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PHYLOGENY AND ZOOGEOGRAPHY OF THE CYPRINID GENUS *Spinibarbus* (Pisces: Cyprinidae)

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Abstract The cyprinid genus *Spinibarbus* consists of 5 species. They form into a monophyly by three synapomorphies. Based on 19 external and skeletal characters, the most parsimonious cladogram is constructed for *Spinibarbus* fishes. Sister groups A (*S. hollandi*) and B–E (*S. sinensis* + *S. denticulatus* + *S. yunnanensis* + *S. polylepis*) represent the first phyletic branching within the genus *Spinibarbus*. The phyletic division of second sister groups B (*S. sinensis*) and C–E (*S. denticulatus* + *S. yunnanensis* + *S. polylepis*) is supposed to be resulted from the upheaval of Yunnan–Guizhou Plateau and the subsequent drainages' division. The phyletic division of third sister groups C (*S. denticulatus*) and D–E (*S. yunnanensis* + *S. polylepis*) is supposed to be resulted from the environmental differentiation between Yunnan–Guizhou Plateau and the lowlands of middle and lower Pearl and Yuanjiang Rivers.

Key words Phylogeny, Zoogeography, *Spinibarbus*

1 Introduction

The cyprinid genus *Spinibarbus* of the subfamily Barbinae consists of 5 species. They can be easily distinguished from any other barbid fishes by having a precumbent predorsal spine, 5 branched anal fin rays, a simple lower lip without any mental lobe. They occur in southern China (including Taiwan and Hainan Islands) as well as northern Vietnam.

The first species of *Spinibarbus* was reported by Bleeker (1871) in the nomenclature ***Puntius (Barbodes) sinensis*** Bleeker from Yangtze River. Henceforth, 8 specific nomenclatures which are now placed in the genus *Spinibarbus* have been reported, they are: *Spinibarbus hollandi* Oshima (1919), *Spinibarbus elongatus* Oshima (1920), *Spinibarbus nigrodorsalis* Oshima (1926), *Barbus caldwelli* Nichols (1925), *Spinibarbichthys*

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denticulatus Oshima (1926), *Barbus (Spinibarbichthys) pingi* Tchang(1931), *Barbodes (Spinibarbus) denticulatus yunnanensis* Tsu (Wu *et al.*, 1977) and *Spinibarbus denticulatus polylepis* Chu (Zheng, 1989). First revision of the *Spinibarbus* fishes was made by Wu *et al.* (1977), 5 species and subspecies were recognized valid. Henceforth, some previously reported species of *Spinibarbus* have been recorded repeatedly from provinces of southern China (Fang, in Guangxi Institute of Fisheries *et al.*, 1981; Shaanxi Institute of Zoololgy *et al.*, 1987; Zhujiang Institute of Fisheries *et al.*, 1986, 1991 ; Chu *et al.*, 1989; Zheng, 1989). Recently the genus was systematically revised by us (Yang *et al.*, in press) and 5 species were considered valid, they are: *S. hollandi*, *S. sinensis*, *S. denticulatus*, *S. yunnanensis*, *S. polylepis*.

About the generic status, some different opinions have been proposed for *Spinibarbus* fishes. Oshima (1926) created the genus *Spinibarbus* by the type species *Spinibarbichthys denticulatus* Oshima (= *Spinibarbus denticulatus*). *Spinibarbichthys* is exactly the synonym of *Spinibarbus* (Chu, in Zheng, 1989; Chu *et al.* , 1989). Wu *et al.* (1977) considered *Spinibarbus* as a subgenus of *Barbodes*. Some previously reported species were placed in *Barbus* (Nichols, 1925; Nichols *et al.*, 1927; Tchang, 1931), *Puntius* (Bleeker, 1871), *Mystacoleucus* (Wu *et al.*, 1931) or *Matsya* (Hora, 1937; Chang, 1944). These disagreements on the generic status is resulted mainly from the poor knowledge about the phylogeny of *Spinibarbus* fishes.

All of the previous studies are focused on classification of the genus *Spinibarbus*. No attempts have been made to study its phylogeny. Therefore the present paper is focused on studying the phylogyeny and zoogeography of *Spinibarbus* fishes.

