Zoological Studies **44**(1): 130-143 (2005)

Zoological Studies

Phylogenetic Relationships of Labeonine Cyprinids of the Disc-Bearing Group (Pisces: Teleostei)

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(Accepted September 30, 2004)

E Zhang (2005) Phylogenetic relationships of labeonine cyprinids of the disc-bearing group (Pisces: Teleostei). *Zoological Studies* **44** (1): 130-143. The disc-bearing group is composed of 4 currently recognized cyprinid genera: *Discocheilus*, *Discogobio*, *Garra*, and *Placocheilus*. This group is defined as having a lower lip modified to form a mental adhesive disc whose posterior margin is not continuous with the mental region, and includes 91 widely distributed species in tropical Africa and Asia. So far, it is represented in China by 28 species (about 1/3 of the total number) of all 4 genera. A phylogenetic analysis, based on 29 morphological characters scored from first-hand observations of 23 of the Chinese species examined, revealed that the disc-bearing group forms a monophyletic clade in which *Garra* is the basal lineage, and *Placocheilus* constitutes a subclade with the sister pair of *Discocheilus* and *Discogobio*. In such a phylogenetic framework, the validity of each genus of the disc-bearing group was evaluated. It was confirmed that *Discocheilus*, *Discogobio* and *Placocheilus* represent 3 valid cyprinid genera. Evidence provided in this phylogenetic analysis, incorporated with conclusions reached in the known literature, reveals that the monophyly and validity of *Garra* need to be further studied using observations of more *Garra* species. Additional characters should also be examined, as the characters utilized in this study and in Abebe's with Getahun's (1999) study are insufficient to resolve the monophyly of *Garra*. http://www.sinica.edu.tw/zool/zoolstud/44.1/130.pdf

Key words: Phylogenetic relationship, Disc-bearing group, Labeoninae, Cyprinidae, China.

The subfamily Labeoninae defined by Chen et al. (1984) (= Labeine cyprinids of Reid (1982, 1985) or Labeonin of Rainboth (1991)) consists of at least 26 genera and about 300 species known from tropical Africa and Asia, which account for 15%~20% of the total number of cyprinids fishes (Reid 1982, Rainboth 1991, Zhang et al. 2000). Most of these species are adapted to rapid-water habitats and feed on diatoms, filamentous algae, and organic detritus. Unmatched by other cyprinid fishes, Labeoninae exhibits a high degree of modification in its oromandibular structures, which is the basis for recognition of the inclusive genera. Within the Labeoninae, 4 genera are unique in having the lower lip modified into a mental adhesive disc whose posterior margin is discontinuous with the mental region: *Discocheilus* Zhang, 1997, *Discogobio* Lin, 1931, *Garra* Hamilton, 1822, and *Placocheilus* Wu, 1977. They are therefore designated as the disc-bearing group hereafter.

The disc-bearing group has 91 currently recognized species (Table 1). *Garra* is the largest and most widely distributed genus consisting of 78 species with a range from Borneo, China, and South Asia, through the Middle East, the Arabian Peninsula, and East Africa to West Africa. Among them, at least 14 species occur in South China (pers. obs.). The 2nd-largest genus is *Discogobio* with 9 species from the Yangtze River (Chang Jiang), Pearl River (Zhu Jiang), and Red River (Yuan Jiang) basins of China. *Placocheilus* has 3 species from the Red River and Salween River (the section in China) (Nu Jiang) basins, with *Discocheilus* having 2 species restricted to the

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Pearl River basin. Together, the disc-bearing group is represented in China by 28 species (about 1/3 of the total number of this group) and includes all 4 genera.

Currently, the generic recognition of the disc-bearing group is mainly based on the morphology of the mental adhesive disc and the number of rows of pharyngeal teeth (Wu et al. 1977, Chu and Cui 1989, Zhu 1995, Zhang et al. 2000 2002). *Garra* shares a crescentic anteromedian fold with *Placocheilus* that is derived from the anterior margin of the mental adhesive disc; but differs from that genus in having 3 rows of pharyngeal teeth. *Placocheilus* resembles *Discogobio* and *Discocheilus* in having 2 rows of pharyngeal teeth, but both can be easily diagnosed by the different morphologies of the anteromedian fold of the mental adhesive disc. This fold is crescentic, flattened and more thickened in *Discocheilus* and is horseshoe-shaped in *Discogobio*. Despite the number of rows of pharyngeal teeth and the morphology of the mental adhesive disc being very significant characters for distinguishing among genera of the disc-bearing group, their validities need to be evaluated in a phylogenetic context.

Phylogenetic relationships among genera of the disc-bearing group still remain unelucidated. Some ideas about intergeneric relationships of the group, though, have been put forward by Chinese workers. Wu et al. (1977) maintained that the 3 then-known genera, *Discogobio*, *Garra*, and *Placocheilus*, uniquely characterized by having a mental adhesive disc modified from the lower lip, were more closely related to each other than to other cyprinid genera, and that *Placocheilus* and *Discogobio* are more derived than *Garra* in having 2 rows of pharyngeal teeth. Zhang et al. (2000) also asserted that the disc-bearing group perhaps resides within the most-phylogenetically derived among the Labeoninae. Unfortunately, these hypotheses were based only on characters related to the pharyngeal teeth and mental adhesive disc, as well as being proposed without use of cladistic methodology. Moreover, none of them concentrated on evaluating the monophyly of the disc-bearing group and each inclusive genus.

The purpose of the present paper was to assess the intergeneric phylogenetic relationships among the disc-bearing group by employing a cladistic method and morphological data based on examination of Chinese species and then evaluate the validity of each inclusive genus in a phylogenetic framework.

MATERIALS AND METHODS

Comparative morphological data were used to assess phylogenetic relationships among the disc-bearing group. Specimens examined in the present study are listed in the appendix. Specimens were dissected following the method outlined by Weitzman (1974) and cleared and double-stained for cartilage and bone utilizing methods modified from Dingerkus and Uhler (1977) and Taylor and Van Dyke (1985).

Hypotheses of phylogenetic relationships were proposed by employing the cladistic method originally formalized by Hennig (1966). Detailed explanations about cladistic principles and their

Table 1. Distribution and species number of each genus of the disc-bearing group

Distribution	Generic name	Species number	Sources of information
East Asia (North Vietnam and South China)	*Garra*	19	Kottelat, 2001a; Zhang et al., 2000 Zhang & Chen, 2002
	Discogobio	9	Kottelat, 200la; Zhang et al, 2000
	Discocheilus	2	Zhang et al, 2000
	Placocheilus	3	Zhang et al. 2002
Southeast Asia (Indochinese Pennisula)	*Garra*	10	Kottelat, 1989 1998 2000 2001a; Roberts, 1989; Kottlet et al, 1993; Raiboth, 1996; Doi, 1997
South Asia (Indian and its adjacent area)	*Garra*	23	Talwar & Jhingran, 1991; Vishwanath, 1993; Kosygin & Vishwanath, 1998; Gopi, 2001
West Asia (Middle east, Arabian Peninsula)	*Garra*	9	Krupp, 1983; Krupp & Schneider, 1989
Africa	*Garra*	17	Gatahun, 1999
Total number	4	91	

operational aspects are widely available from the literature (Wiley 1981, Nelson and Platnick 1981, Sworfford et al. 1996). Given that the phylogenetic relationship of the disc-bearing group to the remainder of the Labeoninae is not better understood, representative species of most genera of this subfamily were examined in the present study. In order to simplify the data presentation, the outgroups directly used for phylogenetic analysis were *Epalzeorhynchos*, *Pseudocrossocheilus*, *Rectoris*, *Parasinilabeo*, *Semilabeo*, and *Sinocrossocheilus*. These are conventionally believed to be closely associated with the disc-bearing group in that their upper lip is replaced by a pendulous rostral fold that entirely covers the upper jaw and is separated from it by a deep groove.

