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Larvae, Adults and Relationships of the Monotypic Perciform Fish Family Lactariidae

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ABSTRACT. The development of *Lactarius lactarius* larvae is described based on three relatively poorly preserved specimens, 6 to 23 mm SL. Aspects of adult external morphology and osteology relevant to assessing the relationships of this taxon are also described. Larvae are notable for their limited head spination, large swim bladder and unusual pigmentation. They otherwise resemble carangids. *Lactarius* possess numerous adult autapomorphies. Previous suggestions that *Lactarius* is a member of the Sciaenidae, Scombridae or Serranidae are rejected. The conventional placement of *Lactarius* near the carangoid fishes cannot be rejected. A number of larval and adult characters indicate that *Lactarius* and *Mene* are the second and first sister groups, respectively, of the carangoid fishes *sensu* Smith-Vaniz and Johnson. However, none of these characters are unequivocal, and the relationships of *Lactarius* remain uncertain pending availability of larvae of the carangoid *Nematistius* and more larvae of *Lactarius*.

The false trevally or milk trevally, *Lactarius lactarius* (Bloch & Schneider, 1801) is a pelagic, nearshore, marine fish (Fig. 1) that occurs over soft bottoms on the continental shelf from the Persian Gulf eastward to Taiwan and the Admiralty Islands, and south to Australia and Fiji (Springer, 1982). Kumaran's (1984) report of its occurrence along the east African coast and islands in the western Indian Ocean needs confirmation. The species is common and of commercial importance throughout much of its range (however, Day, 1878, considered the flesh 'insipid'), and is frequently taken in trawls and seines in shallow water.

The relationships of this species have been a matter of dispute since the original description. Bloch & Schneider (1801) described the species as a member of

Scomber; however, in that genus they also included many pelagic marine species today distributed among several families, including the Scombridae, Carangidae, and Pomatomidae. Cuvier (1829) placed the species in the carangid genus *Seriola*. Valenciennes (*in* Cuvier & Valenciennes, 1833) described the genus *Lactarius* with *Scomber lactarius* as the type species, and placed it in his "tribe Scomberoides" among such genera as *Lichia* and *Seriola* (now in the carangoid family Carangidae), *Pomatomus* (now in the scombroid family Pomatomidae), and *Nomeus*, *Naucrates* and *Psenes* (now in the stromateoid family Nomeidae). Günther (1860) placed *Lactarius* in the Carangidae, but noted it "approaches Sciaenidae", and Day (1878) did not disagree. Seale (1910) agreed with Bloch & Schneider that *Lactarius* was

a scombrid, but did not state why, and Regan (1913) felt it had the general characteristics of the Serranidae. Jordan (1923) created the monotypic family Lactariidae within the Carangiformes, and this rather vague arrangement has since been followed by most authors (but see Deng & Zhan, 1986).

Thus, there has been a general consensus over the last 70 years that *Lactarius* is relatively closely related to the carangoid fishes. However, this has been based on nothing more than general similarity, and the literature contains little other than general descriptions of the external morphology of *Lactarius lactarius*. Similarly, until the work of Johnson (1984) and Smith-Vaniz (1984), the Carangoidei had not been rigorously defined, and the taxa included in it have varied with author. Here, I consider the Carangoidei to include the Nematistiidae, the 'echeneoids' (Coryphaenidae, Echeneididae, Rachycentridae) and the Carangidae (Smith-Vaniz, 1984).

The Lactariidae is one of the few Indo-Pacific shorefish families for which egg and larval development is completely undescribed (Leis & Trnski, 1989). Chacko (1944) briefly described the ovarian eggs of *L. lactarius*. Nair (1952) provided a life-size photograph and brief descriptive notes of some juvenile fish (greater than 21 mm total length) he identified as *L. lactarius*. Unfortunately, the fish are not identifiable from the photograph, and the fin-ray counts given by Nair do not match those of *L. lactarius*, so the identification is questionable.

Recently, I was able to identify three larvae from northern Australia and the Gulf of Thailand as *Lactarius lactarius*. This stimulated me to examine the relationships of the family. To this end, I also studied aspects of adult morphology and osteology. Ultimately, it was obvious, that my larval material was too limited for the task (it is unlikely more larvae will be available soon), and I was unable to convincingly place *Lactarius* amid the complex Percoidei. The purpose of this paper is to present the information gathered during the course of this study with the aims of describing the larval development of this taxon, and of providing a basic description of adult morphology and osteology, both for the first time. These data provide some suggestions as to the relationships of *Lactarius*, and can serve as a basis for future study.

