

## Phylogeny and Zoogeography of the Cyprinid Hemcultrine Group (Cyprinidae: Cultrinae)

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**Ying-Gui Dai and Jun-Xing Yang (2003)** Phylogeny and zoogeography of the cyprinid hemcultrine group (Cyprinidae: Cultrinae). *Zoological Studies* 42(1): 73-92. The hemcultrine group consists of middle-sized cyprinids in Asia which taxonomically belong to the subfamily Cultrinae in the Cyprinidae (Cypriniformes), but there has been no convincing generic phylogenetic hypothesis proposal so far. On the basis of a morphological study of 65 specimens soaked in formalin and 14 skeletal specimens of 8 species in 6 genera within the hemcultrine group as an ingroup, a 70-character matrix was obtained. The generic phylogenetic relationships of the hemcultrine group are hypothesized with the matrix by the method of cladistic analysis. When the species *Rasborinus lineatus* or *Cultrichthys erythropterus* is used as the sole outgroup, the matrix gives the same single most-parsimonious tree of generic phylogenetic relationships within the hemcultrine group which shows that the hemcultrine group forms a monophyletic group. However, when *Rasborinus lineatus* is used as the sole outgroup and *Cultrichthys erythropterus* and *Paralaubuca barroni* are included in the ingroup, the hemcultrine group is validated to represent a paraphyletic group, and the hemcultrine group and the genus *Paralaubuca* form a monophyletic group. The tree of generic relationships and zoogeography of the monophyletic group comprising the hemcultrine group and the genus *Paralaubuca* suggest the following: (1) The monophyletic group comprises 2 smaller monophyletic groups: the genera *Hemiculterella* + *Pseudohemiculter* + *Hainania* and the genera *Hemiculter* + *Paralaubuca* + *Pseudolaubuca* + *Toxabramis*. (2) The sister groups of the monophyletic group show both overlapping and vicariant distribution patterns; therefore the generic distribution pattern of the monophyletic group maybe have resulted from both dispersal and vicariance events. (3) The monophyletic group probably originated on the Asian mainland from the Yangtze River to the Pearl River and on Hainan Island in China. (4) The monophyletic group probably originated after the Japanese Archipelago was separated from the Asian mainland at the beginning of the Quaternary Period in the Cenozoic but before Taiwan, Hainan Island, and Indonesia were completely isolated from the Asian mainland after the ice age in the Quaternary Period. (5) Speciation of the genus *Hemiculter* should have been the earliest, and those of the genera *Paralaubuca*, *Pseudolaubuca*, and *Hainania* ought to be the latest in the process of evolution of this monophyletic group. <http://www.sinica.edu.tw/zool/zoolstud/42.1/73.pdf>

**Key words:** Cladistic analysis, Ingroup, Outgroup, Monophyly, Origin.

The hemcultrine group, consisting of middle-sized cyprinids in Asia, taxonomically belongs to the subfamily Cultrinae in the Cyprinidae (Cypriniformes). The group comprises 6 valid genera (Yue et al. 1996): *Hainania* (Koller, 1927), *Hemiculter* (Bleeker, 1859), *Hemiculterella* (Warpachowsky, 1887), *Pseudohemiculter* (Nichols and Pope, 1927), *Pseudolaubuca* (Bleeker, 1865), and *Toxabramis* (Günther, 1873). To date, sixteen species and subspecies have

been described in the group. From 1855 to 1942, four species and subspecies were described in the genus *Hemiculter*: *Her. leucisculus* (Basilewsky, 1855), *Her. lucidus lucidus* (Dybowsky, 1872), *Her. bleekeri* Warpachowsky 1887, *Her. lucidus warpachowskii* (Nicholsky, 1903), and *Her. tchangi* Fang 1942. From 1865 to 1925, two species were recorded in the genus *Pseudolaubuca*: *Psl. sinensis* Bleeker 1865 and *Psl. engraulis* (Nichols, 1925). From 1873 to 1934, three species were

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described in the genus *Toxabramis*: *T. swinhonis* Günther, 1873, *T. houdemeri* Pellegrin, 1932, and *T. hoffmanni* Lin, 1934. From 1887 to 1989, three species were recorded in the genus *Hemiculterella*: *Hea. sauvagei* Warpachowsky, 1887, *Hea. wui* (Wang, 1935), and *Hea. macrolepis* Chen, 1989. From 1880 to 1942, three species were described in the genus *Pseudohemiculter*: *Psh. dispar* (Peters, 1880), *Psh. hainanensis* (Boulenger, 1899), and *Psh. kweichowensis* (Tang, 1942). Koller (1927) recorded *Hainania serrata* in the genus *Hainania*.

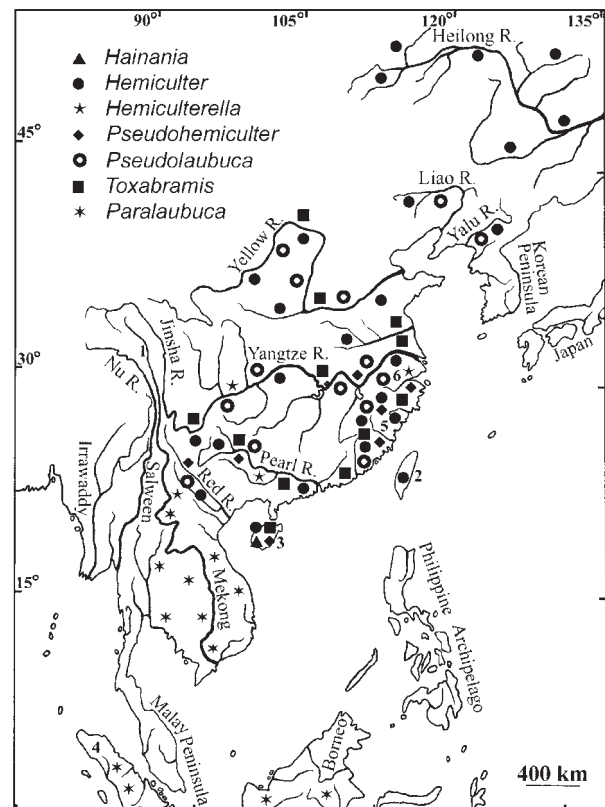
The 6 genera of the hemicultrine group share the following characters with the other genera in the subfamily Cultrinae: a compressed body with a ventral keel but no barbel on the head, 2-3 rows of compressed, curved, and tipped pharyngeal teeth, a complete lateral line, a neural complex including 2 or 3 bony plates, a basioccipital the posterior part of which is a thin and compressed keel, a big aperture between the coracoid and cleithrum, three unbranched dorsal rays, seven branched dorsal rays, eight pterygiophores of the dorsal fin, three unbranched anal rays, a long base to the anal fin, and a deeply forked caudal fin. However, the group is distinguished from all other genera in the subfamily Cultrinae by the combination of the following 3 characters: a 2-chamber air-bladder with a small lobe at the end of the 2nd one, the 3rd circumorbital bone significantly enlarged and much wider than the 4th, and 2 rows of scales present from the lateral line to the base of the pelvic fin.

The hemicultrine group occurs only in East Asia, which includes China, the far-eastern region in Russia, the northern Korean Peninsula, and the northern Vietnam. Of the 6 genera in the hemicultrine group, the genus *Hainania* occurs only on Hainan Island in China, the genus *Hemiculterella* is confined to the South China mainland, and the genus *Pseudolaubuca* is distributed throughout the East Asia mainland (Luo and Chen 1998) (Fig. 1).

On the basis of the skeletal comparisons between *Macrochirichthys macrochirus* (Valenciennes, 1844) and the remaining genera in the subfamily Cultrinae, Howes (1979) considered that the subfamily Cultrinae includes at least 2 monophyletic groups, i.e., the cultrine group and the hemicultrine group, and for the 1st time indicated that the hemicultrine group comprises the genera *Hemiculter*, *Pseudolaubuca*, and *Toxabramis*. However, Howes (1979) gave no synapomorphy for the hemicultrine group in his paper. Thereafter, Yue and Luo (1996) preliminarily studied the phylogeny of the subfamily Cultrinae using the meth-

ods of classical taxonomy and classified the subfamily Cultrinae into 3 monophyletic groups—the Anchidaniorine, the Cultrine, and the Rasborine; they believed that the Rasborine comprises the hemiculter and rasborinus branches. In their paper, Yue and Luo (1996) considered the hemiculter branch to be a monophyletic group composed of the genera *Hainania*, *Hemiculter*, *Hemiculterella*, *Pseudohemiculter*, *Pseudolaubuca*, and *Toxabramis* and based the similarity of the group on the following 6 characters: a 2-chamber air-bladder with a small lobe at the end of the 2nd one, the 3rd circumorbital bone significantly enlarged and much wider than the 4th, the pelvic girdle superficially forked, the neural complex including 3 bony plates, the ventral keel extending from the isthmus to the anus, and the lateral line extending ventrad sharply before the tip of the pectoral fin. They further classified the group into 3 clades: *Hainania* and *Toxabramis*, *Hemiculter* and *Pseudolaubuca*, and *Hemiculterella* and *Pseudohemiculter*.

In this paper, we congruously call the



**Fig. 1.** Map showing the geographical distribution of the genera in the hemicultrine group and the genus *Paralaubuca*. 1, Lancang (Mekong) River; 2, Taiwan; 3, Hainan Island; 4, Sumatra; 5, Min River; 6, Qiantang River.

hemiculter branch the hemicultrine group which comprises the genera *Hainania*, *Hemiculter*, *Hemiculterella*, *Pseudohemiculter*, *Pseudolaubuca*, and *Toxabramis*.

No convincing generic phylogenetic hypothesis has yet been advanced about the hemicultrine group until now. This research focuses on the generic phylogenetic hypothesis of the hemicultrine group by the methods of cladistic analysis based on careful inspection of both formalin-preserved specimens and skeletal specimens of *Hainania serrata*, *Hemiculter leucisculus*, *Hemiculterella macrolepis*, *Hea. sauvagei*, *Pseudohemiculter dispar*, *Pseudolaubuca engraulis*, *Toxabramis houdemeri*, and *T. swinhonis* in the hemicultrine group as the ingroup. Because significant differentiations within the subfamily Cultrinae are present between the genera *Cultrichthys* and *Rasborinus*, both of which are close relatives of the hemicultrine group, we selected *Rasborinus lineatus* and *Cultrichthys erythropterus* as outgroups to polarize the characters for the ingroup. The monophyly, zoogeography, and origin of the hemicultrine group are also evaluated herein.

## MATERIALS AND METHODS

Sixty-five specimens soaked in formalin and 14 skeletal specimens of 8 species in 6 genera within the hemicultrine group as the ingroup and 20 specimens soaked in formalin and 3 skeletal specimens of 2 species in the genera *Rasborinus* and *Cultrichthys* as outgroups were examined. Ten specimens soaked in formalin and 1 skeletal specimen of 1 species in the genus *Paralaubuca* was also inspected for inclusion in the ingroup for the monophyly test of the hemicultrine group. Specimens examined were all adults of the 11 species and belong to the collection of the Kunming Institute of Zoology, Chinese Academy of Sciences, except for specimens of the species *Hainania serrata*, which were donated by the Hydrobiology Institute, Chinese Academy of Sciences, Wuhan, Hubei.

