Campanian (Late Cretaceous) nautiloids from Sakhalin, Far East Russia

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Three nautiloid taxa, *Cymatoceras pseudoatlas* (Yabe and Shimizu, 1924b), *C.* cf. *bifidum* Shimansky, 1975, and *C.* cf. *honmai* Matsumoto and Miyauchi, 1983, are recorded from the Campanian of Sakhalin, Far East Russia. These are the first biostratigraphically well dated nautiloids from Sakhalin, which show close affinities to nautiloid faunas from Japan (Hokkaido), the two areas having formed part of a southerly palaeobiogeographical subprovince of the North Pacific Province. Possible relationships between shell form/ornament and preferred habitats of Late Cretaceous nautiloids are discussed. Coarsely ribbed ("cymatoceratid"), depressed nautiloids seem to predominate in nearshore environments. This may be regarded as an adaptive response to increasing predation pressure by durophages, especially in shallow water settings, which may have triggered the development of defensive morphologies (i.e., ornamented, predation-resistant shells) in Cretaceous shallow-water nautiloids.

Key words: Nautiloidea, *Cymatoceras*, Cretaceous, Campanian, Russia, Sakhalin.

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Introduction

Unlike ammonites, Cretaceous nautiloids are a poorly studied invertebrate group. Usually, data on these cephalopods are dispersed in papers dealing mainly with ammonites and the most recent, comprehensive accounts are those of Wiedmann (1960) and Shimansky (1975). Kennedy (2002) presented a brief summary of British Chalk nautiloids. As a result, the phylogeny and taxonomy of the group are still poorly understood. These deficiencies are partly also related to the fact that nautiloids are relatively rare fossils in many formations (e.g., Kennedy 2002) and show only few taxonomically significant characters, such as suture and embryonic shell. Convergences further complicate the situation.

The aim of the present paper is to document and systematically describe a biostratigraphically well-constrained Campanian nautiloid faunule from Sakhalin, Far East Russia (Pacific Realm). In contrast to Santonian–Maastrichtian ammonites from this region (e.g., Matsumoto 1988, 1995; Yazykova 1994, 1996, 2002; Alabushev and Wiedmann 1997; Yazykova et al. 2002), nautiloids have received little attention and only a few specimens have been described or mentioned from Sakhalin so far. Yabe and Shimizu (1924a: 6) first recorded (but did not figure) a nautiloid find from the "Cape de la Jonquière Group" (i.e., Santonian–Campanian Zhonkier Formation of central Sakhalin) from the "*Inoceramus schmidti* beds" (lower Upper Campanian). Shimizu (1929: 910) stated that "*Nautilus* (*Cymatoceras*) *pseudoatlas* Yabe and Shimizu is another fossil characteristic of this zone, being found from the Zone of *Inoceramus schmidti* at Santan-gawa, a tributary of the Naibuchi, south Saghalin, [...]". Shimizu (1935) mentioned a few specimens of *Cymatoceras* cf. *carlottense* (Whiteaves, 1900) and *Eutrephoceras* cf. *indicum* (d'Orbigny, 1850) from the "Lower Maastrichtian" of Sakhalin ("Naibuchi district", i.e., Naiba River valley). However, this record is now dated as early Late Campanian as the nautiloids co-occur with *Schmidticeramus schmidti*. Regrettably, these nautiloid specimens are now missing from Japanese collections (see Matsumoto 1988, 1995). Shimansky (1975) recorded from the Naiba area *Pseudocenoceras proximum* Shimansky, 1975 (82, pl. 11: 4, uppermost Santonian), *Cymatoceras bifidum* Shimansky, 1975 (108, pl. 23: 1, Lower Campanian), and *Cymatoceras* sp. (113, pl. 24: 1, Lower Campanian). Matsumoto and Muramoto (1983: 92) introduced a new species of *Cymatoceras*, *C. pacificum*, a paratype of which was collected from "South Sakhalin".

Geological setting and stratigraphy

The material was collected from predominantly siliciclastic Campanian strata in Sakhalin representing marine nearshore to middle shelf environments. Co-occurring ammonite and inoceramid bivalve faunas provide precise age assignments.

Sakhalin Island (Fig. 1) formed part of an extensive complex of island arcs and marginal seas that developed in Juras-