2 Materials and Methods

All specimens examined belong to the collections of Kunming Institute of Zoology, Academia Sinica (KIZ). Skeletal specimens were prepared by the method of Dingerkus and Uhler (1977). The genus *Barbodes* is considered as the outgroup of *Spinibarbus* because it shares a close relationship with and is more primitive than the genus *Spinibarbus* (Wu *et al.*, 1977). Counts of vertebrae are illustrated in Fig. 1. The vertebra beneath 1st pterygiophore of dorsal fin is named here as 1st DA (between dorsal and anal fins) vertebra and the one above 1st pterygiophore of anal fin the 1st caudal vertebra. Those vertebrae set before 1st pterygiophore of dosal fin are counted here as predorsal vertebrae (Pv) and those set from 1st pterygiophore of anal fin to caudal fin base as caudal vertebrae (Cv). Those set between the last predorsal vertebra and 1st caudal vertebra are recognized here as DA vertebrae (DA). Other abbreviations used in this paper are as following: Nc, neural complex; Ns4, 4th neural spine; P, posttemperal; Pa4, parapophysis of 4th vertebra; Ps, precumbent predorsal spine; Pt, pterygiophore; S, squamosal; Sc, supracleithrum; Sn, supraneural.

The following cleared and stained skeletal specimens have been prepared: *Barbodes* *huangchuchieni* (Tchang): KIZ734085(Menghan of Yunnan); *B. verayi* (Norman): KIZ736081 (Manzhe of Yunnan); *B. wynaadensis* (Day): KIZ8110101 (Daojie of Baoshan, Yunnan); *B. hexagonolepis* (McClelland): KIZ7801063 (Yingjiang of Yunnan); *Spinibarbus hollandi* Oshima: KIZ8811396, 8811397 (Guanling of Guizhou); *S. sinensis* (Bleeker): KIZ79304, 79305 (Chenghai Lake of Yunnan); *S. denticulatus* (Oshima): KIZ6440017, 6440349 , 6440355 (Hekou of Yunnan); *S. yunnanensis* Tsu: KIZ892067-892069 (Fuxian Lake of Yunnan); *S. polylepis* Chu: KIZ775400 (Luxi of Yunnan), 8811122 (Xingyi of Guizhou).

3 Character Analysis of the Genus *Spinibarbus*

The genus *Spinibarbus* consists of 5 species. They form into a monophyletic lineage by three synapomorphies: (a) disappearance of last supraneural from above the last predorsal vertebra; (b) a strong and tall 4th neural spine; (c) presence of a precumbent predorsal spine at dorsal fin origin. These synapomorphies and some 16 interspecific characters are described and discussed in detail as following.

3.1 Disappearance of last supraneural from above the last predorsal vertebra. A supraneural is a laminar bone set above each of predorsal vertebra and between neural spines. In *Spinibarbus*, the supraneurals are very developed with a triangular form from lateral view. In all species of *Spinibarbus*, the last supraneural is disappeared from above the last predorsal vertebra (Fig. 1; Fig. 2b, c). By contrast, the last supraneural is present above the last predorsal vertebra (Fig. 2a) in *Barbodes*. Outgroup comparison indicates that the disappearance of last supraneural is a synapomorphy of *Spinibarbus* fishes.

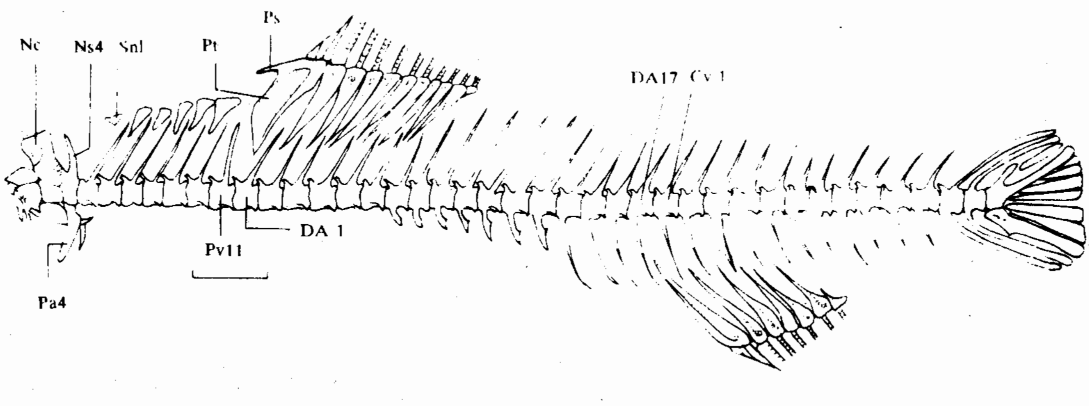

Figure 1 Vertebral column of *Spinibarbus hollandi*

Scale bar 10 mm Abbreviations see the Materials and Methods.

