

Redescription of †*Cobitis longipectoralis* Zhou, 1992 (Cypriniformes: Cobitidae) from late early Miocene of East China

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Here we revise a fossil cobitid species †*Cobitis longipectoralis* Zhou, 1992, based mainly on a well-preserved specimen collected recently from the taxon's type locality of the late early Miocene of Shanwang, Shandong Province, East China. The new specimen, along with those collected by Zhou, enables us to provide an emended diagnosis and more detailed description of the species by focusing on the characters such as the structures of the suborbital spine and the presence and shape of the lamina circularis at the base of the second pectoral fin ray in adult males, the presence of a frontoparietal fontanelle, and a quadrate-metapterygoid fenestra, etc. The long pectoral fin, initially considered by Zhou as the most important character of the species, however, turns out to be not diagnostic for the species. †*Cobitis longipectoralis* Zhou, 1992 is not only the most informative and best-preserved early cobitid fossil known thus far but also the only and earliest cobitid fossil from East Asia.

†*Cobitis longipectoralis*, late early Miocene, East China

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The family Cobitidae is a group of small primary freshwater fishes, dwelling in the bottom of water. Their body is elongated, covered with various color patterns, and often with a truncated or rounded caudal fin. Their mouth is subterminal, and lateral ethmoid is modified into a bifid erectile spine. They are widely distributed in Eurasia and Morocco, with the greatest diversity in southern Asia [1]. The phylogenetic rank of the Cobitidae used here is similar to that in Nalbant [2], Tang et al. [3], and Šlechtová et al. [4]. *Cobitis* is a genus of the Cobitidae. Despite the doubt cast on monophyly of the genus *Cobitis* by some phylogenetic analysis [5], the

genus is still used in its conventional sense and kept growing with newly established species. Here we follow the conventional wisdom of a monophyletic genus *Cobitis* and base our research on previous morphological studies in the absence of a more precise phylogenetic framework.

Known fossil cobitids are scarce [6], and only include several species of *Cobitis* and a species of *Sabanejewia* [7–16]. Most of the materials consist of either detached suborbital spines or poorly preserved skeletons with little information about the suborbital spines. †*Cobitis longipectoralis* Zhou, 1992 (Figure 1), from the late early Miocene of Shanwang, Shandong Province, eastern China (Figure 2), is the only species with well preserved specimens, which

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Figure 1 The holotype (IVPP V 9933.1) of †*Cobitis longipectoralis*, part and counterpart. Scale bars equal 5 mm.

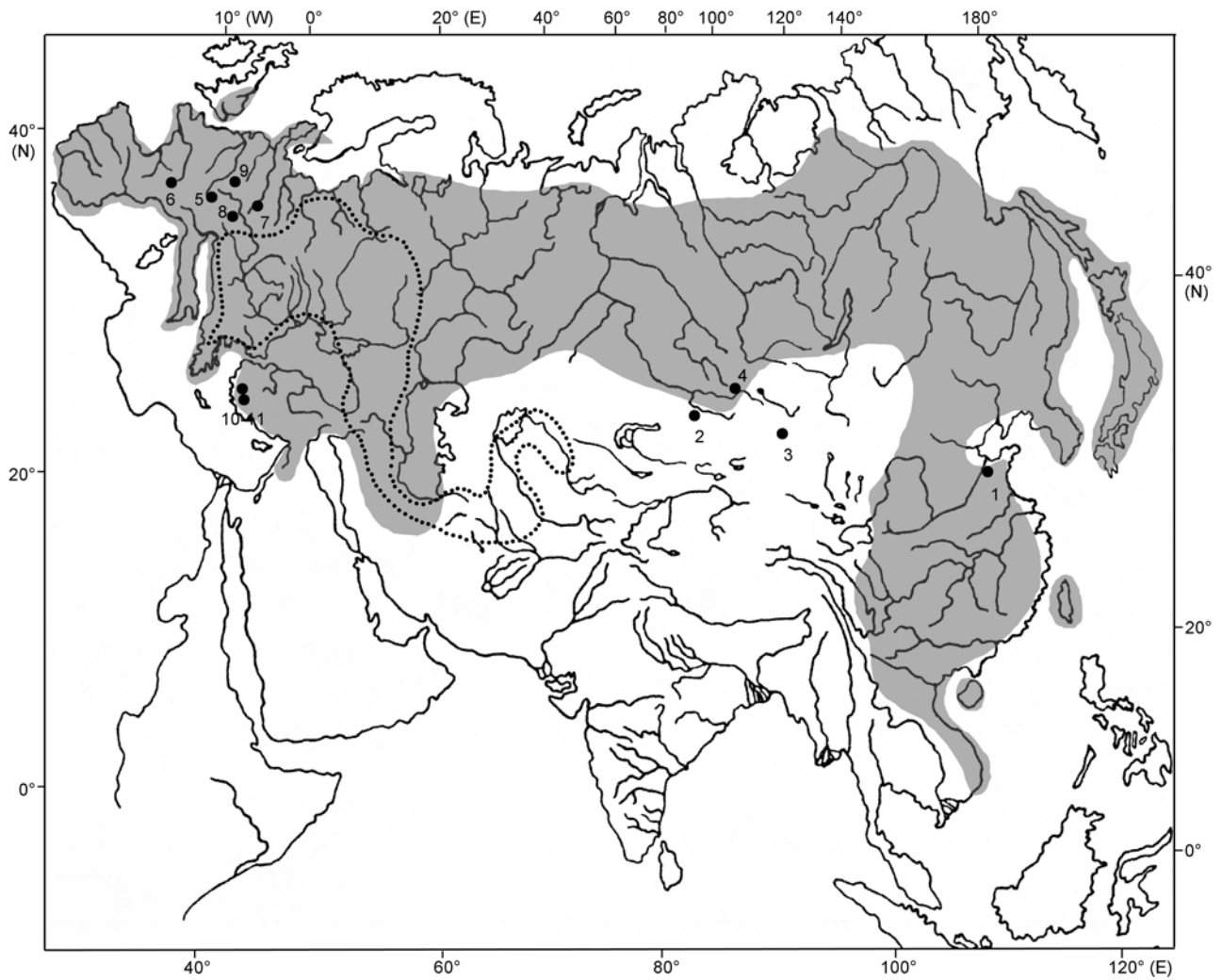


Figure 2 Localities of fossil cobitids (black circle) and distribution of living *Cobitis* (shaded) and *Sabanejewia* (area circled by dots) (modified from Fig. 2/30 in ref. [17]). 1. Shanwang, Shandong Province, East China; 2. Zaisan Basin, eastern Kazakhstan; 3. Shargain-Gobi, Mogolia; 4. Chui Basin, Altai Mountains; 5. Oeningen, Baden, Germany; 6. Rochefort-Montagne, France; 7. Browncoal Basin, North Bohemia, Czech; 8. Sandberg, Vienna Basin, Austria; 9. Oberleichtersbach, Rhon Mountains, Germany; 10. Develikoy; 11. Safran Coal Section, western Turkey.

were previously not well prepared and thoroughly described. Recently, a new, better-preserved specimen of †*Cobitis longipectoralis* was found from the same locality and thus provides new information of the early *Cobitis*. In this paper, we restudy †*Cobitis longipectoralis* Zhou, 1992, based on additional information derived from the new specimen as well as those collected before but further prepared more recently.

