PALEOBIOLOGY AND PALEOECOLOGY OF *PALAEOAPLYSINA* AND *EOPALAEOAPLYSINA* NEW GENUS IN ARCTIC CANADA

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ABSTRACT—*Palaeoaplysina* is an enigmatic platy macrofossil with a cellular skeleton and internal canal system common to upper Carboniferous–lower Permian reefs of the northern hemisphere. Its rapid flourishing from the Moscovian and subsequent extinction near the end of the Sakmarian, as well as its unique combination of physical features, are poorly understood. In addition to *Palaeoaplysina* reefs forming major petroleum exploration targets in Russia, *Palaeoaplysina* is abundant and well preserved in the Sverdrup Basin in the Canadian Arctic Archipelago. A new genus of Palaeoaplysinaceae, *Eopalaeoaplysina* n. gen., is also widespread in the Sverdrup Basin and identified based on a simple morphology with broad canals distributed in roughly even rows. The distribution of paleoaplysinids in strata from the Moscovian to the Sakmarian in the Sverdrup Basin reveals *Eopalaeoaplysina* and *Palaeoaplysina* represent two distinct reef-building forms with an increase in complexity over time. The aragonitic composition of *Palaeoaplysina*, in addition to its distribution within the photic zone and differentiated cellular skeleton, suggests paleoaplysinids were ancestral red algae. *Palaeoaplysina* occurs in both low-energy back-reef and higher-energy reef front facies. Preserved thin edges of *Palaeoaplysina* plates indicate it was encrusting, at least in low-energy conditions. The exclusion of *Palaeoaplysina* from the late Paleozoic tropics and the southern hemisphere, its rapid appearance and proliferation, and its eventual extinction may point towards an evolutionary niche optimized for warm-water conditions at unusually high latitudes along the western margin of Pangea.

INTRODUCTION

PALAEOAPLYSINA KROTOV, 1888 is an enigmatic macrofossil (Fig. 1) common in upper Carboniferous–lower Permian reefs along the northwest margin of Pangea. *Palaeoaplysina*, alongside phylloid and dasycladacean algae, occurs in reefs (West, 1988; Kiessling et al., 1999) and bedded shelf deposits (Morin et al., 1994). In the Ural Mountains, *Palaeoaplysina* build-ups have been successfully drilled, and of 74 lower Permian reefs dominated by phylloid algae and *Palaeoaplysina* catalogued by Kiessling et al. (1999), more than half were productive reservoirs or held reservoir potential. *Palaeoaplysina* is particularly abundant in Moscovian to Sakmarian reefal and non-reefal deposits of the Sverdrup Basin of the Canadian Arctic Archipelago (Beauchamp et al., 1989a; Nassichuk and Davies, 1992).

Palaeoaplysina grew as broad, undulating plates categorized by three features (Fig. 1.1): 1) a branching canal system perpendicular to the plate surface; 2) the common appearance of protuberances referred to as mamelons on one side of the plate; and 3) a cellular skeleton. The canals and mamelons led early researchers to suggest a hydrozoan affinity (Chuvashov, 1973; Davies and Nassichuk, 1973). More recent authors (e.g., Vachard and Kabanov, 2007) have suggested an algal affinity on the basis of the cellular skeleton. *Palaeoaplysina* is inferred to have been aragonitic (Nassichuk and Davies, 1992) because its original skeleton was partially to completely dissolved or replaced early during diagenesis. It appears *Palaeoaplysina* grew well within the photic zone in reef margins and lagoons (Morin et al., 1994), and favored shallow, clean marine conditions. It has been variously argued to be encrusting (Davies, 1971; Breuninger, 1976; Skaug et al., 1982), erect or semi-erect (Davies and Nassichuk, 1973; Beauchamp et al., 1989a; Davies, 1989).

The spatio-temporal distribution of *Palaeoaplysina* was restricted from latest early Moscovian (Kashirian) to the Sakmarian/early Artinskian (Chuvashov, 1983), along the northwest margin of Pangea (Fig. 2.1). The oldest reported occurrence of *Palae-oaplysina* is Middle Pennsylvanian (mid- to late Moscovian) of Utah (Ritter and Morris, 1997). It persisted at least until the late Sakmarian, with some reports from the early Artinskian (Davies, 1989). Of note, however, is conodont biostratigraphic zones considered early Artinskian two decades ago (e.g., Beauchamp and Henderson, 1994) are now considered Sakmarian in age (Chernykh, 2006; Henderson et al., 2012). Descriptions of *Palaeoaplysina* exist from the Moscow Basin, Timan-Pechora, and the Ural Mountains (Chuvashov, 1973, 1983; Ilkhovskii, 1973; Wahlman and Konovalova, 2002; Vennin et al., 2002), Svalbard and Bjørnøya (Skaug et al., 1982; Lonøy, 1988; Stemmerik et al., 1994), the Barents Sea (Rafaelsen et al., 2008), the Canadian Arctic islands (Davies and Nassichuk, 1973; Beauchamp et al., 1989a; Beauchamp, 1992), the Yukon Territory (Davies, 1971, 1989), through British Columbia (Macqueen and Bamber, 1977; Bamber and Macqueen, 1979; Zubin-Stathopoulos et al., 2012), and the Western United States including Utah (Ritter and Morris, 1997), Idaho (Breuninger, 1976; Breuninger et al., 1989), Nevada (Wardlaw et al., 1996) and California (Watkins and Wilson, 1989), as well as Japan (Igawa, 2003; Nakazawa and Ueno, 2009; Nakazawa et al., 2011). One isolated Asselian or lower Sakmarian occurrence in Texas (Wahlman, 2002) represents the southernmost extreme of its paleogeographic range.

This paper investigates the biological affinity and modes of life of *Palaeoaplysina* and some related forms, previously referred to as "ancestral paleoaplysinids" (Beauchamp, 1992) and some as *Palaeoaplysinella* (Vachard and Kabanov, 2007). All these forms are grouped under the general term "paleoaplysinids." Using exceptional material from the Sverdrup Basin, Arctic Canada (Fig. 2.2), this paper discusses the morphology, cellular skeleton, original mineralogy, preservation, and unique stratigraphic and geographic distribution of paleoaplysinids. Our study reinforces previous interpretations of
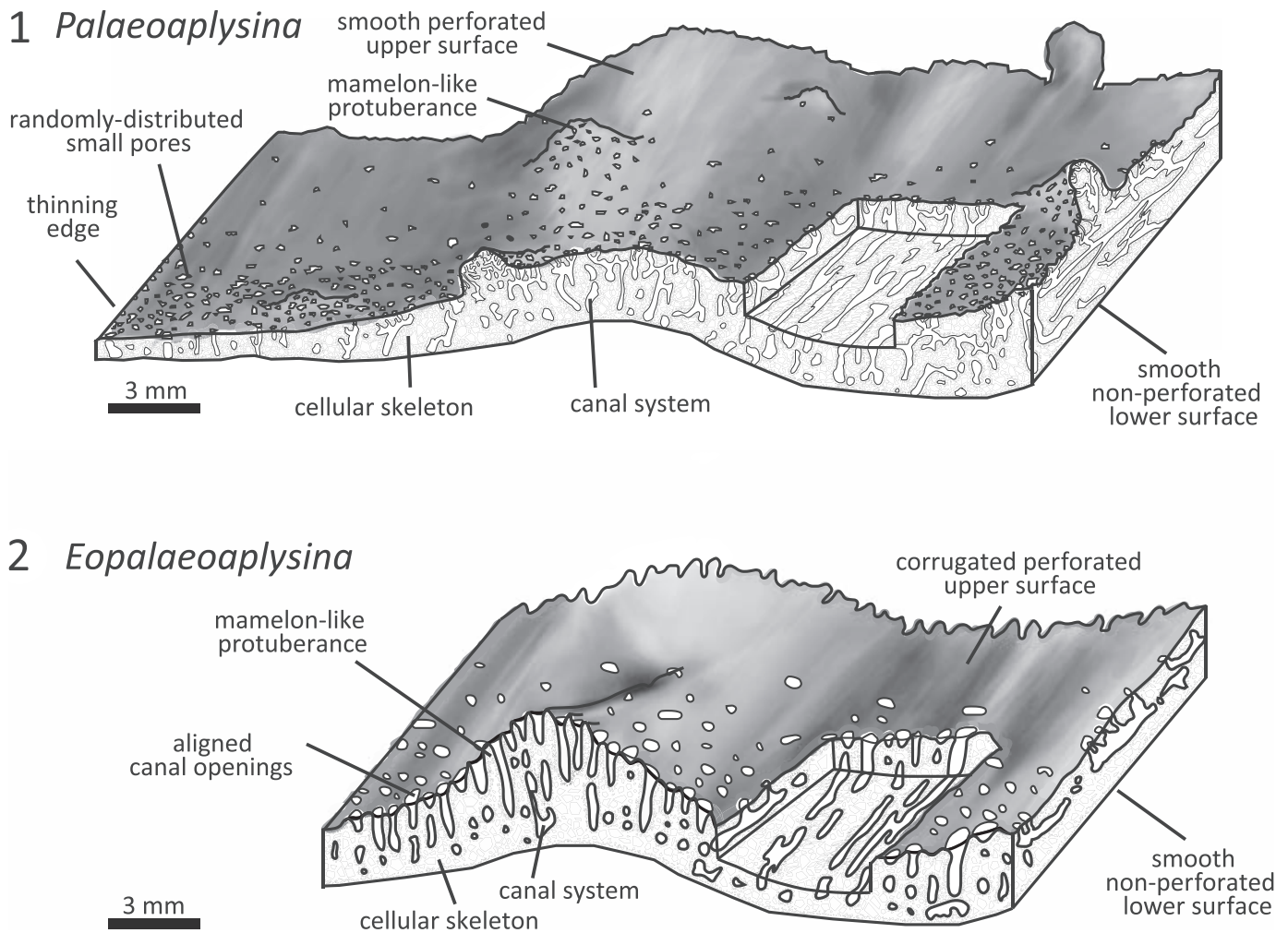
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1 *Palaeoaplysina*

smooth perforated
upper surface

mamelon-like
protuberance

randomly-distributed
small pores

thinning
edge

3 mm

cellular skeleton

canal system

smooth
non-perforated
lower surface

2 Eopalaeoaplysina

corrugated perforated
upper surface

mamelon-like
protuberance

aligned
canal openings

3 mm

canal system

cellular skeleton

smooth
non-perforated
lower surface

FIGURE *1*—Idealized morphology of paleoaplysinids: *1, Palaeoaplysina* Krotov 1888; *2, Eopalaeoaplysina* n. gen.; diagram shows hummocky nature of the plate with thinning edges at the distal margin; protuberances (mamelons) and pore openings on the presumed upper surface; three different canal appearances are possible depending upon orientation of cut through plate; distribution of pores is idealized and incomplete as only a few pores and mamelons are drawn.