3.2 A strong and tall 4th neural spine. In all species of *Spinibarbus*, the 4th neural spine is well developed, being almost as tall as neural complex (Fig. 2b, c). This spine is slightly inclined posteriorly and widely separated from the posterior border of neural complex. In other genera of Barbinae, the 4th neural spine is usually weak and short, its height being less than a half of the height of neural complex (Fig. 2a); this morphotype commonly occurs in species of *Barbodes*, for example *B. chonglingchungi*, *B. hexagonolepis*. The foregoing analysis reveals that a weak and short 4th neural spine occurs in the outgroup and is reasonably considered here to be a plesiomorphic state. A well developed 4th neural spine is only possessed by *Spinibarbus* fishes and regarded as a synapomorphy of *Spinibarbus*.

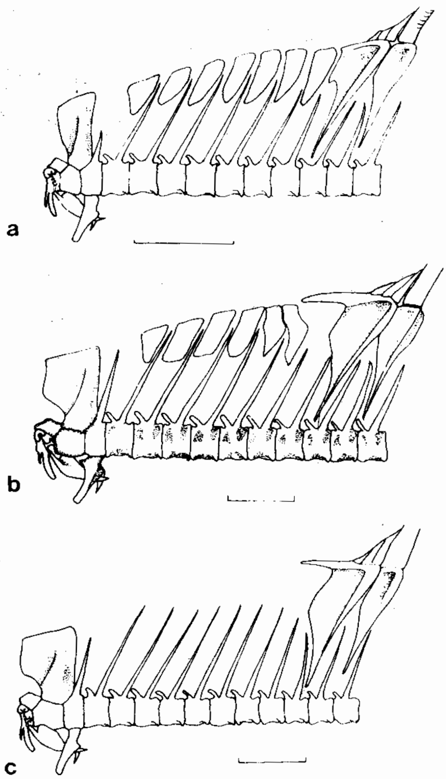

Figure 2 Anterior vertebral column

a: *Barbodes wynaadensis*; b: *Spinibarbus sinensis*; c: *S. denticulatus*. Scale bars 10 mm.

3.3 Presence of a precumbent predorsal spine. In *Spinibarbus*, a well developed spine is protruded forwardly from superior–anterior angle of the first pterygiophore (Fig. 1; Fig. 2b, c). The posterior half of the spine is fused to the first pterygiophore without any sutures. Although the basal portion is embedded under skin, the spine forms a sharp tip protruded outwardly from dorsal skin. In the subfamily Barbinae, this spine is only possessed by the species of *Spinibarbus*, *Mystacoleucus* and some species of *Tor*. About this spine, two opinions have been proposed. Hora (1937) proposed that the spine of *Spinibarbus* and *Spinibarbichthys* (= *Spinibarbus*) was homologous to that of *Mystacoleucus*. By contrast, Wu *et al.* (1977) considered that this spine was independently obtained by *Spinibarbus*, *Tor* and *Mystacoleucus*. It is worthy noting that the three genera show great differenc. *Mystacoleucus* fishes possess 8–9 branched anal fin rays which is fairly different from all other genera (including *Spinibarbus* and *Tor*) of Barbinae. In the genus *Tor*, a unique mental lobe is present at middle of lower lip and the postlabial groove is not disrupted at mental area. By contrast, most genera (including *Spinibarbus* and *Mystacoleucus*) of Barbinae have no mental lobe and the postlabial groove is disrupted at mental area. These characters indicate that a remote relationship lies among *Spinibarbus*, *Mystacoleucus* and *Tor*, and that the precumbent predorsal spine is independently obtained by each of the three genera. So the spine is inferred here to be a synapomorphy of the genus *Spinibarbus*.

The particular combination of synapomorphies discussed above clearly indicates that the genus *Spinibarbus* represents a monophyletic lineage within Barbinae. Of the 3 synapomorphies shared by all species of *Spinibarbus*, the strong and tall 4th neural spine and the disappearance of last supraneural particularly identify the uniqueness of the genus *Spinibarbus*.

