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To cite this article: Pingfu Chen & Gloria Arratia (2010) Oldest known Mylopharyngodon (Teleostei: Cyprinidae) from the Mongolian Plateau and its biogeographical implications based on ecological niche modeling, *Journal of Vertebrate Paleontology*, 30:2, 333-340, DOI: [10.1080/02724631003620930](https://doi.org/10.1080/02724631003620930)


To link to this article: <http://dx.doi.org/10.1080/02724631003620930>

 Published online: 24 Mar 2010.

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## OLDEST KNOWN *MYLOPHARYNGODON* (TELEOSTEI: CYPRINIDAE) FROM THE MONGOLIAN PLATEAU AND ITS BIOGEOGRAPHICAL IMPLICATIONS BASED ON ECOLOGICAL NICHE MODELING

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**ABSTRACT**—*Mylopharyngodon wui*, sp. nov., based on a completely preserved right pharyngeal bone with teeth from a middle Miocene deposit of the IVPP 346 Locality (43°24'53.4"N, 113°07'06.1"E) in the Tairum Nor area of Suniteyou Qi (Banner), Inner Mongolia, China, is described and compared with the living counterpart. It is different from the living black carp in having a generally smaller anterior angle, pharyngeal teeth  $a_1$  and  $a_2$  almost similar in size, and much rounder teeth  $a_2$  and  $a_3$ . The ecological niche model of the living black carp, based on the Genetic Algorithm for Rule-set Production (GARP), shows that the fossil black carp is no longer in the niche model area, indicating that the regional environment has changed greatly, and that the black carp's niche has shrunk southeastward. The niche model also confirms that the distribution of the black carp is restricted by altitude above sea level. It may be inferred that the Inner Mongolia Plateau has risen more than 1000 m since the middle Miocene if the niche remained stable or evolved little over a long period of time.

### INTRODUCTION

Cyprinidae are the largest family of freshwater fishes, containing 220 genera and about 2420 species and occurring widely in Eurasia, Africa, and North America (Nelson, 2006). The greatest generic diversity and number of species is in China and Southeast Asia (Nelson, 2006). Amongst the great cyprinid diversity, 132 genera and 532 species and subspecies of living cyprinids have been recorded in China (Chen et al., 1998), and more than 28 genera and 34 species of fossil cyprinids have been reported from Chinese Tertiary sediments (Zhou, 1990; Chang and Chen, 2000). The earliest fossil cypriniforms (cyprinid and catostomid) are from the Eocene of China and North America, but very few fossil cyprinids have been found in deposits earlier than Miocene (Chang and Chen, 2000; Chang and Chen, 2008). Most subfamilies of living cyprinids have appeared in the Miocene, although very few species belong to the living genera. Almost all fossil cyprinids from Chinese Pliocene deposits can be compared to living genera, and more than half of them to living species (Chang and Chen, 2000). Although many fossil cypriniforms are represented in Asia, their study has been largely neglected in China, owing to the poor preservation of most specimens and their limited significance to higher-level systematics (Chen et al., 2005). The origin, evolution, and interrelationships within the Cyprinidae are still uncertain (e.g., Howes, 1991; Cavender and Coburn, 1992; Chen et al., 1998), mainly due to scarce morphological information on fossil members of the group as well as many extant species and incomplete knowledge on the early diversification of cyprinids.

*Mylopharyngodon* Peters, 1880, is a cyprinid genus native to eastern Asia and represented only by one species—*Mylopharyngodon piceus* (Richardson), 1846, known as 'the black carp.' The black carp is one of the four Chinese pond-cultured carps, which

constitute the most important part of freshwater aquaculture in China. It was recorded in ancient Chinese literature as early as the Tsin dynasty (A.D. 265–420). Fossil remnants of black carp have been recorded from a few geological deposits, and more frequently, in archaeological sites, e.g., the Yingxu archeological site of Anyang, Henan (Wu, 1948); the Jiahu Grave of Wuyan, Henan (Wu Xinzhi, pers. comm. 2001); the Houjiazai archeological site of Dingyuan, Anhui (Jiao-jian Zhou, pers. comm. 2001); the Lijiaohe archaeological site of Neolithic Age at Yichang, Hubei (Liu, 1957); the Dingchun archaeological site of Xiangfen, Shanxi (Liu, 1958); the Pleistocene deposit at Sanmenxia, Henan (Huang, 1957); and the Pliocene deposit of the Yushe basin, Shanxi (Liu and Su, 1962). Single pharyngeal teeth of the black carp were also reported in the lower Miocene deposits of Woniushan, Tongxin County, Ningxia, the Guantao Formation in Binxian County, Shandong (Zhang et al., 1985), and in the upper Eocene Tongjun Formation in the Baise basin of Guangxi Province (Ding et al., 1977). As an individual pharyngeal tooth of the black carp is very similar to the first tooth in the main row of the common carp and that of certain species of the subfamilies Barbinae and Rasborinae (Cyprinidae), these reports of isolated pharyngeal teeth will require additional specimens and comparisons with living black carp to confirm whether or not they actually belong to the same species.

