Original Article

Vampyromorph : past and present
— Cretaceous Vampyromorph (Coleoidea : Cephalopoda) as the diet of plesiosaur —

Yasumitsu KANIE[1], Yoshikazu HASEGAWA[2], Yoshihiko OKAZAKI[3], and Masae TATEMATSU[4]

[1] *Yokosuka City Museum*
[2] *Gunma Museum of Natural History*
[3] *Kitakyushu Museum and Institute of Natural History*
[4] *Aichi Cancer Center Research Institute*

Abstract

The Cretaceous Vampyromorpha *Provampyroteuthis giganteus* swam at the surface or in shallow waters, differing from the modern species *Vampyroteuthis infernalis*. Among many kinds of coleoids, the weaker *Vampyroteuthis* were driven to inhabit the deeper parts of the sea, an adaptation enabling them to survive as living fossils.

Cephalopod jaw remains were discovered as the stomach contents of an elasmosaurid plesiosaur from the Upper Cretaceous deposits of Hokkaido, Japan. Many pieces were embedded around the ribs together with gastroliths. The predator Elasmosaurid were interpreted as surface or shallow sea swimmers from their body morphology and they could not bite shelly ammonites and nautilid with their teeth. The living *Vampyroteuthis* is a weak swimmer in the water columns of 300—2500 m depths, whereas the assemblage of molluscan fossils associated with *Provampyroteuthis* remains suggests an off—estuary environment at a moderate depth.

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

Introduction

At least two pairs of cephalopod jaw apparatuses were found in association with the remains of elasmosaurid plesiosaur (Figures 1, 2). The cephalopod jaws were identified with *Provampyroteuthis giganteus* (Kanie, 1998). We interpret this occurrence as indicating that *P. giganteus* was a prey item of the elasmosaur. These interesting association of two kinds of animals was named the Obira specimens no. 1 and no. 2. The Obira fossil material was embedded in a calcareous nodule from the Lower Santonian of the Upper Cretaceous deposits in the Obira area, northwestern Hokkaido (Matsumoto *et al.*, 1982).

In the present paper, we describe the morphology of the elasmosaurid specimens, discuss this habitation, and interpret the life habits of extinct *Provampyroteuthis*.

Description of the elasmosaurid specimens

Obira specimen no. 1 (Figures 1, 2 ; Table 1)

From the Lower Santonian. M. Tatematsu collection (MT, partly banked in the Gifu Prefectural Museum) Loc. R4701 of Matsumoto *et al.*, (1982), the middle steam of the Obirashibe River, northwestern Hokkaido.

Received : 1998. 1. 15, Accepted : 1998. 2. 17

Table 1. Measurements (mm) of the elasmosaurid bones in the Obira specimen no. 1

Vertebral centrum (V)	Ant.-post. length	Width
V1	40+	69
V2	44	75
V3	48	71
V4	46	58+
V5	42	59
V6	31+	68

Rib (C)	Length	Width
C1	85+	—
C2	50+	31
C3	44+	28
C4	105+	28
C5	200+	26
C6	210+	27

Vent. rib (G,Gastralia)	Length	Width
G1	134+	13+
G2	210+	14
G3	270+	14
G4	170+	14
G5	290+	14
G6	120+	14
G7	260+	14
G8	75+	13
G9	100+	12
G10	140	13

Phalange (P)	Length	Width
P1	20	10
P2	41	28
P3	31	28
P4	32	24
P5	43	26
P6	33	20
P7	26	12
P8	24	9
P9	35	21
P10	29	14
P11	27	16

Humerus (H)	
Total length	180
Right head length	72
Right head width	70
Minimum width	72
Minimum thickness	51
Maximum width of distal part	90+
Maximum width of distal end	52

The bones are various parts of an incompletely preserved specimen. They consist of 8 vertebral centra (V), 6 ribs (C), 10 ventral ribs (G, gastralia), 2 humeri (H), 3 carpi and 11 phalanges (P). The skull and femora are not preserved.

Humerus (H), ventral ribs (G) and ribs (C) are small-sized with round joints, therefore it is difficult to identify the species of the genus. Little ridges for muscle attachment and the heads of joints are coarse-inevenness. The specimen no. 1 regarded juvenile body for the small size and spherical humerus as Caldwell (1997, fig. 5) has pointed out. The ellipsoid vertebral centra (V) only with neural arch of joint surface which are separated from a neural spine (ns). The slender bones of both margins are sharp-topped with shallow grooves are identified ventral ribs. These morphologies are similar to the 2nd thoracic-lumber centrum of *Scanisaurus* cf. *nazarowi* under the Elasmosauridae which Persson (1959, pl. 8, 2a-b) pointed out. We identify the specimen no. 1 as *Elasmosaurus* sp.

The specimens is partially articulated. At least ten gastroliths and 15 cephalopod jaws are located in the ventral part of the body.

Obira specimen no. 2 (Figures 3, 4 ; Table 2)

From the Lower Santonian. Hamamoto collection (Hm). Loc. Uppermost stream of east branch of the Shimo-kinenbetsu River, a tributary of the Obirashibe River. Incomplete bones are consist of 6 vertebrae (V), 8 ribs (C). A ischium is observed at the opposite side (Figure 3-I). No tooth preserved.

Vertebrae (V) are fairly large-sized. They are compared with the dorsal vertebrae for the joint with neural spines (ns), without joint surface in the caudal rib. Eight ribs (C) are incomplete. The marginal part of the ischium made of triangular-flat bone, is similar to ischium of *Alzadasaurus riggi*. Based on these characters, the specimen no. 2 is presumed an adult body of the Elasmosauridae.

