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Additions and revisions to the inflated Pachydiscidae from the Campanian (Upper Cretaceous) strata of Denman and Hornby islands, British Columbia, Canada; taxonomic implications and insights into mode of life

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Abstract

Anapachydiscus (*Anapachydiscus*) *haegerti* n. sp., an ammonite belonging to the Pachydiscidae, is reported for the first time from the upper Campanian Northumberland Formation of Hornby Island, British Columbia. Thirty-five specimens have allowed for the complete ontogenetic reconstruction of the taxon as well as thanatocoenosic (death assemblage) observations with paleoecological implications for ammonoid early life. Although isolated juvenile specimens occur, instances of concretions containing a multitude of individuals are typical. One concretion yielding twenty-six early-stage juveniles lends support to a mode of preservation reflective of life association through a taphonomic process of capture and burial. The new species presents age-diagnostic utility as a distinct fossil within the molluscan assemblage of the *Nostoceras* (*Didymoceras*?) *adrotans* regional subzone; a highly constrained interval of the upper Campanian in the eastern North Pacific. A specimen attributed to *Anapachydiscus* (*Anapachydiscus*) cf. *A.* (*A.*) *fascicostatus* from the upper Campanian of the Cedar District Formation on Denman Island is also described, and the genus *Anapachydiscus* is retained with an emended diagnosis. Additional collections have enabled revised conceptualizations of *Pachydiscus* (*Pachydiscus*) *hornbyense* and *Pachydiscus* (*Pachydiscus*) *ootacodensis* accounting for the spectrum of variance within these species. Recognition of an upper Campanian *P.* (*P.*) *ootacodensis*–*Pachydiscus* (*Pachydiscus*) *suciaensis* Concurrent-range Zone is proposed for the eastern North Pacific to assist broader efforts of interregional biostratigraphic correlation given the endemic limitation of the latter taxon.

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Non-technical Summary

A study of a group of conservative ammonites from the Late Cretaceous, which lived approximately 90–66 million years ago, allows for greater refinement of age placement and paleoecological interpretations. Over 100 specimens were examined from the Nanaimo Group rocks among the Gulf Islands of southern British Columbia in the eastern North Pacific. A reappraisal of this group addresses the range of variation within several forms, proposes a consistent framework of diagnostic characters, and sees the erection of a new species with description of the full development from juvenile to adult. Exclusive death assemblages of the new species support the inference of a gregarious mode of early life.

Introduction

Upper Cretaceous ammonites of Campanian age have been described extensively from the eastern North Pacific ranging from Alaska (Imlay and Reeside, 1954; Jones, 1963), through British Columbia and Washington State (e.g., Meek, 1876; Whiteaves, 1903; Usher, 1952; Ward, 1978a; Haggart, 1989), to California and Mexico (e.g., Smith, 1900; Anderson, 1958; Matsumoto, 1960; Ward et al., 2012, 2015). Among the most renowned localities, exposures of the upper Campanian Northumberland Formation along western Hornby Island have reached legendary status in the region due to the abundance of well-preserved macrofossils that have been the focus of professional researchers and amateur collectors alike for over a century (e.g., Whiteaves, 1879; Usher, 1952; Ludvigsen and Beard, 1998). Namely the beds of Collishaw Point, a syncline platform projecting up to one kilometer outward into the Salish Sea from northwestern Hornby Island, present a major extent of outcrop at low tide, which has been the source of a diverse array of invertebrate (e.g., Usher, 1952; Haggart, 1989; McLachlan and Haggart, 2018; Nyborg et al., 2019) and vertebrate (e.g., Dyke et al., 2011; Martin-Silverstone et al., 2016; McLachlan et al., 2017; Cappetta et al., 2021) material.

However, fossiliferous exposures of the Northumberland Formation are not restricted to the western shore, as the section transects the island with its lowermost beds cropping out on the south-eastern coast (Katnick and Mustard, 2001, 2003; Mustard et al., 2003). An older molluscan fauna characterized by previously unknown heteromorph ammonite taxa has recently been described from these beds and assigned to the *Nostoceras* (*Didymoceras*?) *adrotans* subzone of the *Pachydiscus suciaensis* Zone (McLachlan and Haggart, 2018). The section also yields an unusually high concentration of juvenile ammonite death assemblages concentrated in calcareous concretions. Among these ammonites are representatives of a new member of the Pachydiscidae, *(Anapachydiscus) haegerti* n. sp., with taphonomic evidence reinforcing a planktic mode of life and association between individuals of the same species during their early stages. The occurrence of other closely allied species in the eastern North Pacific (e.g., Usher, 1952; Jones, 1963; Saul, 1979; Haggart, 1989; Haggart and Ward, 1989) presents an opportunity to further address the relationships between inflated pachydiscids with projected ornamentation during the Campanian in approach to the end of the Cretaceous.

Geological setting and historical background

The Nanaimo Group is an Upper Cretaceous sedimentary rock succession ranging from at least Turonian to Maastrichtian in age situated along eastern Vancouver Island (e.g., Mustard, 1994; Haggart et al., 2005) overlying the ancestral Wrangellia terrane of the Western Cordillera Insular Belt (e.g., Wheeler and McFeely, 1991; Yorath et al., 1999; Alberts et al., 2021). Investigations into Nanaimo Group stratigraphy followed the discovery of coal measures in the Nanaimo and Comox areas during the mid-nineteenth century, which proved to be of considerable economic significance to the region with mining of these deposits reaching its zenith in the early twentieth century (e.g., Bickford and Kenyon, 1987; Gardner, 1999). The Nanaimo Group succession reflects a multibasinal depositional environment that underwent an evolution from terrestrial to open marine with strata characterized by fluvial to nearshore facies marked by increasing marine influences of finer sedimentary sequences into the Santonian and Campanian (Bain and Hubbard, 2016; Huang et al., 2019; Kent et al., 2020; Girotto et al., 2024). With regard to the upper Nanaimo Group, fossiliferous mudstone to sandstone beds belonging to the Cedar District Formation are exposed continuously along the coast of western Denman Island from Boyle Point on its southern tip 18 km north-west to herein informally named 'Gladstone Bay' accessible via Gladstone Way. Similar rocks of the Northumberland Formation crop out for 2 km along eastern Denman Island and across the Lambert Channel on adjacent northwestern to southeastern Hornby Island intermittently over 10 km (Cathyl-Bickford and Hoffman, 1998; Katnick and Mustard, 2001, 2003; Fig. 1). Although previously interpreted as corresponding to Trent River Formation and Lambert Formation equivalents in the Comox Sub-basin, respectively (Williams, 1924; Usher, 1952; Cathyl-Bickford and Hoffman, 1998), these strata are now understood to have been deposited following early Campanian flooding of the Georgia Basin (Girotto et al., 2024).

The earliest paleontological fieldwork in proximity to the southern coast of Hornby Island was conducted by James Richardson in 1871 for the Geological Survey of Canada, whose exploration of the main islet of Norris Rocks resulted in the collection of a single fossil fragment belonging to the inner whorls of a planispiral ammonite assigned to *Gaudryceras denmanense* Whiteaves, 1901 (Whiteaves, 1879, 1895, 1903). Norris Rocks is comprised of coarse clastic conglomerates of the De Courcy Formation, which are also exposed along southeastern Denman Island 2 km away on the opposite side of the Lambert Channel (Katnick and Mustard, 2001). It is therefore likely that this material was reworked from the underlying Cedar District Formation where the species is also noted to occur (Haggart, 1989).

Although early mapping efforts would see various nomenclatural assignments for the finer-grained sedimentary units of Hornby Island (e.g., Williams, 1924; Usher, 1952; Muller and Jeletzky, 1970), the highly fossiliferous beds along the southeastern shore at informally named 'Paradise Bay' are now recognized as belonging to the lowermost Northumberland Formation, following adoption of unified basin terminology for the upper Nanaimo Group (Huang et al., 2022). The lower beds of the Northumberland Formation are also exposed west of the ferry terminal on southeastern Denman Island where detrital zircon analysis of lithic arenite established their maximum depositional age as 74.2 ± 1.4 Ma (Matthews et al., 2017; Coutts et al., 2020, fig. 4; Fig. 2). In a southwest to northeast transect along the southeastern shore of Hornby Island, they constitute an approximately 60-m-thick contiguous interval between the conglomeratic sandstones of the overlying Geoffrey Formation and underlying De Courcy Formation (McLachlan and Haggart, 2018). The 'Paradise Bay' locality, which had been largely overlooked for more than a century, would continue to remain uninvestigated until 1978, following the arrival of prolific local fossil collector, Joseph Haegert of Victoria, British Columbia, after having viewed the coastal cliffs across the straight from Qualicum Beach on Vancouver Island.

Materials and methods

Fossil materials were obtained from exposures of the Cedar District Formation on western Denman Island and the Northumberland Formation along western and southeastern Hornby Island in accordance with British Columbia provincial law through surface collection using hand tools. All localities comprise coastal outcrops within the intertidal zone to cliff face, and all geospatial coordinates are presented in decimal degrees corresponding to the WGS84 datum. Specimens were prepared using a suite of pneumatic and rotary tools to enable accurate measurement, diagnosis, and photographic presentation. In some cases, a balance between complete and partial removal of the surrounding matrix was achieved to preserve taphonomic context. Photography was conducted using a Nikon D7100 digital camera and through a Leica M205A stacking microscope with DFC450 camera using Leica Application Suite X version 3.0.12.21488. Composite specimen figures were assembled using Macromedia Fireworks 8 software and image modification was limited to the balancing of brightness and contrast through black-level adjustments.

Vector line tracing of sutural elements was conducted in Adobe Illustrator CS2 over photographs sequentially rotated to compensate for shell surface curvature. Measures of sutural complexity follow the lateral saddle proxy method of Ward et al. (2015, fig. 3.2) wherein the length of the full run of the lateral saddle is divided by its narrowest width. This was achieved with a traced path in Adobe Illustrator CS2. Herein termed Fractal Dimension Index (FDI) values were obtained from the most mature sutures available using the Lateral Lobe Saddle (LLS) method of Marriott and Chamberlain (2021) to ascertain parameters of sutural complexity. Lateral Lobe

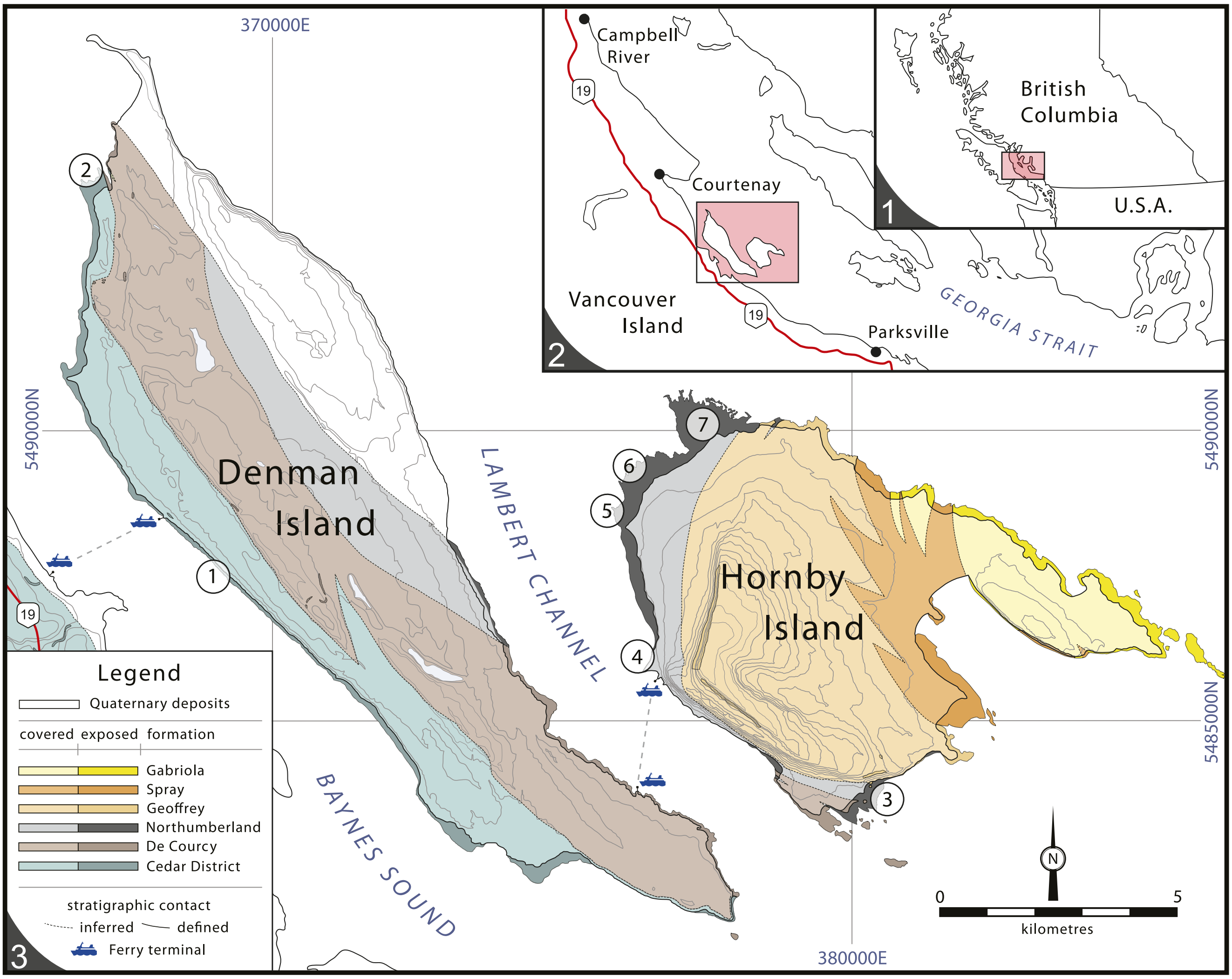

Figure 1. (**1**) Location of study area in western Canada. (**2**) Location of Denman and Hornby islands in the Georgia Straight, British Columbia, Canada. (**3**) Geological map of Denman and Hornby islands after Katnick and Mustard (2001, 2003), Mustard et al. (2003), and McLachlan and Haggart (2018) with representation of the Cedar District, De Courcy, Northumberland, and Geoffrey formations belonging to the Upper Cretaceous Nanaimo Group. Localities mentioned in this study: 1, western coast, Denman Island; 2, 'Gladstone Bay', northwestern Denman Island; 3, 'Paradise Bay', southeastern Hornby Island; 4, Shingle Spit, western Hornby Island; 5, Phipps Point, western Hornby Island; 6, Manning Point, northwestern Hornby Island; 7, Collishaw Point, northwestern Hornby Island.

