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SKELETAL ANATOMY AND CLASSIFICATION OF THE NEOTENIC ASIAN SALMONIFORM SUPERFAMILY SALANGOIDEA (ICEFISHES OR NOODLEFISHES)

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Abstract: The distinctive, largely cartilaginous skeletal anatomy of the Asian icefishes or noodlefishes is described and figured from cleared specimens stained with alcian and alizarin. This information, together with examination of types and other material in North American and European museums, leads to the following revised classification of these neotenic Salmoniformes:

Salangoidea new superfamily (coordinate with Osmeroidea, Salmonoidea)
  Salangidae
  Protosalanginae: *Protosalanx chinensis*
  Salanginae: *Salanx* (*Salanx*) *ariakensis*, *S.* (*S.*) *cuvieri*, *S.* (*Hemisalanx*) *prognathus*, *S.* (*Leucosoma*) *reevesi*
  Salangichthyinae new subfamily: *Neosalanx andersoni*, *N. brevirostris*, *N. jordani*, *N. reganius*, *Salangichthys ishikawae*, *S. microdon*
  Sundasalangidae: *Sundasalanx microps*, *S. praecox*

The introduction includes a summary of salangoid natural history and a key for their identification. The systematic account includes all primary and secondary synonyms of genera and species recognized. New information is presented on pectoral girdle morphology in teleosts, relationships of salangoids and other salmoniforms, and breeding tubercles, meristic variation, and neoteny in salangoids.

INTRODUCTION

The slender, soft-bodied, and transparent or translucent salmoniform fishes of the family Salangidae inhabit the sea coasts, rivers, and lakes of East Asia including Japan from Sakhalin, Vladivostok, and the Amur River south to northern Vietnam (Tonkin). The greatest concentration of genera and species is in China and Korea. Of 11 species herein recognized, eight occur in China, eight or nine in Korea, and four in Japan. Only *Salangichthys microdon* occurs along the outer coast of Korea and in Siberia, and only *Salanx reevesi* and *Neosalanx brevirostris* have been reported as far south as Tonkin (or Haiphong).

Members of the Salangidae have almost always been referred to in English as icefishes. In Japanese, however, they are usually referred to as *shirauwo* (whitefishes) and rarely as *hiagio* (icefishes). In Russian they are usually referred to as *lapsha-ryba* or noodlefish, and an equivalent name exists in Chinese, *mien-tiao-yu* (麵條魚). They have been referred to as *Nudelfische* in German, but noodlefishes, a highly appropriate and distinctive name, seems not to have appeared in English except in a translation of a Russian work (Berg 1962:480). The flesh is tasty, whether cooked as a soup, eaten with vinegar or scrambled eggs, or fried (Okada 1955:60). The species most commonly eaten in Japan is *Salangichthys microdon*, and in China probably *Neosalanx brevirostris* or *N. jordani*. *Protosalanx* and *Salanx* are also consumed, but I doubt that tiny *Sundasalanx* has ever been dined upon.

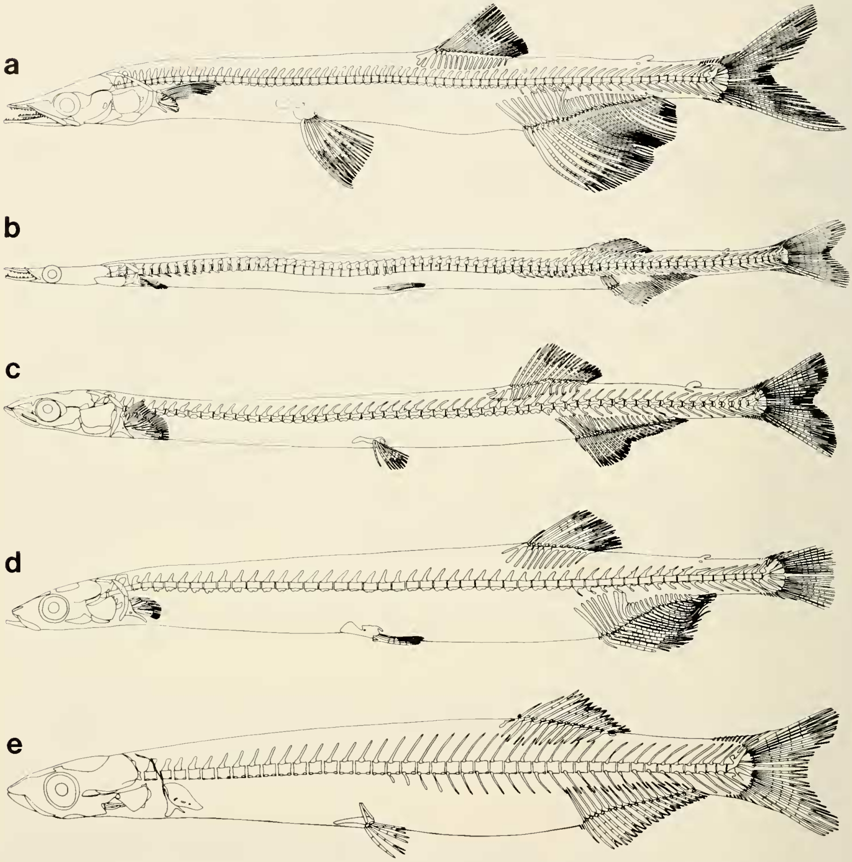

FIGURE 1. Axial skeleton. (a) *Protosalanx chinensis,* CAS-SU 6306, 85.5-mm adult male; (b) *Salanx cuvieri,* CAS-SU 32454, 61.7-mm juvenile sex undetermined; (c) *Salangichthys ishikawae,* CAS 6780, 74-mm adult female; (d) *Neosalanx jordani,* CAS 52028, 38.3-mm adult male; (e) *Sundasalanx microps,* CAS 44220, 17-mm adult sex undetermined.

Despite their standing as a delicacy—sufficient for them to be imported by the Chinese and Japanese communities of San Francisco and served in the city's sushi bars—relatively little is known about the systematics and biology of noodlefishes. An impression of their morphological diversity can be obtained from Figures 1 and 2.

The present study was undertaken in connection with the discovery of some minute, scaleless, and transparent fishes during my fieldwork in the Malay Peninsula (1971, 1973) and on the Kapuas River in Kalimantan Barat, Indonesia (1976). When first found, although in fresh water, they were living close to the sea and were mistaken for elopoid leptocephali, which they resemble only superficially. In the Kapuas River, however, they were living 800 km upriver in the midst of a rich riverine fish fauna dominated by Ostariophysi and with no elopoids. The observation that the maxillary bones curved inwards below

Table 1. Reproductive biology of Salangoids (Wakiya and Takahasi 1937, Okada 1960, Senta 1973a, b, Roberts 1981, and pers. obs.).

	Smallest mature male (mm)	Largest male (mm)	Largest female (mm)	Diameter egg (mm)	Fecundity	Remarks
Protosalanx chinensis	82	168	146	1.15	—	Breeds January–February (Korea)
Salanx ariakensis	—	—	147	0.75	—	Breeds October–November (Korea)
Salanx cuvieri	—	—	144	—	—	—
Salanx prognathus	100	111	119	0.85	—	Breeds April–May
Salanx chinensis	130	130	153	—	—	—
Neosalanx andersoni	79	100	95	—	—	Breeds April–May (Korea)
Neosalanx brevirostris	—	64	60	0.7	—	—
Neosalanx jordani	34	56.5	59.5	0.5	—	Breeds March–May
Neosalanx reganius	—	56	58	0.9	—	Breeds February–March
Salangichthys ishikawae	—	71	74	0.95	—	Breeds April–May
Salangichthys microdon	65	90	100	0.91–0.99	1300–2700	Breeds March–May
Sundasalanx microps	—	—	—	—	—	Largest specimen (sex unknown) 19.9 mm
Sundasalanx praecox	14.9	18.3	17.3	0.20–0.25	50	Both sexes ripe in June

the head led to an hypothesis that they are salangoids, and observations of their skeletal anatomy and particularly the suspensorium confirmed this (Roberts 1981). These fishes differ in a number of respects from Salangidae and constitute a separate family, Sundasalangidae, with one genus, and two or more species, one in the Malay Peninsula and one or two in the Kapuas River (Roberts 1981). *Sundasalanx* also occur in the Mekong basin, as reported herein. This is the only truly tropical genus in the entire order Salmoniformes. *Sundasalanx praecox,* with males and females sexually ripe at only 14.9 mm, is the smallest member of the order, and provides a striking example of a minute secondary freshwater fish living in the midst of a rich freshwater ichthyofauna dominated by primary freshwater Ostariophysi.

Interest in Sundasalangidae and its relationships led me to examine other salangoids but my observations and drawings quickly became too extensive to incorporate in the original description of the new taxa; hence the present monograph.

Food Habits

All salangoids, including tiny *Sundasalanx,* appear to be predators. The largest species, *Protosalanx chinensis* and *Salanx reevesi,* both with well-developed teeth on the tongue and jaws, apparently feed mainly on fishes. *Salangichthys microdon* taken in the Takahashi River had fed on larvae of the goby *Chaenogobius* sp. and on the mysid shrimp *Neomysis* sp. (Senta 1973b). Other species of Salanginae and Salangichthyinae feed mainly on small crustacea (in marine environments) or on insects (in fresh water). *Sundasalanx* are known only from fresh water and feed on tiny insects (Roberts 1981).

Reproduction

While some species are primarily marine or at least brackish water inhabitants (e.g., *Protosalanx chinensis*), and many spend part of their lives in the sea, others are restricted to fresh water or have populations which presumably repeat their life cycle without leaving fresh water. Basic information on salangoid reproductive biology is summarized in Table 1. Fecundity ranges from several thousand eggs in Protosalanginae and Salanginae (no precise numbers available) down to only about 50 in Sundasalangidae.

The external egg membrane is adhesive, eggs becoming attached to any solid object at the spawning site. Wakiya and Takahasi (1937, pl. 21) published drawings of the basal portion of the adhesive strands on the eggs of *Protosalanx chinensis, Salanx ariakensis* and *S. prognathus, Salangichthys microdon* and *S. ishikawae,* and *Neosalanx jordani.* The eggs illustrated are presumably ovarian, since the adhesive strands are not detached. For photomicrographs of the

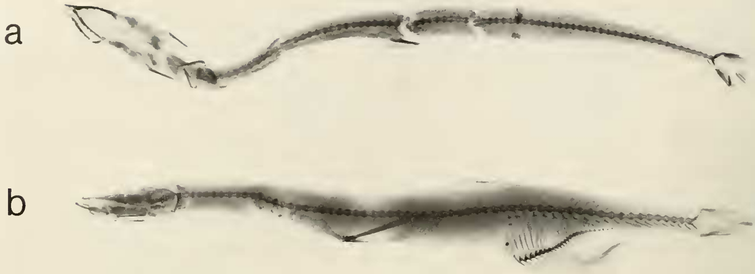

Figure 2. Radiographs. (a) *Salanx cuvieri*, MNHN 9900, 112 mm, holotype; (b) *Neosalanx andersoni*, NRM 10287, 79 mm, holotype.

spawned eggs with detached adhesive threads of unfertilized and fertilized eggs of *Salangichthys microdon* see Okada (1960, pl. 18). Spawning ecology of this species is described by Senta (1973a). According to Wakiya and Takahasi (1937:269), after spawning "the body becomes very lean and the vertebrae become visible through the skin, whence it is generally assumed that death then ensues." I suspect that this is true in Salanginae as well as Salangichthyinae but not in *Protosalanx*.

Sexual Dimorphism

A notable feature of salangoids is their unique sexual dimorphism. In all Salangidae except *Neosalanx*, sexually mature males have the pectoral fins longer and more pointed (falcate) and the pelvic fins larger. In all adult male Salangidae the anal fin is larger than in females and has modified rays. The anterior rays of the anal fin are greatly enlarged, the middle rays thin and strongly curved, and the posterior rays short and widely separated at the base. The morphology of the anal fin is very similar in sexually mature males of all of the genera and species of Salangidae. In all Salangidae, mature males have a row of large, tightly adherent scales on the body parallel to the anal fin base (sometimes extending posteriorly a short distance beyond the anal fin base onto the caudal peduncle). The number of anal scales ranges from 14 to 28. Sexual dimorphism has not been observed in Sundasalangidae.

Although salangids differ greatly in the size of adult males, the morphology of the modified male anal fin is remarkably uniform (Fig. 1a, d). The total range of anal fin-rays is 23–32. The first two or three rays are simple, the first one or two small or minute. The last simple ray and the first four to six branched rays are greatly enlarged and somewhat thickened; near the base of each of these rays is a very large lateral projection. The next 12 or so rays are noticeably thinner and are deflected backwards near the middle of their length, so that their distal portions lie close together. In *Protosalanx* these rays are simple, but in other Salangidae they are branched. The posteriormost rays may be simple or branched, are reduced in size and not modified, except that their bases tend to be relatively wide apart (much more so than the bases of the preceding rays or of the corresponding rays in females), especially in Salanginae. The proximal pterygiophores, especially for the anterior portion of the anal fin, are also enlarged in males. In alcian-alizarin preparations the anal fin-rays and pterygiophores of sexually mature males are deeply stained with alizarin, whereas those of females tend to be less well stained with alizarin or in some instances stained only with alcian.

Near the middle of the rays in the most modified part of the male anal fin, a tough, almost tendonlike membrane arises from each ray and extends obliquely and posteroventrally across the densely webbed portion of the fin to end in a thickened, obliquely oriented non-muscular pad of tissue. The distal portion of this oblique pad is free from the surface, so it can be readily lifted, and even when not lifted forms a sort of groove for the length of the pad. This portion of the anal fin can be flexed in such a way that it forms a slight concavity. The fin may be expanded manually by pulling on the anteriormost rays; when released, it snaps back into a less expanded condition. Spawning behavior has not been reported upon, but presumably the male's anal fin remains in contact with the vent region of the female in such a way that it temporarily retains eggs and sperm in proximity while fertilization occurs externally.

In addition to the modified anal fin, sexually mature males of all Salangidae bear a row of large, cycloid scales on the side of the body above and co-extensive with the anal fin or extending a short distance beyond it onto the caudal peduncle. The scales are tightly adherent and broadly overlapping (more so anteriorly than posteriorly). In addition to the main row of anal scales, some specimens exhibit two or three smaller scales in a separate row overlying the vent. These usually have been overlooked by previous authors, and are not included in the counts of anal scales in Table 2.

Breeding tubercles and other forms of temporary sexual dimorphism have not been reported previously in salangoids. I have observed breeding tubercles in adult males and females, apparently in spawning condition, of *Protosalanx chinensis,* and in adult males of *Salangichthys microdon* and *Neosalanx jordani.* This presumably temporary tuberculation is most extensive and easily observable in an 120-mm male *Protosalanx* (CAS-SU 36025). In this specimen breeding tubercles occur on the anal, pectoral and pelvic fins, abdominal keel, and head. The strong lateral projections on the anterior face of the first nine branched anal fin-rays are entirely or almost entirely covered by a thickened, longitudinal band of thickened skin 9 mm long and 1.2 mm high. The surface of this spongy band of skin is covered with hundreds of small, overlapping, scale- or leaflike breeding tubercles, with their raised free margins projecting anteriorly. There are about 12–20 of these tubercles in a vertical series. Discrete pads of similarly thickened skin covered with similar breeding tubercles extend obliquely posteroventrally on the basal third of the first five branched anal fin-rays. There are up to eight tubercles across each ray. The skin on the middle third of the same rays appears to be only slightly thickened and bears only a few, small widely spaced, low-lying round (not scalelike) tubercles. The distal third or branched portion of the first eight branched rays is covered with thick skin densely coated with scalelike tubercles. There are up to about eight tubercles across each ray-branch. The leading edge of the third (enlarged) simple anal fin-ray bears a thick, lamellar projection of skin, 11.5 mm long and up to 2.2 mm wide, covered with widely scattered, low-lying round tubercles without free margins. The midventral abdominal keel is also notably thickened, and covered with minute, closely spaced round or granular tubercles which extend for a short distance onto the abdomen and sides of the body just anterior to the anal fin. The pelvic and pectoral fins bear round tubercles dorsally and ventrally; these are most noticeable on the enlarged outermost pectoral fin-ray. The dorsal fin is slightly tuberculate, the adipose and caudal fins non-tuberculate. The dorsal, lateral, and ventral surfaces of the head bear irregularly scattered, round, low-lying tubercles without free margins. These are largest and most numerous on its ventral surface. The skin of the oral margin of the upper and lower jaws and gular margin of the lower jaw is thickened and tuberculate. Fine granular projections, which may be minute breeding tubercles, extend in a dorsomedian longitudinal band from the dorsal fin origin anteriorly halfway to the occiput. In the two gravid females the skin is less modified, and although tuberculation is very much lighter, there are small, low-lying round tubercles on the anal, pelvic, and pectoral fins and on the head. In one of them the skin on the jaws is thickened as in the male; in the other it is not. The first female has the median abdominal fold somewhat thickened, suggestive of the more pronounced thickening of this fold seen in the male; the other female does not. Tubercles have not been observed in females of any other salangoid.

In other salangoids breeding tubercles have been observed only on the anal fin of males. An 83.1-mm male *Salangichthys microdon* (CAS 52033) has small scalelike breeding tubercles on the branched portion of the anteriormost branched anal fin-rays. These are arranged uniserially on each fin-ray branch. A 47.5-mm male *Neosalanx jordani* (AMNH 51704) has very similar scalelike tubercles on thickened skin surrounding the lateral projection at the base and on the basal half of the first four branched anal fin-rays (which are enlarged); fin-rays 6–14, which are bent, each have three to four melanophores on the basal one-fourth of their length. (Similar coloration has been observed on the anal fin in occasional males of *Salangichthys microdon*.)

Breeding tubercles apparently do not occur in Sundasalangidae, in which neither secondary sexual dimorphism nor dichromatism has been observed.

Pigmentation

The only pigmentation known to be exhibited by salangoids, apart from that of their eyes, is in melanocytes or melanophores, which tend to occur as widely separated single cells or isolated clumps of relatively few cells. In life all, or almost all, salangoids (except *Protosalanx*) are transparent or translucent, except for the prominent eyes. The most constant pigmentary feature of the salangoids is a row of melanophores at the interface of the ventral myotomic musculature and the non-segmentally muscularized ventral abdominal wall. This series of melanophores, with a single cell at about the middle of the ventral end of each myotome, from the most anterior myotome to the anal fin origin, is present in nearly all salangoid specimens examined. Usually these melanophores are longitudinally elongate, giving the appearance of a series of widely spaced thin black dashes. A second pigmentary feature found in many salangoids is a ventromedian row of widely spaced melanophores, one for each body segment. These melanophores tend to be dendritic when expanded or round when contracted, and may extend the entire length of the abdomen; sometimes they are restricted to the preanal membranous keel. These two pigmentary features of salangoids occur in many teleost larvae and in adults of other neotenic teleosts.

Some salangoids exhibit a row of melanophores along the anal fin base, one between each anal fin-ray. This row of melanophores, lying deep in the body and median rather than paired, may be the continuation of the midabdominal row of melanophores described above. This row usually extends the length of the anal fin; sometimes it continues beyond the anal fin onto the caudal peduncle near its ventral margin.

Clusters of a few melanophores occur just anterior to the bases of the pectoral and pelvic fins in most salangoids, at the tip of the snout and chin, especially in *Salangichthys,* and infrequently on the dorsal surface of the head overlying the fore- and hind-brain. In sexually mature (spawning?) males of *Salanx* and *Salangichthys* there may be a cluster of melanophores on the proximal portion of the middlemost anal fin-rays. The dorsal, anal, pectoral, and pelvic fins are otherwise usually devoid of melanophores, but the caudal fin lobes frequently are dark or dusky due to numerous fine melanophores. The anal scales of the males are always entirely devoid of melanophores.

