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Original Article  
~~~~~New Vampyromorph (Coleoidea: Cephalopoda) jaw apparatuses  
from the Late Cretaceous of JapanYasumitsu KANIE
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Abstract

Some cephalopod jaw remains predated by a Late Cretaceous Elasmosaurid are identified as those of a vampyromorph species. They are described as *Provampyroteuthis giganteus*, gen. et sp. nov. herein. Lower and upper jaws are distinguishable. The lower jaw is more similar to that of modern *Nautilus* than *Vampyroteuthis*, whereas the upper jaw resembles that of Octopoda and Vampyromorpha. No calcareous covering is observed. The jaw apparatus of this species is considerably larger than that of *Vampyroteuthis infernalis*. The new discovery of *Provampyroteuthis* indicates that the evolutionary history of Vampyromorpha dates back to early Santonian.

Key words : *Provampyroteuthis*, *Vampyroteuthis*, Cephalopoda, Plesiosaur, Cretaceous

Introduction

Fossil information on extinct coleoid groups is very poor except for the Belemnitida, Aulacoceratida and Phragmoceratida. Among them, the living dibranchiate cephalopods are Decapoda and Octopoda. Only one representative of the Vampyromorpha, *Vampyroteuthis infernalis* Chun, seems to be the common ancestor of modern dibranchiates (Pickford, 1946; 1949), presumed to originate in the Jurassic by way of the Phragmoteuthida, then Loligosepiina (Donovan, 1977). Jeletzky (1966) believed that the Loligosepiina appeared to represent the common root of most known Teuthid except the Vampyromorphina. The Vampyromorphina was placed under the order Teuthida based on anatomical consideration. Dzik (1986) has illustrated an upper jaw from the Middle Jurassic of Poland and it probably belongs to the Teuthida or Vampyroteuthida, and unsolved because of the poor fossil evidence. Phylogenetic

history of these group is, however still puzzling.

Matsumoto *et al.* (1982) reported some cephalopod jaw specimens (Obira specimen no. 1) without taxonomic identification which occurred together with gastoliths of an Elasmosaurid. As the result of the present further examination, it is concluded that the specimens may be attributed to the jaw apparatuses of a vampyromorph cephalopod based on similarity to those of modern *Vampyroteuthis infernalis*. This is the first discovery of vampyromorph remains from the Cretaceous rocks.

In the present article, I describe the vampyromorph jaws. Inferred interaction between the prey (Vampyromorpha) and the predator (*Elasmosaurus*) was already shown in Kanie *et al.* (1998)

The depositories of the specimens examined are as follows (abbreviations are shown in parentheses).

Yokosuka City Museum (Yokosuka 238–0016 : YCM)

Department of Earth and Planetary Sciences,

Kyushu University (Fukuoka 812-0053 : GK)

Obira specimen no. 1 (M. Tatematsu's private collection, 4-26-2, Takemi-cho, Mizuho-ku, Nagoya 467-0043 : MT)

H. Kokubu's private collection (264-1, Honcho, Mikasa 068-2141 : Ra)

Obira specimen no. 2 (A. Hamamoto's private collection, 2, E1, Suehiro, Asahikawa 071-8121 : Hm)

Comparison with fossil and modern cephalopod jaws

Materials. The Obira sample is composed of 15 jaw fragments : four of them are upper jaws and two are lower ones. Two pairs of the upper and lower jaws were found in close association (Figure 2-1, 4). Size reconstruction is possible on the basis of comparison with jaws of modern coleoids.

The terminology of modern coleoid jaws is followed from Clarke (1962, 1986) and the measurements are partly adapted from Kanie (1982a).

General comparison. As described below, the Obira specimen no. 1 is distinguished from hitherto known jaw apparatuses of Cretaceous ammonites in Japan by the difference in the lower jaw and the absence of calcareous covering, from *Nautilus* by the absence of calcareous covering, and from modern coleoids except for Vampyromorpha by the difference in reduced lateral wall of the lower jaw (Figures 4, 5).

Identification of the Endocochlia and Ectocochlia. All of the Cephalopoda have a jaw apparatus. The lamellae of the jaw plates of the Endocochlia are made from chitinous substances (Saunders *et al.*, 1978 ; Lowenstam *et al.*, 1984), although the lamellae of *Nautilus*, the only representative of living Ectocochlia, are usually composed of a chitinous layer with calcareous coverings (Figure 5). The calcareous coverings make up denticles at the rostra. The denticle made of calcite and calcareous covering on the lamellae is aragonite.

If the specimen belongs to Endocochlia, the calcareous covering should be absent. While, in the Endocochlia, it is unknown whether the dissolution of calcareous layer by Elasmosaurid gastric juice occurred or not. In a specimen GK.H 8094 (=RH1242b) collected by S. Toshimitsu from the Lower Santonian of the

Haboro area, preserved maximum length is 20.8 mm. Wing (rostral part) angle is 45° by Kanie (1982a). Calcareous covering of the lamella is, however, considered to have been originally absent because calcic shells of *Polyptychoceras* sp. and *Sphenoceramus naumanni* are preserved in the same calcareous nodule (Figure 3A).

Another jaw specimen Ra2 collected by H. Kokubu from the Lower Santonian of the Obira area, is associated with calcic shells of *Tetragonites glabrus*, *Damesites damesi*, *Kitchnites ishikawai*, and *Polyptychoceras* sp. (Figure. 3B).