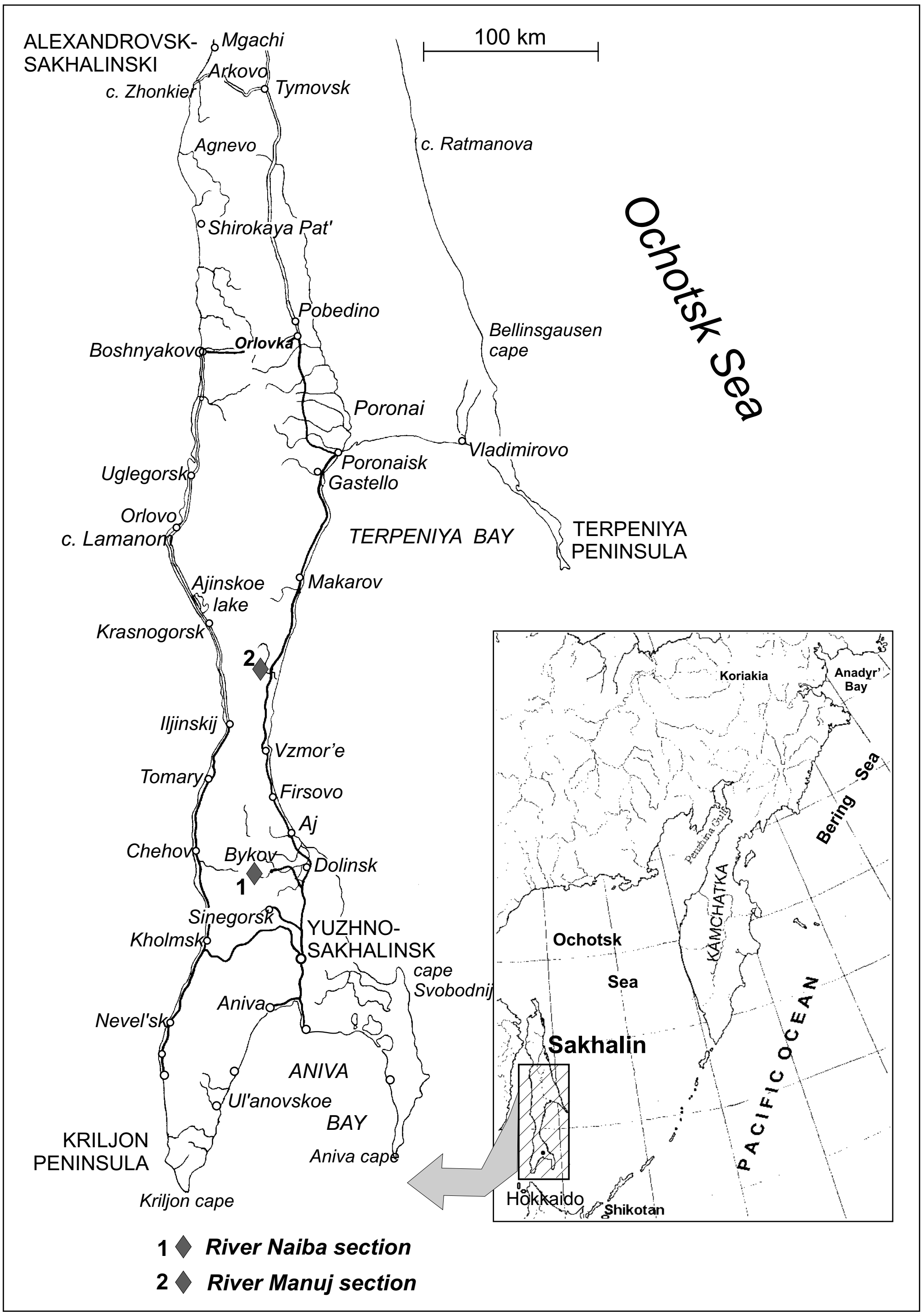

Fig. 1. Locality map of Sakhalin, Far East Russia with indication of the studied sections (no. 1 at River Naiba, no. 2 at River Manuj).

sic–Cretaceous times along the periphery of the Pacific Ocean. Two sections in southern Sakhalin were studied: a southerly section in the "Naiba River Valley", and a northerly one in the "Manuj River Valley" (see Fig. 1), situated in the West Sakhalin Mountains. The Santonian–Campanian succession of these sections comprises marine siliciclastics (sandstone, siltstone, mudstone) with intercalated tuffaceous silt- and sandstone and may attain a thickness in excess of 1,000 m (e.g., Poyarkova 1987; Shigeta et al. 1999; Yazykova 2002). In the Santonian part, sandstones predominate whereas in the Campanian, silt- and mudstones are more widespread (Fig. 2). Biostratigraphic schemes are based on ammonites and inoceramid bivalves (Zonova et al. 1993; Yazykova 2002; Yazykova et al. 2002). Palaeobiogeographically, the area belongs to the North Pacific Province of the Pacific Realm; its rich ammonite and inoceramid faunas are characterized by a high degree of endemism and show close affinities to Japan which is in the same biotic province (Noda

