

rare because salt does not survive at the land surface except in a few extremely arid regions.

Figure 1 shows the variety of sources for the water responsible for the development of caves. Most of the caves are dissolved by the movement of groundwater in contemporary drainage basins. In coastal regions, the mixing of fresh groundwater with saltwater produces an aggressive solution that can dissolve out caves. Some caves (for example, the large caves of the Black Hills of South Dakota) are formed from hot water rising up from deep within the rock. Carlsbad Caverns in New Mexico and other caves of the Guadalupe Mountains have been formed by sulfuric acid derived from the oxidation of hydrogen sulfide migrating upward from the oil fields to the east.

In summary, caves form in a great variety of rocks by a great variety of geological and chemical processes. Each has its importance to geology. However, the common theme that binds this diverse collection of cavities together is their interest to human explorers and their use as habitat by cave-adapted organisms.

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CAVEFISH OF CHINA

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THE DISTRIBUTION AND DIVERSITY OF CHINESE CAVEFISH

Cavefishes, or hypogean fishes, are a distinctive group of fishes. Their life history binds them to be located

in caves and other subterranean waters. In 1854, Schiner divided all creatures that live in subterranean and underground waters into three types: troglobites, troglaphiles, and troglaxenes. Troglobites have typical adaptive characteristics allowing them to complete their entire life cycles in caves; troglaphiles lack special adaptations to caves but nonetheless rely heavily on subterranean waters during their life cycles; and troglaxenes enter the cave accidentally and their life cycles and characteristics do not necessarily require caves.

Globally, most species of cavefish are distributed in the tropics and subtropics, with 75% of all known populations predominantly located in Southeast Asia or Central and South America, where the landscape is composed of limestone and other soluble rock types (also known as a karst landscape). The southern and western parts of China have more than 620,000 km² of karst (Huang *et al.*, 2008), which provides suitable conditions for cavefish evolution. The earliest record of cavefish in Chinese history was in 1436 when a local doctor, Mao Lan, recorded cavefish in South Yunnan. This was the well-known golden-line fish, which lives mostly in Dian Lake near caves in Yunnan Province. This golden-line fish, now recognized as *Sinocyclocheilus grahmi*, is a troglaphilic, partially cave-dwelling fish. The earliest paper report on a troglaphitic fish is also in China. In 1540, Yingjing Xie, a local governor of Guangxi, went to A'lu Cave and recorded "there was a kind of transparent fish coming out if the subterranean river rose very much" in his travel notes on A'lu Cave. This transparent (also blind) fish still lives in the same cave and was described as *Sinocyclocheilus hyalinus* (Fig. 1) in 1994 (Chen *et al.*, 1994).

At the end of 2010, China had 95 described species of hypogean (cave and phreatic) fishes which belong to three families: Cyprinidae, Cobitidae, and Balitoridae (Romero *et al.*, 2009; Table 1). There are 55 species of Chinese hypogean cyprinids that include 4 genera: *Onychostoma*, *Sinocrossocheilus*, *Sinocyclocheilus*, and *Typhlobarbus*. *Onychostoma macrolepis* is a cavefish that was found to "hibernate" during winter. This is the only hypogean species in China found north of the Yangtze River. The family Cobitidae is a family characterized by a wormlike or fusiform body, whose members are mostly bottom dwellers in freshwater. Two troglomorphic species of the genus *Protocobitis* have been described and both are from China. The family Balitoridae is another freshwater family of the order Cypriniformes, which is characterized by having three or more pair of barbels. Some species are scaleless. Many tend to hide underneath rocks. The Chinese hypogean fishes of this family include 7 genera: *Heminoemacheilus*, *Oreonectes*, *Paracobitis*, *Paranemacheilus*, *Schistura*, *Triplophysa*, and *Yunnanilus*.

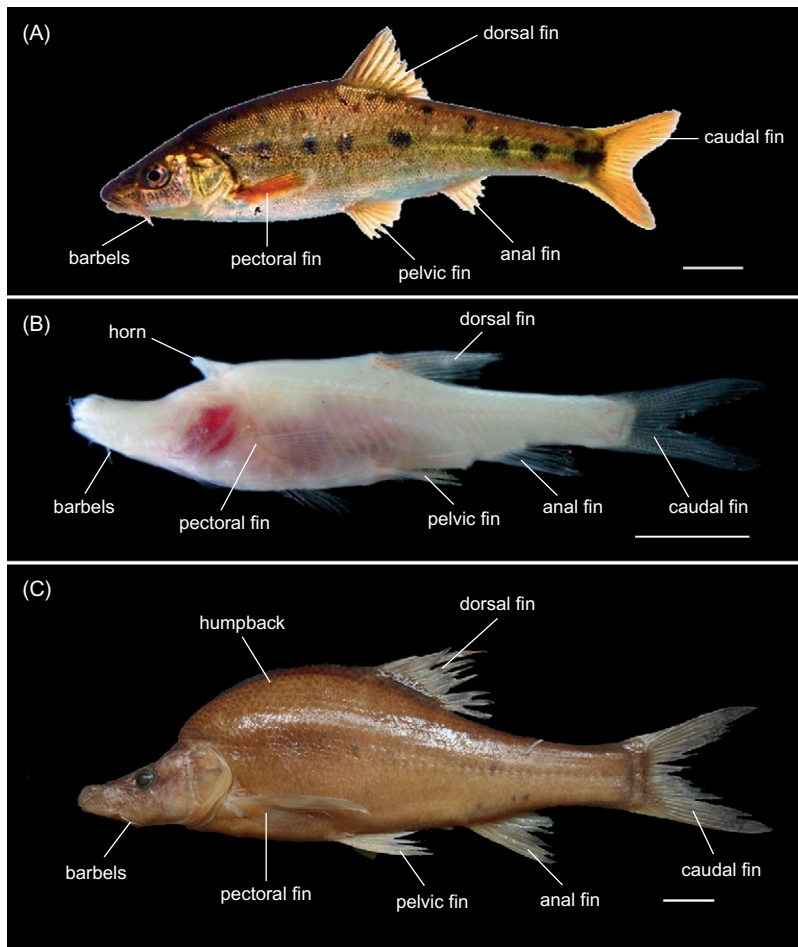


FIGURE 1 A comparison between the general morphologies of (A) adult *S. grahami*, (B) *S. hyalinus*, and (C) *S. brevibarbus*. Scale bars = 1 cm.

The genus *Sinocyclocheilus* (Cypriniformes, family: Cyprinidae), established by Fang Bingwen in 1936, is endemic to China and can be found in the karst cave waters and surface rivers or lakes in Yunnan-Guizhou Plateau and the surrounding region (including east of Yunnan Province, south central of Guizhou Province, and northwest of Guangxi Zhuang Autonomous Region) (Fig. 2). Almost all *Sinocyclocheilus* species live in caves for at least part of their life cycles. Yunnan has the most *Sinocyclocheilus* species, which is mainly attributed to an abundance of troglophiles, while Guangxi and Guizhou contain about half of the troglotic cavefish in China. The genus *Sinocyclocheilus* is mainly distributed near 25°N. In river systems, most species of *Sinocyclocheilus* are found in the Qianjiang River north tributary of Xunjiang River, upstream of the largest Xijiang River tributary of the Zhujiang River system, and more upstream of the Hongshuihe Valley (including the associated underground river). *Sinocyclocheilus* may be the biggest cyprinid genus in China with more than 60 nominal species currently described. At least 50 species are valid among them, and 25 (50%) are trogllobites (Zhao and Zhang, 2009).

BIOLOGY OF CHINESE CAVEFISH

Chinese cavefish vary greatly in their size. For example, the maximum length of adult cavefish is quite variable. Some species are large, like *Sinocyclocheilus altishoulder* and *S. hugeibarbus*, where the largest recorded individual is 200 mm (standard length); whereas in *Oreonectes anophthalmus*, the average adult length is around 30 mm.

Due to the absence of photosynthesis in caves, almost all Chinese cavefish are predators. Based on stomach contents, their diet seems to consist of fish scales, mollusks, and insects. The diet also can include algae (mostly diatoms), insect larvae, and other less defined organic materials.

Reproduction also varies considerably in the genus *Sinocyclocheilus*. Some species show continuous reproductive activity in all four seasons, a phenomenon that is seldom seen at other cyprinid fish. Normally most fish in the subtropical zone of the Northern Hemisphere multiply during the first half of each year. Perhaps because these areas have four distinct seasons, and the winter temperature is low, fish in these areas

TABLE 1 All the Valid Species of Chinese Hypogean Fishes

Species	Namer	Year	Distribution
Family: Cyprinidae			
Genus <i>Onychostoma</i>	Günther	1896	
1. <i>Onychostoma macrolepis</i>	Bleeker	1871	Beijing, Hebei, Shandong, Shanxi, Henan
Genus <i>Sinocrossocheilus</i>	Wu	1977	
2. <i>Sinocrossocheilus bamaensis</i>	Fang	1981	Guangxi, Guizhou
3. <i>Sinocrossocheilus liuchengensis</i>	Liang	1987	Guangxi
4. <i>Sinocrossocheilus megalophthalmus</i>	Chen, Yang, and Cui	2006	Guangxi
Genus: <i>Sinocyclocheilus</i>	Fang	1936	
5. <i>Sinocyclocheilus altishoulderus</i>	Li and Lan	1992	Guangxi
6. <i>Sinocyclocheilus anatirostris</i>	Lin and Luo	1986	Guangxi
7. <i>Sinocyclocheilus angularis</i>	Zheng and Wang	1990	Guizhou
8. <i>Sinocyclocheilus angustiporus</i>	Zheng and Xie	1985	Guizhou, Yunnan
9. <i>Sinocyclocheilus anophthalmus</i>	Chen and Chu	1988	Yunnan
10. <i>Sinocyclocheilus aquihornes</i>	Li and Yang	2007	Yunnan
11. <i>Sinocyclocheilus bicornutus</i>	Wang and Liao	1997	Guizhou
12. <i>Sinocyclocheilus brevibarbus</i>	Zhao, Lan, and Zhang	2009	Guangxi
13. <i>Sinocyclocheilus brevis</i>	Lan and Chen	1992	Guangxi
14. <i>Sinocyclocheilus broadihornes</i>	Li and Mao	2007	Yunnan
15. <i>Sinocyclocheilus cyphotergous</i>	Dai	1988	Guizhou
16. <i>Sinocyclocheilus donglanensis</i>	Zhao, Watanabe, and Zhang	2006	Guangxi
17. <i>Sinocyclocheilus furcodorsalis</i>	Chen, Yang, and Lan	1997	Guangxi
18. <i>Sinocyclocheilus grahami</i>	Regan	1904	Yunnan
19. <i>Sinocyclocheilus guilinensis</i>	Ji	1982	Guangxi
20. <i>Sinocyclocheilus guishanensis</i>	Li	2003	Yunnan
21. <i>Sinocyclocheilus huaningensis</i>	Li	1998	Yunnan
22. <i>Sinocyclocheilus hugeibarbus</i>	Li and Ran	2003	Guizhou
23. <i>Sinocyclocheilus hyalinus</i>	Chen and Yang	1994	Yunnan
24. <i>Sinocyclocheilus jii</i>	Zhang and Dai	1992	Guangxi
25. <i>Sinocyclocheilus jixuensis</i>	Li and Lan	2003	Guangxi
26. <i>Sinocyclocheilus lateristris</i>	Li	1992	Yunnan
27. <i>Sinocyclocheilus lingyunensis</i>	Li, Xiao, and Luo	2000	Guangxi
28. <i>Sinocyclocheilus longibarbus</i>	Wang	1989	Guangxi
29. <i>Sinocyclocheilus longifinus</i>	Li and Chen	1994	Yunnan
30. <i>Sinocyclocheilus luopingensis</i>	Li and Tao	2003	Yunnan
31. <i>Sinocyclocheilus macrocephalus</i>	Li	1985	Yunnan
32. <i>Sinocyclocheilus macrolepis</i>	Wang	1989	Guizhou, Guangxi
33. <i>Sinocyclocheilus macrophthalmus</i>	Zhang and Zhao	2001	Guangxi