1 Materials and methods

Fossil specimens were collected from the famous fossil locality—Shanwang, Linqu County, Shandong Province, East China. The fossils are from the Shanwang Formation. The fish-bearing deposits consist of diatomite. Its geologic age is late early Miocene, 18 Ma, corresponding to MN4 of the European Neogene Mammal units [18].

Fossil materials include specimens studied by Zhou [12]: IVPP V 9933.1 (numbered as H11.082, holotype of †*Cobitis longipectoralis* in Zhou, 1992), IVPP V 9933 [12]; and a nearly complete skeleton IVPP V 9933.2, newly collected from the same locality. The specimens were prepared mechanically.

The methods of measuring and counting follow those conventionally used for the extant fishes. All measurements were made point-to-point. For the abdominal vertebrae counts, in addition to those that can be seen behind the opercle we add four more, which are supposedly present under the opercle, related to the Weberian apparatus. The caudal vertebrae include the last half centrum.

The osteological terminology used in this paper follows Sawada [19] but that of the suborbital spine is according to Nalbant [20].

The drawings were executed under a Wild M7A microscope with camera lucida attachment.

A dagger symbol “†” is used to denote extinct taxa.

Anatomical abbreviations. aa, anguloarticular; br, branchiostegal ray; cc, compound centrum; cl, cleithrum; co, coracoid; d, dentary; ect, ectopterygoid; ep, epural; fr, frontal bone; h, hypural; hy, hyomandibular; iop, interopercle; lc, lamina circularis; lcp, laterocaudal process of suborbital spine; mco, mesocoracoid; mcp, mediocaudal process of suborbital; mep, metapterygoid; mp, medial process of suborbital spine; mx, maxilla; ns, neural spine; op, opercle; p, parietal bone; ph, parhypural; plu, pleurostyle; pmx, premaxilla; pop, preopercle; ps, parasphynoid; pu, preural centrum; q, quadrate; ra, retroarticular; sb, suborbital spine; sc, scapula; sec, supraethmoid-ethmoid complex; sop, subopercle; spe, second preethmoid; so, supraoccipital; sop, subopercle; sy, symplectic; uh, urohyal.

Measurement abbreviations. A-C, distance between origin of anal fin and base of caudal fin; A-P, distance between origin of anal fin and insertion of pelvic fin; BD, body depth; CPD, caudal peduncle depth; CPL, caudal peduncle length;

D-C, distance between origin of dorsal fin and caudal fin base; HD, head depth; HL, head length; PAL, length of preanal; PDL, length of predorsal; PL, length of pectoral fin; P-P, distance between origin of pectoral fin and insertion of pelvic fin; PPL, length of prepelvic; SL, standard length; SPL, length of second pectoral fin ray; SSL, length of suborbital spine; TL, total length.

Institutional abbreviation. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.

2 Systematic paleontology

Superorder Ostariophysi Sagemehl, 1885

Order Cypriniformes Bleeker, 1859/60

Family Cobitidae Nalbant, 2002

Genus *Cobitis*, Linnaeus, 1758

†*Cobitis longipectoralis* Zhou, 1992

Emended diagnosis: *Cobitis* with standard length about eight times the body depth; nine pectoral fin rays; total number of vertebrae about 43; number of abdominal vertebrae about equal to that of caudal ones; suborbital spine stout, mediocaudal process slightly curved and long, laterocaudal process short and less than half of the mediocaudal process in length, medial process prominent; second pectoral fin ray in adult male thickened and elongated, with an approximately square-shaped lamina circularis at its base; origin of dorsal fin midway between snout and caudal fin bases or slightly posteriorly situated; insertion of pelvic fin opposed to middle of dorsal fin base.

Description

(1) General appearance. A small-sized cobitid with known total length of 72.0–115.1 mm. The body is elongate and laterally compressed, with its dorsal and abdominal outlines almost parallel. The head length is longer than the body depth. The mouth is subterminal. The standard length is about 7.9–8.0 times the body depth but 5.2–5.9 times the head length, 7.4 times the caudal peduncle length, and 11.9–12.2 times the caudal peduncle depth. The eye is middle-sized, situated in the upper-middle part of the head. The preorbital and postorbital distances are almost equal. The caudal peduncle length is 1.6–1.7 times its depth. The pectoral fin is long, with the longest ray about 15% of the standard length in IVPP V 9933.1 and 19.7% in IVPP V 9933.2. The first branched pectoral fin ray in IVPP V 9933.2 is elongated and thickened with a nearly square-shaped lamina circularis at the base. The origin of the dorsal fin is anterior to the insertion of the pelvic fin, about at the midpoint of (in IVPP V 9933.2) or slightly behind the midpoint of the dorsal border of the body (in IVPP V 9933.1). The insertion of the pelvic fin is slightly closer to the origin of the anal fin than to the origin of the pectoral fin, opposed to the middle of dorsal fin base (Figures 1 and 3). The morphometric char-

acters are listed in Table 1.

