

COMPLEX NONCALCIFIED MACROALGAE FROM THE SILURIAN OF
CORNWALLIS ISLAND, ARCTIC CANADA

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ABSTRACT—Thin beds of silty limestone within Ludlovian (Ludfordian) strata of the Cape Phillips Formation on Cornwallis Island, Arctic Canada, contain numerous specimens of noncalcified macroalgae in association with dendroid and graptoloid graptolites, brachiopods, and trilobites. The algal material, preserved as carbonaceous compressions, represents three new taxa, each characterized by a central axis surrounded by laterals. Laterals of *Eocladus xiaoi* n. gen. n. sp. are thin and branch to the fifth order whereas those of *Chaetocladus capitatus* n. sp. are undivided and form a distinctive capitulum. Thalli of *Palaeocymopolia nunavutensis* n. gen. n. sp. have a branched, serial-segmented form and a corticated structure. On the basis of thallus architecture, all three taxa are assigned to the extant green algal order Dasycladales. Parallels exist between this macroalgal assemblage and a modern macroalgal association in Florida Bay.

INTRODUCTION

NONCALCIFIED MACROALGAE are, on the whole, rarely represented in the fossil record. That this is the case is, of course, not surprising given that these forms lack mineralized hard parts. Nonetheless, fossil deposits are known in which these key primary producers are both abundant and well preserved. Indeed, in some of these, noncalcified macroalgae are not only abundant, but comprise the primary or even sole constituents. These distinctive Konservat Lagerstätten (sensu Seilacher et al., 1985) are fittingly referred to as algal-Lagerstätten.

Important occurrences of algal-Lagerstätten of early Paleozoic age are known from the Cambrian of China (Yang et al., 2001) and Utah (Conway Morris and Robison, 1988; Brett et al., 2009), the Ordovician of Wisconsin (Whitfield, 1894) and Manitoba (Fry, 1983), and the Silurian of Estonia (Tinn et al., 2009), Ukraine (Ishchenko, 1985), the Czech Republic (Bouček, 1941), Ontario (LoDuca, 1995; von Bitter et al., 2007), and New York (LoDuca, 1995; LoDuca and Brett, 1997). Here, we provide the first report of such an occurrence from the Canadian Arctic, material from which is assigned to three new macroalgal species.

Two major morphological diversification events have been identified in the early history of macroalgae, key details of which have emerged in the last decade through studies of new and previously poorly known algal-Lagerstätten. The first unfolded during the Ediacaran. Forms that originated during this event include thalli with true dichotomous branching, thalli with upright central axes bearing spirally arranged appendages (monopodial architecture), and blade-shaped thalli with rhizoidal holdfasts (Xiao and Dong, 2006). Prior to this event, macroalgal thalli were exclusively of simple morphology, consisting of spherical, ellipsoidal, tomaculate (sausage-shaped), and cylindrical forms, with such forms extending back into the Paleoproterozoic. The "trigger" for the Ediacaran event remains unknown (if indeed there is a single cause), but studies

of form-function relationships for dasycladalean algae suggest that, for the siphonous body plan at least, morphological innovation at this time is best explained as a response to the advent of grazing pressure by mesograzers rather than changes in the physical environment (LoDuca and Behringer, 2009). In the aftermath of this event, morphological diversity and complexity were still rather low relative to modern macroalgae.

The second event, initially recognized by Chuvashov and Riding (1984) based on study of calcareous algae, unfolded during the Ordovician, within the context of the Ordovician radiation (Nitecki et al., 2004). That this signals a true biodiversification event, as opposed to a preservational artifact related to the rise of widespread calcification among algae at this time, is supported by a concomitant rise in thallus diversity and complexity among noncalcified macroalgae (LoDuca et al., 2003) and by a recent molecular study that points to initial divergences of extant clades within the green algal orders Dasycladales and Bryopsidales during the Ordovician (Verbruggen et al., 2009). Further study of this event is needed, including quantitative analysis of morphospace occupation and ecological assessment of thallus morphology, both of which were examined for the Ediacaran event by Xiao and Dong (2006).

The three Silurian macroalgal taxa described herein contribute to knowledge of algal diversity in the aftermath of the second macroalgal diversification event. All three taxa have approximate analogues, at least in terms of external thallus morphology, among rather complex forms of living macroalgae.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENT

Fossils described herein were collected by M. Melchin in 1991 during systematic (decimeter-scale) sampling of an outcrop of the Cape Phillips Formation along an unnamed

stream approximately 5 km southwest of Cape Manning on northeastern Cornwallis Island, Nunavut (75° 26.5' N, 94° 08.9' W) (Fig. 1). The section at this locality comprises slightly more than 13 m of strata, but the lower 6 m and strata above 13 m are exposed only intermittently (Fig. 2). Most of the section consists of thin beds of silty limestone alternating with thin packages of calcareous shale. Beds of the former range in thickness from 2 to 8 cm and are thinly laminated near the top. The entire section is devoid of trace fossils. Near the 11 m mark, the strata display small-scale folds developed during synsedimentary slumping (Fig. 2). The silty limestones are interpreted as turbidite beds, sourced from an adjacent carbonate platform, whereas the shales are regarded as hemipelagic in origin. A coarser, graded, fossiliferous lime packstone unit near the top of the section, like the other limestone units, is considered to represent a turbidite bed.

Algal material was recovered from seven beds in the section (Fig. 2), each composed of the silty limestone lithology, as well as from float material of this lithology adjacent to the section. *Eocladus xiaoi* n. gen. n. sp. is abundant in all of the alga-bearing beds whereas the other two algal taxa described herein were found within the section only at the 12.8 m level. The presence of noncalcified algae in multiple beds across a 5 m interval of section indicates that unusual taphonomic conditions persisted, or at least were intermittently developed, across an extended interval of time. A similar stratigraphic distribution applies to algal-Lagerstätten within the Middle Cambrian Wheeler Formation of the Great Basin, in which multiple thin alga-bearing beds are distributed across a meter or more of section at several stratigraphic levels (Brett et al., 2009).

Specimens of the biostratigraphically useful graptoloid *Saetograptus linearis* (formerly regarded as a subspecies of *Saetograptus fritschi*) occur at several levels in the studied section (Fig. 2, 6.13). The range of this species is restricted to the lower Ludfordian, and Lenz (1990)

used its occurrence to define a *S. fritschi linearis* Zone in Arctic Canada. This zone is regarded as correlative with the *Saetograptus leintwardinensis* Zone of Britain, the base of which defines the base of the Ludfordian.