The specimen reported in this paper was collected by Dr. Xiaoming Wang (Natural History Museum of Los Angeles County, Los Angeles, California) in Inner Mongolia on July 5, 2000. This specimen was found in the IVPP 346 Locality (43°24'53.4"N, 113°07'06.1"E; altitude 1550 m) in the Tairum Nor area of Suniteyou Qi (Banner). The Tertiary deposit here is well exposed along the southern rim of the Tunggur Tableland. The Tairum Nor exposure consists of a sequence of upper and lower red mudstones, 34 m in total thickness, and a 3-m grayish yellow cross-bedded sandstone unit between the red mudstones (Wang et al., 2003). The entire sequence belongs to the lower part of the Tunggur Formation, which is paleomagnetically dated to be

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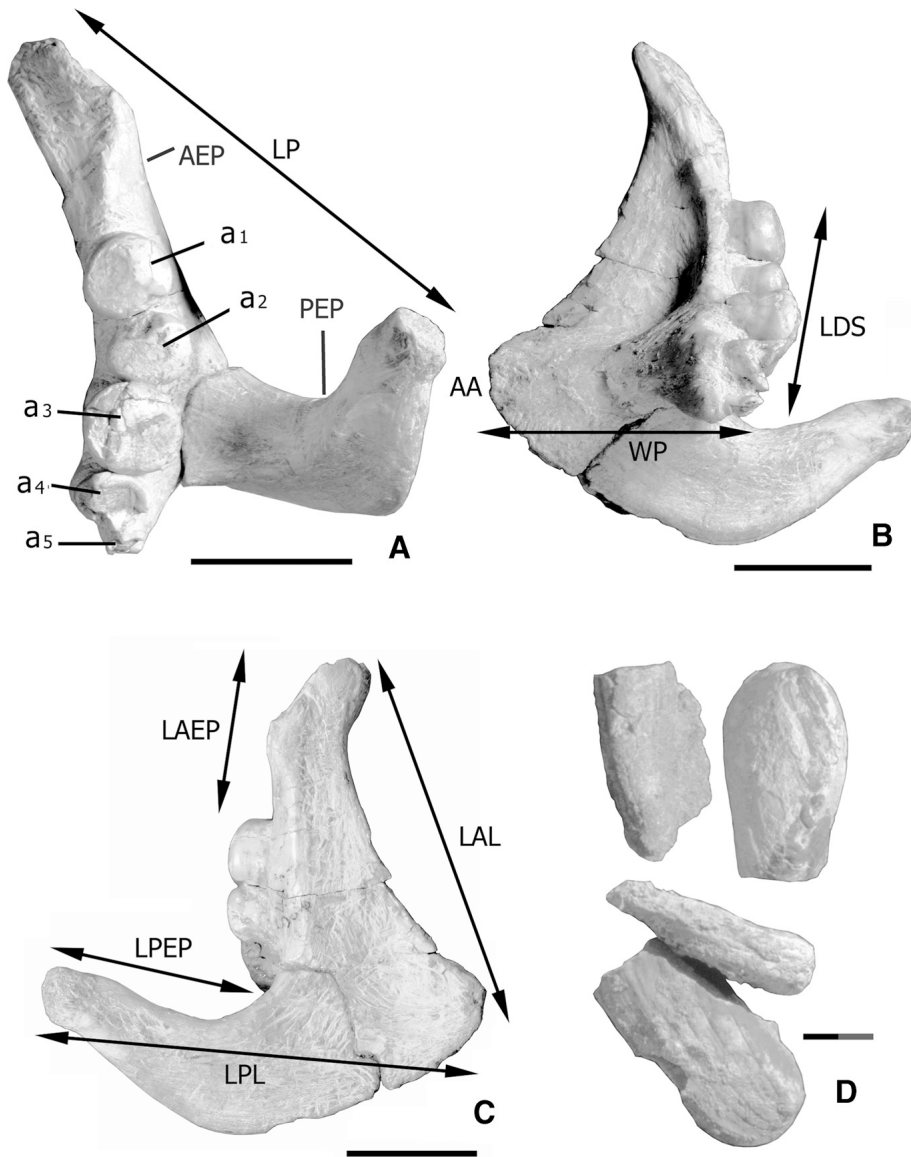


FIGURE 1. Pharyngeal bone and teeth of †*Mylopharyngodon wui*, sp. nov. (IVPP V12533), middle Miocene, Inner Mongolia. **A**, dorsal view; **B**, inner lateral view; **C**, outer lateral view; **D**, undetermined bivalves unearthed with the holotype. Scale bars equal 1 cm.

approximately 12.5 Ma in the late middle Miocene, although recent analysis of small mammals in the red mudstones seems to indicate a somewhat older age (Qiu et al., 2006). The fossil remains of the black carp were found near the top of the sandstone unit and were associated with fossil bivalves (Fig. 1D), and large mammals such as *Platybelodon grangeri*, *Tungurictis spocki* (Wang, 2004), *Sansanosmilus* sp., and *Turcoceros* sp. The red sandstones and mudstones are rich in small fossil mammals, indicating a middle Miocene age (Qiu and Wang, 1999).