Saddle values were first acquired using step counts based on a rule size of 1/10 Lmax in keeping with the Richardson method of complete end-to-end hemisutural transect stepping employed by Lutz and Boyajian (1995). Fractal Dimension Index values were then established following the formula $\mathrm{FDI} = \log(\mathrm{Nlls}/V)/\log(1/L)$ where Nlls is the number of steps recorded, L is the step size (or divisor of Lmax), and V is the Richardson-equivalent conversion value. A Richardson conversion value of 1.56 was determined from the intermediary inflated species *Pachydiscus* (*Pachydiscus*) *hornbyense* Jones, 1963, given the formula $V = \mathrm{Nlls}/\mathrm{Nr}$ where V is the conversion value, Nlls is the LLS step count, and Nr is the Richardson step count (Marriott and Chamberlain, 2021) (Supplementary Data, Fig. 1.2). This conversion value was then applied as a baseline to enable FDI calculations for other species from which LLS values were obtained.

Measurements ≥ 1 mm were taken with a digital vernier caliper and those below were obtained through the Leica Application Suite. All measurements were taken between ribs (intercostal). For instances where shell was not present at a point of measurement but intact on an adjacent surface, the shell thickness was recorded and added to the reading obtained from the internal mold to extrapolate a more accurate value. To maximize use of material, the two measurement end points from the whorl expansion rate formula of Raup (1966, 1967; see Tendler et al., 2015, fig. 2) were reduced from those corresponding to one full 360° volution to two measurements separated by one half volution. As such, vertical and lateral whorl expansion rate values were obtained by dividing the later of two directly opposing whorl heights or widths by the earlier. The descriptive approach traces ontogenetic progression to provide clarity of differentiation between stages of shell development. Terminology and conch morphometric indices follow those of Korn (2010). The reader is also referred to Klug et al. (2015) for a detailed discussion on terminology and conventions.

Morphometric abbreviations. D = whorl volution diameter; Uw = umbilical width; Wh = whorl height (umbilical margin to mid-venter); Ww = whorl width (flank to flank); WWI = whorl width index established from Ww/Wh; CWI = conch width index

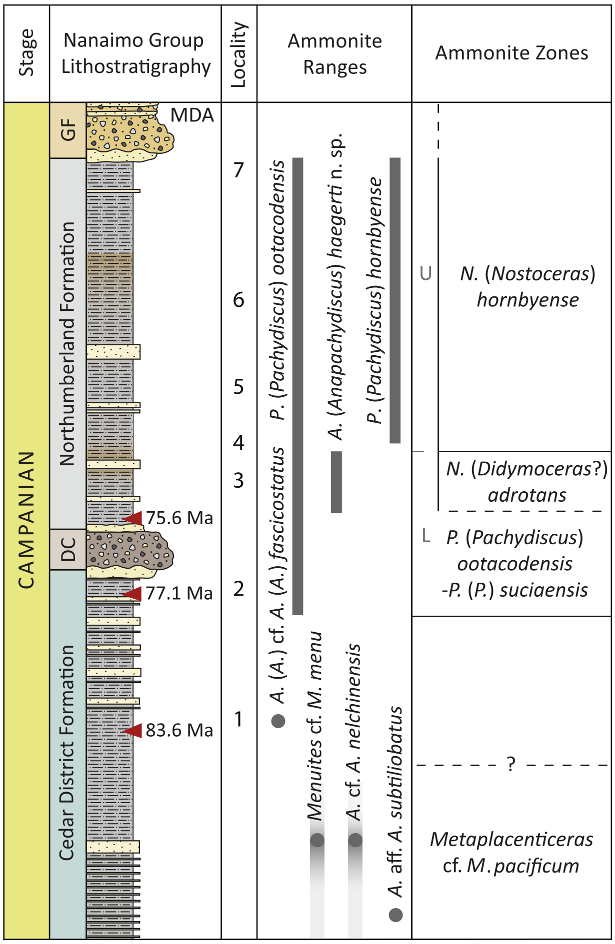

Figure 2. Biostratigraphic distribution and spot occurrences of inflated pachydiscid taxa throughout the Campanian of the Upper Cretaceous Nanaimo Group succession as inferred from occurrences on Saturna Island (Haggart, 1989), South Pender Island (Haggart and Ward, 1989), North Pender Island (Haggart and Ward, 1989), Denman Island (herein), and Hornby Island (Whiteaves, 1903; Usher, 1952; Jones, 1963; herein). Lithostratigraphy adapted from Mustard (1994), Katnick and Mustard (2001, 2003), Mustard et al. (2003), and McLachlan and Haggart (2018) presented as a simplified schematic diagram (stratigraphy not to scale); DC = De Courcy Formation; GF = Geoffrey Formation. Position (red arrows) and maximum depositional ages (MDA) of selected detrital zircon samples from Denman and Hornby islands (determined by Coutts et al., 2020, fig. 4D; samples CD1, CD2, and NU3 after Matthews et al., 2017). Molluscan biozones adapted from Haggart et al. (2009, 2011), Haggart and Graham (2018), and McLachlan and Haggart (2018). Localities: 1, western coast, Denman Island; 2, 'Gladstone Bay', north-western Denman Island; 3, 'Paradise Bay', southeastern Hornby Island; 4, Shingle Spit, western Hornby Island; 5, Phipps Point, western Hornby Island; 6, Manning Point, north-western Hornby Island; 7, Collishaw Point, northwestern Hornby Island.

calculated from Ww_2/D; UWI = umbilical width index obtained from Uw/D; LX = lateral conch expansion rate derived from Ww_2/Ww_1; VX = vertical conch expansion rate determined from Wh_2/Wh_1; RI = rib index representing the primary ventral rib count per one half volution between Wh_1 and Wh_2. FDI = suture fractal dimension index after Marriott and Chamberlain (2021). Sc = measure of sutural complexity after Ward et al. (2015, fig. 3.2). High quality specimen preservation enabled the illustration of suture line elements from a range of ontogenetic stages for certain taxa. As such, sutural terminology follows the system proposed by Wedekind (1916) and reviewed by Kullmann and Wiedmann (1970), where E = external lobe; I = internal lobe; L = first lateral lobe; U = umbilical lobe.

Repositories and institutional abbreviations. The specimens incorporated in this study are reposited within the paleontological collections of the Royal British Columbia Museum (RBCM, Victoria, BC, Canada), the Geological Survey of Canada (GSC, Vancouver, BC, Canada), the Courtenay and District Museum and Palaeontology Centre (CDMPC, Courtenay, BC, Canada), and the Smithsonian National Museum of Natural History (NMNH and USNM, Washington, DC, USA).

Systematic paleontology

Order **Ammonoitida** Hyatt, 1889
Suborder **Ammonitina** Hyatt, 1889
Superfamily **Desmoceratoidea** Zittel, 1895
Family **Pachydiscidae** Spath, 1922
Genus ***Anapachydiscus*** Yabe and Shimizu, 1926

Type species. *Pachydiscus* (*Parapachydiscus*) *fascicostatum* (Yabe and Shimizu, 1921, p. 57, pl. 8, fig. 5; pl. 9, figs. 2–5) by original designation.

Emended diagnosis. Inflated pachyconic pachydiscids with ventral depression throughout ontogeny such that Ww exceeds Wh in ephebic to intermediate growth stages with Ww ≥ Wh in the gerontic stage. Conches subinvolute, narrowly umbilicate with rounded umbilical margin, convex flanks, and broadly arched venter. Ornamentation consisting of rectiradiate to feebly sinuous or prorsiradiate primary ribs becoming more pronounced, retaining expression, or diminishing throughout the intermediate to gerontic stage. Intermediate stage marked by the development of tubercles or conical spines projecting from the umbilical shoulder. Constrictions may or may not occur.

Occurrence. Members of the genus *Anapachydiscus*, as corresponding to the refined diagnostic parameters of the present study, are restricted to strata of at least early Coniacian to late Campanian age, having been recovered from Europe (Schlüter, 1872; Błaszkiewicz, 1980), Madagascar (Collignon, 1955) and the Circum-Pacific region encompassing Japan, Far East Russia, the Western Americas, and Antarctica (e.g., Yokoyama, 1890; Paulcke, 1907; Anderson and Hanna, 1935; Matsumoto, 1951, 1954, 1984a; Jones, 1963; Leanza, 1963; Saul, 1979; Kennedy et al., 2007; Olivero, 2012; Reguero et al., 2022).

Remarks. The original description of Yabe and Shimizu (1926) offered little more than comparative remarks for a group pertaining to densely rectiradially ribbed forms that occupied intermediary morphospace between their '*Mesopachydiscus*' and '*Neopachydiscus*' genera; the former characterized by *Pachydiscus haradai* Jimbo, 1894 (now *Eupachydiscus*; see Spath, 1922; Wright et al., 1996) and the latter characterized by *Pachydiscus naumanni* Yokoyama, 1890 (now *Anapachydiscus* following Matsumoto, 1984a; *Menuites* according to Wright et al., 1996). Subsequent diagnoses given by Matsumoto (1951, 1954, 1984a) accommodate a wide range of forms that express coarsening, retention, or disappearance of rib ornament into maturity as well as the presence or absence of constrictions (Haggart, 1989, p. 197). Seventeen described species have been attributed to the genus: *A. arrialoorensis* (Stoliczka, 1865) (e.g., Collignon, 1952); *A. constrictus* Olivero, 1984; *A. deccanensis* (Stoliczka, 1865) (e.g., Matsumoto, 1955); *A. fascicostatus* (Yabe and Shimizu, 1921) (e.g., Matsumoto, 1951); *A. franciscae*

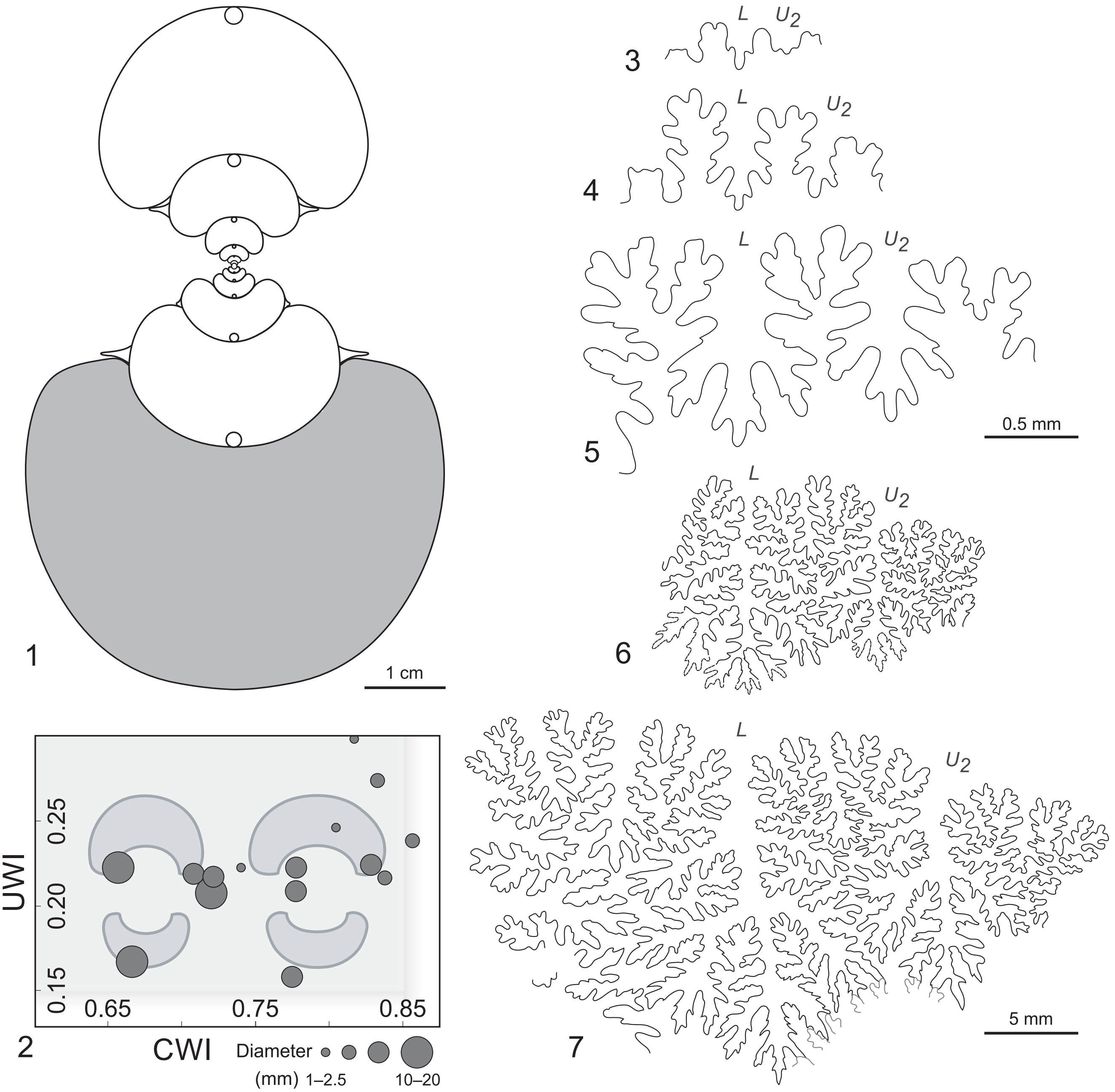

Figure 3. Illustrations of morphological progression and ontogenetic development in *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. from the upper Campanian Northumberland Formation, 'Paradise Bay', Hornby Island. (**1**) Schematic rendition with final volution cross-section reconstructed at 90° through body chamber (gray) based on the holotype RBCM P2022.185.0002. Note spines at mid flank in intermediary stage. (**2**) UWI (umbilical width index) and CWI (conch width index) comparative ratio plot; bubble size refers to maximum-diameter bracket; images in the background show the shape of the last complete whorl (see morphosectors of Korn, 2010). (**3–5**) Juvenile septal suture lines, scale bar = 0.5 mm; (**3**) paratype RBCM P2022.185.0019 at whorl height (Wh) = 0.5 mm; (**4**) paratype RBCM P2022.185.0013 at Wh = 1.5 mm; (**5**) paratype RBCM P2022.185.0027 at Wh = 2.5 mm. (**6**) Suture line of paratype GSC 142951 at Wh = 19.5 mm; dashed regions inferred based on succeeding suture on the same specimen at Wh = 20 mm. (**7**) Penultimate suture line of holotype RBCM P2022.185.0002 at Wh = 26 mm; tips of overlying folioles from preceding saddles illustrated in gray. *L* = lateral lobe; U_2 = second umbilical lobe.

Collignon, 1955; *A. fresvillensis* (Seunes, 1890) (Ward and Kennedy, 1993); *A. hauthali* (Paulcke, 1907) (e.g., Katz, 1963; as *A. patagonicus* of Olivero, 1984; Riccardi and Aguirre-Urreta, 1988; *Menuites hauthali* comb. Kennedy et al., 2007); *A. hourcqi* Collignon, 1955; *A. naumanni* (Yokoyama, 1890) (e.g., Matsumoto, 1951); *A. nelchinensis* Jones, 1963; *A. peninsularis* (Anderson and Hanna, 1935) (Saul, 1979); *A. steinmanni* (Paulcke, 1907) (Leanza, 1963); *A. subtililobatus* (Jimbo, 1894) (e.g., Matsumoto, 1951); *A. sutneri* (Yokoyama, 1890) (e.g., Matsumoto, 1951); *A. terminus* Ward and Kennedy, 1993; *A. vistulensis* Błaszkiewicz, 1980; and *A. wittekindi* (Schlüter, 1872) (e.g., Collignon, 1955).

