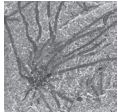


# Systematics of pterobranchs from the Cambrian Period Burgess Shales of Canada and the early evolution of graptolites

GRETA M. RAMÍREZ-GUERRERO & CHRISTOPHER B. CAMERON



Pterobranchs originated in the basal Cambrian (Fortunian) and are mostly known by their tubes preserved in the fossil record. The earliest forms are represented by bushy erect growing colonies that are not widely studied due to their scarcity, preservation quality and species misidentification. For this reason, early phylogenetic relationships within the group are not clearly established. Middle Cambrian Burgess Shale graptolites were poorly known, based on the presence of *Chaunograptus scandens*, some debatable species of the genus *Yuknessia*, and other undetermined fragmented material. This study represents a complete description of *C. scandens*, a consensus for *Yuknessia simplex* and *Y. stephenensis*, and new reports of *Protohalecium hallianum* and *Mastigograptus* sp. from the Burgess Shale localities, which have also been found in other Burgess Shale type localities in Utah and Australia. Phylogenetic analyses of 34 discrete morphological traits from these Burgess Shale genera and some known benthic and planktic taxa ( $n = 22$ ), place these Cambrian species as basal forms closer to the pseudocolonial pterobranch *Cephalodiscus* and the living graptolite *Rhabdopleura*. • Key words: graptolites, Hemichordata, middle Cambrian, Burgess Shale.

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Graptolithina is a subclass of cosmopolitan marine colonial pterobranch hemichordates mostly known by their tubes, preserved in the fossil record since the Cambrian Period. Graptolites differ from their sister group Cephalodiscida, by the presence of a stolon system that supports a colonial lifestyle, the presence of a larval prosicula, and the anatomy of the zooids. Although zooids with preserved morphological details are essentially unknown among fossil graptolites, zooid anatomy is well known from the extant species *Rhabdopleura* (Mitchell *et al.* 2013, Maletz & Beli 2018). The subclass comprises the orders Dendroidea, which includes the benthic organisms with an encrusting to erect, bushy morphology formed by irregular branching, as well as the derived, planktic Graptoloidea (Maletz 2014b, Maletz & Cameron 2016).

Due to poor fossil preservation, taphonomic processes, and similarities in morphology between taxonomic groups, identification of the specimens is difficult and sometimes mistakenly done, especially in Cambrian forms. The useful criteria to define a graptolite, when the soft-tissue material is not available, include an organic tubarium with fusellar structures surrounded by secondary cortical tissue, and the stolon system (Mitchell *et al.* 2013).

Even when these characteristics are preserved, scanning electron microscopy is frequently used to obtain the most details from the specimens; otherwise, mostly outlines of organic-walled fossils are available for determination (Maletz *et al.* 2005, LoDuca *et al.* 2015a).

An example of misidentified pterobranchs is the genus *Yuknessia*, which was originally regarded as an alga (Walcott 1919), but is now recognized as one of the earliest known pterobranchs from the Cambrian Series 3, based on the SEM identification of fuselli in two species (Steiner & Maletz 2012, LoDuca *et al.* 2015a). Like *Yuknessia*, a closer look at other taxa may establish a pterobranch affinity (*e.g.*, *Dalyia racemata* and *Malongitubus*; Maletz & Steiner 2015, Hu *et al.* 2018. See Maletz & Beli 2018 for further discussion). We refer to these early forms simply as pterobranchs, based on their organic tubes with fusellar structures, because it is nearly impossible to classify them as cephalodiscids or graptolites.

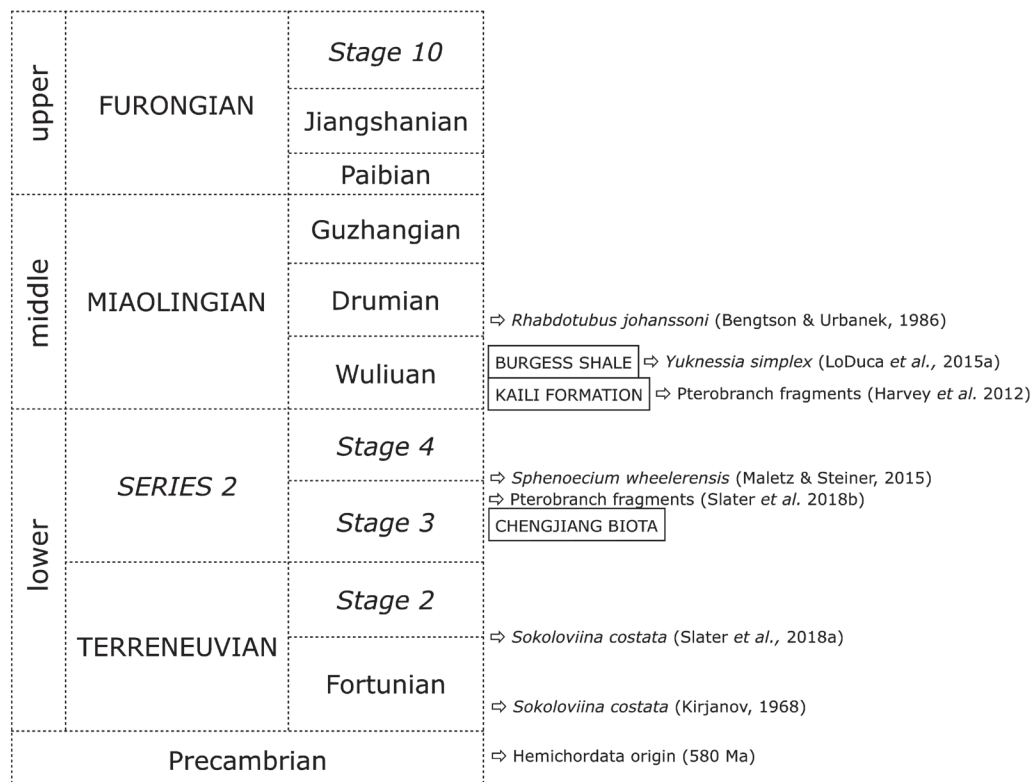
The pterobranch fossil record from the early and middle Cambrian is less complete compared to the Ordovician and Silurian periods (Rickards & Durman 2006), making difficult our understanding of the origin and early evolution of graptolites. It is known that early graptolites

represent benthic forms that originated in the Cambrian, some *incertae sedis* taxa persisted into the Recent, and the order Dendroidea until the Carboniferous. Less long is the existence of the planktic Graptoloidea, which lived from the Early Ordovician until the Early Devonian (Rickards & Durman 2006, Maletz 2014a).

Maletz (2019a) recognized the oldest pterobranch record from the early Cambrian (Terreneuvian, possibly Fortunian) from fragments identified as *Sokoloviina costata* from the Rovno Horizon, Ukraine (Kirjanov 1968). *S. costata* was also identified in the transition between the Fortunian and Stage 2, from the Lontova Formation in Estonia (Slater *et al.* 2018a). Other small pterobranch fragments have been found in a Burgess Shale-type deposit in North Greenland (Series 2, Stage 3) (Slater *et al.* 2018b). True colonial pterobranchs (Graptolithina) are known from the early middle Cambrian (Series 2, Stage 4) such as *Sphenoecium wheelerensis* (Maletz & Steiner 2015) (Fig. 1). Graptolites then radiated and exhibited a large disparity before the Late Ordovician extinction (Bapst *et al.* 2012), and until recently were thought to

have gone extinct during the Carboniferous. Mitchell *et al.* (2013) placed the living benthic *Rhabdopleura* within the Graptolithina, however, based on similarities of the tubarium construction and structure. Rhabdopleurids then, are living benthic graptolites that have survived from the Cambrian to the present (Mitchell *et al.* 2013).

Acorn worms (Cameron *et al.* 2000, Simakov *et al.* 2015) and pterobranchs (Romer 1967, Jefferies 1986) are generally regarded as key groups to understand the origin of the deuterostome phyla. Rickards & Durman (2006) and Maletz & Steiner (2015) described some Cambrian graptolites and provided a possible scenario of their early evolutionary relationships, but neither made detailed reference to Burgess Shale forms. Herein we provide a taxonomic classification of the pterobranchs from Burgess Shales of British Columbia, Canada within the context of other early Paleozoic pterobranch species. We then use these taxa and characters to revise the phylogenetic character matrix of Mitchell *et al.* (2013), to resolve the origins and early evolution of Pterobranchia.



**Figure 1.** Earliest Cambrian pterobranch records, based on organisms that show some features that recognize them as authentic pterobranchs. Molecular clocks estimate the origin of hemichordates in the Ediacaran (580 Ma). Oldest record is *Sokoloviina costata* from the Rovno Horizon, Ukraine (basal Cambrian) and some possible fragments identified as the same species from the Lontova Formation, Estonia from the transition between Fortunian–Stage 2. *Galeaplumosus abilus* was identified as a possible pterobranch zooid from the Chengjiang Biota (Hou *et al.* 2011), however, a cnidarian affinity has more support. Small carbonaceous fragments of pterobranchs were collected from the Buen Formation, Sirius Passet, Greenland from the Stage 3. Later records consist of more complete species found in different localities. *Sphenoecium wheelerensis* is considered the oldest record of a true colonial graptolite and *Rhabdotubus johanssoni* as the oldest recognized rhabdopleurid.

## Methods

All the specimens were collected in the middle Cambrian localities of Walcott Quarry, Miller Pass, Haiduk Peak, and Trilobite Beds, in Southeastern British Columbia, and curated at the Royal Ontario Museum and the Royal Tyrrell Museum. Since the specimens are flat and reflective, they were photographed using direct and cross-polarized light, under dry and wet conditions to capture different details; high resolution photographs were obtained using a Leica M125C stereoscopic microscope.

