

## Phylogeny of the Specialized Schizothoracine Fishes (Teleostei: Cypriniformes: Cyprinidae)

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**Zi-Ming Chen and Yi-Feng Chen (2001)** Phylogeny of the specialized schizothoracine fishes (Teleostei: Cypriniformes: Cyprinidae). *Zoological Studies* 40(2): 147-157. To elucidate phylogenetic relationships within the specialized schizothoracine fishes, we used 41 variable osteological and external characters among this groups, three species of *Schizothorax*, and 1 fossil species. When the 3 species of *Schizothorax* were designated as an outgroup and all 41 characters were set as unordered with equal weighting, the data matrix yielded a single most-parsimonious tree with a tree length of 71 steps, a consistency index of 0.6761, and a retention index of 0.7416. Meanwhile, a bootstrap test was conducted to verify the reliability of the results. The matrix was also analyzed for different conditions: all characters were ordered and the fossil species was added as an outgroup. The phylogenetic analyses presented herein support the following hypotheses. 1) All species of the specialized schizo-thoracines fishes form a monophyletic group. 2) Monophyly of the genus *Ptychobarbus* is not supported by the bootstrap test or when these characters are ordered. 3) The genus *Gymnodiptychus* forms a monophyletic group. 4) All species of *Ptychobarbus* and *Gymnodiptychus* form a monophyletic group with *Diptychus* as its sister group.

**Key words:** Cyprinidae, Specialized schizothoracine fishes, Character analysis, Phylogenetic relationships, Tibetan Plateau.

The subfamily Schizothoracinae is contained within the family Cyprinidae and is diagnosed by 2 lines of enlarged scales along both sides of the anus and urogenital opening. This group is endemic to the central plateau of Asia, and its members are the most typical representatives of the ichthyofauna of this region. According to the degree of specialization of the barbels, scales, and pharyngeal teeth, the schizothoracine fishes are divided into 3 grades: primitive schizothoracine fishes; specialized schizothoracine fishes; and highly specialized schizothoracine fishes (Cao et al. 1981). The specialized schizothoracine fishes include 3 genera (*Diptychus*, *Ptychobarbus*, and *Gymnodiptychus*) containing 9 species and subspecies (*D. maculatus*, *P. conirostris*, *P. dipogon*, *P. kaznakovi*, *P. chungtienensis chungtienensis*, *P. chungtienensis gezaensis*, *G. dybowskii*, *G. integrigymnatus*, and *G.*

*pachycheilus*). Compared to other fishes in the same subfamily, the specialized schizothoracine fishes have the following characters: 1) a single pair of barbels, 2) 2 rows of pharyngeal teeth, and 3) moderately degenerate scales (degenerated entirely in the genus *Gymnodiptychus*).

The specialized schizothoracine fishes are a group of middle- to small-sized fishes. The body is fusiform, and the transverse plane of the body is slightly flattened and nearly round. There is no sharp horny edge on the front of the lower jaw, except in *D. maculatus*. Most species live in rapidly flowing streams and feed on aquatic insects. They occur on the central plateau in Asia, mainly on the Tibetan Plateau (Qinghai-Xizang Plateau) in China at elevations of 2000-4000 m.

*Ptychobarbus* was first erected by Steindachner (1866) based on the type species, *P. conirostris*.

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Regan (1905) first placed *P. dipogon* in *Schizothorax* owing to discarding of the characters of 2 rows of pharyngeal teeth and of single pair of barbels. *Diptychus* is a monotypic genus erected by Steindchner (1866) based on the type species, *D. maculatus*. Herzenstein erected *Gymnodiptychus* in 1892; the type species is *D. dybowskii*, now placed in the genus *Gymnodiptychus*. The 3 genera were once looked on as a subgenus belonging to the genus *Diptychus* (Berg 1949, Cao 1964); other research upgraded the 3 subgenera to independent genera (Day 1889), and this view is widely accepted now (Wu and Wu 1992, Chen 1998, Chen and Cao 2000).

With *Barbodes hexagonolepis* (which belongs to the subfamily Barbinae) as an outgroup and 45 species and subspecies (which represent the 11 genera of Schizothoracinae) as the ingroup, the relationships between the genera of the Schizothoracinae was discussed based on 25 external and osteological characters (Wu and Wu 1992). Chen (1998) pointed out that some of the characters which Wu and Wu (1992) used are adaptive characters and their parallel ones. Chen also discussed the relationships of the genera in Schizothoracinae based on 24 characters (including 34 character states) using *B. daliensis* as an outgroup and 13 species (which represent all genera of Schizothoracinae) as the ingroup. The phylogenetic tree demonstrated that *Diptychus* + *Ptychobarbus* + *Gymnodiptychus* form a monophyletic group with *Diptychus* as the basal clade. An analysis of the relationship between *Diptychus* (*P.*) *chungtienensis* (= *P. chungtienensis*) and *D.* (*P.*) *kaznakovi* (= *P. kaznakovi*) was conducted by Huang and Chen (1986). They concluded that *P. chungtienensis* was more primitive in morphology, and *P. kaznakovi* exhibited specific characters in adaptation to rapid torrents produced by uplift of the Tibetan Plateau. At the same time, Huang and Chen (1986) divided *P. chungtienensis* into 2 subspecies, *P. chungtienensis chungtienensis* and *P. chungtienensis gezaensis*, based on the number of gill-rakers and the degree of development of the lower lip.

Previous studies suffer from: 1) not including all the species and subspecies of the specialized schizothoracine fishes; 2) the low number of characters used in the analyses; and 3) the absence of rigorous cladistic analyses, with the exception of Chen (1998). Hence there is no comprehensive phylogenetic hypothesis for the specialized schizothoracine fishes at present. This paper mainly attempts to resolve the interspecific and generic relationships of this group.

## MATERIALS AND METHODS

*Schizothorax* and *Plesioschizothorax macrocephalus* were taken as the outgroup because *Schizothorax* is the primitive genus in the Schizothoracinae (Cao et al. 1981, Wu and Wu 1992, Chen 1998), and *P. macrocephalus* which is the only fossil species discovered in northern Tibet had been hypothesized to be closely related to *Schizothorax* (Wu and Chen 1980). Having 39 species and subspecies (Chen and Cao 2000), *Schizothorax* is the largest genus in the subfamily. Thus we selected *S. (Racoma) kozlovi*, *S. (Schizothorax) wangchiachii*, and *S. (S.) lissolabiatus* to represent 3 typical compound mouth structures in *Schizothorax*.