Kennedy (1986c) and Cobban and Kennedy (1993) hypothesized sexual dimorphism wherein smaller, bituberculate forms constitute microconchs belonging to *Menuites* and macroconchs assignable to *Anapachydiscus*, with the implication that the latter genus is a dimorphic junior synonym of the former. This is of important consideration with Matsumoto (1984a) having suggested that *Menuites sanadai* Matsumoto, 1984a, could represent

Figure 4. (**1**–**23**) *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. from the upper Campanian of the lower Northumberland Formation, 'Paradise Bay', south-eastern Hornby Island. (**1–3**) Paratype RBCM P2022.185.0009; (**1**) protoconch with view of siphuncle at junction with first septum; (**2**) ventral view; (**3**) left flank. (**4, 5**) Paratype RBCM P2022.185.0007, protoconch partially enveloped by first volution septae; (**4**) right flank; (**5**) ventral view. (**6**) Paratype RBCM P2022.185.0008, with succeeding volutions in cross-section. (**7–9**) Paratype RBCM P2022.185.0019; (**7**) left flank; (**8**) apertural view; (**9**) right flank. (**10–12**) Paratype RBCM P2022.185.0013; (**10**) left flank; (**11**) apertural view; (**12**) right flank. (**13–17**) Paratype RBCM P2022.185.0030; (**13**) ventral view; (**14**) left flank; (**15**) apertural view; (**16**) right flank; (**17**) ventral view at max Ww. (**18**) Paratype RBCM P2022.185.0028, left aperturolateral view, retained in situ next to (**19**) paratype RBCM P2022.185.0029, left ventrolateral view. (**20, 21**) Paratype RBCM P2022.185.0020; (**20**) ventral view; (**21**) right flank. (**22**) Paratype RBCM P2022.185.0025, ventral view, retained in situ next to (**23**) paratype RBCM P2022.185.0026 in cross-section.

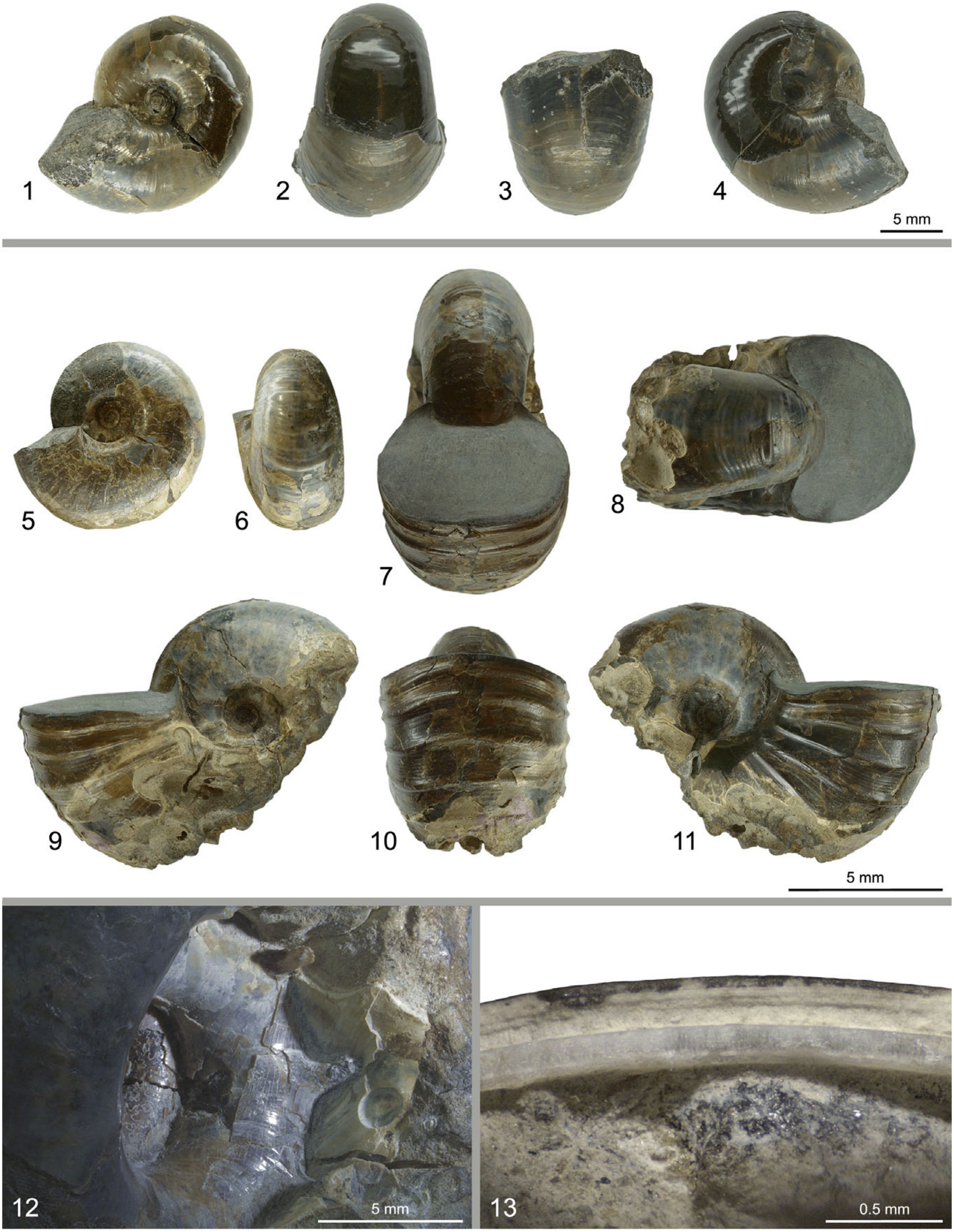

Figure 5. (**1**–**13**) *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. from the upper Campanian of the lower Northumberland Formation, 'Paradise Bay', southeastern Hornby Island. (**1–4**) Paratype RBCM.EH2008.011.11254; (**1**) left flank; (**2**) ventral view; (**3**) ventral view at max whorl width = 11.6 mm; (**4**) right flank. (**5, 6**) Paratype GSC 142951. (**7–13**) Holotype RBCM P2022.185.0002; (**7**) apertural view; (**8**) terminal phragmocone ventral view; (**9**) left flank; (**10**) ventral view of gerontic body chamber; (**11**) right flank; (**12**) spines at intermediate stage both free standing and appressed to umbilical wall; (**13**) cross-section of multi-layered ventrolateral shell at whorl height = 28 mm.

the dimorphic counterpart to the type species *A. fascicostatus*, the likely basis upon which Wright et al. (1996) synonymized *Anapachydiscus* under *Menuites*. Although discussion of taxa co-occurrence lending to this interpretation has been based on extensive material from Japan (Matsumoto, 1951, 1955), the United States Western Interior (Cobban and Kennedy, 1993), and Europe (e.g., Kennedy, 1986c; Kennedy and Summesberger, 1986; Kennedy and Kaplan, 1997), Cobban and Kennedy (1993) acknowledged that dimorphic counterparts have yet to be established and linked for all species, including the holotype *Menuites menu* (Forbes, 1846). Jagt et al. (2006) later suggested *Menuites* as a subgenus of *Anapachydiscus* without explanation, whereas Jagt-Yazykova (2011) maintained *Anapachydiscus* as a subgenus of *Menuites* in her examination of ammonite bio-events in the western North Pacific. More recently, *Anapachydiscus* has been retained and assigned to specimens recovered from the James Ross Basin, Antarctica (Olivero, 2012; Reguero et al., 2022).

Members of the genus *Menuites* are distinctly bituberculate, characterized by umbilical as well as ventrolateral projections and a pre-apertural constriction (Spath, 1922; Matsumoto, 1955). Dimorphism demonstrable among the Hornby Island pachydiscids cannot be defined on the basis of quadrituberculate ornament as recognized in *Menuites*, since all known examples are devoid of constrictions and tuberculate to spinous ventrolateral projections. For this reason, the present study refrains from adopting the classification of Wright et al. (1996). While resolution of the taxonomic placement of all pachydiscid species is beyond the scope of the present study, prevalence and general consistency of ventral depression and projected umbilical ornament as associated traits among pachyconic forms lend support to the *Anapachydiscus* genus concept. However, establishment of definitive generic parameters remains to be borne out through broader comparative character analysis among the Pachydiscidae.

Future investigations could determine that certain taxa placed within *Anapachydiscus* may indeed be more appropriately reassigned to other genera. *Anapachydiscus arrialoorensis*, from the Campanian of southern India, Madagascar, and eastern Europe (e.g., Kennedy and Summesberger, 1984), was regarded by Kennedy (1986b) to be a possible senior synonym of *A. vistulensis* from the upper Campanian of eastern Europe (Błaszkiewicz, 1980). This would render both species potential candidates for *Eupachydiscus* as was surmised for the latter by Matsumoto (1955; pers. comm. in Haggart, 1989) on the basis of reduced whorl depression and similar rib prominence from an early stage. The lectotype for *Anapachydiscus wittekindi* (Schlüter, 1872, pl. 22, figs. 1–3) designated by Błaszkiewicz (1980) from the original German suite has Wh ≥ Ww, while other forms he assigned to the species from Poland do not indicating a need for review of the species concept given inconsistent expression in a genus-level character. While all occurrences of *A. wittekindi* are noted within upper Campanian strata, Błaszkiewicz (1980, p. 50) made the important observation that "specimens which are higher [Wh] than thick [Ww] mostly occupy a higher stratigraphic position." *Anapachydiscus fresvillensis* (Seunes, 1890), from the upper Maastrichtian of Europe, Asia, South Africa, Madagascar, Australia, Chile, and possibly Brasil (Klinger et al., 2001), is another distinct outlier in possessing Wh ≥ Ww at maturity (Salazar et al., 2013) and is therefore of closer affinity with *Pachydiscus*, as acknowledged by Henderson and McNamara (1985). Likewise, with *Anapachydiscus terminus* Ward and Kennedy, 1993, described from the uppermost Maastrichtian strata of France, Spain, Denmark, and Azerbaijan. All specimens of this species reported by Ward and Kennedy (1993) are crushed prohibiting cross-sectional conch reconstruction, although Machalski (2005, fig. 6D–F) figured a coeval specimen from Poland that confirms Wh ≥ Ww. Regardless, assignment of this species to *Anapachydiscus* cannot be based on the presence of umbilical tubercles alone.

In the Nanaimo Group, the only record of specimens attributable to *Menuites* hails from middle Campanian exposures of the Cedar District Formation on South Pender Island, within the regional *Metaplacenticeras* cf. *M. pacificum* zone (*Menuites* sp. of Ward, 1976a, unpublished data; *Menuites* cf. *menu* of Haggart and Ward, 1989). These specimens of *Menuites* sp. have been recovered from the same interval as several examples of *Anapachydiscus nelchinensis* on North Pender Island (Ward 1976a, unpublished data; Haggart and Ward, 1989). The latter species exhibits umbilical tubercles and is nearly smooth throughout ontogeny. Other taxa attributed to *Anapachydiscus* from Nanaimo Group strata are also limited to isolated occurrences of fragmentary specimens from exposures of the Cedar District Formation (Fig. 2). These include a specimen assigned to *A.* cf. *A. nelchinensis* Jones, 1963, from North Pender Island with only sparse, weakly pronounced ribs that arise at the umbilical shoulder and terminate mid-flank (Haggart and Ward, 1989) and a partial whorl collected on Saturna Island attributed to *A.* sp. aff. *A. subtililobatus* (Jimbo, 1894) of Haggart (1989) characterized by evenly spaced, radial ribs.

Subgenus ***Anapachydiscus*** (***Anapachydiscus***)
Yabe and Shimizu, 1926

Type species. *Pachydiscus* (*Parapachydiscus*) *fascicostatum* Yabe and Shimizu, 1921, p. 57, pl. 8, fig. 5; pl. 9, figs. 2–5; by original designation.

Diagnosis. Inflated pachyconic pachydiscids with ventral depression throughout ontogeny such that Ww ≥ Wh is ever present. Conches subinvolute, narrowly umbilicate with rounded umbilical margin, convex flanks, and broadly arched venter. Ornamentation consisting of rectiradiate to feebly sinuous or prorsiradiate primary ribs becoming more pronounced or retaining expression throughout the intermediate toherontic stage. Intermediate stage marked by the development of tubercles or conical spines projecting from the umbilical shoulder. Constrictions absent.

Occurrence. Members of the subgenus *Anapachydiscus*, as corresponding to the diagnostic parameters upheld herein, are restricted to strata of at least Santonian to late Campanian age recovered from Europe (Schlüter, 1872; Błaszkiewicz, 1980), Madagascar (Collignon, 1955), Japan (Yokoyama, 1890; Matsumoto, 1984a), Far East Russia (Matsumoto, 1951, 1954), and western North America (Anderson and Hanna, 1935; Saul, 1979).

Remarks. Haggart (1989) noted that Matsumoto (1984a) retained *Neopachydiscus* of Yabe and Shimizu (1926) as a subgenus within *Anapachydiscus* for forms with periodic constrictions accompanied by major ribs. These taxa are exemplified by *A. naumanni* from the lower Campanian of Japan and Far East Russia (Matsumoto 1954, 1984a), *A. constrictus* from the lower Campanian of James Ross Island, Antarctica (Olivero, 1984, 2012), *A. hauthali* from the Campanian of Chile (Paulcke, 1907) and upper Coniacian–lower Campanian of James Ross Island, Antarctica (Kennedy et al., 2007), and *A. steinmanni* from the Campanian of Chile (Paulcke, 1907; Leanza, 1963) and lower Coniacian–lower Campanian of James

Ross Island, Antarctica (Kennedy et al., 2007). Likewise, *A. nelchinensis*, described from the lower Campanian of Alaska (Jones, 1963), should belong to a separate subgenus as well with rib ornament diminishing to a state of virtual absence at maturity in keeping with the concept of *Pachydiscus* (*Neodesmoceras*) (e.g., Matsumoto, 1951; Kennedy and Summesberger, 1984).

Anapachydiscus* (*Anapachydiscus*) *haegerti new species

Figures 3.1–3.7, 4.1–4.23, 5.1–5.13

Holotype. The holotype is specimen RBCM P2022.185.0002 (Figs. 3.1, 3.7, 5.7–5.11) reposited within the collections of the RBCM, recovered from a float concretion having weathered from the intertidal outcrop of the upper Campanian Northumberland Formation at 'Paradise Bay' along the southeastern coast of Hornby Island, British Columbia (Fig. 1.3, loc. 3; 49.49508°, −124.65217°).

Paratypes. Specimens RBCM.EH2008.011.11254, RBCM P2022.185.0007, RBCM P2022.185.0008, RBCM P2022.185.0009, RBCM P2022.185.0013, RBCM P2022.185.0019, RBCM P2022.185.0020, RBCM P2022.185.0025, RBCM P2022.185.0026, RBCM P2022.185.0027, RBCM P2022.185.0028, RBCM P2022.185.0029, and RBCM P2022.185.0030 housed within the collections of the RBCM. Specimen GSC 142951 is reposited within the collections of the GSC.

