April 1990 *Asiatic Herpetological Research* Vol. 3, pp. 37-45

Studies on Hynobiid Salamanders, With Description of a New Genus

KRAIG ADLER[1] AND ERMI ZHAO[2]

[1]*Cornell University, Section of Neurobiology and Behavior, Mudd Hall, Ithaca, New York 14853, USA*
[2]*Chengdu Institute of Biology, P.O. Box 416, Academia Sinica, Chengdu, Sichuan, China*

Abstract. -The types of *Hynobius chinensis* Günther, 1889, were reexamined and are redescribed; the known range in China is mapped. *Hynobius yiwuensis* Cai, 1985, is relegated to the synonymy of *chinensis*. *Hynobius retardatus* Dunn, 1923, of Japan, differs markedly from all other *Hynobius* and is here placed in a new genus (*Satobius*). The new genus is characterized and compared to the other eight genera of hynobiids.

Key words: Amphibia, Caudata, salamanders, Hynobiidae, *Hynobius*, *Satobius*, China, Japan.

Introduction

As part of our work on a handbook of Chinese amphibians and reptiles, we have had to re-study certain Chinese hynobiid salamanders described in the literature and consider their relationships to extralimital species, especially those native to Japan. This paper is a result of these current investigations and concerns the identity and distribution of *Hynobius chinensis* Günther, 1889, the taxonomic status of *H. yiwuensis* Cai, 1985, and the proper generic status of a Japanese species, *H. retardatus* Dunn, 1923.

Results and Discussion

1. Identity and Distribution of Hynobius chinensis *Günther, 1889*

In 1889, Albert Günther described *Hynobius chinensis* from two specimens collected in Hubei Province. Previously, *Hynobius* species had been known only from Japan and Korea, thus Günther's records from central China were quite isolated from the ranges of the then-known species. Since 1889, however, no other specimens of *Hynobius* have been reported from Hubei, despite much collecting there, leading Zhao and Hu (1983, English translation 1988) to suggest that either the locality data for Günther's specimens are wrong or that *chinensis* is not, in fact, a species of *Hynobius*.

We have examined Günther's two syntypes (British Museum [Nat. Hist.] numbers 1946.9.6.54 and .55, formerly catalogued as 1889.6.25-26). Both are females, as judged from the external appearance of their cloacae (the specimens are too hardened to examine internally).

Based on our examination of the types, *H. chinensis* is a true *Hynobius* as defined by Zhao and Hu (1984, English translation 1988). Since Günther's (1889) original description is brief, we provide the following redescription: Head large, its length from snout to gular fold longer than its width (15.2 x 10.6 mm; 12.8 x 9.5 mm); tip of snout rounded. Eyes are dorsolateral in position, slightly protruded; diameter of eye shorter than the distance from its anterior corner to the tip of snout; pupil rounded. Nostril between eye and tip of snout, and slightly closer to the latter; distance between nostrils slightly larger or equal to the distance between eyes. A "V"-shaped bulge on top of head. No labial fold. An indistinct gular fold. Angle of jaw just behind the posterior corner of eye. Both maxilla and mandible with tiny teeth. Tongue elliptical, large, almost covering the entire floor of mouth. Series of vomerine teeth "ʅʃ"-shaped, the outer branch comprising 6-9 and inner branch 11-15 teeth; the angle formed by outer and inner branches just beyond the anterior margin of choanae; inner branches much longer than the outer ones and extending backwards to the level of the middle of eye ball; the

FIG. 1. Map of central China illustrating all known localities for *Hynobius chinensis*. The inset shows the location of the more detailed map. Locality records in Zhejiang and Fujian provinces are noted by solid circles; the star-shaped symbol in Hubei Province is the type locality (Yichang). Other localities mentioned in the text are noted by hollow circles; some major cities are added for reference. The river mapped in Sichuan Province (upstream from Chongqing) that is continuous with the Chang Jiang (Yangtze River) is known variously as the Dajin, Dadu, and Min.

