

## It's a wonderful hypogean life: a guide to the troglomorphic fishes of the world

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### Synopsis

There are at least 86 species of troglomorphic fishes belonging to 18 families. Some of those families are characterized by features that can be labeled as preadaptations to the hypogean life; others are not. The level of structural reduction in eye development and pigmentation is highly variable, even within some populations. Reduction in number and complexity of scales does occur but has yet to be fully documented. Reduction in the size and structure of the swim(gas)bladder may be another troglomorphic feature. There is considerable doubt on the taxonomic position of many species of troglomorphic fishes given that a number of them have been described solely on the basis of morphology while genetically they may be very closely correlated to genera different from those they have been assigned to. Geographically speaking there are no evident patterns since many of those species are not found in karstic areas but in phreatic waters. These fishes represent an excellent example of convergent evolution.

### Introduction

The rate of discovery of new species/populations of troglomorphic fishes continues to increase rapidly. Although a list of these fishes has been published recently (Weber 2000), since Thinès (1969) there has been no comprehensive attempt to summarize the most important information about them. This paper aims to fill that gap and to serve as a general reference for this volume. We have not included non-troglomorphic fishes found in caves for this account because they have been summarized elsewhere in the volume (Poly 2001). At least one species, *Varicorhinus (Scaphistes) macrolepis*, hibernates for six months in caves (Zhang 1986). Also, we are aware that a number of troglomorphic species have been reported but not formally described (e.g., Trajano 1997c) and others seem to show only a few signs of troglomorphy (e.g., Burr et al. 2001). However, for the sake of simplicity, we decided to stick with those whose taxonomic status and troglomorphy has been clearly established.

### Methods

We collected all available information on troglomorphic fishes published up to January 2001 following the methodology described in Romero (2001). The species were grouped by family following Nelson's (1994) systematic order. For each family a general summary of their biology is given to indicate whether or not they present generalized characters that could be understood as preadaptations to hypogean life, e.g., nocturnal habits or sensory systems that enhance information-gathering in dark waters. Some remarks are also made about the proportion of species known in comparison to how many of them are troglomorphic.

Given that for most genera and species their phylogenetic relationships with the rest of the family is uncertain, genera within families, as well as species within genera, were listed alphabetically. The species were numbered in order to facilitate the reading of the maps (Figures 1, 2). Unless otherwise indicated, the information for each species comes from the

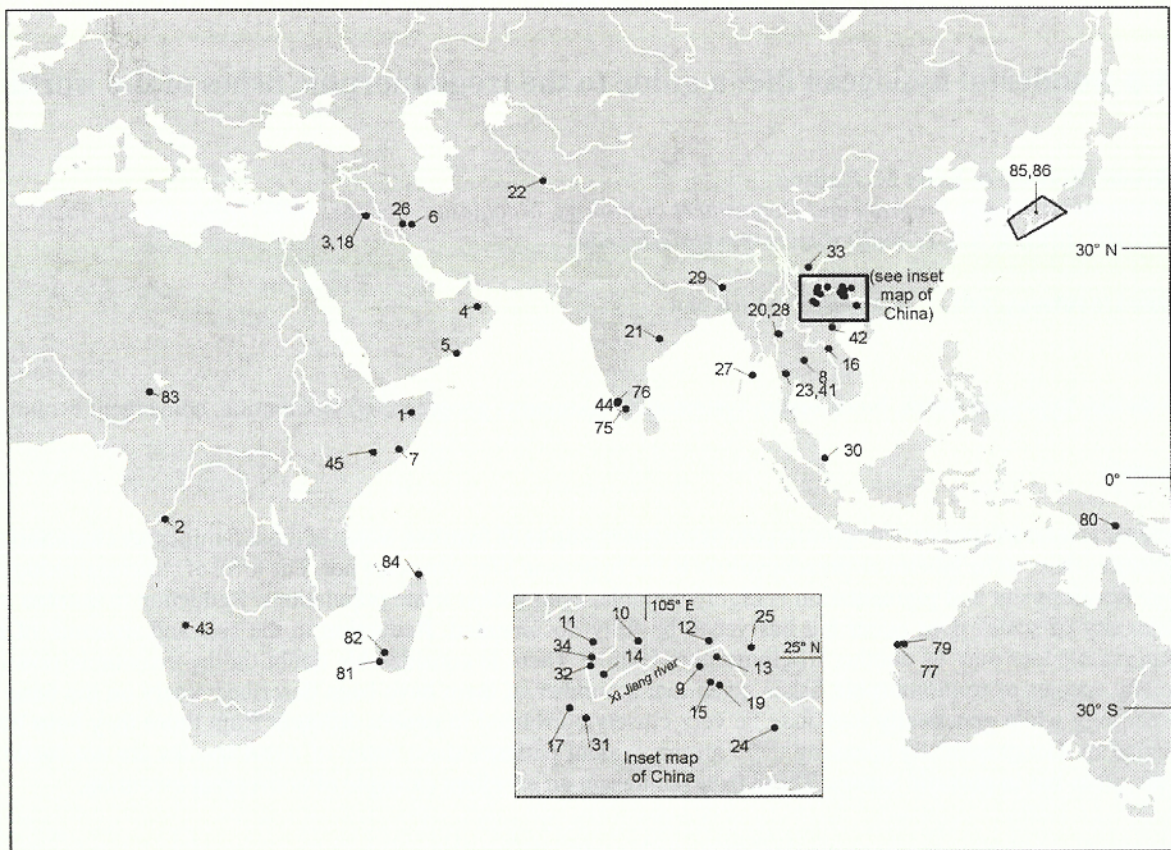


Figure 1. Localities and distributional areas for troglomorphic fishes in the Old World. Numbers represent species as cited in the text.

original description. Common name(s) are given if known. Etymology is given only for those names that were created to identify the hypogean/troglomorphic species/populations. Style for referring to etymologies follows Brown (1956) and Gotch (1995). Major synonyms are given only if they represent or have represented a source of confusion. Historical information is provided only if available. The remarks section aims to summarize information about troglomorphic features (reduction in eyes, pigmentation, and scales), behavioral features and phylogenetic relationships. Information on their conservation status is not included since it is summarized elsewhere in this volume (Proudlove 2001).

The maps accompanying this article (Figures 1, 2) were created using Arc View software in the Macalester College Cartography Laboratory in January 2001. The maps are projected with the Mercator projection, which does create some distortion in the area of landmasses

towards the poles, but since these maps exclude much of the polar landmasses and that troglomorphic fishes are not found at high latitudes, this is not much of an issue. Latitudes and longitudes of troglomorphic fish distributions were determined using one of several methods: sometimes latitude and longitude information was found in the article describing the species; sometimes a description of the location was given (with varying degrees of accuracy and reproducibility), and latitude and longitude were determined using atlases and other sources; other times a range was given (as in the southeastern US and in Japan), and the best attempt was made to draw a polygon encompassing these regions; finally, some articles gave no more than a sketchy description of the location (as with some of the fishes from China) and difficulties in translation and finding the locations on maps make the latitudes and longitudes for these few species rather vague. The latitude and longitude information included in

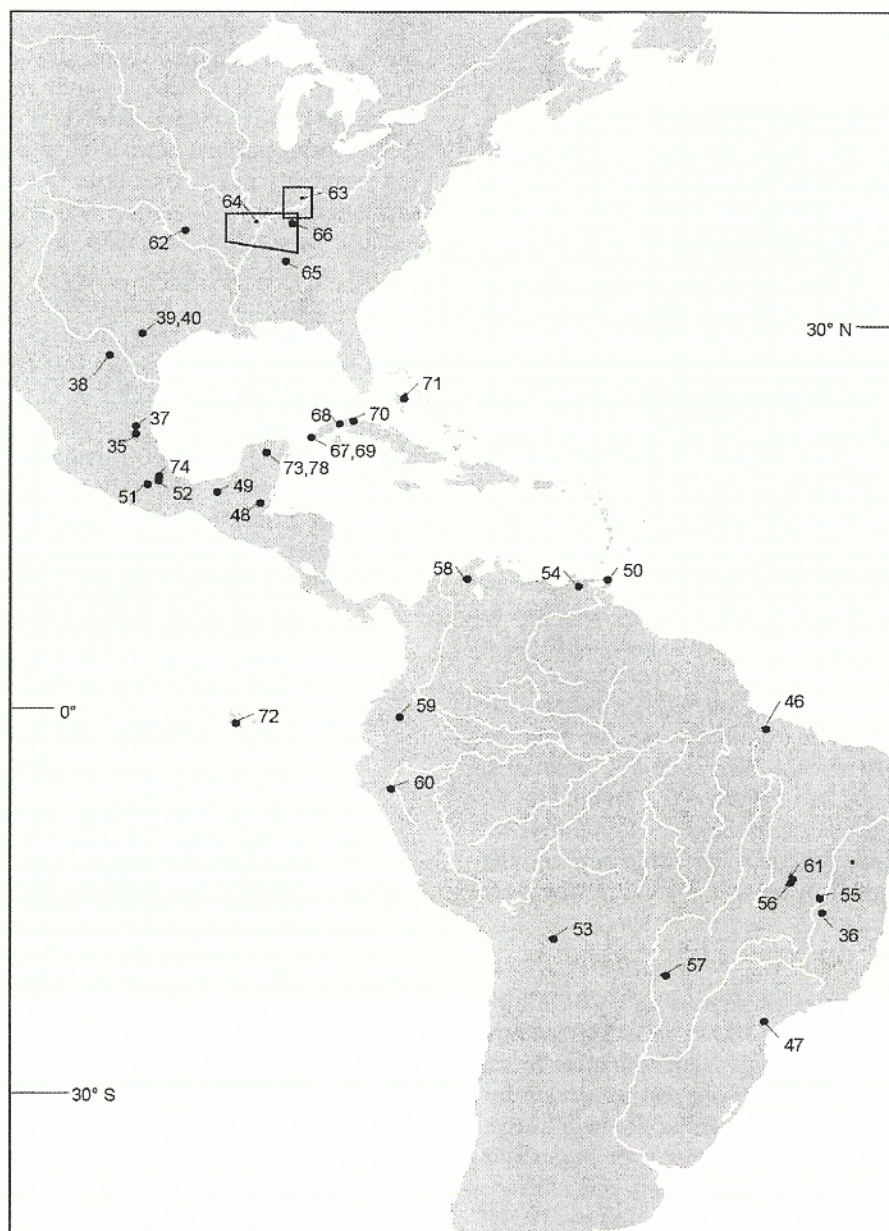


Figure 2. Localities and distributional areas for troglomorphic fishes in the American continent. Numbers represent species as cited in the text.

the article is the same as that which was used in the creation of the maps; where 'ca.' appears before the latitude and longitude, it means that it was determined using an atlas and should reflect a slightly lesser degree of accuracy. The reader should, therefore, take several things into consideration when using these maps. The maps are on a global scale and are intended to

do little more than provide a general idea of where these species are located and provide a reference to the species numbers as described in the article. The nature of the methods used and the scale of the maps mean that the dots are not always (though in some cases are accurate to the tenth of a second) in the *exact* location.

## Results

Family: Cyprinidae

Cyprinidae is the largest family of freshwater fishes with more than 2000 species distributed throughout Eurasia, Africa, and North America (Nelson 1994). Eighteen species/populations of troglomorphic hypogean cyprinids have been described so far. Three are from Africa and the rest are from Asia, ranging from the Middle East to Southeast Asia. Most cyprinids have scales to some degree. Nothing in their morphology, physiology or behavior seems to support the idea of a family being preadapted to the hypogean environment. Thus, the large number of hypogean representatives seems to be just the result of the fact that this is a highly speciosed family.

Most of the troglotic species have been discovered in the last ten years in China and southeast Asia. Many of their descriptions have been published in Chinese and specimens of those species have yet to be examined by researchers others than those who described them. For those that have been more thoroughly studied, there are indications that their taxonomy may be wrong. For example, it is quite possible that *Barbopsis devechii*, *Phreatichthys andruzzii*, *Caecobarbus geertsi* and *Iranocypris typhlops* should all be assigned to the genus *Barbus* (Ercolini et al. 1982). A very close genetic relationship between the first two is supported by allozyme studies (Sbordoni et al. 1996).

1. *Barbopsis devechii* Di Caporiacco, 1926. **Common name:** Somalian blind barb (E). **Etymology:** *barb* (L) for its apparent relationship with other fishes of the genus *Barbus*; *ops* (Gr) eyes; *devecchii* for C.M. De Vecchi, governor of Italian Somalia at that time. **Major synonyms:** *Eilichthys microphthalmus* (Pellegrin, 1929), *Barbopsis stefaninii* (Gianferrari, 1930), and *Zaccarinia stefaninii* (Gianferrari, 1934). Also, the name was originally spelled once as *devecchi* and once as *devecchii*; named after De Vecchi, so *devecchii* is correct. **History:** Original description was based on 19 specimens collected in a well by two local doctors, G. Stefanini and N. Puccioni in the spring of 1925 (Di Caporiacco 1927). Because of variability in eye reduction, specimens of this species have been mistakenly assigned to several genera and species. **Distribution:** Several localities in north-central Somalia (see Ercolini et al. 1982 for map and list of specific locations) (ca. 9°10'00" N, 48°22'10" E).