Therefore, the Obira specimen no. 1 must belong to the Endocochlia. In short, it is regarded as jaw apparatuses of an undescribed vampyromorph. The jaw morphology of modern Vampyromorpha is illustrated for the comparison (Figure 4).

Description of new vampyromorph jaws

Order VAMPYROMORPHA Pickford, 1936

Family VAMPYROTEUTHIDAE Thiere, 1915

Provampyroteuthis, gen. nov.

Type species. *Provampyroteuthis giganteus*, sp. nov.

Generic diagnosis of the jaw. Jaw is composed of upper and lower apparatuses. Lamellae are made of black film. No calcareous covering in the anterior part of the lamellae (rostra). Body size of the type species was much larger than that of living *Vampyroteuthis infernalis*. Upper jaw is smaller than lower one. Soft parts are unknown.

Upper jaw is smaller than that of modern *Nautilus* species in the presence of wings and hood cover reduced lateral wall and round crest.

Comparison. The basic morphology of *Provampyroteuthis* jaw is similar to that of modern *Vampyroteuthis* except for the reduced crest and lateral wall in the lower jaw. It is similar to the jaws of extant *Nautilus* and some Cretaceous ammonites, *Gaudryceras* and *Tetragonites*, but the surface of the rostrum and wing of these genera are covered by calcareous layers. Uncalcified upper jaw with sharp jaw angle from Lukow of the Middle Jurassic was regarded as Teuthida or Vampyroteuthida by Dzik (1986, figure 3A, 3B). Naef (1922, figure 42f) named the upper jaw from the Solnhofen Upper Jurassic as *Plesioteuthis prisca*, and judged vampyroteuthid because of similarity to the

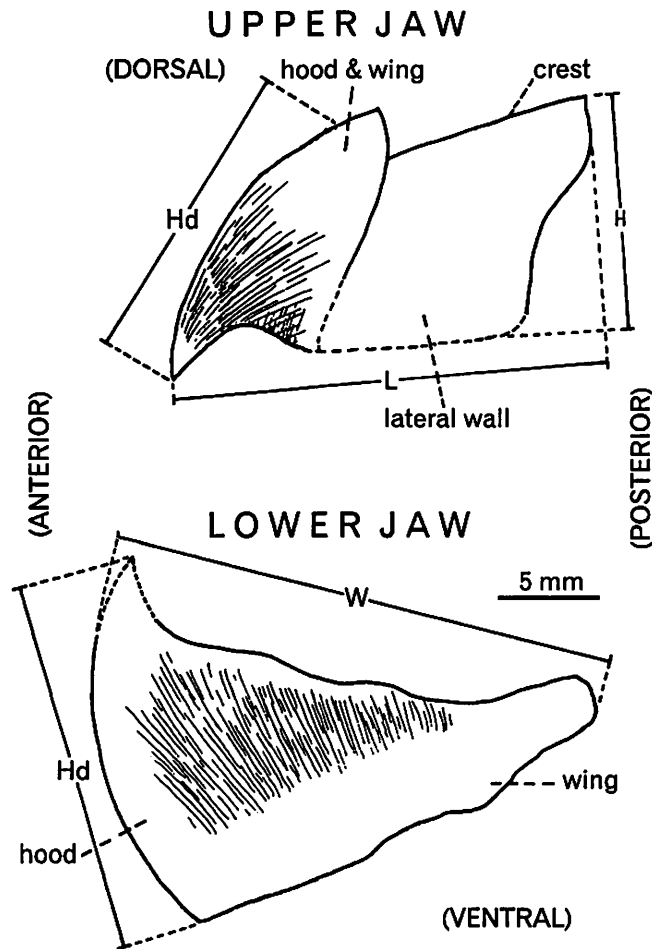


Figure 1. Restoration on the jaw of *Provampyroteuthis giganteus*, gen. et sp. nov. and the measurements based on the holotype specimen. L : length of lateral wall, W : length of wing, Hd : length of hood. Terminology is based on Clarke (1962) and the measurements are adapted from Kanie (1982a). Crest and lateral wall are covered by hood and wing.

Lukow specimen.

Provampyroteuthis giganteus, sp. nov.

Upper jaw

Figure 1 and 2-1, 2, 3.

Material. Holotype : YCM-GP (Yokosuka City Museum) 693=MT12; paratype : MT1, MT13 and YCM-GP 1170 (=MT14). Loc. R4701 of Matsumoto *et al.* (1982), Takishita-juhassen, the upper part of the Obirashibetsu River, Tappu, northwestern Hokkaido (44°05'27"N, 141°57'29"E). Lower Santonian (I. Nakajima coll.); Referred specimens : GK.H 8094, Loc. RH1242b of Toshimitsu (1985), Sakasa-gawa,

Haboro, northwestern Hokkaido. Lower Santonian (S. Toshimitsu coll.); YCM-GP 692. Loc. RH2507p1, Naka-no-futamata River, Haboro. Lower Santonian (Y. Kanie & S. Toshimitsu coll.); H. Kokubu private collection. Loc. Ra1 of Kanie (1982b), Kawakami, the upper part of the Obirashibetsu River. Lower Santonian (H. Kokubu coll.); Loc. Ra2 at 300 m lower stream from loc. R4701a; Hm1 and Hm3. Loc. east tributary of the Shimokinenbetsu River, a tributary of the Obirashibetsu River. Lower Santonian (A. Hamamoto coll.).