29 potentially phylogenetically informative morphological characters, which exhibit variability within the disc-bearing group, were identified and described under the character analysis. Character polarity was determined utilizing the outgroup comparison method of Watrous and Wheeler (1981). 7 multistate characters (4 and 26) were analyzed as unordered in order to avoid imposing an unjustifiable model of evolution on them. Missing entries in the data matrix (represented by "?" in table 2), were applied to inapplicable character states (coded in some taxa for characters 5, 23, 24, 25, and 26). In order to understand the impact of characters showing missing entries on the resulting phylogenetic hypothesis, analyses were conducted that both included and excluded all of those characters. 2 autapomorphic characters (1 and 20) were not included in the computation of the tree statistics.

Phylogenetic analysis was performed using the MS-Windows version of PAUP* 4.0b (Swofford 1998) under the maximum parsimony optimality criterion. The data matrix was analyzed by utilizing heuristic search algorithms with the following settings: addition sequences random; number of replications = 100, tree-bisection-and-reconnection (TBR) branch-swapping performed, MUL Trees option in effect, steepest descent option not in effect, branches having maximum length 0 collapsed to create polytomies, trees unrooted, uninformative characters excluded, and multistate taxa interpreted as polymorphisms. Analyses were unconstrained, and relationships among outgroups were treated as unresolved. The distribution of character states was examined by employing the accelerated transformation (ACCTRAN) optimization in PAUP. A bootstrap analysis was performed with 100 replications using the heuristic search options in PAUP.

Character analysis

1. Anteroventral projection of the ethmoid-vomerine region: (0) slight; (1) marked. When viewed laterally, the ethmoid-vomerine region is somewhat anteroventrally projected in *Discocheilus*, *Discogobio*, and *Placocheilus*, such that the vomer is incorporated with the anterior portion of the parasphenoides to form a short, shallow concavity on the ventral profile of the anterior neurocranium (Fig. 1A); the same state is also present in all selected outgroups. *Garra* possesses a markedly anteroventrally projected ethmoid-

Table 2. Data matrix for ten genera (six of the outgroups and four of the disc-bearing group). 0 = plesiomorphic state, 1 and 2 derived state, and ? = inapplicable state

Taxon	Characters																														
										1										2											3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	
Rectoris	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	1	0		
Pseudocrossocheilus	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	1	0		
Epalzeorhynchos	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	1	0		
Parasinilabeo	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	0	0		
Sinocrossocheilus	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	?	?	1	1	0		
Semilabeo	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	0	1		
Garra	1	1	0	2	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	1	0		
Placocheilus	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0		
Discogobio	0	1	1	2	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	1	1	0		
Discocheilus	0	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	1	2	0	0	1		

vomerine region which forms a long, deep concavity on the ventral profile of the anterior neurocranium (Fig. 1B).

2. Fossa on the ventral surface of the lateral ethmoid: (0) present; (1) absent. According to Howes' (1987) observation, *Labeo* (sensu Reid, 1985) has a lateral ethmoid whose ventral surface bears a fossa that cups an entopterygoid condyle. This type of fossa is variably found in all selected outgroups (Fig. 2A). Howes stated as well that *Garra* has a narrow lateral ethmoid wing, which is connected by a ligament to the entopterygoid. His statement is confirmed in the present study; the fossa on the ventral surface of the lateral ethmoid is lacking in *Discocheilus*, *Discogobio*, and *Placocheilus* as well as *Garra* (Fig. 2B).

3. Broadened anterior portion of the parasphenoides: (0) absent; (1) present. The parasphenoides usually has a lateral ascending wing (articulating with the anteroventral portion of the prootics) that divides it into anterior and posterior portions. In *Discogobio* and *Discocheilus*, the anterior portion of the parasphenoides is broadened and somewhat smaller anteriorly than posteriorly in width (Fig. 3A). This portion is narrow and somewhat enlarged anteriorly in *Placocheilus*, some examined species of *Garra*, and all selected outgroups (Fig. 3B). It is greatly enlarged anteriorly in other examined species of *Garra* (Fig. 3C).

4. Distal end of the pharyngeal process of the basioccipital: (0) pointed; (1) rounded; (2) triangular. Among cyprinid fishes, there is remarkable morphological variation in the shape of the pharyngeal process of the basioccipital, which is putatively believed to be phylogenetically informative (Howes 1981, Chen et al. 1984). In all selected outgroups except *Sinocrossocheilus*, the pharyngeal process is depressed or terete, more or less expanded from the middle of its length to form a broadly rounded distal end (Fig. 4C); the same state is also present in *Placocheilus* (Fig. 4A). This process narrows evenly from 3/4 of its length in *Discocheilus*, *Discogobio*, and *Garra*, therefore resulting in the formation of a triangular distal end (Fig. 4B). In *Sinocrossocheilus*, the pharyngeal process of the basioccipital is elongate and compressed with a pointed distal end, a state also ubiquitously present in the barbine genera (Chen et al. 1984: 432, fig. 3).

5. Ventromedial ridge on the pharyngeal process of the basioccipital: (0) short; (1) long. In the disc-bearing group, the basioccipital has a long ventromedial ridge running nearly along the entire length of the pharyngeal process (Fig. 4A, B). A short ventromedial ridge occurs in all selected out-

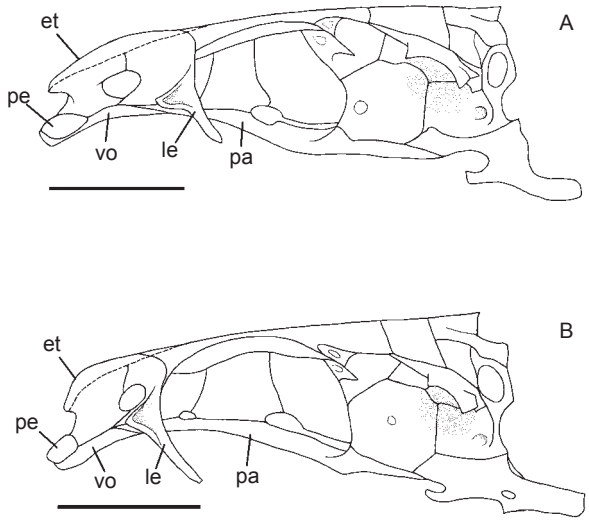

Fig. 1. Lateral view of the neurocranium in (A) *Discogobio longicorpus* and (B) *Garra cambodgiensis*. et, ethmoid; le, lateral ethmoid; pa, parasphenoides; pe, preethmoid; vo, vomer. Scale bar = 5 mm.

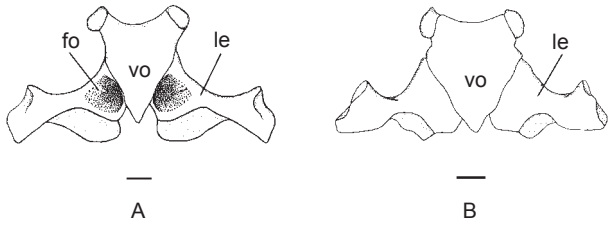

Fig. 2. Ventral view of the ethmoid-vomerine region in (A) *Epalzeorhynchos bicornis* and (B) *Discogobio tetrabarbatus*. fo, fossa on ventral surface of lateral ethmoid; le, lateral ethmoid; vo, vomer. Scale bar = 1 mm.