Methods and Materials

The three *Lactarius* larvae available for this study were in relatively poor condition, limiting the amount of information that I could obtain. Adults were x-rayed, and some specimens cleared and stained for study of bone and cartilage (Dingerkus & Uhler, 1977; Potthoff, 1984). However, in a few specimens, cartilage staining was unsuccessful.

Terminology and measurements of larvae follow Leis & Trnski (1989) except orbit rather than eye diameter was measured. Size refers to standard length. References to pigment are to melanin. Illustrations were done with the aid of a camera lucida, and show the left side unless noted otherwise.

Identification. I established the three larvae were of the same species by general body shape, a large gas bladder, fin-ray counts, myomere number, head spination, and pigment pattern. The myomere counts (24) and complete fin-ray counts of D VIII + I,22-23 and A III,26-27 eliminate from consideration all of the taxa occurring in the area except some carangids and *Lactarius*. The three larvae have an opercular spine (Leis & Trnski, 1989) and lack a space between the last two spines of the anal fin, so carangids could be eliminated. Additionally, no carangid species has more soft rays in the anal fin than in the dorsal fin (Leis & Trnski, 1989), whereas *Lactarius* does. Further confirmation of the
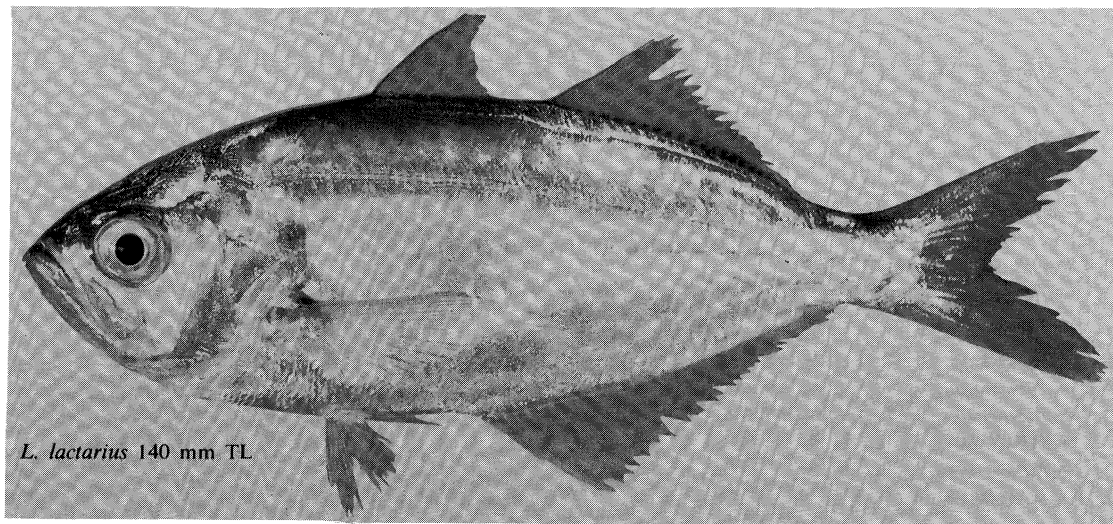

Fig. 1. *Lactarius lactarius* adult (140 mm total length). Figure after Sainsbury *et al.* (1985: 157), reproduced with permission.

identification is the presence in the largest larva of enlarged, recurved, symphysial canine teeth in both jaws – a characteristic of juvenile and adult *L. lactarius*.

Material examined. (Museum acronyms follow Leviton *et al.*, 1985, and are AMS unless noted otherwise; C&S indicates cleared and stained, X indicates x-rayed as well as examined specimen, L indicates larva) – Lactariidae, *Lactarius lactarius* – USNM 315570: 6.0 mm, L, Gulf of Thailand (Naga station S9-21, 60-959), plankton net; USNM 315571: 10.3 mm, L, Gulf of Thailand (Naga station S3-202, 60-105), stramin net; NTM S.10247-002: 23 mm, L, Shoal Bay, Northern Territory, Australia, capture method unknown; X, I.15557-121: 3, 110-145 mm; X, I.20826-010: 2, 180-200 mm; C&S I.21830-010: 133 mm; C&S I.31371-001: 2, 67-100 mm. Menidae, *Mene maculata* C&S I.15557-122: 70 mm; C&S unregistered, L. Coryphaenidae, *Coryphanea hippurus* C&S I.23606-001: 47 mm. Carangidae, *Caranx* sp. C&S I.28949-001: 60 mm; *Decapterus russelli* C&S I.32145-002: 95 mm; *Pseudocaranx dentex* C&S I.30872-002: 57 mm; *Scomberoides lysan* C&S I.24551-004: 42 mm; *Trachurus* sp. C&S I.30866-010: 52 mm. Sciaenidae, *Seriphus politus* X, I.564: 163 mm. In addition, a number of C&S perciform fishes were examined (AMS material): Apogonidae, *Fowleria variagata* I.26723-055,

