

A PRIMITIVE *HALOBIA* (BIVALVIA: HALOBIOIDEA) FROM THE TRIASSIC OF NORTHEAST BRITISH COLUMBIA

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ABSTRACT—*Halobia daonellaformis* new species is described from the lowermost Carnian of northeast British Columbia. *Halobia daonellaformis* n. sp. is regarded as a primitive *Halobia* characterized by external ornamentation similar to *Daonella lommeli*, but with a poorly developed anterior auricle. Morphologic characters of *H. daonellaformis* n. sp. suggest that *Halobia* may be not a natural taxon but a polyphyletic group with one or more ancestors from *Daonella* and *Aparimella* and/or other posidoniid(s). The sudden appearance of *Halobia* throughout the marine Triassic suggests a rapid dispersal mechanism following a Ladinian origin. Larval shell morphology indicates a planktotrophic developmental strategy for *H. daonellaformis* n. sp., and by extension to other halobiids, which may explain the widespread distribution of many halobiid species.

INTRODUCTION

HALOBIIID BIVALVE genera *Daonella*, *Aparimella*, and *Halobia* were widely distributed throughout the Middle to Late Triassic Tethys, Panthalassa, and Arctic seas. As in other Mesozoic thin-shelled pteriomorphs and pectinoideans (e.g., *Clariaia*, *Peribositra*, *Bositra*, *Posidonotis*, and some monotiids and inoceramids), *Halobia* and its allies have been of considerable interest to paleobiologists because of their very thin shells, narrow valve widths, and cosmopolitan occurrence frequently in black shale facies typical of anoxic or dysoxic environments. In addition, *Halobia* species are among the most short-lived and widely distributed bivalves of the Mesozoic, making them excellent biostratigraphic indices—in certain instances equaling or exceeding even the resolution of ammonoids (McRoberts, 1997). For these and other thin-shelled pteriomorphs, the quality of preservation is often exceedingly poor, leaving many of the morphologic features, which could aid in deciphering their paleoecology or in resolving their phylogeny, unknown. These preservational shortcomings are compounded by the taxonomic philosophies of earlier workers (e.g., Mojsisovics, 1874; Kittl, 1912) who employed typological approaches in naming over 300 species of *Halobia*.

This paper highlights the biostratigraphic, paleoautecologic, and phylogenetic significance of what may be an important transitional form between *Halobia* and *Daonella*. *Halobia daonellaformis* new species has morphologic features transitional between *Daonella* and more advanced *Halobia*. Of particular interest is its stratigraphic position; this species occurs from approximately the same age as halobiids attributed to *Aparimella*, a genus introduced by Campbell (1994) as a potential intermediate between *Daonella* and *Halobia*. The phylogenetic significance of *Halobia daonellaformis* n. sp. is that the transition from *Daonella* to *Halobia* through *Aparimella* may not be as straightforward as previously thought, and that *H. daonellaformis* n. sp. may represent an alternative *Halobia* ancestor to forms typically regarded as primitive, such as *H. zitteli*.

Geologic and stratigraphic setting.—*Halobia daonellaformis* n. sp. described herein comes from two collections of the same stratigraphic section located about four km northeast of Clearwater Lake in the Pine Pass area (Calazon Creek NTS Map 93 O/10) of northeastern British Columbia (see Fig. 1). Specimens from GSC loc. 45687 were collected by Triad Oil Company and referred to the Geological Survey of Canada for identification. Those from GSC loc. 94956 were collected by E. T. Tozer in 1969 from approximately the same horizon of the same section. *Halobia daonellaformis* n. sp. occurs about 45 m below beds containing the ammonoids *Clionites reesidei*, *Trachyceras* sp.,

and species of *Halobia* (Tozer, 1967, 1994) and can be assigned to the Lower Carnian Desatoyense Zone of Tozer (1994). At its type locality along the Liard River just over 400 km to the north, the Liard Formation overlies the Toad Formation and is dominated by carbonate rich sandstones and siltstones of a near-shore, subtidal setting (Kindle, 1946). Ammonoids, conodonts, and bivalves from the type Liard, and especially in the Williston Lake area, indicate a Ladinian to Early Carnian age (Orchard and Tozer, 1997). Farther west, the Liard Formation is not recognized and coeval strata are assigned to the Toad Formation.