The length, width and height of the vertebrae are

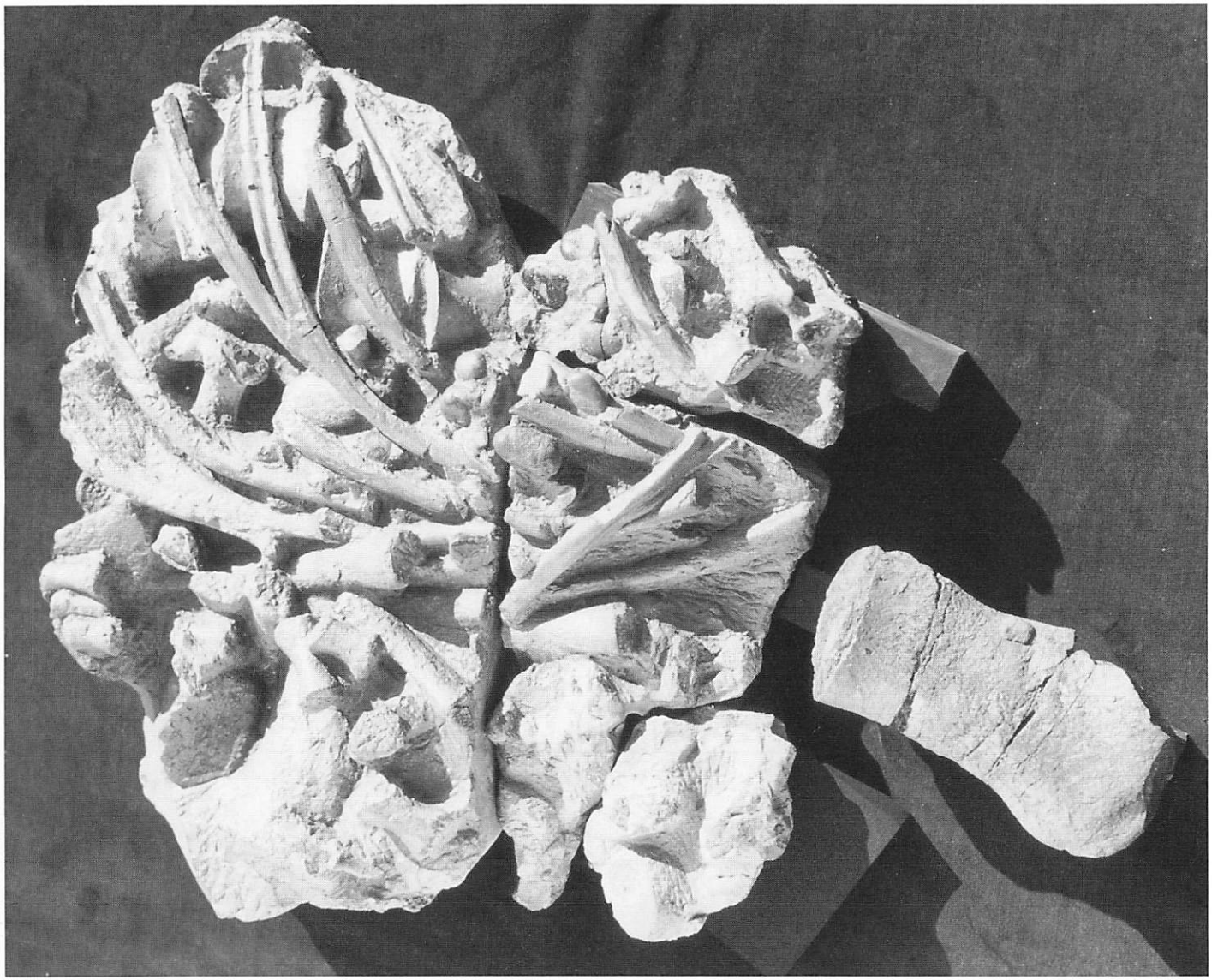

Figure 1 Photo of the Obira specimen no. 1 (MT) ×1/6.