The skeletal specimens were cleared and stained following modifications of the methods proposed by Dingerkus and Uhler (1977) and Taylor and Van Dyke (1985). Outgroup comparisons followed the method of Maddison et al. (1984). Data were analyzed by the cladistic methods originally proposed by Hennig (1950 1966) and summarized by Wiley et al. (1991). The dataset analysis fol-

lowed Paup (vers. 3.11, Swofford 1993) using heuristic searches with starting trees obtained by random stepwise addition (1000 replications of a heuristic search), tree bisection reconstruction (TBR) branch-swapping, and by saving all optimal trees (MULTREES option). Multistate characters were run ordered and unordered and the results were compared. The consistency index (CI), retention index (RI), and homoplasy index (HI) were generated for the phylogeny as a whole, and the CI and RI were also generated for each informative character by PAUP (vers. 3.11, Swofford 1993) (Farris 1989). MacClade (vers. 3.04, Maddison and Maddison 1992) was used to assemble the dataset and visualize character changes on the cladograms. A bootstrap analysis (Felsenstein 1985) was performed with 1000 replications, using heuristic searches with simple stepwise addition, TBR branch-swapping and the MULTREES option. According to the outgroup substitution approach proposed by Donoghue and Cantino (1984), *Rasborinus lineatus* and *Cultrichthys erythropterus* were used as sole outgroups respectively to test the stability of the internal nodes in the final most-parsimonious tree of the generic relationships within the hemicultrine group. Also, the monophyly of the hemicultrine group was preliminarily tested by PAUP (vers. 3.11, Swofford 1993) using *Rasborinus lineatus* as the sole outgroup with *Cultrichthys erythropterus* and *Paralaubuca barroni* included in the ingroup. Statements about the character state for every genus in the ingroup and outgroups are based on species examined in this research.

## RESULTS

A total of 70 morphological characters was found on the basis of careful inspection of specimens soaked in formalin and skeletal specimens of the 8 species in 6 genera within the hemicultrine group in this research. Characters are described and arranged below in anatomical sequence from anterior to posterior and are numbered (in parenthesis) as in table 1.

*Mouth.* *Cultrichthys erythropterus* has a superior mouth (#1-0. Note: #i-n means state n of character i). In species of the hemicultrine group in this study, and *Paralaubuca barroni* and *Rasborinus lineatus*, the mouth is terminate (#1-1). In *C. erythropterus*, the mouth extends towards the rear caudal to verticals through the anterior margins of the nostrils (#2-0). In *Hemiculterella*

*macrolepis*, *Hea. sauvagei*, *Hainania serrata*, *Pseudohemiculter dispar*, and *Paralaubuca barroni*, the mouth extends towards the rear caudal to verticals through the anterior margins of the eyes on the sides of the head (#2-2). In the remaining species of the hemicultrine group in this study and *R. lineatus*, the mouth extends towards the rear caudal to verticals through the posterior margins of the nostrils (#2-1).

**Jaws.** In *Hea. macrolepis*, *Hea. sauvagei*, *Hainania serrata*, *Psh. dispar*, *Pseudolaubuca engraulis*, and *Paralaubuca barroni*, there is a notch at the tip of the upper jaw in which a process at the tip of the lower jaw can be inserted (#3-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, there is neither a notch at the tip of the upper jaw nor a process at the tip of the lower jaw (#3-0).

**Premaxilla.** In *Hea. macrolepis*, *Hea. sauvagei*, and *Paralaubuca barroni*, the process at the anterior end of the premaxilla is lower than the anterodorsal process on the maxilla (Fig. A1b; #4-0). In *Toxabramis houdemeri*, the process at the anterior end of the premaxilla is higher than the anterodorsal process on the maxilla (Fig. A1c; #4-2). In *Toxabramis swinhonis* and *C. erythropterus*, the process at the anterior end of the premaxilla is as high as (#4-1) or higher than (#4-2) the anterodorsal process on the maxilla. In the remaining species of the hemicultrine group in this study and *R. lineatus*, the process at the anterior end of the premaxilla is as high as the anterodorsal process on the maxilla (Fig. A1a; #4-1). In *T. houdemeri* and *T. swinhonis*, the posterior 1/2 of the premaxilla is as wide as the anterior 1/2 (Fig. A2a; #5-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *Paralaubuca barroni*, the premaxilla swiftly narrows towards the rear caudal (Fig. A2b; #5-0). In *C. erythropterus*, the premaxilla swiftly narrows towards the rear caudal (#5-0) or widens about its middle point (Fig. A2c; #5-1).

**Maxilla.** In *Psl. engraulis*, the maxilla extends towards the rear caudal to a vertical through the middle of the nostril (#6-0). In *Hea. macrolepis*, *Hea. sauvagei*, *C. erythropterus*, and *Paralaubuca barroni*, the maxilla extends towards the rear caudal to a vertical through the anterior margin of the eye (#6-2). In the remaining species of the hemicultrine group in this study and *R. lineatus*, the maxilla extends towards the rear caudal to a vertical through the posterior margin of the nostril (#6-1).

**Supraorbital canal.** The supraorbital canal is

the canal on the frontal just above the upper margin of the eye. The supraorbital canal pore refers to the pore on the supraorbital canal, not the pore between the nasal and frontal or the one between the frontal and the 5th infraorbital. *Pseudolaubuca engraulis* has 4-6 supraorbital canal pores (#7-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the number of supraorbital canal pores are 3 (#7-0).

**Interorbital back of head.** In *Psl. engraulis*, *T. houdemeri*, *T. swinhonis*, and *Paralaubuca barroni*, the interorbital back of the head is significantly convex (#8-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, the interorbital back of the head is flat or almost flat (#8-0).

**Lacrimal.** In *T. houdemeri* and *T. swinhonis*, the lacrimal is rectangular (Fig. A3c; #9-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the lacrimal is pentagonal (Fig. A3a, b; #9-0). In *Hemiculter leucisculus*, *Hea. macrolepis*, *Hea. sauvagei*, and *R. lineatus*, the sense canal on the lacrimal is curved (Fig. A3a; #10-0). In the remaining species of the hemicultrine group in this study, and *C. erythropterus* and *Paralaubuca barroni*, the sense canal on the lacrimal is straight (Fig. A3b, c; #10-1). In *Psl. engraulis*, the sense canal on the lacrimal has 3 pores (Fig. A3b; #11-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the sense canal on the lacrimal has 2 pores (Fig. A3a, c; #11-0).

**The 2nd infraorbital.** In *Psl. engraulis*, *R. lineatus*, and *Paralaubuca barroni*, the anterior 1/2 of the 2nd infraorbital remains as wide as its posterior 1/2 (Fig. A3b; #12-0). In the remaining species of the hemicultrine group in this study and *C. erythropterus*, the 2nd infraorbital gradually narrows from its anterior end to its posterior end (Fig. A3a, c; #12-1).

**The 3rd infraorbital.** In *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the 3rd infraorbital is almost as wide as the 4th (Fig. A3d; #13-0). In species of the hemicultrine group in this study, the 3rd infraorbital is significantly wider than the 4th (Fig. A3a-c; #13-1).

**The 4th infraorbital.** In *Psl. engraulis*, *T. houdemeri*, *T. swinhonis*, and *Paralaubuca barroni*, the 4th infraorbital abruptly widens below its middle point (Fig. A3b, c; #14-1). In the remaining species of the hemicultrine group in this study, and

*R. lineatus* and *C. erythropterus*, the 4th infraorbital remains the same width or the lower 1/2 of the 4th infraorbital slightly and smoothly widens compared to its upper 1/2 (Fig. A3a; #14-0).

**The 5th infraorbital.** In *Hea. macrolepis*, *Hea. sauvagei*, *Hainania serrata*, and *Psh. dispar*, the 5th infraorbital is narrower than the upper end of the 4th infraorbital (Fig. A3a; #15-0). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, the 5th infraorbital is as wide as the upper end of the 4th infraorbital (Fig. A3b, c; #15-1). In *Paralaubuca barroni*, the 5th infraorbital is wider than the upper end of the 4th infraorbital (Fig. A3e; #15-2).

**Quadrate.** The quadrate comprises 2 sections: a vertical bony plate and an elongate, horizontal shaft. In *Hea. macrolepis* and *Hea. sauvagei*, the anterior margin of the vertical bony plate of the quadrate is perpendicular to the elongate and horizontal shaft (Fig. A4b; #16-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the anterior margin of the vertical bony plate of the quadrate is not perpendicular to the elongate and horizontal shaft (Fig. A4a; #16-0).

**Urohyal.** The urohyal is on the ventral side of the splanchnocranium and includes ventral and dorsomedial parts. The ventral part is a wide horizontal plate; the dorsomedial part is a keel. In *T. houdemeri* and *T. swinhonis*, the entire urohyal is longer than the combined total length of the hypohyal, ceratohyal, and epihyal (#17-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the entire urohyal is shorter than the combined total length of the hypohyal, ceratohyal, and epihyal (#17-0).

**Pterotic.** In *Psl. engraulis*, two notches are present along the anterior margin of the pterotic (Fig. A5c; #18-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, one or no notch is present along the anterior margin of the pterotic (Fig. A5a, b; #18-0).

**Prepercular.** In *T. houdemeri*, *T. swinhonis*, and *C. erythropterus*, the posterior margin of the prepercular is straight (Fig. A6a; #19-1). In *Hea. sauvagei*, the posterior margin of the prepercular is concave (#19-0) or straight (#19-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *Paralaubuca barroni*, the posterior margin of the prepercular is concave (Fig. A6b; #19-0).

**Opercular.** In *Her. leucisculus*, *Psl. engraulis*, *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, a process extends towards the front from the anterior end of the upper margin of the opercular (Fig. A7b; #20-0). In *Hea. sauvagei*, a process extends towards the front (#20-0) or up (#20-1) from the anterior end of the upper margin of the opercular. In the remaining species of the hemicultrine group in this study, a process extends up from the anterior end of the upper margin of the opercular (Fig. A7a; #20-1). In *Psl. engraulis* and *Paralaubuca barroni*, the posterior margin of the opercular is concave (Fig. A7b; #21-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, the posterior margin of the opercular is convex (Fig. A7a; #21-0).

**Postorbital head length.** In *Hainania serrata*, *Psh. dispar*, *T. houdemeri*, *T. swinhonis*, *R. lineatus*, and *Paralaubuca barroni*, the postorbital head length is 100% of the caudal peduncle depth (#22-0). In *Hea. sauvagei*, the postorbital head length is 100% (#22-0) to 114% (#22-1) of the caudal peduncle depth. In the remaining species of the hemicultrine group in this study and *C. erythropterus*, the postorbital length of the head is 110% - 144% of the caudal peduncle depth (#22-1).

**Outer gill rakers on the 1st gill arch.** In *T. houdemeri*, *T. swinhonis*, *C. erythropterus*, and *Paralaubuca barroni*, the length of the outer gill raker on the 1st gill arch is 50% - 80% that of the branchial filament at the same locus on the 1st gill arch (#23-1), but in the remaining species of the hemicultrine group in this study and *R. lineatus*, the lengths are 25% - 40% that of the branchial filament at the same locus on the 1st gill arch (#23-0).

