化石研究会会誌 Journal of Fossil Research, Vol. 54(2), 41-49(2022)

[Lecture Report]

Restoration of fluke outline of *Basilosaurus* (Mammalia: Archaeoceti)

Norihisa Inuzuka* and Utako Kikutani*

Abstract

Although many restoration figures of *Basilosaurus* have been drawn, the body shape is various and there is no study indicating the theoretical basis for restoration. The flukes in previous works are crescent-shaped same as those of living whales, not suitable for the body shape of *Basilosaurus*. The main subject of the present study is a suggestion of new life restoration with a different-shaped fluke based on new method for restoration. Life restoration is more difficult than skeletal reconstruction, because soft tissues like skin, subcutaneous tissues, and sense organs are not preserved as fossils. But aquatic body outline is correlated with the swimming pattern, so this correlation can be utilized. The fluke shape cannot be restored directly from skeletal characteristics, so a swimming pattern which matches the body shape was presumed, and then the fluke shape most suitable for the swimming pattern was considered. As a result, it is concluded that *Basilosaurus*, which had anguilliform body shape and anguilliform swimming pattern, had a rhombic fluke long along the sides of the body.

Key words: Archaeoceti, *Basilosaurus*, figure, flukes, restoration

Introduction

Accurate morphological restoration is first required to estimate the ecology of extinct animals. So far, many extinct vertebrate skeletons and biological restorations have been exhibited in museums, and have been published in general books such as pictorial books and encyclopedias, as well as in textbooks and specialized books. However, most of them do not have the scientific basis for the restoration posture and the appearance of the body surface as shown in the reconstruction examples of desmostylians (Inuzuka, 1984a) and dinosaurs (Inuzuka, 1997). For this reason, despite the same animal, different postures and appearances are taken depending on the exhibition halls and the books, and so it is difficult for the viewers of the exhibition or the book readers to judge which is true, and to have a constant image of the extinct animals.

Paleobiology, which emphasizes the biological aspects of fossils and seeks to use them as evidence of the evolution by neontological techniques, requires accurate morphological restoration prior to ecological restoration. So, the authors decided to check past domestic and foreign restoration figures.

In the exhibition skeleton of the museum, the same animal may be exhibited in multiple postures in different poses such as swimming or feeding. Since animals are movable, they can take various postures, especially in the parts related to locomotion. However, if the animal's unique characteristics such as the curvature of the spinal column and the orientation of the limbs and toes with respect to the torso differ greatly depending on the exhibition pose, it is not clear which is the original normal pose of the animal (Inuzuka, 1984b). From this point of view, when exhibiting the skeleton of an extinct animal, it is desirable to first restore the normal pose that the animal usually takes for the longest time and then assemble it.

On the other hand, in specialized books and

Received: 6 September, 2021; Accepted: 24 December, 2021

*Palaeo-Vertebrate Laboratory.
Saiwai-cho 45-25-303, Itabashi-ku, Tokyo 174-0034, Japan
e-mail: ashoroa@yahoo.co.jp

pictorial books on vertebrate paleontology and evolution, each animal is represented by a single skeleton or life restoration. Moreover, the author and supervisor of the figure are usually not specified. Therefore, if the same animal is depicted almost identical or similar in different books, the newer one can be presumed to be quoted from the older. In this paper, unless the supervisor is mentioned, the author of the treatises or books containing the skeletal illustrations or biological drawings is regarded as the supervisor of the restoration.

Here, *Basilosaurus* is taken up as an example of life restoration for which scientific basis has not been shown, although it has been drawn in many works so far. In particular, the contour of the fluke requires a new method because of no internal skeleton. Inuzuka (1984a) distinguished the methods of skeletal reconstruction of extinct animals into comparative morphological, functional morphological, and paleontological, and biomechanical methods (Inuzuka, 1984c). The method of life restoration was summarized in Inuzuka (1984b), who restored the skin and the shape of facial sense organs of desmostylians by the comparative and functional morphological methods. However, since this method alone is not sufficient for the fins of aquatic animals, we discuss the swimming style of *Basilosaurus* from its body shape, and then estimate the fluke shape suitable for it.

This paper was given at the 159th Annual Meeting of the Paleontological Society of Japan held at the Lake Biwa Museum in Shiga Prefecture. We would like to express our sincere gratitude to Dr. Hiroshi Sawamura of the Ashoro Museum of Paleontology, National Museum of Nature and Science, Tokyo, Dr. Hajime Taru of the Kanagawa Prefectural Museum of Natural History, and Dr. J. G. M. Thewissen for their cooperation in this research. Dr. Hiroto Ichishima of the Fukui Prefectural Dinosaur Museum and Dr. Toshiyuki Kimura of the Gunma Museum of Natural History reviewed the manuscript, and provided valuable advice as expert paleocetologists.