**Habitat and ecology:** In springs and wells throughout a wide and continuous phreatic layer in the Nugal Valley in an area with a wide range of salinity.

**Remarks:** This species exhibits a lower degree of troglomorphy than other hypogean species, including variability in eye size; little, but still present, pigmentation; thin but existing scales; and a somewhat reduced nervous system related to visual functions. It can be best described as a fish with a variable degree of microphthalmia. It also shows marked scotophilia (photophobia) (Ercolini & Berti 1978) and does not form schools (Jankowska & Thinès 1982). It has a low metabolic rate (Ercolini et al. 1987). Allozyme studies suggest that this species is troglomorphic to a lesser degree because of a more recent isolation from its epigeal ancestor (probably a *Barbus* sp.) Gene flow among the different populations seems to be rather constant when compared to that of *P. andruzzii* (Sbordoni et al. 1996; see also remarks for *P. andruzzii*).

2. *Caecobarbus geertsi* Boulenger, 1921. **Common name:** Congo blind barb (E); barbu aveugle (F). **Etymology:** *caeco* (L) blind; *barbus* (L) for its barbs but also because of its relationship with fishes of the genus *Barbus*; *geertsi* after M.G. Geerts who sent the first specimens to Europe on which the original description was made. **Major synonyms:** None. **History:** M. Delporte, a Belgian explorer, may have been the first European to see this fish in 1915. In 1917, during the dry season, a party of amateur cave explorers penetrated 500 m into a limestone cave situated about 700 m above sea level. This cave is located in lower Congo near Thysville (today Kanka near Mbanza-Ngungu, 5°18' S, 14°50' E). One of those amateur explorers, M. Geerts, waited until after the end of World War I, when it was safe for him to go back to Belgium, where he carried with him a few specimens of this fish. He sent them to George Albert Boulenger, a well known specialist on African fishes (and a Belgian). E. Randour may have found this fish in other caves in the early 1920s. Being easy to transport alive, many European scientists did some experimental work with this species early on. It became so famous that in May 1951, it was exhibited at the New York Aquarium (Romero & Benz 2000). **Distribution:** Congo, caves in the lower Congo river system (ca. 5° S, 15° E) (see Heuts & Leleup 1954 for a distributional map). **Habitat and ecology:** In caves characterized by cyclic food scarcity (Heuts 1951). **Remarks:** It has vestigial eyes that are not externally visible (Gerard 1936). It was

the first troglomorphic species described outside the American continent. After *Astyanax fasciatus*, it is one of the most-studied hypogean fish. Despite numerous attempts, breeding in captivity has failed. It tends to aggregate based on conspecific odors (Berti & Thinès 1980), is scotophilic (Thinès 1953), and responds to the alarm substance (Thinès & Legrain 1973). This species seems to be related to primitive members of the genus *Barbus* (Heuts op. cit.).

3. *Caecocypris basimi* Banister & Bunni, 1980. **Common name:** None given. **Etymology:** *caeco* (L) blind; *cypris* (L) because it is a cyprinid; *basimi* (L) after Basim M. Al-Azzawi, the collector of the specimens. **Major synonyms:** None. **History:** Collected for the first time by Basim M. Al-Azzawi, a collector with the Natural History Research Center of the University of Baghdad, on 21 October 1977 while visiting the locality of *T. widdowsoni* in order to collect specimens of the latter species. **Distribution:** Iraq, Al Anbar province, Al Hadithah, natural well in the Sheik Hadid shrine (ca. 34°04' N, 42°24' E). Same as for *T. widdowsoni*. **Habitat and ecology:** Same as for *T. widdowsoni* with which it is found syntopically. **Remarks:** Eyeless with the orbit filled with fatty tissue; vestigial eyes are present only in juveniles. Depigmented. Scales present only in large specimens.

4. *Garra barreimiae* Fowler & Steinitz, 1956. **Common name:** Omani blind cave fish (E). **Etymology:** *barreimiae* (L) after the type locality, Barreime, Oman. **Major synonyms:** None. **History:** The epigeal form was first known from several specimens sent to the Academy of Natural Sciences of Philadelphia between 1950 and 1951. The first hypogean, troglomorphic population was discovered in May 1980 by Andy Dunsire and M. Gallagher who collected 100 dead and 56 live individuals (Banister et al. 1992). **Distribution:** Arabian peninsula, Oman, Barreime. From a deep cave on the south flank of the Jabal Akhdar mountains, 9 km E.S.E. of Al-Hamra (23°05' N, 57°21' E). **Habitat and ecology:** pH range 6.5–7.5; dH range 10.0–20.0. **Remarks:** No externally visible eyes. Depigmented. Optic lobes not fully developed. It has weak squamation. Some increased development of melanin and the optic lobes occurred among individuals exposed to light under artificial conditions.

5. *Garra dunsirei* Banister, 1987. **Common name:** None given. **Etymology:** *dunsirei* (L) after Andy

Dunsire, the collector. **Major synonyms:** None. **History:** The first four specimens were received at the British Museum (Natural History) in 1984 and were collected by A. Dunsire and D. Green on 16 May 1980. Another 19 live specimens were collected by C. Maclelland on 26 February 1983. **Distribution:** Oman, Dhofar, Jabal Qara (variously Jabal Samhan) mountains, in pools inside caves at the bottom of a large sinkhole at Tawi Atair (17°06' N, 54°34' E). It seems to be very geographically isolated, even from any other species of fish; the closest species is found more than 600 km away. **Habitat and ecology:** The fish were caught in a pool in a side passage 200 m down a sink hole. **Remarks:** Eyes apparently normal. Depigmented. Less squamation than epigeal *G. barreimiae*. There are only a few casual behavioral observations of this fish in captivity.

6. *Iranocypris typhlops* Bruun & Kaiser, 1944. **Common names:** mahi-ye kurgar (Farsi), Iran cave barb (E). **Etymology:** *iran* (L) because it is found in Iran; *cypris* (L) because it is a cyprinid; *typhlos* (Gr) blind; *ops* (Gr) eye. **Major synonyms:** None. **History:** E.W. Kaiser collected seven specimens from a well in Kaaje-Ru, valley of Ab-i-Serum, Iran, while researching fauna in the freshwaters of that country on 6 May 1937. **Distribution:** Iran, Lorestan (Khorramabad) province, Zagros mountains, Ab-i-Serum Valley near Tang-e-haft railway station, Baq-e-Loveh Oasis, a natural well at Kaaje-Ru (33°05' N, 48°36' E) (for full locality description see Coad 1996). **Habitat and ecology:** The well-like water resurgence in which it has been found seems to be the result of a collapsed subterranean system. This is probably part of a larger but complex, narrow, and inaccessible network of underground waters. This locality is shared by another species of hypogean fish, *Paracobitis smithi* (see below). **Remarks:** This species is rare and may be endangered due to overcollecting in its only known locality (Coad op. cit.).

7. *Phreatichthys andruzzii* Vinciguerra, 1924. **Common name:** Somalian cavefish (E). **Etymology:** *phreas* (L) well; *ikhthus* (Gr) fish; *andruzzii* (L) for Alcibiade Andruzzii who secured the first specimens. **Major synonyms:** None. **History:** Six specimens were collected by lieutenant Zaccarini at Bud-Bud (4°11'19" N, 46°28'21" E), central Somalia. He gave them to a Alcibiade Andruzzii, a local physician who, in turn, sent them to the Museo Civico de Storia Naturale di Genova. Since then, this species has been studied

from morphological, ecological, and behavioral perspectives by a number of researchers (e.g., Berti & Zorn 2001). **Distribution:** In central Somalia (see Ercolini et al. 1982 for map and list of specific localities) (ca. 4°11'50" N, 46°28'00" E). **Habitat and ecology:** The different localities at which it is found have different levels of salinity within what probably is the same underground, karstic hydrographic system. Elevations of the wells range between 135 and 150 m a.s.l. **Remarks:** This species lacks visible eyes. Depigmented. Scaleless. Parts of the nervous system associated with vision are highly reduced in complexity. It exhibits specific chemical recognition (Berti 1990), responds to light (Ercolini & Berti 1975), and has low oxygen consumption (Ercolini et al. 1987). Allozyme studies have suggested that this species and *Barbopsis devechii*, another hypogean species of the same general area but allopatric to *P. andruzzii*, may have descended from the same hypogean ancestor (probably a primitive *Barbus*). Furthermore, the genetic distance between the two does not support the contention that they belong to different genera. Gene flow among the different populations of *P. andruzzii* is probably highly restricted or even absent (Sbordoni et al. 1996).

8. *Poropuntius speleops* (Roberts, 1991). **Common name:** None given. **Etymology:** *speos* (Gr) cave; *ops* (Gr) eyes. **Major synonyms:** *Barbus speleops* (original description). **History:** It was collected by Phillip Chapman in April 1989. **Distribution:** Thailand, Tham Phu Khieo, Phu Khieo Wildlife Sanctuary (16°02'05" N, 101°32'10" E), and in the nearby Tham Pathewada (Tham means cave). **Habitat and ecology:** The cave seems to be a major flood-sink during the rainy season. A small stream flowing directly into Tham Pathewada may provide the only permanent year-round input into the underground system. The fish seems to be very abundant, with 65 to 150 individuals per 100 m over 500 m of cave length. **Remarks:** Eyes are vestigial and pigmentation is reduced among adults. Generalized squamation.

9. *Sinocyclocheilus anatirostris* Lin & Luo, 1986. **Common name:** duck-billed golden-line fish (E, translation from Chinese); cave dragon (E). **Etymology:** *anatis* (L) duck-like; *rostris* (L) beak. **Major synonyms:** None. **History:** No information available. **Distribution:** China, Guangxi, Ling-Yün and Le-Ye (ca. 24°45' N, 106°30' E). **Habitat and ecology:** Found in two caves at about 30 m from their entrance at

1.5 m in depth. **Remarks:** No externally visible eyes. Depigmented. Scaleless. Reduced swim bladder.

10. *Sinocyclocheilus angularis* Zheng & Wang, 1990. **Common name:** golden-line angle fish (E, translation from Chinese). **Etymology:** *angularis* (L) because at the end of the posterior portion of the head there is a bone in a form of an angle. **Major synonyms:** None. **History:** First collected in June 1986 by Zheng and Wang. **Distribution:** China, Guizhou, Panxian county, Cave is located at 25°26' N, 104°45' E, at 1540 m a.s.l. **Habitat and ecology:** Karstic cave. **Remarks:** Microphthalmic. Depigmented. Scales embedded.

11. *Sinocyclocheilus anophthalmus* Chen, Chu, Luo & Wu, 1988. **Common name:** eyeless golden-line fish (E, translation from Chinese). **Etymology:** *an* (Gr) without; *ophthalmus* (Gr) eyes. **Major synonyms:** None. **History:** Collected on 18 April 1986. **Distribution:** China, Yunnan, Yiliang county, subterranean river at 25°24' N, 103°27' E. **Habitat and ecology:** Limestone cave. **Remarks:** Eyes not externally visible. Little pigmentation. The scales cover only part of the body.

12. *Sinocyclocheilus cyphotergous* (Dai, 1988). **Common name:** None given. **Etymology:** *cypho* (Gr) curved, convexed; *terg(o)us* (L) back, because of its humpback. **Major synonyms:** *Gibbibarbus cyphotergous*. **History:** No information available. **Distribution:** China, Guizhou province, Luodian county, cave at Daxiao Dong, village of Dajing (ca. 25°26' N, 106°47' E). **Habitat and ecology:** 300 m from the entrance of the cave. **Remarks:** Microphthalmic. Depigmented.

13. *Sinocyclocheilus furcodorsalis* Chen, Yang & Lan, 1997. **Common name:** crossed-fork back golden-line fish (E, translation from Chinese). **Etymology:** *furco* (L) forked; *dorsalis* (L) on the back, because the anterior part of the humpback is bifurcated. **Major synonyms:** None. **History:** Collected in September 1993 by the authors who described it. **Distribution:** China, Guangxi, in an underground river in Tiane County (ca. 25°00' N, 107°00' E). **Habitat and ecology:** No information available. **Remarks:** No externally visible eyes. Depigmented. Scales on the body but not on the head.

14. *Sinocyclocheilus hyalinus* Chen & Yang in Chen, Yang & Zhu, 1994. **Common name:** translucent golden-line barbel (E, translation from Chinese); hyaline fish (E, translation from Chinese). **Etymology:** late Latin *hyalinus*, from *hyalinus* (Gr) of glass, referring to the transparency of the fish. **Major synonyms:** None. **History:** Two specimens were collected in June 1991. This may have been the first troglomorphic fish ever reported in print (Romero 2001). **Distribution:** China, Yunnan, Luxi county, Alu limestone caves (24°33' N, 103°45' E). **Habitat and ecology:** In an underground river (Yusun River) of a cave of 625 m in length at an elevation of 1712.87 m a.s.l. Feeds on microscopic animals and aquatic insects. **Remarks:** No externally visible eyes. Depigmented. Scaleless. May be related to the epigeic *S. angustiporus*.

