Taxonomic Evaluation of Various Morphological Characters in the Late Cretaceous Desmoceratine Polyphyletic Genus "Damesites" from the Yezo Group in Hokkaido and Sakhalin

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Taxonomic evaluation of various morphological characters in the Late Cretaceous desmoceratine polyphyletic genus "*Damesites*" from the Yezo Group in Hokkaido and Sakhalin

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Abstract. Intra- and interspecific variation and ontogenetic changes in various shell characters of the Late Cretaceous desmoceratine ammonoid "*Damesites*" are described, and their taxonomic implications are discussed based on specimens from the Cretaceous Yezo Group in Hokkaido and Sakhalin. Our study reveals that many "diagnostic" features (e. g., appearance of longitudinal striations, height of ribbing, regularity of ribbing as well as constriction curvature) and early internal shell structures, are in fact inappropriate as diagnostic features of "*Damesites*" morphotypes. In contrast, ontogenetic changes in shell ornament, curvature of growth lines and whorl expansion ratio are herein demonstrated to be key characters for species recognition and reconstructing the phylogenetic relationships of the taxa of the subfamily Desmoceratinae. Based on these results, previously described "*Damesites*" species from the uppermost Turonian-lower Campanian interval should be reclassified into three groups. "*Damesites damesi*," "*D. damesi intermedius*," "*D. semicostatus*," and "*D. laticarinatus*" are assigned to the first group. "*D. ainuanus*" and "*Damesites* sp." are assigned to the second group. "*D. sugata*" from the Yezo Group represents the third group. Furthermore, analysis of ontogenetic changes in shell ornament, curvature of growth lines, and whorl expansion ratio suggests that the second and third groups together belong to a different evolutionary lineage from the first group.

Key words: Cretaceous, "*Damesites*," desmoceratine ammonoid, ontogenetic changes in shell, taxonomy, *Tragodesmoceroides*

Introduction

Desmoceratine ammonoids range from Aptian to Maastrichtian in age (Wright, 1957; Wright *et al.*, 1996). As recorded in the Cretaceous Yezo Group in Hokkaido and Sakhalin (Figures 1, 2), this subfamily became particularly diversified into many genera and species in the northwestern Pacific realm during the above time interval. Among them, the keeled genus "*Damesites*" (Figures 3–6) is one of the most important genera in the evolutionary history of desmoceratine ammonoids because of its successive stratigraphic occurrence and abundance. The genus "*Damesites*" was first proposed by Matsumoto (1942) with the type species "*D. damesi*" (Figures 4A–C, Jimbo, 1894), based on a specimen from the Tappu area in northwestern Hokkaido (Figure 1). Since then, "*Damesites*" species have been reported from different parts of the world including South Africa (Spath, 1921), Angola (Howarth, 1968; Cooper, 2003a, b), Madagascar (Collignon, 1961, 1965), India (Forbes, 1846; Stoliczka, 1865; Kossmat, 1895–1898), Japan and Sakhalin (Matsumoto, 1942; Matsumoto, 1954; Matsumoto and Obata, 1955; Poyarkova, 1987; Alabushev and Wiedman, 1993; Shigeta *et al.*, 1999; Kodama *et al.*, 2002; Maeda *et al.*, 2005), Kamchatka (Alabushev, 1995), California (Anderson, 1958; Matsumoto, 1959), and British Columbia (Haggart, 1989).

In the Cretaceous Yezo Group distributed in Hokkaido and Sakhalin, desmoceratine ammonoids occur abundantly from the Cenomanian to Campanian (Figure 2). Six species and one subspecies of "*Damesites*" have been extensively

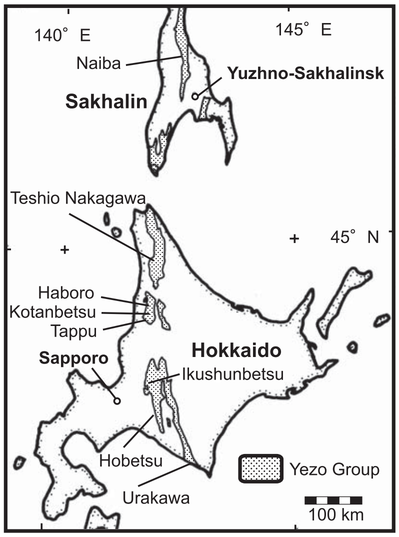

Figure 1. Index map showing location of the Haboro, Kotanbetsu, and Tappu areas and distribution of the Cretaceous Yezo Group in Hokkaido and Sakhalin.

described by many authors since Yokoyama (1890) and Jimbo (1894) (Table 1). After extensive taxonomic studies (Matsumoto, 1942, 1954, 1957; Matsumoto and Obata, 1955; Saito and Matsumoto, 1956), the taxonomic scheme of desmoceratine ammonoids was thought to be well established. Recent paleobiological and biostratigraphic studies on desmoceratines have followed this scheme (hydrodynamic analyses: Tanabe and Shigeta, 1987; Seki *et al.*, 2000; early internal shell structures: Tanabe *et al.*, 1979, 2003; Tanabe and Ohtsuka, 1985; Ohtsuka, 1986; biostratigraphy: Toshimitsu *et al.*, 1995; Okamoto *et al.*, 2003; cladistic analysis: Nishimura, 2003).

However, a recent expansion in available specimens exposed inconsistencies and discrepancies in previous taxonomic and biostratigraphic schemes (Nishimura *et al.*, 2006). In particular, in "*Damesites*" systematics, the identification of species has become controversial. For example, Okamoto *et al.* (2003) listed many "*Damesites*" species, although taxonomic names in that study were ambiguously treated as *D. damesi* (="*D. semicostatus*"), *D.* aff. *damesi*, *D.* aff. *sugata*, etc. There are many intermediate forms among "species" in which ontogenetic shell development has not yet been sufficiently elucidated.

The present study aims to develop a new systematic scheme for the desmoceratine ammonoids, particularly "*Damesites*" species. To reestablish the systematics of desmoceratine ammonoids, the evaluation of ontogenetic changes and individual variation at a given growth stage of each character is highly significant (Nishimura *et al.*, 2006). The purpose of the present study is to evaluate intra- and interspecific variation in various morphological characters of "*Damesites*" as a basis for establishing desmoceratine am-

Table 1. Brief correlation of diagnostic features of previous "*Damesites*" morphotypes and "*Damesites* sp." Single bar represents characters undescribed in previous studies. Double bar represents characters which cannot be compared, because ribs appear in some morphotypes but not in others. Characters with double quotation marks show discrepancies between previous diagnoses and actual shapes.

"morphotype" / characters	"D. damesi"	"D. damesi intermedius"	"D. semicostatus"	"D. laticarinatus"	"D. ainuanus"	"Damesites sp."	"D. sugata" from the Yezo Group
shell form							
profile of keel	moderate to obtuse	moderate	moderate	broad	moderate	moderate to high	obtuse
whorl breadth	moderate	moderate	moderate	—	compressed	compressed	compressed
umbilical width	narrow	narrow	narrow	narrow	narrow	narrow	wide
shell surface ornament							
shape of rib	weak, low	═	sharp, high	═	═	═	═
interspace of rib	irregular wide	═	regular narrow	═	═	═	═
longitudinal striations	present	present	"absent"	present	present	present	present
curvature of constriction	"strong sigmoidal"	weak sigmoidal	"strong sigmoidal"	—	weak sigmoidal	weak sigmoidal	concave
ornament	smooth ribbing	smooth	ribbing	smooth	smooth	smooth	smooth
constrictions in late growth stage	few	—	few	—	frequent	frequent	frequent
curvature of growth line	sigmoidal	sigmoidal	sigmoidal	—	—	concave	concave

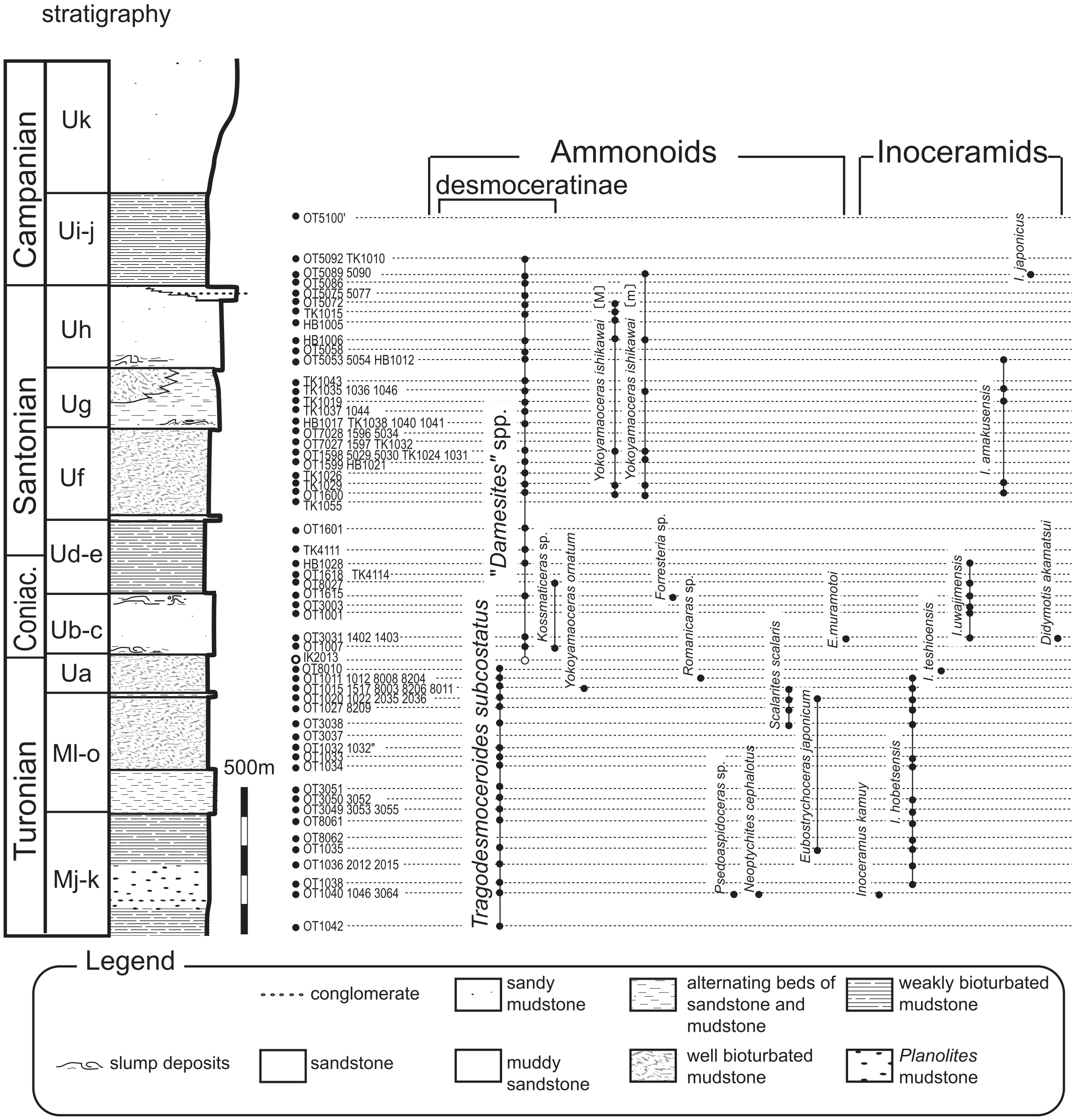

Figure 2. Columnar section of the Turonian to Campanian sequence in the Haboro-Tappu area showing stratigraphic occurrence of desmoceratine ammonoids and some selected fossils. Loc. IK 2013, Pombetsu area (near Ikushunbetsu area, hollow circle) corresponds to the type locality of "*Damesites ainuanus.*" Detailed fossil localities and route maps will appear in a separate paper.

monoid species. Then, the type specimens of the University Museum, University Tokyo (UMUT), National History Museum, London (BMNH), and Kyushu University, and large population samples (collected mainly by T. Nishimura), are referred to these species.

Repository of specimens.—Previous type specimens are housed in UMUT, BMNH, and Kyushu University. NSM PM 9264, 9293, and 9483 (listed in Futakami *et al.*, 1980) are housed in the National Museum of Nature and Science, Tokyo. In addition, a total of 193 newly recovered specimens (KUM MM TN 099-291) are housed in the Kyoto University Museum.

Brief notes on previous morphotypes

Six "species" and one "subspecies" of "*Damesites*" have been described from the Cretaceous Yezo Group (Figures 4–6, Table 1). In addition, "*Damesites sugata* (Forbes, 1846)" first described in South India, has been reported from the Yezo Group.