### Materials examined

In total, 202 specimens of 12 species and subspecies including ingroup and outgroups were examined. Among them, fifteen specimens of 12 species and subspecies were cleared and stained following the method of Dingerkus and Uhler (1977). All specimens were obtained from the Freshwater Fishes Museum, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, Hubei Province.

*Diptychus maculatus*: 989121, another one without a label.

*Ptychobarbus conirostris*: 6290227, 6290230, 631026-1031, 6290237, 6290241, 747177, 748073, 76VIII1046-1047.

*P. dipogon*: 610288-610290, 74IX6286, 74IX6288-6289, 75IX0633.

*P. kaznakovi*: 76VI1675-1679, 82VII1027, 590029, No: 1, No: 2, 76VII1750, 76VII1801, 76VII1803-1808, 76VII1811-1812, 0103, 0769-0770, 0780, 9118-9120, 0772-0774.

*P. c. chungtienensis*: 81IX3223-3238, 81IX3240-3243, 81IX3250-3251, 81IX3253, 81IX3256, 81IX3258, 81IX3260-3261, 81IX3266-3267, 81IX3269, 81IX3285-3286, 81IX3287-3292, 81IX3294-3298, 81IX3301-3304, 989001, 989018-9019.

*P. c. gezaensis*: 989012-9016.

*Gymnodiptychus dybowskii*: 57VIII0824-0825, 6290218-0221, 6290228-0229, 6290232-0235, 6290251-0256, 89IV0288, 89IV0291-0292, 89IV0308, 89IV0316, 89IV0321, 89IV0324, 89IV0326-0327, 89IV0331-0332, 989122.

*G. integrigymnatus*: 780980-0985.

*G. pachycheilus*: 56X0763, 57VIII0769, 59VI0947-0952, 59V0789-0793, 615028, 615031, 615045, 616074, 618298, 618305, 82VIII1137-1141,

82VIII1479-1480, 82VIII2070, 82VIII2072-2083, 82VIII2086-2087, 821229, 824773, 90IX0171, 989123.

*Schizothorax (Racoma) kozlovi*: 989059-9060.

*S. (Schizothorax) wangchiachii*: 989020-9023.

*S. (Schizothorax) lissolabiatus*: 81X4164, 989115-9117.

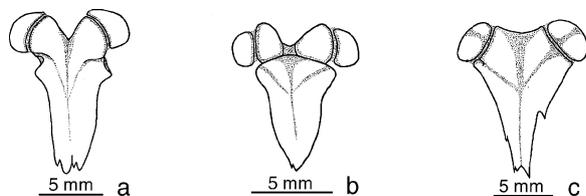
Statements of character condition for the 12 species and subspecies are based on the specimens examined. Characters of *Plesioschizothorax macrocephalus* were based on Wu and Chen (1980), and the a question mark (?) represents characters that we could not determine from that fossil species. A bootstrap test was conducted to verify the reliability of the final most-parsimonious tree(s). Data were analyzed using the cladistic methods originally proposed by Hennig (1950 1966) and summarized by Wiley et al. (1991). Outgroup comparison followed the method of Maddison et al. (1984). The dataset was analyzed using PAUP (version 4.0b4a for Macintosh). Osteological observations and figures were made on cleared and stained specimens, using a binocular microscope equipped with a drawing attachment.

## RESULTS

### Characters and character states

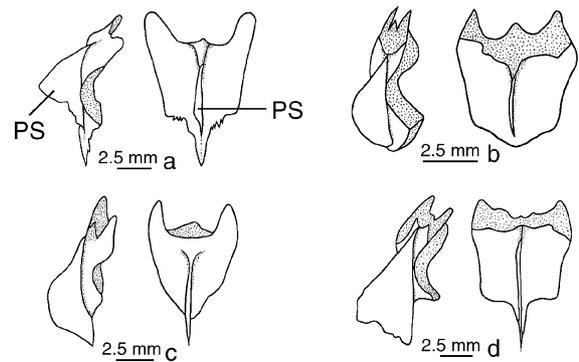
**Vomer:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatus*, and *Gymnodiptychus*, the posterior part of the vomer is blunt (Fig. 1a; #1-0; #1-*n* means state *n* of the *i*th character). In *D. maculatus* and *Ptychobarbus*, the posterior part of the vomer is sharply pointed (Fig. 1b-c; #1-1).

In *Schizothorax (Racoma) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatus*, *Diptychus maculatus*, *Ptychobarbus dipogon*, and *P. kaznakovi*, the anterior part of the vomer is V-shaped concave (Fig. 1a-b; #2-0). In *Gymnodiptychus* and the remaining *Ptychobarbus*, the anterior part of the vomer is slightly concave even forming a concave arc (Fig. 1c; #2-1).



**Fig. 1.** Ventral view of vomer. (a) *Schizothorax (Racoma) kozlovi*, (b) *Diptychus maculatus*, (c) *Ptychobarbus conirostris*.

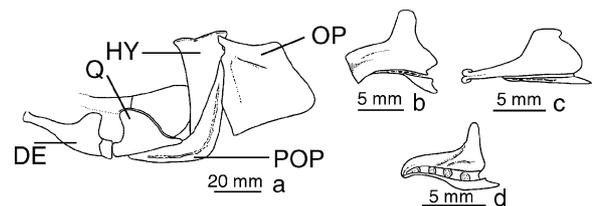
**Supraoccipital:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatus*, and *Ptychobarbus* except for *P. chungtienensis*, the posterior sheet (PS) of the supraoccipital forms a triangular facet (Fig. 2a, d; #3-0). In *D. maculatus*, *Gymnodiptychus*, and *P. chungtienensis*, the posterior sheet of the supraoccipital forms an arc facet (Fig. 2b-c; #3-1).



**Fig. 2.** Left view (left) and dorsal view (right) of supraoccipital. (a) *Schizothorax (Racoma) kozlovi*, (b) *Diptychus maculatus*, (c) *Ptychobarbus chungtienensis*, (d) *P. conirostris*. PS, posterior sheet.

In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatus*, and *Diptychus*, the posterior sheet of the supraoccipital does not exceed the base of the supraoccipital (Fig. 2a-b; #4-0). In *Ptychobarbus* and *Gymnodiptychus*, the posterior sheet exceeds the base of the supraoccipital (Fig. 2c-d; #4-1).