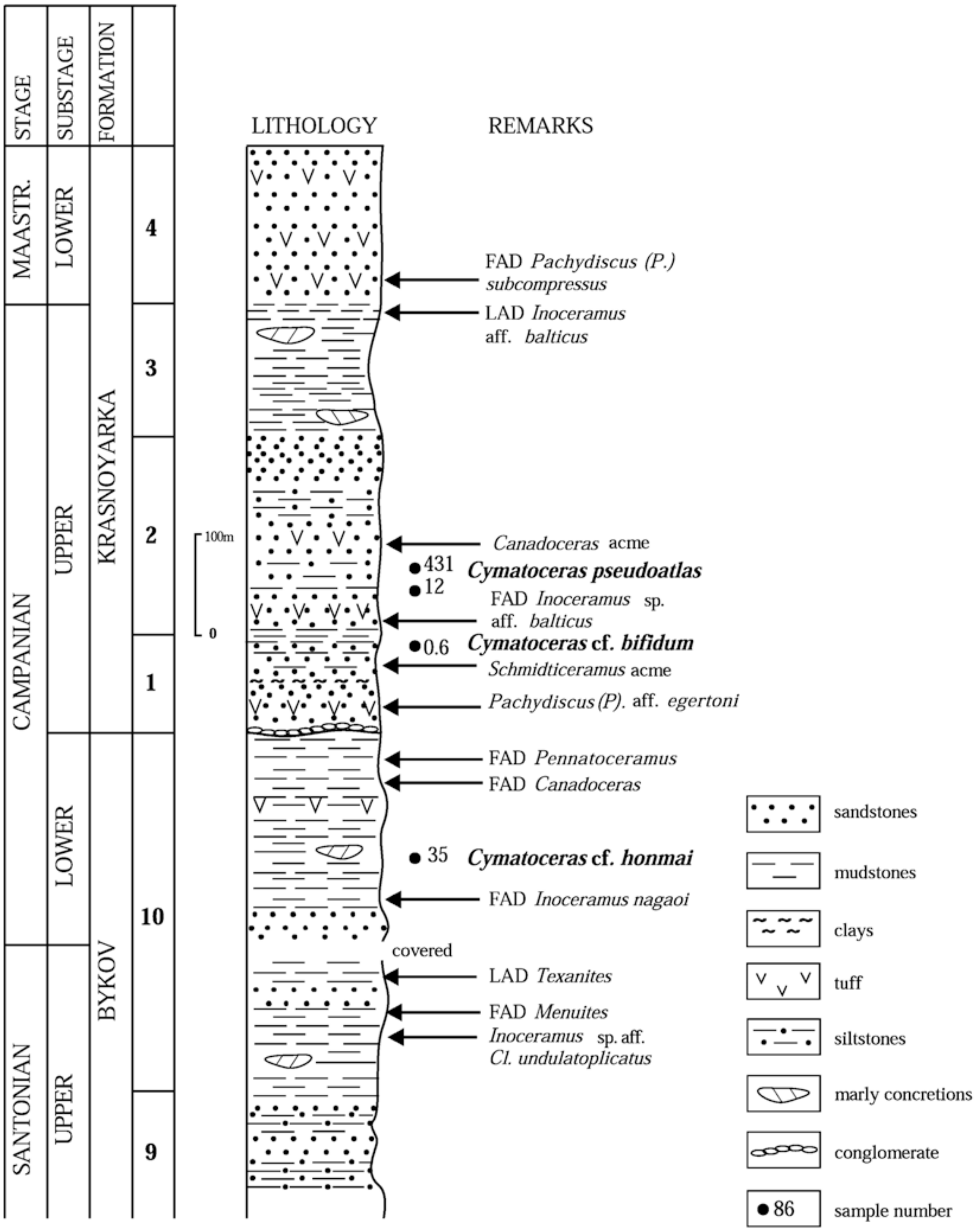

Fig. 2. Stratigraphic log of the Upper Santonian to Lower Maastrichtian of Sakhalin; numbers of lithostratigraphic members, nautiloid occurrences and biostratigraphic events (first and last appearance data, FAD/LAD) are indicated (modified after Yazykova 2002: fig. 2).

and Matsumoto 1998; Zonova and Yazykova 1998; Yazykova et al. 2002).

In the Campanian, four ammonite biozones have been recognized (Zonova et al. 1993; Yazykova 1996, 2002; Shigeta et al. 1999; Yazykova et al. 2002; see Fig. 3). Lithostratigraphically, the Campanian succession comprises the upper, fine siliciclastic part with marly concretions of the Bykov Formation (Member 10) and the lower part of the Krasnoyarka Formation (members 1–3; see Fig. 2). These formations are separated by an unconformity marking the Lower/Upper Campanian boundary (Poyarkova 1987, Yazykova et. al. 2002). The lower two members of the Krasnoyarka Formation are characterized mainly by sandstones and intercalated tuffaceous horizons. The third member consists predominantly of mudstones, containing marly concretions.

Material and methods

Nautiloid preservation is moderate, with specimens retaining (portions of) their shell. Unfortunately, some are more or less strongly deformed. The nautiloids were prepared and mea-

Stage	Substage	Formation	Member	Sakhalin: ammonite zones	Sakhalin: inoceramid zones	Japan: ammonite zones	Japan: inoceramid zones
Campanian	Upper	Krasnoyarka	3	*Canadoceras multicostatum*	*Inoceramus* aff. *balticus*	*Pachydiscus (P.) awajiensis*	*Inoceramus (Endocostea)* aff. *balticus*
			2			*Patagiosites laevis*	
			1	*Pachydiscus (P.)* aff. *egertoni*	*Schmidticeramus schmidti*	*Anapachydiscus fascicostatus*	*Mytiloides shimanukii*
	Lower	Bykov	10	*Canadoceras kossmati*	*Pennatoceramus orientalis*	*Canadoceras kossmati*	*Sphenoc. schmidti* *Sph. orientalis* *I. (P.) chicoensis*
				Anapachydiscus (N.) naumanni	*Inoceramus nagaoi*	*Anapachydiscus (N.) naumanni*	*Inoceramus (Pl.) japonicus*
Sant.	Upper			*Menuites menui*	*Inoceramus (Pl.) japonicus hokkaidoensis*	*Eupachydiscus haradai*	*Inoceramus amakusensis*
	?			*Eupachydiscus haradai*	*I. amakusensis*		

Fig. 3. Synoptic ammonite and inoceramid bivalve biostratigraphy of the areas discussed in the text (compiled after Zonova et al. 1993; Toshimitsu et al. 1995; Shigeta et al. 1999; Yazykova 2002; Yazykova et al. 2002). Abbreviation: Sant., Santorians.

sured using a sliding caliper. Prior to photography, they were coated with magnesium oxide. The material is housed in the collections of the "Institut für Paläontologie" at Würzburg University (repository PIW2002IV).

For taxonomic analyses, the suture is considered to be a very important feature, supplemented by measurements of shell dimensions (D = maximum diameter of shell; Wb = maximum breadth of last whorl; Wh = maximum height of last whorl; U = diameter of umbilicus; all in mm) and calculations of proportions (Wb/D, Wh/D, Wb/Wh, and U/D) (see Fig. 4). The position of the siphuncle is also of significance (for morphological terms see Teichert 1964). Due to poor preservation, some specimens are kept in open nomenclature and recommendations put forward by Bengtson (1988) are followed here.