posterior ends of two inner branches close but do not meet at midline. Body short and stout; limbs well developed and tips of digits meet when limbs adpressed. Costal grooves 11, very prominent and meeting on ventral midline. Fingers four, 2-3-4-1 in order of length, the first finger almost equal in length to the fourth. Toes five, 3-4-2-5-1 in order of length. Digits flattened, free; without palmar and tarsal tubercles; no cornified covering on palms, tarsa, fingers, and toes. Tail length shorter than snout-vent length; tail compressed, but cylindrical at the base and pointed at the end, without crest on ventral edge and only slightly so on its dorsal side. Skin smooth. The dimensions cannot be re-measured due to the specimens' hardened condition; only head length and width can be given (above). Further details about the types are given in Zhao and Adler (1989). Cai et al. (1985) have described the embryonic development and larval features of *chinensis*.

Lectotype: We hereby designate BMNH 1946.9.6.54 as the lectotype of *H. chinensis*.

Type Locality: Günther (1889) stated that "two specimens were collected by Mr. Pratt at Ichang [=Yichang]." (Here and below, modern spellings of place names, where different, are given in brackets. All localities are mapped in Fig. 1.) A. E. Pratt explored China during 1887-1890 and summarized his experiences in a book (1892). As Günther noted in the appendix to Pratt's book, herpetological specimens were collected at various localities in Hubei and Sichuan provinces, and he repeated the "Ichang" locality for the two *Hynobius* specimens. Pope and Boring (1940), however, stated that "Mell ('29) claims that Pratt's records from 'Ichang' were collected in the mountains south of the Yangtze River near Changyang." Curiously, no such paper by Mell is listed in the bibliography of Pope and Boring's monograph, nor can we find such a statement in any of Mell's publications, so we are unable to verify the basis of Pope and Boring's information attributed to Mell.

In his book, Pratt (1892) mentioned finding salamanders only twice (pages 179 and 224) but both localities are in Sichuan: a lake above Ta-tsien-lu [=Kangding], at

14,070 feet elevation, and at Kia-ting-fu [=Leshan], both of which are localities far to the west of Yichang (see Fig. 1). Four other new species of reptiles and amphibians were described by Günther in his 1889 paper, all having "Ichang" as their type locality, and for these taxa the locality has never been questioned, to our knowledge. Thus, we are inclined to accept the type locality as stated by Günther, until new evidence comes to hand, although this locality is about 700-900 km west of the other known localities for this species (see Fig. 1 and below).

Distribution: Subsequent to Günther's report, several other specimens of *H. chinensis* have been reported. Here we summarize all known records (see Fig. 1):

Fujian: Kuatun [=Guadun, 27° 42' N 117° 50' E, a town at Mt. Wuyi], Ch'ungan Hsien [=Chong'an County, 27° 46' N 118° 01' E] (Pope, 1931).

Hubei: Ichang [=Yichang, 30° 42' N 111° 17' E] (Günther, 1889).

Zhejiang: Dachen, 29° 28' N 120° 06' E, 140 m, and Chalin, (both in Yiwu County, 29° 18' N 120° 04' E), Zhenhai, 29° 57' N 121° 42' E, and Xiaoshan, 30° 10' N 120° 15' E, (Cai, 1985; types of *H. yiwuensis*); Wenling, 28° 22' N 121° 22' E, 1500 ft., (Boring and Chang, 1933; Chang, 1933).

Boring and Chang's specimens from Zhejiang Province have been examined and their identifications verified. Cai's species, *H. yiwuensis*, is a synonym of *H. chinensis* (see section 2, below). Thus, *chinensis* is the only *Hynobius* found in mainland China, except for two species in the extreme northeast; three other species are endemic to Taiwan.

