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Late Cretaceous record of large soft-bodied coleoids based on lower jaw remains from Hokkaido, Japan

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The origin and phylogenetic relationships of most modern coleoid groups have not yet been explained by reliable fossil evidence, in large part because of the reduction or disappearance of a calcified chambered shell during their evolutionary history. Herein we describe two exceptionally large coleoid lower jaws from the Upper Cretaceous strata in Hokkaido, Japan. On the basis of the comparison of gross morphology and morphometric data of the lower jaws of modern and fossil coleoids, we assigned the two lower jaws to the following new taxa: *Nanaimoteuthis hikidai* sp. nov. of the order Vampyromorpha (superorder Octobranchia) and *Haboroteuthis poseidon* gen. et sp. nov. of the order Teuthida (superorder Decabranchia). The lower jaw of *N. hikidai* is distinguished from other species of the same genus from the Upper Cretaceous of Vancouver Island (Canada) and Hokkaido by having a broader, more anteriorly curved hood of the outer lamella. The lower jaw of *H. poseidon* seemingly exhibits mosaic features like those of modern teuthids and sepiids but is assigned to Teuthida on the basis of the overall shape of the outer lamella and the development of a distinct fold on the lateral wall. Because of the unusually large lower jaws, these new taxa appear to be comparable in body size to modern giant squids (*Architeuthis* spp.) and the Humboldt squid (*Dosidicus gigas*). This and other discoveries of large jaws referable to octobranchian and decabranchian coleoids from the Upper Cretaceous strata of the North Pacific fill the gap in the relatively poor fossil record of mainly soft-bodied coleoids.

Key words: Cephalopoda, Coleoidea, Vampyromorpha, Teuthida, jaws, Cretaceous, Hokkaido, Japan.

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Introduction

Cephalopod molluscs have been one of the dominant and highly diversified groups of marine invertebrates since the late Cambrian to the present (House 1988). This is confirmed by the abundant fossil record of chambered shells in externally shelled (ectocochleate) taxa such as Nautiloidea and Ammonoidea. In contrast, the fossil record of Coleoidea, a group that is largely characterised by an internally shelled (endocochleate) body plan, is much poorer than that of the ectocochleate cephalopods, other than the extinct taxa with an aragonitic phragmocone and calcitic rostrum (Belemnitida, Aulacocerida, and Phragmoteuthidida). This is because a calcified chambered shell has been much reduced to a

chitinous gladius or completely lost in most of the remaining group during their evolutionary history (Donovan 1977; Doyle et al. 1994; Fuchs 2006a; Kröger et al. 2011). For this reason, most previous studies on extinct coleoids lacking a chambered shell relied on extremely well-preserved fossils with soft tissue remains that were recovered from the Konservat-Lagerstätten of the late Palaeozoic to Cretaceous ages (e.g., Naef 1922; Donovan 1977; Donovan and Toll 1988; Fischer and Riou 1982a, b, 2002; Engeser and Reitner 1983, 1985, 1986; Engeser 1990a; Fuchs 2006a, b; Fuchs et al. 2009, 2013b; Fuchs and Larson 2011a, b).

The jaw apparatus, which is the primary feeding organ of cephalopods, appears to compensate for the relatively poor fossil record of Coleoidea because it has a preservation po-

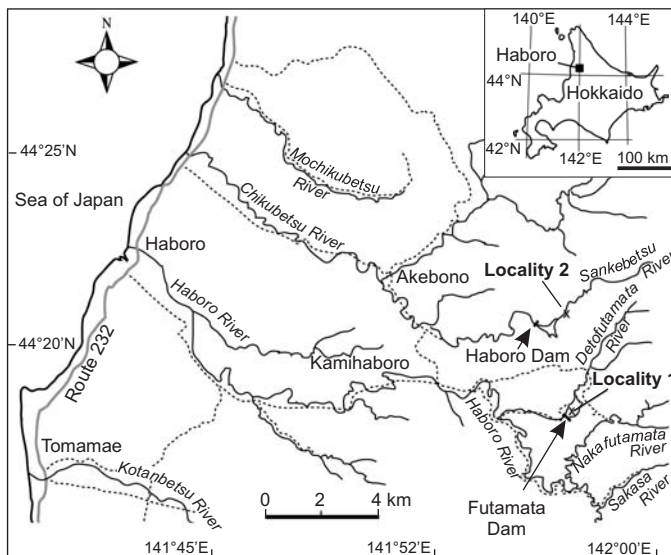


Fig. 1. Map of Haboro area, northwest Hokkaido, Japan, showing the locations of the coleoid lower jaws examined.

tential as a fossil even in taxa without a calcified chambered shell (Harzhauser 1999; Tanabe et al. 2006, 2008; Tanabe and Hikida 2010) and has been extensively used in taxonomical studies of modern fauna (Naef 1923; Clarke 1962, 1986; Clarke and Maddock 1988; Kubodera 2005). In modern cephalopods, the jaw apparatus consists of upper and lower elements (synonymous with beaks and mandibles) that are connected to each other by surrounding jaw muscles and housed within a globular-shaped muscular organ called the buccal mass in the proximal portion of the digestive tract (Nixon 1988; Tanabe and Fukuda 1999). The anterior portion of the upper and lower jaws is projected anteriorly to bite and cut prey, and chewed pieces of prey are conveyed to the oesophagus with the aid of the radula, which is accommodated in the space surrounded by the jaws (see Tanabe and Fukuda 1999: fig. 19.1). The jaw apparatus of modern coleoid cephalopods is made of a darkly tinted, organic hard tissue composed of a chitin-protein complex (Saunders et al. 1978; Hunt and Nixon 1981; Gupta et al. 2008), whereas in nautilids (*Nautilus* and *Allonautilus*), calcareous tips developed on the chitinous lamellae of upper and lower jaws (Saunders et al. 1978; Lowenstam et al. 1984). Fossilized chitinous and calcareous remains of cephalopod jaws have been discovered from the Devonian and younger marine deposits (Tanabe and Fukuda 1999; Tanabe et al. in press). They usually occur solitarily but are occasionally found in situ within the body chambers of ammonoids (e.g., Lehmann 1976, 1980, 1990; Tanabe and Landman 2002; Kruta et al. 2011; Tanabe et al. 2013) and nautilids (e.g., Dietl and Schweigert 1999; Klug 2001). Flattened jaws have also been preserved in situ in the buccal portion of exceptionally well-preserved late Palaeozoic and Mesozoic coleoid fossils retaining soft tissue remains (Saunders and Richardson 1979; Klug et al. 2005; Fuchs 2006a, b; Mapes et al. 2010; Fuchs and Larson 2011a, b). In addition to these flattened in situ jaws, unflattened isolated

jaws referable to Coleoidea have recently been found from the Upper Cretaceous forearc basin deposits of Hokkaido, Japan (Yezo Group), and Vancouver Island, Canada (Nanaimo Group). Their comparative morphological examination with the jaws of modern coleoids allowed us to distinguish the following new genera and species (Tanabe et al. 2006, 2008; Tanabe and Hikida 2010; Tanabe 2012): *Yezoteuthis giganteus* of the order Teuthida, *Nanaimoteuthis jeletzkyi* and *N. yokotai* of the order Vampyromorpha, and *Paleocirroteuthis haggarti* and *P. pacifica* of the order Cirroctopoda.