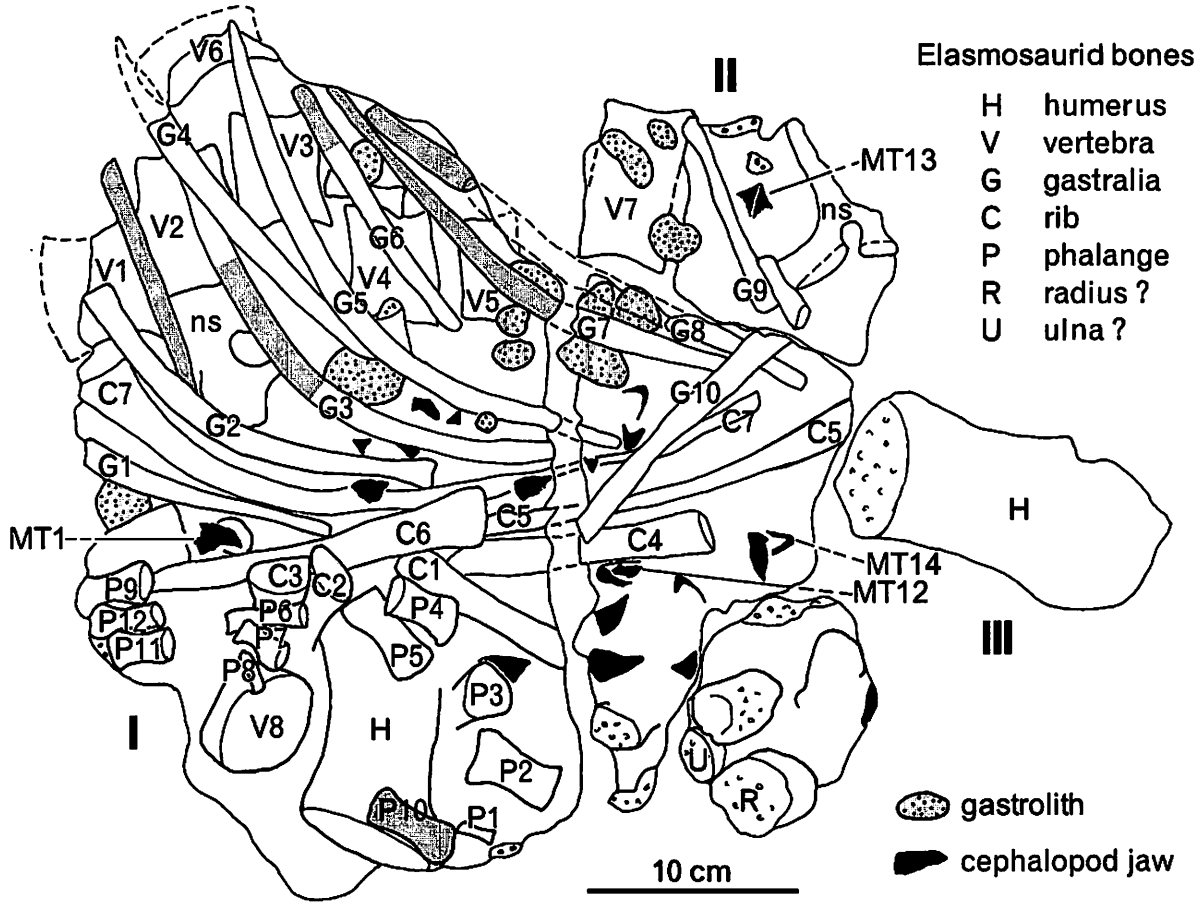

Figure 2. The Obira specimen no. 1 (MT) made of elasmosaurid bones with gastroliths and Vampyromorph jaws. V : vertebral centra, ns : neural spine, C : rib, G : ventral rib (gastralia), H : humerus, P : phalange. Bones reticulated have been removed. ×1/5.

analogous to those of the Lower Santonian *Elasmosaurus* n. sp. from Iwaki, Fukushima Prefecture.

Elasmosauridae reported from Japan

Several plesiosaurs were discovered in the Cenomanian to Maastrichitian deposits of the Japanese Islands, although the head parts was not discovered, excluding *Elasmosaurus* n. sp., "Futaba–suzuki–ryu". They are regarded to belonged to the Elasmosauridae under Plesiosauria. The following is a list of principal Elasmosauridae from Japan.

1) *Elasmosaurus* (?) sp.
Nanbu–no–sawa, Obira, northwestern Hokkaido. Turonian (Obata, Hasegawa & Otsuka, 1972)

2) *Elasmosaurus* (?) sp.
Ponbetsu, Mikasa. Upper Turonian (Obata, Hasegawa & Otsuka, 1972)

3) Elasmosauridae gen. et sp. indet.
Sanushube–gawa, Hobetsu, southern–central Hokkaido. Early Campanian (Nakaya, 1985, 1989)

4) *Elasmosaurus* n. sp., "Futaba–suzuki–ryu"
Irima–zawa, Iwaki, Fukushima Pref. Lower Santonian (Obata, Hasegawa & Suzuki, 1970 ; Hasegawa & Obata, 1972)

5) *Elasmosaurus* (?) sp.
Kumaoi–zawa, Mikasa. Lower Santonian (Obata, Hasegawa & Otsuka, 1972)

6) *Elasmosaurus* (?) sp.
Urakawa, southern–central Hokkaido. Lower Campanian (Obata, Hasegawa & Otsuka, 1972)

7) Elasmosauridae gen. et sp. indet.
Nakagawa, northern–central Hokkaido. Late

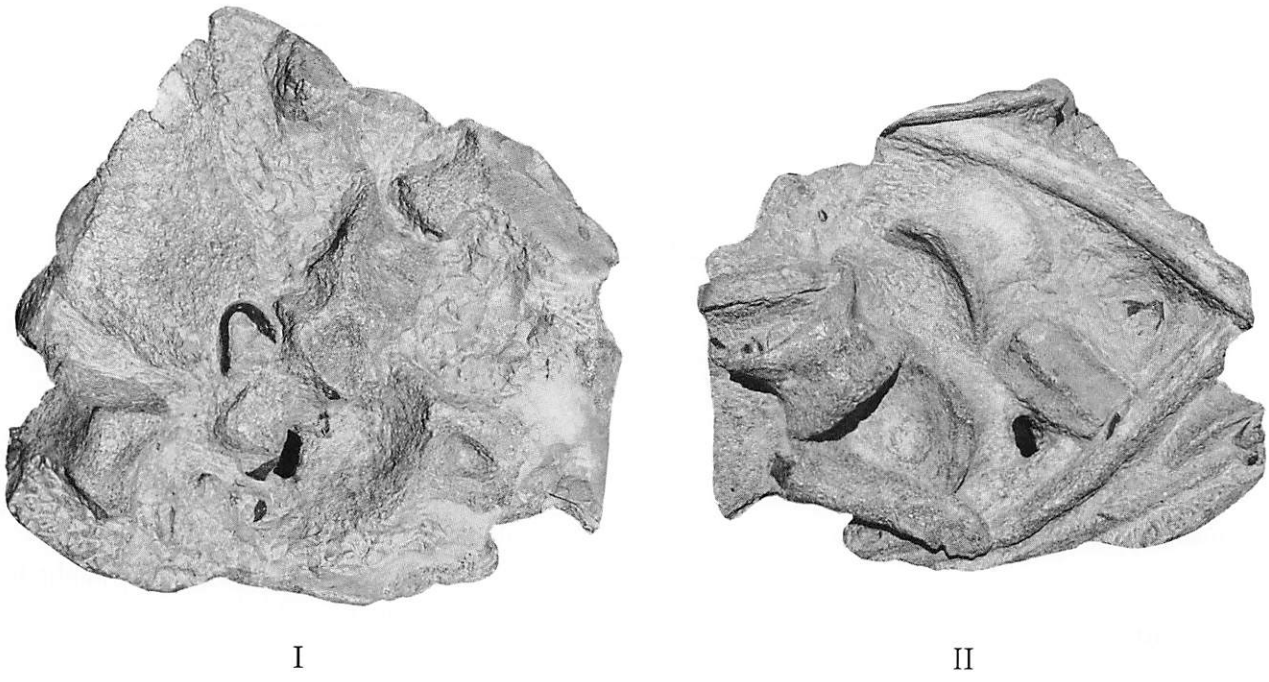

Figure 3. I, II. Photos of the Obira specimen no. 2 (Hm). ×1/3.