**Pharyngeal tooth.** *Toxabramis houdemeri* and *T. swinhonis* have 2 rows of pharyngeal teeth on each pharyngeal bone, respectively (Fig. A8a; #24-1). The remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni* have 3 rows, respectively (Fig. A8b, c; #24-0). *Toxabramis houdemeri* and *T. swinhonis* each have a total of 12-14 pharyngeal teeth on both the left and right pharyngeal bones (#25-1). The remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni* have a total of 21-22 pharyngeal teeth each on both left and right pharyngeal bones (#25-0).

**Pharyngeal bone.** The anterior branch of the pharyngeal bone is the part of the pharyngeal bone from its anterior end to the anterior margin of

the base of the 1st pharyngeal tooth. The posterior branch of the pharyngeal bone is the part of the pharyngeal bone from its posterior end to the posterior margin of the base of the last pharyngeal tooth. In *T. houdemeri* and *T. swinhonis*, the anterior branch of the pharyngeal bone is longer than its posterior branch (Fig. A8a; #26-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the anterior branch of the pharyngeal bone is as long as its posterior branch (Fig. A8b, c; #26-0). An anterior process and a posterior process are usually present along the outer margin of the pharyngeal bone within the hemicultrine group. In *Psl. engraulis*, *T. houdemeri*, and *R. lineatus*, the posterior process is absent (Fig. A8a; #27-0). In *T. swinhonis*, the pharyngeal bone has no posterior process (#27-0) or has a tipped posterior process (#27-2). In the remaining species of the hemicultrine group in this study and *Paralaubuca barroni*, the end of the posterior process is tipped (Fig. A8b; #27-2). In *C. erythropterus*, the posterior process is a fold (Fig. A8c; #27-1).

**Supraoccipital carinate.** In *C. erythropterus*, the supraoccipital carinate rises much higher than the back of the head (#28-1). In species of the hemicultrine group in this research, and *R. lineatus* and *Paralaubuca barroni*, the supraoccipital carinate rises as high as the back of the head (#28-0).

**Basioccipital.** The basioccipital is on the ventral side of the neurocranium. In *Her. leucisculus*, *Hea. macrolepis*, and *Psl. engraulis*, the posterior end of the basioccipital extends towards the rear caudal to the posterior margin of the 4th centrum (#29-1). In *T. swinhonis*, the posterior end of the basioccipital extends towards the rear caudal to the middle of the 3rd centrum (#29-0). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the posterior end of the basioccipital extends towards the rear caudal to the posterior margin of the 3rd centrum (#29-0).

**Cleithrum.** In *Hea. macrolepis*, *Hea. sauvagei*, and *R. lineatus*, the anterior margin of the cleithrum is straight (Fig. A9a; #30-0). In *Psh. dispar*, the anterior margin of the cleithrum is straight (#30-0) or convex (#30-1). In the remaining species of the hemicultrine group in this study, and *C. erythropterus* and *Paralaubuca barroni*, the anterior margin of the cleithrum is convex (Fig. A9b; #30-1).

**Postcleithrum.** *Toxabramis houdemeri* and *T. swinhonis* each has a C-shaped postcleithrum

(#31-1). The remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni* have an S-shaped postcleithrum (#31-0).

**Flesh slip at the pectoral fin base.** The flesh slip at the pectoral fin base is the slip of flesh which is folded at the base of the pectoral fin and extends towards the rear caudal. In *Psl. engraulis* and *Paralaubuca barroni*, the flesh slip at the pectoral fin base is as long as or longer than the eye diameter (#32-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, the flesh slip is shorter than the eye diameter (#32-0).

**Total vertebrae.** *Hainania serrata* has 42 vertebrae (#33-0). *Toxabramis houdemeri* has 40 vertebrae (#33-0). *Pseudolaubuca engraulis* and *C. erythropterus* have 44-45 vertebrae (#33-1). In the remaining species of the hemicultrine group in this study, the total number of vertebrae is 43 (#33-0). *Rasborinus lineatus* has 36 vertebrae (#33-0). *Paralaubuca barroni* has 41 vertebrae (#33-0).

**Trunk vertebrae.** Trunk vertebrae refer to vertebrae without a hemal spine. In *Her. leucisculus* and *C. erythropterus*, the number of trunk vertebrae is 23-24 (#34-1). In the remaining species of the hemicultrine group in this study, the number of trunk vertebrae is 20-22 (#34-0). *Rasborinus lineatus* and *Paralaubuca barroni* each has 18-19 trunk vertebrae (#34-0).

**Vertebrae before the insertion of the 1st pterygiophore of the dorsal fin.** *Hemiculter leucisculus*, *Psl. engraulis*, and *Paralaubuca barroni* each has 15-16 vertebrae before the insertion of the 1st pterygiophore of the dorsal fin (#35-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, the number of vertebrae is 12-14 (#35-0).

**Trunk vertebrae with a developed prezygapophysis.** A trunk vertebra with a developed prezygapophysis refers to a trunk vertebra whose prezygapophysis is significantly higher than the postzygapophysis of the trunk vertebra just before it. In *Her. leucisculus*, *Psh. dispar*, *R. lineatus*, and *C. erythropterus*, the number of trunk vertebrae is 13-18 (#36-0). In the remaining species of the hemicultrine group in this study and *Paralaubuca barroni*, the number of trunk vertebrae is 9-12 (#36-1).

**Lateral process of the neural arch of the 3rd vertebra.** In *Psh. dispar* and *Psl. engraulis*, the lateral process is developed, and the width of the lateral process is equal to or greater than the centrum length of the 3rd vertebra (Fig. A10a; #37-1).

In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the lateral process is undeveloped, and the width of the lateral process is 25% - 75% of the centrum length of the 3rd vertebra (Fig. A10b; #37-0).

**Neural complex.** The neural complex is made up of the neural spine of the 3rd vertebra and the prezygapophysis of the 4th vertebra. The upper 1/2 of the neural complex within the hemicultrine group includes 2 or 3 bony plates which are separated from one another. In *Psl. engraulis*, *T. houdemeri*, *T. swinhonis*, *R. lineatus*, and *Paralaubuca barroni*, the upper 1/2 of the neural complex has 2 bony plates (Fig. A11b; #38-0). In the remaining species of the hemicultrine group in this study and *C. erythropterus*, the upper 1/2 of the neural complex has 3 bony plates, the middle one of which is more developed than the others (Fig. A11a; #38-1).

**Tripus.** In *Hea. macrolepis* and *Hea. sauvagei*, the anterior process of the tripus extends towards the front just to a vertical through the anterior margin on the outer side of the tripus (Fig. A12b; #39-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, the anterior process of the tripus extends towards the front over the vertical through the anterior margin on the outer side of the tripus (Fig. A12a, c; #39-0). In *Paralaubuca barroni*, the anterior process of the tripus does not extend towards the front to the vertical through the anterior margin on the outer side of the tripus (Fig. A12d; #39-2). In *Her. leucisculus*, *Psl. engraulis*, *T. houdemeri*, and *T. swinhonis*, the anterior margin on the outer side of the tripus is straight (Fig. A12a; #40-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the anterior margin on the outer side of the tripus is convex (Fig. A12b-d; #40-0).

**Parapaphysis of the 4th vertebra.** The parapaphysis of the 4th vertebra comprises 2 parts: a dorsal branch and a pelvic branch. In *Hea. macrolepis*, *Hea. sauvagei*, *R. lineatus*, and *C. erythropterus*, a fold is present at a point 33% up the length of the dorsal branch of the parapaphysis of the 4th vertebra (Fig. A13b; #41-0). In *Psh. dispar*, a fold is present at a point 33% (#41-0) or 50% (#41-1) up the length of the dorsal branch of the parapaphysis of the 4th vertebra. In the remaining species of the hemicultrine group in this study and *Paralaubuca barroni*, a fold is present at the mid-point of the dorsal branch of the parapaphy-

sis (Fig. A13a, c; #41-1). In *Hainania serrata*, *Psh. dispar*, and *Paralaubuca barroni*, the end of the dorsal branch of the parapaphysis of the 4th vertebra is tipped (Fig. A13a; #42-0). In *Hea. macrolepis*, *Hea. sauvagei*, *R. lineatus*, and *C. erythropterus*, the end of the dorsal branch is blunt (Fig. A13b; #42-1). In the remaining species of the hemicultrine group in this study, the end of the dorsal branch widens and is shovel-shaped (Fig. A13c; #42-2).

**Neural spine of the 4th vertebra.** In *Psh. dispar*, *T. houdemeri*, and *T. swinhonis*, the neural spine of the 4th vertebra is wider than that of the 5th one (#43-1). In the remaining species of the hemicultrine group in this study, and *C. erythropterus* and *Paralaubuca barroni*, the neural spine of the 4th vertebra is as wide as that of the 5th one (#43-0). In *R. lineatus*, the neural spine of the 4th vertebra is narrower than that of the 5th one (#43-0).

**Suspensorium.** The parapaphysis of the 4th vertebra comprises 2 parts: a dorsal branch and a pelvic branch. The pelvic branches of the left and right parapaphyses of the 4th vertebra form the suspensorium. In *Psl. engraulis*, the end of the suspensorium extends ventrad over a horizontal through the end of the dorsal branch of the parapaphysis of the 4th vertebra (#44-1). In the remaining species of the hemicultrine group in this study, and *C. erythropterus* and *Paralaubuca barroni*, the end of the suspensorium extends ventrad just to a horizontal through the end of the dorsal branch (#44-0). In *R. lineatus*, the end of suspensorium extends ventrad to a horizontal through the midpoint of the dorsal branch (#44-0).

**Air-bladder.** In *R. lineatus* and *Paralaubuca barroni*, the air-bladder has 2 chambers (Fig. A14a; #45-0). In species of the hemicultrine group in this study, the air-bladder has 2 chambers with a small lobe at the end of the 2nd one (Fig. A14b; #45-1). In *C. erythropterus*, the air-bladder has 3 chambers (Fig. A14c; #45-2).

**Rib before the anterior end of the pelvic girdle on each side of body.** *Hemiculterella macrolepis*, *Hea. sauvagei*, and *C. erythropterus* each has 3 ribs before the anterior end of the pelvic girdle on each side of the body (#46-0). In the remaining species of the hemicultrine group in this study, the number of ribs is 4-6 (#46-1). *Rasborinus lineatus* and *Paralaubuca barroni* each has 1-2 ribs before the end of the pelvic girdle on each side of the body (#46-0).

**Branched pelvic fin rays.** *Pseudolaubuca engraulis*, *T. swinhonis*, and *R. lineatus* each has 7

branched pelvic fin rays (#47-0). *Hemiculter leucisculus* and *Paralaubuca barroni* each has 7 (#47-0) or 8 (#47-1) branched pelvic fin rays. The remaining species of the hemicultrine group in this study and *C. erythropterus* each has 8 branched pelvic fin rays (#47-1).