#### MATERIAL AND METHODS

The pharyngeal bone with teeth was mechanically prepared. Measurements were taken with a digital caliper. Pharyngeal bones and teeth of living black carp were used for comparison. The comparative study was limited to a few specimens, because

only a few pharyngeal bones belonging to large individuals were located in museum collections, which possess mainly small pharyngeal bones belonging to young specimens.

Pharyngeal tooth terminology used here follows Chu (1935) and Nakajima and Yue (1995). Tooth positions in the adult dentition are numbered according to the classic work of Vasnetsov (1939). The most medial row is named major row (row a), and lateral rows are named minor rows (rows b and c). Tooth position is numbered from anterior to posterior in each row; tooth a<sub>1</sub> is the first tooth of the major row (row a), and a<sub>5</sub> is the last tooth (see Fig. 1A).

**Institutional Abbreviations**—**AMNH**, American Museum of Natural History, New York; **BIZ**, Beijing Institute of Zoology, Chinese Academy of Sciences, Beijing; **CAS-SU**, California Academy of Sciences specimens previously catalogued at Stanford University, San Francisco, California; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese

TABLE 1. Measurements (in mm) of the pharyngeal bone and teeth of †*Mylopharyngodon wui*, sp. nov.

Bone/teeth	Measurement	Bone/teeth	Measurement
LP	74.72	AA	84°
WP	37.32	Length/width of a <sub>1</sub>	10.43/11.09 = 0.94
LAL	58.00	Length/width of a <sub>2</sub>	9.2/11.0 = 0.84
LPL	70.04	Length/width of a <sub>3</sub>	11.79/14.2 = 0.83
LAEP	30.60	Length/width of a <sub>4</sub>	7.5/10.0 = 0.75
LPEP	51.00	Length/width of a <sub>5</sub>	4.1/5.5 = 0.75
LDS	41.30		

See Anatomical Abbreviations for definitions.

Academy of Sciences, Beijing; **KIZ**, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming; **MCZ**, Museum of Comparative Zoology, Harvard University; **WIH**, Wuhan Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan.

**Anatomical Abbreviations**—a<sub>1</sub>–a<sub>5</sub>, teeth 1–5 of row a; **AA**, anterior angle; **AEP**, anterior edentulous process; **LAEP**, length of anterior edentulous process; **LAL**, length of anterior limb; **LDS**, length of dentigerous surface; **LP**, length of pharyngeal bone; **LPEP**, length of posterior edentulous process; **LPL**, length of posterior limb; **PEP**, posterior edentulous process; **WP**, width of pharyngeal bone.

#### SYSTEMATIC PALEONTOLOGY

Superorder OSTARIOPHYSI Sagemehl, 1885

Order CYPRINIFORMES Bleeker, 1859

Family CYPRINIDAE Cuvier, 1817

Genus *MYLOPHARYNGODON* Peters, 1880

†*MYLOPHARYNGODON WUI*, sp. nov.

(Fig. 1A–C)

**Diagnosis**—Anterior limb curves outward in a bow-shape; posterior limb strongly bent upward from the middle; the anterior angle is less than 90°; teeth a<sub>1</sub> and a<sub>2</sub> are nearly cylindrical and almost similar in size; and tooth a<sub>3</sub> has a much larger length/width ratio than the others.

**Holotype**—IVPP V12533, a completely preserved right pharyngeal bone with teeth.

**Etymology**—The specific name honors the late Dr. Xianwen Wu, in recognition of his great contribution to the study of cyprinids in China.

**Type Locality and Horizon**—Near the top of the sandstone in the lower part of the Tunggur Formation, IVPP 346 Locality (43°24'53.4"N, 113°07'06.1"E) in the Tairum Nor area in Suniteyou Qi (Banner), Inner Mongol, middle Miocene.

#### DESCRIPTION

The pharyngeal bone IVPP V12533 is embowed and robust; it is 74.72 mm in length, and its width is half of its length (for other measurements and ratios, see Table 1). The anterior limb (Fig. 1B, C) arches outward in a bow-shape, obviously different from that of living black carps, which have a triangular shape (Fig. 2B<sub>2</sub>, B<sub>3</sub>, C<sub>2</sub>, C<sub>3</sub>). The posterior limb bends strongly upwards from the middle region, about 1.2 times the length of the anterior one (Table 1). The posterior edentulous process is compressed, tapering to a blunt end. The anterior edentulous process extends into a triangle, its inner side of the extreme end connected to the left pharyngeal bone. The length of the posterior edentulous process is about 1.67 times of that of the anterior. The anterior angle is extended out from the middle of the pitted surface. About five pits (Fig. 1C) are observed along the outer part of the pitted surface, and are filled with quartz sandstone. The anterior angle is less than 90° (Fig. 1B, C), smaller than that of the living species

in which it is greater than 90° (Fig. 2A<sub>2</sub>, A<sub>3</sub>, B<sub>2</sub>, B<sub>3</sub>, C<sub>2</sub>, C<sub>3</sub>). Two pits are observed in the dorsal tooth side of the pharyngeal bone, which are also filled with quartz sandstone.