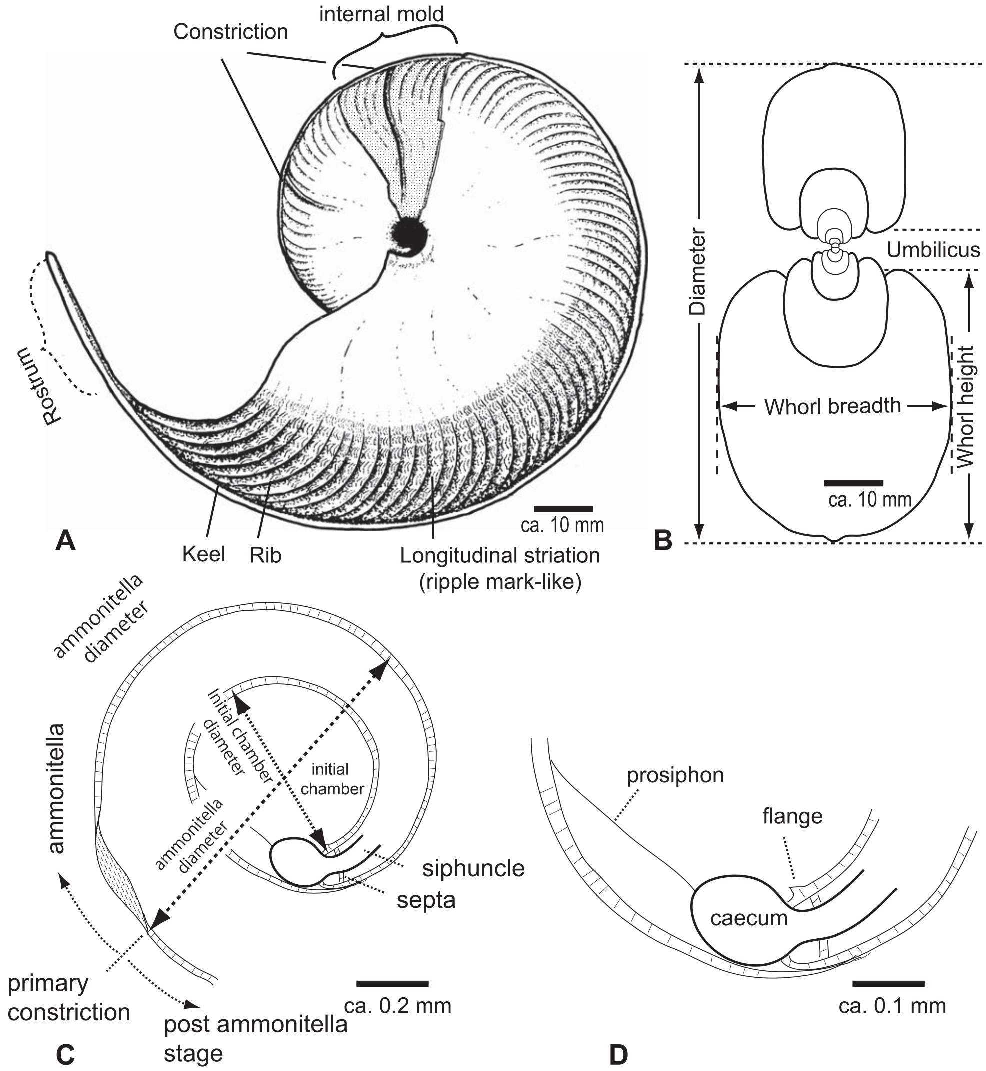

Figure 3. Schematic illustrations of "*Damesites*" shells. **A.** Shell ornamentation. Desmoceratid constriction is thicker internally. Constrictions are parallel to growth lines at ventral shoulder, although they are sometimes oblique. **B.** Median cross section. **C, D.** Longitudinal cross section and measurements showing early internal shell structures.

The present study mainly considers the Turonian to Campanian "*Damesites*" species and provisionally ranks them as morphotypes that are represented by double quotation marks (" "). A Maastrichtian species "*D. hetonaiensis*" was excluded because insufficient material was available. Notes on the genus "*Damesites*" and on each morphotype of "*Damesites*" are briefly summarized as follows (Table 1).

"*Damesites* Matsumoto, 1942"

Original denomination.—*Damesites*, Matsumoto, 1942, p. 25, table 1

Type species.—"*D. damesi* (Jimbo, 1894)"

Diagnosis.—Very involute, more or less compressed, distinct keel with sigmoidal or concave constrictions and in some species fine ribs (compiled from Matsumoto, 1942, 1954; Matsumoto and Obata, 1955; Wright *et al.*, 1996).

"*Damesites damesi* (Jimbo, 1894)"

Original denomination.–*Desmoceras Damesi*, Jimbo, 1894, p. 172, lines 11–37, p. 174, pl. 1, fig. 2a, b.

Lectotype.—UMUT MM 7500, from a floating pebble from the Obirashibe River, Tappu, Hokkaido (Figure 4A–C).

Diagnosis.—Almost smooth shell surface. Sometimes rounded ribs (subcostae) are developed on the ventral half. Strong sigmoidal growth lines and constrictions. Constrictions are less frequent. Faint longitudinal striations like ripple marks (shell microstructure on the outermost shell surface, Figure 3A) develop at ventrolateral and venter. Sometimes,

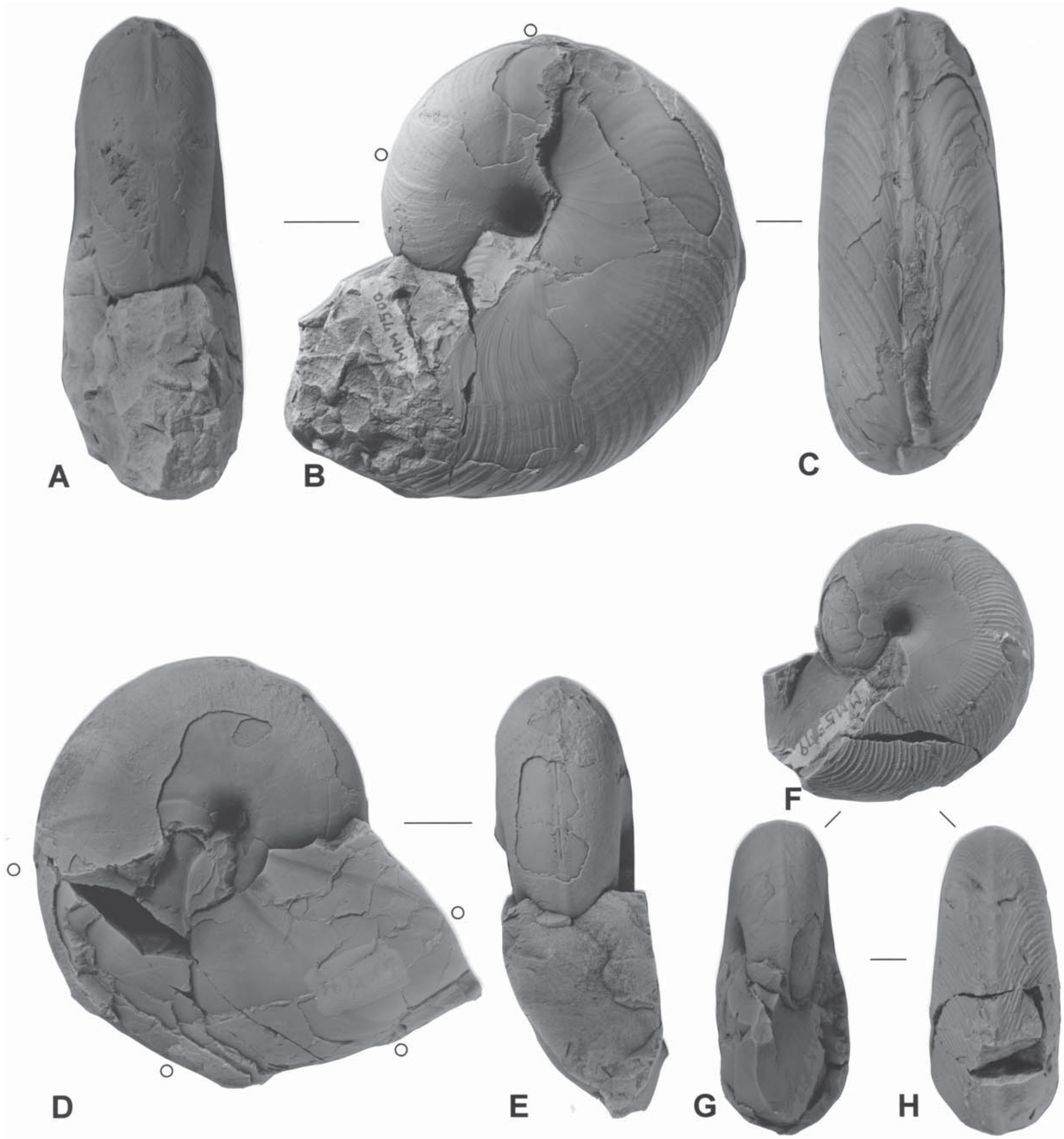

Figure 4. Type specimens of “*Damesites*” morphotypes. **A–C.** “*D. damesi*” (lectotype, UMUT MM 7500). **D, E.** “*D. damesi intermedius*” (holotype, GK. H3269). **F–H.** “*D. semicostatus*” (holotype, UMUT MM 5579). All specimens are natural size. Hollow circles show position of constrictions.

shallow furrows are also present on both sides of the keel. Whorl flanks are somewhat rounded to flat (compiled from Matsumoto, 1942, table 3; 1954, p. 269).

“*Damesites damesi intermedius* Matsumoto, 1954”

Original denomination.—*Damesites damesi intermedia*, Matsumoto, 1954, p. 270–271, pl. 6(12), fig. 4a, b.

Holotype.—GK. H3269, loc. U513, Santonian, Urakawa, Hokkaido (Figure 4D, E).

Diagnosis.—Shell surface is almost smooth. Constriction curvature is less sigmoidal, nearly simple concave (compiled from Matsumoto, 1954, p. 270–271).

Remarks.—Matsumoto (1954) and Matsumoto and Obata (1955) ranked this subspecies as the end member of “*Damesites damesi,*” and it was regarded as an intermediate form between “*Damesites damesi*” and “*D. sugata*” from the Yezo

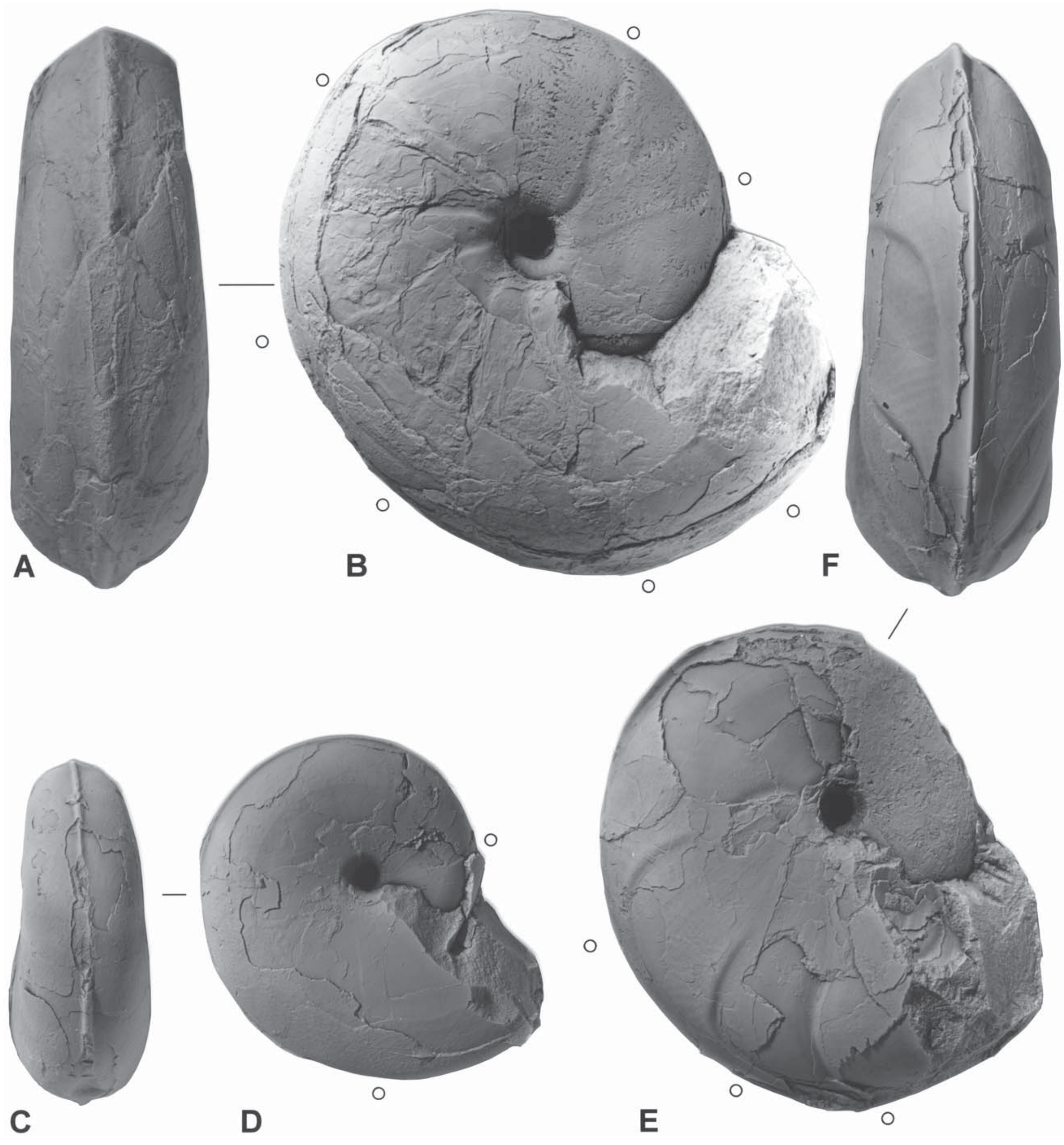

Figure 5. Type and actual specimens (hypotypes) of "*Damesites*" morphotypes. **A, B.** "*D. ainuanus*" (holotype, GK. H4198). **C–F.** "*Damesites* sp." (C, D, KUM MM TN 109; E, F, KUM MM TN 129). All specimens are natural size. Hollow circles show positions of constrictions.

