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The Dentary of a Choristodere (Reptilia: Archosauromorpha) from the Okurodani Formation, Tetori Group (Lower Cretaceous) of Japan

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Abstract An isolated choristoderan dentary is described from the Lower Cretaceous Okurodani Formation, Tetori Group, of Japan. The dentary was collected from the locality where the holotype of *Shokawa ikoi* was found, and is most likely to belong to that species. Only two fragmentary dentaries have been provisionally assigned to *S. ikoi*. This is the first report of an almost complete choristoderan dentary from Japan.

Key words: Choristodere, Early Cretaceous, Tetori group, *Shokawa ikoi*, Gifu, Japan

Introduction

Choristoderans are neodiapsid reptiles that are specialized for an aquatic way of life. They range in size from small to large, and in morphology from short-necked to long-necked, and from short-snouted to gavial-like (Evans and Hecht, 1993). The group has been recorded from deposits of Late Triassic to Late Oligocene age, and had a broad geographical range from western North America (Brown, 1905; Parks, 1927; Erickson, 1972, 1985, 1987; Gao and Fox, 1998), through Europe (Gervais, 1877; Dollo, 1884; Russell-Sigogneau and Russell, 1978; Sigogneau-Russell, 1981a; Evans, 1990, 1991; Hecht, 1992; Storrs and Gower, 1993; Storrs *et al.*, 1996) and Asia (Efimov, 1975, 1979; Sigogneau-Russell, 1981b; Brinkman and Dong, 1993; Gao *et al.*, 1999, 2000), to Japan (Evans and Manabe, 1999a), and from subtropical latitudes to the Arctic (Tarduno *et al.*, 1998). As yet, no choristodere has been recovered from Gondwana.

Shokawa ikoi provided the first record of the Choristodera from Japan (Evans and Manabe, 1999a). The isolated dentary described herein was found at the type locality of *S. ikoi* in the Lower Cretaceous Okurodani Formation, Tetori Group, near Shokawa, Gifu Prefecture. However, the type specimen lacked any trace of the skull or lower jaws. Although many isolated reptile bones are known from this locality, to date the only skull elements to be provisionally assigned to *S. ikoi* were a few fragmentary lower jaw elements from juvenile stages in ontogeny.

Shokawa ikoi is characterized by the following combination of features: at least 16 cervical vertebrae; cylindrical vertebral centra persistently separated from the neural arches except in the neck; caudal vertebrae with deep descending ventral flanges; anterior caudals with tall slender neural spines; rhombic interclavicle with clavicles meeting at a strong angle in the ventral midline; strong quadrangular coracoids and reduced scapular blades; humerus, forearm and hand relatively short and broad; ilium with narrow vertical blade bearing strong vertical striations; ribs, limb bones and gastralia pachyostoic (Evans and Manabe 1999a). Phylogenetic analysis (Evans and Manabe, 1999a) places *Shokawa* in small clade

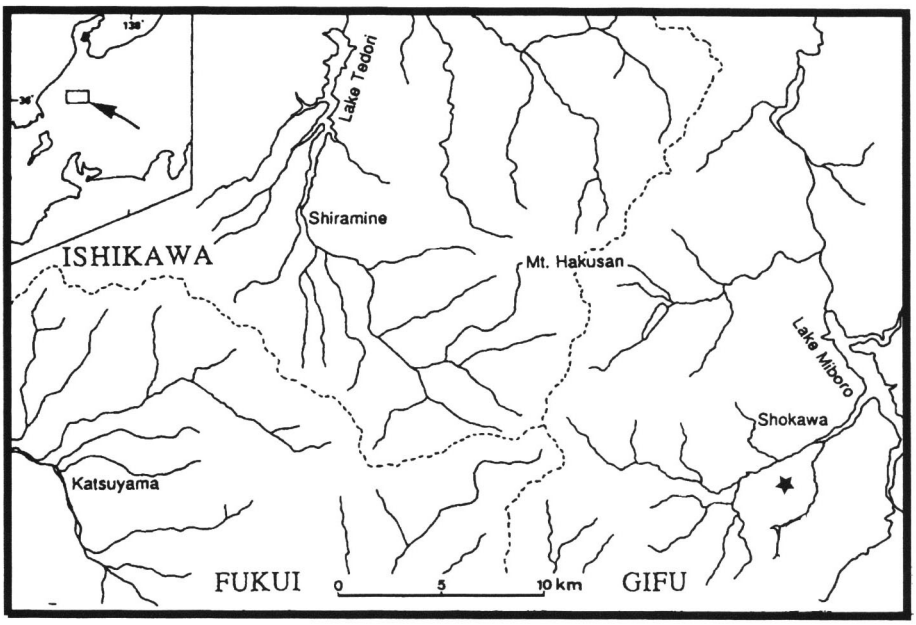

Fig. 1. Map showing the locality (Star mark) of the described specimen. (Modified from Hasegawa et al., 1995).

with the Middle Jurassic to Late Cretaceous genus *Cteniogenys* and the Late Triassic genus *Pachystropheus*. This clade forms the sister taxon of crown-group Neochoristodera (Evans and Hecht 1993) including *Champsosaurus*, *Simoedosaurus*, *Ikechosaurus* and *Tchoiria*.