Five flat, round, molar-like pharyngeal teeth are present. Crowns are smooth and high, except those of the last two teeth (a<sub>4</sub>, a<sub>5</sub>), which are partially damaged. No grooves or lines are observed on their surfaces. Tooth a<sub>1</sub> is cylindrical; the length/width ratio is 0.94. The crown is round, different from that of the living black carp in which the crown of a<sub>1</sub> is oval (Fig. 2A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub>). The chewing surface is smooth except for some worn regions on the inner side. Tooth a<sub>2</sub> is cylindrical and almost the same size as tooth a<sub>1</sub>. The crown is round and smooth, with a dent in the middle of the lateral surface. Tooth a<sub>3</sub> is the largest of the five pharyngeal teeth, located opposite to the end of the posterior edentulous process. The crown is smooth with a backward-inclined chewing surface; the length/width ratio is 0.83. The crowns of teeth a<sub>4</sub> and a<sub>5</sub> are damaged but discernable; they are compressed and elliptic, and the length/width ratios of both teeth are estimated as 0.75. From teeth a<sub>3</sub> to a<sub>5</sub>, the size decreases considerably, so that tooth a<sub>5</sub> is about nine times smaller than tooth a<sub>3</sub>.

Living black carp may weigh 70 kg or more (Chen et al., 1998). Recently, a large black carp of 181 cm in length and 83 kg in weight was reported. Its age was estimated at 70 years (<http://www.sznews.com/n2/ca1513290.htm>, accessed on June 6, 2005). According to the measurements of a pharyngeal bone of an extant black carp of 63 kg from Fuxian Lake, Yunnan (Junxin Yang, pers. comm. 2003), it is reasonable to extrapolate that the fossil pharyngeal bone studied here belongs to a specimen of about 37–43 kg.

#### COMPARISON

The black carp is a unique cyprinid native to eastern Asia, different from all other species of Cyprinidae because of the presence of one row of molariform pharyngeal teeth (Chu, 1935). Six pharyngeal bones and their teeth of *M. piceus* were measured and used to compare with *M. wui*, sp. nov. (Table 2). Specimen IVPP V852 was recovered from the Lijiaohe archaeological site of Neolithic Age in Yichang, Hubei (Fig. 2B<sub>1</sub>–B<sub>3</sub>), and specimen IVPP P40 (Fig. 2C<sub>1</sub>–C<sub>3</sub>), IVPP P41 (Fig. 2A<sub>1</sub>–A<sub>3</sub>), and BIZ45158 are Recent black carps without specific locality data. Specimen IVPP P41 (Fig. 2A<sub>1</sub>–A<sub>3</sub>) is from the Shisanling Reservoir of suburban Beijing. AMNH 10893 is a small Recent specimen from Hunan, China. KIZ is a Recent uncatalogued specimen from Wuxian Lake, Yunnan, China, with a gross weight of 63 kg. Most pharyngeal bones and teeth of black carps in museum collections are too small to be useful for a significant comparison (e.g., CAS-SU 29456, CAS-SU 31171, and MCZ 32654).

All measurements of the fossil pharyngeal bone are within the measurement range of Recent ones (see Table 2), but the anterior angle is 84° in *M. wui*, whereas it is about 90° or more in living black carp. Tooth a<sub>2</sub> is relatively round in *M. wui*, and has almost the same size as tooth a<sub>1</sub>, in contrast to the living black carp specimens in which a<sub>2</sub> is much smaller than a<sub>1</sub> and oblong in shape; the length/width ratio of tooth a<sub>3</sub> is larger than that of the living black carp (see Table 2).

The fossil specimen described above is different from the observed pharyngeal bones and teeth of living black carp and from the archaeological remains found so far in China. Therefore, a new species, *Mylopharyngodon wui*, is established. *Mylopharyngodon* was assigned to Leuciscinae according to Chinese authors such as Chu (1935), Chen et al. (1984), and Chen et al. (1998), or to Squaliobarbinae after Arai and Kato (2003) and Nelson (2006). Because the structure of the pharyngeal bone and teeth of *Mylopharyngodon* is unique within the family Cyprinidae, a discussion of concerning both subfamilies and the position of *Mylopharyngodon* is far beyond the scope of this paper.

TABLE 2. Comparison of measurements (in mm) of †*Mylopharyngodon wui*, sp. nov., and living *Mylopharyngodon piceus*.