In most salangoids the entire dorsal and most of the lateral body surfaces are devoid of melanophores. *Protosalanx chinensis* and *Neosalanx andersoni* provide notable exceptions. Young of *Protosalanx* and *Neosalanx* exhibit very few melanophores. Large and sexually ripe individuals of these two species, however, may have the dorsal and lateral surfaces of the body with numerous melanophores. Those on the dorsal body surface are fine, exceedingly numerous, and generally scattered over the entire musculature, but those on the sides are few and peculiarly restricted along the course of the myotomal septae. About a dozen melanophores lie on each myotomal septa; the melanophores of successive septae are more or less parallel to each other; the cells are obliquely elongate, conforming to the thinness and obliquity of the septae and thus forming a series of widely spaced thin black slashes. This pattern, sometimes barely evident or absent in *P. chinensis,* is very well developed in two gravid females of 129–132 mm (USNM 120746). Wakiya and Takahasi (1937) show it well developed in female *P. chinensis* (not gravid?) and *N. andersoni* (gravid); and relatively weakly developed in males of both species. It is present only on the upper part of the body in the relatively small male holotype of *N. andersoni* (NRM 10287, 79 mm). Chyung (1961) shows it well developed in a gravid *N. andersoni.* I have seen clupeomorphs but no osmeroids or other salmoniforms with similarly distributed melanophores.

Some Misconceptions

Some misconceptions about Salangidae should be noted. These concern the reported presence of scales other than anal scales, presumed absence of the swimbladder, and reputed oral brooding of eggs. The most persistent misinformation concerns the occurrence of scales on the body other than the anal scales. Günther (1866: 205) stated that the body is "naked or covered with small, exceedingly fine, deciduous scales (?)" and added in a footnote, "There is no trace of scales in specimens preserved in spirits for some time; but others, which we received lately, show scattered fragments of scales, without any regular arrangement." He was unaware of the anal scales of males. Regan (1908b:444), in diagnosing Salanginae (=Salangidae), stated simply "scales deciduous" but described the anal scales of males in a footnote. Fang (1934a:239) stated body "naked or with a few exceedingly thin, large, scattered, deciduous scales, without any regular arrangement" in addition to the anal scales of males. Nichols (1944) referred to several species with "scales small, deciduous, little evident." Nelson (1976:104) cautiously stated "body generally scaleless" without referring to the anal scales of males. As noted by Wakiya and Takahasi (1937) all salangids are totally scaleless except for the anal scales of sexually mature males; as noted above, the anal scales are large and strongly adherent. Reports of scales on other parts of the body are all attributable to dislodged scales from other fishes.

Various authors, including Günther (1866: 205), Fang (1934a:239), and Nelson (1976:104) have stated that salangids lack a swimbladder. Wakiya and Takahasi (1937:268, fig. 1) reported a physostomous swimbladder in *Protosalanx chinensis, Salanx ariakensis, S. prognathus, Neosalanx jordani, Salangichthys ishikawae,* and *S. microdon.* In *P. chinensis* and *S. ishikawae* the swimbladder is depicted as relatively large and oval, and in the others as equally long but almost uniformly slender for its entire length. The condition of the swimbladder in Sundasalangidae is unknown.

Fang (1934a:238, 252, fig. 7) suggested that Salangidae are oral brooders. In a series of 61 males and 27 females identified as *Hemisalanx* (=*Salanx*) *prognathus* collected at Chinkiang in April 1933, Fang found 6 males and 19 females with 1–21 eggs in the mouth. He also reported one *Protosalanx* (sex not mentioned) with eggs in its mouth. I have also observed a few specimens of both sexes, especially of Salanginae, with small numbers of eggs in the mouth; this is attributable to rupture of the ovaries and spillage of eggs after the fish had been caught. There is no information indicating that salangoids practice oral brooding or any other form of parental care.

This introduction to salangoids concludes with a key for their identification.

Key to Salangoidea

1a. Pelvic fin with 5 rays; adipose fin absent; pectoral fin rayless throughout life; sexually mature males without anal scales or enlarged anal fin; vertebrae 37–43; standard length to 22 mm (Sundasalangidae) 11

1b. Pelvic fin usually with 7 rays (rarely 6 or 8); adipose fin present; pectoral fin with rays except in larvae; sexually mature males with a row of large anal scales and enlarged anal fin; vertebrae 48–79; adults at least 35 mm in standard length (Salangidae) 2

2a. Teeth on palatal toothplate and lower jaw in two rows; teeth on tongue in two marginal rows or widely spread over basihyal toothplate (Protosalanginae) .... *Protosalanx chinensis*

2b. All oral teeth in single rows 3

3a. Head extremely depressed; snout very elongate and relatively pointed; cranial fontanel entirely closed in juveniles and adults; premaxillae larger than maxillae, those of opposite sides meeting broadly in front of snout; premaxillary teeth relatively large; supramaxilla absent; vertebrae 66–79 (Salanginae) 4

3b. Head moderately depressed; snout moderately elongate and broadly rounded; cranial fontanel with anterior and posterior portions open throughout life, premaxillae smaller than maxillae, more or less separated from each other in front of snout; premaxillary teeth relatively small, tiny, or absent; supramaxilla present; vertebrae 48–65 (Salangichthyinae) 7

4a. Tongue with a median row of conical teeth (subgenus *Leucosoma*) .... *Salanx reevesi*

4b. Tongue toothless 5

5a. Head strongly pointed; lower jaw not projecting beyond upper jaw; presymphyseal fleshy appendage, bone, and teeth frequently present in adults; vertebrae 72–79 (subgenus *Salanx*) 6

5b. Head less strongly pointed; lower jaw projecting slightly beyond upper jaw; no presymphyseal fleshy appendage, bone, or teeth; vertebrae 70–73 (subgenus *Hemisalanx*) .... *Salanx prognathus*

6a. Presymphyseal bone usually present in specimens over 100 mm standard length, relatively elongate and with up to 17 teeth on each side; vertebrae usually 77–78 (rarely 76 or 79) .... *Salanx cuvieri*

6b. Presymphyseal bone usually absent, or relatively short and with no more than 6 teeth on each side; vertebrae 72–75 .... *Salanx ariakensis*

7a. Palatal toothplate with minute teeth; premaxilla with numerous small or minute teeth, snout relatively elongate; vertebrae 59–65 (*Salangichthys*) 8

7b. Palatal teeth absent; premaxilla usually toothless or with 1–5 minute teeth; snout relatively short except in *Neosalanx andersoni*; vertebrae 48–65 (*Neosalanx*) 9

8a. Pectoral fin-rays 14–19 .... *Salangichthys microdon*

8b. Pectoral fin-rays 20–28 .... *Salangichthys ishikawae*

9a. Snout relatively short, standard length to 64 mm, males with 14–21 anal scales, vertebrae fewer than 60 10

9b. Snout relatively elongate, standard length to 100 mm, males with 20–28 anal scales, vertebrae 63–65 .... *Neosalanx andersoni*

10a. Vertebrae 55–59; standard length to 64 mm; total rakers on first gill arch 15–19 (mainland Asia) .... *Neosalanx brevirostris*

10b. Vertebrae usually 50–53, rarely 49 or 54; standard length usually less than 50 mm; total rakers on first gill arch 9–15 (mainland Asia) .... *Neosalanx jordani*

10c. Vertebrae 52–56, average 53.75 (after Wakiya and Takahasi 1937); standard length to 58 mm; total rakers on first gill arch 15 (known only from Ariake Bay, Kyushu, Japan) .... *Neosalanx reganius*

11a. Horizontal diameter of eye less than 4% of standard length; ceratobranchial 5 with 0–3 small conical teeth; total rakers on first gill arch 0–2; vertebrae 41–43 .... *Sundasalanx microps*

11b. Horizontal diameter of eye more than 5% of standard length; ceratobranchial 5 with about 8–10 large conical teeth; total rakers on first gill arch 10–12; vertebrae 37–41 .... *Sundasalanx praecox*

MATERIAL EXAMINED

Salangoid specimens deposited in the following institutions have been examined for this study: American Museum of Natural History, AMNH: British Museum (Natural History), BMNH; California Academy of Sciences, CAS, including specimens formerly deposited at Stanford University, CAS-SU; Museum national d'Histoire naturelle, Paris, MNHN; Naturhistoriska Riksmuseet, Stockholm, NRM: Museum of Zoology, University of Michigan, UMMZ; Smithsonian Institution, USNM; and Zoologisch Museum, Universiteit van Amsterdam, ZMA.

A detailed list of material examined (including alcian-alizarin preparations) is given under each species in the systematic account.

SKELETAL ANATOMY

Salangoid skeletal anatomy cannot be observed adequately from alizarin preparations because it is largely cartilaginous, and even ossified portions (including dermal bones) often fail to stain with alizarin. The only previous observations of salangoid skeletal anatomy are brief and relatively uninformative. The only general account, that of McDowall (1969:815), is limited to three paragraphs, one on the cranium, one on the jaws, and one on the remainder of the skeleton emphasizing the median fins. Wakiya and Takahasi (1937) figured toothed portions of the jaws, palate, and tongue of various salangids. Nelson (1970) described and figured the gill arches in *Salanx reevesi* and *Neosalanx brevirostris*

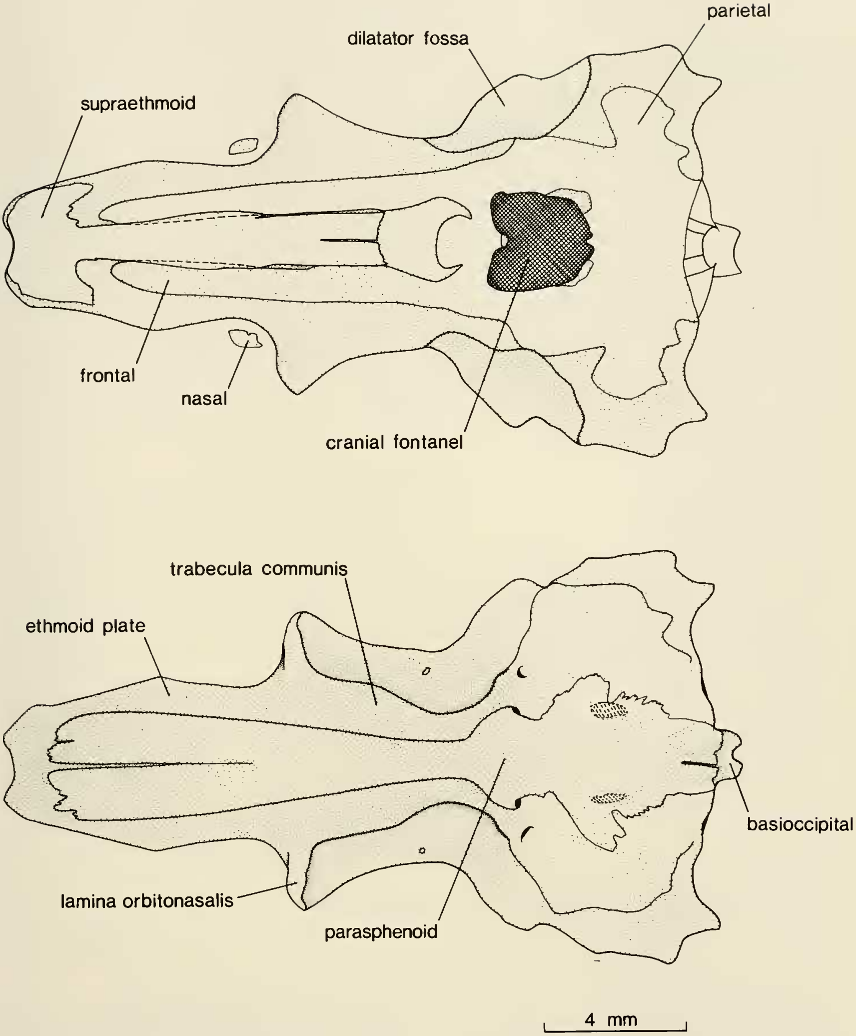

FIGURE 3. Dorsal and ventral view of cranium. *Protosalanx chinensis*, CAS-SU 6306, 158 mm.

(his *Salanx chinensis* and *Salangichthys microdon*). He particularly noted the well-developed fourth hypobranchials, "which so far as known are absent from all other adult teleostean fishes." My own observations and drawings of salangid gill arches agree closely with Nelson's. Rosen (1974; figs. 16g, 26a & b) figured and commented briefly upon the caudal skeleton and portions of the gill arches of *Neosalanx brevirostris* (his *Salangichthys microdon*).

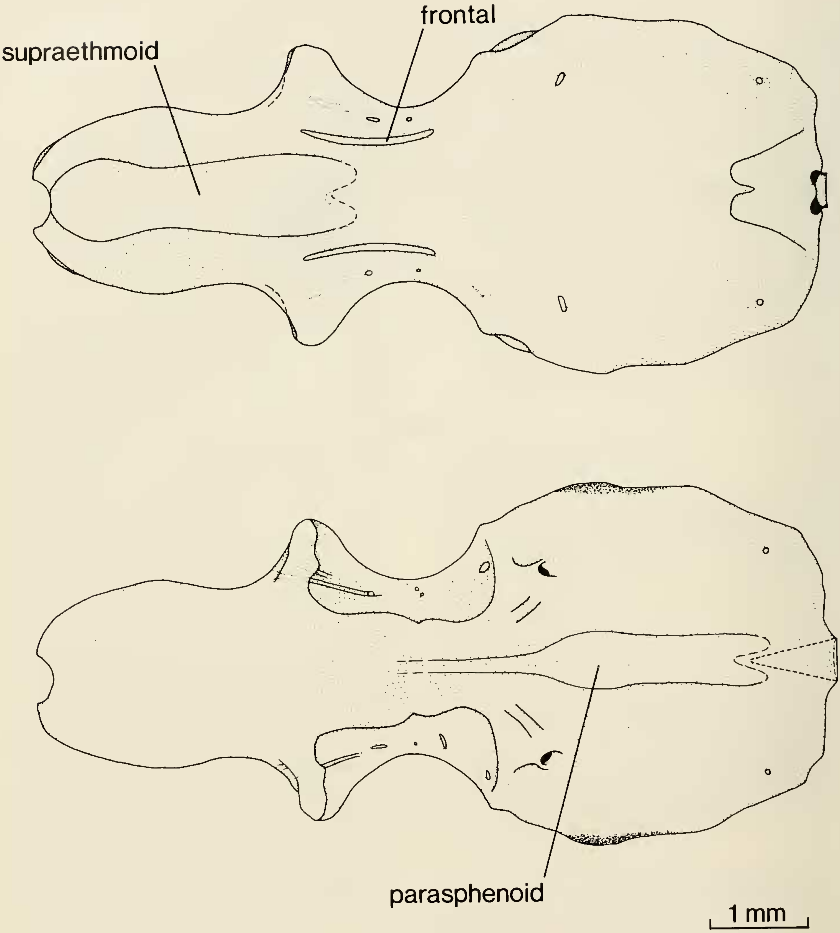

Figure 4. Dorsal and ventral view of cranium. *Salanx cuvieri*, CAS-SU 32454, 69.4 mm.

The advent of a technique for staining whole specimens with alcian and alizarin (Dingerkus and Uhler 1977) made the present relatively extensive observations possible but even so there have been difficulties. Some specimens stained well with alcian but not with alizarin, or vice versa, and in some specimens that otherwise stained well with both stains there are still portions of the skeleton which failed to take up noticeable amounts of either stain. Such difficulties could not always be made up for by staining additional specimens.

In general, alizarin stains only bone. Alcian stains cartilage but also stains some skeletal features which are obviously bony and have no cartilaginous precursors, such as fin-rays. Cartilaginous structures, however, often stain much more deeply with alcian than such non-cartilaginous structures. Thus the salangoid hyopalatine is almost always stained deep blue and the opercle

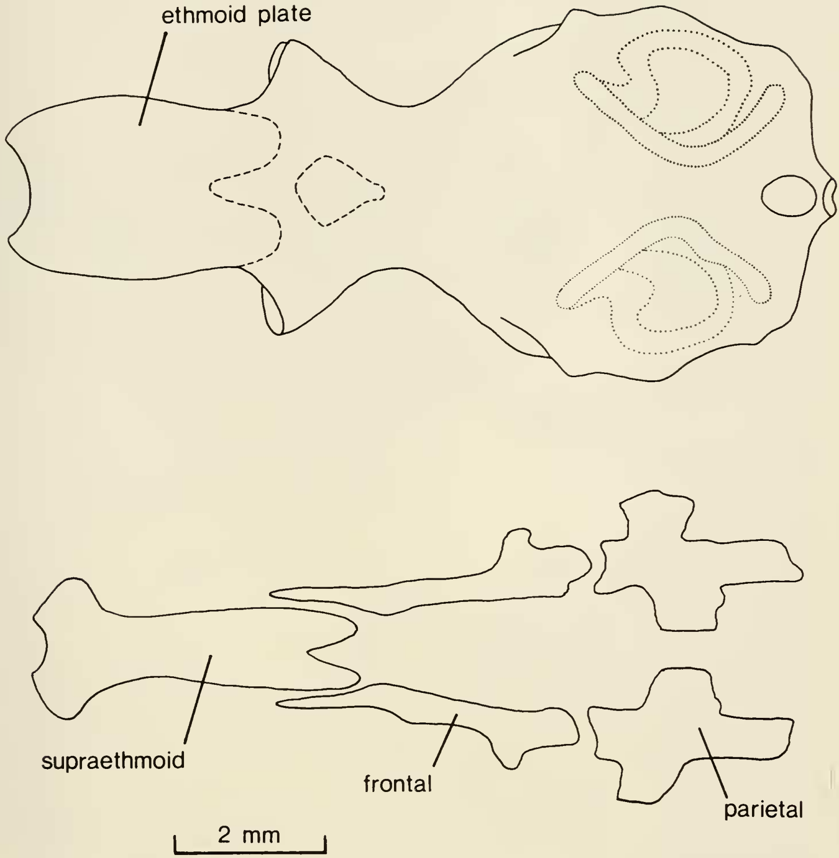

FIGURE 5. Dorsal view of cranium and membrane bones on dorsal surface of cranium. *Salanx prognathus*, CAS 51439, 110 mm.

appears variably pale blue and/or red. In a few of my figures such differences are indicated by the intensity of stippling, but in general the distribution of stain is far too complex to permit its representation in black-and-white illustrations. Some idea of the difficulty involved may be gained from Figure 20 (pelvic girdle of *Protosalanx*), in which the distribution of stain is indicated. In the cranium the distribution is far more complicated and could be conveyed only by illustrations in full color.

CRANIUM

(Figures 3–8)

The cranium of all salangoids is depressed, very strongly in Salanginae and almost as strongly in Protosalanginae, but relatively moderately in Salangichthyinae and Sundasalangidae. Some other features correlated with the cranial depression are the peculiarly underslung maxilla, ventrolateral eye position (especially in Salanginae), and perhaps the posteriorly recurved jaw teeth (especially in Salanginae and Protosalanginae).