In the search for additional fossil material, we discovered two well-preserved coleoid lower jaws that we refer to here as another new species of *Nanaimoteuthis* and a new genus and new species of Teuthida from the Upper Cretaceous strata of Hokkaido. In this article, we describe the gross morphological and morphometric features of the jaws of these new taxa by comparing with those of modern coleoids and discuss the phylogenetic implications of the coleoid fauna from the Late Cretaceous of North Pacific.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CDM, Courtenary and District Museum and Palaeontology Centre, Courtenary, Canada; KMNH, Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan; NSM, National Museum of Nature and Science, Tsukuba, Japan; UMUT, University Museum of the University of Tokyo, Tokyo, Japan.

Other abbreviations.—HL, hood length of the lower jaw; ML, mantle length; RW, relative warp.

Material and recognition of jaw type

Two large cephalopod jaws that were recovered from Upper Cretaceous strata in the Haboro area of northwestern Hokkaido were used in this study. Both jaws were found individually in calcareous nodules; one (KMNH IvP 902,001) was collected from an outcrop exposed in the Detofutamata River before construction of the Haboro-futamata Dam (200 m north-northeast of the dam site; 44°18'19"N, 141°56'40"; Fig. 1: Locality 1), and the other (KMNH IvP 902,002) was recovered as float in the Sankebetsu River, about 1.2 km east-northeast of the Haboro Dam site (44°20'56"N, 141°56'35"; Fig. 1: Locality 2). KMNH IvP 902,001 came from the uppermost part of the Haborogawa Formation (Takashima et al. 2004), which was correlated to the Member Ui-j of the Nagareya Formation and dated the lower Campanian by Okamoto et al. (2003). The nodule that yielded KMNH IvP 902,002 was presumably derived from the upper part of the Haborogawa Formation (Takashima et al. 2004), which was correlated to the Member Uf-g of the Upper Haborogawa Formation and dated the upper Santonian by Moriya and Hirano (2001).

Since the two cephalopod jaws were preserved in calcareous nodules, their three-dimensional architecture is fa-

avourably preserved. The two jaws consist of outer and inner lamellae that are jointed together in the anterior portion, forming a sharply pointed tip. The outer lamella is gently arched and extended posteriorly, while the inner lamella is partly enclosed by the outer lamella and projected postero-ventrally. These features are commonly observed in the lower jaws of modern and fossil coleoids (Clarke 1986; Tanabe and Fukuda 1999; Neige and Dommergues 2002; Kubodera 2005; Tanabe 2012), indicating that the two jaws examined are identified as lower jaws of coleoids. Both lamellae are wholly composed of a black homogeneous material without any trace of calcification. We interpret that the lamellae were originally made of a chitin-protein complex as in those of modern cephalopod jaws (Saunders et al. 1978; Hunt and Nixon 1981; Gupta et al. 2008).

One of the two jaw specimens, KMNH IvP 902,001, is identified as a new species of *Nanaimoteuthis* Tanabe in Tanabe et al., 2008, of the order Vampyromorpha because it shares common generic features with other species of the same genus (see Diagnosis described in Systematic palaeontology). The other jaw specimen, KMNH IvP 902,002, seemingly exhibits mosaic features of the lower jaws of modern coleoids, especially sepiids and teuthids. To determine its higher taxonomic relationship, we performed morphometric analysis for the latter specimen with the lower jaws of 94 modern and 1 fossil coleoid species (listed in SOM 1: Supplementary Online Material available at http://app.pan.pl/SOM/app60-Tanabe_et_al_SOM.pdf), each represented by a single specimen. We followed Doyle et al. (1994) for higher systematics of coleoid cephalopods and Clarke (1962, 1986) and Clarke and Maddock (1988) for descriptive terms and measurements of a coleoid lower jaw (Fig. 2).

Morphometric analysis

Data source and methods

Geometric morphometrics is useful for detecting slight differences in shape among taxa with great within-group variation because it retains full geometric information on the spatial configuration of landmarks throughout analysis. In the present study, two-dimensional geometric morphometrics was used to assess among-species variation in the form of the lower jaw in extant and fossil coleoid species and to compare the specimen KMNH IvP 902,002 with Recent taxa.

Landmark and outline data were collected from photographs by Clarke (1986) and Kubodera (2005) and from photographs taken by us for the specimens housed at UMUT, AMNH, and CDM. Some of the latter specimens have been provided in Tanabe et al. (2008) and Tanabe (2012). Specimens were photographed from the right or left side using a digital camera, and the image was saved as a jpeg file. The left-side images were used for morphometric analysis, if available, and the right-side images were reflected to obtain reversed images prior to analysis. Eight landmarks were fixed

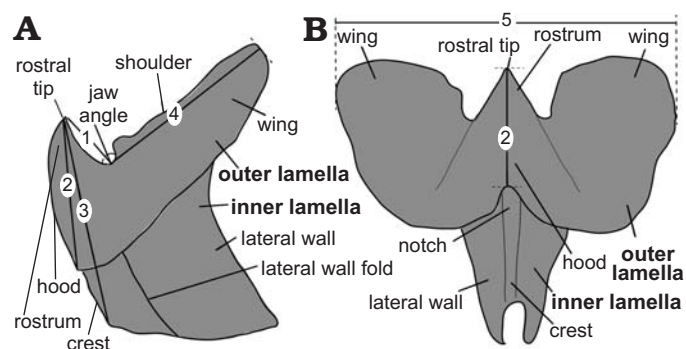


Fig. 2. Diagrammatic drawing of a coleoid lower jaw. Left lateral (A) and frontal (B) views. 1, rostral length; 2, hood length; 3, crest length; 4, wing length; 5, width of outer lamella. After Clarke (1962, 1986), see Clarke and Maddock (1988) for terms and measurements.

