

TWO COLEOID JAWS FROM THE UPPER CRETACEOUS OF HOKKAIDO, JAPAN

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ABSTRACT—Two isolated cephalopod jaws recovered from the middle Turonian of the Obira area and the Campanian of the Nakagawa area, Hokkaido, Japan, consist of short outer, and large and posteriorly elongated inner “chitinous” lamellae, with a sharply pointed rostrum in the outer lamella. These features are common with the upper jaws of Recent cephalopods. Comparison with the upper jaws of ammonoids and Recent cephalopods indicates that the two Cretaceous upper jaws are attributed to the Coleoidea other than the Octopodida. This assignment is also suggested by the cladistic analysis of the Nakagawa specimen compared with five upper jaw characters on 22 Recent cephalopod species. The Obira specimen differs from the Nakagawa specimen in having a much smaller jaw and a larger jaw angle, but its order-level assignment could not be determined because of imperfect preservation. The Nakagawa specimen shares several common features with the upper jaws of Recent Oegopsina; thus we assigned its higher systematic position to this suborder. Based on the extremely large upper jaw (97 mm maximum length), a new genus and species (*Yezoteuthis giganteus*) is proposed. This new taxon would have been as large as the modern giant squid *Architeuthis*, which commonly exceeds more than 5 m in body length. Our study postulates that studies of jaws are important to reconstruct the phylogeny of the Coleoidea.

INTRODUCTION

JAWS (=BEAKS OR MANDIBLES) are the primary feeding apparatus of cephalopod mollusks. They consist of articulated upper and lower elements, and the upper jaw encloses the lower jaw. Each jaw is made up of outer and inner lamellae, which are joined anteriorly. In Recent cephalopods, upper and lower jaws and a radula are accommodated in the proximal portion of the digestive system (buccal mass) and their function is to bite and shear food by means of the strong jaw-radular muscular system (Kear, 1994; Tanabe and Fukuda, 1999). Cephalopod jaws are composed mainly of a hard chitinous material (Saunders et al., 1978; Hunt and Nixon, 1981), so that they have a preservation potential as fossils when they have been diagenetically replaced by phosphatic material (Tanabe and Fukuda, 1983; Tanabe et al., 2001). More commonly, calcified elements of jaws of nautilids (rhyncholites and conchorhynchids) and some Mesozoic ammonoids (aptychi) are preserved as fossils. Indeed, fossil remains of cephalopod jaws have been found in Silurian and younger marine deposits (Tanabe and Fukuda, 1999). The taxonomic value of the jaws of Recent cephalopods has been extensively studied by previous workers (Clarke, 1962, 1986; Saunders et al., 1978; Clarke and Maddock, 1988a; Neige and Dommergues, 2002), allowing a generic-level identification on the basis of their morphology.

In fossil cephalopods, the overall shape and architecture of jaws and their taxonomic variation are best known in the Ammonoidea, because they are occasionally found in situ within the body chambers of specimens whose taxonomic identities are known (e.g., Lehmann, 1980, 1990; Nixon, 1988, 1996; Tanabe and Fukuda, 1999; Tanabe and Landman, 2002). In contrast, jaws of the Nautiloidea and Coleoidea are rather rare as fossils.

We recently discovered two well-preserved cephalopod jaws that can be assigned to the Coleoidea, from the Upper Cretaceous marine deposits in Hokkaido, North Japan. Here, we describe morphological features of the two jaws and discuss their taxonomic relationships by comparing them with the jaws of Recent cephalopods and ammonoids.

MATERIALS

Two cephalopod jaws were found individually in calcareous nodules collected as float; one came from the middle course of Kamikinenbetsu Creek, a tributary of the Obirashibe River, Obira Town, northwestern Hokkaido (lat. 44°02'22"N; long. 142°00'18"E), and the other from the small southern tributary

branch of the lower course of Wakkawenbetsu Creek, Nakagawa Town, northern Hokkaido (lat. 44°37'51"N; long. 142°03'04"E). The nodule that yielded the Obira specimen contains micro- and macroconchs of the scaphitid ammonite *Yezoites puerculus* (Jimbo, 1894) and the bivalve *Inoceramus hobetsensis* Nagao and Matsumoto, 1939. This nodule was presumably derived from the middle Turonian Saku Formation of the Middle Yezo Group, which yields the same molluscan assemblage. The nodule in which the Nakagawa specimen was found is rich in the bivalve *Sphenoceramus naumanni* (Yokoyama, 1890) and the heteromorph ammonite *Polyptychoceras* sp. These fossils, as well as the silty mudstone lithology, suggest that the nodule came from the Campanian Osousyunai Formation of the Upper Yezo Group. The Obira and Nakagawa specimens are respectively housed in the University Museum, University of Tokyo (UMUT), and the Nakagawa Museum of Natural History (NMA).