(2) Skull roof. The frontal can be seen in the holotype and IVPP V 9933.2. It is the largest bone in the roof. The bone is long and narrow. Its length/width ratio is slightly larger than 6. The anterior half of the bone is narrow, then the bone widens gradually, reaching its maximal breadth near its posterior margin. Anteriorly, the frontal bone sutures with the supraethmoid-ethmoid complex, whereas posteriorly it sutures with the parietal bone (Figure 4). There is an obvious notch along the median margin of the posterior part of the frontal, which indicates that a frontoparietal fontanella is present and the fontanella is wider anteriorly and narrower posteriorly (Figure 4). The upper part of supraethmoid-ethmoid complex, which forms a vertical septum separating the two olfactory sacs, is observed in IVPP V 9933 and 9933.2. The bone sutures with the frontal and orbitosphenoid posteriorly. The incompletely preserved orbitosphenoid lies in front of the orbit. The lateral ethmoid extends backward, modified into bifid spine (suborbital spine). The left spine in IVPP V 9933.2 and the right spine in IVPP V 9933 can be detected. The spine is at least 17% of the head length, reaching a point under the middle of the

eye (in IVPP V 9933.2, Figure 4). The mediocaudal process of the spine is slightly curved and long. The laterocaudal process is short, less than half the length of the mediocaudal process. The medial process is prominent (Figures 4, 5(a) and (b)). The lateral process, however, was not observed because of the unfavorable preservation. The length and width of the parietal bone are about equal. The width of the parietal seems to match the posterior margin of the frontal, but its length is less than 1/6 of the latter. The median margin of the parietal is smooth, straight, and slightly thickened, which means that they form the lateral margin of the posterior part of the frontoparietal fontanella. The length of the frontoparietal fontanelle is about 32% of the length of the frontal + parietal. The supraoccipital bone is very short, suturing only with the parietals anteriorly (Figure 4).

(3) Opercular series and cheek bones. The opercular series is preserved in the holotype and IVPP V 9933.2 (Figures 1, 3 and 4). The opercle is a large bone and its anteroventral corner is stretching slightly forward. Its anterior margin is more or less straight. Its ventral margin is strongly concave as the situation in many cobitids, owing to the reduction of the ossification [19]. The socket at the antero-

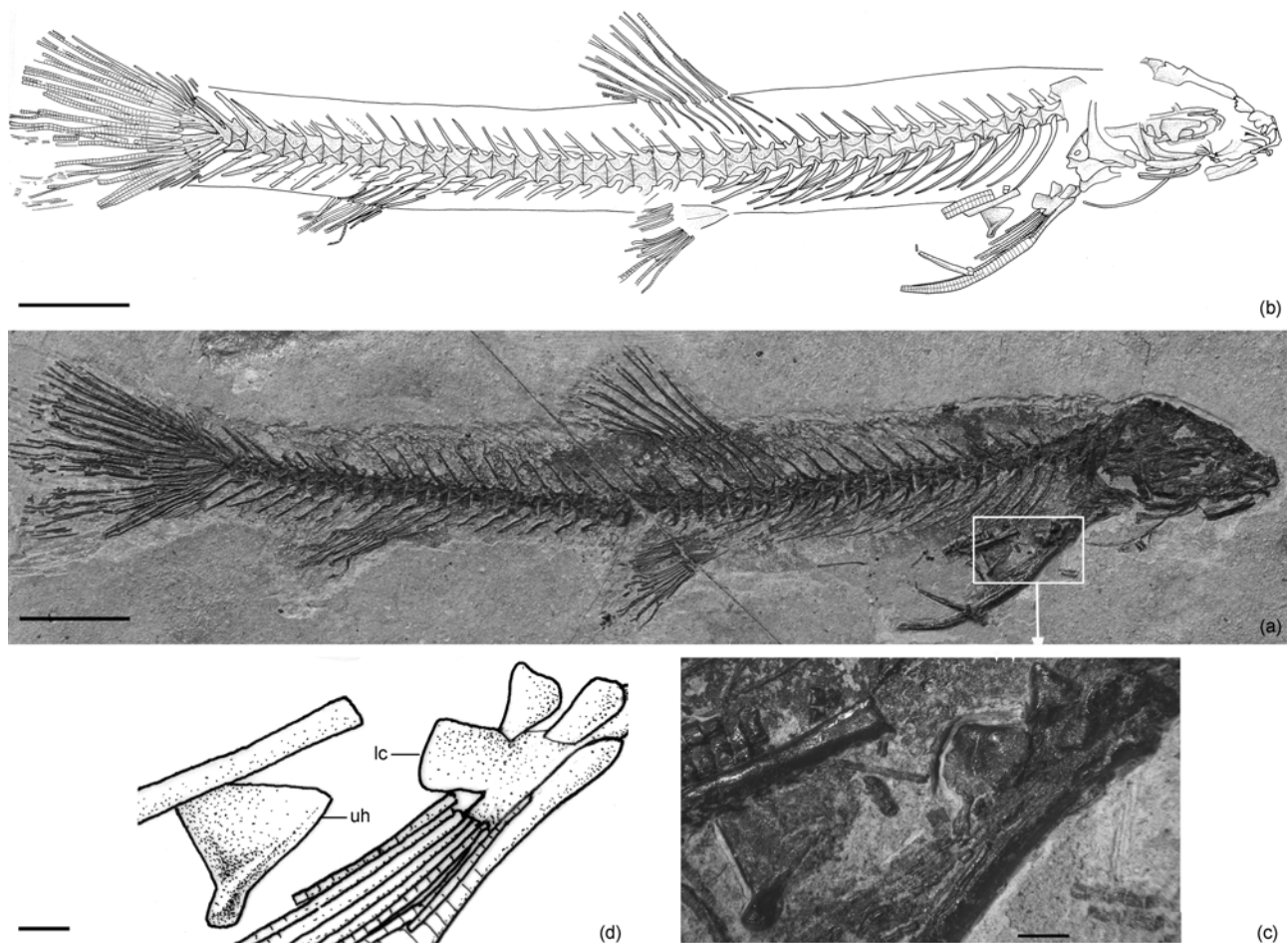
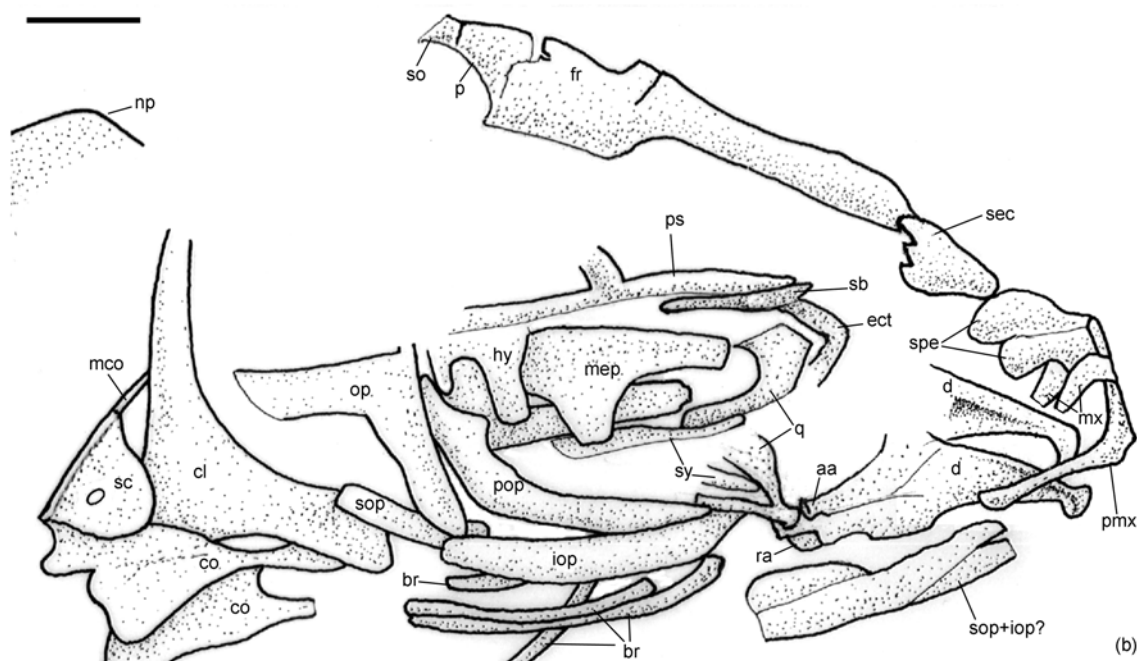
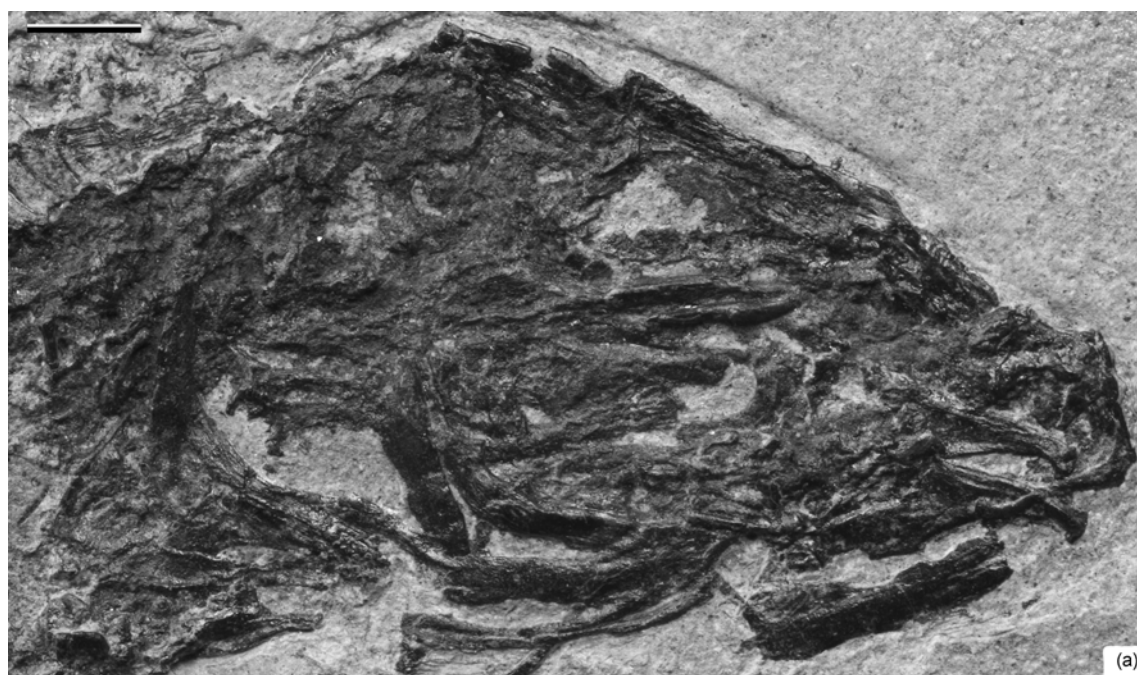