Abbreviations: SBEG, Shokawa Board of Education, Gifu Prefecture; IBEF, Izumi Board of Education, Fukui Prefecture.

Systematic Palaeontology

Diapsida Osborn, 1903

Neodiapsida Benton, 1985

Choristodera Cope, 1884

aff. ***Shokawa ikoi*** Evans and Manabe, 1999a

Material: An isolated right dentary, SBEG 044.

Locality and horizon: Stream section, Shokawa, Gifu Prefecture, Japan (36°03′N, 136°53′E; Fig. 1); bone bed horizon in the Okurodani Formation, Lower Cretaceous Tetori Group, Japan. The horizon has been provisionally dated 120 to 140 Ma based upon fission track dating (Gifu-ken Dinosaur Research Committee, 1993). A preliminary Ar/Ar dating, however, has suggested the possibility of a Late Jurassic in age for the horizon, although further work would be necessary to confirm it (Chris Nicholas and Sarah Sherlock, pers. comm., 2001).

Description: SBEG044 is an almost complete right dentary embedded in the matrix with the lateral surface exposed. Additional preparation has uncovered part of the anteromedial symphysial region. As preserved, the bone has a length of 60 mm and a maximum height of 8 mm (Fig. 2-A). The anterior end is missing about 1 mm and there is a 5 mm break in the middle of the bone caused at the time of its collection in the field. The external surface of the dentary bears a row of grooved sensory foramina as in all choristoderes (Evans, 1990). As preserved, SBEG044 has 56 tooth positions; 41 teeth remain in place and there are 15 empty alveoli. In addition, there must have been up to 4 more tooth positions at the missing parts, the anterior end and the middle of the bone (Fig. 2-A, B). Anterior teeth are more slender than posterior teeth (Fig. 3), and the tooth sockets are circular. The teeth are homodont, re-