Previous works

Basilosaurus was discovered in Louisiana, USA in 1832, and described in 1834 (Harlan, 1834). It includes, '*saurus*' in its name because it was originally identified as a reptile, but it was later found to be a mammal and a new name *Zeugulolon* was proposed to substitute *Basilosaurus* (Owen, 1839). But the original name has been used due to the nomenclatural stability.

The creature was initially estimated to be 60-70 feet long (Lucas, 1929), and Koch considered the monster to be 114 feet long, composed vertebrae from two individuals. Subsequently, the skeleton was divided into two parts and exhibited at the National Museum of Natural History, Smithsonian Institution, remaining 55 feet in length (Gregory, 1951).

The illustration of the whole skeleton of *Basilosaurus* by Kellogg (1936) is very popular (Fig. 1). The 18 m long skeleton of *Basilosaurus cetoides* is a composite from the two individuals. *Basilosaurus isis* found in Egypt preserves a vestigial hind limb (Gingerich et al., 1990; Uhen, 1998).

The first attempt of *Basilosaurus* restoration in the inferred ancient natural environment would have probably been conducted by Osborn (1921). This figure (Fig. 2) is from the American Museum of Natural History, supervised by F. A. Lucas and painted by Charles, R. Knight. The body is elongated, with the fluke similar to those of living whales. According to Osborn (1921) and Lucas (1929), the diameter of the trunk would have been 6 to 8 feet or less at the thickest point, and the body length, 50 to 70 feet, of which 40 feet was the tail. In Lucas' opinion, it would have been an underwater swimming mammal because it had a fluke at the end of the tail. It is considered that the hind limbs were vestigial but presumably jutted out from the body.

The colored ecological restored figure (Fig. 3) by Zdeněk Burian has a good reputation as a restored figure of vertebrates, and is extremely complete as a painting (Burian, 1972). However, as far as this *Basilosaurus* is concerned, there are some doubts. First of all, we

Fig. 1. Whole skeleton of *Basilosaurus cetoides* (Owen) (Kellogg, 1936).

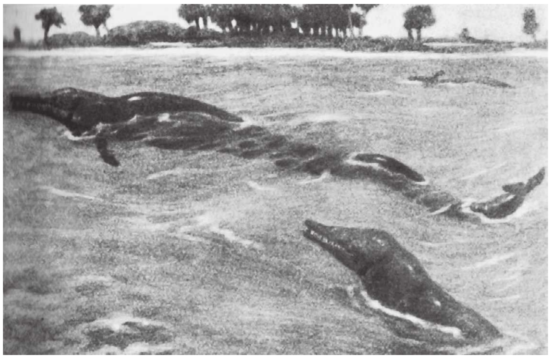

Fig. 2. Restoration figure of *Basilosaurus* drawn by Charles R. Knight under the direction of F. A. Lucas (Osborn, 1921).

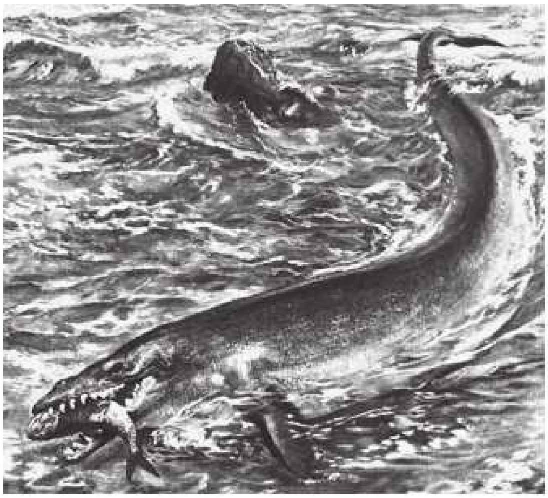

Fig. 3. Restoration figure of *Basilosaurus* drawn by Zdeněk Burian (Burian, 1972).

get an impression that the body is too much exposed from the sea surface like a floating log. Although it is extinct, it should have a specific gravity of around 1 as long as it is a cetacean, and even when breathing, most of the body surface must have been submerged under the surface of the water.