Figure 3 †*Cobitis longipectoralis* in right lateral view. Photograph (a) and drawing (b) of IVPP V 9933.2; photograph (c) and drawing (d) of lamina circularis and urohyal in IVPP V 9933.2. Scale bars equal 10 mm for (a) and (b), and 1 mm for (c) and (d).

Table 1 Morphometric characters of †*Cobitis longipectoralis* (in mm)

	TL	SL	BD	HL	HD	CPL	CPD	PDL	PPL	PAL	D-C	A-P	A-C	P-P	SPL	SPL
V 9933.1	72.0	61.8	7.8	11.8	8.4	8.4	5.2	33.2	33.4	49.3	28.7	15.1	11.7	22.2	9.3	>2.0
V 9933.2	115.1	99.1	12.4	16.8	10.2	13.4	8.1	50.2	53.3	80.0	50.0	27.2	19.7	37.1	19.5	>3.0

**Figure 4** †*Cobitis longipectoralis* (V 9933.2), skull in right lateral view, photograph (a) and camera lucida drawing (b). Scale bars equal 2 mm.

dorsal angle of the opercle, articulating with the condyle of the hyomandibular, was detected in IVPP V 9933. The preopercle is slender. Its ventral branch is longer than the dorsal one. The two branches intersect at an obtuse angle about 135°. Different from the situation in cyprinidae, no

sensory canal running along the preopercle can be observed. Interopercle and subopercle are narrow, long, blade-like and slightly arched bone plates. Branchiostegal rays are slender, acinaciform, three on each side.

