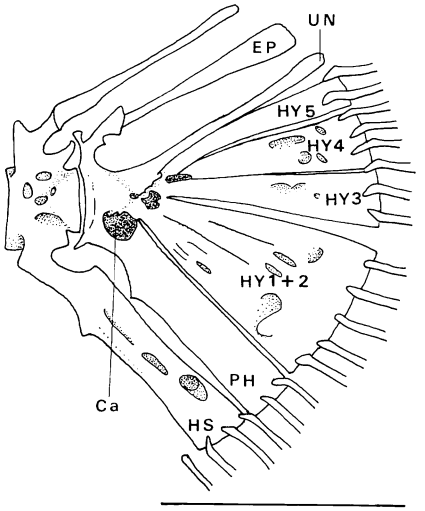

Fig. 29. Caudal skeleton of *Silurus microdorsalis*. Abbreviations as in Fig. 8. Scale bar indicates 1 cm.

Fig. 31. Tip of maxillary barbels in *Silurus soldatovi*. Scale bar indicates 1 cm.

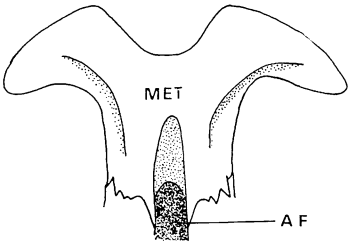

Fig. 32. Dorsal view of mesethmoid of *Silurus soldatovi*. Abbreviations as in Fig. 5.

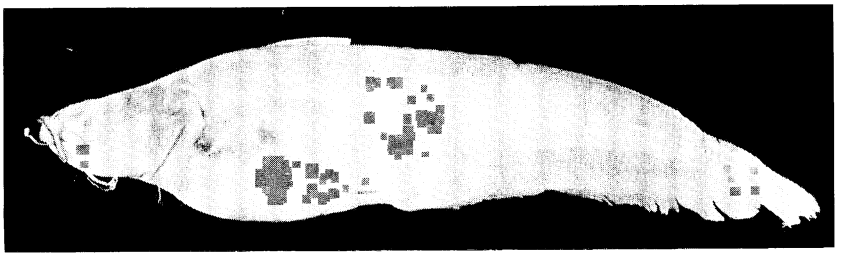

Fig. 30. *Silurus soldatovi*, ZUMT 55084, 249 mm SL.

Silurus soldatovi Nikolsky et Soin, 1948
(Fig. 30)

Silurus soldatovi Nikolsky and Soin, 1948: 1359; Berg, 1949: 474.
Silurus soldatovi soldatovi: Chen, 1977: 208.

No specimen was dissected, but one specimen was skinned in the head region to examine the dorsal view of the skull. Since the adult of this species grows over 1 m, all the specimens observed here were young or juvenile.

Dorsal fin rays 5–6; pectoral fin rays I, 11–14; pelvic fin rays i, 9–11; anal fin rays 78–87; caudal fin rays 7–8+7–8; vertebrae 17, 18+49, 51=67, 68 (2 specimens); branchiostegals 13–16; gill rakers 1–3+8–12.

Lower jaw prominently longer than upper; head 3.75±0.21 in standard length and extremely large; eye with free orbital rim; dorsal surface of body uniformly black and ventral surface white; one obscure white vertical line present along lateral line running along middle of body; two pairs of mandibular barbels; minute papillae clustered on tip of pair of maxillary barbels (Fig. 31); pectoral spine very weak and its anterior surface slightly granulated; vomerine teeth in broad non-separated patch with its posterior margin sharply notched.

Skull: Mesethmoid remarkably broad and its lateral process stout (Fig. 32); prominent sagittal crest rising in posterior part of skull.

Distribution. The Amur River, USSR and the Liao River, China.

Silurus torrentis sp. nov.
(Fig. 33)

Silurichthys leucopodus (not of Fowler, 1939): Wongrat, 1967: 85.

Specimens examined. Holotype—NSMT-P 50234. Adult female from Lampae stream, Khaoluk Village,

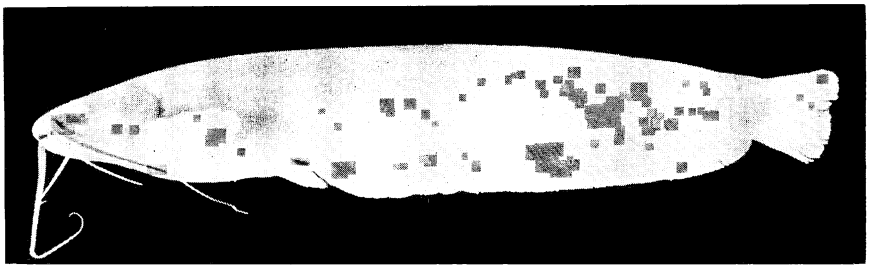

Fig. 33. *Silurus torrentis* sp. nov., NSMT-P 50235, paratype, 148.5 mm SL.

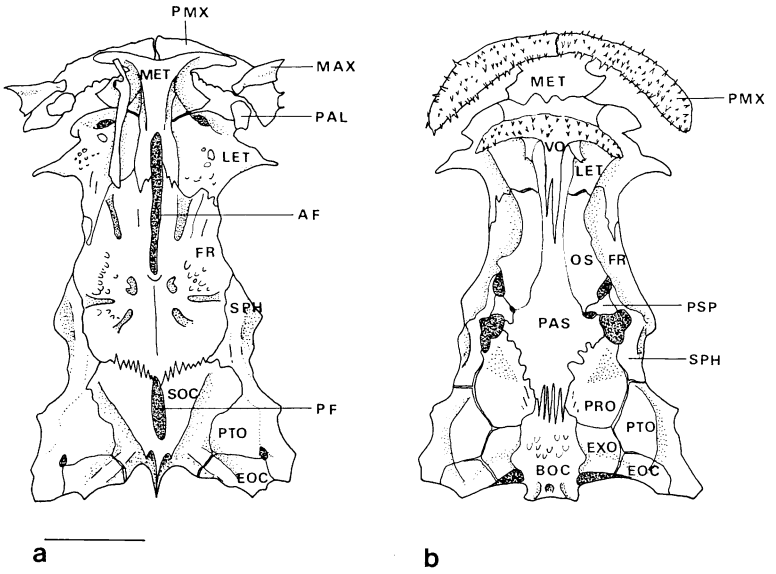

Fig. 34. Skull of *Silurus torrentis* sp. nov. a, dorsal view; b, ventral view. Abbreviations as in Fig. 5. Scale bar indicates 1 cm.