Palaeoaplysina as a red alga (Archaeolithophyllaceae) with an unusual growth form.

LOCALITY AND MATERIAL

The samples used in this study were collected from 1983 to 2010 in the Sverdrup Basin on Axel Heiberg and southwest Ellesmere Islands in the Canadian Arctic Archipelago, Nunavut (Figs. 2.2, 3). All samples are archived at the Geological Survey of Canada, Calgary (GSC). Sections from Arthaber Creek (Section 1A and 1B) GSC locality C-115323–C-115512 (N 80°34′16″, W 95°35′31″; N 80°33′46″, W 95°26′4″), and Griesbach Creek (Section 2) GSC locality C-115515–C-115618 (N 80°27′41″, W 94°24′26″) were collected in 1983 from Axel Heiberg Island from the Hare Fiord and Nansen formations GSC locality C-119358–C-119500 and C-123100–C-123237. Section 3 was collected from a Nansen Formation reef complex west of Blind Fiord (WBF) on southwest Ellesmere Island (N 78°20′14″, W 85°57′05″). GSC locality C-131810–C-132080, collectively referred to as East Blind Fiord (EBF), includes Sections 4A (N 78°25′10″, W 85°31′17″) and 4B (N 78°24′56″, W 85°34′20″). EBF displays the Canyon Fiord, Belcher Channel, and Raanes formations in a setting paleogeographically landward of WBF. In addition, exceptionally well-preserved *Palaeoaplysina* plates were collected from the Belcher Channel Formation at GSC locality C-125272–

C-125276, in a section located about three km south of Section 4B in a locality referred to as Section 4BP. Ages are based on conodonts and foraminifers (Beauchamp et al., 1989b; Beauchamp and Henderson, 1994; Henderson et al., 1995; Pinard and Mamet, 1998).

SVERDRUP BASIN GEOLOGY

The Sverdrup Basin is a large pericratonic rift basin located within the northern part of the Canadian Arctic Archipelago (Fig. 2.2). Filled with clastics, carbonates, cherts, and evaporites, the basin displays a nearly complete record of early Carboniferous to Eocene sedimentation (Thorsteinsson, 1974; Balkwill, 1978). Early Carboniferous extension created a northeast-trending rift zone through Precambrian to Devonian rocks of the Franklinian Basin, which had already undergone several episodes of tectonism, the latest of which was the latest Devonian–earliest Carboniferous Ellesmerian Orogeny (Thorsteinsson, 1974; Harrison, 1995). The subsequent rift collapse of the orogen created the Sverdrup Basin (Balkwill, 1978).

By the Bashkirian, rifting and basement collapse had progressed enough to allow marine incursions (Nassichuk and Davies, 1980; Embry and Beauchamp, 2008) resulting in the initiation of a large basin-fringing carbonate platform (Fig. 2.2). The period from the mid late Carboniferous to the early Permian
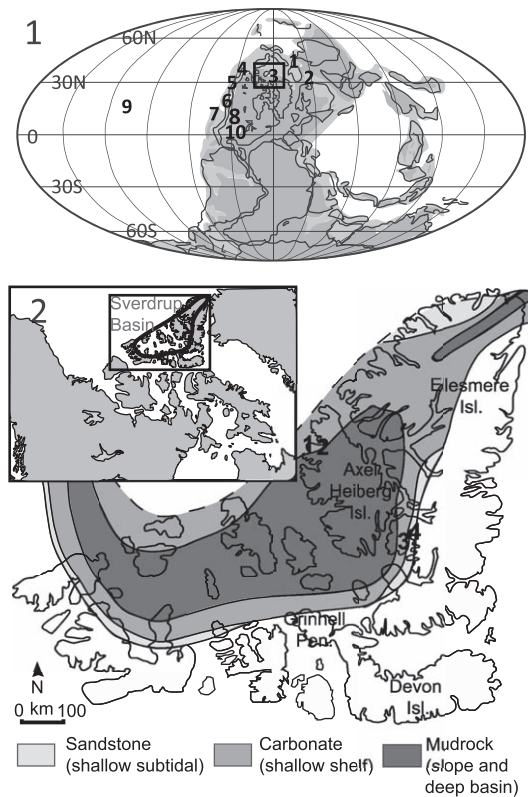
FIGURE 2—Study area. *1,* global paleobiogeography of paleoaplysinids along the northwest margin of Pangea during the Early Permian (map modified from Golonka and Ford, 2000); key: 1=Russian Platform, 2=Svalbard and Barents Sea, 3=Canadian Arctic Archipelago, 4=Yukon Territories, 5=British Columbia, 6=Idaho, 7=California and Nevada, 8=Utah, 9=Japan, 10=Texas; distribution data from Chuvashov (1973), Vennin et al.(2002), Skaug et al. (1982), Lonøy (1988), Stemmerik et al. (1994), Davies and Nassichuck (1973), Beauchamp et al. (1989a), Davies (1971), Macqueen and Bamber (1977), Wardlaw et al. (1996), Breuninger (1976), Watkins and Wilson (1989), Ritter and Morris (1997), Igawa (2003), and Wahlman (2002); red box indicates Canadian Arctic Archipelago; *2,* Late Carboniferous paleogeography of Sverdrup Basin showing shallow water carbonates rimming a deep basin; modified from Embry and Beauchamp (2008). Studied localities: 1=Arthaber Creek, 2=Griesbach Creek, 3=West Blind Fiord, 4=East Blind Fiord.

was a tectonically quiet period of subsidence interspersed by periodic tectonic events that led to fault-controlled subsidence. Rapid generation of accommodation space allowed the growth of a very thick (up to two km) platform carbonate (Davies and Nassichuk, 1990; Embry and Beauchamp, 2008).

The interval from the Bashkirian to the Sakmarian was marked by warm tropical conditions (Beauchamp and Desrochers, 1997; Beauchamp and Baud, 2002), which allowed the formation of thick carbonate shelves of the Nansen Formation characterized by photozoan biotic elements, including ooids, oncoids, and abundant reef mounds constructed of various types of calcareous algae (red, phylloid, dasycladacean) as well as palaeoaplysinids. The Nansen Formation comprises a series of cyclothems—high-order sequences on the scale of a few meters to tens of meters (Fig. 3). These cycles are likely to have formed in response to glacio-eustatic fluctuations (Morin et al., 1994; Beauchamp and Olchowy, 2003; Embry and Beauchamp, 2008), as suggested by similar-aged cycles found throughout the world (Heckel, 2002) and widespread evidence of glaciation in Gondwana (e.g., Montañez et al., 2007; Fielding et al., 2010; Henry et al., 2010). Nansen shelf carbonates grade laterally into deep basin shales of the Hare Fiord Formation, marginal

sandstones and conglomerates of the Canyon Fiord Formation, carbonates of the Antoinette, Tanquary, and Belcher Channel formations, and evaporites of the Otto Fiord and Mount Bayley formations (Fig. 4). Across the Asselian-Sakmarian boundary following a major base-level drop (Beauchamp and Henderson, 1994; Beauchamp and Baud, 2002), the rich (photozoan) biotic assemblage of the Nansen Formation shifts to the impoverished (heterozoan) assemblage of the Raanes Formation (Fig. 4). The Artinskian represents a return to progradation (Bensing et al., 2008; Embry and Beauchamp, 2008) and a significant cooling event, as shown by widespread heterozoan carbonates of the Great Bear Cape Formation and correlative deep-water Trappers Cove Formation (Beauchamp and Henderson, 1994).

Paleoaplysinid plates are common in the Nansen Formation, where they contribute to large build-ups hundreds of meters thick (Beauchamp et al., 1989a). They also occur in the carbonate shelf cycles of the Belcher Channel and Tanquary Formations and as fragments in the transitional slope-to-basin argillaceous limestone and debris flows of the Hare Fiord Formation (Davies and Nassichuk, 1973). *Palaeoaplysina* also occurs in the lower part of the Raanes Formation (Beauchamp and Henderson, 1994), and has been reported at one locality in the Great Bear Cape Formation (Bensing et al., 2008). These latter occurrences place the uppermost range of *Palaeoaplysina* in late Sakmarian to earliest Artinskian at the latest (Fig. 4).

SYSTEMATIC PALEONTOLOGY

Because of the widespread usage in the literature of terms such as "mamelons" or "canals" when referring to these features, morphological terminologies are used here according to their classical application to the features of *Palaeoaplysina* by the first formal English descriptions (Chuvashov, 1973; Davies and Nassichuk, 1973) irrespective of the biological origins of some terms. All specimens are archived at the Geological Survey of Canada (GSC), Calgary, Alberta.

Class RHODOPHYCEAE Ruprecht, 1851
Order ARCHAEOLITHOPHYLLALES Chuvashov *in* Chuvashov et al., 1987
Family PALAEOAPLYSINACEAE Vachard and Kabanov, 2007
Genus PALAEOAPLYSINA Krotov, 1888
PALAEOAPLYSINA LAMINAEFORMIS Krotov, 1888
Figures 1.1, 5.1–5.3, 5.5, 5.6, 6.1–6.9

Diagnosis.—Hummocky lamellar thalli penetrated by a series of tubular canals. Lower surface smooth and parallel upper surface. Stacked levels of canals parallel the plate's long axis in plate center. Eventually, canals angle or branch upwards and narrow into complexly branched vertical to sub-vertical canals. Canals pierce upper surface randomly through numerous small subrounded pores. Lower surface not penetrated by canals. Polygonal cellular skeleton between canals. Coarse cellular tissue central to the thallus, and fine cellular tissue lining the peripheral surfaces, including upper and lower surfaces and canals. Rounded mamelons on upper porous surfaces abundant to absent.