Description. Upper jaw is smaller and narrower than lower one. It consists of hood (outer lamella),

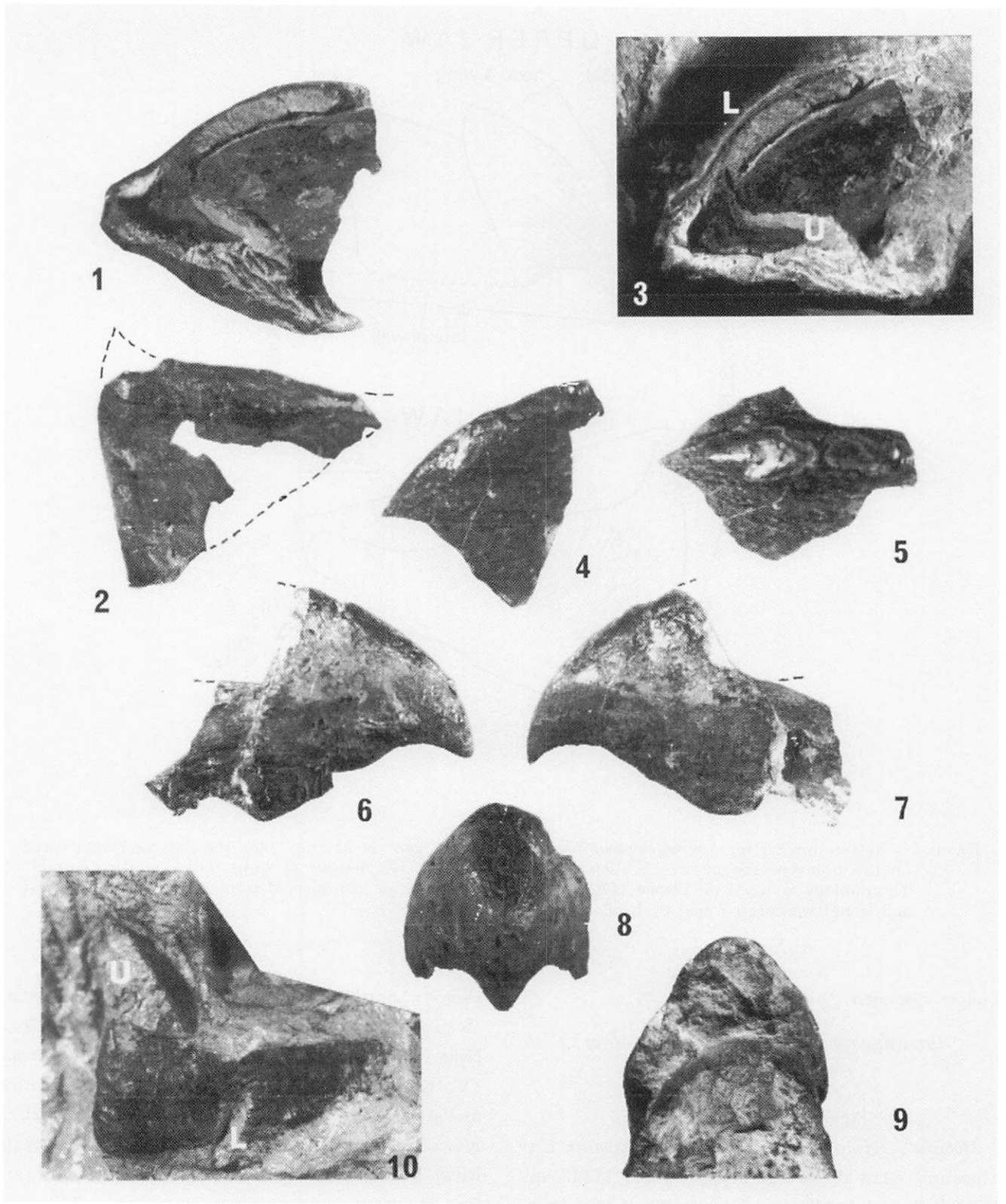


Figure 2. Jaw apparatuses of *Proxamproteuthis giganteus*, gen. et sp. nov. Loc. R4701, Takishita-Juhassen, the upper part of the Obirashibetsu River, northwestern Hokkaido. Lower Santonian. All figures are twice of the natural size.

1-3. Holotype, YCM-GP 693 (=MT12). 1, dorsal; 2, lateral; 3, mode of occurrence of upper (U) and lower (L) jaws. 4-5. paratype, MT13. upper jaw. 4, lateral; 5, dorsal. 6-9. paratypes, YCM-GP 1170 (=MT14). upper jaw. 10. mode of occurrence of upper (U) and lower (L) jaws.