(Continued)

TABLE 1 (Continued)

Species	Namer	Year	Distribution
34. <i>Sinocyclocheilus macroscalus</i>	Li	1992	Yunnan
35. <i>Sinocyclocheilus maculatus</i>	Li	2000	Yunnan
36. <i>Sinocyclocheilus maitianheensis</i>	Li	1992	Yunnan
37. <i>Sinocyclocheilus malacopterus</i>	Chu and Cui	1985	Yunnan
38. <i>Sinocyclocheilus microphthalmus</i>	Li	1989	Guangxi
39. <i>Sinocyclocheilus multipunctatus</i>	Pellegrin	1931	Guangxi, Guizhou
40. <i>Sinocyclocheilus oxycephalus</i>	Li	1985	Yunnan
41. <i>Sinocyclocheilus purpureus</i>	Li	1985	Yunnan
42. <i>Sinocyclocheilus qiubeiensis</i>	Li	2002	Yunnan
43. <i>Sinocyclocheilus qujingensis</i>	Li, Mao, and Lu	2002	Yunnan
44. <i>Sinocyclocheilus rhinocerosus</i>	Li and Tao	1994	Yunnan
45. <i>Sinocyclocheilus robustus</i>	Chen and Zhao	1988	Guizhou
46. <i>Sinocyclocheilus tianlinensis</i>	Zhou, Zhang, and He	2003	Guangxi
47. <i>Sinocyclocheilus tileihornes</i>	Mao, Lu, and Li	2003	Yunnan
48. <i>Sinocyclocheilus tingi</i>	Fang	1936	Yunnan
49. <i>Sinocyclocheilus wumengshanensis</i>	Li, Mao, and Lu,	2003	Yunnan
50. <i>Sinocyclocheilus xunlensis</i>	Lan, Zhao, and Zhang	2004	Guangxi
51. <i>Sinocyclocheilus yangzongensis</i>	Tsü and Chen	1977	Yunnan
52. <i>Sinocyclocheilus yaolanensis</i>	Zhou, Li, and Hou	2009	Guizhou
53. <i>Sinocyclocheilus yimenensis</i>	Li and Xiao	2005	Yunnan
54. <i>Sinocyclocheilus yishanensis</i>	Li and Lan	1992	Guangxi
55. <i>Typhlobarbus nudiventris</i>	Chu and Chen	1982	Yunnan
Family: Cobitidae—loaches			
Genus <i>Protocobitis</i>			
	Yang	1994	
56. <i>Protocobitis polylepis</i>	Zhu, Lu, Yang, and Zhang	2008	Guangxi
57. <i>Protocobitis typhlops</i>	Yang, Chen, and Lan	1994	Guangxi
Family: Balitoridae			
Genus <i>Heminoemacheilus</i>			
	Zhu and Cao	1987	
58. <i>Heminoemacheilus hyalinus</i>	Lan, Yang, and Chen	1996	Guangxi
59. <i>Heminoemacheilus zhengbaoshani</i>	Zhu and Cao	1987	Guangxi
Genus <i>Oreonectes</i>			
	Günther	1868	
60. <i>Oreonectes anophthalmus</i>	Zheng	1981	Guangxi
61. <i>Oreonectes furcocaudalis</i>	Zhu and Cao	1987	Guangxi
62. <i>Oreonectes macrolepis</i>	Huang, Chen, and Yang	2009	Guangxi
63. <i>Oreonectes microphthalmus</i>	Du, Chen, and Yang	2008	Guangxi
64. <i>Oreonectes retradorsalis</i>	Lan, Yang, and Chen	1995	Guangxi
65. <i>Oreonectes translucens</i>	Zhang, Zhao, and Zhang	2006	Guangxi
Genus <i>Paracobitis</i>			
	Bleeker	1863	

(Continued)

TABLE 1 (Continued)

Species	Namer	Year	Distribution
66. <i>Paracobitis maolanensis</i>	Li, Ran, and Chen	2006	Guizhou
67. <i>Paracobitis posterodarsalus</i>	Ran, Li, and Chen	2006	Guangxi
Genus <i>Paranemacheilus</i>	Zhu	1983	
68. <i>Paranemacheilus genilepis</i>	Zhu	1983	Guangxi
Genus <i>Schistura</i>	McClelland	1838	
69. <i>Schistura dabryi microphthalmus</i>	Liao and Wang	1997	Guizhou
70. <i>Schistura linyunensis</i>	Liao and Luo	1997	Guangxi
Genus <i>Triplophysa</i>	Rendahl	1933	
71. <i>Triplophysa aluensis</i>	Li and Zhu	2000	Yunnan
72. <i>Triplophysa gejiuensis</i>	Chu and Chen	1979	Yunnan
73. <i>Triplophysa longibarbus</i>	Chen, Yang, Sket, and Aljancic	1998	Guizhou
74. <i>Triplophysa nandanensis</i>	Lan, Yang, and Chen	1995	Guangxi
75. <i>Triplophysa nasobarbatula</i>	Wang and Li	2001	Guizhou
76. <i>Triplophysa qiubeiensis</i>	Li and Yang	2008	Yunnan
77. <i>Triplophysa rosa</i>	Chen and Yang	2005	Chongqing
78. <i>Triplophysa shilinensis</i>	Chu and Yang	1992	Yunnan
79. <i>Triplophysa tianeensis</i>	Chen, Cui, and Yang	2004	Guangxi
80. <i>Triplophysa xiangshuingensis</i>	Li	2004	Yunnan
81. <i>Triplophysa xiangxiensis</i>	Yang, Yuan, and Liao	1986	Hunan
82. <i>Triplophysa yunnanensis</i>	Yang	1990	Yunnan
83. <i>Triplophysa zhenfengensis</i>	Wang and Li	2001	Guizhou
Genus <i>Yunnanilus</i>	Nichols	1925	
84. <i>Yunnanilus bajiangensis</i>	Li	2004	Yunnan
85. <i>Yunnanilus beipanjiangensis</i>	Li, Mao, and Sun	1994	Yunnan
86. <i>Yunnanilus discoloris</i>	Zhou and He	1989	Yunnan
87. <i>Yunnanilus longidorsalis</i>	Li, Tao, and Lu	2000	Yunnan
88. <i>Yunnanilus macrogaster</i>	Kottelat and Chu	1988	Yunnan
89. <i>Yunnanilus macrolepis</i>	Li, Tao, and Mao	2000	Yunnan
90. <i>Yunnanilus nanpanjiangensis</i>	Li, Mao, and Lu	1994	Yunnan
91. <i>Yunnanilus niger</i>	Kottelat and Chu	1988	Yunnan
92. <i>Yunnanilus obtusirostris</i>	Yang	1995	Yunnan
93. <i>Yunnanilus paludosus</i>	Kottelat and Chu	1988	Yunnan
94. <i>Yunnanilus parvus</i>	Kottelat and Chu	1988	Yunnan
95. <i>Yunnanilus pulcherrimus</i>	Yang, Chen, and Lan	2004	Guangxi

finish their breeding activity as early as possible, so that the young fry have time to grow before the next cold season. Thus, it is likely that breeding of most *Sinocyclocheilus* species occurs between the spring and

summer. Since the streams in all caves inhabited by *Sinocyclocheilus* connect with surface rivers, their water levels are affected by regional precipitation and can change radically within a short time period. These

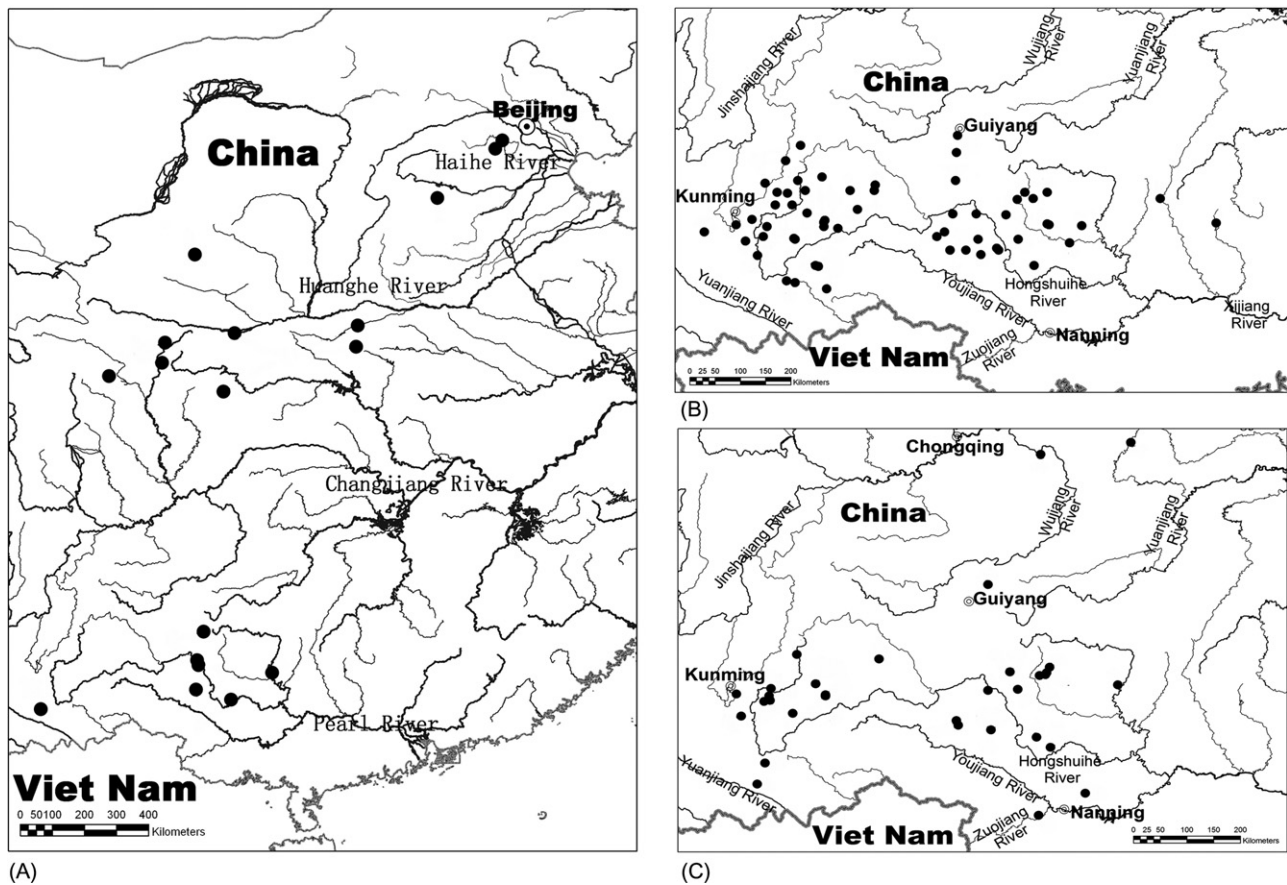


FIGURE 2 Distribution map of Chinese hypogean fishes. (A) Distribution of hypogean *Cyprinidae* (excluding the genus *Sinocyclocheilus*). (B) Distribution of the species in the genus *Sinocyclocheilus*. (C) Distribution of hypogean *Cobitidae* and *Balitoridae*.