Trang, Thailand. Collected by a local fisherman on March 16, 1986. Paratypes—NSMT 50235–50239 (5 specimens). Data as for holotype. Specimens referred to—FBKU, uncatalogued, 2 specimens, same data as the type series; FBKU, uncatalogued, 2 specimens, collected in Klong Bang Son, Trang, Thailand (8°33′N, 98°55′E) by Jarjin Nabithabata on March 13, 1985; NIFI 00414, 3 specimens, Krating Waterfall, Chantaburi, Thailand; NIFI, uncatalogued, 2 specimens, locality unknown; NHRM 1934. 467. 5007, 3 specimens, collected in Mahlwedaung, Ye State, Burma, 18 Nov. 1934; NHRM 1934. 168. 3225, 7 specimens, collected in Patao, Kachin State, Burma, April 1934.

Diagnosis. Dorsal fin extremely small; colour in life dark olive dorsally and white ventrally; vomerine tooth band slender and nearly continous; corner of mouth just reaching or beyond anterior border of eye.

Description of holotype. Dorsal fin rays 3; pectoral fin rays I, 13; pelvic fin rays i, 7; anal fin rays 69; caudal fin rays 7+8; vertebrae 13+42=55; branchiostegals 12; gill rakers 1+4.

Head well depressed, 5.35 in SL; body compressed; eye covered with skin; snout short, 13.89 in SL; nostrils separated by 30.37 in SL; mouth inferior; a single pair of mandibular barbels, 8.45 in SL; maxillary barbel extending over pectoral fin, 2.96 in SL; anterior edge of pectoral spine smooth; posterior edge of pectoral spine serrated; dorsal origin 3.63 in SL; dorsal fin height 27.15 in SL; caudal fin almost truncated; gill rakers slender and small in number. Colour in life dark olive on dorsal and lateral surface, and white on ventral surface; rim of pectoral and anal fins white.

Standard length 179.2 mm; head length 33.5 mm; predorsal 49.3 mm; preanal 66.7 mm.

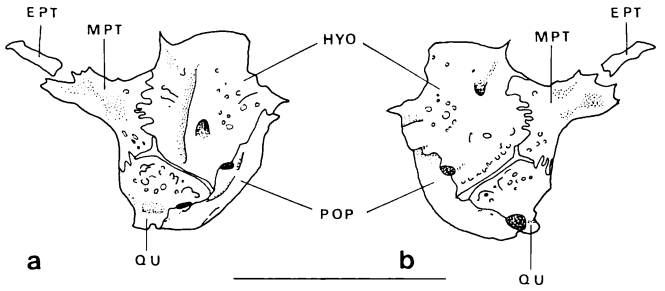

Fig. 35. Suspensorium of *Silurus torrentis* sp. nov. a, lateral view; b, medial view. Abbreviations as in Fig. 6. Scale bar indicates 1 cm.

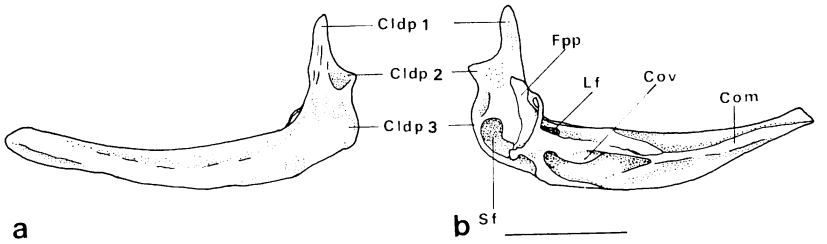

Fig. 36. Shoulder girdle of *Silurus torrentis* sp. nov. a, lateral view; b, medial view. Pectoral fin is removed. Abbreviations as in Fig. 7. Scale bar indicates 1 cm.

Paratypes. Dorsal fin rays 2–3 ($\bar{x}$=2.8; N=5); pectoral fin rays I, 12–13 ($\bar{x}$=I, 12.2; N=5); pelvic fin rays i, 6–8 ($\bar{x}$=i, 7.2; N=5); anal fin rays 63–70 ($\bar{x}$=66.6; N=5); vertebrae 12–13+41–44=54–56 ($\bar{x}$=55.2; N=5); branchiostegals 12–13 ($\bar{x}$=12.2; N=5); gill rakers 1+3 ($\bar{x}$=1+3; N=5).

Two specimens were dissected.

Skull (Fig. 34): Lateral process of lateral ethmoid prominent; antero-median margin of mesethmoid indented posteriorly with a gentle angle; base of lateral projection of mesethmoid strongly compressed; frontal extremely flat, sensory canals on it forming mere groove; sagittal crest broad and confined to posterior part of supraoccipital; posterior part of epioccipital and supraoccipital elevated to form a bump for origin of epaxial muscles; vomer having postero-lateral processes for attachment of a ligament connecting with entopterygoid.

Suspensorium (Fig. 35): Metapterygoid small compared with hyomandibular; entopterygoid an elongate and sheet-like bone; hyomandibular process well-developed and, in one specimen from Chantaburi, forming a pterygoid process to separate adductor mandibulae 3 and levator arcus palatini.

Shoulder girdle (Fig. 36): Vertical part of cleithrum short; ventral coracoid lamina poorly developed; bridge of coracoid strongly bending upward; coracoid connected with cleithrum by complex suture.

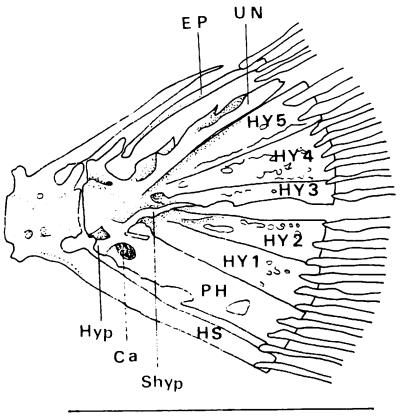

Fig. 37. Caudal skeleton of *Silurus torrentis* sp. nov. Abbreviations as in Fig. 8. Scale bar indicates 1 cm.

Caudal skeleton (Fig. 37): All hypural bones separated from each other; hypurapophysis fused with secondary hypurapophysis, both moderately developed; secondary hypurapophysis forming a well-developed shelf on hypurals 1 and 2.

Remarks. Theis species has been reported by Wongrat (1967) as *Silurichthys leucopodus* Fowler.