(4) Circumorbital bones. Because of the poor preserva-

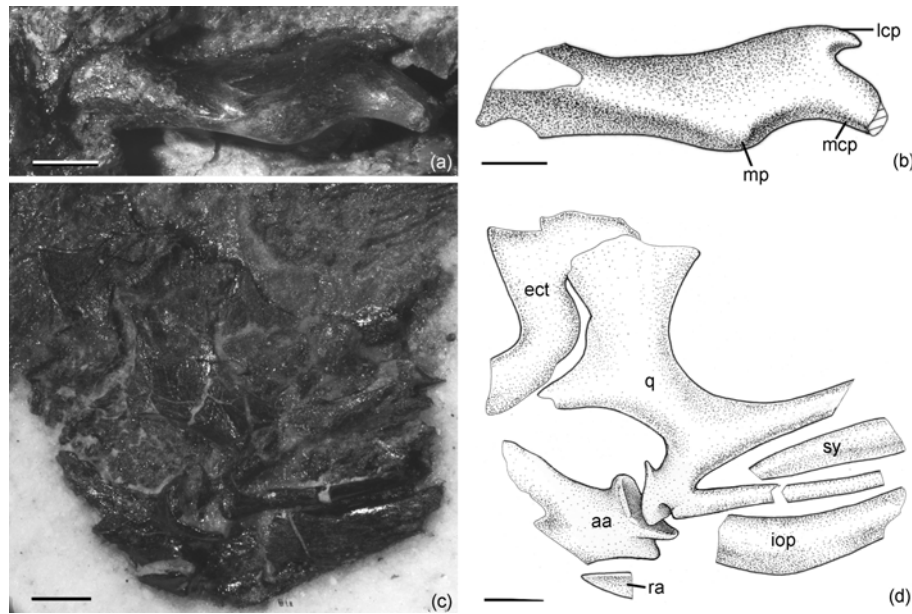


Figure 5 †*Cobitis longipectoralis* (IVPP V 9933), right suborbital spine in dorsoinner view, photograph (a) and camera lucida drawing (b); quadrate in lateral view, photograph (c) and camera lucida drawing (d). Anterior all face to left. Scale bars equal 0.5 mm.

tion in the orbital region, it is difficult to judge if there is a supraorbital bone or not (Figures 1, 3 and 4). No infraorbital bones and infraorbital sensory canal are observed either. Siebert [21] pointed out that in cobitines (now cobitids), only species of *Acanthopsoides*, *Acantopsis*, and *Somileptes* are known to possess an infraorbital lateral line canal.

(5) Jaw and Palate. The snout protrudes slightly. The mouth is subterminal. Its margin is devoid of teeth (Figures 1, 3 and 4). The premaxilla is long and slender, bearing an equally long ascending process at its anterodorsal end. The maxilla is preserved incompletely. The anterior part of the dentary narrows anteriorly and slightly curved ventromedially. The coronoid process of dentary is developed and situated at the posterodorsal margin of the bone. Posteriorly, the dentary sutures with the anguloarticular bone. The anguloarticular is large and flat. On its posterior end, there is a socket accommodating the articular head of the quadrate. The second preethmoid is a short and stout cylindrical bone, with its two ends enlarged to form articular processes. The parasphenoid is straight and elongated, situated between the lower parts of the orbits. Zhou [12] assumed that the posterior part of the parasphenoid met the frontal dorsally, a character usually present in genera *Misgurnus* and *Acanthopthalmus* [19], but we cannot confirm that due to the inadequate preservation. The quadrate, as it usually is in teleosts, consists of a fan-like plate and a rod-like posteroventral process. The process is relatively long. The plate is high with its posterodorsal margin concave to form the anterior margin of the metapterygoid-quadrate fenestra. The articular head of the quadrate fits into the socket at the posterior end of the anguloarticular bone (Figures 4, 5(c) and (d)).

(6) Hyoid arch. The hyomandibular is preserved in IVPP V 9933 and 9933.2. The upper part of the bone is extensive. Ventrally, the bone is shaft-like. Posterior to the ventral shaft is a short downward projection. The symplectic shown in the holotype and IVPP V 9933.2 is long and slender, inserting between the plate and the rod-like process of the quadrate. The ectopterygoid is a laminar bone in front of the quadrate (Figures 4, 5(c) and (d)). The endopterygoid is not preserved. The metapterygoid is a large bone. Its anteroventral margin is concave, forming the upper and posterior edge of the metapterygoid-quadrate fenestra (Figure 4). A detached urohyal (Figure 3) is observed in IVPP V 9933.2. Its anterior end is a condyle; its vertical plate is triangle-shaped, with its depth about equal to the length of its horizontal plate.

(7) Pectoral girdle and fin. The supracleithrum can be observed in IVPP V 9933. It is an elongated, flat bone, attached to the lateral surface of the dorsal branch of the cleithrum. The upper part of the dorsal branch of the cleithrum is narrow, with a thin tip, but its ventral part is broadening towards the bend to the ventral branch. The ventral branch of the cleithrum is broad and is obviously shorter than the dorsal branch. The posteroventral edge of the cleithrum extends slightly ventrally and is in contact with the coracoid (Figures 1 and 4). The postcleithrum is absent as in other cobitids. The bone labeled as postcleithrum in Zhou [12], Figure 1, is, in fact, the mesocoracoid. The mesocoracoid is a slender, elongated bone with its upper end connecting the inner face of the cleithrum. The scapula is somewhat oval in shape with a rod-like process in its posteriodorsal part. The bone is in contact with the cleithrum anteriorly and coracoid ventrally. The foramen in

the center of the scapula can be clearly seen (Figure 4). The coracoid is a relatively long bone. It is narrow in the middle but broad at its two ends. It contacts the anteroventral margin of the cleithrum anterodorsally, the posteroventral process of the cleithrum posterodorsally, and the anteroventral margin of the scapula posteriorly. The median part of the coracoid is not in contact with the cleithrum. A coracocleithrum foramen is present between the two bones (Figure 4).

The pectoral fin is long. In the holotype, there is no thickened pectoral fin ray. The length of the longest fin ray is about 15% of the standard length, almost reaching the middle point of the distance between the origin of the pectoral and the insertion of the pelvic fin. The number of pectoral fin rays is nine (Figure 1). However, in specimen IVPP V 9933.2, there is a very long thickened branched pectoral fin ray, the length of which exceeds the middle point of the span between the pectoral and pelvic fin, reaching 19.7% of the standard length. At the base of the ray is a square-shape lamina circularis (osseous plate) (Figure 3). Though the pectoral fin is not well preserved, from the position of the thickened fin ray we can still judge that it is probably the first branched ray. Sexual dimorphisms are common in cobitids [22]. In most genera, the males are smaller than females, and the pectoral fin in adult male bears elongate and/or thickened fin ray with or without lamina circularis at its base. Thus, based on presence vs. absence of elongate and/or thickened fin ray, IVPP V 9933.2 is most probably an adult male whereas IVPP V 9933.1 is likely a female. However, IVPP V 9933.2 (♂) is actually much larger than IVPP V 9933.1 (♀), a contradiction that could only be attributed to their age difference.