The Pine Pass area, along with much of eastern British Columbia and western Alberta, is part of the Western Canada Sedimentary Basin (WCSB) and is generally believed to be part of a miogeosynclinal and clastic wedge sequence deposited at mid-paleolatitudes on the western margin of the North American Craton (Davies, 1997). The WCSB is distinct from the intermontane, coast, and insular belts further west in Canada and the United States that consist of accreted tectonostratigraphic terranes, such as Stikinia and Wrangellia, whose Triassic paleo-position remain suspect (e.g., Gabrielse, et al., 1991).

SYSTEMATIC PALEONTOLOGY

Because of differences in usage among halobiid workers, shell morphology and dimensional terminology are provided in Figure 2. All figured specimens are housed in the Geological Survey of Canada (GSC) collections in Ottawa.

Class BIVALVIA Linnaeus, 1758

Subclass PTERIOMORPHIA Beurlen, 1944 [emend. Waller, 1978]

Order PTERIOIDA Newell, 1965 [emend. Waller, 1978]

Suborder PTERIINA Newell, 1965 [emend. Waller, 1978]

Superfamily HALOBIOIDEA Campbell, 1994

Discussion.—Halobiid bivalves are here interpreted as belonging to the Pterioida based on shell microstructure and ligament type. Although a simple prismatic outer shell layer observed in the Halobioidea is consistent with placement within the Pectinoidea or Pterioidea, an inner nacreous layer is more consistent with a pterioid affinity, as most possible pectinoid ancestors have, by Middle Triassic time, already evolved aragonitic crossed lamellar or calcitic cross lamellar structure (Carter, 1990). Similarly, the alvincular and more importantly the multivincular ligament of some *Halobia* are morphologic states shared with certain Bakevillidae, Isognomidae, and Inoceramidae and unknown in the Pectinoidea (Carter, 1990). An argument can possibly be made for inclusion of the halobioids in the subclass Cryptodonta—a group whose taxonomic status was recently re-evaluated by Johnston and Collom (1998). Inclusion of Halobioidea in the Cryptodonta would require the edentulous

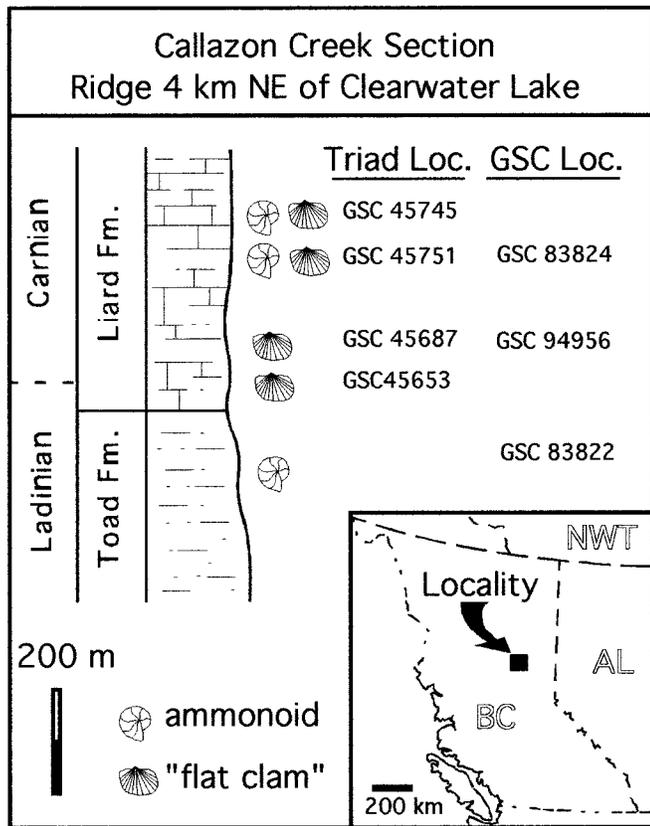


FIGURE 1—Locality map and generalized stratigraphy of the Callazon Creek section of the Pine Pass Area of northeast British Columbia. Biostratigraphic control by ammonoids and flat clams (*Halobia* and *Daonella*) are indicated by symbols. See text for discussion. Stratigraphy from Tozer (personal commun., 1999).

