Paleontological Research, vol. 10, no. 1, pp. 11–28, April 30, 2006

Ontogenetic shell development of a Cretaceous desmoceratine ammonoid "*Tragodesmoceroides subcostatus*" Matsumoto, 1942 from Hokkaido, Japan

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Received June 24, 2005; Revised manuscript accepted October 25, 2005

Abstract. **Ontogenetic shell development of the Turonian desmoceratine ammonoid *Tragodesmoceroides subcostatus* is examined based on more than 200 specimens collected by detailed biostratigraphic survey in the Tappu and Saku areas, Hokkaido, Japan. After the ammonitella stage, the mode of ribbing on the shell surface becomes coarser with growth. The shell surface ornament changes from stage 1 (almost smooth) to stage 3 (coarse ribbing) via stage 2 (weak ribbing). Stage 1 is subdivided into an earlier substage 1a with desmoceratid-type constrictions and a subsequent substage 1b without constrictions. Appearance order of these four ornament stages and substages seems to be ontogenetically fixed in the present species. Other characters, such as ammonitella and early shell shape and whorl geometry are also stable.**

On the other hand, the shifting-timing from stages 1 to 2 and from stages 2 to 3 changes chronologically, i.e., it becomes ontogenetically earlier in upward sequence. In the Lower and Middle Turonian, the adult or subadult shells still remain stage 1 or 2. In contrast the strongly ribbed holotype and paratypes showing stage 3 are regarded as the Upper Turonian peramorphic endmembers of the single biospecies *T. subcostatus*. Taking these features into consideration, *T. subcostatus* should be taxonomically revised.

Key words: Cretaceous, ontogeny, peramorphic evolution, shell surface ornament, *Tragodesmoceroides subcostatus*, Turonian

Introduction

Desmoceratine ammonoids range from the Aptian to the Maastrichtian and are distributed worldwide (Wright, 1957; Wright *et al*., 1996). In the circum-north Pacific realm, species of this subfamily are particularly abundant in the Cretaceous Yezo Supergroup exposed in Sakhalin and Hokkaido (Figure 1). For example, *Desmoceras* (*Pseudouhligella*) spp. occur abundantly in the Upper Albian and Cenomanian sequences (Matsumoto, 1954; Maeda, 1991; Kawabe, 2003; Matsumoto and Nishida, 2004). *Damesites* spp. are also abundant from the Coniacian and Santonian (Matsumoto and Obata, 1955; Okamoto *et al*., 2003). *Tragodesmoceroides* known from the Turonian (Figures 2–7) is a key taxon linking the evolutionary lineage from Cenomanian *Desmoceras* (*Pseudouhligella*) to Coniacian-Santonian *Damesites*.

The type species of this genus, *Tragodesmoceroides subcostatus*, diagnosed by having coarse and sharp sigmoidal ribs, was first described by Matsumoto (1942a) (Figure 7). After that, many authors have reported this species from the Turonian in the Yezo Supergroup (Tsushima *et al*., 1958; Tanaka, 1963; Hirano *et al*., 1977; Tanabe *et al*., 1977; Kawabe, 2000; Funaki and Hirano, 2004). The stratigraphic occurrence is typically demonstrated in the Tappu section (Figure 3).

However, there is a large morphological discrepancy between the holotype and most of the rest of the individuals assigned to the present species. For example, most "*Tragodesmoceroides subcostatus*" specimens are almost smooth or weakly ribbed. The sharp and coarse ribbing, one of the diagnostic features of the present species, does not appear in most individuals (Figures 4, 5).

In order to clarify these discrepancies, more than 200 specimens of "*Tragodesmoceroides subcostatus*" collected from the Tappu and Saku areas (Figure 1) are examined from the viewpoint of the population

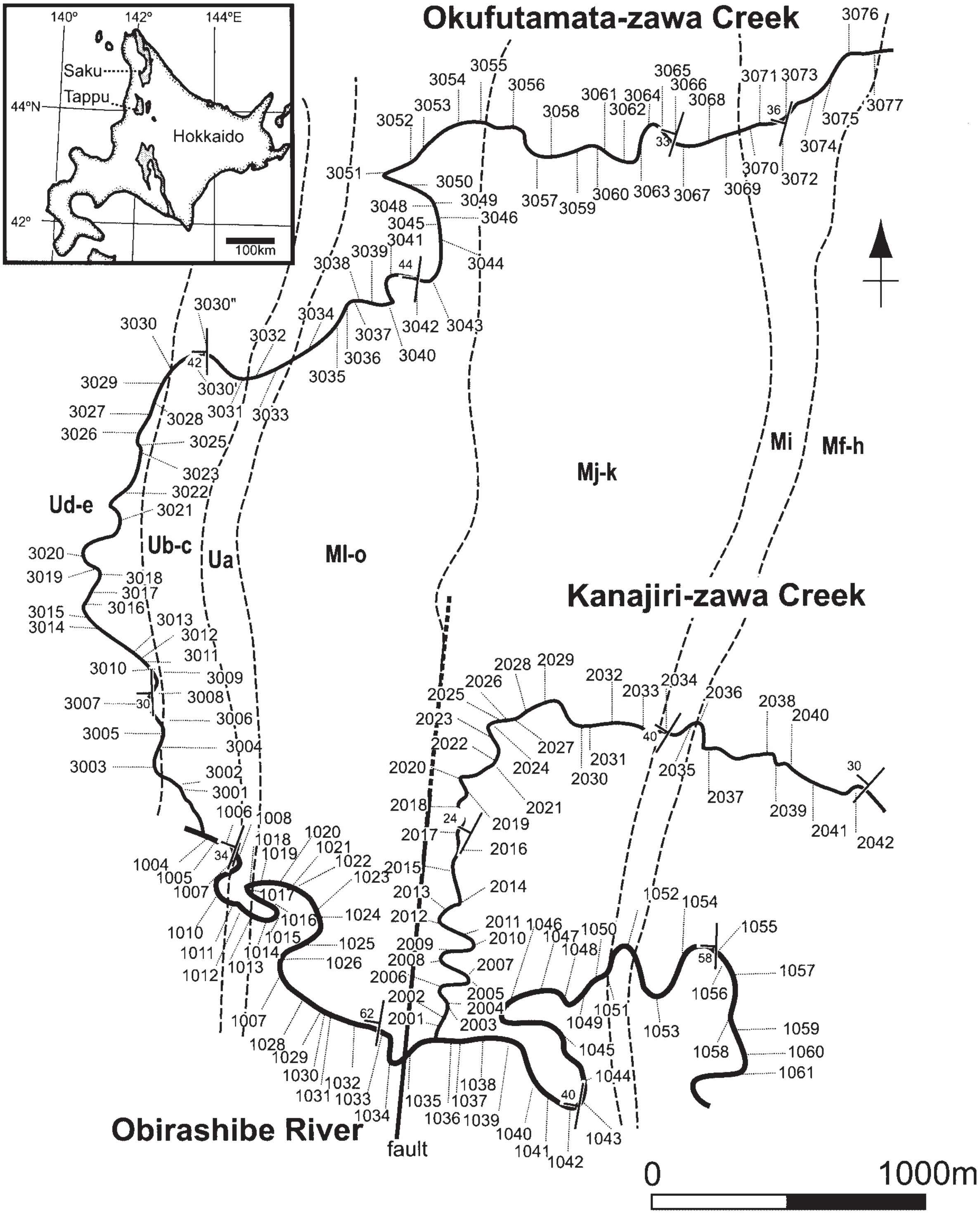


Figure 1. Index map of Hokkaido (left upper) showing the Tappu and Saku areas and route map of the Tappu area showing the sample localities. Dotted area in Central Hokkaido shows distribution of the Yezo Supergroup. Prefix: OT—is abbreviated the locality numbers.