If this figure was drawn with the intention of showing the animal's body better to the readers, it would be a problem as a restored figure. This is the same as Osborn (1913), who took an unreasonable posture when exhibiting the reconstructed skeleton of *Tyrannosaurus* in order to show the skull appealing to the viewers, and it resulted in a distorted reconstruction, departed from the correct appearance of the animal.

More important point is the fluke shape, which is the subject here. *Basilosaurus* belongs to the suborder Archaeoceti, constituting the order Cetacea, together with two other suborders, Odontoceti and Mysticeti and it is presumed that it had a horizontally long crescent-shaped flukes as in modern whales and dugongs.

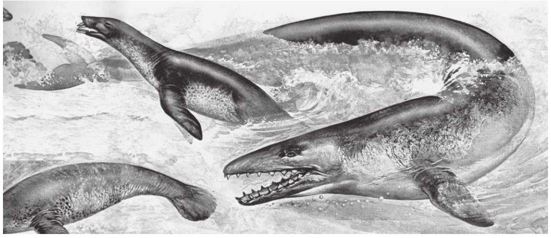

Fig. 4. Life restoration of *Basilosaurus* (Halstead, 1978).

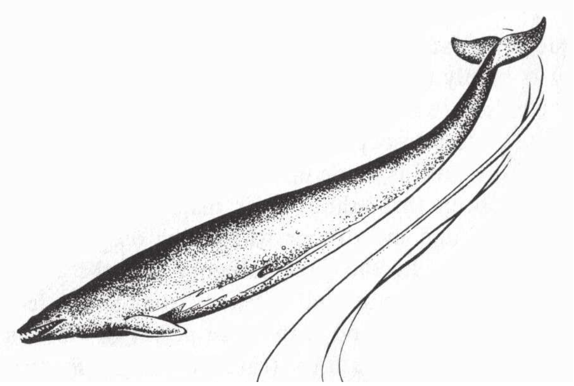

Fig. 5. Life restoration of *Basilosaurus* drawn by Lois M. Darling (Colbert, 1980).

Halstead (1978) draw *Basilosaurus* swimming on the surface of the sea (Fig. 4). However, since the Miocene desmostylian *Desmostylus* and *Paleoparadoxia*, and modern manatees are included in the same figure, it is an illustration that summarizes aquatic mammals rather than an ecological restoration figure.

In addition to these, there are several life restoration figures depicting the animal body only without background by Colbert (1980), Barnes and Mitchell (1978), Shikama(1979), Savage and Long (1986), Cox et al. (1988) etc.

A figure (Fig. 5) appeared in the third edition of the textbook by Colbert (1980), and the text of the 5th edition of 2004 adds a description of the complete hind limb found in Egypt. It has small leg relative to the body, but is well grown foot with three toes.

In the figure by Barnes and Mitchell (1978) the trunk is deeper than that of Burian (1972), with small

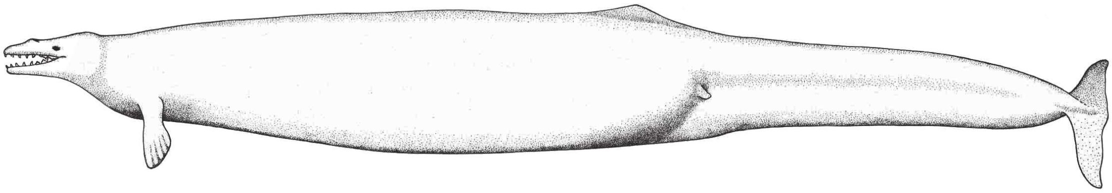

Fig. 6. Life restoration of *Basilosaurus* (Barnes and Mitchell, 1978).

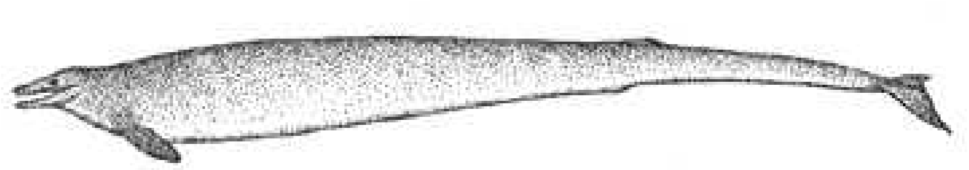

Fig. 7. Life restoration of *Basilosaurus* (Shikama, 1979).