2. *Taxonomic Status of* Hynobius yiwuensis *Cai, 1985*

Cai (1985) described *Hynobius yiwuensis* as new, based upon a series of adults (16 males, 11 females), juveniles, larvae, and eggs from Zhejiang Province. Unfortunately, he was unable to compare his specimens directly with the types of *H. chinensis*. Based on our comparison with those types, however, we believe that the two taxa are synonymous. We base our conclusion primarily on the six features used by Cai to diagnose his new form.

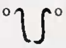
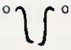
Vomerine Teeth. Cai described the length of the inner branch of vomerine teeth in *yiwuensis* as longer than that of *chinensis*, yet our examination reveals no significant difference. Moreover, the shape of the vomerine teeth series is very similar and the numbers of teeth in both the inner and outer branches are within the same ranges in the two forms.

Head and Body Proportions. Cai stated that in *yiwuensis* the head is much longer than broad, in contrast to Günther's measurements for one specimen in which the length was only slightly greater (11 x 10 mm). Our re-measurement of Günther's specimens, taking snout to gular fold as head length, shows that in both types of *chinensis* the head is much longer than broad (see measurements in section 1, above). Cai also claimed that *chinensis* and *yiwuensis* differ somewhat in body proportions, the latter being less stout. Our comparisons failed to notice significant differences, when relative sizes are taken into account.

Adpressed Limbs. In both types of *chinensis*, the tips of the digits touch when the limbs are adpressed, but Cai's diagnosis states that in *yiwuensis* the tips usually do not touch. However, in Cai's specimens there is variation in this character and in about one third of them the tips of the digits do meet.

Costal Grooves. In his diagnosis, Cai stated that *yiwuensis* has 10 costal grooves, in contrast to *chinensis* which has 11. We have confirmed the presence of 11 in the types of *chinensis*. However, in Cai's type series there are a few individuals having 11 costal grooves, as Cai himself even noted (1985, p. 110). In a series of ten specimens of *chinensis* from Wenling, about 160 km southeast of Cai's type

TABLE 1. Comparison of the genera of hynobiid salamanders. See text for further details.

	*Batrachuperus**	*Hynobius*	*Liua*	*Onychodactylus*	*Pachyhynobius**	*Pachypalaminus**	*Ranodon**	*Salamandrella*	*Satobius*
Distribution	Western China, Afghanistan, Iran	Japan, China, Korea, Mongolia, Eastern Siberia	Central China	Japan, Korea, Northeast China, Eastern Siberia	Eastern China	Japan	Northern China, Siberia	Japan, Siberia to East Europe, Mongolia, Northern China	Hokkaido (Japan)
Number of species	6	21	1	2	1	1	2	1	1
Costal grooves	12-14	11-14	10	13-14	13	13	12	14	11
Costal folds between toe tips of adpressed limbs	-2 to +1	-5 to +3	+1	-2 to 0	-4	-2 to 0	0	-4 to 0	+1 to +4
Tail length vs. head and body	t>h+b or t<h+b	t<h+b	t<h+b	t>h+b	t<h+b	t<h+b	t>h+b	t<h+b	t>h+b
Premaxillary fontanelle	present	absent	present	present	absent	absent	present	absent	absent
Basibranchial radii	present	absent	present	present	present	absent	present	absent	absent
Vomerine teeth (o=position of internal naris)	 or 								
Vomer vs. parasphenoid	sutured	broadly overlaps	sutured	sutured	overlaps	overlaps	sutured	overlaps	sutured, may overlap tip
Lungs	reduced	present	reduced	absent	reduced	present	reduced	present	present
Chromosome number (2*n*)	62, 68	56, 58, 60	64	78	64	58	66	62	40
Larval duration	2-3 years	1 year	2-3 years	2-3 years	?	1 year	2-3 years	1 year	1 year or more
Habitat in non-breeding period	water	land	water	land	water	land	land	land	water or land

**Batrachuperus* includes *Paradactylodon*, *Pachyhynobius* includes *Xenobius*, and *Randon* includes *Pseudohynobius*. According to some authorities *Pachypalaminus* is a synonym of *Hynobius* (Nishio et al., 1987).

locality, the number of costal grooves varied from 10 to 12 (Chang, 1933).