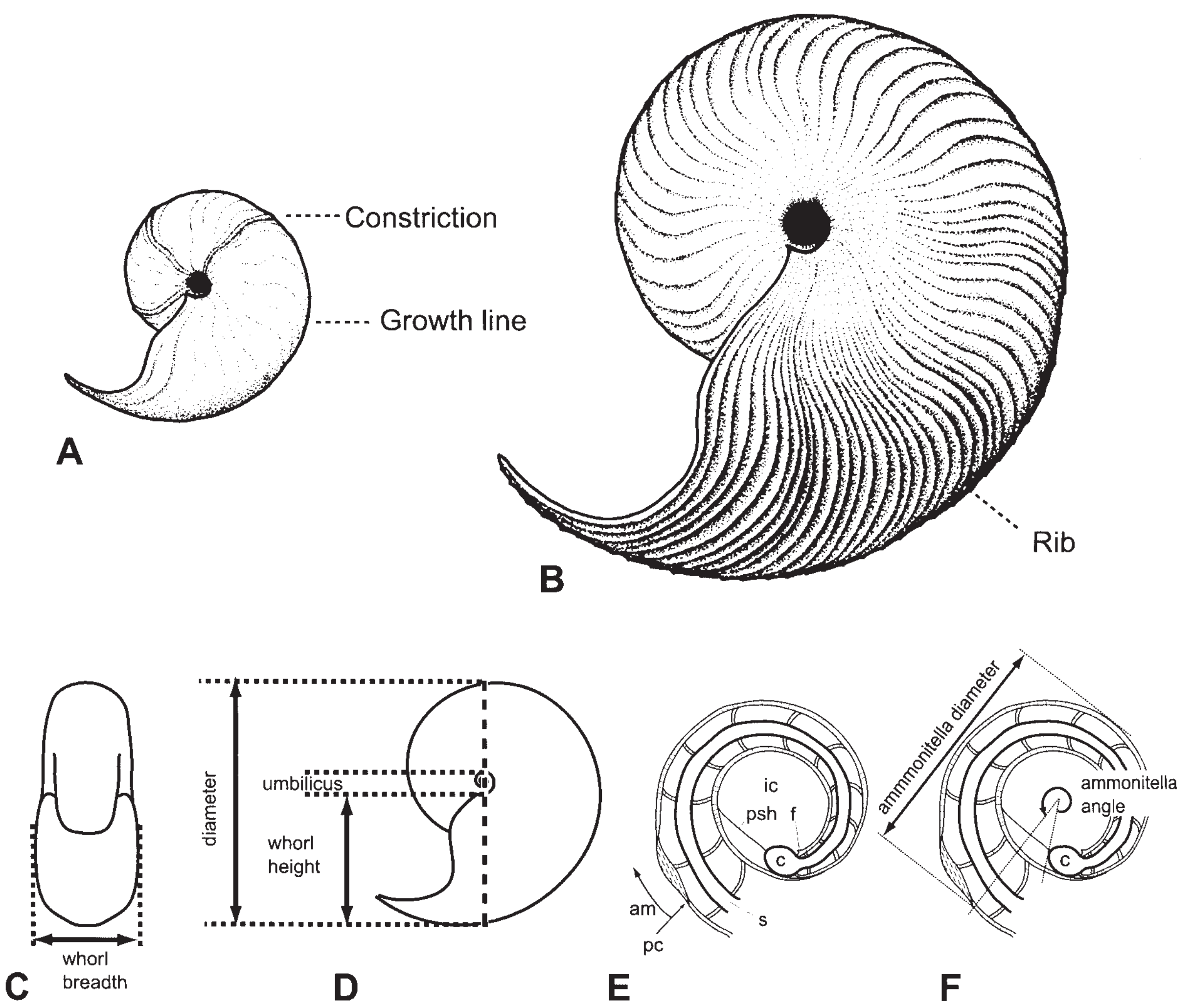


Figure 2. Schematic illustrations of Turonian *Tragodesmoceroides subcostatus* shells. **A, B.** Shell surface ornament. A. Shell at middle growth stage. B. Subadult shell or adult shell. **C, D.** Measured parameters on whorl shape. **E.** Terminology for the early internal shell structures in median longitudinal section. **F.** Measured parameters in early internal shell structure. s, siphuncle; pc, primary constriction; am, ammonitella; ic, initial chamber; f, flange; ps, prosiphon.

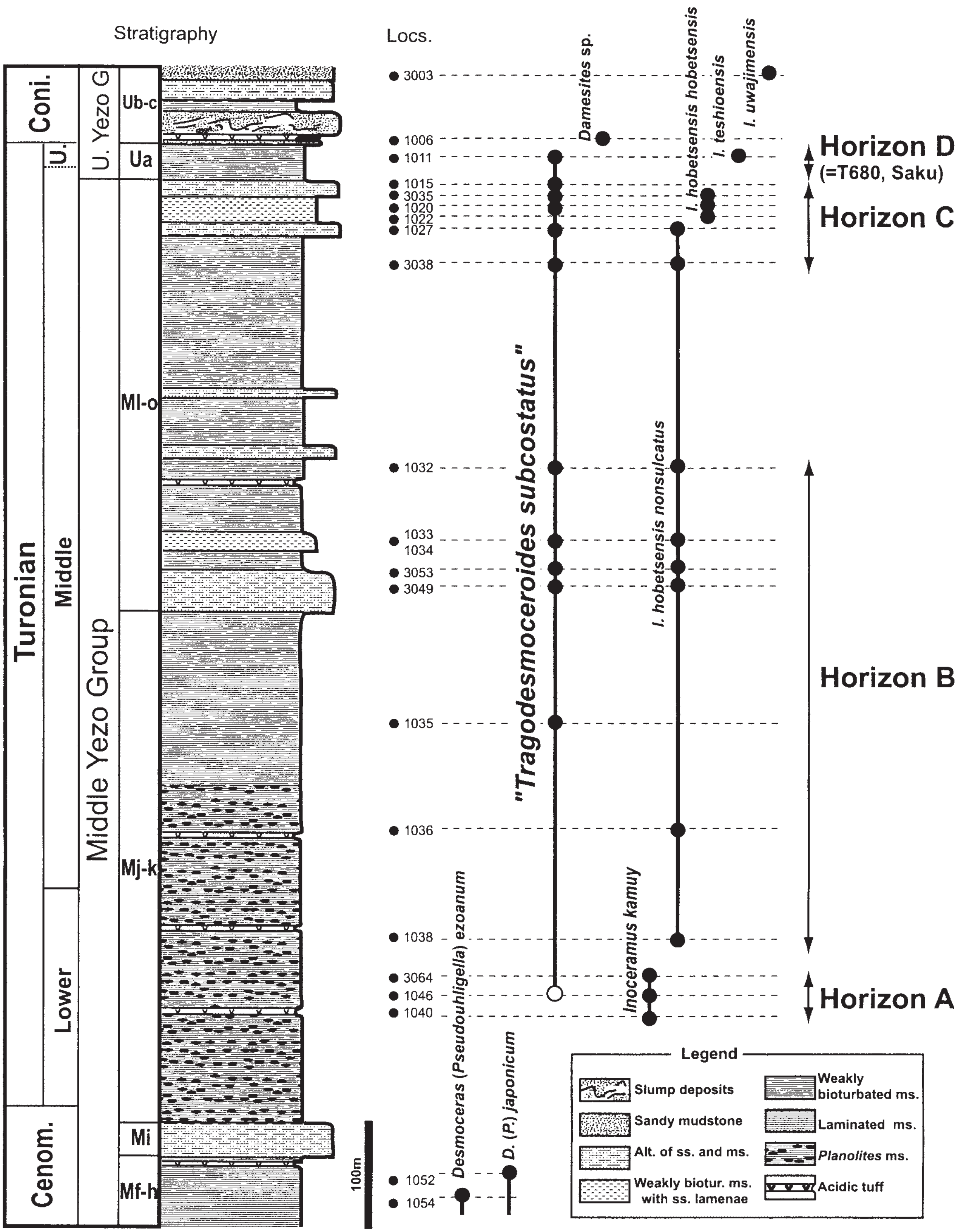
concept. This study aims to reveal the ontogenetic shell growth, the intraspecific variation and the stratigraphic occurrence of "*T. subcostatus*".

In this paper, we provisionally lump all morphotypes of *Tragodesmoceroides subcostatus* except *T. matsumotoi* as a morphospecies "*T. subcostatus*" with double quotation marks.

Repository of specimens.—All the specimens utilized in this study are housed in the Kyoto University Museum with prefix KUM. MM. TN. except for the holotype (UMUT. MM6718) and the paratypes (UMUT. MM6719, UMUT. MM6723), which are registered in the University Museum, the University of Tokyo.

Previous studies on *Tragodesmoceroides*

The genus *Tragodesmoceroides* was first established by Matsumoto (1942a). The type species is *T. subcostatus*, whose holotype was collected from loc. T680 (Matsumoto, 1942b, pl. 12) in the Saku area, about 140 km north of the Tappu area (Figures 1, 7A, 7B). Generic diagnoses given for *Tragodesmoceroides* are summarized as follows.


Stratigraphy
Locs.
Coni.
Turonian
Cenom.
U.
Middle
Lower
U. Yezo G
Middle Yezo Group
Ub-c
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Ml-o
Mj-k
Mi
Mf-h
3003
1006
1011
1015
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1038
3064
1046
1040
1052
1054
100m
Damesites sp.
I. hobetsensis hobetsensis
I. teshioensis
I. uwajimensis
"Tragodesmoceroides subcostatus"
I. hobetsensis nonsulcatus
Inoceramus kamuy
Desmoceras (Pseudouhligella) ezoanum
D. (P.) japonicum
Horizon D
(=T680, Saku)
Horizon C
Horizon B
Horizon A
Legend
Slump deposits
Sandy mudstone
Alt. of ss. and ms.
Weakly biotur. ms. with ss. lamenae
Weakly bioturbated ms.
Laminated ms.
Planolites ms.
Acidic tuff

Figure 3.