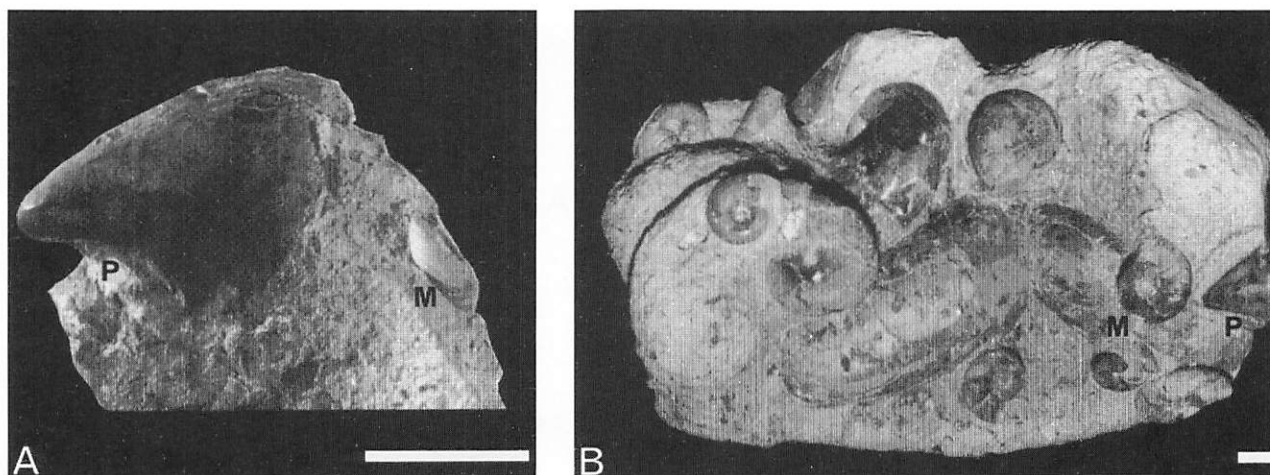


Figure 3. Occurrence of the upper jaw of *Provampyroteuthis giganteus* (P) accompanied by shelled molluscs composed of calcite (M). A. GK.H 8094 from loc. RH1242b; B. Ra2. 1 cm bar scale.

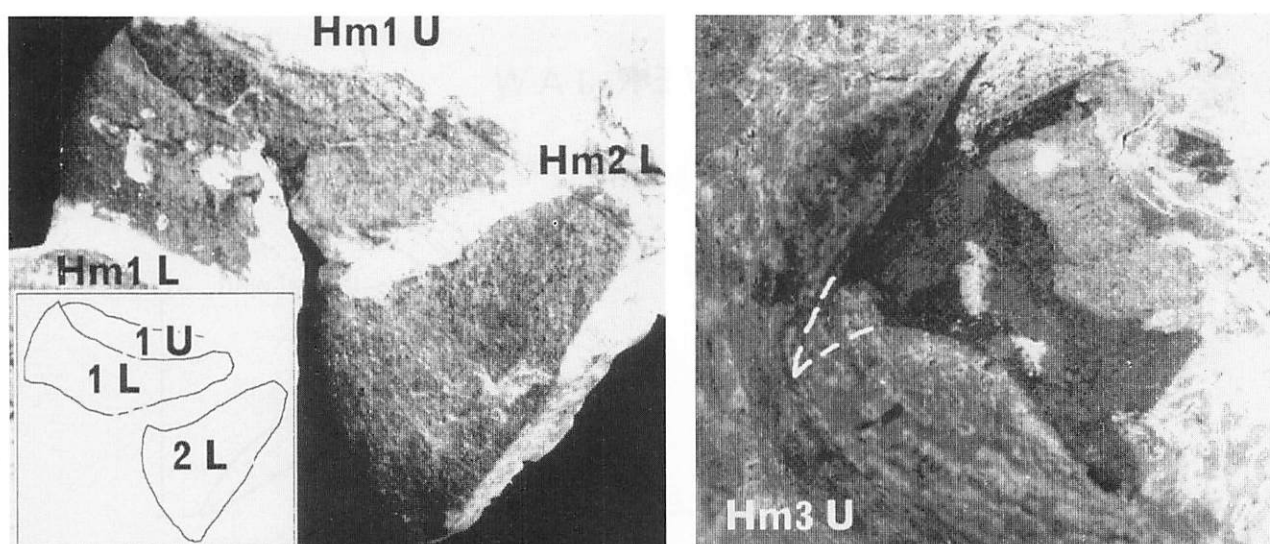


Figure 4. Occurrence of the upper jaw of *Provampyroteuthis giganteus* (P) from east branch of the Shimokinenbetsu River, a tributary of the Obirashibe River, Obira-cho, northwestern Hokkaido. Hm1 and Hm2: lower jaws (L) $\times 1.4$.; Hm1, Hm3: upper jaw (U). $\times 1.4$

and lateral wall plus crest (inner lamella). Lateral wall makes up the greater part of the upper jaw; wings are scarcely extended. In a specimen MT12, the maximum length of the jaw plate is 22.4 mm, and lateral walls are triangular, projecting in a postero-lateral direction, rounded crest dorsal part (Figure 2-1); growth lines are not marked on the lamella surface; hood situates in the anterior part. The specimens MT14, MT1, and MT13 make up a beak, ranging from 13.8+, 23.7+, and 23.6 mm in length, respectively. Lateral wall angle (α) is 45° to 60° . No calcareous covering is recognized.

Remarks. The upper jaw of *Provampyroteuthis giganteus* resembles that of decapods in more rounded

outlines (Figure 5; Kanie, 1982a, figure 2). The upper jaw of this species is most similar to that of modern *Vampyroteuthis infernalis* (Pickford, 1949; Iverson & Pinkas, 1971) and living *Nautilus* in the absence of calcareous covering at the rostra (Figures. 4, 5). The upper jaw of *Permorrhynchus dentatus*, possibly belonging to a Permian Endocochlian species, is characterized by the narrow hood which is widely extended in the ventral area (Zakharov & Lominadze, 1983). The upper jaw of the Late Cretaceous ammonites, *Tetragonites* and *Gaudryceras* (Kanie, 1982a), has calcareous rostra, wide wings, and shortly reduced lateral walls.