Fig. 38. *Silurus triostegus*, BMNH 1920. 3. 3: 168–176. 220 mm SL.

The meristic characters are nearly identical with the original description by Fowler (1939) (Table 1). However, the condition of the continuous anal and caudal fins is quite different. In the genus *Silurus*, the anal fin is continuous with the caudal fin and possesses a definite notch, whereas in the genus *Silurichthys* the two fins are completely united without any break and the posterior rays of the anal fin are longer than the anterior ones. Furthermore this species differs from *Silurichthys leucopodus* described by Fowler (1939) in the following characters: the form of the vomerine tooth patch, length of the maxillary barbels, and the colour of the pectoral fin and the border of the anal fin.

Based on these differences, this form was recognized as a species different from *Silurichthys leucopodus* Fowler.

Wongrat (1967) mentioned specimens only from Chantaburi, but the same forms were also collected in Trang and several places in Burma. A comparison of the meristics and body proportions of the specimens from these three different localities is given in Tables 2 and 3. Slight differences are evident among the specimens from Chantaburi, Trang and Burma, especially in the dorsal fin height, and the number of fin rays and gill rakers. In addition to these differences the colour of the specimens in life from Chantaburi is different from that from Trang. The whole body is black in the specimens from Chantaburi. The body proportions, however, do not differ significantly from each other, and therefore specimens from these three localities are regarded as a single species.

Etymology. The name *torrentis* (Latin) refers to the habitat of this species, torrents.

Distribution. Trang and Chantaburi, Thailand, and eastern Burma.

Silurus triostegus Heckel, 1841
(Fig. 38)

Silurus triostegus Heckel, 1841: 1090.

No specimen was dissected, but radiographs available.

Dorsal fin rays 4; pectoral fin rays I, 12–13; pelvic fin rays i, 9; anal fin rays 78–87; caudal fin rays 7–8+8; vertebrae 17+53=70; branchiostegals 14–15; gill rakers 2–3+10.

Lower jaw longer than upper; head 4.09±0.05 in standard length; two pairs of mandibular barbels in one specimen and only one in others; eye surrounded by free orbital rim; outer surface of pectoral spine smooth; dorsal surface of body mottled in pale yellowish brown and black, and black spots scattered on ventral surface in alcohol-preserved specimens; vomerine teeth in two patches forming a gentle curve separated by a small break. The mesethmoid is broad and not narrowed bilaterally at the base of the well-developed lateral process of this bone.

Distribution. Iraq.

Silurus wynaadensis Day, 1873

Silurus punctatus (not of Cantor, 1842): Day, 1868: 155.
Silurus wynaadensis Day, 1873: 237.

Dorsal fin rays 4; pectoral fin rays I, 10; anal fin rays 56; vertebrae 13+39=52.

Pelvic fin rays could not be counted. Upper jaw longer than lower; head 5.45 in standard length; body uniformly pale brown (specimen not well preserved); mandibular barbels two pairs and rather long, longer one nearly reaching base of pectoral fin; maxillary barbels extending over pectoral fin, but not reaching base of pelvic fin.

Distribution. India.

The meristics of the 17 species of the genus

Table 1. Comparison of *Silurichtys leucopodus* with *Silurus torrentis* sp. nov.

	Dorsal fin	Pectoral fin	Pelvic fin	Anal fin	Branchiostegals	Vomerine tooth patch
Silurichthys leucopodus (original description)	4	I, 10	i, 6	67	—	broad, continuous
Silurichthys leucopodus (from Wongrat, 1967)	4	I, 12–13	i, 8–9	62–68	12–14	—
Silurus torrentis sp. nov.	1–3	I, 10–13	i, 6–9	68–74	11–15	slender, continuous

Table 2. Comparison of the meristic characters of *Silurus torrentis* sp. nov. from three different localities.

Locality	N	Dorsal fin	Pectoral fin	Pelvic fin	Anal fin	Total vertebrae	Branchiostegals	Gill rakers
Chantaburi, Thailand	7	3	I, 10–12	i, 6–9	68–73	56–57	11–13	2–6
		($\bar{x}$=3)	($\bar{x}$=11.1)	($\bar{x}$=i, 6.1)	($\bar{x}$=71.4)	($\bar{x}$=56)	($\bar{x}$=12.1)	($\bar{x}$=4.4)
Trang, Thailand	10	2–3	I, 12–13	i, 6–8	63–74	54–56	12–13	4–5
		($\bar{x}$=2.7)	($\bar{x}$=12.2)	($\bar{x}$=i, 7.1)	($\bar{x}$=68.9)	($\bar{x}$=55.3)	($\bar{x}$=12.2)	($\bar{x}$=4.3)
Burma	10	1–2	I, 10–12	i, 7	68–74	55–57	12–15	2–5
		($\bar{x}$=1.8)	($\bar{x}$=10.4)	($\bar{x}$=i, 7)	($\bar{x}$=67.9)	($\bar{x}$=56)	($\bar{x}$=13.5)	($\bar{x}$=3.4)

Table 3. Comparison of the body proportions (in standard length) of *Silurus torrentis* sp. nov. from three different localities.

Locality	N	Head length	Dorsal height	Predorsal	Preanal	Snout	Caudal pednucle depth	Mandibular barbel	Maxillary barbel
Chantaburi, Thailand	7	5.40	26.3	3.64	2.78	13.3	11.4	3.0	8.5
		±0.161	±1.39	±0.087	±0.114	±1.10	±0.39	±1.10	±0.75
Trang, Thailand	10	5.32	25	3.57	2.64	13.6	13.3	2.7	8.3
		±0.252	±5.8	±0.161	±0.056	±1.07	±1.30	±0.42	±1.04
Burma	10	5.40	31	3.63	2.60	14.2	13.1	3.2	8.8
		±0.133	±4.8	±0.069	±0.114	±1.27	±0.93	±0.37	±1.46

Silurus are shown in Table 4.

Notes on *Silurus goae*

In addition to the 17 valid species mentioned above, *Silurus goae* Haig, 1950 (two specimens including holotype) was examined. The meristics of this species were as follows: dorsal fin rays 4; pectoral fin rays I, 11, 12; pelvic fin rays 8; anal fin rays 67, 72; vertebrae 10+44=54; branchiostegals 13; gill rakers 3+5. *S. goae* externally resembles some members of *Silurus*, but has several unique features in osteology and other morphological characters. These include a smaller number of abdominal vertebrae, a remarkably developed sagittal crest on the supraoccipital, a black spot behind the gill opening, and a forked caudal fin with rounded tips. All of these characters are in good agreement with diagnostic characters of the genus *Ompok*, and I therefore conclude that *S. goae* does not belong to *Silurus* but to *Ompok*.