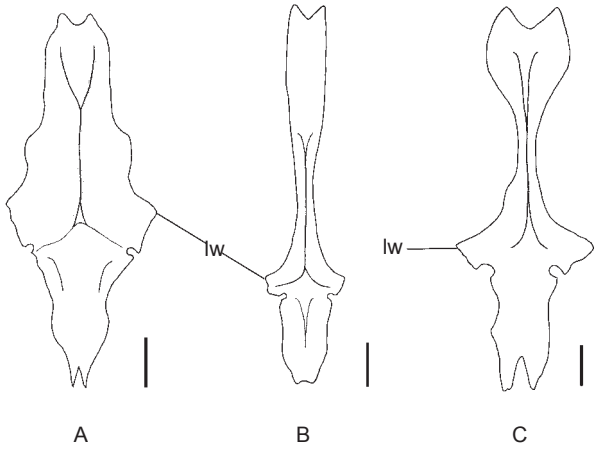

Fig. 3. Ventral view of the parasphenoides in (A) *Discogobio tetrabarbatus*, (B) *Rectoris luxiensis*, and (C) *Garra orientalis*. lw, lateral ascending wing. Scale bar = 1 mm.

groups except *Sinocrossocheilus*, and extends only along the posterior 1/2 of the pharyngeal process (Fig. 4C). This character is inapplicable to *Sinocrossocheilus* as it possesses a basioccipital with a compressed and elongate pharyngeal process, a character not shared with any other genera of the Labeoninae (Chen et al. 1984), and therefore it was coded as a missing entity herein.

6. Ventral masticatory plate of the basioccipital: (0) large; (1) small. In the illustration of the type species of *Garra*, *G. lamta*, by Ramaswami (1955: 17, fig. 9), the basioccipital has a small ventral masticatory plate whose maximal length is less than the length of the pharyngeal process, and the maximal width is less than the corresponding basioccipital width. The same state is also exhibited by all examined Chinese *Garra* species, *Discocheilus*, *Discogobio*, and *Placocheilus* (Fig. 4A, B). The reverse state, however, occurs in all selected outgroups: the ventral masticatory plate of the basioccipital is large, its maximal length is greater than the length of the pharyngeal process, and its maximal width is greater than the corresponding width of the basioccipital (Fig. 4C).

7. Medial portion of the maxilla: (0) shallow and broad; (1) deep and narrow. When viewed ventrally, the maxilla is coarsely L-shaped; its medial portion is wide, and its lateral portion is short and laminar. As found in *Semilabeo*, the maxilla has a deep narrow medial portion in *Discocheilus* (Fig. 5D). This portion is shallow and broad in *Discogobio*, *Garra*, *Placocheilus*, and all selected outgroups except *Semilabeo* (Fig. 5A-C).

8. Broadened ventral edge of the medial portion of the maxilla: (0) slight; (1) marked. In *Discocheilus*, the medial portion of the maxilla has a markedly broadened ventral edge (Fig. 5D), a state also found in *Semilabeo*. This edge is slightly broadened in *Garra*, *Discogobio*, *Placocheilus*, and all selected outgroups except *Semilabeo* (Fig. 5A-C).

9. Ventrolateral process of the medial portion of the maxilla: (0) slight; (1) prominent. In *Discocheilus*, the medial portion of the maxilla has a prominent ventrolateral process (Fig. 5D), to which the *adductor mandibulae* A1 is attached; the same state is present in *Semilabeo* as well. This projection is slight in *Discogobio*, *Garra*, *Placocheilus*, and all selected outgroups except *Semilabeo* (Fig. 5 A-C).

10. Notch on the dorsal margin of the lateral portion of the maxilla: (0) slight or absent; (1) deep. In *Discogobio* and *Discocheilus*, the maxilla has a deep notch on the dorsal margin of its lateral portion, a state also shared with *Epalzeorhynchos*, *Rectoris*, *Parasinilabeo*, and *Pseudocrossocheilus* (Fig. 5B, D). This notch is slight or absent in *Placocheilus*, *Garra*, *Sinocrossocheilus*, and *Semilabeo* (Fig. 5A, C).

11. Triangular flange on the ventral margin of the lateral portion of the maxilla: (0) absent; (1) present. In both *Discogobio* and *Discocheilus*, the maxilla has a conspicuous triangular flange on the

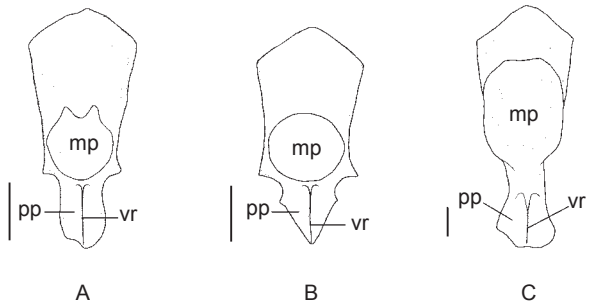

Fig. 4. Ventral view of the basioccipital in (A) *Placocheilus cryptonemus*, (B) *Discocheilus wui*, and (C) *Rectoris luxiensis*. mp, ventral masticatory plate; pp, posterior pharyngeal process; vr, ventromedial ridge. Scale bar = 1 mm.

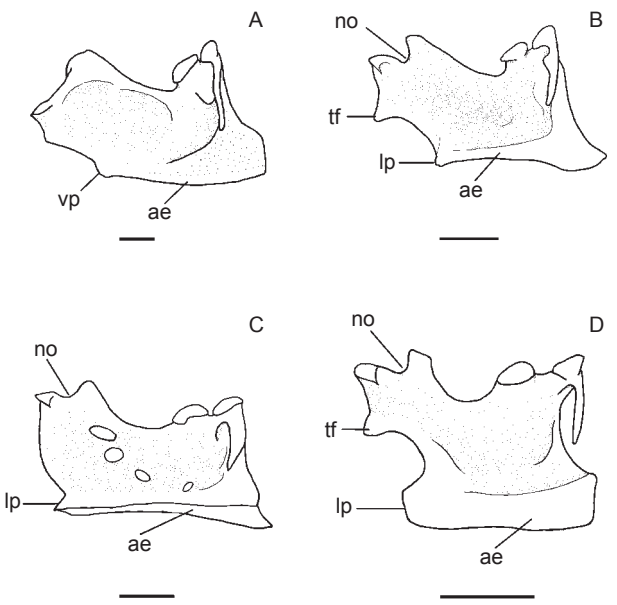

Fig. 5. Ventral view of the maxillae in (A) *Epalzeorhynchos bicornis*, (B) *Discogobio yunnanensis*, (C) *Placocheilus cryptonemus*, and (D) *Discocheilus wui*. no, notch on the dorsal margin of the lateral portion; tf, triangular flange on the ventral margin of the lateral portion; ve, ventral edge of the medial portion; vp, ventrolateral process of the medial portion. Scale bar = 1 mm.

ventral margin of its lateral portion (Fig. 5B, D), just as that found in *Parasinilabeo*. This flange is absent from *Garra* and *Placocheilus* and also from all selected outgroups except *Parasinilabeo* (Fig. 5A, C).

12. Second infraorbital: (0) elongate; (1) square. In all selected outgroups, the 2nd infraorbital is elongate, its length being at least twice its maximal depth (Fig. 6A-C); the same state is present in both *Garra* and *Placocheilus*. This bone is fairly expanded into a square plate in both *Discocheilus* and *Discogobio*, its length being about 1.5 times its maximal depth (Fig. 6D).

13. Third infraorbital: (0) slender; (1) broad. The 3rd infraorbital is slender and slightly expanded medially in *Garra*, *Placocheilus*, and all selected outgroups (Fig. 6A-C). This bone is expanded into a broad plate in both *Discogobio* and *Discocheilus* (Fig. 6D).