Cheilodipterus quinquelineatus I.26723-056; Callanthiidae, *Callanthias australis* I.22871-004; Centrogenysidae, *Centrogenys vaigensis* I.24694-012; Girellidae, *Girella tricuspidata* unregistered; Kuhliidae, *Kuhlia rupestris* I.21262-002; Leiognathidae, *Leiognathus elongatus* I.20829-018; Lutjanidae, *Pristipomoides argyrogrammicus* I.25829-005; Nandidae, *Nandus pallidus* I.22130-003; Percichthyidae, *Nannoperca australis* unregistered; Pinguepididae, *Parapercis cylindrica* I.26723-059; Plesiopidae, *Belonepterygion fasciolatum* I.26723-058, *Plesiops coeruleolineatus* I.31487-004; Pomatomidae, *Pomatomus saltatrix* I.31372-001; Scorpididae, *Scorpis lineolatus* I.31238-006; Serranidae, *Pseudanthias squamipinnis* I.32478-002, *Epinephelus merra* I.20988-013, *Pseudogramma polyacantha* I.21540-048; Terapontidae, *Leiophtherapon unicolor* unregistered.

Results

Description of larvae. Description is based on three larvae of 6.0, 10.3 and 23 mm, standard length (Fig. 2, Table 1). Therefore, many structures were fully developed in the smallest larva, and any characters present only in smaller larvae will have been missed.
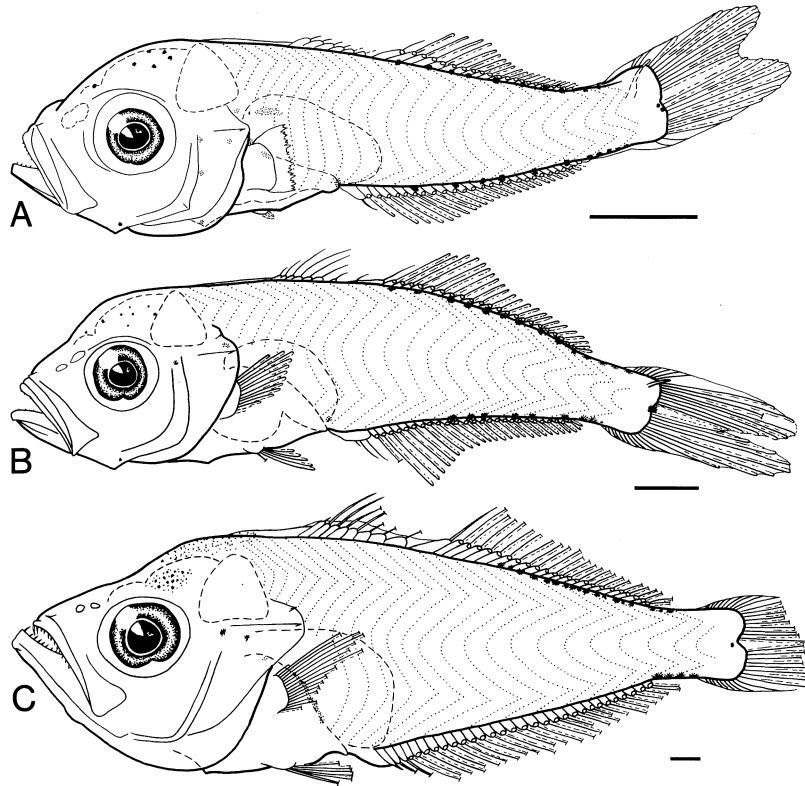

Fig. 2. Larvae of *Lactarius lactarius*. Small, terminal hatch mark across axis of fin elements indicates broken spine or ray. Scale bars = 1 mm. A) 6.0 mm from the Gulf of Thailand (USNM 315570). Broken lines for posterior spines of the dorsal fin represent incompletely formed spines. B) 10.3 mm from the Gulf of Thailand (USNM 315571). Head drawn from right side due to damage on left side. C) 23 mm from near Darwin, Australia (NTM S.102447-002). Specimen in poor condition: most fin rays are broken, and no attempt has been made to show their true length.

Furthermore, two of the larvae are relatively faded, the 10.3 mm specimen has been damaged, particularly on the left side of the head, and the 23 mm specimen appears to have dried out at some stage. In spite of these limitations, a relatively complete description of the larvae can be provided.