Key to species of *Silurus*

1a Lower jaw prominent.....2
1b Upper jaw prominent.....13
2a Anterior surface of pectoral spine smooth 3
2b Anterior surface of pectoral spine unsmooth 4
3a Vomerine teeth in a continuous band ..... *S. glanis*
3b Vomerine teeth in two patches..*S. triostegus*
4a Anterior surface of pectoral spine with granules 5
4b Anterior surface of pectoral spine serrated 10
5a Anterior surface of pectoral spine with a row of granules 6
5b Anterior surface of pectoral spine with scattered granules 8
6a Total vertebrae less than 60; maxillary barbel not extending over base of pectoral fin .... *S. mento*
6b Total vertebrae 61 and more; maxillary barbel extending base of pectoral fin....7
7a Total vertebrae less than 63; maxillary barbel reaching anterior one-third of pectoral fin ..... *S. grahami*
7b Total vertebrae more than 67; maxillary extending to half the pectoral fin..... .....*S. lanzhouensis*
8a Standard length less than 4 times head length; numerous papillae at tip of maxillary barbel .....*S. soldatovi*
8b Standard length more than 4 times head length; papillae absent on maxillary barbel 9
9a Maxillary barbel extends over base of pectoral fin; gape very wide, extending over middle of eye.....*S. meridionalis*
9b Maxillary barbel not reaching base of pectoral fin; gape not reaching middle of eye ..... *S. biwaensis*
10a Total vertebrae less than 70.....11
10b Total vertebrae more than 70..*S. aristotelis*
11a Anterior surface of pectoral spine strongly serrated; standard length less than 5 times head length; caudal fin separated into two lobes 12
11b Serration of pectoral spine weak; standard length more than 5 times head length; caudal fin not separated into two lobes..... ..... *S. microdorsalis*
12a Dorsal view of snout slightly pointed; vomerine teeth in two patches...*S. lithophilus*
12b Dorsal view of snout rounded; vomerine teeth usually in a continuous band..... ..... *S. asotus*
13a Adults with four mandibular barbels; vomerine tooth patch continuous 14
13b Adults with two mandibular barbels....15
14a Vomerine tooth patch continuous; border of anal fin white.....*S. gilberti*
14b Vomerine teeth in two separate patches ..... *S. wynaadensis*
15a Vomerine teeth in a continuous band....16
15b Vomerine teeth in two patches; body surface smooth..... *S. cochinchinensis*
16a Body surface smooth; dorsal fin rudimentary; body dorsally black, ventrally white .....*S. torrentis* sp. nov.
16b Body surface rough with sensory tubercles; body entirely dark brown.....*S. afghana*

Taxonomic invalidity of *Parasilurus*

The genus *Silurus* discussed here was formerly divided into two genera, *Silurus* Linnaeus, represented by *S. glanis*, and *Parasilurus* Bleeker, represented by *P. asotus*. The only diagnostic char-

Table 4. Meristic characters of 18 species of the genus *Silurus* and *Hito taytayensis*. * Radiographs included; ** after Sauvage (1882). ——: no data. D., dorsal fin rays; P., pectoral fin rays; Pel., pelvic fin rays; A., anal fin rays; GR., gill rakers; B., branchiostegals; SL, standard length; HL, head length.

Species	N	D.	P.	Pel.	A.	GR.	B.	Vertebrae	Manibular barbel	SL/HL	Anterior surface of pectoral spine
S. glanis	5*	3-4	I, 15	12-13	83-87	12	15-16	18−19+54−56=72−74	4	4.65	smooth
S. triostegus	3	4	I, 12-13	10	78-87	12-13	14-15	17+53=70	2	4.09	smooth
S. lanzhouensis	10*	4-5	I, 11-13	9-11	70-88	9-11	13-15	16+52−53=68−69	2	4.55	granulated
S. mento	19	3-4	I, 9-11	8-10	61-73	12-15	12-15	12−15+41−46=54−60	2	4.01	granulated
S. grahami	8	4-5	I, 10-12	9-11	67-75	10-13	13-15	14−15+46−49=61−63	2	4.35	granulated
S. soldatovi	12	5-6	I, 11-14	10-12	78-87	10-14	13-16	17−18+49−51=67−68	4	3.79	granulated
S. meridionalis	17	5-6	I, 13-16	10-12	71-85	12-17	12-17	15−18+47−50=64−68	2	4.15	granulated
S. biwaensis	16	4-6	I, 13-15	10-13	71-83	11-15	14-16	13−17+49−52=63−68	2	4.29	granulated
S. asotus	18	4-6	I, 10-13	9-12	59-88	9-12	12-16	12−14+46−50=59−64	2	4.64	serrated
S. lithophilus	9	4-5	I, 10-12	10-12	77-82	9-11	14-17	12−15+48−55=62−69	2	4.62	serrated
S. aristotelis	2	2, 3	I, 11	9	75	14, 15	13	15+45, 46=60, 61	2	4.10	serrated
S. cochinchinensis	12*	4	I, 8-10	8-9	58-66	4-5	10-13	11−13+41−45=53−57	2	5.25	smooth
S. gilberti	7	4	I, 10-11	8-9	57-66	4-7	10-12	11−13+39−42=50−55	4	5.25	smooth
S. microdorsalis	14	1-3	I, 9-11	9-11	61-74	6-8	12-13	13−14+45−47=59−60	2	5.58	serrated
S. wynaadensis	1	4	I, 10	—	56	—	—	13+39=52	4	5.45	smooth
S. afghana	1	2	I, 11	9	74	—	—	15+45=60	2	5.26	smooth
S. torrentis sp. nov.	27	1-3	I, 10-13	7-9	63-74	2-6	11-15	12−13+41−45=55−57	2	5.42	smooth
*S. chantrei***		3	I, 13	10	65	—	—	—	—	—	smooth
Hito taytayensis	20	4	I, 10-11	6-8	59-68	9-13	10-11	9−10+38−41=48−51	4	4.92	smooth

acter separating these two genera was the number of mandibular barbels: *Silurus* having two pairs, while *Parasilurus* had only one pair (Bleeker, 1862; Smith, 1945; Berg, 1949); Nikolsky, (1961). However, Haig (1950) and Chen (1977) reported that the adults of *P. cochinchinensis* and *S. gilberti* were variable in the number of mandibular barbels; individuals with a single pair and two pairs of barbels were found within a species. This variation was confirmed in the present study and also documented for the first time in another species, *S. triostegus*. It has been reported that in juvenile *P. asotus*, one of the two pairs of mandibular barbels disappears in the course of ontogeny (Atoda, 1935). My own observations of the growth and development of the Japanese *Silurus* species (Kobayakawa, unpublished) have confirmed this change in *S. asotus*, and similar ontogenetic changes in barbels were also observed in two other Japanese species, *S. biwaensis* and *S. lithophilus*. Examination of a series of preserved specimens revealed that *S. mento* and *S. meridionalis* also have two pairs of mandibular barbels in their juvenile stage, but similarly change the number of mandibular barbels during their ontogeny.