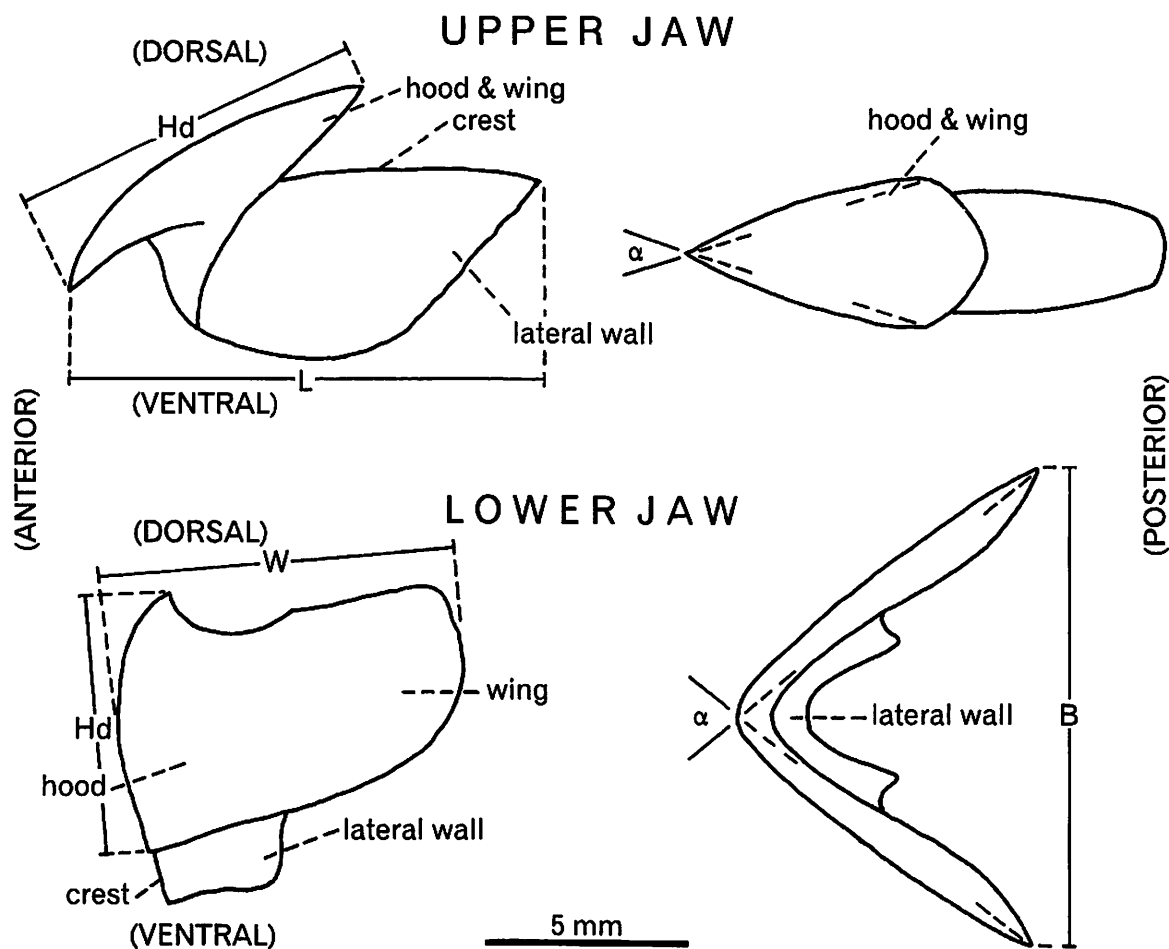


Figure 5. Basic jaw morphology of modern *Vampyroteuthis infernalis*. Upper jaw based on Iverson & Pinkas (1971) and lower jaw based on Clarke (1980). Right, lateral; left, dorsal aspects. L: length of lateral wall, W: length of wing, Hd: length of hood, B: jaw breadth, α : wing (lateral wall) angle.

Lower jaw

Figures 1; 2-3, 2-10

Material. Holotype: YCM-GP 693=MT12; paratype: MT14. Loc. R4701, Takishita-juhassen, the upper part of the Obirashibets River, Tappu, northwestern Hokkaido. Lower Santonian (I. Nakajima coll.). Referred specimen: Hm1. Loc. east tributary of the Shimokinenbetsu River, a tributary of the Obirashibetsu River. Lower Santonian (A. Hamamoto coll.).

Description. Lower jaw is larger (1.1 times in the holotype) and wider than upper one. Wing length is 25.1 mm in the holotype and 27.0 mm in the paratype. The lower jaw is clearly distinguished from the upper jaw in the larger hood which turns into triangular wings. Wing angle is 22° . Hood length is 18.4 mm in the holotype and 12.7 mm + in paratype, and gently swells toward the ventral part. Anterior part of the jaw is semicircular; beak is sharp-topped at the antero-dorsal part.

Lateral wall and crest areas are poorly developed in the inner side of "rostral part" of the holotype and MT14 specimens, with resemblance to that of modern *Nautilus*. Numerous growth lines or scratches exist in parallel to the curve of hood at dorso-lateral part of the jaw. Wing angle (α) is 22° .

Remarks. The lower jaw morphologically differs from that of modern decapods and octopods in the developed crest and lateral wall, although it closely resembles that of *Vampyroteuthis infernalis* (Pickford, 1949; Iverson & Pinkas, 1971; Clarke, 1980) except for the less extended lateral wall and crest. In this point, the lower jaw of *Provampyroteuthis giganteus* is similar to that of *Nautilus* (Okutani & Mikami, 1977; Saunders *et al.*, 1978; Kanie, 1982a, figure 4), but the former differs from the latter in the wing developed into fan form and the rostra covered by calcareous layers.