The sampled section lies within the southern part of the Cape Phillips Embayment, a southern extension (subbasin) of the early Paleozoic Franklinian Basin (Fig. 1). Within the Cape Phillips Embayment, the Cape Phillips Formation comprises Upper Ordovician to Lower Devonian strata and consists primarily of calcareous shales and mudstones with occasional limestones and, in the lower part of the formation, cherts (de Freitas et al., 1999). The formation exceeds 2,500 m in thickness, including at least 1,000 m of Upper Silurian strata on northeastern Cornwallis Island (Lenz, 1990). During the Silurian, this setting was located slightly north of the equator (Scotese, 2001). The portion of the Cape Phillips Embayment within the study area was a slope setting with deeper water to the north and west and a shallow carbonate platform with reefs a short distance to the south and east (Melchin, 1989) (Fig. 1). Notably, the early Ludfordian was a time of major transgression within the basin (de Freitas et al., 1999). Other examples of Silurian algal-Lagerstätten occur within transgressive intervals (see LoDuca and Brett, 1997), and the same has been noted for algal-Lagerstätten recently described from the upper Proterozoic of the East European Platform (Grazhdankin et al., 2007) and the Middle Cambrian of the Great Basin in Utah (Brett et al., 2009), the latter occurring repeatedly and predictably within fourth-order cycles. A causal relationship between transgressions and the formation of Konservat-Lagerstätten in peri- and epicontinental seas in general may be tied to upward displacement of the oceanic oxygen minimum zone or the development of widespread density stratification (see LoDuca and Brett, 1997).

TAPHONOMY AND PALEOECOLOGY

Much of the algal material in the Cape Phillips Formation is highly fragmentary and alignment of thalli is evident on the largest specimen-bearing slab in the collection (Fig. 3). Based on these taphonomic attributes, together with the sedimentological characteristics of the alga-bearing beds, the algal assemblages are regarded as allochthonous — transported by turbidity currents from the adjacent carbonate platform into the slope setting. Exceptional preservation of the assemblages appears to have been facilitated by a combination of rapid burial (obration) in fine-grained carbonate sediment and anoxic conditions below the sediment/water interface, the latter indicated by the lack of bioturbation. Other examples of Silurian algal-Lagerstätten are associated with similar depositional conditions, but for the particular occurrences cited above obrution appears to have occurred more or less in-situ within shallow marine settings (see LoDuca 1995; LoDuca and Brett, 1997). In common with most other examples of algal-Lagerstätten, thalli are preserved as carbonaceous compressions and invertebrate skeletal material is largely, and in some cases entirely, decalcified (see LoDuca and Brett, 1997; von Bitter et al., 2007).

Apart from algae, fossils within the alga-bearing beds are limited to dendroid and graptoloid graptolites, small brachiopods, and styginid trilobites (pygidia) (see Fig. 6.10-6.13). Algal material is abundant, but the other groups are rare. Such a biotic composition is characteristic of thalloid-alga-dominated (TA) biotas (LoDuca, 1995), one of three distinctive types of biotas represented among Silurian marine Konservat Lagerstätten, the others being the eurypterid-phyllocarid-dominated (EP) biota and the dendroid-graptolite-characterized (DG) biota (Kluessendorf, 1994). Worms and lightly sclerotized arthropods, however, which are known from other TA biotas, have not been observed among material from the Cape Phillips

Formation. In general, TA biotas are thought to have colonized restricted (poorly circulated) shallow marine settings with dysoxic to anoxic conditions below and extending for some distance above the seafloor, the lack of oxygen serving to exclude most animal taxa (LoDuca, 1995). Because the material in the Cape Phillips Formation shows evidence of transport, it is possible that it represents the remnants of TA biotas dislodged from the adjacent shallow platform by storm activity.

Parallels exist between the macroalgal assemblages of the Cape Phillips Formation and a modern macroalgal association in Florida Bay, the shallow but expansive lagoon between the Florida Keys and the mainland. The initial colonizer of cleared areas in Florida Bay is the dasycladalean alga *Batophora* (Thayer et al., 1994). The open thallus form of this taxon corresponds to that characteristic of the Filamentous functional-form group and is consistent with its ecological role as an opportunistic species (see Littler et al., 1983). *Eocladus xiaoi* n. gen. n. sp. is an approximate morphological analogue for *Batophora* in the Cape Phillips Formation. In Florida Bay, *Batophora* patches are eventually populated by the bryopsidalean algae *Halimeda* and *Penicillus*, late-successional forms with corticated thalli that enhance survival at the expense of productivity (Littler et al., 1983). The external morphology of these taxa closely approximates that of *Palaeocymopolia nunavutensis* n. gen. n. sp. and *Chaetocladus capitatus* n. sp., respectively, within the Cape Phillips Formation. That the algae preserved within the Cape Phillips Formation were similar in an ecological context to their modern morphological counterparts is suggested by their relative abundances and stratigraphic distributions. Specifically, *Eocladus xiaoi* is abundant in every alga-bearing bed, as expected for an opportunistic species, whereas *Palaeocymopolia nunavutensis* and *Chaetocladus capitatus* are rare and have limited stratigraphic distributions, consistent with late-successional species in

settings subject to frequent disturbance. Thus, although the algal assemblages within the Cape Phillips Formation must be interpreted with caution because of potential biases introduced by post-mortem transport, the evidence at hand suggests that the algal flora represented within this unit roughly paralleled that of Florida Bay in terms of both morphological and ecological aspects.

SYSTEMATIC PALEONTOLOGY

Division CHLOROPHYTA Pascher, 1914

Order DASYCLADALES Pascher, 1931

Family TRIPLOPORELLACEAE Berger and Kaeffer 1992, emend. LoDuca 1997

Genus EOCLADUS new genus

Type species.—*Eocladus xiaoi* n. gen and sp.

Diagnosis.—As for species.

Etymology.—From the Greek *eo*, early, and *cladus*, branch, with reference to the age and branched form of this genus.