15. *Sinocyclocheilus microphthalmus* Li, 1989. **Common name:** Small eye golden-line fish (E, translation from Chinese). **Etymology:** *micro* (Gr) small; *ophthalmus* (Gr) eyes. **Major synonyms:** None. **History:** Li collected it in 1986, between April and May. **Distribution:** China, Guangxi Zhuang autonomous region, Ling Yun county, karst cave at Luo-lou Village (24°20' N, 106°49' E). **Habitat and ecology:** Karst cave from which a river flows. **Remarks:** Microphthalmic. Depigmented. Covered by large scales.

16. *Troglocyclocheilus khammouanensis* Kottelat & Bréhier, 1999. **Common name:** paa kham khom (Laotian for 'fish which crosses the streams'). **Etymology:** *troglo* (Gr) hole; *cyclocheilus* (L) a generic name proposed for cyprinid fishes with which this genus is supposedly related; *khammouanensis* (L) after the limestone formation where it was found. **Major synonyms:** None. **History:** Holotype collected 24 February 1998 by F. Bréhier. Only one specimen has been collected but more have been observed. **Distribution:** Laos, Khammouan province, Khoung Nam Dôn, resurgence of Nam Dôn (stream) near Ban Phôndou (village) (17°33'50" N, 104°52'20" E). May have a wider distribution. **Habitat and ecology:** Cave. Swims close to the bottom and hides near the bottom. **Remarks:** No externally visible eyes. Depigmented. Body entirely scaled. Several rows of sensory papillae on lateral and dorsal sides of the head. May be related to species of the genus *Cyclocheilichthys*.

17. *Typhlobarbus nudiventris* Chu & Chen, 1982. **Common name:** None given. **Etymology:** *typhlo* (Gr) blind; *barbus* (L) for its relationship with the genus *Barbus*; *nudi ventris* (L) for the naked ventral portion. **Major synonyms:** None. **History:** Known from only three specimens. No other information available. **Distribution:** China, Yunnan province, Jian Jianshui county, known only from a sinkhole about 100 m below the surface at an altitude of 1450 m, in Yangjieba (ca. 23°39' N, 102°46' E). **Habitat and ecology:** No information available. **Remarks:** No externally visible eyes. No known phylogenetic relationships except for the fact that it has been placed in the subfamily Barbinae.

18. *Typhlogarra widdowsoni* Trewavas, 1955. **Common name:** Iraq blind barb (E). **Etymology:** *typhlo* (Gr) blind; *garra* (L) because of its close relationship to the genus *Garra*; *widdowsoni* (L) after A.G. Widdowson who secured the first specimens. **Major synonyms:** None. **History:** Dr. Donald and Mr. Khosraf, by request of Mr. A.G. Widdowson, all of them with the Iraq Petroleum Co., collected two specimens of these fish which ended up in the British Museum (Natural History) in July 1953. Three living individuals were later captured and also sent to that institution. **Distribution:** Iraq, in two caves, one about 8 m below ground, 10 km north of Haditha (34°04' N, 42°24' E), and the other, known as Pigeon Hole, is found about 8 km south of Haditha, near the Euphrates. **Habitat and ecology:** Little is known except that the type localities are large caves fed by underground streams. It shares its habitat with *Caecocypris basini*. **Remarks:** No externally visible eyes. Depigmented. Has scales only along the lateral line. The nervous system associated with vision is very much reduced. A few melanophores are present in the tissue between the optic lobes and the cerebellum. This species is slightly scotophilic (Marshall & Thinès 1958). It is closely related to *Garra rufa*.

#### Family: Cobitidae

This is a family composed of more than 110 species of freshwater fishes from Eurasia and Morocco. They have a wormlike to fusiform body and are mostly bottom dwellers (Nelson 1994). Only one troglomorphic species has been described so far.

19. *Protocobitis typhlops* Yang, Chen & Lan, 1994. **Common name:** None given. **Etymology:** *proto*

(Gr) primitive; *cobitis* (L) a generic name for members of the subfamily Cobitinae; *typhlos* (Gr) blind; *ops* (Gr) eye. **Major synonyms:** None. **History:** Specimens collected in August 1991 by Lan Jia-Hu. **Distribution:** China, Guangxi, Duan county, Xiaao town (24°15' N, 107°05' E). **Habitat and ecology:** In a cave at 210 m a.s.l. **Remarks:** No externally visible eyes. Depigmented. Scales rudimentary and only along the midline of the sides of the body. Lacks lateral line. It also lacks a bony swimbladder capsule, which may be a primitive character.

Family: Balitoridae

This is a family of freshwater species from Eurasia composed by more than 600 species. They have three or more pair of barbels. Some species are scaleless. Many tend to hide underneath rocks (Nelson 1994). They have 14 troglobitic representatives. Yang et al. (1994) mentioned a *Oreonectes* sp. for a limestone cave near Xiaao, Duan county, Guanxi, China, yet to be described.

20. *Cryptotora thamicola* (Kottelat, 1988). **Common name:** waterfall climbing cave fish of Thailand (E). **Etymology:** *Cryptotora* (Gr) is a contraction of *kryptos* (hidden, an allusion to the hidden cave life of this monospecific genus) and *balitora*, the name-sake of the family; *tham* (L) transcription of the Thai word for cave; *cola* (L) *colere*, to inhabit. **Major synonyms:** *Homaloptera thamicola* (original description) (Kottelat 1998). **History:** First collected by J. Taylor on 7 May 1985. **Distribution:** Thailand, Mae Hong Son province, Susa Cave (19°28' N, 98°08' E). **Habitat and ecology:** The holotype was found on a ledge, apparently climbing up a small waterfall about 0.6 km from the cave entrance. **Remarks:** No visible eyes. Depigmented except for some appendages. Scaleless.

21. *Nemacheilus evezardi* Day, 1872. **Common name:** hill stream loach (E). **Etymology:** not applicable. **Major synonyms:** Kottelat (1990) changed the generic status of this species to *Indoreonectes* but without explaining why. Singh & Yazdani (1993) gave it the name of *Oreonectes evezardi*. **History:** At the British Museum there are two specimens of *N. evezardi* (BMNH 1960, p. 6.2, pp. 1–2) collected from 'a cave in India', one of which is fully pigmented and the other somewhat depigmented but

apparently with normal eyes. Menon (1987) mentioned the existence of 13 specimens collected in Bhaje Cave, Karla, Poona, but without saying whether or not these fish displayed any troglomorphic characters. **Distribution:** India, Madhya Pradesh state, Bastar district, Kotumsar Cave (18°52'09" N, 81°56'05" E) at 560 m a.s.l. (Kottelat 1990). **Habitat and ecology:** A cave subject to frequent flooding during the monsoon season. **Remarks:** Hypogean forms exhibit lower oxygen consumption than the epigean forms (Biswas 1991). The hypogean individuals also exhibit circadian and circannual rhythmicity (Biswas et al. 1990).

22. *Nemacheilus starostini* Parin, 1983. **Common name:** Kughitang blind loach (E). **Etymology:** *starostini* (L) after I.V. Starostin, a fish researcher and collector specialized in Turkmenia. **Major synonyms:** *Noemacheilus (Troglobitis) starostini* (original description), *Paracobitis starostini* (Weber, 2000). **History:** Seven live individuals and four preserved specimens were captured in December 1981 by V. Dolzansky, a member of a Moscow speleological expedition. The head of that expedition, Vladimir Maltsev, had first found the fish in that very sinkhole five years earlier and caught several specimens which were lost during shipment. **Distribution:** Turkmenistan, Chardzhou province, Khrebet Kughitang (mountains) (several sinkholes) (ca. 37°55' N, 66°23' E). **Habitat and ecology:** The type locality is a sinkhole of about 19 m in depth with a seasonally fluctuating water level. A large portion of the pool is exposed to light part of the time. The pool is connected to an underwater stream. Up to 40 fish can be observed at a time in the pool. They feed on insect larvae and small benthic crustaceans (Smirnov 1983). **Remarks:** No externally visible eyes. Depigmented. Scaleless. No swimbladder.

23. *Nemacheilus troglotaractus* Kottelat & Géry, 1989. **Common name:** None known. **Etymology:** *troglo* (Gr) hole; *cataracta* (L) waterfall. **Major synonyms:** None. **History:** Collected in February 1986 by R. Brouquisse and in June 1986 by the Thais-Maros expedition. **Distribution:** Thailand, Kanchanaburi province, Tham Sai Yok Noi [=Tham Nam Tok], 3 km north-northwest of Nam Tok (14°15' N, 99°04' E). **Habitat and ecology:** Underwater stream. Syntopic with *Pterocryptis buccata*. **Remarks:** No externally visible eyes. Depigmented. Scales embedded.



24. *Oreonectes anophthalmus* Zheng in Anonymous, 1981. **Common name:** None given. **Etymology:** *an* (Gr) without; *ophthalmus* (Gr) eyes. **Major synonyms:** *Nemacheilus anophthalmus* (Kottelat, 1988). **History:** No information available. **Distribution:** China, Guangxi, Wuming county, Qifeng Shan (hill), Taiji Cave (ca. 23°06' N, 108°40' E). **Habitat and ecology:** No information available. **Remarks:** No externally visible eyes.
25. *Paracobitis longibarbus* Chen, Yang, Sket & Aljancic, 1998. **Common name:** None given. **Etymology:** *longi* (L) long; *barbatus* (L) barbels. **Major synonyms:** None. **History:** The first three specimens were collected during February and March 1995 by a joint Slovenian-Chinese expedition. **Distribution:** China, Guizhou province, Libo county, in a cave 13 km northeast of the town of Libo (ca. 25°15' N, 108°00' E). **Habitat and ecology:** The cave contains both streams and lakes with a sandy/rocky bottom. **Remarks:** No externally visible eyes. Depigmented. Rostral and maxillary barbels are well developed. It is related to *Paracobitis variegatus longidorsalis*, which occurs in the same basin of Xijiang. They appear to be scotophilic.
26. *Paracobitis smithi* (Greenwood, 1976). **Common name:** blind loach (E). **Etymology:** *smithi* (L) after Anthony Smith who collected the first specimens. **Major synonyms:** *Noemacheilus smithi* (original description) (Nalbant & Bianco, 1998). **History:** First collected in April 1976. **Distribution:** Iran, Lorestan (Khorramabad) province, Zagros mountains, Ab-i-Serum Valley near Tang-e-haft railway station, Baq-e-Loveh Oasis, a natural well at Kaaje-Ru (33°05' N, 48°36' E) (for full locality description see Coad 1996). **Habitat and ecology:** The well-like water resurgence in which it has been found seems to be the result of a collapsed subterranean system. This is probably part of a larger but complex, narrow, and inaccessible network of underground waters. Syntopic with *Iranocypris typhlops* (see above). **Remarks:** No externally visible eyes. Depigmented.
27. *Schistura jarutanini* Kottelat, 1990. **Common name:** Srisawat blind cave loach (E). **Etymology:** *jarutanini* (L) after Kitipong Jarutanin, who collected the first specimens. **Major synonyms:** None. **History:** First collected by K. Jarutanin in November 1987. **Distribution:** Thailand, Kanchanaburi province, Amphoe Sri Sawat, Tham (cave) Ba Dan (ca. 14°02' N, 94°32' E). **Habitat and ecology:** Underground stream. **Remarks:** Eyes reduced to absent. Slightly depigmented. Scales embedded.
28. *Schistura oedipus* (Kottelat, 1988). **Common name:** None given. **Etymology:** *schistura* (Gr) or *skhizeîn* to split; *oura* (Gr) tail, an allusion to forked caudal fin; *oedipus* for Oedipus, a mythic Theban king who tore out his eyes. **Major synonyms:** *Nemacheilus oedipus* (original description). **History:** The holotype and paratype were collected by J. Dunkley on 7 May 1985. **Distribution:** Thailand, Mae Hong Son province, Tham (cave) Nam Lang (19°31' N, 98°09' E) (see Kottelat 1990 for distributional map). **Habitat and ecology:** An outflow cave with a stream which is probably part of Nam Lang, part of a karstic endorheic basin. **Remarks:** Microphthalmic. Depigmented. Scales embedded.
29. *Schistura sijuensis* Menon, 1987. **Common name:** None given. **Etymology:** *sijuensis* (L) after Siju, the name of the cave where they were discovered. **Major synonyms:** *Noemacheilus sijuensis* original combination/description; *Noemacheilus Mesonoemachilus sijuensis* on plate caption of original description; *Mesonoemacheilus sijuensis*. Pillai & Yazdani (1977) refer to this hypogean fish as *Nemacheilus multifasciatus*, yet, but Talwar & Jhingran (1991) consider them separate species, and when referring to *N. multifasciatus* make no mention of being found in a cave. **History:** The first cave individuals belonging to this species may have been reported by Hora (1924) who described three specimens as '*Nemacheilus* sp.' from the 'Siju Cave, Assam, India'. One specimen, caught within 35 m of the cave mouth, showed coloration comparable to the epigeal forms. Two others, netted about 550 m from the entrance of the cave, were paler in color and apparently had reduced eyes. **Distribution:** India, Meghalaya, Garo Hills, Siju Cave (ca. 25°25' N, 90°30' E). **Habitat and ecology:** No information available. **Remarks:** Eye size and pigmentation variable.
30. *Sundoreonectes tiomanensis* Kottelat, 1990. **Common name:** None given. **Etymology:** *tiomanensis* (L) after Pulau Tioman, the type locality. **Major synonyms:** None. **History:** First collected by Mark

Day on 17 August 1988. **Distribution:** Malaysia, Pulau Tioman (island), cave in Mount Gunung Kajang at 1000 m a.s.l. (ca. 2°50' N, 104°15' E). **Habitat and ecology:** In shallow pools of a small granitic cave system. **Remarks:** Reduced, partly embedded eyes. Partially depigmented.