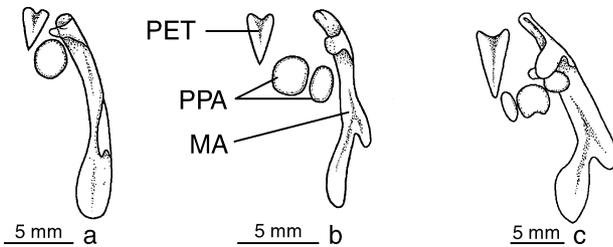
**Dentary:** In *P. macrocephalus* (fossil species), *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatus*, *G. integrigymnatus*, and *G. dybowskii*, the dorsal protuberance in the posterior part of the dentary is very developed and forms a fingerlike shape (Fig. 3a, b, d; #5-0). In *D. maculatus*, *Ptychobarbus*, and the remaining *Gymnodiptychus*, the upward protuberance in the rear part of the dentary is not so developed, and its height is less than its width (Fig. 3c; #5-1).



**Fig. 3.** Lateral view of dentary. (a) *Plesioschizothorax macrocephalus* (according to Wu and Chen 1980), (b) *Schizothorax (S.) wangchiachii*, (c) *Ptychobarbus chungtienensis*, (d) *Gymnodiptychus integrigymnatus*. DE, dentary; Q, quadrate; OP, opercular; POP, preopercular; HY, hyomandibular.

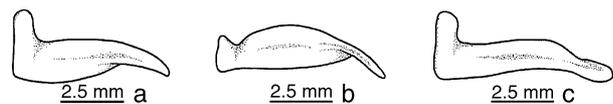
**Canalis of the mandibula:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *Ptychobarbus*, *Diptychus*, and *Gymnodiptychus* except for *G. integrigymnatus*, the canalis of the mandibula is small (Fig. 3a-c; #6-0). In *G. integrigymnatus*, the canalis of the mandibula is large and round in shape (Fig. 3d; #6-1).

**Prepalatine:** The prepalatine is ball-shaped cartilage, connecting the maxilla and palatine. In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, and *Diptychus*, there is only 1 prepalatine on each side (Fig. 4a; #7-0). In *Gymnodiptychus* and *Ptychobarbus* except for *P. conirostris*, there are 2 prepalatines on each side (Fig. 4b; #7-1). In *P. conirostris*, there are 3 prepalatines on each side, among which 1 is bigger and the remaining 2 are smaller (Fig. 4c; #7-2).



**Fig. 4.** Dorsal view of prepalatine. (a) *Schizothorax (Racoma) kozlovi*, (b) *Ptychobarbus dipogon*, (c) *P. conirostris*. MA, maxilla; PET, preethmoid; PPA, prepalatine.

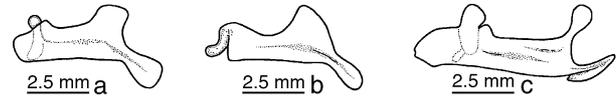
**Premaxilla:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *Gymnodiptychus*, and *Ptychobarbus*, the anterior protuberance of the premaxilla is developed and is the widest part of the bone (Fig. 5a, c; #8-0). In *D. maculatus*, the anterior protuberance of the premaxilla is weak, and the widest part lies in the middle part of the bone (Fig. 5b; #8-1).



**Fig. 5.** Lateral view of premaxilla. (a) *Schizothorax (Racoma) kozlovi*, (b) *Diptychus maculatus*, (c) *Ptychobarbus conirostris*.

**Maxilla:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *D. maculatus*, *P. c. chungtienensis*, and *P. c. gezaensis*, the anterior part of the maxilla is equal to or slightly overruns the inner joint projection (Fig. 6a; #9-0). In the remaining *Ptycho-*

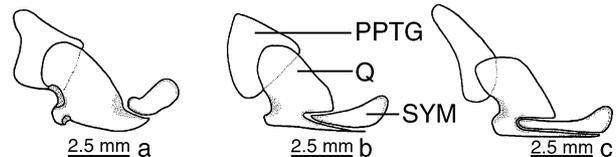
*barbus* and *Gymnodiptychus* except for *G. integrigymnatus*, the anterior part of the maxilla overruns the inner joint projection (Fig. 6c; #9-1).



**Fig. 6.** Lateral view of maxilla. (a) *Schizothorax (Racoma) kozlovi*, (b) *Gymnodiptychus integrigymnatus*, (c) *Ptychobarbus conirostris*.

There is an anterior part of the maxilla in all examined fishes (Fig. 6a, c; #10-0) with the exception of *G. integrigymnatus* in which the anterior part of the maxilla is degenerated, and the inner joint projection overruns the anterior part of the maxilla (Fig. 6b; #10-1).

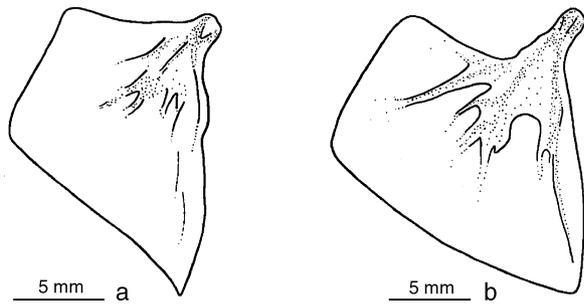
**Prepterygoid:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, and *G. pachycheilus*, the prepterygoid forms a triangular facet (Fig. 7a-b; #11-0). In *D. maculatus*, *Ptychobarbus*, and *Gymnodiptychus* except for *G. pachycheilus*, the prepterygoid forms a belt facet (Fig. 7c; #11-1).



**Fig. 7.** Lateral view of prepterygoid and quadrate. (a) *Schizothorax (S.) lissolabiatu*, (b) *S. (Racoma) kozlovi*, (c) *Ptychobarbus chungtienensis*. PPTG, prepterygoid; Q, quadrate; SYM, symplectic.

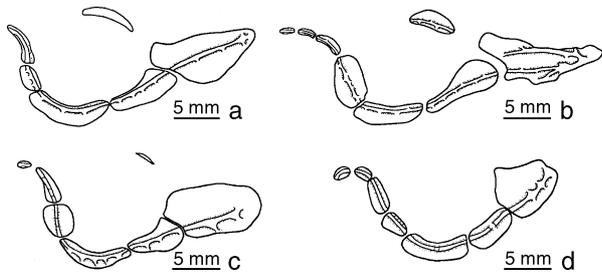
**Quadrate:** In *Plesioschizothorax macrocephalus*, *S. (S.) lissolabiatu*s, and *P. conirostris*, the part that articulates with the symplectic is not concave or is only slightly concave (Fig. 7a; #12-0). In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *D. maculatus*, *Gymnodiptychus*, and *Ptychobarbus* except for *P. conirostris*, the part that articulates with the symplectic is deeply concave (Fig. 7b-c; #12-1).