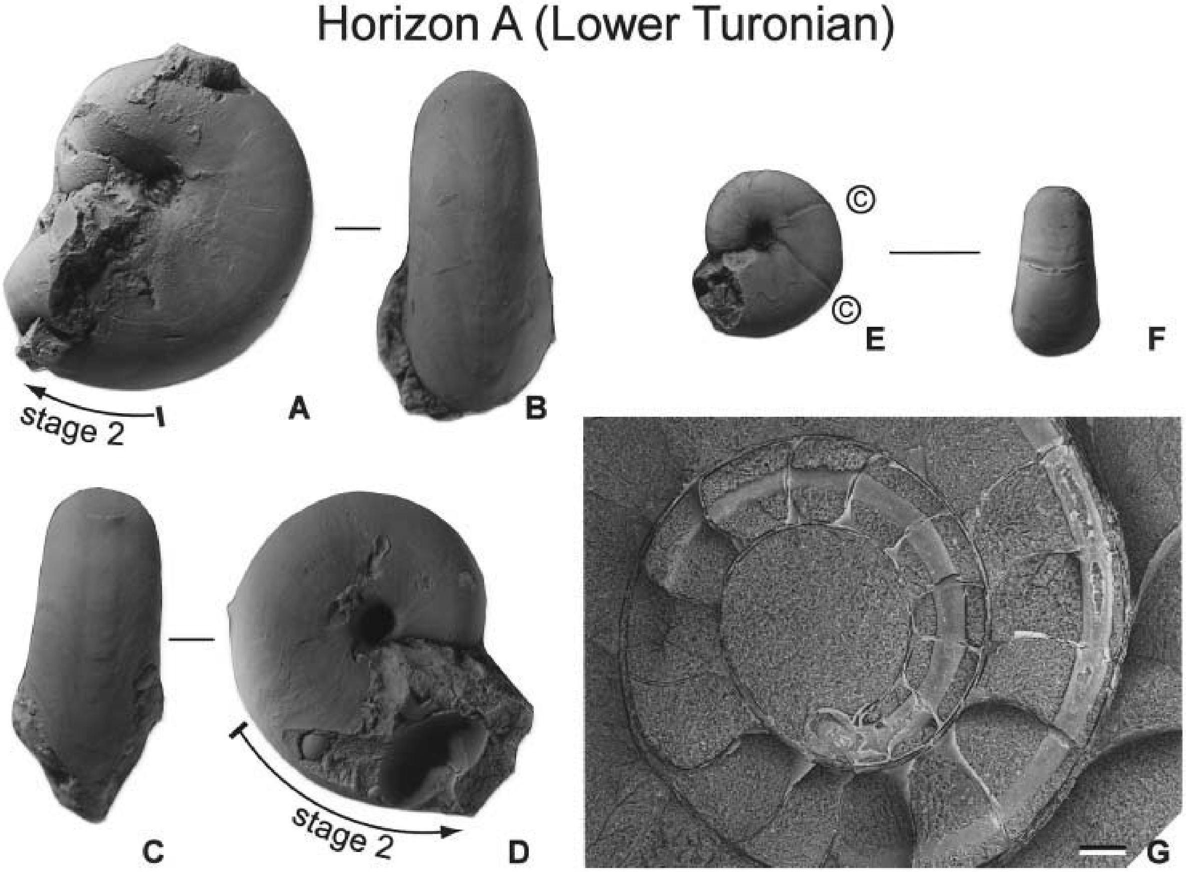

Figure 4. "*T. subcostatus*" collected from horizon A, Lower Turonian. All specimens were recovered from the same calcareous nodule collected from river gravel at OT 1046. **A, B.** KUM. MM. TN. 067. **C, D.** KUM. MM. TN. 070. **E, F.** KUM. MM. TN. 083. **G.** KUM. MM. TN. 084. A–D in natural size. E, F, ×3. G, scale bar = 0.1 mm. c, constriction.

1) Distinct, sharp, narrowly interspaced ribs cover ventral half in the adult (Matsumoto, 1942a, p. 25, lines 13–15; Matsumoto, 1954, p. 262, lines 24–26, p. 263, lines 36–38).

2) Very involute shell with a narrow craterlike umbilicus (Matsumoto, 1942a, p. 25, lines 17–18; Matsumoto, 1954, p. 262, lines 26–27, p. 263, lines 32–35).

3) Biconcave apertural margin with strongly projected ventral rostrum (Matsumoto, 1954, p. 262).

4) Midline of the venter tends to be raised, and forms tonguelike elevation (Wright *et al.*, 1996, p. 83, lines 7–8).

Specific diagnoses for *Tragodesmoceroides subcostatus* are summarized as follows.

5) Weak subcostae in middle growth stage (Matsumoto, 1954, p. 263, lines 35–36).

6) Infrequent constrictions (Matsumoto, 1954, p. 263, l. 38).

7) Occurrence from the Turonian (common in Neogyliakian in Hokkaido and Sakhalin, Matsumoto, 1954, p. 266, l. 5).

⬅ **Figure 3.** Columnar section of the Turonian sequence in the Tappu area showing stratigraphic occurrence of desmoceratine ammonoids and inoceramids. Open circle shows that the samples come from a river gravel and were presumably derived from a lower stratigraphic level in the Turonian, while solid circles were recovered *in situ*. For convenience, horizons A to D are used to describe stratigraphic levels in the text. Horizon D is biostratigraphically correlated with the strata at T680 (type locality of *Tragodesmoceroides subcostatus*) in the Saku area (Matsumoto, 1942b). The specimens used from horizon D were collected from T680, the Saku area. Prefix OT denotes the locality numbers. ss, sandstone; ms, mudstone.

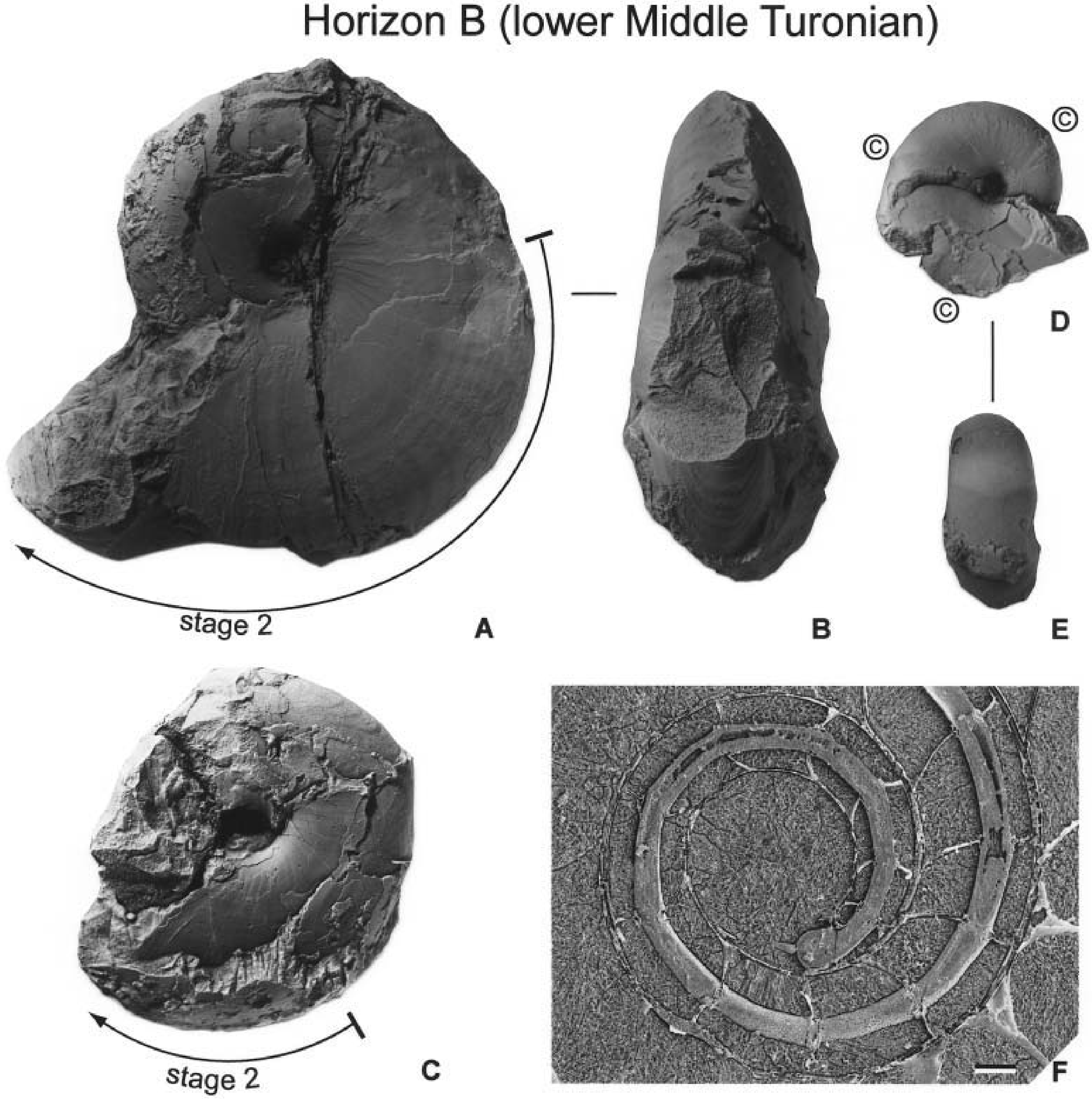

Figure 5. "*T. subcostatus*" collected from horizon B, lower Middle Turonian. **A, B.** KUM. MM. TN. 039. OT1035. **C.** KUM. MM. TN. 042. OT1034. **D, E.** KUM. MM. TN. 053. OT1035. **F.** KUM. MM. TN. 064. OT3051. A–C in natural size. D, E, ×3. F, scale bar = 0.1 mm. Abbreviations are the same as in Figure 4.

We reexamined the holotype and paratypes. Most of them are secondarily deformed adult shells, about 80–90 mm in diameter. The ribs show wide variation, and number 18–35 per half whorl in the subadult shell (about 50 mm diameter). The rib profile is rounded to sharp.

Some Lower and Middle Turonian specimens have been identified as *Damesites ainuanus*. However, they do not possess periodic constrictions which are diagnostic of *D. ainuanus* (e.g., Tanabe, 1983, pl. 71, fig. 2a), but have a tonguelike elevation at the midline of the venter like *T. subcostatus*. Therefore, those specimens are treated as "*Tragodesmoceroides subcostatus*" in this study.

