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Phylogeny of the Genus *Pseudecheneis* (Sisoridae) with an Explanation of Its Distribution Pattern

Wei Zhou* and Yong-Wu Zhou

Faculty of Conservation Biology, Southwest Forestry College, Kunming, Yunnan 650224, China

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Wei Zhou and Yong-Wu Zhou (2005) Phylogeny of the genus *Pseudecheneis* (Sisoridae) with an explanation of its distribution pattern. *Zoological Studies* **44**(3): 417-433. In the present paper, the cladistics method was used to analyze the phylogenetic relationships of 6 recorded species in the genus *Pseudecheneis*. *Bagarius yarrelli* and *Glyptothorax honghensis* were designated as outgroup species. Seventy-three characters of external morphology, internal myology, and osteology were chosen for comparison. Five ingroup species were included, but not *P. sympelvicus* because the examination of its myological and osteological characters is incomplete. All characters were set as unordered with equal weighting, and the data matrix produced a single most-parsimonious tree with a tree length of 110 steps, a consistency index of 0.7364, and a retention index of 0.6947. Meanwhile, a bootstrap test was conducted to verify the reliability of the results. The matrix was analyzed for different conditions: *P. sympelvicus* was combined into the ingroup and all characters were ordered. Each method yielded a single most-parsimonious phylogenetic tree whose structure was completely consistent with each other. The cladogram shows that all species in *Pseudecheneis* form a monophyletic group and can be divided into 2 clades: one includes *P. paviei* and *P. intermedius*, and the other includes the remaining 4 species (*P. immaculatus*, *P. sulcatus*, *P. sulcatoides*, and *P. sympelvicus*). Based on fossil records of the Sisoridae and the phylogenetic tree of *Pseudecheneis*, it is inferred that the genus *Pseudecheneis* originated in the Late Pliocene. With the uplift of the Qinghai-Xizang Plateau, this genus has differentiated 4 times, an inference consistents with the geography of the river systems in Yunnan Province, China.
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Key words: *Pseudecheneis*, Phylogeny, Distribution pattern, Sisoridae.

Before 1982, three catfish species possessing a thoracic apparatus with transverse folds were recorded in the Sisoridae of the Siluriformes, and they were assigned to 3 different genera: *Glyptosternon* (*G. sulcatus*), *Pseudecheneis* (*P. paviei*), and *Propseudecheneis* (*P. tchangi*) (Blyth 1860, Hora and Chabanaud 1930, Hora 1937). However, there was no convincing conclusion about their taxonomic status and relationships, although these problems were discussed (Hora 1937 1952). Chu (1982) discussed their taxonomic status and considered that they should be classified into the genus *Pseudecheneis*, and that only *P. sulcatus* and *P. paviei* were valid species. Meanwhile, he described 2 new species: *P. immaculatus* and *P. intermedius*. Lacking specimens of *P. paviei*, that study based on the principle that the systematic division was predictable and on the resemblance of their outline, indicated that the skeletal system of *P. paviei* was similar to that of *P. intermedius*. On the basis of the principle of cladistics, a cladogram of the 4 recorded species was constructed, showing *P. sulcatus* and *P. immaculatus* as a sister group, and *P. paviei* and *P. intermedius* as another sister group.

In the mid to late 1980s, specimens of *P. paviei* were collected from Pinbian and Luchun (the Red River system) in southern Yunnan

*To whom correspondence and reprint requests should be addressed. Tel: 86-871-3862458. Fax: 86-871-3863635.
E-mail: weizhou@public.km.yn.cn

Province, China near the border with Vietnam. At the same time, additional specimens of *P. sulcatus* were collected from the Lancangjiang (the upper Mekong River), the Nujiang (the upper Salween River), and branches of the Irrawaddy River in Yunnan Prov. Results of comparisons of the skeletal morphology of specimens from the 3 river systems showed that specimens from the Lancangjiang obviously differed from those of the Nujiang and Irrawaddy although their outlines were similar to that of *P. sulcatus*. So specimens collected from the Lancangjiang were described as a new species, named *P. sulcatoides* (Zhou and Chu 1992).

In the late 1990s, some specimens of *Pseudecheneis* sp. were collected from the Nam Theun (a branch of the Mekong River) in Laos, and it was discovered that its shape was the same as that of *P. sulcatus* except that its pelvic fins were fused medially. Those specimens were separated from other recorded species by this morphological character, and so it was named *P. sympelvicus* (Roberts 1998).

There are 6 currently known valid species of *Pseudecheneis*, and their distributions are as follows: *P. sulcatus* (McClelland) in Yunnan and Tibet of China, and throughout Myanmar and India; *P. immaculatus* Chu in the middle reaches of the Lancangjiang, including Deqin and Weixi Counties of Yunnan Prov.; *P. paviei* Vaillant in the Red River system, including Pinbian, Wenshan, Xinpin, Jinpin, and Luchun Counties of Yunnan Prov., and Laichow Prov. of Vietnam; *P. intermedius* Chu in the Babianjiang, a branch of the Red River, in China; *P. sulcatoides* Zhou et Chu in the Lancangjiang River system of China; and *P. sympelvicus* Roberts in the Laotian Nam Theun basin of the Mekong River system.

The reliability of the results of *Pseudecheneis* phylogeny presented by Chu (1982) was affected by the lack of specimens of *P. paviei*. Then *P. sulcatoides* and *P. sympelvicus* were found in the Mekong basin. To date, no discussion has been offered as to where those new species should be placed in the evolutionary process. The facts stated above stimulated the authors to once again study the taxonomy and phylogeny of *Pseudecheneis*.

MATERIALS AND METHODS

Data collection

Characters used for phylogenetic analysis were derived from external features, muscles, and the skeletal system. Observations, dissections, and drawings were made using a binocular microscope (Motic D400, MICRO-OPTIC Industrial Group CoLtd, Xiamen, China) equipped with a drawing attachment. Osteological characters were determined from stained specimens prepared by the methods of Dingerkus and Uhler (1977), but the step of cartilage staining was omitted. Some osteological characters of *P. sympelvicus* were determined by radiographs (taken with a Philips, Tele Diagnost, Royal Philips Electronics, Netherlands; condition: 1000 mA, 40 kV).

The genus *Bagarius* is called a “living fossil”, and *Glyptothorax* resembles *Pseudecheneis* in appearance due to the thoracic apparatus, which is recognized as a primitive genus species in the family Sisoridae (Chu 1982, He 1996). So *Bagarius* and *Glyptothorax* were chosen as the outgroup. Nomenclature of muscles and the skeleton follow Saxena (1961 1962), Gauba (1968), and Mo (1986).

Phylogenetic analysis

Recorded species of the ingroup and outgroup were respectively treated as operating taxonomic units (OTUs). However, specimens of *P. sulcatus* collected from the Nujiang (the upper Salween River) and Irrawaddy River were treated as independent OTUs because their morphological characters obviously differ.

Characters were polarized using the outgroup comparison method (Maddison et al. 1984). Multistate characters were coded into multi-states, i.e., the plesiomorphic state was coded “0”, while the apomorphic state was coded “1” or “1, 2” if there were multi-states. Characters for which the state could not be confirmed were coded as “?”. Then a matrix of character states was produced. The data matrix was analyzed by the software, PAUP* (Phylogenetic Analysis Using Parsimony) (Swoford 2002). All characters had equal weightings and were separately set as unordered and ordered. Phylogenetic analyses were carried out using Parsimony and Bootstrap (the number of bootstrap replicates was 1000) methods with the Branch-and-Bound search program of PAUP*. Trees were unrooted cladograms, which were redrawn using Treeview (Page 1996 2001).

Phylogenetic trees were first constructed with only 5 species included, i.e., *P. sympelvicus* was excluded because its examined myological and osteological characters were incomplete. The phylogenetic trees including all 6 species were again reconstructed. The phylogenetic position of *P. sympelvicus* was discussed after comparison of the congruence among the trees.

Material examined

The 269 examined specimens are preserved in the following institutions and collections: Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ), Kunming, China; Museum of Zoology Section, Southwest Forestry College (SWFC), Kunming, China, and the collections of Dr. Maurice Kottelat, Switzerland ichthyologist (CMK, 1 specimen of *P. sympelvicus* was borrowed from him) (Fig. 1). Examined specimens are listed in alphabetic order of species, and the catalog number of each specimen, the total number of examined specimens (exsp.), standard length (SL) range of specimens in millimeters, collecting locality, and river system were also included. Numbers of dissected specimens and stained skeleton specimens (DS) are given in parentheses.

Bagarius yarrelli: Yuanjiang (Red River) basin: SWFC 97121454, 1 exsp. (1 DS), 135 SL, Yuanjiang R., Hekou, Yunnan, China.

Glyptothorax honghensis: Yuanjiang (Red R.) basin: SWFC 0005098, 1 exsp. (1 DS), 71 SL, Sanjiangkou, Xinping Co., Yunnan; SWFC 97121008, 1 exsp. (1 DS), 85 SL, Baihejiao, Pingbian Co., Yunnan, China.

Pseudecheneis immaculatus: All from China, Yunnan: Lancangjiang (Mekong R.) basin: KIZ 748742 1 exsp., holotype, 98 SL, KIZ 748650~748652, 748735~748739, 748741, 9 exsp., paratypes, 72.8~104 SL, Baijixun, Weixi Co.; KIZ 748636, 748638~748640, 748673, 5 exsp., paratypes, 74.5~89.2 SL, Liutongjiang, Deqin Co.; SWFC 9908007, 0004081-0004085, 0004095, 7 exsp., 76.5~94.2 SL (1 DS), Liutongjiang, Deqin Co.