radical changes in water levels may trigger reproductive activity. The sex ratio of *S. tingi* varies from 1.31 to 4.2, with females being more abundant than males. The egg diameter of *S. macrolepis* is 1.5~2.0 mm, whereas the diameter of mature *S. bicornutus* and *S. angularis* eggs is 1.5~2.0 mm, and the mature egg of *S. tingi* averages 2.1 mm. According to dissection and observation, it was found that the absolute brood size of *S. macrolepis* is about 2000 and the average brood size of *S. tingi* is 2595~3087. In both species, embryos develop synchronously, suggesting that ovulation occurs simultaneously. The fecundity of 2-year-old *S. yangzongensis* is 3585, and increases to 22,000 eggs after 5 years.

THE CHARACTERISTICS OF CHINESE CAVEFISH

Chinese cavefish have five main characteristics that make them unique among the cavefish of the world.

1. China hosts the greatest and most diverse number of troglobitic fish species. So far, at least 46 species of troglobites have been found in China with the

number still increasing with the discovery of new species.

2. Although China has the richest variety of troglobite fish species, they mainly belong to two genera from Cypriniformes, *Sinocyclocheilus* and *Triplophysa*, which together account for 71.7% of the Chinese troglobitic cavefish.
3. The range of preferred habitat is relatively narrow. Chinese troglobitic fish, excluding *Triplophysa xiangxiensis* which lives in Hunan Province and *T. rosa* that lives in Chongqing, are all distributed in Yunnan Province, Guizhou Province, and the Guangxi Zhuang Autonomous Region. In particular, the Guangxi Zhuang Autonomous Region has the largest number of troglobitic cavefish (22 species, accounting for 48% of all Chinese troglobite fish). Chinese troglobitic fish species are most concentrated in the karst areas of the Yunnan-Guizhou Plateau. Most of these species are located only in one independent water body, such as one small river, one brook, even one cave. For example, *Oreonectes anophthalmus* is unique to Taiji Cave of Wuming, Guangxi.

4. Intense speciation is seen among Chinese cavefish, despite the narrow area of habitat in which they live. The genus *Sinocyclocheilus* is a good example. Its range reaches from Yunnan Yimen in the west to Guangxi Fuchuan in the east, and north from Guizhou Huaxi to Yunnan Yanshan in the south. The distance between east and west is 900 km, but the distance between south and north is only 300 km. In this relatively small area, 50 species of *Sinocyclocheilus* have been recorded, making *Sinocyclocheilus* the largest genus of Chinese Cyprinidae, as well as the genus with the greatest amount of adaptive morphology. The large diversity of *Sinocyclocheilus* species is probably the result of strong selective pressures of isolated cave environments, combined with the unique environmental effects that might be present in the Qinghai-Tibet Plateau uplift. It is interesting to note that this intense speciation is seldom seen in the other areas of the world where cavefish are distributed.
5. Each species of Chinese cavefish tends to have a small population size. Limited food resources are probably responsible for this. A good example is *S. hyalinus*, of which only very few specimens were found in their only habitat, A'lu cave in Guangxi Zhuang Autonomous Region.

MORPHOLOGY AND ADAPTATION

Cave habitats are unique environments characterized by permanent darkness, the absence of green plants, and

seasonal scarcity. Chinese cavefish have evolved a series of constructive and regressive morphological changes to survive in these harsh conditions. Constructive features often include a protruding jaw, an increase in the number of taste buds, over-developed barbels, and various specialized appendages, while regressive changes mainly include eye degeneration, reduction or loss of pigmentation, and the disappearance of scales. In addition to these common adaptations, Chinese cavefish have other unique features, such as the development of a humped back, a horn, and a head drape. Below we discuss the morphology and adaptation of Chinese cavefish from the perspective of their constructive and regressive structures.

Changes in Body Shape

Cavefish often have a very different outward appearance compared to their surface counterparts. There are three different body shapes of cavefish, the fusiform type, the humpback type, and the head-horn type. In *Sinocyclocheilus*, the head shape of the surface species is very similar to the normal shape of other fishes (e.g., *S. grahami*), in which the length of the head is longer than the height of the body; the snout is slightly pointed; the mouth is subinferior; and the upper jaw is elongated (Fig. 1). In some cave-dwelling fish, the head is duckbilled, with the anterior half-depressed and the posterior half-raised, and the jaws are wider and more protruding than their related surface species. For instance, the jaws of *S. hyalinus* and *S. anophthalmus* are wider and more protruding than *S. grahami* (Fig. 3). The pleat on the head ridge that is found in *S. hyalinus*

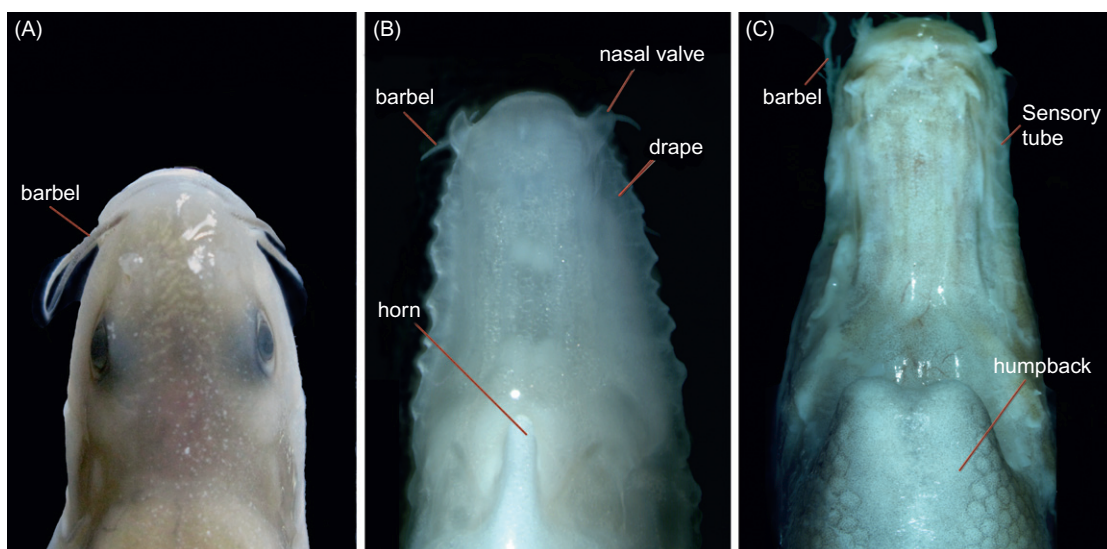


FIGURE 3 Differences in head shape between (A) *S. grahami*, (B) *S. hyalinus*, and (C) *S. anophthalmus*. The jaws of *S. hyalinus* and *S. anophthalmus* adults are wider and more protruding than the jaw of *S. grahami*.

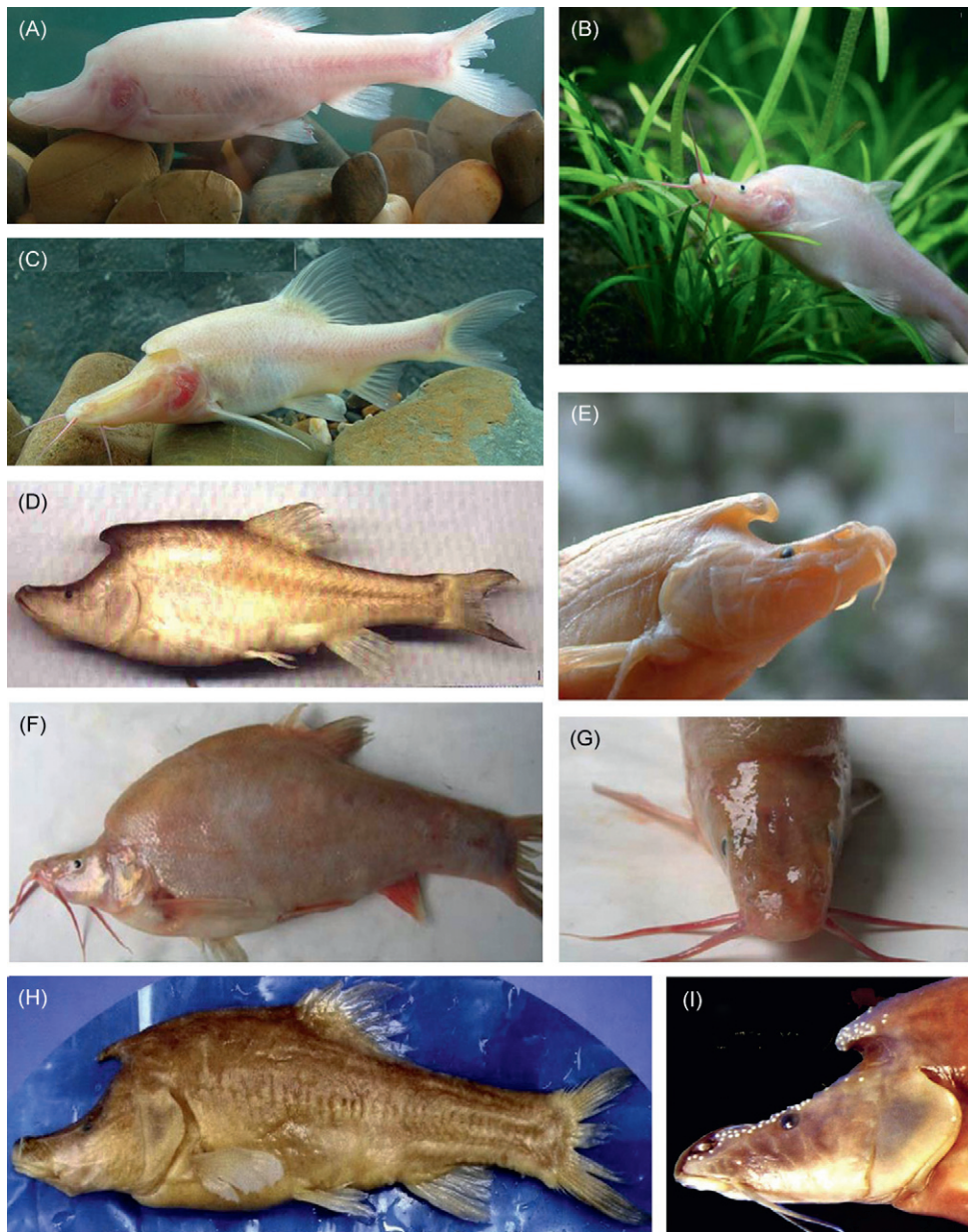


FIGURE 4 Examples of the different species of *Sinocyclocheilus*. (A) *S. tianlinensis*; (B) *S. microphthalmus*; (C) *S. furcodorsalis*; (D) *S. broadihornes*; (E) *S. tileihornes*; (F) *S. hugeibarbus*; (G) enlarged image of *S. hugeibarbus* head; (H) *S. rhinoceros*; (I) enlarged image of *S. rhinoceros* head.

is also a very unique morphological feature (Fig. 3), and may have the function of increasing sensitivity to fluctuations in water flow.

