

Nitecki considered the two species synonymous and assigned them both to *C. gregarius*. We agree that it is unreasonable to establish separate species based solely on size difference; the variation is much more probably ecophenotypic.

Great Britain. Llandovery cyclocrinids are known from the Craighead Inlier of the Girvan district, Ayrshire, Scotland, and at Haverfordwest in Pembrokeshire, Wales. These two populations existed at the same time, but they lived in very different environments.

British cyclocrinids were carefully examined by Salter (1851), who described them as *Nidulites favus* (reprinted in Nitecki 1970). They were later redescribed as *Mastopora fava*, and then as *C. favus* (Currie and Edwards 1942; Nitecki 1970, p. 100). Salter's specimens came from 'Mulloch Quarry' (= Mulloch Hill Formation) in Scotland and from 'Haverfordwest' (= Gasworks Mudstone) in Wales. The specimens consist mostly of flattened thalli, but lateral head width can be used as an indicator of relative thallus size. Salter noted that the lateral heads of the Scottish specimens were 'a line wide' ($= \frac{1}{12}$ in or 0.21 cm), while those of the Welsh specimens were 'something less'.

The Mulloch Hill quarries contain well-preserved, diverse fossil communities, with conspicuous *C.* (= *Nidulites*) *favus* (Peach and Horne 1899). The classic quarry faunas, in sandstones with interbedded shales and siltstones, were examined by Cocks and Toghil (1973), who considered them all variants of the shallow-water *Cryptothyrella* community. This is considered a precursor to the *Eocoelia* community (Ziegler *et al.* 1974).

The Haverfordwest material is from the Gasworks Mudstone of the Haverford 'Stage'. In the type section, described in detail by Strahan *et al.* (1914, pp. 90–91), the deep-water brachiopod *Stricklandia* (= *Stricklandinia*) *lens* is clearly dominant. *Cyclocrinites* (= *Nidulites*) *favus* is common in association with *Stricklandia*.