Tail Proportions. Cai noted that the tail of *yiwuensis* is compressed, with fin folds especially distinct in the males, whereas Günther stated that *chinensis* was without a tail crest. Günther did not mention the sexes of his two specimens, which are both females (see section 1), and this was not known to Cai. Thus, we believe that the differences in the tail may be due to sexual dimorphism and, in addition, perhaps also to further elaboration of the crests during the breeding season.

Color Pattern. Günther's description was based on specimens that had been preserved for some time. Moreover, Cai noted that the color pattern changes during the breeding season, when it becomes lighter and mostly green in color. Nevertheless, our comparisons of the two forms do not reveal any striking differences.

Further details of our comparison between the types of *chinensis* and Cai's specimens of *yiwuensis* are given in Zhao and Adler (1989). In summary, we believe that all of these specimens represent a single taxon which, because of the priority of Günther's name, must be designated *Hynobius chinensis*.

3. Generic Status of Hynobius retardatus *Dunn, 1923*

The identity of this Japanese species was first recognized by E. R. Dunn, who briefly characterized it (Dunn, 1923a) and soon described it in more detail (Dunn, 1923b). The animal itself had been known to Japanese biologists since at least 1907 under the names *Hynobius fuscus*, *H. lichenatus*, and *H. nigrescens*. These names, however, are now known to be properly applied to species found elsewhere in Japan (*fuscus* is a synonym of *nigrescens*). Dunn (1923a) noted that *H. retardatus* was a "well-marked species" and, as knowledge of this animal increased in succeeding years, its distinctiveness from other *Hynobius* and hynobiids generally became more apparent.

In 1932, Makino reported that *H. retardatus* has a diploid somatic chromosome number of 40, but since the comparable numbers for most other hynobiids were not known at that time, the full significance of this very low number was not recognized. In fact, *retardatus* has by far the lowest number of chromosomes in the family Hynobiidae (Table 1). Only in 1943, with Sato's magnificent review of Japanese salamanders, in which he included a special comparative study of their chromosomes, could the matter be properly evaluated, and Sato himself (1943, p. 489) suggested that *retardatus* might be worthy of generic rank. Unfortunately, Sato's premature death in August 1945, during the atomic bombing of Hiroshima (for a biography of Sato, see Adler, 1989), prevented him from pursuing this matter. In subsequent years, additional data on anatomy, karyology, and biology have accumulated which further support the separation of *retardatus* into a new genus, which we name:

Satobius, new genus

Type Species: *Hynobius retardatus* Dunn, 1923a.

Content: A single species.

Diagnosis: A genus of hynobiid salamanders (family Hynobiidae) characterized by very long limbs and toes (tips of digits of adpressed limbs overlap +1 to +4 intercostal spaces in adults); a very long tail (in adults, 100 to 118% of head and body length combined); a long neck and small head; no premaxillary fontanelle or basibranchial radii; two short series of vomerine teeth arranged in transverse arcs between the internal nares; vomer sutured to anterior end of parasphenoid; lungs present; diploid (2*n*) chromosome number of 40; larval duration of one year or more (neoteny sometimes occurs); and both terrestrial and aquatic habits in adults during non-breeding season.

These characteristics are discussed below and, for easy access, are tabulated for each of the nine genera of hynobiid salamanders (Table 1).

Costal Grooves. These vertical grooves on the side of the body correspond to the position of ribs and, thus, to trunk vertebrae; generally, the number of costal grooves that can be counted is one less than the number of trunk vertebrae.

The typical number of costal grooves in *S. retardatus* is 11. In the Japanese species of *Hynobius* the modal numbers of grooves range from 11 to 13 (Misawa, 1989) and some mainland species have as many as 14 (Dunn, 1923b). For species in other hynobiid genera, the modal numbers of costal grooves range from 10 to 14.