Humpback and Horn

One of the prominent constructive structures of *Sinocyclocheilus* is the humpback and horn, which can be very well developed in some of the troglobitic species. The humpback is free of bone and mainly consists

of adipose tissue (Wang *et al.*, 1995), while the horn consists of the frontal and parietal bones. The horn structure is found in both sexes of the same species, and the shape of the horn also varies between different *Sinocyclocheilus* species: some are small (*S. angularis*), some are forked (*S. bicornutus*), some show a thin protrusion (*S. rhinoceros*), and several show a tile shape (*S. tileihornes*) (Fig. 4).

The histology of the *S. hyalmus* head horn has been extensively studied (Fig. 5). Overall, the structure of horn can be divided into three segments, from anterior

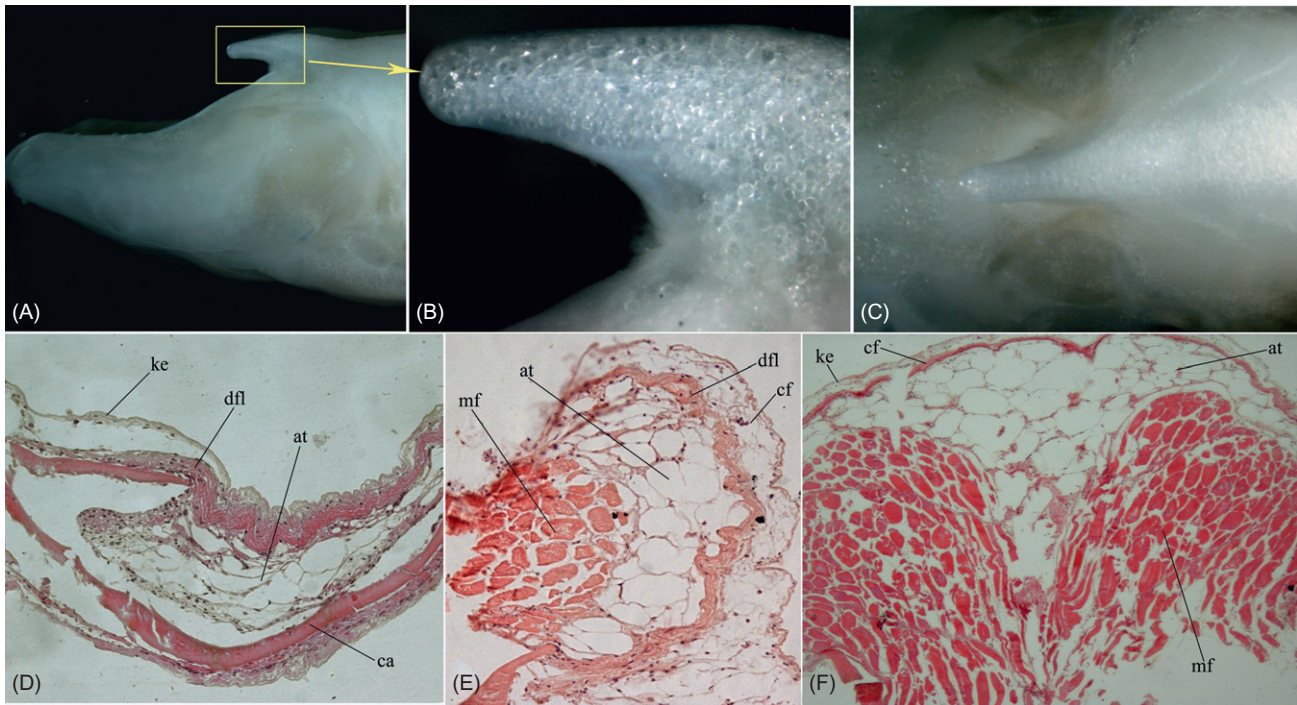


FIGURE 5 Horn structure of *S. hyalmus*. (A) Lateral view of head; (B) magnified image of horn; (C) dorsal view of horn. The horn is divided into three segments; (D), (E), and (F) show the histological structure of horn. ke, keratinized epithelium; dfl, dense fibrous layer; at, adipose tissue; mf, muscle fibers; cf, collagen fibrils; ca, cartilage.

to posterior: the first is the apical section, the second is the middle section, and the third is the basal section. The apical section is characterized by a thick layer of keratinized epithelium containing thick collagen fibrils (Fig. 5D). The middle section is composed of keratinized epithelium, lying over a compact fibrous layer, adipose tissue, and muscle fibers. A thick dermal reticular layer forms the compact fibrous layer under the thick keratinized epithelium. There are adipose tissue and muscle fibers under the fibrous layer (Fig. 5E), and the basal section has a much thinner layer of collagen fibrils and a compact fibrous layer under the keratinized epithelium, which is characterized by the presence of very thick adipose tissue and muscle fibers under the fibrous layer (Fig. 5F). Neither nerve ending nor glands are present in the horn. These characteristics suggest that the function of the horn may be to store fat for nourishment of the adjacent brain.

The horn may also be used for protecting the brain from bumping into rock walls. Li and Tao (1994) studied horn structure in *S. rhinoceros*, and found that its bony part is composed of three pieces, each shaped like a right-angled triangle (Fig. 6A). As shown in the schematic diagram (Fig. 6B), "A" stands for the tip of the horn and "BCD" stands for the base of horn. Thus when "A" hits a rocky surface, the pressure will transmit downward to line "BE," "CE," and "DE" and then disperse and decrease greatly, thereby protecting

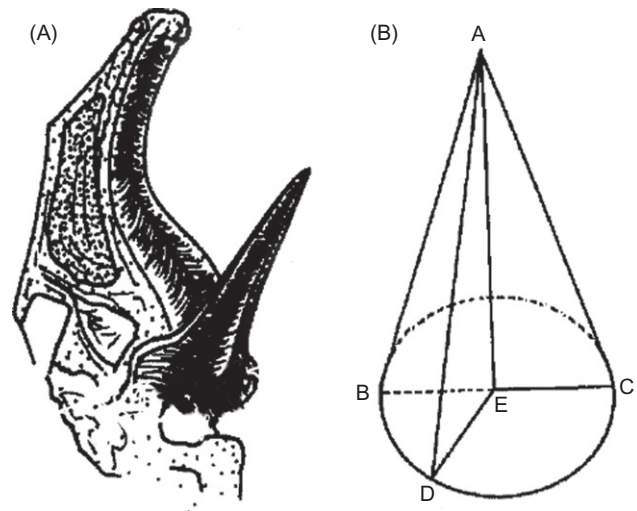


FIGURE 6 Bone structure of the horn of *S. rhinoceros* (A) with a schematic diagram (B).

the brain during swimming in rocky caves (Li *et al.*, 1997). Although the bony horn of *S. rhinoceros* can't completely protect the body from injuries produced by bumping into rock walls, it could disperse pressure equally throughout the head surface to reduce the magnitude of the force. There are also some other hypotheses on functions of horn-like character, but real answers still need further studies.

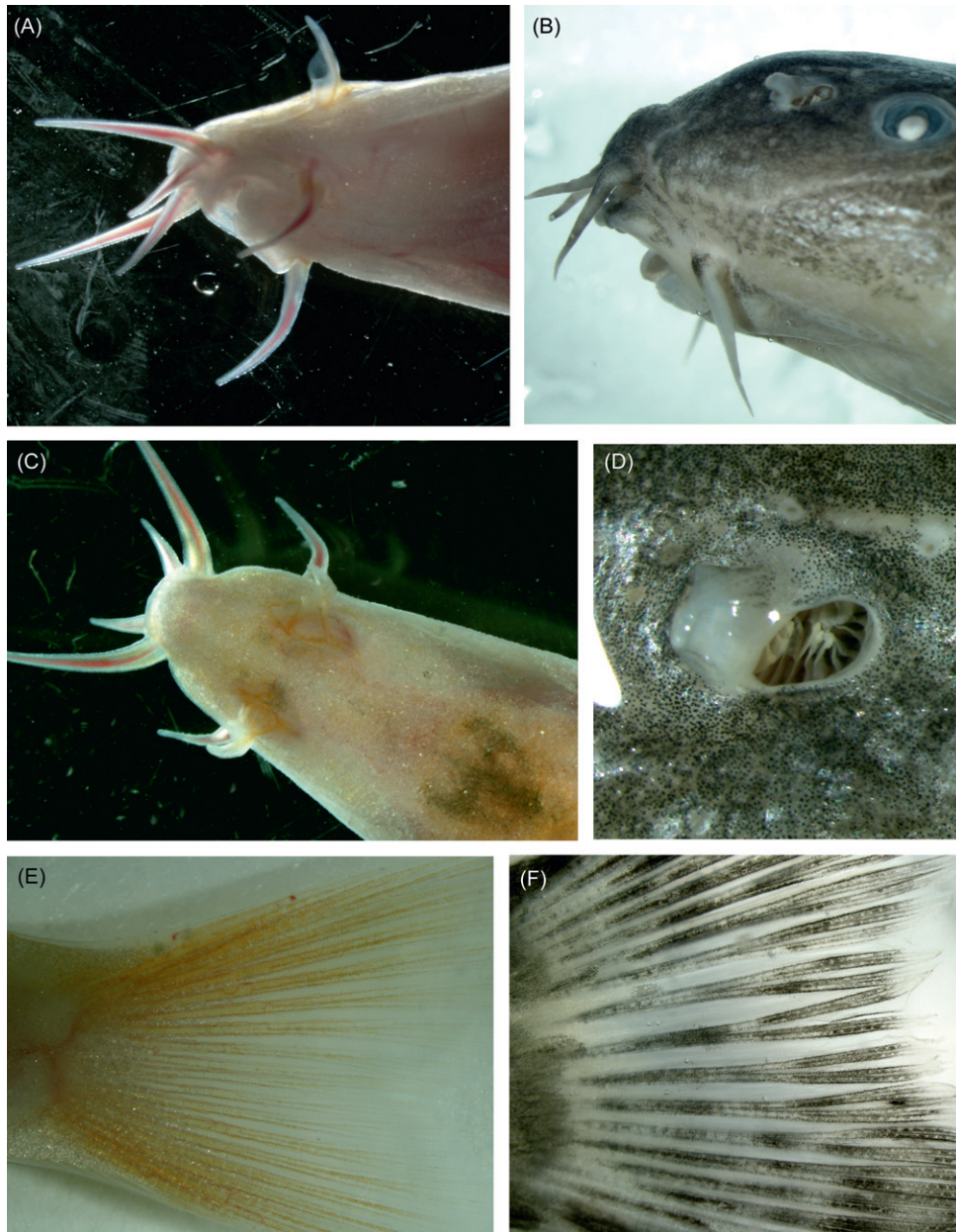


FIGURE 7 The barbels, nostril, and caudal fin of *Triplophysa*.