3.4 The last simple dorsal fin ray. The last simple dorsal fin ray of *S. hollandi* is unossified and flexible, its posterior edge being smooth. In *S. sinensis*, *S. denticulatus*, *S. yunnanensis* and *S. polylepis*, the last simple ray of dorsal fin is heavily ossified with a serrated posterior edge. Although both states occur in outgroup *Barbodes*, most primitive species of *Barbodes* possess an unossified last simple ray of dorsal fin with a smooth posterior edge. The ontogenetic data of *S. yunnanensis* are also helpful for polarity determination of this character. 3 larvae specimens of *S. yunnanensis* with 20–25 mm SL have been examined. Their last simple ray of dorsal fin is flexible with a smooth posterior edge. In adults of *S. yunnanensis*, the last simple ray of dorsal fin become ossified and serrated posteriorly. Both outgroup comparison and ontogenetic data suggest that the ossified last simple dorsal fin ray with a serrated posterior edge should be an apomorphic state.

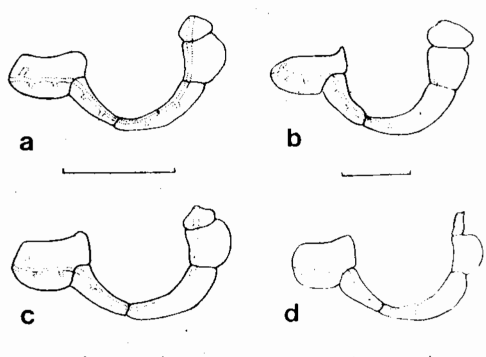

Figure 3 Infraorbital series

a: *Barbodes wynaadensis*; b: *Spinibarbus hollandi*; c: *S. sinensis*; d: *S. denticulatsus*. Scale bars 10 mm

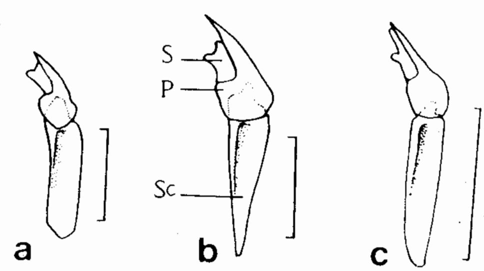

Figure 4 The lateral view of supracleithrum, posttemporal and squamosal

a: *Spinibarbus hollandi*; b: *S. sinensis*; c: *S. denticulatus*. Scale bars 10 mm

3.5 Lachrymal. In *S. hollandi*, the lachrymal is a slightly elongate, laminar bone, its length being obviously larger than its depth (Fig. 3b); this morphotype commonly occurs in most species of *Barbodes* (Fig. 3a) and is reasonably supposed to be a plesiomorphic state. In *S. sinensis*, *S. denticulatus*, *S. yunnanensis* and *S. polylepis*, the lachrymal is a square-like bone, its length being almost equal to its depth (Fig. 3c, d); this morphotype is supposed to be an apomorphic state.

It is worthy mentioning that the larvae (less than 40 mm SL) of *S. denticulatus* possess the former morphotype of lachrymal, but the adults possess the latter morphotype of lachrymal. Here the ontogenetic data further support the inferrence that the former morphotype of lachrymal should be a plesiomorphic state.

3.6 Neural complex. In *S. hollandi*, the neural complex forms into a rectangular bone, its width being apparently smaller than its depth, the dorsal edge being lower than the dorsal level of cranium (Fig. 1); this morphotype is shared by *Barbodes* fishes and inferred here to be a plesiomorphic state. In the rest of *Spinibarbus* species except *S. hollandi*, the neural complex forms into an axe-shaped bone with a well forwardly inclined anterior edge, the dorsal edge being higher than the dorsal level of cranium (Fig. 2b, c); this morphotype does not occur in the outgroup *Barbodes*, and is considered as an apomorphic state.

3.7 Color pattern of dorsal fin. In *S. hollandi*, a deeply black stripe is present on the distal margin of dorsal fin. In the area of this stripe, both the fin rays and the membrane between rays become deeply black. This colour pattern does not occur in *Barbodes* and is reasonably inferred here to be an apomorphic state. In the rest species of *Spinibarbus* except *S. hollandi*, the dorsal fin are greyish and unmottled. This state is shared by most species *Barbodes* and is inferred to be a plesiomorphic state.

3.8 First pterygiophore of dorsal fin. The length of first pterygiophore of dorsal fin is variable in *Spinibarbus*. In *S. hollandi*, the first pterygiophore is short, its ventral tip not reaching to the anterior zygapophysis of first DA vertebrae (Fig. 1); this morphotype is not shared by species of *Barbodes*. It is reasonably to treat this morphotype as an apomorphic state. In rest of *Spinibarbus* species except *S. hollandi*, the first pterygiophore of dorsal fin is fairly elongate, its ventral tip reaching to the anterior zygapophysis of first DA vertebrae (Fig. 2b, c); this morphotype also occurs in species of *Barbodes* (Fig. 2a) as well as most genera of Barbinae and is considered here as a plesiomorphic state.