Pseudecheneis intermedius: All from China, Yunnan: Yuanjiang (Red R.) basin: KIZ 737173, 1 exsp., holotype, 56.5 SL, KIZ 737172, 737179, 737183, 737184, 737188, 737189, 6 exsp., paratypes, 49~56.5 SL, Chuanhe R., Jingdong; SWFC 9810001~9810014, 14 exsp. (2 DS), 36~83.5 SL, Chuanhe R., Jingdong.

Pseudecheneis paviei: All from China, Yunnan: Yuanjiang (Red R.) basin: SWFC 97121278~97121285, 9801013, 9812001~9812010, 9903001, 20 exsp. (3 DS), 69~121 SL, Nanxi R.,

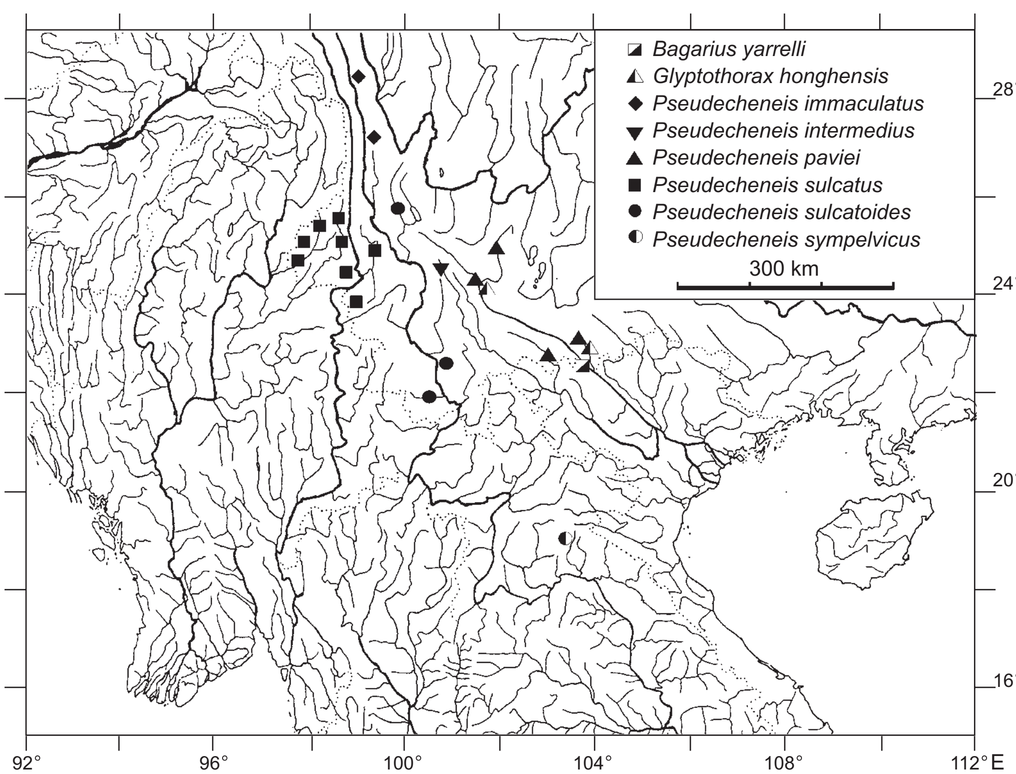

Fig. 1. Collecting localities of the examined specimens. A symbol may represent several adjacent localities.

Pinbian; SWFC 9902101, 0005151~0005154, 0010001~0010020, 25 exsp. (2 DS), 42~84, Tentiao R., Jinping Co.; SWFC 0005080~005084, 5 exsp. (2 DS), 59~69 SL, Sanjiangkou, Xinping Co.; KIZ 914106, 914107, 2 exsp., 60.5~73 SL, Xiaoluzhi, Yimen Co.

Pseudecheneis sulcatus: All from China, Yunnan: Irrawaddy R. basin: SWFC 9904095~9904099, 5 exsp., 80~139 SL, Mangyun, Yingjiang Co.; SWFC 0101001, 0101002, 0103303, 0103304, 4 exsp., 105~121 SL, Tongbiguan, Yingjiang Co.; SWFC 0103248~0103251, 4 exsp., 56~89 SL, Laza, Yingjiang Co.; SWFC 0103289~0103302, 0103394, 15 exsp. (1 DS), 107.6~137 SL, Sudian, Yingjiang Co.; SWFC 0102125~0102128, 0102135~0102148, 18 exsp. (1 DS), 62~168 SL, Qushi, Tengchong Co.; SWFC 9904035~9904058, 9904060, 25 exsp. (2 DS), 63.5~155 SL, Gudong, Tengchong Co.; SWFC 010665~010667, 3 exsp., 56~134 SL, Daju, Tengchong Co.; SWFC 0102155, 0102156, 0102198, 3 exsp., 120~154 SL, Guyong, Tengchong Co. Nujiang (Salween R.) basin: SWFC 9902138, 9902139, 0005237, 0104001~0104003, 3 exsp. (1 DS), 73.8~114 SL, Nangun R., Canyuan Co.; SWFC 9902133~9902136, 4 exsp., 83~133 SL, Fengweihe R., ZhenKang Co.; SWFC 0102063, 1 exsp., 122 SL, Xiangda, Longlin Co.; SWFC 9904113, 9904114, 0202002~0202034, 35 exsp. (1 DS), 58.5~108 SL, Kejie, Channing Co.

Pseudecheneis sulcatoides: All from China, Yunnan: Lancangjiang (Mekong R.) basin: KIZ 839059, 1 exsp., holotype, 105 SL, KIZ 839060, 839063, 748792, 749945, 4 exsp., paratypes, 88~100 SL, Yangbi, Yangbi Co.; KIZ 76, 1 exsp., paratype, 83 SL, Xiaoganlanba, Simao Co.; KIZ 764006, 1 exsp., paratype, 73 SL, Xiaohejiang, Simao Co.; KIZ 737016, 863867, 864868, 863871, 4 exsp., paratypes, 74~95 SL, Menghai, Menghai Co.; SWFC 9910001, 0005015~0005052, 39 exsp. (2 DS), 49~100 SL, Yangbi, Yangbi Co.

Pseudecheneis sympelvicus: Mekong R. basin: CMK 15237, 1 exsp. 61.5 SL, Nam Ngiap about 2 km S of Old Xiang Khouang, Xiangkhouang Prov., Laos.

RESULTS

Character description

According to the morphological comparison results, 73 steady characters were selected. Character descriptions are given as follows:

1. Ray end shape of dorsal, pectoral, and caudal fins. The ray end of the dorsal, pectoral, and caudal fins extending threadlike (#1-0); the ray end of all fins not extended (#1-1).

2. Length of caudal fin lobes. The upper lobe longer than the lower lobe (#2-0); lobes equal (#2-1); the lower lobe longer than the upper lobe (#2-2).

3. Depth of caudal fin fork. The longest ray 2 times longer or equal to the shortest ray (#3-0); the ratio < 2 (#3-1).

4. State of last unbranched ray of dorsal fin. Last unbranched ray strong like a spine (#4-0); a normal soft ray (#4-1).

5. Length of pectoral fin. Pectoral not extending to posterior edge of pelvic fin base (#5-0); pectoral extending beyond posterior edge of pelvic fin base (#5-1).

6. Denticles on pectoral spine. Posterior edge of pectoral spine with denticles (#6-0); its posterior edge without denticles (#6-1).

7. State of posterior edge of adipose fin. Posterior edge of adipose fin free (#7-0); posterior not free (#7-1).

8. Structure of paired fins. Pectoral and pelvic fins not modified as an adhesive apparatus with no special structure on ventral surface (#8-0); paired fins modified as an adhesive apparatus with feather-like gauffers on ventral surface (#8-1).

9. Feather-like cartilage. Outside of paired fins with feather-like cartilage (#9-1); outside without cartilage (#9-0).

10. Shape of eyes. Eye horizontally oval (#10-0); eye rounded (#10-1).

11. Way of connection between gill membranes and isthmus. Gill membranes free from isthmus (#11-0); membranes connected to isthmus (#11-1).

12. Number of branchiostegal rays. Branchiostegal rays 8~12 (#12-0); rays 6 or 7 (#12-1).

13. Gill opening size. Gill openings wide, extending to ventral surface (#13-0); openings narrow, extending to pectoral fin base (#13-1).

14. Surface case of lips. Lips thin, not papillate (#14-0); lips fleshy and papillate (#14-1).

15. Surface case of mandibular and maxillary barbels. Two pairs of mandibular and 1 pair of maxillary barbels without papillae (#15-0); 3 paired barbels with papillae (#15-1).

16. Nasal barbels. Nasal barbels short, not connected when pressed towards each other (#16-

0); nasal barbels long, overlapping when pressed towards each other (#16-1).

17. Shape of premaxillary teeth band. Posterior corner of teeth band strongly recurved (#17-0); shape of teeth band crescentic (#17-1); shape of teeth band semicircular (#17-2).

18. Blotches on body surface. Body surface with blotches (#18-0); surface without blotches (#18-1).

19. Spot on the upper gill openings. Upper gill openings without a small spot (#19-0); with a small oval yellow spot (#19-1).

20. Stripe on back of caudal peduncle. Back of caudal peduncle without stripe, or stripe interrupted (#20-0); back of peduncle with continuous yellow stripe (#20-1).

21. Folds on thoracic apparatus. No thoracic apparatus in outgroup species, or seen as folds on thoracic apparatus (#21-0); based on the speculation that evolutionary direction of folds would be increased in ingroup species, so 8~14 folds as apomorphy 1 (#21-1), 14~21 folds as apomorphy 2 (#21-2).

