# Notes on the anatomy and relationships of Sundasalanx Roberts (Teleostei, Clupeidae), with descriptions of four new species from Borneo 

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#### Abstract

Synopsis. Sundasalanx has a prootic bulla and a recessus lateralis. Thus it is a clupeiform. The degree of caudal skeleton consolidation found in Sundasalanx suggests relationship to the clupeid genus Jenkinsia. Sundasalanx is unusual among known miniature clupeiforms. Its somatic development is equivalent to that of late stage unmetamorphosed larvae of other clupeiforms; Sundasalanx is highly progenetic. Among fishes perhaps only Schindleria attains a comparable degree of progenesis. Sundasalanx is widely distributed over Southeast Asia, with considerable species diversity. Descriptions are provided for four new Bornean species: S. malleti Siebert and Crimmen; S. mesops Siebert and Crimmen; S. megalops Siebert and Crimmen; and S. platyrhynchus Siebert and Crimmen.


## INTRODUCTION

Roberts (1981) described two new species of minute transparent fishes, one from Khlong Falamee, Isthmus of Kra, southern Thai-
land, and the other from the Kapuas River, Kalimantan Barat, Indonesia, as Sundasalanx praecox and Sundasalanx microps, respectively. Sundasalanx is now known also from peninsular Malaysia (Roberts, 1984; Kreutzman, 1993), Thailand north of the peninsula (Roberts, 1984), and eastern Borneo north of the Kapuas River basin
(L. Parenti, pers. comm.). Four new species of Sundasalanx are described below, three from the Barito River, Central Borneo, Indonesia and one from the Kapuas river, West Borneo, Indonesia. The new species of Sundasalanx appear to be larger than S. praecox and $S$. microps but are very small fishes nevertheless, with observed standard lengths not exceeding 30 mm .

Roberts (1981) considered Sundasalanx to be so unlike other known fishes he erected a new family for it. While recognising its unusual nature Roberts nevertheless felt it is allied with Salangidae (icefishes), hence the name Sundasalanx, and its familial derivative, Sundasalangidae. The following list of features was presented as evidence in support of this conclusion: 1) jaw suspensorium consisting of a single cartilaginous element; 2) $4^{\text {th }}$ hypobranchial element present; 3) pedunculate pectoral fins; 4)scaleless body; 5) absence of symplectic; 6) absence of circumorbital bones; 7) myotomal muscles not meeting at the ventral midline of the body; and 8) distal two-thirds of maxilla curved beneath the head so that its ventral edge is directed medially. Others have regarded Sundasalanx simply as a salangid, arguing that if its relationship is with salangids then recognition of a Sundasalangidae would render Salangidae paraphyletic (Fink, 1984; Begle, 1991), if co-ordinate ranking is maintained in classification. Johnson \& Patterson (1996) recently have proposed a classification of the Salmoniformes in which salangids are nested within the Osmeridae. In their classification salangids are given lower rank. They plus Mallotus make up the tribe Salangini.

All of the features enumerated above as suggestive of a relationship with salangids, except possibly the curve of the posterior portion of the maxilla to beneath the head, are simply aspects of a physiognomy that is paedomorphic to an extreme. They are in fact features suggestive of a larval stage of development and are a consequence of a truncated ontogeny. As such they might not each constitute independent evidence of relationship as each might be the result of the same process or event that altered the development of Sundasalanx. Furthermore, they amount to statements of absence, which renders them ineffectual as evidence of relationship in the absence of corroboration from other characters. Different evidence, and a new radical hypothesis of relationship for Sundasalanx are presented below.

## MATERIALSAND METHODS

Comparative morphometry is presented with reference either to Standard length (SL) or Head length (HL), each measured as recommended in Hubbs \& Lagler (1947). Head width (HW) was taken as the width of the widest part of the head. Eye diameter was measured from camera lucida tracings of heads. Counterstained (C\&S) materials were prepared following Dingerkus \& Uhler (1977). Since ossification in Sundasalanx is slight some materials were cleared and then stained with alizarin only. Some very lightly ossified elements were only apparent in material prepared this way. Whether very lightly ossified elements were obscured by the blue counterstain or dissolved by the acidic alcian blue solution during the counterstaining process was not determined. Institutional abbreviations follow Leviton et al. (1985).

Anatomical notes are based on observations of cleared and stained specimens: 17 Sundasalanx malleti sp. nov., from the Barito River; 10 Sundasalanx mesops sp . nov., from the Barito River, 3 Sundasalanx platyrhynchus sp. nov., from the Kapuas River; 2 paratypes of Sundasalanx microps Roberts, from the Kapuas River, 1 paratype of S. praecox Roberts, from peninsular Thailand; and 1 paratype of $S$. megalops sp. nov., from the Barito River.

Material Examined. Materials of the new species are listed below in the descriptions of new species.

Sundasalanx microps, paratypes, CAS 44220, 5 of 9 alc., 2 of 7 C\&S, Indonesia, Kalimantan Barat, Kapuas R. basin, Kapuas R. mainstream at Kampong Nibung, ca 100 km northeast of Selimbau, 5-6 Jul 1976, T.Roberts.

Sundasalanx praecox, paratypes, BMNH 1981.5.19:80-84, 4 alc. ex., 1 C\&S, Thailand, Isthmus of Kra, Khlong Falamee, a tributary of Tale Sap, ca. 2 km W of Pak Payoon, 20 Jun 1970, T.Roberts.

## NOTES ON THE ANATOMY OF SUNDASALANX ROBERTS, 1981

Small size and light ossification make Sundasalanx difficult subjects to study. Observations and interpretations that augment, or differ from, those of Roberts $(1981,1984)$ and Kottelat (1991) are presented below. Although the relationships of Sundasalanx are discussed later, comparisons are made here to clupeomorph, clupeiform, or clupeid anatomy as an aid in interpretingSundasalanx. This is based on the conclusion that Sundasalanx is a clupeid, not a salangoid.

Sundasalanx does not look like other juvenile or adult clupeids. Rather, their physiognomy is very much like that of a late stage premetamorphosis larva. Although there is a large literature concerning the identification of larval clupeomorphs (McGowan \& Berry, 1984) surprisingly little has been written about their internal anatomy (O'Connell, 1981).An exception is the gas bladder-inner ear-lateral line system, of which detailed anatomical descriptions are available for a number of clupeiforms (Allen et al., 1976; Blaxter \& Hunter, 1982; O’Connell, 1981; Shardo, 1996).

Sundasalanx is distinctive. The peculiar structures Roberts (1981) termed parapelvic cartilages (or bones; Fig. 1) are unknown elsewhere among teleosts. Sundasalanx also possesses a highly derived caudal skeleton (described below; Fig. 7A). A number of other features listed by Roberts, mostly paedomorphic and not unique to Sundasalanx, contribute to the generic diagnosis (Roberts, 1981). The absence of hypobranchials $1-3$ but with presence of hypobranchial 4 , a cartilage bar uniting the shoulder girdle across the ventral midline and a rayless pectoral fin supported by a single cartilaginous plate rather than by separate radials are particularly striking among the list.

## Colour Pattern

Previous descriptions of Sundasalanx have been based on single


Fig. 1 Pelvic girdle of Sundasalanx malleti (anterior to left); A = parapelvic bones, $\mathrm{B}=$ basipterygium, $\mathrm{C}=1^{\text {st }}$ pelvic fin-ray, $\mathrm{D}=$ radial, scale $\mathrm{bar}=0.5 \mathrm{~mm}$.
samples, albeit relatively large ones. Roberts (1984) suggested a more detailed investigation of the colour pattern of different populations of Sundasalanx was needed since every population seemed to exhibit its own distinctive pattern, and implied that the observed variation might be intra- rather than interspecific. Preserved materials studied here indicate that Sundasalanx species share a basic colour pattern, but some species differ in certain aspects and it varies with size and between sexes. Sex and size are the two factors that appear to influence colour pattern most. Larger specimens have more strongly developed colour patterns and males have more vivid patterns than females or juveniles.