Backscatter scanning electron microscopy was used as a non-destructive technique to reveal ultrastructural characteristics of thin-walled fossils with organic remains, such as the presence of preserved diagnostic fusellar or stolon structures. The fossils analyzed were preserved on sediment surfaces and no isolation attempts were made. Specimens were glued on sample holders and covered with carbon tape to reduce electron charging. All the samples were examined uncoated under low and high vacuum conditions with accelerating voltages of 5–15 kV, at different working distances depending on the thickness of the slabs, on a JEOL JSM-6610LV, in the Department of Earth Sciences, University of Toronto. Measurements of the specimens were made through digitally processed images.

## Phylogenetic analysis

A phylogenetic analysis was performed using 22 taxa and 34 discrete morphological traits. The taxa included most of the pterobranch genera examined in Mitchell *et al.* (2013), plus the taxa reported here from the Burgess Shale (*Yuknessia*, *Chaunograptus*, and *Protohalecium*). The two species of tubicolous Cambrian acorn worms (*Spartobranchus tenuis* and *Oesia disjuncta*) were used as outgroups. The morphological character traits used were those of Mitchell *et al.* (2013), with some modifications based on recent literature (Tab. 1), and character states for the acorn worm outgroups including aspects of their tubes. These changes are indicated in bold in the character matrix (Tab. 2).

*Chaunograptus* is very likely a graptolite yet this has not been confidently demonstrated because we did not identify fuselli. It was included in the analysis because the thecal organization is similar to other benthic forms (acute conical alternated thecae). *Cephalodiscus Orthoecus/Idiothecia* and *Cephalodiscus Cephalodiscus/Acoelothecia* were included as in-groups, rather than treated as paraphyletic outgroups as per Mitchell *et al.* (2013), due to the inclusion of the basal tubicolous enteropneusts as the new outgroup.

The main challenge when trying to find diagnostic characters in pterobranch fossils is the poor preservation

**Table 1.** Updated list of literature consulted for the character matrix coding and discussion additional to the sources cited by Mitchell *et al.* (2013).

Genus	Reference
<i>Chaunograptus</i>	Ruedemann (1931), Ruedemann (1947), Urbanek (1986), Caron & Jackson (2008), Maletz & Beli (2018)
<i>Yuknessia</i>	Walcott (1919), LoDuca <i>et al.</i> (2015a, b), Maletz & Steiner (2015)
<i>Spartobranchus</i>	Caron <i>et al.</i> (2013)
<i>Oesia</i>	Nanglu <i>et al.</i> (2016)
<i>Epigraptus</i>	Bengston & Urbanek (1986), Mitchell <i>et al.</i> (2013)
<i>Protohalecium</i>	Quilty (1971), Rickards & Durman (2006)
<i>Callograptus</i>	Ruedemann (1931)
<i>Dendrotubus</i>	Maletz <i>et al.</i> (2016)
<i>Kozlowskitubus</i>	Mierzejewski (1988)
<i>Dictyonema</i>	Maletz (2019b)
<i>Bulmanicrusta</i>	Maletz (2014b)
<i>Bithecocamara</i>	Maletz (2014b)
<i>Cephalodiscus</i>	Maletz & Gonzalez (2017)
<i>Rhabdopleura</i>	Kozlowski (1966)

of the tubes and the almost total absence of zooids. In most cases, only outlines or dim imprints of the organic tube remain for identification. Poor preservation hampers the identification of small differences in tube structure. In these cases, we sometimes found additional characters states using computed tomography or scanning electron microscopy.

A list of phylogenetically informative external characters and character states including absence/presence or multistate attributes is provided below. The character descriptions were taken from Kozlowski (1949), Bulman (1970), Urbanek & Mierzejewski (1984), Rickards & Durman (2006), Mitchell *et al.* (2013), Maletz *et al.* (2014), Maletz *et al.* (2016) and focus on structures usually observed in dendroid-like graptolites, meaning that the planktic forms may not accurately fit into this terminology.

- 1) Prosicula: Proximal conical part of the sicula (initial zooid constructed tube) where the larva undergoes metamorphosis [0 – absent; 1 – vesicular (rounded or truncated); 2 – tubular; 3 – caudal/pointed];
- 2) Helical line: Spiral outline around the prosicula (do not confuse with regular fuselli) (0 – absent; 1 – present);
- 3) Metasicular opening in prosicula: Refers to the pore left by the emergence of the first zooid in the early development of the tube; it is observed between the prosicula and metasicula. If the change is gradual and smooth is considered as ‘primary’, whereas ‘resorption’ is observed as an abrupt angular transition formed

**Table 2.** A – data matrix including 22 pterobranch and enteropneust species of 34 morphological characters used to establish the group relationships. Bold face states are modified from the morphological matrix of Mitchell *et al.* (2013), plus two additional characters, the new Burgess Shale graptolite species (*Chaunograptus*, *Yuknessia* and *Protohalecium*), and the enteropneusts outgroup (*Spartobranchus* and *Oesia*). • B – statistics.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
<i>Acanthograptus</i>	2,3	?	2	?	0	1	?	1	2	1	2	1	4	0	1	0	1	1	0	2	0	1	2	?	0	0	0	1	1	2	3	1	0	1
<i>Koremagraptus</i>	?	?	?	?	0	1	?	1	2	?	2	1	4	0	1	0	1	1	0	2	0	1	2	?	0	0	0	1	1	2	3	?	0	1
<i>Anisograptus</i>	3	1	2	2	0	1	1	3	2	0	2	1	4	0	1	1	1	0	1	2	0	2	1	2	0	0	0	1	1	2	3	1	0	1
<i>Rhabdinopora</i>	3	1	2	2	0	1	1	3	2	0	2	1	4	0	1	1	1	2	1	2	0	2	1	2	0	0	0	1	1	2	3	1	0	1
<i>Dictyonema</i>	2,3	?	2	?	0	1	1	1	2	1	2	1	4	0	1	0	1	3	1	2	0	2	2	?	0	0	0	1	1	2	3	1	0	1
<i>Dendrograptus</i>	2	1	2	2	0	1	1	1	2	1	2	1	4	0	1	0	1	0	0	2	0	2	1	2	0	0	0	1	1	2	3	?	0	1
<i>Mastigograptus</i>	2	?	2	?	0	1	?	1	2	1	2	1	4	0	1	0	0	0	0	1	0	1	1	1	0	0	0	1	1	2	3	1	0	1
<i>Reticulograptus</i>	?	?	?	?	?	1	?	1	2	?	1	1	?	0	1	0	0	1	1	1	0	1	2	2	0	0	1	1	1	?	?	?	0	1
<i>Kozlowskitubus</i>	1	1	2	1	1	1	1	1	1,2	1	1	1	1	1	1	0	0	2	0	1	0	1	2	2	0	0	0	1	1	2	3	0	0	1
<i>Dendrotubus</i>	1	1	2	1	1	1	1	1	2	1	1	1	3	1	1	0	0	1	0	1	0	1	2	2	1	0	0	1	0	?	?	?	0	1
<i>Bulmanicrusta</i>	1	0	2	2	?	1	0	2	1	1	2	1	1	1	0	0	0	0	0	1	1	1	0	2	0	2	0	1	1	1,2	2,3	0	0	1
<i>Bithecamara</i>	?	?	?	?	?	1	?	1	2	1	2	1	2	1	0	0	0	0	0	1	1	1	0	2	0	0	0	1	1	?	?	?	0	1
<i>Cysticamara</i>	?	?	?	?	?	1	?	1	3	1	1	0	0	1	0	0	0	0	0	1	1	1	0	2	0	0	0	0	0	?	?	?	0	1
<i>Epigraptus</i>	1	0	1	2	1	1	0	1	2	?	2	1	3	1	0	0	0	0	0	1	0	1	0	2	0	0	1	1	0	?	?	0	0	1
<i>Rhabdopleura</i>	1	0	1	2	1	1	0	1	2	1	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	2	0	0	0	1
<i>Cephalodiscus CA</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	2	
<i>Cephalodiscus OI</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	2	
<i>Chaunograptus</i>	?	?	?	?	?	1	?	?	?	?	1	1	?	?	0	0	0	0	1	1	0	1	1	?	0	0	0	0	?	?	?	?	0	1
<i>Yuknessia</i>	?	?	1	?	?	1	?	?	?	?	1	1	?	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	?	?	?	?	0	1
<i>Spartobranchus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oesia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Protohalecium</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	0	0	1	0	1	1	1	0	0	0	?	?	?	?	?	0	1

## A

	All taxa; enteropneusts as outgroup	All taxa; enteropneust + <i>Cephalodiscus</i> as outgroup	<i>Chaunograptus</i> excluded	<i>Chaunograptus</i> + <i>Dendrotubus</i> excluded	<i>Chaunograptus</i> + <i>Epigraptus</i> + <i>Epigraptus</i> excluded	<i>Dendrotubus</i> + <i>Epigraptus</i> excluded	<i>Chaunograptus</i> + <i>Epigraptus</i> excluded
Eugraptolithina	100	100	64	71	75	100	71
Tree length	73	73	72	69	65	66	69
Consistency index	0.753	0.753	0.764	0.783	0.815	0.803	0.797
Retention index	0.876	0.876	0.879	0.885	0.904	0.899	0.896

## B

- by resorption by the first thecal zooid (Mitchell *et al.* 2013) (0 – absent; 1 – resorption; 2 – primary);
- 4) Metasicular fuselli: Fusellar growth bands observed in the metasicular (distal tubular part of the sicula) (0 – absent; 1 – irregular; 2 – regular zigzag suture);
- 5) Spiral astogeny: Coiled growth pattern of the first tube around the sicula (0 – absent; 1 – present);
- 6) Serial budding: Sequential zooid budding that originates from the serial stolon system and not another structure like the basal disc (0 – absent; 1 – present);
- 7) Internal autothecae in prosicula: Autothecae originates within the prosicula and not in distal regions of the sicula (0 – absent; 1 – present);
- 8) Stolon type: General form of the stolon (0 – absence; 1 – tubular; 2 – beaded; 3 – unsclerotized/not preserved);
- 9) Stolon position: Location of the stolon within the tube (0 – absent; 1 – embedded in basal wall; 2 – central; 3 – embedded in upper wall);
- 10) Stolon diaphragms: Globular or cup-like expansion in