3.9 The rostral groove. The rostral groove of *S. hollandi* is relatively short, reaching forwardly only to the base of rostral barbel; this state does not occur in *Barbodes* and is supposed here to be an apomorphic state. In the rest of *Spinibarbus* species except *S. hollandi*, the rostral groove extending beyond the base of rostral barbel and runs along the ventral-anterior edge of lachrymal; this state is commonly shared by *Barbodes* species and considered as a plesiomorphic state.

3.10 Dorsal fin origin. In *S. hollandi* and *S. sinensis* , the dorsal fin origin is set before pelvic fin origin. In *S. denticulatus*, *S. yunnanensis* and *S. polylepis*, the dorsal fin origin is set behind pelvic fin origin. Because most primitive species of *Barbodes* such as *B. benasi*, *B. wynaadensis* and *B. hexagonolepis* (Wu *et al.*, 1977; Chu *et al.*, 1989) possess an anteriorly positioned dorsal fin. So a posteriorly positioned dorsal fin is inferred here to be an apomorphic state.

3.11 The number of DA vertebrae. The vertebrae between dorsal and anal fin origins are defined here as DA vertebrae. The number of DA vertebrae is variable in *Spinibarbus*. Two states are recognized: 16–17 and 14–15 DA vertebrae. The former state occurs in *S. hollandi* and *S. sinensis*; the latter state occurs in *S. denticulatus*, *S. yunnanensis* and *S. polylepis*. Because the number of DA vertebrae is closely related both to dorsal fin origin and the number of predorsal vertebrae, the state of 14–15 DA vertebrae is correspondingly treated as an apomorphic state.

3.12 Supracleithrum. The supracleithrum of *Spinibarbus* is an elongate, laminar bone. Its ventral half is connected to the dorsal tip of cleithrum, and its dorsal half to the post-temporal. Two states of supracleithrum are recognized in *Spinibarbus*. In *S. sinensis*, supracleithrum is a triangle – like bone with a wide dorsal edge and a narrow ventral tip (Fig. 4b), its posterior margin not running along its anterior margin, this state does not occur in *Barbodes*. So it is reasonably supposed to be an apomorphic state. In rest of *Spinibarbus* species except *S. sinensis*, supracleithrum is rectangle-like, its posterior margin running along its anterior margin (Fig. 4a, c). Because this morphotype is commonly shared by most species of *Barbodes*, it is inferred to be a plesiomorphic state.

3.13 Parapophysis of 4th vertebra. In *Spinibarbus*, the parapophysis is attached to the ventral-lateral portion of 4th vertebra. It forms into two limbs: posterior and ventral limbs. Posterior limb prolongs backwardly and forms into the suspensorium. Ventral limb is extended ventrally. In *S. sinensis*, the anterior edge of the ventral limb projected forwardly and forms into a triangular process (Fig. 2b). Because this morphotype does not occur in *Barbodes* species (Fig. 2a), it is supposed here to be an apomorphic state. In rest of *Spinibarbus* species except *S. sinensis*, the anterior edge of the ventral limb does not form into a triangular process (Fig. 1; Fig. 2c). This morphotype is commonly shared by species of *Barbodes* and treated as a plesiomorphic state.

3.14 Predorsal scales. The number of predorsal scales exhibits interspecific differentiations in *Spinibarbus*. *S. hollandi* possesses 8–12 predorsal scales, *S. sinensis* 6–10, *S. denticulatus* 9–12, *S. yunnanensis* 13–15 and *S. polylepis* 13–14. Here two states can be recognized: 6–12 and 13–15 predorsal scales. Most primitive species of *Barbodes* such as *B. benasi*, *B. wynaadensis* and *B. hexagonolepis* (Wu *et al.*, 1977) possess 7–11 predorsal scales. Based on this recognization, the state of 13–15 predorsal scales is considered as an apomorphic state.

3.15 Number of caudal vertebrae. Vertebrae between anal fin origin and caudal fin base are defined here as caudal vertebrae. *S. hollandi* possesses 14 caudal vertebrae, *S. sinensis* 14–15, *S. denticulatus* 13–14, *S. yunnanensis* 16–17 and *S. polylepis* 15. Two states of caudal vertebrae are identified here: 13–14 and 15–17 caudal vertebrae. Because a high number of vertebrae is usually considered as an apomorphic state within Barbinae (Chen, 1989), a low number of caudal vertebrae is supposed here to be a plesiomorphic state and a high one to be an apomorphic state.