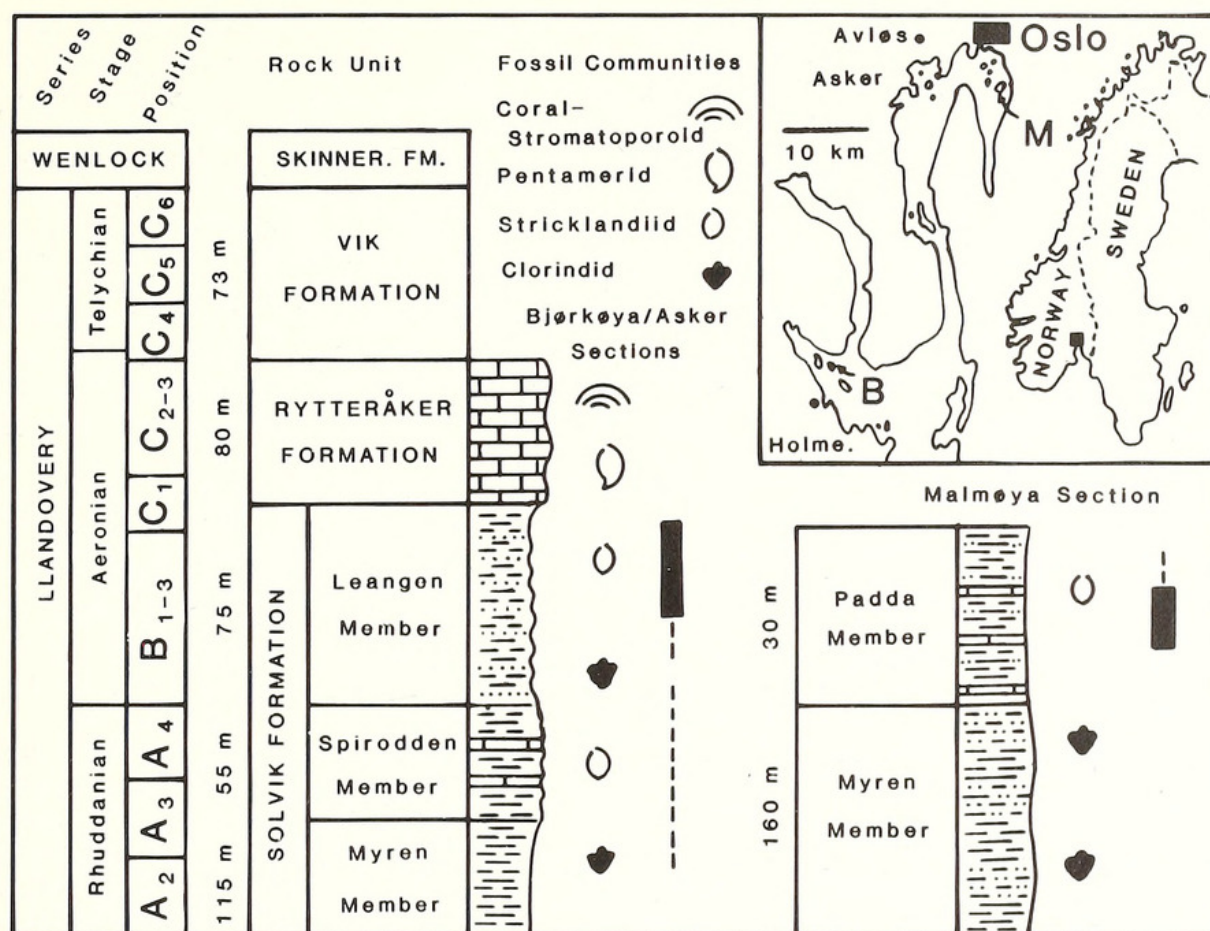
Both the Mulloch Hill and the Gasworks Mudstone indicate an A₃ to A₄ position (Ziegler *et al.* 1974). The faunal evidence suggests that the Gasworks Mudstone represented a deeper water environment, and the cyclocrinids from this unit have smaller lateral heads than those from the shallow-water environments of the Mulloch Hill. It would also be interesting to compare the Mulloch Hill cyclocrinids with those of the overlying Newlands Formation, which contains *C. favus* (= *M. fava*) in a deep-water community with *Clorinda* and *Stricklandia* (Cocks and Toghil 1973). There are presently no data available on the Newlands forms.

Norway. Cyclocrinids are common in the Solvik Formation of Oslofjorden in southeastern Norway (text-fig. 8). The Solvik (= 'Etage' 6 of Kiaer 1908) consists primarily of shale with siltstone and limestone interbeds; the fauna and sedimentary structures suggest generally shallowing conditions throughout the unit (Johnson and Worsley 1982; Baarli 1985). The palaeoshoreline lay to the west and trended south-south-west to north-north-east. In relatively proximal areas (e.g. Asker), cyclocrinids occur throughout most of the Solvik, but in more distal areas (e.g. Malmøya) they are found only near the top. Cyclocrinids are usually preserved as flattened thalli which are conspecific with the British form *Cyclocrinites favus* (= *M. fava* of Kiaer 1908, 1920). As in Britain, lateral head width can be used as a measure of relative thallus size.

Cyclocrinids are most abundant on the island of Bjørkøya, in west-central Oslofjorden north of Holmestrand, where they occur with *Stricklandia* on shale bedding planes. Only the uppermost 24.5 m of the Solvik (the Leangen Member of Baarli, 1985) are exposed; Mørk and Worsley (1980) found that this section represented gradually shallowing environments. The basal beds, representing the deepest conditions, have more siltstone, less shale and limestone, and fewer cyclocrinids than the overlying beds (Mørk and Worsley 1980, fig. 3). The mean lateral head width of *C. favus* thalli from the basal 4 m of section is significantly less than that of thalli from the upper beds (Table 1c). The difference is small (about 10%) but statistically significant due to the large number of samples. The lateral heads of *C. favus* grew slowly, and it is likely that a 10% increase in lateral head width reflects a somewhat larger increase in thallus diameter, probably 15–20%.