14. Posterior margin of the hyomandibular: (0) rounded; (1) triangular. In *Discogobio* and *Discocheilus*, the hyomandibular has a prominent triangular posterior margin (Fig. 7C) instead of a rounded one as in both *Placocheilus* and *Garra* and also in all selected outgroups (Fig. 7A, B).

15. Preoperculum: (0) thin and tall; (1) thick and low. The preoperculum, which approximates a right-angled triangle, is thick and low, and its vertical height is greater than its horizontal width in the disc-bearing group except in *Garra* (Fig. 8C). In *Garra*, the bone is thin and tall, and its vertical height is less than its horizontal width; the same state also occurs in all selected outgroups (Fig. 8A, B).

16. Posterior margin of the vertical plate of the urohyal: (0) truncate; (1) concave. Typically, the urohyal is composed of a ventral horizontal plate and a dorsomedial vertical plate. In the disc-bearing group, the vertical plate of the urohyal has a deep concavity on its posterior margin, resulting in the formation of an elongate and posterodorsally directed process (Fig. 9A). A process of this kind, as figured by Yang and Winterbottom (1998: 61, fig.13a), is exhibited by some species of *Epalzeorhynchos*, but the genus actually has no deep concavity on the posterior margin of the vertical plate of the urohyal. In remaining selected outgroups, the vertical plate of the urohyal has a truncate or slightly concave posterior margin, and its posterodorsal process is short and blunt (Fig. 9B).

17. V-shaped notch on the posterior margin of the horizontal plate of the urohyal: (0) absent; (1) present. In the disc-bearing group, the urohyal possesses a horizontal plate bearing a V-shaped notch medially on its posterior margin (Fig. 9A). In contrast, the horizontal plate of the urohyal has a convex, truncate, or slight concave posterior margin in all selected outgroups (Fig. 9B).

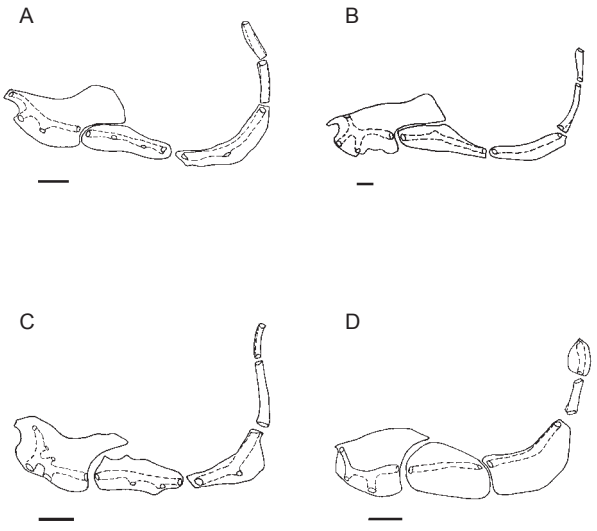

Fig. 6. Lateral view of the infraorbital series in (A) *Rectoris posehensis*, (B) *Semilabeo notabilis*, (C) *Placocheilus cryptonemus*, and (D) *Discocheilus wui*. Scale bar = 1 mm.

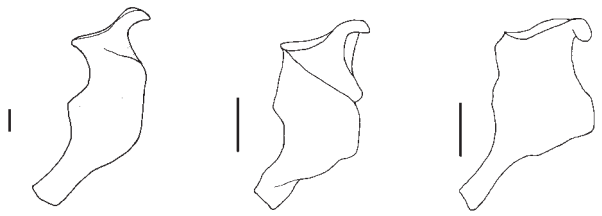

Fig. 7. Lateral view of the hyomandibular in (A) *Semilabeo notabilis*, (B) *Placocheilus cryptonemus*, and (C) *Discocheilus wui*. Scale bar = 1 mm.

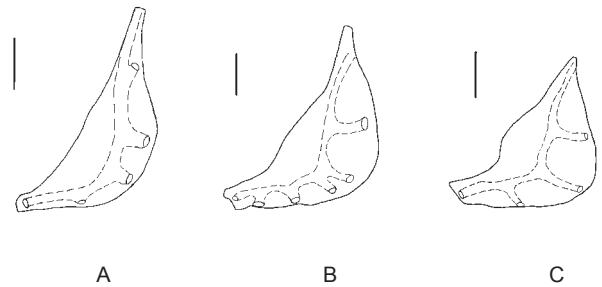

Fig. 8. Lateral view of the preoperculum in (A) *Sinocrossocheilus guizhouensis*; (B) *Rectoris luxiensis*; (C) *Placocheilus cryptonemus*. Scale bar = 1 mm.

18. Rows of pharyngeal teeth: (0) three; (1) two. Rows of pharyngeal teeth are useful indicators of phylogenetic relationships among cyprinid fishes (Wu et al. 1977, Ramaswami 1955). *Garra* shares 3 rows of pharyngeal teeth with all selected outgroups except *Sinocroossocheilus*. Two rows of pharyngeal teeth are found in *Discocheilus*, *Discogobio*, *Placocheilus*, and *Sinocroossocheilus*.

19. Ventrolateral process of the 3rd neural arch: (0) absent; (1) present. The 3rd neural arch has a ventrolateral process which is slightly inclined posteriorly in *Discocheilus*, *Discogobio*, and *Placocheilus* (Fig. 10A, C). This process is absent from *Garra* and also from all selected outgroups (Fig. 10B).

20. Pleural rib of the 4th vertebra: (0) long; (1) short. The pleural rib of the 4th vertebra is short in *Placocheilus*, and its length is less than the height of the 4th neural arch plus its spine (Fig.10C). This pleural rib is long in *Discocheilus*, *Discogobio*, and *Garra*, and its length is greater than the height of the 4th neural arch plus its spine (Fig.10A, B); the same state is also found in all selected outgroups.

21. Anterodorsal process of the pleural rib of the 4th vertebra: (0) absent; (0) present. The pleural rib of the 4th vertebra has an anterodorsal process in *Discocheilus*, *Discogobio*, and *Placocheilus* (Fig. 10A, C). This process is absent from *Garra* (Fig. 10B) and also in all selected outgroups.

22. Mental adhesive disc: (0) absent; (1) present. *Discogobio*, *Discocheilus*, *Garra*, and *Placocheilus* are unique within the Labeoninae in that the lower lip is modified into a mental adhesive disc whose posterior margin is discontinuous with the mental region (Fig. 11A-C). The mental adhesive disc of this kind does not occur in any of the selected outgroups. Despite *Sinocrossocheilus* having a suctorial lower lip whose central portion protrudes to form a round and fleshy pad (Fig. 11D), the structure is posteriorly continuous with the mental region.

23. Anteromedian fold of the mental adhesive disc: (0) crescentic; (1) horseshoe-shaped. The

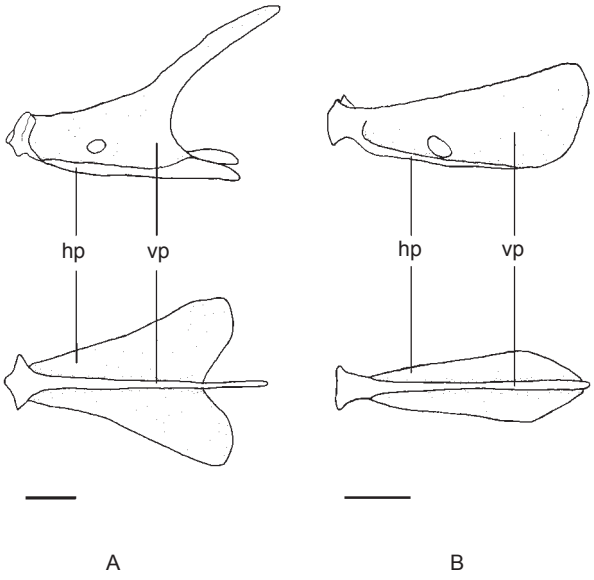

Fig. 9. Lateral (upper) and dorsal (bottom) views of the urohyal in (A) *Garra orientalis* and (B) *Rectoris luxiensis*. hp, horizontal plate; vp, vertical plate. Scale bar = 1 mm.