Diagnosis. A moderate to large-sized species of *Anapachydiscus*. Conch transitioning from thickly globular, involute, to thinly pachychonic, subinvolute. Whorl cross-section strongly embracing and depressed progressing to moderately embracing, weakly depressed. CWI avg. = 0.82. WWI ranges from 7.5 to 1.08 with ontogeny. UWI avg. = 0.22. LX and VX rates avg. = 1.32 and 1.58, respectively. Ornamentation consisting of laterally sinuous to biconvex lirae with intermittent prorsiradiate ventral primary ribs separated by transverse lirae. Rib projection and frequency increasing significantly on gerontic body chamber; ventrally prorsiradiate becoming weakly sinuous to biconvex in continuation across flanks separated by lirae. Spines present at intermediate stage along umbilical margin. Suture line complex and florid.

Occurrence. All specimens of *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. were collected from concretions either occurring as float or excavated in-situ among the intertidal exposures of the upper Campanian Northumberland Formation from the 'Paradise Bay' embayment along the southeastern coast of Hornby Island, British Columbia. The species is constrained within the *Nostoceras* (*Didymoceras*?) *adrotans* subzone (McLachlan and Haggart, 2018) of the *Pachydiscus* (*Pachydiscus*) *ootacodensis*–*Pachydiscus* (*Pachydiscus*) *suciaensis* Concurrent-range Zone (see biozonation of Haggart et al., 2009, 2011, and Haggart and Graham, 2018, emended herein).

Description. The combination of specimens representative of earliest ephebic to latest gerontic stages allows for a virtually complete reconstruction of a 7- to 8-volution conch at maturity (Fig. 3.1) and the extent of morphological change throughout ontogeny (Table 1). In paratype RBCM P2022.185.0007, the protoconch (~550 × 940 μm) is of greater width than the initial half volution (850 μm), which expands with LX = 0.90, transitioning to 1.08 at completion of the first volution (Fig. 4.4, 4.5). This is not the case in paratype RBCM P2022.185.0009, which has a markedly smaller protoconch (390 × 600 μm) and initial half volution LX of 1.07 (Fig. 4.1–4.3). Juvenile conches comprise the bulk of the dataset (Fig. 3.2), and the earliest volutions are seen to be thickly globular, involute, and reniform in cross-section (Figs. 3.1, 3.2, 4.6, 4.8, 4.11). The shell appears essentially smooth at D ≤ 2.0 mm, above which fine growth lines begin to become discernable. These growth lines gradually transition into more pronounced, low-relief lirae analogous to the robust ribs present at maturity separated by finer intermediary lirae (Fig. 4.16, 4.17). The ventrally prorsiradiate primary ribs of the intermediary conch are somewhat broadly spaced becoming weakly sinuous to biconvex in continuation across the flanks, and increasingly more proximate until they are ultimately separated by only 6–8 lirae on the gerontic body chamber (Fig. 5.9–5.11). Over the last 270° of the final volution, the ventral ribs increase in frequency such that their separation is reduced from 22° to 4° in approach to the aperture. Spines develop along the umbilical margin during the intermediate stage where D = ~30–60 mm (Fig. 5.12), at which point the conch has progressed from thinly globular to thickly pachyconic, subinvolute. Across the final volution in the holotype, RBCM P2022.185.0002, WWI reduces from 1.32 to 1.08 (avg. 1.19), accompanying an overall decrease in ventral depression with growth resulting in a thinly pachyconic, subinvolute profile. The holotype apertural dimensions (Wh = 47.1 mm; Ww = 53.8 mm) present a WWI of 1.14. The holotype maximum CWI could not be measured due to erosion of the ventral face, although a UWI of 0.22 is attainable at D = 101.8 mm. Near the gerontic aperture, the shell thickness is greatest at 0.9 mm on the umbilical shoulder, tapering along the flanks to 0.6 mm on the venter.

Table 1. Dimensions of *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. at successive stages of ontogeny. D = whorl volution diameter (mm); WWI = whorl width index; CWI = conch width index; UWI = umbilical width index; LX = lateral conch expansion rate; VX = vertical conch expansion rate; *n* = number of specimens; * = holotype; () = averages

D	WWI	CWI	UWI	LX	VX
< 3.0	1.62 (2.69) 7.50 *n* = 5	0.74 (0.95) 1.45 *n* = 5	0.22 (0.26) 0.30 *n* = 3	0.90 (1.25) 1.67 *n* = 5	1.1 (1.9) 4.1 *n* = 5
3.0–6.0	1.72 (1.96) 2.06 *n* = 4	0.83 (0.84) 0.86 *n* = 3	0.18 (0.22) 0.27 *n* = 6	1.3 (1.4) 1.4 *n* = 3	1.3 (1.5) 1.7 *n* = 6
6.0–12.0	1.48 (1.71) 2.16 *n* = 12	0.66 (0.75) 0.83 *n* = 8	0.16 (0.21) 0.22 *n* = 13	1.3 (1.3) 1.4 *n* = 7	1.3 (1.5) 2.0 *n* = 13
17.4	1.33	0.67	0.17	1.49	1.4
57.0	1.55		0.22		1.58
101.8*	1.08 (1.19) 1.32		0.22	1.40	

The shell is composed of two major inner layers of approximately equal thickness (~0.2 mm at Wh = 28) supporting a thin outer layer (Fig. 5.13). The largest Ww measurement of 63.8 mm was obtained from apertural fragment RBCM.EH2008.011.11234. The mature suture line is complex and florid, marked by intricate lobe-incision elements and narrow-stemmed external, lateral, and second umbilical saddles (Fig. 3.6, 3.7); an FDI of 1.94 and Sc of 4,466 was obtained from the holotype at Wh = 26 mm.

Etymology. The species name honors Joseph John Haegert (b. 1939) of Victoria, British Columbia, a prolific collector of Nanaimo Group fossils who discovered what he deemed the 'Paradise Bay' locality on southeastern Hornby Island in 1978.

Material. Thirty-seven specimens housed within the collections of the GSC and RBCM (Supplementary Data, Table 1.1) recovered from concretionary matrices of the upper Campanian Northumberland Formation at 'Paradise Bay' (Fig. 1.3, loc. 3) along the southeastern coast of Hornby Island, British Columbia. GSC 142951 (paratype, in situ; 49.495485°, −124.653039°), RBCM.EH2008.011.00484 and paratype -11254 (float; 49.49618°, −124.65346°), -11233 (float; 49.49527°, −124.65405°), -11234 (float; 49.49609°, −124.65353°), RBCM P2022.185.0002 (holotype, float; 49.49508°, −124.65217°), -0003–0006 (float; 49.4944°, −124.6535°), and -0007–0033 (in situ; 49.49598°, −124.65308°).

Remarks. *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. is distinct from all other species assigned to the genus due to the presence of fine, flexuous ribs with periodicity of increased ventral projection, which undergo a pronounced transition to greater proximity across the final volution. This is the first time that the complete ontogenetic progression of a species of *Anapachydiscus* has been incorporated into its description, as well as the first time that the earliest stage has been photographed, since Matsumoto (1951, fig. 1a) observed and illustrated the protoconch of *Pachydiscus yezoensis* Yabe, 1909 (= *Anapachydiscus deccanensis*, Matsumoto, 1955). However, limited specimens combined with the development of spines at what can only be characterized as the intermediary stage (D = ~30–60 mm) in the holotype RBCM P2022.185.0002 and paratype GSC 142951 provide no evidence of sexual dimorphism in the species as could be argued if projected ornament were restricted to a diminutive form (microconch).

The closest comparable pachydiscid is *Pachydiscus* (*Pachydiscus*) *hornbyense* Jones, 1963, also from within the Nanaimo Group as reported from the overlying upper Campanian Northumberland Formation exposures of western Hornby Island on the grounds of spinous ornament in the intermediary stage and periodicity of projected transverse ventral ribbing. However, the latter trait is uniformly expressed throughout later ontogeny in the aforementioned species and lacks the sinuosity observed in *A.* (*A.*) *haegerti* n. sp. *Pachydiscus* (*Pachydiscus*) *neevesi* Whiteaves, 1903, known from isolated specimens from the middle Campanian of the Cedar District Formation on Sucia Island, Washington State (Usher, 1952), and possibly the Trent River Formation at Northwest Bay, eastern Vancouver Island (D. Nunnallee, pers. comm. in Haggart, 1989), presents similar sinuosity and cord-like sculpture in its ribbing, although expressed with uniformity in proportionate relief and density. Both *P.* (*P.*) *hornbyense* and *P.* (*P.*) *neevesi* are taxa firmly placed within the genus *Pachydiscus* in being more compressed, evolute, and discoidal than species attributable to *Anapachydiscus.*

Anapachydiscus* (*Anapachydiscus*) cf. *A.* (*A.*) *fascicostatus (Yabe and Shimizu, 1921)

Figures 6.1–6.3

Occurrence. Within the Nanaimo Group, *Anapachydiscus* (*Anapachydiscus*) cf. *A.* (*A.*) *fascicostatus* is known only from a spot occurrence in the middle Campanian of the Cedar District Formation within or above the *Metaplacenticeras* cf. *M. pacifcum* Zone (see biozonation of Haggart et al., 2009, 2011; Haggart and Graham, 2018). Indisputable specimens of *A.* (*A.*) *fascicostatus* are otherwise known only from Campanian rocks of the Yezo Group, Hokkaidō (Matsumoto, 1951, 1954, 1984a; Shigeta et al., 2016).

Description. A fragmentary specimen composed of two partial volutions of phragmocone. The right flank of the outer volution is convex with subdued, densely concentrated rectiradiate ribs of low relief at Wh = 45 mm (Fig. 6.1). The ventrolateral surfaces of the inner volution are essentially smooth. The ventral region is moderately depressed on both inner and outer volutions, and the outer volution is strongly embracing (Fig. 6.2). The extrapolated WWI of the outermost volution is 1.37 at Wh = 45 mm. The external lobe and ventrolateral saddles visible on the inner volution are complex and florid (Fig. 6.3).

Material. A single partial specimen, RBCM.EH2013.047.0003.001, housed within the RBCM (Supplementary Data, Table 1.2) collected on western Denman Island (Fig. 1.3, loc. 1; 49.52555°, −124.80620°), 1.56 km southeast of the ferry terminal, in situ at the base of the coastal cliff face.

Remarks. The specimen is left in open nomenclature due to its fragmentary nature rendering any bifurcation or fasciculation of ribs indiscernible. Otherwise, the flank exhibits a fine, dense rib ornament, depressed, broadly inflated whorl section, and complex septal suture consistent with examples of the type species figured by Yabe and Shimizu (1926, pl. 8, fig. 5, pl. 9, figs. 2a–2e) and Matsumoto (1954, pl. 7(23), fig. 3a, 3b, text-fig. 13(59)c; 1984a, pl. 4, figs. 2a, 2b, pl. 5, fig. 2, text-figs. 4a–4c).

Genus ***Pachydiscus*** Zittel, 1884

Type species. *Ammonites neubergicus* von Hauer (1858, p. 12, pl. 2, figs. 1–4, pl. 3, figs. 1, 2) by the subsequent designation of de Grossouvre (1894, p. 177).

Emended diagnosis. Discoidal pachydiscids ranging from depressed to compressed, becoming more compressed throughout ontogeny. Conches subinvolute, with high, flat, or convex flanks. Ornament consisting of rectiradiate to feebly sinuous or prorsiradiate primary ribs, which may or may not be feebly umbilically bullate, with well-differentiated intercalaries. Ornament may persist, reduce to umbilical ribs, with or without feeble umbilical bullae, or disappear completely in approach to maturity. Sexual dimorphism distinguished on the basis of microconch diminutive size with presence of umbilical bullae, or greater development of umbilical bullae and presence of ventrolateral tubercles.

Occurrence. Members of the genus *Pachydiscus* span an interval from Santonian to latest Maastrichtian in age with a worldwide distribution reflected by abundant records from Europe (Kennedy, 1986b, c; Kennedy et al., 1995), the Middle East (Lewy, 1990), Africa