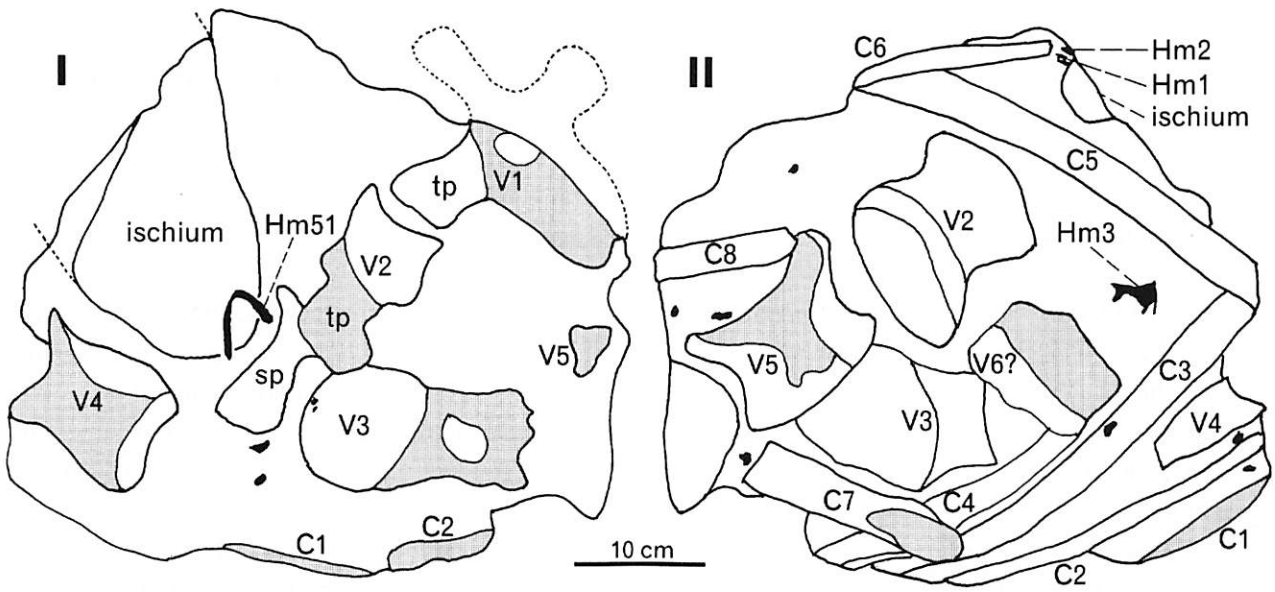

Figure 4. I, II. Mode of occurrence of the specimen no. 2 (Hm) composing of elasmosaurid bones with Vampyromorph jaws (solid : Hm1−3, Hm51). ×1/3.
V : vertebra, C : rib, tp : transverse process, sp : spinous process. Symbols as in Figure 2.

Table 2. Measurements (mm) of the elasmosaurid bones in the Obira specimen no. 2

Vertebra (V)	Length (L)	Width (W)	Height (H)
V1	62	93	—
V2	60	94	170
V3	56	91	65+
V4	61+	94	46+
V5	63	98	62+
V6	31	74	41+

Rib (C)	Length (L)
C1	95+
C2	195+
C3	265+
C4	270+
C5	267+
C6	120+
C7	125+
C8	90+

Ischium	
Length	180
Width	72

Campanian—Maastrichtian (Hikida, 1997)

Gastroliths and food of Elasmosaurs

The Obira specimen no. 1 shows the occurrence of two pairs of upper and lower cephalopod jaws, without calcareous covering, associated with stomach stones in the ventral part of the elasmosaurid. We conclude, the cephalopods were swallowed as food by the elasmosaurid. The existence of paired cephalopod jaws indicates that they were not ground or crushed by gastroliths. The chitinous lamellae made of were indigestible by gastric juices.

The *Provampyroteuthis* jaw remains were situated among vertebrae, ribs, gastralia, phalanges and other remains in the ventral part of the elasmosaurs. The cephalopod jaws occur in the stomach area of the reptile, along with 12 pieces of round to oval pebbles identified as gastroliths. The maximum size of stomach stone is 42×23×8 mm (chert), minimum size is 16×6×10 mm (sandstone) and mean size is 25×18×12 mm. The main composition of stomach stones is chert, next in abundance is sandstone, then mudstone and andesite.

An Early Santonian *Elasmosaurus* n. sp. (estimated body length 7 m with 3 m breadth between body paddles) has gastroliths of 0.7—13.5 cm in diameter (Obata *et al.*, 1970 ; Hasegawa & Obata, 1972). The Early Campanian elasmosaurid from Hobetsu bears 16 oval pebbles of 2—7.5 cm in diameter near the gastralia. The Elasmosauridae from Nakagawa have 102 pebbles of 0.2—3.8 cm diameter made of chert, sandstone, mudstone, and andesite which situate around the gastralia (Hikida, 1997).

The Obira elasmosaurid specimen no. 1 might be juvenile condition based on the size of gastroliths as compared with those of the specimens from Futaba, Hobetsu and Nakagawa. This can be supported by anatomical features of fusion between neural arches and vertebral centra (Brown, 1981).

As previously known, the Elasmosauridae species have stomach stones. Brown (1904) suggested the function to be the breakup of food, based on the remains of the gastric part of the elasmosaurid specimen from the Coniacian—Santonian Niobrara Formation ; the remains consist of great numbers of fish vertebrae, several pterodactyl bones in small pieces, seven broken scaphitid ammonite shells. Masarre (1987) estimated the function of the Cretaceous elasmosaurs among Mesozoic marine reptiles that is suitable for prey preference of soft bodies, based on slender and curved tooth morphology. Thereafter, many ideas on gizzard stones have been proposed (e.g., Skoczylas, 1978 ; Steel, 1989). It is known that the Nile crocodiles *Crocodylus niloticus* commonly have gastroliths. Cott (1961) noted that chitinous opercula of ampullar gastropods, their main diet, are usually found unbroken in the stomachs containing stones, after the calcareous shells and soft parts have been digested with gastric juice. He suggested the stones serve a hydrostatic function for stability in swimming. Based on the assumption that stones weigh one percent of adult body weight ; they could lower the center of gravity. This idea was applied to *Caiman latirostris* by Dieffenbach (1979). Darby & Jakangas (1980) suggested that the Campanian

plesiosaur *Alzadasaurus* (?) of two meters long between both paddles used the stones to increase body stability while in the water, i.e., for hydrodynamic purposes rather than for grinding foods. The sphericity of gastroliths (197 pieces, total weights 8841 gm) is similar to that of river pebbles ; the stones may have been ingested by the plesiosaur in an estuarine environment of a river. An interesting food link is also known between late Liassic reptiles and cephalopods. The chitinous arm hooks of coleoids (prey) exist in the ventral part of ichthyosaurid *Stenopterygius crassicostatus* (predator) at the display in the museum of Tübingen University.