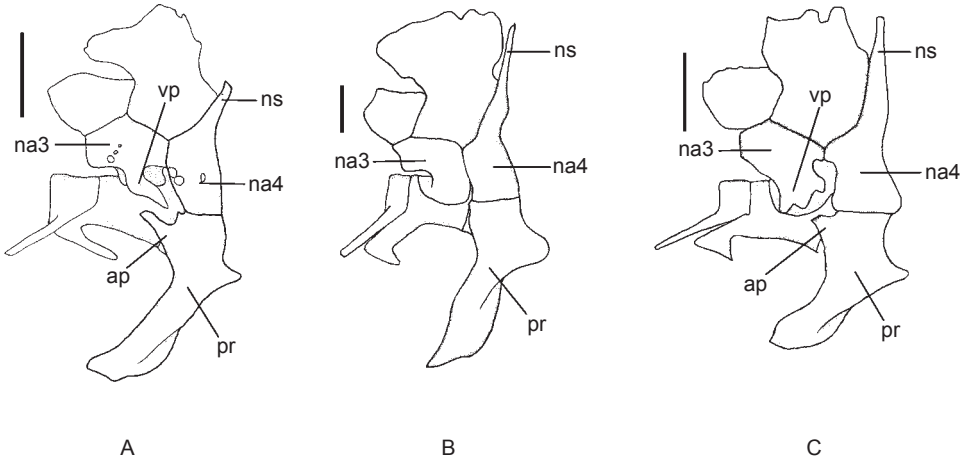

Fig. 10. Lateral view of the Weberian apparatus in (A) *Discocheilus wui*, (B) *Garra orientalis*, and (C) *Placocheilus caudofasciatus*. ap, anterodorsal process of the 4th pleural rib; na3, 3rd neural arch; na4, 4th neural arch; ns, 4th neural spine; pr, 4th pleural rib; vp, ventrolateral process of the 2nd neural arch. Scale bar = 1 mm.

mental adhesive disc is a soft-tissue complex that is usually composed of an anteromedian fold, an anterolateral lobe, a central callous pad, and a lateroposterior flap (Zhang et al. 2002). In *Discogobio*, the anteromedian fold is a horseshoe-shaped structure surrounding the central callous pad anteriorly and laterally (Fig. 11B). It is crescentic in *Discocheilus*, *Placocheilus*, and *Garra* (Fig.11A, C). This character is not found in any of the selected outgroups and was thus coded as a missing entity herein.

24. Central callous pad of the mental adhesive disc: (0) small; (1) large. In both *Garra* and *Placocheilus*, the mental adhesive disc has a large central callous pad, which is wider than 1/2 the disc width (Fig.11A). A small central callous pad is found in *Discogobio* and *Discocheilus*, and its width is less than 1/2 the disc width (Fig.11B, C). This character is not found in any of the selected outgroups, and was thus coded as a missing entity herein.

25. Overlap between the central callous pad and the antermedian fold of mental adhesive disc: (0) absent; (1) present. The mental adhesive disc has a central callous pad which anteriorly overlaps with the anteromedian fold in *Discocheilus* (Fig. 11C). This overlap does not occur in *Discogobio*, *Garra*, or *Placocheilus*, all of which have a central callous pad bordered in a groove with the anteromedian fold anteriorly or anterolaterally (Fig. 11A, B). This character is absent from all selected outgroups and was therefore coded as a missing entity herein.

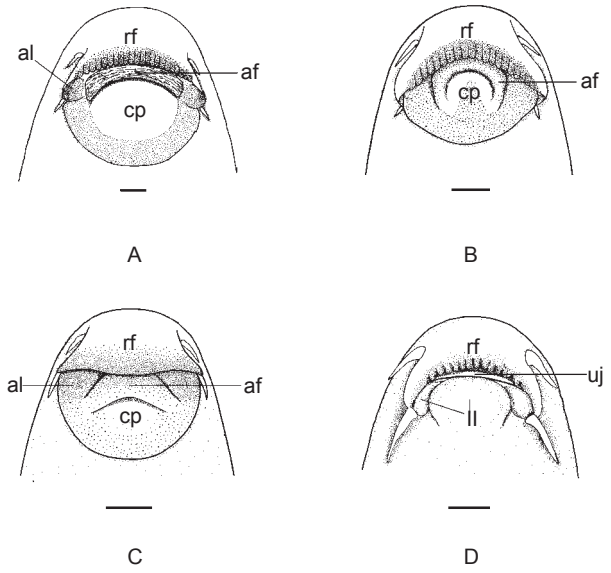

Fig. 11. Ventral view of oromandibular structures in (A) *Garra imbera*, (B) *Discogobio tetrabarbatus*, (C) *Discocheilus wui*, and (D) *Sinocrossocheilus guizhouensis*. af, anteromedian fold of the mental adhesive disc; al, anterolateral lobe of the mental adhesive disc; cp, central callous pad of the mental adhesive disc; ll, lower lip; rf, rostral fold; uj, upper jaw. Scale bar = 4 mm.

26. Anterolateral lobe of the mental adhesive disc: (0) absent; (1) small and oval; (2) large and triangular. The mental adhesive disc has a large triangular anterolateral lobe fully covered by tiny papillae in *Discocheilus* (Fig. 11C). The anterolateral lobe is small and oval in both *Garra* and *Placocheilus* (Fig. 11A), but it is absent from *Discogobio* (Fig. 11B). This character was coded as a missing entity for all selected outgroups as they lack this kind of anterolateral lobe.

27. Distal margin of the rostral fold: (0) non-crenulated; (1) crenulated. In *Discocheilus*, the rostral fold has a non-crenulated distal margin, just as that found in both *Parasinilabeo* and *Semilabeo* (Fig. 11C). A crenulated distal margin occurs in *Discogobio*, *Garra*, and *Placocheilus*, and the same state also occurs in *Epalzeorhynchos*, *Pseudocrossocheilus*, *Rectoris*, and *Sinocrossocheilus* (Fig. 11A, B, D).

28. Anterior margin of the lower lip/horny sheath on the lower jaw: (0) continuous; (1) discontinuous. The lower jaw of *Discocheilus* is separated from the lower lip and has a sharp horny sheath edge continuous with the anterior margin of the lower lip (or anteromedian fold); the same state is also found in *Parasinilabeo* and *Semilabeo*. This continuity does not occur in *Discogobio*, *Placocheilus*, *Garra*, *Epalzeorhynchos*, *Pseudocrossocheilus*, *Rectoris*, or *Sinocrossocheilus*; the horny sheath on the lower jaw is separated from the anterior margin of the lower lip (or anteromedian fold) by a groove running along the entire lower jaw.

29. Mouth opening: (0) wide; (1) narrow. *Discocheilus* has a narrow mouth opening, less than 1/2 the head width, just as in *Semilabeo*, whereas the mouth opening is wider than 3/4 of the head width in *Discogobio*, *Placocheilus*, and *Garra*; the same state is also exemplified by all selected outgroups except *Semilabeo*.