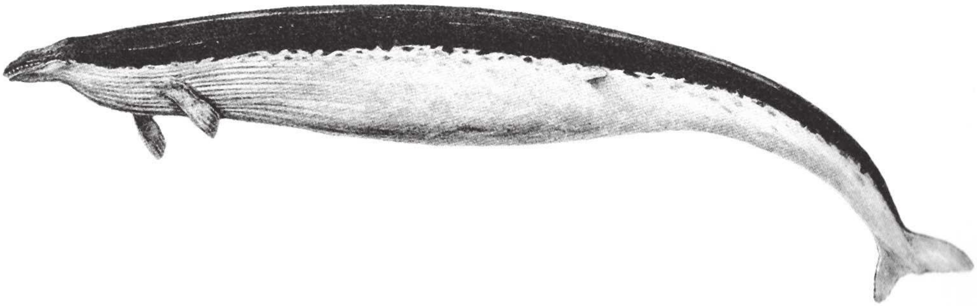

Fig. 8. Life restoration of *Basilosaurus* (Savage and Long, 1986).

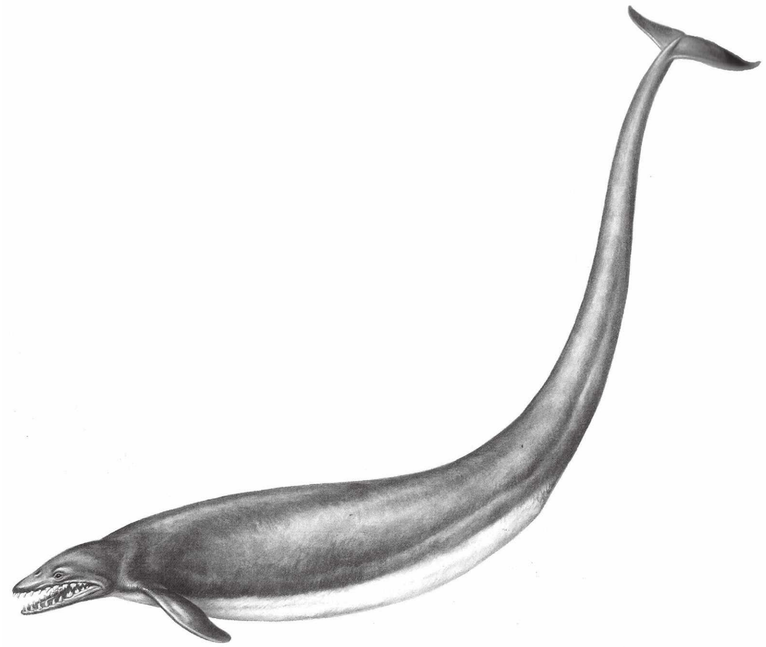

Fig. 9. Life restoration of *Basilosaurus* (Cox et al., 1988).

hind limb projecting from the flank (Fig. 6). Most of cetaceans have fewer thoracic vertebrae and therefore fewer ribs than terrestrial mammals, but the diameter in the trunk without costae should not be much larger than the diameter in the thorax.

The figure (Fig. 7) of Shikama (1979) seems to be faithfully fleshed out from the skeleton of the figure by Kellogg (1936). If you look at both figures together, they almost exactly overlap. However, it does not appear to have restored the swimming creature, probably because the original skeleton was reconstructed with unnaturally linearly arranged vertebrae.

The figure (Fig. 8) of Savage and Long (1986) is similar to the body shape of Colbert (1980) or Halstead (1978), in which the thickest is in the thorax and tapers backward.

Cox et al. (1988) is a color pictorial book depicting only animals on a white background (Fig. 9). *Basilosaurus* in Cox et al. (1988) is very similar to that of Burian (1972) in terms of body shape, posture, and drawing angle, and it seems that only the background sea was erased from the original drawing. In all of the above, the fluke shape is crescent-shaped, similar to Osborn's (1921) reconstruction (Barnes and Mitchell, 1978; Uhen, 1998).

Restoration method and consideration

In general, life restoration of extinct animals is more difficult than skeletal reconstruction, because it is necessary to estimate volume and shape of soft tissue, which does not remain in the fossil. On the other hand, the contour of the body surface of the natatorial animal correlates with the mode of locomotion in water. Therefore, the body shape is first obtained from the body length and height, the swimming style suitable for the body shape is then estimated, and the fluke shape suitable for the swimming style is restored.