Group (Matsumoto, 1954; Matsumoto and Obata, 1955). According to these studies, this subspecies possesses the "*D. damesi*" type of whorl shape and the Yezo Group "*D. sugata*" type of constrictions. However, a definite subspecific diagnosis was not clearly provided, which has now been compiled by us based on a description of this subspecies (Matsumoto, 1954, p. 270–271).

"*Damesites semicostatus* Matsumoto, 1942"

Original denomination.—*Damesites semicostatus*, Matsumoto, 1942, table 3, fig. 1h.

Lectotype.—UMUT MM 5579, an immature shell of 40

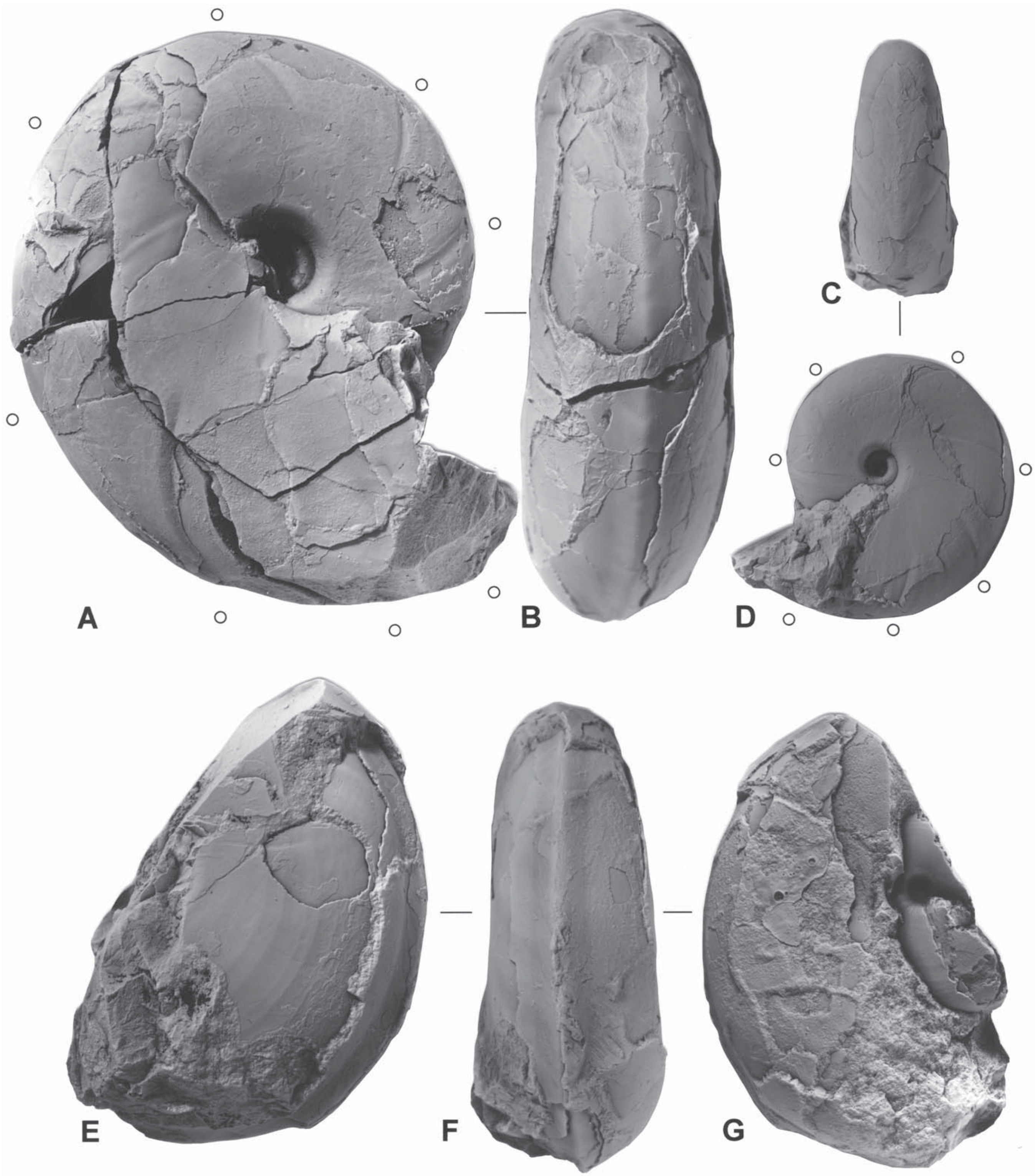

Figure 6. Type and actual specimens (hypotypes) of "*Damesites*" morphotypes. **A–D.** "*D. sugata*" from the Yezo Group (A, B, KUM MM TN 285; C, D., KUM MM TN 282). **E–G.** "*D. laticarinatus*" (holotype, unnumbered specimen, housed in Kyushu University). All specimens are natural size. Hollow circles show position of constrictions.

mm diameter from loc. T592, Coniacian?, Teshio Nakagawa (Figure 4F–H).

Diagnosis.—Strong sigmoidal growth lines and constrictions. Constrictions are less frequent. Sharp and dense ribs develop in the ventral half. Longitudinal striations are not developed. Dentation of the keel is better developed than in "*Damesites damesi*" (compiled from Matsumoto, 1942; table 3; Matsumoto and Obata, 1955, p. 127).

Remarks.—"*Damesites semicostatus*" is very similar to "*D. damesi*." "*D. semicostatus*" possesses elevated and sharper ribs and interspaces between ribs are more regular and the ribbing denser than in "*D. damesi*." However, the diagnostic feature, the dentation of the keel (Matsumoto, 1942, table 3; Matsumoto and Obata, 1955, p. 127), is not well developed in the holotype.

"*Damesites sugata* (Forbes, 1846)"

Original denomination of Indian specimens.—*Ammonites Sugata*, Forbes, 1846, p. 113, pl. 10, fig. 2a–c.

Lectotype.—BMNH C22675 (Natural History Museum, London) designated by Kossmat (1895–1898) and Spath (1921). This specimen is said to be from the Coniacian or Santonian (?) of the Trichinopoly Group, Vridachellum, Madras State (Forbes, 1846, pl. 10, fig. 2a–c, Kennedy and Henderson, 1991, fig. 1A, B.).

Illustrated specimens.—Matsumoto and Obata, 1955, pl. 26, fig. 4, pl. 27, figs 3, 4.

Diagnosis of "Damesites sugata" from the Yezo Group.—Shell surface is almost smooth with frequent prorsiradiate (simple concave) constrictions. Much of the whorl was compressed with parallel and flattened flanks. Ventral keel is obtuse, wide, and low. The umbilical width is wide, and umbilical shoulder is subrounded to subangular (compiled from Matsumoto, 1942, table 3; Matsumoto and Obata, 1955. p. 129) (Figure 6A–D).

Remarks.—Matsumoto and Obata (1955, p. 129) gave a diagnosis based on specimens from Hokkaido and Sakhalin. However, study of a series of specimens (discussed in a separate paper) revealed that the Yezo Group morphotype of "*D. sugata*" should be assigned to a new species.

"*Damesites laticarinatus* Saito and Matsumoto, 1956"

Original denomination.—*Damesites laticarinatus* Saito and Matsumoto, 1956, p. 192–193, fig. 1a–c.

Holotype.—Unnumbered specimen showing deformed body chamber and abraded fragment from the Mikasa Formation along the main course of the Ikushunbetsu River, by monotypy; deposited in the Department of Earth and Planetary Sciences, Kyushu University (Figure 6E–G).

Diagnosis.—Shell surface is almost smooth. Faint longitudinal striations develop at the ventral half. Keel is somewhat broad (compiled from Saito and Matsumoto, 1956, p. 192).

"*Damesites ainuanus* Matsumoto, 1957"

Original denomination.—*Damesites ainuanus*, Matsumoto, 1957, p. 86–88, pl. 15, figs. 1a–d, 2a–c.

Holotype.—GK. H4198. IK 2013g_2, Pombetsu, uppermost Turonian (Figure 5A, B).

Diagnosis.—Shell surface is almost smooth with periodic constrictions. Constrictions show weak flexuosity on both sides in the late growth stage (80 mm diameter). Compressed whorl narrowly umbilicate. Flanks of whorl are flat and nearly parallel (compiled from Matsumoto, 1957, p. 86–87).

In addition, another morphotype, "*Damesites* sp." (="*D.* aff. *sugata*", Okamoto *et al.*, 2003) (Figure 5C–F), has been reported from the Coniacian of the Haboro area, northwestern Hokkaido. The present study briefly describes the characteristic ("diagnostic") features of this morphotype.

Diagnostic features.—Shell surface is almost smooth with periodic constrictions. Growth line curvature is simple concave in the interspaces between constrictions. In the late growth stage (about 60 mm diameter), constrictions become weakly sigmoidal and convex on both flanks. Faint longitudinal striations develop at the ventral half. From the early growth stage, a sharp, narrow, and high ventral keel is developed. Umbilical edge is rounded and umbilicus is somewhat wide. Whorl is compressed.

Materials and methods

To reconsider the adequacy of the previous taxonomic scheme, we closely examined all type specimens of "*Damesites*" morphotypes from the Yezo Group (see repository specimens) and measured and photographed them. Plastotype specimens of Indian "*Damesites sugata*" deposited in the Natural History Museum, London were also observed. In addition, newly recovered specimens (193 specimens) that were collected from the uppermost Turonian to Campanian were utilized here.

Thirty-two specimens belonging to "*Damesites*" morphotypes were cut and polished longitudinally using corundum powder up to #3000 and were etched with 5% acetic acid for a few minutes. Then the samples were observed with a scanning electron microscope (SEM, JEOL, JSM-6100). These specimens were used to observe early internal shell structures (see Section A, below).

To observe the shell surface ornament (see subsections B-1 to B-5 below) and keel shape (see subsection C-1 below), a total of 206 specimens, including type specimens of "*Damesites*," were observed under a binocular microscope. To examine "diagnostic features" between "*Damesites damesi*" and "*D. semicostatus*," the prorsiradiate ribs and longitudinal striations of a total of 52 specimens collected from the lower Santonian strata were carefully observed.

The whorl shape of 122 specimens of "*Damesites*" was measured. Nine specimens were crosscut and polished using corundum powder up to #3000 for precise biometric analysis. The parameters measured were diameter, umbilical width, whorl breadth, whorl height, and whorl expansion ratio (see subsections C-1, C-2, and C-3 below). Forty-nine specimens of *Tragodesmoceroides subcostatus*, a presumed ancestor of "*D. damesi*," were also measured for comparison (detailed relationships between "*Damesites*" and *Tragodesmoceroides* will be described in a separate paper). All measurements were made using a profile projector (Nikon model V-12B, magnification to 100×, accuracy ± 1 um).

Definition of growth stage and dimorphism

"*Damesites*" morphotypes change whorl shape and shell ornament after the 5–7π stage, which they attain at approximately 5 mm diameter. The largest shell diameter attained is 90–100 mm. Like other desmoceratine ammonoids, "*Damesites*" morphotypes do not show remarkable adult features such as apertural modifications, lappet formation or abrupt changes of body chamber shape except for the following two examples. In "*Damesites* sp." (KUM MM TN 129, Figure 5E) and "*D. sugata*" from the Yezo Group (KUM MM TN 285, Figure 6A), spaceing between the last two constrictions are approximated. This condition might represent an adult feature of "*Damesites*."

This study tentatively defines early, middle, and late growth stages for individuals larger than 5 mm diameter. The early growth stage has less than 30 mm diameter, the middle growth stage ranges from 30 mm to 60 mm diameter, and the late growth stage has a diameter over 60 mm.

"*Damesites*" morphotypes do not clearly show dimorphic features. There is no evidence of adult size discrepancies or lappet formation in "*Damesites*" morphotypes, unlike *Yokoyamaoceras* (Desmoceratoidea, Kossmaticeratidae; Maeda, 1993).