For comparison, we examined the jaws of the following nine extant species: *Sepia officinalis* Linnaeus, 1758, *S. esculenta* Hoyle, 1885 (both Sepiidae, Sepiida), *Loligo bleekeri* Keferstein, 1866 (Loliginidae, Myopsina, Teuthida), *Architeuthis* sp. (Architeuthidae, Oegopsina, Teuthida), *Todarodes pacificus pacificus* (Steenstrup, 1880), *Dosidicus gigas* d'Orbigny, 1835 (both Ommastrephidae, Oegopsina, Teuthida), *Octopus vulgaris* Cuvier, 1797, *Enteroctopus membranaceus* Rochebrune and Mabille, 1889 (both Octopodidae, Incirrina, Octopodida), and *Nautilus be-lauensis* Saunders, 1981 (Nautilidae, Nautilida, Nautiloidea). The jaws of these extant species are deposited in the UMUT and the American Museum of Natural History, New York (AMNH).

RECOGNITION OF JAW TYPES

The Obira and Nakagawa specimens, respectively, measure 33 mm and 97 mm in maximum length (Fig. 1), although the posterior portion of the inner lamella in the former is partly missing. Both specimens consist of short outer, and large, posteriorly elongated inner lamellae, with a sharply pointed anterior tip (rostrum) in the outer lamella. The lamellae are strongly convex dorsally and are made of a black, possibly phosphatic material without any trace of a calcareous element (Fig. 1.3, 1.6).

To distinguish the jaw types of the two specimens, we compared their morphological features with those of upper and lower jaws of Recent Cephalopoda. The upper jaws of Recent cephalopods are similar in their overall morphology and all consist of a short, reduced outer lamella and a posteriorly elongated, large inner lamella; both are prominently convex dorsally (see Tanabe