22. Snout shape. Ratio of snout width at mouth corner to distance between pectoral fin base expressing snout shape: wide and flat, ratio larger than 0.75 (#22-0); round and pointed, ratio smaller than 0.75 (#22-1).

23. Length of maxillary barbel. Maxillary barbel long, extending to or beyond pectoral fin base (#23-0); maxillary barbel short, not extending to pectoral fin base (#23-1).

24. Length of lateral mandibular barbels. Lateral mandibular barbels long, reaching to or beyond front of thoracic apparatus (#24-0); lateral mandibular barbels short, not reaching to front of thoracic apparatus (#24-1).

25. Shape of pelvic fin. Pelvic fin separated, not united (#25-0); pelvic fin united (#25-1).

26. Muscle dissociator in pectoral girdle. Ventral of pectoral girdle without muscle dissociator (#26-0) (Fig. 2A, B); girdle with muscle dissociator (#26-1) (Fig. 2C-G).

27. Number of pectoral superficialis muscles. Pectoral superficialis muscle undifferentiated with only 1 muscle (#27-0) (Fig. 2A); modified as an abductor and 1 or 2 adductors (#27-1) (Fig. 2B-G).

28. Origin of pectoral superficialis muscles. Original of pectoral superficialis muscles apart from ventral midline (#28-0) (Fig. 2A-C, E); its origin near ventral midline (#28-1) (Fig. 2D, F, G).

29. Presence of inscription of superficialis pelvic girdle muscle. Superficialis pelvic girdle muscle with inscription (#29-0) (Fig. 3A-C, F, G); muscle without inscription (#29-1) (Fig. 3D, E).

30. Presence of abductor pelvic superficialis muscles. Left and right abductor pelvic superficialis muscles not cicatrized (#30-0) (Fig. 3A, B, E, F); anterior part cicatrized (#30-1) (Fig. 3D); or totally cicatrized (#30-2) (Fig. 3C, G).

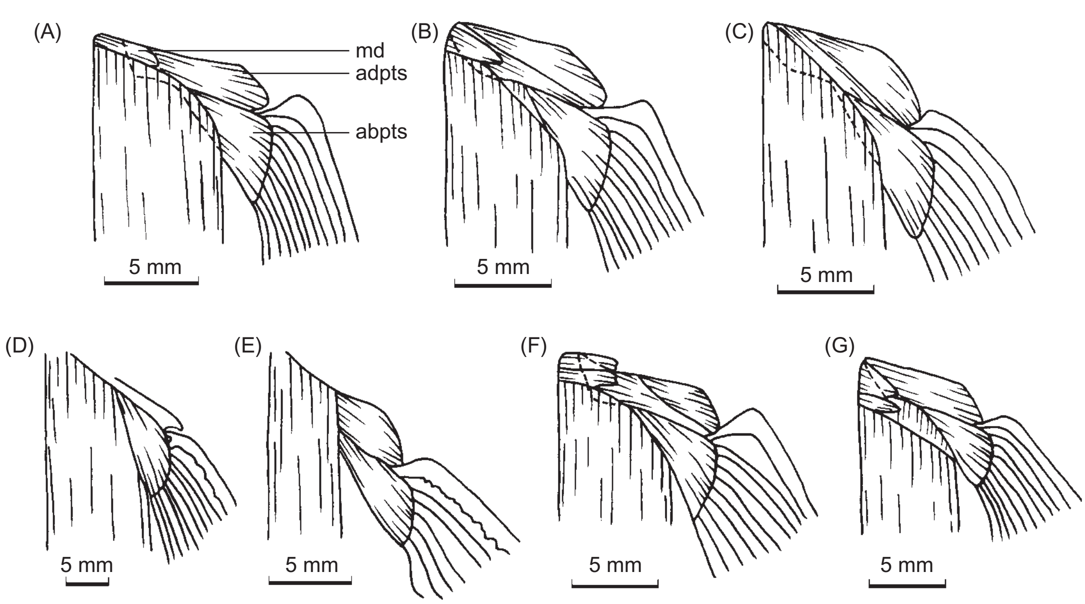

Fig. 2. Ventral view of the pectoralis superficialis muscles. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis paviei*; (D) *P. sulcatoides*; (E) *P. intermedius*; (F) *P. sulcatus* (from the Irrawaddy R.); (G) *P. sulcatus* (from the Nujiang). abpts, m. abductor pectoralis superficialis; adpts, m. adductor pectoralis superficialis; md, muscle dissociator.

31. Shape of anterior part of abductor pelvic profundus muscle. Anterior part of abductor pelvic profundus muscle not bifurcate (#31-0) (Fig. 4A-C); anterior part bifurcate (#31-1) (Fig. 4D).

32. Location between super and infra interfilamenti caudalis muscles. Super and infra interfilamenti caudalis muscles separate (#32-0) (Fig. 5A, D); those muscles connected at their bases (#32-1) (Fig. 5B, C).

33. Shape of ethmoid. Ethmoid "T"-shaped, its anterior protruding, (#33-0) (Fig. 6A); ethmoid "Y"-shaped, its anterior concave (#33-1) (Fig. 6B-F).

34. Connection between sphenotic and supraoccipital. Sphenotic directly connecting to supraoccipital (#34-0) (Fig. 6A, B); they are not connected to each other (#34-1) (Fig. 6C-F).

35. Shape of lateral ethmoid. Lateral ethmoid extending posterolaterally as a narrow rec-

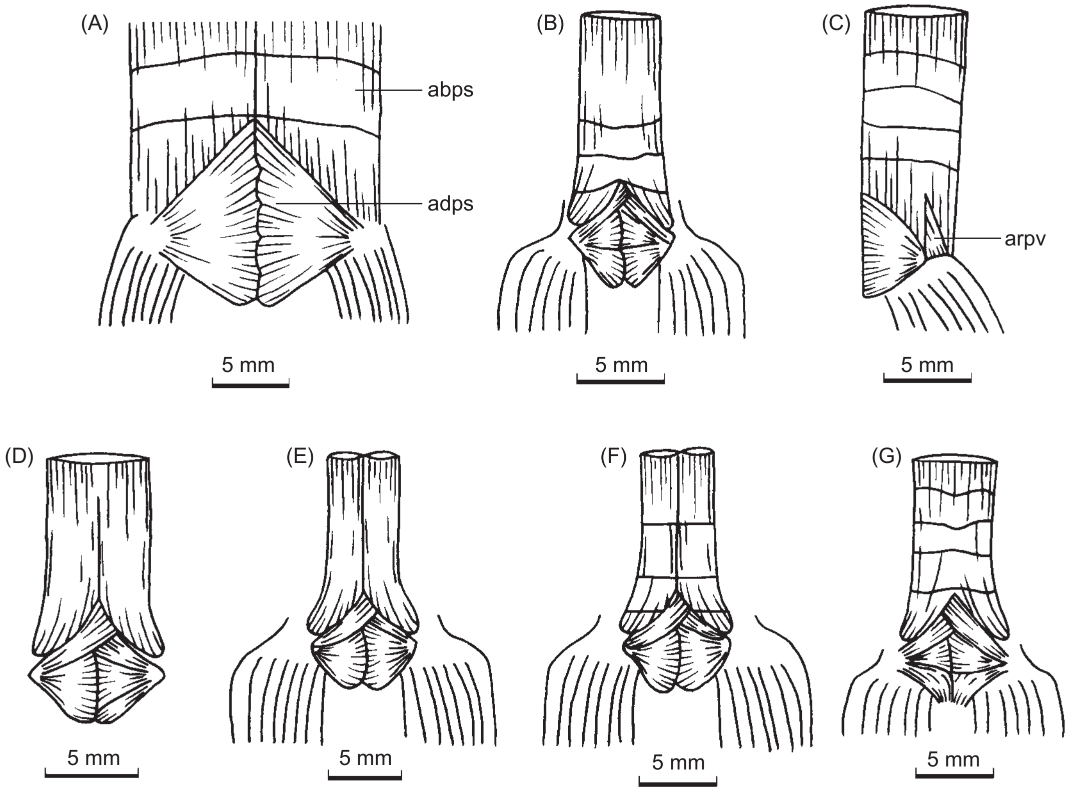

Fig. 3. Ventral view of the superficialis pelvic girdle muscles. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis immaculatus*; (D) *P. sulcatus* (from the Irrawaddy R.); (E) *P. sulcatoides*; (F) *P. intermedius*; (G) *P. sulcatus* (from the Nujiang). abps, m. abductor pelvicalis superficialis; adps, m. adductor pelvicalis superficialis; arpv, m. arrector pelvicalis ventralis.

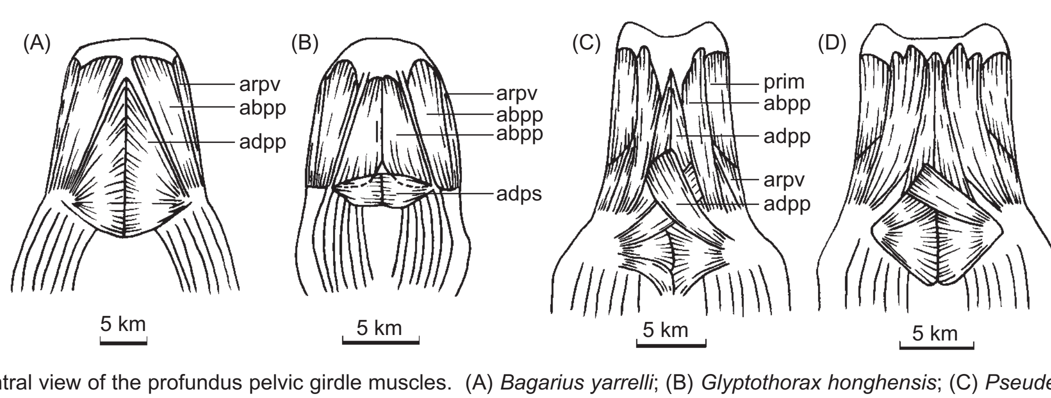

Fig. 4. Ventral view of the profundus pelvic girdle muscles. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis sulcatus* (from the Nujiang); (D) *P. paviei*. abpp, m. abductor pelvicalis profundus; adpp, m. adductor pelvicalis profundus; adps, m. adductor pelvicalis superficialis; arpv, m. arrector pelvicalis ventralis; prim, pars retractor ischii of the m. mesiovental.

tangle (#35-0) (Fig. 6A, F); extending only as a small projection (#35-1) (Fig. 6B-E).