Thus the number of mandibular barbels is proved to be an unreliable generic diagnosis, as already indicated by Haig (1950) and Chen (1977).

The results of observations of other morphological characters are also not in favour of recognizing *Parasilurus*. *P. asotus*, the type species of the genus *Parasilurus*, is more similar to the type species of *Silurus*, *S. glanis*, than to "*Parasilurus*" *cochinchinensis* in various characteristics, such as the shape of the skull and hyomandibular, the sagittal crest on the skull, the entopterygoid, the pectoral spine, and the cleithrum. Since no biologically significant difference is recognized at present, the genus *Parasilurus* is regarded as invalid and relegated to a synonym of *Silurus*.

Taxonomic status of several forms

Examination of the radiograph of the holotype revealed several diagnostic characters of *S. bedfordi* Regan (1908), such as the serration of the anterior surface of the pectoral spine, numbers of vertebrae, anal fin rays, and morphometrics, to fall well within the variation range of *S. asotus*. Accordingly, *S. bedfordi* is synonymized with *S. asotus* in the above revision.

Chen (1977) described *S. meridionalis* as a subspecies of *S. soldatovi*, but the difference in the skull shape between these two forms is so great that they are believed to represent two distinct species. Chen also recognized *S. grahami* as a subspecies of *S. mento*, but the two forms greatly differ in the proportion of the body, colour pattern, and the shape of the mesethmoid, and are therefore considered here as different species.

Haig (1950) considered *S. wynaadensis* and *S. afghana* to be synonyms of *S. cochinchinensis*, but from my observations of type specimens of these species they are judged to be clearly independent species as revealed by the difference in their body colour, body proportion, and number of vertebrae.

Phylogenetic relationships

Monophyly and outgroup of the genus *Silurus*. Based on only three morphological characters, Chen (1977) divided Chinese species of *Silurus* into three groups, represented by *S. cochinchinensis*, *S. asotus*, and *S. soldatovi*, respectively. However, he failed to consider species distributed outside China, and the relationships of species in the genus *Silurus*, as a whole, have not been studied. In recognizing the 17 valid species in the genus *Silurus*, I studied almost all of the hitherto-named taxa from the whole genus range. I utilized cladistic methodology to analyze the phylogeny among 12 species of *Silurus* for which adequate data were available on the basis of a larger number of characters. The genus *Silurus* is one of the nine genera belonging to the family Siluridae and is characterized by the following autapomorphies: 1) anal and caudal fins confluent with a distinct notch between, i.e. the last anal fin ray is shorter than the penultimate ray; 2) dorsal fin small; 3) caudal fin either rounded, truncated or emarginated medially. On the basis of these characters it is argued that the genus *Silurus* is monophyletic.

In order to determine the sister group of the genus *Silurus*, 20 morphological characters of nine nominal genera of the family Siluridae (*Belodontichthys*, *Ceratoglanis*, *Hemisilurus*, *Hito*, *Kryptopterus*, *Ompok*, *Silurichthys*, *Silurus*, and *Wallago*) were analyzed (Kobayakawa, unpublished). In this study, Bagridae, Ictaluridae, and Plotosidae were considered the outgroups of

Siluridae (Howes, 1983). As the result, the genus *Hito* was found to be the sister group of *Silurus*.

Character analysis. Out of the 38 morphological characters examined, the 18 characters discussed below were chosen as suitable for phylogenetic analysis. The character polarity was determined on the basis of outgroup comparison and ontogenetical data were not considered; the ontogeny of several species will be discussed later.

Character 1. Condition of anterior surface of pectoral spine. Four states of this character are observed in the genus *Silurus*; smooth, granulated in a single row, granulated, and serrated. On the basis of the condition in the outgroup, a smooth surface is determined as plesiomorphic, and a granular or serrated surface as apomorphic.

State 0: smooth. State 1: granulated in a single row. State 2: granulated. State 3: serrated.

Direction of change. 0→1→2, 0→3

Character 2. Ratio of standard length to head length. The outgroup has the value intermediate between the extremes seen in the species of *Silurus*. It is difficult to determine the polarity for the morphometric data, because the values vary from species to species, and usually it is subjective to cut a continuous value at a certain point. The relative head length, however, has a correlation with character 1; species with a large ratio have a smooth pectoral spine, and this condition is considered to be plesiomorphic. The outgroup has low value (ratio 4.92).

State 0: ratio 3.7–5.0. State 1: ratio 5.0–6.0.

Direction of change. 0→1

Character 3. Shape of testis. The testis of the outgroup is not split into slender ribbons but only fringed; a fringed testis is considered plesiomorphic and split testis apomorphic.

State 0: fringed. State 1: split.

Direction of change. 0→1

Character 4. Number of vertebrae. As in morphometric data, it is difficult to determine a morphocline for the number of vertebrae. The total number of vertebrae in the outgroup vaies from 48 to 51. These values are relatively low among the family Siluridae. A lower number of vertebrae is inferred plesiomorphic.

Character 5. Secondary hypurapophysis. Lundberg and Baskin (1969) studied the caudal skeleton of Siluriformes, but were unable to reach a firm conclusion regarding polarity. They assumed that species with an eel-like locomotion possessed a weak and undeveloped hypurapophysis. The secondary hypurapophysis of the outgroup forms a shelf on hypurals 1 and 2, and is not fused with the hypurapophysis. It is inferred that the presence of a shelf on hypurals 1 and 2 is plesiomorphic, whereas a shelf on hypural 1 is apomorphic.

State 0: shelf on hypurals 1 and 2. State 1: shelf on hypural 1.

Direction of change. 0→1

Character 6. Fusion of hypurapophysis and secondary hypurapophysis. The hypurapophysis of the outgroup is not fused with secondary hypurapophysis. An unfused condition of hypurapophysis and secondary hypurapophysis is hypothesized to be plesiomorphic and a fused condition apomorphic.