hinge and multivincular ligament of inoceramids and potential ancestral groups (e.g., the eurydesmids) to be synapomorphies shared with halobioids. However, the hypothesis of halobioids as cryptodonts is not supported either by ligament features, that are thought to be homoplastic within the Pterioidea (e.g., Newell and Boyd, 1987), or by the lack of taxodont dentition and possession of simple amphidetic alvincular ligaments along a flat or slightly curved hinge plate (Campbell, 1994).

Family HALOBIIDAE Kittl, 1912 [emend. Campbell, 1994]

Discussion.—Campbell (1994, p. 64) revised the diagnosis of the family and defined the group as thin-shelled pteriaceans with low valve convexity, primitive radial plications, and commarginal rugae retained from a posidoniid ancestor. Although as originally defined, the family Halobiidae represented a phenetic grouping of unrelated taxa (Kittl, 1912), the family as presented by Campbell (1994) and adopted herein is a phylogenetic concept based on inferred shared primitive characters. Established on characteristics of the hinge region and byssal system, three genera are recognized within the Halobiidae: *Daonella* lacks an anterior auricle, *Aparimella* possesses an upper anterior auricle, and *Halobia* has a two-fold anterior auricle. A fourth genus *Enteropleura*, erected by Kittl (1912), is poorly known and may, after further study, be placed in the Halobiidae.

Genus HALOBIA Bronn, 1830

Type species.—*Halobia salinarum* Bronn, 1830, by subsequent designation (Mojsisovics, 1874).

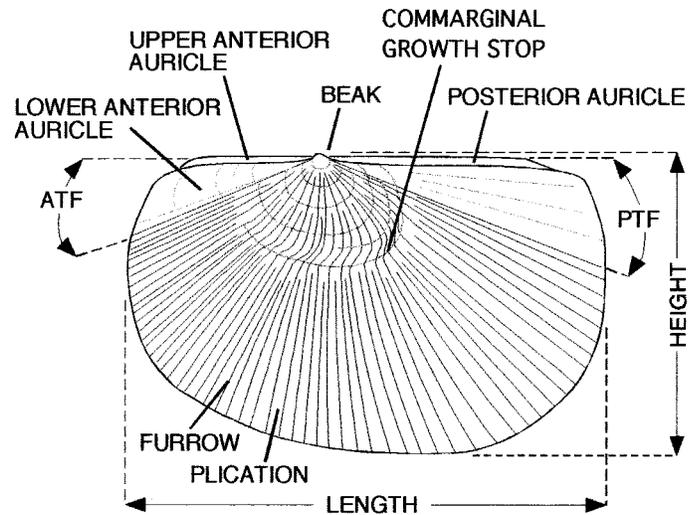


FIGURE 2—Schematic diagram of halobiid morphology. PTF = posterior triangular field; ATF = anterior triangular field (includes the angular value of both upper and lower anterior auricle). Note that lower anterior auricle has often been referred to as the byssal tube (cf. Campbell, 1994) and the growth stop is commonly referred to as the “break” (cf. Polubotko, 1980).

Description.—Shells thin, equivalved, variable in size and outline (usually less than 10 cm in length); narrow valve width (usually less than five mm); amphidetic; equant to slightly prosocline; beak generally prosogyrous, position varies, either central or anterior; anterior and posterior auricles are present to varying degrees in all members; commarginal rugae and radial costae sometimes developed, varying in density, strength, and course.