RESULTS

The data matrix for the 6 selected outgroups and 4 genera of the disc-bearing group is shown in table 2. When *Epalzeorhynchos*, *Parasinilabeo*, *Sinocrossocheilus*, *Pseudocrossocheilus*, *Rectoris*,

and *Semilabeo* were used as a composite outgroup, parsimony analysis of the matrix generated 3 most-parsimonious trees with a tree length of 40, a consistency index (CI) of 0.725, a homoplasy index (HI) of 0.275, a CI excluding uninformative characters of 0.694, an HI excluding uninformative characters of 0.306, a retention index (RI) of 0.766, and a rescaled consistency index (RC) of 0.555. The topologies of the disc-bearing group in these 3 trees are consistent; the strict consensus tree is shown in figure 12. Bootstrap values obtained from 100 replicates are shown in figure 13. The tree topology of the disc-bearing group shown in figure 12 remained constant if the data matrix was performed with exclusion of the mental adhesive disc and pharyngeal teeth (characters 18 and 22), on which the previously hypothesized relationships of the disc-bearing group were based. The same tree topology of the disc-bearing group was also found if the characters (5, 23, 24, 25, and 26) represented in the data matrix by missing entries were excluded, indicating that these characters had no impact on the resultant phylogenetic hypothesis of the group. All findings showed that the disc-bearing group constitutes a monophyletic clade, in which the basal lineage is *Garra*, with *Placocheilus* forming a subclade with the sister pairs *Discogobio* and *Discocheilus*. This corroborates Zhang et al.'s (2000) assertions that the 4 genera of the disc-bearing group are more closely allied with each other than with other cyprinid genera and that *Placocheilus* is closely related to both *Discochelus* and *Discogobio* because they have 2 rows of pharyngeal teeth, with *Garra* distantly associated.

Disc-bearing group. This group being a monophyletic clade was significantly supported with 95% bootstrap values by 7 synapomorphic characters of no fossa on the ventral surface of the lateral ethmoid (2:1), a triangular distal end of the pharyngeal process of the basioccipital (4:2), a long ventromedial ridge extending almost along the entire length of the pharyngeal process of the basioccipital (5:1), a small ventral masticatory plate of the basioccipital (6:1), a concave posterior margin of the horizontal plate of the urohyal (16:1), a V-shaped medial notch on the posterior margin of the horizontal plate of the urohyal (17:1), and a mental adhesive disc (22:1), and by 1 homoplastic character of no or only a slight notch on the dorsal margin of the lateral portion of the maxilla (10:0).

Garra. The examined Chinese species of *Garra* formed a monophyletic lineage supported by only 1 autapomorphic character of a markedly anteroventrally projected ethmoid-vomerine region (1:1).

Placocheilus + *Discogobio* + *Discocheilus*. This subclade was well supported with 86% bootstrap values by 3 synapomorphic characters of a thick low preoperculum (15:1), a ventrolateral process of the 3rd neural arch (19:1), and an anterodorsal process of the pleural rib of the 4th

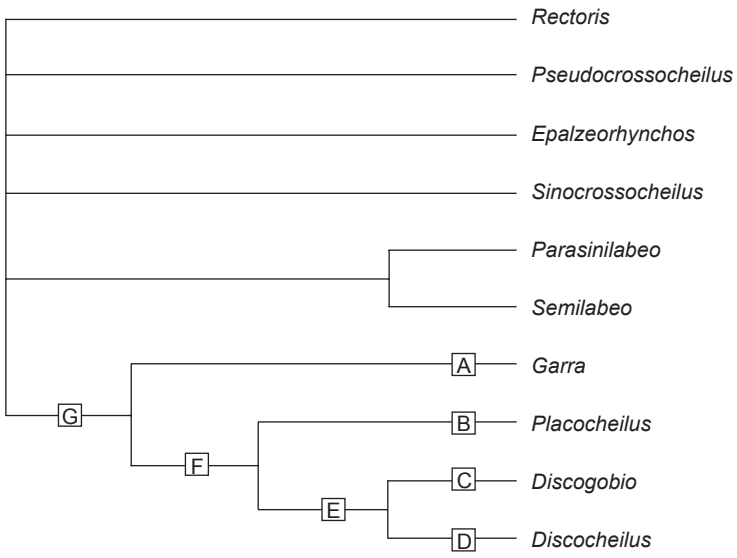

Fig. 12. Strict consensus of the 3 most-parsimonious trees resulting from analysis of the data matrix shown in table 2. Letters refer to the following character state transformations (ACCTRAN optimization): A, **1:1**; B, 4:1 and **20:1**; C, **23:1**; D, 7:1, 8:1, 9:1, **25:1, 26:2**, 27:0, 28:0, and 29:1; E, **3:1**, 10:1, 11:1, **12:1, 13:1, 14:1, 24:0**, and **26:0**; F, **15:1**, 18:1, **19:1**, and **21:1**; G, **2:1**, 4:2, **5:1**, **6:1**, 10:0, **16:1**, **17:1**, and **22:1** (Boldface type indicates synapomorphic or non-homoplastic characters).

vertebra (21:1), and 1 homoplastic character of 2 rows of pharyngeal teeth (18:1).

Placocheilus. This genus was diagnosed by 1 autapomorphic character of a shorter pleural rib of the 4th vertebra than the height of the 4th neural arch plus its spine (20:1), and 1 homoplastic character of a broadly rounded distal end of the pharyngeal process of the basioccipital (4:1).

Discogobio + *Discocheilus*. The sister pairs were significantly supported with 99% bootstrap values by 6 synapomorphic characters of a broadened anterior portion of the parasphenoides (3:1), a square 2nd infraorbital (12:1), a broad 3rd infraorbital (13:1), a triangular posterior margin of the hyomandibular (14:1), a small central callous pad on the mental adhesive disc (24:0), and a small oval anterolateral lobe of the mental adhesive disc (26:0), and by 2 homoplastic characters of a deep notch on the dorsal margin of the lateral portion of the maxilla (10:1) and a prominent triangular flange on the ventral margin of the lateral portion of the maxilla (11:1).

Discogobio. The examined Chinese species of *Discogobio* formed a monophyletic lineage supported by 1 autapomorphic character of a horseshoe-shaped anteromedian fold on the mental adhesive disc (23:1).

Discocheilus. This genus was diagnosed by 2 autapomorphic characters of an anteromedian fold of the mental adhesive disc that extends posteriorly to overlap with the anterior margin of the central callous pad (25:1), and a large triangular anterolateral lobe on the mental adhesive disc (26:2). It is also supported by 6 homoplastic characters of a deep narrow medial portion of the maxilla (7:1), a greatly broadened ventral edge of the medial portion of the maxilla (8:1), a conspicuous ventrolateral process of the medial portion of the maxilla (9:1), a non-crenulated distal margin of the rostral fold (27:0), a horny sheath on the lower jaw continuous with the anteromedian fold (or anterior margin) of the lower lip (28:0), and a narrow mouth opening (29:1).

DISCUSSION

This is the 1st attempt to assess phylogenetic relationships specifically among the disc-bearing group predicated on morphological characters scored from first-hand observations of the 23 Chinese species. The examined material includes all species of *Discogobio* except *G*. *microstoma*, all species of *Discocheilus* and *Placocheilus*, and the majority of Chinese species of *Garra*. Information provided in the present study, incorporated with conclusions reached in the known literature, makes it possible to provide brief comments on the validity of each genus of the disc-bearing group.