Locomotion systems of Plesiosauria

The elasmosaurid, preying upon *Provampyroteuthis*, were surface or underwater "flight" swimmers assumed from their paddle morphologies and characteristic construction made of pectrum, pelvis and gastralia based on the following :

Robinson (1975) considered the functional morphologies of plesiosaurs. They swam by their four paddles resembling those of penguins, sea turtles and otariid pinnipeds. The swimming propulsive hydrofoil paddles of the plesiosaurs transmitted their tension and compression through the paddles to the ventral basket (Robinson, 1977) composed of characteristic pectrum, gastralia and pelvis. Thus, the swimming form of the plesiosaurs was considered to be underwater "flight" manner of hydrofoils.

Life habits of *Vampyroteuthis infernalis*

Vampyroteuthis infernalis, known as a living fossil, i.e., single order, family, genus, and species, has the primitive nature of dibranchiate cephalopod (Robson, 1929 ; Pickford, 1938 ; Jeletzky, 1966). *Provampyroteuthis giganteus*, newly described by Kanie (1998) is considered an ancestor to *V. infernalis*, and the ecology and physiological characteristics of modern species may be used to examine this extinct species.

Bandel & Leich (1986) regarded *Plesiotheuthis*, *Leptotheuthis* and *Trachyteuthis* from the Jurassic Solnhofen Limestone as the Vampyromorpha based on tentacle and gill morphologies without information on jaw morphology.

Vampyroteuthis differs from citrate octopods in having a pair of filaments, photophores, emerged funnel, gladius and two pairs of fins at certain growth stages (Pickford, 1949 ; Okutani, 1984).

Pickford (1946) determined its vertical and horizontal distribution in seawaters, then detailed the external anatomy of the animal. Her view is the following : *V. infernalis* is weak swimmer of the bathypelagic zone ; they live in the waters of the Indo-Pacific and Atlantic Oceans in a depth at 300-2500 meters and are most abundant at 1500-2000 meters. The water temperature at their depth 1.7-15.5° C and most commonly 2.0-5.9° C, thence this species is an oligopaerobic one (oxygen value 1.00-3.99 ml/L). Jaw apparatuses of mature female of are longer than those of males. Roper & Young (1975) reported the vertical distribution of *V. infernalis* in off California waters being 100-200 meters (water temperature 3-6° C; salinity 34.4-35.4 ; oxygen values, 0.3-0.8 ml/L) and 45 % of the captures occurred between 600 and 800 meters.

Young, J. Z. (1977) concluded that *Vampyroteuthis infernalis* probably feeds on diatoms and copepods, judging from crop contents, and has a strange mixture of nervous system characteristics of decapods and octopods. Young, R. E. (1972) discovered the existence of photoreceptors in the mantle cavity and assumed that this may function to detect a luminous content in the waters.

Based on the existence of jaw plates of *Vampyroteuthis infernalis* in the diet of sperm whales caught off Peru and Chile, Clarke *et al.* (1976) reported 3.3 % (wet weight) of vampyromorphs among various kinds of cephalopods. Using trawl nets, Vampyroteuthid jaw plates occurred 0.17 % at off Durban, 0.07~6 % off Donkergat, and 0.02 % in the Atlantic Sea, respectively (Clarke, 1980).

Paleoenvironments

The environments of *Provampyroteuthis* and the elasmosaurid were concluded to be off-estuary moderate depth waters, based on analyses of deposits and associated molluscan fossils.

According to Matsumoto *et al.* (1982), the stratigraphic occurrence of the elasmosaurid specimen was in the

lower part of the U1 Member in the Upper Yezo Group, i. e., Lower Santonian bed. The elasmosaurid and *Provampyroteuthis* were embedded in a calcareous nodule in claystones with thin intercalation of acid tuff, and associated with large bivalvia *Inoceramus* (*Platyceramus*) *amakusensis*. The same horizon of bed (Loc. R470lb) commonly yield *Damesites semicostatus*, *Kitchinites* (*Neopuzosia*) *ishikawai*, *Gaudryceras denseplicatum* and *Polyptychoceras* (*Subptychoceras*) *yubarense*. The same bed just above (R470la) and just below (Loc. R470lc, d) also yield *Inoceramus* (*Platyceramus*) *amakusensis*. The preservation of these fossils is fairly good. Based on Tanabe *et al.* (1977), the molluscan assemblage of the lower Lower part of the U1 Member is *Inoceramus* (*Sphenoceramus*) *naumanni* (62%), *Tetragonites glabrus* (16%), *Damesites damesi* (13%), *Kitchinites* (*Neopuzosia*) *ishikawai* (4%), *Subptychoceras yubarense* (2%), *Gaudryceras denseplicatum* (11%) and individual specimens of *G. tenuiliratum*, *Inoceramus* (*Platyceramus*) *amakusensis* and *Nanonavis sachalinensis*.

Recent studies on Mesozoic ammonites conclude they were mostly benthic animals. Among above species, tetragonitid and desmoceratid ammonites which are smooth or weakly ornate morphotypes inhabited off-shore deeper waters (Tanabe, 1979), although *Inoceramus* (*Sphenoceramus*) *naumanni* had a pseudoplanktonic mode of life (Tanabe, 1978). In the Obira area, the inferred late Cretaceous paleo-landmass was located northwestward not far from southeast off-shore waters (Tanaka & Sumi, 1981). Toshimitsu (1985) presumed a large-scaled estuary and Santonian off-shore delta area about 50 km north or northwest from locality R4701. The depth record of off-shore waters is unclear. However the maximum depth of extant *Nautilus* with chambered outer shells (Tanabe & Kanie, 1978) and jaw apparatuses (Kanie, 1982) similar to tetragonitid ammonites may not exceed 600 m (Kanie & Hattori, 1983), and applied hydrostatic pressure equivalents to the depth of 785 to 830 m is considered to the maximum depth (Kanie & Hattori, 1983). These facts suggest that *Provampyroteuthis* associated with tetragonitid and desmoceratid ammonites inhabited off-shore waters at a moderate depth.