The humpback is found in different clades of *Sinocyclocheilus*, demonstrating that it is the result of convergent evolution, and likely to be adaptive. Although the precise function of the horn-like structure is still unknown, it is found only among some hypogean species of the genus *Sinocyclocheilus*.

Sensory Apparatus

Sensory structures such as barbels, taste buds, nostrils, and the lateral line system have been augmented in cave-fish. Most of the Chinese cave-dwelling species have a

more sensitive sense of smell, with the nostrils more anterior than their surface relatives, and in some species the nasal valve is hyper-developed and takes on a beard shape (Fig. 7). At the same time, cave species often have an increased number of taste buds: for example, *S. hyalinus* has more taste buds than *S. grahami*.

The barbel has a tactile function, and also has taste buds on it, implying both mechanosensory and gustatory functions. Fish can use barbels to detect the surrounding environment and amplify the search for food. There are abundant neurons and sinuses in the barbels of *Sinocyclocheilus anatirostris*, showing

that the barbels have a prominent sensory function. All *Sinocyclocheilus* have two pairs of well-developed barbels; however, the extent of barbel development differs according to the level of exposure to light. Among those Chinese cave-dwelling species that live in both cave and non-cave environments with abundant light, most have barbels that are moderately developed and extend from the anterior edge of the eyes to the preopercular bone. Those partially cave-dwelling species that live in shaded bodies of water have more developed barbels that can extend to the trailing edge of the opercle, and may even extend to the starting point of the pectoral fin, such as is the case in *S. longibarbatulus*. There are several cave-restricted species of Chinese cavefish in which barbel augmentation is often less than that found in partially cave-dwelling species. The least developed barbels do not reach the leading edge of the eye, as in *S. cyphotergous*, while the most developed barbels among the cave-restricted species just touch the preopercular bone, as in *S. microphthalmus*. This shows that the development of the barbels is inversely correlated with eye development: the barbels are long when the eye is smaller, a possible tradeoff for loss of eyesight. This is a very interesting phenomenon if one takes into account that cave-restricted species also have a very developed sensory tube and a special projection on the head. Therefore, it is reasonable to conclude that enhanced barbels is a primitive feature compensating for the loss of eyesight, whereas the sensory tube and projection are more advanced compensatory forms.

The lateral line system of *Sinocyclocheilus* is very developed and specialized. In addition to possessing the tubal system of Cyprinidae, both sides of the lateral line canal also have many short branches named *sensory tubes*. These are especially abundant in the head (Fig. 3C). In species such as *S. cyphotergous*, which shows the most extensive sensory tube network, sensory tubes can even be found under the surface of the skin on both sides of lateral line at the anterior part of the trunk. These special sensory tubes are found in all species of *Sinocyclocheilus*, which suggests that this feature was present in their common ancestor. It is estimated that the initial evolution of the sensory tube system occurred in a common ancestor living in an environment that may have had intimate connections with a karst cave environment. During the course of evolution and adaptation, this common ancestor acquired the trait first, and then passed it to its descendants.

Specialized Appendages

Troglobitic species often have more developed appendages, such as modified pectoral and pelvic fins, than troglophilic species (Fig. 1). The overdeveloped

appendages could diminish the energy consumption of the animal and improve the efficiency of movement, as seen in *Sinocyclocheilus*. In *Sinocyclocheilus*, the degeneration of the opsin system directly weakens the motor skills of the fish and results in a decreased ability to respond quickly to environmental changes. At the same time, the enhanced pectoral fin increases the fish's ability to balance itself. The morphological changes in the pectoral girdle and pectoral fin are detailed as follows. Overall, the pectoral girdle of *Sinocyclocheilus* cave species tends to be more elongated and narrower than surface species. Corresponding to a shorter surface for muscle adherence, the muscle attachment surface composed of the cleithrum and corcoideum has a more flattened concave shape. In some partially cave-dwelling species, the cleithrum and corcoideum are greatly reduced and in some cases they disappear completely. Additionally, the coracoid of surface species is wide, and higher than the cleithrum, with shallow ridges to accommodate muscle attachments. In *Sinocyclocheilus*, the coracoid develops into a triangle with the tip positioned anterior to the plane of the cleithrum.

In partially cave-dwelling species, the pectoral fin is short, with a rear projection that does not reach the starting point of the ventral fin, and an average number of 15 branches in the fin ray. In contrast, the pectoral fin of the cave-restricted species is long, with a rear protrusion that extends past the starting point of the ventral fin, and an average of 13 branches in the fin ray.

Adipose Storage

Chinese cavefish restricted to caves store large amounts of adipose tissue in various parts of the body, such as the forehead, the horn, the base of the dorsal fin, the base of the caudal fin, and the sides of the body (Fig. 8). There is also a considerable amount of adipose tissue stored in the eye socket (Fig. 9F). Fat deposition in the eye sockets should not be dismissed simply as padding, because the storage of fat is very important to cave animals and allows them to survive during seasons in which food does not enter caves. The lack of a primary food source that can be produced in darkness may cause a food limitation and thus require improvements in food-finding and energy storage capabilities. For this reason cave animals store fat wherever they have space, such as in the empty eye sockets and in the horn. Storing fat locally in the horn may function to provide adjacent tissues, such as the brain, nourishment when there is low food input into the cave.

Eye Degeneration

The adaptive changes in the optic system of Chinese cavefish are mainly seen as changes in the size of

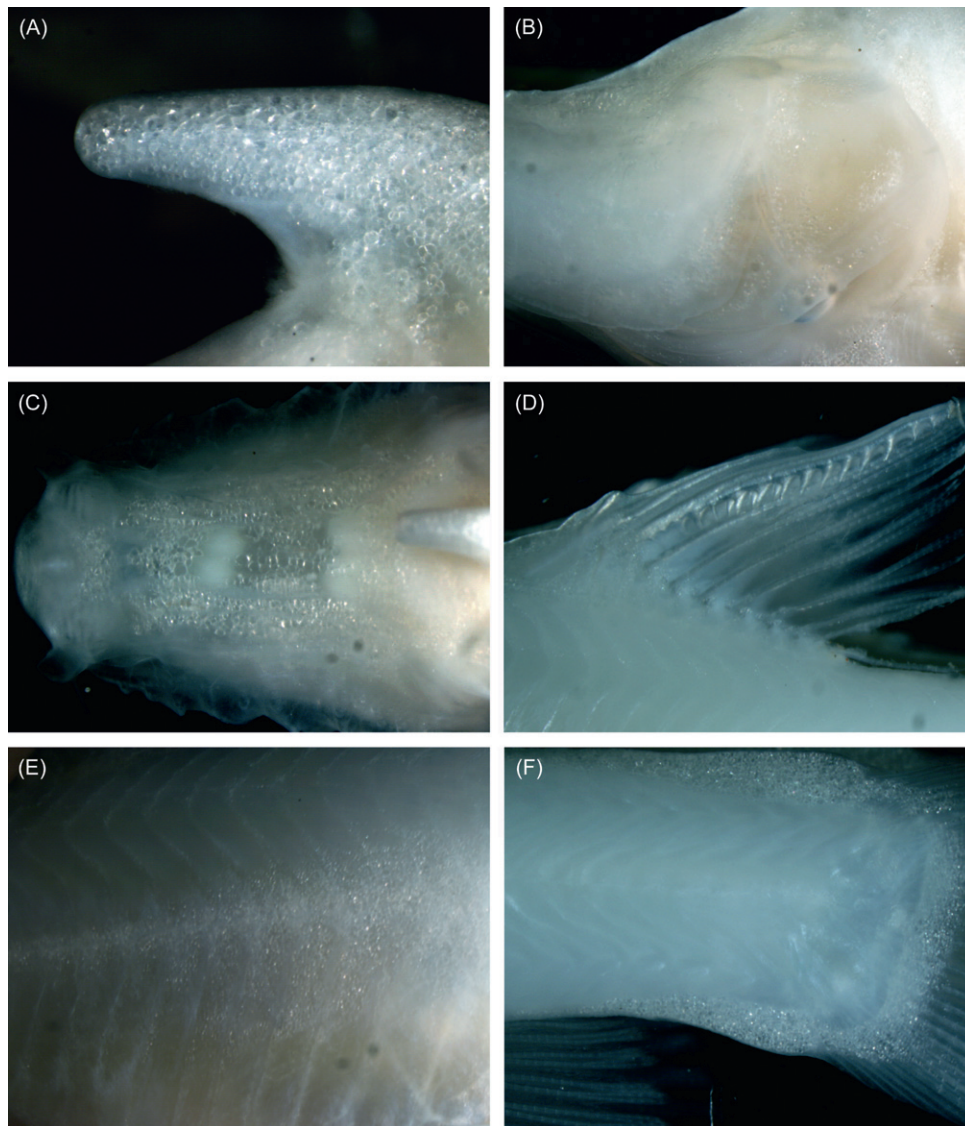


FIGURE 8 The distribution of adipose tissue in *S. hyalinus*. *S. hyalinus* store fat in the horn (A), forehead (B,C), base of the dorsal fin (D), lateral face of the body (E), and at the base of the caudal fin (F).

the eye, the degeneration of the eye's structure, and in some species its complete disappearance. There are three different eye structures seen in the genus *Sinocyclocheilus*: normal, dot-eye, and blind (Fig. 4). These variations are strongly correlated with differing amounts of sunlight each species is exposed to in the caves they inhabit. Those troglomorphic species that are sometimes active at the surface of the water in brighter areas have eyes that are clear but underdeveloped when compared to surface-dwelling species. The circumorbital structures of these fish are also modified, such that the lacrimal and supraorbital bones retain the shapes found in surface-restricted species, while the infraorbital and postorbital bones regress to a tubular shape. In some species, the supraorbital bone and

jawbones have a tendency to fuse, such as in *S. tingi*. In species that live in half-enclosed caves with weak light, such as *S. macrophthalmus*, eyes often tend to be larger, which may be beneficial for detecting weak light. Structural changes are even more pronounced in troglomorphic Chinese cavefish species that spend their entire life cycle in deep caves or underground streams and are only active near the mouth of these caves at night, returning to the depths before daybreak. The eyes of these fish are so small that they are barely visible under the surface of the skin that grows over the eye socket, and in many cases they even disappear completely. The infraorbital and postorbital bones either form tubes or disappear as well, while the supraorbital bone and jawbone fuse together. The sides