In life Sundasalanx is transparent except for the silvery cover around the eyeballs, which decomposes to reveal black pigment around the eye if specimens are conserved in formalin. Close examination, however, of preserved specimens reveals an extensive colour pattern (Figs 2,11,13-15). A small black spot is present behind the eye in the prootic region (best seen in Fig. 14), associated with the posterodorsal surface of what is herein identified as a prootic bulla. This spot was observed in all species examined except S. praecox, studied materials of which were largely depigmented. Pigment deposition on the dorsal surface of the prootic bulla during development has been observed in other clupeoids (Hoss \& Blaxter, 1982), and is possibly a general feature of the group. Absence of prootic bulla pigmentation in S. praecox is likely an artefact of preservation.

A dark prepectoral mark, consisting of $1-5$ melanophores, is present just anterior to the pectoral fin in most individuals examined (present in all large individuals; seen best in Figs 11, 13) of all species except S. praecox. The extent of the mark appears to vary interspecifically with the mark in Barito River species consistently larger than that of species examined from elsewhere. In species with a smaller mark it consists of one or two melanophores on the dorsolateral surface of the connective tissue sheath surrounding the sternohyoideus just anterior to the origin of the muscle on the cleithrum. Species with a larger mark possess up to three more melanophores on the rear wall of the gill chamber, dorsal to those on the sternohyoideus.

Elements of a mid-ventral line of melanophores are present in all species (Fig. 2). A midventral gular streak, dividing the sternohyoideus muscle mass into right and left sides, is present in all species. A midventral line of melanophores from behind the compartment in which the heart lies to the caudal fin, as described for southern peninsular Malaysia materials by Roberts (1984), is present in all species except $S$. praecox. In the region of the body cavity the melanophores are associated with the ventral finfold or its remnants. In the region of the anal fin, ventral midline pigmentation consists of melanophores located between each anal-fin pterygiophore, one per interpterygiophore space (best seen in Fig. 15); behind the anal fin the line is continued as a midventral series of melanophores situated between the ventral ends of myotomes of the caudal peduncle myotomes.

A line of melanophores is present on each side of the body at the ventral edge of myotomes in the region of the body cavity in all species examined (Figs 11, 13-15). The line begins immediately behind the shoulder girdle and ends at the anus, with the frequency of melanophores usually greater than one per myotome, but less than two per myotome. The line is continuous except in the region immediately dorsal to the pelvic fins, from which melanophores are absent.

In all species examined, a dark spot consisting of a single melanophore is located just anterior to the insertion of the pelvic fins (Figs 2, 11, 13-15), below the course of the myotomal line. An additional spot is located near the anterior end of the basipterygium of $S$.


Fig. 2 Schematic representation of the melanophore pattern of Sundasalanx in ventral view (anterior to left); $\mathrm{A}=$ gular streak of midventral line, $\mathrm{B}=$ midventral line of the ventral fin fold, $\mathrm{C}=$ myotomal line, $\mathrm{D}=$ melanophores of cleithral mark associated with the sternohyoideus, $\mathrm{E}=$ cardiac compartment melanophores (present only in males of S. microps, S. mesops, S. megalops, and S. platyrhynchus), F = basipterygium melanophore (present in all species examined).
praecox. Males of S. malleti with mature, or maturing, testes show additional pigmentation of the pelvic-fin girdle, with a ring of melanophores encircling the basipterygium.

The lower caudal-fin lobe is marked by a broad swath of melanophores in all species except possibly S. praecox. This lower caudal-fin lobe swath is especially intense in materials identifiable as male (Fig. 14). A few scattered melanophores were observed on the upper caudal-fin lobe of a few individuals.

The posterior half of the compartment in which the heart lies is marked with melanophores (Fig. 2) in males of S. microps, S. mesops, S. megalops, and S. platyrhynchus, even in quite small individuals. Examination of larger specimens in which it is obvious that maturation of the testes has begun shows the mark is present only in males; specimens with maturing or mature ovaries lack the mark, as do all of the smallest specimens. The juxtaposition of the anterior end of the myotomal lines to the pigmentation of the cardiac compartment creates a very distinctive M-shaped ventral mark just posterior to the pectoral girdle in males of those species with cardiac compartment pigmentation (Fig. 2).

## Soft anatomy

## Gut

The gut of Sundasalanx is straight, with three sections clearly distinguishable under gross microscopical examination of cleared and stained specimens (Fig. 3). Length of gut measures approximately $62 \%$ of SL in the largest cleared and stained specimen examined ( 24 mm SL ). The first section, approximately $20 \%$ of total gut length, is characterised by longitudinal folds, continuous throughout its length. No obvious distinction between oesophagus and stomach is apparent, although the posterior part of this section is somewhat greater in diameter than the anterior part. The pneumatic duct exits from the dorsal side of the posterior half of the stomachal


Fig. 3 Gut and gas bladder of Sundasalanx malleti (anterior to left); A = anterior section of gut (oesophagus/stomach), $\mathrm{B}=$ middle section of gut (anterior part of intestine), $\mathrm{C}=$ parapelvic bones, $\mathrm{D}=$ middle section of gut (posterior part of intestine), $\mathrm{E}=$ posterior section of gut, $\mathrm{F}=$ gas bladder, $\mathrm{G}=$ pneumatic duct, scale $\mathrm{bar}=3 \mathrm{~mm}$.
region. The second section, consisting of the intestine, is separated from the oesophagus-stomach by an obvious sphincter, and measures approximately $73 \%$ of total gut length. The anterior third of the intestine is marked by irregular folds, which are more vertically oriented and regular in the region of the air bladder and parapelvic bones. Posterior to the air bladder the folds are regular, nearly vertical, and wavy. They appear to encircle the gut so that the posterior half of the intestine looks very much like the external appearance of an earthworm. The end of the intestine is conical and projects slightly into the third section. The third section of the gut is short, less than $10 \%$ of total gut length and is slightly greater in diameter than the intestine. It also is characterised by wavy, vertical folds, but these are more numerous (distinctly closer together) and more wavy than those of the intestine.

## Gonads

The gonads lie dorsal to the gut and when mature occupy nearly the entire length of the body cavity, as described for S. praecox (Roberts, 1981). Testes exhibit the vertical striations characteristic of at least some other clupeomorphs (Roberts, 1981; Whitehead \& Teugels, 1985). Judging from enlargement of posterior sections of testes in some individuals, maturation of testes proceeds from posterior to anterior. Ovaries contain eggs of distinct size classes, egg size presumably being an indication of degree of egg maturation. One female contained 18 very large eggs, nine in each ovary arranged in a single file. These eggs were slightly wider than the width of two myotomes (nearly 1 mm in diameter) and occupied nearly the entire length of the ovaries. Smaller eggs of two distinct size classes were interspersed among the larger eggs (Fig. 4). Among clupeomorphs the presence of distinct size classes of eggs in ovaries is considered indicative of repeat spawning within a single breeding season. Sundasalanx may thus have considerable fecundity even though relatively few mature ova are present (can fit) within an ovary. Roberts (1981) reported egg size in S. praecox of only $0.20-0.25$ mm in diameter. Sundasalanx praecox may have smaller ova than other Sundasalanx species, but among clupeiforms that are repeat spawners final enlargement of the egg does not occur until shortly before spawning (Blaxter \& Hunter, 1982). Thus the difference in egg size between Barito River species of Sundasalanx observed here and S. praecox may be due to the stage of egg development at which materials were preserved.


Fig. 4 Outline drawing of the left ovary of Sundasalanx mesops (anterior to left); $\mathrm{A}=$ large ovum, $\mathrm{B}=$ smaller size classes of ova, $\mathrm{C}=$ duct to genital opening, scale bar $=2 \mathrm{~mm}$.

