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On the ontogeny of *Damesites* MATSUMOTO (Ammonoidea, Upper Cretaceous)

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With 2 figures and 1 table in the text

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Abstract: The complete ontogeny of the desmoceratid *Damesites sugata* (FORBES) is investigated for the first time. The appearance of a ventral keel, the suture line with a deep sutural lobe $S = U_{1v}$ and individual lobes U_3 and U_{1d} are the characteristic developmental features of the genus *Damesites* MATSUMOTO.

Zusammenfassung: Die Ontogenese des Desmoceraten *Damesites sugata* (FORBES) wird erstmals beschrieben. Die Bildung eines Ventralkiels und die Lobenlinie mit einem tiefen $U_{1v} = S$ und selbständigen Loben U_3 und U_{1d} sind für *Damesites* MATSUMOTO typisch.

1. Introduction

The genus *Damesites* occurs in the Upper Cretaceous from Cenomanian to Maastrichtian with a maximum distribution in the Indo-Pacific Realm. The following succession of species is best known from Japan (MATSUMOTO 1959):

Damesites laticarinatus SAITO & MATSUMOTO, 1956, Cenomanian
D. ainuanus MATSUMOTO, 1957, Turonian
D. damesi (JIMBO, 1894), Coniacian-Lower Santonian
D. semicostatus MATSUMOTO, 1942, Coniacian–Lower Campanian
D. sugata (FORBES, 1846), Santonian–Campanian
D. hetonaiensis MATSUMOTO, 1942, Maastrichtian.

The Californian specimens, which were described by ANDERSON (1958) under the generic name of *Kotoceras*, are identical with previously described species of *Damesites*. The generic name *Kotoceras* was first given by YABE (1927) to a group of strongly keeled desmoceratids from the Upper Cretaceous of Southern India and Japan. Later, MATSUMOTO (1942) established the new genus *Damesites* with *Desmoceras damesi* JIMBO, 1894, as type species. *Kotoceras*, YABE 1927 (non *Kotoceras* KOBAYASHI, 1934) was

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then included as objective synonym. Nomenclatural problems of the generic name were discussed by WRIGHT & MATSUMOTO (1954) and WRIGHT (1957). As a consequence, the generic name *Damesites* was preserved and used for involute and moderately compressed desmoceratids with gently inflated flanks, small umbilicus, moderately broad ventral keel without accompanying furrows, and with prorsiradiate constrictions which are only slightly biconcave on the flanks and remarkably projected on the venter (COLLIGNON 1966).

Later on, data about the occurrence of *Damesites* in the Tethyan Realm were published (HOWARTH 1968; BEURLEN 1970; IMMEL et al. 1981, 1982; MARTINEZ 1982; COLLIGNON 1983). According to HAGGART (1989), some species from the Tethyan Realm are synonymous with Indo-Pacific taxa.

All authors who studied *Damesites* paid attention to the high morphologic variability comparable with that in many other desmoceratids. The suture ontogeny of *Damesites damesi* (JIMBO) was studied by MATSUMOTO (1954, p. 270, fig. 11), and later corrected by SCHINDEWOLF (1966, p. 608, fig. 372). The reason for a contradictory interpretation of MATSUMOTO's figure was the lack of important stages of suture ontogeny. This is obvious in comparing MATSUMOTO's figure with Figure 2. Here, the description and illustrations of the morphogeny are given for the somewhat younger *Damesites sugata* (FORBES).

All studied specimens were collected from the Upper Santonian/Lower Campanian strata of the Naiba Valley, southern Sakhalin, and are deposited in the North-Eastern Interdisciplinary Scientific Research Institute, Magadan (NEIM) and in the Geologisch-Paläontologisches Institut, Tübingen (GPIT).

2. Morphogeny of *Damesites sugata* (FORBES)

The bulk of the studied material consists of well-preserved shells which were extracted from the limestone concretions occurring commonly in fine-grained sandstones and siltstones of the upper member of the Bykovskaya Formation in its type area. The fossiliferous concretion layers are reiterated every 1,2–1,8 metres. About one hundred specimens were investigated visually, by microscope in median and cross sections, and using the method of suture ontogeny.