Character	Specimen							
	† <i>M. wui</i> , sp. nov. (IVPP V12533)	<i>M. piceus</i> (IVPP V852)	<i>M. piceus</i> (IVPP P40)	<i>M. piceus</i> (AMNHI10893)	<i>M. piceus</i> (BIZ 9710)	<i>M. piceus</i> (BIZ 45158)	<i>M. piceus</i> (KIZ)*	<i>M. piceus</i> (IVPP P41)
Body length	N/A	N/A	N/A	113	174.02	232.16	N/A	N/A
Gross weight (g)	?3700–4300	N/A	N/A	22.6	66.28	350	6300	N/A
LP/LDS	74.72/41.3 = 1.81	100.3/60.7 = 1.65	43.7/27.0 = 1.62	13.2/7.15 = 1.84	18.16/10.56 = 1.72	27.22/17.01 = 1.60	118.08/63.58 = 1.86	76.1/40.05 = 1.9
WP/LDS	37.32/41.3 = 0.90	50.0/60.7 = 0.82	21.8/27.0 = 0.81	6.2/7.15 = 0.87	10.77/10.56 = 1.02	18.54/17.01 = 1.09	69.95/63.58 = 1.10	45.05/40.05 = 1.12
LP/WP	74.72/37.32 = 2.002	100.3/50.0 = 2.006	43.7/21.8 = 2.005	13.2/6.2 = 2.129	18.16/10.77 = 1.6862	27.22/18.54 = 1.4682	118.08/69.95 = 1.6881	76.1/45.05 = 1.69
LAL/LDS	58.0/41.3 = 1.40	81.2/60.7 = 1.34	33.9/27.0 = 1.26	9.6/7.15 = 1.34	11.62/10.56 = 1.10	20.41/17.01 = 1.20	83.2/63.58 = 1.31	69.6/40.05 = 1.74
LP/LDS	70.04/41.3 = 1.70	87.0/60.7 = 1.43	39.8/27.0 = 1.47	12.2/7.15 = 1.71	15.84/10.56 = 1.50	24.66/17.01 = 1.45	116.36/63.58 = 1.83	74.8/40.05 = 1.87
LP/LAL	70.04/58.0 = 1.208	87.0/81.2 = 1.071	39.8/33.9 = 1.174	12.2/9.6 = 1.27	15.84/11.62 = 1.363	24.66/20.41 = 1.208	116.36/83.2 = 1.399	74.8/69.6 = 1.07
LAEP/LDS	30.6/41.3 = 0.74	38.18/60.7 = 0.63	16.3/27.0 = 0.60	4.7/7.15 = 0.66	5.49/10.56 = 0.52	11.23/17.01 = 0.66	55.4/63.58 = 0.87	33.3/40.05 = 0.83
LPEP/LDS	51.0/41.3 = 1.23	66.08/60.7 = 1.09	29.5/27.0 = 1.09	7.5/7.15 = 1.05	9.50/10.56 = 0.90	16.67/17.01 = 0.98	81.83/63.58 = 1.29	51.9/40.05 = 1.30
LPEP/LAEP	51.0/30.6 = 1.67	66.08/38.18 = 1.73	29.5/16.3 = 1.81	7.5/4.7 = 1.60	9.5/4.49 = 1.73	16.67/11.23 = 1.48	81.83/55.4 = 1.48	51.9/33.3 = 1.56
AA	84°	94°	101°	92°	90°	88°	104°	105°
Length/width of a <sub>1</sub>	10.43/11.09 = 0.94	15.2/17 = 0.89	9.0/8.4 = 1.07	2.0/2.4 = 0.83	3.21/3.42 = 0.94	5.28/6.21 = 0.85	14.83/14.19 = 1.05	10.7/12.3 = 0.87
Length/width of a <sub>2</sub>	9.2/11.0 = 0.84	11.5/16.3 = 0.71	5.0/8.0 = 0.63	1.7/2.2 = 0.77	2.24/3.68 = 0.61	3.59/6.30 = 0.57	9.94/14.75 = 0.67	7.6/11.1 = 0.68
Length/width of a <sub>3</sub>	11.79/14.2 = 0.83	16.78/22.76 = 0.74	7.3/11.9 = 0.61	2.2/3.4 = 0.65	1.99/3.55 = 0.56	4.51/6.94 = 0.65	15.94/22.48 = 0.71	11.5/16.5 = 0.70
Length/width of a <sub>4</sub>	7.5/10.0 = 0.75	15.2/21.4 = 0.71	6.6/10.34 = 0.64	1.7/3.2 = 0.53	1.57/3.08 = 0.51	N/A	15.83/18.44 = 0.86	8.3/14.5 = 0.57
Length/width of a <sub>5</sub>	4.1/5.5 = 0.75	6.7/8.2 = 0.82	3.62/5.76 = 0.63	N/A	1.11/2.71 = 0.41	N/A	6.4/10.2 = 0.63	4.8/6.4 = 0.75

See Anatomical Abbreviations for definitions.

\*Uncatalogued specimen from KIZ; locality: Wuxian Lake; gross weight: 63 kg.