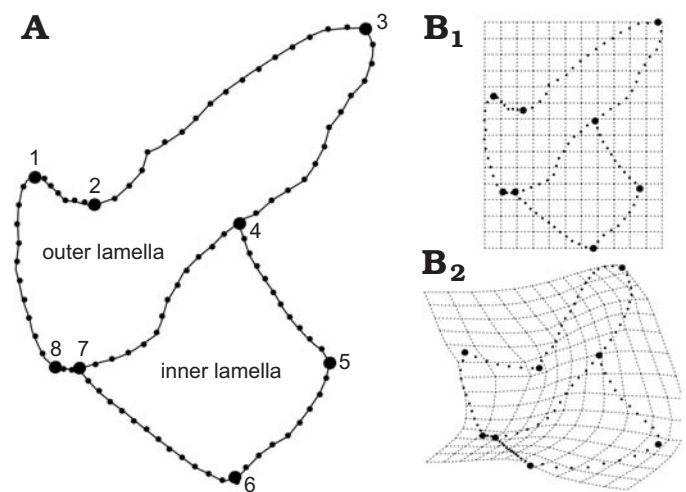


Fig. 3. Eight landmarks and 89 semi-landmarks collected on a coleoid lower jaw (A, B). 1, the rostral tip; 2, the base of the rostrum; 3, the posterior end of the wing; 4, the posterior intersection of the outer and inner lamellae; 5, the posterior end of the inner lamella; 6, the anteroventral end of the crest; 7, the anterior intersection of the outer and inner lamellae; 8, the anteroventral end of the hood. B. A square grid showing shape differences between two individuals as deformation from B₁ to B₂ drawn by use of a thin-plate spline.

on the surface of the lateral-side image of each jaw (Fig. 3A). Neige and Dommergues (2002) defined 10 landmarks on the lateral side of the lower jaw, but two were omitted in the present study because they were poorly defined in some specimens. Coordinates of all landmarks were collected on a computer image using the digitizing program DIGITIZER (Ubukata 2004). Each segment of the outline curve between neighbouring landmarks was equally spaced to define comparable points, or semi-landmarks, along the curve (Fig. 3A). Analysis using semi-landmarks allows us to simultaneously compare an outline curve with a landmark configuration (Bookstein 1997). The outline curves were digitized using the same computer program by locating a series of coordinate points along the curves, and sets of coordinate points were interpolated so that each segment was represented by a fixed number of equally spaced semi-landmarks (Ubukata 2003; Ubukata et al. 2010). A total of 89 semi-landmarks were used in addition to the eight fixed landmarks.

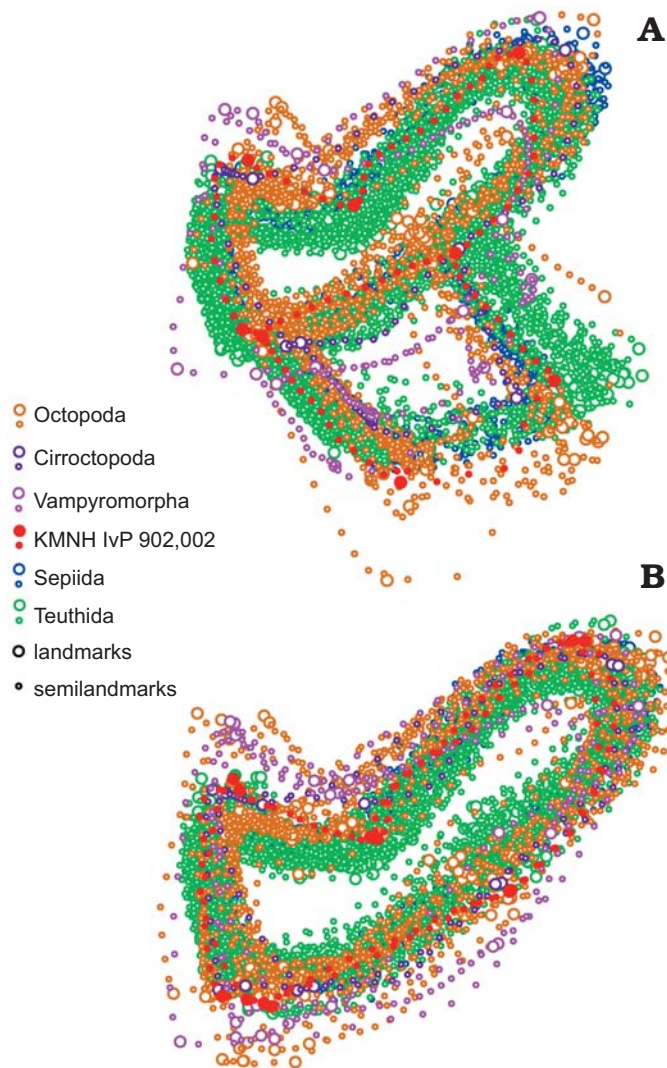


Fig. 4. All coleoid lower jaws registered by the generalized least squares superimposition. **A.** A full set of landmarks (large symbols) and semi-landmarks (small symbols). **B.** A subset of landmarks and semi-landmarks put along the outline of the outer lamella.

Centroid size (Bookstein 1991; Slice et al. 1996) was calculated for each specimen and was used for representing specimen size. A configuration of landmarks and semi-landmarks was translated, rotated, and scaled using generalized least squares (Rohlf and Slice 1990), allowing semi-landmarks to slide to minimize the bending energy of deformation (Bookstein 1997). The mean shape of all specimens was then calculated as the set of mean coordinates of landmarks and semi-landmarks of the aligned specimens by least squares superimposition. The shape of a specimen can be characterised by the deformation of its landmark configuration from the mean shape. An interpolation technique applied for coordinates of landmarks and semi-landmarks using the thin-plate spline function defines a deformation grid (Fig. 3B) for data of two shapes (Bookstein 1989, 1991; Rolf 1996). The thin-plate spline deformation from the mean shape of each specimen can be decomposed into a series of components, called partial warps (Bookstein 1989, 1991). Scores of the partial warps

for each specimen (partial warp scores) were then used as variables in principal component analysis (relative warp analysis) (Bookstein 1991; Rohlf 1993). Relative warps, which correspond to principal components, were estimated in each specimen to examine the variation in shape of the lower jaw.

The lower jaw consists of outer and inner lamellae, and the length and orientation of the inner lamella seem to be highly variable among the species examined. Generalized least squares superimposition adopted here is sensitive to large displacements at one or several landmarks (Zelditch et al. 2004). The “Pinocchio Effect”, a great change concentrated at one landmark with little at others, may considerably affect analytical results in the present case. Therefore, shape of the outer lamella, as well as gross jaw form, was also compared among species of different taxa. In this option, a subset of six landmarks and 64 semi-landmarks along the outline of the outer lamella was used for the analyses.

The morphometric analysis was performed using the computer program TPSRELW version 1.49 (Rohlf 2010). For sliding semi-landmarks, the default setting was used. In computing the partial warps, $\alpha = 0$ (Rohlf 1993) and the estimates of the uniform components by Rolf and Bookstein (2003) were included as an option of the TPSRELW program.

Results

Procrustes analysis.—A set of the lateral views of coleoid lower jaws were registered using Procrustes superimposition to visualize variation in shape. Procrustes analyses for the full set and a subset of landmarks and semi-landmarks both led to a similar result (Fig. 4). Teuthids generally have an outer lamella with a wide jaw angle and a great lower rostral length; the shape of the outer lamella shows remarkable interspecific variation with species of other orders. Interspecific shape variation appears to be greater in the inner lamella than in the outer lamella. Octopods tend to possess a longer crest than most teuthids (Fig. 4A). In KMNH IvP 902,002, the jaw angle is acute (ca. 80°), and the rostral length is relatively as large as the rostral lengths of modern teuthids. However, unlike typical teuthids, its shoulder is distinctly projected dorsally, and its ventral margin of the outer lamella is almost straight (Fig. 4B).