Diagnosis of modern vampyromorph jaws

Genus *Vampyroteuthis* Chun, 1903

Type species. *Vampyroteuthis infernalis* Chun, 1903

Figure 5

Remarks. Chun (1903) gave the first report on *Vampyroteuthis infernalis*, and then Chun (1915)

illustrated an upper jaw of this species. Robson (1929) elected the suborder Vampyromorphina for the archaic octopoda, and thereafter Pickford (1936) raised it to ordinal rank. However, Jeletzky (1966) placed it under the order Teuthida.

Pickford (1949) gave the relationships between the length of lower jaw and the mantle length (Figure 7). The general morphology of the lower jaw is largely different from that of octopods and decapods i.e., lateral wall of octopods and decapods widely projects at the bottom of the wing, although that of *Vampyroteuthis infernalis* slightly thrusts out. This species has a radula within a buccal mass. Mature females have larger jaw apparatuses than those of males. As the characteristics of the lower jaw of *Vampyroteuthis infernalis*, Iverson and Pinkas (1971) showed the broad wing and entirely covered lateral wall. Clarke (1980) showed that 13 mm of crest length in the lower jaw indicates that the body wet weight was 870 g based on Pickford (1949)'s diagram; the largest lower jaw is 16 mm in length, 100 mm in mantle length and 2 kg in total body (male) weight (Figure 7B).

Table 1 Measurements (in mm) of the upper and lower jaws in *Provampyroteuthis giganteus*.
L: length of lateral wall, Hd: length of hood, H: jaw height, α : wing angle, W: length of wing,
B: length between right and left sides of lamellae.

| Specimen No. | Upper jaw | | | | Lower jaw | | | |
|---------------------|-----------|-------|-------|-----------------------|-----------|-------|------|-----------------------|
| | L | Hd | H | α ($^\circ$) | W | Hd | B | α ($^\circ$) |
| MT14 | | 13.8+ | | 50 | 27.0 | 12.7+ | | |
| YCM 693 (Holotype) | 22.4 | 10.0+ | 14.3 | | 25.1 | 18.4 | 22.7 | 22 |
| YCM 692 (RH2507p1) | 28.5 | 20.0 | 18.0+ | 50 | | | | |
| GK.H 8094 (RH1242b) | | 20.8 | | 45 | | | | |
| MT13 | | 23.6 | | | | | | |
| MT1 | | 23.7+ | | 50 | | | | |
| Ra2 | | 24.0 | | 50 | | | | |
| Ra1 | | 29.3 | | 60 | | | | |

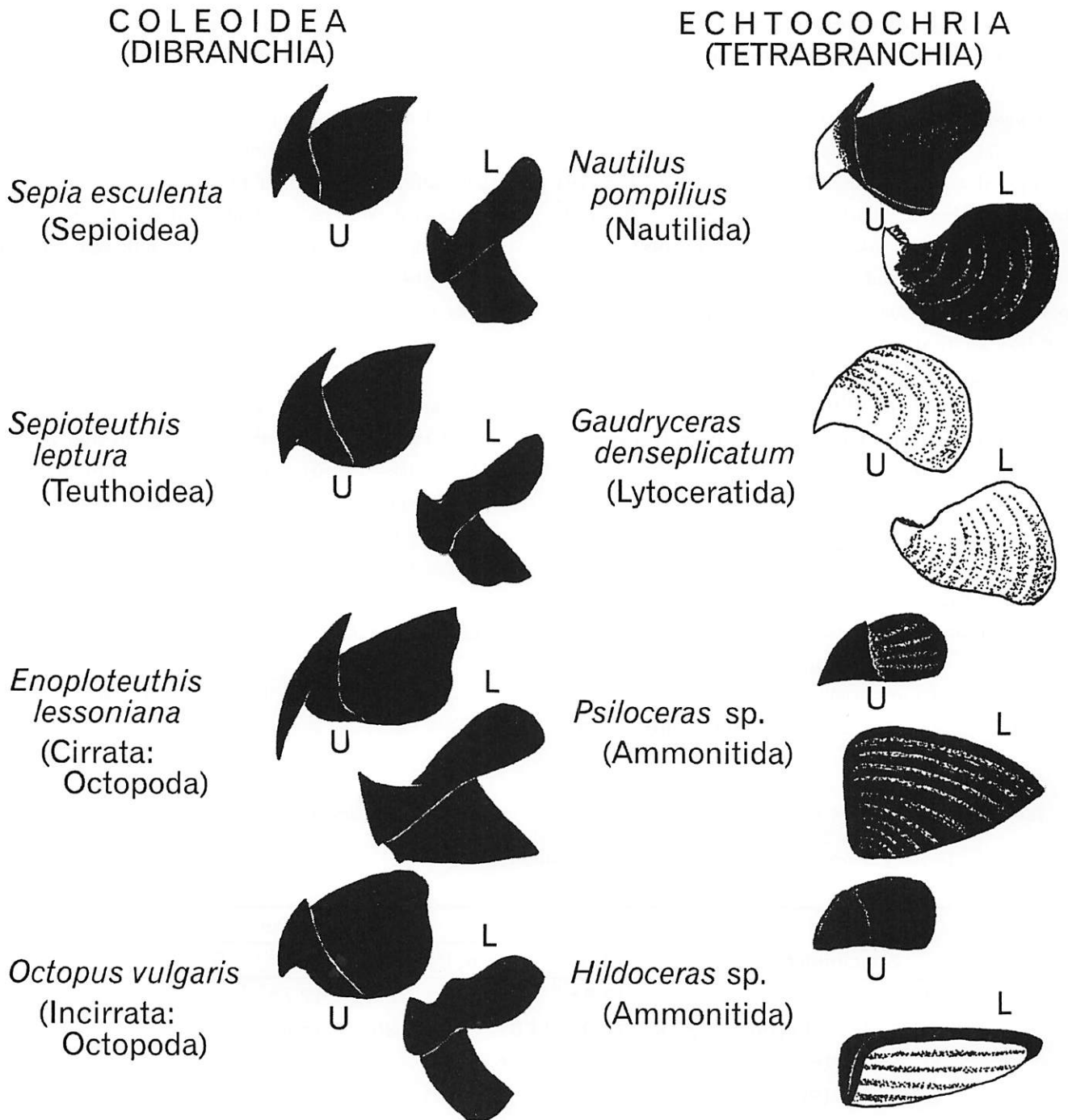


Figure 6. Upper and lower jaws of various kind of cephalopods. Solid : chitinous lamella, open : calcareous covering ; U : upper, L : lower. Sepioidea, Teuthoidea, Cirrata, Incirrata, Nautilida and Lytoceratida are from Kanie (1982a, figure 2). *Psiloceras* from Lehmann (1975) and *Hildoceras* from Lehmann (1972).