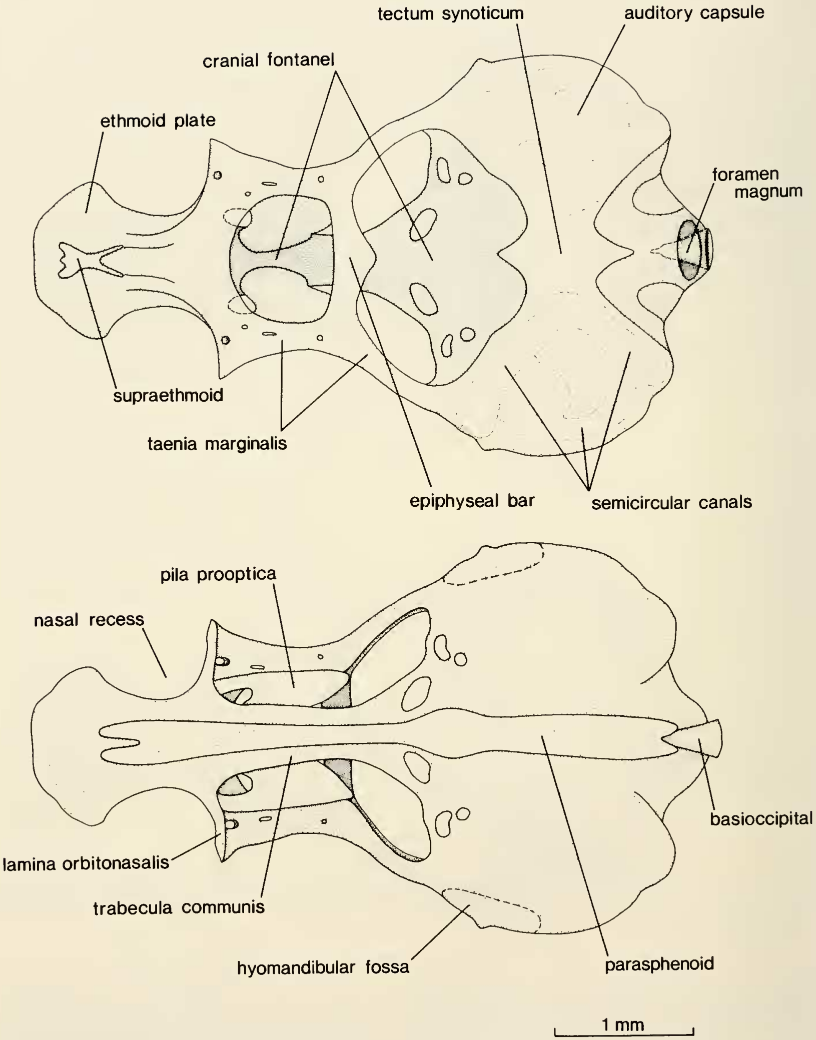

FIGURE 6. Dorsal and ventral views of cranium. *Neosalanx jordani*, CAS 52028, 38.3 mm.

The development of the cranial fontanel exhibits considerable differences. The fontanel apparently remains open anterior and posterior to the epiphyseal bar throughout life in Salangichthyinae and Sundasalangidae, although the anterior portion may be greatly reduced in larger Salangichthyinae. In Protosalanginae the anterior portion closes while the posterior portion always remains open, albeit much reduced in the largest specimens examined. In Salanginae the cranial fontanel is entirely closed in all specimens in which skeletal preparations have been examined.

Young Osmeridae in which the cranium is still

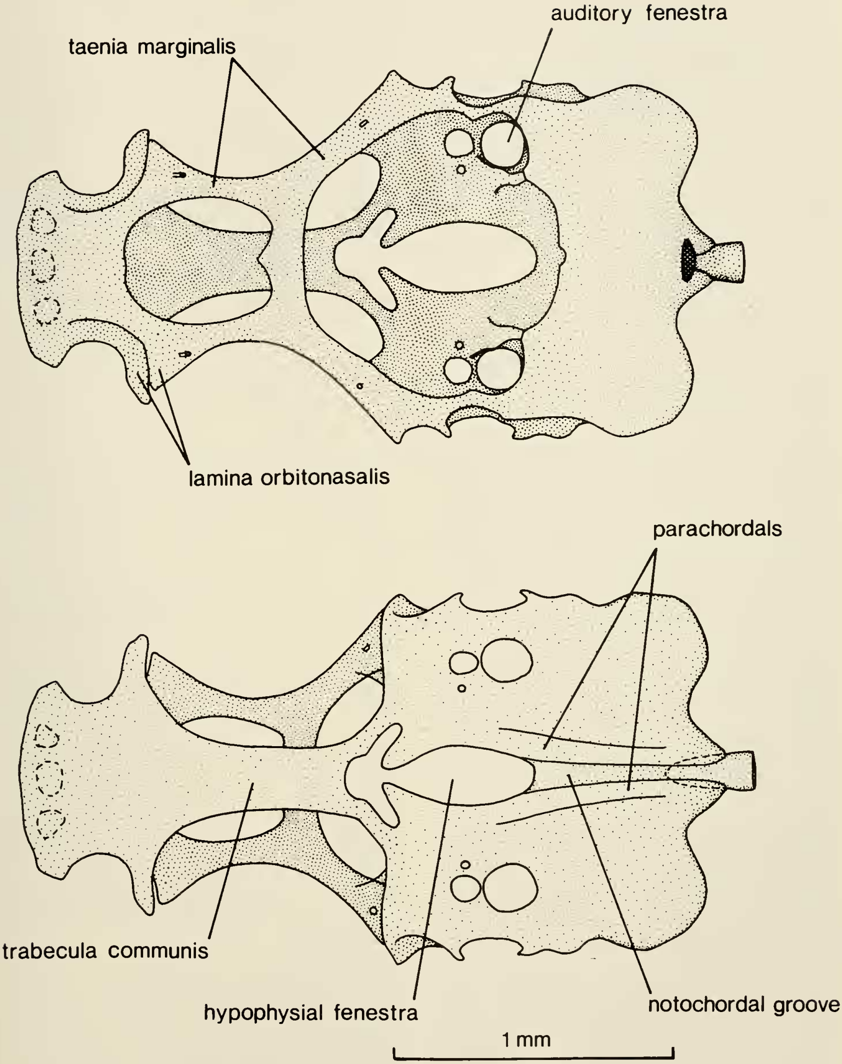

FIGURE 7. Dorsal and ventral views of cranium. *Sundasalanx microps*, CAS 44220, 17 mm.

cartilaginous have a median bar (taenia tecti medialis) separating the anterior and posterior portions of the cranial fontanel into left and right halves. Such a feature is usually but not invariably absent in salangoids. In a series of ten *Neosalanx jordani* (39.7–45.7 mm), nine have the cranial fontanel entirely undivided, but one (41.0 mm) has a median cartilaginous bar dividing both the anterior and posterior portions of the fontanel. The bar is slender posteriorly, but anteriorly it is much wider, so that the anterior portion of the fontanel is represented by two widely

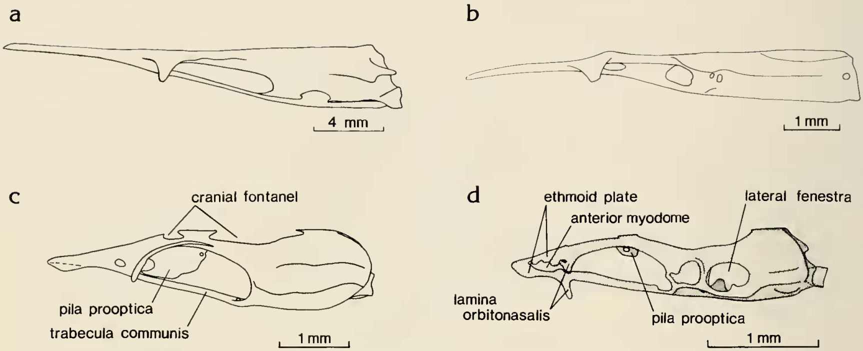

FIGURE 8. Lateral view of cranium. (a) *Protosalanx chinensis*, CAS-SU 6306, 158 mm; (b) *Salanx cuvieri*, CAS-SU 32454, 69.4 mm; (c) *Neosalanx jordani*, CAS 52028, 38.3 mm; (d) *Sundasalanx microps*, CAS 44220, 17 mm.

separated and relatively small openings. The epiphyseal bar in this specimen is also larger than usual. The condition of the cranial fontanel in this specimen closely resembles that observed in osmerid chondrocrania. In *Protosalanx* of 85–89 mm, the anterior portion of the cranial fontanel is similarly divided into greatly reduced left and right openings, which become entirely closed in specimens slightly larger.

The ethmoid plate is greatly enlarged in all salangoids. In Salangichthyinae and Sundasalangidae it is broad and moderately elongate, while in Protosalanginae and Salanginae it is broad and extremely elongate. Ossification of the chondrocranium is relatively poor in all salangoids but varies greatly. The greatest amount of cranial ossification is observed in the skulls of the largest *Protosalanx*, in which the supraethmoid, frontals, parietals, parasphenoid, and basioccipital are all stained more or less deeply with alizarin. In large *Protosalanx* the posterior portion of the parasphenoid has broad lateral wings and the basioccipital has small thin lateral wings (largely obscured by the overlying parasphenoid). Neither of these features has been observed in other salangoids. In all other salangoids the basioccipital ossification is apparently restricted to the basioccipital centrum.

In Protosalanginae the outline of the cranium is more irregular, suggesting a more primitive condition; while in Salanginae it is relatively smooth and streamlined, suggesting a more derived or specialized condition. The auditory capsules are most pronounced or laterally prominent in Salangichthyinae.

The interorbital septum is relatively open in Sundasalangidae and Salangichthyinae, almost as open in Protosalanginae, but greatly reduced in Salanginae. In Salangichthyinae the anterior-medial portion of the orbit is occupied by very large pilae proopticae arising from the ventral surface of the taenia marginalis or anterior supraorbital cartilage. In Sundasalangidae the pilae proopticae are rudimentary.

A number of cranial features that occur in Sundasalangidae have not been observed in the other (mostly juvenile and adult) salangoids examined. Thus the lamina orbitonasalis, which appears as a single apparently simple entity in other salangoids, has two components in *Sundasalanx*: a dorsoanterior contribution from the taenia marginalis and a ventroposterior contribution from the trabecular communis or posteroventral portion of the ethmoid plate. The ethmoid plate is separated by the anterior myodome into dorsal and ventral portions; the anterior myodome extends anteriorly almost to the tip of the snout. In other salangoids the anterior myodome lies much farther posterior, and the ethmoid plate is relatively thin and more or less greatly depressed (least so in Salangichthyinae).

In *Sundasalanx* the base of the cranium is largely occupied by the hypophysial fenestra, a character of all developing teleost chondrocrania usually lost at an early stage. In all other salangoids the hypophysial fenestra is closed off by cartilaginous growth and the area it once occupied may be overlaid by the parasphenoid. In Sundasalangidae the passage for the internal carotid artery is represented by an anterolateral

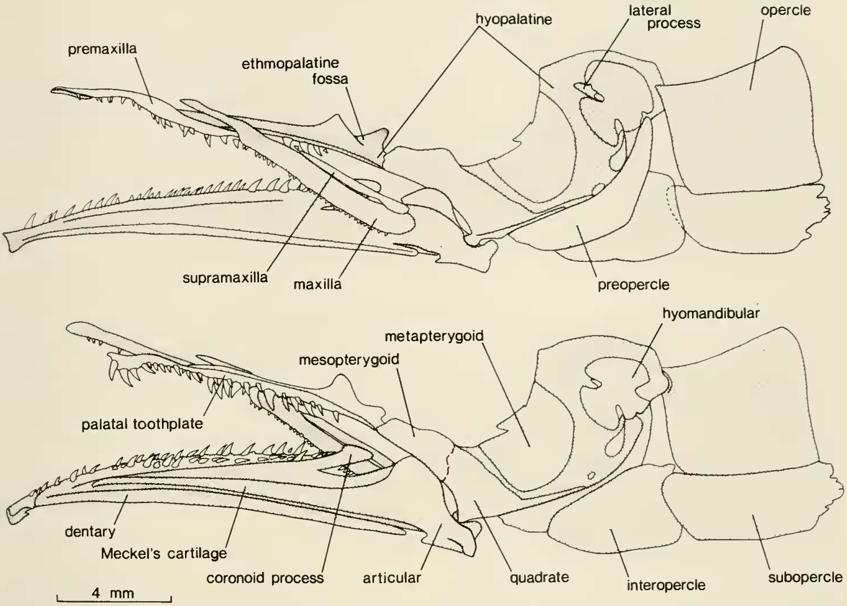

FIGURE 9. Lateral view of jaws, suspensorium, and opercular bones. *Protosalanx chinensis,* CAS-SU 6306, 158 mm.

extension of the hypophysial fenestra; in all other salangoids the passage for this pair of arteries is isolated and widely separated.

In *Sundasalanx* the base of the cranium exhibits a median groove on either side of which extends a slight ridge. This groove probably represents the pathway of the embryonic cranial notochord before its absorption (complete in all other salangoids examined) into the basioccipital centrum. The ridges on each side may be remnants of the parachordal cartilages.

JAWS

(Figures 9–13)

The jaws of salangoids are relatively generalized, in that the jaw bones, their shape, and the distribution of teeth on them are similar to those in many lower teleosts. In all salangoids the maxilla is toothed and enters broadly into the gape. All salangoids have a single supramaxilla, except Salanginae, in which this element is lacking. In some Salanginae the bony tip of the lower jaw is formed not by the dentaries, but by a median presymphyseal bone (usually tooth-bearing). Due in part to poor quality of alcian-alizarin staining of the lower jaw in salangoids, the relationships of bones that constitute it have not been adequately observed. The premaxillae and maxillae are somewhat variable (see remarks in systematic account).

SUSPENSORIUM

(Figures 9–13)

The outstanding feature of the salangoid suspensorium is the union of the hyomandibula (hyosymplectic) and pterygoquadrate, which are united into a single continuous cartilaginous element, here called the hyopalatine (=palatohyomandibuloquadrate of Roberts 1981). Only in *Sundasalanx praecox* is the hyopalatine divided into anterior and posterior portions, but the division apparently is more anterior than the primitive division between hyomandibula (or hyosymplectic) and pterygoquadrate.

In developing vertebrates the rudimentary mandibular arch divides into two cartilages where it bends around the corner of the mouth: the pterygoquadrate bar (dorsal) and the mandibular bar or Meckel's cartilage (ventral). The rudimentary hyoid arch divides into the hyomandibular (dorsal) and hyoid bar (ventral). All salangoids except *Sundasalanx praecox* show the

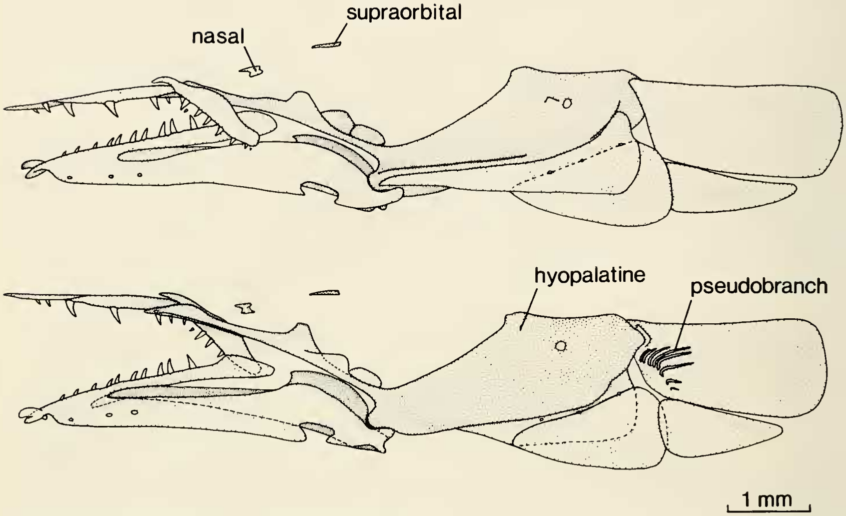

FIGURE 10. Lateral and medial views of jaws, suspensorium, and opercular bones. *Salanx cuvieri*, CAS-SU 32454, 69.4 mm.

most unusual condition of having the dorsal portions of the mandibular and hyoid arches fused into a single element. This salangoid element has readily definable features corresponding to the palatine or pterygoid, quadrate, and hyomandibula of teleosts in which these elements are separate, but it is unclear whether a portion representing the symplectic is present.

No separate symplectic has been detected in any salangoid; the symplectic may be represented by a thickening or ridge near the ventral margin of the quadrate portion of the hyopalatine.

In Sundasalangidae and some Salanginae and Salangichthyinae the suspensorium consists solely of the cartilaginous hyopalatine, but in other Salanginae and Salangichthyinae and in Protosalanginae a number of perichondral, endochondral, or dermal ossifications develop on the suspensorium. The elements most often added are the mesopterygoid and an anterior palatal toothplate (=ectopterygoid?), which may or may not bear teeth. The suspensorium exhibits more ossification in large *Protosalanx* than in any other salangoids examined: heavily toothed palatal toothplate, mesopterygoid, and partial ossification of quadrate and hyomandibula.

Whether the dorsal portions of the mandibular and hyoid arches are similarly fused in any other fishes is unknown. In the few fishes for which the development of these arches has been adequately observed it would appear they are separate, including *Salmo* (DeBeer 1937), *Elops* (pers. obs.), *Hepsetus* (Bertmar 1959). In young salmoniforms I examined (including *Salmo, Galaxias, Lepidogalaxias, Hypomesus,* and *Spirinchus*) cartilaginous pterygoquadrate and hyomandibular or hyosymplectic are always separate.

Circumorbital Bones

(Figure 12)

A supraorbital bone is seen in all Salangidae but is absent in Sundasalangidae. The dermosphenotic or sixth infraorbital appears to be absent in all salangoids. An isolated infraorbital (fourth or fifth?) is seen in some Salangichthyinae but is greatly reduced (Fig. 12).

Gill Arches

(Figures 14–17)

The upper elements of the gill arches of salangoids are relatively generalized and, except in Sundasalangidae, so are the lower elements. Except for the upper and lower pharyngeal toothplates the salangoid gill arches apparently are entirely cartilaginous. Four basibranchials are probably present in all salangoids but in none are all of them separate. In Protosalanginae, Sa-

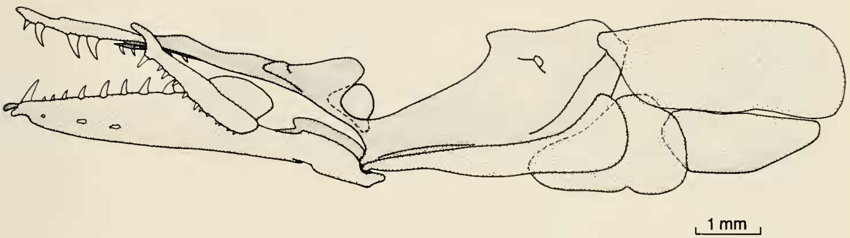

FIGURE 11. Lateral view of jaws, suspensorium, and opercular bones. *Salanx prognathus,* CAS-SU 51439, 110 mm.

langinae, and Salangichthyinae basibranchials 2 and 3 are indistinguishably fused to each other, and in some Salanginae basibranchials 1, 2, and 3 may be so fused.

All salangoids have four hypobranchials; hypobranchial 4 is always separate and relatively large.

The basibranchial series in salangoids is entirely cartilaginous. Not only do the basibranchials themselves not ossify, but basibranchial toothplates, a characteristic feature of many salmoniforms including salmonids, osmerids, and galaxiids, are absent. The basic basibranchial arrangement in Salangidae appears to be basibranchial 1 separate, basibranchials 2 and 3 fused, and basibranchial 4 separate. A basibranchial 5 is fused to basibranchial 4 in various salmoniforms, and is apparently usually present in many salmonoids, osmeroids, and galaxioids (including *Lepidogalaxias*) as a thin cartilaginous shaft projecting posteriorly between the fifth ceratobranchials. In some instances there is a clear demarcation between basibranchials 4 and 5, and they may be separate or at least not completely fused. Basibranchial 5, fused with basibranchial 4, is indicated in Salangidae by Nelson (1970), but in Salangidae I have examined there is no indication of a fusion or demarcation between the presumed basibranchial 5 and basibranchial 4. Basibranchial 5 does not project so far posteriorly nor is it slender and rodlike as in other Salmoniformes in which its presence is less doubtful. I therefore tentatively consider basibranchial 5 absent in Salangidae. That it is absent in Sundasalangidae seems highly likely.