## Gas Bladder and Associated Structures

The gas bladder is located above the gut in the region of the pelvic fins, and is somewhat constricted by the parapelvic bones (Fig. 3). The pneumatic duct appears to enter the anterior end of the gas bladder, an entry position unusual among clupeomorphs (Whitehead and Blaxter, 1989). The gas bladder was deflated in most specimens but in a few the anterior portion was partially filled with gas. Nocturnal, facultative filling of the gas bladder by swallowing air is well known among larval clupeomorphs. Thus no special significance is attached to the observation that in some Sundasalanx specimens the gas bladder is partially filled with air whereas in most


Fig. 5 Photograph of the head of a skeletal preparation of Sundasalanx malleti (BMNH 1996.7.18.15) showing the relative position, size, and shape of the prootic bulla (A).
it is deflated. A duct leading from the gas bladder to the region of the anus, usually present in clupeomorphs, was not observed.

A very large, vertically oriented, spindle-shaped bulla is present in the prootic (Fig. 5). It is approximately $40 \%$ of head depth in height, protrudes ventrally into the branchial chamber, and extends dorsally nearly to the dorsal surface of the head. It is capped with melanophores and is among the few structures other than the eyes that can be seen on living Sundasalanx. A canal for the precoelomic gas duct is apparent but the duct itself was not detected. Ossification of the prootic bulla is not apparent in counter stained preparation, only in preparations stained solely with alizarin.

Lateral to the prootic bulla lies a cavity, identified as a recessus lateralis, on which the supraorbital, temporal, and infraorbital laterosensory canals converge (Fig. 6). A small, circular fenestra on the dorsolateral side of the prootic bulla communicates with the


Fig. 6 Schematic representation of the recessus lateralis and cephalic laterosensory canals of Sundasalanx malleti (anterior to left); A = temporal canal, $\mathrm{B}=$ infraorbital canal, $\mathrm{C}=$ supraorbital canal, $\mathrm{D}=$ infraorbital bone, $\mathrm{E}=$ recessus lateralis chamber, $\mathrm{F}=$ fenestra on the medial wall of the recessus lateralis, $\mathrm{G}=$ prootic bulla.
recessus lateralis. A large fenestra to the rear of the recessus lateralis communicates with the perilymphatic system.

## Laterosensory canals

No laterosensory canals were observed other than the infraorbital, supraorbital, and temporal canals which converge on the recessus lateralis (Fig. 6). All are short. The supraorbital canal does not extend to even over the eye. The temporal canal does not reach the shoulder girdle or form a supratemporal commisure with its counterpart from the opposite side. The infraorbital canal does not extend to beneath the eye.

## Osteology

No part of the skeleton of Sundasalanx is heavily ossified. Ossification of dermal elements appears to be exceptionally slight and many, usually present in other teleosts, may be absent. For example, no parietals or dermal ethmoid element were detected.

## Caudal skeleton

The caudal skeleton of Sundasalanx is highly consolidated, and somewhat reduced (Fig. 7A). Preural centrum 1 and ural centra 1 and 2 are consolidated into a single compound element, to which uroneural 1 is apparently fused. Uroneural 2 is free, and in Barito River Sundasalanx greatly expanded. Only a single epural is present. The parhypural and hypural 1 are fused (observed in an ontogenetic series of cleared and stained materials); the compound parhypuralhypural is autogenous; hypural 2 is fused to the compound centrum; hypural 3 is autogenous; hypural 4 is expanded to about the size of


Fig. 7 A) Caudal skeleton of Sundasalanx malleti (BMNH 1996.7.18.15), scale $=.3 \mathrm{~mm}$; B) Caudal skeleton of Jenkinsia (BMNH 1962.7.21.48-50), scale $=.45 \mathrm{~mm} ; \mathrm{A}=$ compound centrum $(\mathrm{PU} 1+\mathrm{U} 1+\mathrm{U} 2), \mathrm{B}=$ epural, $\mathrm{C}=$ uroneural $2, \mathrm{D}=$ hypural $5, \mathrm{E}=$ hypural $4, \mathrm{~F}=$ hypural $1, \mathrm{G}=$ parhypural
cartilage chevrons, unique among lower teleosts, are associated with the lateral tips of epicentral intermuscular bones in many clupeoids and the derivation of parapelvic bones from these structures should also be considered.

## Vertebral column

Vertebrae of Sundasalanx are lightly ossified, with neural arches present on all vertebrae preceding the compound caudal vertebra. Caudal vertebrae appear to ossify first. All neural arches preform in cartilage and the anterior few may not ossify. The first neural arch has a broader base than the others and neural spines do not appear to form on the first 4 or 5 arches. No supraneurals are present. Haemal arches also preform in cartilage. Cartilaginous basiventrals are present on all preural centra, including the first. No ribs are present.

## Intermusculars

No intermuscular bones or ligaments (Patterson \& Johnson, 1995) are present.

## Dorsal- and anal-fin supports.

Middle radials do not develop in dorsal- and anal-fin pterygiophores. Distal radials are clearly present. Proximal elements (=proximal + middle radials) of the last few dorsal pterygiophores appear to fuse.

## Jaws

Toothed premaxillary and maxillary bones make up the upper jaw. No supramaxillary bones were detected. Dentary, anguloarticular, and retroarticular bones were identified in the lower jaw.

## Gill arches

The primitive complement of structures that make up the median series of hyoid- and gill arch elements of teleosts, not all of which may be present in adult forms, develops from three copulae (copula 1-3; Nelson, 1969). Derivatives of all three copulae are present in Sundasalanx. The series includes (Fig. 8): the basihyal (derived from copula 1); basibranchial 1-2 and basibranchial 3 (derivatives of copula 2); and basibranchial 4-5 (derived from copula 3). Gill arches 1 and 2 articulate with basibranchial 1-2, gill arch 3 articulates with basibranchial 3, and gill arches 4 and 5 articulate with basibranchial 4-5. Hypobranchials are not evident in the first three arches. Roberts (1981) suggested they were fused to the median elements but such fusion of lateral endoskeletal elements to median endoskeletal elements is rare (Nelson, 1969). A more likely explanation is that hypobranchials $1-3$ never condense from the hypo/ceratobranchial precursors and thus never develop at all. Hypobranchial 4 is present in all species examined, and a curious cartilage nodule, located in the ligament between ceratobranchial 4 and 5 , was seen in some specimens of S. praecox, S. malleti, S. mesops, and S. megalops, but not in S. microps or S. platyrhynchus, both from the Kapuas River. Five conventional ceratobranchials are present. Four epibranchials and three pharyngobranchials are present (Fig. 9). Epibranchials 2-4 are short. Epibranchial 1 is large, occupying the space of pharyngobranchial 1 in addition to its own. Epibranchial 4 curves anteromesially to articulate with the lateral posterodorsal corner of pharyngobranchial 4 , dorsal to the tooth plate associated with the posteroventral side of pharyngobranchial 4. The efferent arterial canal of epibranchial 4 is completely closed, with no sign of any line of fusion of interbranchial 4. A small levator process projects dorsally from the top of the ring of cartilage that forms this canal. The levator exturnus IV, which has its origin on the posterodorsal corner of the skull, inserts on this process. Epibranchial 3 is short, and articulates with the posterolateral end of a large pharyngobranchial 3. The mesioposterior end of pharyngobranchial


Fig. 8 Lower branchial arches of Sundasalanx malleti (anterior to left); A $=$ ceratobranchial $1-5, B=$ hypobranchial $4, C=$ basibranchial $1-2, D=$ basibranchial $3, \mathrm{E}=$ anterior and posterior ceratohyals, $\mathrm{F}=$ hypohyal, G = basihyal, scale bar $=1 \mathrm{~mm}$.