2.1 Observations

The protoconch is round in median section (Fig. 1C), has a diameter of 0.30–0.32 mm, and is 0.56–0.61 mm wide. The caecum is small and measures 0.08 mm in cross section. There are 10 septa (starting from the proseptum) up to the primary constriction (Ammonitella stage), which is situated at about 310 degrees from the proseptum. At all post-embrionic

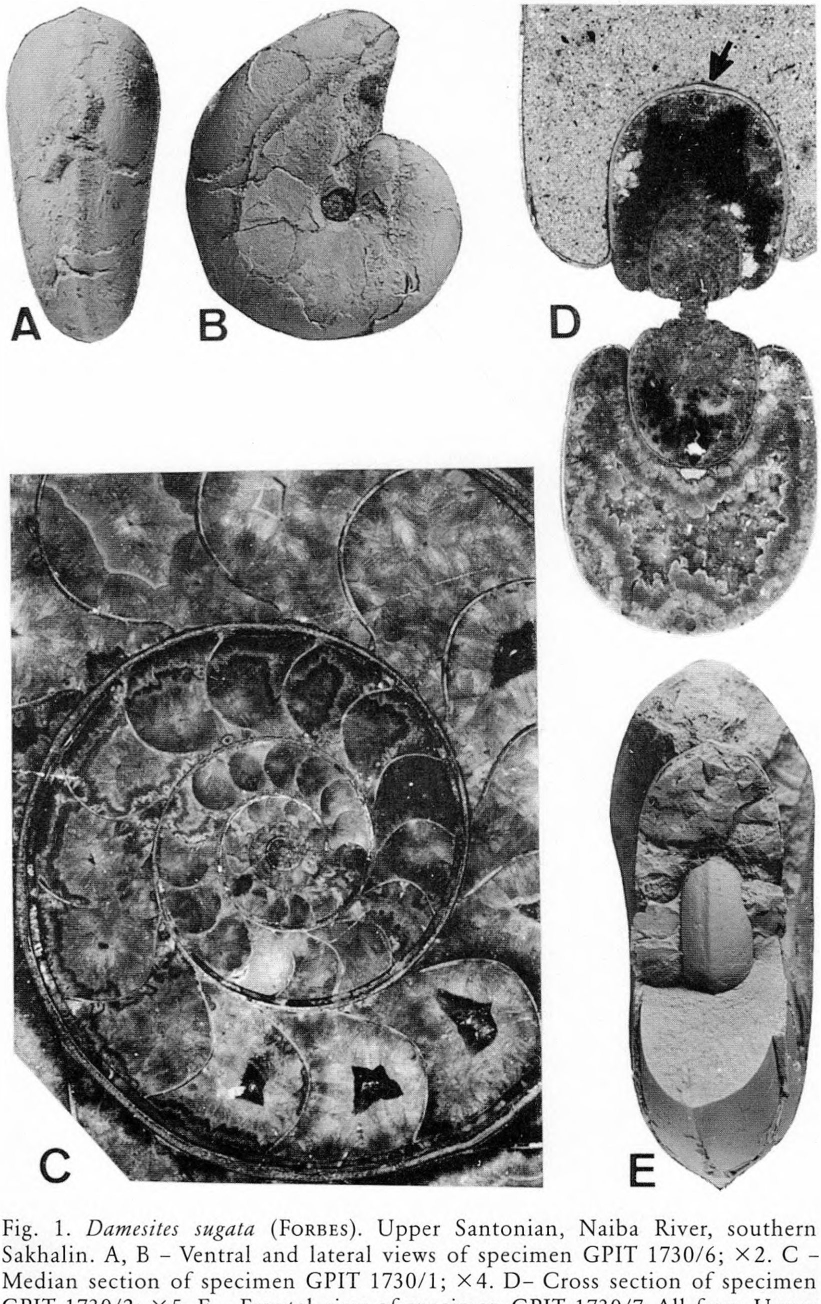


Fig. 1. *Damesites sugata* (Forbes). Upper Santonian, Naiba River, southern Sakhalin. A, B – Ventral and lateral views of specimen GPIT 1730/6; ×2. C – Median section of specimen GPIT 1730/1; ×4. D– Cross section of specimen GPIT 1730/2; ×5. E – Frontal view of specimen GPIT 1730/7. All from Upper Santonian, Naiba River, Southern Sakhalin.

Table 1. Allometrical tendency of shell growth of *Damesites sugata* (FORBES).