Evaluation of morphological characters in desmoceratine taxonomy

Desmoceratine ammonoids have been taxonomically classified mainly on the basis of the existence and appearance of ribs and their shape, keel profile, umbilical width, curvature of growth lines and constrictions, and whorl breadth. However, there have been no clear investigations of the ontogenetic development of these characters based on large samples. We reexamined and evaluated the following characters.

A. Early internal shell structure

Since Branco (1879–1880), many paleontologists have attached importance to the early internal shell structure of ammonoids. These pioneering studies have demonstrated that the shells of ammonoids can be divided into two stages, ammonitella and post-ammonitella, at the boundary of the primary varix and primary constriction (Figure 3C).

Several characters which appear in the ammonitella and early post-ammonitella stages, e.g., initial position and ontogenetic change in siphuncle, shape of caecum, shape of prosiphon, and number of accessory threads of the prosiphon have been used for recognition of higher taxa at a suborder level (e.g., Tanabe and Ohtsuka, 1985; Ohtsuka, 1986; Tanabe *et al.*, 2003). These divisions, based on the characters of the early ontogenetic stages, are concordant with the previously reported results of higher taxonomy. In addition, the diameter of the initial chamber differs somewhat among Mesozoic suborders (Ohtsuka, 1986; Landman *et al.*, 1996). However, Rouget and Neige (2001) and Tanabe *et al.* (2003) have reported wide intraspecific variations in some early internal shell characters.

In the Cretaceous desmoceratine ammonoids, early internal shell characters were not used when defining species and genus. These characters were partly evaluated in some paleobiological studies (Tanabe *et al.*, 1979, 2003; Tanabe and Ohtsuka, 1985; Ohtsuka, 1986). Using 41 ammonitella specimens belonging to three desmoceratine ammonoid species, Tanabe *et al.* (2003) concluded that a long and straight prosiphon, an elliptical caecum, and an initially central siphuncle are common and stable characters of desmoceratine ammonoids.

We reexamined intra- and interspecific variation of these characters. The technical terms and dimensions of each character used by Ohtsuka (1986) and Landman *et al.* (1996) have been followed.

Observation.—Most specimens show typical desmoceratid features (Figures 7A–D, 8C–F; Ohtsuka, 1986; Tanabe *et al.*, 2003; Nishimura *et al.*, 2006), i.e., elliptical caecum, long and straight prosiphon (0.2 mm) attached to the center of the caecum, and very short flange (0–0.02 mm long). There is no secondary prosiphon. The position of the siphuncle gradually shifts towards the venter.

The morphology of the prosiphon and flange is more variable than previously reported. The prosiphon of "*Damesites damesi*" is straight and 0.1–0.23 mm in length (Figure 8A–D). Most specimens belonging to "*Damesites* sp." have a long and straight prosiphon (0.3 mm long, Figure 7C, D). In contrast, some specimens of "*Damesites* sp." possess a somewhat short and straight prosiphon (0.15 mm long, Figure 7E) or a very short and curved prosiphon (0.06 mm long, Figure 7F). In particular, the latter is not common in specimens of other desmoceratids. This wide variation in prosiphon morphology in "*Damesites* sp." is recognized even in a population sample from a single calcareous concretion (Figure 7C–F). Such morphological variations resemble that of the Jurassic oppelids (Rouget and Neige, 2001) and the Cretaceous collignoniceratid ammonoid *Reesidites minimus* (Tanabe *et al.*, 2003).

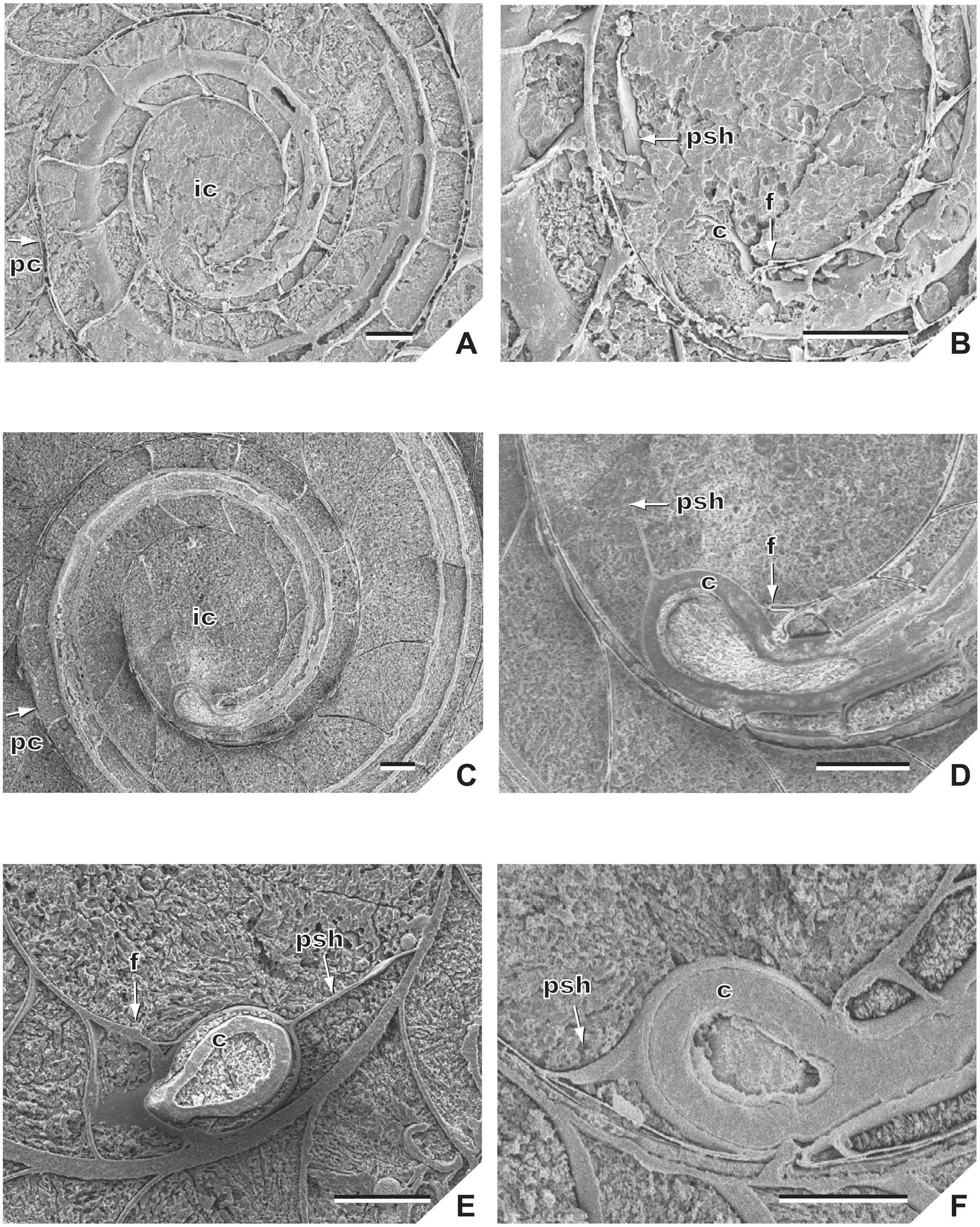

Figure 7. Early internal shell structures of "*Damesites*" morphotypes. **A, B.** "*D. sugata*" from the Yezo Group (KUM MM TN 290). **C–F.** "*Damesites* sp." (C, D, KUM MM TN 141; E, KUM MM TN 116; F, KUM MM TN 122). In "*Damesites* sp." (C–F) from the upper Coniacian, prosiphon and flange also show variable shapes. Scale bar: 0.1 mm. ic: initial chamber, pc: primary constriction, c: caecum, f: flange, psh: prosiphon.

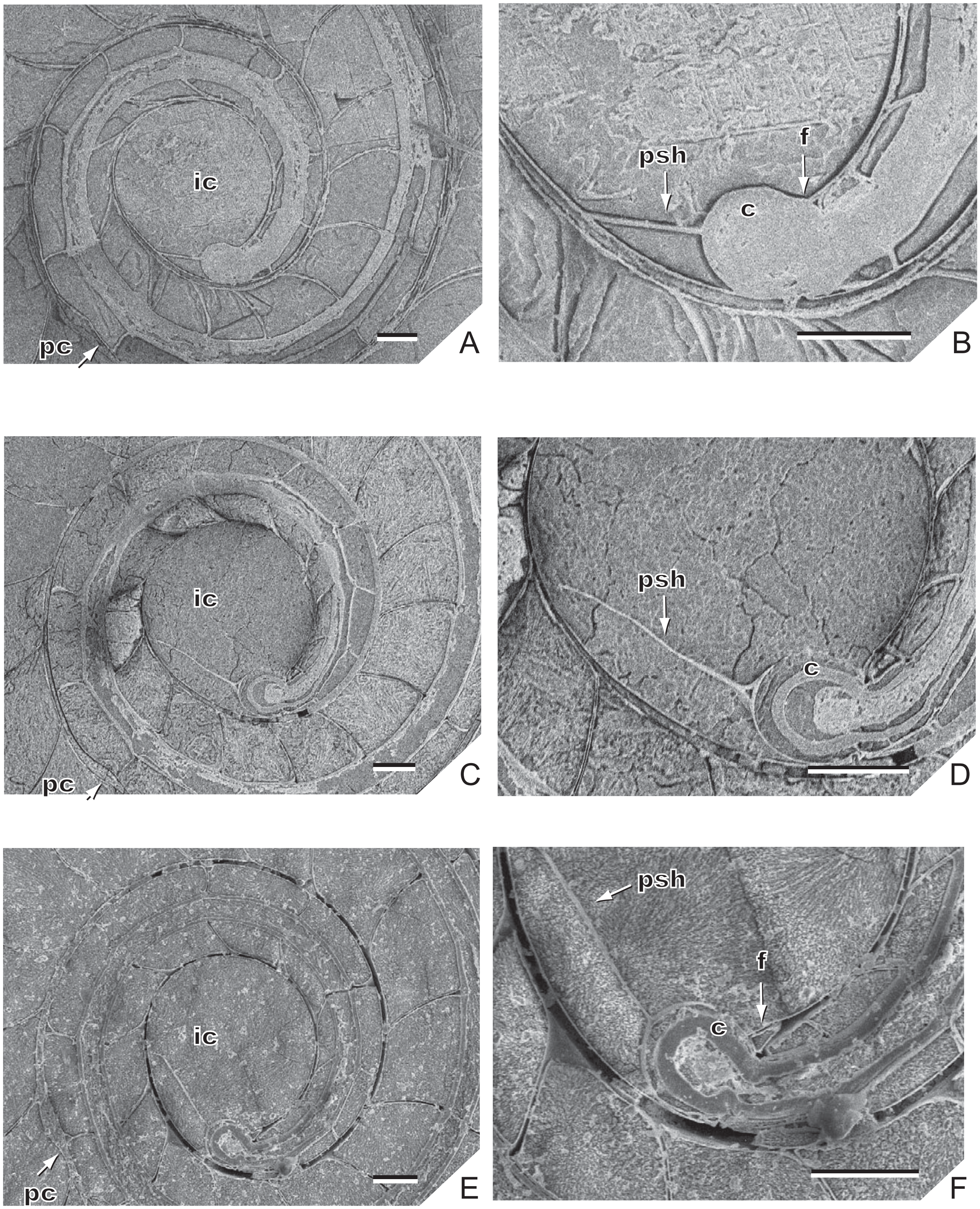

Figure 8. Early internal shell structures of “*Damesites*” morphotypes. **A–D.** “*D. damesi*” (A, B, KUM MM TN 243; C, D, KUM MM TN 212). **E, F.** “*D. semicostatus*” (KUM MM TN 214). In “*D. damesi*” (A–D), prosiphon and flange also show variable shapes. Scale bar: 0.1 mm. Abbreviation is same as Figure 7.