**Opercular:** In *Plesioschizothorax macrocephalus*, *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *D. maculatus*, *G. pachycheilus*, and *Ptychobarbus* except for *P. chungtienensis*, the dorsal edge of the opercular is level or slightly concave (Fig. 8a; #13-0). In the remaining *Gymnodiptychus* and *P. chungtienensis*, the dorsal edge of the opercular is concave (Fig. 8b; #13-1).



**Fig. 8.** Lateral view of opercular. (a) *Schizothorax (Racoma) kozlovi*, (b) *Ptychobarbus chungtienensis*.

**Supraorbital:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *Dtychobarbus*, and *Gymnodiptychus* except for *G. integrigymnatus*, the supraorbital is present (Fig. 9a-b; #14-0). In *D. maculatus*, the supraorbital is degenerated, and almost fused with the frontal (Fig. 9c; #14-1). In *G. integrigymnatus*, the supraorbital is absent (Fig. 9d; #14-2).



**Fig. 9.** Right lateral view of orbital region. (a) *Schizothorax (S.) lissolabiatu*s, (b) *Ptychobarbus conirostris*, (c) *Diptychus maculatus*, (d) *Gymnodiptychus integrigymnatus*.

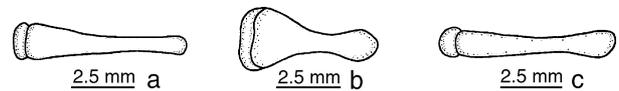
**Infraorbital:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *D. maculatus*, *Ptychobarbus* except for *P. conirostris*, and *Gymnodiptychus* except for *G. integrigymnatus*, the infraorbital consists of 5-6 bones (Fig. 9a, c; #15-0). In *P. conirostris*, and *G. integrigymnatus*, the infraorbital consists of 7 bones (Fig. 9b, d; #15-1).

**Lacrimal:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *D. maculatus*, *Ptychobarbus* except for *P. conirostris*, and *Gymnodiptychus* except for *G. integrigymnatus*, the length of the lacrimal is about 1.5 times (1-2 times) its depth (Fig. 9a, c; #16-0). In *P. conirostris*, the length of the lacrimal is about 3 times its depth (Fig. 9b; #16-1). In *G. integrigymnatus*, the length of the lacrimal is about equal to its depth (Fig. 9d; #16-0).

**Supraorbitale:** The supraorbitale exists in all ex-

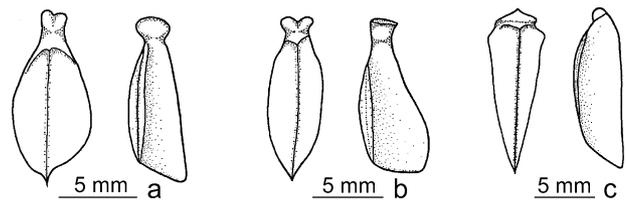
amined species (Fig. 9a-c; #17-0) with the exception of *G. integrigymnatus* (Fig. 9d; #17-1).

**Basihyal:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *D. maculatus*, *P. chungtienensis*, *P. kaznakovi*, and *Gymnodiptychus* except for *G. pachycheilus*, the anterior part of the basihyal is wider than the posterior part (Fig. 10a-b; #18-0). In the remaining *Ptychobarbus* and *G. pachycheilus*, the width of the anterior part is equal to that of the posterior part (Fig. 10c; #18-1).



**Fig. 10.** Dorsal view of basihyal. (a) *Schizothorax (Racoma) kozlovi*, (b) *Diptychus maculatus*, (c) *Ptychobarbus dipogon*.

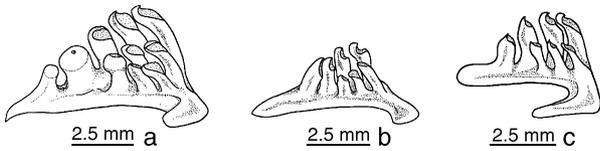
**Urohyal:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, and *S. (S.) lissolabiatu*s, the width of the widest part is more than 3 times that of the neck in the anterior portion of the ventral part (Fig. 11a; #19-0). In the specialized schizothoracine fishes, the width of the widest part is less than or equal to 2 times that of the neck in the anterior portion of the ventral part (Fig. 11b-c; #19-1).



**Fig. 11.** Ventral view (left) and lateral view (right) of urohyal. (a) *Schizothorax (Racoma) kozlovi*, (b) *Diptychus maculatus*, (c) *Ptychobarbus conirostris*.

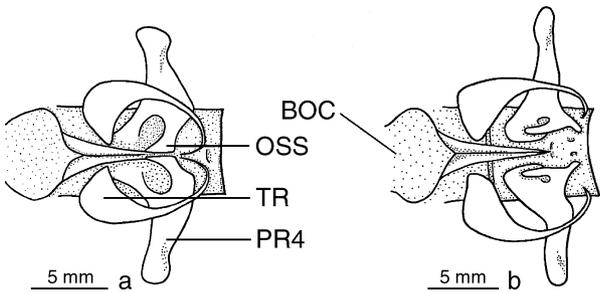
In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *D. maculatus*, *Gymnodiptychus*, *P. dipogon*, and *P. kaznakovi*, the ventral part of the urohyal forms an elliptical facet (Fig. 11a-b; #20-0). In the remaining *Ptychobarbus*, the ventral part of the urohyal forms a triangular facet, and the widest part lies at the front of the facet (Fig. 11c; #20-1).

**Pharyngeal teeth:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, and *P. macrocephalus*, there are 3 rows of teeth on each side of the pharyngeals, and its pattern is 2.3.5-5.3.2 (Fig. 12a; #21-0). In *D. maculatus*, *Ptychobarbus*, and *Gymnodiptychus*, there are 2 rows of teeth on each side of the pharyngeals, and its pattern is 3.4-4.3 (Fig. 12c; #21-1).



**Fig. 12.** Right lateral view of pharyngeal. (a) *Schizothorax* (*S.*) *lissolabiatu*, (b) *Gymnodiptychus dybowskii*, (c) *Ptychobarbus chungtienensis*.