Discussion.—Traditionally, separation of *Halobia* from *Daonella* has been based on the presence of the anterior auricle [byssal tube of Campbell (1994)]. As interpreted here, *Halobia* differs from *Aparimella* in its development of the lower division of the anterior auricle. These distinctions are taken to be the diagnostic criterion distinguishing these three closely related genera. The above criteria for generic recognition suggest that morphologic differences used by several authors (e.g., Gruber, 1976; Polubotko, 1984) to erect separate halobiid genera (e.g., *Perihalobia*, *Zittelihalobia*, and others) are not of generic, but of specific, significance. However, if the anterior auricle of *Halobia* is twice derived by homoplasmy (e.g., once from *Aparimella* and once from *Daonella*) then erection of a new genus and a revision of *Halobia* and its membership will be required to accommodate the separate lineages for which generic names may already exist.

HALOBIA DAONELLAFORMIS new species

Figures 3.1–3.5, 5

Diagnosis.—*Halobia* having poorly developed anterior auricle and radial sculpture; plications flat-topped, occurring in primary and secondary bundles of 4–6, straight or with anterior bend at 1 cm.

Description.—Shell moderately large (maximum width estimated at 10 cm, maximum height estimated at 5.5 cm); length to height ratio variable averaging about 1.5; beak central, slightly extended above hinge margin, prosogyrous; plications developed over entire shell surface, beginning nearly 1.5 mm from beak, primary plications are broad and flat separated by deep furrows, secondary plications begin nearly 3 mm from beak and form by division and insertion of narrow and shallow furrow, tertiary



FIGURE 3—*Halobia daonellaformis* n. sp. All specimens are natural size. 1, Holotype, GSC 118305, RV external; 2–5, paratypes; 2, GSC 118304, LV external; 3, GSC 118306, RV external; 4, GSC 118302, RV external; 5, GSC 118306, LV external.

TABLE 1—Dimensional measurements (in mm) for *Halobia daonellaformis* n. sp. taken on commarginal outlines and angular values of anterior and posterior triangular fields (ATF and PTF respectively).

Specimen	Length	Height	L/H Ratio	ATF ^o	PTF ^o
GSC 118303	4.4	2.5	1.76	34.6	—
	7.2	4.7	1.53	—	—
	8.6	5.4	1.59	—	—
GSC 118304	9.1	8.4	1.08	29.3	36.9
GSC 118305*	4.0	2.5	1.60	36.1	19.1
	6.8	4.0	1.70	—	—
GSC 118306	16.1	11.6	1.39	—	—
	4.5	3.7	1.22	25.3	25.4
	5.6	4.4	1.27	—	—
	7.9	5.4	1.46	—	—
	14.9	8.3	1.80	—	—
	19.7	13.0	1.52	—	—

* = holotype.

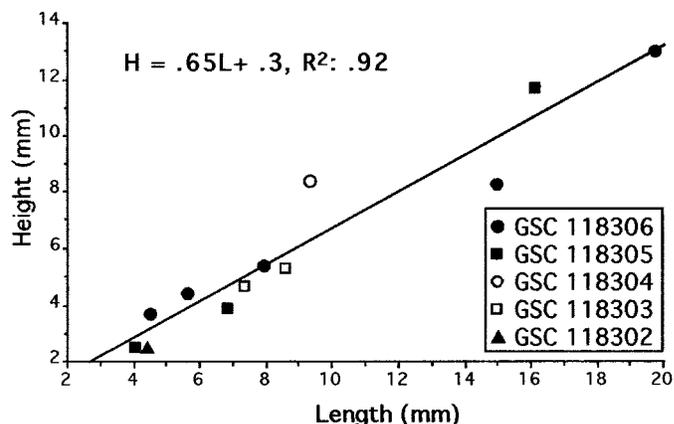


FIGURE 4—Scatterplot of length vs. height for *Halobia daonellaformis* n. sp. All measurements were taken on commarginal rugae. Measurement axes are shown in Figure 2.

plications are present but weakly defined; radial plications are slightly curved anteriorly or bend sharply anteriorly at 12 mm from beak; commarginal rugae moderately developed in umbonal area to about 1 cm, rugae are poorly developed or lacking on remainder of disc; lower anterior auricle poorly developed and dissected with numerous finely spaced plications; upper anterior auricle variably developed, smooth; anterior triangular field variable; posterior auricle poorly developed as flattened flange with weak radial ornamentation. Umbone area characterized by smooth Prodissoconch shell nearly 0.9 mm in length. Dentition, musculature, or other interior morphologic features not observed.