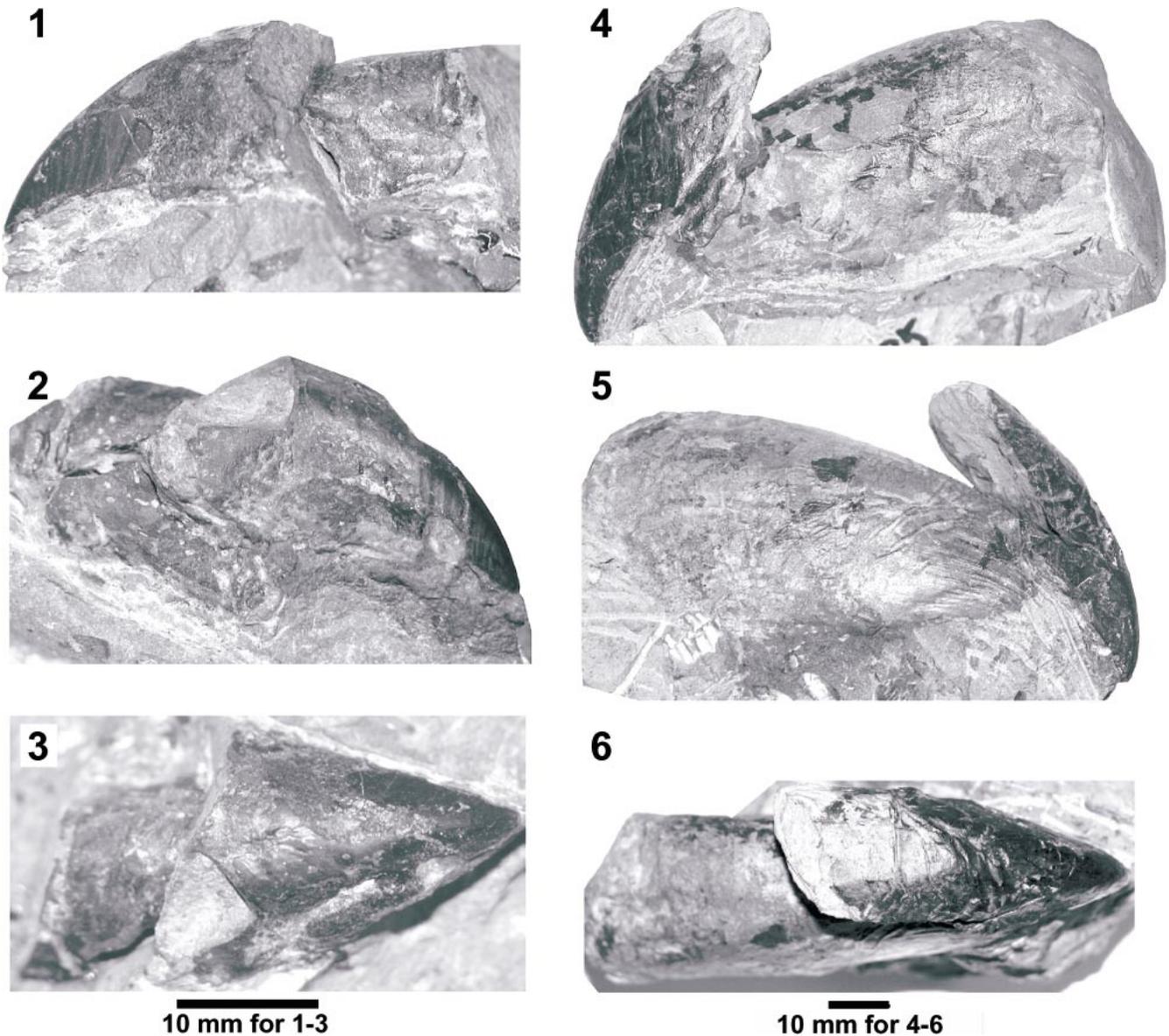


FIGURE 1—3, Coleoidea genus and species indeterminate. An incomplete upper jaw, left lateral (1), right lateral (2), and dorsal (3) views, UMUT MM 28665. From the middle Turonian of the Obira area, northwestern Hokkaido, Japan. 4—6, *Yezoteuthis giganteus* n. gen. and sp. Holotype, an almost complete upper jaw, jaw, left lateral (4), right lateral (5), and dorsal (6) views, NMA-335. From the Campanian of the Nakagawa area, northern Hokkaido, Japan.

and Fukuda, 1999, fig. 19.3; Fig. 2.4–2.7). The upper jaws of ammonoids consist of short outer and large inner lamellae like those of Recent cephalopods, but the former are clearly distinguished from the latter in that the inner lamella is distinctly partitioned into paired portions in the posterior region (Fig. 2.1–2.3).

In both Recent cephalopods and fossil ammonoids, the lower jaw is larger than the upper jaw and its outer lamella is gently arched and extended posteriorly. The three-dimensional architecture of their lower jaws shows a remarkable variation at higher taxonomic levels; namely, in *Nautilus* Linnaeus, 1758 (Nautilida, Nautiloidea), the inner lamella is short and reduced (Saunders et al., 1978, text-fig. 1; Fig. 2.5), whereas in coleoids belonging to the Octopodida, Spirulida, Sepiida, Sepiolida, and Teuthoida it is prominently projected posteriorly (Naef, 1921, pls. 17, 18; Clarke, 1962, 1986; Fig. 2.6, 2.7). The degree of development of the inner lamella in the lower jaw of *Vampyroteuthis* Chun, 1903 (order

Vampyromorphida) is intermediate between those of *Nautilus* and other coleoids (Clarke, 1986, figs. 126, 127; Fig. 2.8).

The overall features observed in the Obira and Nakagawa specimens are compatible with those in the upper jaws of Recent Coleoidea (Figs. 1, 2.6–2.8).

HIGHER SYSTEMATIC POSITIONS

Two left lateral views of a coleoid upper jaw with labeled morphological terms and measurements are diagrammatically shown in Figure 3. We follow Clarke (1962) for jaw terminology.

Recent Coleoidea are currently classified into six orders: Spirulida, Sepiida, Sepiolida, Teuthida, and Octopodida, and Vampyromorphida (Sweeney and Roper, 1998). Fossil records of these orders are scarce as compared with those of ectocochliate cephalopods because of the poor development of a chambered internal shell in these taxa, excluding the spirulid *Spirula* Lamarck, 1799

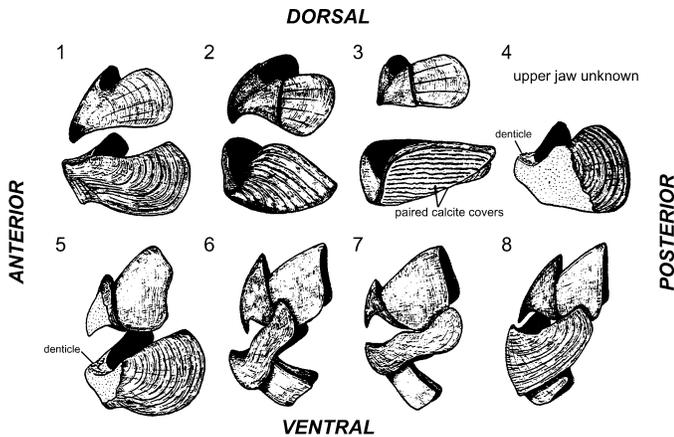


FIGURE 2—Three-dimensional architecture of the jaw apparatuses of selected ammonoids (1–4) and Recent cephalopods (5–8) viewed from the anterolateral side. Modified from Tanabe and Fukuda (1999, fig. 19.3). 1, *Eoasianites* Ruzhencev, 1933 (Late Carboniferous Goniatitina; normal type). 2, *Psiloceras* Hyatt, 1867 (Early Jurassic Ammonitina; anptychus type). 3, *Hildoceras* Hyatt, 1867 (Early Jurassic Ammonitina; aptychus type). 4, *Gaudryceras* Grossouvre, 1894 (Late Cretaceous Lytoceratina; rhynchaptychus type). 5, *Nautilus* Linnaeus, 1758 (Nautilida, Nautiloidea). 6, *Sepia* Linnaeus, 1758 (Sepiida, Coleoidea). 7, *Octopus* Cuvier, 1797 (Octopodida, Coleoidea). 8, *Vampyroteuthis* Chun, 1903 (Vampyromorphida, Coleoidea).