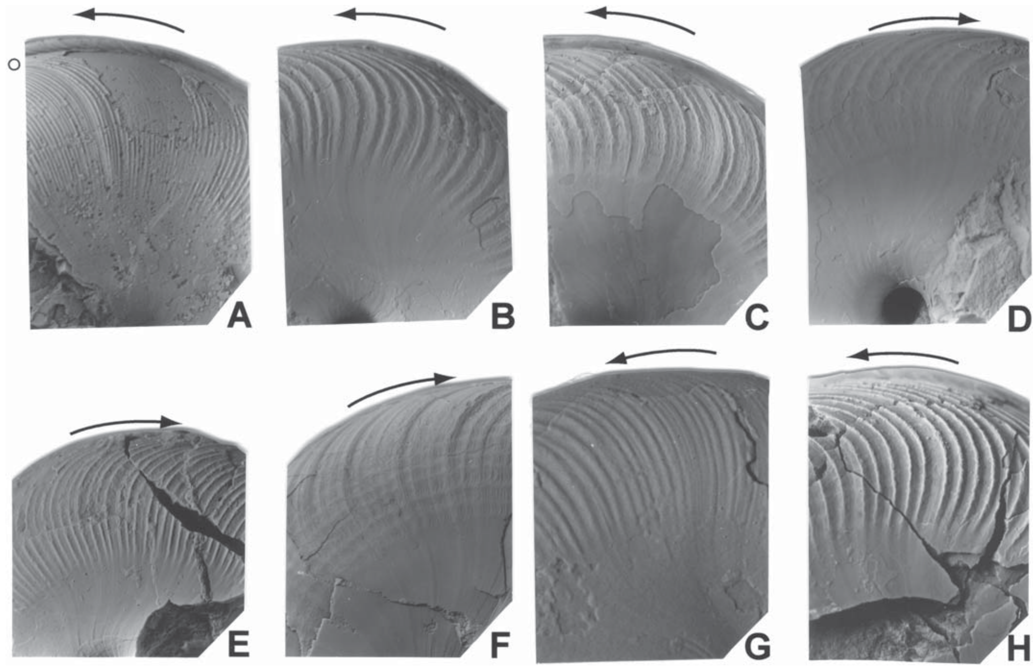

Figure 9. Interspaces and regularity of ribs compared between "*Damesites damesi*" and "*D. semicostatus*." **A.** Narrow interspaces and regular ribbing (KUM MM TN 200). These features are obscure near the constriction (hollow circle). **B.** Moderate interspaces and somewhat irregular ribbing (KUM MM TN 196). **C.** Moderate interspaces and irregular ribbing (KUM MM TN 193). **D.** Wide interspaces and regular ribbing (KUM MM TN 164). **E.** Narrow interspaces and regular ribbing, "*D. semicostatus*" (holotype, UMUT MM 5579). **F.** Moderate interspaces and irregular ribbing, "*D. damesi*" (lectotype, UMUT MM 7500). **G, H.** Ontogenetic change (G to H) of rib shape (KUM MM TN 184). Interspaces and regularity of ribbing vary from "*D. semicostatus*"-type ribbing (narrow interspaces and regular ribbing) to "*D. damesi*"-type ribbing (wider interspaces and irregular ribbing). "*D. damesi*" is difficult to clearly distinguish from "*D. semicostatus*" by previous diagnostic criteria (interspaces and regularity of ribbing), because many intermediate forms exist (interspace: B and C; regularity: B and H). Hollow circles show position of constrictions. Black arrows indicate adoral direction. A–F: ×1; G: ×1.2; H: ×2.0.

The flange also shows wide intraspecific variation in the same population sample. Most "*Damesites* sp." specimens have a very short or no flange (Figure 7E, F), while some specimens have a long flange (Figure 7C, D).

The ammonitella diameter ranges from 0.68 to 1.06 mm, and is variable. For example, it is 0.69–0.87 mm long in "*Damesites damesi*" specimens and 0.79–0.86 mm in specimens of "*D. semicostatus.*" The extent of the variation clearly overlaps in morphotypes.

Results.—The shape and length of the prosiphon are widely variable. Both extreme forms appear even in specimens of a single morphotype from a single population sample contained in a calcareous nodule. The length of the flange is also unstable. The diameter of the initial chamber and ammonitella also show large variation. It is very difficult to classify previous morphotypes by these characters.

B. Shell surface ornament

B-1. Prorsiradiate rib

Modes of ribbing have been used as diagnostic features for systematics in desmoceratine ammonoids. For example, "*Damesites damesi*" is differentiated from "*D. semicostatus*" by having less intense ribbing and highly irregular rib interspaces (Matsumoto and Obata, 1955).

Observation.—The "*Damesites semicostatus*" holotype has much sharper and stronger ribs and much narrower and more regular rib interspaces than those of the "*D. damesi*" lectotype (Figure 9E, F).

The ribs of the "*Damesites semicostatus*" holotype number 10/30° whorl. In "*D. semicostatus*" morphotypes, the ribbing varies from 7 to 26/30° whorl (at 30–50 mm diameter). In the "*D. damesi*" lectotype, the ribs number 8/30° whorl. As in the type specimens of "*Damesites damesi*," the rib interspaces in KUM MM TN 193 (Figure 9C) are irregular. However, KUM MM TN 196 (Figure 9B) has somewhat regular ribs and is regarded as an intermediate form between both morphotypes. Both "*D. semicostatus*"-like regular ribbing and "*D. damesi*"-like irregular ribbing appear within a single individual during growth (KUM MM TN 184, Figures 9G, H, 13C).

The height and sharpness of the rib profile are also variable in the specimens within both morphotypes, "*Damesites damesi*" (almost smooth to sharp, Figures 9F, 10) and "*D.

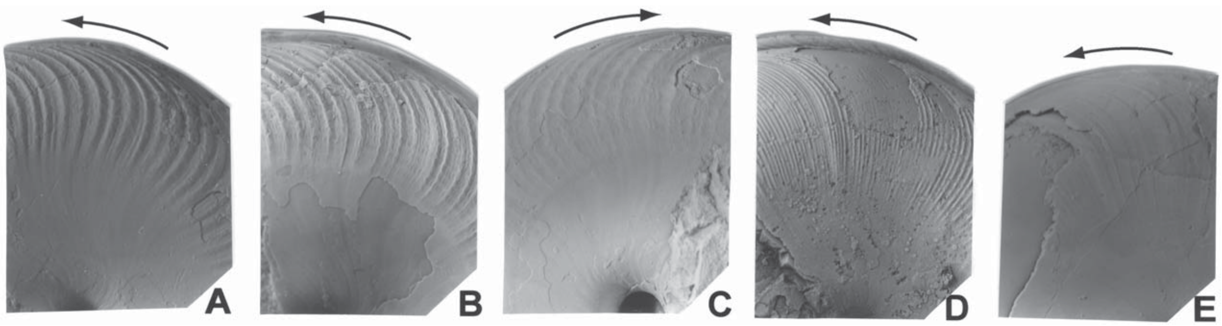

Figure 10. Shape of ribbing (height and sharpness) compared between "*Damesites damesi*" and "*D. semicostatus*". **A.** High and sharp ribs (KUM MM TN 196). **B.** High and sharp ribs (KUM MM TN 193). **C.** Moderately high and rounded ribs (KUM MM TN 193). **D.** Low and rounded ribs (KUM MM TN 200). **E.** Low and sharp ribs, nearly smooth surface (KUM MM TN 201). Differences in height and sharpness of ribs (previous "diagnostic" features) between "*D. damesi*" and "*D. semicostatus*" are not clearly distinguished, because these characters vary from a nearly smooth shell surface (E) to sharp ribbing (A, B) via intermediate forms (C, D) in a population sample from the lower Santonian. Black arrows indicate adoral direction. All specimens are natural size.

semicostatus" (moderate to sharp, Figures 9E, 10).

Results.—Two morphotypes, "*Damesites damesi*" and "*D. semicostatus,*" previously differentiated by differences in the modes of ribbing and longitudinal striation (described later) are actually not clearly distinguishable, because regularity and interspaces are fairly variable not only among specimens of similar shell size but also in individuals during ontogeny.

B-2. Constriction curvature

Constriction has been regarded as one of the diagnostic features of desmoceratine ammonoids (Wright *et al.*, 1996). Constriction curvature is usually described as parallel to growth lines and/or ribs.

Observation.—In cross section, weak periodic constrictions appear on the outer shell surface, but are clearly observable on an internal mold (Figure 11A, B, D). On the exterior, these appear at the ventrolateral periphery, but are very faint on both flanks.

The curvature of each constriction is not exactly parallel to the growth lines but is oblique. The former is usually projected much more forward than the latter. The constrictions show a simple concave or a weak sigmoidal pattern (Figure 11). The pattern sometimes changes from simple concave to weak sigmoidal with growth.

In "*Damesites sugata*" from the Yezo Group (Figure 11C), the constrictions retain a simple concave pattern throughout ontogeny. In "*D. ainuanus*" (Figure 11A) and "*Damesites* sp.," they change from a simple concave to a weak sigmoidal pattern in the late growth stage. In these morphotypes, the constrictions run almost parallel to the growth lines.

In contrast, "*Damesites damesi*" was assumed to have strong sigmoidal constrictions, running in parallel to the growth lines. However, like "*D. ainuanus*" and "*Damesites* sp.," "*D. damesi*" and "*D. semicostatus*" also possess weak sigmoidal constrictions. In both morphotypes, the constrictions are remarkably oblique to the growth lines. For example, the "*D. damesi*" lectotype (UMUT MM 7500, Figures 4A–C, 11B, 11D) has weak sigmoidal constrictions and strong sigmoidal growth lines and ribs (Figure 11A, C).

Results.—Most "*Damesites*" morphotypes have common periodic constrictions that are simple concave in the early growth stage and weak sigmoidal in the late growth stage.

Thus, "*Damesites damesi*" and "*D. semicostatus*" are not differentiated from "*D. ainuanus*" and "*Damesites* sp." by constriction curvature (Figure 11A, B, D). Almost all morphotypes of "*Damesites*" share a similar constriction pattern. However, "*Damesites sugata*" from the Yezo Group differs from the other morphotypes in possessing simple concave constrictions even in the late growth stage, although the difference is slight (Figure 11C).

B-3. Longitudinal striations

As shell microsculpture, longitudinal striations appear only on the outermost shell surface (Figure 12). They are usually seen on the outer flanks and ventrolateral shoulders and cross the prorsiradiate or sigmoidal growth lines and ribs obliquely.

Shell microsculpture, including longitudinal striations, is considered to be important for revealing the ammonoid shell growth pattern (Checa, 1994; Henderson *et al.*, 2002). In desmoceratine ammonoids, longitudinal striae is treated as one of the diagnostic features by which "*Damesites damesi*" is differentiated from "*D. semicostatus*" (Matsumoto and Obata, 1955).

Observation.—Longitudinal striations develop on the outermost shell surface at the ventral periphery, particularly on the ventrolateral shoulder. Usually, 7 to 12 rows of ripple-mark-like striations appear at the middle to the late growth stages (30–90 mm diameter). Striations vary from faint discontinuous lines to ripple-mark-like microundulations among

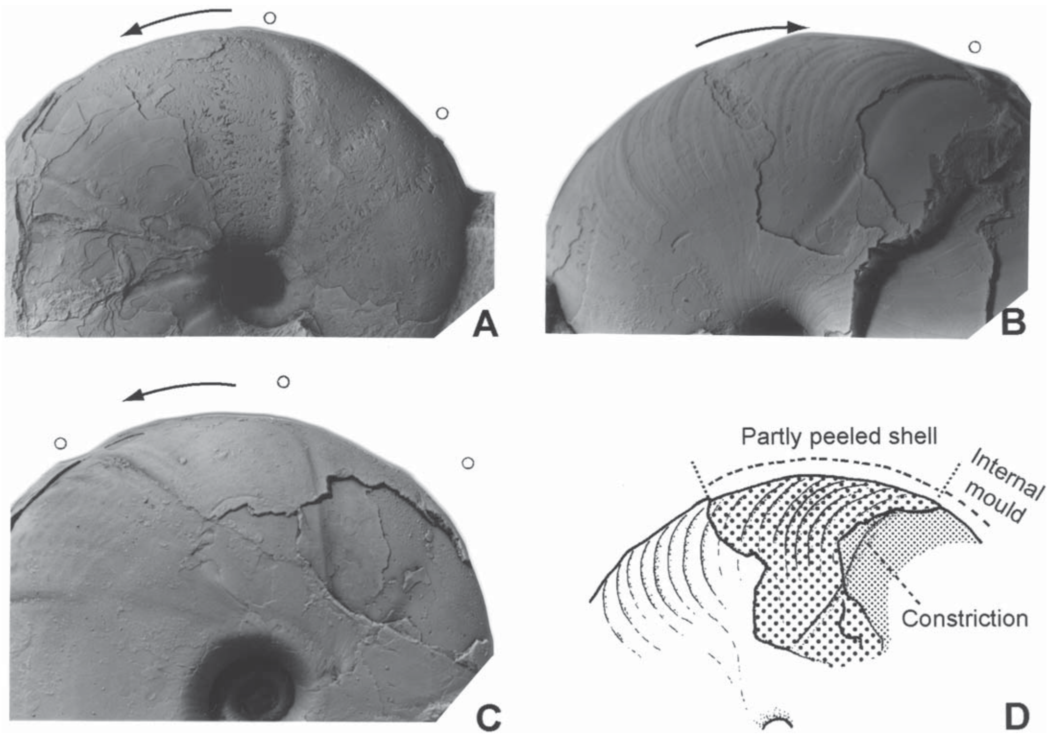

Figure 11. Constriction curvature. **A.** Weakly sigmoidal, "*Damesites ainuanus*" (holotype, GK. H4198, internal mold). **B.** Weakly sigmoidal, "*D. damesi*" (lectotype, UMUT MM 7500). Constriction curvature of "*D. damesi*" was described as strongly sigmoidal, following the same pattern as the growth lines and ribs. However, the curvature of the constrictions in this specimen differs from that of the growth lines and ribs. **C.** Simple concave shape, "*D. sugata*" from the Yezo Group (KUM MM TN 286). **D.** Schematic illustration of B. On the basis of the constriction curvature it is difficult to differentiate previous "*Damesites*" morphotypes, except "*D. sugata*" from the Yezo Group. Hollow circles show position of constrictions. Black arrows indicate adoral direction. A, B: ×1.5; C: ×2.