Growth stage	Size of specimens in mm					P*	dP
	1730/1	1730/2	1730/3	1730/4	1730/5		
Protoconch	0,32	0,32	0,32	0,31	0,30		
Ammonitella	0,73	0,72	0,73	0,72	0,70		
Whorls:							
second	1,40	1,40	1,39	1,39	1.36	1,928	+0,027
third	2,73	2,74	2,72	2,71	2,67	1,955	+0,101
fourth	5,60	5,64	5,60	5,55	5,51	2,056	-0,055
fifth	11,23	11,27	11,17	11,10	11,05	2,001	-0,088
sixth	21,52	21,64	21,35	21,17	21,13	1,913	

*P – coefficient of diameter increase (average)
$P = D_n - D_{n-1}$ (with D – diameter, n – whorl number)
$dP = P_n - P_{n-1}$

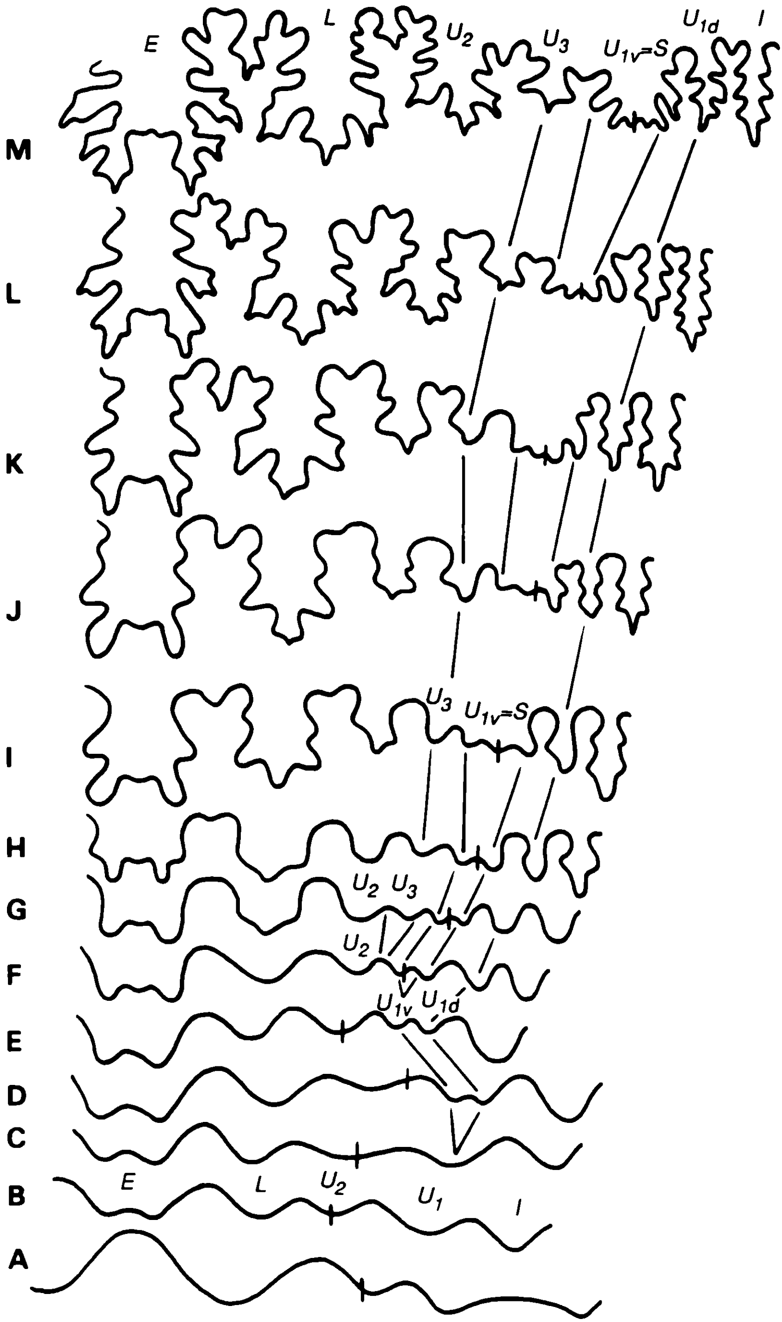
stages, the shell grows allometrically (Table 1). At first, there is a positive gradient of the coefficient P up to the third whorl. Thereafter the diameter increases moderately. At the beginning of the fourth whorl the gradient of the coefficient P is negative.