Relative warp analysis for the full data set.—The first relative warp (RW1) accounts for 46.48% of the total variance, and the first five relative warps together account for approximately 85% (SOM 2). RW1 mainly represents overall stretching or compression in the dorsoventral direction (Fig. 5A). As the score proceeds negatively along the RW1 axis, the outline of the lower jaw is compressed dorsoventrally, with a wider jaw angle and greater lower rostral length. In contrast, a jaw form accommodated in the positive RW1 area of the morphospace is characterised by dorsoventral elongation with a reduced rostrum. The second, and smaller relative warp (RW2) defines local shape variation. In the positive direction of RW2, the posterior ends of the wing are stretched posteriorly, but the outer lamella reduces its anterior, forming a dogleg shape (Fig. 5A). In the negative direction of RW2,

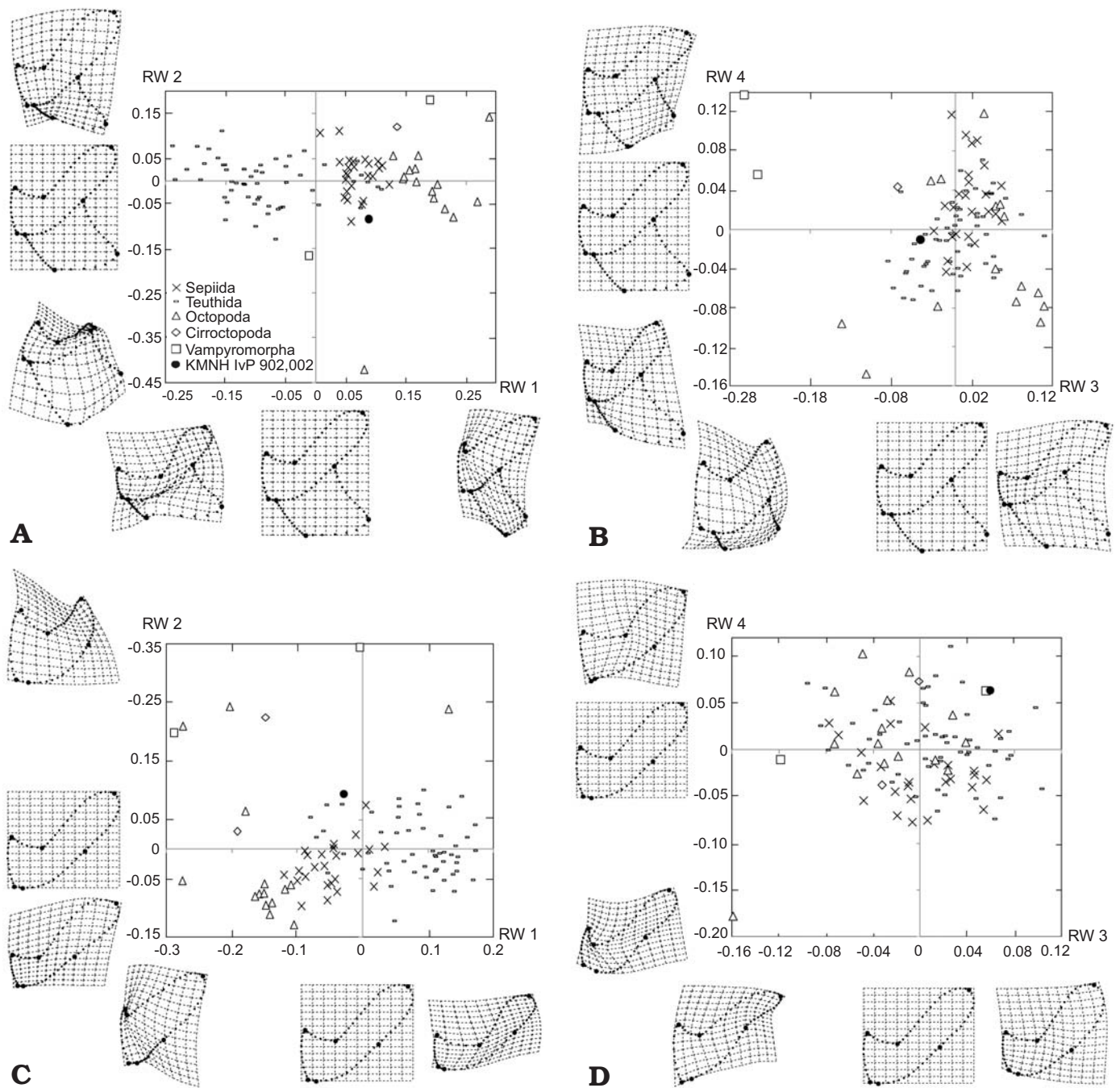


Fig. 5. Plots of the relative warp scores computed for the full set (A, B) or subset (C, D) of landmarks and semi-landmarks and the relative warps displayed as thin-plate splines. The lower and left grids show deformations from the mean shape (undeformed grid) corresponding to perturbations associated with RW1 and RW2, respectively (A, C) or RW3 and RW4, respectively (B, D).

the wing is largely reduced, while the outer lamella is greatly enlarged. The third relative warp (RW3) seems to correlate with the proportion of the inner lamella to the outer lamella as well as with the proportion of wing size to rostrum size. A specimen with a negative RW3 score tends to possess a short lateral wall of the inner lamella, covered mostly by the hood of the outer lamella and with a large rostrum, while a specimen with a positive RW3 score has a developed inner lamella with a flat cap of the outer lamella (Fig. 5B). The fourth relative warp (RW4) is closely related to the length of

the lateral wall (Fig. 5B). As RW4 score decreases, the lateral wall is elongated posteroventrally, and the outer lamella is anteroposteriorly compressed. A positive perturbation along the RW4 axis reduces the lateral wall and elongates the wing.

RW1 fairly separates higher taxa of coleoids. Most teuthids (>85%) have RW1 scores lower than 0.02, while all sepiids examined, excluding *Sepia longipes*, have RW1 scores higher than 0.02 (Fig. 5A). Most species of Octopoda, Cirroctopoda, and Vampyromorpha, all of which are included in the superorder Octobranchia, occupy the larger RW1 re-

gion than the species of Teuthida and Sepiida of the superorder Decabrachia (>0.12). Compared to RW1, RW2 seems useless for higher taxonomy. *Stauroteuthis* sp., an octopod species, has by far the lowest RW2 scores of any coleoid species. Except for this species, species of Vampyromorpha and Cirroctopoda have extreme RW2 values. In RW1–RW2 morphospace, KMNH IvP 902,002 is located near the region predominantly occupied by decabrachian species (sepiids, octopods, and teuthids) and has a higher RW1 score (0.0885) than most teuthid species (Fig. 5A).

In RW3–RW4 morphospace, all the decabrachian species occupy the central region and are surrounded by octobranchian species, most of which have forms that are quite different from the mean shape (Fig. 5B). This result indicates high variability in the lower jaw morphology of octopuses. KMNH IvP 902,002 is distributed at the periphery of the decabrachian species and has a lower RW3 value than any sepiid species.