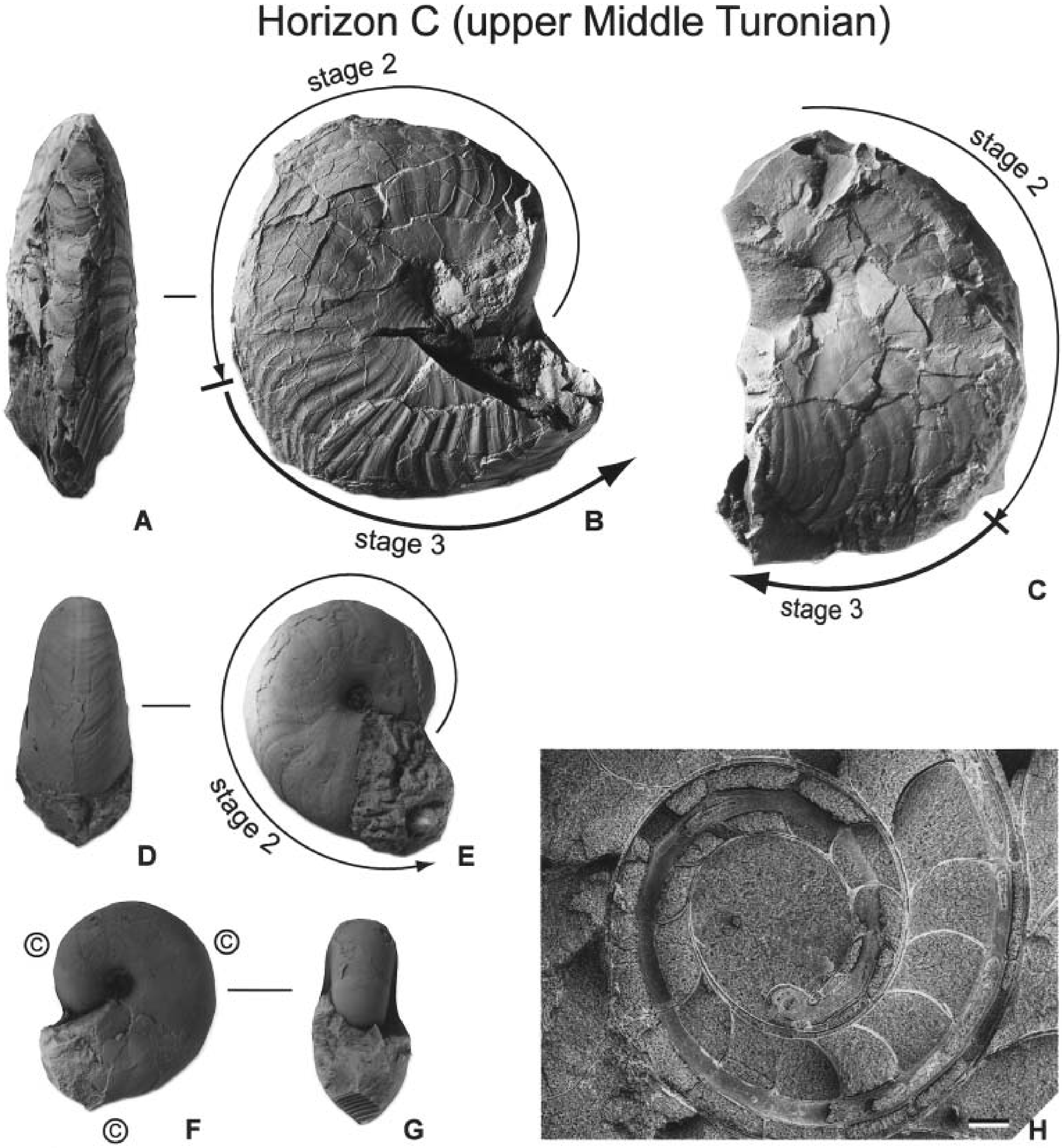

Figure 6. "*T. subcostatus*" collected from horizon C, upper Middle Turonian. **A, B.** KUM. MM. TN. 022. OT1027. **C.** KUM. MM. TN. 023. OT1020. **D, E.** KUM. MM. TN. 025. OT1020. **F, G.** KUM. MM. TN. 031. OT 1027. **H.** KUM. MM. TN. 037. OT 1020. A–E in natural size. F, G, ×3. H, scale bar = 0.1 mm. Abbreviations are the same as in Figure 4.

The early internal shell of *T. subcostatus* has been investigated in a few paleobiological works (Ohtsuka, 1986; Tanabe *et al.*, 2003). The early internal shell of "*T. subcostatus*" has a long and straight prosiphon, an elliptical caecum, and an initially central siphuncle (Figures 2E, F). These features are the grounds for the argument that the present species belongs to the Desmoceratoidea.

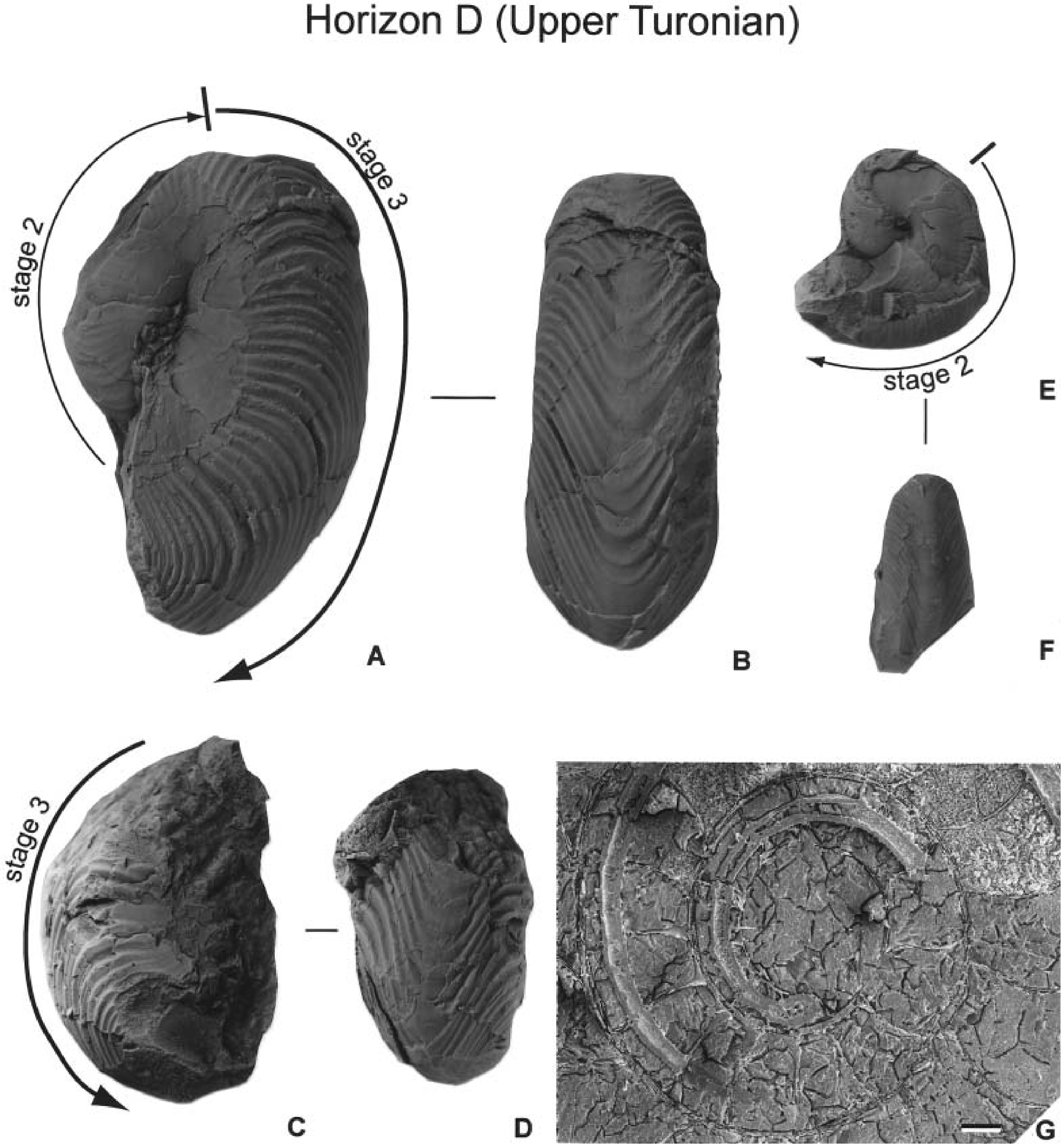

Figure 7. Holotype and topotypes of *Tragodesmoceroides subcostatus* collected from horizon D (T680, type locality of this species, Saku), Upper Turonian. **A, B.** holotype, UMUT. MM 6718 (same specimen as in Matsumoto, 1954, plate IV, 1a, 1b). **C, D.** KUM. MM. TN. 001, fragmented specimen. This specimen is not shown in Figure 11. **E, F.** KUM. MM. TN. 003. **G.** KUM. MM. TN. 020. A–F in natural size. G, scale bar = 0.1 mm.

Hirano *et al.* (1990) studied the growth ratio, breadth/height ratio, umbilical diameter, and "protoconch" (= initial chamber) width of *Tragodesmoceroides* from the Turonian. Based on such measurements, they also described another species of the present genus: *Tragodesmoceroides matsumotoi*. According to them, the whorl-growth ratio of *T. matsumotoi* differs from *T. subcostatus*, and the two species never cooccur. *T. matsumotoi* ranges from upper Middle to Upper Turonian (*Inoceramus hobetsensis hobetsensis* and *I. teshioensis* zones). After that, however, *T. matsumotoi* was not examined in detail because its type locality was submerged under the Obirashibeko Reservoir.

Stratigraphic setting

The Yezo Supergroup, Aptian to Maastrichian forearc basin deposits, is widely exposed in the meridional zone of Hokkaido and Sakhalin (Figure 1; Matsumoto, 1942b, 1954; Okada, 1983).

The Tappu area, located in northwest Hokkaido, has been known as one of the best outcropping areas of the supergroup (Figure 1; Yabe, 1904; Tanabe *et al.*, 1977; Maeda, 1987, 1991; Funaki and Hirano, 2004). The Yezo Supergroup of the area is represented mainly by offshore mudstones of various types (Maeda, 1987, 1993). The Turonian muddy facies is particularly fossiliferous (Tanaka, 1963; Tsushima *et al.*, 1958; Tanabe *et al.*, 1977). Based on Tanaka's stratigraphic division, the Turonian sequence yielding "*Tragodesmoceroides subcostatus*" is subdivided into three lithostratigraphic units, Mj-k, Ml-o and Ua units in upward sequence (Figure 3; Tsushima *et al.*, 1958; Tanaka, 1963; Maeda, 1987; Hirano *et al.*, 1990; Toshimitsu *et al.*, 1995). The Mj-k unit is composed of weakly bioturbated mudstone. Particularly, the lower part of this unit contains numerous *Planolites* isp. burrows (*Planolites* mudstone; Maeda, 1987; Kodama *et al.*, 2002). The Ml-o unit, which is stratigraphically equivalent to the Saku Formation (Matsumoto and Okada, 1973), is composed mainly of mottled mudstone and alternating beds of mudstone and sandstone. The mudstone is more intensely bioturbated than that in the underlying Mj-k unit. The Ua unit is composed of massive mudstone and very fine-grained sandy mudstone.

