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New records of coleoid cephalopod jaws from the Upper Cretaceous of Hokkaido, Japan, and their paleobiogeographic and evolutionary implications

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ABSTRACT

Seven coleoid jaws recovered from Santonian to lower Campanian (Upper Cretaceous) strata in Hokkaido, Japan were taxonomically studied. Based on the comparison with the jaws of modern and fossil coleoids, six of the seven jaw fossils are referred to the following two genera and three species, including one possible new species: *Nanaimoteuthis jeletzkyi* and *N. yokotai* of the order Vampyromorpha, and *Paleocirroteuthis* sp. nov. (?) of the order Cirroctopodida. The other single lower jaw is seemingly similar to those of modern octopods and teuthids with respect to the shape of the inner lamella, but its order-level assignment could not be determined because of its imperfect preservation. *N. jeletzkyi* has been described in the Upper Cretaceous fore-arc basin deposits in Hokkaido (Yezo Group) and Vancouver Island, Canada (Nanaimo Group), whereas *N. yokotai* occurs only in the Yezo Group. These findings, complemented by previous reports of coleoid jaws, gladii, and phragmocones from the Yezo and Nanaimo Groups, demonstrate that a highly diversified, non-belemnitid coleoid fauna including large teuthids had already appeared during the post-Albian Late Cretaceous, in the North Pacific region.

1. Introduction

The Coleoidea is a group of cephalopod mollusks characterized by an internally shelled (endocochleate) body plan. Modern Coleoidea are currently classified into two superorders, Decabrachia Boettger, 1952 (10 arms, the fourth pair modified as tentacles), and Octobrachia Fiorini, 1981 (10 arms, the second pair modified or lost) (Doyle et al., 1994). Decabrachia comprises four orders (Spirulida, Sepiida, Sepiolida, and Teuthida) and Octobrachia comprises three (Octopoda, Cirroctopoda, and Vampyromorpha) (Doyle et al., 1994, table 1).

The fossil record of the Cretaceous Coleoidea excluding the groups with an aragonitic phragmocone and a calcitic rostrum (e.g., Belemnitida and Diplobelida), unlike that of externally shelled ammonoids and nautilids, is poor and sporadic; this is because of the reduction or loss of the calcified shell in most of the remaining groups during their evolutionary history (Doyle et al., 1994; Fuchs, 2006a; Bizikov, 2008; Kröger et al., 2011). For this reason, previous studies on Cretaceous coleoids were largely based on isolated shelly fossils such as calcitic rostra, aragonitic phragmocones, and chitinous gladii from various regions of the world (e.g., Jeletzky, 1966). In addition, exceptionally well-preserved fossils with soft and hard tissue remains have been described from Konservat-Lagerstätten in Europe (e.g., Engeser and Reitner, 1985; Košťák, 2002), Lebanon (e.g., Naef, 1922; Fuchs, 2006b; Fuchs et al., 2009; Fuchs and Larson, 2011a,b; Jattiot et al., 2015; Donovan and Fuchs, 2016), and Mexico (Fuchs et al., 2008, 2010). Previous studies of these fossils have shown that the Cretaceous was an important period for the macroevolution of the Coleoidea, because major groups that flourished during the Mesozoic, such as the Prototeuthina, Loligosepiina, and Teudopseina of the Vampyromorpha, Belemnitida, and Diplobelida became extinct before the end of the Cretaceous (Bizikov, 2008; Kröger et al., 2011; Fuchs et al., 2013), and possible ancestors of modern decabrachian and octobrachian coleoids appeared in the Cretaceous (Woodward,

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1896; Tanabe et al., 2006, 2015b; Fuchs et al., 2008, 2009, 2012a; Iba et al., 2011).