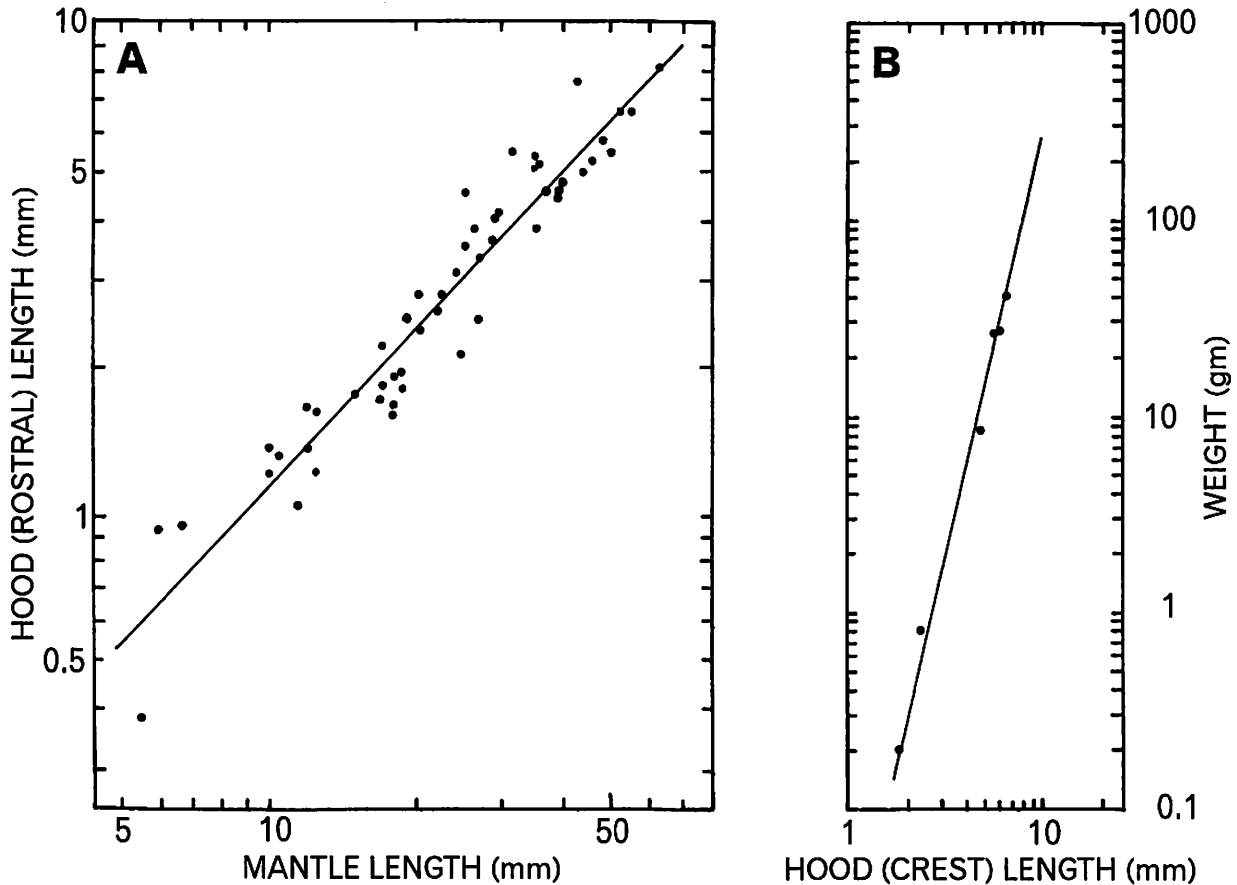


Figure 7. Body length and weight against the length of lower jaw in *Vampyroteuthis infernalis*. A. allometric relationship between hood length and mantle length based on Pickford (1949, figure 67). B. Total wet weight plotted against hood length based on Clarke (1980, figure 236).