State 0: hypurapophysis not fused with secondary hypurapophysis.

State 1: hypurapophysis fused with secondary hypurapophysis.

Direction of change. 0→1

Character 7. Gill rakers. The members of the genus *Silurus* are roughly divided into two groups by the number of gill rakers. This character is correlated to the ratio of the relative head length. The outgroup has 9–13 gill rakers, and these values are intermediate between those of the two groups observed in the genus *Silurus*. Although it is difficult to determine polarity, 9 or more gill rakers are considered to be apomorphic.

State 0: less than 9 gill rakers. State 1: 9 or more gill rakers.

Direction of change. 0→1

Character 8. Mouth. The mouth of the outgroup is inferior, and this condition is con sidered to be plesiomorphic.

State 0: inferior. State 1: superior.

Direction of change. 0→1

Character 9. Caudal fin. Since the outgroup has a forked caudal fin, the forked condition is inferred as plesiomorphic, and unforked apomorphic.

State 0: forked and emarginated medially. State 1: truncated.

Direction of change. 0→1

Character 10. Width of mesethomid. The mesethmoid of the outgroup is constricted at the base of the lateral projection of this bone, and this condition is inferred as plesiomorphic.

State 0: constricted at the base of lateral pro-

jection. State 1: unconstricted.

Direction of change. 0→1

Character 11. Sagittal crest. The sagittal crest of the outgroup is restricted to the posterior part of the supraoccipital, and only a broad bump is formed. On the basis of outgroup comparison, a broad sagittal crest restricted to the posterior part of the supraoccipital is assumed to be plesiomorphic, and a well-developed sagittal crest apomorphic.

State 0: broad and restricted to the posterior part of the supraoccipital. State 1: well-developed.

Direction of change. 0→1

Character 12. Cleithrum. The length of the vertical part of the cleithrum seems to be related with the depth of the skull (Table 5), i.e. a deep skull with a well-developed sagittal crest retains a long vertical portion of the cleithrum. The outgroup has the cleithrum with a short vertical part, and this is considered to be plesiomorphic.

State 0: with short vertical portion. State 1: with long vertical portion.

Direction of change. 0→1

Character 13. Number of mandibular barbels. The outgroup has one pair of mandibular barbels, which is considered to be plesiomorphic. In some species, the juvenile has two pairs of mandibular barbels, and retains this condition. In others, only one pair is present.

State 0: one pair. State 1: two pairs.

Direction of change. 0→1

Character 14. Entopterygoid. The entopterygoid of the outgroup is a sheet bone. On the basis of outgroup comparison, a sheet-like entopterygoid is considered as plesiomorphic, and a rod-like one apomorphic.

State 0: sheet-like. State 1: rod-like.

Direction of change. 0→1

Character 15. Hyomandibular. The hyomandibular of the outgroup is elongated dorsoventrally, and this state is regarded as more plesiomorphic than that of the antero-posteriorly elongated state. State 0: dorso-ventrally elongated. State 1: antero-posteriorly elongted.

Direction of change. 0→1

Character 16. Suture between cleithrum and ventral part of coracoid. The cleithrum and ventral part of the coracoid in the outgroup are connected by a suture. On the basis of the outgroup analysis, connection by suture is considered to be plesiomorphic.

State 0: sutured. State 1: non-sutured.

Direction of change. 0→1

Table 5. Character state distribution of the genus *Silurus* and the outgroup, *Hito taytayensis*. As for the character numbers and state numbers, see the text. /: polarity could not be determined. ?: not examined.

Species	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Silurus afghana	0	1	?	/	?	0	?	0	1	0	?	?	1	?	?	?	0	0
S. aristotelis	3	0	0	/	0	0	1	1	0	1	1	1	0	1	1	1	1	0
S. asotus	3	0	0	/	0	0	1	1	0	1	1	1	0	1	1	1	1	1
S. biwaensis	2	0	0	/	1	0	1	1	0	1	1	1	0	1	1	1	1	0
S. cochinchinensis	0	1	1	/	1	0	0	0	1	0	0	0	0	0	0	1	0	0
S. gilberti	0	1	1	/	1	1	0	0	1	0	0	0	1	0	0	1	0	0
S. glanis	0	0	?	/	0	0	1	1	0	1	1	1	1	1	1	1	1	0
S. grahami	1	0	0	/	0	0	1	1	0	1	1	1	0	1	1	1	1	0
S. lanzhouensis	1	0	?	/	?	?	1	1	0	1	1	?	0	?	?	?	1	0
S. lithophilus	3	0	0	/	0	0	1	1	0	1	1	1	0	1	1	1	1	1
S. mento	1	0	?	/	0	0	1	1	0	1	1	1	0	1	1	1	1	1
S. meridionalis	2	0	?	/	0	0	1	1	0	1	1	1	0	1	1	1	1	0
S. microdorsalis	3	1	1	/	0	0	0	1	1	0	0	0	0	0	0	1	0	0
S. soldatovi	2	0	?	/	?	?	1	1	0	1	1	?	1	?	?	?	1	0
S. torrentis	0	1	1	/	1	1	0	0	1	0	0	0	0	0	0	0	0	0
S. triostegus	0	0	?	/	?	?	1	1	0	1	?	?	0	?	?	?	1	0
S. wynaadensis	0	1	?	/	?	?	?	0	1	0	?	?	0	?	?	?	0	0
Hito taytayensis	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0