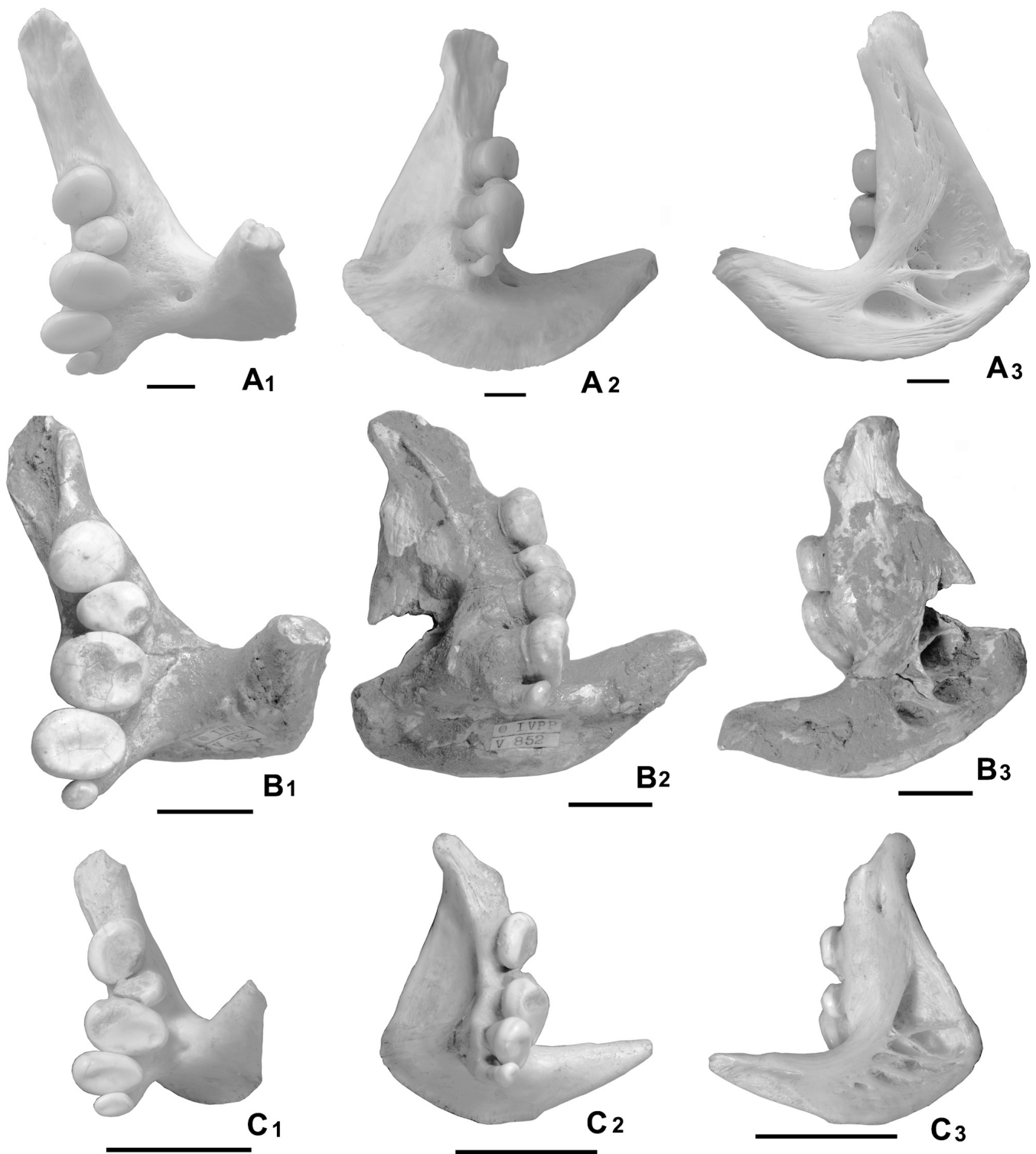


FIGURE 2. Pharyngeal bone and teeth of *Mylopharyngodon piceus*. **A<sub>1</sub>–A<sub>3</sub>**, IVPP P41; **B<sub>1</sub>–B<sub>3</sub>**, IVPP V852; **C<sub>1</sub>–C<sub>3</sub>**, IVPP P40. **A<sub>1</sub>**, **B<sub>1</sub>**, **C<sub>1</sub>**, dorsal view; **A<sub>2</sub>**, **B<sub>2</sub>**, **C<sub>2</sub>**, inner lateral view; **A<sub>3</sub>**, **B<sub>3</sub>**, **C<sub>3</sub>**, outer lateral view. Scale bars equal 1 cm.

The pharyngeal bone and teeth described here has turned out to be the oldest-known specimen of black carp found so far, and, consequently, the oldest-known squaliobarbin or the oldest known leuciscin, depending on the assignment of *My-*

*lopharyngodon* in one or another subfamily. This specimen could doubtless provide some evidence for further study on the origin, evolution, and biogeography of the most diverse and largest family of freshwater fishes.