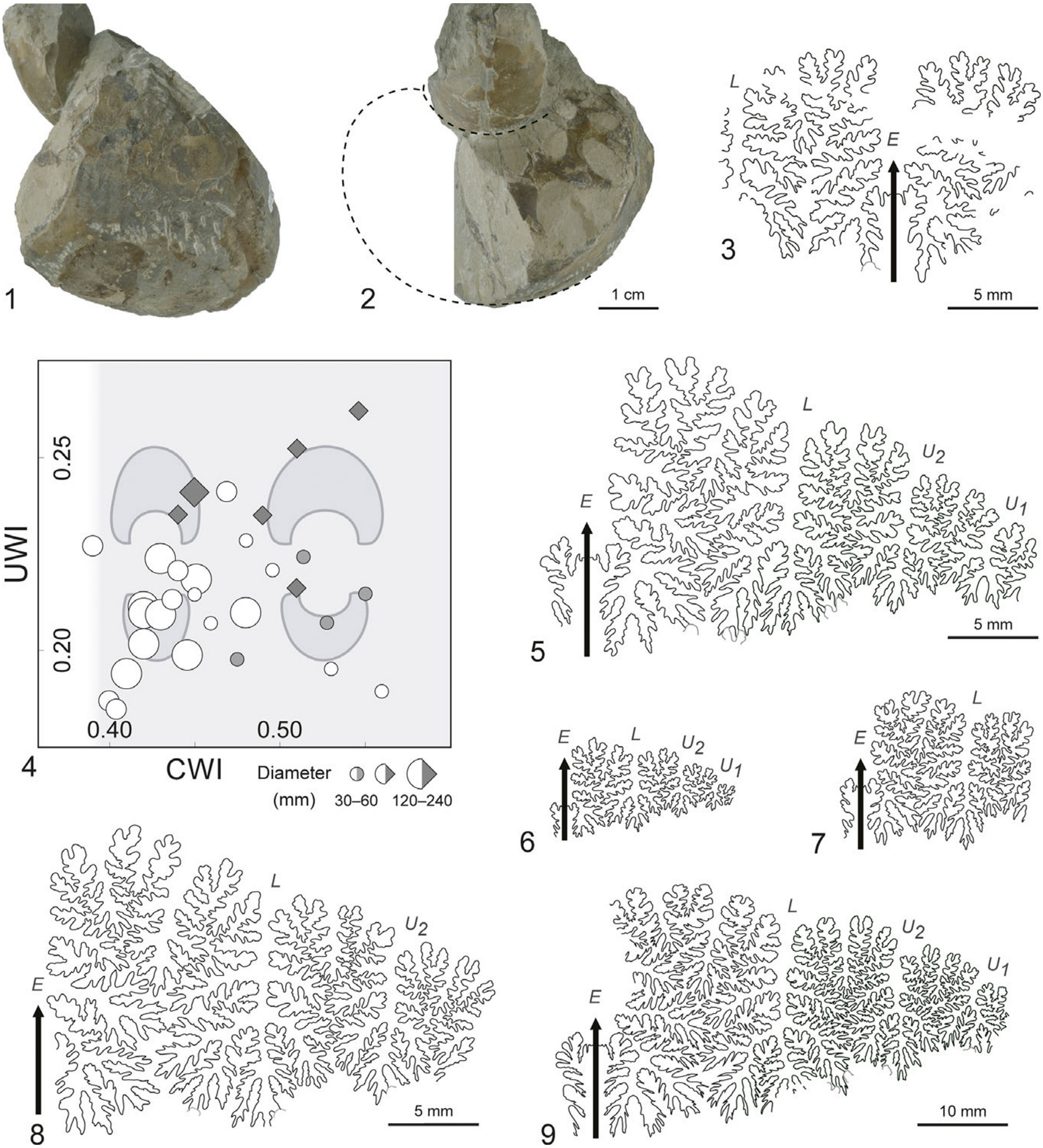

Figure 6. (**1**–**3**) *Anapachydiscus* (*Anapachydiscus*) cf. *A.* (*A.*) *fascicostatus* Yabe and Shimizu, 1921 from the middle Campanian of the Cedar District Formation, western Denman Island, RBCM.EH2013.047.0003.001; (**1**) right flank with faintly discernable rib ornament; (**2**) ventral view, dashed lines denote extrapolated phragmocone cross-section; (**3**) septal suture at Wh = 15 mm. (**4**) UWI (umbilical width index) and CWI (conch width index) comparative ratio plot; bubble size refers to maximum diameter bracket, and images in the background show the shape of the last complete whorl (see morphosectors of Korn, 2010); diamonds denote values pertaining to *Pachydiscus* (*Pachydiscus*) *hornbyense*; circles denote values pertaining to *Pachydiscus* (*Pachydiscus*) *ootacodensis*; white circles = macroconchs, gray circles = mircoconchs. (**5**) Septal suture of *P.* (*P.*) *hornbyense*, RBCM. EH2008.011.11272, western Hornby Island, at whorl height (Wh) = 25 mm. (**6**–**9**) Septal sutures of *P.* (*P.*) *ootacodensis* from the upper Campanian Northumberland Formation, scale bar = 5 mm; (**6**) RBCM.EH2008.011.11257, Collishaw Point, Hornby Island, at Wh = 9.5 mm; (**7**) RBCM.EH2008.011.11264, Collishaw Point, at Wh = 17.5 mm; (**8**) RBCM. EH2008.011.11256, Collishaw Point, Hornby Island, at Wh = 26.5 mm. (**9**) RBCM.EH2008.011.11273, north of Phipps Point, at Wh = 46 mm. *E* = external lobe; *L* = lateral lobe; U_1 = first umbilical lobe; U_2 = second umbilical lobe.

(Spath, 1922; Klinger et al., 2001), Madagascar (Collignon, 1955, 1971), Asia (Stoliczka, 1865; Kossmat, 1898), Japan (Matsumoto, 1951, 1984a), Australia (Henderson and McNamara, 1985), the Americas (Usher, 1952; Matsumoto 1960; Jones, 1963), and Antarctica (Macellari, 1986; Crame et al., 2004).

Remarks. The emended diagnosis essentially reflects that provided by Kennedy (1986b, c) with the adopted terminology of Korn (2010) and microconch ornament morphology. Kennedy (1986c, p. 31) recognized *Pachydiscus* (*Pachydiscus*) *haldemsis* (Schlüter, 1867) as the only dimorphic species in the genus. Unlike *Pachydiscus* (*Pachydiscus*) *ootacodensis* considered in this study, both macro- and microconchs of *P.* (*P.*) *haldemsis* bear umbilical bullae, the principal differentiating factor of ornament being the increase in their projection and presence of ventrolateral tubercles in the microconch (Kennedy and Summesberger, 1984).

Subgenus ***Pachydiscus*** (*Pachydiscus*) Matsumoto, 1947

Type species. *Ammonites neubergicus* von Hauer (1858, p. 12, pl. 2, figs. 1–4, pl. 3, figs. 1, 2) by subsequent designation of de Grossouvre (1894, p. 177).

Emended diagnosis. Discoidal pachydiscids ranging from depressed to compressed, becoming more compressed throughout ontogeny. Conchs subinvolute, with high, flat or convex flanks. Ornament consisting of rectiradiate to feebly sinuous or prorsiradiate primary ribs, which may or may not be feebly umbilically bullate, with well-differentiated intercalaries. Ornament may persist or reduce to umbilical or lateral ribs, with or without feeble umbilical bullae, into maturity. Sexual dimorphism distinguished on the basis of microconch diminutive size and presence of umbilical bullae, or greater development of umbilical bullae and presence of ventrolateral tubercles.

Occurrence. As for the genus.

Remarks. The emended diagnosis essentially reflects that provided by Kennedy (1986b, c) with the adopted terminology of Korn (2010). A number of workers (e.g., Kennedy and Summesberger, 1984; Wright et al., 1996; Ifrim et al., 2010) followed Matsumoto (1947, 1951), as does the present author, in recognizing two subgenera within *Pachydiscus*: *P.* (*Pachydiscus*) as the autonym in contrast to *P.* (*Neodesmoceras*) proposed by Matsumoto (1947) on the basis that members of the former retain some aspect of rib expression into maturity whereas those attributable to the latter see their ornament dimmish early such that the conch appears essentially smooth in the gerontic stage.

Pachydiscus* (*Pachydiscus*) *hornbyense Jones, 1963

Figures 6.4, 6.5, 7.1–7.14

1903 *Pachydiscus otacodensis* (Stoliczka); Whiteaves, p. 340, pl. 46, fig. 1; text-fig. 20.
1952 *Pachydiscus ootacodensis* (Stoliczka); Usher, p. 85, 86, pl. 17, figs. 1–5; pl. 18, fig. 1.
?1958 *Pachydiscus* sp. A Hoen, p. 74, 75, pl. 14, fig. 2.
1963 *Pachydiscus* (*Pachydiscus*) *hornbyense* Jones, p. 38–40, pl. 32, figs. 2–6; pl. 33; text-fig. 19.
?1997 *Pachydiscus* cf. *hornbyense* Larson et al., p. 61, unnumbered fig.
1999 *Pachydiscus* (*Pachydiscus*) *hornbyense* Jones; Kennedy and Cobban, p. 121, 123, pl. 1, figs. 1–3; pl. 2.

Holotype. USNM PAL 131209 recovered from the wavecut platform of the upper Campanian Northumberland Formation at Collishaw Point (Fig. 1.3, loc.7; 49.55°, −124.69°) along the northwestern coast of Hornby Island, British Columbia, as designated by Jones (1963) and reposited within the NMNH.

Emended diagnosis. A large to very large-sized species of *Pachydiscus.* Intermediate conch transitioning from thickly discoidal, subinvolute, to thinly discoidal, subinvolute with maturity. Whorl cross-section strongly embracing and weakly depressed to weakly compressed. CWI avg. = 0.50. WWI avg. = 1.09. UWI avg. = 0.24. LX and VX rates avg. 1.45 and 1.56, respectively. Ornamentation consisting of continuous ribs transverse from the flanks across the venter at even intervals with intercalary ribs. Spines present at intermediate stage along umbilical margin. Suture line complex and florid.

Occurrence. *Pachydiscus* (*Pachydiscus*) *hornbyense* is known from the upper Campanian Northumberland Formation exposed along western Hornby Island, British Columbia (Whiteaves, 1903; Usher, 1952; Jones, 1963) occurring within the *Nostoceras* (*Nostoceras*) *hornbyense* subzone (McLachlan and Haggart, 2018) of the *Pachydiscus* (*Pachydiscus*) *ootacodensis*–*Pachydiscus* (*Pachydiscus*) *suciaensis* Concurrent-range Zone (see biozonation of Haggart et al., 2009, 2011, and Haggart and Graham, 2018, emended herein). Beyond Hornby Island, the species has been reported from the upper Campanian–lower Maastrichtian Bearpaw Formation of Montana (Kennedy and Cobban, 1999) and potentially the upper Campanian of the Pierre Shale of South Dakota based on a few isolated specimens (Larson et al., 1997; Kennedy and Cobban, 1999) as well as possible occurrences within Maastrichtian strata of Madagascar (Collignon, 1971).

Description. Specimens are representative of the intermediate to gerontic stage, reaching large to occasionally very large dimensions with somewhat rounded flanks that become more compressed with maturity (Figure, 6.4; Table 2). Ornamentation consists of ventrally prorsiradiate primary ribs presenting on the intermediary conch (Fig. 7.5, 7.9, 7.11), which become feebly prorsiradiate to rectiradiate in continuation across the flanks with intercalary ribs arising from the flank above the umbilical shoulder (Fig. 7.7, 7.8). Spines begin to develop as tubercles in the intermediary stage where D = ~30 mm and may persist to D = ~90 mm (Fig. 7.1, 7.10). Ribs continue to be raised to the extent that they are reflected on the internal mold with prominent bases on the umbilical shoulder until maturity, with ornament becoming progressively more subdued in some individuals following the intermediate stage. The mature suture line is complex and florid, marked by intricate lobe incision elements and narrow-stemmed external, lateral, and umbilical saddles (Fig. 6.5); an FDI of 1.89 and Sc of 2,013 was obtained from specimen RBCM.EH2008.011.11272 at Wh= 25 mm.

Material. Sixteen specimens reposited within the GSC, NMNH, and RBCM (Supplementary Data, Table 1.3) collected from intertidal outcrops of the upper Campanian Northumberland Formation along the western coast of Hornby Island, British Columbia: RBCM.EH2008.011.11235 from north of Shingle Spit (Fig. 1.3, loc. 4; 49.5215°, −124.7055°); RBCM.EH2008.011.00444 from south of Phipps Point (Fig. 1.3, loc. 5; 49.5342°, −124.7114°); RBCM.EH2008.011.00459, -11236, -11268, and -11270–11272 from the Phipps Point area (Fig. 1.3, loc. 5; 49.5367°, −124.7121°);

Table 2. Dimensions of *Pachydiscus* (*Pachydiscus*) *hornbyense* Jones, 1963, at successive stages of ontogeny. D = whorl volution diameter (mm); WWI = whorl width index; CWI = conch width index; UWI = umbilical width index; LX = lateral conch expansion rate; VX = vertical conch expansion rate; *n* = number of specimens; ex = extrapolation; * = holotype; () = averages

D	WWI	CWI	UWI	LX	VX
50 to < 100	1.0 (1.11) 1.28 *n* = 10	0.41 (0.50) 0.56 *n* = 7	0.22 (0.25) 0.28 *n* = 8	1.41 (1.46) 1.60 *n* = 5	1.50 (1.54) 1.65 *n* = 6
100–200	0.98 (1.00) 1.01 *n* = 3	0.50 (0.53) 0.57 *n* = 2	0.22 (0.23) 0.24 *n* = 4		1.57 *n* = 1
120*	1.01	0.57	0.23		
216.4	0.97	0.45 ex	0.24	1.40	1.62

RBCM.EH2008.011.11274 from the cliffs of Manning Point (Fig. 1.3, loc. 6; 49.5433°, −124.7069°); and GSC 5850, 10051, 10052, RBCM.EH2008.011.11101, RBCM.EH2016.010.0001, holotype USNM PAL 131209, and -131210 from Collishaw Point (Fig. 1.3, loc. 7; 49.55°, −124.69°).

Remarks. Macellari and Zinsmeister (1983) provided unfigured records of what they described as *Pachydiscus* cf. *hornbyense* from the López de Bertodano Formation of Seymour and Snow Hill islands, Antarctica. Macellari (1986) later argued that *Pachydiscus* (*Pachydiscus*) *hornbyense* should remain as a synonym of *Pachydiscus* (*Pachydiscus*) *ootacodensis* due to ambiguity in the definition of the latter species in light of the broad range of variation in the ornamentation of Stoliczka's original type series. However, the specimens in the present study further uphold the lines of evidence established by Jones (1963, p. 40) for distinguishing *P.* (*P.*) *hornbyense* as a distinct species from *P.* (*P.*) *ootacodensis.* Among them, what Jones (1963) described as secondary ribs at an early stage in *P.* (*P.*) *hornbyense.* These would be more appropriately referred to as intercalary ribs, following the terminology of Klug et al. (2015, fig. 1.6) based on the concept of Arkell (1957), given that they develop independently with emergence along the flanks and do not represent furcations or offshoots of primary ribs. The presence of intercalary ribs underscores a tendency of *P.* (*P.*) *hornbyense* to exhibit greater rib frequency at an earlier stage as well. In terms of qualitative rib discernment, *P.* (*P.*) *ootacodensis* has greater sinuosity of the primary ribs, which sweep across the ventrolateral margin to carry forward prorsiradially across the venter. In profile, *P.* (*P.*) *hornbyense* has a higher CWI above D = 50 mm than *P.* (*P.*) *ootacodensis* with even less-compressed flanks and acutely rounded venter. The specimen figured by Hoen (1958, pl. 14, fig. 2) from western Hornby Island, which has a WWI of 0.79 at Wh = 29 mm with transverse and intercalary ribs lending to an RI ≥ 20, as evinced by the plate photograph, is likely assignable to *P.* (*P.*) *hornbyense*, although its UWI of 0.27 is difficult to discern from an eroded umbilical margin. Conversely, it is challenging to definitively place *Pachydiscus* cf. *hornbyense* of Larson et al. (1997, unnumbered fig.) because the specimen is largely an internal mold with a UWI of 0.22.

Ornamentation between *P.* (*P.*) *hornbyense* and *P.* (*P.*) *ootacodensis* becomes difficult to differentiate at more mature stages due to a shared increase in rib density and gradual rib transition to low relief, broadly spaced undulations toward the ultimate smoothing of the ventral region at D > 400 mm (Jones, 1963, p. 38). Not only does ornament become subdued throughout ontogeny in both species, but the flanks of the conch become increasingly compressed. Kennedy and Cobban (1999) recorded considerable compression for *P.* (*P.*) *hornbyense* at D = 230 mm with a WWI of 0.88. For these reasons, consideration needs to be given to differences in shell geometry more clearly expressed in the early to intermediate stages with *P.* (*P.*) *hornbyense* possessing less-compressed flanks, a broadly rounded venter, and a proportionality wider umbilicus reflected in slightly higher UWI values.

Jones (1963) placed emphasis on the presence of umbilical tubercles as a trait that distinguishes examples of *P.* (*P.*) *hornbyense* from those of *P.* (*P.*) *ootacodensis.* In actuality, umbilical tubercles —or bullae—are present in some diminutive specimens of *P.* (*P.*) *ootacodensis* (Jones, 1963, pl. 32, fig. 1; Fig. 8.1–8.6, 8.8), herein attributed to a microconch dimorph. Beyond D = ~40 mm, these forms lack umbilical bullae that progress into the prominent spinous tubercles characteristic of *P.* (*P.*) *hornbyense.* Another point of differentiation lies in *P.* (*P.*) *hornbyense* presenting ridges along the umbilical shoulder in connection with more well-developed transverse primary ribs in comparison to the steplike, smooth umbilical shoulder with an overhanging wall in *P.* (*P.*) *ootacodensis.* In instances where specimens of *P.* (*P.*) *hornbyense* have lost their spines and elevated ridges along the umbilical shoulder following damage, the bases of these features usually remain evident as a bulge on the internal mold and exposed septate surface following complete removal of the outer shell layers.