Description.—Elongate tabular plate at least 50 cm in length and averaging 2–3 mm in thickness. Plates are often preserved as stacked curved or flat broken plates (Fig. 5.1) which may be oriented mamelons-up or mamelons-down. Fragments are often rounded, abraded and variably micritized. Longer plates are often undulated (Figs. 5.2, 6.4) or folded (Fig. 5.3), suggesting an organism that was not fully calcified. Accordingly, ductile folds can be recognized by compression of canals in the inner part of fold axis (Fig. 6.5). In shorter fragments brittle fractures (Fig. 6.6) are equally common, most likely reflecting intra-skeletal early marine cementation. Where preserved, plate edges thin and flatten (Fig. 6.7). In some cases, plate edges thin so much that they lose
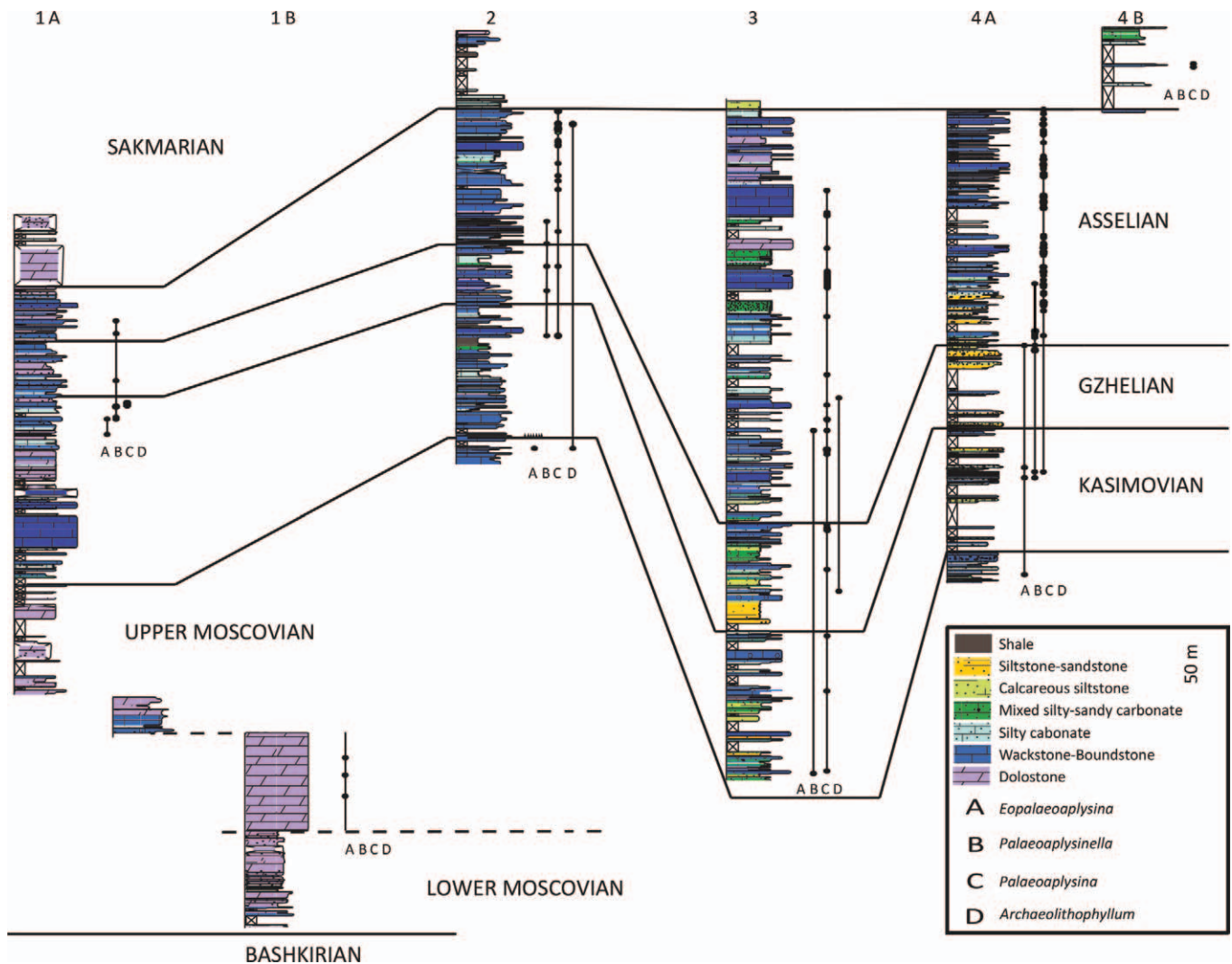
FIGURE *3*—Studied sections and stratigraphic range of paleoaplysinids; frequent repetition of lithologies is a characteristic expression of late Paleozoic cyclothems; see Figure *2.2* for location; biostratigraphic age correlations are based on small foraminifers (Mamet et al., 1987; Henderson et al., 1995; Pinard and Mamet, 1998) and conodonts (C. M. Henderson, unpublished Ph.D. thesis, 1989; Beauchamp and Henderson, 1994; Henderson et al., 1995). Observed occurrences of paleoaplysinids and *Archaeolithophyllum* Johnson, 1956 indicated by dots.

their canals systems and could be mistaken for *Archaeolitho-phyllum lamellosum* Wray, 1964.

Thallus is perforated by canals perpendicular, sub-perpendicular, or parallel to the length of the plate. Canals elongate parallel to long axis of the plate, extending horizontally in a series of sub-parallel layers through plate thallus. Canals are more perpendicular towards superior surface, and subdivide more frequently (Fig. 6.8). Canal diameter is 0.1–0.3 mm in plate center, anastomose and narrow towards superior plate surface into pores that are 0.06–0.14 in mm diameter and appear to open to environment. Stellate canal structures are not observed. Inferior plate surface is smooth and imperforated.

Cellular skeleton is rarely preserved. Where preserved, the cell wall is ~0.002 mm thick and composed of micrite or fine sparite which appears yellow in plane-polarized light. Cell structure is mostly visible through fill by fibrous calcite crystals perpendicular to cell wall, or more rarely micrite fill. Cells are pentagonal, tetragonal, or trigonal, and equant to tabular in shape, and may be elongated parallel to plate surface. There are two cell populations; small cells (0.125–0.37 mm) towards the plate edge and lining the canals, large cells (<0.25 mm) toward plate center (Figs. 7.1, 7.2,

8.1). Common mamelon protuberances on the upper surfaces, ~2–5 mm high, may reach a height of as much as 7 mm and are 3–6 mm wide. In the third dimension, mamelons are most often spherical, or rarely elongated tabular-like protrusions (Fig. 6.9). In some specimens, mamelons are abundant and more or less equally spaced (Fig. 5.5), but are more commonly rare and scattered unevenly (Fig. 5.6). The presence of stellate canal openings (Ryabinin, 1955), and canal septa (Chuvashov, 1973) have been described only once and are not considered here to be characteristic. The upper mamelon-bearing surface may be encrusted by foraminifers, gastropods, and algae. These epibionts rarely cover the entire plate, sometimes penetrating down into the canals (Fig. 6.3). In some instances, mamelons are significantly more encrusted by epibionts than the smoother plate surface in between the mamelons (Fig. 6.9).

Occurrence.—Kasimovian until the late Sakmarian, East Blind Fiord and West Blind Fiord, Ellesmere Island, Canadian Arctic.

Remarks.—The cellular structure is usually dissolved and destroyed (Fig. 6.8), but can be exceptionally preserved through various diagenetic preservation. Figure 8.1 illustrates five different styles of preservation: 1) complete to near-complete dissolution of cellular wall and mould-filling by sparry calcite

cement; ghostly outline of cells are locally present; 2) neomorphic spar replacement of cell walls, and fill of cells interiors by micrite cement; 3) micritization of cellular wall structure and filling of cell interior by sparry calcite cement; 4) well-preserved yellowish cell walls and sparry calcite fill of cells interior; and 5) well-preserved yellowish cell walls and cells interiors lined by early fibrous cement; remaining pore space filled by later sparry calcite cement. The best-preserved cellular structures show cells that grow from small cells lining the canals and plate surface to larger cells in the plate center (Fig. 7.1, 7.2).

Difficulty may exist in differentiating poorly preserved *Palaeoaplysina*, *Archaeolithophyllum* (mostly A. missouriensis Johnson, 1956), and large phylloid algae. Vachard and Kabanov (2007) noted that many algae classified as phylloid in areas of abundant *Palaeoaplysina* may, in fact, be poorly preserved paleoaplysinids. *Palaeoaplysina* and *Archaeolithophyllum* may also be easily mistaken depending on the cut through the plate and the preservation of canals and cellular structure. If preservation of the internal skeleton is poor, and if canals are not easily distinguished by a different matrix fill, it may be difficult to differentiate these two organisms as both have morphologically similar cellular skeleton structure and similar alteration pathways.

A seemingly primitive paleoaplysinid was illustrated by Vachard and Kabanov (2007) as *Palaeoaplysinella*, based on smaller size and simple canals. However, illustrated samples are likely eroded bioclasts and not a distinct genus (Figs. 7.3, 7.4, 8.2). Specimens of this type are found in bioclastic, oolitic, or other high-energy facies, but do not appear in reefs and low energy facies. Clasts are always rounded, variably micritized and may either lack encrusting epibionts or rarely be entirely encrusted as proto-oncoids. Meanwhile, *Palaeoaplysina* typically possesses encrusters on one side of the plate suggesting regular growth without strong erosion. Although mamelons occur in *Eopalaeoaplysina* and *Palaeoaplysina*, they are not present in *Palaeoaplysinella*, and were likely removed during erosion of the plates (Fig. 8.2). The canals in the center of *Palaeoaplysina* are often similar in width and complexity to the simple canals of *Palaeoaplysinella*. In *Palaeoaplysinella* canals may be open to both sides of the plate. On abraded surfaces where the outer layer has been stripped, canals can be visible as fine parallel ridges, which run along the plate long axis. The range of *Eopalaeoaplysina*, *Palaeoaplysina*, and *Palaeoaplysinella* partially overlaps in the Sverdrup Basin (Fig. 3), but *Palaeoaplysinella* occurs predominantly in high-energy basin margin settings, such as in grainstones and packstones of the Belcher Channel Formation at Grinnell Peninsula, Devon Island (Beauchamp et al., 1998; Fig. 6.17a). For these reasons, the genus *Palaeoaplysinella* of Vachard and Kabanov (2007) is here considered invalid. In light of extensive analysis of paleoaplysinids in the Sverdrup Basin, it is suggested *Palaeoaplysinella* synonymous with either *Palaeoaplysina* or *Eopalaeoaplysina* in the Canadian Arctic.