and sepiids. Fortunately, exceptionally well-preserved fossil remains that can be referred to these orders are known from Konservat Lagerstätten of Mesozoic and Cenozoic age (e.g., Naef, 1922; Donovan, 1977), indicating that their ancestors had already appeared in the Mesozoic. Another important extinct coleoid group that can be considered as a possible source of the two upper jaws from Hokkaido is the Belemnitida. Calcified remains (rostra and phragmocones) of belemnoids, however, have not yet been found in the post-Albian deposits in the North Pacific bioprovince, including Hokkaido (Stevens, 1973; Doyle, 1992; our own field observations in Japan and California), for paleobiogeographic reasons, although they flourished in other bioprovinces (Tethyan and Boreal realms, and the Western Interior Seaway) throughout the Late Cretaceous. For this reason, we can safely exclude the Belemnitida as candidates for the Obira and Nakagawa specimens. *Naefia* Wetzel, 1930, a small coleoid genus classified as belonging to the Groenlandibelidae of the order Sepiida (Jeletzky, 1966), occurs in the Upper Cretaceous of the North Pacific region (Hirano et al., 1990; Hewitt et al., 1991), represented by partial phragmocones. However, in view of the small size of its phragmocones, usually only several centimeters in length, this genus can be excluded as a source for the Obira and Nakagawa specimens.

Jaws of representative Recent species of these orders have been described and figured by many authors (e.g., Naef, 1921; Pickford, 1946, 1949; Clarke, 1962, 1986; Iverson and Pinkas, 1971;

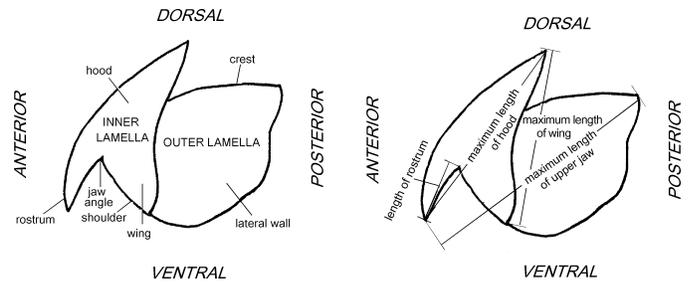


FIGURE 3—Diagrammatic drawings of a coleoid upper jaw, showing the descriptive terms (left) and measurements (right). Modified from Clarke (1962, fig. 1).

Clarke and Maddock, 1988a). Furthermore, Neige and Dommergues (2002) quantitatively compared the upper jaw morphologies of 16 Recent coleoid species by means of a landmark-based phenetic analysis. According to these authors, there are a number of morphological differences in the upper jaws of the Coleoidea at the ordinal level. For example, the upper jaws of the Sepiida, Sepiolida, and Teuthida can be distinguished from those of the Octopodida in having a more acutely projected rostrum and a much larger outer lamella (see Neige and Dommergues, 2002, text-fig. 3). The upper jaw of *Vampyroteuthis infernalis* Chun, 1903, the only extant species of the order Vampyromorphida, also has a relatively short rostrum, as in those of octopods, but the outer lamella of the former is more developed than in the latter (Kaiser and Lehmann, 1971; Iverson and Pinkas, 1971; Fig. 2.7, 2.8). If we consider these features, the Obira and Nakagawa specimens are referable to either Teuthida or Sepiida or Sepiolida, rather than the Octopodida and Vampyromorphida. The order-level assignment could not be determined for the Obira specimen, because the posterior portion of the inner lamella is missing; hence we treat it as a non-octopodid coleoid upper jaw.

In order to determine the exact higher systematic relationships of the Nakagawa specimen, we compared five morphological characters of upper jaws by means of a cladistic analysis on 23 operating taxonomic units (OTUs) which consist of 22 species belonging to 22 genera of 18 families and the Nakagawa specimen. The outgroup used was *Nautilus belauensis* (Nautilida; Nautiloidea). The characters and their observed states are summarized in Table 1. Of the five characters, shape of rostrum and jaw angle may be judged as quantitative characters; nevertheless, two distinct states were observed in the examined OTUs without any intermediate form. The character data matrix shown in Table 2 was analyzed using the PAUP 4.0b10 software package (Swofford, 2004), with a heuristic search option.