Post-Aptian Cretaceous fore-arc basin deposits, called the Yezo Group, in Hokkaido (Japan) and Sakhalin (Russia) yield rich and diversified cephalopod fossils throughout the entire sequence. Cephalopod fossils include mostly ammonoid conchs and jaws, with fewer nautilid conchs, belemnitid rostra, and non-belemnitid coleoid phragmocones (Hewitt et al., 1991; Hirano et al., 1991; Fuchs and Niko, 2010; Fuchs and Tanabe, 2010; Iba et al., 2011; Fuchs et al., 2012a,b, 2013). In the last decade, fairly large isolated upper and lower jaws attributed to the vampyromorph, cirroctopodid, and teuthid coleoids have been discovered from the Turonian to the Campanian strata of the Yezo Group (Tanabe et al., 2006, 2008, 2015b; Tanabe and Hikida, 2010; Tanabe, 2012).

While searching for additional materials, we found seven large jaws in our museum collections; six of them are referred to two genera and three species of octobrachian coleoids. In this article, we describe these jaws, and discuss their implications for Cretaceous coleoid systematics and paleobiogeography.

2. Material

Seven cephalopod jaws were recovered from the Santonian to the lower Campanian strata of the Yezo Group, in the Tomiuchi and Haboro-Tomamae areas, Hokkaido, Japan (Fig. 1). Lithostratigraphic and biostratigraphic positions of the examined material were determined based on definitions given by Takashima et al. (2004) and Toshimitsu et al. (1995,2007), respectively.

Detailed locality, horizon, and age of each specimen are as follows: 1) a lower jaw, HMG-1689, collected as float in the western tributary of the Tosano-sawa Creek, Tomiuchi area, southern central Hokkaido (lat. 42°47′44″N; long. 142°12′49″E; loc. 1 in Fig. 1). It was presumably derived from the Santonian *Inoceramus* (*I.*) *amakusensis* Zone or the lower Campanian *Inoceramus* (*Platyceramus*) *japonicus* Zone, in the middle part of the Kashima Formation (Hayashi et al., 2011); 2) a lower jaw, KMNH IvP 902,004, collected as float in the middle stream of the Nakafutamata River, Haboro area, northwestern Hokkaido (lat. 44°18′11.8″N; long. 141°58′14.8″E; loc. 2 in Fig. 1). It was presumably derived from the Santonian *I.* (*I.*) *amakusensis* Zone, in the middle to the upper part of the Haborogawa Formation (Member Ug of Upper Haborogawa Formation, Okamoto et al., 2003); 3) a lower jaw, KMNH IvP 902,003, discovered in a fallen concretion derived from the lower Campanian *I.* (*P.*) *japonicus* Zone, in the upper part of the Haborogawa Formation (Member Ui-j of Nagareya Formation, Okamoto et al., 2003), exposed in a large road-side outcrop along the Sakasa River, Haboro area, northwestern Hokkaido (lat. 44°16′26.1″N; long. 141°58′24.7″E; loc. 3 in Fig. 1); 4) a large lower jaw, NMA-814, collected as float in the Haboro River, about 1.6 km upstream from the junction with the Chimei-zawa Creek (also called the Ogawa-zawa Creek), Haboro area, northwestern Hokkaido (lat. 44°14′20″N; long. 141°59′27″E; loc. 4 in Fig. 1). It was presumably derived from the Santonian *I.* (*I.*) *amakusensis* Zone, in the middle to the upper part of the Haborogawa Formation (Member Uh of the Upper Haborogawa Formation, Okamoto et al., 2003); 5) upper and lower jaws, MCM-A872, collected as floats in the Kaminosawa Creek, a tributary of the Kotanbetsu River, Tomamae area, northwestern Hokkaido ((lat. 44°11′56.0″N; long. 141°58′59.0″E; loc. 5 in Fig. 1). They were presumably derived from the Santonian *I.* (*I.*) *amakusensis* Zone, in the upper part of the Haborogawa Formation (Member U1 of Middle Haborogawa Formation, Wani and Hirano, 2000; and Member Ug of the same formation, Tsujino and Maeda, 2007); 6) a lower jaw, KMNH IvP 902,005, discovered in a fallen concretion derived from the Santonian *I.* (*I.*) *amakusensis* Zone, in the upper part of the Haborogawa Formation (Member U1 of the Middle Haborogawa Formation, Wani and Hirano, 2000; and Member Ug of the same formation, Tsujino and Maeda, 2007), exposed at the large riverside outcrop near the Kumaoi Bridge in the Kotanbetsu River, Tomamae area, northwestern Hokkaido (lat. 44°10′58.3″N; long. 141°58′20.6″E; loc. 6 in Fig. 1).