Family PALAEOAPLYSINACEAE Vachard and Kabanov, 2007
EOPALAEOAPLYSINA new genus

Type specimen.—*Eopalaeoaplysina daviesi* n. gen. (by monotypy).

Diagnosis.—As for the type species.

Etymology.—Older stratigraphic range than *Palaeoaplysina*.

Occurrence.—Moscovian to Kasimovian reefal limestones of Ellesmere and Axel Heiberg islands, Sverdrup Basin.

Remarks.—*Eopalaeoaplysina* is differentiated from *Palaeoaplysina* by its comparatively simpler canals systems. *Palaeoaplysina* possesses an extremely complex canal system that displays frequent bifurcation and anastomosing. The range of
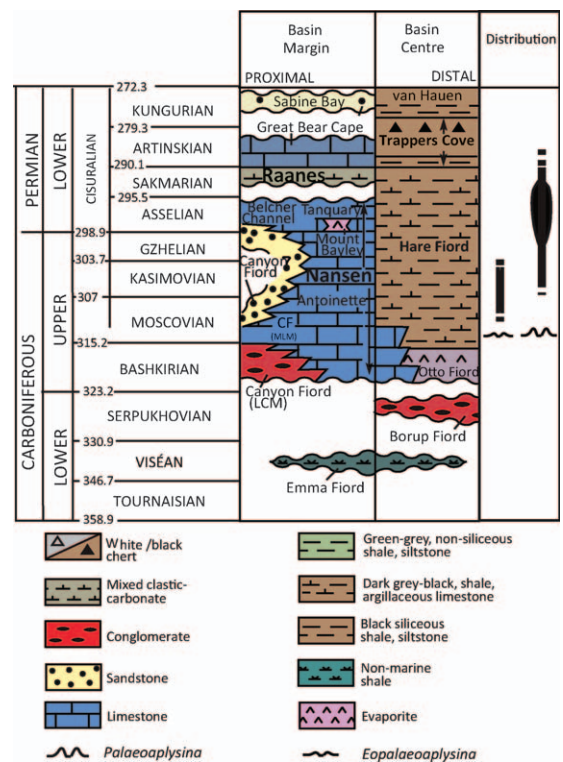

FIGURE 4—Carboniferous to lower Permian stratigraphic chart of the Sverdrup Basin (modified from Embry and Beauchamp, 2008); paleoaplysinids are commonly found in the upper Carboniferous to lower Permian Nansen, Canyon Fiord, Belcher Channel, and Tanquary formations and rarely in the Hare Fiord Formation.

Eopalaeoaplysina and *Palaeoaplysina* overlaps during the Kasimovian.

Although both *Palaeoaplysina* and *Eopalaeoaplysina* are monospecific genera, there are sufficient morphological differences between the primitive *Eopalaeoaplysina* and the more advanced *Palaeoaplysina* to warrant attribution of the former to a new genus. This is in accord with the common practices by specialists in the taxonomy of calcareous algae (e.g., Wray, 1977; Mamet et al., 1987; Vachard and Kabanov, 2007). Additionally, the more advanced (and most common) paleoaplysinid—*Palaeoaplysina*—is known universally by its generic name, and not its species name (*P. laminaeformis*). Establishing *Eopalaeoaplysina* as a separate genus will prevent confusion among carbonate sedimentologists who otherwise are likely to use *Palaeoaplysina* interchangeably for two very different specimens without mention of the species.

EOPALAEOAPLYSINA DAVIESI new species
Figure 9.1–9.5

1990 *Palaeoaplysina* sp., DAVIES AND NASSICHUK, fig. 18a.
1997 *Palaeoaplysina* sp., RITTER AND MORRIS, p. 399, fig. 4.
2012 *Palaeoaplysina* sp., ZUBIN-STATHOPOULOS ET AL., fig. 5H.