The analysis found a single most parsimonious tree (Fig. 4). The tree has a minimum of six steps with a consistency index (CI) of 0.86, a retention index (RI) of 0.96, and a rescaled consistency index (RC) of 0.83, when multistate characters were treated as unordered. It shows a polyphyletic pattern gathering three branches, namely *Nautilus belauensis*, a branch consisting

TABLE 1—List of characters used in the cladistic analysis.

Characters	States and codes
A. Shape of rostrum	Long and sharply pointed 0 Short and weakly pointed 1
B. Jaw angle	Acute (>90°) 0 Obtuse (<90°) 1
C. Shape of shoulder	Straight 0 Convex anteriorly 1
D. Posterior margin of wing	Straight 0 Concave inward 1
E. Posterior margin of lateral wall	Straight 0 Concave medially 1 Convex medially 2

TABLE 2—Character state matrix for 22 species of Recent Cephalopoda and the Nakagawa specimen. See Table 1 for details of abbreviated characters. Major taxonomy of each species is based on Sweeney and Roper (1998). *After Clarke (1962, 1986). **After Pickford (1946, 1949).

Subclass	Order	Suborder	Family	Species	Characters				
					A	B	C	D	E
Coleoidea	Sepiida	Sepiolida	Sepiidae	<i>Sepia officinalis</i> Linnaeus, 1758	0	0	1	1	1
			Sepiolidae	<i>Rossia macrosoma</i> (Chiaie, 1830)*	0	0	1	1	1
	Teuthida	Myopsina	Lolliginidae	<i>Neorossia caroli</i> (Joubin, 1902)*	0	0	0	1	1
				<i>Loligo? forbesii</i> Steenstrup, 1856*	0	0	0	1	1
		Oegopsina		<i>Sepioteuthis</i> sp.*	0	0	0	1	1
				<i>Megalocranchia</i> sp.*	0	0	0	1	1
				<i>Lepidoteuthis grimaldii</i> Joubin, 1895*	0	0	1	1	0
				<i>Mastigoteuthis</i> sp.*	0	1	0	1	1
				<i>Enoploteuthis leptura</i> (Leach, 1817)*	0	1	0	1	1
				<i>Cuciotheuthis</i> sp.*	0	0	0	1	0
Nautiloidea	Octopodida	Incirrata	Thysanoteuthidae	<i>Tanningia</i> sp.*	0	0	1	1	0
			Architeuthidae	<i>Thysanoteuthis rhombus</i> Troschel, 1857*	0	0	1	1	0
			Histiotheuthidae	<i>Architeuthis</i> sp.	0	0	0	1	1
			Onychoteuthidae	<i>Histiotheuthis bonnellii</i> (Férussac, 1834)*	0	1	0	1	1
			Gonatidae	<i>Moroteuthis</i> sp.*	0	1	0	1	1
			Omniastrephidae	<i>Gonatus antarcticus</i> Lönnberg, 1898*	0	1	0	1	1
			Octopodidae	<i>Todarodes pacificus pacificus</i> (Steenstrup, 1880)	0	0	1	1	1
				<i>Eledone cirrhosa</i> (Lamarck, 1798)*	0	0	1	1	0
				<i>Enteroctopus membranaceus</i> Rochebrune and Mabille, 1889	1	1	0	1	1
				<i>Argonauta argo</i> Linnaeus, 1758*	1	1	0	1	1
Vampyromorphida	Nautilida	Argonautidae	<i>Vampyroteuthis infernalis</i> Chun, 1903**	1	1	0	1	1	
		Vampyroteuthidae	<i>Nautilus belauensis</i> Saunders, 1981	1	1	0	1	2	
		Nautilidae	Nakagawa specimen (<i>Yezoteuthis giganteus</i> n. gen. and sp.)	0	0	1	1	1	

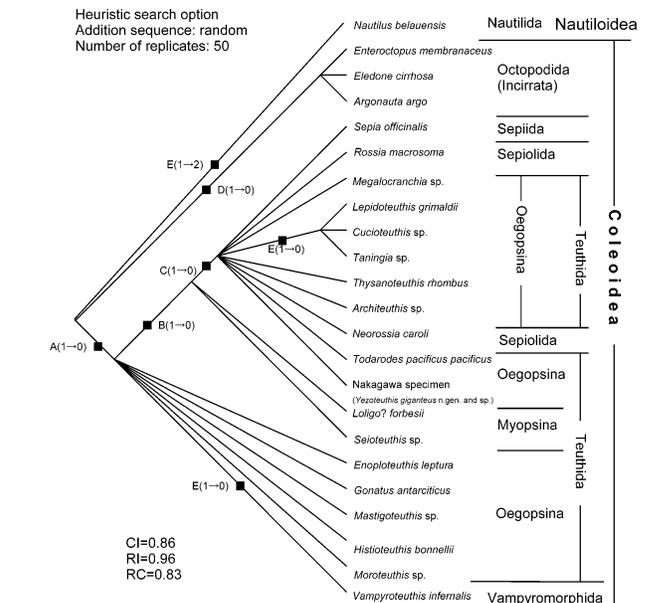


FIGURE 4—Single most parsimonious cladogram obtained from the character analysis of the upper jaw structure of 23 cephalopod taxa including the Nakagawa specimen (*Yezoteuthis giganteus* n. gen. and sp.). Labels on the tree indicate characters that change unambiguously. CI: consistency index, RI: retention index, RC: rescaled consistency index. Major taxonomy of each species is based on Sweeney and Roper (1998).