Strategy and life habits of Vampyromorpha

Strategy

Living *Vampyroteuthis infernalis*, a single genus and species under Vampyromorpha, lives in deeper waters. They are typical living fossils, and preyed upon by sperm whales. Cretaceous *Provampyroteuthis giganteus* was preyed upon by elasmosaurid reptiles. It was larger than modern species presumed to swim at surface or shallow water (Table 3). Vam-pyromorph have changed their mode of lives during the post-Cretaceous time, and could survive as "living fossils".

Life habits

Vampyroteuthis infernalis is a weak swimmer in the water columns of the bathypelagic zone at 300 to 2500 m depth in the Indo-Pacific and Atlantic Oceans (Pickford, 1946 ; Roper & Young, 1975). Its black body and existence of photorecepters are an adaptation to the dark world without light. The jaw apparatuses of *Vampyroteuthis infernalis* are often found in the stomach contents of sperm whales. The larger forms (body of 2 kg wet weight) have jaws of 18 mm hood length (Clarke, 1980). (Figure 5-Present).

Late Cretaceous *Provampyroteuthis giganteus* with giant jaw apparatuses of 29 mm hood length, and had been preyed upon by elasmosaurid plesiosaurs, a surface or shallow water swimmer, therefore Cretaceous Vampyromorphs are thought to flourish at the surface or shallow waters which were rich in foods. The associating molluscan fossils also support an off-shore condition at a moderate depth. (Figure 5-Past)

Cretaceous vampyromorphs succeeded in shallow surface waters bearing various kinds of foods. Thereafter, they were driven to deeper seas with few rivals during post-Cretaceous age by the appea-rances of various kind of decapods and octopods. This enabled modern *Vampyroteuthis infernalis*, a weak swimmer, to survive. The similar strategy was adapted by *Nautilus*.

Conclusions

As already known, the Obira fossil material from the Lower Santonian include *Provampyroteuthis giganteus*

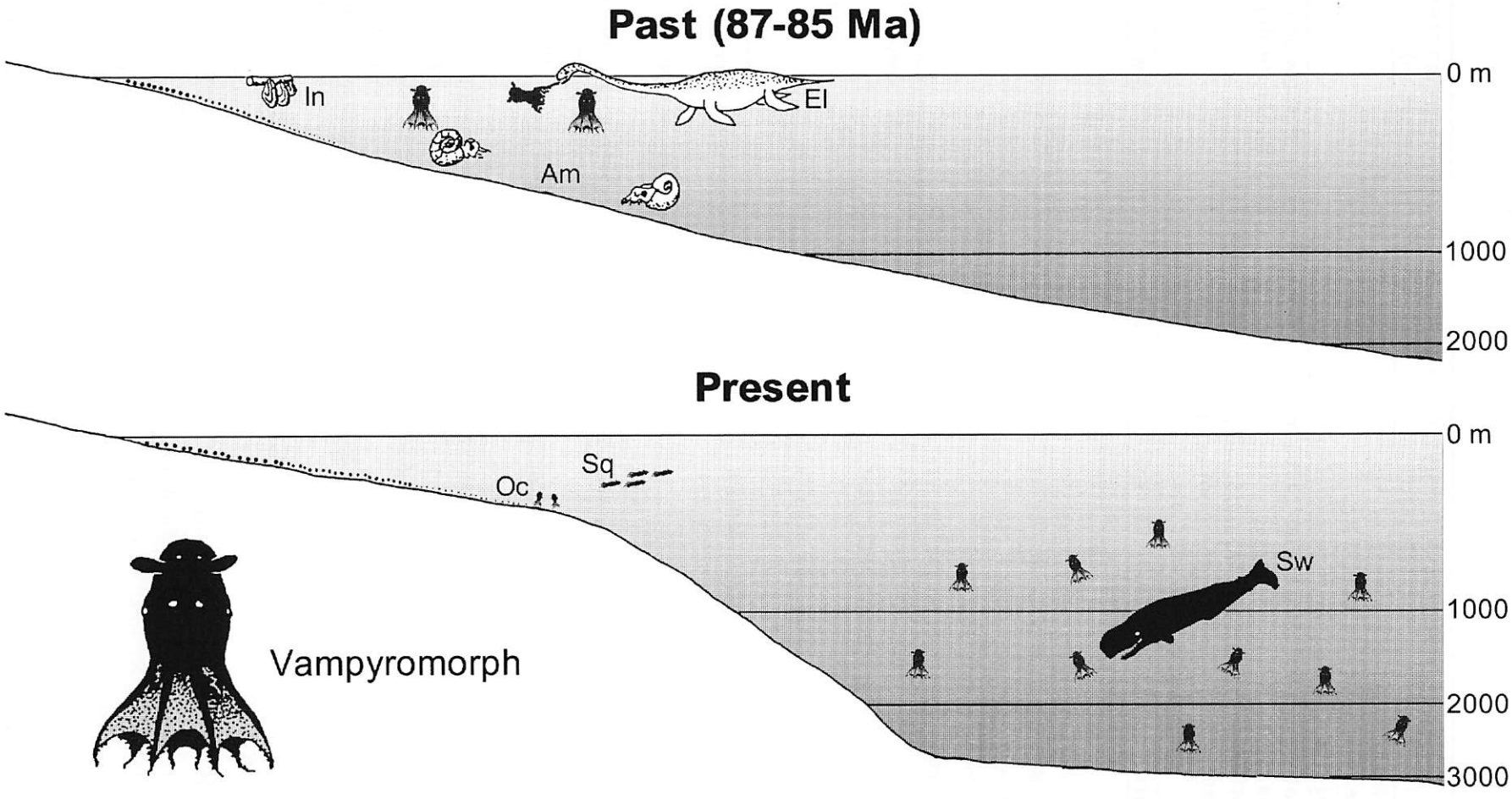

Figure 5. Vampyromorph : past (early Santonioan, 87−85 Ma) and present and their predator in the schematic seas. Body sizes are not in scale. Sq : squid, Sw : sperm whale, El : elasmosaurid, Am : ammonite, In : inoceramid bivalve.