- main stolon at nodes where daughter stolons branch (at the base of autotheca/bitheca); also known as vesicular diaphragms (0 – absent; 1 – present);
- 11) Budding type: Number of zooids (or its respective branching theca or stolons) budding at each division, it involves the presence of a new autothecae and sometimes bithecae (0 – absence; 1 – diad; 2 – triad);
  - 12) Thecae with stolon system: Refers to the old term ‘stolothecae’ that was considered a type of tube enclosing stolon, for almost all dendroid-like graptolites, is the main tube of the colony. If the autotheca is recognized as the main and larger type of graptolite thecae (as it is for graptoloids), under this parameter, the stolotheca is a synonym of autotheca but as an *immature* form (Bulman 1970). This character is included based on the presence of a pterobranch species (*Cysticamara*) where the stolon is not surrounded by thecal tubes but extrathecal tissue (Kozłowski 1949), as well as *Cephalodiscus* and acorn worms where there is no stolon system (0 – absent; 1 – present);
  - 13) Stolon location within thecorhiza: Position of stolon in the thecorhiza (a compact encrusting basal disc, similar to the creeping tubes in other graptolites) (0 – stolon absent; 1 – encrusting; 2 – on top of thecorhiza; 3 – diverse locations within thecorhiza; 4 – thecorhiza absent);
  - 14) Encrusting: Type of tube growth that is sideways the surface and not upwards (as the erect tubes), this characteristic is inferred from preservation and/or presence of basal membrane; a synonym is creeping or repent: (0 – no; 1 – yes);
  - 15) Erect series of interconnected thecae: Erect tubes show any type of stipe connection (see character 18), excluding erect tubes that are single (0 – absent; 1 – present);
  - 16) Planktic: Colonies that have a free lifestyle, inferred from the absence of encrusting tubes or *in situ* preservation: (0 – no; 1 – yes);
  - 17) Paired dimorphic theca: Presence of paired autothecae and bithecae clearly differentiated (0 – absent; 1 – present);
  - 18) Stipe connection: Type of discontinuous lateral interconnection between branches [0 – absent; 1 – anastomosis (temporary fusion of lateral walls); 2 – dissepiments (connection by cortical material); 3 – thecal bridges (permanent, suggested after Maletz 2019b)];
  - 19) Upright planar tubarium: Colony has a two-dimensional arrangement, excluding bushy or colonies growing upwards from their encrusting tubes, that suggest a tridimensional form (0 – absent; 1 – present);
  - 20) Thecal construction: Refers to the arrangement of the tubes as seen in a cross section (0 – irregular; 1 – tubular with unshared walls; 2 – tubular with shared dorsal walls);
  - 21) Vesicular theca: Presence of any vesicular structure along the tube, like a graptoblast (See character 26) (0 – absent; 1 – present);
  - 22) Autothecal isolation: Degree of separation of the new autotheca from the main tube. For some dendroid-like pterobranchs, distal conical branching thecae are called metathecal/autothecal tubes, as assumed to be autotheca (0 – non-tubular or irregular; 1 – complete or partial; 2 – not isolated);
  - 23) Branch condition: Type of stipe branching [0 – undefined/absent; 1 – stipes possess a single thecal series; 2 – compound (single stipe with several thecal series growing along)];
  - 24) Fusellar sutures on autothecal tubes: Type of fusellar pattern in erect tubes (0 – irregular or absent; 1 – zigzag);
  - 25) Autothecal coiling: Autotheca show a spiral coiling of the erect thecal tube (0 – absent; 1 – present);
  - 26) Closed terminal buds: Refers to the presence of a particular enclosing structure where latent budding zooids develop. Graptoblasts are a type of flattened oval resting cyst with fusellar lines located in the stolotheca and usually observed in Crustoidea and Camaroidea. A similar, yet less specialized enclosing structure has been observed in *Rhabdopleura* and is coded as ‘encapsulated’ (See Urbanek 1983) (0 – absent; 1 – encapsulated; 2 – graptoblast);
  - 27) Conotheca: Large conical theca irregularly developed only in some tuboids (0 – absent; 1 – present);
  - 28) Bithecae: Short type of theca, smaller compared with the autotheca, usually shows an alternated growth side along the stipes, present in triad budding individuals (0 – absent; 1 – present);
  - 29) Spongy extrathecal mass: Spongy tissue present around some thecal walls, mostly observed in *Cephalodiscus* and some encrusting species (0 – absent; 1 – present);
  - 30) Endocortex: Structure of the cortex (laminated cortical tissue that forms the periderm) secreted inside the fusellar tissue, produced by multiple secondary depositions of sheets and intersheet material [0 – pseudocortex (intersheet material lacking fibrous elements); 1 – paracortex (intersheet material as a condensed meshwork of fibrous elements); 2 – eucortex (well defined, straight and parallel fibrils) (Urbanek & Mierzejewski 1984)];
  - 31) Ectocortex: Structure of the cortex secreted outside or above the fusellar tissue (0 – absent; 1 – pseudocortex; 2 – paracortex; 3 – eucortex);
  - 32) Vesicular sheet fabric: Material composed of electron dense, homogeneous, or very densely reticulated pellicle delimiting particular fuselli or layers (Urbanek & Towe 1974) (0 – absent; 1 – present);
  - 33) Tube fibrils: Fine fibrous elements that constitute the



thecal tubes, similar to those observed in *Oesia disjuncta* (Fig. 4F, Nanglu *et al.* 2016) (0 – absent; 1 – present);

- 34) Coloniality: Inferred by the presence of serial branching and the presence of stolons reported in the literature (See Landing *et al.* 2018) (0 – absent; 1 – present).

Unknown states were scored as ‘?’ and polymorphic traits as ‘0, 1, 2, 3 or 4’. Missing characters under the parsimony criterion assign to taxa the character state that would be most parsimonious given its placement on the tree. Therefore, only the characters with no missing data will affect the placement of the taxa (Swofford 2002). Characters were treated as unordered and with equal weight. Analysis were run using PAUP 4.0b10 (Swofford 2002) under the assumptions of parsimony using the heuristic and branch-and-bound search algorithm by bootstrapping using 10,000 replicates. Statistics reported include tree length, consistency index, and retention index. New Technology Analyses with default parameters were also performed in TNT (Goloboff *et al.* 2008), and statistics including tree length and absolute and relative Bremer support values were calculated. Changes of individual characters along branches were tracked using Mesquite 3.51 (Maddison & Maddison 2018).

## Systematic Paleontology

Hemichordata Bateson, 1885

Class Pterobranchia Lankester, 1877

Subclass Graptolithina Bronn, 1849

### Genus *Chaunograptus* Hall, 1882

*Type species.* – *Dendrograptus* (*Chaunograptus*) *novellus* Hall, 1882.

*Emended diagnosis.* – Minute organic theca, creeping and branching, bearing conical tubes with simple and straight apertures (Bulman 1970, Maletz & Beli 2018).

*Remarks.* – The genus was initially considered a hydroid until Obut (1964) classified it as a dithecoid graptolite (Family Chaunograptidae). Mierzejewski (1986) suggested that the type species of *Desmohydra* (*D. flexuosa*) and *Epallohydra* (*E. adhaerens*) resemble that of *Chaunograptus* and therefore those genera should be treated as synonyms. Maletz (2014b) considered the genus as a hydrozoan based on the idea of Mierzejewski (1986). Maletz & Beli (2018) included *Chaunograptus* in the family Rhabdopleuridae and we follow that decision here.

### *Chaunograptus scandens* Ruedemann, 1931 Figure 2

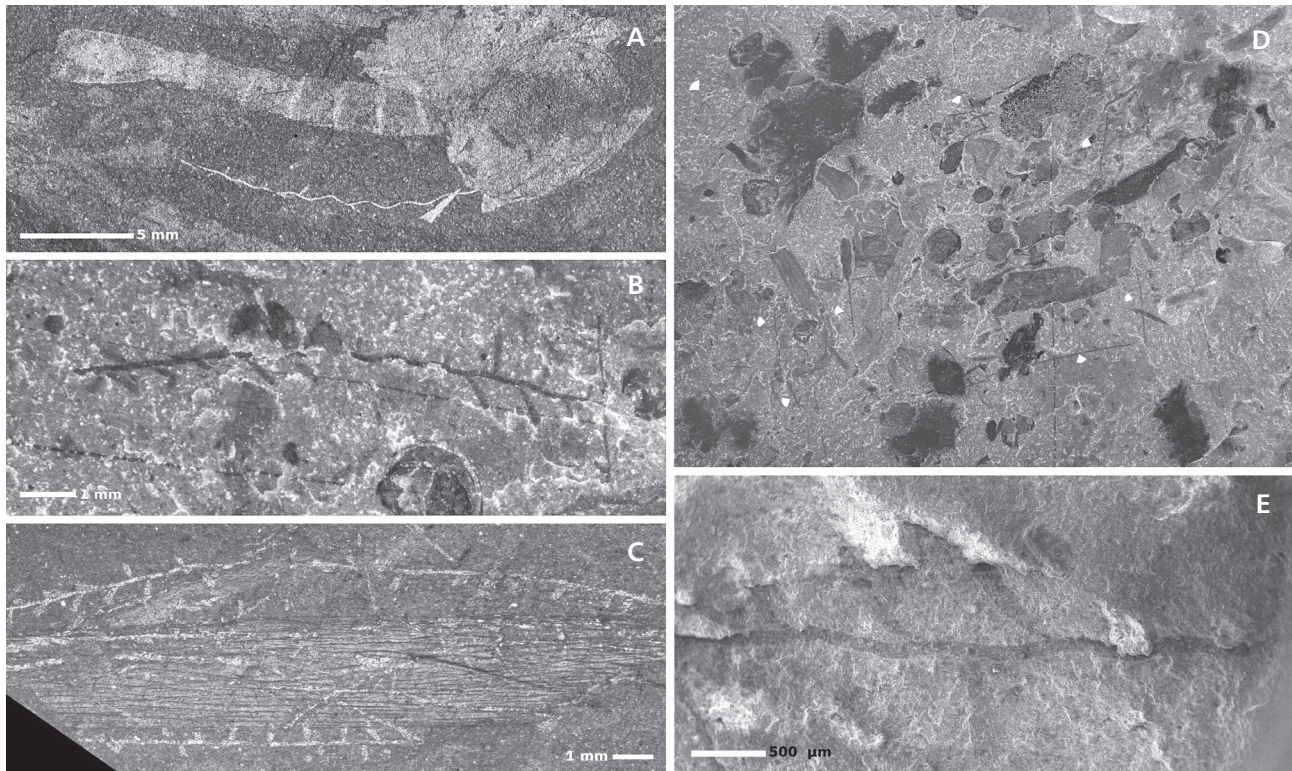
1931 *Chaunograptus scandens* n. sp.; Ruedemann, p. 2, pl. 2, figs 4–6; pl. 4, fig. 1.