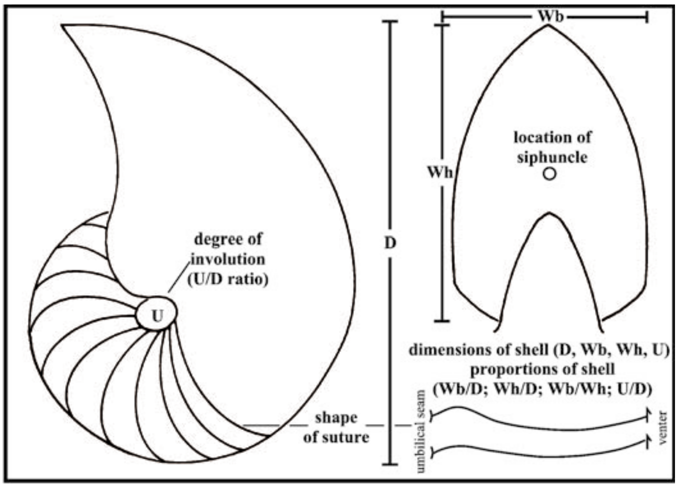

Fig. 4. Criteria for systematic classification of nautiloids used herein.

Systematic palaeontology

The most important contributions on the taxonomy of post-Triassic nautiloids are the papers by Kummel (1956, 1964), Wiedmann (1960), and Dzik (1984). Shimansky (1975) and Matsumoto et al. (1984) focused mainly on Cretaceous nautiloids and their phylogenetic relationships. However, family and genus level classification is still highly controversial (Dzik 1984); e.g., the Treatise proposes a subdivision of post-Triassic nautiloids (superfamily Nautilaceae) into six families (*sensu* Spath 1927). Other authors (e.g., Wiedmann 1960; Shimansky 1975; Wiedmann and Schneider 1979; Wilmsen 2000) have opposed a splitting of this (inferred) monophyletic group which is most probably derived from Late Triassic *Cenoceras* (Kummel 1956: 349, fig. 3). The family Cymatoceratidae Spath, 1927 may serve as an example; it does not exist as a true systematic entity since it demonstrably represents a taxonomic "sink" for ornamented offshoots of the usually smooth nautiloid stock (e.g., Yabe and Ozaki 1953; Tintant 1993). Consequently, Shimansky (1975) included most of the cymatoceratid genera in the family Nautilidae, and his taxonomy is followed here. As this is only a brief palaeontological note, the list of synonymies is kept short.

Subclass Nautiloidea Agassiz, 1848
Order Nautilida de Blainville, 1825
Suborder Nautilina de Blainville, 1825
Superfamily Nautilaceae de Blainville, 1825
Family Nautilidae de Blainville, 1825
Genus *Cymatoceras* Hyatt, 1884

Type species: *Nautilus pseudoelegans* d'Orbigny, 1840 (70, pl. 8), by original designation.