(8) Pelvic girdle and fin. The anterior part of the pelvic bone is forked. The ischiac process of the bone is weakly developed as in other cobitids. The insertion of the pelvic fin is closer to the anal fin than to the pectoral. There are one unbranched and six branched fin rays. In addition, there is a spine-like pelvic splint running along the exterior of the rays (Figures 1 and 3).

(9) Dorsal and anal fins. The origin of the dorsal fin is slightly anterior to the insertion of the pelvic fin, situated in the middle (IVPP V 9933.2, ♂) or slightly posterior to the middle (in holotype, ♀) of the back excluding the caudal fin, similar to the living *Cobitis* in that the origin of dorsal fin is situated slightly forward in male than in female [23]. The dorsal fin base is comparatively short. It contains three unbranched and seven branched fin rays. The length of the fin base is shorter than the head length. Nine dorsal pterygiophores were preserved in the holotype. All are rod-like bones. The first of them is the largest. It is bifurcated, inserting between neural spines of the 16th and 17th vertebrae. The 2nd to 9th pterygiophores reduce in length towards the rear. Inserted between two neural spines are one or two or even three pterygiophores (Figures 1 and 3).

The origin of the anal fin is closer to the caudal fin base

than to the pelvic insertion. The anal fin has three unbranched and five branched rays, with the last ray doubled as the usual case in teleosts. Seven pterygiophores were seen, all rod-like. The first pterygiophore is bifurcated and inserted between the 7th and 8th hemal spines. Posteriorly, one or two pterygiophores insert between two hemal spines.

(10) Vertebral column. Nineteen abdominal vertebrae and 20 caudal vertebrae are observed. On top of these we added four more, which are supposedly lying under the opercle and associated with the Weberian apparatus. Thus, the total number of vertebrae is about 43. Among them the anterior 16 are pre-dorsal. The Weberian apparatus is not well preserved. Only the ventrally downward projection of the incomplete bony gas bladder capsule can be observed in IVPP V 9933 and the holotype. The neural complex is broad and low. Its posterior edge is in close contact with the anterior edge of the 4th neural spine. The 4th and 5th neural spines are slightly wider and shorter than the rest of neural spines. Fifteen pairs of ribs are preserved; they are long, almost reaching the abdominal edge. No supraneurals are present, as in Recent cobitids. The prezygapophyses of the vertebrae are prominent. Numerous thin and long epineural and epipleural intermuscular bones are shown in the holotype and IVPP V 9933.2 (Figures 1 and 3). The epineural series over the vertebral column extends approximately from the 9th vertebra to about the 2nd preural centrum. In the holotype, the proximal ends of the epineurals over the abdominal vertebrae are bifurcated, with an anteromedial and an anteroventral branch. More posteriorly, the two branches of epineural become separate, thin bones. The epipleural series starts approximately from the last two abdominal vertebrae to the 2nd preural centrum. The epipleurals following the pelvic fin are bifurcated; more posteriorly, they became separate thin bones (Figure 1). In IVPP V 9933.2, fewer epineural and epipleural intermuscular bones are observed than in the holotype, and they almost become separate, thin bones (Figure 3).

(11) Caudal skeleton and fin. The 1st preural and the 1st and 2nd ural centra are fused to form a compound centrum. Fused with that compound centrum is the pleurostyle extending posterodorsally. There are five hypurals. The first two hypurals and the parhypural support the lower lobe of the caudal fin. The remaining hypurals support the upper lobe of the fin. There is a gap between the h2 and h3. The first two hypurals fused with each other proximally and fused with the compound centrum. Although the preservation of the proximal end of parhypural is not very well, it still shows that the parhypural is fused with the compound centrum. The 3rd to 5th hypurals attach to the posteroventral side of the pleurostyle and reduce in length dorsally. The neural and hemal spines of the 2nd and 3rd preural centra are longer and broader than those in front of them, supporting the procurrent rays. The neural and hemal spines of the 2nd preural centrum are fused with the centrum. There is a slender, elongated epural on the dorsal side of the pleu-

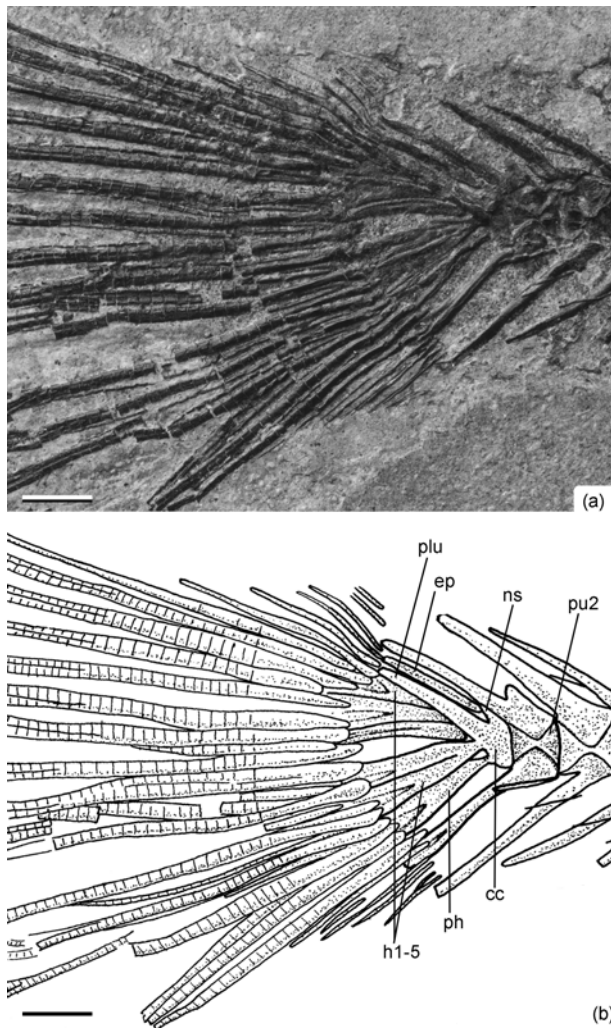


Figure 6 †*Cobitis longipectoralis* (IVPP 9933.2), caudal skeleton in right view, photograph (a) and camera lucida drawing (b). Scale bars equal 2 mm.

rostyle. The compound centrum carries a short incomplete neural spine on its dorsal side. The posterior end of the short neural spine and the proximal end of the epural are almost in contact with each other (Figure 6). The caudal fin is truncated or slightly convex in shape. There are two unbranched and 14 (in holotype) or 13 (in IVPP V 9933.2) branched principal fin rays (Figures 1, 3, 6). Six procurent rays above and under the principal rays respectively can be counted in IVPP V 9933.2.