*Holotype.* – USNM 83484 from the Burgess Shale Member, Stephen Formation (Locality 35k Walcott).

*Material.* – ROM 61106, ROM 981517, ROM 58022 from the Walcott Quarry.

*Description.* – Tubarium consists of a narrow, straight to undulated central tube stem ranging from 55–135 µm in width, 93 µm average width and up to 150 mm length. Alternate short conical tubes typically 700 µm average length, widening gradually towards the aperture from 90 µm at the base to 135 µm. Thecae develop alternately on the stem, projecting irregularly at various angles ranging from 15–80°, frequently at angles of 50–60°. Details of the fusellar ultrastructure have not been observed.

*Remarks.* – Slabs contain several short fragments that suggest a continuous arrangement of a single longer colony. It is possible that the smallest tubes are part of the terminal or budding theca supporting the idea of an upward projecting epibenthic suspension feeder (Caron & Jackson 2008). The narrow central tube can be interpreted, following the traditional use, as the prototheca that form the stipe axis and divergent metathecae. The holotype USNM 83484 also from the Stephen Formation, approaches the shortest and widest values of thecal measurements observed from the ROM specimens. One or two fragments of *C. scandens* are present in several slabs from this locality. Those with abundant specimens were used for this description, particularly one slab (ROM 58022) with counterparts preserved of numerous traces of possibly a single long tube (Fig. 2D). Tubarium ROM 61106 resembles that of the holotype by being closely attached to another organism, possibly a sponge, but not *Tupoia lineata*, as observed in the holotype (Ruedemann 1931). The ROM 981517 and ROM 58022 samples contain several specimens of *C. scandens* preserved in assemblage with other taxa but not attached to or found near to them. The genus *Chaunograptus* from the middle Cambrian Burgess Shale may represent one of the oldest colonial pterobranchs if fusellar construction can be recognized (Maletz 2013), however, due to poor preservation, especially by the lack of organic preserved material in the flat specimens and their minute size, only the outline of the colonies have been found. Rickards & Durman (2006) proposed its taxonomic affinities to the order Dithecoidea based on Obut (1964) but it is



**Figure 2.** *Chaunograptus scandens* Ruedemann, 1931; A – ROM 61106, *C. scandens* in association with an arthropod species; B – ROM 58022 showing the two types of tubes, straight and undulated, from a possible continuous single individual; C – holotype USNM 83484 showing two individuals in association with a sponge-like fossil; D – slab with several fragments of *C. scandens* (indicated by white triangles) together with other associated fauna; E – BSE image showing the tubes and its alternate autothecal segments.

no longer a recognized order, after Maletz (2014b) reclassified some of its species into the *incerta sedis* family Dithecodendridae, making no reference to *Chaunograptus*. Maletz & Steiner (2015) suggested that due to the straightness of the tube (that is not always consistent based on the undulated forms preserved) and the short conical thecae, *C. scandens* may not be related to the type species *Dendrograptus* (*Chaunograptus*) *novellus*, but rather to a possible erect-growing dithecoid. Maletz & Beli (2018) regarded the genus as a member of the Rhabdopleuridae. Backscatter SEM imaging did not show any details of the fusellar sutures or stolon as organic material traces. Instead, most specimens consist of imprints in the sediment, and only the outline of the tubarium is preserved.

**Occurrence.** – Walcott Quarry, Fossil Ridge, Burgess Shale Member, Stephen Formation, Yoho National Park, British Columbia.

### Genus *Yuknessia* Walcott, 1919

Figure 3

**Type species.** – *Yuknessia simplex* Walcott, 1919.

**Emended diagnosis.** – Isolated long, slender and slightly conical erect tubes non-interconnected, arranged in radiating clusters originated from a circular attachment structure at the base. Rarely branched erect tubes, with evidence of irregular fusellar bands (LoDuca *et al.* 2015a, b; Maletz & Steiner 2015; Maletz & Cameron 2016).

**Remarks.** – *Yuknessia* was initially classified as a tentative Chlorophyta by Walcott (1919) and further reports of the genus in the USA (Conway-Morris & Robison 1988, Skinner 2005) and China (*e.g.*, Hou *et al.* 1999, Babcock & Zhang 2001, Guo *et al.* 2010, Zhao *et al.* 2011) supported this algal affinity. Maletz & Steiner (2015) found fusellar patterns in a specimen from Utah using backscatter SEM and, recognizing its resemblance to *Yuknessia simplex*, classified it as a cephalodiscid pterobranch. LoDuca *et al.* (2015a) redescribed the genus as a ‘benthic colonial pterobranch’ based on the identification of fusellar bands and other ultrastructural details, and suggested a close resemblance to rhabdopleurid pterobranchs due to similarities in the suture patterns and budding patterns from the repent tubes, but differing by the distinct zigzag suture and absence of branching in erect tubes of *Rhabdopleura*. Despite these similarities, LoDuca *et al.* (2015a)



did not formally identify the genus as a graptolite. Maletz & Cameron (2016) included *Yuknessia* as *incertae sedis* in the Pterobranchia. The presence of a stolon system has not been identified, though this does not necessarily indicate its absence. It is possible that it lacks the sclerotized sheath that would favour its preservation.

### ***Yuknessia simplex* Walcott, 1919**

Figure 3A

*partim* 1919 *Yuknessia simplex* n. sp.; Walcott, p. 235, pl. 54, fig. 1a [non fig. 1b, c (= *Dalyia racemata*)].

*partim* 1966 *Yuknessia simplex* (Walcott). – Johnson, p. 38, pl. 17, figs 1, 2 (non pl. 17, fig. 5 = *Dalyia racemata*).

*non* 1988 *Yuknessia simplex* (Walcott). – Conway-Morris & Robison, p. 16, figs 11.1–11.6 (= *Yuknessia stephenensis*).

1994 *Yuknessia simplex* (Walcott). – Briggs *et al.*, p. 57, fig. 6.

2015 *Yuknessia simplex* (Walcott). – Maletz & Steiner, p. 1094, fig. 15a–c.

2015a *Yuknessia simplex* (Walcott). – LoDuca *et al.*, p. 83, figs 1.1–1.4, figs 2.4–2.9.

**Holotype.** – USNM 35406 from the Trilobite Beds, Campsite Cliff Shale Member, Mount Stephen, Burgess Shale Formation, Yoho National Park (Locality 14s Walcott).

**Material.** – ROM 62919, ROM 62920, ROM 62921 from the Trilobite Beds.

**Emended diagnosis.** – Tubarium bears several elongated conical tubes arrayed roughly radially around a black granular object. Slender tubes slightly flexuous ranging from 6–8 mm length, up to 13 mm long, widening distally from 0.1 mm at the base to 0.5 mm towards the aperture. Central (assumed as the repent portion) branching pattern at irregular intervals, bifurcation or interconnections not observed or possibly concealed by the dense overlapped tubes. Fusellar sutures from faint to clearly visible with an average distance of 22 µm. All specimens lack evidence of a stolon system (LoDuca *et al.* 2015a).

**Remarks.** – *Yuknessia simplex* is the type species of the genus, described by Walcott in 1919 using the holotype USNM 35406 from the Trilobite Beds and two paratypes, USNM 35407 and 35408, from the Phyllopod Bed. The three specimens show notable morphological differences that indicate two probable species. Maletz & Steiner (2015) considered the holotype as the only specimen that fits in the description of the genus *Yuknessia*. LoDuca *et al.* (2015a) mentioned that some non-types are consistent with the dimensions of *Dalyia racemata* rather than *Y.*

*simplex*, an idea also supported by Maletz & Steiner (2015); however, a final assignment is limited by the quality of the material and it is conceivable, together with both paratypes, that they are not true pterobranchs. With the reexamination of the types made by LoDuca *et al.* (2015a), *Yuknessia simplex* is only known from the holotype and other fragmentary specimens from Mount Stephen and no definitive specimens are known from the Walcott Quarry; therefore it should be considered rare and restricted to a Burgess Shale-type locality. Maletz & Steiner (2015) accepted a possible cephalodiscid affinity, until clear interconnections or stolon systems are observed in newly collected material.

**Occurrence.** – Trilobite Beds, Campsite Cliff Shale Member, Mount Stephen, Burgess Shale Formation, Yoho National Park, British Columbia.

### ***Yuknessia stephenensis* LoDuca *et al.*, 2015a**

1988 ?*Yuknessia simplex* (Walcott). – Conway-Morris & Robison, p. 16, figs 11.1–11.6.

2015a *Yuknessia stephenensis* n. sp.; LoDuca *et al.*, p. 85, figs 2.1–2.3.