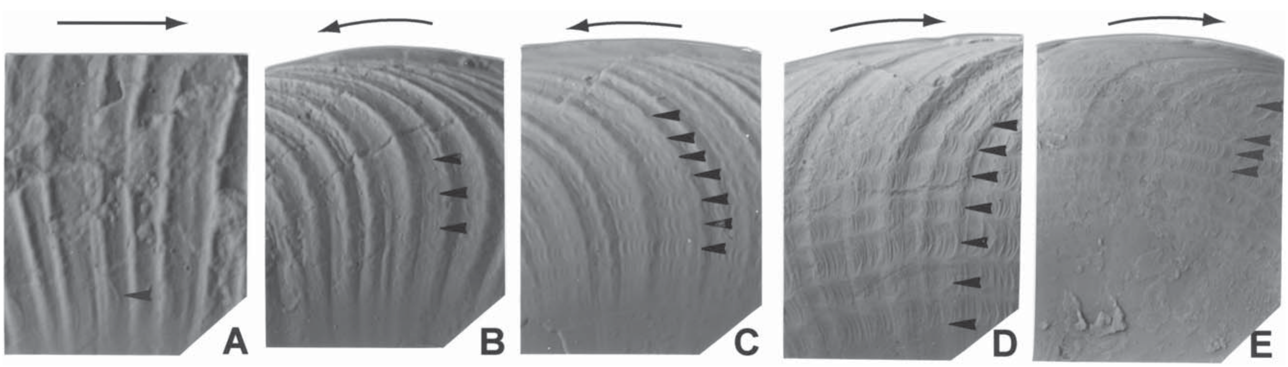

Figure 12. Development of longitudinal striations. Triangles point to longitudinal striations. **A.** "*Damesites semicostatus*" (holotype, UMUT MM 5579). **B.** KUM MM TN 196. **C.** KUM MM TN 193. **D.** "*D. damesi*" (lectotype, UMUT MM 7500). **E.** KUM MM TN 163. Longitudinal striations occur in not only almost smooth (E, "*D. damesi*"-type) specimens but also in intensely ribbed (B, "*D. semicostatus*"-type) ones. Longitudinal striations were formerly a diagnostic feature of "*D. damesi*." In contrast, previous studies claimed that longitudinal striations were not developed in "*D. semicostatus*". However, longitudinal striae does slightly develop along with "*D. semicostatus*"-type ribbing (A, B). Black arrows indicate adoral direction. A, ×20; B–D, ×3; E, ×1.5.

specimens of similar shell size.

Longitudinal striations occur most prominently on almost smooth shells and shells with wide interspaces between ribs (Figure 12C, D). However, they are not always developed in relatively weakly ornamented specimens (="*Damesites damesi*," Figure 12E). This feature is also observed in "*D. semicostatus*"-type specimens that have stronger ribs (Figure 12B). In addition, this character is slightly developed

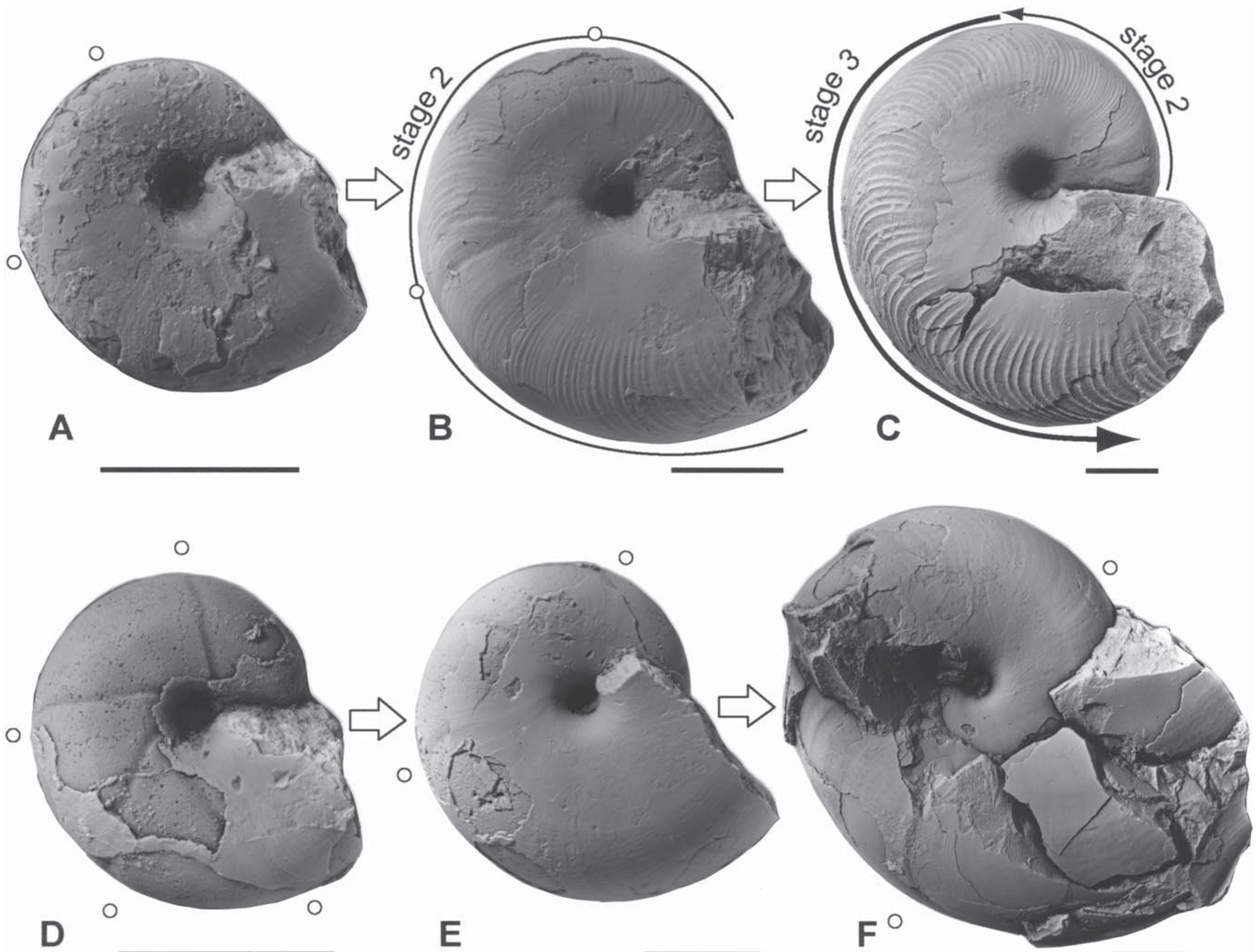

Figure 13. Ontogenetic development of shell ornamentation. **A–C.** "*Damesites semicostatus*" (KUM MM TN 184). Shell ornamentation changes from almost smooth (stage 1) to coarsely ribbed (stage 3) via weakly ribbed (stage 2). **D–F.** "*D. damesi*" (KUM MM TN 229). Shell surface remains almost smooth. Number of constrictions decreases with growth. Hollow circles show position of constrictions. Scale bar: 10 mm.

in the "*D. semicostatus*" holotype (Figure 12A).

Results.—Longitudinal striations are commonly observed in desmoceratine ammonoids. It appears in all morphotypes of "*Damesites*." It is difficult to discriminate the morphotypes "*Damesites damesi*" and "*D. semicostatus*" by this character because longitudinal striations appear in both morphotypes.

B-4. Ontogenetic development of shell ornamentation

Types of shell surface ornamentation (ribs and growth lines) have been often assumed as diagnostic features in desmoceratine ammonoid systematics (Matsumoto, 1954; Matsumoto and Obata, 1955). In spite of their significance, their ontogenetic development remains to be exploited for diagnostic purposes.

Observation.—The ontogenetic development of shell ornamentation is classified into three sequential stages: stage 1, almost smooth with faint growth lines; stage 2, weak ribs; and, stage 3, covered with coarse ribs, as in the case of the Turonian desmoceratine species *Tragodesmoceroides subcostatus* (Nishimura *et al.*, 2006).

Among lower Santonian specimens belonging to the morphotypes "*Damesites damesi*," "*D. damesi intermedius*," and "*D. semicostatus*," stage 2 (weak ribs) and sometimes stage 3 (coarse ribs) appear in the middle to late growth stages (Figure 13A–C). However, many individuals of "*D. damesi*" from the upper Santonian and lower Campanian show only stage 1 throughout ontogeny (Figure 13D–F). The number of constrictions decreases with growth in this morphotype. The timing of stages 2 and 3 is variable, although the order of appearance of ornamentation is fixed in these morphotypes.

Specimens of morphotypes "*Damesites ainuanus*,"

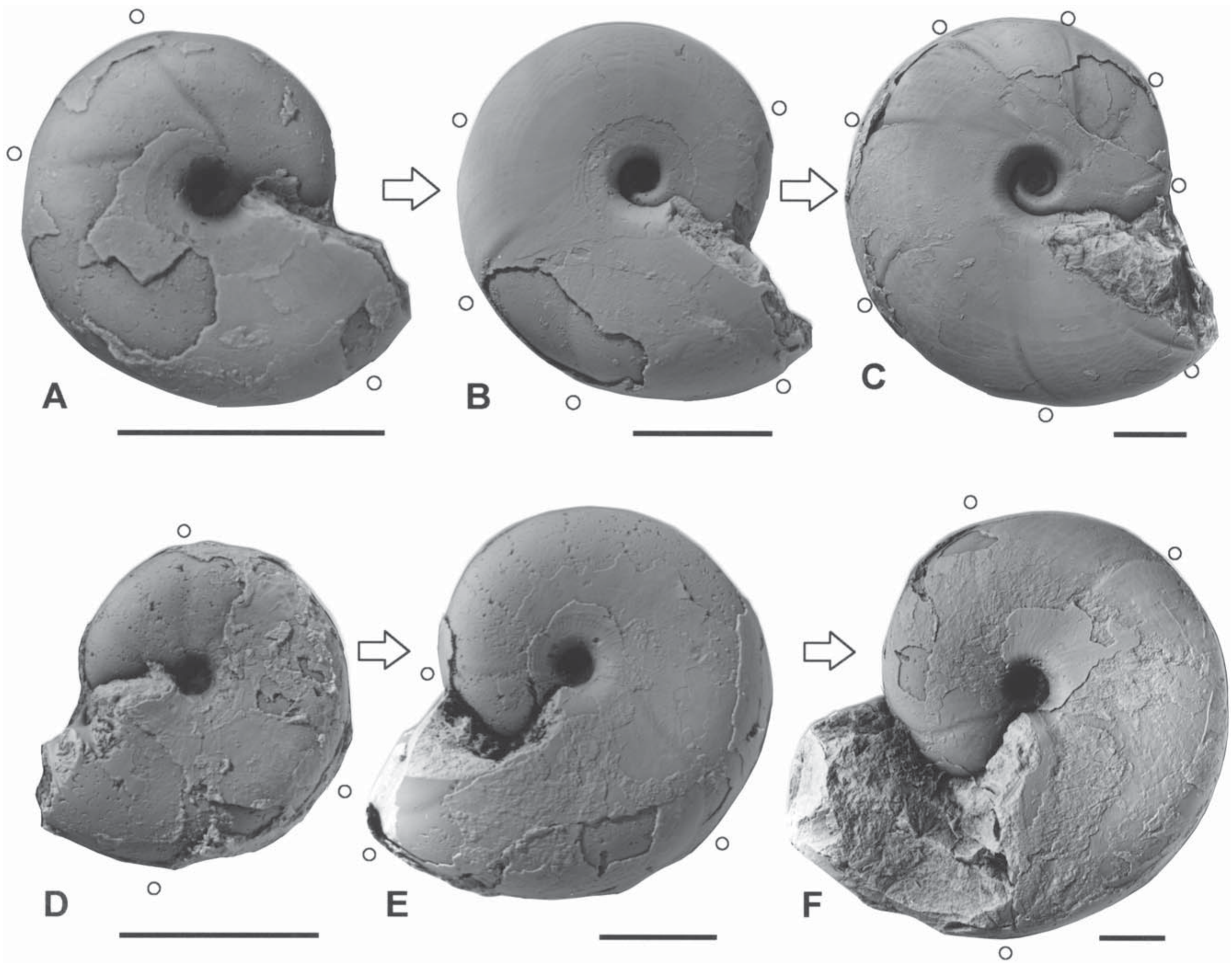

Figure 14. Ontogenetic development of shell ornamentation. **A–C.** "*Damesites sugata*" from the Yezo Group (KUM MM TN 286). **D–F.** "*D. ainuanus*" (topotype, KUM MM TN 099). Shell surface of both morphotypes almost smooth (stage 1) with frequently periodic constrictions throughout thier ontogeny. Hollow circles show position of constrictions. Scale bar: 10 mm.