Placocheilus was erected by Wu et al. (1977) for *Discognathus caudofasciatus* Pellegrin and Chevey, 1936 from the Red River basin in China. Its generic status is currently widely accepted by Chinese workers (Chu and Cui 1989, Zhu 1995, Zhang et al. 2000) and also by Eschmeyer (1998). *Placocheilus* is morphologically very similar to

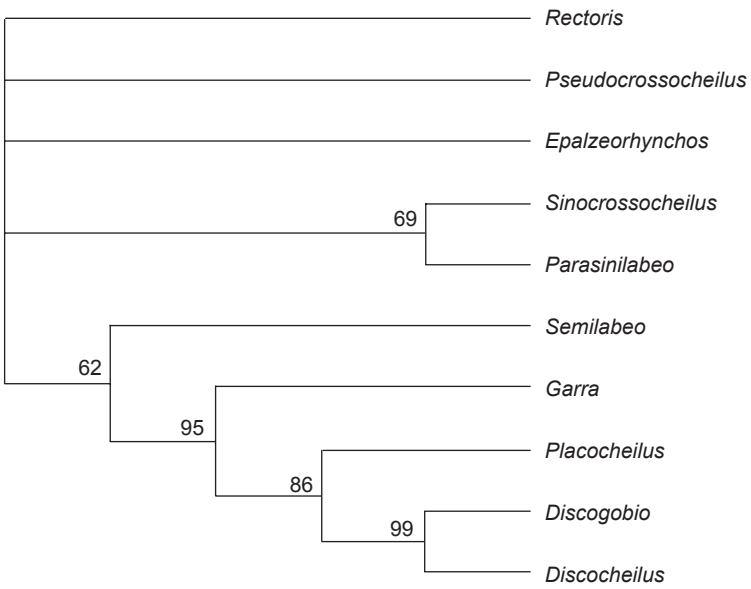

Fig. 13. 50% majority-rule consensus tree with bootstrap values after 100 replicates.

Garra, but differs from it in having 2 (vs. 3) rows of pharyngeal teeth. The validity of *Placocheilus* was recently doubted by Kottelat (2001a), who held that there is no distinct difference between *Placocheilus* and *Garra* with the exception of the number of rows of pharyngeal teeth, and that the loss of 1 row of pharyngeal teeth is a reductive character that is uninformative to diagnose the evolutionary lineages (genera). Kottelat's conclusion is only based on the external morphological characters, though. It is perfectly true that *Garra* shares several characters of the oromandibular structures with *Placocheilus*, e.g., a rostral fold with a crenulated distal margin, a mental adhesive disc having a large central callous pad, and a crescentic anteromedian fold. The phylogenetic hypothesis based on the osteological and external morphological characters in the present study showed that *Placocheilus* clustered with the sister pair of *Discogobio* and *Discochelus* as a subclade which was supported by 3 synapomorphic characters (15:1, 19:1, and 21:1) and 1 homoplastic character (18:1) and that it is a monophyletic lineage supported by 1 synapomorphic character (20:1) and 1 homoplastic character (4:1). Accordingly, *Placocheilus* should be treated as a valid cyprinid genus distinct from *Garra*.

The generic status of *Discocheilus* was confirmed in the present study. This genus was originally described by Chen and Lan (1992) as *Disocolabeo*, a monotypic genus consisting of a single species, *D. wui*. In the original description, *Disococheilus* has a mental adhesive disc which it shares with *Discogobio*, *Garra*, and *Placocheilus*, and 2 rows of pharyngeal teeth which it shares with *Discogobio* and *Placocheilus*. But it is uniquely characterized by the presence of a mental adhesive disc with a crescentic anteromedian fold which is flattened, thickened, and extended posteriorly to overlap with the anterior margin of the central callous pad. Zhang (1997) found that the name *Discolabeo* was preoccupied; it was used by Fowler (1937) for *Discolabeo fisheri*, a new species from the Tachin River, Thailand. The species was subsequently shown by Rainboth (1996) to be a member of *Garra*, an opinion also shared by Robert (1989). It was synonymized by Kottelat (1998) with *Garra fulignosa* Fowler, 1934. In reality, *Discolabeo* Chen and Lan, 1992 is a homonym of *Discolabeo* Fowler, 1937 which is a synonym of *Garra*. So a new replacement name *Discocheilus* was proposed by Zhang (1997) for *Discolabeo* Chen and Lan, 1992. The hypothesized phylogenetic relationship in the present study revealed that *Discocheilus* is sister to *Discogobio*, that both are grouped by 6 synapomorphic characters (3:1, 12:1, 13:1, 14:1, 24:0, and 26:0) and 2 homoplastic characters (10:1 and 11:1), and that it itself is a monophyletic lineage supported by 2 autapomorphic characters (25:1 and 26:2) and 6 homoplastic characters (7:1, 8:1, 9:1, 27:0, 28:0, and 29:1). All findings show that *Discocheilus* should be a distinct cyprinid genus as well.

Discogobio was proposed by Lin (1931), with *D. tetrabartatus* employed as the type species. It is separated from *Garra* in having 2 rows of pharyngeal teeth and a horseshoe-shaped anteromedian fold on the mental adhesive disc. *Discogobio* was historically confused with *Garra*, though. Menon (1964) placed *Discognathus yunnanensis* Regan, 1907, a species currently placed in *Discogobio*, in *Garra*. Also, Mai (1978) made no discrimination between *Discogobio* and *Garra*, misidentifying the Red River basin material as *Garra microstoma*, which was confirmed by Kottelat (2001a) to be a species of *Discogobio*. This is perhaps attributed to the fact that Mai had no access to what had been done by contemporaneous Chinese authors. The proposed phylogenetic relationship in the present study showed that *Discogobio* is sister to *Discocheilus*, both being united by 6 synapomorphic characters (3:1, 12:2, 13:1, 4:1, 24:0, and 26:0) and 2 homoplastic characters (10:1 and 11:1) and that it itself is a monophyletic lineage supported by 1 autapomorphic character (23:1). Apparently, *Discogobio* is in fact a valid genus separate from *Garra*.

The examined Chinese *Garra* species form a monophyletic lineage supported merely by 1 autapomorphic character (1:1, a marked anteroventrally projected ethmoid-vomerine region) in the present study. This does not corroborate Getahun's (1999) conclusion mainly based on an examination of African species, that the monophyly of *Garra* is supported by 3 synapomorphic characters: (1) a short broad ethmoid, (2) an elongated narrow cleithrum, and (3) 2 or more anterior unbranched pectoral-fin rays. None of those were found herein to be shared by the examined Chinese *Garra* species. The incongruence is not surprising, given that *Garra* is a speciose fish group which consists of roughly 78 species known widely from tropical Africa and Asia (pers. obs.), but limited materials have been examined in their respective studies. Also, it is highly likely that *Garra*, as currently known, is a composite group representing many distinct under-

described taxa. Since no African *Garra* species were included in the present study, it is impossible to address this problem in-depth. Apparently, the monophyly and validity of *Garra* need to be further investigated on the basis of an examination of additional species of the genus, especially those from South Asia, the Arabian Peninsula, the Middle East, and Africa.

Acknowledgments: I especially thank 2 anonymous reviewers for their comments on and good suggestions for the original manuscript. This research was supported by a grant (KZCX-SW-126) from the Innovation Program of the Chinese Academy of Sciences.

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Appendix:

Materials Examined

The species name is followed by the institutional catalog number, the number of specimens, and standard length (mm) of examined specimens, and locality data. Specimens that are cleared and double-stained for cartilage and bone are indicated as (CS) in parentheses following the catalog number. Institutional abbreviations are as follows: IHB, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan; KIZ, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming; and YU, Yunnan Univ., Kunming, China.