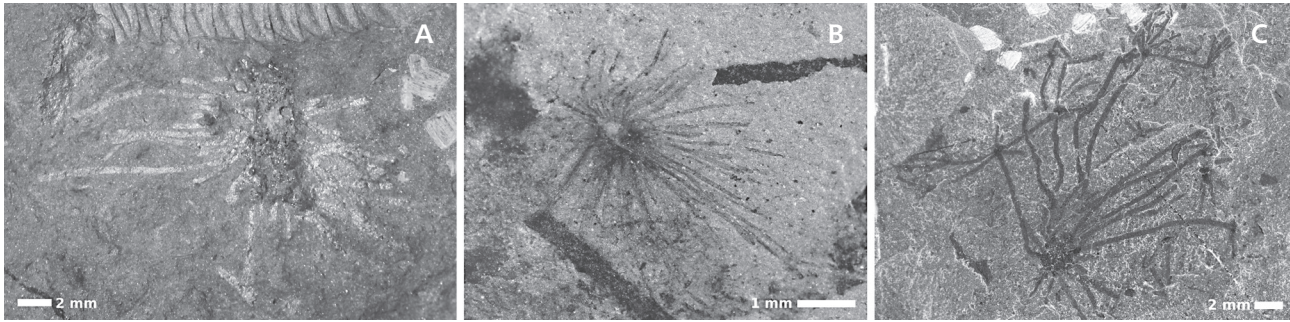
**Holotype.** – ROM 62918 from the Trilobite Beds, Campsite Cliff Shale Member, Mount Stephen, Burgess Shale formation, Yoho National Park (Locality 14s of Walcott).

**Material.** – ROM 62918 from the Trilobite Beds.

**Diagnosis.** – Tubarium consists of several elongated conical tubes arrayed in roughly radial fashion and emerging around a central repent area covered by overlapping tubes. Definitive branching not evident but overlaps are present. Erect tubes form slightly flexuous, from 7 to 20 mm in length and widening gradually distally from ~0.1 mm at the base to a maximum of ~0.8 mm at the straight aperture. Fuselli with strong transverse ridges with an average height of 0.032 mm faintly visible in BSE images. Absence of zigzag sutures, suggest the presence of full rings are present in the erect tubes. All specimens lack evidence of a stolon system (LoDuca *et al.* 2015a).

**Remarks.** – *Yuknessia stephenensis* was a new, true pterobranch species proposed by LoDuca *et al.* (2015a) to accommodate the specimens from the Trilobite Beds and all the material from the Spence and Wheeler formations of Utah (Conway-Morris & Robison 1988), previously assigned to *Y. simplex*, based on the width differences of the erect tubes. Maletz & Steiner (2015) referred some pterobranchs from Germany and that same material from Utah to *Sphenoecium wheelerensis* based





**Figure 3.** *Yuknessia simplex* Walcott, 1919; A – holotype USNM 35406 is the recognized type for the genus and *Yuknessia simplex*, initially described by Walcott from the Trilobite Beds; B – paratype USNM 35407, reexamination does not show a pterobranch affinity and it may possibly be classified as an alga (LoDuca *et al.* 2015a); C – paratype USNM 35408 shows size similarities with *Dalyia racemata* according to Maletz & Steiner (2015), excluding it as a pterobranch form. Photographs of *Yuknessia* structural features can be found in LoDuca *et al.* (2015a), including the specimens here described.

on differences mostly in size, structure and erect tubes branching (apparently absent in *Yuknessia*). Therefore, they suggested that *Y. stephenensis* should be restricted merely to its type specimen ROM 62918. Maletz & Steiner (2015) mentioned that *Sphenoecium* is typically represented by an encrusting basal region and the erect, slowly widening theca, however, several middle Cambrian pterobranchs share this same thecal morphology. It is possible that both species are alike since their differences are based on features that are not clearly distinguished and resolved. Maletz (2019a) recognized that *Yuknessia* and *Sphenoecium* may be closely related but since the proximal parts of the *Yuknessia* specimens are poorly preserved, it is difficult to substantiate. LoDuca *et al.* (2015a) mentioned that *Y. stephenensis* resembles other Cambrian pterobranch species such as *Rhabdopleura obuti* from Siberia (Durman & Sennikov 1993), *Rhabdotubus robustus* from the Czech Republic (Maletz *et al.* 2005), and *Archaeolafoea monegettae* from Utah (LoDuca & Kramer 2014). Detailed comparisons may invalidate these similarities and provide support for its generic designation as *Yuknessia*. For example, *A. monegettae* has an elongated growth rather than the radial arrangement characteristic of *Yuknessia* – although two specimens of *Y. simplex* from the Trilobite Beds show an axial elongated growth (LoDuca *et al.* 2015a). The Utah specimens are noticeably bigger, especially in terms of tube widths, compared to *Yuknessia* but this difference may not be the result of a taxonomical difference but ecological conditions. For example, Spence Shale and Wheeler Shale localities are 300 km apart, and specimens show differences in length. The holotype of *Yuknessia stephenensis* (ROM 62918, figs 2.1–2.3 in LoDuca *et al.* 2015a) does look different from *Y. simplex* (Fig. 3A) and its new denomination is acceptable. However, since we do not study the Utah specimens, we base our arguments on what the authors present, and decide that these Utah pterobranchs most likely belong to *Sphenoecium wheelerensis*. All differences between these

species are merely based in morphological appearance and measurements. The holotype of *Y. stephenensis* from British Columbia, presents radial shorter and more conical thecal tubes, while the holotype of *S. wheelerensis* (Maletz & Steiner 2015, fig. 17a–b, d–e,) from Utah presents encrusting radial, denser, longer and slowly widening theca, more similar to the Utah specimens (particularly KUMIP 204380–24382). A problem for *Yuknessia* species is that both holotypes are preserved in a way that the central portion of their tubarium is either concealed or dim, making difficult the understanding of how the repent or basal tubes develop, and whether the colony is radial or upright. For this reason, we only included the holotype of *Y. stephenensis* as the representative that occurs in British Columbia.

**Occurrence.** – Trilobite Beds, Campsite Cliff Shale Member, Mount Stephen, Burgess Shale Formation, Yoho National Park, British Columbia.

### Genus *Protohalecium* Chapman & Thomas, 1936

**Type species.** – *Protohalecium hallianum* Chapman & Thomas, 1936.

**Emended diagnosis.** – Sinuously branching tubarium with terminal conical thecae dense in the distal part and increasing thecae separation proximally. Thecae narrower at their base than at the aperture. Irregular fuselli with rare zigzag sutures (Bulman 1970, Chapman & Thomas 1936, Rickards & Durman 2006).

**Remarks.** – The genus was defined by Chapman & Thomas (1936) from fragmentary specimens collected from Knowsley East, Victoria, Australia. Quilty (1971) reported more complete and slightly bigger specimens from the Que River. Rickards & Durman (2006) examined and photographed the type specimens and Quilty's

material. Bulman (1970) classified the genus as *incertae sedis* and Maletz (2014b) and Rickards & Durman (2006) as a hydroid. However, our observation of fuselli demonstrates that it is a graptolite.

***Protohalecium hallianum* Chapman & Thomas, 1936**

Figure 4

1936 *Protohalecium hallianum* n. sp.; Chapman & Thomas, p. 204, pl. 16, fig. 22.

1945 *Protohalecium hallianum* (Chapman & Thomas). – Thomas & Henderson, p. 7, pl. 1, fig. 4.

1971 *Protohalecium hallianum* (Chapman & Thomas). – Quilty, p. 181, fig. 3.10; pl. 14, fig. 6.

2006 *Protohalecium hallianum* (Chapman & Thomas). – Rickards & Durman, p. 60, figs 50a–c, 51.1–51.4.

**Holotype.** – NMV P.47748 (ex VMD No. 35972) from the locality 8 of the middle Cambrian in the Parish of Knowsley East, Victoria, Australia.

**Material.** – ROM 54480 and ROM 54417 from Miller Pass and TMP 2004.11.46 from Haiduk Peak.

**Description.** – Elongated tubarium bearing short conical thecae. Colony length 65 and 110 mm, less than 8.5 mm wide. Main axis straight to sinuous in some sections, showing the appearance of slender tubes inclined to the axis but oriented in rotation, as a coiled stem. The most basal part of the main axis ~ 0.4 mm wide, slightly decreasing distally to 0.15 mm, however, this is not a strict pattern along the colony. Autothecae conical, 150–250 µm wide at the base to 350–450 (rarely 600) µm towards the aperture. Thecal length 2.5–4.0 mm (average = 3.5 mm). Autothecae more closely spaced in the distal part of the colony than in the proximal part where spacing ranges from 0.3 to 0.7 mm. (Fig. 5A). Irregular fuselli are observed along the main stipe and autothecae with rare zigzag sutures (Fig. 5C). Fuselli 18–22 µm in height. Other ultrastructural features not visible.

**Remarks.** – Most ROM 54480 measurements are at the lower end of those for TMP 2004.11.46. Total colony length differences can be explained by tubarium fragmentation. The two samples come from different localities but common biotas have been identified with other known British Columbia Burgess Shale-type deposits such as Haiduk Peak, 50 km southeast Mount Stephen (as in Johnston *et al.* 2009). The graptolites from the Duchesnay Unit in Miller Pass belong to a higher zone than those from the Walcott Quarry; however, both are similar in terms of fossil occurrences and strata positions (Johnston *et al.* 2009). The specimens somewhat resemble the species *Archaeolafoea monegettae*, which was reported

from the Wheeler Shale by LoDuca & Kramer (2014); same is the case of *Yuknessia* that is found in both British Columbia and Utah. The similarities are mainly in the uppermost part of the colony where autothecal branching patterns are comparable. However, these ROM and TMP specimens have a distinctive elongated sinuous growth and similar dimensions as *Protohalecium hallianum* Chapman & Thomas, 1936 from Victoria, Australia. Quilty (1971) showed ink drawings of the specimens that were later photographed and more completely described by Rickards & Durman (2006). The sinuous nature of the main axis and arrangement of the autothecae, particularly in the basal section, indicate that the colony may have been arranged helically in life (Rickards & Durman 2006). This description represents the first identification and description of fusellar patterns in the species, and demonstrates that it is indeed a graptolite and not a hydroid. A stolon was not observed.