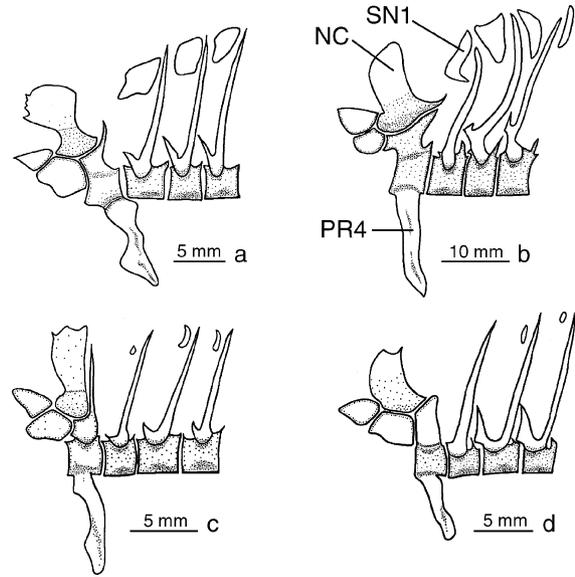
**Os suspensorium:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*, *D. maculatus*, *Gymnodiptychus*, *P. pachycheilus*, *P. conirostris*, and *P. dipogon*, both sides of the os suspensorium are weak, and they stand ventrally together with each other (Fig. 13a; #22-0). In the remaining *Ptychobarbus*, both sides of the os suspensorium are stiff and apart from each other (Fig. 13b; #22-1).



**Fig. 13.** Ventral view of os suspensorium. (a) *Schizothorax* (*S.*) *lissolabiatu*, (b) *Ptychobarbus chungtienensis*. BOC, basio-cipital; TR, tripus; OSS, os suspensorium; PR4, pleural rib of 4th vertebra.

**Neural complex:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *D. maculatus*, and *Ptychobarbus* except for *P. dipogon*, the lateral face of the neural complex is short and broad (Fig. 14a, b, d; #23-0). In *S. (S.) lissolabiatu*, *P. dipogon*, and *Gymnodiptychus*, the neural complex is slender and forms a striplike facet (Fig. 14c; #23-1).

**Supraneural:** Supraneurals are a series of slender platelike bones anterior to the neural spines. In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, and *S. (S.) lissolabiatu*, the lateral faces of the supraneurals are very broad, and the size of the anterior supraneurals is almost equal to that of the posterior ones (Fig. 14a; #24-0). In *P. c. chungtienensis*, *P. c. gezaensis*, and *P. kaznakovi*, the lateral faces of the 1st and 2nd supraneurals are broad and larger, while those of the remaining supraneurals are fine and smaller (Fig. 14b; #24-1). In *D. maculatus*, *Gymnodiptychus*, and the remaining *Ptychobarbus*, the lat-

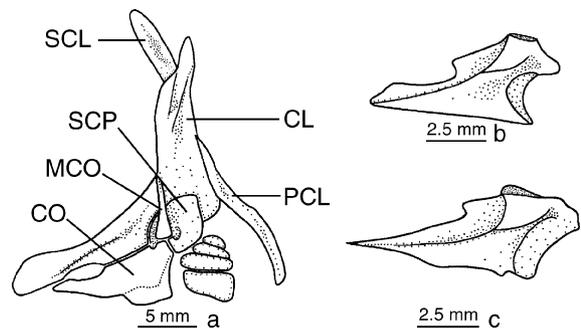


**Fig. 14.** Lateral view of neural complex and supraneural. (a) *Schizothorax* (*S.*) *wangchiachii*, (b) *Ptychobarbus chungtienensis*, (c) *P. dipogon*, (d) *Diptychus maculatus*. NC, neural complex; SN1, 1st supraneural; PR4, pleural rib of 4th vertebra.

eral faces of all supraneurals are fine and small (Fig. 14c-d; #24-2).

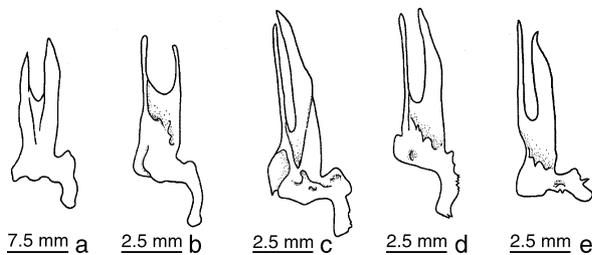
In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*, *Ptychobarbus*, and *P. integrigymnatus*, the 1st supraneural is present (Fig. 14a-c; #25-0). In *D. maculatus* and the remaining *Gymnodiptychus*, the 1st supraneural is absent (Fig. 14d; #25-1).

**Coracoid:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*, *P. c. chungtienensis*, *P. c. gezaensis*, and *P. dipogon*, the anterior part of the coracoid is blunt and broad (Fig. 15a-b; #26-0). In *D. maculatus*, *Gymnodiptychus*, and the remaining *Ptychobarbus*, the anterior part of the coracoid is pointed and slender (Fig. 15c; #26-1).



**Fig. 15.** Lateral view of coracoid. (a) *Schizothorax (Racoma) kozlovi*, (b) *S. (S.) wangchiachii*, (c) *Ptychobarbus chungtienensis*. SCL, supracleithrum; PCL, postcleithrum; CL, cleithrum; CO, coracoid; MCO, mesocoracoid; SCP, scapular.

**Innominatum:** In *Plesioschizothorax macrocephalus*, *S. (R.) kozlovi*, *S. (S.) wangchiachii*, and *S. (S.) lissolabiatius*, the fork in the anterior innominatum is shallow, and its length is less than 1/2 of the total length of the anterior part which is the main part of the innominatum (Fig. 16a-b; #27-0). In *D. maculatus*, *Ptychobarbus*, and *Gymnodiptychus*, the fork length is more than 1/2 of the total length of the anterior part (Fig. 16c-e; #27-1).



**Fig. 16.** Dorsal view of left innominatum. (a) *Plesioschizothorax macrocephalus*, (b) *Schizothorax (Racoma) kozlovi*, (c) *Diptychus maculatus*, (d) *Ptychobarbus kaznakovi*, (e) *Gymnodiptychus integrigymnatus*.

In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatius*, and *G. integrigymnatus*, the length of the inner branch of the anterior innominatum is shorter than that of the outer branch (Fig. 16b, e; #28-0). In *P. macrocephalus*, *D. maculatus*, *Ptychobarbus*, and *Gymnodiptychus* except for *G. integrigymnatus*, the length of the inner branch is longer than that of the outer one (Fig. 16a, c, d, e; #28-1).