Relative warp analysis for subset data on the outer lamella.—RW1 accounts for 44.63% of the total variance, and the first five relative warps together account for approximately 88% (SOM 2). As in the result for the full data set, RW1 also represents stretching or compression in the dorsoventral direction and relative size of the rostrum, although the positive direction of the RW1 axis is reversed in this case (Fig. 5C). RW2 for the subset data corresponds to RW3 for the full data set, i.e., the proportion of wing size to rostrum size. RW3 for the subset data is characterised by compression of the anterior hood and posterior wing (Fig. 5C). The anterior part of the hood is slightly compressed when the RW3 score is positive, whereas the negative perturbation of RW3 reduces the posterior part of the wing. The individual characterised by a positive RW4 score tends to have a well-developed shoulder and a straight ventral margin with great lower rostral length.

Most octobranchian species examined have lower RW1 (less than -0.1) scores than the decabrachian species (Fig. 5C). KMNH IvP 902,002 is accommodated near the origin of the RW1–RW2 morphospace, which is occupied by teuthids as well as by sepiids. This specimen has one of the highest RW2 scores among the decabrachian species. Neither RW3 nor RW4 separates higher taxa of coleoids (Fig. 5D).

Our two-dimensional geometric morphometric suggests that the higher taxonomic relationship of KMNH IvP 902,002 is assigned to the Decabrachia because its morphometric features are more similar to extant decabrachian species than to modern and fossil octobranchian species, especially in the overall shape of the outer lamella. The other characteristic feature observed in KMNH IvP 902,002 is the development of a distinct fold on the lateral wall (see Systematic palaeontology). In modern decabrachian coleoids, this feature is recognised in many genera of Teuthida, such as *Lepidoteuthis* (Octopoteuthidae), *Histioteuthis* (Histioteuthidae), and *Cycloteuthis* (Cycloteuthidae) (Clarke 1986; Kubodera 2005), but does not occur in the lower jaws of Sepiida, Sepiolida, and Spirulida (Clarke and Maddock 1988: fig. 2). For these reasons, we assign the higher taxonomic position of KMNH IvP 902,002 to Teuthida.

Systematic palaeontology

Subclass Coleoidea Bather, 1888

Superorder Octobrachia Fioroni, 1981

Order Vampyromorpha Robson, 1929

Family uncertain

Genus *Nanaimoteuthis* Tanabe in Tanabe et al., 2008

Type species: *Nanaimoteuthis jeletzkyi* Tanabe in Tanabe et al., 2008; Lower Campanian (Upper Cretaceous) Pender Formation, about 10 km northwest of Courtenay, north-central Vancouver Island, Canada.

Species included: *Nanaimoteuthis jeletzkyi* Tanabe, 2008, from the lower Campanian of Vancouver Island, Canada (Tanabe et al. 2008), and the Haboro area, northwestern Hokkaido, Japan (AM unpublished data), and *N. yokotai* Tanabe and Hikida, 2010, from the Turonian of the Tappu (Obira) and Nakagawa areas, Hokkaido (Tanabe and Hikida 2010), and *Nanaimoteuthis hikidai* sp. nov.

Emended diagnosis.—Large lower jaw characterised by large outer lamella with very high wing fold, very broad hood that is prominently convex anteriorly without notch, weakly expanded wing, and short rostrum with pointed hook; short inner lamella with crest portion mostly covered by outer lamella, and lateral wall without fold or ridge.

Discussion.—Vampyromorphid coleoid lower jaws comparable in overall morphology and size to those of the present genus are hitherto unknown in the fossil record. However, large gladii of vampyromorphid genera *Tusoteuthis* Logan, 1898, of the suborder Mesoteuthina Naef, 1921, and *Actinosepia* Whiteaves, 1897, of the suborder Teudopseina Starobogatov, 1983, have been reported from the Campanian strata of Vancouver Island (Fuchs et al. 2007) in addition to the Campanian and Maastrichtian rocks in the Western Interior Province of North America (Whiteaves 1897; Logan 1898; Waaage 1965; Nicholls and Isaak 1987; Larson 2010). The extremely large lower jaws of *Nanaimoteuthis* and gladii of *Tusoteuthis* and *Actinosepia* seem to suggest their taxonomic affinity, but this hypothesis should be verified from future discoveries of exceptionally well-preserved fossils showing a gladius-jaw apparatus association.

Stratigraphical and geographical range.—The genus *Nanaimoteuthis* has been reported from the Turonian to the Campanian rocks of Vancouver Island, Canada (Tanabe et al. 2008), and Hokkaido, Japan (Tanabe and Hikida 2010; Tanabe 2012; this paper).

Nanaimoteuthis hikidai sp. nov.

Fig. 6A–E.

2012 *Nanaimoteuthis* sp. nov.; Tanabe 2012: fig. 4-3a, b.

Etymology: Named for the palaeontologist Yoshinori Hikida (Nakagawa Museum of Natural History, Nakagawa, Hokkaido) in recognition of his significant contribution to the studies of Cretaceous molluscs from Hokkaido.

Holotype: KMNH IvP 902,001, a lower jaw, the only specimen available.

Type locality: A riverside outcrop in the Detofutamata River, now under the Futamata Reservoir, about 200 m north-northeast from the Haboro-futamata Dam site, Haboro, northwestern Hokkaido, Japan (Fig. 1: Locality 1).