The Malmøya section lies south of Oslo in Bunnefjorden. The upper Solvik (Padda Member of Worsley *et al.* 1982) contains common cyclocrinids, both in the predominant shales and in thin siltstone interbeds. An earlier study of Malmøya brachiopods by Worsley (1971) found that those in the shales were generally deposited in place, while those in the siltstone interbeds had been transported down from shallower, more proximal environments. The mean lateral head width of *C. favus* thalli from the shales is significantly less than that of the transported thalli in the siltstones (Table 1d). The difference is about the same as that between the two populations on Bjørkøya.

The size differences among the cyclocrinids of Bjørkøya and Malmøya are relatively small, and this suggests that the depth differences were small as well. The faunal evidence also indicates that the depth changes were



TEXT-FIG. 8. Stratigraphic and geographic distribution of *Cyclocrinites favus* populations in Oslofjorden, Norway. B = Bjerkøya, M = Malmøya. Solid bars = abundant *C. favus*, dotted lines = uncommon *C. favus*. Llandovery Stages after Holland (1985).

relatively minor: all of the sampled cyclocrininitid populations discussed above occur with generally similar *Stricklandia* communities.

Cyclocrininitids are also known from the Asker area where they are preserved in two different ways. Typical flattened *C. favus* thalli occur, but small spherical internal moulds are common as well (text-fig. 2F). Kiaer (1908 p. 327; 1920) referred to these as *M. sp.* but never formally described them. These thalli are far smaller than typical *C. favus* thalli, and they probably represent immature individuals. Similar small spherical thalli occur rarely in the Mulloch Hill Formation of Scotland (Currie and Edwards 1942); these have internal structures which closely resemble those of immature *Bornetella capitata*, a Recent dasyclad (Elliott 1972). Such small thalli were especially vulnerable to currents, and they often occur in large, well-sorted groups. One block from Avløy in Baerum contains some 135 thalli packed tightly together in a single layer (Mørk and Worsley 1980, fig. 5). The moulds consist of mud and bioclastic debris, and their preservation suggests that they were detached, transported along muddy bottoms, and swept together. Such groups are found only in proximal environments, notably Asker but also Bjerkøya.

The Solvik is overlain by the Rytteråker Formation, which is primarily limestone with *Pentamerus*, corals, and stromatoporoids. It was apparently formed in shallower, high-energy water (Johnson and Worsley 1982). Cyclocrininitids are conspicuously absent from this unit, although a few specimens are known from the lower Rytteråker on Bjerkøya and Malmøya (Mørk and Worsley 1980; Baarli, pers. comm.).

CONCLUSIONS

Silurian cyclocrininitids showed considerable intraspecific variation in adult thallus size. This variation was apparently ecophenotypic; populations in certain environments had significantly smaller thalli

than neighbouring populations. Cyclocrinitids are commonly considered calcareous green algae, and they were morphologically and ecologically similar to dasycladaceans. This suggests that the observed size variation was caused by differences in light intensity, since such differences have marked effects on the growth of Recent algae. Cyclocrinitid populations should therefore be useful locally as relative depth indicators: those with small thalli should represent deeper, darker environments, while those with large thalli should indicate shallower, brighter environments.

In all cases the relative depths indicated by cyclocrinitid size variation are the same as those indicated by the invertebrate communities and sedimentary features. In Iowa, Anticosti Island, and Great Britain, large changes in cyclocrinitid thallus size are associated with obvious changes in the composition of the associated invertebrate communities. On Bjørkøya and Malmøya in Norway the size change is much less, and the faunal changes are minor as well. The distribution of Llandovery cyclocrinitid algae reinforces the hypothesis that Llandovery invertebrates were largely zoned by factors related to water depth.

The absolute depths inhabited by these communities are more difficult to define. Boucot (1975 fig. 15) considered the *Stricklandia* community (= Benthic Assemblage 4) to lie below the photic zone, but the abundance of cyclocrinitids in the *Stricklandia* communities of Iowa, Wales, and Norway suggests otherwise. Cyclocrinitids are even known from a *Clorinda-Stricklandia* community in Scotland (Cocks and Toghil 1973, p. 215). By analogy with Recent dasyclads, it is probable that these cyclocrinitids lived at depths of less than 100 m.

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