On the other hand, the type locality of *T. subcostatus* is located in the Saku area, north Hokkaido (loc. T680, Matsumoto, 1942b, pl. 12). The Cretaceous deposits of the area are also represented by an offshore muddy sequence (Matsumoto, 1942b; Nagao, 1962; Matsumoto and Okada, 1973), while the succession is much thinner than that of the Tappu area. The Turonian deposits are lithostratigraphically divided into the Sakugawa and Saku formations in upward sequence (Takahashi *et al.*, 2003). The stratigraphic level of the type locality of *T. subcostatus* (T680, Matsumoto, 1942b, pl. 12) is correlated to the uppermost part of the Saku Formation, which is composed of alternating beds of mottled mudstone and sandstone ranging from 3–60 cm thick.

Environmental interpretation

The Turonian sequence of the Tappu area is interpreted to have been deposited under an offshore environment. A Middle to Upper Turonian part with occasional turbiditic sandstone intercalations is correlated to the Saku Formation (Matsumoto and Okada, 1973), which represents an intermediate facies between shelf and slope basin.

Coarser-grained facies consisting of turbidites, slump deposits, and channel-fill deposits are common in the stratotype of the Saku Formation in the Saku area (Matsumoto and Okada, 1973; Takahashi and Mitsugi, 2002).

The equivalent section in the Tappu area seems to represent a much more offshore environment, because it is much finer-grained and about 1.5 times thicker than the Saku section.

Material and methods

Material

In addition to the holotype (Figures 7A, B, UMUT. MM6718) and the paratypes (UMUT. MM6719, UMUT. MM6723), more than 200 specimens collected from the Upper Cretaceous sequence in the Tappu and Saku areas were examined for precise biometric study. Of these, about 200 specimens were collected from the Lower to Upper Turonian deposits along the Obirashibe River and its tributaries in the Tappu area (Figure 1), and about 20 specimens from the type locality of *T. subcostatus* along the Abeshinai River in the Saku area (loc. T680; Matsumoto, 1942b; Figure 1). Most specimens cooccur with other ammonoids, inoceramids, and wood particles in calcareous nodules.

The holotype of *Tragodesmoceroides matsumotoi* (WEA103T, Waseda University) was also examined. However, *T. matsumotoi* is excluded from our discussion because its type locality is now submerged, so that detailed stratigraphic and paleoecologic data are unavailable.

Population samples of "*Tragodesmoceroides subcostatus*" were collected mainly from four stratigraphic levels (horizons A–D) as follows (Figure 3).

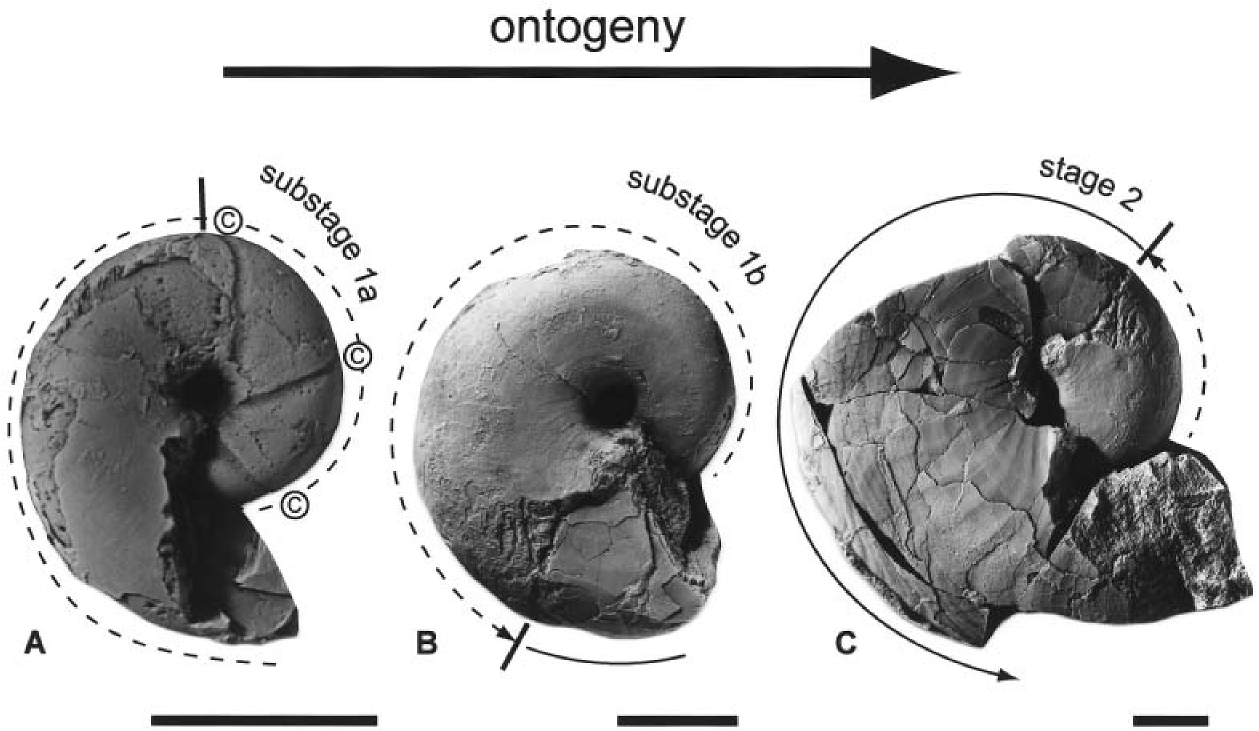

Figure 8. Shell surface ornament change of "*Tragodesmoceroides subcostatus*" through ontogeny. A–C are photos at different stages of the same specimen (KUM. MM. TN. 024) collected from OT 1020 (horizon C). Scale bars are 10 mm. Abbreviations are the same as in Figure 4.

Horizon A.—Lower part of the Mj-k unit (OT 1046) correlated to the *Inoceramus kamuy* Zone (Lower Turonian).

Horizon B.—Upper part of the Mj-k unit to lower part of the Ml-o unit (OT1032–1038, OT2001–2032) correlated to the main part of the *I. hobetsensis nonsulcatus* Zone (lower Middle Turonian).

Horizon C.—Upper Ml-o unit (OT1020–1028, 3031–3034) correlated to the uppermost part of the *I. hobetsensis nonsulcatus* Zone and *I. hobetsensis hobetsensis* Zone (upper Middle Turonian).

Horizon D.—Ua unit correlated to the *I. teshioensis* Zone (Upper Turonian).

Biostratigraphic schemes by Hirano *et al.* (1981), Matsumoto *et al.* (1991), Toshimitsu *et al.* (1995) and Matsumoto and Asai (1996) are adopted in this study.

Methods

Observation of early internal shells.—Fifteen specimens in total were carefully cut and longitudinally polished. The polished longitudinal section of each specimen was etched with 5% acetic acid for a few minutes. Ammonitella diameter and ammonitella angle (Figures 2E, F) were measured by means of a profile projector (Nikon model V-12B, magnification × 100). The other characteristics were observed by a scanning electron microscope (SEM, JOEL, JSM-6100).

We follow Ohtsuka (1986) and Landman *et al.* (1996) for technical terms and dimensions of the characters (Figures 2E, F). The whorl volution is expressed by π (= 180°) scale from the center of the initial chamber.

Observation of shell surface ornament.—In total 55 specimens were examined. Ontogenetic change of shell surface ornament from juvenile shells less than 10 mm diameter to adult shells over 80 mm diameter was observed under a binocular microscope and photographed (Figures 4–8).

Ontogenetic shell development

Early shell

The ammonitella and initial chamber (= "protoconch") of "*Tragodesmoceroides subcostatus*" show typical desmoceratoid features (Figures 2E, F, Ohtsuka, 1986; Tanabe *et al*., 2003), i.e., the elliptical caecum, and the long and straight prosiphon attached to the center of the caecum. The prosiphon is about 0.5 mm long, the caecum is about 0.4 mm long, the ammonitella angle is 320° and the ammonitella diameter is 0.88 mm on average. The siphuncle is located centrally in each camera in the first whorl from the initial chamber (= volution 0–2 π, Figures 4G, 5F, 6H, 7G). The initial chamber of "*T. subcostatus*" is an ellipsoidal shape, about 0.45 mm in diameter and 0.7 mm wide (Figures 9A, B). The siphuncle gradually shifts in position towards the venter. At the second whorl (approximately 1.5 mm in diameter), the siphuncle is settled at the ventralmost position (Figures 4G, 5F, 6H, 7G).

Whorl geometry

Whorl geometry of "*Tragodesmoceroides subcostatus*" changes with growth. Whorls of the present species become compressed and umbilicus/diameter ratio (U/D) decreases with growth (Figures 9C, D). Umbilical shoulders appear in the 3–4 π stage in cross section (about 1.4–2.0 mm diameter), and the desmoceratid umbilical break (Maeda, 1993, fig. 10) appears in the 5–6 π stage (2.7–4.0 mm diameter, Figures 9A, B).

After this stage, the whorl proportions of "*T. subcostatus*" become generally stable, although the breadth/height ratio (B/H) and umbilicus/diameter ratio (U/D) gradually decrease with growth (Figures 9C, D). At about 10 mm diameter (immature to middle growth stage), U/D is about 0.13, B/H is about 0.8 to 1.1. At 40 mm diameter, the subadult stage, U/D is about 0.08 and B/H is about 0.7 (Figures 9C, D). Roughly speaking, the shell becomes compressed and the umbilicus becomes narrower in the adult stage.