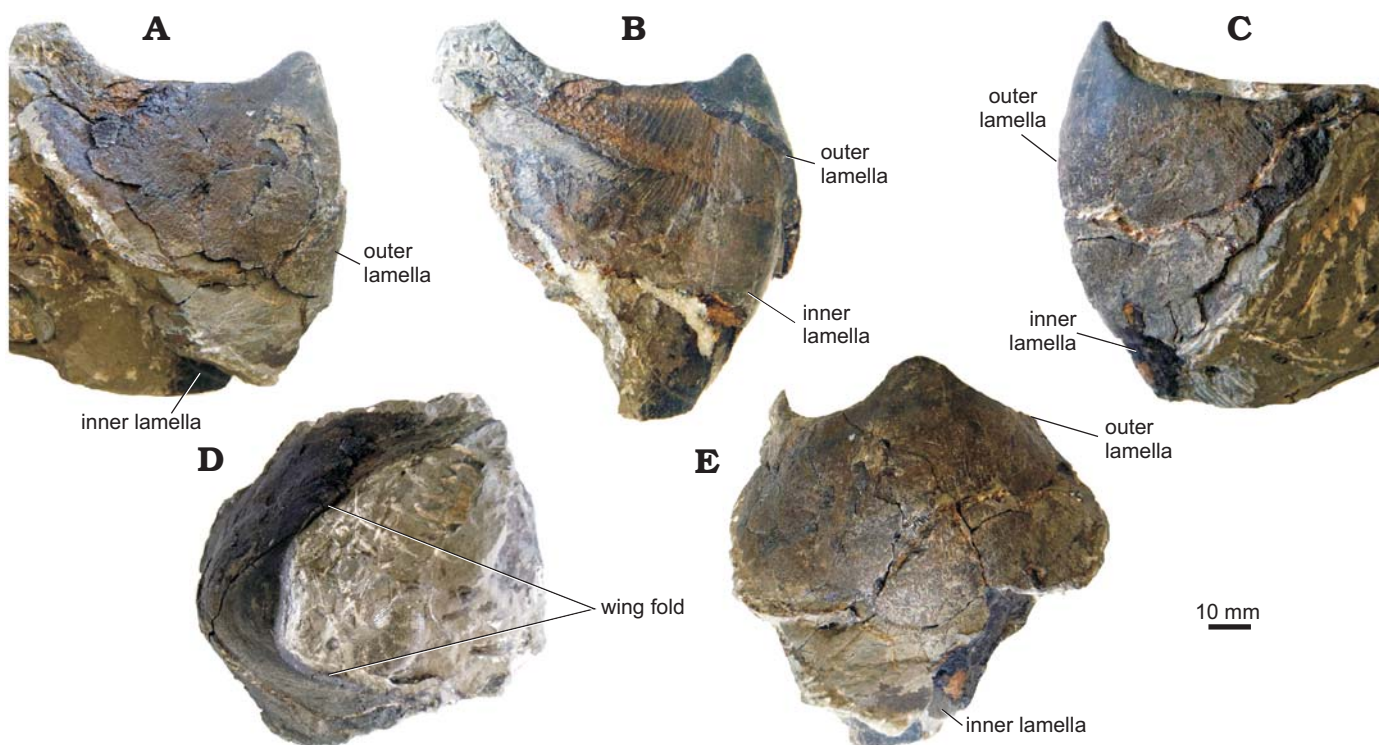


Fig. 6. Octobranchian coleoid *Nanaimoteuthis hikidai* sp. nov. KMNH IvP 902,001, holotype, a lower jaw; early Campanian, Late Cretaceous, Haboro area, Hokkaido, Japan. Right lateral (A), left lateral (C), dorsal (D), and frontal (E) views, and right lateral view after removing part of outer lamella (B).

Type horizon: The Member Ui-j, the uppermost part of the Haborogawa Formation, lower Campanian, Upper Cretaceous.

Diagnosis.—Large lower jaw characterised by well-developed thick outer lamella with high wing fold, very obtuse jaw angle, long and gently arched hood with convex anterior margin, short rostrum with more or less pointed hook; relatively short inner lamella without ridge and fold, with crest portion mostly covered by outer lamella, and lateral wall lacking fold and ridge and instead sculptured by many fine radial striations.

Description.—Lower jaw extremely large, consisting of almost equally sized thick inner and outer lamellae, both of which are made of black, presumably originally chitinous material; rostrum short but sharply pointed with ridge-line-like hook. Outer lamella 3.1 mm thick in rostral region (much thicker than inner lamella), 1.2 mm thick in lateral wall portion, expanded laterally with large open angle of paired wings approximately 115° , with very high wing fold (see Fig. 6D) and very long hood without notch; hood profile from lateral side gently arched anteriorly; wing shortly expanded posteriorly; jaw angle very obtuse (approximately 140°). Inner lamella weakly expanded posteroventrally, crest portion covered by outer lamella over 85% in profile from lateral side; crest narrowly rounded, and lateral wall lacking radial ridge and fold. Both outer and inner lamellae sculptured by many radial striations; those on inner lamella much stronger than those on outer lamella.

Measurements.—Crest length 90.4 mm, wing length 51.1

mm, hood length 78.4 mm, rostral length 13.0 mm, width of outer lamella ca. 87 mm.

Remarks.—The lower jaw of the present species is similar to that of *N. jeletzkyi* from the lower Campanian Pender Formation of the Nanaimo Group of Vancouver Island (Tanabe et al. 2008: figs. 3, 4; Tanabe 2012: fig. 4-1) in overall shape and ornamentation but distinguished from the latter by having a less posteriorly expanded inner lamella and a broader, more anteriorly curved hood portion of the outer lamella. The lower jaw of the present species resembles the lower jaws of *N. yokotai* Tanabe and Hikida, 2010, from the Turonian in the Tappu (Obira) and Nakagawa areas of northern Hokkaido (Tanabe and Hikida 2010: 146, fig. 1) in overall shape, but the latter have a much smaller open angle of paired wings and a shorter inner lamella in relation to the outer lamella.

In modern coleoids, the lower jaw size has a linear relationship with mantle length (Clarke 1962, 1986). In *Vampyroteuthis infernalis* Chun, 1903, the sole living species of the order Vampyromorpha, mature males have approximately 2 kg total body weight and 100 mm mantle length (Pickford 1949), and the relationship between mantle length (ML , in mm) and hood length of the lower jaw (HL , in mm) is approximated by the following equation: $ML = 9.02 HL - 5.8$ (Clarke 1986). When applying the relationship to the holotype of the present new species, its owner would have had a mantle length of approximately 700 mm.

Stratigraphical and geographical range.—Type locality and horizon only.

Superorder Decabrachia Boettger, 1952

Order Teuthida Naef, 1916

Family uncertain

Genus *Haboroteuthis* nov.

Type species: *Haboroteuthis poseidon* sp. nov., see below.

Etymology: After Haboro, a town near to the type species locality.

Diagnosis.—Large lower jaw characterised by long rostrum with sharply pointed tip (hook), dorsally convex shoulder, relatively narrow hood weakly convex anteriorly with distinct radial notch on lateral side, long and anteriorly weakly curved crest, and long lateral wall that is parallelogram-shaped in lateral view and with relatively broad fold.

Discussion.—The lower jaw of the present new genus exhibits mosaic features of modern teuthids and sepiids, such as the modern teuthids *Nototodarus* of Ommastrephidae (Clarke 1986: fig. 28) and *Onychoteuthis* of Onychoteuthidae (Clarke 1986: fig. 32), in which the outer lamella is characterised by a long rostrum with a sharply pointed tip, a dorsally arched shoulder, and a relatively short hood; however, the inner lamella of the present genus is more elongated posteroventrally than that of modern teuthids, which have an inner lamella with a short parallelogram- or rhomboidal-shaped lateral wall. The lower jaw of the present genus resembles that of modern sepiid and sepiolid genera in having a long parallelogram-shaped lateral wall in the inner lamella but is distinguished from the latter in the development of a lateral wall fold (Clarke 1986; Clarke and Maddock 1988; Kubodera 2005).

Lower jaws comparable in size and overall shape to those of the present genus are thus far unknown in the fossil record. However, there is a possibility that the present genus is congeneric with *Yezoteuthis* Tanabe, Hikida, and Iba, 2006, a monospecific teuthid genus represented by a single species, *Y. giganteus*; this species was proposed based on a large upper jaw from the lower Campanian of the Nakagawa area, Hokkaido. This hypothesis might be verified from co-occurring upper and lower jaws that are comparable to the holotypes of the type species of the two genera. Such co-occurrence of upper and lower jaws would be confirmed in stomach and coprolite remains of their probable predators such as large Cretaceous marine reptiles.