3.16 Total vertebrae number. *S. hollandi* possesses 42 vertebrae, *S. sinensis* 41–43, *S. denticulatus* 40–42, *S. yunnanensis* 44–46 and *S. polylepis* 44. Two states are recognized here: 40–43 and 44–46 vertebrae. Because most primitive species of *Barbodes* such as *B. hexagonolepis* possess 40–42 vertebrae, the state of 44–46 vertebrae is supposed here to be an apomorphic state.

Table 1 Character states' distributions of *Spinibarbus* fishes

	S. hollandi	*S. sinensis*	*S. denticulatus*	*S. yunnanensis*	*S. polylepis*
1	A	A	A	A	A
2	A	A	A	A	A
3	A	A	A	A	A
4	P	A	A	A	A
5	P	A	A	A	A
6	P	A	A	A	A
7	A	P	P	P	P
8	A	P	P	P	P
9	A	P	P	P	P
10	P	P	A	A	A
11	P	P	A	A	A
12	P	A	P	P	P
13	P	A	P	P	P
14	P	P	P	A	A
15	P	A, P	P	A	A
16	P	P	P	A	A
17	P	P	A	P	P
18	P	P	P	P	A
19	P	P	P	A	P

The numbers same as the text; A: apomorphic state; P: plesiomorphic state.

3.17 5th infraorbital. The 5th infraorbital of *Spinibarbus* exhibits four external morphotypes. In first morphotype (Fig. 3b), the 5th infraorbital is very short and wide, its width being about twice of its length, the sensory canal runs along the middle of 5th infraorbital; this morphotype is possessed by *S. hollandi*. In second morphotype (Fig. 3c), the 5th infraorbital is square-like, its width being about equal to its length, sensory canal runs through the middle of 5th infraorbital; this morphotype occurs in *S. sinensis*. In third morphotype, 5th infraorbital is triangular, this morphotype is possessed by *S. yunnanensis* and *S. polylepis*. In fourth morphotype (Fig. 3d), 5th infraorbital is almost reduced to a bony tube; this morphotype is possessed by *S. denticulatus*. The morphology of 5th infraorbital is variable in Barbinae (Chen, 1989), so is it in *Barbodes* species. However most primitive species of *Barbodes* (Wu *et al.*, 1977; Chu *et al.*, 1989) such as *B. wynaadensis* usually possess the morphotypes from the first to third (Fig. 3a). Based on this recognization, we consider here the first, second and third morphotypes of 5th infraorbital as a plesiomorphic state and fourth morphotype to be an apomorphic state.

3.18 Lateral line scales. *S. hollandi* possesses 25–29 lateral line scales, *S. sinensis* 29–35, *S. denticulatus* 26–33, *S. yunnanensis* 29–35 and *S. polylepis* 37–39. Two states are here distinguished: 25–35 and 37–39 lateral line scales. Because most primitive species of *Barbodes* possess a low number of lateral line scales, the state of 37–39 lateral line scales is supposed to be an apomorphic state.

3.19 Rostral barbel. The rostral barbel of *S. yunnanensis* is short, its tip not reaching to anterior margin of eye. By contrast, the rest of *Spinibarbus* species have a relatively long rostral barbel, its tip reaching to anterior margin of eye. Because most species of *Barbodes* have a long rostral barbel, the state of a short rostral barbel is supposed to be an apomorphic state.

4 Phylogeny and Zoogeography

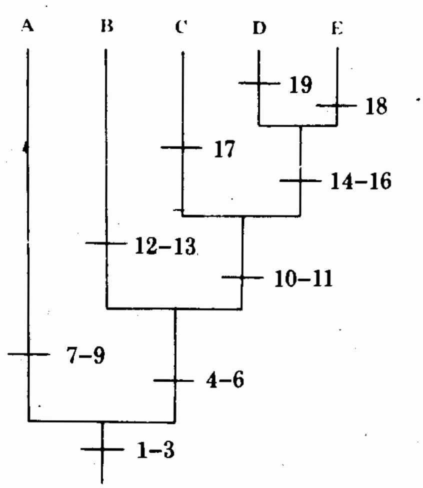

Figure 5 The phylogenetic cladogram of *Spinibarbus* fishes

A: *Spinibarbus hollandi*; B: *S. sinensis*; C: *S. denticulatus*; D: *S. yunnanensis*; E: *S. polylepis*.