Table 3. Comparison between modern *Vampyroteuthis infernalis* and extinct *Provampyroteuthis giganteus* in jaw size, body weights, mode of life, habitats and their predator. Lj : lower jaw

	Vampyroteuthis infernalis (Recent)	*Provampyroteuthis giganteus* (Early Santonian)
Jaw size, body weight	LJ=13 mm, 0.87 kg LJ=16 mm, 2 kg	LJ=25 mm, 3 kg ? LJ=35 mm
Mode of life	Weak swimmer (pelagic)	?
Marine habitats Water depth, Temperature, Ocean	300-2500 (1500-2000) m, 2-6 ℃, Atlantic 1500-2500 m, Indo. —Pac. 100-1200 (600-800) m, 3-6 ℃, Off Calif.	Surface and/or shallow sea at a moderate depth
Predator	Sperm whale, 3. 3 %	Elasmosauridae, 15 jaws

which were predated by elasmosaurid. The existence of *Provampyroteuthis giganteus* in the Mesozoic waters among the little known coleoids gives a clue to restore the ecosystem of the Cretaceous sea.

1) Elasmosaurids were interpreted as surface or shallow sea swimmers from their body forms and it is unlikely could bite shelly animals with their frail teeth.
2) Extinct *Provampyroteuthis giganteus* had a fairly large body judged from its jaw length, and the species was good food for the *Elasmosaurus*, because *Provampyroteuthis* body was soft except for the jaw apparatus.
3) Modern *Vampyroteuthis infernalis* of reduced body size inhabits the low temperate water column of the bathypelagic zone.
4) The Mesozoic Vampyromorpha used to swim as the surface or in shallow waters, differing from the modern species. Among many kinds of coleoids, the weaker vampyroteuthids were driven to inhabit the deeper parts of the sea. This was the way of adaptation enabling them to survive as living fossils.

Acknowledgments

We are grateful to Mr. A. Hamamoto, for providing the Obira specimen No. 2. Dr. H. Nakaya (Kagawa University, Takamatsu), Merrs. R. Aoki (Yokosuka) and Dr. E. L. Nicholls (Royal Tyrell Museum, Alberta) for giving comments on the elasmosaurid. Dr. M. Ota (Kitakyushu Museum and Institute) and Mr. K. Shikano (Gifu Prefectural Museum) gave constant encouragement.

References

With *, in Japanese with English abstract and **, in Japanese.

Bandel, K. & Leich, H.
1986 Jurassic Vampyromorpha (dibranchiate cephalopods). *N. Jb. Geol. Paläont. Mh.*, 1986(3): 129—148.

Brown, B.
1904 Stomach stones and food of Plesiosaurs. *Science, N.S.*, 20 : 184—185.

Brown, D.S.
1981 The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauroidea. *Bull. British Mus. Nat. Hist., (Geol,)*, 35(4): 253—347.

Caldwell, M. W.
1977 Limb osteology and ossification patterns in Cryptoclidus (Reptilia : Plesiosauroidea) with a review of sauroptrerygian limbs. *J. Vert. Paleont.*, 17: 295—307.

Clarke, M. R.
1980 Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. *Discovery Reports*, 37: 1—324. London.

Clarke, M. R., McLeod, N. & Paliza, O.
1976 Cephalopod remains from the stomachs of the sperm whales caught off Peru and Chile. *J. Zool.*, 180: 477—493. London.

Cott, H. B.
1961 Scientific results of an inequity into the ecology and economic status of the Nile Crocodile *Crocodilus niloticus* in Uganda and Northern Rhodesia. *Trans. Zool. Soc. London*, 29: 211—357

Darby, D. G. and Jakangas, R. W. O.
1980 Gastroliths from an Upper Cretaceous Plesiosaur. *J. Paleont.*, 54: 548—556.

Diefenbach, C. O. da C.
1979 Ampullarid gastropod-Staple food of *Caiman latirostris*? *Copeia*, 1979: 162—163.