Fossil records of coleoid shell remains are also important when considering taxonomic affinity with the present genus. Shell remains of the following Late Cretaceous coleoid genera other than Belemnnoidea and Octobrachia have been described previously; *Naefia* Wetzel, 1930, from the Maastrichtian of Chile (Wetzel 1930) and possibly from the Campanian of Antarctica (Wetzel 1930; Stilwell and Zinsmeister 1987) and California (Hewitt et al. 1991); *Cyrtobelus* Fuchs, Keupp, Trask, and Tanabe, 2012, from the upper Campanian to the upper Maastrichtian of Vancouver Island, British Columbia, Canada, and West Greenland (Fuchs et al. 2012); *Groenlandibelus* Jeletzky, 1966, from the upper Maastrichtian of Greenland (Birkelund 1956; Fuchs et al. 2012, 2013a); and *Longibelus* Fuchs, Iba, Ifrim, Nishimura, Kennedy, Keupp, Stinnesbeck,

and Tanabe, 2013 from the Aptian of the Caucasus (Doguzhaeva 1996), the Albian of South Africa and southern India, and the Cenomanian–Maastrichtian of Japan (Hirano et al. 1991; Hewitt et al. 1991; Fuchs and Tanabe 2010), southern India (Doyle 1986), Mexico (Ifrim et al. 2004), and Alaska. Among these genera, the former three were included in either the order Sepiida (Jeletzky 1966) or the order Spirulida (Fuchs et al. 2012, 2013a), while *Longibelus* was assumed to be a taxon linking the Belemnnoidea and the early Decabrachia (Fuchs et al. 2013a). Although jaws and a complete proostracum are unknown, all these genera are represented by small phragmocones, usually less than 10 cm in length, suggesting their smaller body size than *Haboroteuthis*.

Stratigraphical and geographical range.—The genus *Haboroteuthis* is known to occur in the upper Santonian rocks of the Haboro area, Hokkaido, Japan (this paper).

Haboroteuthis poseidon sp. nov.

Fig. 7A–D.

Etymology: Named for Poseidon, the god of the sea in Greek mythology.

Holotype: KMNH IvP 902,002, a lower jaw.

Type locality: Recovered as float in the Sankebetsu River, about 1.2 km east-northeast of the Haboro Dam site, Haboro, northwestern Hokkaido, Japan (Fig. 1: Locality 2).

Type horizon: Possibly derived from the upper part of the Member Uf-g in the upper part of the Haborogawa Formation, upper Santonian.

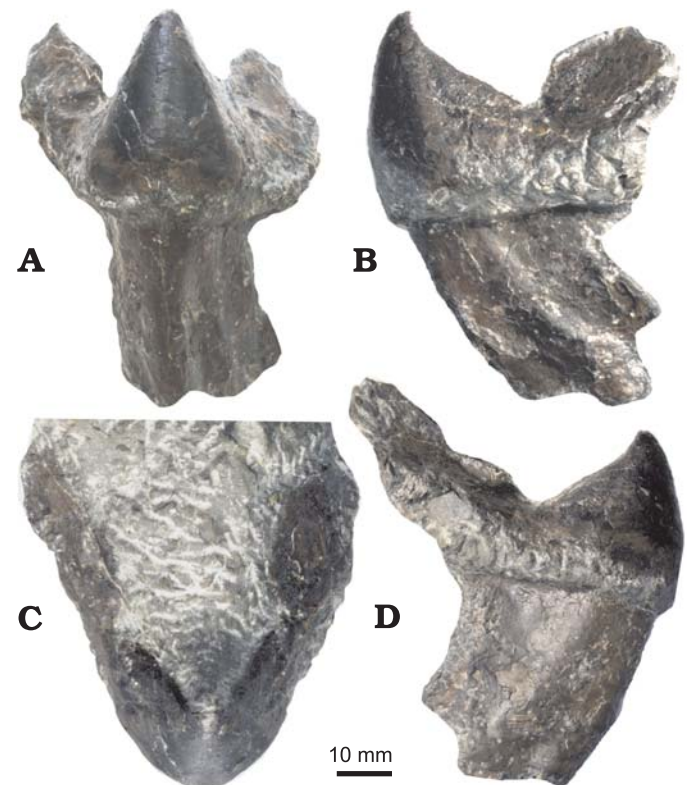


Fig. 7. Decabrachian coleoid *Haboroteuthis poseidon* gen. et sp. nov. KMNH IvP 902,002, holotype, a lower jaw; late Santonian, Late Cretaceous, Haboro area, Hokkaido, Japan. Frontal (A), left lateral (B), dorsal (C), and right lateral (D) views.