Restoration of *Provampyroteuthis giganteus*

The restoration of fossil vampyroteuthid jaw apparatus is possible on the basis of the observations mentioned, and the general morphology and the life habits of *Provampyroteuthis giganteus* are discussed.

Jaw apparatus. Restored morphology of the jaw apparatus is shown in Figure 1. The rostral hood and wings occupy the anterior one third of the upper jaw which covers inner lamella (lateral walls plus crest). The lower jaw makes a triangular hood and wing covering almost all parts of the inner lamellae (lateral wall). The upper jaw is smaller than lower one because the former situates at the inner side of the later one. The rostra of

the lower and upper jaws are discriminated from those of nautiloids and some Cretaceous ammonites in the absence of apparent calcareous covering (Figure 6). The restored length of the upper jaw amounts to more than 50 mm based on the largest specimen MT1 with the hood 23.7 mm long (Table 1). In the lower jaw of the specimen MT12, the length of hood and wing amounts to 18.4 mm to 25.1 mm, respectively (Table 1).

Soft body. Length of the soft part of *Vampyroteuthis infernalis* is inferred from the ratio of the jaw length. According to Pickford (1949), the specimen having 44 mm in mantle length and 5.0 mm in hood length of the lower jaw is female, which a male specimen has 63 mm in mantle length and bears lower jaw of

8.0 mm hood length (Figure 7A). Clarke (1980) mentioned that the body weight of 870 g bears a lower jaw of 13 mm in hood length; the most heavy specimen with body wet weight of 2 kg and the mantle length of 100 mm (male) bears a lower jaw of 16 mm (Figure 7B). According to the above-mentioned ratio between body weight and jaw length, the body weight of the MT12 specimen of 18.4 mm in hood length is inferred to be 3 kg; more than 10 kg of body weight is suggested based on the upper jaw in the specimens of MT1 and MT13. In any case, Late Cretaceous *Provampyroteuthis giganteus* is regarded as having a much larger body than that of modern *Vampyroteuthis infernalis*.

Concluding remarks

Fifteen cephalopod jaw remains, predated by an individual of Late Cretaceous Elasmosaurian reptile, are identified with *Provampyroteuthis giganteus* gen. et sp. nov. belonging to the Vampyromorpha. Two pairs of the upper and lower jaws are preserved in situ position or slightly removed.

Morphological characters of the lower jaw: outer lamellae made up larger hood and wings cover the reduced inner lamellae consisting of crest and lateral walls. The morphological features are similar to those of modern *Nautilus* species and *Vampyroteuthis infernalis*. The morphology of the upper jaw can be correlated with that of the Octopoda and Vampyromorpha rather than with that of the Decapoda. No calcareous covering is observed at the rostral parts of the upper and lower jaws.

The morphological features of the jaw apparatus in *Provampyroteuthis giganteus* suggest phylogenetic similarities or eating habitat resemblance.

The body weight of *Provampyroteuthis giganteus* based on jaw size was far larger than that of living *Vampyroteuthis infernalis*.

The existence of *Provampyroteuthis giganteus* in early Santonian helps disclose the evolutionary history of the Vampyromorpha.

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Haboro 羽幌, Kawakami 川上, Naka-no-futamata River 中二股川, Obira 小平, Obirashibetsu River 小平薬川, Sakasa-gawa 逆川, Shimokinenbetsu River 下記念別川, Takishita-Juhassen 滝下十八線, Wakkanai 稚内

要 旨

後期白亜紀コウモリダコ目（頭足綱：鞘形類）の顎器

蟹 江 康 光

横須賀市自然博物館

白亜紀サントニアン前期の長頸竜によって捕食された頭足類顎器片を，コウモリダコ目の新属・新種の *Provampyroteuthis giganteus* として報告する。そのうちの2対の上・下顎は一緒に保存されていた。下顎は，わい小化した内ラメラを外ラメラがおおって現生オウムガイに似るが，外ラメラの形状は現生コウモリダコに近い。上顎の形状は，ツツイカ目・コウイカ目よりもタコ目・コウモリダコ目に似ている。オウムガイ類および一部のアンモナイト類の顎器先端にある石灰質階状部は認められない。 *P. giganteus* の顎器の形状は，動物の系統分類や捕食生活を示唆しているのかもしれない。現生コウモリダコと比較して，顎器の大きさから復元された化石種は巨大であったと推定される。サントニアン前期における *P. giganteus* の存在は，鞘形類のわずかな情報しか得られていない白亜紀の海における食物連鎖を復元し，現生種への進化を知る手がかりとなりうる。

白亜紀サントニアン前期の長頸竜によって捕食された頭足類顎器片を，コウモリダコ目の新属・新種の *Provampyroteuthis giganteus* として報告する。そのうちの2対の上・下顎は一緒に保存されていた。下顎は，わい小化した内ラメラを外ラメラがおおって現生オウムガイに似るが，外ラメラの形状は現生コウモリダコに近い。上顎の形状は，ツツイカ目・コウイカ目よりもタコ目・コウモリダコ目に似ている。オウムガイ類および一部のアンモナイト類の顎器先端にある石灰質階状部は認められない。 *P. giganteus* の顎器の形状は，動物の系統分類や捕食生活を示唆しているのかもしれない。現生コウモリダコと比較して，顎器の大きさから復元された化石種は巨大であったと推定される。サントニアン前期における *P. giganteus* の存在は，鞘形類のわずかな情報しか得られていない白亜紀の海における食物連鎖を復元し，現生種への進化を知る手がかりとなりうる。

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