"*Damesites* sp.," and "*D. sugata*" from the Yezo Group show almost smooth shell surfaces (stage 1), even in the late growth stage (60–90 mm diameter). In these morphotypes, periodic constrictions numbering 3–8/half whorl are present throughout their ontogeny (Figure 14). These morphotypes never show stage 3, not even in the late growth stage.

Results.—Based on the ontogenetic development of shell ornamentation, the Turonian-lower Campanian specimens of "*Damesites*" are subdivided into two different groups. The first group (S-group in Table 2) has weak and/or coarse ribs (stages 2 and 3) in the late growth stage (60–90 mm diameter). "*Damesites damesi*," "*D. damesi intermedius*," "*D. semicostatus*," and "*D. laticarinatus*" are classified into this category. Periodic constrictions are often developed in the early growth stage, but decrease in number in the late growth stage. The ontogenetic sequence of shell ornament types is stable (stage 1 to stage 3 via stage 2). The other group has an almost smooth shell surface (stage 1) with frequent constrictions throughout growth. The frequency of periodic constrictions does not decrease even in the late growth stage. Morphotypes belonging to this category include "*Damesites ainuanus*," "*Damesites* sp.," and "*D. sugata*" from the Yezo Group (C-group in Table 2).

B-5. Curvature of growth lines

The curvature of the fine growth lines changes with growth. This has not been closely considered in previous studies on systematics, but the present study attaches importance to this character.

Observation.—Curvature of growth lines is classified into two types (Figure 15). The first type forms a simple concave curve adorally, which is nearly straight at the midflank,

Table 2. Brief correlation of diagnostic features of the revised groups of “*Damesites*” (Turonian to Campanian) and *Tragodesmoceroides subcostatus*.

groups / characters	C-group: second group "*D. ainuanus*" and "*Damesites* sp."	C-group: third group "*D. sugata*" from the Yezo Group	S-group: first group "*D. damesi*," "*D. damesi intermedius*," "*D. semicostatus*," and "*D. laticarinatus*"	*Tragodesmoceroides subcostatus*
shell form				
ventral projection	keel	keel	keel	tongue-like elevation
umbilical width	narrow to somewhat wide	wide	narrow	narrow
whorl expansion ratio (late growth stage)	small	small	large	large
shell ornament				
ontogenetic development of shell ornamentation	almost smooth	almost smooth	almost smooth or sigmoid ribs appear	almost smooth or sigmoid ribs appear
shape of growth lines	concave	concave	sigmoidal	sigmoidal

and becomes prorsiradiate at the ventral periphery (simple concave, C-type, Figure 15A, C). “*Damesites ainuanus*,” “*Damesites* sp.,” and “*D. sugata*” from the Yezo Group (Figures 5, 6A–D, 14) belong to the C-group showing a simple concave pattern. Specimens of this group retain the same pattern throughout growth. Only in the late growth stage (60–90 mm diameter) of “*D. ainuanus*” and “*Damesites* sp.” does a very weak sigmoidal curve appear near the constriction (Figure 15A). The other type exhibits a very flexuous sigmoid (biconvex) curve like the Cenomanian *Desmoceras* (*Pseudouhligella*) *japonicum*. The curvature at the venter and mid-flanks projects forward with growth (Figure 15B, D). “*Damesites damesi*,” “*D. damesi intermedius*,” “*D. semicostatus*,” and “*D. laticarinatus*” (Figures 4, 6E–G, 13) belong to the S-group showing a sigmoid or biconvex shape, except for the early growth stage. The growth line changes from a simple concave (C-) to flexuous sigmoidal (S-) shape at 10–50 mm in diameter.

Results.—Based on the curvature of the growth line, the Turonian-lower Campanian desmoceratine ammonoids are clearly classified into two groups: C- and S-groups. “*Damesites ainuanus*,” “*Damesites* sp.,” and “*D. sugata*” from the Yezo Group (C-group showing a simple concave pattern) are clearly distinguished from “*D. damesi*,” “*D. damesi intermedius*,” “*D. semicostatus*,” and “*D. laticarinatus*” (S-group showing a sigmoidal pattern) based on this characteristic.

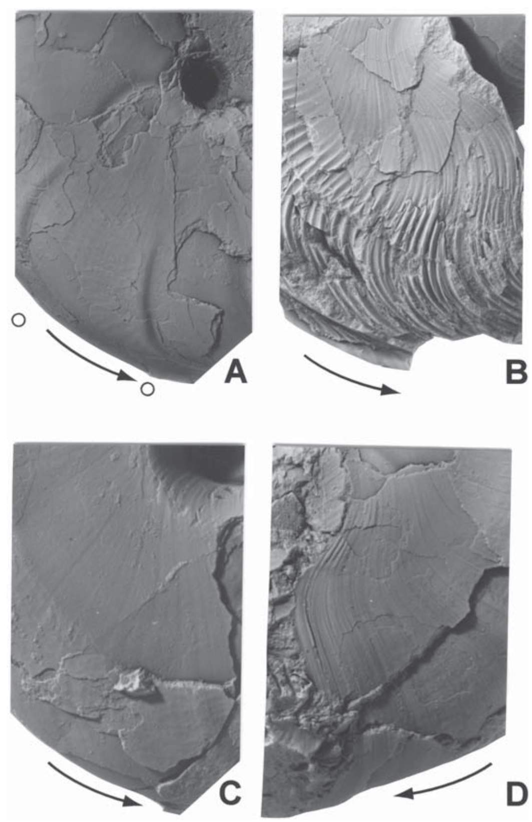

Figure 15. Curvature of growth line. **A.** C-type (concave) growth line, “*Damesites* sp.” (KUM MM TN 129), ×1.2. Only near constrictions, curvature of growth lines changes to weakly sigmoidal. **B.** S-type (sigmoidal) growth line (ribs), “*D. damesi*” (KUM MM TN 196), ×1.0. **C.** C-type growth line, “*D. sugata*” from the Yezo Group (KUM MM TN 286), ×2. **D.** S-type growth line, “*D. damesi*” (KUM MM TN 155), ×2.4. Based on the two observed types of curvature of growth lines, previous “*Damesites*” morphotypes are subdivided into two groups (C- and S-groups). Hollow circles shows position of constrictions. Black arrows indicate adoral direction.

C. Shell form

C-1. Keel

The keel has been considered as a generic character in the systematics of desmoceratine ammonoids (Matsumoto, 1942). In “*Damesites*” spp., the keel appears gradually with ontogeny, generally at 5–10 mm diameter. The profile and time of appearance of the keel differ among “*Damesites*”

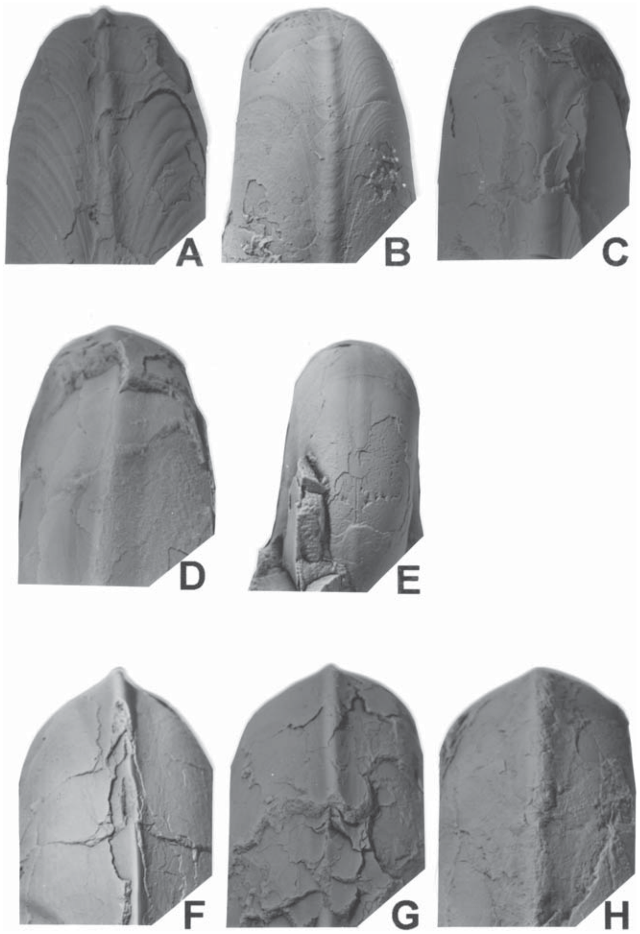

Figure 16. Profile of keel. **A**. "*Damesites damesi*" (lectotype, UMUT MM 7500). **B.** "*D. damesi*" (KUM MM TN 153). **C.** "*D. damesi intermedius*" (UMUT MM 6747). **D.** "*D. laticarinatus*" (holotype), **E.** "*D. damesi intermedius*" (KUM MM TN 145). **F.** "*Damesites* sp." (KUM MM TN 129). **G.** "*Damesites* sp." (KUM MM TN 103). **H.** "*D. ainuanus*" (holotype, GK. H4198). The keel of "*D. laticarinatus*" is broad (D), which is the "diagnostic" feature of this morphotype in the previous study. However, this feature is also found in "*D. damesi intermedius*" (C). In addition, many intermediate forms are recognized (e.g., B, C). Thus, "*D. damesi*," "*D. laticarinatus*," and "*D. damesi intermedius*" are difficult to discriminate by the keel profile. The keel height and width of *D. damesi* are variable, i.e., acute and high (A) to obtuse (E) are connected via intermediate (B–C) forms. The keel profile of "*Damesites* sp." is also variable. "*D. ainuanus*" and "*Damesites* sp." are not clearly discriminated by this character, because intermediate forms (G) exist. All specimens are natural size.

species. These characteristics were used for the classification of "*Damesites*" species, e.g., a broad keel is a diagnostic feature of "*D. laticarinatus*."

Observation.—A keel is absent in the early growth stage (less than 5 mm diameter) and appears gradually from the middle to late growth stages (20–50 mm diameter). Ontogenetic changes in the height and profile of the keel are also variable among specimens of a single morphotype, but the timing of appearance and prominence of the keel differ among "*Damesites*" species. The profile of the keel varies from acute to rounded according to morphotype.

The most common profile patterns of the keel differ among "*Damesites damesi*," "*D. damesi intermedius*," and "*D. laticarinatus*" (Figure 16A–E). The profile of the keel of "*D. damesi*" is acute (holotype, UMUT MM 7500, Figure 16A) to moderate (KUM MM TN 153, Figure 16B), whereas that of "*D. laticarinatus*" (holotype) is broad and moderately high (Figure 16D), and of "*D. damesi intermedius*" is somewhat broad and low (UMUT MM 6747, Figure 16C) to obtuse (KUM MM TN 145, Figure 16E). However, UMUT MM 6747 ("*D. damesi intermedius*") exhibits keel features intermediate with "*D. laticarinatus*" (Figure 16C).

The profile of the keel also varies between "*D. ainuanus*" (obtuse, Figure 16H, GK. H4198) and "*Damesites* sp." (siphonal to moderate, Figure 16F, G, KUM MM TN 129, 103).

Results.—"*Damesites laticarinatus*" is differentiated from the other morphotypes by the presence of a broad keel. However, it is difficult to discriminate "*D. laticarinatus*" from the other morphotypes ("*D. damesi*" and "*D. damesi intermedius*") by the keel shape because of the presence of many intermediate forms (Figure 16B, C).

In specimens of morphotypes "*Damesites ainuanus*" and "*Damesites* sp.," the keel profile also varies, and an intermediate form exists between them (e.g., KUM MM TN 134, Figure 16G).

C-2. Umbilicus

The relative width of the umbilicus is regarded as a diagnostic feature in some desmoceratine ammonoids. For example, a wider umbilicus is diagnostic of "*Damesites sugata*" from the Yezo Group (Matsumoto and Obata, 1955).

Observation.—The umbilical width (U) changes with ontogeny. The U/diameter (D) is variable among specimens of different morphotypes after the 7–9π stage, about 5–10 mm diameter.

The relative umbilical width of "*Damesites damesi*" is constant or somewhat decreases (U/D is 0.08–0.10) in the middle to late growth stages. The U/D ratio of "*Damesites* sp." shows a similar pattern to that of "*D. damesi*" until the middle growth stage (30 mm diameter). In the late growth stage, "*Damesites* sp." has a wider umbilicus than "*D. damesi*"; however, the U/D ratios of both morphotypes overlap. The U/D ratio of "*D. sugata*" from the Yezo Group increases from the early to middle growth stages (10π stage, 10 mm diameter). After this stage, the ratio of "*D. sugata*" from the Yezo Group becomes notably higher than in other morphotypes (Figure 17A, C).