31. *Triplophysa gejiuensis* (Chu & Chen, 1979). **Common name:** Gejiu blind loach (E). **Etymology:** *gejiuensis* (L) for the province of Gejiu. **Major synonyms:** *Noemacheilus gejiuensis* (original description) (Zhou & Cui, 1997), *Schistura gejiuensis* (Zhu, 1989). **History:** The seven original specimens were captured on 30 March 1978. **Distribution:** China, Yunnan province, Gejiu county, Bajiaoqing near Qiafang (23°16' N, 103°09' E). **Habitat and ecology:** In subterranean waters at a depth of 400 m underground. **Remarks:** No externally visible eyes. Depigmented. Scaleless. Has no swimbladder. It was classified as a new species based only on troglomorphic characters. Paired fins and barbels are greatly elongated.

32. *Triplophysa shilinensis* (Chu & Yang in Chen, Yang & Xu, 1992). **Common name:** blind loach (E). **Etymology:** *shilinensis* (L) for the words Shi Lin which in Chinese means 'stone forest', the name of the general area where this species is found. **Major synonyms:** None. **History:** The first two specimens were collected by the authors describing the species on 18 March 1991. **Distribution:** China, Yunnan, Lunan county, cave at Weiboyi village near Stone Forest (24°47' N, 103°22' E). **Habitat and ecology:** The cave has a funnel-like opening and goes down vertically for 109 m before it reaches a horizontal river where this fish can be found. Insects have been found in their stomachs. **Remarks:** Eyes completely degenerated. Completely depigmented; body described as 'translucent'. Scaleless. Posterior chamber of air bladder reduced, and anterior chamber enclosed in a bony capsule.

33. *Triplophysa xiangxiensis* (Yang, Yuan & Liao, 1986). **Common name:** None given. **Etymology:** *xiangxiensis* (L) because it is found in the area of Xiangxi. **Major synonyms:** *Noemacheilus xiangxiensis* (original description), *Schistura xiangxiensis* (in Zhu, 1989). **History:** No information available. **Distribution:** China, Xiangxi, Hunan province, Longshan county, Feihu Cave (ca. 27°52' N, 102°15' E). **Habitat and ecology:** Subterranean waters, Yuan River

system, 20 m underground. **Remarks:** No externally visible eyes.

34. *Triplophysa yunnanensis* Yang, 1990. **Common name:** None given. **Etymology:** *yunnanensis* (L) because it is found in the province of Yunnan. **Major synonyms:** None. **History:** No information available. **Distribution:** China, Yunnan province, Yiliang (ca. 25°00' N, 103°23' E). **Habitat and ecology:** No information available. **Remarks:** Microphthalmic but pigmented.

#### Family: Characidae

This is a highly diversified (ca. 900 species) family of freshwater fishes from America and Africa (Nelson 1994). They show no apparent morphological and/or behavioral preadaptation to the hypogean environment. It is somewhat surprising that more representatives of this family have not been found in caves given its ample distribution and high diversity. Most characids are completely covered with cycloid scales. There are at least two species of troglomorphic characids.

35. *Astyanax fasciatus* species complex (Cuvier, 1819). **Common name:** Mexican blind/cave tetra (E). **Etymology:** not applicable. **Major synonyms:** The epigean form of this species was originally described by Cuvier (1819, p. 352, pl. 26 (figure 2) as *Chalceus fasciatus* based on material from Brazil. The genus *Astyanax* was created by Baird & Girard (1854) and then the species was reassigned to it. The specific status of the epigean form in the areas surrounding the cave localities for the troglomorphic ones is in dispute. The whole family Characidae is very complex, with many species that are difficult to differentiate from each other and are not always allopatric (Géry 1977, Nelson 1994). New species of the genus *Astyanax* have been described in Mexico using morphological characters only (e.g., Contreras-Balderas & Lozano-Vilano 1988, Lozano-Vilano & Contreras-Balderas 1990). Common synonyms are *A. mexicanus*, a rearrangement of *Tetragonopterus mexicanus* (De Filippi, 1853), and *Astyanax fasciatus mexicanus*. The use of *mexicanus* has been most commonly employed by US-based authors, especially when dealing with epigean individuals from Texas. However, clear taxonomic differences and geographic limits between *A. fasciatus* and *A. mexicanus* have yet to be established. Until the taxonomy of the entire genus is fully clarified, the most parsimonious approach is to use the name *Astyanax*

*fasciatus*, clarifying when necessary whether we refer to the epigeal or troglotic populations. We avoid the use of the term 'cave populations' because some hypogean individuals are actually eyed and pigmented. **History:** The first cave, troglotic population (from La Cueva Chica in the San Luis de Potosí area) was described as *Anoptichthys jordani* (Hubbs & Innes, 1936), the second one (from La Cueva El Pachón) was named *Anoptichthys antrobius* (Alvarez, 1946), and a third one (from La Cueva de Los Sabinos) was named *Anoptichthys hubbsi* (Alvarez, 1947). Most if not all of the papers that still use either those names, or a combination of *Astyanax* and the specific names given to cave populations, are written by experimentalists, not field or taxonomic researchers. As more cave populations were discovered it became evident that this typological approach was creating a lot of confusion (Romero 2001). **Distribution:** The epigeal *A. fasciatus* is a freshwater fish with a broad distribution in the New World. Although obligatory and facultative cave populations of the eyed form have been reported for Belize and Costa Rica (Romero 1984), the Yucatán Peninsula (Hubbs 1938), and Brazil (Trajano 2001a), the only region in which they have developed into blind, depigmented individuals is the San Luis de Potosí area, east central Mexico, where at least thirty-one caves supporting subterranean populations of this fish can be found (Espinasa et al. 2001) (ca. 22°05' N, 99°00' W). Not all the cave populations of this area display the same degree of morphological divergence from the surface forms, however. Some are completely blind and depigmented while others are only partially so. Three caves contain only individuals with full eyes and pigmentation. Eleven of these populations include blind, eyed, as well as phenotypically intermediate forms (Mitchell et al. 1977, Romero 1983, Espinasa et al. op. cit.). **Habitat and ecology:** In numerous caves. Some of those caves appear to be very poor from a trophic viewpoint while others (e.g., La Cueva Chica) have a very rich input of nutrients thanks to large bat colonies producing guano on which these fish feed. **Remarks:** Troglomorphic individuals have reduced eyes (most are not externally visible), pigmentation (including totally depigmented), and a larger number of taste buds (Schemmel 1967). The surface and cave forms interbreed in both natural and laboratory conditions, producing fertile hybrids with a phenotypically intermediate form in the F<sub>1</sub> generation, and with an F<sub>2</sub> generation whose individuals range from an almost completely blind and depigmented form to an almost eyed and pigmented

one (Peters & Peters 1973, Sadoglu 1957, Wilkens 1969). Breeding, electrophoretic, and karyotypic studies support the contention that the cave and epigeal forms are the same species (Avisé & Selander 1972, Kirby et al. 1977). The two forms are not only different in their morphology, but also in their behavior: unlike the surface/eyed form, the blind form never schools, is active all the time, and is not aggressive (Boucquey et al. 1965, Breder 1942, Breder & Gresser 1941, Erckens & Weber 1976). Although the blind form does produce an alarm substance, it does not respond to it (Pfeiffer 1966). Schemmel (1980) also reported differences between the two forms in the angle of inclination used when feeding from the bottom. Differences in the level of phototactic responses among different populations have also been reported (Romero 1985).

36. *Stygichthys typhlops* Brittan & Böhlke, 1965. **Common name:** Brazilian blind characid (E). **Etymology:** *stygos* (Gr) from the underworld in the Greek mythology; *ichthys* (Gr) fish; *typhlos* (Gr) blind; *ops* (Gr) eye. **History:** Known from only one specimen captured on 16 May 1962 by Joseph A. Tosi, Jr., an ecologist with the Instituto de Agricultura of the Organization of American States. The fish was captured in water brought up from a depth of 30 m during a well-drilling operation. **Distribution:** Brazil, Minas Gerais state, in one well location at Jaiba. The precise location is unknown. Jaiba may refer to an area (Serra de Jaiba) or to a town, near to which the well could be situated. It is the area between Januária and Janaúba, in northern Minas Gerais State, central-eastern Brazil (Trajano personal communication) (ca. 16°15' N, 44°00' W). **Habitat and ecology:** Groundwater, obtained from a well drilled at 30 m. Although the tooth structure seems to indicate a mostly vegetarian diet, it is unlikely that they maintain such a diet in the underground environment. This may be a relictual morphological feature. **Remarks:** No externally visible eyes. There is no distinct lateral-line system. Totally depigmented. Unlike the Mexican cave tetra, the ancestral form of this fish has yet to be determined. The Brazilian blind characid has a number of features typical of the Tetragonopterinae. More specifically, it may be related to the *Hyphessobrycon-Hasemanina* complex, because of this group's reduction in the circum-orbital bones; however that just may be a coincidence given that the reduction of those bones is a convergent feature among cave fishes. They also differ from other Tetragonopterinae in the large number of inner

premaxillary and maxillary teeth, as well as the small number of anal rays which is unusual for this group of characids (Romero & McLeran 2000).

Family: Ictaluridae

About 45 species of freshwater fishes found in North America from southern Canada to Guatemala. They are scaleless (Nelson 1994). Their possession of barbels as well as their nocturnal habits might be argued to be preadaptive features. Four unrelated eyeless species are known from deep wells and caves. All four species show a remarkable convergence of features that include the lack of externally visible eyes, depigmentation, and reduced lateral line (Walsh & Gilbert 1995).

37. *Prietella lundbergi* Walsh & Gilbert, 1995. **Common name:** phantom blindcat (E); bagre ciego duende (S). **Etymology:** *lundbergi* (L) after John G. Lundberg, an American ichthyologist who has greatly contributed to the systematics and paleontology of ictalurid and neotropical catfishes. **Major synonyms:** None. **History:** Collected by T. Morris on 17 April 1989. **Distribution:** Mexico, Tamaulipas state, Río Tamesí drainage, Nacimiento (spring) de San Rafael de Los Castros, subsurface thermal spring (ca. 22°40' N, 99°00' W). **Habitat and ecology:** Cave subject to periodic flooding. **Remarks:** No visible eyes. Depigmented. Reduced lateral line.

38. *Prietella phreatophila* Carranza, 1954. **Common name:** Mexican blindcat (E), bagre ciego de Múzquiz (S). **Etymology:** *prietella* (L) after Carlos Prieto, sponsor of the expedition to collect these specimens; *phreas* (L) well; *philos* (Gr) loving, with affinity to. **Major synonyms:** None. **History:** Collected on August 1954 by J. Carranza after hearing of the presence of a blind catfish in a well in that area. **Distribution:** Several localities in northern Mexico. Original specimens collected at El Potrero de Doña Mariana, Municipio Múzquiz, Coahuila state, in a well at the base of Sierra de Santa Rosa (ca. 27°55' N, 101°07' W). **Habitat and ecology:** It has been kept under starvation in the laboratory for up to 44 months and it is believed that it may last longer under natural conditions, which suggests that its environment is very poor in nutrients (Hendrickson et al. 2001). **Remarks:** No externally visible eyes. Depigmented. Reduced lateral line. It has a swimbladder.

39. *Satan eurystomus* Hubbs & Bailey, 1947. **Common name:** widemouth blindcat (E). **Etymology:** *satan* (Heb) prince of darkness; *eurys* (Gr) broad; *stomus* (Gr) mouth ('widemouth prince of darkness') (Hubbs liked to name cave fishes with diabolic names based on the idea of hell being underground; see etymology for *Ophisternon infernale*). **Major synonyms:** None. **History:** Carl L. Hubbs visited the Witte Memorial Museum in San Antonio, Texas in 1938 when the director of that museum, Ellen S. Quillin, made available to him two blind catfishes which had been pumped from deep artesian wells in the vicinity of San Antonio. One of them was *Trogloglanis pattersoni* but the other one was of an unknown species. Apparently these fish had been pumped out of wells since the 1920s. **Distribution:** Texas, Edwards Aquifer. Holotype collected at an artesian well (depth 381 m), near San Antonio, Bexar county (ca. 29°30' N, 98°30' W). **Habitat and ecology:** An opportunistic predator. **Remarks:** No externally visible eyes. Depigmented. Exhibits degeneration of the swimbladder.