Discussion.—To date, 10 macroalgal genera characterized by noncalcified thalli with an erect main axis and branched appendages arranged in radial fashion and consisting of cylindrical segments have been established on the basis of fossil material. All are known only from Paleozoic strata and nearly all are monospecific (*Callithamnopsis* and *Dowlingia* are the sole exceptions). Thalli conforming to these characteristics are common among the algal flora of the Cape Phillips Formation but cannot be assigned to any of the aforementioned genera. Specifically, in the context of classification criteria for fossil dasycladalean algae established by

Bassoullet et al. (1977), the new material is excluded from *Archaeobatophora* Nitecki 1976 on the basis of main axis morphology (the diagnosis of *Archaeobatophora* indicating constrictions between the whorls), from *Inopinatella* Elliott 1971 and *Dasycladophycus* Elliott 1982 on the basis of lateral morphology (the former characterized by bulbous primary lateral segments, whereas the laterals of *Dasycladophycus* branch only to the second order), from *Heterocladus* LoDuca, Mikulic, and Kluessendorf 2003 and *Uncatoella* Li and Cai, 1978 by the lack of reproductive structures, and from *Primicorallina* Whitfield 1894 (noncalcified material illustrated in Johnson, 1961, plate 19, 20), *Callithamnopsis* Whitfield 1894, *Kinnowia* Fry 1983, *Whiteavesia* Fry, 1983, and *Dowlingia* Fry, 1983 by the particulars of lateral arrangement, the laterals of the new material being arrayed in discrete whorls (euspondyl) rather than randomly distributed along the length of the main axis (aspondyl).

Only one taxon in the pre-Devonian fossil record of calcified algae merits comparison with the new material, the dasycladalean genus *Arcticella* Poncet 1986. This taxon, known from the Ordovician of the Canadian Arctic, is characterized by euspondyl thalli with a main axis comparable to that of the new material in shape and size. However, in addition to being calcified, *Arcticella* differs significantly in being characterized by unbranched laterals with a vesicular as opposed to cylindrical form and over 30 laterals per verticil.

Thalli of the new material agree in all key areas of morphology with vegetative noncalcified thalli of the extant dasycladalean algae *Batophora* and *Acetabularia*. Indeed, the only differences of note concern minor variances in whorl spacing and total lateral length. These extant taxa, however, develop conspicuous gametophores during the reproductive phase of thallus development (choristosporate reproduction) that have not been observed on any specimens of the new material.

EOCLADUS XIAOI new species

Figures 3, 4.1-4.11

Diagnosis.— Noncalcified thallus comprising a narrow main axis and laterals arranged in verticils (euspondyl); main axis cylindrical, without constrictions between verticils; laterals branched to at least the fourth order, all lateral segments cylindrical; endosporate.

Description.—The thallus of the holotype (ROM 59911a) is 30 mm long and 6 mm wide at its widest point and consists of an undivided main axis surrounded by thin, branched laterals (Fig. 4.1). The main axis is cylindrical in form, approximately 0.3 mm in diameter, and maintains a nearly uniform diameter along its length, without appreciable change either at or between the verticils. The laterals emerge from the main axis in verticils spaced approximately 0.6 mm apart; those along the middle and upper part of the thallus curve upward so that they are at an acute angle to the main axis. Each verticil appears to comprise four primary laterals, but the precise number is difficult to ascertain owing to the flattened condition of the material. Along the middle and upper part of the thallus, laterals are approximately 10 mm in total length and branch to the fifth order. All lateral segments are cylindrical. Branching at each level appears to be dichotomous, but it is possible that branching is trichotomous, with the third segment in each case being obscured by matrix (see Kenrick and Li, 1998). Laterals along the lower part of the thallus lack higher-order segments, but these may have been removed by transport or, like living dasycladalean algae, may have been deciduous. Details of lateral segment morphology are best revealed by a cluster of detached laterals adjacent to the holotype and likely derived from this thallus (see Fig. 4.2), from which the following measurements were obtained (length followed by diameter, in mm): first-order 1.5 by 0.12; second-order 3.6 by 0.1; third-order 3.0 mm by 0.09;

fourth-order 1.7 by 0.08; fifth-order 0.5 by 0.08. For the other thalli examined, main axis diameter ranges between specimens from 0.25 to 0.35 mm. The longest specimen has a length of 40 mm, but it is not clear if any of the specimens in the collection preserve the full length of the thallus. Reproductive structures and holdfasts are not evident among any of the material examined.

Etymology.—Named in honor of Dr. Shuhai Xiao, an ardent student of fossil algae.

Types.—The largest specimen illustrated in Figure 4.1 is designated as the holotype, repositied in The Royal Ontario Museum (ROM 59911a). Specimens illustrated in Figure 4.3 and 4.6 are designated as paratypes, also repositied in The Royal Ontario Museum (ROM 59914A; ROM 59912a, b). All specimens Ludfordian, from the Cape Phillips Formation along an unnamed stream approximately 5 km southeast of Cape Manning on northeastern Cornwallis Island, Nunavut (75° 26.5' N, 94° 08.9' W).

Other material examined.—Over 30 specimens, including ROM 59910a, b, c; ROM 59911b, c; ROM 59913A; ROM 59915; ROM 59917, and ROM 59923c, illustrated herein.

Occurrence.—Known only from the type locality.

Discussion.—*Eocladus xiaoi* is assigned to Dasycladales on the basis its thallus architecture (main axis bearing whorls of branched laterals; see LoDuca, 1997; LoDuca et al., 2003; Kenrick and Vinther, 2006, for additional details). In addition, the lack of evident cross walls is suggestive of a siphonous body plan, consistent with a dasycladalean affinity, but it is possible that this simply reflects preservational limitations. Within Dasycladales, an affinity with the Triploporellaceae is indicated by the euspondyl arrangement of the laterals and by the lack of gametophores, the latter indicating non-choristosporate reproduction. It might be argued that all known material of *E. xiaoi* simply represents pre-reproductive individuals. However, no

definitive evidence of gametophores is known from among the many early Paleozoic taxa assigned to Dasycladales, some of which are represented by dozens of specimens from multiple localities. Noncalcified thalli assigned to Dasycladales with preserved gametophores are known from the Devonian (Kenrick and Li, 1998). In the absence of biochemical and cellular-level details, however, the possibility remains that this taxon represents an algal clade apart from Dasycladales that has no living representatives.

Taxon-specific stable carbon isotope values for this species were reported under the heading “unidentified alga” by LoDuca and Pratt (2002, table 2).

Genus CHAETOCLADUS Whitfield 1894, emend. LoDuca 1997

CHAETOCLADUS CAPITATUS new species

Figures 5.1-5.7, 6.14

Diagnosis.—*Chaetocladus* with laterals 0.25 mm wide and attaining lengths of 12 to 15 mm along the upper part of the main axis; main axis 2 to 2.5 mm wide.