Gill rakers are poorly ossifed (never stained with alizarin) and edentulous (frequently dentigerous in salmonoids, osmeroids, esocoids). Those on the trailing (inner) face of the arches usually are fewer and smaller than those on the leading (outer) face (Figs. 14–17). Total number of gill rakers on leading face of first gill arch is 8–19 in Salangidae and 0–10 in Sundasalangidae (Table 2).

Dentition

The most complete and presumably most primitive dentition in salangoids is observed in

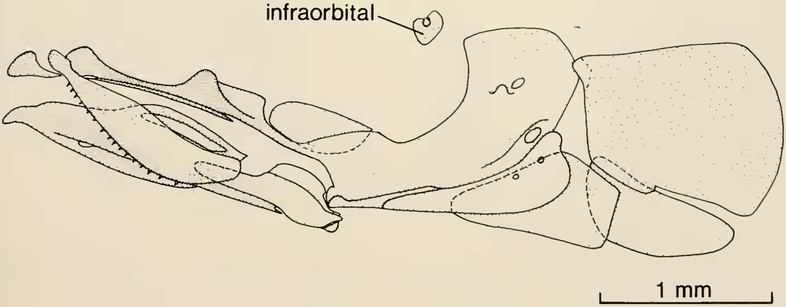

FIGURE 12. Lateral view of jaws, suspensorium, and opercular bones. *Neosalanx jordani,* CAS 52058, 35.1 mm.

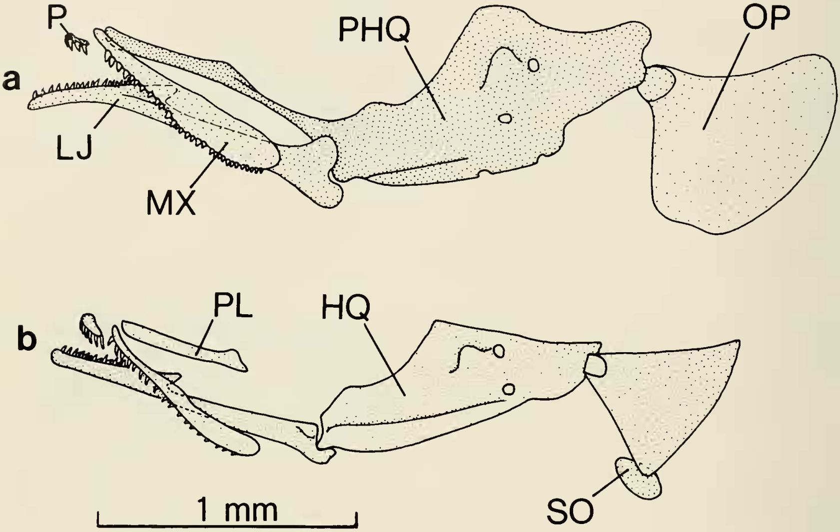

FIGURE 13. Lateral view of jaws, suspensorium, and opercular bones. (a) *Sundasalanx praecox,* CAS 52031, 17 mm; (b) *Sundasalanx microps,* CAS 44290, 17 mm. HQ = hyomandibula + quadrate, LJ = lower jaw or Meckel's cartilage, MX = maxilla, P = premaxilla, PHQ = hyopalatine cartilage, PL = palatine, OP = opercle, SO = subopercle.

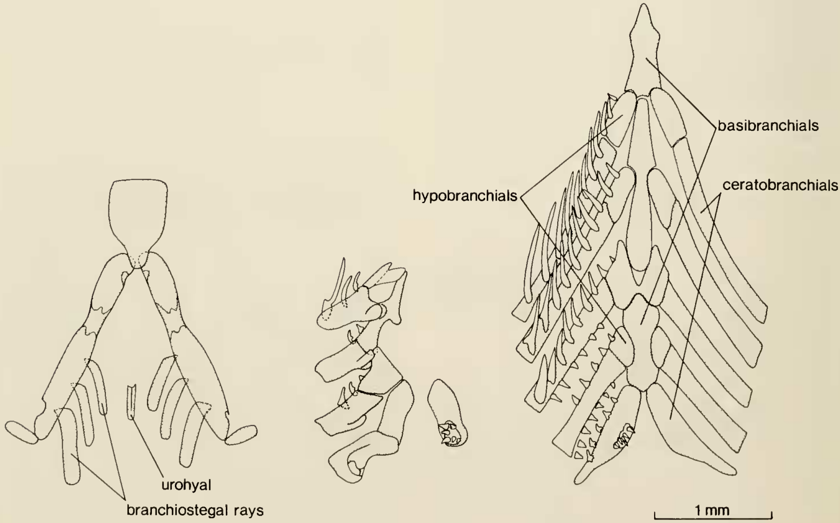

FIGURE 14. Dorsal and ventral views of hyoid and branchial arches. *Protosalanx chinensis,* CAS-SU 6306, 153 mm.

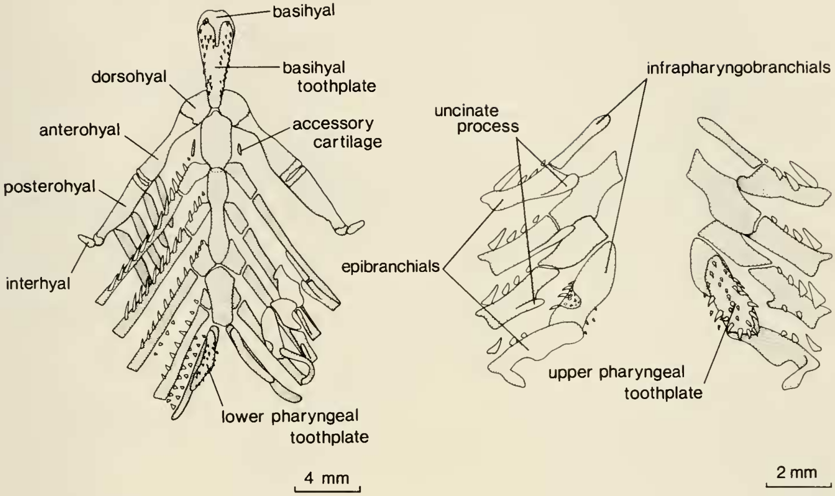

FIGURE 15. Dorsal view of hyoid and branchial arches and ventral view of upper pharyngeal elements. *Salanx cuvieri,* CAS-SU 32454, 69.4 mm.

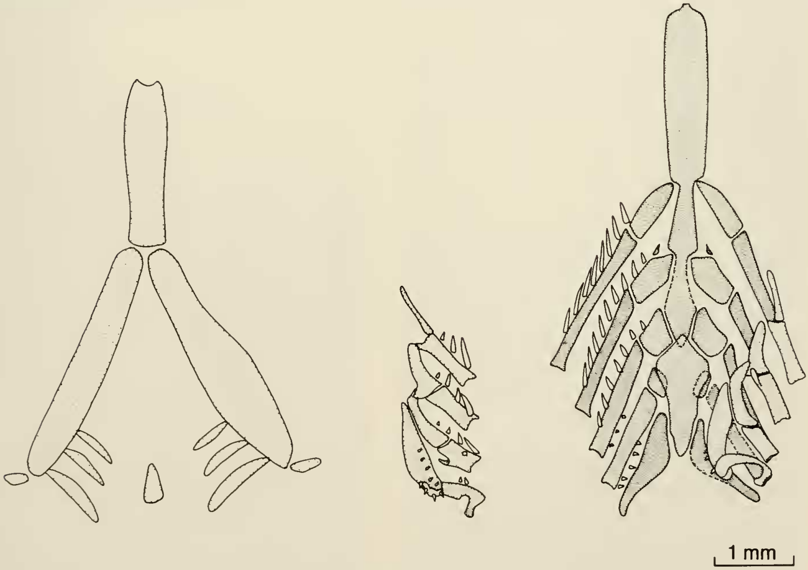

FIGURE 16. Dorsal view of hyoid and branchial arches; ventral view of infrapharyngobranchial 4 and upper pharyngeal toothplate. *Neosalanx jordani,* CAS 52058, 38.3 mm.

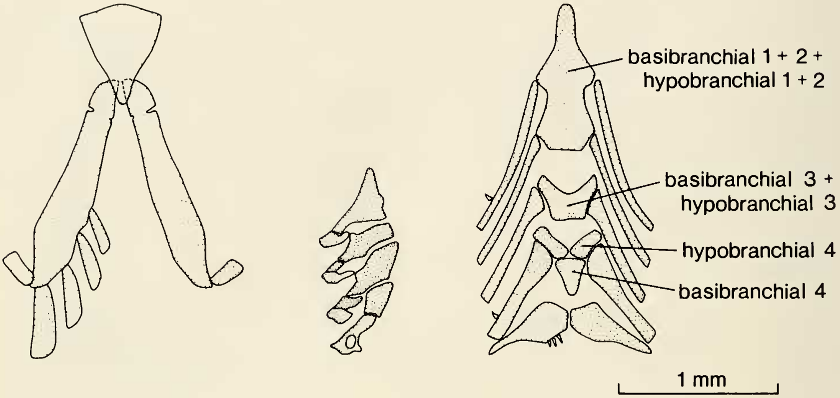

FIGURE 17. Dorsal view of hyoid and branchial arches. *Sundasalanx microps*, CAS 44220, 17 mm.

Protosalanx, with numerous large, conical teeth on the premaxilla, maxilla, palatal toothplate (=ectopterygoid?), tongue (basihyal toothplate), and upper and lower pharyngeal toothplates. As in all Salangidae, there are only two pairs of pharyngeal toothplates: the upper, on infrapharyngobranchial 4, and the lower, on ceratobranchial 5; the branchial arches are otherwise entirely toothless.

In *Protosalanx* the teeth on the palatal toothplate and lower jaw are in two rows, as in many other salmoniforms, but in all other salangoids the teeth on each tooth-bearing element except those in the pharynx are restricted to single rows. In largest specimens of *Protosalanx* the tongue teeth are more or less widely scattered over the surface of the basihyal (as in Fig. 9), but in smaller ones they are restricted to two marginal rows, as in salmoniforms generally. The only other salangoid with tongue teeth, *Salanx* (*Leucosoma*) *reevesi*, has them in a single median row on the basihyal toothplate, a unique specialization for salmoniforms. This character is diagnostic of the subgenus *Leucosoma*.

The maxilla and lower jaw are well-toothed in all salangoids; the palate is toothless in *Neosalanx* and *Sundasalanx*. In *Neosalanx* the teeth on the premaxilla, maxilla, and lower jaw are very small, and frequently the premaxilla and lower jaw are entirely toothless. In *Sundasalanx* bony pharyngeal toothplates apparently fail to form, and the pharyngeal teeth appear to be directly attached to the cartilaginous infrapharyngobranchial 4 and ceratobranchial 5. The only bony tooth-bearing elements in *Sundasalanx* appear to be the premaxilla and maxilla; the lower jaw teeth are loosely attached to Meckel's cartilage.

PECTORAL GIRDLE

(Figures 18–19)

All salangoids have a secondary pectoral girdle (connecting the primary girdle to the back of the cranium) consisting of three dermal bones: posttemporal, supracleithrum, and cleithrum. Postcleithra are absent except in Salanginae, in which there is a single postcleithrum. In Salangidae, the primary shoulder girdle consists of the entirely cartilaginous paired scapulocoracoids and one or two series of radials. The basic number of primary radials appears to be five in all Salangidae. The first primary radial, associated with the outermost (enlarged) pectoral fin-ray, is relatively simple; it is largest in males of Protosalanginae and Salanginae. The other primary radials are complex, with numerous deep divisions approximately corresponding in number to the fin-rays. These divisions are most numerous in Salangichthyinae, particularly *Neosalanx*, but are well developed in all Salangidae. Comparable divisions or fimbriae occur in the pectoral basal plate of

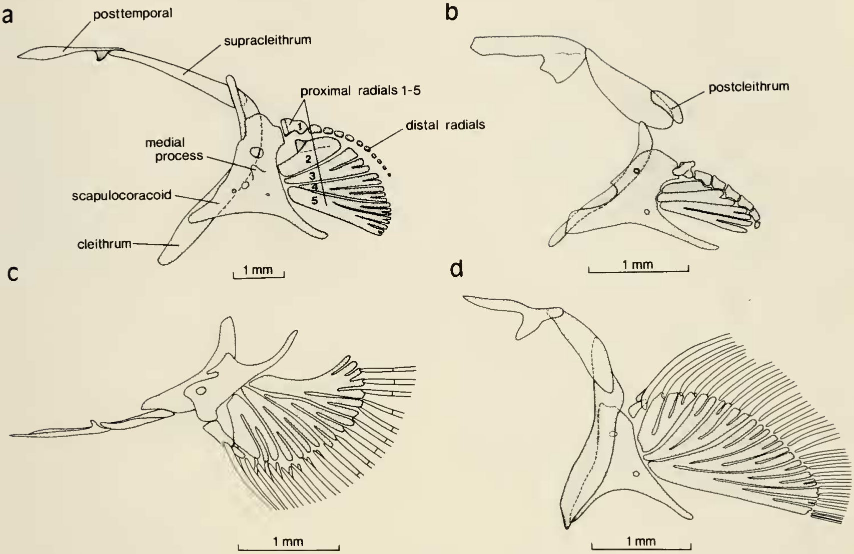

Figure 18. Left half of pectoral girdle. (a) *Protosalanx chinensis,* CAS-SU 6306, 158 mm (medial view); (b) *Salanx cuvieri,* CAS-SU 32454, 69.4 mm (lateral view); (c) *Neosalanx jordani,* CAS 52058, 43.1 mm (dorsal view); (d) *Salangichthys ishikawae,* CAS 6780, 74 mm (lateral view).

the salmoniform *Dallia pectoralis* but are not present in other salmoniforms I have examined and do not seem to have been reported in any other teleosts. Secondary radials, more or less corresponding in number to the pectoral fin-rays, are small and simple. The mesocoracoid is lacking in all salangoids except that *Protosalanx* has a process on the median surface of the scapulocoracoid that may represent the ventral portion of the mesocoracoid (Fig. 18a, medial process). In Sundasalangidae the primary pectoral girdle consists of a U-shaped median scapulocoracoid and a basal plate. Fin-rays are absent.

Pelvic Girdle

(Figure 20)

The left and right halves of the pelvic girdle develop in the ventral myotomic wall, and, as the ventral myotomic progression is arrested in Salangidae while the myotomes are still widely separated, the pelvic girdle halves remain widely apart and fail to form any sort of ligamentous or cartilaginous connection between each other. As pointed out by Klyukanov (1975), in Salmoniformes the two halves of the pelvic girdle are usually joined at least anteriorly for a short distance by strong cartilaginous or ligamentous tissues.

Axial Skeleton

(Figure 1)

All salangoids have a pair of small dorsal cartilages straddling the intervertebral disc between the basiocciptal and first vertebral disc; such cartilages occur in many (perhaps most or all) Salmoniformes.

In all Salangidae the neural arches of vertebrae 1 and 2 are fused dorsally; this condition has not been observed in Osmeridae or any other salmoniforms I have examined. In Sundasalangidae the neural arches of vertebrae 1 and 2 are separate from each other and morphologically similar to those of the vertebrae immediately succeeding them.

In salangoids the mineralized portion of each centrum is relatively elongated and hourglass shaped, so that the intervertebral joints are narrow and the notochord greatly constricted. In

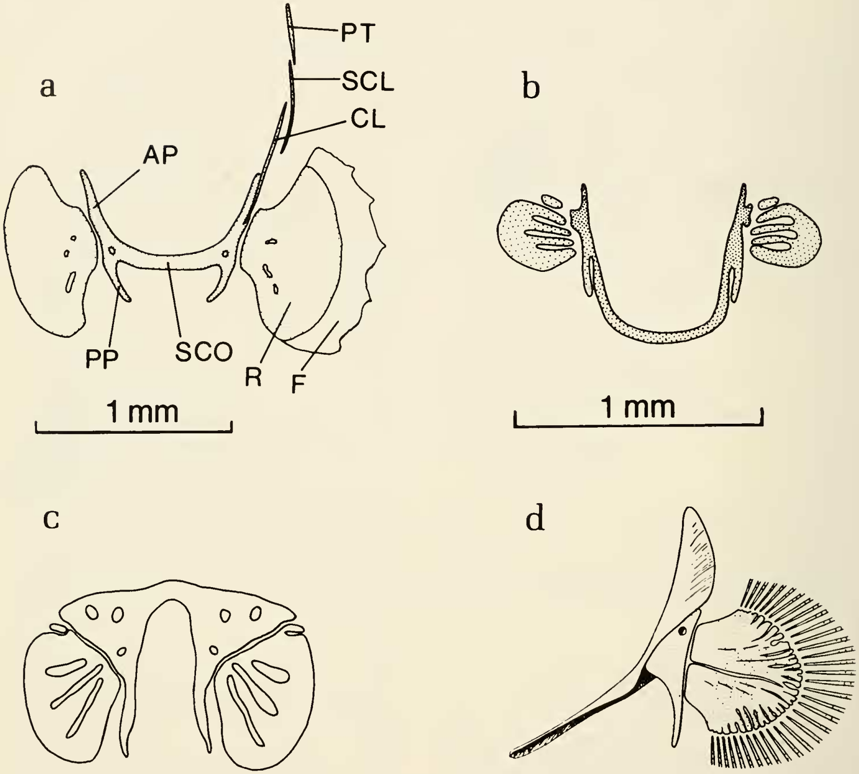

FIGURE 19. Pectoral girdle. (a) *Sundasalanx microps,* CAS 44220, 17-mm adult (posterior view); (b) *Elops hawaiiensis,* CAS 52035, 30-mm leptocephalus larva (posterior view); (c) *Sardina pilchardus,* 20–30 mm (ventral view?, after Goodrich 1922); (d) *Dallia pectoralis,* (lateral view, after Starks 1904; apparently based on CAS-SU 12615, 125 mm, Nushagak River, Alaska); AP = ascending process, CL = cleithrum, F = fin margin, PP = posterior process, PT = posttemporal, R = basal plate, SCL = supracleithrum, SCO = scapulocoracoid. In (b) and (c) the first primary radial has pinched off from the basal plate.

salmonids, osmerids, galaxiids, and other Salmoniformes, especially in the young stages, the mineralized portion of each centrum tends to be relatively short and cylindrical, so that the intervertebral space is much larger and the vertebral section of the notochord is entirely intact. A comparable condition is not present in any salangoid skeletal material I have examined.

Ribs are absent or weakly developed and stain poorly. They are small, weakly stained with alcian when present (Fig. 1b).

Gosline (1960) and others have pointed out that neural and hemal spines of most Salmoniformes, especially posteriorly, may be flattened or laminar, even to the extent of resembling a continuous keel. The neural and hemal spines of salangoids are always relatively slender, especially posteriorly.