40. *Trogloglanis pattersoni* Eigenmann, 1919. **Common name:** toothless blindcat (E). **Etymology:** *troglo* (Gr) cave; *glanis* (Gr) catfish, originally from Glanis, the name of a river; *pattersoni* (L) after J.T. Patterson who secured the first specimen. **Major synonyms:** None. **History:** The holotype was collected on an unknown date by G.W. Brackenridge of San Antonio, Texas, the owner of the well. He gave the specimen to Patterson who, in turn, sent it to Eigenmann. A second specimen was caught in June 1934 by Josef Boecke in a ditch fed by an artesian well on his farm NE to San Antonio, Texas, and a third one was collected sometime before 1955 near Von Ormy, Texas. **Distribution:** Texas, Edwards Aquifer (ca. 29°30' N, 98°30' W). **Habitat and ecology:** Found in artesian waters up to 1300 m deep. This species is a herbivore, feeding on fungal growth and detritus found in the wells. Temperature may be a limiting factor in the distribution of this fish (Longley & Karnei 1979). It may be a scavenger. **Remarks:** Blind. Depigmented. Exhibits rudimentation in a number of regions of the nervous system related to vision.

Family: Siluridae

About 100 species of freshwater in Europe and Asia. Most are scaleless. Silurids have one or two pairs of barbels (Nelson 1994). The presence of barbels and

nocturnal habits could be considered preadaptations. One, maybe two troglomorphic species from south-east Asia.

41. *Pterocryptis buccata* Ng & Kottelat, 1998. **Common name:** None given. **Etymology:** *bucca* (L) mouth, because their cheeks look inflated due to their musculature. **Major synonyms:** None. **History:** The hypogean individuals were collected by L. Deharveng and colleagues in June 1986. **Distribution:** Thailand, Kanchanaburi province, Amphoe Sai Yok, Mae Khlong basin (ca. 14°15' N, 99°04' E). **Habitat and ecology:** Syntopic with *Nemacheilus troglotactaractus*. **Remarks:** There are both epigeal and hypogean populations. The hypogean individuals are depigmented and have sunken eyes.

42. *Pterocryptis cucphuongensis* (Mai, 1978). **Common name:** Cá niết Cúc phurong (Vietnamese). **Etymology:** *cucphuongensis* (L) after Cúc phurong National Park where the fish was found. **Major synonyms:** *Silurus cucphuongensis* (in original description). New name given by Ng & Kottelat (1998). **History:** Collector and date unknown. **Distribution:** Vietnam, Cuc Phuong National Park, foothills of the northern Annamite Mountains, some 100 km southwest of Hanoi. The park comprises parts of Ha Nam Ninh, Ha Son Binh and Thanh Hoa provinces (20°19' N, 105°22' E). **Habitat and ecology:** There is no information in the description that this fish is a hypogean one. **Remarks:** It is microphthalmic. Description based on a single individual that may have not been well preserved. Based on the original description, it is not clear why this fish has been labeled as a 'cave fish' (e.g., Weber 2000).

#### Family: Clariidae

This family includes about 100 species of freshwater fishes found in Africa, Syria and southern and western Asia (Philippines to Java). They have four pairs of barbels and are scaleless. Airbreathing is accomplished with a labyrinthic organ arising from the gill arches ('labyrinth catfishes'). Some species are capable of traveling over short distances on land ('walking catfishes'). Some are burrowers with small eyes (Nelson 1994). These could be considered as preadaptations to the hypogean life. Three troglomorphic species have been described so far.

43. *Clarias cavernicola* Trewavas, 1936. **Common name:** cave catfish (E); spelonkbaber (Afrikaans); blinder höhlenwels (G). **Etymology:** *cavernicola* (L) living in a cave. **Major synonyms:** None. **History:** It may have been encountered first between 1917 and 1919 by geologists Jaeger & Waibel (1921). First collected by Karl Jordan who visited that cave in 1921 but not described until 1936. **Distribution:** Namibia, known only from an underground lake at Aigamas Cave, north of Otavi and west of Grootfontein (19°25' S, 17°18' E). **Habitat and ecology:** Lives in caves over shelves in open, clear water. Usually swims near the surface of the water. Feeds on the remains of insects (mostly beetles), bat and baboon guano, and insects associated with animal carcasses (Bruton 1995). **Remarks:** Eyes not visible but sunken and with variability in development. Depigmented.

44. *Horaglanis krishnai* Menon, 1950. **Common name:** Indian blind catfish (E). **Etymology:** *hora* (L) after S.L. Hora, Director of the Zoological Survey of India; *glanis* (L) catfish; *krishnai* (L) after the collector N. Krishna. **Major synonyms:** None. **History:** Four specimens were collected in July 1948 by N. Krishna Pillay after draining a well. He gave the specimens to K. Gopinath, who in turn sent it to Hora. The two specimens were received in August 1949 and the other two were lost. **Distribution:** India, Kerala state, Travancore, in two dugout wells at Kottayam (between 8°04' N, 76°13' E and 10°21' N, 77°38' E) (Mercy et al. 1982). **Habitat and ecology:** No information available. Syntopic with *Monopterus indicus* (Eapen, 1963). **Remarks:** No externally visible eyes. Free, not enclosed, swimbladder. It has a bulbous stomach that helps store food and the ileo-sphincter helps retain the digested food to maximize absorption (Mercy & Pillai 1984–5).

45. *Uegitglanis zammaranoi* Gianferrari, 1923. **Common name:** None given. **Etymology:** *uegit* (L) after the type locality, a pool in Uegit, El Uegit, Somalia; *glanis* (L) eponymous spirit of the Sacred springs in the town of Glanum in Provence, then there was the Glanicae, a triad of local Mother Goddesses associated with healing springs (all this makes reference to the fact that the this fish was found in a pool associated with a spring); *zammaranoi* (L) after the collector, V.T. Zammaranoi. **Major synonyms:** None. **History:** The first specimens were collected by an Italian army officer, V.T. Zammaranoi at an unspecified

date. **Distribution:** Somalia, several localities in southern Somalia (see Ercolini et al. 1982 for distributional map) (ca. 3°48'30" N, 43°14'47" E). **Habitat and ecology:** Tolerates remarkable variations in salinity and chemicals in the water. It reproduces between January and March, in the dry season (Ercolini et al. op. cit.). **Remarks:** No externally visible eyes. Depigmented. Scaleless. It lacks optic nerves, chiasm, and has a reduced brain size, particularly in the optic lobe and cerebellum (Bianchi 1975, Ercolini & Berti 1977). The epidermis has cells that contain an alarm substance. It does not present any specialization in olfactory structures (Bianchi et al. 1978). Displays aggressive behavior similar to epigean Siluriformes (Berti & Ercolini 1979). Studies on their responses to light have been inconclusive (Ercolini & Berti op. cit.).

Family: Pimelodidae

This is a family of about 300 species of freshwater fishes found in Central and South America (north to southernmost Mexico). They have three pairs of barbels and a naked body. Barbels and nocturnal habits make members of this family preadapted to the hypogean environment (Nelson 1994).

Seven troglomorphic species have been described so far. Additionally, Hubbs (1936, 1938) reported specimens of *R. guatemalensis* with certain degree of depigmentation and eye reduction and called them *Rhamdia guatemalensis decolor* and *Rhamdia guatemalensis stygaea*, respectively. The four other species/populations of *Rhamdia* described for southern Mexico and Belize represent a puzzle not only because of their close similarity to epigean *Rhamdia*, but also because of their great variability in troglomorphic characters and the lack of molecular studies that could shed some light on their evolution. There may be at least two more species of stygobiontic representatives for this family. One reported as *Imparfinis* sp. by Trajano (1997c) for the caves in the Chapada Diamantina, Itaete County, Bahia State, Brazil, and a *Taunayia* sp. also reported by Trajano (op. cit.) for Brazil, Bahia state, Campo Formoso County, Toca do Gonçalo Cave.

46. *Phreatobius cisternarum* Goeldi, 1905. **Common name:** None given. **Etymology:** *phreatos* (Gr) from a spring; *bius* (Gr) alive; *cisternarum* (L) from a deposit; all this in reference to the phreatic origin of this fish. **Major synonyms:** *Heptaterus cisternarum* (Andreas Buckup, 1988). The date of publication is usually cited

as 1904, year in which Goeldi presented the paper describing this species before the Sixth International Congress of Zoology at Berne. However, the proceedings of that meeting were not published until 1905 and, according to article 21.1 of the International Code of Scientific Nomenclature it is the date of publication that must be taken in consideration. **History:** No information available. **Distribution:** Brazil, Pará and Amapá states, at the Rio Amazonas delta, Belém city, Pará, and Macapá city. Original locality: Marajo I., at the mouth of the Amazon, Brazil (in a cistern) (ca. 1°27' S, 48°29' W). **Habitat and ecology:** Phreatic. **Remarks:** Rudimentary eyes. Reduced pigmentation, mostly in the head and anterodorsal parts of the body. Its taxonomic position is very much in question (de Pinna 1998).

47. *Pimelodella kronei* (Miranda-Ribeiro, 1907). **Common name:** ceguinho (P). **Etymology:** *kronoi* (L) after Ricardo Krone, who first reported this fish to Miranda-Ribeiro. **Major synonyms:** *Typhlobagrus kronei* (original description); *Caecorhamdella brasiliensis* (Borodin, 1927), *Pimelodella lateristriga* var. *kronoi* (Haseman, 1911). **History:** This fish may have been known for some time, since the paper describing it has two pictures of the type locality dated 1898 and taken by Krone. **Distribution:** Brazil, southern São Paulo state, Upper Rio Ribeira basin, Iporanga, Areiras, Águas Quentes, Bombas, and Córrego Seco caves, on the right margin of the Rio Betari, and Alambari de Cima and Guruvuta caves, on the left margin (24°25' S, 48°35' W). **Habitat and ecology:** Headwater streams, with rocky beds and rapids intercalated with soft-bottomed pools. **Remarks:** Variable vestigial eyes. Varying pigmentation from dark to almost totally depigmented with most individuals being intermediate. They display agonistic behavior (Trajano 1991). Telencephalon is enlarged probably due to the improvement of olfactory and integrative centers related to social communication. Its putative ancestor is *Pimelodella transitoria*.

48. *Rhamdia laticauda typhla* Greenfield, Greenfield & Woods, 1982. **Common name:** cave chulín (E). **Etymology:** *typhla* (Gr) blind. **Major synonyms:** None. **History:** First specimens were collected on 10 July 1972. **Distribution:** Belize, Mountain Pine Ridge, Las Cuevas (16°45' N, 89°00' W). **Habitat and ecology:** Found in pools together with troglomorphic shrimps. **Remarks:** Variable eye size and

pigmentation. The *R. guatemalensis* reported by Hubbs (1936, 1938) showed a certain degree of depigmentation and eye reduction and was called *Rhamdia guatemalensis decolor* and *Rhamdia guatemalensis stygaea*, respectively; yet these subspecies show a much lesser degree of depigmentation and eye reduction than *R. laticauda typhla*.

49. *Rhamdia macuspanensis* Weber & Wilkens, 1998. **Common name:** None given. **Etymology:** *macuspanensis* (L) after the town of Macuspana, about 20 km from the type locality. **Major synonyms:** None. **History:** The first specimen was provided by V. Sbordoni and specimens used for the species description were collected on 11 April 1996 by Ulrike Strecker, Axel Werber and Horst Wilkens. **Distribution:** Mexico, Tabasco state, ca. 20 km southeast of Macuspana, Grutas de Agua Blanca, Balneario de Agua Blanca at 64.9 km of the road (carretera federal 186) from Villahermosa to Chetumal (17°37'15.5" N, 92°28'22.6" W). **Habitat and ecology:** Crustaceans and epigeal *Rhamdia* have been observed in the same cave. **Remarks:** Sunken eyes. Reduced pigmentation.

50. *Rhamdia quelen* (Quoy & Gaimard, 1824). **Common name:** eyeless catfish of Trinidad (E). **Etymology:** not applicable. **Major synonyms:** *Caecorhamdia urichi* (description of the cave population, Norman, 1926); *R. quelen urichi*, *Caecorhamdella urichi* (Hubbs, 1938). **History:** Cave individuals were first collected by Friederick William Urich in the 'Guacharo' cave (actually Oropouche or Urumaca cave). By July 1924, the British Museum of Natural History had received from Urich a specimen of 'blind' fish. The fish was examined by John Roxborough Norman who, fearing that the specimen could represent an accident of nature rather than a normal fish species, requested two more specimens and Urich complied. In October of 1926 Norman published his paper and named the fish *Caecorhamdia urichi* [*caeco* (L) blind; *rhamdia* (L) the genus of a catfish to which this cave fish seemed most related to; *urichi* (L) honoring Urich, the collector] (Romero & Creswell 2000). **Distribution:** Trinidad and Tobago, Trinidad, northern range, Pool at about 70 m from the entrance to the Oropouche or Urumaca cave (10°42'53" N, 61°10'29" W). **Habitat and ecology:** The cave is linear and limestone with an emergent stream running its full length. It is at an altitude of 185–215 m a.s.l. Fish are only found in the

dark section of the cave. They feed on the droppings of oil birds, *Steatornis caripensis*. **Remarks:** There is some variability in eye size and pigmentation but even the ones with the least visible eyes cannot be considered anything but microphthalmic. Fish are extremely scotophilic (Romero & Creswell op. cit.).