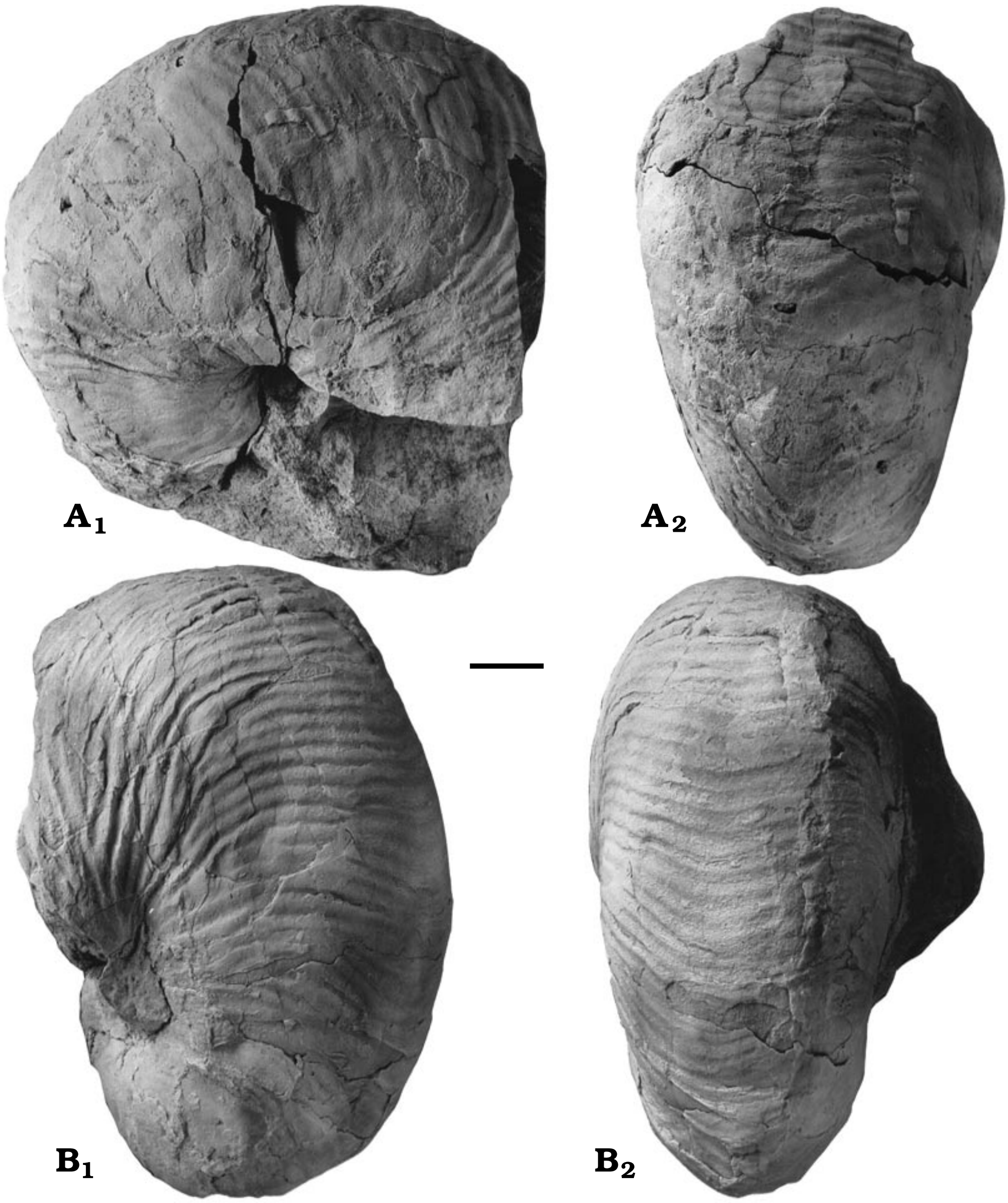

Fig. 5. *Cymatoceras pseudoatlas* (Yabe and Shimizu, 1924b). **A**. PIW2002IV-3 from the Krasnoyarka Formation, Member 2, locality 431 (*Canadoceras multicostatum* Zone, Upper Campanian), Manuj River valley, Sakhalin, in lateral (A_1) and ventral (A_2) views. **B**. PIW2002IV-2 from the Krasnoyarka Formation, Member 2, locality 12 (*Canadoceras multicostatum* Zone, Upper Campanian), Naiba River valley, Sakhalin, in lateral (B_1) and ventral (B_2) views. Scale bar 2 cm.

Cymatoceras pseudoatlas (Yabe and Shimizu, 1924b)

Figs. 5, 6A.

Nautilus (*Cymatoceras*) *pseudo-atlas* Yabe and Shimizu, 1924b: 42, pl. 5.
Cymatoceras pseudoatlas Yabe and Shimizu; Kummel 1956: 426.
Cymatoceras sp.; Shimansky 1975: 113, pl. 24: 1.
Cymatoceras pseudoatlas (Yabe and Shimizu); Matsumoto and Muramoto 1983: 90, pl. 17: 1.

Material.—Two large specimens from Sakhalin, slightly deformed but with shell preserved (no. PIW2002IV-2 from the Naiba River valley, locality 12; no. PIW2002IV-3 from the Manuj River valley, locality 431).

Description.—Very involute, nautiliconic nautiloid with slightly depressed whorl section showing a broadly rounded venter (Fig. 6A). Even though both specimens are slightly deformed, standard measurements are as follows:

Specimen	D	Wb	Wh	U	Wb/D	Wh/D	Wb/Wh	U/D
PIW2002IV-2	165	124	108	–	0.75	0.87	1.15	–
PIW2002IV-3	~140	~110	~95	~10	0.79	0.86	1.16	0.07

Maximum breadth is on the lower flanks close to the umbilical shoulder. The umbilical shoulder is rounded and the umbilical wall steep to overhanging. The umbilicus is narrow to occluded. The shell shows conspicuous, rather fine, flat-