Adpressed Limbs. As a relative measure of limb length, the minimum distance between the tips of the digits is determined with the limbs adpressed along the sides of the body. Distances are then measured in intercostal spaces, the fleshy folds between adjacent costal grooves.

In metamorphosed adults of *S. retardatus* the intercostal distance between the digits of adpressed limbs is +1 to +4; that is, because the limbs and toes are very long, the digits actually overlap by one to four intercostal spaces. Proportionately, these are the longest limbs found in any member of the entire family. In species of *Hynobius*, this measurement ranges from 5 to +3; among hynobiids other than *Hynobius* and *Satobius*, the longest limbs are found in *Pachypalaminus* (-2 to 0), but the toes are shorter than those of *Satobius*.

Tail. The tail of *S. retardatus*, as measured from posterior angle of the vent, is longer than the combined measurements of head plus body length. In adults, tail length varies from 100 to 118% of head-body length, whereas in all other hynobiids it is shorter except in *Ranodon* (about 100-120% of head-body length) and in *Onychodactylus* (about 100-115%). The tail lengths of *Hynobius* species are significantly shorter than the head-body length (60-80%); only in the adults of *H. nigrescens* does the tail occasionally equal head-body in length. Apparently in all hynobiids, tail length relative to head-body increases with overall size, so the numbers given here are all taken, for comparative purposes, from large adults.

Vomer and Vomerine Teeth. The paired vomer bones (or prevomers for those who deny homology to the vomer of mammals) of the palate bear teeth near their posterior edges. The relationship between the vomers and the parasphenoids lying posterior to them varies among hynobiid genera (Table 1). In *S. retardatus*, the posterior edge of the vomer is sutured to the parasphenoid and overlaps very little, if at all in some specimens, onto the palatal surface of the parasphenoid (Inukai, 1932; Sato, 1943). The two series of vomerine teeth extend broadly between the internal nares in two slight arcs which nearly meet at the midline; the overall length of this patch of teeth along the midline is about 30% of the width of the series.

The general pattern of these teeth is like those in the genera *Onychodactylus* and *Ranodon*, and quite unlike that in *Hynobius* where the vomers (and the vomerine teeth on their posterior surface) extend onto the parasphenoids to a degree varying from species to species. In some *Hynobius* this overlap is small (e.g., *H. leechii* and *lichenatus*) but in most it extends onto the palatal surface for from one-third to as much as one-half the length of the parasphenoids (e.g., *H. formosanus* and *sonani*) (Sato, 1943). Since the vomerine teeth are located on this edge of the vomer, in these *Hynobius* the vomerine series has a pattern wholly unlike that in *retardatus*, beginning at the nares and extending far posteriorly on the palate in the shape of a lyre (see Table 1). In *H. formosanus*, for example, the length of the vomerine teeth along the midline of the palate is fully twice the total width of the two series (versus 30% in *S. retardatus*).

Chromosomes. Makino (1932) was the first to report that *S. retardatus* has a diploid chromosome number of 40, as confirmed by others (Azumi and Sasaki, 1971; Morescalchi, 1975). No other hynobiid is known to have fewer than 56. In Japanese species of *Hynobius*, the so-called pond-type species are $2n=56$ (*retardatus* is a pond breeder) and the mountain brook types are $2n=58$ (except *H. okiensis* where $2n=56$); *H. kimurai* is ordinarily $2n=56$, except in one population ($2n=60$) which may represent a separate species (Morescalchi, 1975; Morescalchi et al., 1979; Ikebe et al., 1989). The Korean *H. leechii* is $2n=56$ (Makino, 1934), but the chromosome number is not known for any of the Chinese species of *Hynobius*.