51. *Rhamdia reddelli* Miller, 1984. **Common name:** juil ciego (S). **Etymology:** *reddelli* (L) after James R. Reddell who donated all the type specimens. **Major synonyms:** Considered just a population of *Rhamdia laticauda* by Silfvergrip (1996). **History:** Holotype collected on 9 March 1973. **Distribution:** Mexico, Oaxaca state, ca. 9 km southwest of Acatlán, Cueva del Nacimiento del Río San Antonio (ca. 18°12' N, 98°02' W). **Habitat and ecology:** In a deep lake about 120 m from the entrance of the cave. The cave is at 100 m a.s.l. A rich invertebrate troglomorphic fauna is found in the same cave. **Remarks:** No externally visible eyes. Depigmented. Individuals will darken under light conditions.

52. *Rhamdia zongolicensis* Wilkens, 1993 **Common name:** None given. **Etymology:** *zongolicensis* (L) after Zongolica, the geographic region where it occurs. **Major synonyms:** According to Silfvergrip (1996) it is a local population of *Rhamdia laticauda*. **History:** Collected on 17 December 1992 by Ulrike Strecker and Horst Wilkens. **Distribution:** Mexico, Veracruz state, Sierra de Zongolica, Cueva del Ostoc or Cueva de El Túnel (ca. 18°30' N, 97°10' W). **Habitat and ecology:** No other aquatic fauna has been reported for the same cave. **Remarks:** Slightly depigmented. Individuals will darken under light conditions. This fish is extremely similar to *R. laticauda* but also to *R. reddelli* reason by which some authors (e.g., Silfvergrip op. cit.) do not consider it a valid species.

#### Family: Trichomycteridae

This is a family of about 160 species of freshwater fishes found in Costa Rica, Panama and South America. They have a naked and elongate body. They usually have two pairs of barbels on maxilla, but lack barbels on the chin (Nelson 1994). The presence of barbels and nocturnal habits of some species make them preadapted to the hypogean environment. Of the ca. 100 species of the genus *Trichomycterus*, three species/populations have been found to display troglomorphic characters while other non-troglomorphic,

hypogean populations have been reported for the Colombian Andes (Sket 1988) and two more for Brazil (Trajano & Souza 1994, Trajano 1997c).

53. *Trichomycterus chaberti* Durand, 1968. **Common name:** None given. **Etymology:** *chaberti* (L) after J. Chabert, collector of the first specimens. **Major synonyms:** *Pygidium chaberti* (Ringuelet, 1974). **History:** 30 specimens were collected by Chabert and his companions during a visit to the type locality on September 1966. An earlier specimen may have been captured by B. Antelo in August and sent to R.A. Ringuelet but not described until 1974 (Ringuelet op. cit.). **Distribution:** Bolivia, Charcas province, Potosí department, Cave of Umayalanta, 8 km northwest of the town of Torotoro, 130 km south of Cochabamba (ca. 18°20' S, 65°30' W). **Habitat and ecology:** The cave is at an altitude of 2850 m. The entrance is a sinkhole of 140 m in depth through which a body of water penetrates for 1620 m. **Remarks:** Eye size and pigmentation are variable, from almost normal for a trichomycterid (which in comparison with other fishes appears to be microphthalmic to somewhat reduced) to a typical troglomorphic fish with very reduced, not externally visible eyes.

54. *Trichomycterus conradi* (Eigenmann, 1912). **Common name:** bagre ciego de la cueva del Guácharo (S). **Etymology:** not applicable. **Major synonyms:** *Pygidium conradi* (original description); *T. guianensis* (Galán, 1995). **History:** First reference to fishes from this cave is by Schultz (1949). **Distribution:** Venezuela, Monagas state, Cueva del Guácharo (10°10'33" N, 63°33'06" W). **Habitat and ecology:** This is a large cave in which fish can be found throughout most of its waters. This fish has the tendency to burrow in the sediment, which may make its observation difficult (Romero 1987). **Remarks:** It has reduced eyes and variable pigmentation (Nalbant & Linares 1987). Many of the morphological differences reported by Andreani Armas (1990) may be influenced by the natural variability of this species; some of those are typical of epigeal species whose hypogean population is in status nascendi. Agonistic behavior for this species has been reported (Romero op. cit.). The definite taxonomy of this species has yet to be clarified. Part of the problem is the poor knowledge on the systematics of the genus *Trichomycterus* in general. Although morphological differences have been used to suggest specific differentiation between the hypogean population

and the epigeal one in nearby waters (Andreani Armas op. cit., Galán 1995), such contention is not supported by genetic studies (Pérez & Moodie 1993).

55. *Trichomycterus itacarambiensis* Trajano & de Pinna, 1996. **Common name:** None given. **Etymology:** *itacarambiensis* (L) after the name of the county, Itacarambi, in the state of Minas Gerais, where it was found. **Major synonyms:** None. **History:** Although specimens of this fish had been collected since 1984 and even papers published about it (Carvalho & de Pinna 1986), it was not formally described until 1996. **Distribution:** Brazil, Minas Gerais state, Município (county) de Itacarambi, creek inside Olhos d'Água Cave (15°06'06" S, 44°09'30" W). **Habitat and ecology:** Found throughout most of the cave. Generally, depigmented individuals increase in number as one goes farther into the cave. The estimated population size is between 1500 and 2000 (Trajano 1997b). This fish feeds mostly on living animals such as small arthropods and oligochaetes (Trajano 1997a). **Remarks:** This population consists of both depigmented and pigmented individuals with variable eye size and variable pigmentation.

Family: Loricariidae

This is a large family (ca. 550 species) of freshwater fishes from Costa Rica, Panama and South America. Their body lacks true scales but is generally covered by bony plates. Their mouth is ventral, with or without conspicuous barbels. They are usually found in swift-flowing streams from lowlands up to 3000 m a.s.l. They tend to be detritivorous (Nelson 1994). No remarkable characteristic seems to make fish of this family preadapted to the hypogean environment. The genus *Ancistrus* has 60 species, three of which are hypogean.

56. *Ancistrus cryptophthalmus* Reis, 1987. **Common name:** None given. **Etymology:** *cryptos* (Gr) hidden, covered, concealed; *ophthalmos* (Gr) eye. **Major synonyms:** None. **History:** This fish was known since at least 1972 when a specimen was collected, possibly by Rene Ginot, but then lost. The first specimens in museum collections today are paratypes collected by E. Ferrari and Claude Vidal in 1972. The holotype was collected in 1980 by a group of the Clube Alpino Paulita. **Distribution:** Brazil, Goiás state, Sao Domingos, Rio Sao Vicente system, Caverna Passa



Três, ca. 300 m into the cave (13°20' to 13°52' S, 46°16' to 46°30' W). **Habitat and ecology:** It is a bottom-dweller with a strong preference for rocky substrates in fast-flowing stream sectors. It is found in relatively high population densities (Trajano 2001b). **Remarks:** It coexists with a *Trichomycterus* sp. and *Astyanax* sp. Eyes in different degrees of reduction, sometime sunken under the skin. Small specimens have externally visible eyes which are reduced in size and become completely covered by dermal ossifications and skin during growth. Body almost entirely depigmented.

57. *Ancistrus formoso* Sabino & Trajano, 1997. **Common name:** None given. **Etymology:** *formoso* (L) after the type locality, Rio Formoso. **Major synonyms:** None. **History:** The first specimen was collected in 1995 and the second in 1996. **Distribution:** Brazil, Mato Grosso do Sul state, Município (county) de Bonito, Serra da Bodoquena, Buraco do Ducho cave (21°08' S, 56°28' W). **Habitat and ecology:** It is found in resurgences of caves of difficult access. **Remarks:** Reduced eyes not externally visible. It is totally depigmented. Abdomen naked.

58. *Ancistrus galani* Perez & Vilorio, 1994. **Common name:** None given. **Etymology:** *galani* (L) after Carlos Galán who collected the holotype. **Major synonyms:** None. **History:** The holotype and the paratype were collected on 10 March 1990 and 25 March 1991, respectively. **Distribution:** Venezuela, Zulia state, Sierra de Perijá, Río Socuy, Cueva de Los Laureles (10°45'04" N, 72°27'42" W). **Habitat and ecology:** This cave is inhabited by a number of common epigeal fishes, including *Ancistrus brevifilis bodenhameri*, none of which show true troglomorphic characters. *A. galani* is found only in remote gallery of the cave. **Remarks:** Reduced eyes and pigmentation. Description made based on only two specimens.

#### Family: Astroblepidae

This is a family of about 40 species of freshwater fishes found in the Andean region (South America) and Panama. Astroblepids have two pairs of barbels. They are characterized by their naked body and the presence of a mouth disc which allows some of them to climb the faces of waterfalls of torrental mountain streams. They also have maxillary and nasal barbels (Nelson 1994). These could be considered preadapted characters. There are two hypogean species within the genus

*Astroblepus*. The vague reference to the Colombian *Astroblepus cyclopus* (originally described as *Pimelodus cyclopus*) by Humboldt (1805) as a cave fish cannot be substantiated (Romero & Paulson 2001).

59. *Astroblepus pholeter* Collette, 1962. **Common name:** None given. **Etymology:** *pholeter* (Gr) means 'one who lurks in hole'. **Major synonyms:** None. **History:** Collected in 1961 and 1962 by Pedro I. Porras who sent the specimens to the U.S. National Museum. **Distribution:** Ecuador, Napo province, Jumandi Cave in Latas, 4 km north of Archidona (0°20'–0°40' S, 77°50' W). **Habitat and ecology:** Found between 300 and 2000 m from the entrance of the cave. Hides in holes of rocks. Insect remains have been found in the stomachs of captured specimens. **Remarks:** Microphthalmic and slightly depigmented. It has a reduced swimbladder (Chardon 1966). Precise relationship to other members of the genus *Astroblepus* has yet to be established.

60. *Astroblepus riberae* Cardona & Guerao, 1994. **Common name:** None given. **Etymology:** *riberae* (L) after C. Ribera, the collector of the first specimens. **Major synonyms:** None. **History:** Collected on 20 August 1977 by Ribera. **Distribution:** Peru, Cajamarca region, Río Reque basin, Pacific drainage, Grutas (caves) de Ninabamba (6°19'48" S, 78°30'36" W). **Habitat and ecology:** No information available. **Remarks:** Vestigial eyes under the skin. Depigmented. Scaleless. Precise relationship with other members of the genus *Astroblepus* has yet to be established.

#### Family: Sternopygidae

This is a family made up of 15 species found in the freshwaters of South America. They have an elongated, compressed body. Like other members of the order Gymnotiformes, they possess electric organs that are the result of transformed muscles. They use these organs to search for food, obstacles, other fishes (electrogenic or not) and for defense. They are mainly nocturnal fishes many of which are found only in the deep waters of major rivers of the Amazon basin (Nelson 1994). These characters could be considered preadaptations to the hypogean environment. Only one hypogean species has been described so far.

61. *Eigenmannia vicentespelaea* Triques, 1996. **Common name:** None given. **Etymology:** *vicente* (L)

from the name of the cave; *spelaea* (L) cave. **Major synonyms:** None. **History:** First collected by P. Slavec in July 1978. **Distribution:** Brazil, Goiás state, Rio Sao Vicente system, Rio Tocantins basin, at Sao Domingos, Gruta (cave) Sao Vicente II (13°35'00" S, 46°22'30" W). **Habitat and ecology:** No information available. **Remarks:** The main difference between this species and other members of the same genus is its reduced eyes which are covered by thick skin. It is somewhat depigmented. The body is covered by uniformly cycloid scales whose size decreases from lateral line to dorsal and ventral regions. Scales in the dorsal and ventral regions are two or three times smaller in diameter than those near the lateral line. It is not known whether this fish utilizes its electric organs in the hypogean environment. Even if this was the case, and despite its obvious usefulness in this habitat, this cannot be considered a phylogenetic novelty since this is a character shared by all members of the order Gymnotiformes.

Family: Amblyopsidae

This is a family of freshwater fishes found in the southern and eastern United States. It is composed of six species, four of which are clearly troglomorphic; one is a troglaxene (facultative cavernicole) and one is found in swamps. Scales are cycloid but head is naked. Eyes range from small to vestigial. They have rows of sensory papillae on the head, body, and tail (Nelson 1994). The fact that the only epigeal species of the family lives in dark swamp waters, one is a facultative cavernicole, and the other four are troglomorphic species makes this family the archetypical hypogean fish group.

62. *Amblyopsis rosae* (Eigenmann, 1897). **Common name:** Ozark cavefish (E). **Etymology:** *rosae* (L) after C.H. Eigenmann's wife and ichthyologist Rosa Smith. **Major synonyms:** *Typhlichthys rosae*, original description; *Troglichthys rosae* (Eigenmann, 1899). **History:** First reported from specimens collected from caves near Sarcoxie, Missouri by Garman (1889) as *Typhlichthys subterraneus*. The description was first published by Eigenmann (1897) with brief characterization involving eyes, and then described in more detail in Eigenmann (1898). **Distribution:** U.S.A., it is presently known from 41 caves in the Ozark Plateau, distributed over seven counties in three states, northwestern Arkansas, northeastern Oklahoma, and in the southern corner of Missouri (ca. 36°53' N, 95°03' W).