**Pelvic girdle.** In the hemicultrine group, the pelvic girdle is superficially forked, and therefore the anterior 1/2 of the pelvic girdle is composed of 2 branches: an inner branch and an outer branch which is the longer of the 2. In *Hea. macrolepis*, *Hea. sauvagei*, *Hainania serrata*, *Psh. dispar*, and *Paralaubuca barroni*, the inner branch of the pelvic girdle is narrower than its outer branch (#48-2). In the remaining species of the hemicultrine group in this study and *R. lineatus*, the inner branch of the pelvic girdle is as wide as its outer branch (#48-1). In *C. erythropterus*, the inner branch of the pelvic girdle is wider than its outer branch (#48-0). In *Her. leucisculus*, the outer branch length of the pelvic girdle is 33% of the pelvic girdle length (#49-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, the outer branch length of the pelvic girdle is 50% of the pelvic girdle length (#49-0). In *Paralaubuca barroni*, the outer branch length of the pelvic girdle is 68% of the pelvic girdle length (#49-0).

**Dorsal fin origin.** In *Hea. macrolepis*, *Hea. sauvagei*, *Hainania serrata*, and *Psh. dispar*, the dorsal fin origin is near a vertical through the posterior margin of the pelvic fin base on each side of the body (#50-2). In *Psl. engraulis*, *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the dorsal fin origin is near a vertical through the midpoint of the distance between the origins of the pelvic and anal fins (#50-0). In the remaining species of the hemicultrine group in this study, the dorsal fin origin is near a vertical through a point 25% anteriorly of the distance between the origins of the pelvic and anal fins (#50-1).

**Last unbranched dorsal ray.** In *Hainania serrata*, *T. houdemeri*, and *T. swinhonis*, the last unbranched dorsal ray is serrated posteriorly (#51-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the last unbranched dorsal ray is smooth (#51-0). *Hemiculterella macrolepis*, *Hea. sauvagei*, *Psl. engraulis*, *R. lineatus*, and *Paralaubuca barroni* each has a soft last unbranched dorsal ray (#52-0). Each of the remaining species of the hemicultrine group in this study and *C. erythropterus* has an osseous last unbranched dorsal ray (#52-1).

**Vertebrae between the insertions of the 1st pterygiophores of the dorsal and anal fins.** *Pseudolaubuca engraulis*, *R. lineatus* and *Paralaubuca barroni* each has 5-7 vertebrae between the insertions of the 1st pterygiophores of the dorsal and anal fins (#53-0). In *Hainania serrata* and *Psh. dispar*, the number of vertebrae is 11 (#53-2). In the remaining species of the hemicultrine group in this study and *C. erythropterus*, the number of vertebrae is 9-10 (#53-1).

**Dorsum of body.** In *T. houdemeri*, *T. swinhonis*, *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the dorsum of body is convex around the origin of the dorsal fin (#54-0). In the remaining species of the hemicultrine group in this study, the dorsum of body is flat and straight (#54-1).

**Lateral line.** In *Psl. engraulis*, *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the lateral line curves ventrad smoothly on the sides of the body (#55-0). In the remaining species of the hemicultrine group in this study, the lateral line extends ventrad sharply before the tip of the pectoral fin and has 2 sharp folds respectively near the tip of the pectoral fin and the posterior margin of the anal fin base (#55-1).

**Scales between the pelvic fin origin and lateral line.** *Rasborinus lineatus* has 4 rows of scales between the pelvic fin origin and lateral line (#56-0). *Cultrichthys erythropterus* has 6 rows of scales between the pelvic fin origin and lateral line (#56-0). *Paralaubuca barroni* has 3 rows of scales between the pelvic fin origin and lateral line (#56-0). Species of the hemicultrine group in this study each has only 2 rows of scales between the pelvic fin origin and lateral line (#56-1).

**Color pattern on the sides of the body.** In *Hea. macrolepis*, *Hea. sauvagei*, *T. houdemeri*, and *T. swinhonis*, a broad longitudinal black stripe is present on each side of the body (#57-1). In the remaining species of the hemicultrine group, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, no broad longitudinal black stripe is present on either side of the body (#57-0).

**Ventral keel.** In *Psl. engraulis*, *T. houdemeri*, *T. swinhonis*, and *Paralaubuca barroni*, the ventral keel extends from the isthmus to the anus (#58-2). In *Her. leucisculus* and *C. erythropterus*, the ventral keel extends from the pectoral fin base to the anus (#58-1). In the remaining species of the hemicultrine group in this study and *R. lineatus*, the ventral keel extends from the pelvic fin base to the anus (#58-0).

**Intestine.** In *Her. leucisculus*, *Psh. dispar*, and *R. lineatus*, the total length of the intestine is



longer than the standard length (#59-0). In *Hainania serrata*, *C. erythropterus*, and *Paralaubuca barroni*, the total length of the intestine is equal to the standard length (#59-1). In the remaining species of the hemicultrine group in this study, the total length of the intestine is shorter than the standard length (#59-2).

*Ribs connected to a long, developed parapapophysis on each side of the body.* The ribs connected to a long, developed parapapophysis on each side of the body are the last several ribs on each side of the body, each of which is connected to a long, developed parapapophysis of trunk vertebrae. *Hainania serrata* and *Psh. dispar* have 5 ribs, each of which is connected to a long, developed parapapophysis on each side of the body (#60-1). In the remaining species of the hemicultrine group in this study and *C. erythropterus*, the number of ribs is 3-4 (#60-0). *Rasborinus lineatus* and *Paralaubuca barroni* each has 2 ribs, both of which are connected to long, developed parapapophyses on each side of the body (#60-0).

*Trunk vertebrae with 1 hemal canal.* The last several trunk vertebrae each has 1 hemal canal which is located on the respective vertebra's ventral side. *Hainania serrata* and *Psl. engraulis* have 3 trunk vertebrae each with 1 haemal canal (#61-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the number of trunk vertebrae with 1 hemal canal is 1 or 2 (#61-0).

*Caudal vertebrae.* *Pseudolaubuca engraulis* and *Paralaubuca barroni* each has 23-24 caudal vertebrae (#62-2). In *Hea. macrolepis*, *Hea. sauvagei*, and *C. erythropterus*, the number of caudal vertebrae is 22 (#62-1). In the remaining species of the hemicultrine group in this study, the number of caudal vertebrae is 19-21 (#62-0). *Rasborinus lineatus* has 17 caudal vertebrae (#62-0).

*Hemal spine of the 1st caudal vertebra.* In *Her. leucisculus*, *Psl. engraulis*, *T. houdemeri*, and *T. swinhonis*, a sharp fold occurs along the hemal spine of the 1st caudal vertebra (Fig. A15b; #63-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and *Paralaubuca barroni*, the hemal spine of the 1st caudal vertebra curves slightly and smoothly (Fig. A15a; #63-0). In *Hea. macrolepis*, *Hea. sauvagei*, *R. lineatus*, and *Paralaubuca barroni*, the hemal spine of the 1st caudal vertebra is 50% - 56% as long as that of the 2nd one (#64-0). In the remaining species of the hemicultrine group in this study

and *C. erythropterus*, the hemal spine of the 1st caudal vertebra is 79% - 117% as long as that of the 2nd one (#64-1).

*Caudal vertebrae with 2 hemal canals.* The 1st several caudal vertebrae have 2 hemal canals; each vertebra has 2 hemal canals located at the base of its hemal spine. *Hemiculterella macrolepis*, *Hea. sauvagei*, *Hainania serrata* and *R. lineatus* each has 1 caudal vertebra with 2 hemal canals (#65-0). None of the remaining species of the hemicultrine group in this study or *Paralaubuca barroni* has any caudal vertebra with 2 hemal canals (#65-1). *Cultrichthys erythropterus* has 1 (#65-0) or no (#65-1) caudal vertebra with 2 haemal canals.

*Preanal caudal vertebrae.* The preanal caudal vertebrae are the caudal vertebrae located before the insertion of the 1st pterygiophore of the anal fin. *Pseudohemiculter dispar*, *Psl. engraulis* and *Paralaubuca barroni* each has 2 preanal caudal vertebrae (#66-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus* and *C. erythropterus*, the number of preanal caudal vertebrae is 1 (#66-0).

*Anal fin.* In *R. lineatus*, the outer margin of the anal fin is straight (#67-0). In the species of the hemicultrine group in this study, and *C. erythropterus* and *Paralaubuca barroni*, the outer margin of the anal fin is concave (#67-1).

*Branched anal fin rays.* *Pseudolaubuca engraulis* has 21-24 branched anal fin rays (#68-1). *Cultrichthys erythropterus* and *Paralaubuca barroni* each has 26-30 branched anal fin rays (#68-1). The remaining species of the hemicultrine group in this study and *R. lineatus* each has 12-19 branched anal fin rays (#68-0).

*Pterygiophore of the anal fin.* *Pseudolaubuca engraulis* has 24 pterygiophores of the anal fin (#69-3). *Cultrichthys erythropterus* and *Paralaubuca barroni* each has 27 pterygiophores of the anal fin (#69-3). In *T. houdemeri* and *T. swinhonis*, the number of pterygiophores of the anal fin is 18-19 (#69-2). In *Her. leucisculus*, the number of pterygiophores is 8-12 (#69-0). In the remaining species of the hemicultrine group in this study and *R. lineatus*, the number of pterygiophores is 14-17 (#69-1).

*The last 3 caudal vertebrae.* In *Hainania serrata*, *Psh. dispar*, and *Psl. engraulis*, the neural spine of the last 3 caudal vertebrae is long and extends towards the rear caudal to touch the anterior ends of the caudal fin rays (#70-1). In the remaining species of the hemicultrine group in this study, and *R. lineatus*, *C. erythropterus*, and

*Paralaubuca barroni*, the neural spine of the last 3 caudal vertebrae is short and extends towards the rear caudal but is not near the anterior ends of the caudal fin rays (#70-0).

## DISCUSSION

A 70-character matrix was obtained for the cladistic analysis of the hemicultrine group in this research (Table 1).

When *Rasborinus lineatus* is used as the sole outgroup, sixty-four characters can be polarized (excluding characters 1, 13, 28, 45, 56, and 67 as unpolarized characters) and 54 of them (excluding characters 7, 11, 18, 21, 32 - 34, 44, 49, and 68 as autapomorphies) are potentially informative in the phylogenetic reconstruction. The 54 informative characters give a single most-parsimonious tree (Fig. 2) of 111 steps, a consistency index (CI) of 0.67, a retention index (RI) of 0.67 and a homoplasy index (HI) of 0.41 when all multi-state characters are run ordered; the same single topological tree of 105 steps, a CI of 0.69, a RI of 0.67, and a HI of 0.39 with all clades (except for the clade of the genera *Pseudolaubuca* + *Toxabramis*) supported by high bootstrap values (greater than 60%) which are produced when all multi-state characters are run unordered (Tables 2, 3). When *Cultrichthys erythropterus* is used as the sole outgroup, sixty-one characters can be polarized (excluding characters 1, 4, 5, 13, 28, 45, 56, 65, and 67 as unpolarized characters), and 53 of them (excluding characters 7, 11, 12, 18, 21, 32, 44, and 49 as autapomorphies) are potentially informative in the phylogenetic reconstruction. The 53 informative characters give a single most-parsimonious tree of 109 steps, a CI of 0.67, a RI of 0.66, and a HI of 0.40 when all multi-state characters are run

ordered, which also has the same topology when *R. lineatus* is used as the sole outgroup. The same single topological tree of 104 steps, a CI of 0.69, a RI of 0.66, and a HI of 0.38 with all clades supported by high bootstrap values (greater than 60%) which are produced when all multi-state characters are run unordered.