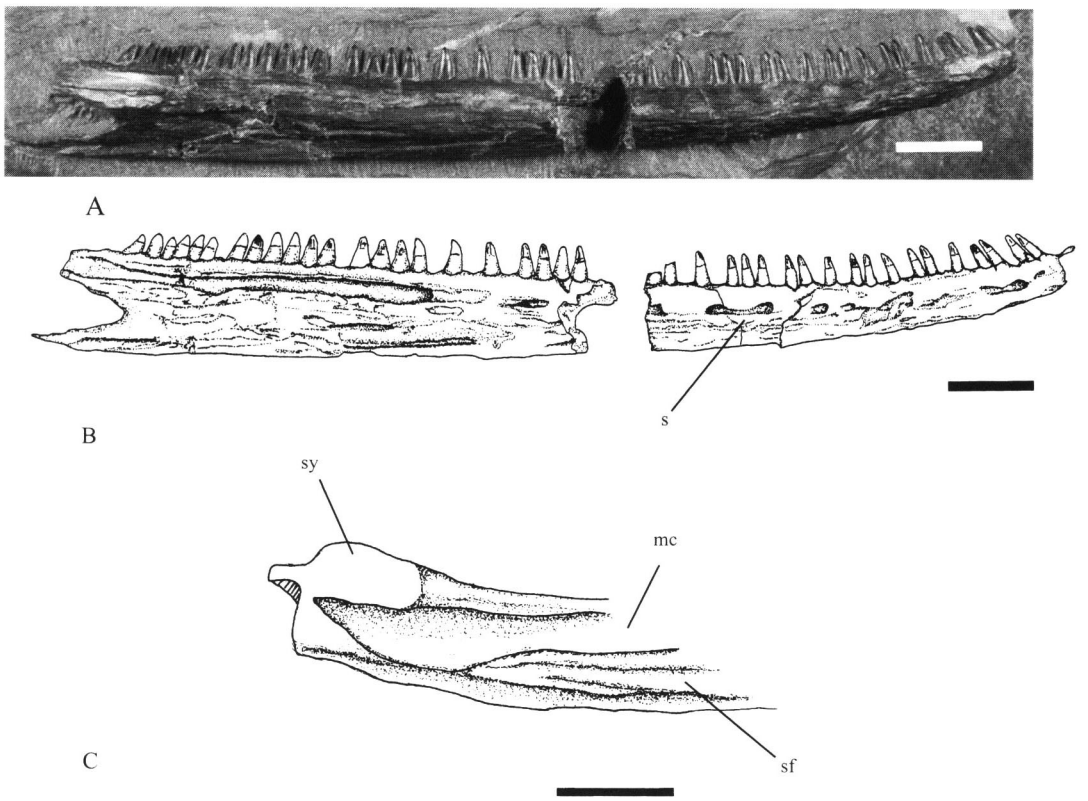

Fig. 2. SBEG044: Right dentary. A and B, Lateral view. C, Medial view. mc: meckerian canal, s: sensory foramina, sf: splenial facet, sy: symphysis. Scale bar=5 mm.

sembling slender cones, and the upper parts bear weak striae. The root partially exposed from the tooth socket is smooth. The mandibular symphysis is small and terminal (Fig. 2-C) and evidently lacked the posterior elongation seen in *Champsosaurus* (Erickson, 1972), *Ikechosaurus* (Brinkman and Dong, 1993) and *Tchoiria* (Efimov, 1975, 1979). Overall, the morphology of the dentary suggests a relatively short-snouted animal, rather than the long gavial-like snout seen in *Champsosaurus* and *Tchoiria*.

The splenial is missing from SBEG044, exposing the internal structure of the Meckelian canal, which has a deep anteroventral wall (Fig. 2-C). There is no anterior groove on the subdental shelf for articulation of the splenial, but a deep depression on the ventral wall of the Meckelian canal, probably indicates the termination of the spleniodentary articulation, at a point below the seventh tooth position (Fig. 2-C).

Discussion

Several reptilian groups have been identified amongst the small vertebrate remains in Shokawa, including turtles, dinosaurs, pterosaurs, lizards, and choristoderes. SBEG044 is clearly not attributable to either a dinosaur or a turtle, and differs from those of pterosaurs on the basis of tooth implantation and tooth morphology. Lizard jaws are substantially shorter than SBEG 044 and show little or no development of the mandibular symphysis (Evans and Manabe, 1999b). In contrast, SBEG044 shows a striking similarity to the jaws of choristoderan reptiles, in length, in tooth morphology (homodont cones with striae), and in the row of grooved external sensory foramina. Attribution to a choristodere is

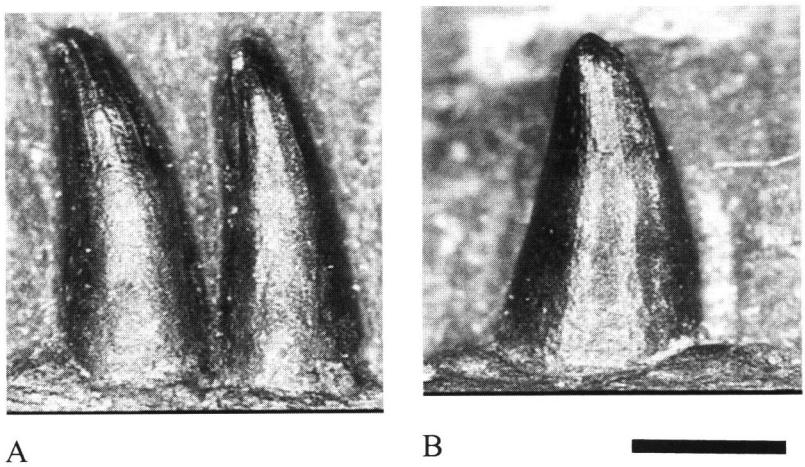

Fig. 3. A, anterior dentary tooth in lateral view. B, posterior dentary tooth in lateral view (SBEG044). Scale= 0.5 mm.