Fig. 9 Dorsal view of left side upper gill arch elements of Sundasalanx malleti (anterior to left); $\mathrm{A}=$ epibranchial $1, \mathrm{~B}=$ epibranchial $4, \mathrm{C}=$ tooth plates (circles indicate tooth positions diagramatically), $\mathrm{D}=$ pharyngobranchial $2-4$, scale $\mathrm{bar}=0.25 \mathrm{~mm}$.

3 articulates broadly with the anterior end of pharyngobranchial 4.A large tooth plate is associated with the ventral surface of the posterior half of pharyngobranchial 3. The uncinate process of epibranchial 3 is modified to form a canal for efferent artery 3. The artery is completely ringed inS. praecox, so that the lateral end of epibranchial 3 looks similar to the lateral end of epibranchial 4. It is almost completely ringed inS. platyrhynchus, but only partially encircled in S. malleti, S. mesops, and S. megalops. Epibranchial 2 is also short, but with a long uncinate process that articulates with the lateral edge of pharyngobranchial 3, the point of articulation on pharyngobranchial 3 drawn out to form an 'uncinate' process in S. malleti. Pharyngobranchial 2 is much longer than wide, extending from the medial edge of epibranchial 2 in an anteromedial direction to the tip of pharyngobranchial 3. No tooth plate was found to be associated with pharyngobranchial 2 . Epibranchial 1 is narrow near the articulation with ceratobranchial 1, broadly spatulate at its medial edge. It possesses a long uncinate process that articulates with the uncinate process of pharyngobranchial 2. A separate pharyngobranchial 1 was not observed. Enlargement of epibranchial 1 may be the result of fusion between it and pharyngobranchial 1 , or of failure of condensation of pharyngobranchial 1 from the epi-pharyngobranchial anlagen in a shortened developmental programme.

Very thin perichondral ossification of ceratobranchial 5 was the only ossification detected for endoskeletal gill arch elements. If other elements are ossified their ossification is beyond the limit of


Fig. 10 Schematic illustration of the opercular and branchiostegal series of Sundasalanx malleti (anterior to left); A = opercle, B = subopercle, C = interopercle, $\mathrm{D}=$ branchiostegals, $\mathrm{E}=$ preopercle, $\mathrm{F}=$ infraorbital bone.
resolution of the staining procedures used, or the materials prepared as whole mount preparations.

## Dentition

Roberts (1981, 1984) reported teeth on the premaxilla and maxilla, and that teeth are embedded directly in cartilage on the lower jaw (Meckel's cartilage), ceratobranchial 5, and pharyngobranchial 4 of S. praecox and S. microps. Kottelat (1991) reported a pharyngobranchial 4 tooth plate in the species here named S. platyrhynchus, rather than teeth embedded directly in cartilage. Materials prepared only as alizarin preparations in this study indicate the conclusion that some teeth in Sundasalanx are directly embedded into cartilage is erroneous, and most likely due to examination of specimens prepared by counter-staining for cartilage and bone.

In addition to those structures listed above, all species of Sundasalanx examined were found to also have a tooth plate and teeth associated with the underside of the posteromedial part of pharyngobranchial 3 . The size of the tooth plate appears to vary among species. Sundasalanx praecox was found also to possess teeth on the posterior end of basibranchial 1-2) in the floor of the mouth, and small 'vomerine' tooth patches were found also in the roof of the mouth, one on either side of the anterior tip of the parasphenoid. The largest cleared and stained specimen of S. malleti appears to have a tooth plate (toothless) associated with the posterior end of the basihyal.

## Suspensorium

The suspensorium is weakly ossified and not well differentiated. Independent quadrate, metapterygoid, symplectic, or hyomandibula ossifications were not detected in any species of Sundasalanx. The posterior articulation of the suspensorium with the skull is broad. An independent cartilaginous palatine was observed in all examined species except S. praecox, the smallest species, in which a thin strut of cartilage communicates between the palatine and the hyomandibular complex. An extremely thin, sheet-like ossification under the eye between the palatine and hyomandibular is here identified as the mesopteryogoid.

## Lower hyoid arch

The basihyal is a large expansive structure that essentially fills the floor of the mouth anterior to the hyoid arch A cartilaginous hypohyal is present, but apparently without differentiation into upper and lower hypohyoid elements. Ossified anterior and posterior ceratohyals are present, as is an unossified interhyal. Two, three,
or four branchiostegals, subequal in size, were found to be associated with the ventrolateral side of the posterior ceratohyal. The number of branchiostegals present is not constant in any species of Sundasalanx examined. The anteriormost branchiostegal is positioned at the anterior edge of the posterior ceratohyal, partially overlapping the gap between the posterior- and anterior ceratohyal. Succeeding branchiostegals are positioned posteriorly along the ceratohyal and there is a distinct gap between the branchiostegal series and the interopercle, which is associated with the posterolateral side of the posterior ceratohyal near the articulation of the interhyal. The interopercle is distinctly larger than any member of the branchiostegal series (Fig. 10).

## Opercular series

An opercle, subopercle, interopercule, and preopercle were found in all species examined (Fig. 10). All elements are very lightly ossified and are easily overlooked, especially the preopercle. The opercle, subopercle and interopercle form an overlapping series, with the ventroanterior corner of the opercle lying external to the posterior edge of the subopercle and the anterior edge of the subopercle lying external to the posterior edge of the interopercle. The interopercle is associated with the posterolateral side of the posterior ceratohyal, near the interhyal. The preopercle is an elongate element. Its anterior end lies lateral to the undifferentiated quadrate. More posteriorly it lies lateral to the ventral portion of the cartilaginous structure that is the undifferinated hyomandibula. Its posterior portion occupies the space between the infraorbital and the opercle. No lateral sensory canal was observed to be associated with the preopercle.

## Infraorbital series

A single infraorbital element was detected. It is an extremely thin ossification located in the interior of the bend of where the infraorbital laterosensory canal turns in an anterior direction. The infraorbital canal emerges from the recessus lateralis well behind the eye. Consequently the sole infraorbital is positioned well posterior to the eye.

## Skull Roofing Bones

The only roofing bone identified is an ossification associated with the supraorbital laterosensory canal and recessus lateralis. The bone is very weakly ossified and difficult to detect. The pair, one on each side, are here identified as frontals, because of the association between the supraorbital laterosensory canal, the recessus lateralis and the frontal in clupeiforms. Parietals, and dermal ethmoid elements were not detected.

## RELATIONSHIPS

In the discussion that follows, the informal term salangid refers to icefishes (=Salangidae of Roberts, 1984). This does not imply criticism of the rank ascribed to them by Johnson and Patterson (1996). Features identified as suggesting a relationship between Sundasalanx and salangids (Roberts 1981, 1984; listed previously [p. 5]) are all paedomorphic, with the possible expection of the orientation of the posterior part of the maxilla. If maxilla orientation in other larval clupeoids is found to be like that Sundasalanx then this feature also is paedomorphic. The features are plesiomorphic too, being features found in larvae of lower teleosts, and in larvae of some euteleosts. Such a list, no matter how long, is nothing more than an appeal to symplesiomorphy as evidence for the hypothesis of relationship. However, as Roberts (1984) indicated the question
remains as to whether the apomorphic condition of neoteny in Sundasalanx and salangids is a synapomorphy or a homoplasy. Derived, non-paedomorphic, features unique to both Sundasalanx and salangids can corroborate a Sundasalanx-salangid relationship, thereby establishing neoteny as synapomorphic for Sundasalanx and salangids.