Hasegawa, Y. & Obata, I.
1972 Notes on the excavation of new plesiosaur.** *Nat. Sci. & Mus.*, 39: 107–121., Tokyo.
Hikida, Y.
1997 Gastroliths of the Cretaceous plesiosaurs from Nakagawa, Hokkaido.** *Abstr. 104th Ann. Meet. Geol. Soc. Japan* : 414.
Jeletzky, J. A.
1966 Comparative morphology, phylogeny, and classification of fossil Coleoidea. *Univ. Kansas Paleont, Contrb., art 7* : 1–162, 25 pls.
Kanie, Y.
1982 Cretaceous tetragonitid ammonite jaws : a comparison with modern *Nautilus* jaws. *Trans. Proc. Palaeont. Soc. Japan, N.S.*, no. 125: 239–258, pls. 39–40.
1998 New Vampyromorph (Coleoidea : Cephalopoda) jaw apparatuses from the Late Cretaceous of Japan. *Bull. Gunma Mus. Nat. Hist.*, no. 2: 23–34.
Kanie, Y. & Hattori, M.
1983 Shell implosion depth of living *Nautilus*. *Kagoshima Univ., Res. Center S. Pacific, Occ. Paps.*, no. 1: 1–35, pls. 1–2.
Massare, J. A.
1989 Tooth morphology and prey preference of Mesozoic marine reptiles. *J. Vert. Paleont.*, 7(2),: 121–137.
Matsumoto, T., Obata, I., Okazaki, Y. & Kanie, Y.
1982 An interesting occurrence of a fossil reptile in the Cretaceous of the Obira area, Hokkaido. *Proc. Japan Acad., Ser. B*, 58: 109–113.
Nakaya, H.
1985 Preliminary report of plesiosaurian fossil (HMG 1) from Hobetsu–cho, Hokkaido, Japan.** *Bull. Hobetsu Mus.*, no. 2: 43–49, pl. 1.
1989 Upper Cretaceous Elasmosaurid (Reptilia, Plesiosauria) from Hobetsu, Hokkaido, northern Japan. *Trans. Proc. Palaeont. Soc. Japan, N.S.*, no. 154, 96–116
Obata, I., Hasegawa, Y. & Suzuki, T.
1970 Discovery of elasmosaur from the Upper Cretaceous Futaba Group.** *J. Geol. Soc. Japan*, 76: 161–164.
Obata, I., Hasegawa, H. & Otsuka, H.
1972 Preliminary report on the Cretaceous Reptile fossils from Hokkaido.* *Mem. Natn. Sci. Mus., Tokyo*, no. 5: 213–223, pl. 5.
Okutani, T.
1984 *Vampyroteuthis infernalis* Chun.* *Aquabiology*, 8: 402–404.
Persson, P. O.
1959 Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). *Arkiv Mineralogi och Geologi*, 2(35): 431–478, pls. 1–20.
Pickford, G. E.
1936 A new order dibranchiate cephalopods. *Anat. Rec.*, 67, suppl. 1, 1–71.
1946 *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. I . *Dana–Rept.*, no. 29, 40 p. Copenhagen.
1949 *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. II. *Dana–Rept.*, no. 32, 132 p.
Robinson, J. A.
1975 The locomotion of plesiosaurs. *N. Jb. Geol. Paläont., Abh.*, 149: 286–332.
1977 Intracorporal force transmission in plesiosaurs. *N. Jb. Geol. Paläont., Abh.*, 153: 86–128.
Robson, G. C.
1929 On the rare abyssal octopod, *Melanoteuthis beebei*. *Proc. Zool. Soc. London*, 1929 : 469–488.
Roper, C. F. E. & Young, R. E.
1975 Vertical distribution of pelagic cephalopods. *Smith. Contrb. Zool.*, no. 209, iv+51 p.
Skoczylas, R.
1978 Physiology of the digestive tract. In Gans, C. and K. A. *Biology of the Reptilia*, 8 (Physiology B): 589–717. Academic Press, London & N.Y.
Steel, R.
1989 Crocodiles. 198 p. Christopher Helm, London.
Tanabe, K.
1973 Evolution and mode of life of *Inoceramus* (*Spheno–ceramus*) *naumanni* Yokoyama emend., an Upper Cretaceous bivalve. *Trans. Proc. Palaeont. Soc. Japan, N. S.*, no. 92 : 163–184, pls. 27–28.
1979 Palaeontological analysis of ammonoid assemblages in the Turonian *Scaphites* facies of Hokkaido, Japan. *Palaeontology*, 22 : 609–630.
Tanabe, K., Hirano, H., Matsumoto, T. & Miyata, Y.
1987 Stratigraphy of the Upper Cretaceous deposits in the Obira area, northwestern Hokkaido.* *Sci. Rept., Dept. Geol., Kyushu Univ.*, 12 : 181–202.
Tanabe, K. & Kanie. Y.
1978 Colour markings in two species of tetragonitid ammonites from the Upper Cretaceous of Hokkaido, Japan. *Sci. Rept. Yokosuka City Mus.*, no. 25: 1–6, pl. 1.
Tanaka, K. & Sumi, Y.
1981 Cretaceous paleocurrents in the central zone of Hokkaido, Japan.* *Bull. Geol. Surv. Japan*, 32: 85–127.
Toshimitsu, S.
1985 Biostratigraphy and depositional facies of the Cretaceous in the upper reaches of the Haboro River, Hokkaido. *J. Geol. Soc. Japan*, 91 : 599–618.
Young, J. Z.
1977 Brain, behavior and evolution of cephalopods. *In* Nixon, M. and Messenger, J. B. eds. The Biology of Cephalopods *Symp. Zool. Soc. London*, no. 38 : 377–434. Academic Press, London & N. Y.
Young, R. E.
1972 Function of extra–ocular photoreceptors in bathypelagic cephlopods. *Deep–See Res*, 19 : 651–660.

要　旨

コウモリダコ目の過去と現在
―長頸竜の餌としての白亜紀コウモリダコ目（頭足類：鞘形綱）―

蟹江康光[1]・長谷川善和[2]・岡崎美彦[3]・立松正衛[4]

[1] 横須賀市自然博物館
[2] 群馬県立自然史博物館
[3] 北九州市立自然史博物館
[4] 愛知県がんセンター研究所

白亜紀のコウモリダコ目*Provampyroteuthis giganteus*は，現生のコウモリダコ*Vampyroteuthis infernalis*と異なり，浅海の表面あるいは水中を遊泳していた．多様な鞘形類の中で，ひ弱なコウモリダコ属は，生きている化石として生き残るために深海の生息域に追いやられて適応していった．

頭足類の顎片が，エラスモサウルス科長頸竜の胃の内容物として北海道の後期白亜系から発見された．多数の顎片が腹肋骨のまわりに胃石とともに埋没していた．頭足類の捕食者としてのエラスモサウルス類は，その体型とアンモナイト類・オウムガイ類などの殻を噛めない歯をもった，浅海あるいは水面付近の遊泳者と解釈される．現生コウモリダコは水深300－2500 mの弱遊泳者であるが，*Provampyroteuthis*の顎片と共産する軟体動物化石は沖合中浅海のものである．

蟹江康光
横須賀市自然博物館：〒238-0016　神奈川県横須賀市深田台95
Yasumitsu KANIE.
Yokosuka City Museum：95 Fukadadai, Yokosuka, Kanagawa, 238-0016, Japan.

長谷川善和
群馬県立自然史博物館：〒370-2345　群馬県富岡市上黒岩1674-1
Yoshikazu HASEGAWA.
Gunma Museum of Natural History：1674-1, Kamikuroiwa, Tomioka, Gunma, 370-2345, Japan.

岡崎美彦
北九州市立自然史博物館：〒805-0061　福岡県北九州市八幡東区西本町3-6-1，八幡駅ビル内
Yoshihiko OKAZAKI.
Kitakyushu Museum and Institute of Natural History：Yahata, Yahata-higashi-ku, Kitakyushu, Fukuoka, 805-0061, Japan.

立松正衛
愛知県がんセンター研究所：〒464-8681　愛知県名古屋市千種区鹿子殿1-1
Masae TATEMATSU.
Aichi Cancer Center Research Institute：Kanokoden Chikusa-ku, Nagoya, Aichi, 464-8681, Japan.