Yue and Luo (1996) considered the hemicultrine group to be monophyletic based on the similarity of 6 characters of the group. Following the methods of cladistic analysis, when *R. lineatus* is used as the sole outgroup, the tree of the generic relationships within the hemicultrine group indicates that it is monophyletic, and is supported by 14-15 synapomorphies (Fig. 3). When *C. erythropterus* is used as the sole outgroup, the phylogenetic tree of the hemicultrine group indicates that it is monophyletic, and is supported by 9 synapomorphies.

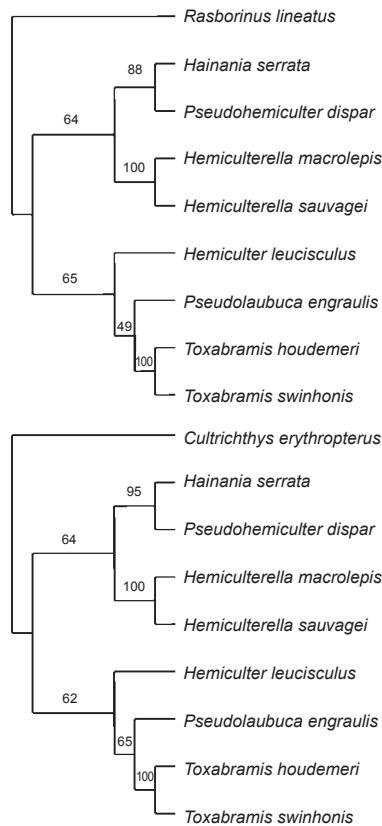
To further test the monophyly of the hemicultrine group, dataset analysis was performed using by Paup (vers. 3.11, Swofford 1993) using *R. lineatus* as the sole outgroup with *C. erythropterus* and *Paralaubuca barroni* included in the ingroup. When *R. lineatus* is used as the sole outgroup with *C. erythropterus* and *Paralaubuca barroni* included in the ingroup, sixty-nine characters can be polarized (excluding characters 67 unpolarized characters), and 62 of them (excluding characters 1, 7, 11, 18, 28, 44, and 49 as autapomorphies) are potentially informative in the phylogenetic reconstruction. The 62 informative characters give a single most-parsimonious tree (Fig. 4) of 160 steps, a CI of 0.57, a RI of 0.58 and a HI of 0.51 when all multi-state characters are run ordered; the same single topological tree of 152 steps, a CI of 0.59, a RI of 0.59, and a HI of 0.49 with all clades (except for clades 1, 5, and 6) supported by high bootstrap values (greater than 55%) which

**Table 1.** Character state distribution of the hemicultrine group in the subfamily Cultrinae

Species	Character no.																			
	123	4	5	6789012345678	9	0	1	2	2222	2	22	3	3333333334	4	44444	4	4455555555566666	6	66667	
<i>Rasborinus lineatus</i>	110	1	0	1000000001000	0	0	0	0	0000	0	00	0	0000000000	0	10000	0	1000000000000000	0	00010	
<i>Cultrichthys erythropterus</i>	000	(12)	(01)	2000101001000	1	0	0	1	1000	1	10	1	0011000100	0	10020	1	00001100001100101	(01)	01130	
<i>Paralaubuca barroni</i>	121	0	0	2010100012000	0	0	1	0	1000	2	00	1	0100110020	1	00000	(01)	20000000002100200	1	11130	
<i>Hainania serrata</i>	121	1	0	1000101100000	0	1	0	0	0000	2	00	1	0000010100	1	00011	1	20211211100111001	0	01011	
<i>Hemiculter leucisculus</i>	110	1	0	1000001101000	0	0	0	1	0000	2	01	1	0001100101	1	20011	(01)	11101111101000011	1	01000	
<i>Hemiculterella macrolepis</i>	121	0	0	2000001100100	0	1	0	1	0000	2	01	0	0000010110	0	10010	1	20200111110200100	0	01010	
<i>Hemiculterella sauvagei</i>	121	0	0	2000001100100	(01)	(01)	0	(01)	0000	2	00	0	0000010110	0	10010	1	20200111110200100	0	01010	
<i>Pseudohemiculter dispar</i>	121	1	0	1000101100000	0	1	0	0	0000	2	00	(01)	0000001100	(01)	01011	1	20201211100010001	1	11011	
<i>Pseudolaubuca engraulis</i>	111	1	0	0110110111001	0	0	1	1	0000	0	01	1	0110111001	1	20111	0	10000010102201211	1	11131	
<i>Toxabramis houdemeri</i>	110	2	1	1011101111010	1	1	0	0	1111	0	00	1	1000010001	1	21011	1	1011101112200011	1	01020	
<i>Toxabramis swinhonis</i>	110	(12)	1	1011101111010	1	1	0	0	1111	(02)	00	1	1000010001	1	21011	0	1011101112200011	1	01020	

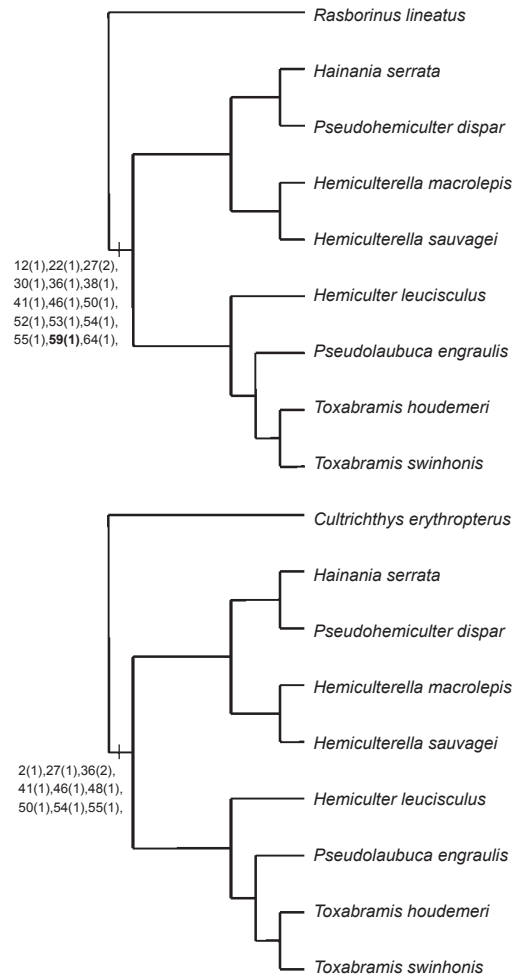
are produced when all multi-state characters are run unordered (Table 2). The tree in figure 5 shows that the clade including the hemicultrine group has the same topology as the tree in figure 1. In this tree, the genus *Paralaubuca* is the sister group of the genus *Pseudolaubuca* and both form a monophyletic group supported by 12 synapomorphies. As a result, the hemicultrine group + the genus *Paralaubuca* form a monophyletic group supported by 9 synapomorphies. Therefore, the hemicultrine group is not a monophyletic group but a paraphyletic group. Even so, it is certain that the monophyly of the hemicultrine group needs to be eventually tested by a more extensive examination of the generic relationships within the entire Cultrinae subfamily.

The following discussion is based on the tree of generic relationships within the hemicultrine group obtained using *R. lineatus* as the sole out-



**Fig. 2.** Trees of the generic relationships within the hemicultrine group using *Rasborinus lineatus* or *Cultrichthys erythropterus* as the sole outgroup, respectively. The number above each branch represents the bootstrap value, and the bootstrap analyses were performed by PAUP (vers. 3.11, Swofford 1993) with all multistate characters run as 'unordered'.

group with *C. erythropterus* and *Paralaubuca barroni* included in the ingroup when all multi-state characters are run unordered (Fig. 5). According to the tree in figure 5, the hemicultrine group + the genus *Paralaubuca* form a monophyletic group, i.e., clade 1, which is supported by 9 synapomorphies. Members of this clade occur in the far-eastern region of Russia, the northern Korean Peninsula, Vietnam, Thailand, Burma, the Greater Sundas (Malay Peninsula, Sumatra, Java, and Borneo) and China except for the Qinghai-Tibetan Plateau and Xinjiang (Fig. 1). The tree shows that the monophyletic group comprises 2 smaller monophyletic groups—a pair of sister groups. The



**Fig. 3.** Trees of generic relationships within the hemicultrine group using *Rasborinus lineatus* or *Cultrichthys erythropterus* as the sole outgroup, respectively, and with all multistate characters run as 'ordered' or 'unordered'. The numbers are synapomorphies, states of which are indicated by the numbers in parentheses. The number in boldface is 1 of synapomorphies obtained by Paup (vers. 3.11, Swofford 1993) with all multistate characters run as 'ordered'.

genera *Hainania* + *Pseudohemiculter* + *Hemiculterella* form a monophyletic group, i.e., clade 2, which is supported by 8 synapomorphies including 4 homoplastic changes and 2 reversed characters (Table 4). The genera *Hemiculter* + *Toxabramis* + *Pseudolaubuca* + *Paralaubuca* form another monophyletic group, i.e., clade 7, which is supported by 6 synapomorphies including 1 homoplastic change and 1 reversed character.

The monophyletic group *Hemiculterella* + *Pseudohemiculter* + *Hainania* is distributed only in the northern Vietnam and South China, but not Taiwan, but its sister group *Hemiculter* + *Toxabramis* + *Pseudolaubuca* + *Paralaubuca* covers the far-eastern region of Russia, the northern Korean Peninsula, Vietnam, Thailand, Burma, the Greater Sundas, and China except for the Qinghai-Tibetan Plateau and Xinjiang. So this pair of sister groups show an overlapping distribution pattern, but only by a small portion.

The genera *Hainania* + *Pseudohemiculter* form a monophyletic group, i.e., clade 3, which is supported by 5 synapomorphies including 2 homoplastic changes and 1 reversed character. This monophyletic group is distributed in the northern Vietnam and South China but not Taiwan; its sister group, the genus *Hemiculterella*, is a monophyletic group, i.e., clade 4, which is supported by 13 synapomorphies including 7 homoplastic changes and 6 reversed characters, and occurs in the

**Table 2.** Comparison of tree statistics of the generic relationships for the hemicultrine group in the subfamily Cultrinae (first with multistate characters run as ordered transformation series, then with multistate characters run unordered) using different outgroups

Outgroup	Tree length	Number of polarized characters	Number of informative characters	Consistency index	Retention index	Homoplasy index
<b>A</b>	111	64	54	0.67	0.67	0.41
	105	64	54	0.69	0.67	0.39
<b>B</b>	109	61	53	0.67	0.66	0.40
	104	61	53	0.69	0.66	0.38
<b>C</b>	160	67	62	0.57	0.58	0.51
	152	67	62	0.59	0.59	0.49

**A**, *Rasborinus lineatus* only; **B**, *Cultrichthys erythropterus* only; **C**, *Rasborinus lineatus* only with *Cultrichthys erythropterus* and *Paralaubuca barroni* included in the ingroup.

upper Yangtze River, the Qiantang River, the Pearl River and the Lancang River. So this pair of sister groups still show an overlapping distribution pattern; the size of the range of the genus *Hemiculterella* is slightly smaller than that of the monophyletic group.