of three octopodids *Eledone cirrhosa* (Lamarck, 1798), *Argonauta argo* Linnaeus, 1758, and *Enteroctopus membranaceus*, and a branch consisting of 18 species belonging to the orders Sepiida, Sepiolida, Teuthida, and Vampyromorphida, and the Nakagawa specimen. The three octopod species constituting the second branch share an inward concave posterior margin of wing as an unambiguous synapomorphy. The taxa in the third branch share a sharply pointed rostrum as an unambiguous synapomorphy, though the species belonging to the Oegopsina show polyphyletic distributions in the obtained tree. In the third branch, the Nakagawa specimen constitutes a cluster, together with 10 species of the Sepiida, Sepiolida, and Oegopsina. These taxa share an anteriorly convex shoulder as an unambiguous synapomorphy. The results of the cladistic analysis did not demonstrate whether the Nakagawa specimen is referable to the Oegopsina, Sepiida, or Sepiolida. However, in the Nakagawa specimen and the Oegopsina, the ventral margin of the wing is less expanded posteriorly and the rostrum is more sharply projected than in the Sepiida and Sepiolida (see Naef, 1921, pl. 18, figs. 1–3; Neige and Domergues, 2002, text-fig. 3). Judging from these observations, we referred the Nakagawa specimen to the upper jaw of the Oegopsina.

It should be noted that the phylogenetic relationships of Recent coleoids are still poorly understood even when numerous characters (but none from the jaws) are taken into account (e.g., Young and Vecchione, 1996; Young et al., 1998). Therefore, our analysis using characters of upper jaws should be considered only a first step in determining their relationships.

ESTIMATION OF BODY SIZE

In Recent coleoids, there is an intimate allometric relationship between jaw size and total body weight at intra- and interspecific levels (e.g., Pickford, 1949; Clarke, 1962, 1980; Nixon, 1969, 1988). To estimate the body size of the owners of the Obira and

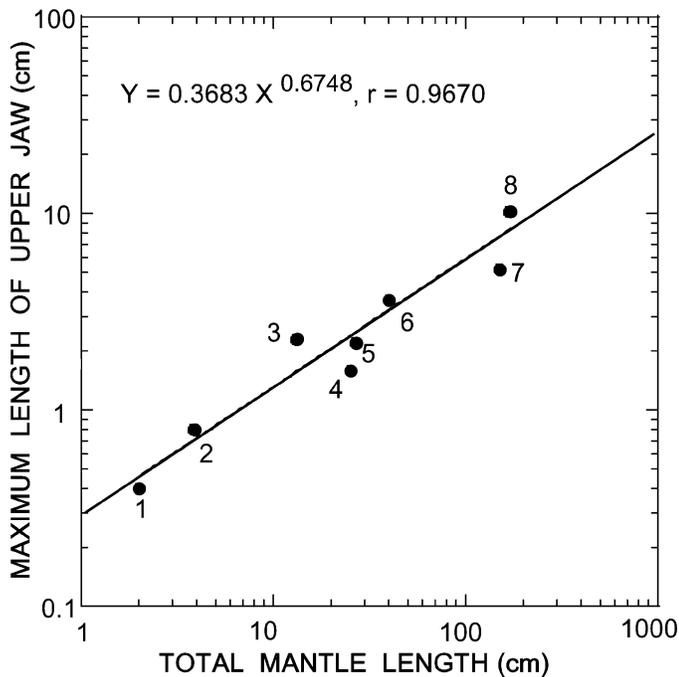


FIGURE 5—Double logarithmic scatter plots of maximum upper jaw length versus total mantle length in selected eight Recent coleoid species. Regression line with the reduced major axis indicates a strong negative allometry. 1, *Euprymna morsei* (Verrill, 1881) (Incirrina, Octopodida). 2, *Enteroctopus membranaceus* Rochebrune and Mabile, 1889 (Incirrina, Octopodida). 3, *Sepia esculenta* Hoyle, 1885 (Sepiida). 4, *Loligo bleekeri* Keferstein, 1866 (Myopsina, Teuthida). 5, *Todarodes pacificus pacificus* (Steenstrup, 1880) (Oegopsina, Teuthida). 6, *Sepia officinalis* Linnaeus, 1758 (Sepiida). 7, *Dosidicus gigas* d'Orbigny, 1835 (Oegopsina, Teuthida). 8, *Architeuthis* sp. (Oegopsina, Teuthida). Measurements of *Architeuthis* sp. after Roeleveld and Lipinski (1991).