Restoration of body shape

According to Web and Weihs (1983), the relationship between body shape and movement mode of fish is high-speed cruising type for spindle-shaped tuna with crescent-shaped tail fin, sudden start acceleration type for pike, and slow swimming type with high turning performance for high fish like butterflyfish. In addition, regarding the relationship between the body shape and part of the body that produces thrust and the swimming speed, the high-speed cruising type such as tuna oscillates only the tip of the tail and the tail fin quickly, while the elongated body shape such as eel swims slowly, making most of the body meander. This way of swimming is called oscillation and undulation, respectively. The tail fin of a fish that swims in undulation like an eel has not a crescent shape, but a ribbon shape along the body wall. But sea snakes without a tail fin can swim without problem.

Therefore, prior to the restoration of the fluke of *Basilosaurus*, it is necessary to restore the body shape of the living body from the skeleton. According to Kellogg (1936), *B. cetoides* (USNM12261) preserves almost the whole skeleton, including 21 caudal vertebrae, which make up 34% of the body length. The vertebral body length of the caudal vertebrae in total is about 5.4 m, and assuming that the thickness of the intervertebral disc is about 10% of the vertebral body length, the body length would be about 17.5 m. The maximum width of the thorax is about 1.3 m. In general, two-limbed aquatic animals such as whales and sea cows have a thoracic cross section close to a circle, so the diameter of the thoracic can be considered to be equal to the height and width.

In the whale body with reduced hind limbs, the skeleton located caudal to the thorax is mostly the vertebrae, and the height and width of the latter half of the body must be estimated in order to restore the body outline. By superimposing both of them on a modern whale whose skeleton and living body are known, the height of the living body can be estimated from the abdomen to the tail. Many whales and dolphins show the maximum diameter at the posterior part of the thorax and often taper smoothly backward. Looking at the restoration of *Basilosaurus* from this point of view, In tail reconstruction, Barnes and Mitchell (1978)'s is too thick, and in Shikama (1979), too tapered. Barnes and Mitchell (1978)'s reconstruction is too thick, and Shikama (1979)'s is too tapered in tail.

The body shape of *Basilosaurus* restored in this way is compared with that of modern whale and eel-shaped fish. Since we seldom have a chance to measure the actual specimens of the present life, the body length and height were measured with an accurately drawn picture book, and the value was obtained by multiplying by the reciprocal of the scale. Since the purpose of this study is to clarify the body proportions, the accuracy of the measured value itself is not strict. A scatter plot with body length on the X-axis and body height on the Y-axis shows the difference in proportions of the

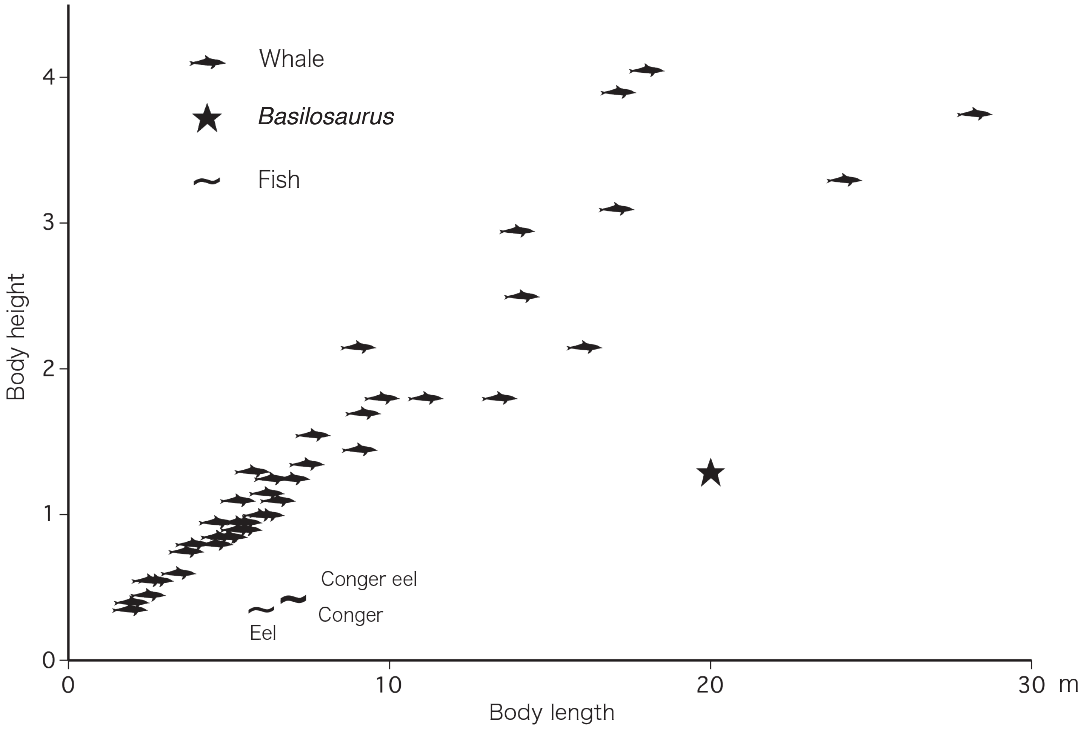

Fig. 10. Scattergram showing body proportion of whales and eel-shaped fish.