Etymology.—In reference to its general *Daonella*-like characteristics.

Types.—The collection consists of five incomplete valve exteriors (three left valves and two right valves). Holotype, GSC 118305; paratypes, GSC 118302–118304, 118306.

Occurrence.—The material comes from the lower part of the Liard Formation, of northeast British Columbia Canada and is likely from the lowermost Carnian Desatoyense Zone.

Discussion.—*Halobia daonellaformis* n. sp. differs from similar species of *Halobia* and *Aparimella* in the poorly developed and radially sculptured anterior auricle and from species of *Daonella* by development of the anterior and posterior auricles. The radial sculpture of *H. daonellaformis* n. sp. is quite variable,

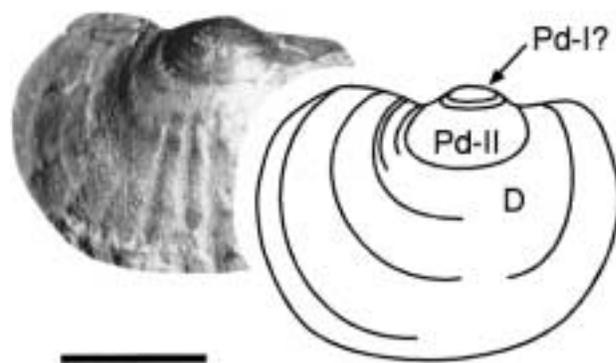


FIGURE 5—Larval and post-larval shell morphology of *Halobia daonellaformis* n. sp., GSC 118303, Callazon Creek, British Columbia. Pd-I = Prodissoconch-I larval stage, Pd-II = Prodissoconch-II larval stage, and D = post-larval Dissoconch stage. Scale bar = 1 mm.

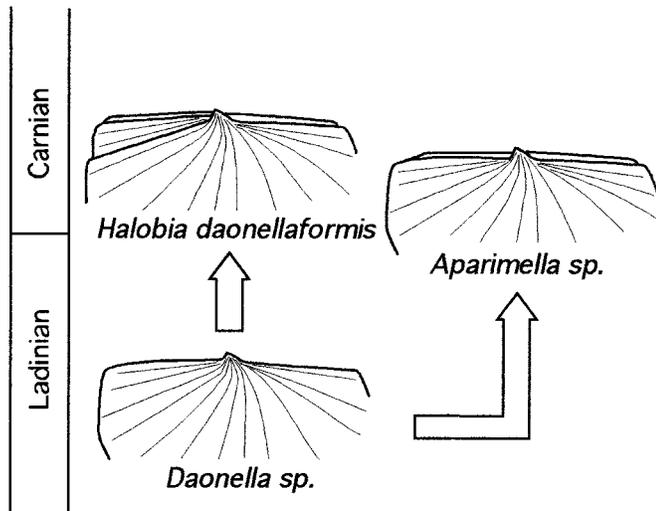


FIGURE 6—Proposed phylogenetic relationships between *Halobia*, *Daonella*, and *Aparimella*. Note that the transition from *Aparimella* to *Halobia* (sensu Campbell, 1994) is questionable given the primitive apomorphy of the lower auricle in *Halobia daonellaformis* n. sp.

probably depending on slight differences in preservation. In perhaps the best preserved specimen (see Fig. 3), the ribbing is nearly identical to *Daonella lommeli*, being broad and flat-topped and diverging away from a medial line extending from the beak to ventral margin. The *Daonella*-like radial plications that are strongly developed on the lower anterior auricle suggests this form to be closely related to, and likely descendent from, a form similar to *Daonella lommeli*.