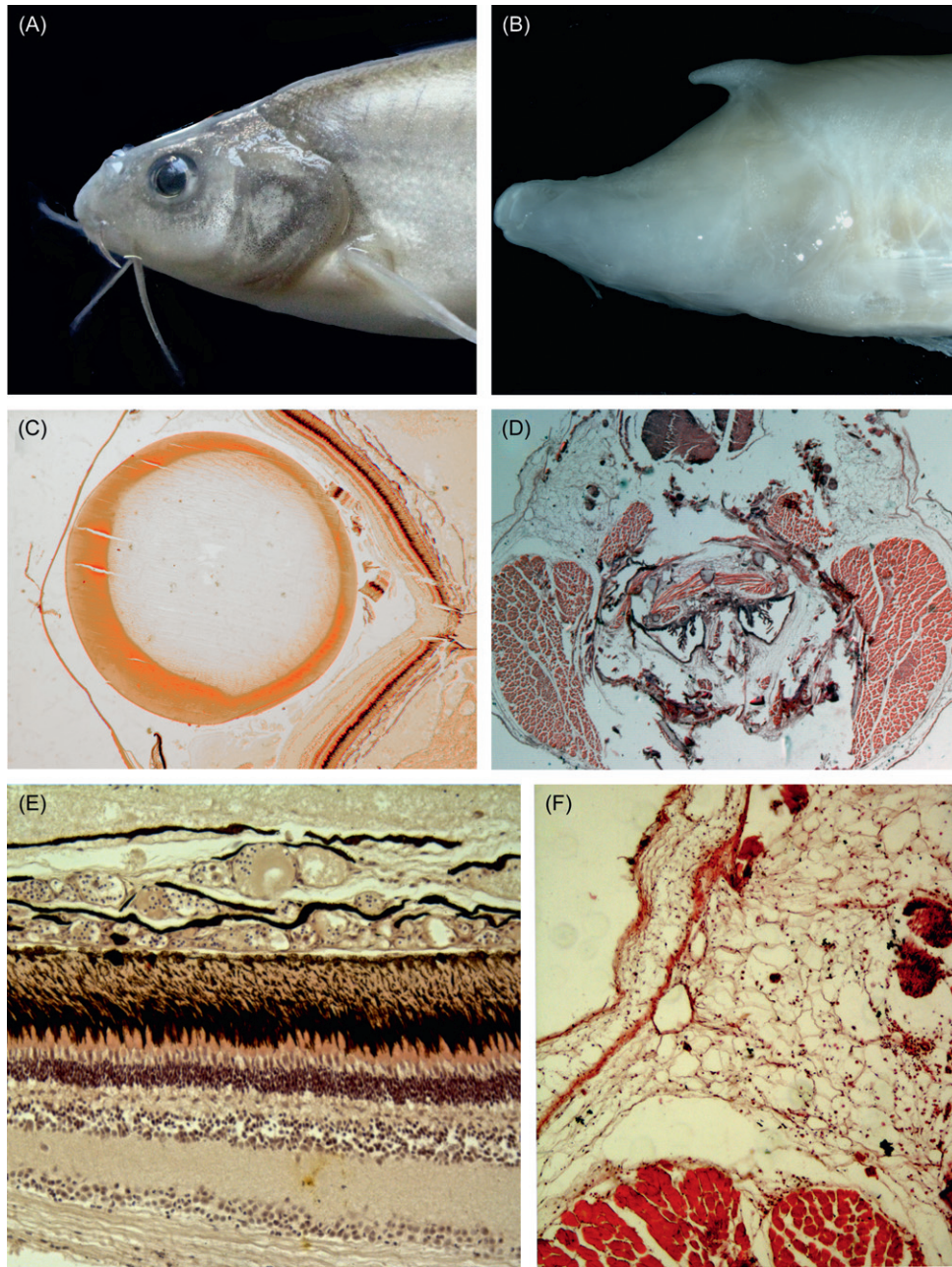


FIGURE 9 Comparison of the eye structures of *S. grahami* (A,C,E) and *S. hyalinus* (B,D,F). (A) Lateral view of *S. grahami* with normal eyes; (B) lateral view of *S. hyalinus* without eyes; (C) section of a *S. grahami* eye; (D) transversal section through the eye region of *S. hyalinus* showing the region containing fat tissue and a flap of skin; (E) retinal structure of *S. grahami*; (F) enlarged image of *S. hyalinus* eye region.

of the jawbone are widened and the rima oculi narrowed. The skin of the jaw has elongated and fused with the inferior skin to seal up the rima oculi completely. In addition, adipose tissue is deposited around the eye as it degenerates and can even replace it completely, as in *S. anatirostris* and *S. hyalmus* (Fig. 9).

Here we use *S. grahami* and *S. hyalinus* to demonstrate the details of the various changes in the eyes of Chinese cavefish (Fig. 9). On examination of the

external features of these fish, it can be seen that the *S. grahami* has fully developed eyes located toward the front section of the head (Fig. 9A), while the eyes of *S. hyalinus* seem to disappear (Fig. 9B). The eye structure of *S. grahami* is complete and includes the cornea, iris, pupil, and retina, with its fully developed neural structure (Fig. 9C,E). In *S. hyalinus*, the eye disappears completely, to the point that only adipose tissue is found in the eye orbit when the head is serially

sectioned (Fig. 9D,F). In contrast, *S. anophthalmus* does have small eyes buried deep within the orbits of the skull, which are also reduced in size, as seen in skeletal comparisons between species (Fig. 10D). Sometimes, the level of degeneration is different even within same species, as is known to occur in *S. anophthalmus* and *Triplophysa tianeensis*. Most individuals of these species have lost eyes completely; however, a few individuals have vestigial eyes buried under the skin (Fig. 11B) on one side or both sides. Histological sections of *S. rhinoceros* showed only a single rod cell and no cone cells, thus demonstrating that their eyes have lost light sensitivity.

Loss of Pigmentation

Body pigmentation in teleosts is due to three types of dermal chromatophores: black melanophores, which contain melanin; silver iridophores, which contain purines; and yellow xanthophores, which contain pteridines. There is a dramatic decline in the total number of melanophores in Chinese cavefish, as well as a strong reduction in the ability of these cells to synthesize melanin. Those cavefish species that live exclusively in subterranean streams where there is no

light are often completely albino, whereas those species that live around cave entrances and are only partial cave dwellers often have light black-brown or dark brown pigment on their bodies. This is seen in all three of our sample species (Fig. 1): the surface species *S. grahami*, which has a deep yellow body color; the cave-dwelling species *S. hyalinus*, which is an albino with no scales; and *S. brevibarbatus*, which is normally semitransparent with milky white fins. Of greater interest is the fact that individuals of the same species, captured in a cave environment, are often lightly colored or colorless, while those captured outside of the cave often have a much darker body color (*S. microphthalmus*). Some Chinese cavefish can gain pigmentation when they enter a bright environment. It seems likely that the disappearance of pigmentation in Chinese cavefish is mainly caused by the inhibition of gene expression in the pigment production pathway, rather than by the total loss of pigmentation genes.

Disappearance of Scales

The development of scales in cave-adapted *Sinocyclocheilus* takes on an obvious regressive trend,

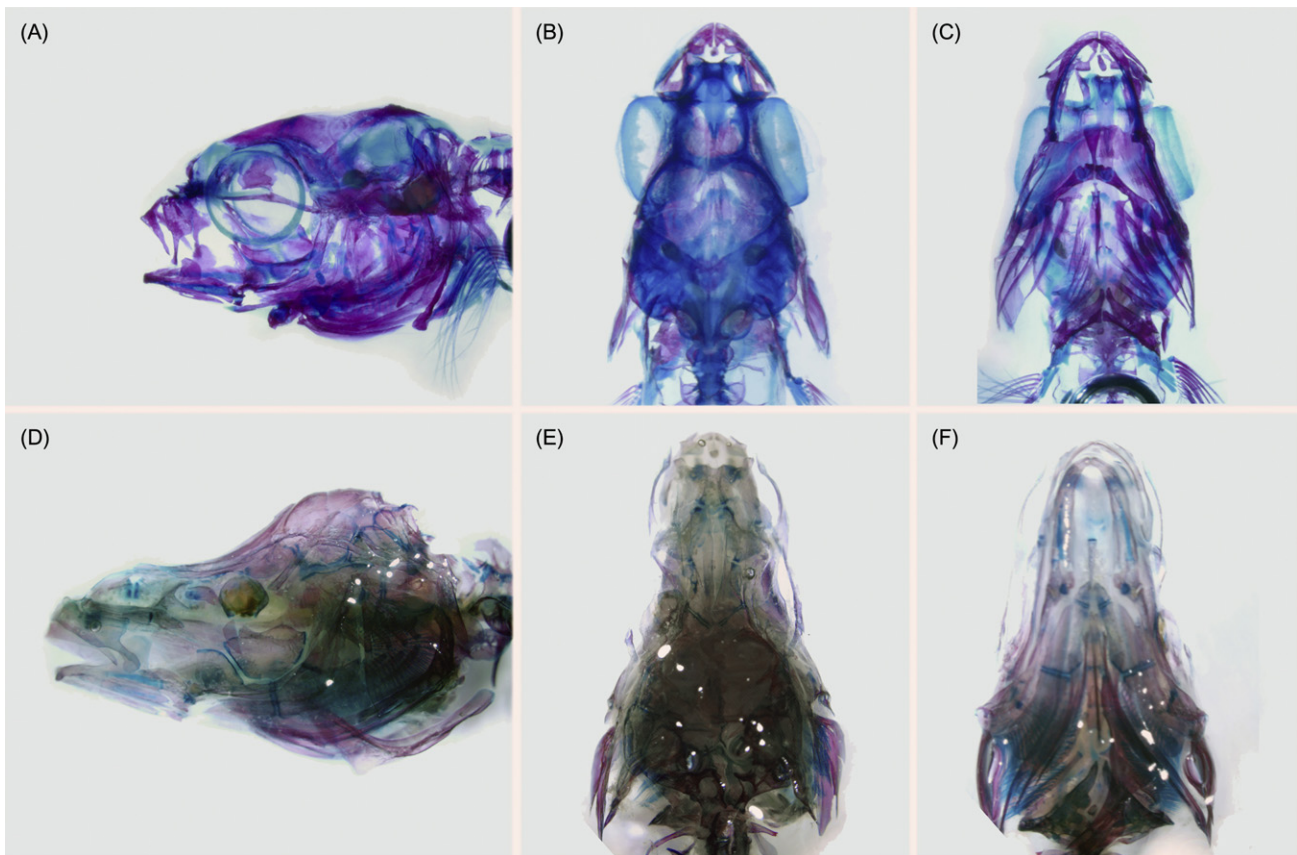


FIGURE 10 Comparison between the head skeleton of *S. grahami* (A,B,C) and *S. anophthalmus* (D,E,F). (A,D) lateral views; (B,E) dorsal views; (C,F) ventral views.