side view of the body shape (Fig. 10). Whales and dolphins are plotted on a scale of 1 meter. Eel-shaped fish (Ueno and Sakamoto, 1999) are multiplied by 10 for convenience of comparison. Cetaceans (Yamada, 2003) are represented by dolphin-shaped marks, eel-shaped fish by wavy lines, and *Basilosaurus* to be restored is indicated by a diamond.

Then, the slope of the regression line that penetrates the modern cetaceans and eel-type fish is divided into two, and the position of *Basilosaurus* is on the extension of the line of eel-type fish, and it becomes clear that the body shape belongs to the eel-type.

Swimming style and restoration of flukes

Modern whales and dolphins, like tuna, are high-speed cruising type, and all have crescent-shaped or triangular flukes or tail fins.

According to Buchholtz (1998), a series of elongated vertebrae of constant size shows undulation with constant amplitude, which supports the interpretation of a vertical eel-type swimming style. The caudal peduncle and tail fin are relatively small and only come out of the body modestly.

However, *Basilosaurus*, which resembles eel-shaped fish, should have swum slowly with its body meandering dorsoventrally, and modern tetrapods with eel-type movement have no caudal peduncle or tail fin. Therefore, it can be said that the triangular fluke is not suitable for this way of swimming.

Anguilliform fish meander bilaterally the entire body to generate thrust over the entire body wall. For this reason, the dorsal fins, tail fins, and anal fins are continuous, and in many cases, the height of the rear part of the body is increased. However, the anguilliform swimming reptile sea snake has no fins at all, but the meandering of the body is sufficient to swim. Thus, in the extinct mammal *Basilosaurus*, which has an anguilliform body and is thought to have swum in an eel, it needs a basis for deciding what extent the fins should be attached.

Since none of the living mammals have an eel-shaped body (Buchholtz, 1998), it is difficult to infer the degree of expanse of the fluke in *Basilosaurus*. It is known that in modern cetaceans, the caudal vertebrae are quite small near the posterior end where the tail fin is attached. The vertebral body of the last 6 caudal vertebrae of *Basilosaurus* is also particularly small (Buchholtz, 1998). Therefore, it is probable that a tail fin of *Basilosaurus* was also situated only at the rear

Fig. 11. Flukes of a fetal minke whale. Stored by Ashoro Museum of Paleontology.

end of the body like modern whales.

Even if the range of the fluke base is limited, the contours are variable. In fact, even modern whales have a wide variety of shapes such as crescents, triangles, and ginkgo leaves (Fish, 1998). However, as discussed above, all of these shapes correspond to the swimming style due to the oscillation of the tail. The shape of the fins suitable for swimming in eellike fashion should not be protruding than laterally protruding from the body in a wing shape.

In the whale embryo, the developmental process of a fluke can be observed. Initially, the skin folds along the side of the body, and as it grows, the central part rises to form a rhombus (Fig. 11), and then only the rear part protrudes bilaterally to form a triangle or crescent shape. It is generally known that the fetal and larval stages trace the shape of their ancestors in phylogeny. Since *Basilosaurus* is a species of Eocene ancestral cetaceans, it is not impossible that the shape of flukes of *Basilosaurus* hold the developmental stage of the modern whales.

Ecological Restoration

Based on the above biological restoration, we try to restore the appearance during swimming. Even if the reconstructed skeleton is unnaturally straight, it must have meandered during swimming. Since *Basilosaurus* is a mammal, it should have taken a dolphin kick to swing the vertebral column dorsoventrally like modern whales and dolphins. The problem is about meandering, and how many wavelengths fit in the body length. Compared to eels and sea snakes with similar body shapes, *Basilosaurus* has longer vertebrae and fewer vertebrae for its diameter of the vertebral body. From this, it is considered that the flexibility of the vertebral column is not so different from that of modern whales. Therefore, it can be estimated that only one wavelength of meandering would be included despite of its long body.

Basilosaurus is thought to have swum slowly near the surface of the sea (Gingerich, 1998), so the body color should have been dark on the back and white on the ventral side, similar to modern whales and dolphins. Many shallow-sea fish also have this kind of body color, but this color scheme is said to be a protective color that blends into the background when viewed from above or below.