Pachydiscus (*P.*) *hornbyense* approaches *Anapachydiscus* morphology based on inflation, ventral depression, spinous-tuberculate umbilical ornament, and rib pronunciation, but the key CWI and WWI metrics reflect Wh ≥ Ww as the conch becomes more compressed with maturity. Jones (1963) remarked that *P.* (*P.*) *hornbyense* can be perceived as an intermediary form between members of *Pachydiscus* and *Anapachydiscus.* Among species attributed to the latter genus, *P.* (*P.*) *hornbyense* bears greatest similarity to *Anapachydiscus peninsularis* known from the upper Campanian–?lower Maastrichtian of the Great Valley Sequence and Santa Ana Mountains of California (Anderson and Hanna, 1935; Ward and Signor, 1983), as well as the strata of Baja California (Anderson and Hanna, 1935; Beal, 1948; Saul, 1979; Ward et al., 2012), and probably Oregon (cf. *peninsularis* of Howard, 1961; Bourgeois, 1980; see Taylor and Lucas, 2018, for biostratigraphic commentary), with the differences becoming apparent in late ontogeny. The former species differs from *A. peninsularis* in having greater consistency of rib continuity and projection across the venter as well as in being less depressed. The whorls of *A. peninsularis* remain wider than high among the largest specimens where D > 350 mm (Anderson and Hanna, 1935)—an inflation parameter retained to over twice the diameter of the most depressed individuals of *P.* (*P.*) *hornbyense.* In addition, the UWI at 0.22 is slightly lower in *A. peninsularis* compared to *P.* (*P.*) *hornbyense* with an average of 0.24 between the specimens measured herein and by Jones (1963). Both taxa lose their spinous ornament where D > 90 mm.

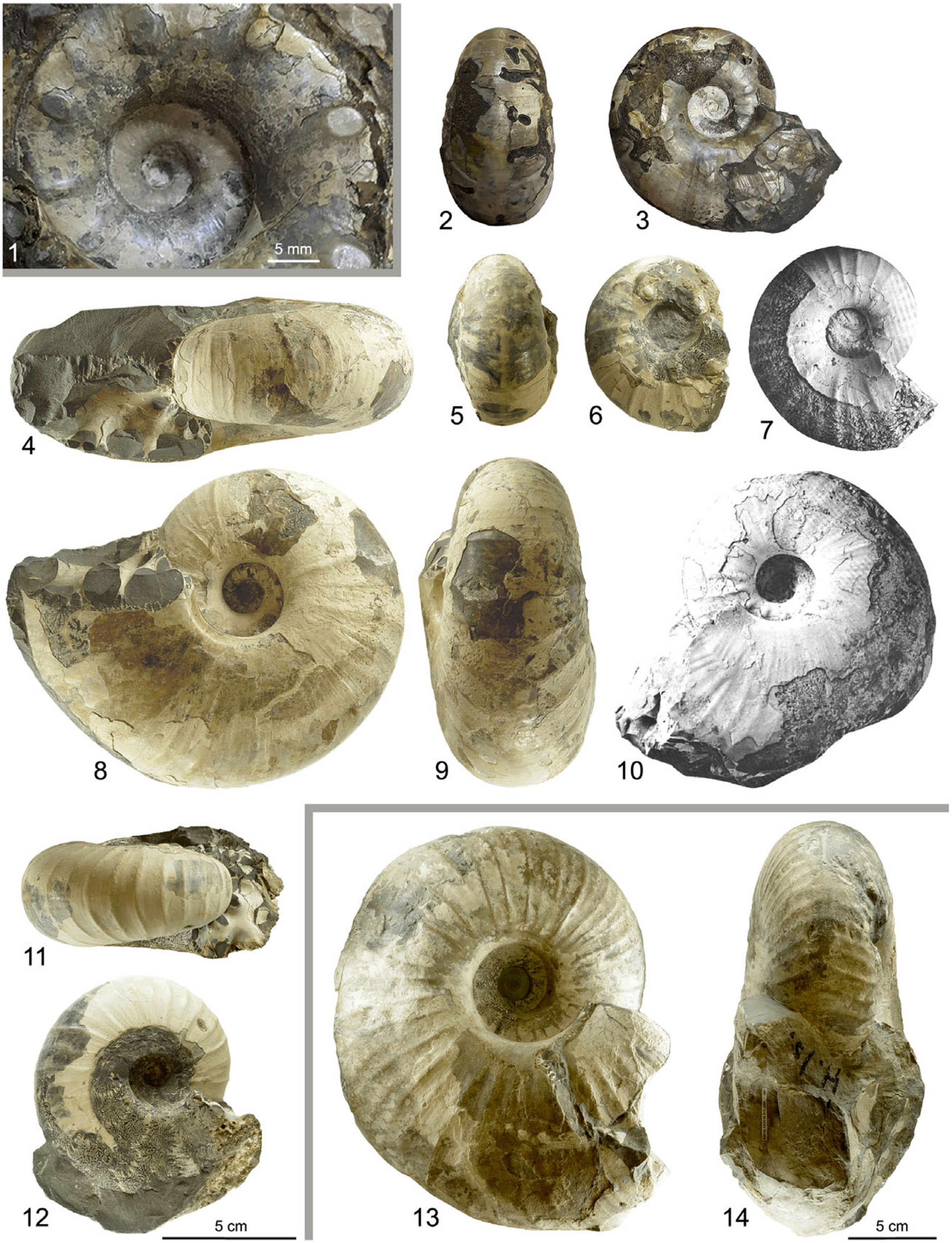

Figure 7. (**1–14**) *Pachydiscus* (*Pachydiscus*) *hornbyense* Jones, 1963 from the upper Campanian of the upper Northumberland Formation, western Hornby Island. (**1–3**) RBCM. EH2008.011.00459, Phipps Point area; (**1**) left flank exhibiting prominent spine bases along the umbilical shoulder; (**2**) ventral view; (**3**) right flank. (**4, 8, 9**) RBCM.EH2008.011.11270, Phipps Point area; (**4, 9**) ventral views; (**8**) left flank. (**5, 6**) RBCM.EH2008.011.11268, Phipps Point area; (**5**) ventral view; (**6**) right flank. (**7**) Paratype USNM PAL 131210 of Jones (1963, pl. 33, fig. 4), right flank, Collishaw Point. (**10**) Holotype USNM PAL 131209 of Jones (1963, pl. 32, fig. 6), left flank with band-slit pathology, Collishaw Point. (**11, 12**) RBCM. EH2008.011.11271, Phipps Point area; (**11**) ventral view; (**12**) right flank. (**13, 14**) RBCM.EH2016.010.0001, Collishaw Point; (**13**) right flank; (**14**) apertural view.

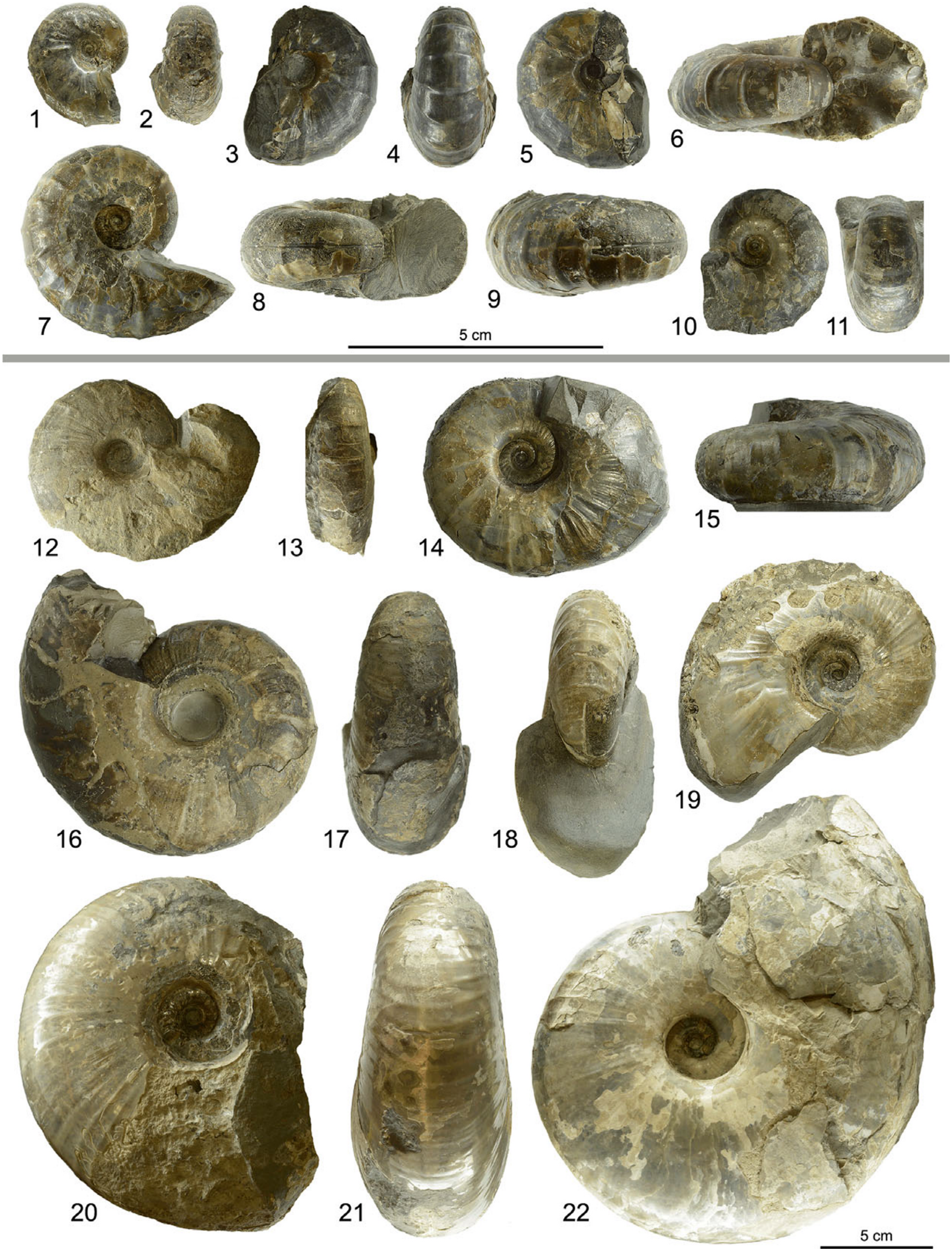

Figure 8. (**1–22**) *Pachydiscus* (*Pachydiscus*) *ootacodensis* (Stoliczka, 1865) from the upper Campanian of the Cedar District and Northumberland formations exposed on Denman and Hornby islands, respectively. (**1–9**) Inferred microconchs with bullae and intermittent rib projection along the umbilical shoulder. (**1, 2**) RBCM.EH2008.011.11246, north of Shingle Spit; (1) right flank; (2) ventral view. (**3–5**) RBCM P2022.183.0001, south of Phipps Point; (**3**) left flank; (**4**) ventral view; (**5**) right flank. (**6**) RBCM.EH2008.011.11250, north of Shingle Spit, ventral view. (**7–9**) RBCM.EH2008.011.11264, Collishaw Point; (**7**) right flank; (**8**) apertural view; (**9**) ventral view with unusual ribbing obliquity along left ventrolateral margin. (**10–22**) Inferred macroconchs with subdued ornamentation along the umbilical shoulder throughout ontogeny. (**10, 11**) RBCM.EH2008.011.11248, south of Phipps Point; (**10**) left flank; (**11**) ventral view. (**12, 13**) RBCM.EH2008.011.27501, ‘Gladstone Bay’; (**12**) right flank; (**13**) ventral view. (**14, 15**) RBCM P2022.183.0003, Collishaw Point; (**14**) right flank; (**15**) ventral view. (**16, 17**) RBCM P2022.183.0002, ‘Gladstone Bay’; (**16**) left flank; (**17**) ventral view. (**18, 19**) RBCM.EH2008.011.11256, Collishaw Point; (**18**) apertural view; (**19**) right flank with band-slit pathology. (**20, 21**) RBCM.EH2008.011.11258, ‘Paradise Bay’ (**20**) right flank; (**21**) ventral view. (**22**) RBCM.EH2008.011.11284, Manning Point, right flank.

Pachydiscus* (*Pachydiscus*) *ootacodensis (Stoliczka, 1865)

Figures 6.4, 6.6–6.9, 8.1–8.22

1865 *Ammonites ootacodensis* Stoliczka, p. 109, 110, p1. 54, figs. 3, ?4, pl. 56, figs. 1, 2a, 2b (not p1. 57).
1898 *Pachydiscus ootacodensis* (Stoliczka) Kossmat, p. 98–101, p1. 16, figs. 1a, 1b, p1. 17, fig. 1.
1922 *Parapachydiscus* aff. *ootacodensis* (Stoliczka), Spath, p. 132, 133, p1. 7, fig. 6.
1935 *Parapachydiscus ootacodensis* (Stoliczka); Anderson and Hanna, p. 20, 21, pl. 6, figs. 1, 2.
?1952 *Pachydiscus ootacodensis* (Stoliczka); Usher, p. 85, 86, pl. 19, fig. 1, pl. 20, figs. 1, 2.
1958 *Pachydiscus ootacodensis* (Stoliczka); Hoen, p. 70–72, pl. 13, figs. 1, 1a, 2, 2a.
1963 *Pachydiscus* (*Pachydiscus*) *ootacodensis* (Stoliczka); Jones, p. 38, pl. 29, figs. 1–3, 13–16, pl. 30, figs. 1–3, pl. 31, figs. 1, 2, pl. 32, fig. 1.
?1971 *Pachydiscus otacodensis* (Stoliczka); Collignon, p. 40, pl. 656, fig. 2419.
?2013 *Pachydiscus* cf. *ootacodensis* (Stoliczka); Zakharov et al., fig. 4.

Holotype. Undesignated with no lectotype instated following a lack of confirmation from the Curatorial Division of the Geological Survey of India as to the status of Stoliczka's (1865) original material. The author agrees with Jones (1963) that in the absence of a holotype from the series of Stoliczka (1865), the specimen illustrated by Kossmat (1898, p1. 16, fig. la, b) from the Ariyalur Group of southern India stands as a suitable representative of the predominant species morphotype.

Emended diagnosis. A small to very large-sized species of *Pachydiscus.* Intermediate conch transitioning from thickly discoidal, subinvolute, to thinly discoidal, subinvolute with maturity. Whorl cross-section strongly embracing and weakly depressed to weakly compressed with step-like umbilical shoulder. Ornamentation consisting of strongly projected prorsiradiate ventral primary ribs, which vary in continuity across the flanks. Microconch: generally small with umbilical bullae; CWI avg. = 0.52; WWI avg. = 1.10; UWI avg. = 0.22; LX and VX rates avg. 1.47 and 1.50, respectively. Macroconch: large to very large with progressively diminishing ribbing; CWI avg. = 0.46; WWI avg. = 0.94; UWI avg. = 0.21; LX and VX rates avg. 1.53. Suture line complex and florid.