3 Comparison and distribution

From the description above, †*Cobitis longipectoralis* shows many typical cobitid characters, such as, the cobitid-type bifid suborbital spine [20]; the premaxilla with a long ascending process but without anterior process; the opercle deeply concave posteroventrally; the presence of a quadrate-metapterygoid fenestra and a cheithrum-coracoid fora-

men, the absence of the postcleithrum; the presence of bony gas bladder capsule with a pair of ventral projections; the ischiac process of pelvic bone weakly developed; the truncated or slightly convex posterior margin of caudal fin; the hypural 1–2 and parhypural fused with the compound centrum; the number of principal branched caudal fin rays being 14 or 13 [19, 20]. At the same time, †*Cobitis longipectoralis* also demonstrates a number of characters of *Cobitis*, such as the number of vertebrae (around 43), the origin of dorsal fin about in the mid-point along body back, slightly anterior to the insertion of the pelvic fin, the number of the pectoral fin rays (nine) and branched dorsal fin rays (seven), and the most important—the enlarged and elongated first branched pectoral fin ray with lamina circularis at its base in adult males [19, 23].

In delimitation of the genera within cobitids, in addition to the color pattern, the morphometric characters, the fin formula, the development of the barbels and mental lobes, the shape and size of scales and their extent over the body, and the extension of the lateral line, the structure of suborbital spine and sexual dimorphism are also frequently used [20, 21, 24–31]. In fossil loaches, it is not possible to observe the color pattern, mental lobes, scales, and lateral line, so the characters of suborbital spine and pectoral fin rays are used as diagnostic. Among the cobitid fishes, erectile bifid suborbital spine is present in all genera except *Misgurnus* and *Paramisgurnus* [19, 32]. Enlarged first branched pectoral fin ray with the lamina circularis at the base of the ray in adult male exists in only five genera [22] (*Cobitis*, *Iksookimia*, *Koreocobitis*, *Misgurnus*, and *Paramisgurnus*). Based on the presence of the bifid suborbital spine and the presence of lamina circularis at the base of the first branched pectoral fin ray in adult male, †*Cobitis longipectoralis* can be easily distinguished from all other cobitid genera except *Cobitis*, *Iksookimia*, and *Koreocobitis*. *Iksookimia* is stouter than *Cobitis*, and its suborbital spine is generally reduced, with the laterocaudal process less than half of the mediocaudal process. Its lamina circularis in adult males is elongated or more or less semicircular, with a beak-like projection [27, 33]. Therefore, †*Cobitis longipectoralis* can be easily separated from *Iksookimia* by its much-developed suborbital spine and square-shaped lamina circularis. *Koreocobitis* is very similar in shape and size to *Misgurnus* (in adult up to 160 mm in standard length) but with relatively small suborbital spines [34]. Consequently, †*Cobitis longipectoralis* cannot be referred to any other genus but *Cobitis*.

Cobitis is the most speciose genus within the family Cobitidae. The family Cobitidae includes approximately 100 species, among which about 40 are referred to the genus *Cobitis* [35]. The classification of living *Cobitis* is based mainly on the pigmentary zones of Gambetta (color pattern), the shape and number of lamina circularis, and morphometric characters [29, 32]. †*Cobitis longipectoralis* differs from all other species of *Cobitis* in morphometric characters and

the shape of *lanima circularis* [23, 27, 29, 31, 36–41]. The comparison of †*Cobitis longipectoralis* with some living congeneric species is shown in Table 2. Zhou [12] believed that the pectoral fin of †*Cobitis longipectoralis* is especially long compared with that of other species of *Cobitis* and the species is named after this character. In fact, based on the description of Vladykov [25] and Chen [23], the ratio of the pectoral fin length and standard length in †*Cobitis longipectoralis* falls in the variation range of that in *Cobitis dolichorhynchus* (♀, 11.5%–16.6%; ♂, 17.4%–25.4%). Thus, it seems unsuitable to regard the long pectoral fin as diagnostic for the species †*Cobitis longipectoralis*.

Fossil cobitids are very rare. Most of them are referred to the genus *Cobitis*, and only one species of *Sabanejewia* has been found to date. Agassiz [7] was the first to describe fossil cobitids including †*Acanthopsis angustus* (later transferred to *Cobitis* by Sauvage [42]), †*Cobitis centrochir*, and †*C. cephalotes* from the upper Miocene of Öhningen, Baden, Germany [7]. Several decades later, Winkler [8] erected two additional fossil species of *Cobitis*, †*C. bredai* and †*C. teyleri*, from the same locality. The four fossil species of *Cobitis* were transferred to *Nemachilus* (Nemacheilidae) by Sauvage [42] but later rejected by Woodward [43]. Woodward [43] treated the †*C. bredai* and †*C. teyleri* as synonyms of †*Cobitis centrochir* and †*C. cephalotes* respectively. Although they are all represented by complete skeletons, the preservation is poor and does not show the details. Described by Agassiz were the slender body form and the counts of vertebrae and fin rays in all species, but the counts were not always complete. The head skeletons in all specimens are badly preserved except the suborbital spine in †*C. angustus* and three branchiostegal rays in †*C. centrochir*. Well-developed pectoral fin with strong first fin ray was described in †*C. centrochir*; however, the lamina circularis at the base of the first pectoral ray was not mentioned in any of the three species. †*C. cephalotes* bears a deeply forked caudal fin [7, 43], containing I-8-9-I principal fin rays, and thus differs obviously from the extant species of *Cobitis*,