**Occurrence.** – Miller Pass, Mount Assiniboine Provincial Forrest, Stephen Formation, Burgess Shale Member and Haiduk Peak, Kootenay National Park, Duchesnay Unit, British Columbia, Canada.

Order Dendroidea, Nicholson, 1872

Family Mastigograptidae Bates & Urbanek, 2002

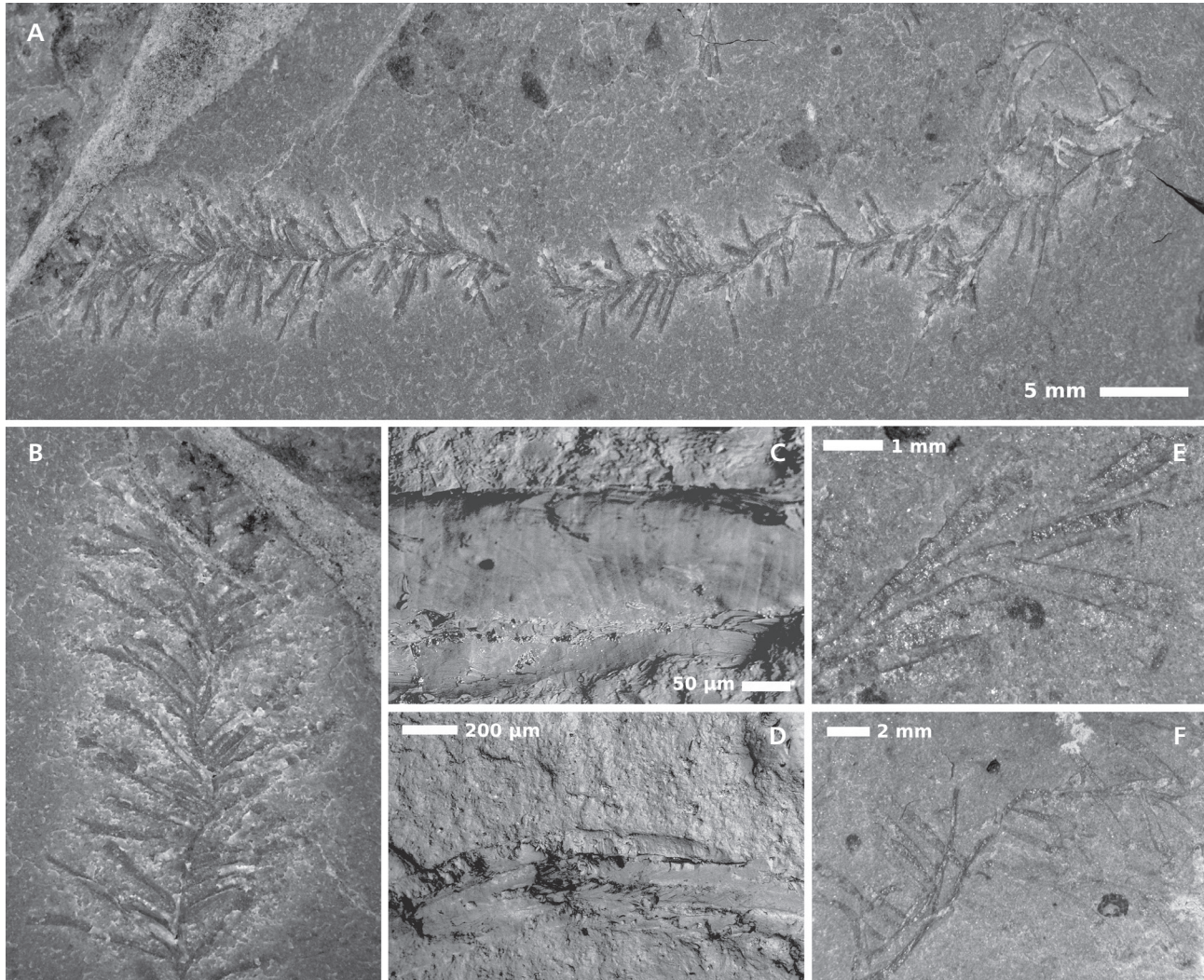
**Genus *Mastigograptus* Ruedemann, 1908**

**Type species.** – *Dendrograptus tenuiramosus* Walcott, 1879.

**Emended diagnosis.** – Bushy, dendroid tubarium with slender, dense-walled stipe and thin-walled, distinctly widening thecae arranged in pairs. Fusellar structure with complete fusellar rings and irregular half-rings sutures. Triad budding present and autothecae/bithecae are not differentiated by size (Bulman 1970, Maletz 2014b).

**Remarks.** – Ruedemann (1908) established this genus based on the notable differences between the type species of the genera *Mastigograptus* and *Dendrograptus* (type is *D. hallianus*). Its taxonomic position is not clear. It was initially referred to the family Chaunograptidae by Bulman (1955), and later to the same family, but in the order Dithecoidea by Obut (1964) that included taxa that preceded dendroids. Afterwards, it was treated as a dithecoid with affinities to dendroids and considered a transitional genus between the two (Chapman *et al.* 1996). Rickards (1993) placed it in the order Dendroidea and then Bates & Urbanek (2002) decided that it did not belong to the dithecoids or dendroids, and separated it into its own family Mastigograptidae and the order Mastigograptida. Maletz (2014b) referred the genus to the





**Figure 4.** *Protohalecium hallianum* Chapman & Thomas, 1936; A – ROM 54480 complete specimen; on the right, the basal part of the upright growing colony; B – detail of distal thecae showing a brush-like arrangement and no evidence of branching; C – SEM showing regular fusellar sutures from the single-tubed autotheca; D – SEM showing fusellar sutures and twisted-tubes detail from the central axis in the mid region segment of the colony; E – TMP 2004.11.46 detail of distal thecae comparative to B; F – basal tubes to be compared with the right-most portion of A.

Order Dendroidea due to the presence of triad budding. We decided to include *Mastigograptus* within the family Mastigograptidae based on their non-differentiated isolated metathecal tubes with complete fusellar rings, according to Bates & Urbanek (2002) and Maletz (2014b) diagnosis.

***Mastigograptus* sp. sensu Ruedemann (1947)**

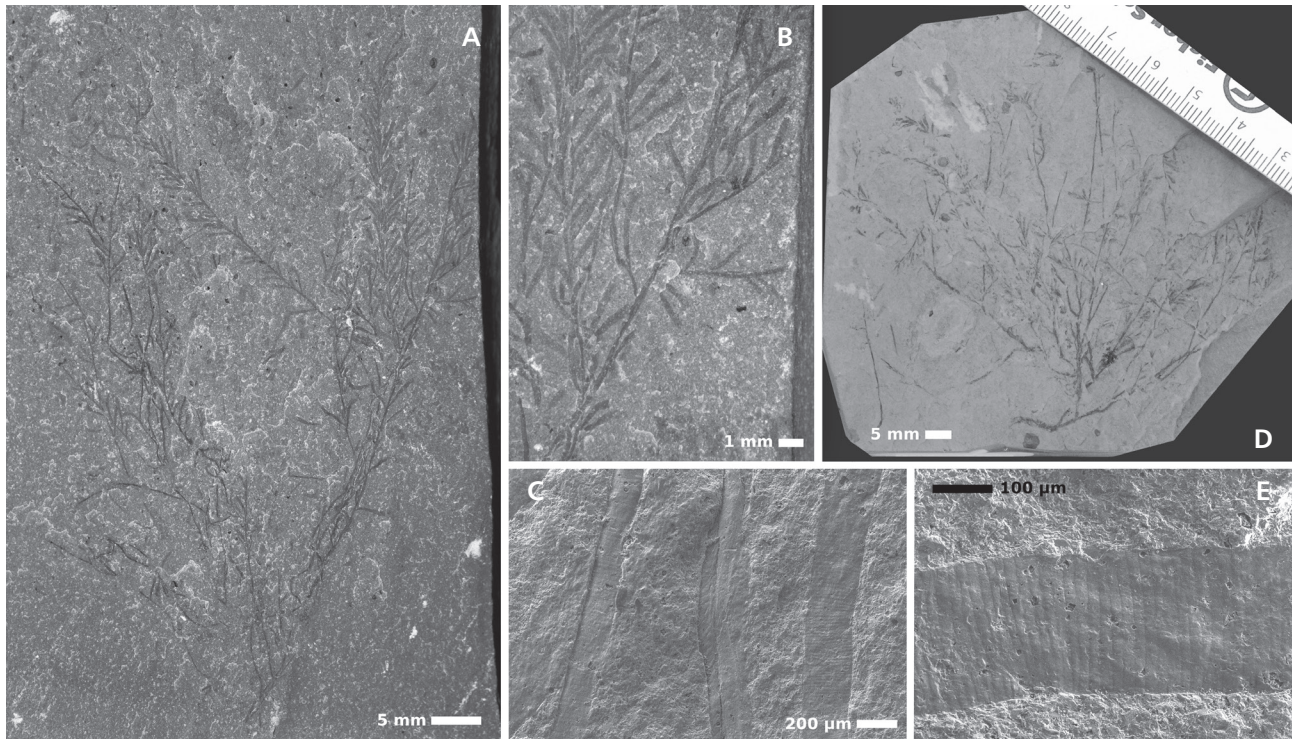
Figure 5

**Material.** – ROM 54458, ROM 54417, and several smaller fragments from the ROM collection from Miller Pass and TMP 2004.11.7 from Haiduk Peak.