36. Process of frontal bone. Frontal with an evident lateral process (#36-0) (Fig. 6A-E); frontal without a lateral process (#36-1) (Fig. 6B).

37. Location of posterior fontanelle. Posterior fontanelle located on supraoccipital only (#37-0) (Fig. 6A, B); posterior fontanelle straddling frontal and supraoccipital (#37-1) (Fig. 6C-F).

38. Length of supraoccipital. Length of supraoccipital longer than or equal to its width (#38-0) (Fig. 6A, C); its length shorter than its width (#38-1) (Fig. 6B, D-F).

39. Length of occipital process. Length of occipital process equal to or shorter than its body length (#39-0) (Fig. 6A, C); process longer than its body length (#39-1) (Fig. 6B, D-F).

40. Distance between lateral edges of sphenotic bones. Distance between lateral edges of sphenotic bones equal to width of Weberian ossicles (#40-0) (Fig. 6A, D-F); distance not equal to width (#40-1) (Fig. 6B, C).

41. Angle made by parapophysis of complex vertebra and vertical axes of skull. Angle almost a right angle (#41-0) (Fig. 6A, B, D, E); angle acute (#41-1) (Fig. 6C, F).

42. Shape of neural spine of complex vertebra. Neural spine of complex vertebra bifurcate (#42-0) (Fig. 6A-C, E); spine single (#42-1) (Fig. 6D, F).

43. Relationship between neural spine of complex vertebra and 1st proximal radials. First proximal radials just mounted in forked neural spine of complex vertebra (#43-0); radials not mounted in spine (#43-1).

44. First dorsal spine. First dorsal spine exists (#44-0) (Fig. 7A-D); 1st dorsal spine absent (#44-1) (Fig. 7E).

45. Shape of 1st proximal radials. Anterior end of 1st proximal radials rounded (#45-0) (Fig. 7A, B, E); end pointed (#45-1) (Fig. 7C, D).

46. Depth of 2nd proximal radials. Depth of 2nd proximal radials less than 1/2 its width (#46-0); its depth exceeding 1/2 its width (#46-1).

47. Development of pelvic girdle. Pelvic girdle not covering 1/2 of abdomen (#47-0); covering more than 1/2 of abdomen (#47-1).

48. Number of lateral processes on pelvic girdle. Pelvic girdle without lateral processes (#48-0) (Fir. 8A, B); with 1 lateral process (#48-1) (Fig. 8C, D); with 2 lateral processes (#48-2) (Fig. 8E).

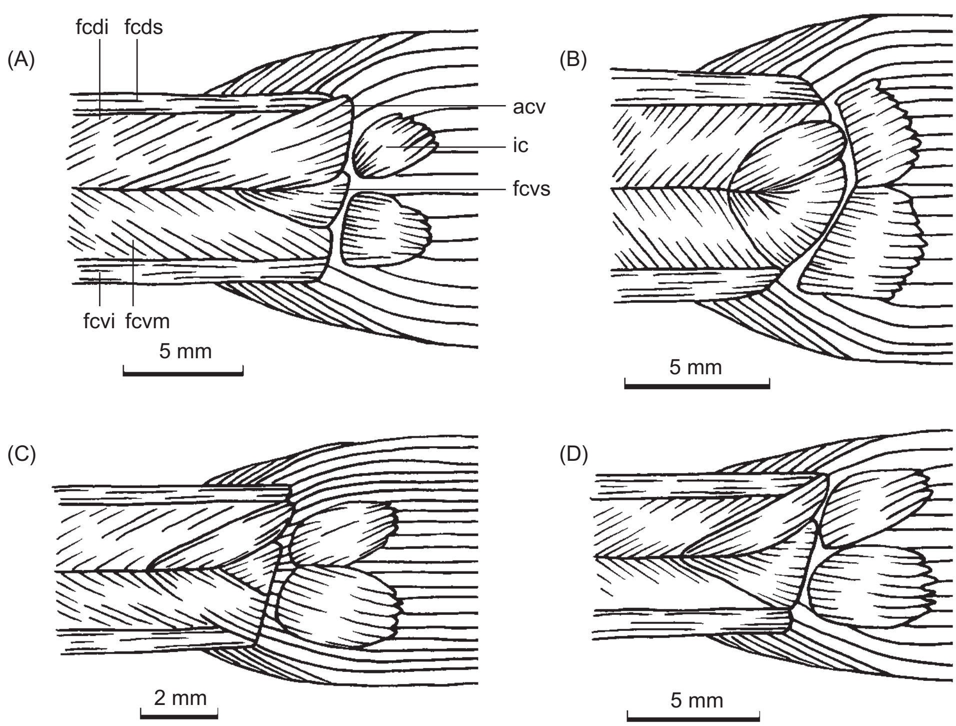

Fig. 5. Left lateral view of the caudal fin muscle. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis sulcatoides*; (D) *P. intermedius*. acv, m. adductor caudalis ventralis; fcdi, m. flexor caudalis dorsalis inferior; fcds, m. flexor caudalis dorsalis superior; fcvi, m. flexor caudalis ventralis inferior; fcvm, m. flexor caudalis ventralis medialis; fcvs, m. flexor caudalis ventralis superior; ic, m. interfilamenti caudalis.

49. Contact state of pelvic plates. Bones of pelvic plates at a distance and connected by cartilage (#49-0) (Fig. 8A); bones of pelvic plates contacting along midline (#49-1) (Fig. 8B-E).

50. Shape of pelvic plate posterior process. Posterior process of pelvic plates not prolonged (#50-0) (Fig. 8A-D); process prolonged (#50-1) (Fig. 8E).

51. Location of small foramen on pelvic plate. Small foramen close to base of inner process in pelvic plate (#51-0) (Fig. 8A); foramen separate from base of inner process in pelvic plate (#51-1) (Fig. 8B-E).

52. Number of vertebra. Vertebrae 37~40 (#52-0); 34~36 (#52-1).

53. Vertebrae number after 1st pterygiophore of anal fin. Eighteen vertebrae after 1st pterygiophore of anal fin insertion (#53-0); 17 vertebrae after insertion (#53-1).

54. Posterior process of coracoid. Coracoid without posterior process (#54-0) (Fig. 9A, D); coracoid with posterior process (#54-1) (Fig. 9B, C).

55. Shape of posterior edge of coracoid. Coracoids connected along ventral midline, their posterior edges concave forwards (#55-0) (Fig. 9A); their posterior edge almost straight or projecting to rear (#55-1) (Fig. 9B-D).

56. Shape of anterior edge of cleithrum anterior limbs. Cleithrum anterior limbs connected along ventral midline, its anterior edge pointed forwards sharply or smoothly (#56-0) (Fig. 9A, B, D); its anterior edge pointed and the tip with an incision (#56-1) (Fig. 9C).