Description.— The shaving brush-shaped thallus of the holotype (ROM 59925A) is 45 mm long and 20 mm wide at its widest point and consists of an undivided main axis surrounded by numerous unbranched lateral appendages (Fig. 5.6). The main axis is cylindrical, with a diameter of 2.5 mm. Laterals are developed in verticils (euspondyl), spaced approximately 1 mm apart, and are borne at an acute angle. Each verticil comprises approximately 20 laterals of cylindrical form. Laterals along the lower and middle part of the main axis are short, ranging from 1 to 1.5 mm in length (Fig. 5.8). The whorls in this area have the appearance of a series of nested cups. Laterals along the uppermost part of the main axis are elongate and form a distinctive capitulum

approximately 20 mm wide. Capitulum laterals are 0.25 mm wide and 12 to 15 mm long, with rounded terminations. Along the left side, a cluster of capitulum laterals appears to have been pulled downward, perhaps as a consequence of transport. Some of the laterals in this area appear to branch, but this is regarded to reflect overlapping of separate elements. The lowermost part of the main axis is at a 90° angle relative to the rest of the thallus and may represent the rhizoid. The same applies to ROM 59924. The lower and middle part of the main axis of ROM 59923a is devoid of laterals, but the former presence of these structures is indicated by dark transverse bands comprising rows of faint circular attachment scars, each with a diameter corresponding to the width of a lateral (Fig. 5.1, 5.3). ROM 59924 presents an intermediate case, in that most, but not all, of the laterals along the lower and middle part of the main axis are missing (Fig. 5.5). Reproductive structures and cellular-level details are not evident among the study material.

Etymology.—After the Latin *caput*, meaning head.

Types.—The specimen illustrated in Figure 5.6 is designated as the holotype, repositied in the Royal Ontario Museum (ROM 59925A). The specimen illustrated in Figure 5.1 is designated as a paratype, also repositied in The Royal Ontario Museum (ROM 59923a). Ludfordian, from the Cape Phillips Formation along an unnamed stream approximately 5 km southeast of Cape Manning on northeastern Cornwallis Island, Nunavut (75° 26.5' N, 94° 08.9' W).

Other material examined.—A specimen missing most of the main axis below the capitulum, illustrated in Figure 5.4 (ROM 59923b), and a specimen lacking most of the capitulum, illustrated in Figure 5.5 (ROM 59924).

Occurrence.—Known only from the type locality.

Discussion.—*C. capitatus* closely resembles other species of *Chaetocladus* Whitfield 1894, a taxon known from Ordovician to Devonian strata and regarded by LoDuca (1997) as a

noncalcified member of the green algal order Dasycladales. Like other *Chaetocladus* taxa, thalli of *C. capitatus* are unbranched and comprise a cylindrical main axis bearing whorls of unbranched cylindrical laterals. *C. capitatus* differs from the five *Chaetocladus* species recognized by LoDuca (1997) and an additional species recently described by Kenrick and Vinther (2006) from the Silurian of Sweden with regard to lateral length. Specifically, the laterals of *C. capitatus* along the upper part of the main axis are markedly longer than those of all but *C. hefteri* Kräusel and Weyland 1962, by a factor of nearly two or more, whereas those of *C. hefteri* are longer than those of *C. capitatus* by a factor of two. In addition, only *C. ruedemanni* LoDuca 1997 has laterals with a diameter similar to that of *C. capitatus* (0.2 vs 0.25 mm, respectively), the other *Chaetocladus* taxa differing in this regard by a factor of nearly two or more, but the longest laterals known for *C. ruedemanni* are only one-third the length of the capitulum-forming laterals of *C. capitatus*.

The stipitate capitulum thallus form displayed by the four known specimens of *C. capitatus* is developed, albeit to a somewhat lesser degree, among thalli of *C. dubius* (Spencer 1884) and *C. plumula* Whitfield 1894, from the Silurian of Ontario and the Ordovician of Wisconsin, respectively (see LoDuca, 1997, figs. 5.5, 5.13). In addition, like *C. capitatus*, capitate individuals of *C. dubius* in some cases have short laterals along the lower part of the main axis, relative to those along the upper part, and in others have lost the laterals from along the lower part of the main axis. Capitate thalli are also known for *Medusaegraptus mirabilis* Ruedemann 1925 and *M. graminiformis* (Pohlman 1886), noncalcified dasycladalean alga taxa with aspondyl thalli from the Silurian of New York (see Ruedemann, 1925, pl. 8 fig. 4, pl. 10 fig. 4; LoDuca, 1990, fig. 3.1-3.3), and are a diagnostic feature of a number of fossil calcified dasycladalean taxa, including the Jurassic genera *Goniolina* d'Orbigny 1850 and *Petrascula*

Gümbel 1873 (see Berger and Kaefer, 1992). Among living algal taxa, this thallus form is known for both *Penicillus* and *Chamaedoris*. The former, commonly known as merman's shaving brush, differs markedly from *C. capitatus* in that the stipe is multiaxial. *Chamaedoris*, a member of the green algal order Siphonocladales (Graham and Wilcox, 2000), like *C. capitatus*, is characterized by a uniaxial stipe. Nonetheless, three factors collectively argue against a close affinity between *Chamaedoris* and *C. capitatus*. First, *Chamaedoris* develops appendages only at the extreme base and top of the stipe, these forming the rhizoid and capitulum, respectively, whereas *C. capitatus* produced appendages along the entire length of the main axis. Second, *Chamaedoris* forms distinctive small outgrowths along the capitulum filaments, termed tenacular cells (see Leliaert et al., 2007), and these have not been observed among material of *C. capitatus*. Finally, all fossil taxa currently assigned to Siphonocladales from Neoproterozoic and Paleozoic strata (see Vologdin, 1966; Butterfield et al., 1994; Berchenko, 2000) are characterized by simple thallus morphologies, these having the form of smooth balls or thin, branched filaments.

Genus PALAEOCYMOPOLIA new genus

Type species.—*Palaeocymopolia nunavutensis* n. gen and sp.

Diagnosis.—As for species.

Etymology.—The name refers to similarity between this genus and the living alga *Cymopolia* and to the age of the material.

Discussion.—The thalli that form the basis of this new genus bear a striking resemblance to those of the extant dasycladalean alga *Cymopolia barbata*. In both cases, thalli with a dichotomously branched, serial-segmented form and a corticated structure comprise a cylindrical

main axis and cylindrical primary laterals arranged in radial fashion (compare Fig. 6.1 - 6.6 with 6.7 - 6.9). Main axis diameter, primary lateral length and diameter, segment size, and segment shape are also similar between these taxa. Thalli of the new material are assigned to a genus apart from *Cymopolia*, however, because they appear to be endosporate, not choristosporate, and because they do not have whorls of branched, hairlike laterals between the segments. In addition, thalli of *Cymopolia* are calcified.