Occurrence. In British Columbia, *Pachydiscus* (*Pachydiscus*) *ootacodensis* has its first occurrence in exposures of the upper Campanian of the Cedar District Formation at 'Gladstone Bay' on northwestern Denman Island with continuation into the Northumberland Formation on Hornby Island (Hoen, 1958; Jones, 1963; cf. *ootacodensis* of Zakharov et al., 2013), sharing the same range of the regional zonal index taxon *Pachydiscus* (*Pachydiscus*) *suciaensis* (Meek, 1862) (see biozonation of Haggart et al., 2009, 2011; Haggart and Graham, 2018). *Pachydiscus* (*P.*) *ootacodensis* was originally described from southern India by Stoliczka (1865) where it was later re-examined by Kossmat (1898). Forms attributed to the taxon have subsequently been reported from the upper Campanian of Alaska (Keller and Reiser, 1959; Popenoe et al., 1960; Jones, 1963; Jones in Grantz, 1964; Koepnick et al., 1985; cf. *ootacodensis* of Imlay and Reeside 1954), California (Matsumoto, 1960; Popenoe et al., 1960; Vedder et al., 1977; Ward, 1978a; Elder and Miller, 1993; cf. *ootacodensis* of Matsumoto, 1960); Baja California (Anderson and Hanna, 1935; Beal, 1948), eastern Europe (Pratz, 1910), the Middle East (Lewy, 1990), South Africa (aff. *ootacodensis* of Spath, 1922), and the Maastrichtian of Madagascar (Collignon, 1938, 1971). Isolated specimens from upper Maastrichtian strata of Antarctica have also been assigned to the species (Macellari, 1986; Crame et al., 1991, 2004).

Description. Specimens are representative of the late-juvenile to gerontic stages, attaining large to very large dimensions with increasingly compressed flanks and an evenly rounded venter throughout ontogeny (Figure, 6.4; Table 3). Approximately 93% of all measured specimens where D > 100 mm express a WWI < 1. The CWI for the largest specimen, NMNH "1" of Jones (1963), is 0.45 at Wh = 442 mm, consistent with a gradual trend toward lateral compression with maturity. Ornamentation consists of characteristic prorsiradiate ribs with greatest projection along the venter (Fig. 8.4, 8.13, 8.15), which vary in their expression of continuity across the flanks.

Among inferred microconchs, bullae develop along the umbilical margin from the inception point of raised ribs, which diminish to mid-flank at D = 20–50 mm (Fig. 8.1–8.6, 8.8). These projections may present as tubercles but are more commonly characterized as elongate nodes arising from 'pinched' ribs. Mature microconchs seldom exceed D = 50 mm and retain raised, projected ribs and bullate ornament. In forms lacking umbilical bullae, herein regarded as macroconchs, the continuity of ribs can be seen to

Table 3. Dimensions of *Pachydiscus* (*Pachydiscus*) *ootacodensis* (Stoliczka, 1865) at successive stages of ontogeny. D = whorl volution diameter (mm); WWI = whorl width index; CWI = conch width index; UWI = umbilical width index; LX = lateral conch expansion rate; VX = vertical conch expansion rate; *n* = number of specimens; * = microconch values; () = averages

D	WWI	CWI	UWI	LX	VX
33–56*	0.99 (1.09) 1.18 *n* = 6	0.47 (0.52) 0.55 *n* = 5	0.20 (0.21) 0.23 *n* = 6	1.38 (1.47) 1.58 *n* = 4	1.32 (1.50) 1.65 *n* = 4
19 to < 50	0.90 (1.08) 1.27 *n* = 4	0.45 (0.53) 0.57 *n* = 6	0.19 (0.21) 0.23 *n* = 6	1.38 (1.48) 1.54 *n* = 4	1.46 (1.61) 1.78 *n* = 4
50 to < 100	0.72 (0.92) 1.08 *n* = 15	0.39 (0.44) 0.48 *n* = 8	0.19 (0.22) 0.24 *n* = 9	1.37 (1.57) 1.70 *n* = 5	1.33 (1.54) 1.70 *n* = 9
100 to < 200	0.69 (0.89) 1.03 *n* = 18	0.40 (0.44) 0.49 *n* = 12	0.19 (0.21) 0.23 *n* = 14	1.41 (1.57) 1.80 *n* = 11	1.37 (1.57) 1.72 *n* = 12
200–400	0.67 (0.85) 0.93 *n* = 5	0.42 (0.44) 0.46 *n* = 3	0.18 (0.21) 0.24 *n* = 4	1.70 *n* = 1	1.30 (1.42) 1.53 *n* = 2
442	0.94 *n* = 1	0.45 *n* = 1	0.22 *n* = 1		

more readily dissipate at mid-flank with termination prior to a smooth step-like umbilical shoulder.

In the macroconch morphotype, the RI of the broad, ventral ribs increases with ontogeny while ribs in general exhibit diminishing relief as to render them subdued undulations along an essentially smooth shell surface typically where D > 150 mm (Fig. 8.20–8.22). The mature suture line is complex and florid, marked by intricate lobe incision elements and narrow-stemmed external, lateral, and umbilical saddles (Fig. 6.6–6.9); an FDI of 1.96 and Sc of 4,005 were obtained from specimen RBCM.EH2008.011.11273 at Wh = 46 mm.

Material. Fifty-eight specimens reposited within the collections of the RBCM, NMNH, and CDMPC (Supplementary Data, Table 1.4). Three specimens, RBCM.EH2008.011.27500, -27501, and RBCM P2022.183.0002, were collected from intertidal outcrops of the upper Campanian of the Cedar District Formation, 'Gladstone Bay', northwestern Denman Island (Fig. 1.3, loc. 2; 49.584°, −124.841°), and 54 from exposures of the upper Campanian Northumberland Formation along the southeastern and western coasts of Hornby Island, British Columbia; RBCM.EH2008.011.11251 and -11259 from 'Paradise Bay' (Fig. 1.3, loc. 3; 49.4953°, −124.6533°); RBCM. EH2008.011.00472, -11246, and -11250 from north of Shingle Spit (Fig. 1.3, loc. 4; 49.5215°, −124.7055°). RBCM P2022.183.0001, RBCM.EH2008.011.11237, -11239, -11240, -11242–11245, -11248, -11265, -11275, and -11276 from south of Phipps Point (Fig. 1.3, loc. 5; 49.533°, −124.712°); RBCM.EH2008.011.11241, -11252, -11260, -11261, -11267, -11273, -11277, -11279, -11286, and RBCM. EH2016.011.0001 from north of Phipps Point (Fig. 1.3, loc. 5; 49.5367°, −124.7121°); RBCM.EH2008.011.11278 and -11284 from the Manning Point area (Fig. 1.3, loc. 6; 49.5438°, −124.7111°); RBCM P2022.183.0003, RBCM.EH2008.011.11058, -11108, -11256–11258, -11262–11264, -11266, -11280–11283, and -11285 from Collishaw Point (Fig. 1.3, loc. 7; 49.55°, −124.69°); and CDM 2008.1.20 HUN, -78 HUN, -86 HUN, RBCM.EH2008.011.11247, and -11253 from broadly western Hornby Island. Data from six specimens measured by Jones (1963, p. 38) were included: USNM PAL 131202 and -131203 from USGS Mesozoic loc. 16398, USNM PAL 131204 from USGS Mesozoic loc. 25327, USNM PAL 131208 from USGS Mesozoic loc. 25856, and specimens "1" and "2" of unknown provenance, southern Alaska.

Remarks. Exceptionally large pachydiscids having attained a size in excess of D = 1 m have been recovered from the Northumberland Formation on Hornby Island, with their greatest frequency of occurrence in the section north of Shingle Spit that is characterized by an interval of heightened oxidation resulting in the rusty red exterior of concretionary matrices. It is likely that these specimens represent mature macroconchs of *Pachydiscus* (*Pachydiscus*) *ootacodensis.* However, these examples are fragmentary or, at best, preserved in a single-sided manner such that only one flank of the outermost volutions was immersed in the substrate upon deposition. A step-like umbilical shoulder is clearly evident, but due to the diminishment ornament, shells retaining only faint rib expression, if not exhibiting a virtually smooth surface, at these diameters preclude a definitive diagnosis.

Henderson and McNamara (1985) followed Stoliczka (1865) in considering *P.* (*P.*) *ootacodensis* to be a junior synonym of *Pachydiscus* (*P.*) *colligatus* (Binkhorst van den Binkhorst, 1861). Kennedy (1986b) refuted this interpretation in his revised treatment of the latter species toward resolution of the confusion stemming from the wide range of variability between forms originally accommodated within the *P.* (*P.*) *ootacodensis* concept as presented by Stoliczka (1865). The specimen illustrated by Kossmat (1898) is an adequate representative for *P.* (*P.*) *ootacodensis* in the absence of a lectotype designated from Stoliczka's (1865) figured series.

As noted by Kennedy et al. (2000, p. 560), the Antarctic specimens assigned to *P.* (*P.*) *ootacodensis* by Macellari (1986) lack the characteristic broadly spaced prorsiradiate ventral primary ribs, while exhibiting ribs that extend across the flanks, and umbilical tubercles. These features see Antarctic material bearing closer resemblance to *Pachydiscus* (*Pachydiscus*) *hornbyense*, differing only in a lack of intercalary ribs with lesser proximity and an ornamental affinity to *Anapachydiscus peninsularis* in the lack of rib continuity across the venter (Macellari, 1986, fig. 40.3). As such, unless more definitive specimens are figured, the Antarctic occurrence of *P.* (*P.*) *ootacodensis* sensu Macellari (1986) upon which all subsequent inference and discussion relating to the species in the region is based (e.g., Crame et al., 1991, 2004; Pirrie et al., 1991; Olivero and Medina, 2000; Olivero, 2012; Harper et al., 2018) is more appropriately assigned to a separate taxon. The specimen figured by Collignon (1971) from the Maastrichtian of Madagascar is questionably referred to this species due to the transverse continuity of coarse ribs across the venter, its rib density (RI > 20), UWI (0.18), and VX value of 1.55 obtained from the figured image.

Discussion

Biostratigraphic correlation. *Anapachydiscus* (*Anapachydiscus*) *fascicostatus*, known from rocks of the upper Yezo Group in Hokkaidō, is a constituent molluscan fossil of the middle Campanian *Metaplacenticeras subtilistriatum* Zone in the region (e.g., Matsumoto, 1982, 1984a; Shigeta et al., 2016). In Japan, the *M. subtilistriatum* Zone occurs as an interval below the range of *Baculites subanceps* Haughton, 1925 (Shigeta et al., 2016), the latter species of which has been identified as a biostratigraphically important index heteromorph ammonite for the North Pacific with presence in the Cedar District Formation of the Nanaimo Group exposed along eastern Vancouver Island, western Denman Island, South Pender Island, and Sucia Island (e.g., Muller and Jeletzky, 1970; Ward, 1978b; Ward et al., 2012, 2015; Bookstein and Ward, 2013). The specimen herein attributed to *Anapachydiscus* (*Anapachydiscus*) cf. *A.* (*A.*) *fascicostatus* from the Denman Island coast was recovered from below the highest occurrence of *Metaplacenticeras* cf. *M. pacificum* (Smith, 1900), ~500 m northwest of the Denman Island West ferry terminal (Muller and Jeletzky, 1970). However, due to the chaotic nature of the fossils in situ, the site yielding *M.* cf. *M. pacificum* may represent a down-slope deposit of reworked material (R. Graham, pers. comm., 2023). Nevertheless, a position equivalent to or overlying the middle Campanian *Metaplacenticeras* cf. *M. pacificum* Zone erected for the eastern North Pacific can be inferred (e.g., Popenoe, 1942; Matsumoto, 1960; Popenoe et al., 1960; Muller and Jeletzky, 1970; Ward, 1978a; Haggart and Ward, 1989) supported by sub- and superjacent occurrences of the bivalve *Opis vancouverensis* Whiteaves, 1879, assigned to the middle–upper middle Campanian by Squires and Saul (2009). Other specimens assigned to *Anapachydiscus* have been reported from this zone in California including *A. deccanensis* and *A.* cf. *A. arrialoorensis* (e.g., Matsumoto, 1960; Popenoe et al., 1960). Haggart (1989) indicated that some overlap is apparent between the ranges of *B. subanceps* and *M.* cf. *M. pacificum* in the Nanaimo Group as has been recognized in California (e.g., Matsumoto, 1959, 1960; Matsumoto and Obata, 1963; Ward et al., 2012). While there may be diachroneity between the zones of endemic placenticeratid fauna in the eastern and western North Pacific, it is reasonable to regard the *M.* cf. *M. pacificum* Zone as approximately equivalent to the *M. subtilistriatum* Zone (Matsumoto, 1960; Popenoe et al., 1960). As such, the position of a pachydiscid comparable to *A.* (*A.*) *fascicostatus* within or superjacent to the corresponding interval for the Nanaimo Group succession is entirely consistent with the Japanese biochronology.

Usher (1952) recognized specimens possibly attributable to *Pachydiscus* (*Pachydiscus*) *ootacodensis* from the upper Campanian of the Nanaimo Group within an interval subsequently renamed the *Pachydiscus suciaensis* Zone by Jeletzky (1970a, b) who also recognized the regional co-occurrence of the species. Matsumoto (1960), Ward (1978a, b), Ward and Stanley (1982), and Elder and Saul (1996) have also noted *P.* (*P.*) *ootacodensis* as an age-diagnostic species for the Pacific Slope of North America.

It is herein considered practical to instate *Pachydiscus* (*Pachydiscus*) *ootacodensis* as a zonal index fossil due to its broader geographic recognition beyond the eastern North Pacific (e.g., Stoliczka, 1865; Kossmat, 1898; Pratz, 1910; Spath, 1922; Lewy, 1990), whereas *Pachydiscus* (*Pachydiscus*) *suciaensis* is endemic to the region with a distribution ranging from Alaska (Keller and Reiser, 1959; Popenoe et al., 1960; Jones, 1963) south through Haida Gwaii (Haggart et al., 2009) to the Gulf Islands (e.g., Meek, 1862, 1876; Whiteaves, 1879, 1903; Usher, 1952; Hoen, 1958; Ward et al., 2012) and California (Ward et al., 2012). Notably, the faunal assemblage of the Lawn Hill section of the informally named Tarundl formation exposed on the east coast of Graham Island, Haida Gwaii (Haggart et al., 2009) shares a striking similarity to that of southeastern Hornby Island as described by McLachlan and Haggart (2018). The only possible exception to *P.* (*P.*) *suciaensis* endemism is an isolated report from strata of the Izumi Group, Awaji Island, Japan, which Matsumoto (1978) assigned to *Pachydiscus* cf. *P. suciaensis*. Save for reports attributed to the species from the Maastrichtian of Madagascar (Collignon, 1971) and its use as a zonal indicator for the upper Maastrichtian of the López de Bertodano Formation of Antarctica (e.g., Macellari, 1986, 1988; Crame et al., 1991, 2004; Olivero and Medina, 2000), it would appear that *P.* (*P.*) *ootacodensis* sensu Jones (1963) maintained herein is constrained to strata of late Campanian age. Therefore, the present study proposes the adoption of a *P.* (*P.*) *ootacodensis*–*P.* (*P.*) *suciaensis* Concurrent-range Zone for the upper Campanian of the eastern North Pacific.