A round, oval, or elongate and splintlike adipose fin cartilage lies at the base of the adipose fin in all Salangidae. A survey of lower teleosts for the adipose fin cartilage by Matsuoka and Iwai (1983) revealed its presence in Salangidae, Osmeridae, Plecoglossidae, Myctophidae, and Neoscopelidae; it was not observed in other lower teleosts with an adipose fin including Sal-

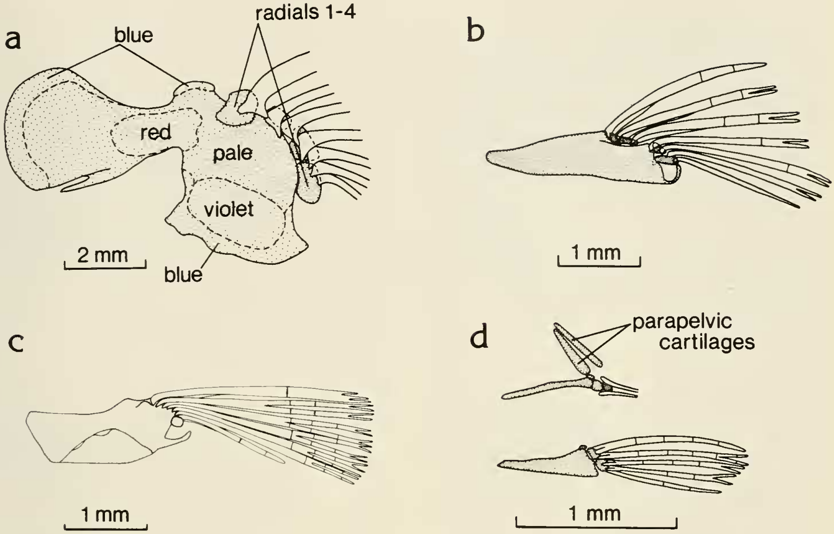

FIGURE 20. Ventral view of left half of pelvic girdle. (a) *Protosalanx chinensis*, CAS-SU 6306, 158 mm; (b) *Salanx cuvieri*, CAS-SU 32454, 69.4 mm; (c) *Neosalanx jordani*, CAS 52028, 43.1 mm; (d) *Sundasalanx microps*, CAS 44220, 17 mm (with lateral view of pelvic girdle and parapelvic cartilages above).

monidae, Retropinnidae, Prototroctidae, Aulopodidae, Synodontidae, Chlorophthalmidae, Argentinoidei, Characoidei, or Siluriformes. The similar morphology of the adipose fin cartilages in Salangidae and Osmeridae, as noted by Matsuoka and Iwai, is possibly indicative of relationship between these two families.

Caudal Fin Skeleton

(Figure 21)

The caudal fin is more or less deeply forked, and the upper and lower lobes are about equal. Principal caudal fin-rays are invariably 10+9; upper and lower procurrent caudal fin-rays are moderately numerous (to 14). The complex ural or hypural centrum apparently consists of three centra and uroneural 1 (sometimes also uroneural 2?) fused into a single unit. The three centra involved are the terminal centrum and postterminal centra 1–2, according to the nomenclature of Gosline (1960), or preural centrum 1 and ural centra 1–2, according to Rosen (1974). In none of the skeletal material examined is there any indication of separate centra posterior to the complex hypural centrum. Epurals 0–3. A separate uroneural 2 is sometimes present, but uroneural 1 is apparently always fused to complex hypural centrum. Free radial or pterygial cartilages are sometimes present, usually between ray halves at the base of the anteriormost 2–3 upper or lower procurrent rays and the lowermost upper and uppermost lower principal rays. Hypurals six. Six separate hypurals occur in *Salangichthys microdon* (Rosen 1974, Fig. 26). *Protosalanx chinensis* occurs with hypurals 1–2 and 5–6 separate, but with 3–4 fused near the base. The hypurals are more fused in *Neosalanx, Salanx,* and *Sundasalanx*. In *Salanx* parhypural and hypurals 1–2 are fused near the base; hypurals 1–2 and 3–4 are fused for their entire length except for oblong basal foramina where fusion evidently failed to complete. In *Sundasalanx* parhypural and hypurals 1–3 are evidently fused into a single element.

SYSTEMATICS

In the present account the salangoids are recognized as a salmoniform superfamily separate from osmeroids, which they superficially resemble. There are two families, Sundasalangidae, with

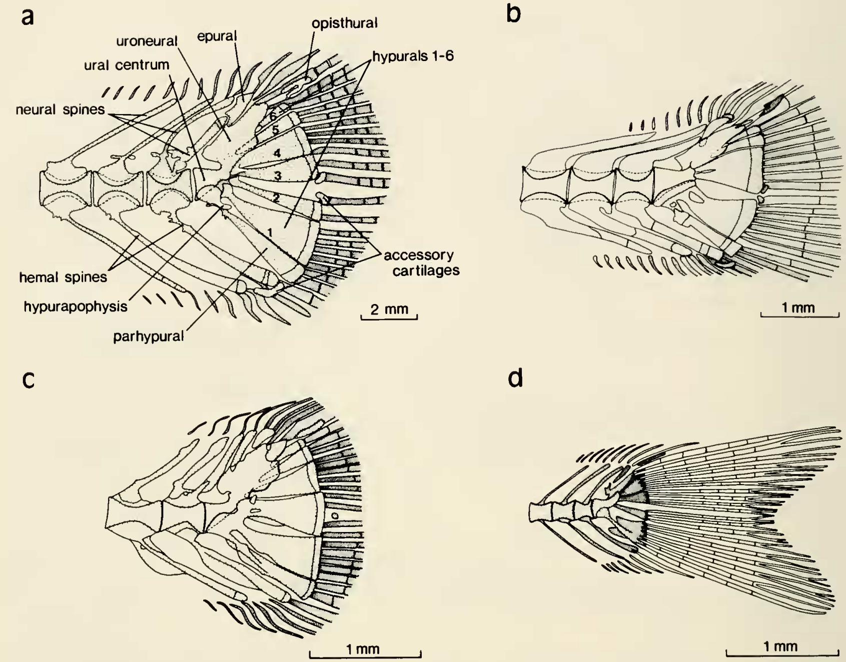

FIGURE 21. Lateral view of caudal fin skeleton. (a) *Protosalanx chinensis*, CAS-SU 6306, 158 mm; (b) *Salanx cuvieri*, CAS-SU 32454, 61.7 mm; (c) *Neosalanx jordani*, CAS 52028, 43.1 mm (note: hypurals 2 and 3, normally separate from each other in all salangoids, are fused in this specimen); (d) *Sundasalanx microps* CAS 44220, 17 mm. In a–c left half of fin rays removed to facilitate observation of median structures.

only a single genus and two species, and Salangidae. Salangidae is further divided into three subfamilies, four genera, and eleven species. The genus *Salanx* is further divided into three subgenera; this taxonomic category is not employed in the other genera of salangoids. In addition to the new superfamily Salangoidea, the new subfamily Salangichthyinae is proposed for *Neosalanx* and *Salangichthys*, leaving the subfamily Protosalanginae with only the genus *Protosalanx*. No new genera or species are proposed. Some previous workers, particularly Regan (1908b) and Fang (1934a, b) recognized far more species than I have, especially in the subgenus *Salanx* (genera *Salanx* and *Parasalanx* of Regan). This is attributable in part to their basing species on only one or a few type-specimens and utilizing characters such as cranial proportions, body depth, and relative position of dorsal and anal fins which vary considerably within the species. Neither Regan nor Fang utilized vertebral counts, which I find extremely useful in distinguishing species. My extensive data on vertebral counts of types and other material are presented in Table 2.

My counts of vertebrae, fin-rays (except pelvic) anal scales, branchiostegal rays, and gill rakers are presented in Table 2. This table includes all species of salangoids herein recognized as valid except *Neosalanx reganius*, which I have not examined. Pelvic fin-ray counts are excluded because they are invariably 5 in Sundasalangidae and almost invariably 7 in Salangidae (6 in one observed specimen of *Neosalanx jordani*, 8 in two specimens of *Salangichthys microdon*). Previous authors have presented data on most of the species but have often lumped data from various localities (and frequently of two or more species). In order to minimize this problem, my data are presented separately for each locality.

Although Table 2 includes meristic data obtained from whole specimens, radiographs, and cleared and stained specimens, the stained specimens provide the best material for accurate count of fin-rays, teeth, and gill rakers. It is difficult to observe the jaw teeth and lowermost pectoral fin-rays in *Neosalanx* except in stained material. In dorsal and anal fin-ray counts the last "two" rays ("divided to base") are counted as one ray. In vertebral counts the basioccipital centrum is not counted and the hypural complex centrum is counted as one. In salangoids, especially in females, the anteriormost anal-fin pterygiophore does not provide a ready basis for distinguishing abdominal and caudal vertebrae. In order to obtain additional meristic data from the vertebral column and at the same time obtain more precise data on the relative position of fin origin, I have taken data on the vertebrae parallel to the origins of the pelvic, dorsal, and anal fins. The number of vertebrae posterior to a vertical line through the base of the last anal fin-ray is also recorded.

Radiographs are usually satisfactory for obtaining vertebral counts of salangoids and sometimes for fin-ray counts. Sometimes the vertebrae may show up very faintly but it is almost always possible to obtain a count repeatable to within one vertebra. Fin-rays, however, frequently cannot be accurately counted on radiographs, and I have only incorporated data on fin-ray counts taken from radiographs when the radiographs seemed reliable.

Some characters utilized by other workers to distinguish species are not emphasized here because they do not seem useful. This particularly applies to pectoral fin-ray counts in *Neosalanx* and to the elongation of the head or cranium, relative position of the dorsal- and anal-fin bases, and body depth, especially in *Salanx*. In salangids the number of pectoral fin-rays generally continues to increase slightly with growth, especially so in those such as *Neosalanx*, in which the rays are exceptionally numerous. The elongation of the cranium (particularly its anterior portion) is extremely variable in *Salanx*, as noted also by Wakiya and Takahasi (1937:289). This variation is individual and is probably enhanced by growth. The position of the dorsal and anal fins relative to each other is also highly variable in salangids, subject to individual variation as well as sexual dimorphism. In defining species of *Salanx* too much reliance has been placed on slight differences in fin positions based on only one or two specimens. *Salanx, Salangichthys,* and other salangids vary enormously in body depth due to sex-related body changes and nonsexual factors of condition and preservation.

In discussing salmonoid classification, Gosline (1971:119) stated:

> The suborder Salmonoidei as here recognized (Families Salmonidae, Osmeridae, Plecoglossidae, Salangidae, Retropinnidae, Aplochitonidae, and Galaxiidae) is a group of highly diverse inshore and freshwater salmoniform fishes. Though the included families no doubt should be divided into superfamily groupings, inadequate knowledge of the Salangidae and the Southern Hemisphere forms would seem to make any formal superfamily classification premature at the present time. Informally, the members may be divided between Northern and Southern Hemisphere forms. The diverse forms from the Southern Hemisphere seem to be most closely related to the northern osmerids. . . . The Northern osmeroids are represented by four quite distinct lines: Salangidae, Plecoglossidae, Osmeridae, and Salmonidae.

Rosen (1974) divided the suborder Salmonoidei into two superfamilies, Salmonoidea—including the Southern Hemisphere families (except Retropinnidae) and Salmonidae—and Osmeroidea (with four families listed as incertae sedis: Osmeridae, Plecoglossidae, Retropinnidae, and Salangidae). I have not investigated Retropinnidae or the highly aberrant Plecoglossidae but suspect that Retropinnidae (particularly *Prototroctes*) and *Plecoglossus* may indeed be closely related to each other and perhaps to Osmeridae. But I have not been able to find any good evidence (in the form of shared specializations or derived characters) between Salangidae and any one or combination of these families. I have therefore designated the new superfamily Salangoidea, which is coequal with the superfamilies Osmeroidea and Salmonoidea (and Galaxioidea, if this is also to be recognized).

SALANGOIDEA, NEW SUPERFAMILY

This superfamily apparently differs from all other Pisces in having a suspensorium in which the cartilaginous palatine and pterygoid (of the mandibular arch) and quadrate and hyomandibular (of the hyomandibular arch) are fused into a single element, the hyopalatine. Gill arches with well-developed fourth hypobranchials—so far as known absent from all other adult teleosts (Nelson 1970). Pharyngobranchials 4. Anterior pharyngobranchial modified as an elongate "suspensory pharyngeal"; only fourth pharyngobranchial bears teeth (teeth absent in *Sundasalanx*). Fifth ceratobranchial with well-developed teeth (absent in osmeroids; McAllister 1963:4). Branchiostegal rays 2–5 (7–19 in salmonoids, 5–10 in osmeroids, 3–9 in galaxioids). Cranium moderately to excessively flattened (more so than in any other salmoniforms). Maxillary bone, bearing teeth for its entire length, with its posterior half abruptly curved medially beneath head (so that teeth on posterior half of maxillary are directed anteriorly rather than ventrally). Scales entirely absent except for a row of strongly adherent anal scales in adult male Salangidae.

Dermosphenotic and circumorbital bones absent, except for a single small troughlike bony element observed in *Neosalanx,* which may represent a fifth or sixth circumorbital (not dermosphenotic). Supraocciptal bone absent (present in most other salmoniforms).

Pectoral fins pedunculate throughout life (with pectoral radials in a fleshy pedestal separate from body). Pelvic fin-rays usually 5 or 7 (rarely 6 or 8; 8 in osmeroids). Principal caudal fin-rays invariably 10+9 (as in most lower teleosts including salmoniforms with generalized caudal fins; galaxioids have fewer).

Salangoids apparently have no laterosensory canals on the body. The cephalic laterosensory canals, although well developed, are superficial (i.e., not enclosed in bony tubules) and often difficult to observe in their entirety. Those of *Salanx chinensis,* illustrated by Nelson (1970, Fig. 15), do not exhibit any particularly unusual features for lower teleosts. There are preopercular, mandibular, supraorbital, infraorbital, and extrascapular canals. The mandibular is not continuous with the preopercular. The supraorbital and infraorbital extend anteriorly only a short distance in front of the nostrils, i.e., not significantly onto the greatly depressed and enlarged snout. The infraorbital has 8 pores, the preopercular 6, and the mandibular 5.

Alimentary canal a relatively simple, straight tube. Pyloric caecae absent. Gonads paired.

Salangidae Jordan and Snyder, 1902

Pelvic fin almost invariably with 7 rays (8 observed in one specimen of *Salangichthys ishikawae* and two *S. microdon,* 6 in one *Neosalanx jordani*). Pelvic girdle without parapelvic cartilages. Pectoral fin-rays 8–34. Pectoral girdle with five proximal radials; distal ends of one or more proximal radials with more or less numerous branches; adult males with a series of anal scales and enlarged, modified anal fins; total vertebrae 49–79.

The family Salangidae comprises three subfamilies: Protosalanginae, Salangichthyinae, and Salanginae.

Protosalanginae Wakiya and Takahasi, 1937

This subfamily, here restricted to the monotypic genus *Protosalanx,* differs from all other salangoids in having the premaxilla, palatal toothplate (=ectopterygoid?), and dentary with two rows of teeth instead of at most a single row; the basihyal toothplate of the tongue also has the teeth in two marginal rows (a primitive condition for salmoniforms) or irregularly scattered over its entire surface; the only other salangoid with basihyal teeth has them in a single median row. Pelvic fins relatively larger and more anterior than in any other salangoids (see Fig. 1, Table 2).

Cranium strongly depressed (almost as much as in Salanginae); adults with anterior portion of cranial fontanel closed, posterior portion of cranial fontanel greatly reduced but remaining open throughout life (both portions closed in adult Salanginae, open throughout life in Salangichthyinae and Sundasalangidae). Lower jaw weakly projecting beyond upper jaw; premaxillae projecting anteriorly beyond snout tip as in Salanginae but failing to form a membrane-covered space through which symphyseal teeth of lower jaw project. Lower jaw without enlarged symphyseal teeth (present in Salanginae), sometimes with a weakly developed fleshy presymphyseal process but without presymphyseal teeth or bony process. Adults attaining slightly greater standard length (Table 1) and heavier-bodied than any other salangoids. Dorsal fin-rays 16–18 and anal fin-rays 30–32 (vs. 10–15 and 14–32 in all other salangoids); vertebrae 66–70 (Table 2).

Protosalanx Regan, 1908

Eperlanus Basilewsky, 1855:242.

Salanx Abbott, 1901:490.

Protosalanx Regan, 1908b:444 (type-species, by monotypy, *Salanx hyalocranius* Abbott, 1901 = *Eperlanus chinensis* Basilewsky, 1855).

Paraprotosalanx Fang, 1934a:246 (type-species, by monotypy, *Protosalanx andersoni* Fang, 1934a (non Rendahl, 1923) = *Protosalanx chinensis* Basilewsky, 1855).

Protosalanx chinensis (Basilewsky, 1855)

Eperlanus chinensis Basilewsky, 1855:242 (type-locality "in sinu Tschiliensis habitat" [not "Pekin" as usually cited]).
Salanx hyalocranius Abbott, 1901:3490 (type-locality Pei-ho at Tien-tsin).
Protosalanx hyalocranius Regan, 1908b:445.
Paraprotosalanx andersoni Fang, 1934a:246 (Figs. 4–6, text in part [non *Paraprotosalanx andersoni* Rendahl, 1923]).
Protosalanx chinensis Chyung, 1961:163.

Material Examined.—BMNH 1929.2.5.2.–3, 61–65 mm, Kiangyin; CAS 52026, 60:48.2–70.7 mm, no locality (purchased in San Francisco); CAS-SU 6306, 25:80.5–163 mm, Pei-ho at Tien-tsin, paratypes of *Salanx hyalocranius* (7:85.5–158 mm alcian-alizarin); CAS-SU 23639, 1:137 mm, Seoul; CAS-SU 36025, 3:120–136 mm, no locality; UMMZ 180096, 2:127–129 mm, Korea; USNM 120746, 2:129–132 mm, Korea.

Protosalanx appears to be the most primitive salangoid. There is no indication that it comprises more than a single species. Although Abbott's account begins "*Salanx hyalocranius* new species," it concludes "this species is probably identical with *Eperlanus chinensis* Basilewsky, from Pekin, but the name chinensis is already used for the 'whitebait of Makao' " (Abbott 1901: 490–491). In Abbott's time Salangidae were so poorly known it was reasonable for him to assume that his material might represent an undescribed species, but even so it is clear from this statement that Abbott was really proposing a replacement name. Now that Salangidae are better known it seems Basilewsky's account could only refer to this species, as explicitly recognized by Wakiya and Takahasi (1937), although they retained the name *P. hyalocranius.* The holotype of *P. chinensis* cannot be found (Barsukov, pers. comm. 1983). Since the "whitebait of Makao" has been referred to as *Leucosoma* or *Salanx chinensis* but never as *Eperlanus* or *Protosalanx chinensis,* the epithet *chinensis* is available for a species of *Protosalanx.* As this is also the earliest name proposed it must replace *hyalocranius,* and the species should be known as *Protosalanx chinensis.* The only publication to come to my attention in which this name is correctly applied is by Chyung (1961).

Wakiya and Takahasi (1937) correctly identified *Paraprotosalanx andersoni* Fang, 1934a with this species. Fang's figures agree in every respect with *P. chinensis.* The fleshy presymphyseal appendage, presumed by Fang to differentiate his *Paraprotosalanx* from *Protosalanx,* is also present in some of Abbott's type-specimens of *S. hyalocranius.* Fang's figures presumably are based upon the single large male, "S. 4374," 153 mm (total length according to Table 4, but standard length according to p. 247) from Nanking. All or almost all of the other specimens referred to *Paraprotosalanx andersoni* by Fang are probably *Neosalanx.*

It should be noted that small specimens in museum collections identified as *Protosalanx* are usually *Neosalanx* and that all or almost all published reports of smaller *Protosalanx* up to the present time are based on *Neosalanx.* For example, I find that all of the small specimens in Abbott's type-series of *S. hyalocranius* are *Neosalanx.* Young *P. chinensis* are relatively rare in collections. Those I examined (smallest 48.2 mm) closely resemble the largest adults in every way except they lack the sexually dimorphic characters of adult males. The strongly pointed snout and large teeth arranged in two rows on the palate, tongue, and lower jaw are easily observable. *Neosalanx* have no teeth on the tongue or palate, and the jaw teeth except on the maxillary are absent or minute and difficult to observe, while the males are sexually mature and provided with greatly enlarged anal fins and anal scales at relatively small size. The smallest male *Protosalanx* with anal scales is probably considerably larger than any *Neosalanx.*

Protosalanx chinensis appears heavier-bodied at all sizes and to attain a greater size than any other salangoid. The 163-mm specimen is the largest that has been reported.