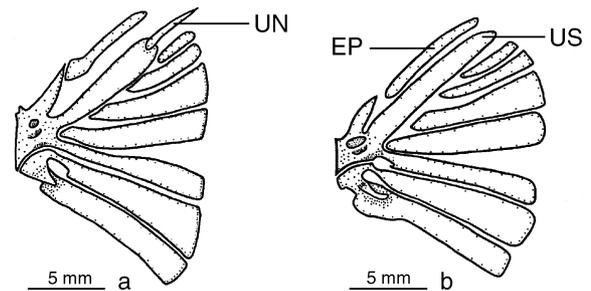
In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, and *S. (S.) lissolabiatius*, both branches of the anterior innominatum are slender, and the width of the outer branch is larger or equal to that of the inner branch (Fig. 16b; 29-0). In *P. macrocephalus* and the specialized schizothoracine fishes (9 species and subspecies), the width of the outer branch is smaller than that of the inner one (Fig. 16a, c, d, e; #29-1).

In *P. macrocephalus*, *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatius*, *D. maculatus*, *Ptychobarbus*, and *Gymnodiptychus* except for *G. integrigymnatus*, the projecting facet in the posterior innominatum is straight (Fig. 16a-d; #30-0). In *G. integrigymnatus*, the facet is slanted medially (Fig. 16e; #30-1).

In *P. macrocephalus*, *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *S. (S.) lissolabiatius*, *D. maculatus*, *Ptychobarbus*, and *Gymnodiptychus* except for *G. integrigymnatus*, the length of the projecting facet in the posterior innominatum is twice its width (Fig. 16a-d; #31-0). In *G. integrigymnatus*, the facet

length is about equal to its width (Fig. 16e; #31-1).

**Uroneuralia:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, and *S. (S.) lissolabiatius*, there is a pair of uroneuralias detached on each side of the urostyle (Fig. 17a; #32-0). In the specialized schizothoracine fishes, the uroneuralia is absent (Fig. 17b; #32-1).



**Fig. 17.** Lateral view of uroneuralia. (a) *Schizothorax (S.) lissolabiatius*, (b) *Ptychobarbus conirostris*. UN, uroneuralia; US, urostyle; EP, epural.

**Numbers of unbranched dorsal-fin rays:** In *P. macrocephalus*, *S. (R.) kozlovi*, *S. (S.) wangchiachii*, and *S. (S.) lissolabiatius*, there are 4 unbranched dorsal-fin rays (#33-0). In *Ptychobarbus*, there are 4 unbranched dorsal-fin rays, but the 1st unbranched ray is degenerated, and only its remnant can be observed (#33-1). In *D. maculatus* and *Gymnodiptychus* except for *G. integrigymnatus*, there are 3 unbranched dorsal-fin rays (#33-2). In *G. integrigymnatus*, there are only 2 unbranched dorsal-fin rays (#33-3).

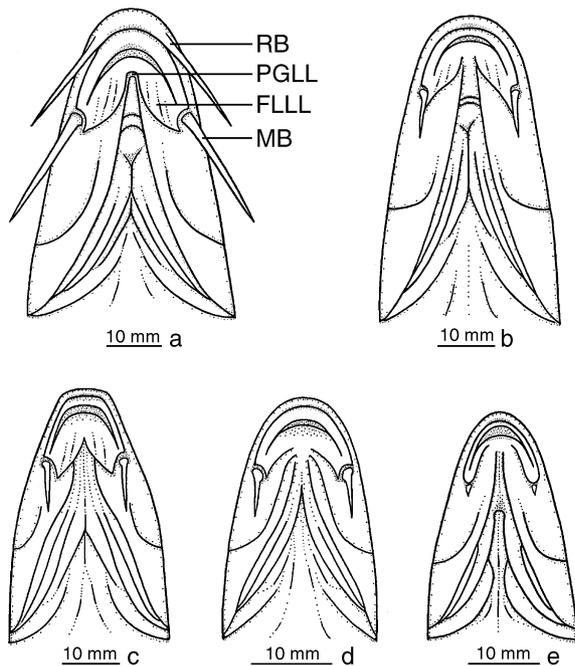
**The last unbranched dorsal-fin ray:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, and *S. (S.) lissolabiatius*, the last unbranched dorsal-fin ray is stiff, and there are sawteeth on its posterior edge (#34-0). In *Plesioschizothorax macrocephalus* and the specialized schizothoracine fishes, the last unbranched dorsal-fin ray is soft and there are no sawteeth on its posterior edge (#34-1).

**Numbers of unbranched anal-fin rays:** In *Plesioschizothorax macrocephalus*, the primitive schizothoracine fishes (referring to *Schizothorax*), *D. maculatus*, and *Gymnodiptychus*, there are 3 unbranched anal-fin rays (#35-0). In *Ptychobarbus*, there are 4 unbranched anal-fin rays (#35-1).

**Sexual dimorphism:** In *Plesioschizothorax macrocephalus* and the primitive schizothoracine fishes, the 4th and 5th branched rays of the anal-fin in the male do not become stiff when the fish mature (#36-0). In the specialized schizothoracine fishes, the 4th and 5th branched rays in the male become stiff when the fish mature (#36-1).

**Barbels:** In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, and *S. (S.) lissolabiatu*s, there are 2 pairs of barbels (Fig. 18a; #37-0). In the specialized schizothoracine fishes except for *G. integrigymnatus*, there is a single pair of barbels which are moderate (Fig. 18b-d; #37-1). In *G. integrigymnatus*, the single pair of barbels is degenerate (Fig. 18e; #37-2).

**Structure of the mouth:** In *S. (S.) wangchiachii*, *S. (S.) lissolabiatu*s, *D. maculatus*, and *G. integrigymnatus*, there are no free fleshy lips attached to the jaw (Fig. 18d-e; #38-0). In *S. (R.) kozlovi*, *Ptychobarbus*, and the remaining *Gymnodiptychus*, free fleshy lips attached to the jaw are present (Fig. 18a-c; #38-1).



**Fig. 18.** Ventral view of head. (a) *Schizothorax (Racoma) kozlovi*, (b) *Ptychobarbus dipogon*, (c) *P. chungtienensis*, (d) *Diptychus maculatus*, (e) *Gymnodiptychus integrigymnatus*. RB, rostral barbel; MB, maxillary barbel; PGLL, posterior groove of lower lip; FLLL, fleshy lobe of lower lip.