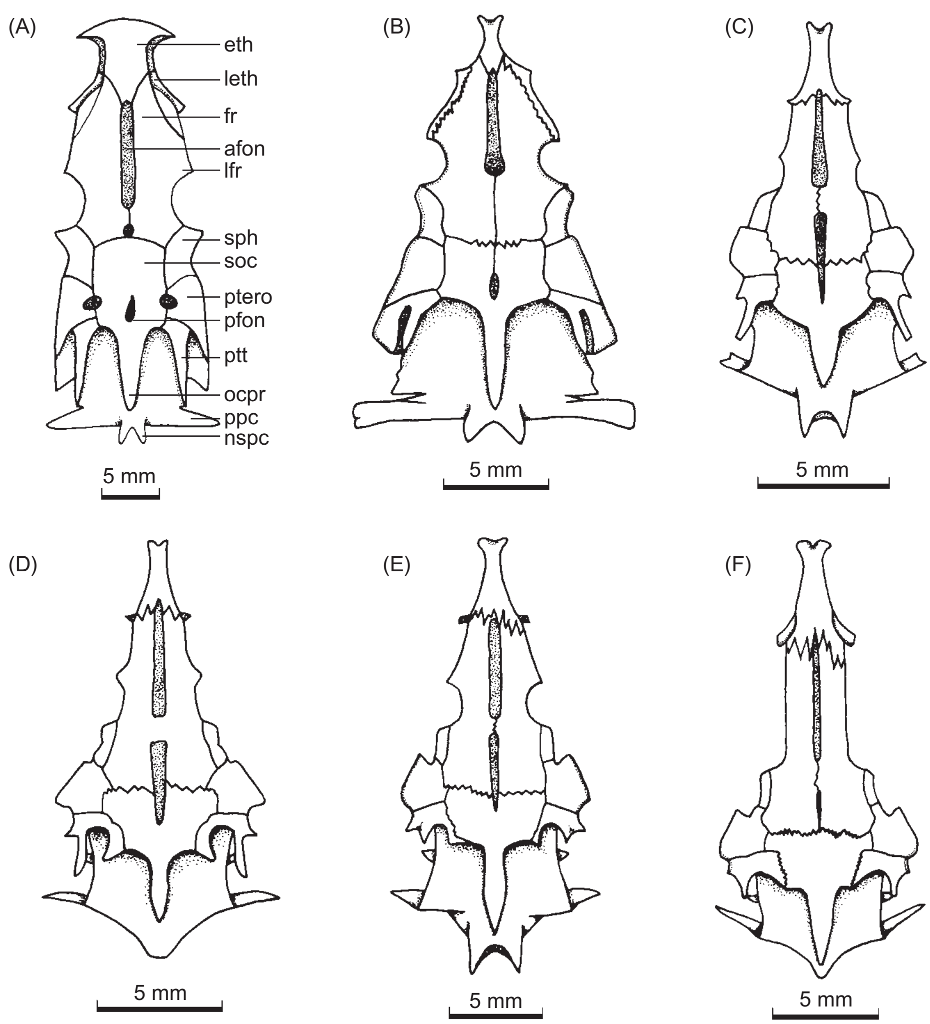

Fig. 6. Dorsal view of the cranium. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis immaculatus*; (D) *P. sulcatoides*; (E) *P. sulcatus* (from the Irrawaddy R.); (F) *P. paviei*. afon, anterior fontanelle; eth, ethmoid; fr, frontal; leth, lateral ethmoid; lfr, lateral process of frontal; nspc, neural spine of complex vertebra; ocpr, occipital process; ptero, pterotic; pfon, posterior fontanelle; ptt, posttemporal; ppc, parapophysis of complex vertebra; soc, supraoccipital; sph, sphenotic.

57. Location between metapterygoid and hyomandibula. Metapterygoid located before hyomandibula and connected to it (#57-0) (Fig. 10A, B); metapterygoid located above hyomandibula and not connected with it (#57-1) (Fig. 10C, D).

58. Location between metaterygoid and ectopterygoid. Metapterygoid separated from ectopterygoid (#58-0) (Fig. 10A-C); metapterygoid closely contacting ectopterygoid and their posterior ends cicatrized (#58-1) (Fig. 10D).

59. Location between ectopterygoid and hyomandibula. Hyomandibula contacting posterior edge of ectopterygoid (#59-0) (Fig. 10A, B); because metapterygoid is inserted between them, hyomandibula no longer contacting ectopterygoid (#59-1) (Fig. 10C, D).

60. Shape of urohyal. Urohyal without posterior process or not distinct (#60-0) (Fig. 11A, B); with posterior process and rounded (#60-1) (Fig. 11C); or sharply pointed (#60-2) (Fig. 11D, E).

61. Number of premaxilla. Premaxilla made up of 2 bones (#61-0); of only 1 bone (#61-1).

62. Ratio of palatine length to maxilla length. Ratio 0.72 (#62-0); ratio > 1 and < 2 (#62-1); ratio > 2 (#62-2).

63. Number of ribs. Twelve or more ribs (#63-0); fewer than 12 ribs (#63-1).

64. Number of vertebrae with hemal arch. Eleven vertebrae with hemal arch (#64-0); 4~6

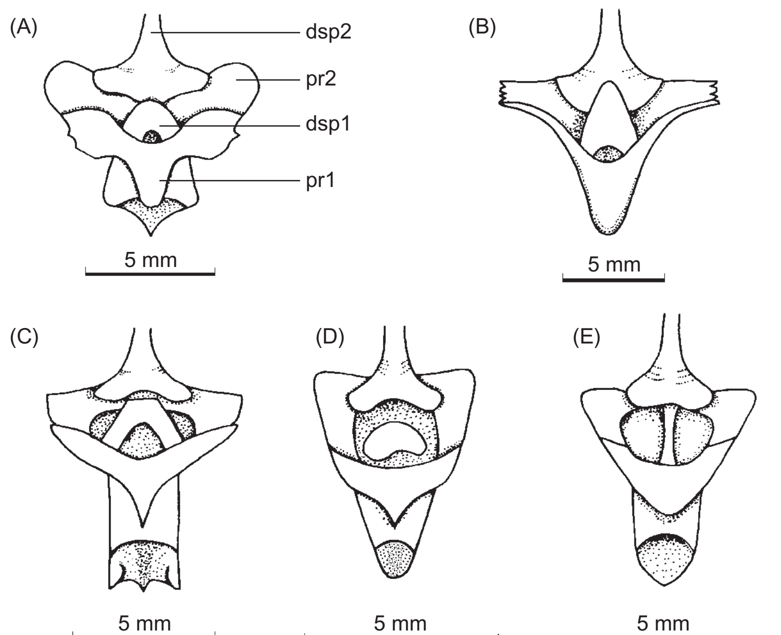

Fig. 7. Dorsal view of the dorsal fin base bones. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis immaculatus*; (D) *P. paviei*; (E) *P. sulcatoides*. dsp1, 1st dorsal spine; dsp2, 2nd dorsal spine; pr1, 1st proximal radials; pr2, 2nd proximal radials.

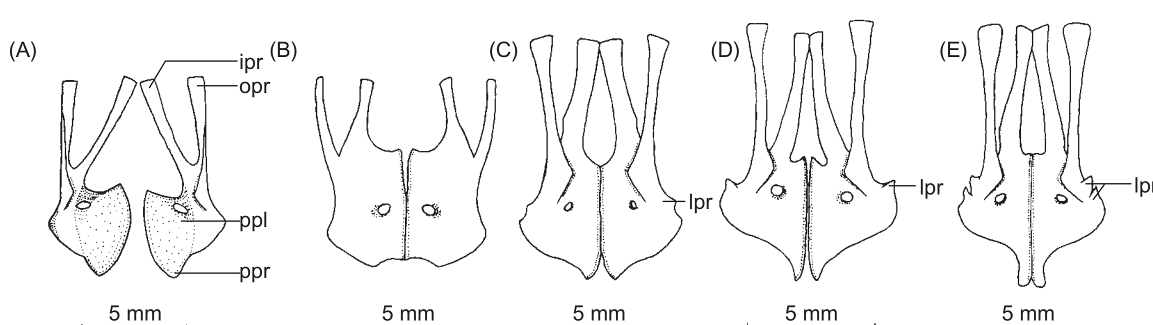

Fig. 8. Ventral view of the pelvic girdle. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis sulcatus* (from the Nujiang); (D) *P. paviei*; (E) *P. sulcatus* (from the Irrawaddy R.). ipr, inner process; lpr, lateral process; opr, outer process; ppl, pelvic plate; ppr, posterior process.

vertebrae with arch (#64-1).

65. Shape of neural spines. Neural spines of vertebrae above anal fin with a flat end (#65-0); spines with a needle-like end (#65-1).

66. State of neural spine before adipose fin. Neural spine before adipose fin extruded, can be felt when its back is pressed, and with some light dots on its surface along back midline (#66-0); cannot be not felt when its back is pressed, and without light dots on its surface along back midline (#66-1).

67. Relationship between epural and pre-

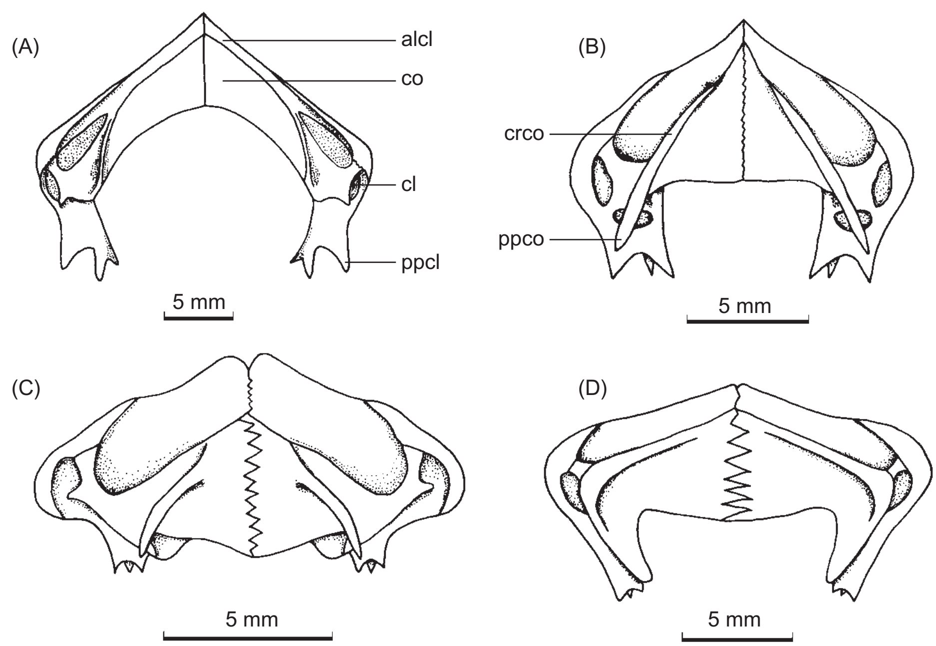

Fig. 9. Ventral view of the pectoral girdle. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis sulcatoides*; (D) *P. paviei*. alcl, anterior limb of cleithrum; cl, cleithrum; co, coracoid; crco, crest of coracoid; ppcl, posterior process of cleithrum; ppco, posterior process of coracoid.