Salanginae Regan, 1908b

Cranium and especially ethmoid plate very strongly depressed and elongate, more so than in any other salmoniforms. Adults with cranial fontanel entirely closed (posterior and sometimes also anterior portion of cranial fontanel open throughout life in all other salangoids). Upper and lower jaws with strongly pointed or projecting tips. Teeth relatively large and few in number. Premaxillae projecting beyond concave anterior margin of ethmoid plate to form a membrane-covered space penetrated by enlarged symphyseal teeth of lower jaw. Lower jaw often with a fleshy or bony presymphyseal process and presymphyseal teeth (Wakiya and Takahasi 1937, pl. 20, figs. 31–34). Supramaxilla absent (present in all other salangoids). Pectoral fin-rays 7–11 (20–32 in all other Salangidae). Pectoral girdle with a single postcleithrum (absent in all other salangoids). Body extremely elongate, more so than in any other salmoniforms. Basal portion of neural and hemal arches expanded, frequently covering centrum laterally and fusing with each other. Distal portion of neural arches with anterior and posterior projections, those of successive vertebrae articulating with each other. Vertebrae 68–79 (37–70 in all other salangoids).

The enlarged symphyseal teeth of the dentary and the membrane in the roof of the mouth through which they project presumably form a puncturing device to kill prey. Similar devices, with foramina in the roof of the mouth through which fanglike lower jaw teeth pass, occur in other piscivorous or predatory teleosts, including the characoids *Hepsetus, Hoplias,* and *Acestrorhynchus* (Roberts 1969).

In many respects Salanginae appear to be the most highly specialized members of the family. Even the low pectoral fin-ray count, which might be considered primitive, may be secondarily evolved, since primary pectoral radials 2–4 of Salanginae exhibit the distally fimbriate or digitate condition that is probably associated with the retention of pedunculate pectoral fins (probably a neotenic character) and evolution of large numbers of pectoral fin-rays (a specialization shared by all other Salangidae).

Salanx Oken, 1817

"Les Salanx" Cuvier, 1817:185 (French vernacular; not available for zoological nomenclature).

Salanx Oken, 1817:1183 (Latinization of Cuvier's "Les Salanx," and the earliest name available for zoological nomenclature; see ICZN Declaration 87, paragraph 12. Type-species, by monotypy, *Salanx cuvieri* Valenciennes, 1849).

Leucosoma Gray, 1831:4 (type-species, by monotypy, *Leucosoma reevesi* Gray, 1831).

Hemisalanx Regan, 1908b:444 (type-species, by monotypy, *Hemisalanx prognathus* Regan, 1908b).

Parasalanx Regan, 1908b:444 (type-species, by subsequent designation of Fang, 1934a:259, *Parasalanx gracillimus* Regan, 1908b = ?*Salanx cuvieri* Valenciennes, 1849).

Reganisalanx Fang, 1934b:509 (type-species, by monotypy, *Reganisalanx normani* Fang, 1934b = *Salanx ariakensis* Kishinouye, 1901).

Metasalanx Wakiya and Takahasi, 1937:293 (type-species, by monotypy, *Metasalanx coreanus* Wakiya and Takahasi, 1937, a nomen nudum).

The four species herein recognized as constituting the genus *Salanx* have been placed by other authors in three genera, *Salanx, Hemisalanx,* and *Leucosoma.* Wakiya and Takahasi (1937) even placed *Hemisalanx* in a subfamily of its own, Hemisalanginae, regarded by them as intermediate between Protosalanginae and Salanginae. Because these four species differ strikingly from all other salangids in several features of skeletal anatomy but agree closely with each other in conformation of the cranium and jaws, distribution and size of jaw teeth, number of pectoral fin-rays, and the peculiar modification of their neural and hemal arches and high vertebral counts, I prefer to recognize them as belonging to three subgenera in the sole genus of the subfamily Salanginae.

Salanx (*Salanx*) **ariakensis**
(Kishinouye, 1901)

Salanx ariakensis Kishinouye, 1901:359 (type-locality Ariake Bay, Kiushiu).

Salanx acuticeps Regan, 1908a:360 (type-locality Lake Candidius, Formosa).

Parasalanx acuticeps Regan, 1908b:446.

Parasalanx longianalis Regan, 1908b:446 (type-locality Liao-ho, northern China).

Parasalanx annitae van Dam, 1926:342 (type-locality Peitaiho, China).

Reganisalanx normani Fang, 1934b:509 (type-locality Ichang, as herein restricted).

Material Examined.—AMNH 10327, 7:125–147 mm, Hunan; BMNH 1888.5.15.11–12, 2:141–143 mm, Ichang (lectotype and paralectotype of *R. normani*); BMNH 1898.2.8.20–23, 4:114–123 mm, Liao-ho, northern China (syntypes of *P. longianalis*); BMNH 1904.4.2835–36, 2:116–118 mm, Lake Candidius, Formosa (syntypes of *S. acuticeps*); BMNH 1927.3.26.3, 125 mm, Nanking; BMNH 1928.6.22.6, 115 mm, Wenchow; CAS-SU 8574, 2:99.1–104 mm, Ariake Sea (identified by Kishinouye); CAS-SU 23103, 107 mm, Maruyama, Taihoku, Formosa; ZMA 112.587, 128 mm, Peitaiho, China (holotype of *P. annitae*).

In vertebral counts and in all other respects so far as known the four syntypes of *P. longianalis* agree well with other material herein referred to as *Salanx ariakensis,* except for their consistently high anal fin-ray counts of 30–32 (reported by Regan 1908b:446). Most samples of *S. ariakensis* examined have only 26–29 anal fin-rays, but two specimens from Ariake Bay have 27 and 31.

Reganisalanx normani is based primarily on the description by Regan (1908b) and supplementary notes by Fang (1934b:509) of two specimens from Ichang (BMNH 1888.5.15, 11–12), identified by Regan (ibid.) as *Salanx cuvieri.* Fang declared that the specimens represented a distinct genus but did not provide a proper generic diagnosis or description; apparently he distinguished it from *Salanx* based on the lack of a presymphyseal bone. In my opinion the character cannot be used to split the genus *Salanx*.

I have reidentified these specimens as *S. ariakensis,* a species in which the presymphyseal bone may be present or absent. I have not seen the third specimen referred to *R. normani* by Fang (ibid.). It is clear from Fang's account that he did not compare this specimen directly with the two specimens from Ichang, and it might not be conspecific. In order to fix the identity of this nominal taxon, the 141-mm undamaged specimen from Ichang (BMNH 1888.5.15.11) is hereby designated the lectotype. The 143-mm specimen, with the body damaged just behind the head and at mid-abdomen, is a conspecific paralectotype (BMNH 1888.5.15.12).

Fang (1934a) reported 11 specimens (as *Parasalanx longianalis*) with the following anal finray counts: 28(5), 29(2), 30(3), 32(1). The vertebral counts are unknown for these specimens but it seems likely from Fang's account that they are all *S. cuvieri.*

The holotype of *P. annitae* has the head relatively short and broad (for the subgenus *Salanx*) and in this respect is more like *S. ariakensis* than *S. cuvieri.* A presymphyseal bone is present, but it is short considering the large size of the specimen, and has only 2 teeth on each side. The premaxilla has 7 teeth, maxilla 12, and dentary about 10.

Salanx (*Salanx*) **cuvieri** Valenciennes, 1849

Salanx cuvieri VALENCIENNES *in* CUVIER AND VALENCIENNES, 1849:360 (type-locality unknown).

?*Parasalanx gracillimus* REGAN, 1908b:446 (type-locality Shanghai).

Parasalanx angusticeps REGAN, 1908b:446 (type-locality China).

Parasalanx cantonensis HERRE, 1932:425 (type-locality Canton).

MATERIAL EXAMINED.—AMNH 51689, 3:88.6–106 mm, Canton; BMNH 1855.9.19.1539, 144 mm (holotype of *P. angusticeps*); BMNH 1891.1.31.20, 111 mm, Shanghai (holotype of *P. gracillimus*); BMNH 1936.10.7.13, 119 mm, Sharp Peak, Fukien; CAS 52057, 4:76.5–98.0 mm, Hong Kong (1 alizarin); CAS-SU 225732, 112 mm, Canton (holotype of *P. cantonensis*); CAS-SU 32454, 18:56–66 mm, Chuan Is. (4:61.7–69.4 mm alcian-alizarin); CAS-SU 32943, 117 mm, near Pakhoi, SW Kwangtung; MNHN 9900, 112 mm, no locality (holotype).

So far as I have been able to determine, variation in the presymphyseal bone within each species, including its presence or absence and its length or amount of dentition, is correlated chiefly with size and is not sexually dimorphic.

NOTES ON HOLOTYPE.—The holotype (Fig. 2a) is dried but complete and in fair condition. The body immediately posterior to the head is badly damaged and fin-rays brittle, so it must be handled with care. Cranial width (at anterior margin of eyes) 3.5 in cranial length. Presymphyseal bone, 2.1 mm long, with 1–2 moderately large teeth basally and at least 2 minute teeth distally. Premaxilla considerably elongated anteriorly, with 7–8 teeth. Maxilla with about 7 teeth. Dentary with about 13 teeth of variable size. Palatal teeth 7, very small and in a single row. The following proportional measurements are expressed as times in standard length. Length of cranium about 7; length of head (to end of gill cover) 4.7; length from anterior midline of ethmoid plate (concave) to anterior rim of orbit 16; length from tip of upper jaw (premaxilla) to anterior rim of orbit 10; diameter of eye (slightly shrunken) approximately 28.

NOTES ON SYNONYMY.—*P. angusticeps* is distinguished by Regan primarily on the basis of its exceptionally elongate head: "head nearly 4 times as long as broad; snout a little longer than postorbital length of head" versus head 3 times or a little more than 3 times as long as broad, and snout only as long as or a little shorter than postorbital length of head in all other *Parasalanx* and *Salanx* (Regan 1908b:445–446). The dentition of the holotype of *P. angusticeps,* a gravid female of 144 mm, is complete and undamaged. Presymphyseal bone elongate with 5–6 teeth on each side; premaxilla with 7 teeth; maxillary teeth 10 or 11; dentary with a small tooth anteriorly (just behind symphysis), then an enormous canine tooth, followed by 7 small teeth and 6 moderately large teeth; palatine with 8 small teeth in a single straight row.

The holotype of *P. gracillimus* is in poor condition, dried, twisted, and slightly shrunken. Its body depth, reported as 18 times its length, is attributable to the poor condition (emaciation) of the specimen. Its dentition is as follows: presymphyseal bone with 3 teeth on each side, premaxillary 5, maxillary 8, dentary with 1 moderately large, 6 small, and 5 moderately large, and palatal 7 moderately large. The vertebral column is broken anteriorly, making all of the counts based on vertebrae doubtful. Wakiya and Takahasi (1937:288) tentatively placed *P. gra-*

TABLE 2. MERISTIC CHARACTERS OF SALANGOIDS BASED ON MATERIAL EXAMINED.

	Total vertebrae	Vert. to pelvic o.	Vert. to dorsal o.	Vert. to anal o.	Caudal vert.	Dorsal rays	Anal rays	Pect. rays	Anal scales	Branch. rays	Gill rakers	Remarks
Protosalanx chinensis												
CAS-SU 6306, Tien Tsin	68–70	21–25	38–39	47–48	6–8	16–18	30–32	22–27	26–30	4(6)4(1)	16(2)	Paratypes *hyalocranius*
CAS-SU 23639, Seoul	67	23	39	45	8	16	33	25	26	–	15	
CAS-SU 36025, no. loc.	66(3)	22–23	36–37	44–48	6–8	16	31–33	20–30	22	–	13–15	
UMMZ 180096, Korea	–	–	–	–	–	16–17	31–33	23–24	23	–	12–16	
Salanx ariakensis												
AMNH 10327, Hunan	74(5)75(1)76(1)	30–31	51–52	54–55	10–11	13–14	26–28	9	22–25	–	8–12	
BMNH 1888.5.15.11–12, Ichang	74–75	31	52–53	55	10?	–	–	–	–	–	–	Syntypes *normani*
BMNH 1898.2.8.20–23, Liao-ho	73(2)75(2)	29–31	51–53	54–55	10–11	–	–	–	–	–	–	Syntypes *longianalis*
BMNH 1909.4.28–35–36, Formosa	72–73	30–31	51–52	52	10	–	27?	10?	20–21	–	–	Syntypes *acuticeps*
BMNH 1927.3.26.3, Nanking	75	30	52?	54?	–	–	–	–	–	–	–	
BMNH 1928.6.22.6, Wenchow	72	31	52	54	10	–	–	–	–	–	–	
CAS-SU 8574, Ariake Bay	74(2)	29–30	52–53	54–55	9–10	12–14	27–31	10	–	–	14	
CAS-SU 23103, Formosa	74	30	53	53	10	13	28	10	21	–	8	
ZMA 112.587, Peitaiho	75	28	51	53	–	13	27?	9	–	–	11	Holotype *annitae*
Salanx cuvieri												
AMNH 51689, Canton	77(1)78(1)79(1)	31–32	54–56	56–57	–	13–14	29	9–10	–	–	9–10	
BMNH 1855.9.19.1539, China	77	31	56	57	11?	–	29?	9	–	–	–	Holotype *angusticeps*
BMNH 1891.1.31.20, Shanghai	76?	31?	54?	57?	–	–	–	–	–	–	–	Holotype *gracillimus*
BMNH 1936.10.7.13, Fukien	77	31	–	–	–	–	–	–	–	–	–	
CAS 52027, Hong Kong	77(1)78(1)79(1)	30–32	54–56	55–58	–	12–14	27–30?	9–10	–	–	8–9	
CAS-SU 25732, Canton	77	31	55	57	10	13	28	9–10	–	–	11?	Holotype *cantonensis*
CAS–SU 32454, Chuan Is.	76(2)77(5)78(4)	31–32	53–55	55–57	12	13	27	–	–	3	11	
CAS-SU 32943, Kwantung	78	32	55	56	11	14?	27?	9	–	–	11	
MNHN 9900, no loc.	77	31–32	55	56	10	12	29	9	–	–	–	Holotype *cuvieri*
Salanx prognathus												
BMNH 1873.7.30.69, Shanghai	71	30?	52	53	9	12?	25	–	–	–	–	Holotype *prognathus*
CAS 51439, Kiangsu	71(5)	30–31	51–52	51–53	10	12–14	25–28	7–8	16–20	3	10–11	
CAS-SU 33990, Hong Kong	70–73	30–31	51–52	52–53	10–11	13–14	26–29	7–9	18–21	–	9–11	
Salanx reevesi												
AMNH 10336, Fukien	68	28	47	53	6	11	27	10	–	3	–	
AMNH 11161, Fukien	68	27	46	52	7	10	28	10	–	3	16	
CAS-SU 1511, Swatow	70–73	28–30?	48–49	53–55	7–9	10–11	30(1)	11	19	3	13	
CAS-SU 25738, Canton	71	29	48	55	6	11	28	10	–	–	13?	
CAS-SU 61189, Hong Kong	70	27	47	54	7	12	28	11	–	3	15	

Table 2. Continued.

	Total vertebrae	Vert. to pelvic o.	Vert. to dorsal o.	Vert. to anal o.	Caudal vert.	Dorsal rays	Anal rays	Pect. rays	Anal scales	Branch. rays	Gill rakers	Remarks
Neosalanx andersoni												
NRM 10287, Chihli	63	24	37	43	9	15	30	34	20–21?	—	15	Holotype *andersoni*
Neosalanx brevirostris												
AMNH 10337, Hunan	55(9)56(11)57(2)	20–22	31–34	39–42	6–8	12–14	25–28	—	—	3	15(3)	
AMNH 10480, Tung Ting	55	20	32–33	40	6	13	26	—	—	—	14	
AMNH 11155, Fukien	57	21	33–34	41	7	14	25	—	—	—	17	
AMNH 37044, Foochow	56(1)57(1)	20	33–34	41–42	6–7	14–15	25(2)	—	—	—	17	
AMNH 51690, Canton	57(6)58(14)59(3)	20–22	32–35	42–44	7	14	26–30?	—	—	—	17(2)	
CAS 52032, Hong Kong	58	21	32	41	—	14	28	—	—	—	—	
CAS-SU 1540, Swatow	58(2)59(1)	21	33	42	5	13–14	28(3)	26–30	—	3	19	
CAS-SU 68888, Seoul	55(1)56(1)57(1)	20–21	31–33	40–42	—	15	24(1)	28	15?	—	15–16	
MNHN 1922.184–189, Tonkin	57(3)58(2)59(1)	19–21	34–35	41–44	6–7	14–15	25–26	24–27	—	—	—	Syntypes *brevirostris*
Neosalanx jordani												
AMNH 51705, Canton	51(1)52(6)54(1)											
AMNH 51704, Foochow	53	21	32	40	8	13	23	—	—	—	14 or 15	
CAS 52028, Kiangsu	50(7)51(3)52(1)	18–20	30–32	35–37	5–8	11–13	23–25	20–26	13–16	2–3	9–10	
CAS 52029, Hong Kong	48	20	32	41–42	—	14	29	—	—	—	17?	
CAS-SU 68625, Tien Tsin	50(3)51(5)52(9)53(1)	19–20	30–32	36–38	5–7	12–14	23–25	21–22	—	3–4	12–14	
Salangichthys ishikawae												
CAS-SU 6780, Same	59(2)60(1)	25–26	37–39	42–43	8–9	14–15	25–26	25–28	—	3–4	16–17	
CAS-SU 68889, Ariake Bay	61	26	38	43	9	15	24?	26	—	—	19	
Salangichthys microdon												
CAS 52033, Kawasaki	61(2)62(3)63(1)	26–27	40	43–44	9	12–13	25–28	14–18	17	—	18	
CAS 53034, Kituara	59(2)60(1)61(4)62(1)	23–26	36–39	42–45	8–9	10–13	22–25				14–16	
CAS-SU 134, Tokyo	61(2)62(3)	25–26	39–40	43–45	8–9	12–13	24–27	14–16	—	3–4	16	
Sundasalanx microps												
CAS 44220, Kapuas	41(2)42(4)43(1)	15–16	25–27	29–31	3–4	12–14	17–21	0	0	3	0–2	Paratypes *microps*
Sundasalanx praecox												
CAS 52031, Tale Sap	37(2)38(7)	13–14	23–24	26–28	3–4	12–13	16–19	0	0	3	10	Paratypes *praecox*
CAS 52036, Mekong	39(1)40(3)	14–15	24–25	29	3–4	12–15	16–21	0	0	3	10–12	
CAS 52037, Muar	37(1)40(4)41(7)	14–15	25–26	30–31	3–4	12–14	14–16	0	0	3	10?	

cillimus as a synonym of *P. ariakensis*, and perhaps they were correct. This matter is of some nomenclatural significance, since *P. gracillimus* is type-species of Regan's *Parasalanx.*

The holotype of *P. cantonensis* has a very elongate presymphyseal bone with 10 teeth; premaxillary teeth 8, maxillary teeth 10, dentary teeth 13; palatal teeth 11.