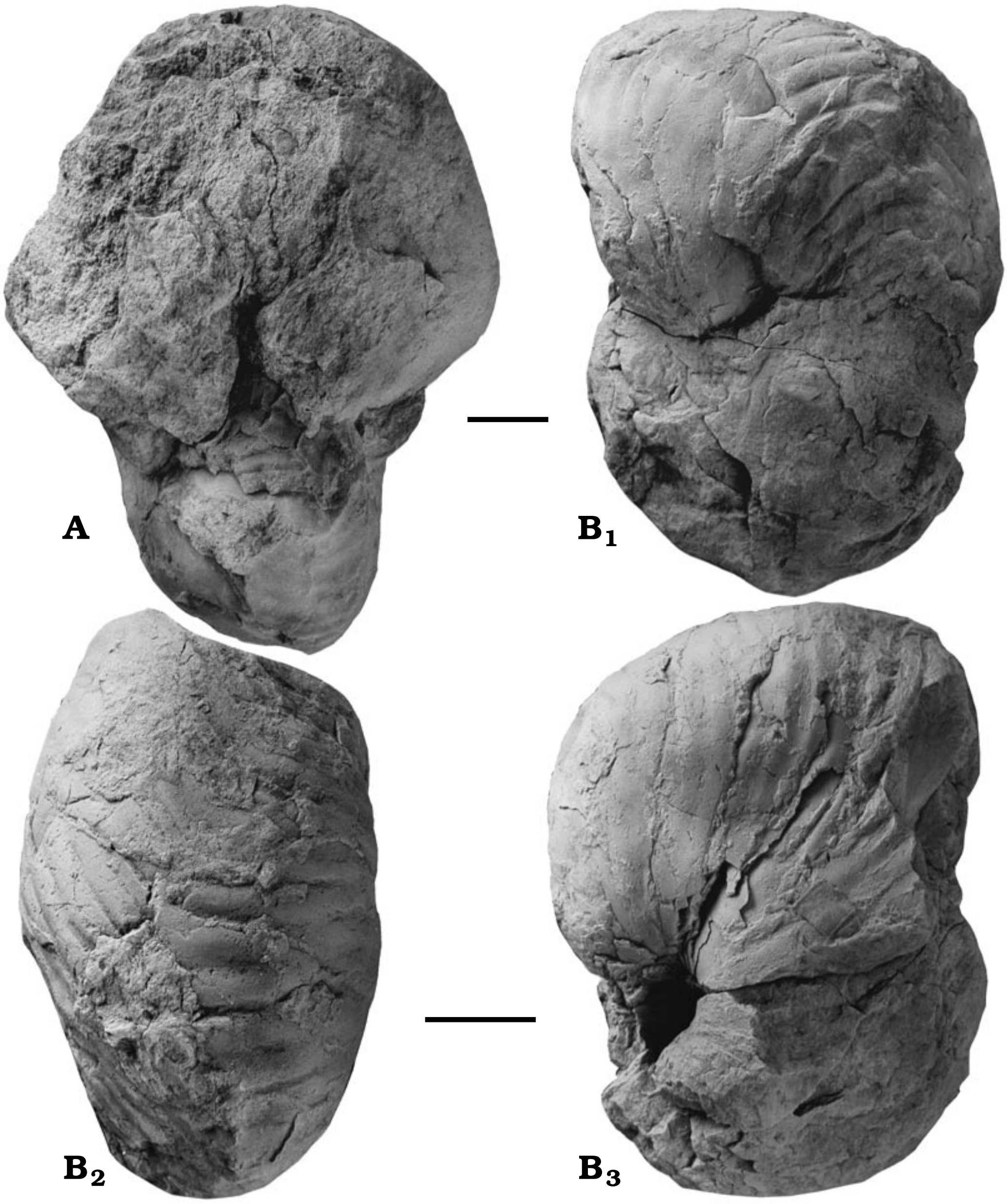

Fig. 6. **A**. *Cymatoceras pseudoatlas* (Yabe and Shimizu, 1924b). PIW2002IV-2 from the Krasnoyarka Formation, Member 2, locality 12 (*Canadoceras multicostatum* Zone, Upper Campanian), Naiba River valley, Sakhalin; apertural view [see also Fig. 5B]. **B**. *Cymatoceras* cf. *bifidum* Shimansky, 1975. PIW2002IV-4 from the Krasnoyarka Formation, Member 1 (*Pachydiscus* (*P.*) aff. *egertoni* Zone, Upper Campanian), locality 0.6, Naiba River valley, Sakhalin; in lateral (B_1, B_3) and ventral (B_2) views. Scale bar in the middle is for A, B_1, and B_3. Scale bars 2 cm.

tened ribs (mean width 2–4 mm) separated by narrow, 1–2 mm wide grooves. The ribs originate at the umbilical wall, are slightly prorsiradiate on the lower flank, curve backwards near the middle part and cross the external part with a rounded, shallow ventral sinus (Fig. $5A_2$, B_2). They bifurcate preferentially on the lower to middle part of the flanks (Fig. $5B_1$), and may occasionally also divide on the ventrolateral part or the venter. Due to shell preservation, the suture cannot be seen; the position of the siphuncle is not visible either.

Remarks.—In terms of dimensions and shell proportions as well as ribbing pattern, these specimens are very close to *C. pseudoatlas* as figured by Yabe and Shimizu (1924b: pl. 5) and Matsumoto and Muramoto (1983: pl. 17: 1). This species was erected by Yabe and Shimizu (1924b) in order to distinguish more irregularly ribbed representatives from *Cymatoceras atlas* (Whiteaves, 1876), which appears to be more finely ribbed and is stronger depressed than *C. pseudoatlas* (observations by M.W. on specimens of *C. atlas* in the collections of the Natural History Museum, London; Wb/Wh of a specimen figured by Sharpe 1853: pl. 4: 1, is 1.32). However, these species appear closely related and *C. pseudoatlas* may have been derived from *C. atlas* which is known from the Cenomanian to Santonian of England (Wright and Wright 1951); Kennedy (2002) indicates only a Cenomanian distribution for *C. atlas*. A Campanian specimen from the Naiba River valley described and figured by Shimansky (1975: pl. 24: 1) as *Cymatoceras* sp. is here also placed in *C. pseudoatlas*. It shows the same ornament and shell form and may be of the same age as the specimen described here. *Cymatoceras bifidum* Shimansky, 1975, from the Campanian of Sakhalin, has broad, flat ribs on the flanks which bifurcate near the ventrolateral shoulder (see also below). *Cymatoceras carlottensis* (Whiteaves, 1900: 269) from the (?Lower) Cretaceous "Lower Shales" of Skidegate Inlet, Maple Island (British Columbia), is a generally similar species but appears to be somewhat coarser ribbed and is characterized by a ventral depression or grove and a slightly deeper sinus. *Cymatoceras loricatum* (Schlüter, 1876) from the Upper Campanian of northern Germany shows imbricated ribs with intervening fine lirae.

Occurrence.—*Cymatoceras pseudoatlas* is known from the Upper Santonian of Japan (*Inoceramus amakusensis* Zone; Matsumoto and Muramoto 1983) and from the lower Upper Campanian of Sakhalin (Shimizu 1929). Our specimens are from the Upper Campanian Krasnoyarka Formation, Member 2, from localities 431 and 12 (*Canadoceras multicostatum* Zone; see Figs. 2, 3).

Cymatoceras cf. *bifidum* Shimansky, 1975

Fig. 6B.

cf. *Cymatoceras bifidum* Shimansky, 1975: 108, pl. 23: 1.

Material.—A single deformed specimen with shell preserved (no. PIW2002IV-4 from locality 0.6 in the Naiba River valley, Sakhalin).

Description. —Involute nautiloid with broadly rounded venter. The umbilical shoulder is rounded, grading into a steeply inclined to overhanging umbilical wall. The funnel-like umbilicus is narrow but not occluded (Fig. $6B_3$). Due to lateral compaction, only maximum diameter (~157 mm), whorl height (~90 mm) and umbilical diameter (~20 mm) could be measured (Wh/D = 0.57; U/D = 0.13). Maximum breadth of whorl seems to be in the lower part of the flanks. The flank is covered by band-like ribs which broaden up to mid-flank, reaching a width of up to 12 mm. Intercalated grooves are 2–4 mm wide. Bifurcations or intercalatories appear on the outer flanks and on the ventrolateral shoulders rather irregularly. On the venter, the ribs are regularly spaced and approximately 5–7 mm wide (Fig. $6B_2$). On the inner to middle part of the flanks the ribs are slightly prorsiradiate, then curve backwards and cross the venter with a moderately rounded sinus (Fig. $6B_2$). Neither suture nor the position of the siphuncle are visible.