Recent studies by Japanese and Italian workers show that the karyology of *S. retardatus* is even more different from that of *Hynobius* species than the low number of chromosomes would suggest. The combined lengths of the chromosomes in the genomes of *Hynobius* species and in *retardatus* are nearly equal at the same degree of condensation, and the amount of nuclear DNA is also approximately equal (Morescalchi, 1975). Despite these similarities, there are important differences that set *retardatus* apart from species of *Hynobius*. Kuro-o et al. (1987, as modified in 1989) were able to compare chromosome pairs in four *Hynobius* (3 Japanese and 1 Korean species) and *retardatus*, using the R-banding technique (RBG method), allowing them to identify 18 of 28 pairs in *Hynobius* and 16 of 20 in *retardatus*. Based on this analysis, chromosome pairs 2 and 8 of *retardatus* are not at all represented in the genomes of these *Hynobius* species, whereas pairs 2, 12, 20, and 22, found in all four *Hynobius*, were lacking altogether in that of *retardatus*; other chromosome pairs were completely (11 pairs) or partially (3 pairs) homeologous. To summarize, among these four *Hynobius* species homeologies totalled about 90%, but this value fell to 65% when *retardatus* was included. DNA analysis was also performed by these authors, using highly-repetitive DNAs as probes on Southern blot hybridization, which showed that *retardatus* was distinctively different from the five *Hynobius* species tested (4 Japanese and 1 Korean).

Breeding Biology. The reproductive biology of *S. retardatus* has been studied in detail (Sasaki, 1924; Makino, 1933; Sato, 1989 and references cited therein). The larval period is normally less than a year, but at high elevations can take more than one year. Neotenous individuals are well known (Sasaki, 1924). Adults breed in ponds and are terrestrial during non-reproductive periods. However, unlike species of *Hynobius* which remain on land while not breeding, *retardatus* often visits the water during non-breeding periods (Sasaki, 1924).

Distribution. Satobius retardatus is found only in Hokkaido, the northernmost of the main Japanese islands. No *Hynobius* are known from Hokkaido and, among hynobiids, only *Salamandrella keyserlingii* is found there.

Relationships. Historically, *S. retardatus* has been said to be most closely related to *H. nigrescens* of neighboring Honshu Island, Japan (Sato, 1943). Indeed, the two species are superficially similar in that, as adults, both are blackish in color with little pattern and both possess relatively long tails. However, on closer examination, these two species are fundamentally different. *H. nigrescens* is a large-headed and short-necked species, as are all *Hynobius*, when compared with *S. retardatus*. The skull of *nigrescens*, in particular the vomer-parasphenoid relationship and the pattern of vomerine teeth, are typical of *Hynobius* and unlike the situation in *Satobius*. Furthermore, the number of chromosomes and details of chromosome structure, based on both C-banding and R-banding methods, are distinctly different. In short, we believe that the similarities between *nigrescens* and *retardatus* are due to convergence and do not reflect close phylogenetic relationship.

Several of the diagnostic characteristics of *S. retardatus* are similar to those of members of the *Ranodon* group of hynobiids, which includes *Batrachuperus*, *Liua*, *Onychodactylus*, and *Ranodon* (Zhao and Hu, 1984). The suturing of the vomer and parasphenoid, the pattern of vomerine teeth, and the relative lengths of limbs and tail in *retardatus* are similar to the condition in one or more members of the *Ranodon* group, but in most other respects *Satobius* is clearly a member of the *Hynobius* group of genera: *Hynobius*, *Pachypalaminus* (synonymized with *Hynobius* by Nishio et al., 1987) and *Salamandrella* (for discussion of these two groups of genera, see Zhao and Hu, 1984). Within this group, the closest living relative of *retardatus* may be *H. leechii* of Korea and northeastern China, according to their chromosome structure; indeed, as Ikebe et al. (1989) point out, based on C-banding patterns, *retardatus* is more similar to the northernmost populations of *leechii* rather than those in the southern part of the Korean peninsula.