The verified historic range was larger (Romero 1998a). **Habitat and ecology:** Found mostly in small cave streams with chert or rubble bottom. Also occasionally found in pools over silt and sand bottom. Stomachs examined contained copepods which constituted about 70–90% by volume with the balance being primarily small salamanders, crayfish, isopods, amphipods and young of their own species (Poulson 1963). **Remarks:** Rudimentary eyes hidden under the skin. Depigmented body with few nonfunctional pigmented cells. It is a very old and highly genetically distinct clade of amblyopsid fishes. It has been proposed that there are two subspecies of this fish: *A. rosae whitae* for the White River drainage and *A. rosae arkansasus* for the Middle Arkansas River drainage (Romero op. cit.).

63. *Amblyopsis spelaea* DeKay, 1842. **Common name:** northern cavefish (E). **Etymology:** *amblyus* (Gr) blunt, point taken off; *ops* (Gr) eyes; *spelaea* (L) cave. **Major synonyms:** Originally described as *Amblyopsis spelaeus*. **History:** This was the first troglitic species of fish ever described in the scientific literature. **Distribution:** U.S.A., in about 2500 caves in Kentucky and about 1800 caves in southern Indiana (ca. 37°–39° N, 85°–87° W). Its distribution may be limited by competition with another amblyopsid cavefish, *Typhlichthys subterraneus*. **Habitat and ecology:** Found only in caves and subterranean passages of well-developed karst terrain whose water comes from the precipitation diverted underground through sinkholes and sinking streams. It is most often found in caves with uniform silt-sand substrates. It is a top predator (Romero & Bennis 1998). **Remarks:** Rudimentary eyes hidden under the skin. Body depigmented with non-functional pigment cells. It has small cycloid scales. It has a well-defined annual cycle: breeding occurs during high water from February to April, the females carry the eggs in their gill cavities until hatching and carry the young until they lose their yolk sacs, a total period of 4–5 months, then the young appear in late summer and early fall. Low reproductive rate. It is scotophilic (Green & Romero 1997).

64. *Chologaster agassizii* Putnam, 1872. **Common name:** spring cavefish (E). **Etymology:** *agassizii* (L) after Louis Agassiz who allowed Putnam to study the specimens. **Major synonyms:** *Forbesella agassizi* (Page & Burr, 1991), *Forbesichthys agassizi* (Boschung, 1992, Etnier & Starnes, 1993).

Preoccupied by *Forbesella* in tunicates, replaced by *Forbesichthys* Jordan, 1929. **History:** First collected in a well in Lebanon, Tennessee, and presented to the Museum of Comparative Zoology at Harvard, by J.M. Safford in January 1854. **Distribution:** U.S.A., central and western Kentucky (west to Tennessee River) to southern central Tennessee; west across southern Illinois to southeastern Missouri (ca. 35°00'–37°30' N, 86°–92° W). **Habitat and ecology:** Occurs in springs and caves (but almost always near surface). Lives underground but emerges above ground in springs (Page & Burr op. cit.). **Remarks:** Active in springs at night and usually retreats underground during the day. The few individuals which venture into the spring portions of their habitat may show strong rheotaxis for half to one-minute periods but usually show strong thigmotaxis and hide under rocks or debris (Poulson 1963). Feeds at night on amphipods, midge larvae, tiny worms and microcrustaceans. Fecundity averages about 100 eggs per female (Etnier & Starnes op. cit.).

65. *Speoplatyrhinus poulsoni* Cooper & Kuehne, 1974. **Common name:** Alabama cavefish (E). **Etymology:** *speos* (Gr) cave; *platys* (Gr) flat; *rhinus* (Gr) nose, referring to the greatly flattened snout; *poulsoni* (L) after American cave fish researcher T.L. Poulson. **Major synonyms:** None. **History:** Captured by J.E. Cooper and his spouse on 19 March 1967 while collecting crayfish in Kay Cave, Alabama. **Distribution:** U.S.A., Alabama, apparently restricted to Key Cave, Lauderdale county, in the north bank of the Tennessee River. **Habitat and ecology:** The habitat is mostly lacustrine (lentic, phreatic groundwater) (for more details see Romero 1998c). Population is estimated to be no more than 100 individuals, which would make of this one the most endangered fish species in the world. **Remarks:** No externally visible eyes. Body depigmented with few scattered non-functional melanophores. Body covered by embedded cycloid scales.

66. *Typhlichthys subterraneus* Girard, 1859. **Common name:** southern cavefish (E). **Etymology:** *typhlops* (Gr) blind, *ichthys* for iktus (Gr) fish; *subterraneus* (L) underground. **Major synonyms:** *Typhlichthys wyandotte* (Eigenmann, 1905), *T. osborni* (Eigenmann, 1905), *T. eigenmanni* (Hubbs, 1938). **History:** The first specimen was taken from a well near

Bowling Green, Warren Co., Kentucky, and sent to the Smithsonian Institution by J.E. Younglove. **Distribution:** U.S.A., subterranean waters in two major disjunct ranges being separated by the Mississippi River, Ozark Plateau of central and southeastern Missouri and north-eastern Arkansas, and Cumberland and Interior Low plateaus of northwest Alabama, northwest Georgia, central Tennessee and Kentucky and southern Indiana (ca. 37°00' N, 86°29' W). **Habitat and ecology:** Mostly lentic but also in pools of streams at or near water table (for more details see Romero 1998b). **Remarks:** Rudimentary eyes hidden under the skin. Body depigmented with few non-functional pigment cells. Scales minute and embedded. It does not respond to light (Green & Romero 1997).

Family: Bythitidae

This is a family composed of about 90 species of mostly marine fishes with a few representatives living in brackish and fresh waters. Their distribution includes the Atlantic, Indian, and Pacific Oceans. They usually have scales and the swimbladder is present. Their opercles usually have a strong spine. All members of this family are viviparous (Nelson 1994). They have no characters that can be labeled as preadapted to the hypogean environment, yet seven species belonging to two genera of the family are hypogean. Of the six species of *Lucifuga*, five are hypogean. *Lucifuga* is divided into two subgenera; the difference between the two is that *Lucifuga* (*Lucifuga*) has palatine bones but without teeth with pectoral fin rays numbering 12–14, usually 12–13, while *Lucifuga* (*Stygicola*) has palatine teeth and pectoral fin rays numbering 15–20. The species of this genus need to be studied using genetic techniques. Given that some of these species can be found together as well as the large overlap of characters among them, it raises questions of whether they represent just populations of no more than two species. Hybridizations may also occur. Until these species are studied from a population genetics perspective, rather than purely morphological, we will not know for sure. Of the five species of *Ogilbia*, two are hypogean.

67. *Lucifuga* (*Lucifuga*) *subterraneus* Poey, 1858. **Common name:** Cuban cusk-eel (E). **Etymology:** *fugere lucem* (L) because it is photophobic; *subterraneus* (L) underground. **Major synonyms:** None. **History:** The first person to report this fish was Tranquilino Sandalio de Noda in 1831, which predates the first reports of *Amblyopsis spelaea*. Through him and

others, Poey secured the specimens he used in his first published description (Romero 2001). **Distribution:** Cuba, in several anchialine caves of the Pinar del Rio and Habana provinces (ca. 21°50' N, 84°57' W). **Habitat and ecology:** In caves and sink-holes formed by solution of underlying limestone. Frequently found syntopically with *L. dentatus*. It can tolerate brackish waters. It feeds on cirrolanid isopods. **Remarks:** Eyes poorly developed and not externally visible in many preserved specimens. Yellowish-white pigmentation. The body is covered with small, imbricate scales.

68. *Lucifuga (Lucifuga) teresinarum* Díaz Perez, 1988. **Common name:** None given. **Etymology:** *teresinarum* (L) after Maria Teresa del Valley Portilla and Maria Teresita de la Hoz Gonzalez, both faculty at the Universidad de la Habana. **Major synonyms:** None. **History:** Both the holotype and the paratype were captured on 20 October 1986 by A. Montoto Lima and E. García Machado, both skin divers. **Distribution:** Cuba, Habana province, Cuevas de Ashton (Cueva de la Lechuza and Cueva Baño II), Barrios de las Cañas Artemisa (ca. 22°50' N, 82°40' W). **Habitat and ecology:** In the Cueva de la Lechuga it is found with isopods and introduced guppies. In the Cueva Baño II is found with *L. subterraneus* and *L. dentatus* as well as several species of crustaceans. This fish species is prey of crustaceans, *Epilobocera* sp. **Remarks:** Eyes not visible externally. Depigmented. Cycloid scales on parts of the body. It has a number of characteristics that place it as a composite of *L. (L.) subterraneus* (upper profile of the head, lack of palatine teeth, number of pectoral rays) and *L. (S.) dentatus* (free caudal fin and male intromittent organ).

69. *Lucifuga (Stygicola) dentatus* Poey, 1858. **Common name:** toothed Cuban cusk-eel (E). **Etymology:** *dentatus* (L) with teeth. **Major synonyms:** *Stygicola dentatus* (original description). **History:** Same as for *L. (L.) subterraneus*. **Distribution:** Same as for *L. (L.) subterraneus* (ca. 21°50' N, 84°57' W). **Habitat and ecology:** Same as for *L. subterraneus*. Found syntopically with *L. (L.) subterraneus* and *L. (L.) teresinarum*. Feeds on cirrolanid isopods. **Remarks:** Eyes not externally visible. Depigmented. Viviparous.

70. *Lucifuga (Stygicola) simile* Nalbant, 1981. **Common name:** None given. **Etymology:** *simile* (L) because of its intermediate features between *L. subterraneus* and *L. dentatus*. **Major synonyms:** None.

**History:** Collected by C. Jubertie on 7 November 1970. **Distribution:** Cuba, Matanzas province, Grieta Punta de Guana, ca. 100 m from shoreline of Atlantic Ocean (ca. 23°04' N, 81°35' W). **Habitat and ecology:** Found in a sinkhole near the ocean. The only stomach contents reported so far for this species have been plant remains. **Remarks:** Completely depigmented, 57–60 anal rays. This species has palatine teeth as the other representatives of the subgenus *Stygicola*, but at the same time its caudal fin is confluent with both dorsal and anal fins, which is unique to *L. subterraneus*.

71. *Lucifuga (Stygicola) spelaotes* Cohen & Robins, 1970. **Common name:** New Providence cusk-eel (E). **Etymology:** *spelaotes* (Gr) cave dweller. **Major synonyms:** None. **History:** The first specimens were collected by Carleton Ray on 24 October 1967. **Distribution:** Bahamas, New Providence Island, Mermaid's Pool, SW Nassau (ca. 25°05' N, 77°20' W). **Habitat and ecology:** This fish lives in anchialine caves (Illife 1992) on several Bahamian Islands. Some of them (e.g., Mermaids Hole, Uncle Charlie's Blue Hole) are typical inland holes of the cenote type, circular openings between 30 and 250 m across and from 2 to 110 m depth. **Remarks:** Eyes not very well developed and small. The entire body is covered by small, rounded imbricate scales. It has more coloration than *L. dentatus* and seems more primitive than *L. dentatus*.

72. *Ogilbia galapagosensis* (Poll & Leleup, 1965). **Common name:** Galapagos cuskeel (E). **Etymology:** *galapagosensis* (L) because it is found in the Galápagos Islands. **Major synonyms:** *Caecogilbia galapagosensis* (original description). **History:** Collected on 4 December 1964 by A. De Roy and N. Leleup. **Distribution:** Chile, Galápagos Archipelago, Santa Cruz Island (ca. 1°00' S, 90°55' W). **Habitat and ecology:** In crevices of a lagoon. Rare and difficult to observe (Illife 1991). **Remarks:** Eyes and pigmentation reduced and variable. However, in the pictures of this fish (Allen & Robertson 1994) examined by us there is no noticeable difference between *O. galapagosensis* and other species of the same genus living in the same area. It has small scales. Hardly a 'cave' fish, despite the fact that it is usually listed as such.

73. *Ogilbia pearsei* (Hubbs, 1938). **Common name:** Dama ciega blanca (S). **Etymology:** *pearsei* (L) after A.S. Pearse who collected the first specimens. **Major synonyms:** *Typhlias pearsei* (original description),

*Typhliasina pearsi* (e.g., Wilkens 1973, Chumba-Segura 1983). **History:** Collected by Pearse on 22 June 1936. **Distribution:** Mexico, Yucatán peninsula (see Chumba-Segura 1983 for distributional map) (ca. 20°40' N, 88°32' W). **Habitat and ecology:** Stable environments, clear waters. Does not seem to be very abundant (Chumba-Segura op. cit). **Remarks:** Eyes and pigmentation variable. Small scales covering only parts of the body. Sex ratio may be skewed towards females.

Family: Poeciliidae

This family is represented by about 300 species of freshwater and brackish water fish found from eastern United States to South America and in Africa, including Madagascar (Nelson 1994). No characters that could be assigned as preadapted. Only one hypogean species.