The genera *Hainania* and *Pseudohemiculter* represent a terminal pair of sister groups. The genus *Hainania* is a monophyletic group, i.e., clade 5, which is supported by 3 synapomorphies including 2 homoplastic changes, and is only found on Hainan Island, China. Its sister group, the genus *Pseudohemiculter*, forms a monophyletic

**Table 3.** Consistency index (CI) and retention index (RI) for each informative character on the phylogenetic tree in figure 5

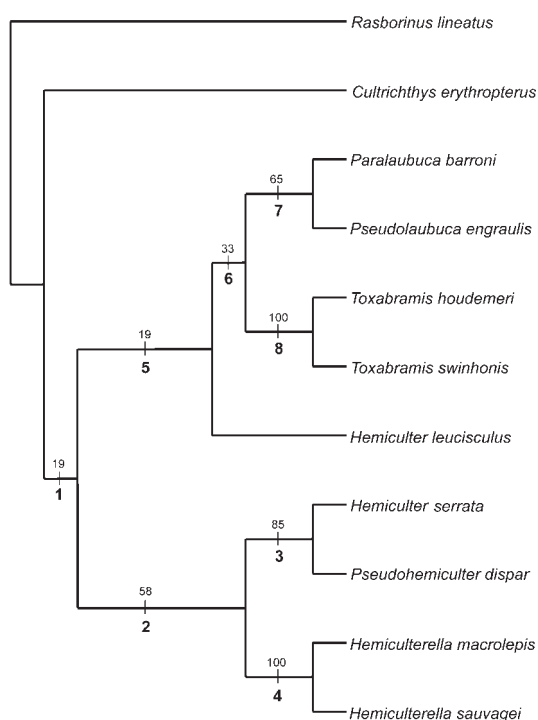
Character	CI	RI	Character	CI	RI
<b>1</b>	—	—	<b>36</b>	0.33	0.33
<b>2</b>	0.67	0.75	<b>37</b>	0.50	0.00
<b>3</b>	0.50	0.75	<b>38</b>	0.50	0.75
<b>4</b>	0.80	0.50	<b>39</b>	1.00	1.00
<b>5</b>	1.00	1.00	<b>40</b>	0.50	0.67
<b>6</b>	0.50	0.33	<b>41</b>	0.67	0.67
<b>7</b>	—	—	<b>42</b>	0.67	0.80
<b>8</b>	1.00	1.00	<b>43</b>	0.50	0.50
<b>9</b>	1.00	1.00	<b>44</b>	—	—
<b>10</b>	0.33	0.33	<b>45</b>	0.67	0.00
<b>11</b>	—	—	<b>46</b>	0.33	0.50
<b>12</b>	0.50	0.50	<b>47</b>	0.60	0.00
<b>13</b>	0.50	0.50	<b>48</b>	0.67	0.75
<b>14</b>	1.00	1.00	<b>49</b>	—	—
<b>15</b>	1.00	1.00	<b>50</b>	0.67	0.80
<b>16</b>	1.00	1.00	<b>51</b>	0.50	0.50
<b>17</b>	1.00	1.00	<b>52</b>	0.33	0.50
<b>18</b>	—	—	<b>53</b>	0.67	0.67
<b>19</b>	0.67	0.50	<b>54</b>	0.33	0.50
<b>20</b>	0.67	0.75	<b>55</b>	0.50	0.67
<b>21</b>	1.00	1.00	<b>56</b>	0.50	0.50
<b>22</b>	0.40	0.00	<b>57</b>	0.50	0.67
<b>23</b>	0.33	0.33	<b>58</b>	0.67	0.75
<b>24</b>	1.00	1.00	<b>59</b>	0.40	0.25
<b>25</b>	1.00	1.00	<b>60</b>	1.00	1.00
<b>26</b>	1.00	1.00	<b>61</b>	0.50	0.00
<b>27</b>	0.60	0.00	<b>62</b>	0.67	0.67
<b>28</b>	—	—	<b>63</b>	0.50	0.67
<b>29</b>	0.33	0.00	<b>64</b>	0.33	0.33
<b>30</b>	0.67	0.50	<b>65</b>	0.67	0.67
<b>31</b>	1.00	1.00	<b>66</b>	0.50	0.50
<b>32</b>	1.00	1.00	<b>67</b>	+	+
<b>33</b>	0.50	0.00	<b>68</b>	0.50	0.50
<b>34</b>	0.50	0.00	<b>69</b>	0.75	0.67
<b>35</b>	0.50	0.50	<b>70</b>	0.50	0.50

CI and RI were calculated using PAUP (vers. 3.11, Swofford 1993) with multistate characters run unordered.

Unpolarized characters are indicated by the symbol "+", and autapomorphies indicated by the symbol "-" in the table.

group, i.e., clade 6, which is supported by 5 synapomorphies including 5 homoplastic changes and 1 reversed character, and occurs in the northern Vietnam and South China, but not Taiwan. So the distributional area of the former is only a very small part of that of the latter.

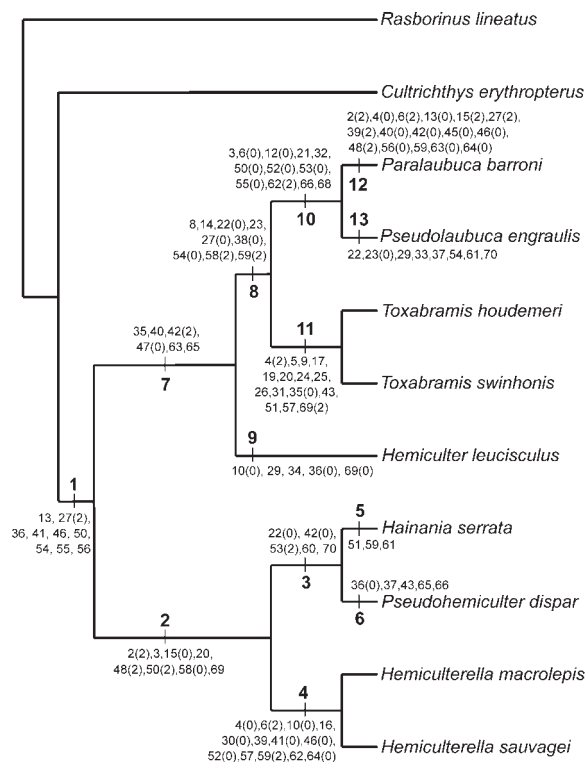
The genera *Toxabramis* + *Pseudolaubuca* + *Paralaubuca* form a monophyletic group, i.e., clade 8, which is supported by 9 synapomorphies including 2 homoplastic changes and 4 reversed characters. It ranges from the Liao River southwards to Hainan Island in China, but not the Qinghai-Tibetan Plateau or Xinjiang, and it also occurs in the northern Korean Peninsula, Vietnam, Thailand, Burma, and the Greater Sundas, but is not found in Taiwan. Its sister group, the genus *Hemiculter*, is a monophyletic group, i.e., clade 9, which is supported by 5 synapomorphies including 3 homoplastic changes and 2 reversed characters, and occurs in the far-eastern region of Russia, the northern Korean Peninsula, the northern Vietnam, and China except for the Qinghai-Tibetan Plateau and Xinjiang. So this pair of sister groups also



**Fig. 4.** Tree of the generic relationships within the hemicultrine group using *Rasborinus lineatus* as the sole outgroup and with *Cultrichthys erythropterus* and *Paralaubuca barroni* included in the ingroup. Numbers in boldface are clade numbers, while the remaining ones represent bootstrap values. Bootstrap analyses were performed using PAUP (vers. 3.11, Swofford 1993) with all multistate characters run as 'unordered'.

show an overlapping distribution pattern. The range of the monophyletic group, the genera *Toxabramis* + *Pseudolaubuca* + *Paralaubuca*, is larger than that of its sister group, the genus *Hemiculter*.

The genera *Pseudolaubuca* + *Paralaubuca* represent a monophyletic group, i.e., clade 10, which is supported by 12 synapomorphies including 3 homoplastic changes and 5 reversed characters, and is distributed on the mainland from the Liao River southwards to the Red River in China except for the Qinghai-Tibetan Plateau and Xinjiang and also occurs in the northern Korean Peninsula, Vietnam, Thailand, Burma, and the Greater Sundas. Its sister group, the genus *Toxabramis*, is a monophyletic group, i.e., clade 11, which is supported by 15 synapomorphies including 4 homoplastic changes and 1 reversed character, and is distributed in China from the Yellow River southwards to Hainan Island exclud-



**Fig. 5.** Tree of the generic relationships within the hemicultrine group using *Rasborinus lineatus* as the sole outgroup and with *Cultrichthys erythropterus* and *Paralaubuca barroni* included in the ingroup. Numbers in boldface are clade numbers, while the remaining ones along each branch are synapomorphies obtained by Paup (vers. 3.11, Swofford 1993) with all multistate characters run as 'unordered'. Character states are indicated by the numbers in parentheses, and character states with no indication are 1.

ing the Qinghai-Tibetan Plateau, Xinjiang, and the Red River; it is not found in Taiwan. The range of the former is much larger than that of the latter.

The genera *Pseudolaubuca* and *Paralaubuca* belong to another terminal pair of sister groups. The genus *Paralaubuca* forms a monophyletic group, i.e., clade 12, which is supported by 16 synapomorphies including 5 homoplastic changes and 7 reversed characters, and occurs in Vietnam (except for the Red River), Thailand, Burma, the Greater Sundas, and the Lancang River in China. The genus *Pseudolaubuca* is its sister group which represents a monophyletic group, i.e., clade 13, which is supported by 8 synapomorphies including 4 homoplastic changes and 1 reversed character, and is distributed in the mainland from the Liao River southwards to the Pearl River and the Red River in China except for the Qinghai-Tibetan Plateau and Xinjiang and also ranges to the northern Korean Peninsula and the northern Vietnam (the Red River). So this pair of sister groups are a typical case of vicariant speciation.

The tree of the generic relationships and the zoogeography of the monophyletic group comprising the hemicultrine group and the genus *Paralaubuca* reveal that (1) the sister groups of the monophyletic group show both overlapping and vicariant distribution patterns, and (2) the generic distribution pattern of the monophyletic group maybe have resulted from both dispersal and vicariance events. The cladistic dispersal method was first proposed by Brundin (1966) and is very useful for deciding the origin center and dispersal

routes of the species groups. Following the cladistic dispersal method (Brundin 1966), the tree and the distribution pattern of the monophyletic group indicate that the origin center of the group is probably situated on the mainland from the Yangtze River to the Pearl River and on Hainan Island in China. The cladistic vicariance method attempts to guess the sites of vicariant speciation of species group and determines the relationships of different rivers or ranges in which the species group live (Platnick et al. 1978). According to the cladistic vicariance method, vicariance events between the Red River and the Lancang River probably resulted in the vicariant speciation of the genera *Pseudolaubuca* and *Paralaubuca*, which also indicates the distant relationships between the Red River and the Lancang River in Asia. Therefore, the distribution pattern of the monophyletic group is due to both dispersal events from the origin center and to vicariance events between the Red River and the Lancang River.