Diagnosis.—Plate-like thalli penetrated by a series of tubular canals. Canals in plate center run parallel to plate surface in a series of somewhat regularly spaced semi-continuous parallel rows from which straight, unconstricted secondary canals branch perpendicularly. These are unlike the complexly bifurcated and anastomosing canals in *Palaeoaplysina*. Secondary canals connect to the upper surface through numerous wide round perforations roughly aligned into rows. Canals penetrate thalli on one side only and form blind terminations within plate. Polygonal
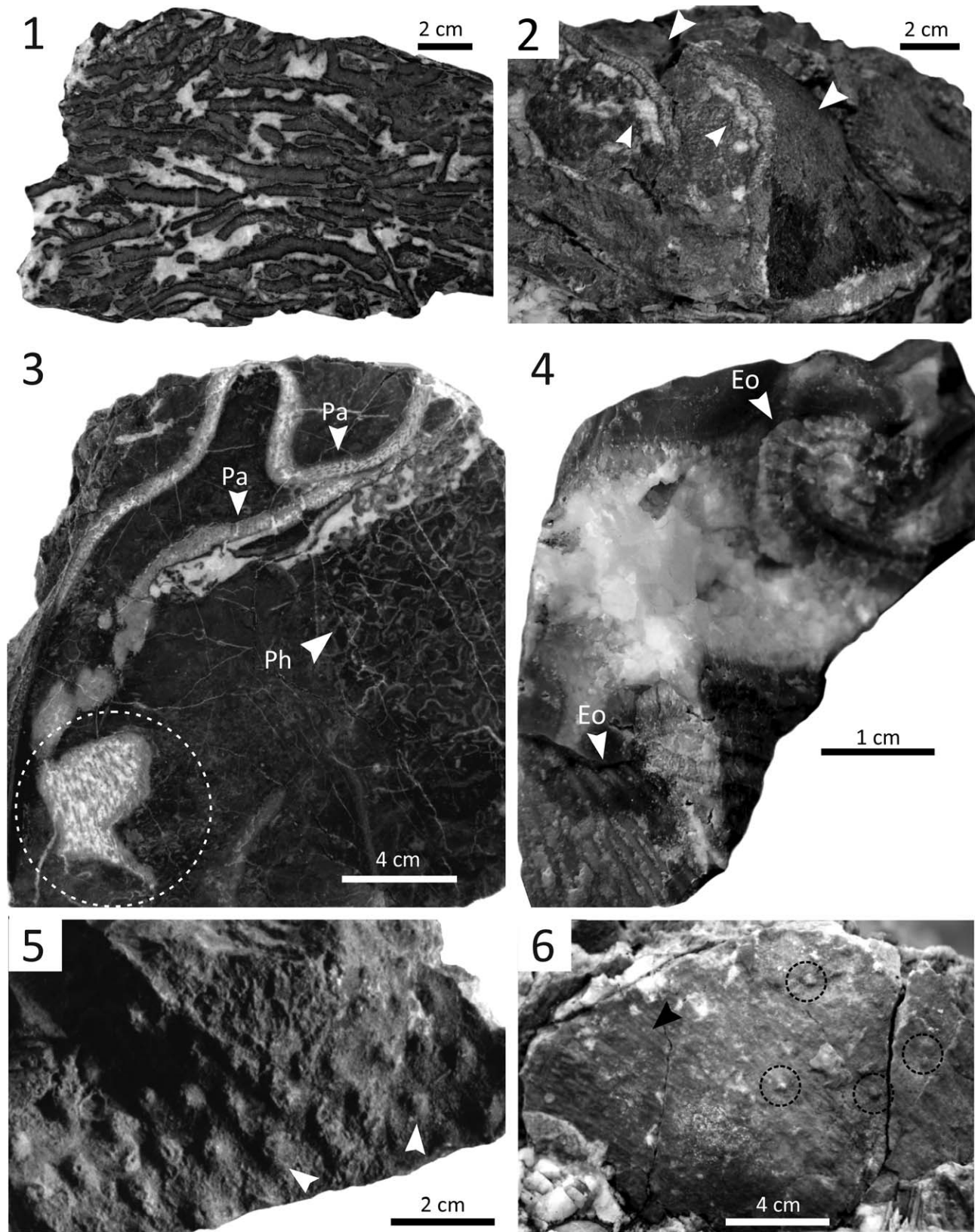
FIGURE 5—General morphology of paleoaplysinids in hand sample. *1,* stacked *Palaeoaplysina* Krotov, 1888 plates; (C-540849, Section 3); *2,* overturned *Palaeoaplysina* plate displaying irregular contouring (arrows) and smooth lower plate surface (C-540849, Section 3); *3,* recumbent long (46 cm) *Palaeoaplysina* plate (Pa), partly cut in plan view (circle); numerous phylloid algae (Ph) are present beneath geopetal fabric (C-540849, Section 3); *4, Eopalaeoaplysina* n. gen. partial erosion of lower surface reveals parallel canals (arrows) (C-115613, Section 1); *5,* top view of *Palaeoaplysina* plate with closely and evenly spaced mamelons (white arrows); *6,* top view of *Palaeoaplysina* plate with scattered mamelons (circles) and faint parallel canals and striations (black arrow) (C-540849, Section 3).
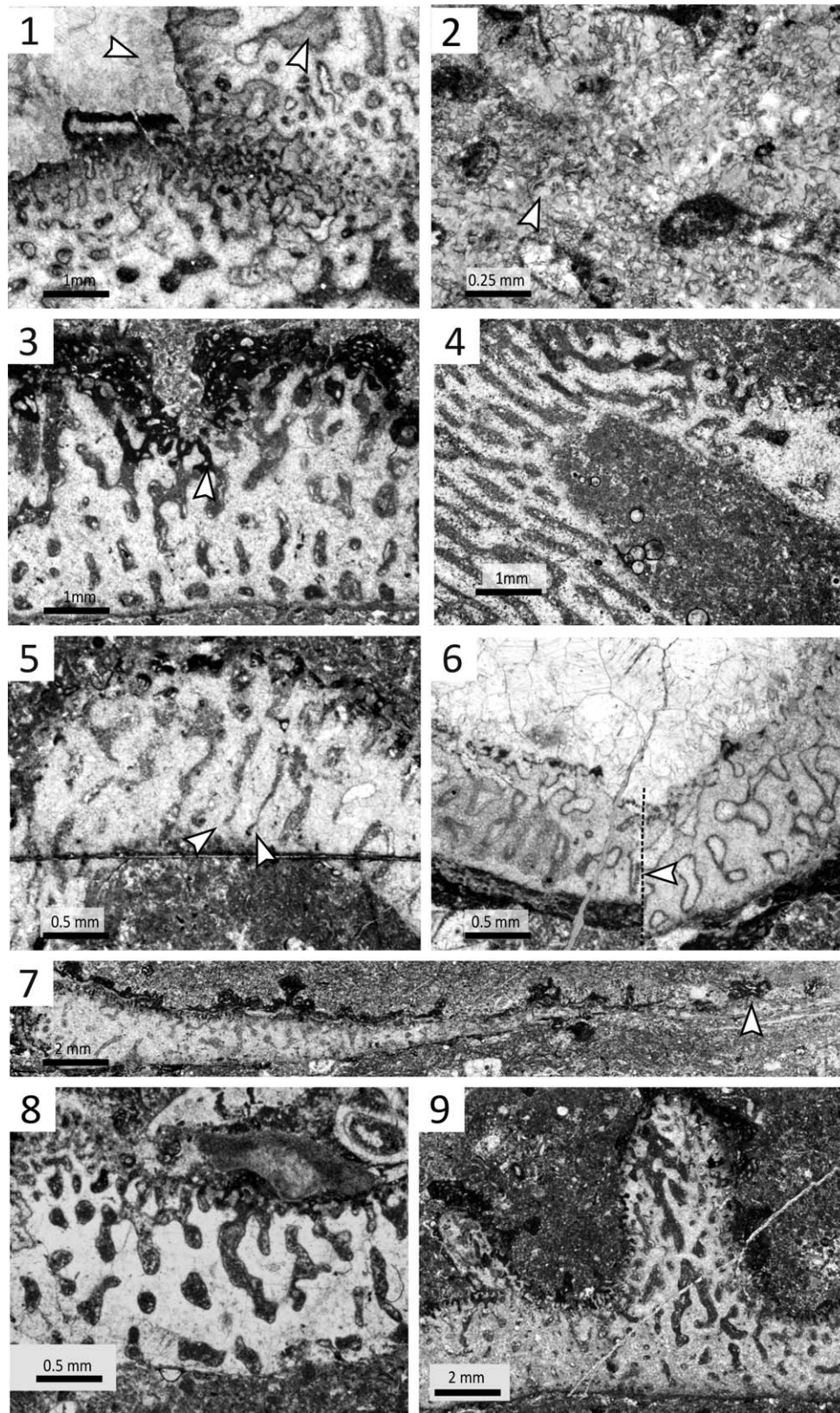
FIGURE 6—Photomicrographs of *Palaeoaplysina* Krotov, 1888 in plane polarized light. All specimens from Section 4BP (C-125272–C-125276); *1,* fine crystalline cement rim lining canals grading into coarse crystalline spar in the plate center; isopachous cement lines the plate and canals (arrows); *2,* detailed view of cellular skeleton with fibrous cement fill growing perpendicular to cell wall (arrow); *3, Palaeoaplysina* with closely spaced mamelons; encrusters penetrate into canal system (arrow); *4,* undulated *Palaeoaplysina* plate showing change in orientation of canals; *5,* ductile deformation of folded plate; note the distortion of the canals in the center of the fold axis (arrows); *6,* brittle fracturing (arrow) of a bent *Palaeoaplysina* plate; *7,* encrusted *Palaeoaplysina* plate thinning along length (arrow); *8, Palaeoaplysina* plate with complexly branched canals bifurcating upwards; *9,* elongated mamelons with encrusting epibionts.
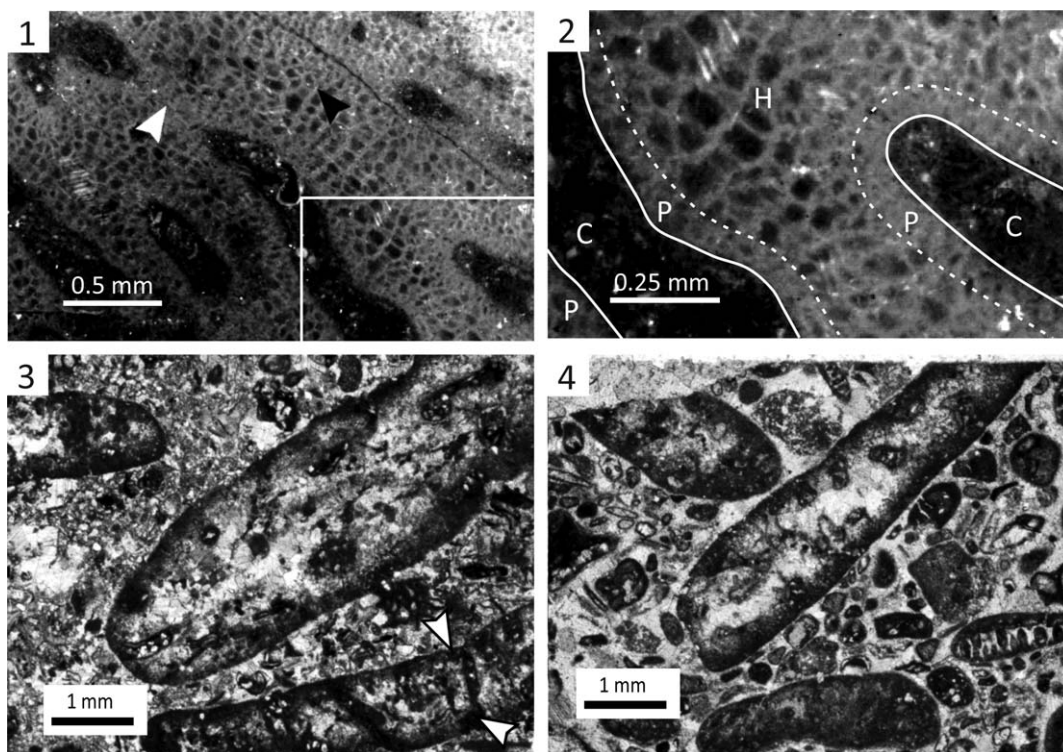
FIGURE 7—Preservation extremes of paleoaplysinid plates. *1,* excellent preservation of paleoaplysinid cellular skeleton in reflected light; larger cells (black arrow) midway between the canals (dark areas) with fine cells (white arrow) surrounding the canals (Section 4BP); area shown in *2* outlined by white rectangle; *2,* details of *1* showing clear distinction between small cells of perithallus (P) and much larger cells of hypothallus (H), occupying the space in between the micrite-filled canals (C); *3,* poor preservation of abraded paleoaplysinid plate with simple wide canals that penetrate both sides of the plate (white arrows) (C-131892, Section 4); similar abraded specimens have been described as *Palaeoaplysinella* by Vachard and Kabanov (2007); *4,* rounded and abraded paleoaplysinid clast in bioclastic packstone (C-131891, Section 4).

cellular skeleton between canals with fine cellular tissue lining the peripheral surfaces, including upper and lower surfaces and canals. Coarser cellular tissue away from surfaces. Rare rounded mamelon thickenings on porous side.

Description.—Hummocky lamellar thalli. Lower surface smooth and parallel upper surface. The average plate thickness is 2–3 mm, or up to 4.5 mm where rare rounded protuberances (mamelons) on one side create local thickening (Fig. 9.1). Maximum length of plate fragments is 50 cm, however broken plate ends suggests much larger size. The plate is penetrated by broad canals with a constant diameter of 0.3–0.4 mm. These canals are manifested by their micrite, early marine fibrous, or sparry cement fills. Canals open to the superior surface of the plate as sub-rounded to oval pore openings 0.3–0.4 mm in diameter (Fig. 9.5). The inferior surface is smooth and featureless. Longitudinal to canal long axis, canals are parallel to the plate surface, ~0.5–1 mm depth into the plate. When erosion removes the plate surface, canals are exposed parallel to sub-parallel down the plate length. From long canals, secondary canals branch at uneven intervals perpendicular upwards to the plate surface. In transverse cut, canals are broad, parallel, non-anastomosed and unbranched (Fig. 9.1, 9.3).

Where preserved, a cellular skeleton is present within plate (Fig. 9.2). Cellular fabric often removed by early diagenetic solution and later mold filling by sparry calcite. Cells are polygonal to tabular, grading from fine (0.01–0.06 mm) along plate edges and around canals, to coarse (0.01–0.06 mm) in the plate center. Cell walls are preserved as dark micrite or yellowish-hued cement. Epibiont encrusters are unknown on any of the example specimens.

Etymology.—After seminal English descriptions of *Palaeoaplysina* in the Sverdrup Basin by Dr. Graham Davies, whose benchmark research was done in collaboration with Dr. Walter Nassichuk of the Geological Survey of Canada in the 1970s.

Occurrence.—Arthaber Creek B on Axel Heiberg Island, 188 m above base, C115618. Early late Moscovian–Kasimovian, GSC locality C-115518–C-115618, lower Nansen Formation, Sverdrup Basin, Canadian Arctic Archipelago; Moscovian, Belcourt Formation, British Columbia; early Desmoinesian (mid to late Moscovian), Ely Limestone, Utah.

Types.—Twelve specimens in eight samples reposited at the GSC, Calgary. Holotype: C115618, (Fig. 9.1). Paratypes: C115016, C115010. Arthaber Creek on Axel Heiberg Island.