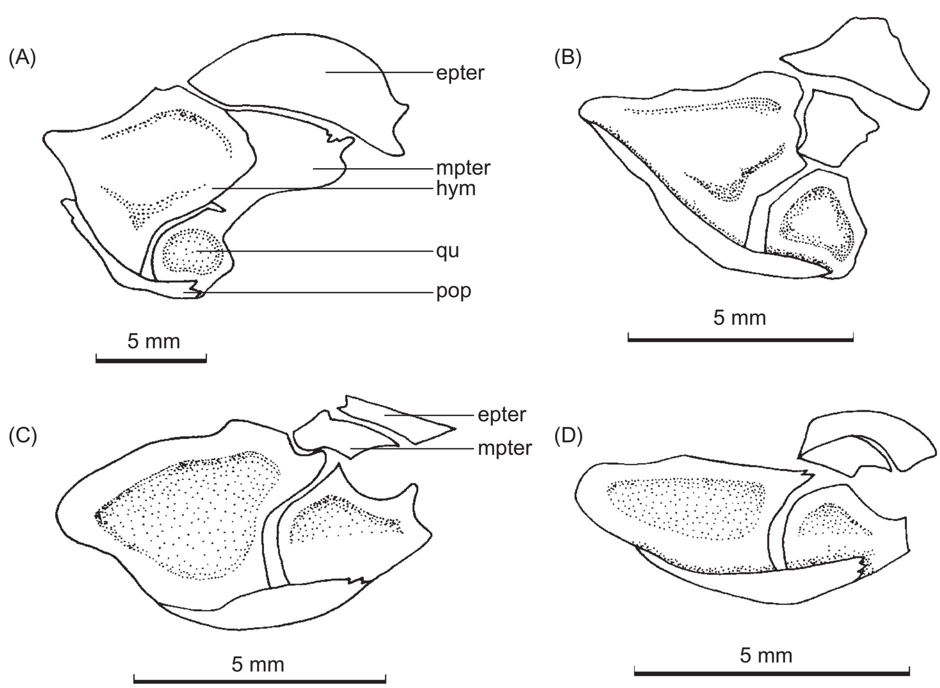

Fig. 10. Right lateral view of the pterotic. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis paviei*; (D) *P. sulcatoides*. epter, ectopterygoid; mpter, metapterygoid; hym, hyomandibula; qu, quadrate; pop, preoperculum.

ceding vertebra neural spine. Base of epural not cicatrized with neural spine of preceding vertebra (#67-0) (Fig. 12A-C); only cicatrized on base or entirely (#67-1) (Fig. 12D-G).

68. State of uroneural fusion with hypural 6. Uroneural fused with hypural 6 (#68-0) (Fig. 12A, B, G); not fused (#68-1) (Fig. 12C-F).

69. State of hypural 6 fusion with hypural 5. Hypural 6 fused with hypural 5 (#69-0) (Fig. 12A-E, G); not fused (#69-1) (Fig. 12F).

70. State of hypural 5 fusion with hypural 4. Hypural 5 not fused with hypural 4 (#70-0) (Fig. 12A); hypural 5 fused with hypural 4 (#70-1) (Fig. 12B-G).

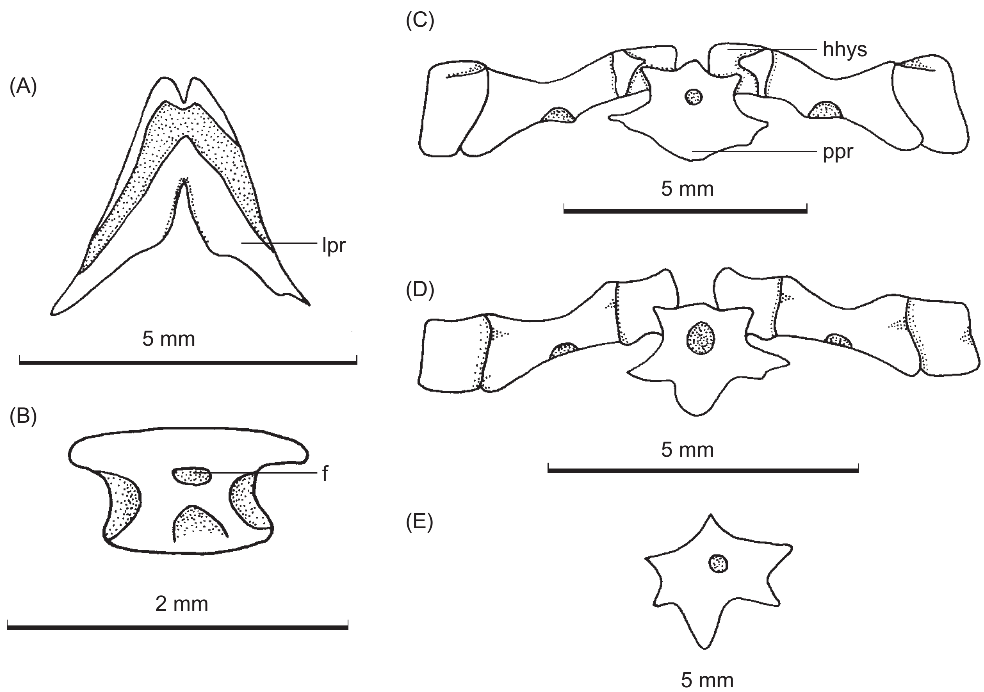

Fig. 11. Ventral view of the urohyal. (A) *Bagarius yarrelli*; (B) *Glyptothorax honghensis*; (C) *Pseudecheneis sulcatoides*; (D) *P. sulcatus* (from the Nujiang); (E) *P. intermedius*. f, fenestra; hhys, hypohyals; lpr, lateral process; ppr, posterior process.

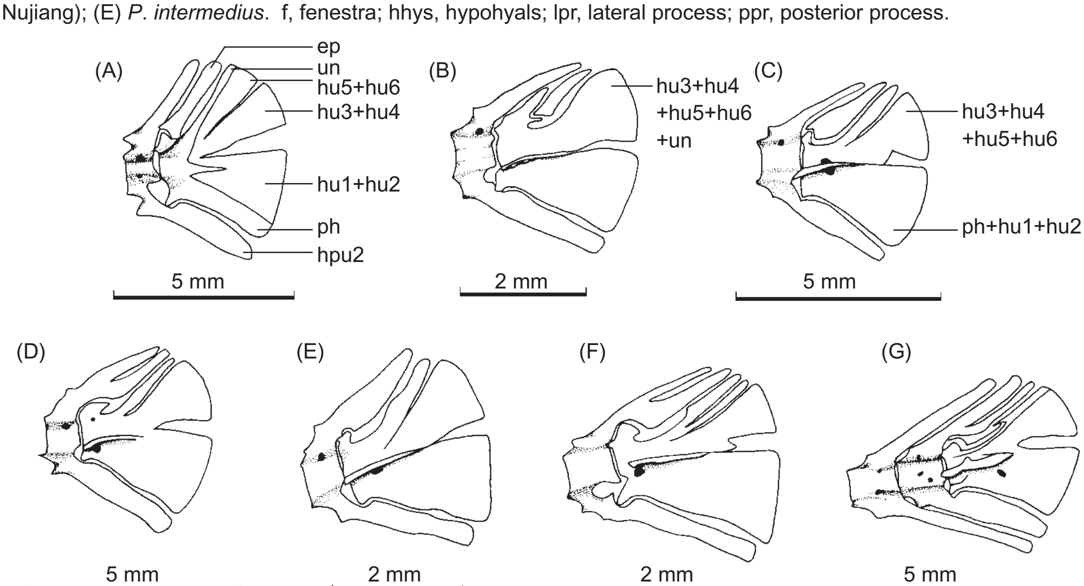

Fig. 12. Left lateral view of the caudal fin skeleton. (A) *Bagarius yarrelli*; (B) *Pseudecheneis intermedius*; (C-E) *P. paviei*, (C, from Pingbian; D, from Jinping, and E, from Xinping); (F) *P. immaculatus*; (G) *P. sulcatus* (from the Irrawaddy R.). ep, epural; hpu, hemal spine of preural centrum; hu, hypural; ph, parhyural; un, uroneural

71. Ratio of body length to head length. Ratio < 3.9 (#71-0); ratio 4.1~4.4 (#71-1); or ratio 5.4~5.9 (#71-2).

72. Ratio of body length to body depth. Ratio < 5.6 (#72-0); ratio 6.3~6.5 (#72-1).

73. Ratio of caudal peduncle length to its depth. Ratio < 4.0 (#73-0); ratio 5.2~5.5 (#72-1); or ratio 6.3~6.5 (#72-2).

Cladogram

Seventy-three morphological characters were selected for comparisons. They were polarized using the outgroup comparison method (Table 1).