The extant alga *Halimeda*, a member of the green alga order Bryopsidales, is also characterized by bifurcating thalli with a serial-segmented form and a corticated structure. *Halimeda*, however, in addition to being calcified, stands apart from the new taxon with regard to the structure of the medullary region, this being multiaxial as opposed to uniaxial, and with regard to the morphology of the cortical filaments, these developing conspicuous inflated portions termed utricles. Extant taxa within the Rhodophyta that are characterized by serial-segmented or otherwise constricted thalli comprising medullary and cortical zones, such as *Scinaia* and *Galaxaura* among the Nemaliales, and *Amphiroa* and *Cheilosporum* among the Corallinales, similarly differ by having a multiaxial construction for the medullary region.

Among extinct algal taxa, thalli of the new material closely resemble those of *Callisphenus gracilis* Høeg, 1937, a noncalcified taxon erected on the basis of Wenlockian material from the island of Kommersøy, Norway. Additional material from the Wenlockian of Gotland and Estonia was assigned to the genus in open nomenclature by Nitecki and Spjeldnaes (1993). The 22 mm long club-shaped thallus of the type specimen of *C. gracilis* comprises a cylindrical "central cell" 0.3 to 0.5 mm in diameter from which extend thin "tubes" 0.1 to 0.13 mm in diameter. The remainder of the thallus consists of "a dense tissue, which in the central parts is seen as a reticulation, whereas towards the sides it has the form of lines curving out

towards the surface and reaching it at a right angle." Høeg (1937, p. 44) further notes: "The original nature of the of the superficial tissues cannot be made out. There may have been a kind of cortical layer, which has now more or less completely disappeared." Thalli assigned to the new genus compare closely with those of *C. gracilis* with regard to the preserved internal structure. Specifically, in both cases, thalli consist of a central cylindrical axis, 0.25 to 0.5 mm in diameter, that bears a series of thinner cylindrical appendages, these in turn giving rise to a thin cortical layer preserved as a film of carbon. In addition, maximum segment width for the former is only slightly less than thallus width for the latter (4 vs. 5 mm). Thalli of the new material, however, differ from those of *C. gracilis* in that they have a serial-segmented form. It is strictly on this basis that the new material is assigned to a genus apart from *Callisphenus*.

Among fossil calcified algae, cyclocrinitids, which are locally abundant in Ordovician and Silurian strata and are regarded by most workers as dasycladalean algae (see Beadle, 1988; Berger and Kaefer, 1992), also have corticated thalli with a central axis. In addition, a noncalcified example of a cyclocrinitid is known, a specimen of *Mastopora parva* from the Ordovician of Scotland (see comment in Nitecki and Spjeldnaes, 1993, p. 350). This specimen, however, like all cyclocrinitids, differs from the new material in that it lacks a serial-segmented form. Fossil calcified dasycladalean algae with serial-segmented thalli, but in other respects similar to cyclocrinitids, are known, and include the Permian genus *Mizzia* Schubert, 1907. These forms, in addition to being calcified, differ from the new material with regard to segment shape. Several genera within the Lanciculaceae Shuysky 1987, a Paleozoic bryopsidalean taxon, also bear some similarity to the new material, particularly *Lancicula* Maslov 1956, *Cauculicula* Shuysky and Schirschova (in Shusky, 1987), and *Voycarella* Shuysky and Schirschova (in Shusky, 1987), in that they are characterized by serial-segmented, corticated thalli comprising

segments that increase in width upward from their bases. The segments of *Voycarella* are a particularly close match for the new material in terms of external form. The segments of these taxa, however, have a multiaxial construction. The well known Paleozoic bryopsidalean taxa *Dimorphosiphon* Høeg 1927 and *Palaeoporella* Stolley 1893 also differ from the new material in being characterized by a medullary region with a multiaxial construction, and the same applies to serial-segmented, corticated members of the Gymnocodiaceae (reviewed in Mu, 1991), a taxon known from upper Paleozoic to lower Cenozoic strata and assigned by Elliott (1955) to the Rhodophyta. In addition, Gymnocodiaceae are characterized by reproductive structures in the cortical region that have not been observed among specimens of the new material.

PALAEOCYMOPOLIA NUNAVUTENSIS new species

Figures 6.1-6.6

Diagnosis.— Noncalcified serial-segmented thallus with dichotomous branching and a corticated structure; segments cylindrical to clavate in form, each comprising a cylindrical main axis and cylindrical laterals arranged in radial fashion; endosporate.

Description.— The thalli of this form are distinctly serial-segmented. The largest, designated as the holotype (ROM 59918), has a length of 72 mm (Fig. 6.1) and is sharply bent near the base. The 16 mm long portion of the thallus below the bend appears to comprise a single segment and is nearly cylindrical, expanding in width from 2.5 mm at the base to 3.0 mm at the top. Above the bend, the thallus is divided into a number of segments, each of which widens noticeably toward the top. The initial segments are approximately 6 mm in length and expand in width from 2.5 mm at the base to 4 mm at the top, whereas those along the upper part of the thallus are approximately 5 mm in length and expand in width from 2 mm at the base to 3 mm at the top. At

the center of each segment is a cylindrical main axis, 0.25 to 0.5 mm in diameter. This structure extends from the base of the specimen to the top and passes from one segment to the next without obvious constriction. The remainder of each segment consists of a granular film of carbon that often partially, and in some cases totally, conceals the central axis. This film has fairly smooth outer edges and appears to represent the remnants of a thin cortical layer. At approximately the midpoint from the base, the thallus bifurcates, the two branches being of roughly equal size and form, but the segments above the bifurcation are slightly smaller than those immediately below. Other specimens provide additional details. On ROM 59919a, the central axis, with a diameter of 0.25 mm, is clearly evident and retains its three-dimensional form, indicating without doubt that this structure was cylindrical in life (Fig. 6.3). On the same specimen, this structure bears a series of cylindrical laterals, each approximately 0.045 mm in diameter and 1 mm in length. From the material at hand, it appears that the laterals were arranged in radial fashion around the central axis, but too few have been preserved to determine whether or not they were arrayed in discrete whorls. Scars marking the attachment points of laterals along the central axis have not been observed. Reproductive structures are not evident.

Etymology.—From the Canadian Territory that includes the type locality.