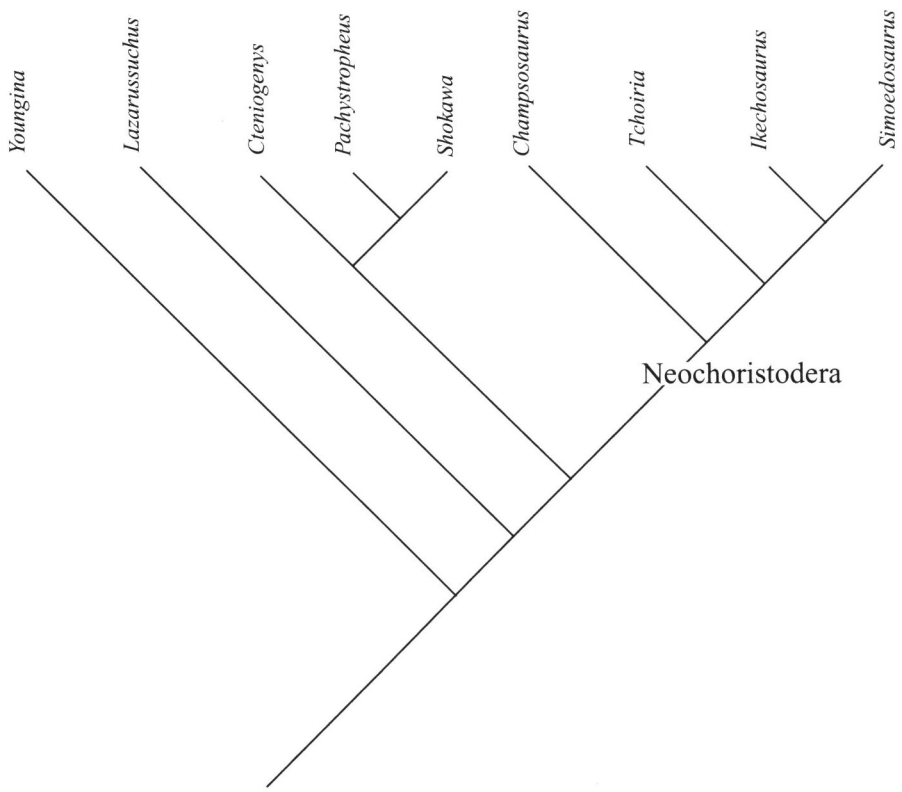

Fig. 4. A cladgram of the Choristodera. Modified from Evans and Manabe (1999a). Phylogenetic positions of *Hyphalosaurus* and *Monjurosuchus* are yet to be resolved.

therefore the most parsimonious conclusion.

SBEG044 can be distinguished from the dentaries of Neochoristodera (*Champsosaurus*, *Ikechosaurus*, *Simoedosaurus*, *Tchoiria*) by the lack of basal infolding of the tooth enamel (character 35 in the data matrix of Evans and Manabe,

1999a). SBEG044 also differs from the dentary of *Lazarussuchus* (Hecht, 1992) that has a moderately elongated mandibular symphysis equalling one-third or less of the length of the tooth row, with little inclusion of the splenial (character 41, Evans and Manabe 1999a). Therefore remaining possibilities among described species are *Cteniogenys*, *Monjurosuchus*, *Hyphalosaurus*, *Pachystropheus* and *Shokawa* (Fig. 4). However, there are no lower jaw elements reported for *Pachystropheus* (Storrs *et al.*, 1996), and no detailed descriptions have been published for *Monjurosuchus* (Gao *et al.*, 2000) and *Hyphalosaurus* (Gao *et al.*, 1999). SBEG 044 is similar to the dentary of *Cteniogenys* (Evans, 1990) in the following characters: the tooth sockets are circular, the root partially exposed from the tooth socket is smooth, and the mandibular symphysis is small and terminal. However, these are primitive character states within choristoderes. In addition, SBEG044 has a deep anterior groove on the ventral wall of the Meckelian canal for articulation with the splenial. This is quite different from the condition in *Cteniogenys* where there is a shallower depression and no groove for articulation of the splenial. According to Evans and Manabe (1999a), *Cteniogenys* and *Shokawa* are sister taxa within a clade lying outside Neochoristodera. The differences between SBEG044 and *Cteniogenys* confirm the generic distinction of these two basal choristoderan taxa.

The holotype specimen of *S. ikoi* represents a small choristodere with a snout-vent length of about 250 mm, and a total length (with the tail) of about 370–400 mm (Evans and Manabe, 1999a). Based on jaw proportions in other choristoderes, SBEG 044 is from an animal similar in size to the holotype of *Shokawa ikoi*. Two dentaries (IBEF VP8, IBEF VP9) from the Shokawa locality were provisionally attributed to *S. ikoi* (Evans and Manabe, 1999a), but they are both fragmentary and immature, and no detailed descriptions have been published. SBEG 044 is similar to them in tooth, socket, and symphysial morphology, and it is therefore reasonable to suggest that they all belong to *S. ikoi*. Nonetheless, firm assignment of SBEG 044 to *S. ikoi* must await the discovery of more complete specimens. The Yixian Formation of China has yielded two similar sized choristoderan species: the short-necked *Monjurosuchus* (Endo, 1940 Gao *et al.*, 2000) and a new long-necked form, *Hyphalosaurus* (Gao *et al.*, 1999). There is new evidence to suggest that choristoderans were similarly diverse in the Tetori Group. A microvertebrate assemblage from the contemporaneous Kuwajima Formation, Shiramine Village, Ishikawa Prefecture, has yielded highly unusual choristoderan remains that appear to represent a genus as yet unknown either in the Tetori Group or the Yixian Formation.

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