The venter is rounded throughout ontogeny. In some middle-sized and adult specimens, however, the venter become raised up and form a tonguelike elevation (Figures 4C, 6A, 7F, 7B). The tonguelike elevation differs from a true keel because the basal part of the elevation is extremely wide. It is about 1/2–1/3 of the whorl breadth.

Adult features and dimorphism

Like other desmoceratine ammonoids, "*Tragodesmoceroides subcostatus*" does not show remarkable adult features such as apertural modifications or abrupt change of body chamber shape and ornament (Kennedy and Cobann, 1976). Approximation of the last few septa has not yet been clarified because of a small sample number.

On the other hand, "*T. subcostatus*" never exceeds 100 mm in shell diameter even as an adult. The adult shell, about 70–90 mm diameter, has a strongly projected rostrum which is not developed in immature shells (Figures 5A, 5B, 5D, 5E, 6A, 6B, 6D, 6E, 6F, 6G, 7A, 7B, 7E, 7F). A shell size larger than 70 mm as well as development of the rostrum can be used for recognition of the adult stage in the present species.

Like other desmoceratines, "*T. subcostatus*" never shows dimorphic features. Adult shells are never lappeted. Large discrepancy of shell sizes within a species is not observable, unlike the kossmaticeratid *Yokoyamaoceras* belonging to the same superfamily Desmoceratoidea (Maeda, 1993).

Shell surface ornament

The shell surface ornament of "*Tragodesmoceroides subcostatus*" consists mainly of fine growth lines and sigmoid ribs. The modes of ribbing change with growth. The following three successive stages are observable in "*T. subcostatus*" specimens (Figure 10).

Stage 1 (*almost smooth, Figures 10A, 10B*).—This stage is almost smooth only with very fine growth lines. It is recognized in immature to middle-sized shells, about 5–15 mm whorl height (10–25 mm diameter).

Concave or slightly sigmoid fine growth lines are weakly convex on both flanks and moderately projected on the venter. They are very weak in relief on the shell surface, while the internal mold is smooth. The growth lines are very faint, particularly on the internal half of the flanks.

Stage 1 can be subdivided into two substages. The earlier substage 1a is represented by an almost smooth shell surface with desmoceratid-type constrictions (Figure 10A). The presence of sigmoidal or prorsiradiate constrictions numbering 3–6 per whorl is one of the diagnostic features of the desmoceratids (= desmoceratid-type constriction: Figures 4E, 5D, 6F, 8A). Desmoceratid-type constrictions are thicker in the internal mold and each accompanies a collared rib. These are well discernible on internal molds of the shell. Each constriction runs somewhat obliquely to adjacent growth lines. The latter never cross but converge on the former. Substage 1a is recognized in immature shells, about 5–10 mm whorl height (approx. 10–18 mm diameter).

The subsequent substage 1b is covered only with fine growth lines without desmoceratid-type constrictions (Figure 10B). This substage appears in the later half of stage 1, at about 8–15 mm whorl height (approx. 15–25 mm diameter).

Stage 2 (*weak ribbing, Figure 10C*).—This stage is characterized by weak ribbing on the shell surface. This stage follows stage 1, and appears in middle to

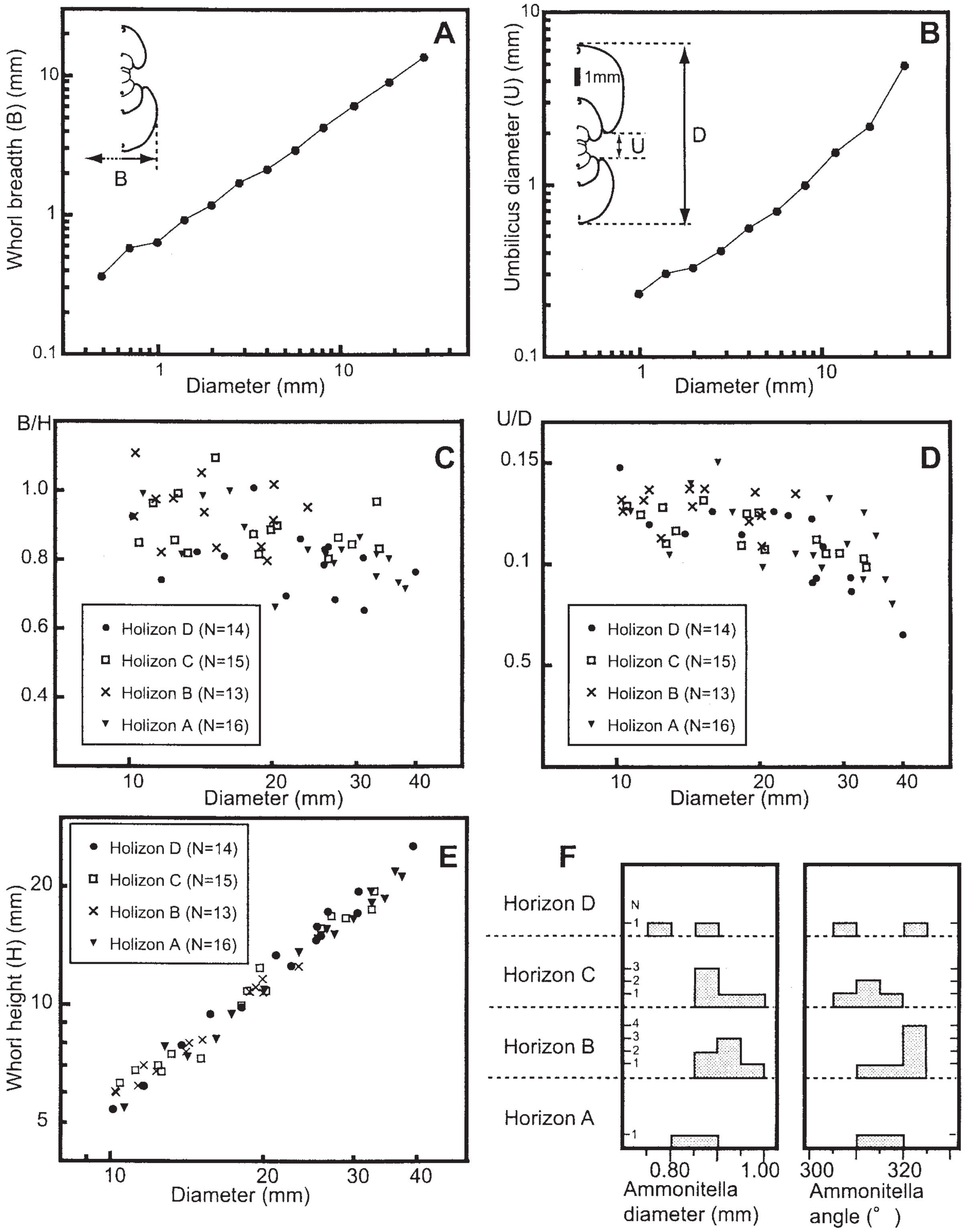

Figure 9. Measurements of "*Tragodesmoceroides subcostatus*" collected from four horizons. **A.** Whorl diameter/breadth change with ontogeny in specimen KUM. MM. TN. 009. **B.** Whorl diameter/umbilicus diameter change with ontogeny in specimen KUM. MM. TN. 009. **C.** Whorl breadth/Height ratio (B/H) in relation to shell diameter for juvenile to near-adult stage. **D.** Umbilicus/Diameter ratio (U/D) in relation to shell diameter for juvenile to near-adult stage. **E.** Whorl diameter/Whorl height relationship. **F.** Ammonitella diameter and angles from horizon A–D. All parameters do not show choronologically significant changes.

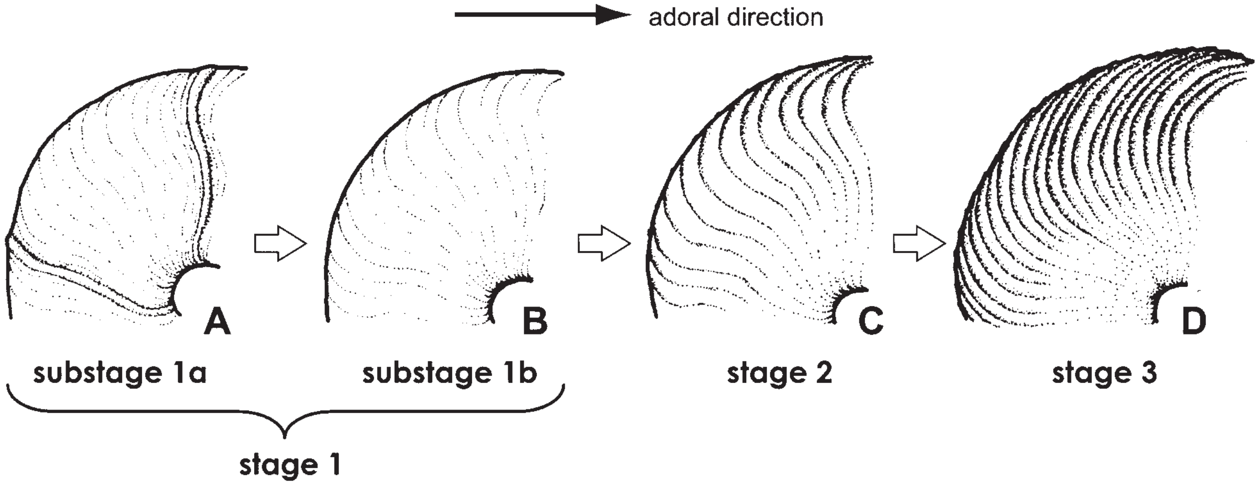

Figure 10. Schematic diagrams illustrating typical shell surface ornament stages and substages in "*Tragodesmoceroides subcostatus*". **A.** substage 1a; Desmoceratid-type constriction. **B.** substage 1b; Almost smooth with fine growth line. **C.** Stage 2; Weak ribbing. **D.** Stage 3; Coarse ribbing (diagnostic feature). Not to scale. A black arrow indicates adoral direction.

adult stages, at about 20 mm whorl height (approx. 33 mm diameter). The change from stage 1 to stage 2 is rather abrupt (Figures 4A, 4D, 5A, 5C, 7E).