Institutional abbreviations. NMA, Nakagawa Museum of Natural History, Nakagawa Town, Hokkaido, Japan; MCM, Mikasa City Museum, Mikasa City, Hokkaido, Japan; HMG, Hobetsu Museum, Mukawa Town, Hokkaido, Japan; KMNH, Kitakyushu Museum of Natural History and Human History, Kitakyushu City, Fukuoka, Japan; UMUT, University Museum, The University of Tokyo, Tokyo, Japan; CDM, Courtenay and District Museum and Paleontological Center, British Columbia, Canada.

3. Jaw types and higher taxonomic positions

To determine jaw types and higher taxonomic positions of the seven Late Cretaceous cephalopod jaws examined, we compared their overall morphology and lamellar compositions to those of the jaw apparatuses of modern and fossil cephalopods described previously (Clarke, 1986; Clarke and Maddock, 1988; Neige and Dommergues, 2002; Klug et al., 2005, 2010; Kubodera, 2005; Tanabe et al., 2006, 2008, 2015b; Tanabe and Hikida, 2010; Tanabe, 2012; Nixon, 2015, for coleoids; Tanabe et al., 2015a and references in it for ammonoids; Saunders et al., 1978; Klug, 2001, for nautilids). Of the seven jaw fossils, six consist of a widely open outer lamella and a posteriorly projected inner lamella with a pointed rostrum. These features are commonly observed in the lower jaws of modern as well as fossil coleoids, nautilids, and ammonoids (see Tanabe and Fukuda, 1999, fig. 19.3; Tanabe et al., 2015a, fig. 10.4); hence, they were identified as lower jaws. The seventh jaw consists of a short outer lamella and a partly broken, posteriorly elongated inner lamella with a pointed rostrum. These features are characteristic for the upper jaws of modern and fossil cephalopods (see Tanabe et al., 2015a, fig. 10.4) and thus, we identified it as an upper jaw.

The six lower jaws consist of a widely open outer lamella and a posteriorly projected inner lamella, both of which are composed of dark, possibly primarily chitinous material, without any trace of calcification. The posteriorly projected inner lamella is commonly observed in the lower jaws of modern and fossil coleoids (see Tanabe, 2012, figs. 3, 4), and never occur in the lower jaws of nautilids and ammonoids, both of which possess a very short inner lamella. Furthermore, in modern and fossil nautilids and many Jurassic and Cretaceous ammonoids, the chitinous outer lamella of the lower jaw is wholly or partly covered by a calcified deposit. Based on this evidence, the six lower jaws examined can be referred to the Coleoidea. The upper jaw shares common features with the upper jaws of modern and fossil coleoids, such as a posteriorly elongated inner lamella and a short outer lamella without a calcified rostral tip (see Clarke, 1986); accordingly, it is referred to the Coleoidea.

We followed the definitions given by Doyle et al. (1994) for higher taxonomy of coleoid cephalopods, and Clarke (1962, 1986), Clarke and Maddock (1988), and Tanabe et al. (2015b) for descriptive terms and measurements of coleoid jaws (Fig. 2).

4. Systematic paleontology

Subclass Coleoidea Bather, 1888
Superorder Octobrachia Fioroni, 1981
Order Vampyromorpha Robson, 1929
Family uncertain