When *Bagarius yarrelli* and *Glyptothorax honghensis* were designated the outgroup, the ingroup species of *P. sympelvicus* was omitted, and all 73 characters were set as unordered and had equal weightings, the 73 character matrix yielded a single most-parsimonious tree (Fig. 13) with a tree length of 110 steps, a consistency index (CI) of 0.7364, and a retention index (RI) of 0.6947. At the same time, a bootstrap test was completed (number of bootstrap replicates of 1000), and a bootstrap 50% majority-rule consensus tree resulted (Fig. 14). Relationships among ingroups of all species from the 2 trees were consistent. When all 73 characters were set as

Table 1. Matrix of character states

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Bagarius yarrelli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyptothorax honghensis	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0
Pseudecheneis paviei	1	2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	2	0	0	0	1	0	0	0
Pseudecheneis intermedius	1	2	1	1	1	1	0	1	1	1	1	1	1	1	1	1	2	0	0	0	1	0	0	0
Pseudecheneis immaculatus	1	2	0	1	1	1	0	1	1	1	1	1	1	1	1	1	2	1	0	0	2	1	0	0
Pseudecheneis sulcatoides	1	2	0	1	0	1	1	1	1	1	1	1	1	1	1	0	2	0	1	0	2	1	1	1
Pseudecheneis sympelvicus	1	2	1	1	0	1	1	1	1	1	1	?	1	1	1	0	2	0	1	0	2	1	1	1
NJ- *Pseudecheneis sulcatus*[a]	1	2	1	1	1	1	0	1	1	1	1	1	1	1	1	0	2	0	0	1	2	1	1	1
YJ- *Pseudecheneis sulcatus*[b]	1	2	0	1	0	1	1	1	1	1	1	1	1	1	1	0	2	0	0	1	2	1	1	1

Character	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Bagarius yarrelli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyptothorax honghensis	0	0	1	0	0	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0
Pseudecheneis paviei	0	1	1	0	1	0	1	0	1	1	0	1	1	1	1	0	1	1	1	0	1	1	1	1
Pseudecheneis intermedius	0	1	1	0	0	0	1	0	1	1	0	1	1	1	1	0	1	1	1	0	1	1	1	1
Pseudecheneis immaculatus	0	1	1	1	0	2	0	1	1	1	1	0	1	0	0	1	1	0	0	0	1	0	1	1
Pseudecheneis sulcatoides	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	1	1
Pseudecheneis sympelvicus	1	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
NJ- *Pseudecheneis sulcatus*[a]	0	0	1	1	0	2	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	1	1
YJ- *Pseudecheneis sulcatus*[b]	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	1	2

Character	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
Bagarius yarrelli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyptothorax honghensis	1	0	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Pseudecheneis paviei	1	0	1	1	1	0	1	0	1	0	1	12	1	1	1	1	1	1	01	1	0	1	1	0	0
Pseudecheneis intermedius	1	0	1	1	0	0	1	0	1	0	1	2	1	1	1	1	1	1	0	0	0	1	1	0	0
Pseudecheneis immaculatus	1	0	1	1	1	1	1	1	1	1	1	1	1	2	1	1	0	1	1	1	1	1	2	1	2
Pseudecheneis sulcatoides	1	0	1	1	1	1	1	1	1	1	1	1	1	2	0	1	0	0	1	1	0	1	2	1	1
Pseudecheneis sympelvicus	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	2	1	1
NJ- *Pseudecheneis sulcatus*[a]	1	0	1	1	0	1	1	1	1	1	1	2	1	2	1	1	0	0	1	0	0	1	2	1	2
YJ- *Pseudecheneis sulcatus*[b]	1	1	1	0	0	1	1	1	1	1	1	1	1	2	0	1	0	0	1	0	0	1	2	1	2

[a]Specimens of *Pseudecheneis sulcatus* collected from the Nujiang River system (the upper Salween River); [b]Specimens of *Pseudecheneis sulcatus* collected from the Irrawaddy River system.

ordered and had equal weightings, 1 most-parsimonious tree could be generated with a tree length of 112 steps, a CI of 0.7232, and an RI of 0.7103. The consensus tree of the bootstrap test (the number of bootstrap replicates was 1000) was the same as that shown in figure 14 except for the percentages.

When the species *P. sympelvicus* was included in the ingroup, the undetermined characters in *P. sympelvicus* were coded as missing data (i.e., "?"), and all characters were unordered and unweighted, the computational analysis resulted in 1 most-parsimonious tree (Fig. 15) with a length of 113 steps, a CI of 0.7257, and an RI of 0.6961. The consensus tree of the bootstrap test (with 1000 bootstrap replicates) was constructed (Fig.

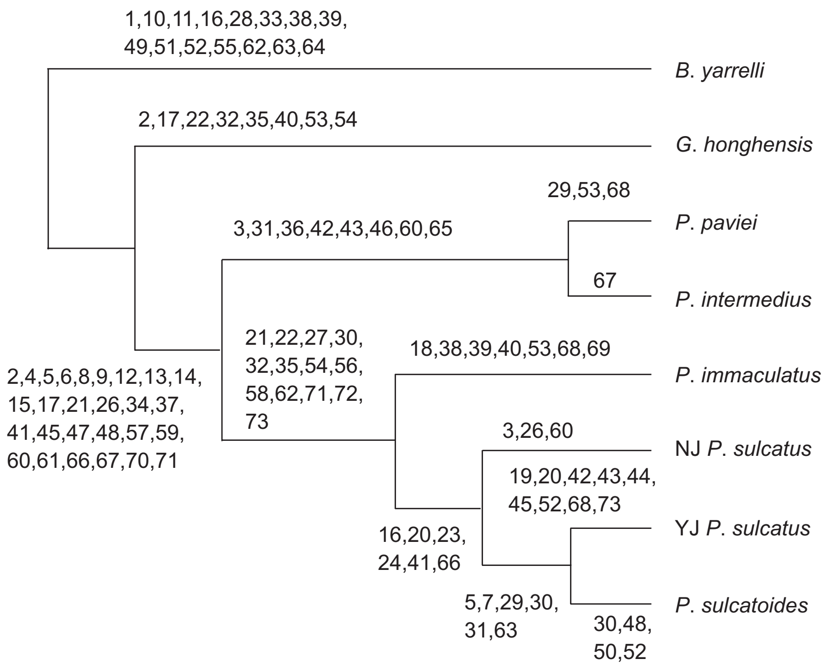

Fig. 13. Cladogram of genus *Pseudecheneis* except *P. sympelvicus*. *Bagarius yarrelli* and *Glyptothorax honghensis* were designated as the outgroup, and all 73 characters were set as unordered and had equal weight. Tree length = 110 steps, CI = 0.7364, RI = 0.6947.

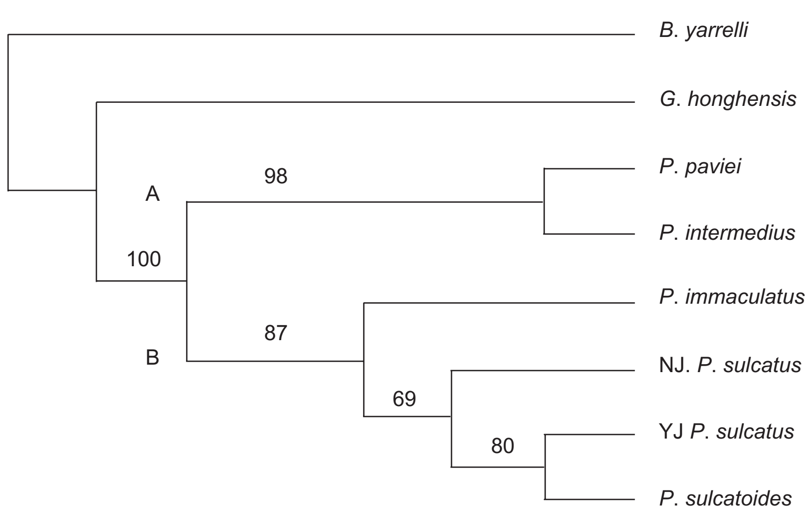

Fig. 14. Bootstrap 50% majority-rule consensus tree of genus *Pseudecheneis* except *P. sympelvicus*. *Bagarius yarrelli* and *Glyptothorax honghensis* were designated as the outgroup, and all 73 characters were set as unordered and had equal weight. Number of bootstrap replicates = 1000, starting seed = 121021786.

16). When all characters were set as ordered and had equal weightings, a single most-parsimonious tree could be retained with 115 steps, a CI of 0.7130, and an RI of 0.7080. The results of the bootstrap test (with 1000 bootstrap replicates) was also the same as that shown in figure 16 except for the percentages.

By comparing the trees between figures 13 and 15, interrelationships of the ingroup with all species except *P*. *sympelvicus* were highly congruent. This means that the phylogenetic position of *P*. *sympelvicus* as suggested in the tree from figure 15 stands a higher chance of being correct.

According to the phylogenetic trees (Figs. 13-16), the analysis of relationships among *Pseudecheneis* species can be summarized as follows.

(1) All 6 ingroup species of *Pseudecheneis* form a monophyletic group supported by 27 synapomorphies (2, 4~6, 8, 9, 12~15, 17, 21, 26, 34, 37, 41, 45, 47, 48, 57, 59~61, 66, 67, 70, and 71).

(2) The ingroup can be divided into 2 clades. Clade A includes *P*. *paviei* and *P*. *intermedius*,

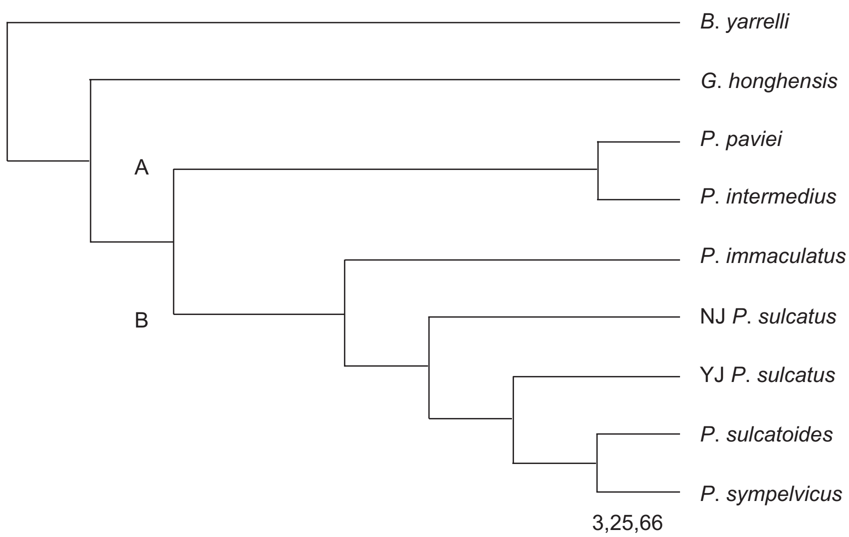

Fig. 15. Cladogram of all six recorded species of genus *Pseudecheneis*. *Bagarius yarrelli* and *Glyptothorax honghensis* were designated as the outgroup, and all 73 characters were set as unordered and had equal weight. Tree length = 113 steps, CI = 0.7257, RI = 0.6961.