Remarks.—This specimen is very close to *Cymatoceras bifidum*, especially in the style of ornament (broad ribs on flank, irregular bifurcations), but also the general shell form and the funnel-like, deep umbilicus (U/D = 0.15 in the holotype) are similar. That species was erected by Shimansky (1975) on the basis of a single specimen from the "Santonian" of Naiba, Sakhalin. According to the locality details (see below) and refined stratigraphy of that area, this find has now to be regarded as Lower Campanian. The holotype figured by Shimansky (1975) in pl. 23: 1a, seems to have suffered a non-fatal shell injury, partly causing the irregular ribbing pattern on the flank. Due to the poor preservation, only some of the specific characters are unequivocally discernible (general ribbing pattern, umbilicus), and, therefore, our specimen is referred to *C. bifidum* only with reservation. *Cymatoceras pacificum* Matsumoto and Muramoto, 1983 (92, pl. 18: 1, pl. 19: 1, pl. 20: 1, 2, text-fig. 3) from the lower Upper Campanian of Hokkaido, is a similar species concerning shell parameters. However, its style of ribbing is more regular and the ribs are finer. Furthermore, the whorl section is slightly more depressed in this species and the umbilicus is very narrow to occluded. *Cymatoceras kayeanus* (Blanford, 1861), a common species in the Lower Campanian of Madagascar (Kabamba 1983), is similar in respect to the form of the ventral sinus. It, however, has more densely spaced, finer ribs, and is slightly more evolute and clearly compressed.

Occurrence.—Our specimen is from the Krasnoyarka Formation, Member 1, locality 0.6 in the Naiba River valley (*Pachydiscus* (*P.*) aff. *egertoni* Zone, lower Upper Campanian; see Figs. 2, 3). The holotype of *C. bifidum* comes from the Lower Campanian of Sakhalin, Naiba River, near the River Seim estuary (left tributary of Naiba) (Shimansky 1975).

Cymatoceras cf. *honmai* Matsumoto and Miyauchi, 1983

Fig. 7.

cf. *Cymatoceras honmai* Matsumoto and Miyauchi, 1983: 225, pl. 48: 2; pl. 49: 1, 2.

Material.—A single, wholly septate, strongly weathered internal mould (specimen PIW2002IV-5) from locality 35 in the Manuj River valley, Sakhalin.

Description.—Involute, depressed nautiloid with broadly rounded, nearly flat venter. Dimensions and proportions are as follows: D = ~52 mm; Wb = 39.6 mm; Wh = 33.3 mm; U = ~5 mm; Wb/D = 0.76; Wh/D = 0.64; Wb/Wh = 1.19; D/U = ~0.10. The whorl section is broadly elliptical with maximum breadth in the lower part of the flanks. The flanks are only weakly convex and gently converge towards the broadly rounded ventrolateral shoulders. The umbilicus is deep and narrow with steep umbilical walls; the umbilical shoulders are rounded. The siphuncle is positioned subcentrally, slightly nearer to the venter than to the dorsum. The prorsiradiate suture is of low sinuosity and characterized by an inconspicuous saddle at the umbilical shoulder, a broad, shallow lateral lobe and a shallow lobe on the broad venter, separated by a saddle at the ventrolateral shoulder. The septa are fairly densely spaced (ca. 11–12 septa per half whorl).

Remarks.—With respect to outline of whorl section, proportions of shell, density of septa per whorl, position of siphuncle and degree of involution, our specimen is very close to *Cymatoceras honmai*. However, due to its incom-

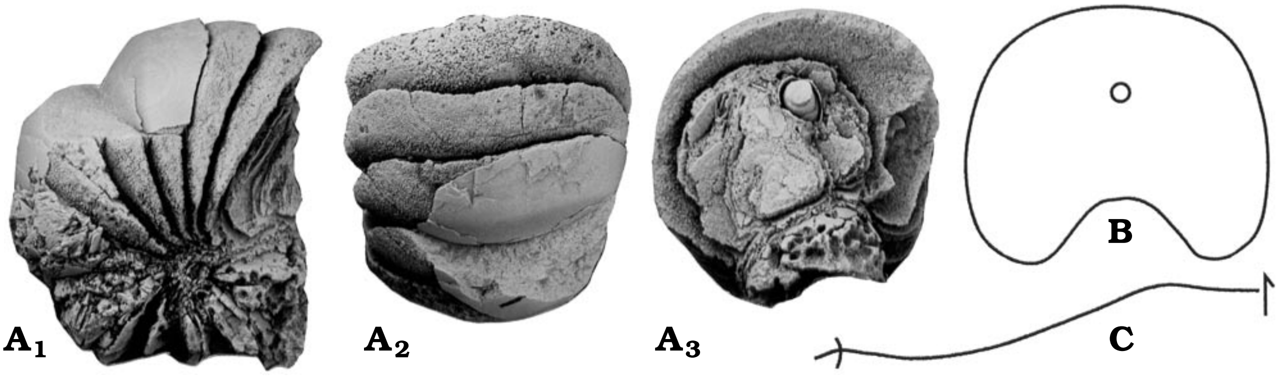

Fig. 7. **A**. *Cymatoceras* cf. *honmai* Matsumoto and Miyauchi, 1983 (specimen PIW2002IV-5 from the Lower Campanian Bykov Formation, Member 10, locality 35 at the Manuj River section, Sakhalin) in lateral (A_1), ventral (A_2), and septal (A_3) views. **B**. Reconstruction of whorl section. **C**. Suture line (not to scale) (all figures natural size except C).

plete preservation and slight differences in sutural sinuosity, it is assigned to *C. honmai* with a query.