Types.—The specimen illustrated in Figure 6.1 is designated as the holotype, repositied in The Royal Ontario Museum (ROM 59918). Ludfordian, from the Cape Phillips Formation along an unnamed stream approximately 5 km southeast of Cape Manning on northeastern Cornwallis Island, Nunavut (75° 26.5' N, 94° 08.9' W).

Other material examined.—Two small slabs with fragmentary thalli, four of which are illustrated herein (ROM 59919a, b, c; ROM 59920).

Occurrence.—Known only from the type locality.

Discussion.—Although the material at hand provides much information about this distinctive alga, several details remain unclear. The first concerns the form of the rhizoid. It is possible that the lower part of the holotype specimen, below the bend, comprises a simple, hook-shaped rhizoid, similar in form to that of the Silurian taxon *Medusaegraptus* (LoDuca, 1990). However, because all other material of *P. nunavutensis* is highly fragmentary, this must remain speculative. Uncertainty also surrounds the nature of the cortex. That the black granular film forming the bulk of each segment comprises the remnants of a cortical layer, in general, is supported by analogy with living dasycladalean algae. For the latter, the cortex is supported by numerous cylindrical laterals arising in radial fashion from a central axis. A similar structure is evident in material of *P. nunavutensis*. It may be that the vesicles forming the cortex of this alga were particularly thin-walled, so that they decayed more rapidly than other thallus elements, leaving behind only a rather amorphous film of carbon. Finally, although direct evidence of calcification is lacking, it is conceivable, particularly in view of its corticated structure, that this alga was calcified in life and subsequently decalcified during diagenesis, as observed for the associated shelly biota.

P. nunavutensis is assigned to Dasycladales on the basis of its distinctive thallus architecture (central axis surrounded in radial fashion by laterals). In addition, the lack of evident cross walls is suggestive of a siphonous body plan, consistent with a dasycladalean affinity, but it is possible that this simply reflects preservational limitations. Material of this taxon lacks the gametophores characteristic of living dasycladalean algae but, as noted above, no definitive examples of these structures are known among the many fossil taxa assigned to this order from strata older than Devonian. The similar fossil taxon *Callisphenus gracilis* was regarded by Høeg (1937) as a dasycladalean alga on similar grounds, a view later supported by Nitecki and Spjeldnaes (1993). An affinity with Bryopsidales is considered unlikely because all living

corticated members of this group with serial-segmented thalli have a multiaxial construction. In the absence of biochemical and cellular-level details, however, a dasycladalean affinity cannot be established with certainty, and the possibility remains that *P. nunavutensis* represents an algal clade with no living representatives. Within Dasycladales, *P. nunavutensis* is assigned to the family Triploporellaceae on the basis of an inferred euspondyl thallus form, an assumption drawn on constructional grounds from the form of the cortex. In the absence of definitive evidence regarding lateral arrangement, however, this assignment must be regarded as tentative.

The description of *P. nunavutensis* increases the already substantial proportion of living dasycladalean genera that have approximate morphological analogues among early Paleozoic macroalgal taxa, the others being *Acetabularia*, *Batophora*, and *Bornetella*. *Acetabularia* is similar to *Heterocladus waukeshaensis*, known from the Silurian of Wisconsin (LoDuca et al., 2003), *Batophora* is similar to *Archaeobatophora typha*, known from the Ordovician of Michigan (Nitecki, 1976), and *Eocladus xiaoi* (this report), and *Bornetella* is similar to the calcified cyclocrinitids (Beadle, 1988). The precise phylogenetic relationships between living dasycladalean taxa and their early Paleozoic *doppelgängers* remain to be determined. One viable hypothesis is that the early Paleozoic taxa represent early members of various extant dasycladalean clades, with each of these clades independently evolving choristosporate reproduction. Alternatively, it is conceivable that the early Paleozoic taxa belong to extinct dasycladalean lineages and reflect cases of convergent evolution in the area of vegetative thallus form. Results from a recent molecular study by Verbruggen et al. (2009) seem to support the first view, but more work is needed in this area.

Phylogenetic uncertainties aside, *P. nunavutensis* is significant because it is the oldest macroalgal taxon with a serial-segmented thallus form comprising corticated segments that

widen toward their tops, the next oldest being members of the Laniculaceae from the Devonian (Shuysky, 1987; Hubmann et al., 2008). Interestingly, material even older than *P. nunavutensis*, from the Llandoveryan of Estonia (see Tinn et al., 2009, Fig. 2I), also appears to have such a morphology, but has yet to be described in detail.

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FIGURE CAPTIONS

FIGURE 1—Location of the study area in the Canadian Arctic (modified after Melchin and Holmden, 2006). On the detailed map of Cornwallis Island, the sampled section is marked by the black dot along an unnamed stream near Cape Manning (CM), located at 75° 26.5' N, 94° 08.9' W. Thick dashed line indicates approximate position of boundary between carbonate platform and more basinal strata of the Cape Phillips Embayment. Thin dashed line shows approximate position of boundary between the Cape Phillips Embayment and deeper water strata of the Hazen Basin.

FIGURE 2—Generalized stratigraphic section of the Upper Silurian Cape Phillips Formation at the study area.

FIGURE 3—Slab with numerous current-aligned specimens of *Eocladus xiao*, collected 8.0 m from base of section (ROM 59910), x1.

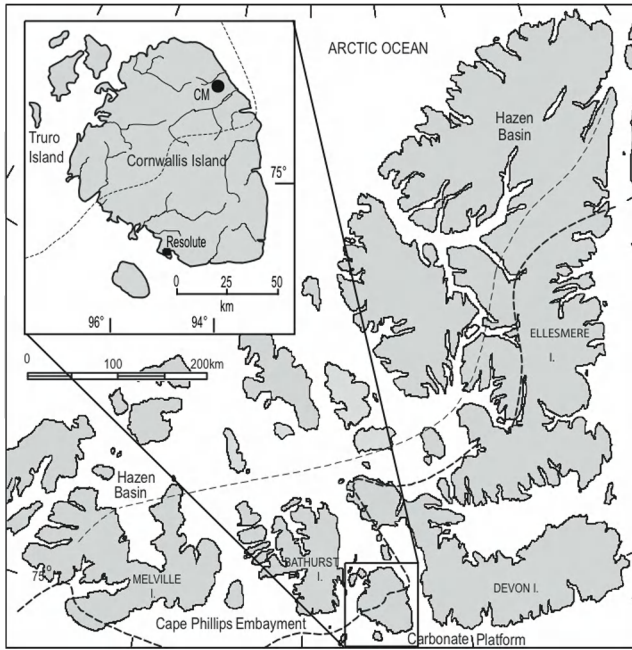
FIGURE 4—*Eocladus xiaoi* n. gen. and sp. 1, holotype (at center) (ROM 59911a), note second partial thallus at top (ROM 59911b) and detached set of laterals at lower right (ROM 59911c), x3; 2, enlargement of the set of detached laterals shown in 1, x6; 3, main axis stripped of laterals (ROM 59914; paratype), x2; 4, specimen interpreted to represent a young thallus (ROM 59917), x4; 5, an enlargement of the slab shown in Figure 3 with two current-aligned thalli (ROM 59910a, b), x2; 6, two partial thalli (ROM 59911c, d), x2; 7, two large thalli (ROM 59912a, b; paratypes), x2; 8, enlargement of a thallus from the slab shown in Figure 3 (ROM 59910c), x2;