The recent re-examination of lower eutelostean relationships by Johnson \& Patterson (1996) provides a context for the search for non-paedomorphic features that might confirm a Sundasalanxsalangid relationship. The relevant groups and characters (numbered sequentially) are: euteleosts -1 ) supraneurals develop caudally, 2) uroneural 1 with a membranous outgrowth (stegural), 3) caudal median cartilages present; salmoniforms -4) epicentrals with cartilage rods distally, 5) epicentral and epineural intramuscular bones lacking proximal forks; salmonoids + osmeroids -6 ) derm- and supraethmoid separate, 7) postemporal fossa open, 8) a single supramaxilla, 9) upper pharyngeal tooth plate 4 absent, 10) anterior epineurals not fused to neural arches; 11) epipleurals absent, 12) distal parts of posterior neural and haemal arches forming a keel, 13) uroneural 2 anterodorsal to uroneural 1,14 ) scales without radii, 15) nuptial tubercles present, 16) diadromy; osmeroids -17 ) orbitosphenoid absent, 18) basisphenoid absent, 19) articular reduced, 20) gill rakers toothless, 21) preural centrum 1 and ural centrum 1 fused, 22) cleithrum with a narrow columnar process toward coracoid, 23) no postcleithrum; osmerids -24 ) short hyomandibular crest, 25) opercular with anterodorsal notch, 26) levator process present on epibranchial 4,27 ) uroneural 1 fused to preural centrum $1,28)$ caudal scutes absent, 29) extrascapular fragmented into several ossicles, 30) posterior dorsal pterygiophores fused, 31) adipose cartilage present, 32) egg with adhesive membrane; osmerines - 33) otic bulla (=saccular recess) somewhat inflated, 34) keel formed by posterior neural and haemal spines absent; salangins - 35 ethmoid endoskeleton long and unossified, 36) 1st pectoral radial unmodified, 37) 4th pectoral radial multifid distally, 38) males with modified anal fin endoskeleton; and Icefishes (=salangids) 39) anterior margin of metapterygoid above quadrate, 40) antorbital bone absent, 41) 1 supraneural present, 42) 4th pectoral radial articulates with glenoid, 43) dermal plate absent from basibranchials.

At least 19 of these characters are 'absence characters', or 'reversals' to a more primitive condition, leaving just 24 as 'presence characters'.As with Roberts'list, resemblance between Sundasalanx and salangids due to the first class characters requires confirmation from congruence with the second class of characters. Character 32, egg with adhesive membrane, was not checked in this study. Of the remaining 24 characters from the second class of characters Sundasalanx can be shown to have only four, fusion of preural centrum 1 with ural centrum 1 (21), levator process on epibranchial 4 present (26), uroneural 1 fused to preural centrum 1 (27), and posterior dorsal pterygiophores fused (30). Sundasalanx simply lacks the rest, either because they are primitively absent or because Sundasalanx is so underdeveloped they never appear in its ontogeny. All of the four that are present in Sundasalanx are also present among clupeocephalan, or even elopocephalan, fishes. The evidence for a close relationship among Sundasalanx and icefishes should be regarded as non-existent.

Sundasalanx is highly paedomorphic and as obvious from comparison to the above lists establishing its relationship presents certain difficulties. It is not, however, wholly paedomorphic and the non-paedomorphic features of Sundasalanx suggest a relationship not with salangids, nor any other euteleostean, but with clupeiforms, and further to dussumieriine clupeids.

Prootic bullae are found only among clupeomorph fishes and the recessus lateralis is found only among clupeiforms (Greenwood et
al, 1966; Grande, 1985). Sundasalanx is thus a clupeiform. Establishing the relationships of Sundasalanx within Clupeiformes is less easy. Many external and internal features used to elucidate relationships within the order (Grande, 1985) are absent; all scute and scale characters widely used in the identification of clupeiforms are absent from Sundasalanx, which is completely scaleless and lacks ribs and supraneurals. However, Sundasalanx exhibits a derived, highly consolidated, caudal skeleton. Derived features are: 1) fusion of preural centrum 1 (PU1), ural centrum 1 (U1), ural centrum 2 (U2), and the first uroneural into a single element; 2) reduction of the number of epurals to $1 ; 3$ ) reduction of the number of hypurals to 5 ; 4) fusion of the parhypural and hypural $1 ; 5$ ) an expanded hypural 4; and 6) absence of the extensions of the middle caudal fin rays characteristic of clupeiforms. Among clupeiforms only the spratelloidin dussumieriine genus Jenkinsia, a marine, Caribbean endemic, approaches the degree of caudal skeleton consolidation found in Sundasalanx (Fig. 7B). The pertinent modifications are (Grande, 1985): 1) fusion of PU1, U1, and U2 into a single element; 2) reduction of the number of epurals to one; and 3) expansion of hypural 4 to a size equal to that of hypural 1. Fusion of PU1 with U1 is also known in some pellonulines, some engraulids and Clupeonella, but these lack the other derived caudal skeleton features of spratelloidins (Grande, 1985). Sundasalanx is thus a spratelloidin, and possibly the sister-group of Jenkinsia.

## DISTINCTIVENESS OF SUNDASALANX PRAECOX

The discovery of materials seemingly intermediate in eye size betweenS. praecox and S. microps led Roberts (1984) to suggest that distinction between them at the species level needed further consideration, with the implication that there might be only one widespread species of Sundasalanx. Sundasalanx praecox and S. microps were re-examined for this study. I conclude that Roberts' (1981) original assessment of the specific status of $S$. praecox is correct. It is different from other species of Sundasalanx in so many details that it stands out as the most distinctive of all the described species. No other known species of Sundasalanx possesses any palatal or basibranchial teeth. It has far fewer vertebrae, many more upper jaw teeth, larger pharyngeal tooth plates with many more teeth, larger and more numerous gill rakers, a relatively longer posterior parapelvic bone than any species known from Kalimantan, and lacks a midventral line of melanophores associated with the ventral fin-fold.

## DESCRIPTIONS OF NEW SPECIES

Sundasalanx malleti Siebert and Crimmen, sp. nov.
(Fig. 11)
Holotype. MZB 6096, 26.4 mm SL, Indonesia, Kalimantan Tengah, Barito River basin, Sungai Barito at Muara Laung, dip nets and seines, 20-22 Feb 1991, D. Siebert, A. Tjakrawidjaja, O. Crimmen, and A. Effendi.

PARATYPES. MZB 6097 (20), collection data as for holotype. BMNH 1996.7.18.147-311 (164), collection data as for holotype. USNM 320689 (5), collection data as for holotype.

Referred material. BMNH 1996.7.18.315-324 (10), C\&S, Indonesia, Kalimantan Tengah, Barito River drainage, sand bars of

Table 1 Selected mensural characters of Sundasalanx malleti, S. mesops, S. megalops, and S. platyrhynchus; the mean $\pm$ standard deviation is followed by the sample minimum - maximum; sample size is reported in parentheses if different from that reported under each species' name.

|  | S. malleti $\mathrm{n}=10$ |  |  | S. mesops $\mathrm{n}=30$ |  | S. megalops $\mathrm{n}=2$ | S. platyrhynchus $\mathrm{n}=20$ |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Eye (\% SL) | $4.2 \pm 0.3$ | 3.8-4.7 |  | $5.2 \pm 0.3$ | 4.5-5.7 | 5.9-6.0 | $5.1 \pm 0.4$ | 4.2-5.7 | (18) |
| Eye (\% HL) | $21.3 \pm 1.1$ | 19.9-23.2 |  | $25.5 \pm 1.3$ | 21.4-27.5 | 27.5-29.0 | $23.8 \pm 1.2$ | 21.7-25.9 | (16) |
| Snt (\% SL) | $4.3 \pm 0.4$ | 3.5-4.8 | (9) | $3.8 \pm 0.4$ | 3.1-4.8 | 3.5-4.9 | $4.0 \pm 0.7$ | 2.9-5.2 |  |
| Snt (\% HL) | $21.2 \pm 1.7$ | 18.4-23.9 | (9) | $18.6 \pm 1.7$ | 15.6-22.9 | 17.3-22.6 | $18.1 \pm 1.9$ | 15.3-21.4 | (19) |
| Snt:eye | $1.0 \pm 0.1$ | 0.8-1.2 | (9) | $0.7 \pm 0.1$ | 0.6-1.0 | 0.6-0.8 | $0.8 \pm 0.1$ | 0.6-1.0 | (18) |
| Head d. (\% SL) | $8.2 \pm 0.8$ | 6.3-9.0 |  | $7.9 \pm 0.5$ | 7.3-9.1 | 9.4-9.6 | $8.3 \pm 0.7$ | 7.2-9.5 |  |
| Head I. (\% SL) | $20.0 \pm 0.8$ | 18.8-21.1 |  | $20.7 \pm 0.7$ | 18.7-21.8 | 20.4-21.6 | $21.4 \pm 1.2$ | 19.6-23.2 | (18) |
| Head w. (\& SL) | $9.7 \pm 0.7$ | 8.6-10.6 | (9) | $10.5 \pm 0.4$ | 9.8-11.2 | 9.4 (1) | $10.9 \pm 0.5$ | 10.2-12.0 | (21) |