Nakagawa specimens, we analyzed the allometric relationship between the maximum length of the upper jaw (LUJ) and the total mantle length (ML) in eight selected species belonging to the Teuthida, Sepiida, and Octopodida (Fig. 5). The growth of LUJ versus ML shows a strong negative allometry (slope of the regression line with the reduced major axis = 0.6748), and therefore, even in the giant squid *Architeuthis* Steenstrup, 1857, with total body length < 5 m and ML ≈ 1.7 m, the LUJ rarely exceeds 10 cm. If we apply the above allometric relationship to the Nakagawa coleoid jaw (LUJ = 97 mm), its body would have been as large as that of the giant squid. The Obira coleoid is estimated to have had an ML of approximately 40–50 cm.

SYSTEMATIC PALEONTOLOGY
Subclass COLEOIDEA Bather, 1888
Order and Family UNCERTAIN
Genus and species INDETERMINATE
Figures 1.1–1.3, 6.1, 6.2

Description.—Medium-sized upper jaw, 33 mm in preserved maximum length, although posterior margin of inner lamella partly missing; outer lamella well developed, 15.8 mm in maximum width, markedly expanded posteriorly, ornamented with fine and dense concentric lirae; rostrum 18.2 mm in length, sharply pointed anteriorly; jaw angle approximately 120°. Inner lamella imperfectly preserved, 13.5 mm in maximum width, partly wrinkled by secondary shrinkage on dorsal side.

Material examined.—UMUT MM 28665, an imperfect upper jaw.

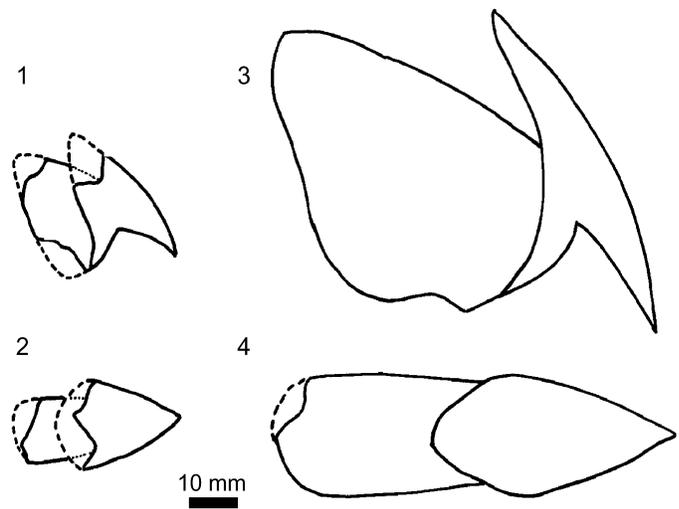


FIGURE 6—Diagrammatic drawings of upper jaws. 1, 2, Coleoidea genus and species indeterminate. Right lateral (1) and dorsal (2) views, UMUT MM 28665. 3, 4, *Yezoteuthis giganteus* n. gen. and sp. Right lateral (3) and dorsal (4) views of holotype, NMA-335.

Occurrence.—Middle Turonian, Saku Formation, Middle Yezo Group, Kamikinenbetsu Creek, a tributary of the Obirashibe River, Tappu area, Obira Town, Rumoi Province, northwestern Hokkaido, North Japan.

Discussion.—One of the characteristic features of the present specimen is the long and sharply pointed rostrum. This feature is commonly observed in the upper jaws of Recent Oegopsina, Myopsina, Sepiida, Sepiolida, and Vampyromorphida. For this reason, the order-level assignment of this specimen could not be determined because of imperfect preservation of the inner lamella. The isolated upper jaws from the Santonian of the Obira area, which were described as the vampyromorph *Provampyroreuthis giganteus* Kanie (1998, figs. 2.3–2.9, 4), somewhat resemble the present specimen, but *P. giganteus* is distinguished from the present specimen in having a much larger jaw angle and a shorter rostrum.

Order TEUTHIDA Naef, 1916
Suborder OEGOPSINA d'Orbigny, 1845
Family UNCERTAIN
Genus YEZOTEUTHIS new genus

Type species.—*Yezoteuthis giganteus* new genus and species.

Diagnosis.—Extremely large upper jaw, consisting of shorter inner lamella and larger outer lamella, both made up of black horny material; anterior rostral portion of outer lamella thick and sharply pointed; hood expanded posteriorly with gently convex margin; wing concave inward at midlateral margin and its ventral margin weakly expanded posteriorly; shoulder gently arched ventrally; lateral wall margin concave medially; crest line gently convex dorsally; outer lamella smooth on dorsal side; inner lamella sculptured by equally spaced, very fine concentric growth lines with fine radial striations on ventrolateral side of lateral wall.