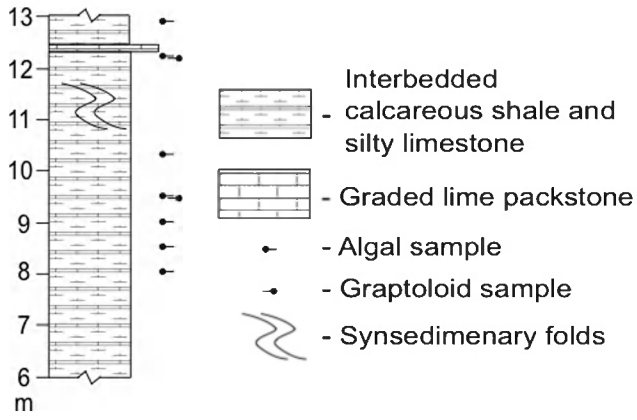
9, thallus with laterals along upper part lying parallel to main axis (ROM 59915), x2; 10, specimen collected 12.8 m from base of section (ROM 59913A), x2; 11, schematic reconstruction of the upper part of a thallus with multiple close-spaced whorls comprising four branched laterals per whorl, the two laterals along the lower part of the illustration are provided to show details of the lateral branching pattern used in this reconstruction, x2. All specimens photographed immersed in water. Specimens recovered from float material unless otherwise indicated.

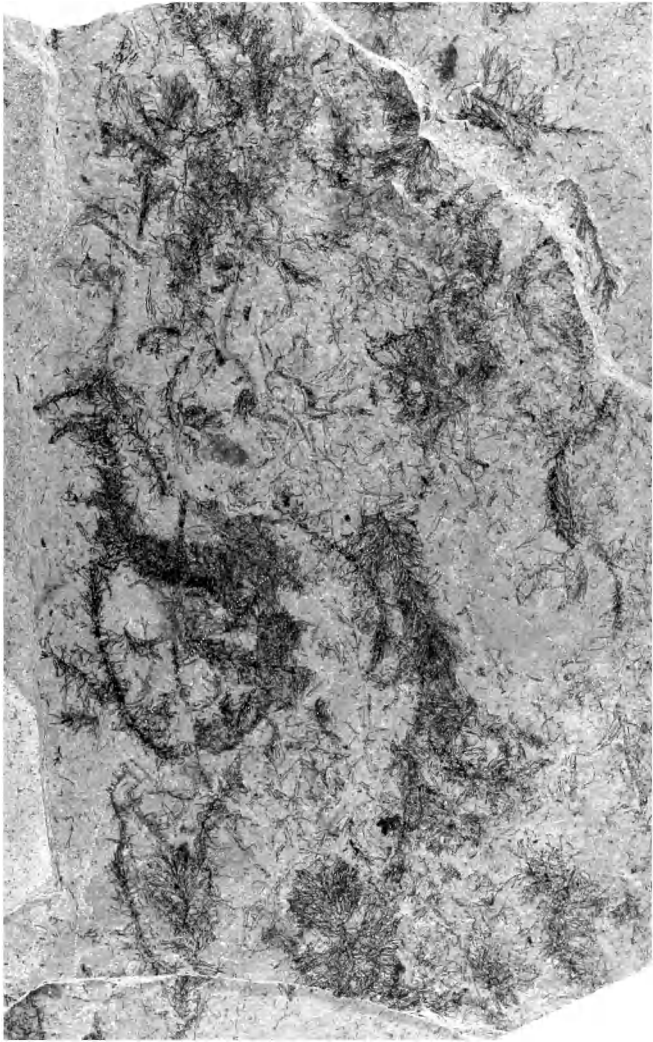
FIGURE 5—1-7 *Chaetocladus capitatus* n. sp. 1, specimen with laterals missing along the lower and middle part of the main axis and with elongate laterals along the upper part of the main axis forming a conspicuous capitulum (ROM 59923a; paratype), note specimen of *Eocladus xiaoi* at right (ROM 59923c), x2; 2, enlargement of the upper part of the specimen shown in 1, x4; 3, enlargement of the middle part of the main axis shown in 1, note dark transverse bands with faint circular scars marking former positions of laterals, x10; 4, specimen missing most of the main axis below the capitulum (ROM 59923b), x1; 5, specimen missing most of the capitulum, collected 12.8 m from base of section (ROM 59924), x1; 6, nearly complete thallus (ROM 59925A; holotype), note dendroid graptolite at top left and putative rhizoid at base, x2; 7, counterpart of specimen shown in 6 (ROM 59925B), x2 8, enlargement of the middle part of the thallus shown in 7, note whorls of short laterals, x8. All specimens photographed immersed in water. Specimens recovered from float material unless otherwise indicated.