Of the 7 genera in the monophyletic group comprising the hemicultrine group and the genus *Paralaubuca*, there is 1 genus (*Hemiculter*) which occurs in Taiwan, one genus (*Paralaubuca*) in Thailand, Burma, and Indonesia (Sumatra, Java, and Borneo), and 4 genera (*Hemiculter*, *Pseudohemiculter*, *Toxabramis*, and *Hainania*) on Hainan Island, but none is distributed in the Japanese Archipelago (Fig. 1). The island distributional pattern of the monophyletic group shows that: (1) during the geological history of Asia, the Japanese Archipelago most likely first separated

**Table 4.** Homoplastic changes and reversed characters of synapomorphies in each clade on the phylogenetic tree in figure 5

Clade no.	2	3	4	5	6	7	8	9	10	11	12	13
	2 (1→2)	22 (1→0)	4 (1→0)	51 (0→1)	36 (1→0)	65 (0→1)	22 (1→0)	10 (1→0)	3 (0→1)	20 (0→1)	2 (1→2)	29 (0→1)
	3 (0→1)	70 (0→1)	10 (1→0)	61 (0→1)	37 (0→1)		59 (0→2)	29 (0→1)	52 (1→0)	43 (0→1)	4 (1→0)	37 (0→1)
	20 (0→1)		46 (1→0)		43 (0→1)			36 (1→0)	66 (0→1)	51 (0→1)	46 (1→0)	61 (0→1)
Homoplastic changes	48 (1→2)		52 (1→0)		65 (0→1)					57 (0→1)	48 (1→2)	70 (0→1)
			57 (0→1)		66 (0→1)						64 (1→0)	
			59 (0→2)									
			64 (1→0)									
Total	4	2	7	2	5	1	2	3	3	4	5	4
	58 (1→0)	22 (1→0)	10 (1→0)		36 (1→0)	47 (1→0)	22 (1→0)	10 (1→0)	12 (1→0)	35 (1→0)	13 (1→0)	23 (1→0)
	69 (3→1)		30 (1→0)				27 (2→0)	36 (1→0)	50 (1→0)		40 (1→0)	
Reversed characters			41 (1→0)				38 (1→0)		52 (1→0)		45 (1→0)	
			46 (1→0)				54 (1→0)		53 (1→0)		46 (1→0)	
			52 (1→0)						55 (1→0)		56 (1→0)	
			64 (1→0)								63 (1→0)	
											64 (1→0)	
Total	2	1	6		1	1	4	2	5	1	7	1

The synapomorphies were calculated using PAUP (vers. 3.11, Swofford 1993) with multistate characters run unordered. Clade numbers correspond to the numbers in boldface used in figure 5. Changes in character states are shown in parentheses.

from the Asian mainland, and while Indonesia was probably the last to be completely isolated from the Asian mainland; Taiwan was completely isolated from the Asian mainland earlier than Hainan Island; and (2) the group was probably originated after the Japanese Archipelago was separated from the Asian mainland at the beginning of the Quaternary Period in the Cenozoic (Department of Geography, Nanjing Univ. 1961), but before Taiwan, Hainan Island, and Indonesia were completely separated from the Asian mainland after the ice age in the Quaternary Period. The trees of the generic relationships (Fig. 5) and the island distributional pattern of this monophyletic group reveal that the speciation of the genus *Hemiculter* probably occurred the earliest in the group, and those of the genera *Pseudolaubuca*, *Paralaubuca*, and *Hainania* possibly occurred the latest. The genus *Hemiculter* is at the base of clade 7 and is broadly distributed in the far-eastern region of Russia, the northern Korean Peninsula, the northern Vietnam, China including Hainan Island, and Taiwan but not the Japanese Archipelago, so it should have originated after the Japanese Archipelago was isolated from the Asian mainland but before both Taiwan and Hainan Island were separated. Neither genera of *Pseudohemiculter* nor *Toxabramis* is a basal clade in figure 5, and they range over the Chinese mainland and Hainan Island, so their speciations probably occurred between the time when Taiwan and Hainan Island were completely separated from the Asian mainland. The genus *Hemiculterella* which is situated at the base of clade 2 is distributed only in mainland South China, but the genus *Pseudohemiculter*, a terminal monophyletic group of clade 2 ranges over the South China mainland and Hainan Island. Therefore it is possible that the genus *Hemiculterella* also differentiated to the generic level between the time when Taiwan and Hainan Island were completely separated from the Asian mainland. The genus *Hemiculterella* was perhaps previously distributed on Hainan Island, but now it has disappeared from the island. The genus *Hainania*, which is a terminal monophyletic group of clade 2, occurs only on Hainan Island, and therefore the genus should have originated after the complete segregation of the Japanese Archipelago, Taiwan, and Hainan Island from the Asian mainland. The genera *Pseudolaubuca* and *Paralaubuca* are 2 terminal monophyletic groups of clade 7 and form a pair of sister groups. Because neither is distributed in the Japanese Archipelago, Taiwan, nor Hainan Island, their spe-

ciations should have occurred after these areas were completely isolated from the Asian mainland. The genus *Pseudolaubuca* ranges north and east to the Red River, but the genus *Paralaubuca* occurs in the south and west to the Lancang River including Thailand, Burma, and the Greater Sundas, so this pair of sister groups probably originated from vicariance events between the Red River and the Lancang River after the Japanese Archipelago, Taiwan, and Hainan Island were completely isolated from the Asian mainland but before the segregation of Indonesia from the Asian mainland. Of the 7 genera, both genera of *Hemiculterella* and *Paralaubuca* occur in the Lancang River. Therefore, the genus *Hemiculterella* ought to have originated before the vicariance events between the Red River and the Lancang River but the speciation of the genus *Pseudohemiculter* probably occurred after the vicariance events.

In the genera of *Toxabramis* and *Hainania* within the hemicultrine group, the last unbranched dorsal ray is serrated posteriorly; the remaining genera within the subfamily Cultrinae all have a smooth last unbranched dorsal ray. So it seems that the genus *Toxabramis* is a closest relative to the genus *Hainania* in the hemicultrine group. However, the genus *Toxabramis* was found to differ from the genus *Hainania* in 31 morphological characters (characters 2, 3, 5, 8, 9, 14, 15, 17, 19, 23-26, 31, 38, 40, 42, 43, 48, 50, 53, 54, 57-61, 63, 65, 69, and 70) in this research. For example, the genus *Toxabramis* has 2 rows of pharyngeal teeth on each pharyngeal bone, a ventral keel extending from the isthmus to the anus, an intestinal length which is shorter than the standard length, and a broad longitudinal black stripe present on each side of the body, but neither a notch at the tip of the upper jaw nor a process at the tip of the lower jaw; while the genus *Hainania* has 3 rows of pharyngeal teeth on each pharyngeal bone, a ventral keel extending from the pelvic fin base to the anus, an intestinal length which is equal to the standard length, a notch at the tip of the upper jaw and a process at the tip of the lower jaw, but no broad longitudinal black stripe on either side of the body. The phylogenetic tree in figure 5 shows that the genus *Toxabramis* and the genus *Hainania* respectively belong to clades 2 and 7. Therefore both these genera are distant relatives of each other in the monophyletic group comprising the hemicultrine group and the genus *Paralaubuca*.

## MATERIALS EXAMINED

Specimens examined belong to the collections of the Kunming Institute of Zoology, Chinese Academy of Sciences except for specimens of the species *Hainania serrata* which were donated by the Hydrobiology Institute, Chinese Academy of Sciences, Wuhan, Hubei. Numbers and standard lengths (mm) of specimens are given in parentheses. The symbol "S" in parentheses indicates skeletal specimens. Ingroup: *Hainania serrata* (2, 98.0-109.0; 1S, 109.0), *Hemiculter leucisculus* (10, 104.0-123.0; 2S, 87.0-110.0), *Hemiculterella macrolepis* (10, 86.0-107.0; 2S, 86.0-97.0), *Hemiculterella sauvagei* (10, 85.0-98.0; 1S, 84.0), *Pseudohemiculter dispar* (9, 63.5-216.0; 1S, 101.0), *Pseudolaubuca engraulis* (3, 122.0-142.0; 1S, 126.0), *Toxabramis houdemeri* (10, 56.0-90.0; 3S, 72.5-97.0), *Toxabramis swinhonis* (10, 88.0-116.0; 3S, 94.0-95.0) and *Paralaubuca barroni* (10, 71.0-114.0; 1S, 101.0). Outgroups: *Rasborinus lineatus* (10, 71.0-88.0; 1S, 78.0) and *Cultrichthys erythropterus* (10, 108.0-152.0; 2S, 109.0-128.0).

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## APPENDIX

Fig. A1

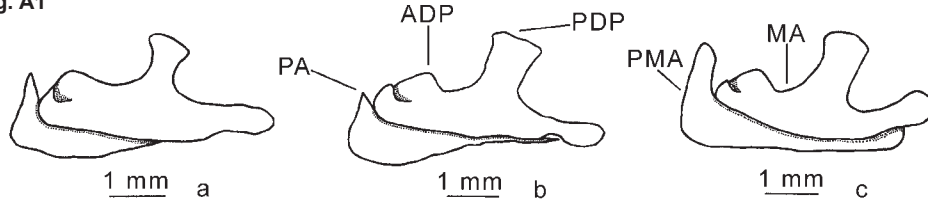


Fig. A2

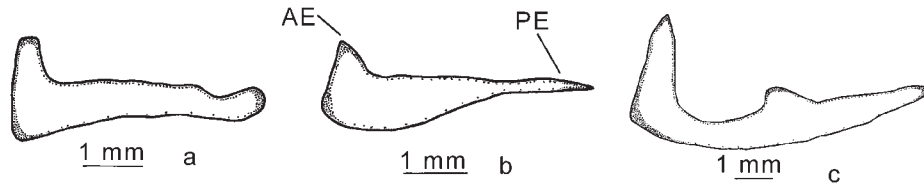


Fig. A3

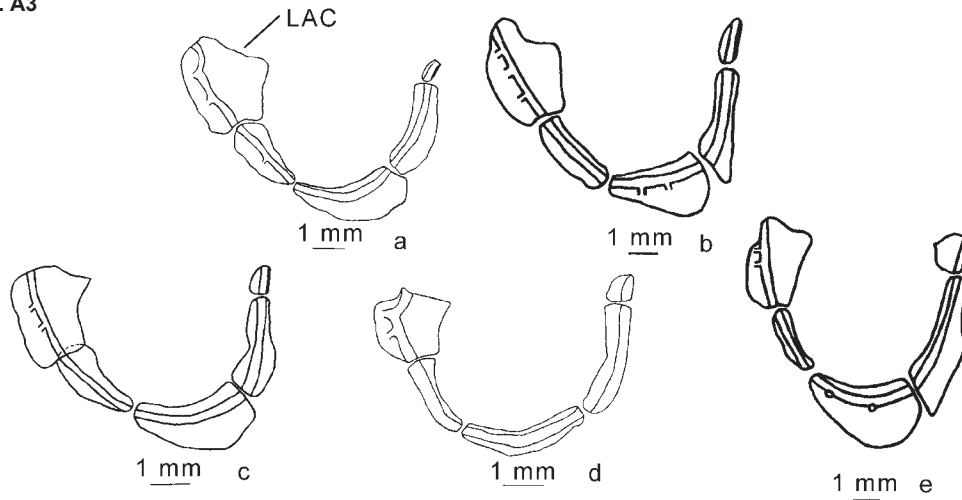
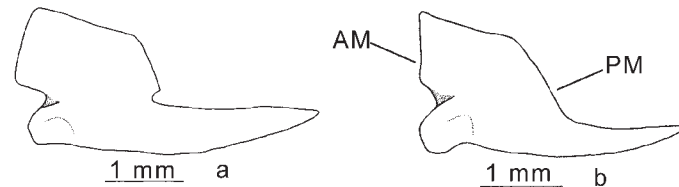