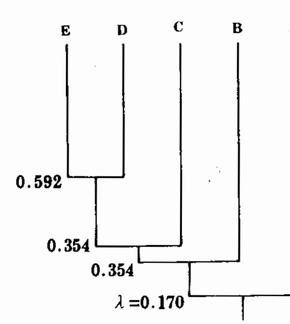

Figure 6 The cluster cladogram of *Spinibarbus* fishes (taxa same as Fig. 5)

Based on Table 1, the most parsimonious phylogenetic cladogram is constructed for the genus *Spinibarbus* (Fig. 5). As a test, "0" is substituted for the plesiomorphic state and "1" for the apomorphic state; then the cluster analysis has been employed to analyse the phylogenetic relationships of *Spinibarbus* fishes and resulted in a most parsimonious phylogenetic cladogram (Fig. 6). Both cladograms are exactly the same. From Fig. 5 and Table 1, several points can be concluded as following.

4.1 The division of sister groups A (*S. hollandi*) and B–E (*S. sinensis* + *S. denticulatus* + *S. yunnanensis* + *S. polylepis*) represents the first phyletic branching within the genus *Spinibarbus*. Group A is defined by 3 synapomorphies (characters 7–9), and B–E by 3 synapomorphies (characters 4–6). Group A occurs in middle and lower reaches of Yangtze, Qiantangjiang, Pearl, Yuanjiang (= Red River), Mingjiang Rivers and Hainan, Taiwan Islands; group B–E distributes over the wide areas of southern China (Fig. 7). The distribution ranges of first sister groups overlap greatly upon south–eastern China.

4.2 The division between group B (*S. sinensis*) and C–E (*S. denticulatus* + *S. yunnanensis* +*S. polylepis*) represents the second phyletic branching within *Spinibarbus*. Group B and C–E are respectively identified by 2 (characters 12–13) and 2 (characters 10–11) synapomorphies. Group B is confined to the north of Yunnan–Guizhou Plateau, occurring in upper and middle Yangtze River; group E–C is confined to southern slope of Yunnan–Guizhou Plateau and Nanling mountains, occurring in Pearl, Yuanjiang Rivers and Hainan Island (Fig. 7). This unique congruence between the distribution pattern and phylogenetic cladogram suggests that the upheaval of Yunnan–Guizhou Plateau during Pliocene and the subsequent drainages' division between upper Yangtze (Jinshajiang River) and upper Pearl River (Nanpanjiang River) be an important vicariant event which might have resulted in the phyletic division of the second sister groups B and C–E. Similar cases also happened in the phyletic division between first sister groups of the cyprinid genus *Anabarilius* (Yang *et al.*, 1987). The present geological data indicate that the Yangtze River and Pearl River respectively captured the Jinshajiang and Nanpanjiang drainages when Yunnan–Guizhou Plateau uplifted strongly during Pliocene (Li 1981; Chen *et al.* 1986).

4.3 Sister groups C (*S. denticulatus*) and D–E (*S. yunnanensis* + *S. polylepis*) represent the third phyletic splitting within *Spinibarbus*. Group C and D–E are respectively defined by 1 (character 17) and 3 (characters 14–16) synapomorphies. Group C widely occurs in the lowlands of Hainan Island, middle and lower Pearl and Yuanjiang Rivers (Fig. 7). The distribution range of group D–E is confined to Nanpanjiang and Beipanjiang Rivers (belonging to upper Pearl River) which are situated on southern part of Yunnan–Guizhou Plateau (Fig. 7). This unique congruence between distribution pattern and the phylogenetic cladogram suggests that the upheaval of Yunnan–Guizhou Plateau and the environmental differentiation between the plateau and the lowlands subsequent to the upheaval of Yunnan–Guizhou Plateau be a major vicariant event which might have resulted in the phyletic division of the third sister groups C and D–E.