In cross-section (Fig. 1D), a ventral keel develops at the fifth whorl. The thickness of shell layers increases on the ventral side (ibidem, indicated by arrow). It is interesting that constrictions become indistinct at this stage. Thus, the intermediate growth stage, 4th to 6th whorl, is characterized by a slowdown in the increase of the diameter, a weakening of constrictions and the formation of a ventral keel (Figs. 1A, 1B). At the adult growth stage, 7th to 9th whorl, the keel is moderately strong (Fig. 1E) and the constrictions, 5–7 per whorl, are distinct and projected forward on the venter. The lirae are biconcave on the flanks and likewise strongly projected on the venter.

2.2 Suture line

The suture ontogeny is in accordance with that of all desmoceratids, but has some particular features (Fig. 2): The lateral lobe *L* is shorter than the ventral lobe *E* during all stages of ontogeny. The two first "metalobes"

Fig. 2. Suture line ontogeny of *Damesites sugata* (FORBES), specimen NEIM 22s/1. Lower Campanian, Naiba River, southern Sakhalin. A-F – 1st, 2nd, 5th, 7th, 10th (primary constriction) and 15th suture lines (1,3 whorls), ×50; G–I – 21st (1,7 whorls), 24th (2,0 whorls) and 29th suture lines (2,4 whorls), ×35; J–K – 33rd (2,7 whorls) and 37th suture lines (3,0 whorls), ×20; L – 44th suture line (3,5 whorls), ×15; M – 52nd suture line (4,0 whorls), ×8.


E
L
U2
U3
U1v=S
U1d
I
M
L
K
J
U3
U1v=S
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F
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in U_1 occur early in ontogeny (Fig. 2D), while the lobe U_2 remains situated on or near the umbilical seam, up to the 7th suture line. At the 21st suture line a new element, U_3, is inserted between U_2 and U_{1vv} (Fig. 2G). In the adult, there are 5 to 7 incisions between the lateral lobe L and the umbilical seam. The deeply suspending sutural lobe is formed by the lobe U_{1v} in the following way $U_1 \rightarrow U_{1v}U_{1d} \rightarrow U_{1vv}U_{1vd}U_{1d} \rightarrow U_{1v} = SU_{1d}$ (Figs. 2 I–M). The adult suture formula is: $ELU_2U_3U_{1v} = SU_{1d}I$.

2.3 Comparison with *Damesites damesi* (Jimbo 1894)

The specimens of *D. sugata* are more compressed than typical forms of *D. damesi* and have a weaker keel and shallower constrictions, which are indistinct at the intermediate growth stage. The suture line of *D. sugata* is characterized by more compressed lobes and saddles at the adult growth stage, the umbilical suture line is not suspending (cf. Matsumoto 1954).

Conclusions

In the family Desmoceratidae Zittel, 1895, most genera are characterized by shells without a ventral keel and by a suture ontogeny with a deeply suspending sutural lobe S. For the time being, there is no unanimity about the interpretation of the sutural lobe S. While Schindewolf (1966, figs. 370–392) and Wiedmann (1966, figs. 14–19) favoured a suture formula $ELU_2U_3U_4 = SU_{1v}U_{1d}I$, Mikhailova (1983, figs. 77–80) preferred an adult suture formula $ELU2U_{1v} = SU_{1d}I$ (transferred to German terminology). The genus *Damesites* Matsumoto exhibits a similar type of individual development. However, the appearance of a ventral keel, the formation of a suture line with a deeply suspending sutural lobe $S = U_{1v}$ and the individualization of the lobes U_3 and U_{1d} are different from typical desmoceratids. Morphometric data show that the formation of shell and sculpture features was intensive at an early stage, slow at an intermediate stage and moderate at the adult growth stage. The fine lirae are projected forward on the venter during the whole ontogeny. Especially in this feature juvenile specimens of *Damesites* having not yet established the distinctive keel differ from morphologically similar small forms of *Desmophyllites*. In the latter, the lirae form a rounded ventral sinus, there are more septa per whorl, the lateral lobe L is deeper than E, and much more incicions appear between L and the umbilical seam at the adult stage. *Damesites* differs from *Desmoceras* (*Pseudouhligella*), which was the possible ancestor, by the ventral keel and a suture line with short lateral lobe L, $U_{1v} = S$ and individualized lobes U_3 *and* U_{1d}.

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