Definition of the Pachydiscus (Pachydiscus) ootacodensis–Pachydiscus (Pachydiscus) suciaensis Concurrent-range Zone. A biostratigraphic unit herein designated as an interval for the uppermost Campanian of the eastern North Pacific realm as defined by the mutual first and last occurrences of the ammonite species *Pachydiscus* (*Pachydiscus*) *ootacodensis* (Stoliczka, 1865) and *Pachydiscus* (*Pachydiscus*) *suciaensis* (Meek, 1862). The proposed type section for the base of the *P.* (*P.*) *ootacodensis*–*P.* (*P.*) *suciaensis* Concurrent-range Zone (Fig. 2) lies within Nanaimo Group exposures of the Cedar District Formation at 'Gladstone Bay' on northwestern Denman Island (Fig. 1.3, loc. 2; 49.584°, −124.843°). At this location, specimens of the eponymous species have their first occurrence and are found in association with the ammonite taxa *Baculites rex* Anderson, 1958, *Gaudryceras denmanense* Whiteaves, 1901, and *Hypophylloceras* (*Neophylloceras*) *ramosum* (Meek, 1857). Specimens of *P.* (*P.*) *ootacodensis* have not been recognized from strata of the Cedar District Formation previously, although Ward (1976a, table 3.2) noted rare occurrence at Shelter Point, south of Campbell River on Vancouver Island; an intertidal locality with exposures attributed to this unit (Haggart and Graham, 2022) also reported to yield pachydiscids assignable to *P.* (*P.*) *suciaensis* (Jeletzky in Richards, 1975; Haggart, 1989). Ward et al. (2012) would later report the presence of *P.* (*P.*) *suciaensis* within the formation on western Denman Island. However, their claim that the *P.* (*P.*) *suciaensis* range extends to the basal level of the Denman Island section and into the underlying zone of *M.* cf. *M. pacificum* is dubious, given that the specimens available from the lowest beds are incomplete representatives of more evolute, constricted forms akin to *Canadoceras newbarryanum* (Meek, 1857).

On Hornby Island, *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. is part of a distinct molluscan assemblage that characterizes a narrow interval within the *P.* (*P.*) *ootacodensis*–*P.* (*P.*) *suciaensis* Concurrent-range Zone represented by lower Northumberland Formation exposures at 'Paradise Bay', along the southeastern coast (Fig. 1.3, loc. 3) overlying the zonal base in the upper Cedar District Formation on western Denman Island (Fig. 2). *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. occurs within the *Nostoceras* (*Didymoceras*?) *adrotans* subzone of McLachlan and Haggart (2018) at this locality alongside *P.* (*P.*) *ootacodensis* in addition to the following ammonites: *Baculites* cf. *B. occidentalis* Meek, 1862, *Damesites* cf. *D. damesi* (Jimbo, 1894), *Exiteloceras* (*Neancyloceras*) aff. *E.* (*N.*) *bipunctatum* (Schlüter, 1872), *Gaudryceras denmanense* Whiteaves, 1901, *Gaudryceras* cf. *G. tenuiliratum* (Yabe, 1903), *Hypophylloceras* (*Neophylloceras*) *ramosum* (Meek, 1857), *Hypophylloceras* (*Neophylloceras*) *surya* (Forbes, 1846), *Nostoceras* (*Didymoceras*?) *adrotans* McLachlan and Haggart, 2018, *Pachydiscus* (*Pachydiscus*) *subcompressus* Matsumoto, 1954, *Pseudophyllites indra* (Forbes, 1846), *Phyllopachyceras forbesianum* (d'Orbigny, 1850), *Phylloptychoceras horitai* Shigeta and Nishimura, 2013, *Solenoceras exornatus* McLachlan and Haggart, 2018, and *Zelandites* sp. Curiously, specimens of *P.* (*P.*) *suciaensis* are unknown at 'Paradise Bay', perhaps reflecting an ecological limitation of the species in addition to its biogeographical constraints.

The *Nostoceras* (*Nostoceras*) *hornbyense* subzone (e.g., Jeletzky, 1970b; Ward, 1978a; = *Nostoceras hornbyense* Zone of Haggart et al., 2009) spans the western coast of Hornby Island upsection from Shingle Spit toward the highest level of the Northumberland Formation at Collishaw Point. An appropriate reference section for the top of the *P.* (*P.*) *ootacodensis*–*P.* (*P.*) *suciaensis* Concurrent-range Zone would be placed at the cliff face perpendicular to the syncline axis at Collishaw Point (Fig. 1.3, loc.7; 49.549°, −124.692°). In addition to the aforementioned index taxa, this interval is marked by a rich ammonite fauna including: *Baculites occidentalis* Meek, 1862, *Desmophyllites diphylloides* (Forbes, 1846), *Diplomoceras* (*Diplomoceras*) *cylindraceum* (Defrance, 1816), *Diplomoceras* (*Diplomoceras*) cf. *D.* (*D.*) *cylindraceum* (Defrance, 1816), *Gaudryceras* cf. *G. tenuiliratum* (Yabe, 1903), *Hypophylloceras* (*Neophylloceras*) *ramosum* (Meek, 1857), *Nostoceras* (*Nostoceras*) *hornbyense* (Whiteaves, 1895), *Nostoceras* (*Nostoceras*) aff. *N.* (*N.*) *pauper* (Whitfield, 1892), *Pachydiscus* (*Pachydiscus*) *hornbyense* Jones, 1963, *Pachydiscus* (*Pachydiscus*) sp., *Pachydiscus* (*Neodesmoceras*) sp., and *Pseudophyllites indra* (Forbes, 1846). Rarer assemblage constituents consist of: *Anagaudryceras politissimum* (Kossmat, 1895), *Damesites* cf. *D. damesi* (Jimbo, 1894), *Exiteloceras* (*Exiteloceras*) *densicostatum* McLachlan and Haggart, 2018, *Exiteloceras* (*Neancyloceras*) aff. *E.* (*N.*) *bipunctatum* (Schlüter, 1872), *Fresvillia constricta* Kennedy, 1986a, *Gaudryceras* aff. *G. venustum* Matsumoto, 1984b (Haggart, 1989), *Hypophylloceras* (*Neophylloceras*) *surya* (Forbes, 1846), *Phyllopachyceras forbesianum* (d'Orbigny, 1850), *Phylloptychoceras horitai* Shigeta and Nishimura, 2013, and *Solenoceras* cf. *S. reesidei* Stephenson, 1941.

Taphonomic considerations and paleoecological implications. Molluscan shells such as the elaborately coiled and ornate conchs of heteromorph ammonites belonging to the Baculitidae, Diplomoceratidae, and Nostoceratidae are rarely recovered as complete specimens from Nanaimo Group strata (e.g., Usher, 1952; Ward, 1976b; Ward and Mallory, 1977), and examples known from the Northumberland Formation are no exception (McLachlan and Haggart, 2018). However, planispiral taxa such as members of the Pachydiscidae are typically compact and robust, and therefore less prone to processes of post-depositional disarticulation. The predominantly fine-grained mudstone of the Northumberland Formation allows for high-quality preservation of shell materials (e.g., Zakharov et al., 2013), although planispiral ammonites commonly exhibit single-sided preservation presumably due to effacement of the side not impressed within the substrate after settlement as a result of breakage or scavenging. The best preservation of ammonites is generally observed in calcareous concretions where the cameral chambers are filled by calcite crystals, which developed after the shell became waterlogged and sank to the sea floor under circumstances conducive to complete sediment immersion (Maeda and Seilacher, 1996). Sections of phragmocone are generally the most well preserved due to septal buttressing while shattered body chambers provide evidence of unsupported shell wall susceptibility to compaction at depth.

A phenomenon commonly observed within the Northumberland Formation mudstone is the tendency of juvenile ammonites from a wide range of species to occur in clusters within concretions. Such concretions are often densely fossiliferous containing a wide variety of micro- and macrofossils. Unlike modern *Nautilus*, which has a deep-sea reproductive strategy (e.g., Haven, 1977; Saunders, 1984; Saunders and Ward, 2010), ammonoids are largely regarded to have been planktic drifters in early life (Ward and Bandel, 1987; Landman et al., 1996; Wani et al., 2011; Laptikhovsky et al., 2012; De Baets et al., 2015). While these death assemblages have been attributed to ocean chemistry changes such as those in proximity to methane seeps (Rowe et al., 2020), the frequent presence of terrestrial botanical matter in these concretions—such as seeds, cones, and wood—suggests the possibility that planktic juveniles became bound in drifting masses conducive to agglutination prior to their deposition. It has been surmised that the transport mediums in question may have been floating algal mats (Stinnesbeck et al., 2016) or the gelatinous egg masses or membranous brood sacs of these very ammonoids (Landman et al., 1996; Westermann, 1996) either suspended in the water column or attached to subsurface debris (Etches et al., 2009; Mapes and Nützel, 2009).

A heightened diversity of ammonite assemblages has been interpreted as a function of proximity to nearshore oxygenated environments (Landman and Klofak, 2012; Slattery et al., 2018). Sedimentological and microfacies analyses have also led to speculation that ammonoids may have spawned in shallow waters below storm wave base (Ifrim et al., 2018). The energetic and tumultuous conditions of an inner neritic setting that would have contributed to the entrapment and rapid burial of juvenile ammonoids are supported by the presence of broken inoceramid shells (Landman and Klofak, 2012), gastropods, and scaphopods (Wendler et al., 2016) as well as an abundance of terrestrial plant detritus (Linzmeier et al., 2018), all of which are observed in the concretions of the Northumberland Formation section.

It is difficult to discount the associative bias of 26 juvenile specimens of *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. within one concretion as having reflected a gregarious mode of living (Fig. 9). Whether or not this occurrence is indicative of social cohesion is certainly debatable, although the benefits of schooling behavior in extant coleoids are well understood (e.g., Oshima et al., 2016). It has long been speculated that certain ammonites, such as baculitids, travelled in schools not unlike modern squid, given instances of mass occurrence (Lewy, 2002). This is also due to their associative death assemblages (Klinger and Kennedy, 2001). However, unlike modern squid that swim and spawn in schools, which may or may not precede mass die-offs (e.g., Hanlon et al., 2004; Boyle and Rodhouse, 2005; Shashar and Hanlon, 2013), the cluster of *A.* (*A.*) *haegerti* n. sp. individuals contained within the Hornby Island concretion in question were far from sexual maturity. If not freely adrift, it is possible their association was a function of enclosure within a medium that hastened their demise amidst adverse conditions. While most specimens in the aggregate have a conch size ranging from D = 5–10 mm, a few are notably smaller, and one body-chamber fragment is indicative of an individual having attained several cm in diameter. These juveniles appear to represent members of multigenerational clutches, suggesting that they occupied the same level in the euphotic zone, although older individuals could very well have been captured in the mass upon its descent.

Figure 9. Artistic rendition of *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. by Katherine L. Marriott. A school of juvenile ammonoids navigates through a drifting algal mass to feed while two adults are seen emerging from the depths below amid turbulent waters.

Mature individuals belonging to *Pachydiscus* (*Pachydiscus*) *hornbyense*, *Pachydiscus* (*Pachydiscus*) *ootacodensis*, and potentially other inflated pachydiscids, may have favored a demersal life habit beginning into early adulthood as evinced by the presence of band-slit pathologies in some Hornby Island specimens (Fig. 7.10, redux Jones, 1963, pl. 32, fig. 6; Fig. 8.19). These features, reflecting healed shell damage, have been observed among numerous ammonite taxa (e.g., Landman and Waage, 1986; Landman et al., 2010; Keupp, 2012). Various authors (e.g., Keupp, 2006;

Hoffmann and Keupp, 2015; Hoffmann et al., 2021) have surmised that band-slit pathologies were caused by injuries incurred following attempted predation by benthic crustaceans (stomatopods), requiring an ammonoid to have lived in close proximity to the substrate. A shell thickness of 0.4 mm in the *A.* (*A.*) *haegerti* n. sp. holotype (Fig. 5.13) is entirely consistent with that of analogous modern *Nautilus pompilius* Linnaeus, 1758, at equivalent Wh = 28 mm, suggesting the capacity of the species to have withstood pressure at similar depths in excess of 300 m (e.g., Saunders and Wehman, 1977; Ward et al., 2016). This is contrary to the observation of Saul (1979) with respect to a Baja Californian specimen referred to morphologically allied *Anapachydiscus* cf. *A. arrialoorensis*, questionably reported by Matsumoto (1959, 1960), that the shell is one-half as thick as that of *Nautilus* in exhibiting an umbilical margin shell thickness of 0.6 mm at D = 90.5 mm. Regardless of advancing factors of marine predation into the Late Cretaceous (e.g., Ward, 1983; Kauffman, 2004; Takeda et al., 2016), the morphological variance of these inflated pachydiscids and their life associations are indicative of specialization toward a range of niche adaptations illustrating their versatility as successful *r*-strategists (e.g., Lukeneder, 2015).

Conclusion

Pachydiscid ammonites can exhibit dramatic change in the progression of their shell ornamentation, profile, and structural geometry throughout ontogeny. The range of morphospace occupied by a given species is only recently becoming appreciated in the literature due to the early description of specimens based on a particular stage of development limiting diagnostic application and, at worst, lending to ambiguity surrounding what were generally intended to be discrete species concepts. Recently collected specimens from upper Campanian strata of the Cedar District and Northumberland formations of the Nanaimo Group serve to illustrate the wide spectrum of variance within the inflated species *Pachydiscus* (*Pachydiscus*) *hornbyense* and *Pachydiscus* (*Pachydiscus*) *ootacodensis* at intermediate and adult stages. A detailed taxonomic treatment has provided greater resolution of the diagnostic criteria for these species, with biostratigraphic importance reaching beyond the North Pacific realm. Additionally, a review of published records has enabled revision of the morphometric parameters that define and warrant retention of the genus *Anapachydiscus.* Furthermore, the suite of *Anapachydiscus* (*Anapachydiscus*) *haegerti* n. sp. from the lower Northumberland Formation on Hornby Island enables full reconstruction of the complete developmental progression of the ammonoid shell. The highly inflated pachyconic geometry and character of dense, sinuous ribbing with increasing pronunciation into maturity set specimens of *A.* (*A.*) *haegerti* n. sp. apart from all other pachydiscids in the section. The ontogenetic transition and expression of the ornament distinguish it from all known species. The inference of gregarious behavior in early life is also supported by the depositional circumstances of inner neritic aggregate burial with the exclusion of other ammonite taxa.

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