Table 2 Number of vertebrae of species of Sundasalanx; counts for $S$. praecox and S. microps are from Roberts (1981). Analysis of variance with a post hoc test of location reveals $S$. praecox to be significantly different from S. microps, S. platyrhynchus, S. malleti, and S. mesops at $p<0.001$.

|  | Vertebrae |  |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 |
| S. praecox | 2 | 7 |  |  |  |  |  |  |
| S. microps |  |  |  |  | 2 | 4 | 1 |  |
| S. patarhynchus |  |  |  | 2 | 1 | 5 | 3 | 2 |
| S. malleti |  |  |  | 2 | 8 |  |  | 2 |
| S. mesops |  |  |  |  | 1 |  |  |  |
| S. megalops |  |  |  |  |  |  |  |  |

Table 3 Dorsal- and anal-fin branched ray counts for species of Sundasalanx. Sundasalanx praecox, S. microps, S. platyrhynchus, S. malleti, and $S$. mesops were tested for difference in number of dorsaland anal-fin branched rays with one-way analysis of variance, with Tukey's post hoc HSD test to locate differences of means. Sundasalanx platyrhynchus differs from S. mesops in number of branched dorsal-fin rays at $p<0.01$; for branched anal-fin rays $S$. microps and $S$. platyrhynchus test as significantly different from S. praecox, S. malleti, and $S$. mesops with $p<0.01$.

|  | D-fin rays |  |  |  | A-fin rays |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
|  | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| S. praecox |  | 4 | 1 |  |  | 1 | 2 | 2 |  |  |
| S. microps | 2 | 5 |  |  |  |  | 2 | 3 | 2 |  |
| S. platyrhynchus |  | 3 | 15 | 4 | 1 |  | 4 | 3 | 12 | 4 |
| S. malleti | 4 | 16 | 23 | 3 |  | 9 | 16 | 13 | 5 | 1 |
| S. mesops | 2 | 28 | 8 |  |  | 3 | 23 | 9 | 2 |  |
| S. megalops |  |  | 2 |  |  |  | 1 | 1 |  |  |



Fig. 11 Holotype of Sundasalanx malleti, female. MZB 6096, 26.4 mm SL.

Sungai Murung around Project Barito Ulu basecamp on Sungai Murung, seine, 12 Feb 1991, D. Siebert, O Crimmen, and A. Tjakrawidjaja.
Diagnosis. A photograph of $S$. malleti is presented as Fig. 11; selected morphometrics are summarised in Table 1 and vertebral and fin-ray counts are summarised in Table 2 and Table 3. It is a species of Sundasalanx with a relatively small eye (3.8-4.7\% SL, 19.7$23.2 \% \mathrm{HL}$ ); snout long ( $18.4-23.9 \% \mathrm{HL}$ ); and with snout:eye ratio usually greater than 1 ( $0.8-1.2$ ). Prepectoral blotch extensive; maturing or mature males (large individuals) with basipterygium ringed by melanophores; no melanophores on posterior wall of cardiac compartment; lower caudal-fin lobe with a broad swath of melanophores. Vertebral number 40-44 (median=42); dorsal-fin rays $8-11$ (median $=10$ ); anal-fin rays $13-17$ (median=14). Premaxilla with 4-5 teeth, maxilla with 15-17 teeth; dentary with 10-12 teeth; 5th ceratobranchial tooth plate large, with 5-6 teeth in principal posterior row, 2 or 3 rows of smaller teeth anterior to principal row; 3rd pharyngobranchial tooth plate large, longer than wide, subequal to or larger than 4th pharyngobranchial tooth plate; 4th pharyngobranchial tooth plate large, nearly $1 / 2$ size of 4th pharyngobranchial, with principal row of larger teeth along posterior edge.
Sundasalanx malleti is easily distinguished from its Barito River


Fig. 12 Scatter plot of Eye versus Standard length for Barito River species of Sundasalanx, with linear smoothing function superimposed on points for $S$. malleti and $S$. mesops $; \Delta=S$. megalops, $\mathrm{O}=S$. mesops, $x=S$. malleti.


Fig. 13 Holotype of Sundasalanx mesops, female, MZB 6098, 20.7 mm SL.


Fig. 14 Holotype of Sundasalanx megalops, MZB 6100, male, 25.5 mm SL. The melanophore cap of the prootic bulla is clearly visible, the myotomal pigment line is clearly interrupted above the pelvic fins, melanophores associated with anal fin pterygiophores are clearly visible, and the vivid swatch of melanophores on the lower caudal fin lobe characteristic of males is clearly evident. The wavy striations of the posterior half of the intestine are discernible posterior to the pelvic fins.


Fig. 15 Holotype of Sundasalanx platyrhynchus, MZB 5944, 19.2 mm SL.
congeners and S. platyrhynchus by size of eye, snout length, and colour pattern. Other Barito River Sundasalanx have discernibly larger eyes (Figs 11-15; Table 1), have a snout:eye ratio <1, lack a ring of melanophores around the basipterygium in maturing males,


Fig. 16 Dorsal view of the head of Sundasalanx platyrhynchus.
and possess melanophores on the posterior wall of the cardiac compartment in males. Table 4 summarises diagnostic features of all described species of Sundasalanx.

Sexual dimorphism. Sundasalanx malleti is sexually dimorphic for colour pattern. Unbleached cleared-and-stained materials that are identifiable as male or as female show a difference between sexes in pigmentation of the basipterygium and lower caudal-fin lobe. Males have a more intense mark on the lower caudal-fin lobe, the result of a greater density of melanophores that make up the lower caudal lobe swath. Males with maturing or mature testes also possess additional pigmentation around the basipterygium that was not observed in any female. Minimally, females, males, and juveniles possess a single melanophore just anterior to the pelvic-fin origin. The basipterygium of males is marked by additional melanophores along its side and across its posterior edge between the pelvic-fin bases so that it is completely encircled with melanophores.

Ecology. Sundasalanx malleti was captured in turbid flowing waters over silty, clayey substrates along banks adjacent to mainstream currents and at depths up to 1 m . Children with fly-screen scoop nets, working bankside shallows before dusk for small fishes for the evening meal, captured them in great abundance. The same shallows worked during daylight usually yielded no or few Sundasalanx. Thus S. malleti probably inhabits deeper waters during daylight hours, moving to shallower areas at dusk, possibly to escape predation. Fishes captured in the same habitat with S. malleti were many species of small and juvenile cyprinids and catfishes, Nemacheilus sp., Homaloptera sp., and chandids.

Remains of insects and crustaceans are observable in guts of cleared and stained specimens.

Etymology. This species is named after JohnValentine Granville Mallet, former Prime Warden of the Worshipful Company of Fishmongers, whose enthusiasm, encouragement, and support have made possible the continuation of a research programme on freshwater fishes of Southeast Asia.