Remarks.—*Palaeoaplysina* and *Eopalaeoaplysina* have similar cellular skeletons in size, distribution and coloration. *Palaeoaplysina* and *Eopalaeoaplysina* canals have the same maximum diameter. However, *Eopalaeoaplysina* pore diameters are the same as in the plate center, while in *Palaeoaplysina* canals branch and narrow upwards to create constricted pores. *Eopalaeoaplysina* has a strongly ridged appearance in hand specimen (Fig. 5.4), due to the lack of constriction of pores and more even spacing of canals along the plate length compared to the smooth appearance of unweathered *Palaeoaplysina*. *Eopalaeoaplysina* canals in longitudinal cut are long semi-continuous horizontal tubes parallel plate surface with intermittent straight vertical branches. These simple, straight canals are diagnostic features of *Eopalaeoaplysina*. In *Palaeoaplysina* these horizontal tubes are multi-leveled with many complex branches that gradually angle upwards to become complexly branched upright canals. Unlike sponges, paleoaplysinid canals do not form a network or latticework of interconnected tubes. Plate thickness between the two genera is nearly the same, although *Palaeoaplysina* is slightly thicker. Mamelons are rare in *Eopalaeoaplysina*, and appear to be simple plate thickenings. Mamelons in *Palaeoaplysina* are more hemispherical, spherical to elongate protrusions, which may
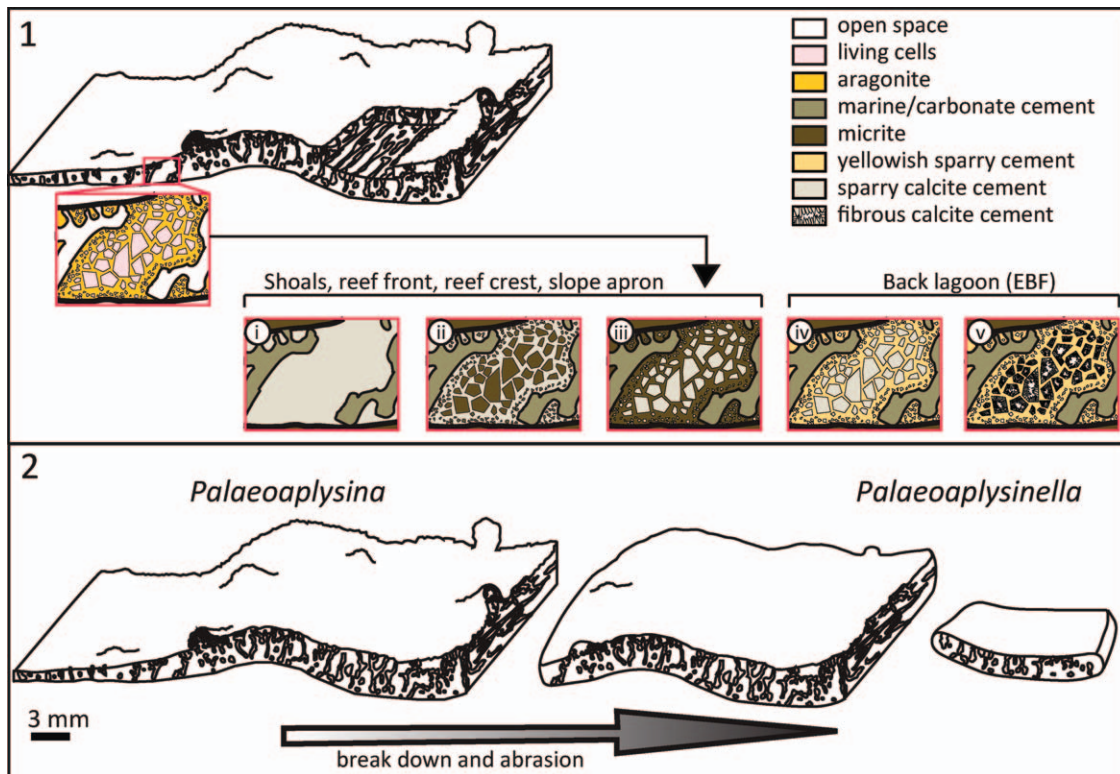
FIGURE *8*—Schematic depiction of the physical and chemical alteration steps responsible for the final appearance (megascopic and microscopic) of *Palaeoaplysina* Krotov, 1888 plates. *1,* preservation styles of *Palaeoaplysina* plates and their cellular skeleton; steps (i) to (v) are discussed in the text; *2,* advanced physical abrasion leads to smaller, variably rounded pebble-sized bioclasts with apparent simple canals and without mamelons that may be misidentified as a separate form, i.e., *Palaeoaplysinella* of Vachard and Kabanov (2007). Note preferential erosion of finely porous upper surface.

range from common to absent. Both are associated with carbonate reef build-ups, as well as shoal sediments.

BIOLOGICAL AFFINITY

Three morphologically distinct genera are recognized in the Sverdrup Basin. Kasimovian–Sakmarian reef-building *Palaeoaplysina* is equivalent to *Palaeoaplysina laminaeformis* Krotov, 1888. Simpler morphologies have been observed (e.g., Beauchamp, 1992; Ritter and Morris, 1997; Vachard and Kabanov, 2007) and were generally grouped informally as "ancestral *Palaeoaplysina*" (Beauchamp, 1992) (Figs. 5.4, 9). These simpler forms are recognized as *Eopalaeoaplysina* in this study. *Eopalaeoaplysina* n. gen. was observed to occur in early late Moscovian–Kasimovian reef-buildup settings. Vachard and Kabanov (2007) erected the genus *Palaeoaplysinella* from Russian samples of Moscovian age based on a smaller size, simple and wide canals that do not constrict towards pore openings, a lack of mamelon protuberances, and a restriction to non-reef building facies. A number of specimens described in this study correspond closely to *Palaeoaplysinella*. However, the eroded and abraded nature of the bioclasts in addition to their restriction to high-energy bioclastic and oolitic facies indicate this appearance is related to taphonomic preservation factors, rather than a distinct genus. In the Canadian Arctic, *Palaeoaplysinella* comprises abraded bioclasts of *Palaeoaplysina* and likely *Eopalaeoaplysina* as well. It is also thus likely that the Moscovian specimens of *Palaeoaplysinella* described and illustrated by Vachard and Kabanov (2007) are reworked *Eopalaeoaplysina*, however diagnostic features have been removed by abrasion.

Palaeoaplysina was initially defined as a sponge (Krotov, 1888), but was later reinterpreted as a hydrozoan (Ryabinin,

1955; Breuninger, 1976; Davies, 1971; Davies and Nassichuk, 1973), and subsequently as an alga (Watkins and Wilson, 1989; Kiessling et al., 1999; Wahlman, 2002; Scholle and Ulmer-Scholle, 2003; Flügel, 2004; Vachard and Kabanov, 2007). Table 1 lists the biologic arguments for each proposed affinity.

Some authors have raised the possibility that *Palaeoaplysina* represents a symbiotic or parasitic relationship between multiple organisms (Wahlman, 2002). For instance, it has been suggested either as an animal (sponge?, hydrozoan?) in which an ancestral coralline alga, such as *Archaeolithophyllum,* has invaded the inner tissue (Mamet et al.,1987), or as an alga that was invaded by protists, sponges, or algae without a calcareous wall, creating canal-like openings (Vachard and Kabanov, 2007). Most modern photosynthetic symbionts in hydrozoans or corals are round unicellular dinoflagellates known as zooxanthellae (Flügel, 2004). These zooxanthellae themselves do not form a calcified skeleton structure. One genus of Hydrozoa—*Hydra*—is known to have symbiosis with unicellular green algae, however these algae are contained within the vacuoles of the cells, and do not colonize the tissue itself (Ahmadjian and Paracer, 1986).

Chuvashov (1973) made comparisons to the Stromatoporoidea on the basis of the internal canal system and mamelon-like protuberances, as well as the rare occurrence of stellate canal openings associated with the mamelons, which was reported only once (Ryabinin, 1955). Since their original classification, the stromatoporoids have been redefined as a sclerosponge, or coralline sponge (Stern et al., 1999; Finks and Rigby, 2004). The removal of the stromatoporoids from the hydrozoans reduces the fossil record of the latter to a few genera restricted to the Mesozoic (Flügel, 2004). Paleoaplysinids exhibit no
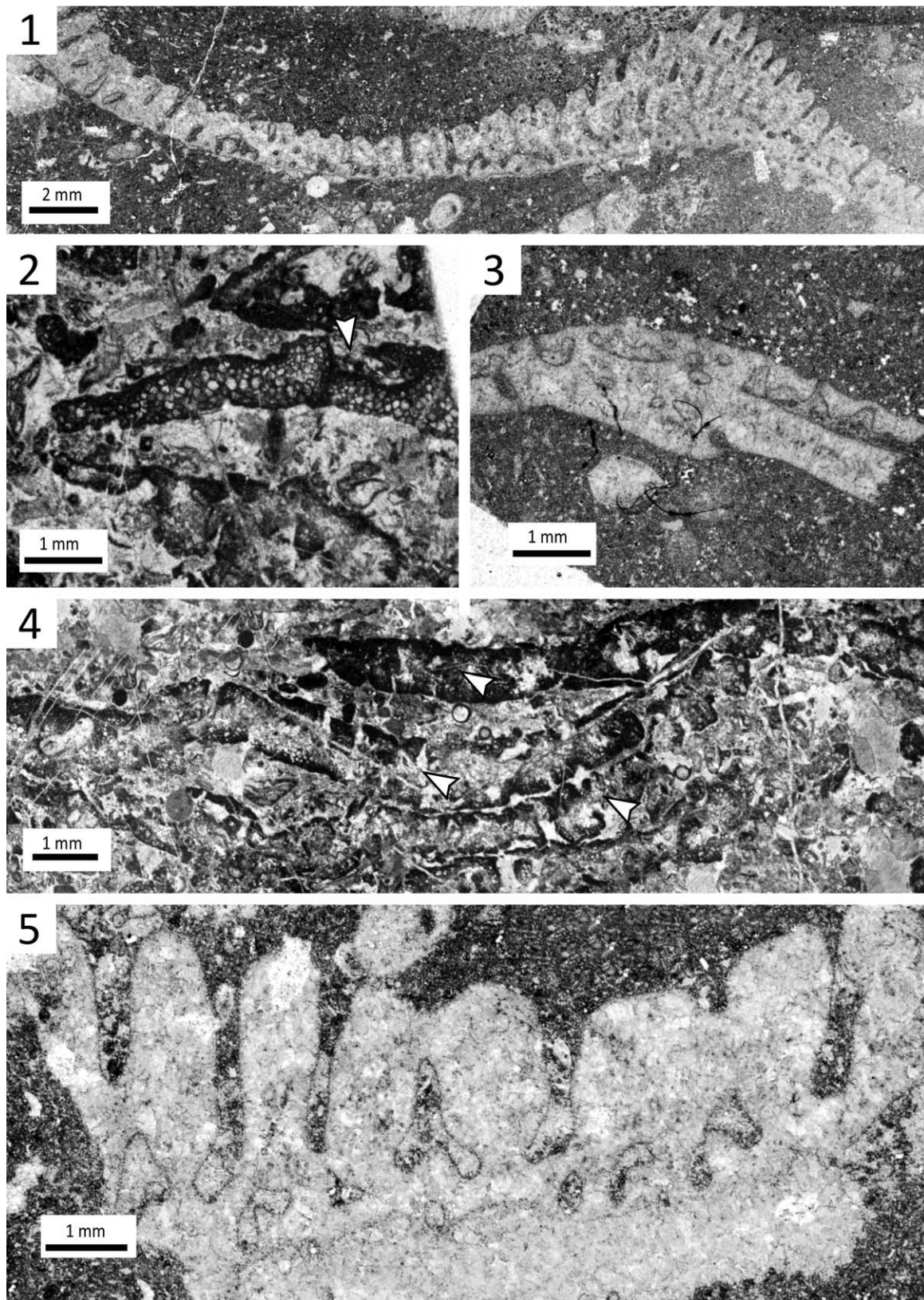
FIGURE *9*—Photomicrographs of *Eopalaeoaplysina* n. gen. in plane polarized light. *1,* large *Eopalaeoaplysina* plate displaying simple, non-bifurcated canals, wavy plate surface, and a simple mamelon (C-115615, Section 2); *2,* preserved cellular structure with finer cells lining the plate surface the single, simple canal (arrow) (C-115016, Section 2); *3,* shallowly penetrating canals which coalesce into a single main canal; view parallel to long direction of plate (C-115618, Section 2); *4,* accumulation of *Eopalaeoaplysina* plates in packstone with poorly preserved but still observable cellular structure, and simple, shallow canals (arrows) (C-115010, Section 2); *5,* fragment of thick (>4 mm) plate with broad canals that do not constrict into pores at the surface (C-115618, Section 1).