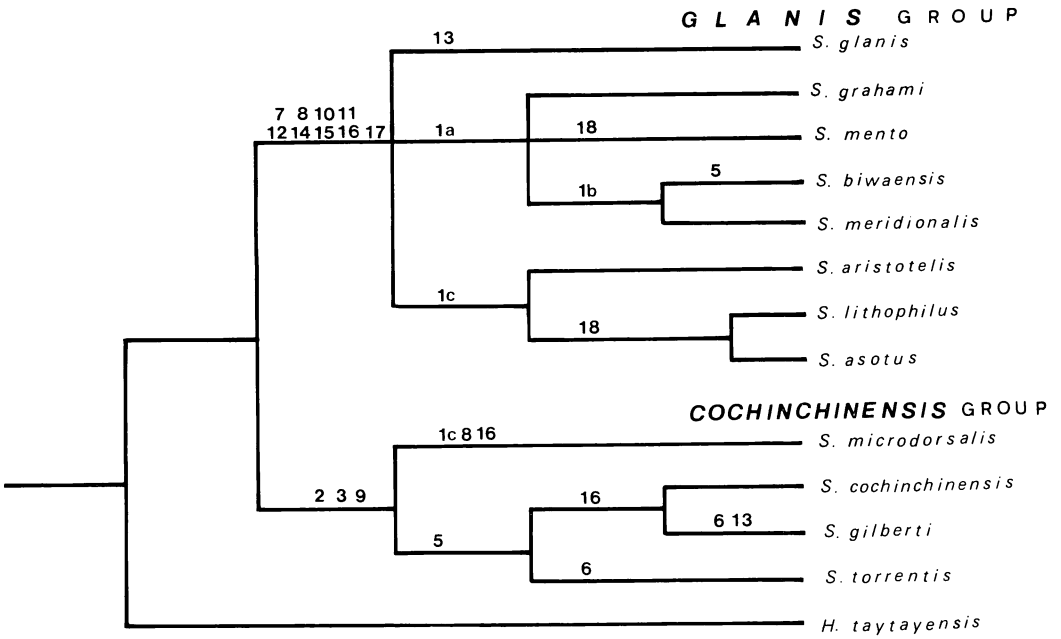

Fig. 39. Phylogenetic relationships of 12 species available for anatomical study of the genus *Silurus*. Numbers on each branch indicate character numbers of synapomorphy. 1 a–c, character state 1–3 of character 1, respectively.

Character 17. Margin of eye. In some species, the eye is covered with skin, while in others, the eye has a free orbital rim. The outgroup shows the former condition, and the eye covered with skin is considered to be plesiomorphic.

State 0: covered with skin. State 1: with free orbital rim.

Direction of change. 0→1

Character 18. Lateral line. The lateral line of the outgroup runs only vertically. Some species of *Silurus* have a horizontal lateral line in addition to the usual vertical one. On the basis of outgroup analysis, the condition with horizontal lateral line only is regarded as plesiomorphic.

State 0: only vertical. State 1: both vertical and horizontal.

Direction of change. 0→1

The character state distribution of these 18 characters is shown in Table 5.

Inferred phylogeny. The phyletic relationships among the 12 species thus inferred are shown in Fig. 39, from which this genus is revealed to be split into two major species groups. Chen (1977) recognized three species groups in the Chinese *Silurus*, as noted above. Unfortunately, I could not dissect any specimens of *S. soldatovi*, and the species is therefore not included in the above phylogenetic analysis. From my observation, however, the differences between *S. asotus* and *S. soldatovi* is minor compared with the differences found between either of these two species and *S. cochinchinensis*. Accordingly, it would be safe to conclude that this genus should be divided into two, and not three, major species groups. Here these groups are named the *glanis* group and the *cochinchinensis* group. A comparison of the main differences between these two groups is given in Table 6.

The *glanis* group is composed by *S. asotus*, *S. aristotelis*, *S. biwaensis*, *S. glanis*, *S. grahami*, *S. mento*, *S. meridionalis*, and *S. lithophilus*. From the main characteristics listed in Table 4, *S. lanzhouensis*, *S. soldatovi*, and *S. triostegus* are also regarded as members of this group. The *cochinchinensis* group consists of *S. cochinchinensis*, *S. gilberti*, *S. microdorsalis*, and *S. torrentis*. *S. afghana* and *S. wynaadensis* are also included in this group on the basis of the characteristics given in Table 6. Although *S. chantrei* Sauvage was not treated in the present work, the species may be a member of the *cochinchinensis* group, since the description of this species (Sauvage, 1882)

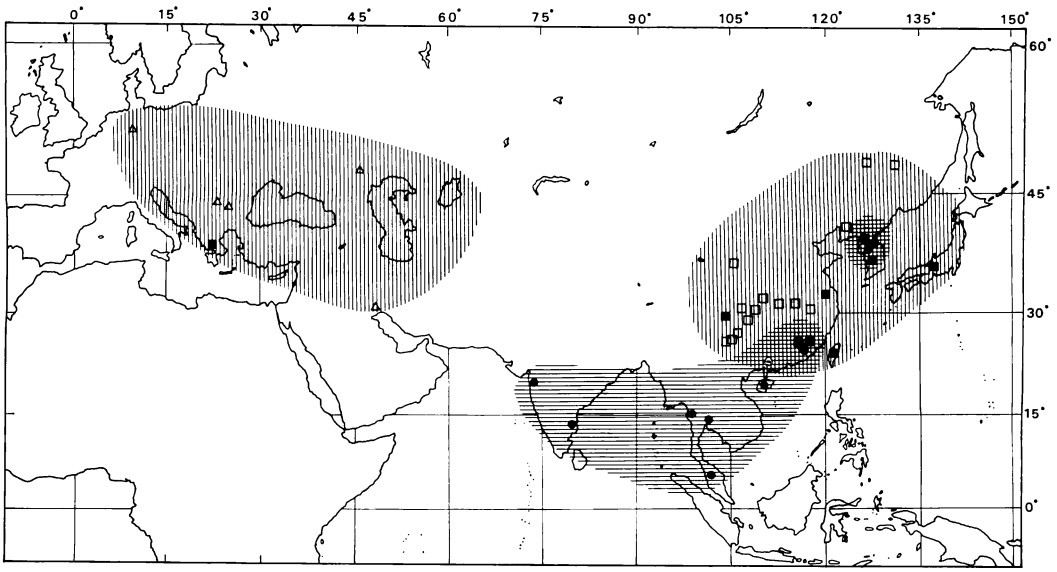

Fig. 40. Distribution of the genus *Silurus*. Horizontally hatched area indicates the distribution range of *cochinchinensis* group, vertically hatched area that of the *glanis* group. Localities of specimens examined are shown: solid circle, species of *cohcinchinensis* group; triangle, species with smooth anterior surface of pectoral spine in *glanis* group; square, species with granulated anterior surface of pectoral spine in *glanis* group; solid square, with serrated anterior surface of pectoral spine in *glanis* group.

indicates its close resemblance to *S. afghana*.