The weak ribs are moderately interspaced, sigmoid, weakly convex on both flanks, and moderately or strongly projected forward on the venter-like rostrum. Number of ribs varies from 2–9/30° of whorl volution. The rib profile is rounded to sharp. These ribs run parallel to fine growth lines. The ribs are most elevated on the ventrolateral shoulders and the venter. Elevation of the ribs weakens at the umbilical shoulder. The internal mold shows the same relief as the shell surface. In a few specimens, the weak ribs are associated with faint longitudinal striations (Figures 5A, 8C).

Stage 3 (*coarse ribbing*).—This stage is characterized by sharp, narrowly interspaced coarse ribbing. This stage follows stage 2 (weak ribbing), and appears in subadult and adult shells, at about 30 mm whorl height (approx. 45 mm diameter). The transition from stage 2 to this stage is rather gradual (Figures 6B, 6C, 7A).

The coarse ribs are narrowly interspaced, sigmoid, weakly convex on both flanks, strongly projected forward on the venter, and number 4–13/30° of whorl volution. The rib profile is flat-topped to sharp. The coarse ribs run parallel to growth lines and weak ribs. They are most elevated on ventrolateral shoulders and the venter. In some specimens, the coarse ribs are associated with longitudinal striations on the external half of the shell like the weak ribs in stage 2.

Besides discrimination by visual rib intensity, the coarse ribs in stage 3 are different from the weak ribs in stage 2 in interspace and height of ribs. The interspace of the former ones is narrower than that of the latter ones. The number of weak ribs per 30° of whorl volution is 2–9, while that of coarse ribs is 4–13. In general, in the coarse ribs of stage 3, the rib height/whorl height ratio exceeds 0.0005 at the ventrolateral or ventral profile in which the ribs are most elevated. In contrast, in the weak ribs of stage 2, the ratio is less than 0.0005.

The appearance order of the shell surface ornament is stable (stages 1a–1b–2–3) in all specimens examined.

Chronological changes of shell morphology

The examined specimens of "*Tragodesmoceroides subcostatus*" generally share the same ontogenetic shell developmental patterns in most morphologic characters. Likewise, successive order of shell ornament stages (substages 1a,b – stage 2 – stage 3) is also very stable throughout the Turonian. However, precise stratigraphic observation reveals that the shifting-timing of shell surface ornament stages varies by levels.

Early internal shell morphology

Caecum and prosiphon shapes are almost invariable in every specimen throughout the Turonian. The ammonitella diameter and ammonitella angle both exhibit some extent of variation. The ammonitella diameter ranges from 0.79–0.96 mm and ammonitella angle ranges from 310–325° in horizons A–D. The ranges of variation almost overlap in most samples, and there is no significant change throughout the Turonian sequence of the Tappu area (Figure 9F).

Whorl geometry

B/H and U/D ratios are not so variable, and stratigraphic tendencies are not discernible. The ontogenetic variation of both characters closely overlap in most samples (Figures 9C, D). The mean B/H ratio of the middle-sized specimens, about 20 mm diameter, is about 0.85 in horizon A, 0.9 in horizon B, 0.9 in horizon C, and 0.8 in horizon D (Figure 9C). The mean U/D ratio of the same-sized specimens is about 0.12 in horizon A, 0.13 in horizon B, 0.12 in horizon C and 0.12 in horizon D. The height/diameter ratio is stable throughout samples from horizons A–D (Figure 9E).

Shell surface ornament

Shell surface ornament of "*Tragodesmoceroides subcostatus*" changes with growth, and stages 1–3 appear successively (Figures 4A, 4D, 5A, 5C, 6B, 6C, 6E, 7A, 7C, 7E, 8). However, the shifting-timing between stages varies chronologically. This study precisely examines the shifting–timing among four population samples successively collected from the Turonian sequence of the Tappu and Saku areas (horizons A–D, Figure 11).

The measured shifting-points from substage 1a to stage 3 via substage 1b and stage 2 are plotted in Figure 11.

Substage 1a changes to substage 1b at 8–10 mm whorl height (approx. 15–18 mm diameter) throughout the Turonian (horizons A–D). It is difficult to determine the mean and standard deviation of whorl height in this substage because the interspace between constrictions is wide, but the shifting-timing of substages 1a–1b is stable throughout the Turonian sequence.

On the other hand, stage 2 appears approximately at 17 mm whorl height (approx. 30 mm diameter) in horizon A, at 30 mm whorl height (approx. 55 mm diameter) in horizon B, at 13 mm whorl height (approx. 24 mm diameter) in horizon C, and at 12 mm whorl height (approx. 22 mm diameter) in horizon D. Particularly in horizon B, the appearance of stage 2 is delayed relative to the other horizons. Stage 2 appears ontogenetically at smaller diameters in upward sequence.

The most significant difference in the ontogenetic appearance of growth stages in the "*T. subcostatus*" lineage is the appearance of stage 3. This stage is recognized only in horizons C and D (upper Middle to Upper Turonian) and appears at 25 mm whorl height (approx. 40 mm diameter).

To sum up, the stratigraphic change of the shifting-timing from substage 1a to substage 1b is obscure in the Turonian sequence. In contrast, the ontogenetic appearance of stage 2 becomes earlier toward the top of the Turonian sequence, particularly in horizons C and D (Figure 11). Only in horizons C and D does the last shell surface ornament stage (stage 3) appear.

Besides the Tappu and Saku areas, stratigraphic occurrence and the chronologic trends of "*Tragodesmoceroides subcostatus*" were examined, e.g., in the Kamiashibetsu and Oyubari areas. Although stratigraphic records are imperfect, "*T. subcostatus*" also shows the same chronologic trend in other areas in Hokkaido.

Discussion

Interpretation of the holotype

The holotype of *Tragodesmoceroides subcostatus* from the Upper Turonian (*Inoceramus teshioensis* Zone) exhibits diagnostic sharp and narrowly interspaced coarse ribbing (stage 3, Figures 7A, 7B). However, individuals having such coarse ribs at the last half whorl to last whorl (stage 3) occur rarely. Except for shell surface ornament, other morphologic characters, such as B/H, U/D and so on are similar among individuals from different horizons (Figures 9A–E). Early internal shell structures of a *T. subcostatus* specimen collected from the type locality are very similar to those of 13 specimens from lower stratigraphic levels (horizons A–C; Figures 4G, 5F, 6H, 7G, 9F).

Precise observation reveals that the coarse-ribbed individuals showing stage 3 restrictedly occur in horizons C and D (Figure 11). All subadult and adult shells from the type locality, including paratypes and topotypes over 30 mm in whorl height, are ornamented with sharp and coarse ribs of stage 3 as in the holotype (Figures 7A–D, 11).

On the other hand, the diagnostic sharp and coarse ribbing of stage 3 never appear even in the large adult shells from the lower levels, i.e., horizons A and B (Figures 4A–D, 5A–C, 11). In lower stratigraphic levels, most specimens of "*T. subcostatus*" are represented by the less ornamented morphotype without stage 3.

As described above, the ontogenetic appearance of shell surface ornament stages in "*T. subcostatus*" tends to be earlier with time. The change is gradual, showing fairly wide extent of individual variation at a