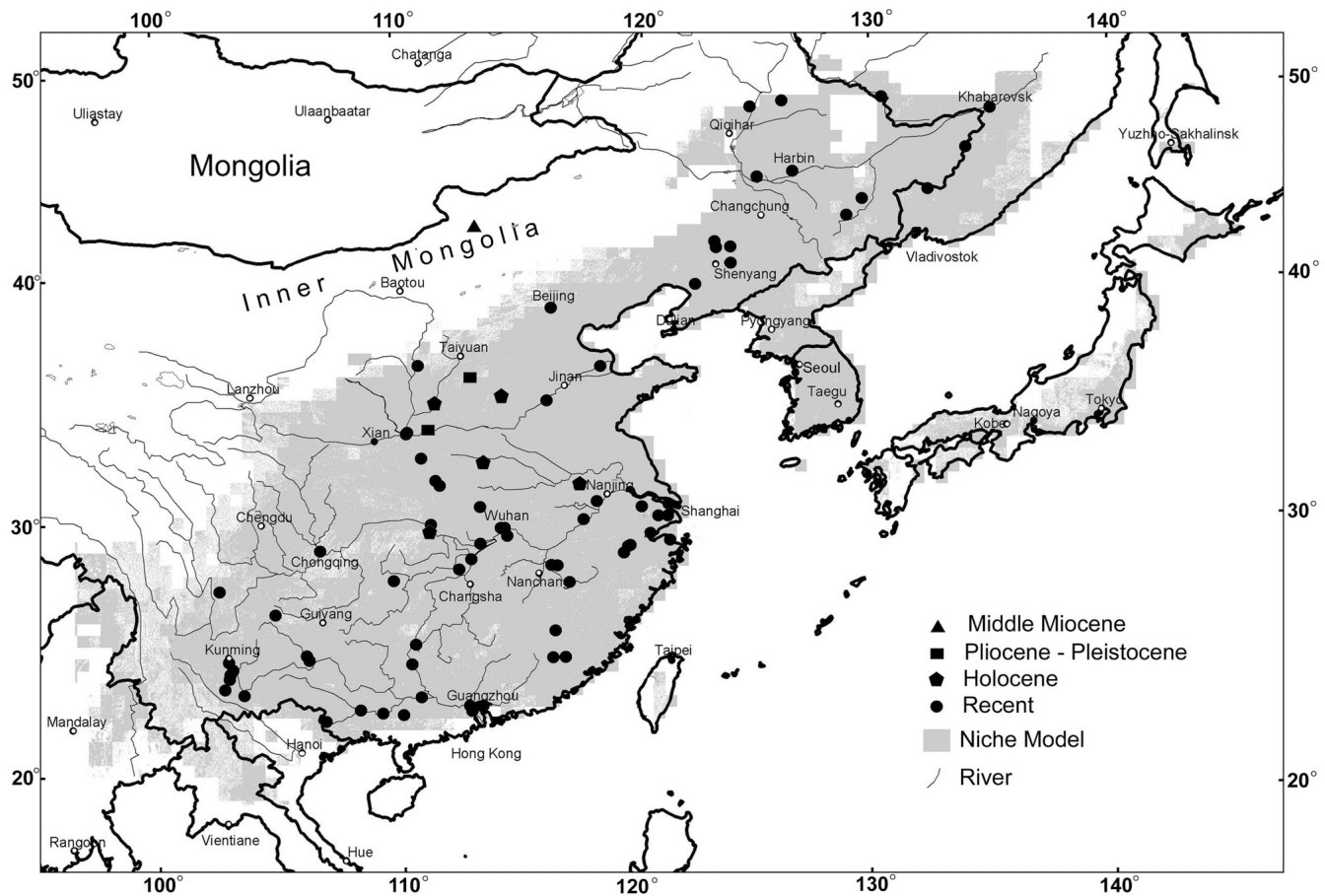


FIGURE 3. Locality of *Mylopharyngodon wui*, sp. nov., and geographical distribution of the black carp in East Asia. Triangle indicates locality of *Mylopharyngodon wui*, sp. nov.; circles indicate localities of extant black carps; squares indicate localities of black carps in Pliocene–Pleistocene deposits; pentagons indicate localities of black carps in Holocene deposits; the shaded area is the predicted distribution of the black carp based on niche modeling.

### ECOLOGICAL AND BIOGEOGRAPHICAL IMPLICATIONS

The living black carp, *Mylopharyngodon piceus*, mainly inhabits the middle and lower layers of waters, and rarely swims to the water surface. Its optimum water temperature is 22–28°C. In its growing season it stays in river bends, lakes, and ancillary waters, mainly feeding on mollusks and crustaceans, and survives the winter by staying in deep water (Chen et al., 1998). The larvae of black carp feed on zooplankton and fingerlings, and they start to feed on small mollusks and crustaceans when they reach 15 cm in length. The powerful molar-like pharyngeal teeth and the hard callous pad on the basioccipital process permit the adult black carp to crush the thick shells of large mollusks. *Mylopharyngodon wui* was found near the top of the sandstone unit, which is interpreted as river-bend deposits, and was associated with fossil bivalves, revealing that the black carp inhabited clear mollusk-rich water during the middle Miocene.