TABLE 1—Biological affinity arguments for paleoaplysinids. Typical characteristics of each group are summarized in the table. Features that are in agreement with those features found in fossil paleoaplyinids are in bold.

	Mamelons	Reproduction	Canal system	Cellular skeleton	Mineralogy	Other
Palaeoaplysina	**present** **populated by canal system**	**unknown**	**parallel multi-level rows** **upper(?) surface pore openings** **non-partitioned**	**polygonal** **fine outer, coarse inner cells**	**aragonite**	**rhizomes** **photic zone**
Sponges sclerosponge	none	larvae	complex, radiating **non-partitioned** incurrent and excurrent	non calcified cellular skeleton	non calcified cellular skeleton fibrous aragonite fans/ sclerodermites	perforated cortex
stromatoporoidea	**present** populated by radiating canals	larvae	radiating evenly throughout entire body	**cellular skeleton** square cells (laminae/ pillar)	**aragonite** or high Mg-calcite	uncommon from the Carboniferous-Triassic
Hydrozoans	**present**	budding/ larvae	partitioned radiating	thick walled, porous cells jelly-like mesoglea colonial specialization of body	**aragonite** or high Mg-calcite	**no spicules** no fossil analogues **rhizomes** radial symmetry
Algae green	none		branched filament system filaments small, round cross-section	none	**aragonite**	**photic zone**
red coralline	**non-functional 'warts'**	calcified conceptacles	none	**polygonal** **fine outer, coarse inner cells** arcuate rows	calcite	**encrusting**, branching, nodules, erect **photic zone**
peyssonellid	**non-functional 'warts'**	non-calcified structures	none	**polygonal** **fine outer, coarse inner cells** arcuate rows	**aragonite**	**rhizomes** **prone-semi-erect crusts** basal calcification **photic zone**
Symbiotic	possible	possible	possible	intercellular or intracellular		often dinoflagellates or green algae **photic zone**

evidence of hydrozoan colonialism, and the fossils still considered calcareous hydrozoans exhibit no evidence of cellular preservation (Hill and Wells, 1956), greatly weakening the argument for a hydrozoan affinity of *Palaeoaplysina* and *Eopalaeoaplysina*.

Paleozoic stromatoporoids have a basal calcareous skeleton of cellular tissue and lack spicules (Stern et al., 1999). The wall structures of stromatoporoids display laminae with pillars that create horizontal and radial arrangements. Chuvahov (1973) also suggested there may be transverse septa in the canals that he compared to the tabulae of the stromatoporoids. However, no subsequent researchers have described septa within the canals. Unlike *Palaeoaplysina*, stromatoporoid canals are narrow and ramify throughout the body creating an interconnected canal network rather than forming discrete tubular openings isolated from one another. Furthermore, stromatoporoid canals are astrorhizal and coalesce towards the center to form a central axial canal. Stromatoporoid cells are thick, subspherical porous elements, unlike the finely walled polygonal cells of paleoaplysinids.

Inozoan sclerosponges (unsegmented sponges) also possess a superficial resemblance to *Palaeoaplysina. Pseudopalaeoaplysina* is an inozoan sponge named for its resemblance to *Palaeoaplysina* (Fan et al., 1991). However, inozoan skeletons were fibrous, not cellular (Rigby et al., 1989), with a wall microstructure composed of spherulitic or radiating fans of aragonite or sclerodermites (Finks and Rigby, 2004). Inozoan canals are arranged radially and include both inhalant and exhalant canals arranged in a functional network (Finks and Rigby, 2004).

Some authors (Kiessling et al., 1999; Flügel, 2004) favor an algal origin for *Palaeoaplysina* supported by the presence of the cellular skeleton with cells similar in shape to the hypothallus of *Archaeolithophyllum* (Vachard and Kabanov, 2007) and environmental restriction to the photic zone in association with phylloid and dasycladacean algae. Some authors support a codiacean green algal association (Watkins and Wilson, 1989; Wahlman, 2002; Scholle and Ulmer-Scholle, 2003) by suggesting the progressively branched tubular utricles, which pierce the thallus of modern algae, are comparable to the canals of *Palaeoaplysina* (Watkins and Wilson, 1989). However, this affinity is unlikely as the canals of *Palaeoaplysina* are disparate and complexly intertwined, whereas codiaceans lack cellular structure and possess thin round utricles (Davies and Nassichuk, 1973; Vachard and Kabanov, 2007). Arguing against a red algal origin is the presence of the canals. No known rhodophyte exhibits a canal system (Flügel, 2004), and hypotheses are rarely attempted to explain these more animal-like characteristics. The universal connectivity of the canals to the environment through pores on the upper surface and the fact that internal cells increase in size away from them suggests the canals are integral parts of paleoaplysinid plates, and are unlikely to be merely borings. The perithallus lining of the canals indicate they represent invaginations of the upper surface of the plates possibly to increase the surface area exposed to sunlight descending from above. Additionally, an algal origin was originally rejected due to the lack of cellular organization in *Palaeoaplysina* into arcuate rows as in *Archaeolithophyllum* (Davies and Nassichuk, 1973). However, closer examination of exceptional specimens shows that both *Palaeoaplysina* and *Eopalaeoaplysina* clearly have tissue differentiation into a coarse hypothallus and fine perithallus lining the plate edge and canals (Fig. 7.1, 7.2).

Vachard and Kabanov (2007) proposed an association with *Archaeolithophyllum*, generally characterized as an ancestral

coralline red alga (e.g., Wray, 1964, 1977; Flügel, 2004). As mentioned above, paleoaplysinids lack the advanced organization of cells into arcuate rows, as observed in many (but not all) specimens of *Archaeolithophyllum missouriensum* Johnson, 1956 and *Archaeolithophyllum johnsoni* Racz, 1964, as documented in Mamet et al. (1987). Nevertheless, these authors attributed the cellular structure of *Palaeoaplysina* from the Yukon Territory to *Archaeolithophyllum missouriensum*. However, these authors believed *Archaeolithophyllum* and *Palaeoaplysina* to be two distinct organisms, and alga and an animal. They interpreted *Palaeoaplysina*'s cellular skeleton to have been *Archaeolithophyllum* encrusting and replacing the internal soft parts of the former. The principal argument against this interpretation is the fact that individual cells forming the cellular fabric become increasingly large inward away from both the outside plate surface and the internal canal walls. Clearly, the cells and canals belonged to the same organism. The cellular organization of *Palaeoaplysina* and *Eopalaeoaplysina* is also very similar to other genera of Archaeolithophyllaceae, especially *Neoprincipa* (Cozar and Vachard, 2003, figs. 5, 6) with a randomly arranged coarse hypothallus and a fine outer perithallus lining. The similar preservation of cell structure, aragonitic plate composition, and similar paleoenvironments suggest paleoaplysinids are likely related to the Archaeolithophyllaceae.

It has been shown that the plates of *Archaeolithophyllum* were originally aragonitic (Moshier and Kirkland, 1993). Although generally classified as ancestral coralline red algae (Wray, 1964), this composition is divergent from the Mg-calcite composition of other Corallinaceae. It has been proposed that this, and the occasional appearance of pendant aragonitic botryoids on *Archaeolithophyllum* plates, may demonstrate a relationship to the rhodophyte group Peyssonneliaceae (Squamariaceae) (James et al., 1988; Moshier and Kirkland, 1993) which are a type of encrusting red algae with similar cellular tissue to that of the corallinaceans, but composed of aragonite, instead of high-Mg calcite (Wray, 1977). This family possesses widely varying styles of calcification, which may or may not include calcification of the thallus (James et al., 1988). It is possible Palaeoaplysinaceae and perhaps Archaeolithophyllaceae may be ancestral peyssonnelids.

Fossil peyssonnelaceans are known from the Early Cretaceous, but may include some questionable phylloid algae from the late Carboniferous and Permian (Wray, 1977). Fossils such as *Pseudolithothamnium* may present excellent cellular structure preservation and a yellowish-brown tint in thin section (Wray, 1977; James et al., 1988), similar to specimens of *Palaeoaplysina* from EBF. Other lines of evidence linking *Palaeoaplysina* to the Peyssonneliaceae are the ventral spines of *Archaeolithophyllum* (Forsythe, 2003) and the newly described rhizoids of *Palaeoaplysina* (Nakasawa et al., 2011). A peyssonellid affinity may resolve one argument against an algal origin. Reproductive organs in living peyssonnelids are not protected by conceptacle walls (James et al., 1988) and thus do not fossilize, providing a possible explanation for lack of conceptacles in *Palaeoaplysina* and *Eopalaeoaplysina*.