Length of the head (and cranium) is exceptionally variable in all genera of Salangidae, even including the relatively short-snouted genus *Neosalanx*, and is particularly variable in the long-snouted subfamily Salanginae. Variable elongation of the head and particularly the snout with its flattened ethmoid plate is evident in the large series of *Protosalanx chinensis* and *Neosalanx jordani* I examined, even though these are relatively small specimens. *P. angusticeps* is based on a single specimen, the holotype, which happens to be the largest referred to *S. cuvieri* that I have examined. In vertebral counts and other characters it apparently agrees well with other material of *S. cuvieri.*

Salanx (*Hemisalanx*) **prognathus** (Regan, 1908b) new combination

Hemisalanx prognathus Regan, 1908b:445 (type-locality Shanghai).
?*Salanx brachyrostralis* Fang, 1934a:257 (type-locality Nanking).
?*Reganisalanx brachyrostralis* Fang, 1934b:509.
Metasalanx coreanus Wakiya and Takahasi, 1937 (otherwise unpublished manuscript name placed in synonymy of *H. prognathus* by Wakiya and Takahasi 1937:293).

Material Examined.—BMNH 1873.7.30.69, 111 mm, Shanghai (holotype); CAS 51439, 34:97.5–120 mm, Kiangsu Prov. (12:97.5–112 mm alcian-alizarin); CAS-SU 33990, 8: 94–114 mm, Tai Po, New Territory, Hong Kong.

This species has been recognized as representing a monotypic genus since its original description, and Wakiya and Takahasi (1937) even placed it in a monotypic subfamily (Hemisalanginae). Apart from its somewhat shorter, blunter snout, and slight differences in dentition, however, it is very similar to specimens of the subgenus *Salanx* lacking a presymphyseal bone. The magnitude of the differences between *Hemisalanx* and *Salanx* (sensu stricto) is comparable to that between the latter and *Leucosoma*, which I also regard as only subgenerically distinct.

Regarding *S. brachyrostralis*, Wakiya and Takahasi (1937) placed it in the synonymy of *S. prognathus* with a question mark, as is done here. Neither Wakiya and Takahasi nor I have examined the holotype ("S. 4227, 144 mm total length").

Wakiya and Takahasi (1937:293) placed *Reganisalanx normani* in the synonymy of *H. prognathus* with a question mark, but I have examined the type-specimens and have reidentified them as *S. ariakensis.*

Salanx (*Leucosoma*) **reevesii** (Gray, 1831)

?*Albula chinensis* Osbeck, 1757 (type-locality West River at Canton?; original not consulted).
Leucosoma reevesi Gray, 1831:4 (type-locality China).
Leucosoma chinensis Richardson, 1846:303.
Salanx reevesii Valenciennes *in* Cuvier and Valenciennes, 1849:363, Pl. 646.
Salanx chinensis Günther, 1866:205.

Material Examined.—AMNH 10336, 130 mm, Fukien; AMNH 11161, 74.5 mm, Fukien; CAS-SU 1511, 4:87.8–140 mm, Swatow (2:87.8–102 mm alcian-alizarin); CAS-SU 25738, 127 mm, Canton; CAS-SU 61189, 153 mm, Castle Peak Bay?, Hong Kong.

Salanx reevesi is second only to *Protosalanx chinensis* as the largest and heaviest-bodied salangoid. It is the only species of Salangidae in which males with anal scales have not been reported previously. A 130-mm specimen from Swatow (CAS-SU 1511) is a mature male with its anal fin greatly enlarged and 17 anal scales. It is the only member of the subgenus *Leucosoma*, distinguished by a median row of 6–8 teeth on the tongue or basihyal bone.

Albula chinensis Osbeck, 1765, has been identified with this species by various ichthyologists following Richardson (1846) but, as pointed out by Wakiya and Takahasi (1937:291–292), its identity cannot be verified. While *Albula chinensis* evidently is a member of the Salanginae, there apparently are no type-specimen(s) extant (Kullander, pers. commun., 1983) and it is impossible to tell from Osbeck's description which species he had. The presence of teeth on the tongue, which would positively identify it as *S. chinensis*, is not mentioned.

In addition to having teeth on the tongue, *Leucosoma* has jaw teeth that are somewhat larger than those in the subgenera *Hemisalanx* and *Salanx.* In all other features of skeletal anatomy, however, *Leucosoma* falls in the genus *Salanx.* It has nearly the same vertebral counts as the subgenus *Hemisalanx*, and its cranial shape appears to be identical with that in the subgenus *Salanx.*

Salangichthyinae, new subfamily

Cranium only moderately depressed (as in Sundasalangidae). Cranial fontanel with posterior and apparently anterior portions open throughout life. Head rounded anteriorly, premaxillae failing to meet at midline, not projecting significantly beyond snout. Teeth greatly reduced in size, small or minute, those on maxilla very numerous (about 15–40). Maxilla expanded, much larger than premaxilla. Body moderately elongate. Vertebrae 48–65 (66–79 in all other Salangidae).

This subfamily contains two genera, *Neosalanx* and *Salangichthys*, formerly placed in Protosalanginae (Wakiya and Takahasi 1937).

Neosalanx Wakiya and Takahasi, 1937

Neosalanx Wakiya and Takahasi, 1937:282 (type-species, by original designation, *Neosalanx jordani* Wakiya and Takahasi, 1937).

The species of this genus are poorly known. In museum collections and older literature they are usually misidentified as *Protosalanx* or *Salanx*. Wakiya and Takahasi (1937) recognized four species, three of which they described as new. Although they recognized that *Protosalanx andersoni* Rendahl belonged to *Neosalanx*, they overlooked three previously described taxa, which also apparently belong to it: *Protosalanx brevirostris* Pellegrin, 1923; *Protosalanx tangkahkeii* Wu, 1931; and *Salanx argentea* Lin, 1932. All three of these were mistakenly placed by Fang (1934a:240) in the synonymy of *Protosalanx hyalocranius*. I briefly examined the type-specimens of Pellegrin's *P. brevirostris* in Paris, and have since studied radiographs of them, but have not seen the types of the taxa described by Wu and Lin.

Wakiya and Takahasi (1937) distinguished four species of *Neosalanx*, mainly on the basis of differences in counts of vertebrae and fin-rays. Without knowing more about interpopulational meristic and other variation in *Neosalanx*, it is difficult to evaluate the species. Specimens I examined tend to fall into groups, based on vertebral counts, identical to those recognized as species by Wakiya and Takahasi, and I have identified my material accordingly.

Wakiya and Takahasi (1937) described *Neosalanx* as a new genus despite the fact that one of its included species, *Protosalanx andersoni* Rendahl, 1923, was proposed by Fang (1934a) as type-species for his genus *Paraprotosalanx*. It is obvious from Fang's account that he mistook specimens of *Protosalanx chinensis* and probably either *Neosalanx brevirostris* or *N. jordani* as *Protosalanx andersoni* and that his generic diagnosis is based mainly on *P. chinensis*. At this point the nomenclaturally parsimonious solution would have been for Wakiya and Takahasi to recognize *Paraprotosalanx* as a valid genus with *Protosalanx andersoni* Rendahl, 1923 (not of Fang 1934a), as its type-species. They chose, however, to coin a new name and designated as type-species the new species *N. jordani*. Given that they did so, and that no publication has appeared subsequently in which *Paraprotosalanx* is treated except as a synonym of *Neosalanx*, I provisionally recognize *Neosalanx* as valid. It should be noted, however, that judging from Article 70 of the International Code of Zoological Nomenclature (1964 ed.) this case should be referred to the International Commission.

Neosalanx andersoni (Rendahl, 1923)

Protosalanx andersoni Rendahl, 1923:92 (type-locality Chihli, Shan-Hai-Kuan).
Neosalanx andersoni Wakiya and Takahasi, 1937:285.

Material Examined.—NRM 10287, 79 mm, Chihli, Shan-Hai-Kuan (holotype).

This species differs from all other *Neosalanx* by its relatively large size, to 100 mm (vs. only to 64 mm) and more numerous total vertebrae, 63–65 (vs. 59 or less). Wakiya and Takahasi reported anal scale counts of 25–28 in *N. andersoni* and only 14–21 in other *Neosalanx*, but I find only 21 or 22 anal scales on the male holotype. *N. andersoni* is known only from rivers in Korea and China flowing into the Yellow Sea.

The jaws of the holotype of *Neosalanx andersoni* appear to be almost entirely toothless. I detected a single small conical tooth on the right premaxilla, none on the left. The dentaries appear to be entirely toothless. The maxillae, although having irregularities in the margin where teeth may have been affixed, are toothless or almost toothless except for a very few minute teeth. There seem to be no palatal or glossal teeth.

The anterior and posterior portions of the cranial fontanel are widely separated and reduced in size (especially the anterior portion). There is no indication of a tectum medialis.

A small patch of minute, scaly breeding tubercles occurs near the base of the 9th and 10th anal fin-rays, and more extensive areas of tubercles have evidently been sloughed off. Pelvics enlarged but without tubercles; lower jaw very strongly projecting. Snout elongate, as in *Salangichthys* (snout-tip to anterior margin of orbit =4.2 mm).

Anal scale row continues onto ventral margin of caudal peduncle a considerable distance (4 scales).

Tip of snout dorsally and tip of lower jaw, dorsal surface of cranium over brain, dorsal surface of body with irregularly distributed small melanophores. No melanophores on anal fin, and none or almost none on caudal fin, ventral body surface, including pelvic and pectoral fin bases.

Neosalanx brevirostris (Pellegrin, 1923) new combination

Protosalanx brevirostris Pellegrin, 1923:351 (type-locality Tonkin).

?*Protosalanx tangkahkeii* Wu, 1931:219 (type-locality Amoy).

?*Salanx argentea* Lin, 1932 (type-localities Sangchang stream; Henngchow Bay; Canton).

Protosalanx brevirostralis Fang, 1934a:232, 236, 240 (misspelled; referred to synonymy of *Protosalanx hyalocranius*).

Neosalanx hubbsi Wakiya and Takahasi, 1937:284 (type-locality Tien-tsin).

Neosalanx tangkahkeii taihuensis Chen, 1954? (reference not seen).

Material Examined.—AMNH 10337, 22:43.8–60.7 mm, Hunan (2:58.4–60.7 mm alizarin); AMNH 10480, 53.5 mm, Tung Ting Lake, Hunan; AMNH 11155, 60.5 mm, Fukien; AMNH 37044, 2:49.6–60.8 mm, Foochow, Fukien; AMNH 51690, 26:48–65 mm, Canton; CAS 52032, 2:46.1–48.3 mm, Hong Kong (48.3 mm alizarin); CAS-SU 1540, 3:56.8–57.9 mm, Swatow; CAS-SU 68888, 3:56.0–58.2 mm, Seoul; MNHN 1922.184–189, 6:65–70 mm, Tonkin (syntypes of *P. brevirostris*); USNM 219923, 2: 51.0–57.4 mm, Liang tsi Lake, Hupeh (formerly identified as *N. tangkahkeii taihuensis*).

Protosalanx brevirostris has not been recognized as a valid species or even referred to since Fang (1934a), without examining the types, erroneously placed it as a junior synonym of *Protosalanx hyalocranius*. I briefly examined the types, which are in rather poor condition, during a visit to Paris in November, 1982, but did not have specimens of other *Neosalanx* on hand for comparison. I have since examined radiographs of the types. Since their vertebral counts—57(2), 58(2), 59(1)—correspond only to those reported by Wakiya and Takahasi for *Neosalanx hubbsi*, I conclude that they are conspecific.

Neosalanx brevirostris is known from the mainland coast of Asia, from the Yellow Sea coast of Korea south to Tonkin.

In most specimens of *Neosalanx* the premaxillaries are toothless or have relatively few teeth (1–6 reported by Wakiya and Takahasi (1937), presumably based on examination of numerous specimens, and 0–2 in a large number of specimens I examined). Wakiya and Takahasi (1937) reported only 1–2 premaxillary teeth in *N. hubbsi*. Thus it is noteworthy that the 48.3-mm specimen from Hong Kong (CAS 52032) here referred to this species has about 20 minute teeth on each premaxilla. Tooth counts have not been made on the type-specimens of *N. brevirostris*.

Despite considerable effort to trace its original description, the taxon *Neosalanx tangkahkeii taihuensis* is known to me only from an article by Wang et al. (1980), an abstract of which appeared in *Aquatic Sciences and Fisheries Abstracts*. The article reports on its artificial fertilization and larval development (see Addendum).

Neosalanx jordani Wakiya and Takahasi, 1937

Neosalanx jordani Wakiya and Takahasi, 1937:282 (type-locality "River Rakuto, Corea").

Material Examined.—AMNH 51705, 8:29–33 mm, Canton; AMNH 51704, 47.5 mm, Foochow, Fukien; CAS 52028, 177:33.0–45.5 mm, Kiangsu, Chekiang Prov. (14:35.1–44.8 mm alcian-alizarin); CAS 52029, 1:36.8 mm, Hong Kong; CAS 52030, 311:22–58 mm, purchased in San Francisco; CAS-SU 68625, 160:35.3–47.1 mm, and UMMZ 55601, 20:35.5–41.3 mm, Pei-ho at Tien-Tsin (paratypes of *Salanx hyalocranius* Abbott, 1901) (10:39.7–45.7 mm alcian-alizarin).

Wakiya and Takahasi (1937) characterize this species as having 49–54 vertebrae (average 50.95). The range of material I examined is 48–54. The species is known from rivers along mainland coast of Asia, from the Yellow Sea coast of Korea south to Hong Kong.

Neosalanx reganius Wakiya and Takahasi, 1937

Neosalanx reganius Wakiya and Takahasi, 1937:283 (type-locality "Ariake Bay, Kyushu, Japan," possibly erroneous).

Neosalanx regani Matsubara, 1955:214 (unjustified spelling).

Wakiya and Takahasi (1937:283) reported 52–56 (average 53.75) vertebrae for this species. It is known only from the type-specimens, supposedly collected in Ariake Bay. I have not examined any *Neosalanx* from Japan.

Salangichthys Bleeker, 1860

Salangichthys Bleeker, 1860:101 (type-species, by monotypy, *Salangichthys microdon* Bleeker, 1860).

Salangichthys microdon Bleeker, 1860:101

Salangichthys microdon Bleeker, 1860:101 (type-locality Yeddo-Tokyo).
Salangichthys kishinouyei Wakiya and Takahasi, 1913:552 (type-locality Seishin, Korea and Shimane-ken, Japan).

Material Examined.—AMNH 13149, 28:50–64 mm, Daomori-ken, Japan; CAS 52033, 6:74.8–86.7 mm, Kawasaki; CAS 52034, 9:31.6–36.1 mm, Lake Kituara (alcian-alizarin); CAS-SU 134, 10:78–92 mm, Tokyo (5:81–86 mm alcian-alizarin); CAS-SU 22637, 61:32–67 mm, Sendai, Matsushima Bay, Japan.

Salangichthys kishinouyei originally was distinguished from *S. microdon* by Wakiya and Takahasi (1913) on the basis of its having 1) mandibular, maxillary, and palatal teeth more widely spaced; 2) snout shorter; 3) anal fin origin in females more anterior; and 4) threads of external egg membrane thicker, their ends club-shaped and ending freely without fusing to each other to form a ring. They later concluded that these differences represent intraspecific variation in populations of *S. microdon* on the Japan Sea coast of Sakhalin, Korea, Honshu, and Kyushu and placed *S. kishinouyei* as a synonym of *S. microdon* (Wakiya and Takahasi 1937:279–280).

Matsuoka and Iwai (1983, Fig. 2) illustrated an alcian-alizarin preparation of *S. microdon* (locality not indicated) with 65 total vertebrae. The highest number of vertebrae otherwise known in *Salangichthys* is 63 (Table 2).

Salangichthys ishikawae Wakiya and Takahasi, 1913

Salangichthys ishikawae Wakiya and Takahasi, 1913: 552 (type-locality Miyagi-ken, Japan).

Material Examined.—CAS-SU 6780, 9:67.6–74.3 mm, Same, Rikuoku (3:70.3–74.2 mm alcian-alizarin); CAS-SU 68878, 20:48–63 mm, Pacific coast of Aomori-ken, northern Honshu; CAS-SU 68889, 70.7 mm, Ariake Bay, Kyushu (locality possibly erroneous).

Salangichthys ishikawae is distinguished from *S. microdon* mainly by having 20–27 pectoral fin-rays instead of only 14–19 (see Senta 1973c). Differences in counts of vertebrae and anal scales, based on few specimens, are of doubtful significance (see Table 2).

According to Wakiya and Takahasi (1937:281), *S. ishikawae* "lives in water of rather higher salinity than *S. microdon* . . . and seems to be a northern species," known only on the Pacific coast of Honshu. The specimen herein reported from Ariake Bay, Kyushu, represents a southerly range extension of about 500 km if its locality data are correct. It was found with two specimens of *Salanx ariakensis* collected by Kishinouye in Ariake Bay (CAS-SU 8574).

Sundasalangidae Roberts, 1981

Primary pectoral girdle consisting of single median element (identical to the condition in various larval teleosts, but unknown in adults of any other teleost). Pectoral fin rayless, supported by a single undivided basal radial. Pelvic fin with 5 rays. Each half of pelvic girdle with two parapelvic cartilages (unknown in any other teleosts). Adipose fin absent. Adult males without anal scales or sexually dimorphic anal fins. Neural spines much more elongate than in Salangidae. Hemal arches of last 12 or so abdominal vertebrae with elongate hemal spines (abdominal vertebrae without hemal spines in all other salangoids). Vertebrae 37–43. Caudal fin skeleton with parhypural fused to hypurals 1 and 2 (parhypural separate in all other salangoids).

If specialized is defined as deviation from the morphology of any known group of salmoniforms that could possibly serve as the ancestral stock of Salangoidea, then *Sundasalanx* is by far the most specialized of all salangoids.

The samples of *Sundasalanx* available at the time of their original description differed so much (in regard to eye size, non-overlapping vertebral counts, etc.) that it seemed to me that they could not be the same species. Samples examined subsequently, from Muar and the Mekong, tend to be intermediate between the two described species. I have tentatively identified the new samples with *Sundasalanx praecox,* but the question of the number of species in the genus should be reconsidered when more material becomes available. The genus has not been found yet in Sumatra but is to be expected there.

Sundasalanx Roberts, 1981

Sundasalanx Roberts, 1981:297 (type-species, by original designation, *Sundasalanx praecox* Roberts, 1981).

Sundasalanx microps Roberts, 1981

Sundasalanx microps Roberts, 1981:300 (type-locality Kapuas River at Kampong Nibung, about 100 km NE of Sintang and 7 km NE of Selimbau).

Material Examined.—CAS 44220, paratypes, 34:14.6–19.9, Kapuas River at Kampong Nibung (paratypes) (7:13.5–18.0 mm alcian-alizarin).

Sundasalanx praecox Roberts, 1981

Sundasalanx praecox Roberts, 1981:299 (type-locality Khlong Falamee, Tale Sap, about 2 km W of Pak Payoon, Kra Isthmus, Southern Thailand).

Material Examined.—CAS 52031, 6:16.4–17.7 mm Khlong Falamee, Tale Sap, near Songkhla, Thailand (paratypes; alcian-alizarin); UMMZ uncat. and CAS 52036, 65:15.7–22.5 mm, Mekong River and tributaries in Thailand from Ban Dan to Nakon Phanom (4:18.2–20.3 mm alcian-alizarin; USNM 229304 and CAS 52037, 121:12.3–18.0 mm, Muar River 7–18 miles inland from Bandar Maharani (formerly Muar City) (12:16.5–17.8 mm alcian-alizarin).

When more material becomes available and the species of *Sundasalanx* are re-examined, the pigmentation of the Muar specimens (CAS 52037, USNM 229304) should be taken into consideration. In the *Sundasalanx* examined, each sample tends to have a more or less distinctive pigmentation or pattern of melanophore distribution shared by all of the specimens. Thus the type-series of *S. microps* is characterized by having a series of large midventral melanophores, one per myotome, extending from the pectoral fin to the anal fin. Midventral melanophores are absent in the type-series of *S. praecox.* In the Muar specimens here identified as *S. praecox,* however, a series of midventral melanophores extends from about pelvic-fin origin to the anal fin, thus resembling the pigmentation of *S. microps.* On the other hand, each of the Muar specimens has a series of large melanohores along the base of the anal fin, one melanophore between the base of each branched fin-ray. Other samples of *Sundasalanx* examined do not exhibit this feature.