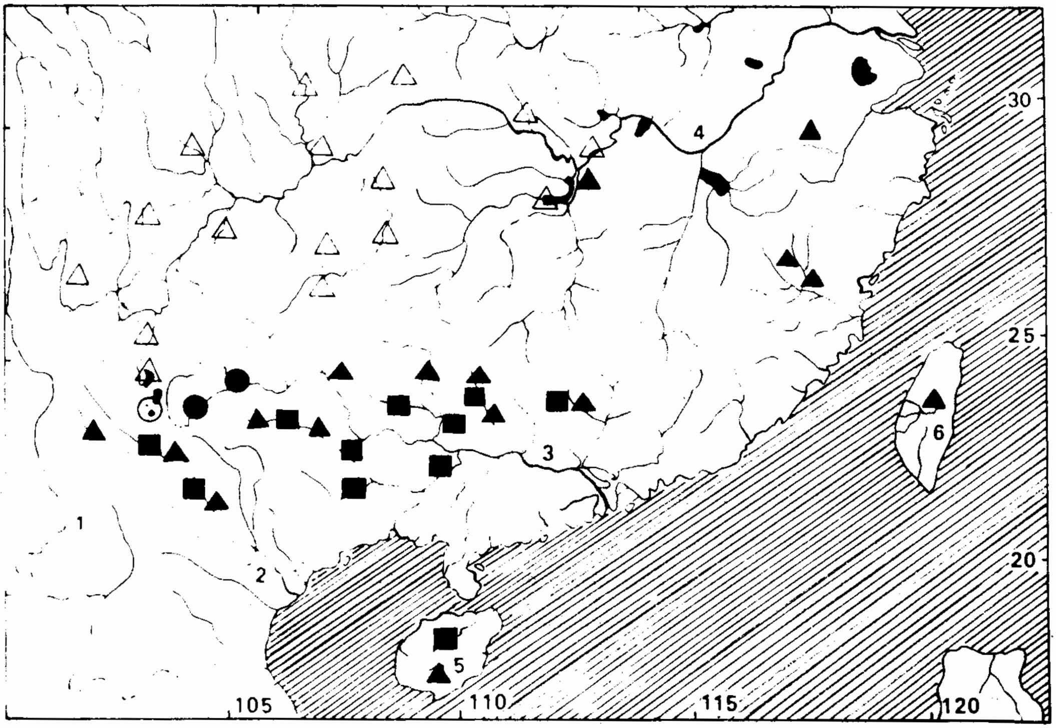

Figure 7 The distribution of the *Spinibarbus* fishes

Spinibarbus hollandi (black triangle); *S. sinensis* (open triangle); *S. denticulatus* (black square); *S. polylepis* (black circle); *S. yunnanensis* (open circle). 1: Lancangjiang River (upper Mekong); 2: Yuanjiang River (upper Red River); 3: Pearl River; 4: Yangtze River; 5: Hainan Island; 6: Taiwan Island.

4.4 Sister groups D (*S. yunnanensis*) and E (*S. polylepis*) represent the fourth phyletic branching within *Spinibarbus*. The distribution of group D is confined to lakes of eastern Yunnan, and that of group E to Nanpanjiang and Beipanjiang Rivers (Fig. 7). It is undoubted that great difference in habitats exists between the lakes and rivers. So it is supposed here that the differentiation of habitats might have played an important role on the phyletic division of the fourth sister groups D and E.

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倒刺鲃属鱼类的系统发育及其动物地理学研究

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摘要 倒刺鲃属 (*Spinibarbus*) 鱼类隶属于鲤科的鲃亚科，共有 5 个有效种。应用分支系统学原理和方法，对该属鱼类的系统发育和地理分化进行了研究。在进行性状分析时，以四须鲃属 (*Barbodes*) 作为倒刺鲃属的外类群，理由是它们的系统发育关系较近，而且四须鲃属较原始。分析结果表明，倒刺鲃属鱼类共有 3 个共同离征，表明该属鱼类为一个单源群。在 19 个外部形态和内部骨骼特征的基础上，构建了倒刺鲃属鱼类的系统发育分支图。姐妹群 A(*S. hollandi*) 和 B-E (*S. sinensis* + *S. denticulatus* + *S. yunnanensis* + *S. polylepis*) 代表了倒刺鲃属内的第一次谱系分化。第二次谱系分化发生于姐妹群 B (*S. sinensis*) 和 C-E (*S. denticulatus* + *S. yunnanensis* + *S. polylepis*) 之间；姐妹群 B 分布于长江水系，而姐妹群 C-E 则分布于珠江水系以南，包括海南岛；基于谱系分化和姐妹群的地理分布，推测此次谱系分化可能是由于云贵高原的抬升及同时发生的水系分流所致。第三次谱系分化则发生于姐妹群 C (*S. denticulatus*) 和 D-E (*S. yunnanensis* + *S. polylepis*)之间；姐妹群 C 分布于珠江和元江水系的低海拔地区，包括海南岛；姐妹群 D-E 则仅分布于云贵高原的南、北盘江；据此推测第三次谱系分化可能是云贵高原和低海拔地区间的环境差异所致。

关键词 系统发育，动物地理，倒刺鲃属