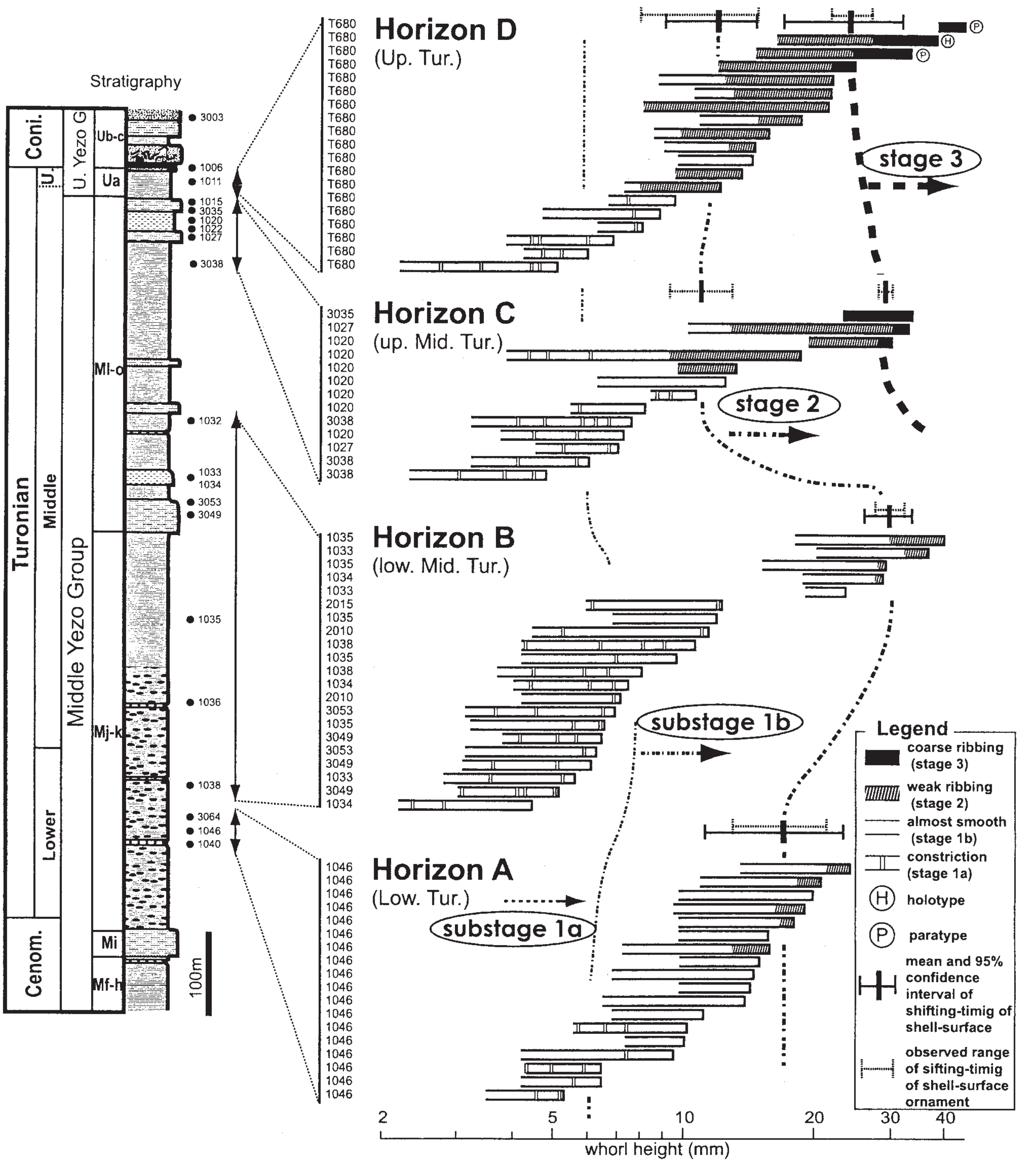

Figure 11. Schematic diagram showing ontogenetic shell-surface ornament change (bars, left to right showing ontogeny) and the chronological trends (lower to upper) of *Tragodesmoceroides subcostatus*. Approximate whorl diameter is presumed from Figure 9E. Prefix: OT—is abbreviated the locality numbers (excludes loc. T680 in Saku area).

given horizon (Figure 11). Therefore, we interpret *T. subcostatus* as a single evolutionary species.

These lines of evidence suggest that *T. subcostatus* shows a clear chronological trend for ontogenetic change of shell surface ornament and that the holotype of *T. subcostatus* represents the Late Turonian morphotype in this evolutionary species. In other words, the holotype can be regarded as a peramorphic endmember in the Upper Turonian (see Landman, 1988, McKinney and McNamara, 1991).

The absence of stage 3 in the Lower and lower Middle Turonian populations has caused great taxonomic discrepancy between the definitions and morphology of the actual specimens. The specific and generic diagnosis needs to be revised. The revised diagnosis is described in the appendix.

Significance in desmoceratine lineage

Ontogenetic change of shell surface ornament common in other ammonoids (i.e., *Gaudryceras tenuiliratum*; Hirano, 1975, Collognoniceratids; Tanabe, 1993, Harada and Tanabe, 2004, Kossmaticeratids; Maeda, 1993, *Polyptychoceras pseudogaultinum*; Okamoto and Shibata, 1996, baculitids; Tsujino *et al*., 2003, etc.). Shell ornament has proven to be one of the most important characters at the lower taxonomic levels.

In desmoceratine ammonoids, the shell surface ornament has been utilized as a key to define genera and species. However, the descriptions of ontogenetic change of shell surface ornament were insufficient in previous work on the desmoceratids. This paper covers this weak point of previous "typological" studies based on small samples, and shows the modes of shell surface ornament change in "*Tragodesmoceroides subcostatus*" with growth.

The ontogenetic change of shell surface ornament with growth will be a useful character by which to reexamine the systematics of several desmoceratine ammonoids whose taxonomic position are still unclear.

Conclusion

The evolutionary pattern in the Turonian desmoceratine species, "*Tragodesmoceroides subcostatus*" Matsumoto, 1942 has been examined on the basis of large samples from the Tappu and Saku areas, Hokkaido.

Shell surface ornament of this species consists of four stages and substages. They are almost smooth with desmoceratid-type constrictions (substage 1a), almost smooth (substage 1b), weak ribbing (stage 2) and coarse ribbing (stage 3). The ontogenetic appearance of shell surface ornament stages is stable throughout Turonian time, while the shifting-timing to the next stage becomes earlier upward. These lines of evidence suggest that the coarse-ribbed holotype showing stage 3 ornament merely represents a peramorphic endmember which occurs only in the Upper Turonian.

Thus, *T. subcostatus* is characterized by a heterochronic change of ribbing (acceleration; McKinney and McNamara, 1991) and should be taxonomically revised as an evolutionary species.

Acknowledgments

We thank Kazushige Tanabe (University of Tokyo), Neil H. Landman (American Museum of Natural History) and Hajime Naruse (Kyoto University) for critical reading of the manuscript and helpful comments. We thank Hiromichi Hirano (Waseda University) and Takenori Sasaki (the University Museum, the University of Tokyo) for their kind assistance in observation of type specimens. Thanks are due to Norihiko Sakakura, Takeshi Matsunaga (Kyoto University), Yasuyuki Tsujino (Tokushima Prefectural Museum) and Yoshinori Hikida (Nakagawa Museum of Natural History) for their constructive advice. The Tappu Forestry Office is thanked for their cooperation in the field, and Narita Lodging House, Murakami Lodging house and Nakagawa Ecomuseum Center for their kind hospitality during field work.

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Appendix

Systematic paleontology
Order Ammonoidea Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Desmoceratoidea Zittel, 1895
Subfamily Desmoceratinae Zittel, 1895
Genus ***Tragodesmoceroides*** Matsumoto, 1942

Revised diagnosis.—Craterlike umbilicus, venter tending to be raised in some specimens. Coarse sigmoidal ribs may appear in some subadult and adult shells, otherwise the shell surface is smooth.

Tragodesmoceroides subcostatus Matsumoto, 1942

Figures 4A–G, 5A–F, 6A–H, 7A–G, 8A–C

Tragodesmoceroides subcostatus Matsumoto, 1942a, p. 28, fig. 1d; Matsumoto, 1954, pl. 4, figs. 1–6; Matsumoto, 1959, pl. 9d; Hirano *et al*., 1990, p. 395, figs. 1–15.

Damesites ainuanus Matsumoto, 1957, Tanabe, 1983, pl. 71, fig. 2a.

Besides the above, the following studies noted the occurrence of *Tragodesmoceroides subcostatus* without giving illustrations; Tsushima *et al*. (1958), Tanaka (1963), Hirano *et al*. (1977), Tanabe *et al*. (1977), Funaki and Hirano (2004).

Diagnosis.—As for genus.

Description.—Caecum is elliptical in shape. Prosiphon is attached to center of caecum. Initial chamber is an ellipsoidal shape, about 0.45 mm in diameter and 0.7 mm wide. Siphuncle is located centrally in each camera in first whorl, shifts in position towards venter and settles at ventralmost position.

Whorl becomes compressed and umbilicus/diameter ratio decreases with growth. Umbilical shoulder appears in 3–4 π stage and desmoceratid umbilical break appears in 5–6 π stage.

The adult is about 6–7 π volutions, 70–90 mm diameter. In the subadult-adult, B/H ratio is 0.7, U/D ratio is 0.08. In some subadult-adult specimens a tonguelike elevation appears at the venter.

Shell surface ornament changes with growth. The surface is almost smooth or without desmoceratid-type constrictions in the early substages 1a and 1b (ca. 10–25 mm diameter), weak ribs develop in the subsequent stage 2 (ca. 10–25 mm diameter), and coarse ribs in the mature stage 3 (ca. 45 mm diameter).

Specimens having coarse ribs (stage 3) restrictedly occur in the upper part of the Turonian.

Comparison.—*Tragodesmoceroides subcostatus* resembles *T. matsumotoi* in whorl shape as well as shell surface ornament. In the latter species, however, growth rates of the whorl radius and the whorl breadth in relation to the whorl volution are much smaller than those of the present species (Hirano *et al*., 1990).

This species resembles Cenomanian *Desmoceras* (*Pseudouhligella*) *japonicum* in many morphologic aspects. In shell surface ornament, both species share a similar smooth stage with periodic constrictions during processes of ontogenetic shell development (stage 1a: see previous chapters). A few fully grown shells of *D.* (*P.*) *japonicum* show weak ribbing on the ventral periphery, which resembles stage 2 of *T. subcostatus*. However, sharp and coarse sigmoidal ribbing (stage 3) never appears in *D.* (*P.*) *japonicum. T. subcostatus* has a narrow craterlike umbilicus throughout ontogeny (U/D = 8%), while the umbilicus of *D.* (*P.*) *japonicum* is much wider in the adult stage (U/D = 15%).

As discussed above, coarse sigmoidal ribbing (stage 3), which has been regarded as the diagnostic feature of *T. subcostatus*, does not always appear in all adult shells of the present species (Figures 4A, 4D, 5A, 5C, 8C). Therefore, the morphotype that lacks the coarse-ribbed stage (stage 3) could have been misleadingly identified as *Desmoceras* species. Close reexamination of Turonian desmoceratines are required to determine the taxonomic relationships among *T. subcostatus* and other desmoceratine species.

T. subcostatus also resembles Santonian *Damesites damesi* both in whorl shape and shell surface ornament. Both species share smooth and subsequent weakly ribbed stages (stages 1 and 2) during ontogenetic shell development. Typical adult shells of *D. damesi* exhibit sharp, coarse sigmoidal ribbing, which is similar to stage 3 of *T. subcostatus* (Matsumoto, 1954, pl. 5, figs. 1a–d; Nishimura, 2003, figs. 1C–F). Unlike *D. damesi*, however, *T. subcostatus* never has a distinct keel, although a broad elevation on the ventral periphery may sometimes appear.

The Upper Turonian species, *Damesites ainuanus* resembles *T. subcostatus*, particularly in the juvenile shell. Unlike *T. subcostatus*, however, *D. ainuanus* has a keel and desmoceratid-type constrictions remain even in the adult stage (Matsumoto, 1957).

The Cenomanian species *Damesites laticarinatus* differs from *T. subcostatus* in having a keel. However, the specific identity of *D. laticarinatus* is still obscure, because this species is monotypic and represented only by a fragmental holotype (Saito and Matsumoto, 1956).