We suggest that the ancestral stock leading to *S. retardatus* was derived from a *Hynobius*-like ancestor and arrived in Japan from the mainland very early, before the formation of the Tsugaru Strait which later isolated Hokkaido from the southern Japanese islands. *Satobius* differentiated in Japan but was later excluded from the more southern Japanese islands by a later invasion of hynobiids from the mainland. Thus isolated by the Tsugaru barrier, *Satobius* further differentiated, yet retained some of its primitive characters, including a few today found only in the *Ranodon* group.

The long isolation from *Hynobius* has led also to the chromosomal differentiation described earlier (although retaining some similarities to *H. leechii* on the mainland). The great reduction in chromosome number in *retardatus* may be due in part to fusions, since the total composite lengths and DNA content are approximately the same as for the *Hynobius* genome (Kuro-o et al., 1989). However, in view of the many differences based on the C-banding and R-banding studies mentioned above, the karyotype of *retardatus* cannot be explained by a simple mechanism of fusions alone.

Etymology. We take great pleasure in naming this new genus for Ikio Sato (1902-1945), who first recognized its distinctiveness from *Hynobius*. The name *Satobius* is derived in part from the stem of *Hynobius* (*hynis* [or *hynnis*], Greek for plowshare, the cutting part of a plow, and *bios*, life).

Acknowledgments

Our research has been supported by the USA National Academy of Sciences (Committee on Scholarly Exchange with the People's Republic of China). We thank Barry Clarke (British Museum [Nat. Hist.]) and Robert C. Drewes and Jens V. Vindum (California Academy of Sciences) for the loan of specimens. We thank Satoshi Amagai (Cornell University) for some translations of articles in Japanese.

Literature Cited

ADLER, K. (ed.) 1989. Contributions to the History of Herpetology. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology 5:1-202.

AZUMI, J. AND M. SASAKI. 1971. Karyotypes of *Hynobius retardatus* Dunn and *Hynobius nigrescens* Stejneger. Chromosome Information Service 12:31-32.

BORING, A. M. AND T.-K. CHANG. 1933. The distribution of the Amphibia of Chekiang province. Peking Natural History Bulletin 8:63-74.

CAI, C.-M. 1985. [A survey of tailed amphibians of Zhejiang, with description of a new species of *Hynobius*]. Acta Herpetologica Sinica 4:109-114. (In Chinese).

CAI, M.-Z., J. ZHANG, AND D.-J. LIN. 1985. [Preliminary observation on the embryonic development of *Hynobius chinensis* Guenther]. Acta Herpetologica Sinica 4:177-180. (In Chinese).

CHANG, T.-K. 1933. Two new amphibian records from Chekiang. Peking Natural History Bulletin 8:75-80.

DUNN, E. R. 1923a. New species of *Hynobius* from Japan. Proceedings of the California Academy of Sciences, ser. 4, 12:27-29.

DUNN, E. R. 1923b. The salamanders of the family Hynobiidae. Proceedings of the American Academy of Arts and Sciences 58:445-523.

GÜNTHER, A. 1889. Third contribution to our knowledge of reptiles and fishes from the Upper Yangtsze-Kiang. Annals and Magazine of Natural History, ser. 6, 4:218-229.

IKEBE, C., M. KURO-O, T. OHHASHI, H. YAMADA, K.-I. AOKI, AND S.-I. KOHNO. 1989. Evolution of chromosome 10 in ten pond-type *Hynobius* from Korea and Japan, with comments on phylogenetic relationships. Pp. 85-90. *In* M. Matsui et al. (eds.), Current Herpetology in East Asia. Herpetological Society of Japan, Kyoto.

INUKAI, T. 1932. Urodelenarten aus Nordjapan mit besonderer Berücksichtigung der Morphologie des Schädels. Journal of the Faculty of Science, Hokkaido Imperial University ser. 6, 1:191-217.

KURO-O, M., C. IKEBE, AND S. KOHNO. 1987. Cytogenetic studies of Hynobiidae (Urodela). VI. R-banding patterns in five pond-type *Hynobius* from Korea and Japan. Cytogenetics and Cell Genetics 44:69-75.