Etymology.—Named for the old name of Hokkaido, “Yezo,” where the type species was found.

Discussion.—Almost complete remains of coleoid fossils have been discovered from Konservat Lagerstätten of Cretaceous age (e.g., the Cenomanian of Hakel, Lebanon: Roger, 1946; Engeser and Reitner, 1986; Campanian of Westphalia, Germany: Riegraf, 1987; see also Riegraf, 1987 for the complete list of Cretaceous coleoid genera), but no examples with an upper jaw comparable in size and shape to *Yezoteuthis* have been described. Apart from

its unusually large size, the upper jaw of *Yezoteuthis* is somewhat similar in overall shape to that of the plesiotheuthid *Plesiotheuthis* Wagner, 1859 [type species, *P. prisca* (Rüppell, 1829)] (see Naef, 1922, fig. 42f) from the Upper Jurassic (Tithonian) lithographic limestone at Solenhofen, southern Germany, but *Plesiotheuthis* has a more posteriorly expanded outer lamella than *Yezoteuthis*. *Plesiotheuthis* ranges from the Tithonian to the Campanian (Riegraf, 1987) and has been regarded as the direct ancestor of modern oegopsid squids (Donovan, 1977, fig. 11; Donovan and Toll, 1988).

The upper jaw of *Yezoteuthis* is comparable to that of the architeuthid *Architeuthis* (type species, *A. dux* Steenstrup, 1857; see Clarke, 1962, pl. 16, fig. a, d; Roeleveld and Lipinski, 1991, pl. 14, fig. a) in overall shape, structure, and unusually large size, but is distinguished in having a more convex crest margin and more prominent concentric growth lines on the inner lamella.

YEZOTEUTHIS GIGANTEUS new species

Figures 1.4–1.6, 6.3, 6.4

Diagnosis.—Same as for the genus.

Description.—Upper jaw very large, 97.0 mm in maximum length; outer lamella 22.5 mm in maximum width, acutely convex dorsally and expanded posteriorly with a gently convex margin; rostrum 25.0 mm in length and sharply pointed anteroventrally; jaw angle 60°; hood 56.2 mm in maximum length, its ventral margin gently convex; wing well developed, 50.4 mm in maximum length, its posterior margin gently concave inward at midlateral region and slightly expanded posteriorly on ventral side. Inner lamella acutely convex dorsally with a gently arched crest margin, 29.4 mm in maximum width, being expanded posteriorly with a slightly concave margin at midlateral point; ventral and posterior margins of lateral wall partly missing on left lateral side but perfectly preserved on right lateral side. Outer lamella smooth and partly wrinkled by secondary shrinkage on dorsal side; inner lamella sculptured by equal-spaced fine concentric growth rings with a flat top, with fine radial striations on lateral side. In view of the unusually large upper jaw size, the present species appears to be the largest fossil coleoid ever described.

Etymology.—Latin *giganteus*, referring to the very large upper jaw.

Type.—Holotype, an upper jaw (NMA-335).

Occurrence.—Campanian; Osousyunai Formation, Upper Yezo Group, southern tributary of Wakkawebetsu Creek, Nakagawa Town, Nakagawa County, northern Hokkaido, North Japan.

CONCLUDING REMARKS

Among extant coleoids, a chambered internal shell is only preserved in sepiids and *Spirula*. It has been much reduced to a chitinous gladius or completely lost in other species of the Sepiolida, Teuthida, Ocotopodida, and Vampyromorphida during their evolutionary history. As a result, these taxa are rarely preserved as fossils; accordingly, their evolutionary history and phylogenetic relationships are still uncertain. Most of the previous works on these nonshelled coleoids relied upon exceptionally well-preserved fossil remains from Konservat Lagerstätten [e.g., the Middle Jurassic (Callovian) Oxford Clay of England and the Late Jurassic (Tithonian) lithographic limestone of Solenhofen, Germany]. As already noted, jaws are the primary feeding organ in all Cephalopoda and have some preservation potential as fossils under special conditions, even in the case of nonshelled coleoids. Furthermore, in Recent cephalopods, generic level identification of jaws has been well established by previous authors (Clarke, 1962, 1980, 1986). Other hard-part remains of coleoids, such as hooks, gladii, and statoliths have been individually found in marine Mesozoic and Cenozoic sediments (Donovan and Toll, 1988;

Engeser and Clarke, 1988; Clarke and Maddock, 1988b), but their taxonomic assignment is more difficult than jaws.

This study has revealed the presence of an unusually large new teuthoid in the Late Cretaceous (Campanian) of the Northwest Pacific, together with other shelled cephalopods (ammonoids, nautilids, and a small coleoid *Naefia*). This species presumably had a high trophic level in the Late Cretaceous marine ecosystem of the region. Our study strongly postulates that although preserved parts are rare, they are as important as those of shells to reconstruct the evolutionary history and paleoecology of the Cephalopoda through time.

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