**Description.** – Colony about 70 mm long by 80 mm wide, branching into slender stems bearing short conical

metathecae with an average width of 215 µm at the base and slightly increasing to an average maximum width of 340 µm. Metatheca vary in length from 1.5 to 3.5 mm. Central tube width varies between 150–200 µm and their arrangements are different depending on the position on the stipes. Upper tubes are the finest and consist of single tubes. Downwards, tubes become somewhat wider by the interconnection of older thecal compartments. Some double branching occurs at the same point, this is an indicator of triad budding, where bitheca and autotheca are not differentiated by length. Distance between thecae varies but tends to be smaller in the uppermost part of the colony. Full rings with regular fusellar sutures 15–20 µm in height, zigzag sutures rare (Fig. 4E). Single stipes frequently clustered at the tip of the colony and are more abundant at this point compared to lower stipes (Fig. 4A, B).





**Figure 5.** *Mastigograptus* sp. sensu Ruedemann (1947); A – ROM 54458 general view; B – ROM 54458 detail of branching theca holding conical appendages, suggesting the presence of a triad budding; C – three different types of tubes in the colony, all showing fuselli: single narrow, twisted, and single wide conical; D – TMP 2004.11.7 represents a less bushy colony but maintains the similar arrangement as the Miller Pass specimen (showed in A and B); E – SEM image showing regular complete fusellar patterns from the uppermost part of the colony.

Colonies show an arborescent growth and most of the branching occurs at the base.

**Remarks.** – Metathecal lengths are difficult to measure precisely due to overlapping tubes and coverage by the matrix, however, they tend to be longer in the distal part of the colony and slightly shorter at the base. Johnston *et al.* (2009) reported the presence of TMP 2004.11.7 and two other graptolite fossils from the Haiduk Peak location, and mentioned their affinity to *M. macrotheca* but because of the absence of triad budding and inflated stolothecae – diagnostics characters according to Bates & Urbanek (2002) – the identification was uncertain. However, the presence of three branches with a shared origin, particularly in the specimens TMP 2004.11.7, ROM 4417 and ROM 54480 (Fig. 4E), indicate the existence of this type of budding. Also, a distinctive twisted tube arrangement (Fig. 4C) can be interpreted as stolonial strands, although stolon was not observed. An undetermined species of *Mastigograptus* has been reported for the Burgess Shale-type Cambrian localities in Wheeler and Marjum, Utah, together with debatable *Yuknessia* specimens (LoDuca & Kramer 2014). Maletz (2019a) referred to specimens from the Tyrrell Museum (see Johnston *et al.* 2009 and Fig. 5 herein) as possible

dithecodendrids, and recognized certain morphological similarity to an Ordovician species of *Mastigograptus* mentioned by Andres (1961).

**Occurrence.** – Miller Pass, Mount Assiniboine Provincial Forest, Stephen Formation, Burgess Shale Member and Haiduk Peak, Kootenay National Park, Duchesnay Unit, British Columbia, Canada.

## Discussion

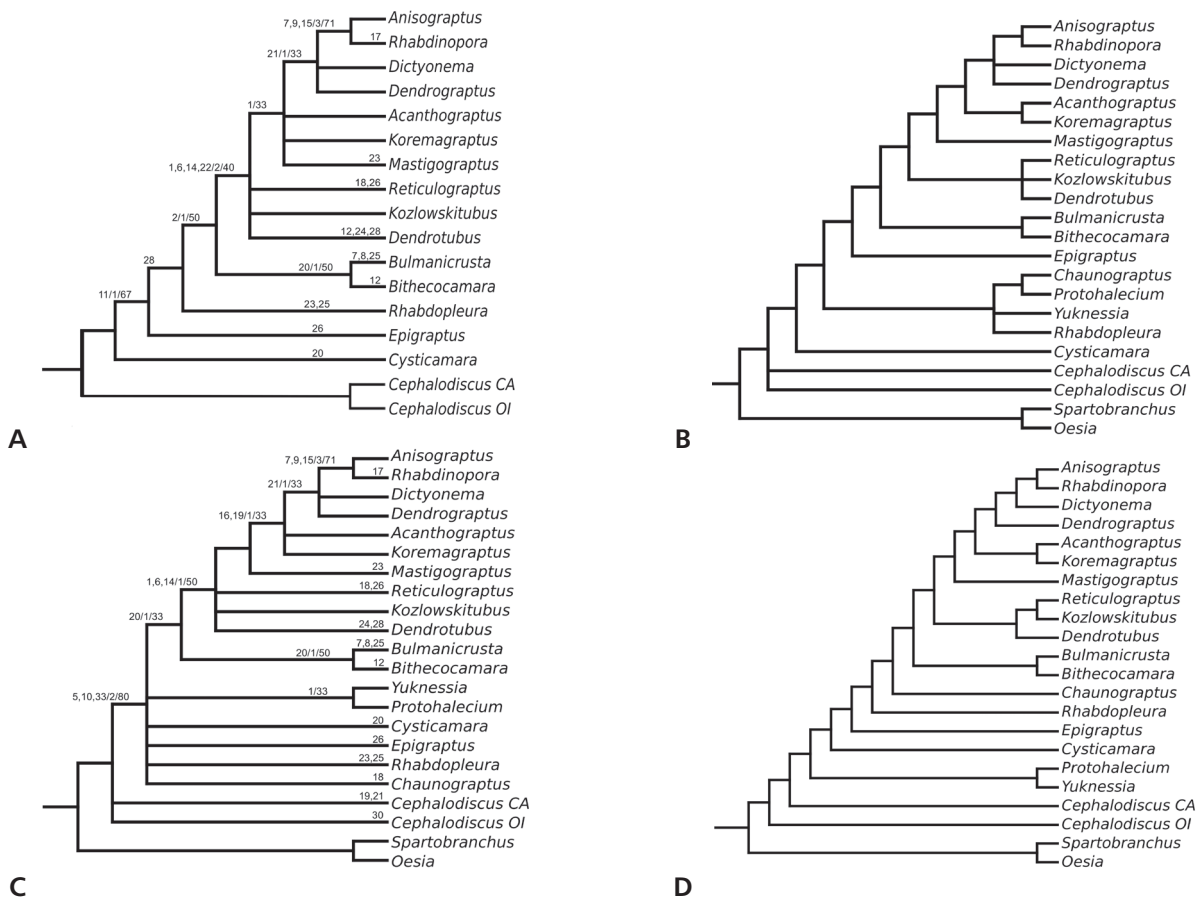
The traditional classification of graptolites by Bulman (1970) recognized most benthic forms in the now disused orders Tuboidea, Camaroidea and Crustoidea and most Burgess Shale or early taxa were considered *incertae sedis* (e.g., *Protohalecium*, *Mastigograptus*, *Chaunograptus*, *Sphenoecium*). The revised classification of Maletz (2014b, 2017) discontinued these orders but maintained their families as uncertain taxa, and recognize the orders Dendroidea and Graptoloidea. Dendroidea includes the families Dendrograptidae, Acanthograptidae, and Mastigograptidae. Cephalodiscida was elevated to a subclass and Rhabdopleuridae is an *incertae familiae*. Mitchell *et al.* (2013), Maletz (2014b), and this phylo-

genetic analysis reject the Bulman (1970) hypothesis that *Cephalodiscus* and *Rhabdopleura* are sister groups, and reject the Rickards & Durman (2006) phylogeny that grouped *Cephalodiscus* with fossil graptolites.

Mitchell *et al.* (2013) employed a character list similar to that of Rickards & Durman (2006), but excluded all genera that were presumably redundant with other taxa or for which little morphological information was available. They placed *Cephalodiscus* as a paraphyletic outgroup, based on initial unrooted trees analysis, and because the tube-building enteropneusts were unknown at that time. The Burgess Shale enteropneusts *Spartobranchus tenuis* (Caron *et al.* 2013) and *Oesia disjuncta* (Nanglu *et al.* 2016) were tubicolous, suggesting that tubes are a hemichordate plesiomorphy, elaborated in the pterobranchs line, and lost in the crown group acorn worms (Caron *et al.* 2013, Nanglu *et al.* 2016, Cameron 2018).

The tubes of *Oesia disjuncta* were porous, made of woven fibres, and previously known as the alga *Margaretia dorus* (Conway Morris *et al.* 1988, Nanglu *et al.* 2016). We conducted one analysis using the tubicolous acorn worms as a monophyletic outgroup to the graptolites, and a second with acorn worms plus *Cephalodiscus* as outgroup taxa, but found no difference in tree shape or statistics, because the alternate outgroups did not produce a polarization of characters. *Cephalodiscus* is distinct from the graptolites in its pseudocolonial habit that lacks connecting stolons, the absence of a larval prosicula, and the relatively simple ultrastructural details of the tube walls (Gonzalez & Cameron 2012).

The genus *Cephalodiscus* is divided into four subgenera corresponding to different types of organization of the coenecium (Ridewood 1920, Markham 1971). The zooids of *Orthoecus* and *Idiothecia* live in individual



**Figure 6.** Cladograms showing the phylogenetic relationships within living and fossil pterobranch genera. • A – strict consensus of 4 equally parsimonious trees from a new technology analysis in TNT including only the same taxa as Mitchell *et al.* (2013) and no Burgess Shale genera. • B – strict consensus of 54 equally parsimonious trees from a branch and bound analysis in PAUP considering all taxa. The heuristic analysis produces 52 equally parsimonious trees with a 52% bootstrap value that supports the node of *Dendrograptus* as the sister group of the Graptoloida (*Anisograptus* and *Rhabdinopora*); the remaining branches are supported 100%. • C – strict consensus of 6 equally parsimonious trees from a new technology analysis in TNT including all taxa. • D – selected strict consensus cladogram of the 6 equally parsimonious trees from the previous analysis that best represents all the relationships from all the trees obtained. Numbers above the nodes and branches represent the synapomorphic characters at that branch followed by the Bremer support values and the relative Bremer support values. Branches where only one value is showed refer to the synapomorphic characters.

tubes (Harmer 1905, Lankester 1905, Andersson 1907, John 1931). The subgenus *Cephalodiscus* (Harmer 1905, Andersson 1907, Johnston & Muirhead 1951, Bayer 1962, Emig 1977) lacks individual tubes. Zooids can move freely inside a common cavity that opens to the outside through ostia placed along or at the end of the branched structure of the coenecium. *Acoelothecia* includes the single species *C. kempi*, whose coenecium also lacks a tubular cavity, instead composed of a network of spines welded to each other (John 1931). Therefore, *Orthoecus* and *Idiothecia* form a clade that is sister to *Cephalodiscus* and *Acoelothecia*. Combined nuclear 18S rDNA and mitochondrial 16S rDNA phylogeny of cephalodiscids (Cannon *et al.* 2013) support these two sister clades, though which pair might represent the ancestral state is unknown. Only two characters regarding thecal arrangement differ between them (characters 20 and 22), and three others are uncertain for *Cephalodiscus* and *Acoelothecia* (characters 30–32, related to the cortex). Zooid characteristics of *Cephalodiscus* may provide more characters to polarize this clade. Despite the lack of resolution among cephalodiscids (Fig. 6), our analyses are congruent with previous studies that position them as sister group to the graptolites (Mitchell *et al.* 2013, Maletz 2014b).