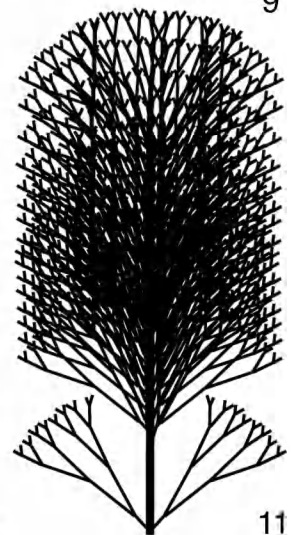
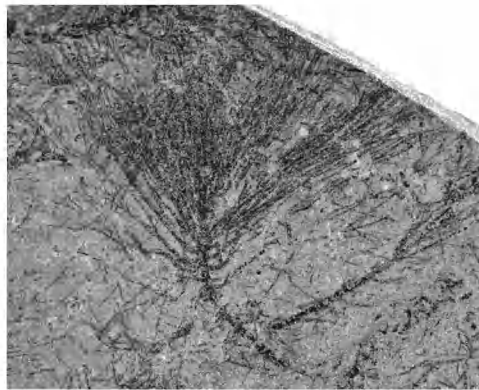
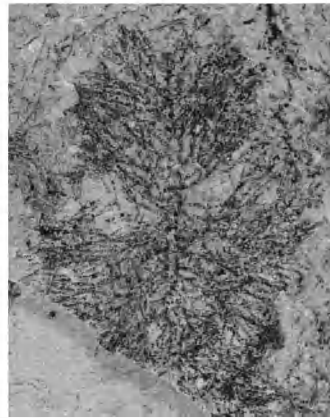
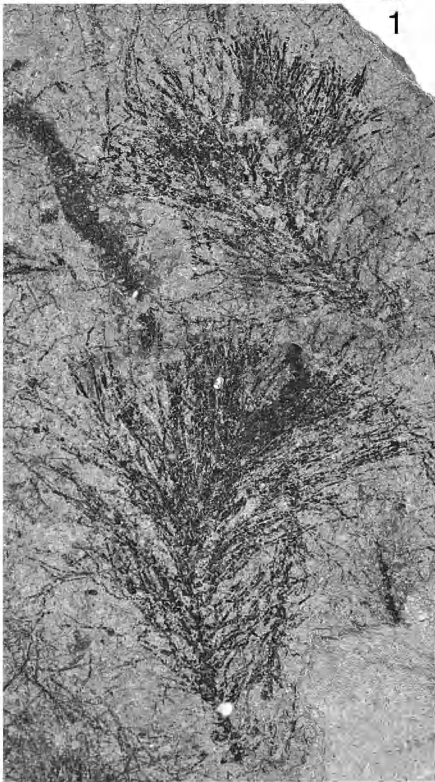
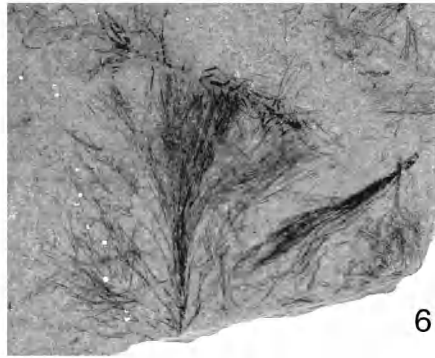
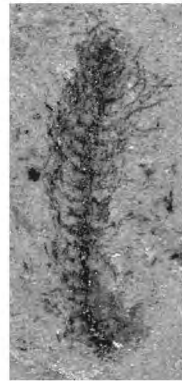
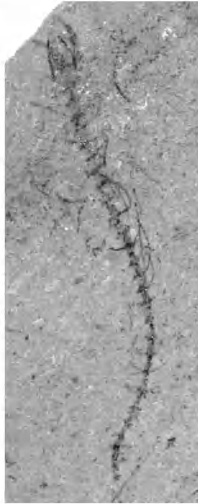
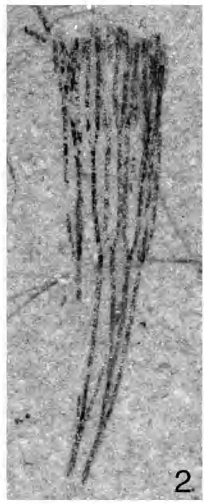
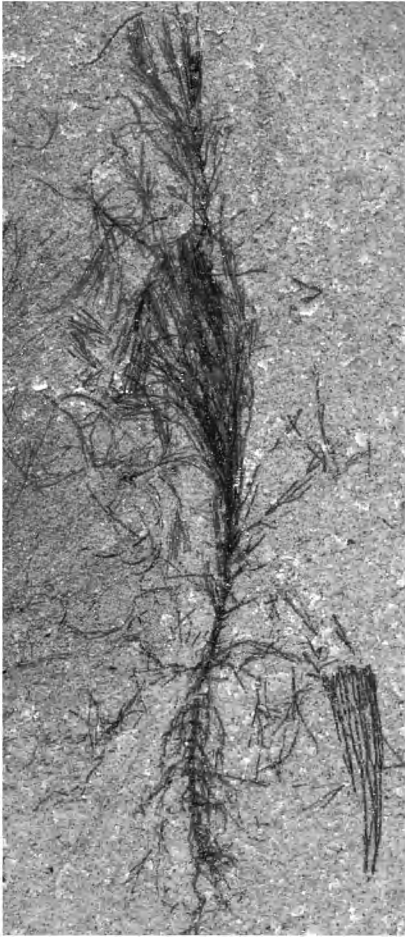
FIGURE 6—1-6, *Palaeocymopolia nunavutensis* n. gen. and sp. 1, large fragment of a thallus collected 12.8 m from base of section (ROM 59918; holotype), x2; 2, enlargement of the middle

part of the thallus shown in *1*, note bifurcation near lower part of image and dark main axis visible at the center of several segments, x6; *3*, enlargement of a single segment, note cylindrical main axis at center and thin cylindrical laterals to each side of this structure (ROM 59919a), x18; *4*, two articulated segments, note dark main axis at center (ROM 59919c), x5; *5*, fragment of a thallus collected 12.8 m from base of section (ROM 59920), x2; *6*, single segment, note dark main axis at center largely concealed by the cortex (ROM 59919b), x12; *7-9*, *Cymopolia barbata* (Recent). *7*, illustration of a nearly complete thallus, note tufts of thin laterals at ends of branches, x0.8 (from Taylor, 1960, reprinted with permission); *8*, detail of a portion of a thallus, note bifurcation at base and clavate form of segments, x2 (from Solms-Laubach, 1887); *9*, cross-section view of a portion of a thallus with main axis at left bearing laterals (white) on right that form a cortex at far right, note spheroidal reproductive structures at tips of cylindrical primary lateral segments and calcification (dark gray areas between laterals), x9 (from Solms-Laubach, 1887); *10*, small brachiopod (ROM 59921a), x9; *11*, small brachiopod (ROM 59921b), x4; *12*, styginid trilobite pygidium collected 12.2 m from base of section (ROM 59922), x1.5; *13*, specimen of *Saetograptus linearis* collected 8.0 m from base of section (ROM 59910d), x2; *14*, schematic reconstruction of *Chaetocladus capitatus*, the isolated whorl along the lower part of the thallus is provided to show details of lateral arrangement within the whorls used in the reconstruction, x1.5. *1*, *2*, *4-6* photographed immersed in water; *3*, *10-13* photographed in air. Specimens recovered from float material unless otherwise indicated.









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