In the original description of *S. praecox* (Roberts 1981:299) it is stated that the type-series has maxillary teeth about 15–19 vs. about 30 in *S. microps*; the reverse is true.

Discussion

Anyone who has looked into recent accounts of salmoniform classification realizes that it is in disarray. In this group current classifications are based largely on skeletal anatomy, and as long as the skeletal anatomy of major groups such as salangoids remain uninvestigated and others only partially investigated, no stable classification can be expected. McDowall (1969) briefly examined the skeletal anatomy of "*Salangichthys microdon*" (actually *Neosalanx*?) stained with alizarin and concluded that Salangidae "is not part of the galaxioid radiation." He also stated "a more complete study (of salangid skeletal anatomy) may be desirable, should a full range of material be available, especially if it should reveal some species with more complete ossification to enable more precise determination of affinities." A species with somewhat more complete ossification actually does exist—*Protosalanx chinensis*—but even in this species truly adequate observations of skeletal anatomy cannot be based on specimens stained solely with alizarin. The question is no longer relevant, however, since adequate skeletal preparations of salangoids usually can be obtained using the alcian-alizarin technique.

All modern accounts of salangid classification agree in placing them in the order Salmoniformes. My information on salangoid skeletal anatomy, however, has not provided me with obvious answers about their relationships to other salmoniforms, but has only emphasized their distinctness. The presence of two (marginal or submarginal) rows of teeth on the basihyal toothplate of *Protosalanx* confirms the integrity of the order Salmoniformes and the placement of Salangoidea within this order but nothing more. The presence of a taenia medialis in the cranium of young *Protosalanx* and a single specimen of *Neosalanx* suggests a shared derived character (synapomorphy) with osmeroids, but this character may well prove primitive for salmoniforms, perhaps to be found in many of them.

Higher classification of Salmoniformes has been the subject of considerable interest in the last two decades or so, with contributions by Gosline (1960), Greenwood et al. (1966), Weitzman (1967), McDowall (1969), Rosen (1974), Klyukanov (1975), and Fink and Weitzman (1982). A major issue is whether esocoids (pikes, northern mud-minnows, and relatives) are Salmoniformes, and should include the southern *Lepidogalaxias,* as advocated by Rosen. This view is contested by Fink and Weitzman, who exclude esocoids from Salmoniformes and relate *Lepidogalaxias* to Galaxiidae and osmeroids. Another major issue is whether relations of the southern "salmonoids" (Galaxiidae, etc.) lie with the northern salmonoids (Salmonidae, etc.) or with osmeroids. The hypothesis that stomiatoids are Salmoniformes (Weitzman 1967) has been rejected by Rosen (1974), Klyukanov (1975), and Fink and Weitzman (1982). Fink and Weitzman also point out that no satisfactory evidence has yet been advanced to support the hypotheses of relationships among osmeroids, salmonids, and galaxioids. Here I shall comment briefly on relationships of the salangoids to other Salmoniformes, particularly osmeroids and galaxioids, and present some evidence bearing on relationships of *Lepidogalaxias.*

Gosline (1960) suggested a close relationship of Osmeridae, Salangidae, and Plecoglossidae, distinguishing them from the Southern Hemisphere Retropinnidae, Aplochitonidae, and Galaxiidae. Greenwood et al. (1966) placed Salangidae in a suborder Galaxioidei including Retropinnidae, Galaxiidae, and Aplochitonidae without explanation. McDowall (1969) concluded that Salangidae are a very specialized offshoot of the salmonoids and not part of the galaxioid radiation.

In observing the skeletal anatomy of salangoids I have been watchful for specialized characters indicative of phyletic relationship to other Salmoniformes. While my study has revealed highly specialized characters (such as the hyopalatine) indicating monophyly of salangoids, it has not provided (or at least I have not noticed) characters that would link salangoids in a monophyletic taxon with Osmeridae or any other group. Rosen (1974) pointed to specializations of the anal fin and associated scales in males of *Lepidogalaxias* and *Mallotus,* but concluded (p. 304) that these do not indicate relationship to Salangidae, and I agree. The anal scales and anal fin modifications of male salangoids appear to be a unique specialization, as does the hyopalatine. Salangoids lack some skeletal features found in Osmeridae, notably in the ethmoid region. Whether this absence is due to loss or reflects a primitive condition is unclear. Development of a tectum taenia medialis in the cranial fontanel, characteristic of the osmeroid chondrocranium, occurs in some salangoids and may be indicative of relationship, but further observation may reveal that the character is widespread in Salmoniformes. The peculiar morphology of the salangoid egg case (Wakiya and Takahasi 1937, Okada 1960) may be similar to that in osmeroids (compare photographs of *Hypomesus olidus* and *Salangichthys microdon* eggs in Chyung 1961, figs. 242–243). Similar specializations possibly also occur in *Plecoglossus* but have not been reported in any of the northern salmonoids or in galaxioids.

According to McAllister (1963:6) "the neotenic Salangidae strongly resemble larval Osmeridae but may be distinguished by their reduced pointed head and elongated anterior portion of the body, as well as osteological characters." Skeletal preparations of larval Osmeridae examined by me differ from salangoids in many respects. There are certain similarities in appearance of the largely transparent and lightly pigmented larvae of osmeroids and salangoids but these are mainly such as are to be found in larvae of non-related teleosts, and their value in assessing relationships is dubious. Skeletal anatomy of larval osmeroids I have examined differs from that of salangoids almost as much as does skeletal anatomy of adult osmeroids. I have not examined skeletal anatomy of Plecoglossidae, but this family appears to be very specialized and there is no evidence that it is particularly closely related to Salangidae. Gosline (1960:346) and others have mentioned certain similarities between the salangids and the extraordinarily specialized galaxoid *Lovettia* but I believe such resemblance is due to independently acquired neotenic characters.

Considerable interest has centered on the phylogenetic significance of the little salmoniform *Lepidogalaxias salamandroides* recently discovered in western Australia (Mees 1961). Among many peculiar features, it has in sexually mature males an extraordinarily modified anal fin partially covered by a sheath of anal scales suggestive of the anal scales of male Salangidae. The extremely complex modifications of the anal finrays go far beyond that seen in the anal fin of the salangids or any other salmoniform, and I doubt that in the relatively simple modifications of the anal fin in male salangids any uniquely shared specializations (or synapomorphies) with *Lepidogalaxias* can be recognized. The presence of a sheath of enlarged anal scales, on the other hand, demands closer comparison with those of salangids, which are otherwise unique among salmoniforms (and perhaps all other teleosts). The anal scales in *Lepidogalaxias* are greatly enlarged and disposed in two main rows, rather than a single row, as in salangids. Two 31–34-mm specimens I examined have seven to eight scales in the upper row and three in the lower. There also appear to be some scales or scalelike structures associated with the vent itself. Unlike that of salangids, however, the anal sheath covers the

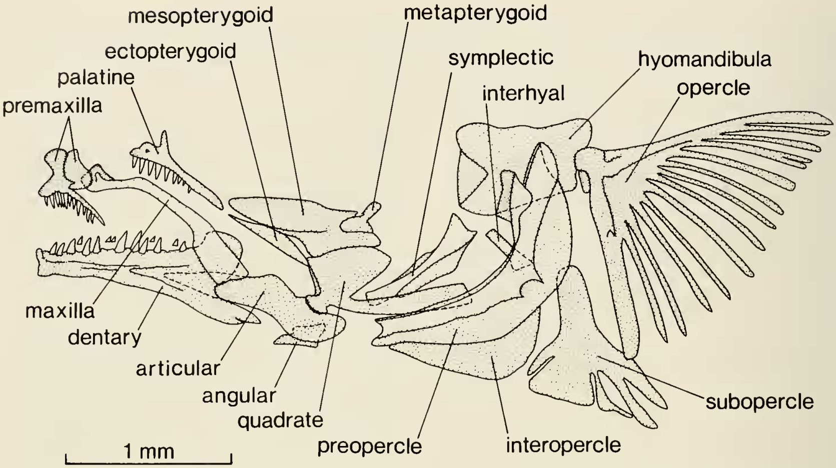

FIGURE 22. *Lepidogalaxias salamandroides* (uncat., 23.5 mm). Jaws, facial ones, and suspensorium (lateral view).

anal fin, especially the modified portions. In salangids the anal scales are on the body above the anal fin, and the rays themselves are entirely exposed. Whatever the phyletic significance, it would certainly be of interest to know more about the functional significance of the anal scales and modified anal fins in *Lepidogalaxias* and in Salangidae.

Fink and Weitzman (1982) suggested that a single row of mesopterygoid teeth is a synapomorphy indicating monophyly for the osmeroids (including Salangidae) and galaxioids (including *Lepidogalaxias*). Although Gosline (1960) stated that the mesopterygoid is absent in Salangidae, it is actually present in most of them. But while most Salangidae have palatal teeth, the salangoid mesopterygoid is invariably toothless, even in *Protosalanx* and *Salanx chinensis* which have well-developed basihyal teeth. Thus the concept of a "tongue-bite" character, based on basihyal and mesopterygoid teeth, and uniting galaxioids and osmeroids, does not hold for salangoids.

While my observations of salangoid skeletal anatomy have not provided me with the key to their higher relationships, I earnestly hope that they may do so for future workers who are able to make more extensive comparisons. In examining *Lepidogalaxias* I find no characters indicative of close relationship to Osmeridae or Salangidae, but the structure of the jaws and gill cover reveals specialized characters linking this strange western Australian fish to the southern galaxioid radiation.

Based largely on the assumption that *Lepidogalaxias* possesses uniserial mesopterygoid teeth, and without having examined skeletal material, Fink and Weitzman (1982) suggested its relationships lie with osmeroids and galaxioids. I have examined skeletal anatomy of several larval and juvenile or subadult *Lepidogalaxias*; the largest of these has a well-developed median patch of teeth on the prevomer and a pair of well-developed tooth patches on the anterior palatine area (ectopterygoid? = endopterygoid of Mees 1960) but the large, well-developed mesopterygoid is toothless. On the other hand, specialization of bones in the jaws and gill cover (Fig. 22) indicates relationship with galaxioids. The extraordinary fimbriate condition of the bony opercle, also of the subopercle, appears to be a highly specialized character shared only (i.e., synapomorphic) with galaxioids (see McDowall 1969, Fig. 3b–e, and Rosen 1974, Fig. 13). The short and laterally directed premaxilla and toothless maxilla with its strongly concave margin may represent another synapomorphy with galaxioids. My observations suggest that *Lepidogalaxias* is indeed related to Galaxiidae, as suggested by Nelson (1970), but I doubt that it represents the "primitive sister group of galaxiids or galaxioids"; it is more likely to be a highly specialized galaxiid or galaxioid derivative. As pointed out by Scott (1966), its osteology should be examined carefully and thoroughly; this has yet to be done. For the present I would like to point out a difference between the branchial arches of *Lepidogalaxias* and Umbridae which merits further investigation. In *Lepidogalaxias* and Umbridae the basibranchial plate has five basibranchials, and the fifth is cartilaginous. In *Lepidogalaxias* the basibranchial plate is apparently immobile; that is, the basibranchials apparently do not move backward and forward in relation to each other. In Umbridae, however, as exemplified by *Novumbra hubbsi*, basibranchial 5 is movably articulated to basibranchial 4 in such a fashion that it can be rocked back and forth beneath it; and thus the pair of toothplate-bearing fifth ceratobranchials, firmly attached to basibranchial 5, are also moved back and forth. Whether such basibranchial mobility occurs in other Umbridae or in esocoids generally is unknown; it has not been observed in galaxioids, osmeroids, or salangoids (the latter apparently lack basibranchial 5).

In assessing phylogenetic relationships one should not be overly impressed by the presence of primitive characters, even in groups in which such characters supposedly have been lost for a long time.

Atavism, the expression of ancient characters "buried in the genome," occurs far more often than generally recognized. This, rather than a Lamarckian interpretation, is doubtless the correct explanation for the appearance of breeding tubercles on the palms of the midwife toads (*Alytes obstetricans*) painstakingly studied by Kammerer (see Koestler 1973). Characters such as eyes, teeth, scales, bone, or the pelvic girdle may be repeatedly suppressed, and may not be physically expressed in any members of quite large groups, without ever having been lost from the genome. For purposes of phylogenetic analysis, I suggest it is parsimonious to assume that primitive characters are never lost from the genome, and that this is really why it is futile to rely on them. Thus the fully scaled condition of *Lepidogalaxias* does not suggest to me that it represents the primitive sister group of the otherwise scaleless galaxioids.

I believe that utilization of the caudal skeleton as a guide to phyletic relationships among teleosts, especially those with the primitive teleost complement of six separate hypurals and 10+9 principal caudal fin-rays, has inevitably resulted in confusion of primitive with advanced characteristics in the caudal fin skeleton. While teleosts as a whole exhibit great diversity in their caudal skeleton (Monod 1968), the main features of the caudal skeleton are remarkably similar in many teleosts with forked caudal fins and the primitive complement of principal caudal fin-rays. Thus the caudal fin skeleton of salangoids is strikingly similar in many respects to that of *Elops*, many clupeoids, characoids, and cyprinoids as well as of osmeroids and other salmoniforms. There are two possible explanations (or hypotheses) for such similarities, both predicated upon the assumption that the caudal fin structure of *Elops* and the others is primitive for teleosts. The first, and traditional, explanation is that all descended from ancestors that never deviated from morphologically primitive caudal fins. The second is that teleosts with secondarily generalized caudal fins have repeatedly reverted to a primitive type of caudal fin skeletal morphology.

Salangoids often have been referred to as neotenic. According to Jordan and Snyder (1902: 592), "the straight alimentary canal, distinct muscle segmentation, very thin ventral wall of the abdominal cavity, and other characters of salangoids suggest a larval stage of development." Among other characters, they were certainly thinking of the near perfectly transparent state of the fish in life. Thus when the fish die, the flesh turns perfectly white, and, in the absence of scales, the myotomes stand out very clearly, as in many larval fish. Berg (1947), Gosline (1960), Weitzman (1967), and McDowall (1969), remarked that Salangidae seem to be neotenic but did not elaborate. If the term *neotenic* means simply attaining sexual maturity while retaining some larval characteristics, salangoids are surely neotenic, probably more so than any other salmoniform fishes. The following characteristic features of salangoids are among those which may be neotenic:

1) Body almost entirely transparent in life.

2) Pectoral fin pedunculate, with a broad, fleshy, pedestallike base more or less free from the lateral musculature of the body, and placed high on

the side of the body, just like the pedunculate pectoral fin of many lower teleost larvae.

3) Skeleton in large measure cartilaginous; many bones found in adults of other salmoniforms absent.

4) Body scaleless throughout life except for anal scales in sexually mature male salangids.

5) Ventral body musculature incomplete, evidently due to an arrested ventral myotomic progression, so that the ventral abdominal wall is thin and non-muscular.

6) Left and right halves of pelvic girdle more or less widely separated from each other, failing to form a cartilaginous union by means of posteromedian processes as in most other salmoniforms.

7) Abdomen posterior to pelvic fin with a membranous median keel.

8) Fourth gill arch with well-developed hypobranchials.

9) Primary pectoral girdle consisting of a median scapulocoracoid in Sundasalangidae (a condition also present in larvae of *Elops* and other lower teleosts).

10) Dorsal and anal fins placed relatively far posteriorly (least so in *Protosalanx*).

On the other hand, salangoids exhibit considerable diversification and a number of peculiar modifications or specializations which are obviously not neotenic, including:

1) Marked sexual dimorphism in Salangidae, involving enlarged pectoral and anal fins, modified anal fin-rays, and development of the anal scales in sexually mature male salangids.

2) Strongly depressed cranium and skull; marked ventromedian curvature of maxilla.

3) Voracious feeding habits and canine dentition, especially in Salanginae.

4) Vertebral counts of 37–79, the highest counts found in Salanginae with excessively elongate body form.

5) Proximal radials of pectoral fin highly modified in all Salangidae; pectoral fin-rays very numerous in all Salangidae except Salanginae.

6) Fusion of cartilaginous hyomandibular and mandibular arches to form a hyopalatine.

7) Fusion of basibranchials and hypobranchials in gill arches of Sundasalangidae.

Thus salangoids resemble larval fish in many ways. But the problem arises of distinguishing between characters that are truly neotenic and characters that represent convergence of adults with larvae. Upon first observing the beautifully simple condition of the primary pectoral girdle in *Sundasalanx*, and taking into consideration the fused condition of ventral elements in the branchial arches of *Sundasalanx* and of the pterygoquadrate and hyomandibula in all salangoids, I was inclined to regard it as due to secondarily evolved simplification and/or reduction and fusion of the primitively separate left and right halves. But a morphologically identical "median" pectoral girdle and "fused" radial plate was reported in larval clupeoids by Goodrich (1922) and I have found it in larval *Elops hawaiiensis* (Fig. 19b) and anchovies. In all of these larvae, as in *Sundasalanx*, the scapulocoracoid has three clearly divided portions (a transverse median bar, an ascending process, and a posterior projection) and the basal radial or plate is perforated by three foramina. In further development, the three foramina of the pectoral plate presumably enlarge until the basal plate in all of these forms except *Sundasalanx* divides into proximal radials 2–5. (The primitive number of proximal radials for all teleosts appears to be 5, observed even in many teleosts having highly modified pectoral fins.) *Sundasalanx* is the only known fish which retains a median scapulocoracoid at sexual maturity. The other salangoids presumably have such a median pectoral girdle as larvae, but although the scapulocoracoid is apparently cartilaginous in all Salangidae examined, it is clearly divided into two halves in all specimens examined, including *Salangichthys microdon* of only 39 mm SL. Goodrich (1922:508) tentatively concluded that the fusion of the endoskeletal pectoral girdle he found in young clupeids represents a specialization peculiar to larval Clupeidae. The present finding that morphologically identical girdles occur in at least some Elopomorpha and Salmoniformes as well suggests that it is indeed a primitive characteristic of teleosts. The duration of the median condition apparently corresponds more or less closely with a period when the pedunculate pectoral fins are being used most actively, the primary pectoral girdle is still largely or entirely cartilaginous, and the mesocoracoid arch has not developed.

ADDENDUM

The galley proofs of this paper were already set when Prof. Xin-Luo Chu of the Kunming Institute of Zoology of Academia Sinica visited the California Academy of Sciences (January

1984) bringing specimens of *Neosalanx tangahkeii taihuensis* for me to examine. These specimens, CAS 54330, 4: 69.7–76.8 mm, were caught in Kunming Lake where the species was introduced in 1981 from artificially reared stock originating in Lake Taihu. The specimens have total vertebrae 56(1), 57(2), 59(1) and gill rakers 15(2), 16(1), 18(1). I therefore conclude that *N. tangahkeii taihuensis* is a junior subjective synonym of *N. brevirostris. N. brevirostris* is a valuable commercial fish and much of the production (especially of Lake Taihu) is marketed abroad. In the near future it may be widely introduced in lakes in China which lie outside the natural range of *Neosalanx.*

It may be worthwhile for Chinese workers to investigate the aquacultural potential of the other two species of *Neosalanx* occurring in China. *N. andersoni,* which may grow slightly larger than *N. brevirostris,* has a relatively restricted northerly distribution, indicating that it is adapted to colder waters. *N. jordani,* the smallest species, has a wide range largely overlapping that of *N. brevirostris,* but my observations indicate that the two species usually do not occur together in nature. *N. jordani* has fewer gill rakers and this together with its smaller size indicates a probable difference in feeding habits. It could be of practical as well as scientific value to compare the ecology and fisheries biology of these three species.

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