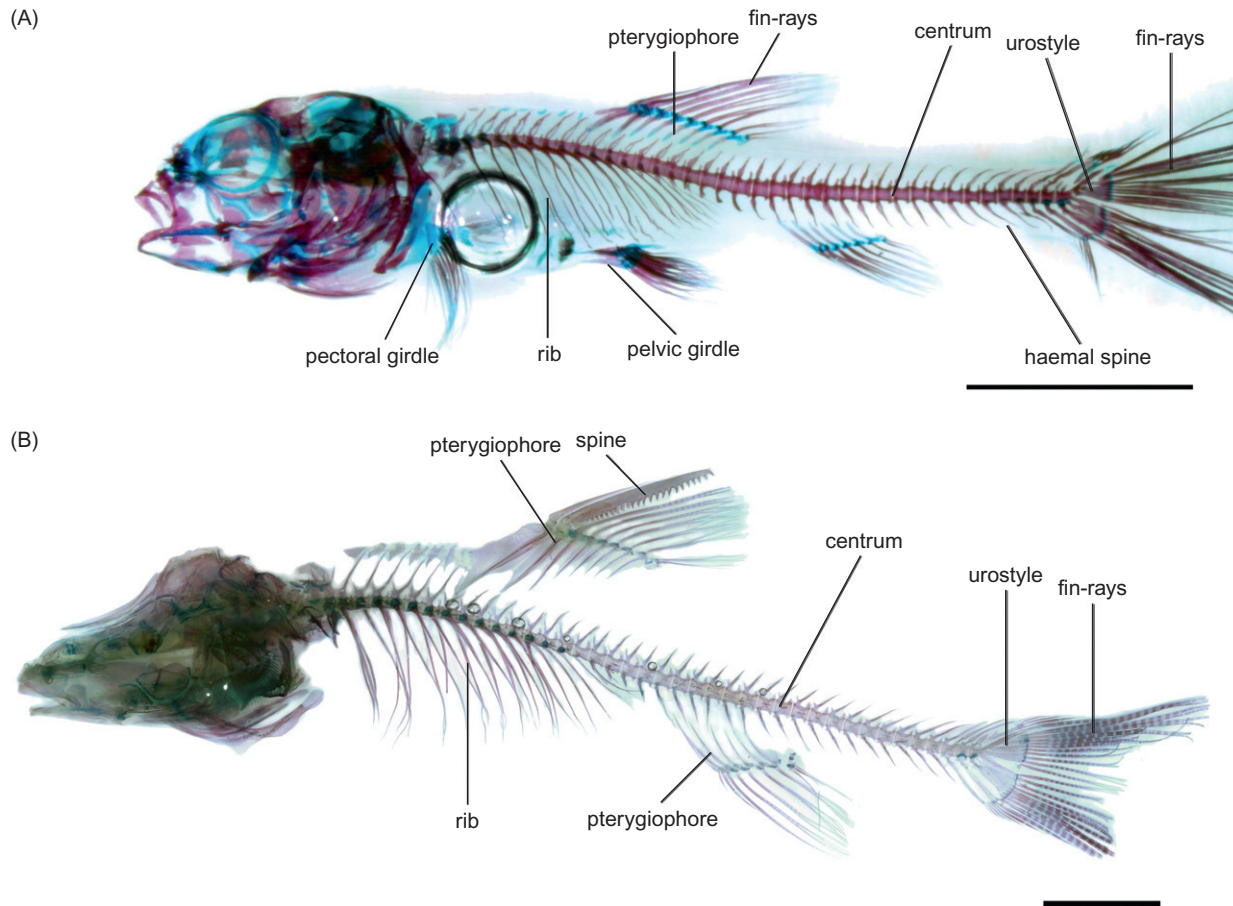


FIGURE 11 Whole-mount staining of bone and cartilage of *S. grahami* (A) and *S. anophthalmus* (B). The cartilage was stained with Alcian blue and the bone was stained with Alizarin red. Scale bars = 50 mm.

as seen in their reduced distribution over the body and the relative size of the lateral line scales. Those species that live in abundant light, such as *S. grahami*, have large well-developed scales that are overlapping over the entire body. The most extreme example of scale regression is seen in cave-restricted species such as *S. tianlinensis*, which have no scales on the body at all. We can only find lateral line pores on the sides.

The rate of scale regression the lateral line due to adaptation to the cave environment is much slower than the speed at which general body scales are lost. As previously mentioned, even those *Sinocyclocheilus* species that have completely lost their body scales still retain the scales of the lateral line, although they are underdeveloped. For those species that have partial regression of body scales, the lateral line scales retain a larger shape than those general body scales above and below them, while in species that have well-developed body scales, those of the lateral line are just as well developed or even larger. This indicates that the lateral line scales of Chinese cavefish are more resistant to regressive evolution during cave adaptation.

PHYLOGENESIS, SPECIATION MECHANISMS, AND BIOGEOGRAPHY

Evolution is at the center of all Chinese cavefish research. Due to the isolated nature of caves, it is possible to combine geological data with the existing records of cavefish distribution to reveal the synergic relationship between cavefish evolution and cave development. The origin of the genera *Sinocyclocheilus* and *Triplophysa* is attributed to the ancient geology and climate of China. Current theory suggests that the primitive ancestor of *Sinocyclocheilus* may have originally lived on the Yunnan-Guizhou Plateau during the late Tertiary period. During the Quaternary period, the Qinghai-Xizang Plateau underwent a sudden upward shift that caused the geological environment to change greatly, while the Yunnan-Guizhou Plateau also underwent an upheaval but settled at a different elevation. At the same time, the temperature of the Earth began to decline, such that the size of the polar ice caps greatly increased. As a result of these drastic environmental changes, the *Sinocyclocheilus* common

ancestor was forced to live in caves and eventually took on such adaptations as tetraploidy of chromosomes, an increase in the number of body scales, and a smaller body size in order to survive.

Sinocyclocheilus is a monophyletic group with four clades, given the names *jii*, *angularis*, *cyphotergous*, and *tingi*, named according to their most representative species. The geographical distribution of these different clades displays very little overlap. The phylogenetic tree of *Sinocyclocheilus* based on combined morphological and molecular data indicates that different cavefish species invaded individual cave waters multiple times and acquired their troglomorphic traits independently (Xiao *et al.*, 2005; Fig. 12). The hypothesized troglophilic ancestor of modern *Sinocyclocheilus* species was presumably distributed throughout the karst region of Yunnan and Guizhou at the beginning of the plateau uplift. After the violent sudden upheaval of the plateau approximately 3.4 Ma BP, also known as Act A of the Qinghai-Xizang Movement, the eastern population became isolated from the other groups and evolved into today's *jii* clade. Phylogenetic trees based on maximum parsimony, Bayesian analysis, or morphology, all show that *jii* is the ancestral clade. Soon afterward, some *Sinocyclocheilus* in the western region became true troglobites, dwelling exclusively in caves and/or subterranean rivers. These became the ecologically isolated *angularis* clade, which became separated from other troglophilic relatives partially in response to the various climate changes and structural changes of the karst landscape. The *angularis* clade emerged from this ancestral group. Most species of *angularis* clade have a horn on the head and a humpback. In addition to the appearance of the horn and humpback, the species in this clade are all troglobites, possessing the usual regressive characteristics typical of caves; their eyes are either reduced in size or absent; and their pigmentation is decreased. Almost at the same time, further upheaval of the land during Act B (2.6 Ma BP) of the Qinghai-Xizang Movement served to isolate the remaining two clades: *tingi* and *cyphotergous*, which are sister groups. These clades share a common characteristic in not forming the parietal bone projection on the head and back. The *tingi* clade, which with one exception exclusively exhibits troglophilic levels of adaptation to hypogean life, became limited to the watershed of the Nanpanjiang River. This clade mainly shows a troglophilic life cycle and will forage out of the cave, although not far away from cave entrances. The troglophilic and troglobitic members of the *cyphotergous* clade are currently distributed among the drainage sites of the Hongshuihe River. The *cyphotergous* clade is characterized by a humpback

and a reduced lateral line scale number, normally 55 scales. Whether a given *Sinocyclocheilus* species emerged as troglobite or a troglophile can be closely tied to the geological characteristics of the Yunnan-Guizhou Plateau as it exists today. Troglobitic species are more heavily concentrated in the central area of the distribution range, where violent upheavals have produced steep slopes and a complicated karst environment. In contrast, troglophilic species tend to be found closer to the eastern and western edges of the overall distribution area, which exhibit less elevation change. Vicariance is the primary mechanism for speciation in the genus *Sinocyclocheilus*, with diversification mainly resulting from genetic drift in isolated populations (Zhao and Zhang, 2009).

Geographical isolation is the main cause of species diversity in *Sinocyclocheilus*. The ancestor of *Sinocyclocheilus* was likely to be a troglophilic cavefish. During its subsequent evolutionary history, some troglophilic cave *Sinocyclocheilus* became isolated in caves, which gradually produced special characteristics adaptive to the dark environment, and thus troglobitic cavefish species appeared. The isolation of cave or subterranean waters prohibited genetic communication between the fish groups living in different caves. In the cave-rich southern areas, which are affected by high temperatures, abundant precipitation, and surface erosion, cave collapse or underground river diversion was frequent, further enhancing the geographical isolation of species that once had a continuous range. Thus, different populations isolated by underground water evolved in different directions, finally resulting in the formation of independent species.

A very interesting phenomenon not often encountered in cave-adapted animals is that different *Sinocyclocheilus* species can be spatially distributed at the same underground river or same cave at the same time. For example, *S. anatirostris*, *S. microphthalmus*, and *S. lingyunensis* all live in Guangxi Lingyun caves. This phenomenon may be attributed to abundant rainfall in these areas, which enters caves and isolates existing fish populations spatially, thus eventually leading to the formation of separate species in the same cave.