In *S. (S.) lissolabiatu*s, *D. maculatus*, *P. c. chungtienensis*, *P. c. gezaensis*, and *Gymnodiptychus* except for *G. pachycheilus*, the posterior groove of the lower lip is broken (Fig. 18b, d, e; #39-0). In *S. (R.) kozlovi*, *S. (S.) wangchiachii*, *G. pachycheilus*, and the remaining *Ptychobarbus*, the posterior groove of the lower lip is continuous (Fig. 18a, c; #39-1).

**Scales:** In the primitive schizothoracine fishes, *D. maculatus*, and *Ptychobarbus*, the entire body is covered with scales except for part of the chest and

abdomen (#40-0). In *Gymnodiptychus*, most of the body is scaleless, with only a few scales distributed on the shoulder and lateral to the anus and urogenital opening (#40-1).

In the primitive schizothoracine fishes, *D. maculatus*, *P. conirostris*, and *P. dipogon*, the scales of the lateral line on the tail are as large as the other scales on the tail (#41-0). In the remaining *Ptychobarbus*, the scales of the lateral line in the tail are bigger than the other scales on the tail (#41-1). In *Gymnodiptychus*, the scales of the lateral line are degenerated, and the scales beside the lateral line have disappeared (#41-2).

### Distribution of character states

All of these character states compose a data matrix with a question mark (?) representing characters that we could not determine from the fossil species (Table 1).

### CONCLUSION AND DISCUSSION

When the 3 species of *Schizothorax* were designated as an outgroup and all 41 characters were set as unordered and had equal weight, the 41-character matrix yielded a single most-parsimonious tree with a tree length of 71 steps, a consistency index (CI) of 0.6761, and a retention index (RI) of 0.7416 (Fig. 19). At the same time, a bootstrap test was completed (number of bootstrap replicates = 1000), and the bootstrap 50% majority-rule consensus tree is shown in figure 20. The differences between the 2 trees are that the relationships among the 4 species of *Ptychobarbus* are resolved or unresolved; and *Gymnodiptychus* is or is not derived from the *Ptychobarbus*.

When all 41 characters were set as ordered and had equal weight, twelve most-parsimonious trees could be generated with a tree length of 74 steps, a CI of 0.6486, and an RI of 0.7320. The consensus tree of the bootstrap test (number of bootstrap replicates = 1000) is the same as that shown in figure 20 except for the percentages.

When the 3 species of *Schizothorax* and *P. macrocephalus* were combined as an outgroup, the undetermined characters in *P. macrocephalus* were coded as missing data (i.e., "?"). With all characters unordered, the matrix generated a single most-parsimonious tree of 72 steps, a CI of 0.6667 and an RI of 0.7474; the structure of the tree is the same as that of figure 19 in regard to the ingroup (all species of the specialized schizothoracine fishes). The consensus

**Table 1.** Character state distribution

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Plesioschizothorax macrocephalus</i>	?	?	?	?	0	?	?	?	?	?	?	0	0	?	?	?	?	?	?
<i>Schizothorax (S.) lissolabiatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. (S.) wangchiachii</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. (Racoma) kozlovi</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Diptychus maculatus</i>	1	0	1	0	1	0	0	1	0	0	1	1	0	1	0	0	0	0	1
<i>Ptychobarbus chungtienensis</i>	1	1	1	1	1	0	1	0	1	0	1	1	1	0	0	0	0	1	1
<i>P. conirostris</i>	1	1	0	1	1	0	2	0	1	0	1	0	0	0	1	1	0	1	1
<i>P. dipogon</i>	1	0	0	1	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1
<i>P. kaznakovi</i>	1	0	0	1	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1
<i>Gymnodiptychus integrigymnatus</i>	0	1	1	1	0	1	1	0	0	1	1	1	1	2	1	0	1	1	1
<i>G. pachycheilus</i>	0	1	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	1	1
<i>G. dybowski</i>	0	1	1	1	0	0	1	0	1	0	1	1	1	0	0	0	0	1	1

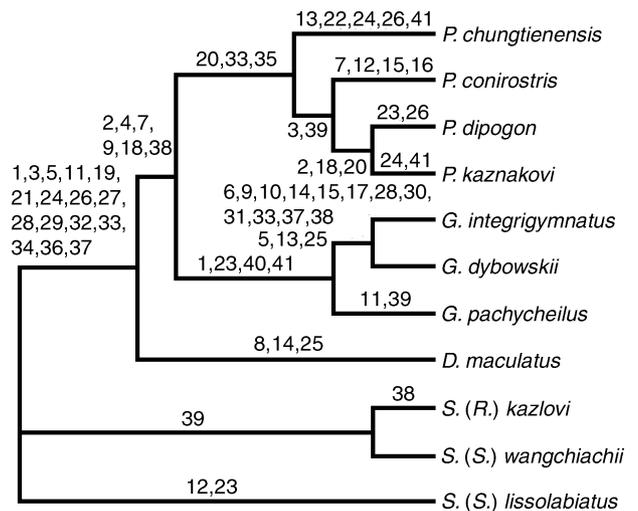
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
<i>Plesioschizothorax macrocephalus</i>	?	0	?	?	?	?	?	0	1	1	0	0	?	0	1	0	0	?	?	?	?	?
<i>Schizothorax (S.) lissolabiatus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. (S.) wangchiachii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>S. (Racoma) kozlovi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Diptychus maculatus</i>	0	1	0	0	2	1	1	1	1	1	0	0	1	2	1	0	1	1	0	0	0	0
<i>Ptychobarbus chungtienensis</i>	1	1	1	0	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1	0	0	1
<i>P. conirostris</i>	1	1	0	0	2	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0	0
<i>P. dipogon</i>	0	1	0	1	2	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	0	0
<i>P. kaznakovi</i>	0	1	0	0	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1
<i>Gymnodiptychus integrigymnatus</i>	0	1	0	1	2	1	1	1	0	1	1	1	3	1	0	1	2	0	0	1	1	2
<i>G. pachycheilus</i>	0	1	0	1	2	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1	2
<i>G. dybowski</i>	0	1	0	1	2	1	1	1	1	1	0	0	1	2	1	0	1	1	1	0	1	2

tree of the bootstrap test (number of bootstrap replicates = 1000) is the same as that shown in figure 20 in regard to the ingroup except for the percentages. When all characters were ordered, twelve most-parsimonious trees could be retained with 75 steps, a CI of 0.6400, and an RI of 0.7379; the results of the bootstrap test (number of bootstrap replicates = 1000) is also the same as that shown in figure 20 in regard to the ingroup except for the percentages.