Occurrence.—Lower Campanian (*Anapachydiscus* (*N.*) *naumanni* Zone) of Sakhalin, Member 10 of the Bykov Formation, locality 35 (see Figs. 2, 3). The types of *Cymatoceras honmai* are from the lower Upper Campanian near Soya, northern Hokkaido (member "E" of Campanian strata of Matsumoto and Miyauchi 1983).

Palaeobiogeographical and palaeoecological implications

Even if the data set of the present study is rather limited, some general conclusions concerning the distribution of Campanian nautiloids are possible. According to published records (see Introduction) and data presented herein, the Campanian nautiloid fauna of Sakhalin is dominated by representatives of the genus *Cymatoceras*. The genus, extensively redescribed by Kummel (1956), is cosmopolitan in distribution and ranges from the Late Jurassic into the Oligocene, reaching its peak diversity during the Cretaceous. According to Kummel (1956: 420), some 60+ species are known. The nautiloids from Sakhalin show close biogeographical affinities to faunas from Japan, Hokkaido (see Matsumoto in Matsumoto et al. 1984: 341–344), which is not surprising since the two areas are only a few hundred kilometres apart in the same biotic province (see Fig. 1). The greater region forms part of the North Pacific Province of the Pacific Realm. In this province, according to Zonova and Yazykova (1998), two separate palaeobiogeographical zones (which should be regarded as subprovinces) may be distinguished; a northerly one, comprising Kamchatka and Koryakia, with close affinities to Alaska, and a southerly one, comprising Sakhalin and the Kuril Islands, with close affinities to Japan (Fig. 1). The nautiloid distribution pattern supports this interpretation.

Recent representatives of the genus *Nautilus* Linnaeus, 1758, are rather deep-dwelling animals with a preferred depth habitat between ca. 150 to 300–400 m (Saunders and Ward 1987) and at least for a part of the smooth-shelled, compressed post-Triassic nautiloids with central to centrodorsal siphuncles, a similar mode of life in deeper water is assumed (e.g., Tintant and Kabamba 1985; Wilmsen 2000; Tintant et al. 2001). The siliciclastic successions of Sakhalin (and Hokkaido, see Matsumoto in Matsumoto et al. 1984), indicating shallow to moderately deep nearshore to inner/middle shelf settings of high to moderate water energy, are dominated by ornamented nautiloids with depressed whorl sections whereas smooth-shelled forms, especially compressed representatives of the genus *Angulithes* de Montfort, 1808 (= *Deltoidonautilus* Spath, 1927), are largely missing. Late Cretaceous *Angulithes* from Cantabria, Spain, were regarded by Wilmsen (2000) as deeper water forms. A corresponding picture is seen in the Upper Campanian of northwest Europe: due to a high sea-level stand (e.g., Hancock 1990), most parts of this area were covered by a deep epicontinental sea in which low-energy sediments (e.g., chalks) were deposited. From these rocks, mostly smooth shelled nautiloids of the genera *Eutrephoceras* and *Angulithes* are known (e.g., Westfalia and Lower Saxony area, Germany: Schlüter 1876; Wilmsen, unpubl. data; Spain: Wiedmann 1960; Wilmsen 2000). In northern Ireland, however, where the Upper Campanian transgressively overlies Permo-Triassic rocks (Hancock 1961), *Cymatoceras bayfieldi* (Foord and Crick 1890) is very common in nearshore sediments containing a high-diversity fauna of gastropods, bivalves and echinoids as well as a shallow-water ammonite fauna dominated by heteromorphs and tuberculated pachydiscids (C.J. Wood, personal communication October 2002). That species also occurs in slightly condensed, fossiliferous Upper Campanian chalks of Norfolk (Wright and Wright 1951; Kennedy 2002) but is apparently absent from pure chalk facies. These observations lend support to the idea of a relationship between shell form/ornament and preferred habitats in Late Cretaceous nautiloids. The development of ornament, e.g., ribbing in *Cymatoceras* or transverse folding in *Anglonautilus* Spath, 1927, was regarded by Tintant and Kabamba (1985: 62–63) as an adaptive response to life in shallow environments, assuming that those shells were more resistant to mechanic damage by agitated water. However, it is more plausible that the coarse shell ornament was of defensive nature. In the course of the "Mesozoic marine revolution" (Vermeij 1977), which intensified during the Jurassic and Cretaceous periods, shell-breaking (durophagous) predators such as carnivorous gastropods, decapod crustaceans, teleost fishes, marine reptiles, rays and sharks were of increasing importance (e.g., Kelley and Hansen 2001). Important Cretaceous durophages were mosasaurid lizards and ptychodontoid sharks. Since attacks of durophagous predators are much more common in shallow than in deeper waters (Ward 1996; Kelley and Hansen 2001), predatory pressure may have triggered the development of defensive morphologies, i.e., ornamented, predation-resistant shells, in Jurassic–Cretaceous shallow-water nautiloids. Correspondingly, Ward (1981, 1996) demonstrated that coarse ornament in ammonites, apparently defensive in nature, became increasingly important during the Mesozoic, especially during the Cretaceous. A similar radiation of durophageous predators and armoured prey, regarded as the "mid-Palaeozoic precursor of the Mesozoic marine revolution" (Signor and Brett 1984), occurred in the Middle to Late Devonian, and sculpture became more pronounced and common among coiled nautiloids.

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