Our analyses support the hypothesis that *Rhabdopleura* is an extant member of the Graptolithina, distinct from the living pterobranch *Cephalodiscus* (Mitchell *et al.* 2013, Maletz 2014b). We add little to the debate regarding the exact position of *Rhabdopleura* among these early forms (Rickard & Durman 2006, Mitchell *et al.* 2013, Maletz, 2014b, Beli *et al.* 2018), because its position is variable, or unresolved (Fig. 6C) depending on the analyses. The only clear conclusion that can be made is that *Rhabdopleura* appears to occupy an important transitional position between the basal group and the derived Eugraptolithina, characterized by a prosicula with a helical line (characters 1 and 2) (Mitchell *et al.* 2013).

Though little new morphological information was obtained for the Burgess Shale *Protohalecium hallianum*, it was included in the analyses to observe its relationship to other graptolites. In some phylogenies (Fig. 6C, D), *Yuknessia* and *Protohalecium* are sister taxa based on an encrusting habit and a simple, isolated and planar tubarium with zigzag fusellar sutures (characters 14, 19, 20, 22, 24, respectively). The encrusting growth (character 13) and the recognition of fuselli (character 23) distinguish this clade from *Chaunograptus*, where these features are unknown. This grouping remains tenuous, however, because the strict consensus branch and bound tree (Fig. 6B) placed *Chaunograptus* and *Protohalecium* as sister taxa, in a trichotomy with *Yuknessia* and *Rhabdopleura*. The encapsulated terminal bud of *Rhabdopleura* is an autapomorphy that collapses the branch with other genera

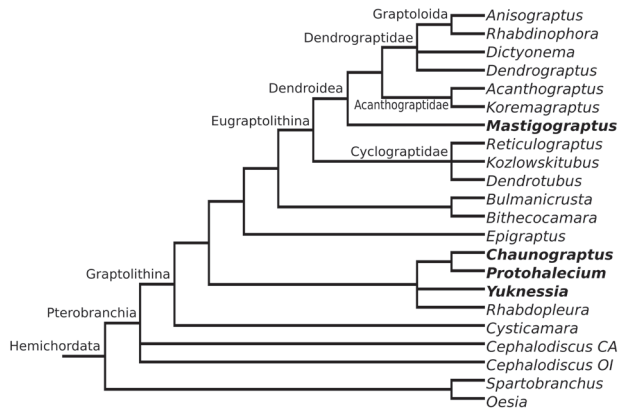
(Fig. 6B, C). These different evolutionary hypotheses for the basal taxa are due to differences in the algorithm and especially the default collapsing conditions. For example, TNT eliminates any branch for which the minimum possible length is zero (Goloboff *et al.* 2008), while PAUP retains a branch if it is supported by at least one most-parsimonious reconstruction of the ancestral states, for at least one character (Swofford 2002). The TNT criteria are stricter, which explains the fewer trees obtained and more collapsed branches (Fig. 6C) compared to results from PAUP (Fig. 6B).

*Cysticamara* occupies a phylogenetic position in-between *Cephalodiscus* and graptolites in most tree constructions (excluding Fig. 6D). Historically, it was considered a camaroid because it has diad budding (no bithecae) (characters 11 and 28) and a vesicular theca (character 21) that it shares with crustoids (Kozłowski 1949). This unique character unified *Bulmanicrusta*, *Bithecocamara* and *Cysticamara* in the Rickards & Durman (2006) phylogeny. Unique to *Cysticamara* is a spongy extrathecal mass that surrounds the stolons embedded in the upper wall, meaning that it is not surrounded by a true stolothea (character 12), a possible primitive character state (Kozłowski 1949). By contrast, *Cysticamara* exhibits derived graptolite character states like erect autothecal tubes and stolon diaphragms (character 10). Our knowledge of *Cysticamara* is mostly based on Kozłowski (1949) and since it may represent one of the very earliest graptolite forms, an in-depth re-examination may fill in some missing character states.

*Bulmanicrusta* and *Bithecocamara* are sister taxa even though they were classically considered crustoids and camaroids, respectively (Bulman 1970). *Bithecocamara* is coded here with triad budding as it has bithecae, not a typical characteristic for the diad budding of the cysticamarids, yet the presence of bithecae in some species has been noted by Kozłowski (1949). This budding type instead of representing a main difference may be a trait that unites these two taxa, despite the differences in stolon type and position (characters 8 and 9) or the presence of graptoblast (character 26). The phylogenetic analysis only included one species of each group because information about their representative species is incomplete. Possibly, camaroids and crustoids are a single group that shares the presence of a vesicular theca (character 21) (Maletz 2014b).

Because *Epigraptus* and *Dendrotubus* possess several homoplastic traits (*e.g.*, *Epigraptus* has bithecae, which is not typical for tuboid graptolites), Mitchell *et al.* (2013) excluded these graptolites singly from some analyses in order to gauge the constraints on their phylogenetic position. The cladogram that lacks Burgess Shale taxa (Fig. 6A), placed *Epigraptus* and *Cysticamara* as intermediate forms between *Cephalodiscus* and *Rhabdopleura* and





**Figure 7.** Strict consensus tree from a heuristic analysis in PAUP of 54 equally parsimonious trees including all 22 taxa showing in each node shows their recognized taxonomic level based on the classification of Maletz (2014b), and Mitchell *et al.* (2013) who recognize the infraclass Eograptolithina.

the branch to *Dendrotubus* at a higher position in the tree within the Eograptolithina. The exclusion of *Epigraptus* and *Dendrotubus*, separately and in combination with *Chaunograptus*, produced poorly resolved trees with lower support.

*Acanthograptus* and *Koremagraptus* are grouped by the presence of a compound branch condition (character 23) showing an anastomosed pattern (character 18). A triad of paired dimorphic thecae with shared dorsal walls defines this branch plus the early planktic genera. Maletz (2014b) included these two taxa within the family Acanthograptidae.

The genus *Dictyonema*, which traditionally belonged in the family Dendrograptidae, is considered central to understand the origin of planktic graptolites with the genus *Rhabdinophora* (Erdtmann 1982, Cooper *et al.* 2012, Maletz 2014b). Strict consensus trees (Fig. 6A–C) show a polytomy with *Dendrograptus* and *Dictyonema* regarding their relationship to the Graptoloidea (*Rhabdinophora* and *Anisograptus*). Maletz (2019b) reexamination of Silurian type specimens, placed *Dictyonema* in the family Acanthograptidae, based on a tubular theca on compound stipes (character 23) and the absence of true dissepiments as stipe connections (character 18). This is not completely supported by the present analysis, as the phylogenetic position of the genus remains unresolved, but closer to the planktic forms and not within the node that groups the acanthograptids (Fig. 6A–C). Here the addition of *thecal bridges* as a character state for character 18 and the presence of compound stipes in the character matrix, produced the collapsed node of *Dictyonema* and *Dendrograptus* but maintained the same phylogenetic relationship with the planktic taxa.

Changes from a benthic to a planktic habitat are mostly related to modifications in the proximal part of the colony,

where the initial zooid constructs the first thecal tube, or sicula, which change may have been driven by the loss of the encrusting habit (character 14). The sicula of planktic graptolites tends to develop a caudal prosicula (character 1; instead of the vesicular shape), and the helical line (character 2) becomes more common. The prothecal portion of the first asexually produced theca, which houses the beginning of the stolon, initiated in a more proximal position within the sicula (character 7) and the central stolon changes from mainly tubular to unsclerotized (character 8), bearing stolon diaphragms (character 10). This contributed to the predominance of a triad budding type with paired dimorphic thecae in the most derived forms (characters 11 and 17), presenting complex stipe connections (character 15) that maintain autothecal tubes that are not completely isolated (character 22).

Graptolites from the Burgess Shale of Canada represent some of the earliest and poorly known forms. Details of the zooids are completely absent and features of the tubes, derived from flattened, poorly preserved, and often fragmented specimens, are also often not satisfactorily revealed. This lack of characters makes it a challenge to establish a robust phylogeny for the species, though their basal position within the Graptolithina is now evident (Fig. 7). With the exception of *Mastigograptus*, the Burgess Shale graptolites are closely affiliated with the graptolite *Rhabdopleura*. Following the taxonomic revision of Maletz (2014b), our analysis places *Mastigograptus* as an early member of the Dendroidea. This result indicates that graptolites had already undergone substantial evolutionary diversification by the mid Cambrian. Indeed, taxonomic revisions and phylogenetic analyses such as this one are key to revealing early hemichordate evolution. Most important, however, is the discovery of new pterobranch specimens from Burgess Shale-type deposits, particularly those that are rich in sessile organisms (Johnston *et al.* 2009, Caron *et al.* 2010, Zhao *et al.* 2013).

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