which have a truncated or rounded caudal fin with I-7-7-I principal fin rays. Accordingly, †*C. cephalotes* can hardly be referred to *Cobitis* for reasons stated above. Moreover, †“*C. teyleri*”, bearing 20 caudal fin rays, is also unlikely to belong to *Cobitis*. Woodward [43] considered †*C. angustus* more elongated than †*Cobitis centrochir* and thus was a separate species, whereas Gaudant [44] believed †*C. angustus* was a synonym of †*Cobitis centrochir*. Yet we inclined to agree with Woodward [43]. Besides, some fossils were once mistaken for species of *Cobitis*, but later moved to other groups, such as *Notogoneus longiceps* (Meyer, 1848) (Gonorhynchidae) from upper Oligocene of Mayence Basin [43] and *Cryptolebias senogalliensis* (Cocchi, 1859) (Cyprinodontiformes) [45]. Based on specimens collected from the lower Miocene (MN3) of Bohemia Basin, Obrhelová [11] erected †*Cobitis ioannis*. Nevertheless, her description and figures indicate that it is probably not a member of *Cobitis*, for it has 12–15 pectoral fin rays, an opercle of the usual cyprinid type with slightly concave ventral margin, and a cleithrum with long ventral and short dorsal limbs. In *Cobitis*, the number of pectoral fin rays is mostly 8–9, the opercle is posteroventrally deeply concave, and the dorsal limb of the cleithrum is longer than the ventral one [19, 46]. Another known fossil *Cobitis*, *C. cf. taenia* L., represented by a relatively complete skeleton from the Pliocene of Rochefort-Montagne, Puy-de-Dome, France was described by Gaudant [9]. It is similar to *Cobitis* in body shape, number of fin rays and vertebrae, but the main osteologic diagnostic characters related to the suborbital spine and *lanima circularis* are absent. Apart from the articulated skeletons, isolated suborbital spine of cobitids were found from the middle-late Miocene and Pliocene of Zaisan Basin in East Kazakhstan, Altai, and West Mongolia [10], the Miocene of Vienna Basin [13], the Neogene of Turkey [15, 16], and the late Oligocene of Northern Bavaria, Germany [14]. Based on the isolated suborbital spines, several new species and subspecies of *Cobitis* (†*C. zaisanica*, †*C. zaisanica orientalis*, †*C. ichberchae*, and †*C. central-*

Table 2 Comparison of the †*Cobitis longipectoralis* with some living congeneric species^{a)}

	† <i>C. longipectoralis</i>	<i>C. sinensis</i>	<i>C. dolichorhynchus</i>	<i>C. macrostigma</i>	<i>C. granoei</i>
SL/BD(♀)	7.9	4.8–6.2	5.0–6.6	6.9–9.2	6.5–8.2
(♂)	8.0	5.5–6.3	5.9–6.5	8.4–8.6	6.6–9.1
SL/HL(♀)	5.2	4.8–5.7	4.3–5.1	5.2–6.4	5.0–5.8
(♂)	5.9	5.0–5.3	4.5–4.8	5.2–5.6	4.7–5.7
CPL/CPD(♀)	1.6	1.1–1.5	1.4–1.8	1.7–2.4	1.5–2.5
(♂)	1.7	1.2	1.3–1.5	1.8–2.2	2.0–2.9
HL / PL(♀)	1.3	1.4–1.7	1.4–1.7	1.4–1.6	1.3–1.6
(♂)	0.9	1.1	1.0–1.2	1.1–1.4	1.3–1.5
odf	m / p	p	p	m / a	p
nv	43	43–44	41–43	50	42–49
Shape of lc	square-like	near circle-like with a handle-like base	ax-like	trapezium	semicircle

a) Data of living species from ref. [23]. a, anterior to the mid-point of body back; m, mid-point of body back; nv, number of vertebrae; odf, origin of dorsal fin; p, posterior to the mid-point of body back.

asiae from East Kazakhstan, Altai, and West Mongolia, †*C. martini* from Vienna Basin, †*C. primigenus* from Northern Bavaria) and *Sabanejewia* (†*S. shargaensis* from West Mongolia and East Kazakhstan) were erected. The presence of suborbital spine is a character shared by Botiidae and Cobitidae. Nalbant [2, 20] pointed out the differences between the spines of these two families. However, the comparative studies of the suborbital spines within the family Cobitidae are few, and only Chen [23] pointed out the discrimination between the spines of *Cobitis*, *Bibarba*, and *Niwaella*. Therefore, the suborbital spines of special type are sufficient to provide evidences for the presence of cobitids but may not be adequate for establishing a new species [6].

Cobitis is the only widespread genus among cobitids. Living species of *Cobitis* have a Palaearctic distribution, throughout East Asia to Europe. They are mainly dwelling in the temperate zone approximately between the latitudes of 35° to 60°N, extending to the south to Morocco and northern part of West Asia in the west, and nearly to 11°N in Southeast Asia in the east, but absent in northern Siberia, most part of Scandinavia, and Scotland [9, 18]. The southern boundary of its distribution, in the region between the two southwardly extending areas, rests at the latitude of further north than 45°N [18] (Figure 2). Living species of *Sabanejewia* are largely distributed in Europe with a small part in West Asia [18]. Most known fossil cobitids fall in the distribution range of the Recent *Cobitis*. Among them, a good number of localities are in Europe, several in Central Asia, and only one in East Asia. We believe that our present knowledge about the distribution of fossils of *Cobitis* is biased due to uneven exploration. It is worth mentioning that the fossil localities from the Central Asia, namely East Kazakhstan, Altai and West Mongolia, are either situated outside the recent distribution range of *Cobitis* or just at the southern boundary. Thus, it is most likely that *Cobitis* had a much wider distribution during the Neogene than the present day, and the absence of *Cobitis* in Central and most part of South Asia today is possibly attributable to the uplift of this area caused by the rigorous tectonic movement during the Cenozoic, as it was suggested by some ichthyologists [47]. The relatively great variety of the suborbital spines indicates considerable diversity of *Cobitis* in this area during the Miocene and Pliocene. Fossil *Sabanejewia* is also found in this area, outside of its present distribution. Together with abundant contemporaneous fossil fishes of other groups, this emphasizes the importance of the area in the formation of recent freshwater ichthyofaunas in Eurasia [10].

To sum up, the earliest cobitid known so far is †*Cobitis primigenus* Böhme, 2008 from the latest Oligocene of Northern Bavaria, Germany, though it is represented only by six lateral ethmoids, i.e., suborbital spines. The late early Miocene †*Cobitis longipectoralis* Zhou, 1992 from East China with complete skeleton, showing many important characters of *Cobitis*, is thus far the earliest representative

of the genus from Asia and most informative fossil form among all referred to the genus. *Cobitis* most probably had a much wider distribution range than it has today. Its present absence in most part of Central and South Asia may be due to the Cenozoic orogeny in this area. The Neogene freshwater fossils from Central Asia may have played an important role in the formation of freshwater ichthyofaunas of Eurasia today. Previous studies suggested a South and Southeast Asiatic origin of Cobitidae [5, 18, 19, 47] and an East Asia [48] or South China origin of *Cobitis* [23]. However, any meaningful discussion of the origin problem must be based on reliable phylogeny and sufficient fossil evidence.

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