Fig. A4

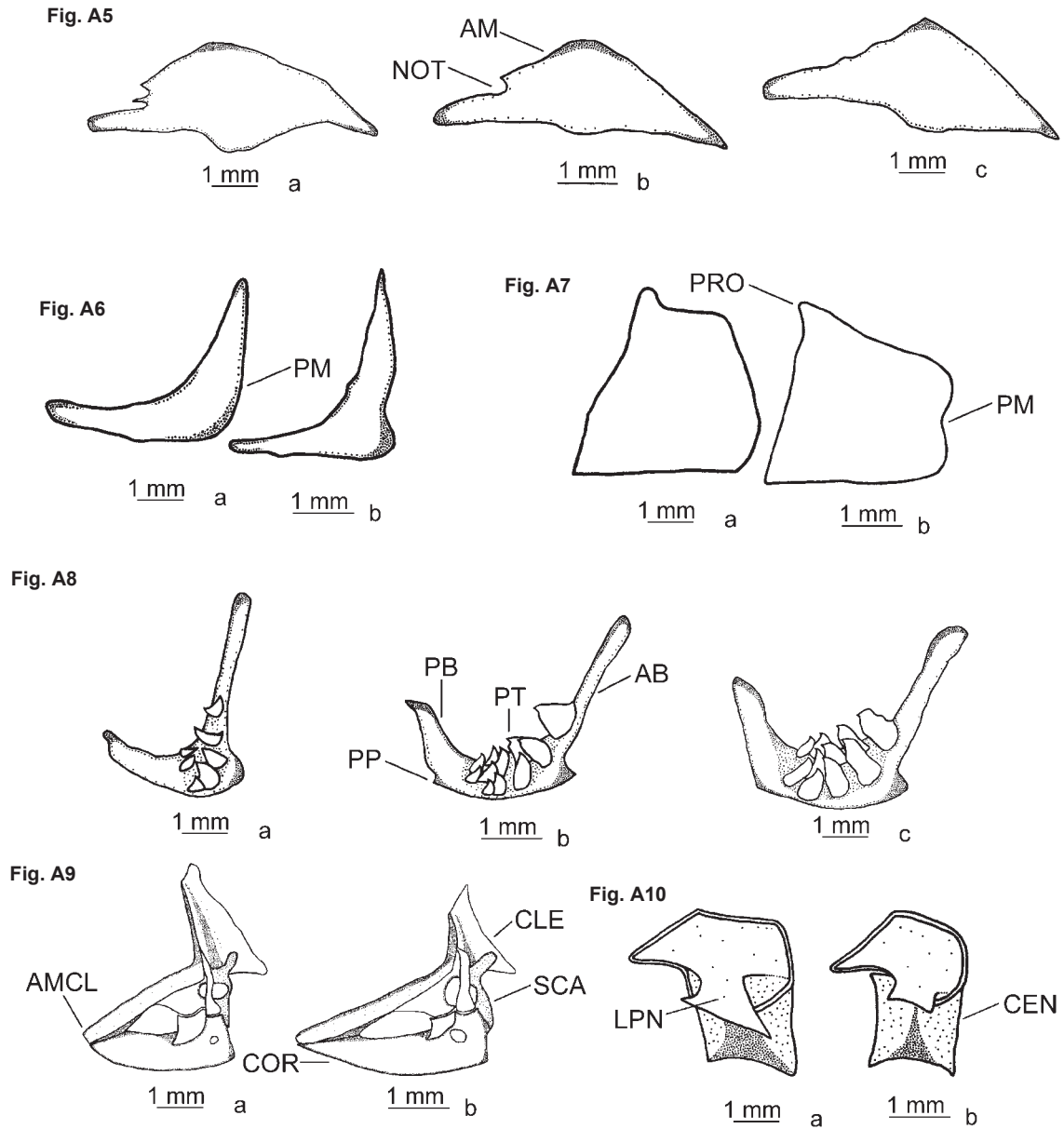


**Fig. A1.** Left lateral view of the left premaxilla and maxilla. (a) *Hemiculter leucisculus*; (b) *Hemiculterella macrolepis*; (c) *Toxabramis houdemeri*. ADP, anterodorsal process on maxilla; MA, maxilla; PA, process at the anterior end of the premaxilla; PDP, post-dorsal process on the maxilla; PMA, premaxilla.

**Fig. A2.** Left lateral view of the left premaxilla. (a) *Toxabramis houdemeri*; (b) *Hemiculterella macrolepis*; (c) *Cultrichthys erythropterus*. AE, anterior end; PE, posterior end.

**Fig. A3.** Left lateral view of the left infraorbital series. (a) *Hemiculterella macrolepis*; (b) *Pseudolaubuca engraulis*; (c) *Toxabramis houdemeri*; (d) *Rasborinus lineatus*; (e) *Paralaubuca barroni*. LAC, lacrimal.

**Fig. A4.** Left lateral view of the left quadrate. (a) *Hemiculter leucisculus*; (b) *Hemiculterella macrolepis*. AM, anterior margin; PM, posterior margin.



**Fig. A5.** Left lateral view of the left pterotic. (a) *Pseudolaubuca engraulis*; (b) *Hemiculterella macrolepis*; (c) *Hemiculter leucisculus*. AM, anterior margin; NOT, notch.

**Fig. A6.** Left lateral view of the left prepercular. (a) *Toxabramis swinhonis*; (b) *Pseudohemiculter dispar*. PM, posterior margin.

**Fig. A7.** Left lateral view of the left opercular. (a) *Hemiculterella macrolepis*; (b) *Pseudolaubuca engraulis*. PM, posterior margin; PRO, process.

**Fig. A8.** Ventral view of the left pharyngeal bone. (a) *Toxabramis houdemeri*; (b) *Hemiculterella macrolepis*; (c) *Cultrichthys erythropterus*. AB, anterior branch; PT, pharyngeal tooth; PB, posterior branch; PP, posterior process.

**Fig. A9.** Left lateral view of the right pectoral girdle. (a) *Hemiculterella sauvagei*; (b) *Hemiculter leucisculus*. AMCL, anterior margin of the cleithrum; CLE, cleithrum; COR, coracoid; SCA, scapula.

**Fig. A10.** Left lateral view of the 3rd vertebra. (a) *Pseudolaubuca engraulis*; (b) *Toxabramis swinhonis*. CEN, centrum; LPN, lateral process of the neural arch.

Fig. A 11

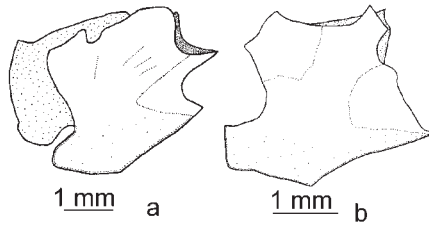


Fig. A12

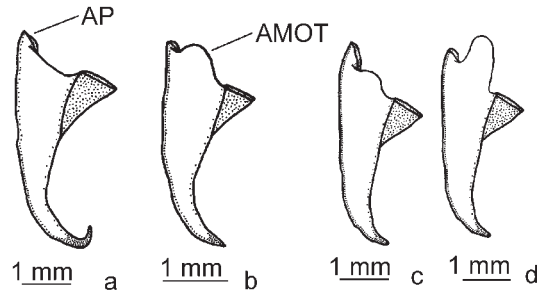


Fig. A13

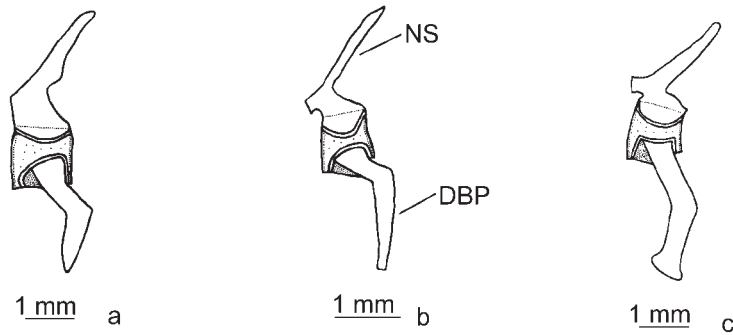


Fig. A14

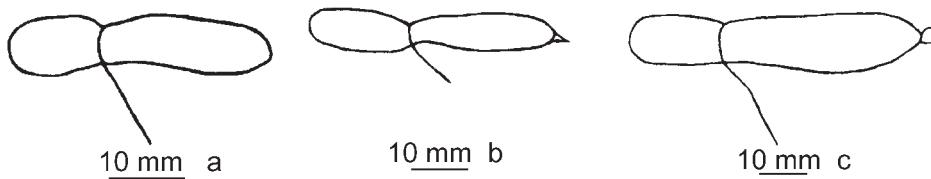
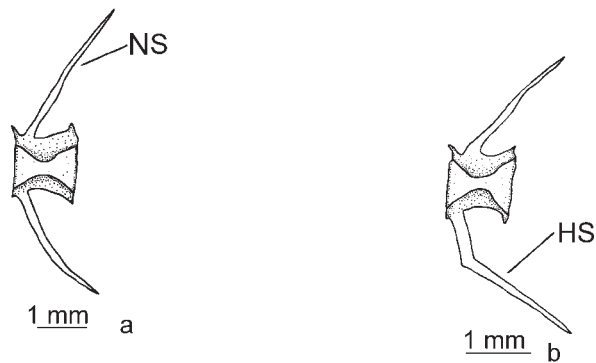


Fig. A15



**Fig. A11.** Left lateral view of the neural complex. (a) *Hemiculter leucisculus*; (b) *Pseudolaubuca engraulis*.

**Fig. A12.** Left lateral view of the left tripus. (a) *Hemiculter leucisculus*; (b) *Hemiculterella macrolepis*; (c) *Pseudohemiculter dispar*; (d) *Paralaubuca barroni*. AMOT, anterior margin on the outer side of the tripus; AP, anterior process.

**Fig. A13.** Left lateral view of the 4th vertebra. (a) *Hainania serrata*; (b) *Hemiculterella macrolepis*; (c) *Hemiculter leucisculus*. DBP, dorsal branch of the parapophysis; NS, neural spine.

**Fig. A14.** Left lateral view of the air-bladder. (a) *Rasborinus lineatus*; (b) *Hemiculter leucisculus*; (c) *Cultrichthys erythropterus*.

**Fig. A15.** Left lateral view of the 1st caudal vertebra. (a) *Pseudohemiculter dispar*; (b) *Pseudolaubuca engraulis*. HS, hemal spine; NS, neural spine.