When the characters were unordered, whether the 3 species of *Schizothorax* or the 3 species plus *Plesioschizothorax macrocephalus* were treated as the outgroup, there was only a single most-parsimonious tree (Fig. 19). In this case, the characters that are unknown in *Plesioschizothorax macrocephalus* are assumed to be the same as those in the 3 species of *Schizothorax*. When the 3 species of *Schizothorax* were selected as the outgroup, the specialized schizothoracine fishes were defined by 16 characters (1, 3, 5, 11, 19, 21, 24, 26-29, 32-34, and 36-37). Thus more characters are presented here to support the monophyly of the specialized schizothoracine fishes. The bootstrap test also supports this outcome by 100%.

The cladogram (Fig. 19) shows that the specialized schizothoracine fishes could be divided into 3

clades: *Diptychus*, *Ptychobarbus*, and *Gymnodiptychus*. *Ptychobarbus* and *Gymnodiptychus* are sisters, and *Diptychus* forms the sister group to *Ptychobarbus* + *Gymnodiptychus*. This result

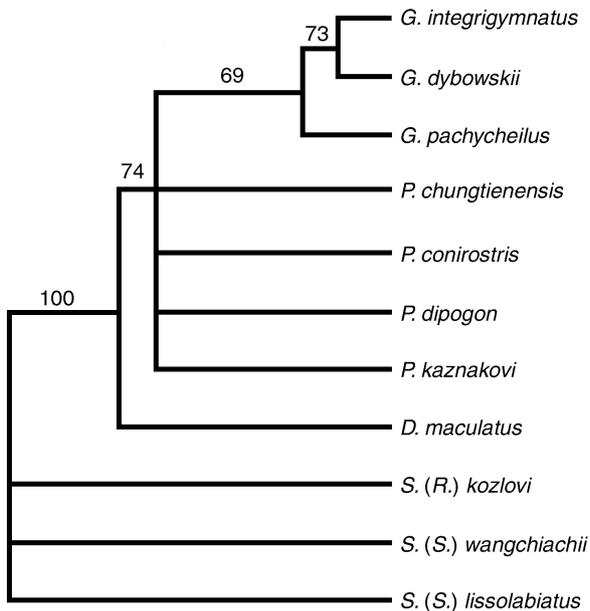


**Fig. 19.** Cladogram of the specialized schizothoracine fishes. Three species of *Schizothorax* are designated as the outgroup, and all 41 characters are unordered. Tree length = 71 steps; CI = 0.6761; RI = 0.7416.

seems congruent with the conclusions reached by Wu et al. (1992) and Chen (1998). But the conclusions from the bootstrap test and the cladogram when all characters were ordered show that *Ptychobarbus* is not a monophyletic group, and support a hypothesis that *Gymnodiptychus* is derived from *Ptychobarbus* instead of being its sister group.

When all 41 characters were ordered, whether the 3 species of *Schizothorax* or the 3 species plus *Plesioschizothorax macrocephalus* were used as the outgroup, twelve most-parsimonious trees could be retained. The bootstrap test shows that the specialized schizothoracine fishes still comprise a monophyletic group (Fig. 20). This result is consistent with the preceding outcome.

Regarding the relationships within the genera, all species of *Ptychobarbus* and *Gymnodiptychus* are resolved when all the characters are unordered. In *Ptychobarbus*, *P. conirostris* + *P. dipogon* + *P. kaznakovi* form a monophyletic group with *P. chungtienensis* as its sister group. *P. dipogon* + *P. kaznakovi*, and *P. conirostris* are sister groups. In *Gymnodiptychus*, *G. dybowskii* and *G. integrigymnatus* form a monophyletic group with *G. pachycheilus* as its sister group. When all the characters are ordered, the relationships within *Gymnodiptychus* are the same as the results when all the char-



**Fig. 20.** Bootstrap 50% majority-rule consensus tree. Three species of *Schizothorax* are designated as the outgroup, and all 41 characters are unordered. Tree length = 77 steps; CI = 0.6234; RI = 0.6742. Number of bootstrap replicates = 1000; number of characters resampled in each replicate = 41; starting seed = 2130346986.

acters are unordered. But the relationships within *Ptychobarbus* remain unsettled. When we order the characters, we infer that which state is primitive and which state is derived and this process is not always correct; in fact, so judging them may unavoidably include some subjectivity. In our study, ordering the characters affected the relationships between *Gymnodiptychus* and *Ptychobarbus*, and the relationships within the 4 species of *Ptychobarbus*. It seems that the results with all characters unordered are more acceptable.

The 2 subspecies of *P. chungtienensis* exhibit no differences in characters detected in our study. Huang and Chen (1986) partitioned *P. chungtienensis* into 2 subspecies according to the number of gillrakers and developmental degree of the free fleshy lip attached to the lower jaw. But when different populations are examined, the 2 subspecies intermix with each other in these 2 characters. Whether this species should be divided into 2 subspecies needs further study.

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## 特化等級裂腹魚類之系統親緣

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本文對特化等級裂腹魚類的系統親緣關係進行了探討。在特化等級裂腹魚類和裂腹魚屬的 3 個種以及一個化石種中發現 41 個有變化的骨骼和形態特徵。當僅以裂腹魚屬的 3 個種作外類群，所有的特徵等權和非秩序化時，可以產生一個最簡約樹，其步長為 71，一致指數(CI)為 0.6761，保留指數(RI)為 0.7416。同時，利用自展法對該樹的可靠性進行檢驗。此外，在不同的條件下，如所有的特徵秩序化和化石種加入作為外類群，也對數據矩陣進行了分析。結果表明：1)特化等級裂腹魚類，即包括重唇魚屬 (*Diptychus*)、葉鬚魚屬 (*Ptychobarbus*) 和裸重唇魚屬 (*Gymnodiptychus*) 3 個屬的 8 個種形成一個單系群；2) 葉鬚魚屬的 5 個種及亞種的單系性並不為自展法或當所有特徵秩序化時所構建的系統樹支持；3) 裸重唇魚屬的 3 個種形成一個單系群；4) 葉鬚魚屬和裸重唇魚屬的關係較近，而重唇魚屬是它們的姐妹群。

**關鍵詞：**鯉科，特化等級裂腹魚類，特徵分析，系統親緣關係，青藏高原。

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