According to Li and Fang (1990), the extant black carp inhabits large rivers and lakes of great plains with distinctive seasonal conditions, e.g., it requires water temperatures below 30°C in summer and slightly higher than 4°C in winter. It cannot live in high-gradient rivers in mountainous regions. The gonads of black carp need low water temperatures (after summer) to mature, and sufficient currents are required to stimulate spawning. Spawning only occurs in rush waters with water temperatures around 26°C. The

river course downstream also must be long enough for the semi-buoyant eggs to hatch, and the river also must have bodies of calm waters for fry to feed and grow. Therefore, the native distribution of *Mylopharyngodon piceus* is generally limited within the lower valleys of large rivers in eastern Asia, but the accurate geographical distribution of this species is unclear due to the very limited sampling and ground surveys. The ecological niche of a species is a critical determinant of its geographical distribution, defined as the ranges of all environmental conditions within which a species is able to maintain populations (Grinnell, 1917; Hutchinson, 1957; MacArthur, 1972). In order to define the accurate geographical distribution of the living black carp for further discussion, the occurrence points of black carp were collected from FishBase (www.fishbase.com), and the institutions and museums in China, then used GARP (the Genetic Algorithm for Rule-set Production, for details refer to <http://nhm.ku.edu/desktopgarp/>) (Stockwell, 1999; Stockwell and Peters, 1999) to calculate the correlations between occurrence points and a set of globally available environmental data, and then to build the ecological niche model for the black carp. GARP has been proven to be an efficient tool for building and predicting the geographical distribution of species (Peterson, 2001; Wiley et al., 2003; Iguchi et al., 2004; Chen et al., 2007). Fifteen environmental variables were used for model building, which well summarize aspects of topography (elevation, topographic index, flow accumulation, slope, and aspect from USGS Hydro-1K data set; available at

<http://edcdaac.usgs.gov/gtopo30/hydro/>), tree cover percentage (Hansen et al., 2003), and climatic conditions (annual means of diurnal temperature range; frost days; precipitation; maximum, minimum, and mean monthly temperatures; solar radiation; wet days; and vapor pressure; for 1960–1990 from the Intergovernmental Panel on Climate Change Worldwide Climate Data Distribution Centre, available at <http://ipcc-ddc.cru.uea.ac.uk/index.html>). Fifty-three out of 73 unique occurrence points were randomly selected for model building, and the remaining 20 points were used for model verification. The niche model for the black carp, which is visualized as the shadow area in Figure 3, is highly statistically significant, and well outlines the area where the black carp is able to live. The niche model for the black carp shows that fossil *Mylopharyngodon wui* is not in the niche model area. Speciation theory (Peterson et al., 1999) supports low niche differentiation between phylogenetically closely related species, and ecological niches evolve little at or around the time of the speciation event and may remain stable over long periods of time. Peterson et al. (1999) compared reciprocal geographic predictions of sister-taxon pairs of birds, mammals, and butterflies in southern Mexico, and found niches quite conservative over several million years of independent evolution below the family level. If the ecological niche of the black carp changes little or remains stable after speciation, we can infer that the provincial environment has changed greatly since the middle Miocene, and that the black carp's niche has shrunk southeastward.

According to the compiled ecological data (Li and Fang, 1990), the distribution of *Mylopharyngodon piceus* is restricted by the altitude above sea level. Its distribution is restricted to localities less than 420 m above sea level in the lower valley of Yellow River, less than 200 m in the drainages of Heilongjian River, and less than 500 m in the middle and down streams of Yangtze River. The niche model for the black carp also generally confirms the above findings. As *Mylopharyngodon wui* is located in the Inner Mongolia Plateau, 1550 m above sea level within the drainages of the Yellow River, it may be inferred that the plateau has risen more than 1000 m since the middle Miocene.

#### ACKNOWLEDGMENTS

We thank Drs. C. Zhang (BIZ), J. Yang (KIZ), S. He (WIH), and H. Liu (WIH), for allowing access to their museum data and helping measure some specimens for comparison; and D. Catania (CAS), A. Williston (MCZ), B. Brown (AMNH), for loaning materials for comparison. P. Chen is particularly indebted to Dr. Xiaoming Wang, Natural History Museum of Los Angeles County, for generously providing the specimen for study, and for his helpful discussion; Dr. H.-P. Schultze, University of Kansas, for his review of an earlier draft of the manuscript and helpful comments; Drs. Mee-mann Chang and Jiao-jian Zhou, IVPP, for their discussions and helps with literature; G. Chen and N. Wang, IVPP, for their collecting materials for comparison; Dr. E. O. Wiley, University of Kansas, for providing necessary informatics infrastructure, and facilities for building the ecological niche model. S. A. Rages, University of Kansas, improved the style of the manuscript. The comments of two anonymous reviewers are greatly appreciated. This research is partly supported by the Chinese National Science Foundation (grant no. 40432003), the Chinese Academy of Sciences (grant no. KZCX3-SW-126), and the Cypriniformes Tree of Life, NSF grant no. 37870 (to G. Arratia).

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Submitted August 6, 2008; accepted June 12, 2009.