74. *Poecilia mexicana* Steindachner, 1863. **Common name:** cave shortfin molly (E). **Etymology:** Not applicable. **Major synonyms:** *Poecilia sphenops* (Valenciennes, 1846), *Mollienisia sphenops* (Regan, 1913), *Mollienisia mexicana* (Hubbs, 1961). **History:** The first cave population was described by Gordon & Rosen (1962). **Distribution:** Mexico, Estado de Tabasco, Cueva de las Sardinias, near Tapijula Village, about 26 km south of Teapa (ca. 18°51' N, 97°08' W). **Habitat and ecology:** The environment is a calcium sulfate stream. **Remarks:** There is a lot of variation in the troglomorphic characters: the deeper you go into the cave, the more the eyes are reduced in size and the lower the pigmentation, while there is an increase in the thickness of the lips of the mouths (Parzefal 2001).

Family: Synbranchidae

This family is made up of about 17 species of freshwater and occasionally brackish water fishes. Found in tropical and subtropical waters in Asia, Indo-Australian Archipelago, West Africa (Liberia), Mexico, Central and South America. They are eellike fishes with no pectoral or pelvic fins; rudimentary dorsal and anal fins; and a caudal fin that is small or rudimentary, or lacking altogether. Scales are absent or confined to the caudal region. They have small eyes and lack swimbladders or ribs. Mostly air breathers. Many are burrowers (Nelson 1994). All these characters can be considered preadaptive to the hypogean environment.

There are two genera with two species each that are hypogean. *Ophisternon* is a genus of six species of circumtropical distribution with a disjunct distribution of species; they all lack scales. *Monopterus* is an Old World genus represented by seven species that also lack scales; two of those species are hypogean. The contention by Galán (1982, 1995) that *M. boueti* was found in caves is erroneous. Given the geographic proximity of the two hypogean species of *Monopterus*, it would be interesting to investigate the genetic relationships between both as well with their putative ancestor *M. albus*. A depigmented individual of *Synbranchus marmoratus* was collected in a cave in northeastern Venezuela in 1979 (Galán 1982), but this fish recovered its pigmentation when exposed to light. Further studies in this locality are needed in order to confirm the troglomorphic nature of this potential hypogean population.

75. *Monopterus (Monopterus) eapeni* Talwar in Talwar & Jhingran, 1991. **Common name:** Malabar swampeel (E). **Etymology:** *eapeni* (L) after K.C. Eapen, who first described the species under a preoccupied name. **Major synonyms:** *Monopterus indicus* (Eapen, 1963). Secondarily preoccupied in *Monopterus* by *Amphipnous indicus* Silas & Dawson, 1961, replaced by *Monopterus eapeni* Talwar, 1991. **History:** No information available. **Distribution:** India, Kerala state, well at Kottayam (9°30' N, 76°33' E). **Habitat and ecology:** No information available except that another troglomorphic fish, *Horaglanis krishnai*, is found in the same well. **Remarks:** Sunken eyes. Scaleless. It may have derived from *M. albus*.

76. *Monopterus roseni* Bailey & Gans, 1998. **Common name:** None given. **Etymology:** *roseni* (L) after Donn E. Rosen, an American ichthyologist. **Major synonyms:** None. **History:** Collected in July 1986 by Carl Gans, S.K. Saraswat and C. Rajasunderam. **Distribution:** India, Kerala state, from a well, Periyam village (10°38' N, 76°22' E). This location is about 102 km slightly west of north from Kottayam, the type locality of *M. eapeni*. **Habitat and ecology:** Collected in the village water supply, 50 m a.s.l. **Remarks:** Blind. Depigmented. Scaleless. The non-troglomorphic differences between these two species are mostly in body proportions and number of vertebrae.

77. *Ophisternon candidum* (Mees, 1962). **Common name:** blind cave eel (E). **Etymology:** *candidum* (L)

whitish, for the pale appearance of the skin. **Major synonyms:** *Anommatophasma candidum* (original description). **History:** First observed by Alf Snell who mentioned the existence of a 'blind eel' sometime in 1959, and in that year A.N. Douglas and G.F. Mees collected the first specimen. **Distribution:** Australia, western and northeastern coastal plain of the Cape Range peninsula. Found in 11 locations (two now destroyed) in numbers ranging from one to three individuals (for a distributional map see Humphreys 1999) (ca. 22°07' S, 113°57' E). **Habitat and ecology:** In wells, sinkholes, and caves, and possibly in groundwater. This species feeds on invertebrates, both hypogean and epigean, that accidentally fall into their habitat (Humphreys & Feinberg 1995). **Remarks:** No externally visible eyes. Whitish coloration in the skin (Romero & Vanselow 2000b). Scaleless. It may have derived from *Synbranchus bengalensis*, the only other synbranchid known to occur in Western Australia.

78. *Ophisternon infernale* (Hubbs, 1938). **Common name:** blind swamp eel (E), anguila ciega de los cenotes (S). **Etymology:** *infernale* (L) from hell (Hubbs liked to name cave fishes with diabolic names based on the idea of hell being underground; see etymology for *Satan eurystomus*). **Major synonyms:** *Pluto infernalis* (original description); *Furmastix infernalis* (Whitley, 1951b); *Synbranchus infernalis* (Mees, 1962). **History:** The holotype was collected by A.S. Pearse on 7 July 1936. **Distribution:** Mexico, in the cenotes of central and northern Yucatan peninsula (see Chumba-Segura 1984 for distributional map) (ca. 20°40' N, 88°30' W). **Habitat and ecology:** Found in shallow waters of sinkholes with sediments that are nutrient-rich. **Remarks:** No externally visible eyes. Depigmented. Scaleless. Most likely is derived from *Synbranchus marmoratus*.

Family: Eleotridae

This is a family of mostly tropical and subtropical fishes, both marine and freshwater, represented by about 150 species (Nelson 1994). No particular characteristics that could be seen as preadapted.

79. *Milyeringa veritas* Whitley, 1945. **Common name:** blind cave gudgeon (E). **Etymology:** *Milyeringa* (L) after Milyering, Yardie, Western Australia, the type locality; *veritas* (L) true, 'because, like Truth, it was found at the bottom of a well' (Whitley 1951a). **Major synonyms:** None. **History:** The first twelve

specimens were collected from a freshwater well by its owner, Eric Payne, on 18 October 1944. It is believed that the existence of this fish was known by the locals since the 1920's. **Distribution:** Australia, western and northeastern coastal plain of the Cape Range peninsula and Barrow Island. Found in 19 locations (now absent from two) in numbers of up to more than 100 individuals (Humphreys 2001) (ca. 22°00' S, 114°00' E). **Habitat and ecology:** In wells, sinkholes, caves, and bores and probably widely in the anchialine and fresh groundwater. It is sympatric with *Ophisternon candidum* but seems much more abundant. **Remarks:** Eyes not externally visible. Whitish coloration in the skin. Scales are reduced and entirely absent from the head; there are about 28 rows in a longitudinal line. *M. veritas* closest affinity is possibly with the eleotrid genus *Butis*, a mangrove dwelling genus of brackish and freshwaters on the Indo-Australian Archipelago (Romero & Vanselow 2000a).

80. *Oxyeleotris caeca* Allen, 1996. **Common name:** ihaaribi (blind, in Yagi language). **Etymology:** *caeca* (L) blind. **Major synonyms:** None. **History:** Rumors of the existence of this fish date back to 1978 but it was not captured until June 1995 by inhabitants of Kafa Village. **Distribution:** Papua New Guinea, creek near Kafa, tributary of the Mubi River, upper Kikori River system (ca. 6°34'30" S, 143°29'30" E). **Habitat and ecology:** In a creek connected to a small cave 100–200 m upstream, at an elevation of 650 m a.s.l. **Remarks:** Eyes not externally visible. Mostly depigmented except for the dorsal region. Most of the scales embedded. Description based on a single specimen. Seems to be closely related to *O. fimbriata*, one of the most widely distributed gudgeons in New Guinea and the only freshwater-restricted member of the genus occurring on both sides of the Central Dividing Range.

81. *Typhleotris madagascariensis* Petit, 1933. **Common name:** toho (in Mihafale). **Etymology:** *typhlos* (Gr) blind; *eleotris* (L) because of its relation to the genus *Eleotris*; *madagascariensis* (L) after the island where it was found. **Major synonyms:** None. **History:** Collected by H. Perrier de la Bâthie at an unspecified date. **Distribution:** Madagascar, province of Toliara: south of Onilahy River, at Mitoho caves, underground waters in Mahafaly, ca. 1 km north of the natural reserve of Lake Tsimanampetsotsa (ca. 24°08' S, 43°48' E). **Habitat and ecology:** In underground lakes below

what is now a desert where it feeds on crustaceans and insects. **Remarks:** Sunken eyes. Variable levels of depigmentation (Angel 1949). Degenerated ctenoid scales (Poisson & Besairie 1947).

82. *Typhleotris pauliani* Arnoult, 1959. **Common name:** None given. **Etymology:** *pauliani* (L) after R. Pauliani who secured the first specimens. **Major synonyms:** None. **History:** Pauliani collected the first specimens in July 1956. **Distribution:** Madagascar, Andalambezo region near Morombe, north of Onilahy River (ca. 23°00' S, 44°30' E). **Habitat and ecology:** In underground lakes below what is now a desert where it feeds on bat guano and aquatic insects. **Remarks:** No externally visible eyes. Depigmented. Irregular (degenerated?) scales that sometimes look cycloid, sometimes ctenoid.

#### Family: Gobiidae

This is a very large family (possibly >2000 spp.) of mostly marine and brackish species. Mostly of small size, they tend to be cryptic bottom dwelling carnivores feeding on small benthic invertebrates. Very common in fresh waters on oceanic islands (Nelson 1994). Thus, it is not surprising that all four hypogean species described thus far are from islands: two from Japan, one from the Philippines and one from Madagascar.

The two species of *Luciogobius* seem to be valid based on the differences in their meristic, nontrogomorphic differences and allopatry; both of them most probably descended from *Luciogobius guttatus*. The third species also seems to be valid: the monotypic genus *Caecogobius* does not appear to be related to any other extant species. More information is needed regarding the fourth, *Glossogobius ankaranensis*, given the fact that it has been found syntopically with the congeneric *Glossogobius callidus*.

83. *Caecogobius cryptophthalmus* Berti & Ercolini, 1991. **Common name:** None given. **Etymology:** *caeco* (L) blind; *gobius* (L) for its relationship to species of the genus *Gobius*; *crypto* (L) hidden; *ophthalmus* (L) eyes. **Major synonyms:** None. **History:** The first four specimens were collected by members of the Federazione Speleologica Veneta in January and February 1987. **Distribution:** Philippines, Samar Island, Calbiga Cave system (12°00' N, 125°00' E). **Habitat and ecology:** No information available. **Remarks:** No externally visible eyes. Strongly

reduced pigmentation. Phylogenetic relationships are unknown.

84. *Glossogobius ankaranensis* Banister, 1994. **Common name:** None given. **Etymology:** *ankaranensis* (L) after the region of Ankarana where this fish was first collected. **Major synonyms:** *Gobius ankaranensis* (Wilson, 1996). **History:** First collected by Jane Wilson and her colleagues in 1986. **Distribution:** Madagascar, Ankarana reserve in a subterranean river (see Wilson op. cit. for a map of the area) (ca. 12°50' S, 49°10' E). **Habitat and ecology:** In a cave where they feed on blind and eyed shrimps. They may also feed on insects and bat guano. It is found syntopically with eyed *Glossogobius callidus*. **Remarks:** Eyes reduced to small spots. Body depigmented. Thin and weak ctenoid scales.

85. *Luciogobius albus* Regan, 1940. **Common name:** dôkutsu-mimizuhaze (J), cave earthworm goby (E). **Etymology:** *albus* (L) white, referring to the color of the skin. **Major synonyms:** None. **History:** First reported by Masatoshi Iwata in 1934 (Torii 1951). Based on two specimens of *Luciogobius guttatus guttatus* of Tomiyama (1936, p. 51, figure 10C). **Distribution:** Asia, Japan, Prefectures of Wakayama, Kochi, Shimane, Nagasaki and the Gotô islands (Masuda et al. 1984). Originally collected in the cave of Daikon-zima in Simani-ken (ca. 32°–36° N, 128°–136° E; but not throughout the entire square defined by these coordinates). **Habitat and ecology:** Inhabits underground waters near the sea. **Remarks:** Vestigial eyes. Depigmented (pinkish due to the color of the blood). Like *L. pallidus*, it lacks free rays on the pectoral fin.

86. *Luciogobius pallidus* Regan, 1940. **Common name:** ido-mimizuhaze (J), well earthworm goby (E). **Etymology:** *pallidus* (L) for pale referring to the color of the skin. **Major synonyms:** None. **History:** First reported by Masatoshi Iwata in 1934 (Torii 1951). Based on artesian well specimens of *Luciogobius guttatus guttatus* of Tomiyama (1936, p. 51, figure 10D). **Distribution:** Asia, Japan, prefectures of Mie, Wakayama, Kochi, Ehime, Kumamoto, and Yamaguchi (Masuda et al 1984, Uéno & Morimoto 1970). Original specimens collected from an artesian well (ca. 32°–36° N, 128°–136° E; but not throughout the entire square defined by these coordinates). **Habitat and ecology:** Inhabits underground waters near

the sea. **Remarks:** Reduced, sunken eyes. Slightly depigmented. Like *L. albus*, it lacks free rays on the pectoral fin.

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