The scene with a parent and a juvenile is based on the idea that it is exactly the same as modern whales. Cetaceans are born underwater, in considerable size, and begin to swim immediately after birth. During parenting, the mother accompanies them to help them breathe. All artiodactyls inhabiting the African savanna are nidifugous and can stand up and run shortly after birth. Since cetaceans are known to have been derived from some of the artiodactyls closely related to hippopotami, Eocene *Basilosaurus* should have these attributes.

Figure 12 is a new ecological restoration of *Basilosaurus* drawn based on the above considerations.

Conclusion

There are few papers on the skeletal reconstructions and life restoration figures of extinct vertebrates that refer to the basis for restoration. Since the restoration of physiology and ecology will be required for the future vertebrate paleobiology, the morphological restoration on the basis of them is indispensable.

In the restoration figure of the archaeocete *Basilosaurus*, a triangular fluke as seen in modern whales and dolphins has been drawn, although it has an eel-shaped body. The shape of the fluke of a whale is not determinable because of lack of bone inside. The body length and height were estimated from the shape and number of vertebrae, and the anguilliform body shape was restored. The vertical undulation like eel-shaped swimming style, is most suitable for its eel-shaped body, and the shape of the fluke is considered to be a longitudinally long rhombus. *Basilosaurus* is thought to swim slowly near the surface of the sea, and a new ecological restoration figure was created in consideration of the ecology of modern whales.