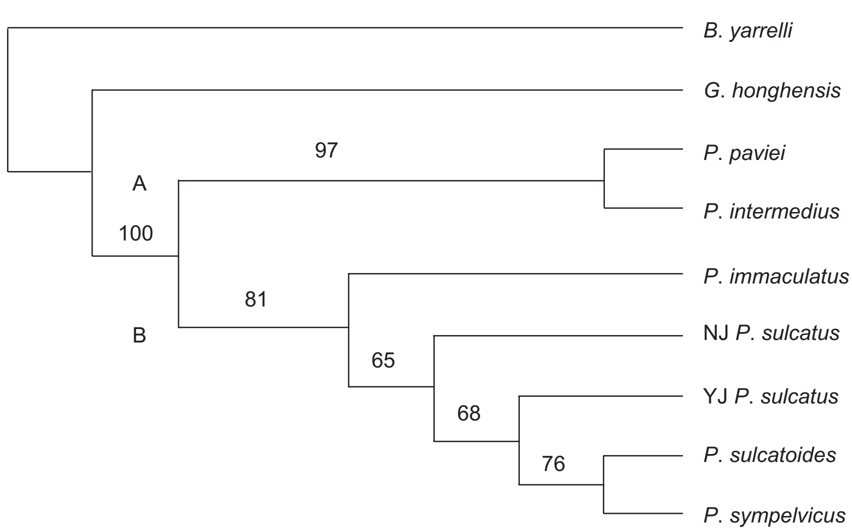

Fig. 16. Bootstrap 50% majority-rule consensus tree of all six recorded species of genus *Pseudecheneis*. *Bagarius yarrelli* and *Glyptothorax honghensis* were designated as the outgroup, and all 73 characters were set as unordered and had equal weight. Number of bootstrap replicates = 1000, starting seed = 89839760.

while clade B includes the remaining 4 species of *Pseudecheneis*.

(3) Specimens of *P. sulcatus* from the Nujiang (NJ) and Irrawaddy (YJ) did not cluster into an independent clade to form a pair of sister species. Their morphologic characters obviously differ, and they may represent different species. It would be worth discussing their taxonomic status in another paper.

(4) In clade B, *P. immaculatus* forms the sister group to *P. sulcatus* (NJ) + *P. sulcatus* (YJ) + *P. sulcatoides* + *P. sympelvicus*.

(5) Based on the morphological characters, phylogenetic trees, and distributions, *P. sympelvicus* is possibly a sister species of *P. sulcatoides*.

PHYLOGENY AND EXPLANATION FOR THE DISTRIBUTION PATTERNS

As geological changes occurred and water systems formed, different populations derived from the same ancestry were gradually and respectively isolated. Gene flow would have been interrupted. Some populations would have developed into different species or subspecies in different environments. As their habitats were not the same, they encountered different evolutionary pressures, so some species or populations evolved rapidly, while some evolved more slowly. According to the fossil records of the Sisoridae, and the cladogram of *Pseudecheneis* (Fig. 12) with data on ancient geography (Yunnan Geology and Minerals Bureau 1995, Sun and Zheng 1998, Wang et al. 2001), it is inferred that the genus *Pseudecheneis* may have evolved in the late Pliocene. With uplift of the Qinghai-Xizang Plateau, the genus *Pseudecheneis* experienced differentiation 4 times. Each geological change would have caused the ancestry to be isolated and form distinct populations. These different populations became new species or subspecies because of the lack of genetic exchange among them.

Origins

The Tethys Sea withdrew south in the early Late Permian period. Remains of the Tethys Sea on the Qinghai-Xizang (Tibetan) Plateau and Yunnan Plateau had entirely disappeared by the late Miocene. All of the plateau had become dry land. Wide valleys and basins characteristic of the Pliocene level plateaus were formed after the process of abrasion and denudation on the plateau in the early Pliocene. In this period, the ground of the Qinghai-Xizang Plateau gently rose and fell. Wide valleys and basins were well connected with each other. River systems looked like a string of pearls made up of small lakes (Sun and Zheng 1998). The geology and landforms of the Yunnan-Guizhou Plateau, at an elevation of 500 m, were generally the same as those of the Qinghai-Xizang Plateau (Yunnan Geology and Minerals Bureau 1995, Wang et al. 2001).

The earliest known fossil record of the Sisoridae is *Bagarius bagarius* found in Sumatra and India of the Pliocene (Hora 1939). This species is still extant. There is no doubt about its primitive status (Chu 1982). So the origin of *Pseudecheneis* could be in the Pliocene or slightly later. At that time, the Gaoligong Mountains and Hengduan Mountains had not yet been uplifted, so that area was still in a subtropical zone with a subtropical climate phase. The possibility exists that some locations were linked up among the different river systems. In these periods, the extent of the connectedness reached Sumatra to the south and the Indian Plate to the southwest.

The first differentiation

The Qinghai-Xizang Plateau rose so rapidly from the late Pliocene to the early Pleistocene that the pattern of river systems of the Pliocene Level was destroyed (Li 2002). The ancestors of *Pseudecheneis* that had originally lived on the plateau underwent the 1st division. As a result, 2 groups were produced: one adapted to the original environment was pushed out to the edge of the Yunnan-Guizhou Plateau, while the other changed its form and gradually adapted to the harsher environment of the upraised plateau. Because the environment in which the former group was distributed varied little, the influences and living pressures caused by environmental changes were small. Fishes in this group retained the original shapes with a few folds on the thoracic apparatus. *Pseudecheneis paviei* and *P. intermedius* were distributed all along the plateau edge, now known as the Yuanjiang river system (upper Red River) in southern Yunnan.

The next three differentiations

Because of the late Himalayan Orogenic Movement in the early Pleistocene, plateaus were lifted and rose higher. Discrepancies in elevation were strengthened. The Red River was considered a boundary dividing Yunnan into 2 parts on the Yunnan-Guizhou Plateau. The eastern part was relatively stable and mainly contained lake basins and marshes while the western part was violently active and mainly contained rivers that were frequently changing. In the northwest, Yunnan received extrusions from the Indian Plate. This area was gradually uplifted, and folds and ruptures formed. The northwestern part of Yunnan was seen as an axis at that time; the entire western part of Yunnan rotated to the southwest and spread out like a broom under pressure with the northwestern part being pushed and the southern part becoming convoluted. In this period, the rivers in the southern region north of latitude 25° frequently divided and linked up. The Mekong, Salween, and Irrawaddy Rivers were separated and progressively formed. It was inferred that the last 3 differentiations of other *Pseudecheneis* species might have taken place in this period.

With plateau imbalance and uplift, the Mekong and Brahmaputra Rivers were formed and separated. Fishes of *Pseudecheneis*, originally adapted to harsh environments of the plateau experienced a 2nd division. They formed ancestors similar to *P. immaculatus* and to "*P. sulcatus* + *P. sulcatoides* + *P. sympelvicus*". The former was only distributed in the Mekong River system, while the latter was widely distributed in the vast area from the Mekong to the Brahmaputra River.

There have been several glacial periods since the Pleistocene (Li et al. 2002). Ancestors similar to *P. immaculatus* occurred in the Mekong and adapted to cold-water environments of the plateau. They remained in areas of high elevation and weather among the cold waters. The color spots already existing on their bodies gradually disappeared. This must have suited the environment better, by avoiding enemy attack and for preying on the benthic macrofauna as food. These eventually evolved into *P. immaculatus* and occupied the upper reaches of the Mekong River.

When a 3rd species division took place, ancestors similar to "*P. sulcatus* + *P. sulcatoides* + *P. sympelvicus*" divided and formed ancestors of *P. sulcatus* (NJ) and ancestors similar to "*P. sulcatus* (YJ) + *P. sulcatoides* + *P. sympelvicus*". Based on the phylogenetic tree of *Pseudecheneis*, there was an inference that at that time, the Indian Plate just connected with Eurasia Plate, and the elevation in extensive areas was not high and retained the state of the ancient plain. There were many linkages among the Mekong, Salween, and Irrawaddy River systems.

The 4th species division occurred separately. (1) Gaoligong Mountain was gradually lifted because the Indian Plate and Eurasia Plates were continually pushing against each other. The Irrawaddy, Salween, and Mekong River systems were completely separated and their communications were interrupted. An ancestor similar to *P. sulcatus* distributed in the Salween River system gradually formed an independent group (NJ *P. sulcatus*), and produced morphological and molecule differences with *P. sulcatus* distributed over an extensive area. (2) The plateau level of western Sichuan and northern Yunnan Provinces sloped southeastward, which was caused by the strong uplift of the Qinghai-Xizang Plateau since the Tertiary. This caused the function of river systems to be strengthened in the southeast, with the Pacific Ocean attacking river valleys on the plateau. Ancient watersheds of Xikang finally disintegrated with waterways of plateau fishes spreading outwards and being completely dredged (Wu et al. 1991, Li et al. 2002). An ancestor similar to *P. sulcatus* distributed in this area gradually spread outwards reaching Pakistan and India. It became the *P. sulcatus* of today and was extensively distributed. (3) Ancestor groups of *P. sulcatoides* and *P. sympelvicus* living in the Mekong River spread to different river sections midstream and downstream. Through adaptations to constant developments in the environment, they eventually formed today's *P. sulcatoides* and *P. sympelvicus* and occupy different respective river sections.

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