KURO-O, M., C. IKEBE, R. KATAKURA, Y. IZUMISAWA, AND S.-I. KOHNO. 1989. Analyses of phylogenetic relationships in the genus *Hynobius* by means of chromosome banding and Southern blot hybridization. Pp. 91-94. *In* M. Matsui et al. (eds.), Current Herpetology in East Asia. Herpetological Society of Japan, Kyoto.

MAKINO, S. 1932. The chromosome number in some salamanders from northern Japan. Journal of the Faculty of Science, Hokkaido Imperial University ser. 6 (Zool.) 2:97-108.

MAKINO, S. 1933. [Several ecological observations on *Hynobius retardatus* Dunn]. Shokubutsu oyobi Dobutsu (Botany and Zoology), Tokyo 1:1136-1142. (In Japanese).

MAKINO, S. 1934. The chromosomes of *Hynobius leechii* and *H. nebulosus*.

Transactions of the Sapporo Natural History Society 13:351-354.

MISAWA, Y. 1989. The method of counting costal grooves. Pp. 129-134. *In* M. Matsui et al. (eds.), Current Herpetology in East Asia. Herpetogical Society of Japan, Kyoto.

MORESCALCHI, A. 1975. Chromosome evolution in the caudate Amphibia. Pp. 339-387. *In* T. Dobzhansky et al. (eds.), Evolutionary Biology, vol. 8. Plenum Press, New York.

MORESCALCHI, A., G. ODIERNA, AND E. OLMO. 1979. Karyology of the primitive salamanders, family Hynobiidae. Experientia 35:1434-1436.

NISHIO, K., M. MATSUI, AND M. TASUMI. 1987. The lacrimal bone in salamanders of the genera *Hynobius* and *Pachypalaminus*: a reexamination of its taxonomic significance. Monitore Zoologico Italiano, new ser. 21:307-315.

POPE, C. H. 1931. Notes on amphibians from Fukien, Hainan, and other parts of China. Bulletin of the American Museum of Natural History 61:397-611.

POPE, C. H. AND A. M. BORING. 1940. A survey of Chinese Amphibia. Peking Natural History Bulletin 15:13-86.

PRATT, A. E. 1892. To the Snows of Tibet Through China. Longmans, Green, and Co., London. 268 pp.

SASAKI, M. 1924. On a Japanese salamander, in Lake Kuttarush, which propagates like the axolotl. Journal of the College of Agriculture, Hokkaido Imperial University 15:1-36 (*"Hynobius lichenatus" = Satobius retardatus*).

SATO, I. 1943. [A Monograph of the Tailed Batrachians of Japan]. Nippon Shuppan-sha, Osaka, 520, 7 pages, 31 color plates. (In Japanese).

SATO, T. 1989. Breeding environment and spawning of a salamander, *Hynobius retardatus*, at the foot of Hidaka Mountains, Hokkaido, Japan. Pp. 292-304. *In* M. Matsui et al. (eds.), Current Herpetology in East Asia. Herpetological Society of Japan, Kyoto.

ZHAO, E.-M. AND Q.-X. HU. 1983. [Taxonomy and evolution of Hynobiidae in western China, with description of a new genus.] Acta Herpetol. Sinica 2(2):29-35 (In Chinese). (English translation published in Zhao et al., 1988, Studies on Chinese Salamanders. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology 4: ix, 1-67).

ZHAO, E.-M. AND Q.-X. HU. 1984. [Studies on Chinese Tailed Amphibians.] Sichuan Sci. Tech. Publ. House, Chengdu, (3), 68 pages (In Chinese). (English translation published in Zhao et al., 1988, Studies on Chinese Salamanders. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology 4: ix, 1-67).

ZHAO, E.-M. AND K. ADLER. 1989. [*Hynobius chinensis*, a re-description on its 100th anniversary]. Sichuan Journal of Zoology 8(2):18-20, 1 plate. (In Chinese).