## Sundasalanx mesops Siebert and Crimmen, sp.nov.

(Fig. 13)
HOLOTYPE. MZB 6098, 20.7 mm SL, Indonesia, Kalimantan Tengah, Barito River drainage, Sungai Laung at desa Maruwei, $\mathrm{O}^{\circ}$ 21.986'S, $114^{\circ} 44.103^{\prime}$ E, miscellaneous catches, $15-18$ Jul 1992, D. Siebert, A. Tjakrawidjaja and O. Crimmen.
Paratypes. MZB 6099 (10), collection data as for holotype. BMNH 1996.7.18.2-51 (50), collection data as for holotype.

REFERRED MATERIAL. BMNH 1996.7.18.52-56 (5), Indonesia, Kalimantan Tengah, Barito River drainage, small tributary of Sungai Maruwei approx. 1 km upstream from desa Maruwei, $\mathrm{O}^{\circ} 21.986^{\prime} \mathrm{S}$, $114^{\circ} 44.103^{\prime} \mathrm{E}$, rotenone, 15 Jul 1992, D. Siebert, A. Tjakrawidjaja and O. Crimmen. BMNH 1996.7.18.57-66 (10), C\&S, collection data as for BMNH 1996.7.18.52-56. BMNH 1996.7.18.67-109 (43), collection data as for BMNH 1996.7.18.52-56. BMNH 1996.7.18.110-146 (37), Indonesia, Kalimantan Tengah, Barito River drainage, Sungai Barito approx. 2 km below Muara Laung, beach seine at dusk, 8 Jul 1992, D. Siebert, A. Tjakrawidjaja and O. Crimmen. BMNH 1996.7.18.312 (1), 26.5 mm , Indonesia, Kalimantan Tengah, Sungai Barito drainage, sand bank of Sungai Joloi upstream from Sungai Busang, seine, 7 Feb 1991, D. Siebert, A. Tjakrawidjaja and O. Crimmen. BMNH 1996.7.18.313-314 (2), 26.0-29.5 mm, Indonesia, Kalimantan Tengah, Barito River drainage, sand bars of Sungai Joloi upstream from Sungai Busang, seine, 8 Feb 1991, D. Siebert, O. Crimmen, A. Tjakrawidjaja.
Diagnosis. A photograph of $S$. mesops is presented as Fig. 13; selected morphometrics are summarised in Table 1 and vertebral and fin-ray counts are summarised in Table 2 and Table 3. It is a species of Sundasalanx with a relatively large eye ( $4.5-5.7 \%$ SL, 21.4 $27.5 \% \mathrm{HL}$ ); and relatively short snout ( $15.6-22.9 \% \mathrm{HL}$ ). Vertebral number 40-41 (median=41); dorsal-fin rays 8-10 (median=9); and anal-fin rays $13-16$ (median=14). Prepectoral mark well developed; posterior wall of cardiac compartment with melanophores; basipterygium without ring of melanophores. Premaxilla with 3-5 teeth; maxilla with 16-18 teeth; dentary with 12-13 teeth in single row; 5th ceratobranchial tooth plate with 3-5 teeth in principal posterior row, teeth anterior to principal row small and few; 3rd pharyngobranchial tooth plate small, with 3 or 4 teeth; 4th pharyngobranchial tooth plate relatively small, about $1 / 3$ size of 4 th pharyngobranchial, with principal row of larger teeth along posterior edge.

Sundasalanx mesops is easily distinguished from its Barito River congeners by size of eye, colour pattern, and upper pharyngeal dentition. The eye of S. malleti is smaller; the eye of S. megalops is larger (Figs 11-14). Colour pattern features that distinguish it from S. malleti are listed above in the diagnosis for S. malleti. Sundasalanx malleti has larger upper pharyngeal tooth plates, with more teeth; $S$. megalops possesses fewer teeth in jaws and smaller upper pharyngeal tooth plates with fewer teeth (see below). Sundasalanx mesops can usually be distinguished from S. platyrhynchus of the Kapuas River, West Kalimantan by dorsal- and anal-fin ray counts (Table 3).

Sexual dimorphism. Cleared and stained materials in which male and female specimens are clearly identifiable reveal Sundasalanx mesops is sexually dimorphic for colour pattern. Females differ from males in pigmentation of the cardiac compartment and lower caudal-fin lobe. Males have a more intense mark on the lower caudal-fin lobe; the lower caudal-fin lobe of the female specimen with the largest eggs is not as dark as that of males with only partially mature testes. Males with maturing or mature testes also possess pigmentation of the posterior wall of the cardiac compartment which was not observed in any female.

ECOLOGY. Sundasalanx mesops was captured downstream from creek mouths in shallows over sandy or silty substrates during daylight hours. During a spate specimens were also taken from inundated grassy stream banks.

Distribution. Sundasalanx mesops was taken from several localities throughout the upper Barito River basin, Central Kalimantan, Indonesia, from the widest variety of habitat sizes. On present evidence it has the widest distribution of Barito River Sundasalanx.

Etymology. The name mesops, is a combination of meso, Greek for middle, and ops, Greek for eye. It is in reference to the size of its eye relative to other Barito River Sundasalanx species.

Sundasalanx megalops Siebert and Crimmen, sp. nov.
(Fig. 14)
Holotype. MZB 6100, 25.5 mm SL, Indonesia, Kalimantan Tengah, Sungai Barito drainage, sand and silt bank at the mouth of Sungai Sapen, a small left hand tributary of Sungai Joloi above Sungai Busang, seine, 6 Feb 1991, D. Siebert and O. Crimmen.

Paratype. BMNH 1996.7.18.1; (1), $25.0 \mathrm{~mm}, \mathrm{C} \& S$, collection data as for holotype.
DiAGnosis. A photograph of S. megalops is presented as Fig. 14; selected morphometrics are summarised in Table 1 and vertebral and fin-ray counts are summarised in Table 2 and Table 3. It is a species of Sundasalanx with a deep head (approximately $9.5 \%$ SL); large eye (approximately 6.0 per cent SL, $28 \% \mathrm{HL}$ ); and short snout (snout:eye ratio $<1$ ). Prepectoral mark well developed; posterior wall of cardiac compartment with melanophores; basipterygium without ring of melanophores. Meristics of paratype as follows: vertebral number 41; dorsal-fin rays 10 , anal-fin rays $14-15$. Premaxilla with 2-3 teeth; maxilla with 12-14 teeth; dentary with 8-10 teeth, arranged in 2 rows in rear portion of dental arcade; ceratobranchial 5 tooth plate with 5-6 teeth in principal posterior row, teeth anterior to principal row small and few; pharyngobranchial 3 tooth plate small, with only 2 or 3 teeth; pharyngobranchial 4 tooth plate small, about $1 / 3$ size of pharyngobranchial 4 , with principal row of larger teeth along posterior edge.

Sundasalanx megalops is easily distinguished from its Barito River congeners by size of eye (Figs 11-15; Table 1), snout length, and colour pattern. Its eye is easily recognisable as the largest. Colour pattern features in which it differs from S. malleti are listed under $S$. malleti. Distinguishing features for all described Sundasalanx are presented in Table 4.
ECOLOGY. Sundasalanx megalops was captured at the mouth of a creek over sandy, silty substrate in flowing turbid water approximately 1.5 m deep. Seining sand and mud bars along Sungai Joloi up- and downstream from its point of capture produced specimens of S. mesops.

DISTRIBUTION. Sundasalanx megalops was captured from a single locality on Sungai Joloi, a large upper basin tributary of the Barito River, Central Kalimantan, Indonesia.
Etymology. This species is named megalops, a combination of mega, Greek for large, and ops, Greek for eye.

Sundasalanx platyrhynchus Siebert and Crimmen, sp. nov.
(Fig. 15, 16)
Holotype. MZB 5944 (ex CMK 6979), 19.2 mm SL, Indonesia, Kalimantan Barat, Kapuas River basin, Kapuas R. mainstream

Table 4 Summary table of diagnostic differences among described species of Sundasalanx.

|  | S. praecox | S. microps | S. platyrhynchus | S. malleti | S. mesops | S. megalops |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Ipb 3 tooth plate | large | small; 1-2 teeth | small; 2-3 teeth | large; row of teeth <br> along post. edge | medium; teeth <br> along post. edge | small; 4-5 teeth <br> Ipb 4 tooth plate |
| Palatal and Bb 1 teeth | present | small | absent | large | large | large |

${ }^{1}$ Median value italicised.
about 7 km SW of Nanga Silat, approx. $0^{\circ} 19^{\prime} \mathrm{N} 111^{\circ} 45^{\prime} \mathrm{E}$, 29-IV1990, M.Kottelat et al.