In addition, the relative umbilical width of *Tragodesmoceroides subcostatus* is greatest (U/D=0.15) in the early growth stage (10–20 mm diameter), and decreases

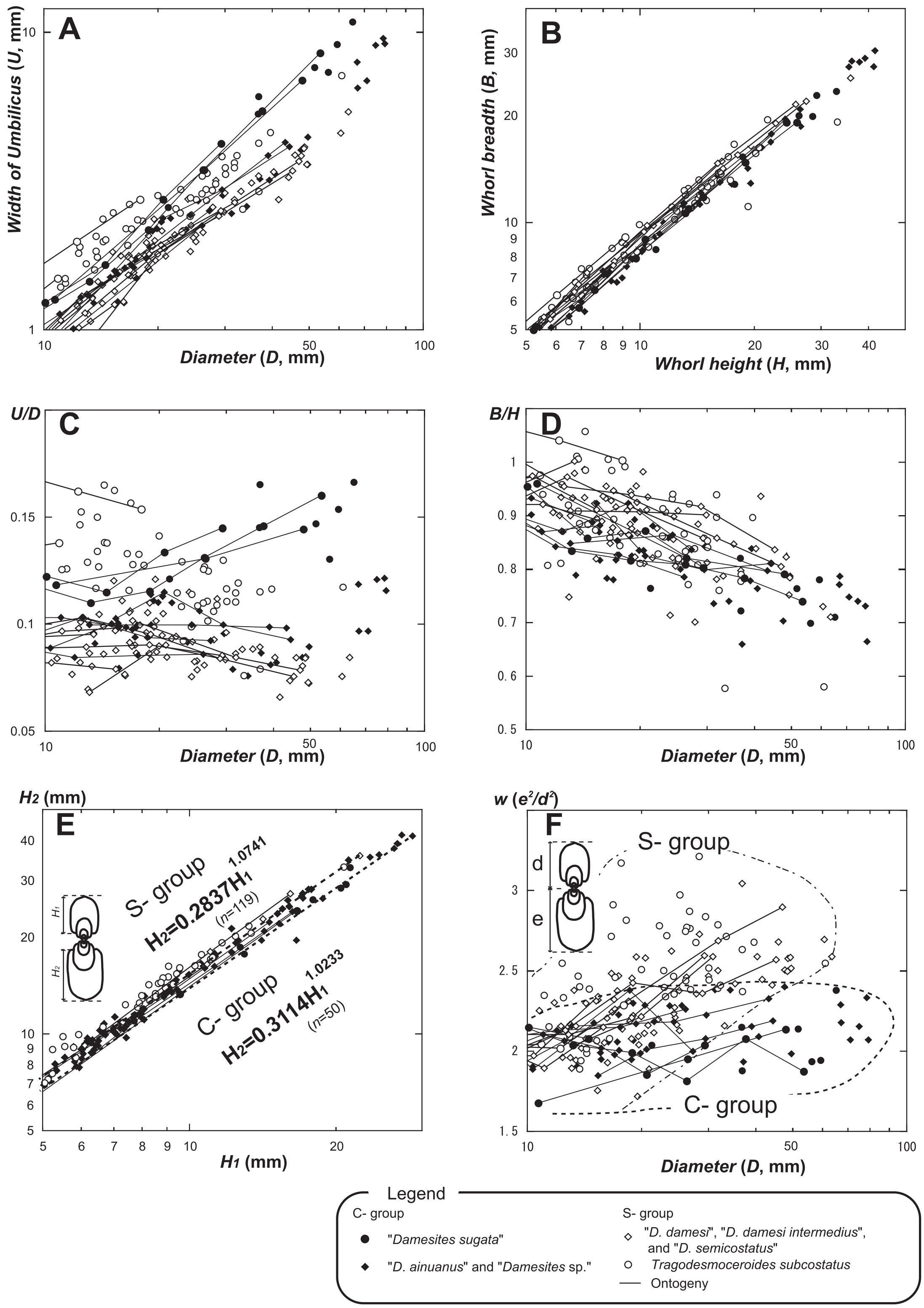

Figure 17. Ontogenetic change of shell geometry. **A, C.** Umbilical width of "*Damesites sugata*" from the Yezo Group is obviously greater than in the other species. **B, D.** Whorl breadth. **E.** Whorl enlargement ratio. Each slope of the reduced major axis is clearly discriminated ($p<0.01$). **F.** Whorl expansion ratio (W, Raup, 1966). Previous "*Damesites*" morphotypes are classified into two groups (C- and S- group) not only by shape of growth line (Figure 15) but also by whorl enlargement ratio (E) and whorl expansion ratio (F).

(U/D=0.10) in the middle to late growth stages (30–50 mm diameter).

Results.—Ontogenetic changes in the U/D ratio shows different patterns among morphotypes (Figure 17A, C). Only "*Damesites sugata*" from the Yezo Group shows a different pattern from the other morphotypes, i.e., their U/D ratios are greater than those of the other "*Damesites*" species (Figure 17A, C). This result is concordant with a previous study (Matsumoto and Obata, 1955).

In contrast, the U/D ratios of other morphotype specimens overlap one another. Therefore, it is not possible to clearly discriminate "*Damesites*" morphotypes using this character, except for "*D. sugata*" from the Yezo Group.

C-3. Whorl breadth

Whorl breadth is also regarded as a diagnostic feature in desmoceratine taxonomy. In "*Damesites*" morphotypes, this character is not considered to be significant for classification, although differences have been shown.

Observation.—In general, the whorl becomes compressed with growth in all morphotypes. After the 8π (about 8 mm diameter) stage, the ontogenetic change in breadth/height (B/H) ratios in relation to shell diameter differs among morphotypes.

"*Damesites* sp." and "*D. sugata*" from the Yezo Group show a similar pattern of change in whorl breadth. The B/H ratio of both morphotypes reaches 0.8 at 20 mm diameter, and decreases to 0.7 at 50 mm diameter. In "*Damesites damesi*," the B/H ratio is 0.8–0.9 at 20 mm diameter and decreases to 0.7–0.8 at 50 mm diameter. In addition, in *Tragodesmoceroides subcostatus*, the B/H ratio is approximately 0.9 at 20 mm diameter, and decreases to 0.75 at 50 mm diameter (Figure 17B, D).

Results.—The changing patterns of whorl breadth during ontogeny are similar among "*Damesites*" morphotypes. Thus, it is difficult to differentiate morphotypes based on this character only. This character should be used as a subordinate character for the identification of desmoceratines.

C-4. Whorl expansion ratio

Whorl expansion ratio has been used as a subordinate character in the taxonomy of desmoceratine ammonoids. In a pioneering study, Obata (1959) first performed allometric analysis with some desmoceratine ammonoids. However, this study emphasized methodology, and few comparisons of actual taxa were demonstrated.

Observation.—The present study revealed that the whorl expansion ratio (*W*; Raup, 1966) varies from 1.6 to 3.2 during ontogeny in the specimens examined (Figure 17F). Above 10-mm diameter (about 9π stage), *W* values show different ontogenetic patterns among different morphotype specimens (Figure 17F).

In morphotype specimens of "*Damesites* sp." and "*D. sugata*" from the Yezo Group, *W* values do not show a marked ontogenetic change, i.e., *W* values are approximately 2.0 in the early to middle growth stages (about 10–30 mm diameter) and approximately 2.2 in the late growth stage (about 60 to 90 mm diameter, Figure 17F). In "*Damesites damesi*," "*D. damesi intermedius*," "*D. semicostatus*," and *Tragodesmoceroides subcostatus*, the *W* value tends to increase from 2.1 to 2.7 with ontogeny.

Results.—Ontogenetic patterns of change in whorl height enlargement per half volution were statistically analyzed by using reduced major axis regression analysis (Figure 17E).

In this section, the slope and intercept of the whorl enlargement ratio are described by each newly defined morphological group that show peculiar evolutionary trends (discussed later).

The first group ("*Damesites damesi*," "*D. semicostatus*," and "*D. damesi intermedius*") (n=72) shows a higher gradient ($H_2=0.1861H_1^{1.110}$, r=0.995). *Tragodesmoceroides subcostatus* (n=49) also shows a higher gradient ($H_2=0.3090H_1^{1.0739}$, r=0.992).

The second group ("*Damesites ainuanus*" and "*Damesites* sp.") (n=40) shows a lower gradient ($H_2=0.1302H_1^{1.010}$, r= 0.996). The third group ("*D. sugata*" from the Yezo Group) (n=10) also shows a lower gradient ($H_2=0.1958H_1^{1.0602}$, r= 0.980).

On comparing the three groups and *Tragodesmoceroides subcostatus*, only the slopes of the reduced major axis between the first and second groups are significantly different ($p<0.05$, K=2.32; discussed later).

Discussion

Among various "diagnostic" features of "*Damesites*," only the umbilical width has proved to be a reliable diagnostic feature. The presence of intermediate forms reveals that other "diagnostic" features (e.g., the appearance of longitudinal striation, height of rib, regularity of ribbing as well as the constriction curvature) and the early internal shell structures are in fact inadequate as diagnostic features for species classification.

However, a few additional characters that have not signified in previous taxonomic studies (e.g., Matsumoto, 1954, 1957; Matsumoto and Obata, 1955) are useful for classifying "*Damesites*" spp. "*Damesites*" morphotypes are classified into C- and S-groups by the shape of growth lines and ontogenetic changes in shell surface ornamentation. This division is also supported by statistical analysis of whorl expansion ratio. The ontogenetic patterns of change in whorl height enlargement per half volution between the C- and S-groups are as follows.

Cluster 1 (S-group) including "*Damesites damesi*," "*D. semicostatus*," and "*D. damesi intermedius*" (first group) and *Tragodesmoceroides subcostatus* (n=119) shows a higher gradient ($H_2=0.2837H_1^{1.0741}$, $r=0.992$).

Cluster 2 (C- group) including "*Damesites ainuanus*" and "*Damesites* sp." (second group) and "*D. sugata*" from the Yezo Group (third group) ($n=50$) exhibits a much lower gradient ($H_2=0.3114H_1^{1.0233}$, $r=0.997$).

The slopes of the reduced major axis of the two clusters are significantly differentiated from each other ($p<0.01$, $K=2.92$).

In addition, the C-group is subdivided into two groups (second and third groups) by umbilical width. The umbilical width of "*Damesites sugata*" from the Yezo Group is wider than that of other morphotypes of the C-group. The simple concave shape of the constrictions of this morphotype also differs somewhat from other morphotypes of the C-group.

"*Damesites sugata*" from the Yezo Group remains as the third group. It is characterized by the possession of simple concave growth lines, wide umbilicus, small whorl expansion ratio, and an almost smooth shell surface with periodic constrictions throughout growth. It resembles "*Damesites* sp." (the second group) in having a lower gradient of whorl expansion ratio. However, the classification of the present morphotype is doubtful because there are some disparities in shell morphology and stratigraphic range between "*D. sugata*" from the Yezo Group and the type specimens of *D. sugata* from India. For example, "*D. sugata*" from the Yezo Group has a much wider umbilicus, while the Indian types possess narrow, craterlike umbilici (Forbes, 1846; Kossmat, 1898; Kennedy and Henderson, 1991). The Yezo Group "*D. sugata*" commonly occurs from the Santonian to the lower Campanian. In contrast, Indian *D. sugata* typically occurs in the Coniacian according to the Indian collection of Dr. K. Ayyasami (GSI).

Besides morphological observations, the paleobiogeography of allied species outside Hokkaido and Sakhalin, particularly that of typical *Damesites sugata* (Forbes) from India, must be considered in reconstructing an up-to-date taxonomic scheme for desmoceratines. Taking the above morphological examination into consideration, the previous typological scheme of "*Damesites*" should be revised or, instead, a new taxonomic scheme that defines several evolutionary biospecies should be developed.

Conclusions

Based on the reevaluation of morphological features and consideration of shell ontogeny, the present study redefines three groups of "*Damesites*" (Table 2).

"*Damesites damesi*," "*D. damesi intermedius*," "*D. semicostatus*," and "*D. laticarinatus*" are assigned to the first group. The characteristic features of this group are sigmoidal growth lines, craterlike narrow umbilicus, large whorl expansion ratio, and weak or coarse ribs that develop in the middle to late growth stages.

"*Damesites ainuanus*" and "*Damesites* sp." are assigned to the second group. Their characteristics are a simple concave growth line, craterlike narrow or somewhat wide umbilicus, small whorl expansion ratio, and an almost smooth shell surface with periodic constrictions throughout growth.

"*Damesites sugata*" from the Yezo Group remains as the third group, having simple concave growth lines, wide umbilicus, small whorl expansion ratio, and an almost smooth shell surface with periodic constrictions throughout growth. However, the shell morphology and stratigraphic range of "*D. sugata*" from the Yezo Group are different from those of the type specimens of *D. sugata* from India. Questions of the systematic paleontology, stratigraphic occurrence, and phylogenetic relationships based on the reexamination outlined in the present study will be described in a separate paper.

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