Mamelons have been proposed to represent reproductive structures (Davies, 1971), due in part to their transitory occurrence. These features may represent some kind of budding feature, however elongated and pinched mamelons are relatively rare. They are unlikely to represent red algae cystocarps, a swelling formed after fertilization (Wray, 1977). Cystocarps contain a reproductive carposporophyte, and are more like a protective envelope. Paleoaplysinid mamelons are connected to the canals system and contain the same cellular skeleton as the

rest of the plate. There is no evidence that mamelons may have been an attempt to avoid encrusting epiphytes. Encrusters are more likely to grow on the mamelons, perhaps because these features provide elevated surfaces, but also less commonly on the plate surface around them, and their penetration into the canals suggests they are likely a post-mortem feature.

PALEOECOLOGY

Eopalaeoaplysina n. gen. and *Palaeoaplysina* occur in similar facies on both the southeastern and northwestern margins of the Sverdrup Basin (Fig. 3). *Eopalaeoaplysina* is found from the lower upper Moscovian to the lowest Gzhelian, while *Palaeoaplysina* ranges from the Kasimovian to the upper Sakmarian. At Arthaber Creek B on Axel Heiberg Island (Section 1B), *Eopalaeoaplysina* is found within boundstones, and has contributed to a reef build-up over 100 m thick. East of Blind Fiord, *Eopalaeoaplysina* is found more rarely as rounded clasts within bioclastic to oolitic facies. *Eopalaeoaplysina* is less common than *Palaeoaplysina*.

Palaeoaplysina may form massive build-ups up to 100 m thick, as in West Blind Fiord. Plates occur in peloidal, spongiostromid (microbial) fabric, and are associated most frequently with phylloid algae and epimastoporid dasycladacean algae. *Epimastopora*, and often *Epimastoporella* are nearly ubiquitous in *Palaeoaplysina*-bearing units. Phylloid algae are also common. Along the reef edges, plates may be found stacked within floatstone and rudstone fabrics (Fig. 5.1). *Palaeoaplysina* may also be found in wackestone or packstone associated with small encrusting foraminifers, or as rounded clasts in mixed bioclastic facies, oolitic facies, or oncoidal facies, which typically preserve most of the fossils also associated with the reef deposits. Best-preserved specimens are found in the back reef packstone of EBF (Section 4BP). *Palaeoaplysina* also colonized the back-reef environment, associated with other algae (phylloid or dasycladacean). Here the dominant matrix is fine-grained muds and peloids, and grains show little sign of abrasion or breaking.

Paleoaplysinids flourished and formed reefs in sub-tropical to warm temperate clear, shallow open marine conditions below fair weather wave base (Beauchamp and Desrochers, 1997). These favorable settings mostly developed on basin-facing carbonate shelves. Model examples of such buildups are found at Arthaber Creek B (*Eopalaeoaplysina*) and WBF (*Palaeoaplysina*) outcrops. Paleoaplysinid plates found in reef build-ups and back-reefs are clearly in situ, often preserved as large, intact plates. In comparison, paleoaplysinids found within bioclastic grainstones, oolitic, or oncoidal grainstones are likely clasts transported from their habitats of reefs or lagoons into the high-energy swash zones (i.e., *Palaeoaplysinella* of Vachard and Kabanov, 2007). The diversity of environments suggests paleoaplysinids may have preferred moderately high energy systems, but was also capable of colonizing moderate energy leeward or lagoonal sites.

The facies distribution of *Palaeoaplysina* is very similar to that of udoteacean phylloid algae of the same time period, although the paleogeographic range of udoteaceans extended much further south (Davies, 1971; Wahlman, 2002). Although paleoaplysinids range from the latest early Moscovian (Kashirian) to the end of the Sakmarian (Mamet et al., 1987), they largely flourished during the Asselian–Sakmarian. Throughout the Sverdrup Basin, a close association of *Palaeoaplysina* with the dasycladacean algae *Epimastopora* was observed. Similarly Breuninger (1976) reported a relationship with *Eugonophyllum* and other calcareous phylloid algae in Idaho. This evidence may

point towards a similar environmental cause behind the flourishing of *Palaeoaplysina* and other forms of algae.

Palaeoaplysina plates are strongly asymmetric, with mamelons and canal openings restricted to one side. It has been variously proposed that *Palaeoaplysina* may have had an erect body and acted as a sediment baffler (Davies and Nassichuk, 1973), semi-erect and acted as a sediment trap (Beauchamp et al., 1989a), or that it may have had an encrusting growth form and acted as a sediment binder (Davies, 1971; Breuninger, 1976; Skaug et al., 1982). Based on availability of substrate area, and in order to increase access to nutrients and light, it was speculated that paleoaplysinids probably grew erect, and the common stacking of plates is a relict of preservation (Davies and Nassichuk, 1973). While it is likely that stacks of plates found along the reef flanks may have been caused by depositional forces in which waves ripped up plates and deposited them flat, plate asymmetry suggests an originally recumbent or flat-lying position of *Palaeoaplysina* plates.

The thin edges of plates (Fig. 6.7) are suggestive of an encrusting habit, as these edges are unlikely to have been able to withstand high-energy water currents. Additionally, the reports of "rootlet"-like ventral rhizomes from paleoaplysinids in Japan (Nakasawa et al., 2011) suggests *Palaeoaplysina* plates were recumbent or, at most, semi-erect in the water column. Davies and Nassichuk (1973) rejected an encrusting habit in part on the basis of lack of evidence for hard-ground encrustation. However, while some peyssonellids grow as petaloids anchored by a basal attachment, many of the Peyssonneliaceae grow as prone arching plates of encrusting algae (Wray, 1977), and can form their own solid substrate on muds (James et al., 1988). If *Palaeoaplysina* was an encruster, it may have contributed to the formation of reefs as a frame-builder, sediment-binder and sediment trap.

Paleobiogeography and evolutionary considerations.—Paleoaplysinids are found along the northwest margin of Pangea (Fig. 2.1) with notable exclusion from the lowermost tropical and equatorial latitudes such as in the Tethyan Ocean. The open connection between the Tethyan Ocean and the Uralian seaway created unusually warm conditions along the northwest margin of Pangea (Reid et al., 2007), extending the range of photozoan biota as far north as 40–45°N during the late Carboniferous–early Permian. There are however, major differences between the tropical Tethyan photozoan biota and the coeval subtropical NW Pangean biota. For instance organisms such as inozoan and sphinctozoan calcareous sponges and the incertae sedis *Archaeolithoporella*, which contributed to widespread reef development in the Tethys (Wahlman, 2002), are absent in coeval deposits along NW Pangea (Beauchamp and Desrochers, 1997). Likewise, there is a significant drop in the abundance and diversity of foraminiferal, algal, and conodont populations along NW Pangea (Mamet et al., 1987; Pinard and Mamet, 1998; Henderson et al., 2012; Schmitz and Davydov, 2012). This indicates a significant temperature gradient existed between both areas.

As the red algal precursor to *Palaeoaplysina* moved into higher latitude sub-tropical waters (substantially cooler than their low latitude counterparts, but unusually warm for the western margin of a continent), it developed adaptations to take advantage of these specific environmental conditions. Beginning in the Moscovian, the simple *Eopalaeoaplysina* begins to develop small invaginations, eventually evolving into the complexly canaled *Palaeoaplysina*. It is possible that these invaginations evolved to increase the surface area of these algae and thus their exposure to sunlight, which would have declined substantially at higher latitudes, especially during the winter months. Meanwhile, *Archaeolithophyllum* which is found in upper Carboniferous and lower Permian deposits throughout the western United States,

but also in Europe (Spain, Yugoslavia, and the Eastern Alps) (Mamet et al., 1987; Flügel, 1981) did not extend far into these waters, remaining within the 15°N limit in spite of presumably favorable warm conditions (Wray, 1977; Wahlman, 2002). Only the much thinner *Archaeolithophyllum lamellosum* is known to occur farther north.

Paleoaplysinids may have been restricted to more northern conditions rather than moving into the significantly warmer temperatures between 15°N and 15°S because they had evolved to take advantage of higher latitudes conditions. *Palaeoaplysina's* distant cousin, *Archaeolithophyllum* was far better adapted to warmer, more direct light, and these conditions may in themselves have formed a formidable barrier to paleoaplysinid southward migration. Whatever the cause, *Palaeoaplysina* was completely maladapted to move in warmer better-lit environments of the southern latitudes. As the Uralian connection began to close, shallow ocean temperatures began to drop, and the northwest margin of Pangea to cool (Reid et al., 2007). *Palaeoaplysina* moved into narrow near-shore refuges from the Sakmarian to possibly early Artinskian (Bensing et al., 2008). It may be speculated that the closure of the Uralian connection in the late Artinskian and subsequent cooling left *Palaeoaplysina* unable to escape from these marginal conditions, thus leading to its subsequent demise.

CONCLUSIONS

Similar to primitive Archaeolithophyllaceae, *Palaeoaplysina* and *Eopalaeoaplysina* n. gen. possess cellular differentiation into a coarse inner hypothallus, and a fine outer perithallus which lines the plate edge and canals. The cellular skeleton, photic zone distribution, aragonitic composition, and close association with other algae suggest paleoaplysinids are rhodophytes. Palaeoaplysinaceae may be related to the Peyssonneliaceae (Squamariaceae).

Two distinct genera of paleoaplysinids have been identified in the Sverdrup Basin; *Eopalaeoaplysina* n. gen, and *Palaeoaplysina*. These genera represent an increase in complexity over time, with simpler *Eopalaeoaplysina* with broad, unbranched, non-anastomed canals found in the Moscovian through the Kasimovian, and the thicker and more complex *Palaeoaplysina* ranging from the early Kasimovian until the earliest Artinskian. Both may occur in large reefs on Ellesmere and Axel Heiberg islands. *Palaeoaplysina* flourished in reef settings, but also inhabited back-reef or lagoonal environments. The asymmetrical nature of the plates and preservation of very thin plate edges suggest *Palaeoaplysina* was an encrusting or procumbent organism.

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