Although geographical isolation is the most important mechanism for *Sinocyclocheilus* speciation, small population sizes also have a role in this process. In small isolated populations there are powerful effects of *genetic drift* as well as natural selection. In small populations derived from a single founding population, genetic differentiation and speciation can occur more rapidly due to the absence of migration and gene pool exchange. In summary, speciation in this genus is attributed to several different factors, including isolation and small population sizes, which result in

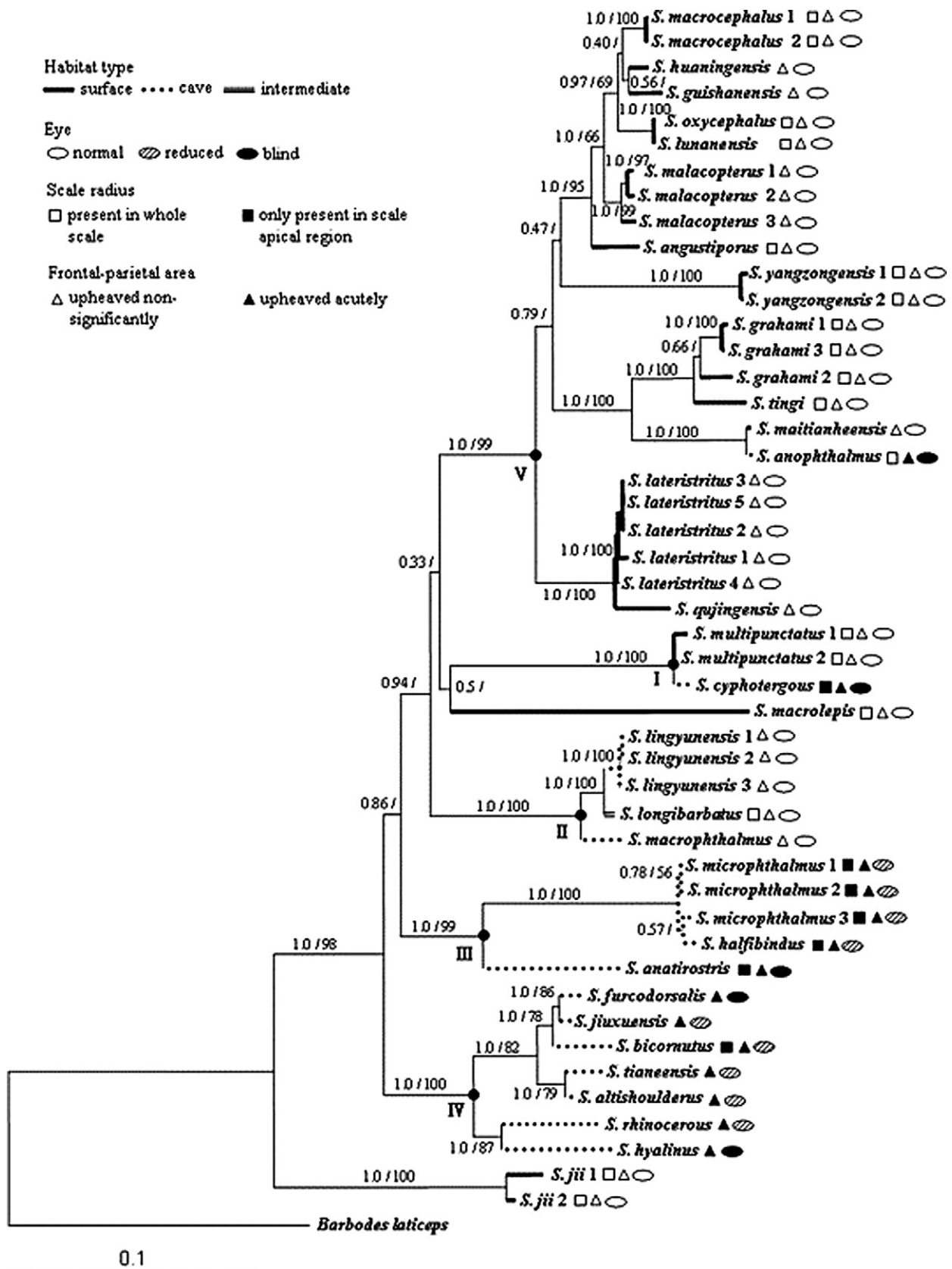


FIGURE 12 A combined phylogenetic tree of *Simocyclocheilus* fishes constructed using both morphological and molecular data.

inbreeding, rapid genetic differentiation, and fixation. For example, *S. anophthalmus* and *S. maitianheensis* have morphological variation, but their genetic difference is small (only 0.36%), suggesting that enormous and sudden selective pressures led to rapid evolution of adaptive features. Small population speciation mechanisms probably accelerate and amplify this process, and have resulted in a particularly rich *Sinocyclocheilus* species diversity.

The distribution of *Sinocyclocheilus* in karst environments is a consequence of drainage system distribution, climate conditions, and karst development. As described above, geographical isolation was probably the most important factor in speciation; however, the distribution of the tingi clade in the upstream parts of the Nanpanjiang River may be the result of diffusion in this area after the third diversity. And the ψ -type structure in Guangxi karst landform, a Cenozoic downfaulted basin and valley, has had a significant effect on this pattern. The distribution of *Sinocyclocheilus* was separated coincidentally by both flanks and extension line of Guangxi ψ -type structure at different areas. The jii clade occupies the east part of the Guangxi ψ -type structure's east flank, including the Guijiang river and Hejiang river; and no distribution records of *Sinocyclocheilus* exist between the middle and east wing of Guangxi ψ -type structure, which is due to the absence of caves in this

area. In contrast, the cyphotergous clade distributes to the east and midline west areas of the Guangxi ψ -type structure. And the distribution of *Sinocyclocheilus* has an obvious relationship to the vertical altitude of karst from Yunnan to Guangxi. The tingi clade is mainly distributed in eastern Yunnan Province, the central eastern plateau, and the upstream parts of the Nanpanjiang River at altitudes between 1500 m and 2000 m. Downstream, in the middle parts of the Nanpanjiang River, the altitude of most areas is between 1000 m and 1500 m, and the angularis clade is found in this region. The cyphotergous clade is located in the far downstream parts of the river, where elevation falls to between 500 m and 1000 m. Finally, the altitude where the jii clade is found is only about 200 m. Thus, the geographical distribution of *Sinocyclocheilus* clades has a vertical basis.

RESEARCH AND CONSERVATION

Hypogean fishes are susceptible to the threats from habitat degradation, hydrological manipulations, environmental pollution, overexploitation of resources, and introduction of alien species. Because most Chinese cavefish are endemic to small areas and have small populations, any of these threats

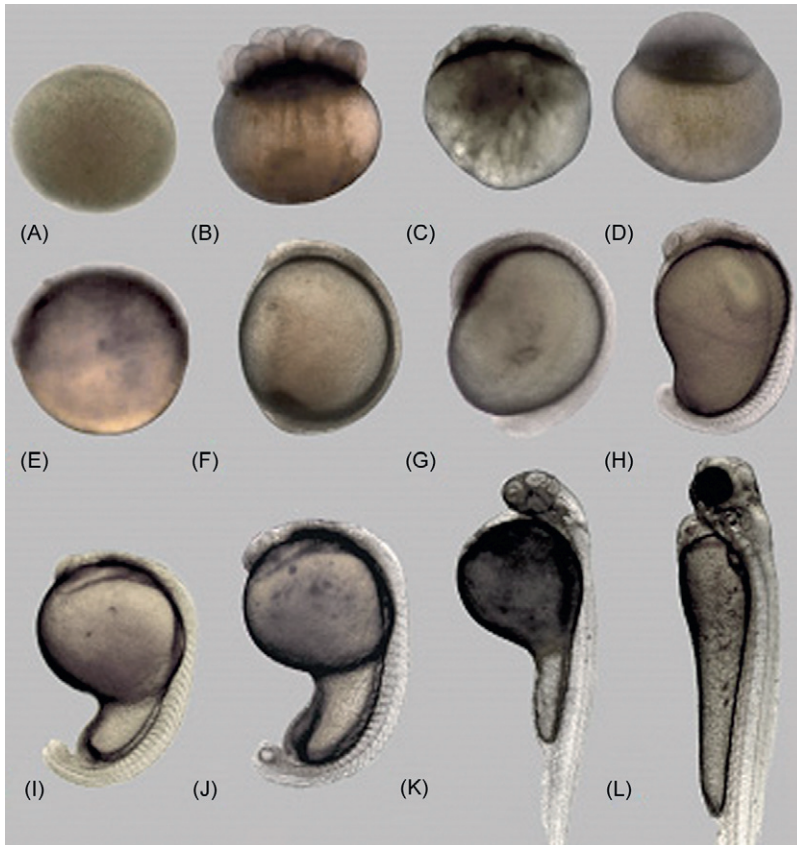


FIGURE 13 The embryonic development of *S. grahami*. (A) The zygote, a few minutes after fertilization; (B) 16-cell stage; (C) 64-cell stage; (D) sphere stage; (E) 50% epiboly stage; (F) bud stage; (G) 5-somite stage; (H) 22-somite stage; (I) 24-somite stage; (J) 28-somite stage; (K) 42-somite stage; (L) long-pec stage.

could have serious consequences. Currently, some populations have been considered “threatened” or “vulnerable.” In fact, most Chinese cavefish are currently placed in the “vulnerable” status. In 2004, 14 species cavefish were placed on the “Chinese red list” (Wang Song, Xie Yan (2004). *China species red list*. Beijing: Higher Education), including 9 species of Cyprinidae (8 species of *Sinocyclocheilus*) and 5 species of Cobitidae.

Chinese cavefish are also threatened by the rapid economic growth, which has depleted their habitats for living and reproduction. To protect these valuable and unique species of hypogean fish, more research should focus on the present habitats that still exist, while practical and effective protective measures must be established for the karst caves and deep pools where they live. Protection should also be put into place so that predation by other animals and humans is prevented. On April 3, 2008, the first “autonomous district level cave rare fish natural area” was set up in Guangxi Lingyun. This was the first natural reserve area to focus on preserving the unique and rare cavefish of China, and it covers an area 684 hectares wide, including areas along an underground river and six distinct caves. Even more promising is the success of researchers at the Yunnan Endemic Species Breeding Center, who in 2007 were able to stimulate artificial reproduction in *Sinocyclocheilus grahami* (Fig. 13). The study of Chinese cavefish has drawn more people’s attention to the urgent need for conservation measures to protect this fascinating group of highly endangered animals.

See Also the Following Article

Astyanax mexicanus—A Model Organism for Evolution and Adaptation

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CHEMOAUTOTROPHY

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INTRODUCTION

Photosynthesis is not possible in the dark zone of a cave. Consequently, the assumption has been that nearly all life on Earth, and especially life in caves, depends on organic carbon and energy derived from photosynthesis. But, reactive rock surfaces and mineral-rich groundwater provide energy sources for specialized microorganisms that gain cellular energy from chemical transformations of inorganic compounds—such as hydrogen, reduced iron, or hydrogen sulfide, present in groundwater or sediments—and convert inorganic carbon sources into organic carbon. Essentially, microorganisms utilize the available chemical energy that might otherwise be lost to a system. In this manner, chemosynthesis provides a rich alternative energy source for organisms, with the results being that ecosystem biodiversity and population densities are higher compared to some nonchemosynthetically based ecosystems that rely on inconsistent and limited inputs of organic carbon.

This article focuses on chemosynthesis and chemosynthetically based ecosystems in caves and karst. In general, our knowledge of the evolution and metabolism of major chemosynthetic microbial groups has increased in recent years, partly due to advances in molecular genetics methods, but also because of expanded efforts to investigate habitats where chemosynthetic microbes exist. Thanks to research from cave and karst settings, as well as from research done on significant chemosynthetic populations at deep-sea hydrothermal vents (Deming and Baross, 1993) and within the deep terrestrial subsurface (Stevens and McKinley, 1995), the “world is green” view is beginning to change. The article concludes with a discussion of the importance of subsurface chemosynthetically based