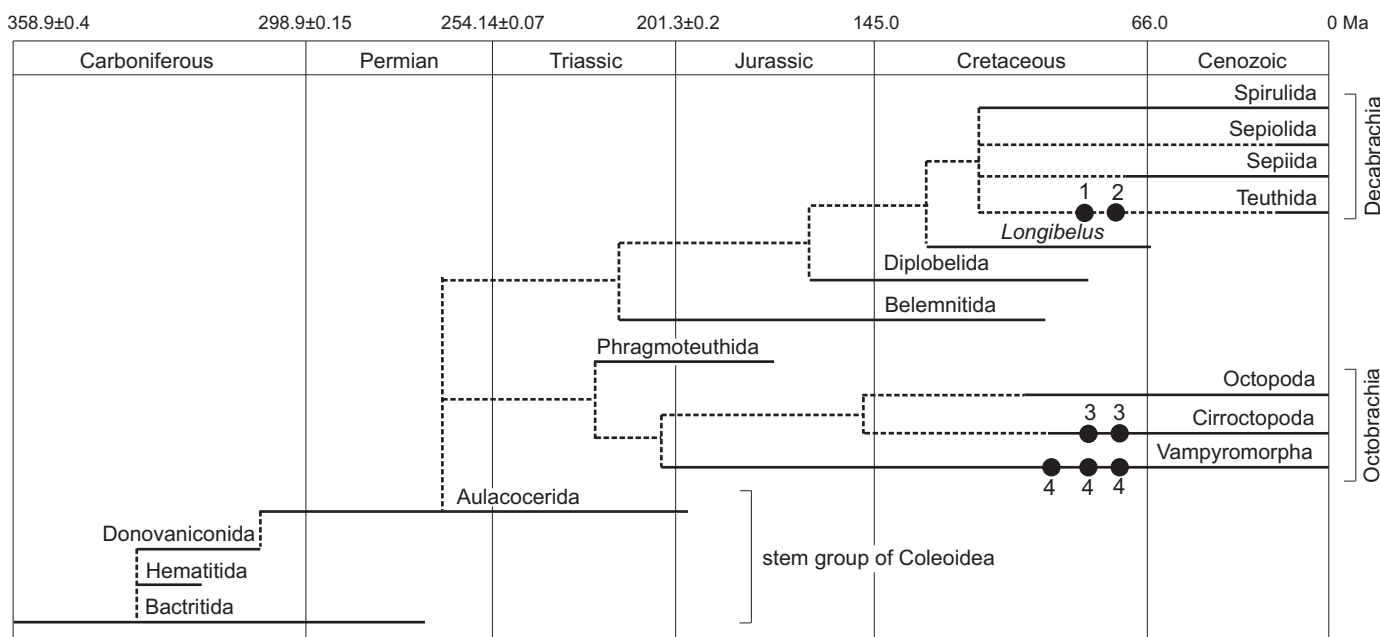


Fig. 8. Phylogenetic relationships of fossil and modern coleoid major taxa compiled from the data by Kröger et al. (2011: fig. 5) and Fuchs et al. (2013: fig. 12). Fossil records of Cretaceous decabrachian and octobranchian coleoids from the North Pacific region are given in black circles. 1, *Haboroteuthis* (this study); 2, *Yezoteuthis* (Tanabe et al. 2006); 3, *Paleocirroteuthis* (Tanabe et al. 2008); 4, *Nanaimoteuthis* (Tanabe et al. 2008; Tanabe and Hikida 2010; this study). Age after Cohen et al. (2012).

Diagnosis.—Same as for the genus, by monotypy.

Description.—Lower jaw large, consisting of moderately open outer lamella and posteriorly elongated inner lamella, both of which are fused together in the anterior portion, forming a sharply pointed rostral tip; they are made up of black, presumably originally chitinous material; outer lamella weakly expanded laterally with open angle of paired narrow wings, approximately 60° , with dorsally arched shoulder and relatively narrow hood with distinct radial notch on lateral side; hood covers 35% of crest in profile from lateral side; hood line weakly convex anteriorly; wing prominently expanded posteriorly; jaw angle acute, approximately 80° . Inner lamella remarkably expanded posteroventrally with narrowly rounded anterior margin; crest line weakly convex anteriorly; lateral wall parallelogram-shaped in lateral view, ornamented with relatively broad fold.

Measurements.—Crest length 63.1 mm, wing length 31.1 mm, hood length 30.0 mm, rostral length 25.7 mm, width of outer lamella 49.0 mm.

Remarks.—The lower jaw of the present new species has a crest length of 63.1 mm, which is larger than the lower jaws of known modern coleoids. For example, in adult specimens of the giant squid *Architeuthis kirki* Robson, 1887, of Architeuthidae, captured off Chatham Rise, New Zealand, with a total body length of approximately 7.7 m (AMNH 291938), and of the Humboldt squid *Dosidicus gigas* Orbigny, 1835, of Ommastrephidae, captured off Baja California, Mexico, with a mantle length of 1.5 m (UMUT 31004), the lower jaws have crest lengths of 47.5 mm and 50.2 mm, respectively (see Tanabe 2012: fig. 3-1, 2). This rough comparison

suggests that the present new species undoubtedly had an extremely large body size comparable to that of modern giant squids.

Discussion

Modern coleoid cephalopods are currently classified into two superorders, Decabrachia Boettger, 1952 (10 arms, fourth pair modified as tentacles), and Octobrachia Fiorini, 1981 (= Vampyropoda Boletzky, 1992) (10 arms, second pair modified or lost) (Doyle et al. 1994). The superorder Decabrachia includes four orders (Spirulida, Sepiida, Sepiolida, and Teuthida), and the superorder Octobrachia includes three orders (Octopoda, Cirroctopoda, and Vampyromorpha) (Doyle et al. 1994: table 1). Molecular clock analysis of modern coleoids using different genes, models, and software suggested a Palaeozoic origin for the coleoid crown (Strugnell et al. 2006; Bergmann et al. 2006; Warnke et al. 2011; Kröger et al. 2011). Although divergence time estimates of the coleoid crown do not match among researchers (453 ± 60 Ma, Ordovician/Silurian boundary interval, Warnke et al. 2011; 415 ± 24 Ma, early Palaeozoic, Bergmann et al. 2006; 276 ± 75 Ma, early to middle Permian, Kröger et al. 2011), they are congruent at several points with the available fossil record (see Kröger et al. 2011: fig. 5). For these reasons, the origin and phylogenetic relationships of individual modern coleoid orders are still controversial.

Well-preserved coleoid fossils with squid-like compressed soft tissue remains (“fossil teuthids”) are known to occur episodically from the Konservat-Lagerstätten of the

late Palaeozoic to Cretaceous ages (Naef 1922; Fischer and Riou 1982a, b, 2002; Fuchs 2006a, b; among others). These “fossil teuthids” sometimes exhibit a mosaic distribution of characteristic features of modern Decabrachia and Octobranchia (see discussion by Vecchione et al. 1999); hence, they have been mostly placed in Decabrachia and Octobranchia (Naef 1922; Donovan 1977; Doyle et al. 1994; Young et al. 1998; Vecchione et al. 1999) or in Octobranchia (Bandel and Leich 1986; Engeser and Bandel 1988; Engeser 1990a, b; Haas 2002; Fuchs 2006a). This discrepancy among previous researchers contributes greatly to the different evaluations of the arm structures and gladii preserved as fossils. Concerning the origin of Decabrachia, Fuchs et al. (2013a) suggested that the Cretaceous belemnoid-like phragmocone-bearing coleoid *Longibelus*, which has a marginal siphuncle, stripe-like dorsal attachment scars, and a poorly developed layer of tabular nacre, represents a sister taxon of the decabrachian clade comprising modern Spirulida, Sepiida, and Teuthida. Meanwhile, Tanabe et al. (2006) described an extremely large coleoid upper jaw from the Campanian (Upper Cretaceous) of Hokkaido as a new genus and species (*Yezoteuthis giganteus*) and assigned its higher taxonomic position as Teuthida based on cladistic analysis of several characters with modern cephalopods.

This study and others (Tanabe et al. 2006, 2008; Tanabe and Hikida 2010; Tanabe 2012) on the jaws from the Upper Cretaceous of Hokkaido and Vancouver Island (Canada) fill the gap in the relatively poor fossil record of the mainly soft-bodied coleoids (Fig. 8).

Conclusions

On the basis of the comparison of gross morphology and morphometric data of the lower jaws of modern and fossil coleoids, two extremely large lower jaws that were recovered from the Upper Cretaceous strata in Haboro area, Hokkaido, Japan, were assigned to the following new taxa: *Nanaimoteuthis hikidai* sp. nov. of the order Vampyromorpha (superorder Octobranchia) and *Haboroteuthis poseidon* gen. et sp. nov. of the order Teuthida (superorder Decabrachia). Because of the unusually large lower jaws, these new taxa appear to be comparable in body size to modern giant squids (*Architeuthis* spp.) and the Humboldt squid (*Dosidicus gigas*). This and other discoveries of large jaws referable to octobranchian and decabrachian coleoids from the Upper Cretaceous strata of the North Pacific fill the gap in the relatively poor fossil record of mainly soft-bodied coleoids and demonstrate that large non-belemnoid coleoids existed in this bioprovince during that time.

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