The larval and post-larval development of *Halobia daonellaformis* n. sp. can be observed on one of the specimens (GSC 118303; see Fig. 5). If the interpretation of the larval shell illustrated in Figure 5 is correct, the prodissoconch-I is relatively small (0.2 mm in length) compared to prodissoconch-II (0.8 mm in length). According to criteria outlined by Jablonski and Lutz (1983) on the ratio between prodissoconch-I and prodissoconch-II sizes, it is likely that *H. daonellaformis* n. sp. utilized a planktotrophic larval strategy. A planktotrophic developmental strategy, alluded to by various authors (e.g., Campbell, 1994; McRoberts, 1997) could explain the very widespread distribution of many halobiid species. It is unfortunate, however, that the proviculum is not evident in the dissoconch of the available specimen, as its recognition could corroborate the larval ecology interpreted above, and potentially aid in phylogenetic reconstruction of the family.

PHYLOGENETIC SIGNIFICANCE

Debate continues regarding the origin and phylogeny of *Halobia*. Several workers suggest that *Halobia* is polyphyletic, having arisen from several *Posidonia* and *Daonella* ancestors (e.g., Gruber, 1976; Polubotko, 1988). Evidence for a polyphyly is threefold: (1) early Carnian *Halobia* differ from *Aparimella* (and *Daonella*) only by the degree of development of anterior auricles; (2) several upper Carnian to lower Norian *Halobia* exhibit posidoniid morphology akin to *Peribositra* early in ontogeny; and (3) ligament types, generally regarded as a conservative feature in bivalve evolution (e.g., Newell and Boyd, 1987), may differ between *Halobia* species. Although the significance of these characters in generic-level determinations has not yet been adequately demonstrated, they do question the concept of *Halobia* as a natural taxon.

The timing of *Halobia*'s origin is also unclear. The oldest undisputed *Halobia* occur almost simultaneously in the earliest Carnian strata in the Arctic, Panthalassa, and Tethys seaways. Earlier reports of Ladinian *Halobia* have now been determined to be either species belonging to other taxa such as *Daonella* and *Aparimella* (e.g., Campbell, 1994), or assigned to younger strata, such as has been determined for the *Halobia* known from Alpine Europe (e.g., Krystyn, 1978) and the Himalayas (e.g., Balini, et al., 1988). The appearance of certain species, such as *H. zitteli* A and similar forms, was not coincident; they first appeared in the earliest Carnian Desatoyense Zone in the Arctic and Panthalassan seas before appearing later in the early Carnian Aonoides Zone in the western Tethys (Gruber, 1976; McRoberts, 1997). Conversely, *H. vixauarita* A is known from the earliest Carnian Aon Zone of the Alpine area in beds associated with *Daonella lommeli* A (Gruber, 1976; Krystyn, 1978). In northeast Siberia, several species of *Halobia*, such as *H. zhilnensis* A and *H. korkodonica* A, first appear at the base of the lowermost Carnian Omkutchanicum Zone, whereas other forms closely related to *H. zitteli*, such as *H. talajaensis* A, *H. seimkanensis* A, and *H. popowi* A, first appear above the base of the Omkutchanicum Zone (Polubotko, 1980). As noted by Polubotko (1980), the lowermost Carnian, *H. korkodonica* A, is similar in many regards to *Daonella subarctica* A and perhaps to *D. indica* A, being differentiated by the presence of lower anterior auricle. The occurrence of *H. daonellaformis* n. sp. in the earliest Carnian rocks of northeast British Columbia as well as that of *H. vixauarita* from the earliest Carnian of the western Tethys, separated as they are by a considerably large paleodistance, does suggest a Ladinian origin and rapid dispersal across nearly all marine Triassic provinces.

CONCLUSIONS

By sharing morphologic features with both *Daonella* and *Halobia*, *H. daonellaformis* n. sp. from the lowermost Carnian of northeast British Columbia represents one of the most primitive halobias known. This species, characterized by external ornamentation similar to *Daonella lommeli* but with a poorly developed anterior auricle, suggests that the evolutionary transition from *Daonella* to *Halobia* may not be a simple series involving *Aparimella*, as suggested by Campbell (1994). Instead, *Halobia*, as traditionally defined, may be polyphyletic, perhaps including an origin directly from *Daonella* and *Aparimella* and/or other posidoniid ancestors. Further morphologic analysis, particularly involving shell microstructure, ligament, and musculature characters, will be needed to more conclusively resolve conflicting phylogenies and the status of *Halobia*.

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