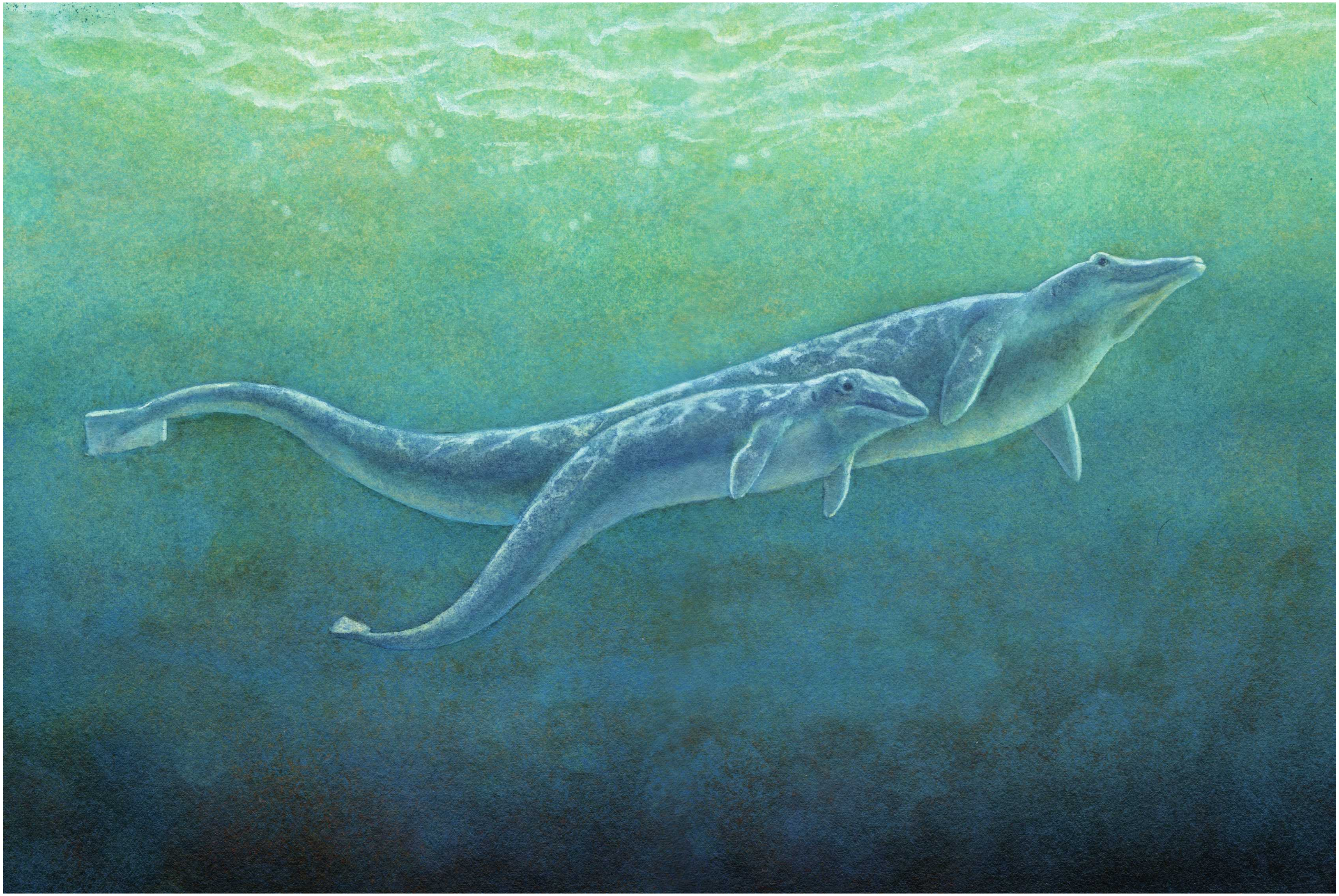

Fig. 12. Restoration figure of *Basilosaurus* drawn by Utako Kikutani under the direction of Norihisa Inuzuka.

References

Barnes LG, Mitchell E (1978) Cetacea. In: Maglio VJ, Cooke HBS (eds) Evolution of African mammals, Harvard Univ. Press, 582-602

Burian Z (1972) Artia, Prague, 220p

Buchholtz EA (1998) Implications of vertebral morphology for locomotor evolution in early Cetacea. In: Thewissen JGM (ed) Emergence of whales, Plenum Press, 325-351

Colbert EH (1980) Evolution of the vertebrates. 3rd ed. John Wiley & Sons, New York, 510p

Cox B, Savage RJG, Gardiner B, Dixon D (1988) Macmillan illustrated encyclopedia of dinosaurs and prehistoric animals, 311p

Fish FE (1998) Biomechanical perspective on the origin of cetacean flukes. In: Thewissen JGM (ed) Emergence of whales, Plenum Press, 303-324

Gingerich PD (1998) Paleobiological perspectives on Mesonychia, Archaeoceti, and the origin of whales. In: Thewissen JGM (ed) Emergence of whales, Plenum Press, 423-449

Gingerich PD, Smith BH, Simons EL (1990) Hind limbs of Eocene *Basilosaurus*: evidence of feet in whales. Science 249, 154-157

Gregory WK (1951) Evolution emerging, Vol. 1. Macmillan, New York, 736p

Halstead LB (1978) The evolution of the mammals. Peter Lowe, 116p

Harlan R (1834) Notice of Fossil Bones Found in the Tertiary Formation of the State of Louisiana. Transactions of the American Philosophical Society 4, 397-403

Inuzuka N (1984a) Skeletal restoration of the desmostylians: herpetiform mammals. Mem. Fac. Sci., Kyoto Univ., Ser. Biol. 9, 157-253

Inuzuka N (1984b) Morphological Restoration of *Desmostylus*. In: Inuzuka N, Takayasu K, Chinzei K, Yoshida K (eds) Monograph of the Association for the Geological Collaboration in Japan, 28 101-118

Inuzuka N (1984c) Restoration of the desmostylians. Kaimeisha, Tokyo, 146p

Inuzuka N (1997) Dinosaur reconstructions. Iwanami Shoten, Tokyo, 128p

Kellogg R (1936) A review of the Archaeoceti. Carnegie Inst. Wash. Publ., 482, 1-366

Lucas FA (1929) Animals of the past. American Museum of Natural History, New York, 206p

Osborn HF (1913) *Tyrannosaurus*, restoration and model of the skeleton, Bull. Amer. Mus. Nat. Hist 32, 91-92

Osborn HF (1921) The age of mammals in Europe, Asia and North America. Macmillan, New York, 635p

Owen R (1839) Observations on the teeth of the *Zeuglodon*, *Basilosaurus* of Dr. Harlan. Proceedings of the Geological society of London 3, 24-28

Savage RJG, Long MR (1986) Mammal evolution an illustrated guide. British Museum (Natural History), London, 259

Shikama T (1979) Illustrated Guide to Vertebrate Paleontology, Asakura Shoten, Tokyo, 212p

Uyeno T, Sakamoto K (1999) Illustrated Guide to Fish Taxonomy, Tokai Univ. Press, 155p

Uhen MD (1998) Middle to Late Eocene Basilosaurines and Dorudontines. In: Thewissen JGM (ed) Emergence of whales, Plenum Press, 29-61

Web PW, Weihs D (1983) Fish biomechanics. Praegar Publishers

Yamada TK (ed) (2003) Cetaceans of the world. National Science Museum