From the phylogenetic tree shown in Fig. 39, it is possible to further subdivide each major group. Regarding the *cochinchinensis* group, *S. microdorsalis* is separable from the other species, but available information is inadequate to recognize clear subgroups. Similarly the *glanis* group seems to be separated into at least three groups (Fig. 39). When the species not shown in the tree (*S. lanzhouensis*, *S. soldatovi*, and *S. triostegus*) are added to this group, a single character (character 1; anterior surface of the pectoral spine) may be used to further divide the *glanis* group into three subgroups. The first subgroup is composed of *S. glanis* and *S. triostegus*, whose anterior surface of the pectoral spine is completely smooth, the second consists of *S. lanzhouensis*, *S. mento*, *S. grahami*, *S. meridionalis*, *S. biwaensis*, and *S. soldatovi*, whose anterior surface of the pectoral spine is granulated, and the third consists of *S. asotus*, *S. lithophilus*, and *S. aristotelis*, whose anterior surface of the spine is well-serrated. In order to confirm the validity of these subgroups, further morphological and anatomical information is required.

Pattern of distribution

Due to the limited amount of available information, it is impossible to accurately determine the exact distribution range of each species at present. However, the locality records attached to the observed specimens give an outline of the range of the two major species groups in the genus *Silurus*. The range of *Silurus*, as a whole, is clearly separated in Europe and Asia (Fig. 40). In Europe, only members of the *glanis* group occur. In contrast, the two species groups occur in Asia, where their ranges are roughly split into two regions. This distribution pattern seems to support the validity of the two major species groups recognized from the phylogenetic analysis based on the external morphology and anatomy.

The outgroup species, *Hito taytayensis*, is endemic to the northern part of Palawan and Caramians, the Philippines. On the basis of this distribution range of *Hito* and its phylogenetic relationships to the two species groups of *Silurus*, it is inferred that the genera *Hito* and *Silurus* have differentiated in Southeast Asia, from where *Silurus* later extended its distribution range.

Table 6. Comparison of the two species groups of the genus *Silurus*.

Character	*cochinchinesis* group	*glanis* group
Mouth	inferior	superior
Standard length/head length	>5	<5
Total vertebrae	<60	>60
Gill rakers	less than 9 and reduced	9 and more and well developed
Anterior surface of pectoral spine	smooth or slightly serrated	smooth, serrated, or granulated
Entopterygoid	sheet bone	rod-like bone
Hyomandibula	vertically elongated	transversally elongated
Testis	split into slender ribbons	fringed

The pattern of distribution and the estimated phylogenetic relationships of the two species groups seem to support this idea. The distribution range of the *cochinchinensis* group is mainly in southeastern Asia and the southern part of eastern Asia, with the exception of *S. microdorsalis* which extends north to Korea. This species is particularly interesting. The distribution of *S. microdorsalis* is slightly separate from other members of the *cochinchinensis* group, and this species is morphologically more similar to the *glanis* group than are other members of the *cochinchinensis* group, as shown in the phylogenetic tree. It is possible that this species might represent a relict, retaining some character states similar to those of the ancestral form of the *glanis* group.

The geographic distribution of the *glanis* group is clearly split into two wide ranges, one in central Europe and the other in East Asia, being separated by the Mongolian Plateau (Lindberg, 1972). *S. aristotelis*, a member of one of the subgroups of the *glanis* group, is isolated in the Balkan Peninsula far from the other two members of the same subgroup, *S. asotus* and *S. lithophilus*, which are distributed in eastern Asia. The Himalayan orogeny might have a serious effect on splitting the distribution range of the *glanis* group. Since the fossil record of this genus is very poorly known (Obrchev, 1964; Kobayakawa and Okuyama, 1984), it is difficult to infer from which of the present centers the ancestral form of the *glanis* group arose.

The distribution ranges of the two major groups overlap at the eastern edge of Asia. Available data indicate that the members of the *cochinchinensis* group inhabit upper streams or more rapid running waters than the members of the *glanis* group (Day, 1878; Uchida, 1939; Joen, personal communication), and therefore it is probable that ecological isolation exists between the members of these two major groups.

Ontogeny and phylogeny

Since the ontogeny of only several members of the *glanis* group has been studied, it is difficult to generalize the relationship between ontogeny and phylogeny in the genus *Silurus*. Regarding the ontogeny of the three Japanese species of the *glanis* group, however, detailed information is available (Kobayakawa, unpublished). From that study, the juveniles, in comparison with adults, have unique conditions in several characters: the anterior surface of the pectoral spine is smooth, the skull is flat both dorsally and ventrally, the cleithrum is gently curved, and the mouth is inferior. When these juvenile features are considered, the conditions of the corresponding chraracters found in the *cochinchinensis* group are regarded as juvenilized ones of the *glanis* group. These ontogenetical considerations again seem to confirm the validity of grouping them into two major species groups, and suggest that the ontogeny has strongly affected the phylogeny in the evolution of the genus *Silurus*. The two major species groups, the *cochinchinensis* group and the *glanis* group, mentioned above seem to deserve generic status, but in this report, I will reserve further discussion until all genera of Siluridae have been studied in detail.

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タイおよびビルマ産の1新種を含むナマズ属魚類の分類学的再検討

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ナマズ科魚類はユーラシア大陸に広く分布するが，これまでに知られている9属のうち，ナマズ属 *Silurus*は，特に分布が広い．本属については分布が広いため標本の入手が容易でないこともあり，系統分類学的な研究はまだなされておらず，属の再検討を行った Haig (1950) と中国産の種の再検討を行った Chen (1977) の研究があるにすぎない．したがって本属にはこれまでに何種が記載されているかも明確ではなかった．また，本属は下顎の鬚の数によって *Silurus* 属と *Parasilurus* 属に分けられていたが，Haig (1950) および Chen (1977) はいくつかの種で下顎の鬚の数には種内変異が認められ，属の特徴とするに値しないことを指摘している．本研究では，1新種を含む17種を有効な種と認め，*S. bedfordi* Regan は *S. asotus* Linnaeus の同物異名とし，*S. goae* Haig は *Ompok* 属とした．また，新種 *S. torrentis* を記載した．これら17種の外部形態を，12種については解剖学的にも比較し，分岐分類法によって系統関係を推定した．その結果，本属を *Silurus* と *Parasilurus* に分けるのは妥当ではなく，*Parasilurus* は前者の同物異名であると認めた．さらにいくつかの形態的特徴により，本属は大きく2つの種群に分けられることがわかり，*cochinchinensis* 種群，*glanis* 種群と名づけた．*cochinchinensis* 種群は *glanis* 種群の稚魚的な特徴を維持していた．これら2つの種群は，例外はあるものの，分布からもその有効性が確かめられた．これら2つの種群は属に相当するとも考えられるが，今後ナマズ科の他の属との比較を行った上で検討すべきであろう．

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