PARATYPES. CMK 6979 (12), collection data as for holotype. CMK 7898 (3), c\&s, data as for holotype. CMK 6892 (8), Indonesia, Kalimantan Barat, Kapuas River basin, Kapuas R. mainstream at Teluk Ujung Bayur, approx. $0^{\circ} 50^{\prime} \mathrm{N} 112^{\circ} 45^{\prime} \mathrm{E}$., 27-IV-1990, M.Kottelat et al.

DiAGNOSIS. A photograph of S. platyrhynchus is presented as Fig. 15; selected morphometrics are summarised in Table 1 and vertebral and fin-ray counts are summarised in Table 2 and Table 3. It is a species of Sundasalanx with a large head (HL 19.6-23.3\% SL, HW $10.2-12.0 \% \mathrm{SL}$ ), relatively large eye ( $4.2-5.7 \% \mathrm{SL}, 21.7-25.9 \%$ HL), and short snout ( $15.3-21.4 \% \mathrm{HL}$ ). Prepectoral mark present; posterior wall of cardiac compartment marked with melanophores; basipterygium without ring of melanophores. Vertebral number 4143 (median=43);dorsal-fin rays $9-12$ (median=10); anal-fin rays 14-17 (median=16). Premaxilla with 5-7 teeth; maxilla with 15-19 teeth; dentary with 15-18 teeth, arranged in 2 rows in posterior part of dental arcade; 3rd pharyngobranchial tooth plate small, with only 2 or 3 teeth; 4th pharyngobranchial tooth plate small, about $1 / 3$ size of pharyngobranchial 4 , with principal row of larger teeth along posterior edge.

Sundasalanx platyrhynchus is easily distinguished from its Kapuas River congener by size of eye and pharyngeal dentition. The eye of $S$. microps is much smaller (Table 4) and pharyngeal dentition in $S$. microps is much reduced. Sundasalanx platyrhynchus can be distinguished from its Barito River congeners by size of eye and vertebral, dorsal- and anal-fin ray counts. S. malleti has a smaller eye; S. megalops has a larger eye. S. mesops has fewer vertebrae and dorsaland anal-fin rays.

Distribution. Sundasalanx platyrhynchus is known from the Kapuas River basin, West Kalimantan, Indonesia.

ETYMOLOGY. The name platyrhynchus is a combination of platys, Greek for broad, and rhynchos, Greek for snout.

## DISCUSSION

Sundasalanx is very small and much of its anatomy is suggestive of the larvae of lower teleosts generally (as realised by Roberts, 1984). Evolution of a tiny adult size among clupeiforms is not unusual; it is known both in engraulids (Cervigón, 1982; Nelson, 1986; Roberts, 1981; Whitehead et al., 1988) and other clupeids (Poll, 1948; Roberts, 1972; Whitehead, 1988; Whitehead \& Teugels, 1985). Among these a good anatomical description is available only for Sierrathrissa leonensis (Whitehead and Teugels, 1985). However 'youthful' an impression small size lends to Sierrathrissa leonensis, it nevertheless is more or less a miniature adult. The degree of ossification, development of the intestinal tract, development of the air bladder, fin positions, etc. are all indicative of at least a juvenile stage in the life cycle, if not of an adult.

Sundasalanx on the other hand is both tiny and underdeveloped. Its level of skeletal and somatic development (straight gut, small air bladder, myotomes not extending ventrally to cover ventral portion of body cavity, presence of ventral fin-fold, undifferentiated cartilaginous plate supporting a rayless pectoral fin, etc.) is comparable to that of other unmetamorphosed clupeid larvae. Migration of the dorsal fin forward to a position characteristic of adults is considered to mark the transition between larvae and adults in clupeiforms. The positions of the dorsal fin, anus, and anal fin, in absolute terms and relative to each other, of the largest Sundasalanx specimens studied are similar to the positions reported for other unmetamorphosed spratelloidins (Leis \& Trnski, 1989) and there is no difference in the positions of any of these structures between the smallest and largest specimen for any species studied. Sundasalanx appears to have attained the ability to reproduce at a stage of development equivalent to larvae of other clupeids. If this assessment of developmental stage of Sundasalanx is correct the size of Sundasalanx may be unusual. Transition, or metamorphosis, in other spratelloidins often begins at sizes of less than half that attained by Sundasalanx.

Small size, lack of somatic development beyond that of the
larvae of other clupeoids, and obvious acceleration of gonadal maturation suggest Sundasalanx are progenetic. Whitehead \& Teugels (1985) attributed the small size of Sierrathrissa leonensis to progenesis, but Sundasalanx exhibits a more extreme condition of the syndrome than Sierrathrissa leonensis since S. leonensis is, morphologically, a miniature 'adult'. Among fishes perhaps only Schindleria (Johnson \& Brothers, 1993) matches Sundasalanx for degree of progenesis. Both Sundasalanx and Schindleria (Schindler, 1932; Gosline, 1959) are obvious larval forms that have attained reproductive capabilities. This may be what sets them apart from other small progenetic fishes, like Sierrathrissa, with paedomorphic reductive tendencies.

Sundasalanx is of such small size an individual probably only goes through one sexual cycle during its lifetime. Mature or maturing specimens have been taken from the Barito River during February and August, suggesting Sundasalanx might breed year around, a reproductive phenomenon observed for other species of tropical Bornean freshwater fishes (Roberts, 1989). Alternatively, it may follow a bimodal breeding pattern tuned to rainfall patterns of the region since February and August are months which correspond to the two periods of low rainfall and low water levels of the annual climatic cycle of Central Kalimantan. Larvae of marine clupeoids can attain the known size of Sundasalanx within two months or less if water temperatures are high enough and resources adequate (Blaxter \& Hunter, 1982). Conditions permitting, Sundasalanx probably is capable of completing its life cycle within a single wet-dry cycle only half a year long, and thus might be capable of completing two generations per annum.

Weitzman \& Vari (1988) and Kottelat \& Vidthayanon (1993) observed that many miniature freshwater fishes are found in still or slow-flowing waters. Within the Barito River basin Sundasalanx was captured adjacent to strong currents and its apparent ability to move in-shore at dusk within a riverine environment suggests it is an exception to this generalisation, as is also one of the other miniature clupeiforms (Thrattidion noctivagus Roberts, 1972; Whitehead, 1988). Barito River Sundasalanx also appears to be found only in larger habitats. It was never taken in small tributary streams, many of which were sampled.

Acknowledgements. The Indonesian Institute of Sciences (LIPI) is gratefully acknowledged for permission to conduct research in Indonesia; Dr. Soetikno Wirjoatmodjo, Dr. Dedy Darnedi, Dr. Arie Budiman, and Mr. Pak Amir, all of the Research and Development Centre for Biology, Bogor, Java, have supported research efforts in the Barito basin and their support is gratefully acknowledged; The Worshipful Company of Fishmongers, the Royal Society, and the Godman Fund are acknowledged for financial support; Project Barito Ulu is acknowledged for logistic support; Dr. Maurice Kottelat kindly made Kapuas River materials available from his private collection. Oliver Crimmen is thanked for his efforts in describing the new species. Colin Patterson, Dave Johnson, Peter Forey, and Lance Grande all made valuable suggestions toward improving the manuscript. Finally my colleague and friend Agus Tjakrawidjaja is warmly acknowledged for his personal attention to research on freshwater fishes in Indonesia.

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