Outgroups

Epalzeorhynochos – *E. bicornis*, IHB 81X4343, 81X4342 (CS), 80IV0098, 80IV0181, 80IV0183, 5 ex., 122.0~153.0 mm SL, Baoshan, Yunnan.

Parasinilabeo – *P. assimilis*: IHB 75IV2647 (CS), 75IV626-27, 75IV29-32, 7 ex., 78.0~93.0 mm SL, Lijiang, Guangxi.

Pseudocrossocheilus – *P. bamaensis*: IHB 8510088 (CS), 1 ex., 87.0 mm SL, Du'an, Guangxi; IHB 743119, 743136, 73422, 76092, 4 ex., 100.0~108.0 mm SL, Bama, Guangxi. *P. liuchengensis*: IHB 82VII1526 (CS), 82VII1521~23, 82VII1528, 5 ex., 68.0~81.0 mm SL, Liucheng, Guangxi.

Rectoris – *R. luxiensis*: IHB 87IV0034 (CS), 87IV0023, 87IV0032, 87IV0018, 87IV0020, 5 ex., 94.0~135.1 mm SL, Dachang, Sichuan. *R. posehensis*: IHB 75IV1068~73, 81XII0281, 7 ex., 94.5~153.4 mm SL, Longzhou, Guangxi; IHB 85051820 (CS), 1 ex., 81.4 mm SL, Baiwang, Guangxi.

Sinocrossocheilus – *S. guizhouensis*: IHB 6650420, 6650510, 6650411, 6650415~16, 6650503~05, 6650417 (CS), 6650508, 10 ex., 53.0~76.0 mm SL, Zhunyi, Guizhou. *S. microstomatus*: IHB 87IV510, 87IV506~7, 87IV509, 4 ex., 78.1~83.2 mm SL, Libo, Guizhou.

Semilabeo – *S. notabilis*: IHB 75IV1058 (CS), 75IV1050, 81XII0204, 81XII 0281, 4 ex., 101.9~144.1 mm SL, Longzhou, Guangxi.

Ingroups

Garra – *G. cambodgiensis*: IHB 742813 (CS), 78V0548, 78V0295~6, 78V0386 (CS), 78V0472~3, 78V02531, 8 ex., 55.1~97.5 mm SL, Xishuang-banna, Yunnan. *G. imbera*: IHB 82V0343 (CS), 82V0346~8, 82V0350, 5 ex., 64.0~133.5 mm SL, Dechang,

Sichuan. *G. kempi*: IHB 74VII2124~5, 74IVII2126 (CS), 3 ex., 56.0~72.0 mm SL, Motuo, Tibet; IHB 73VII0300, 73VII0169~70, 75VII0063~6, 73VII0284, 73VII0135, 8 ex., 58.3~87.0 mm SL; Chayu, Tibet. *G. mirofrontis*: IHB 78IV0528, 78IV0389, 78IV0047, 78IV0388, 4 ex., 40.2~97.4 mm SL, Menghan, Yunnan; uncataloged (CS), 80.5 mm SL, Jinghong, Yunnan. *G. orientalis*: IHB 660755, 660753 (CS), 660757, 660841, 6600844, 5 ex., 69.7~100.2 mm SL, Yangshan, Guangdong. *G. salweenica*: IHB 78IV1546, 78IV1549, 78IV1541, 78IV1536, 78IV1521, 90IV0119, 90IV291, 90IV0121, 90IV288~9, 10 ex., 94.0~174.4 mm SL, Tengchong, Yunnan. *G. hainanensis*: IHB 76V9068, 76V9063 (CS), 76V9062, 76V9064, 76V9070, 5 ex., 100.5~123.0 mm SL, Qiongzhong, Hainan. *G. qiaojienesis*: IHB 60542, 78IV1051~2, 90IV0076~8, 90IV0998 (CS), 78IV1052, 8 ex. 92.3~162.4 mm SL, Tengchong, Yunnan. *G. tengchongensis*: IHB 900189, 9001242~3, 900184 (CS), 90IV0237~43, 11 ex., 53.0~83.2 mm SL, Tengchong, Yunnan.

Discogobio – *D. bismargairtus*: KIZ 776563, 776579, 776568, 776587, 776582, 5 ex., 58.0~108.0 mm SL, Guangnan, Yunnan; IHB 83IV1362-5, 83IV1369~71, 83IV1359 (CS), 8 ex., 85.0~118.0 mm SL, Huangguoshu, Guizhou. *D. branchyphysalloides*: KIZ 775784~5, 775795~6, 7757801, 5 ex., 102.5~132.0 mm, Luoping, Yunnan; IHB 87IV201~2, 87IV197~8, 87IV1998 (CS), 5 ex., 68.3~96.8 mm SL, Kaiyang, Guizhou. *D. elongates*: IHB 8810067~9, 8810081 (CS), 8810088~9, 8810097, 82100253, 82100286, 9 ex., 68.5~98.0 mm, Xuanwei, Yunnan. *D. laticeps*: IHB 87IV733 (CS), 87IV727, 87IV730~1, 87IV736~7, 6 ex., 102.0~141.0 mm SL, Sandu, Guizhou. *D. longibarbatus*: IHB 76XI068, 76XI029, 636548, 636501~2, 5 ex., 65.0~105.0 mm SL, Lake Fuxian, Yunnan. *D. macrophysalliodes*: KIZ 88111077~9, 88111073, 4 ex., 87.0~105.5 mm SL, Xingyi, Guizhou; IHB 6507136 (CS), 65071367, 2 ex. 78.0~80.0 mm SL, Nanjiang, Yunnan; IHB 504015~6, 2 ex., 87.0~105.5 mm, Kunming, Yunnan, *D. multilineatus*: uncataloged, 8 ex., 56.2~75.2 mm SL, of which 1 specimen (CS) attained 68.7 mm SL, Bama, Guangxi. *D. tetrebarbatus*: IHB 75IV2036~7, 75IV2032, 75IV2326~7, 75IV2034, 83V0154, 7 ex., 65.0~95.0 mm SL, Guiling, Guangxi; IHB 86082138 (CS), 80.0 mm SL, Du'an, Guangxi. *D. yunnanensis*: IHB 87VII0667, 87VII0 549 (CS), 87VII 0649, 87VII0 671, 87VII0558 (CS), 87VII 0647, 87VII 0562, 87VII0 683, 87VII0661, 9 ex., 81.6~143.0 mm SL, Xinshan, Hubei.

Discocheilus – *D. multilepis*: IHB 8950001, 8950006 (CS), 8950228, 3 ex., 31.2~99.1 mm SL, Congjiang, Guizhou. *D. wui*: IHB 89XII0023, 89XII0008, 89XII0010, 89XII 0012 (CS), 89XII0003 (CS), 5 ex., 60.5~66.8 mm SL, Donglan, Guangxi; IHB 85VIII068~70, 3 ex., 36.5~44.5 mm SL, Tian'e, Guangxi.

Placocheilus – *P. caudofasciatus*: IHB 20005972 (CS), 20005352~56, 20005985~86, 20005358~60, 11 ex., 49.1~87.3 mm SL, Jingping, Yunnan. *P. cryptonemus*: IHB 81X4311~2, 81X4329 (CS), 81X4303, 81X4308, 5 ex., 79.0~112.0 mm SL, Liuku Yunnan. *P. robustus*: IHB 601128~34, 7 ex., 48.6~109.1 mm SL, Yuanjiang, Yunnan. YU 60253, 60227, 60209, 60205-6, 60201, 60219, 60223~4, 8340525, 10 ex., 53.1~117.4 mm SL, Honghe Yunnan; IHB 81122080 (CS), Xinping, Yunnan.