The body is of moderate depth, laterally compressed, and slightly deeper at the pectoral base than at the anus. There are 9-10 + 14-15 = 24 myomeres. The gut is coiled, and the anus is located at 40-47% of standard length. A very large, conspicuous gas bladder is located above the gut, and extends a considerable distance posterior to the anus. With growth the head becomes increasingly pointed primarily due to increased protrusion of the lower jaw as the mouth becomes more oblique. The mouth is moderate to large, but does not reach the pupil in the two smaller larvae. Small, slightly recurved teeth are present in both jaws of the smallest larva. The 23 mm fish has enlarged, symphysial canines in both jaws. Judging from the size of the orbit, the eye is large, but it appears to have shrunk in the available specimens. Gill membranes are free from the isthmus. No scales are evident on the two smaller larvae. The largest specimen appears to have incipient scales, or perhaps damaged scale pockets.

Head spination is confined to the preoperculum and operculum. Preopercular spination is limited to a small spine at the angle in the 6 mm specimen. There is no preopercular spination in the other two larvae. A weak opercular spine is present in all larvae, and a small second spine, dorsal to the first, is present in the two larger larvae.

The smallest larva is fully flexed, with a full complement of primary caudal rays. All but the posteriormost soft rays in the long-based dorsal and anal fins are present. The anterior rays of the fins are more than twice as long as the posterior rays. The spinous dorsal fin has six incompletely-formed spines. The first spine of the anal fin is present, but the next two elements, which ultimately become spines, appear

to be soft rays. Only incipient rays are present in the pectoral fins, and the pelvic fins are merely buds. In the 10.3 mm larva, the full complement of rays is present in all fins, except the pectoral fin where the lower rays are still incipient. The 23 mm larva appears to have all pectoral rays ossified. The fin spines are all slender and weak, none are particularly elongate, and none have any external ornamentation. There is no gap between the anus and the anterior margin of the first pterygiophore of the anal fin. The only unusual aspect of fin development is the apparent transformation of two anal rays into spines, but this needs to be confirmed when more specimens in better condition become available.

The head and trunk are lightly pigmented, whereas the tail is adorned with two prominent melanophore series. Scattered melanophores are present dorsally on the midbrain. These increase in number with growth and extended posteriorly. A single dorsal melanophore is present on each hemisphere at the juncture of mid- and hindbrains in the two smaller larvae. A single melanophore is present on the angle of the lower jaw in the two smaller larvae; the jaws are otherwise unpigmented. Only the smallest larva has a ventral melanophore just anterior to the cleithral symphysis. In all three larvae a melanophore is present at the base of the opercular spine in line with the centre of the eye. A few faint melanophores are present anteriorly on the gut and dorsally over the anterior portion of the gas bladder. Another melanophore is present on the dorsal surface of the gut at the anus. Along each side of the base of the soft rays of the dorsal fin is a series of melanophores. These are paired in the two larger larvae. The number of melanophores in this series increases with growth from about eight at 6 mm to 15 at 23 mm. A similar series of melanophores is present along the anal fin, but consists of six melanophores at 6 mm and 10.3 mm, and no melanophores at 23 mm. Each series extends onto the midline of the caudal peduncle where three to six unpaired melanophores are present. The

Table 1. Morphometric and meristic characters of larval *Lactarius lactarius*. Measurements in mm are defined in Leis & Trnski (1989) except as noted.

| | Length of Larva | | |
Character	6.0 mm	10.3 mm	23.0 mm
Preanal Length	2.8	4.8	9.3
Predorsal Length	2.5	4.2	9.0
Head Length	2.1	3.4	8.3
Orbit Diameter	0.8	1.2	3.0
Snout Length	0.6	1.1	1.8
Body Depth at Pectoral	1.7	2.8	7.6
Body Depth at Anus	1.4	2.4	7.1
Caudal Peduncle Length	0.9	1.4	2.8
Maxilla Length	1.0	1.5	3.5
Dorsal Fin	VI+I,20	VIII+I,22	VIII+I,23
Anal Fin	I,25	III,26	III,27
Caudal Fin	3/9+8/2	9/9+8/9	9/9+8/9
Pectoral Fin	0	10	16
Pelvic Fin	0	I,5	I,5

only lateral pigment on trunk or tail consists of one or two melanophores midlaterally at the base of the central caudal rays.

Comparison with other taxa. Larvae of *Lactarius* are most likely to be confused with larvae of carangids and nomeids, as these are similar in general morphology and in pigment. Carangids can be distinguished because they have much more extensive spination on the head than does *Lactarius* (Leis & Trnski, 1989), although the latter has an opercular spine which carangids lack. Also, once the fins are formed, carangids have a gap between the last two spines of the anal fin. Nomeids such as *Cubiceps* have shape, pigment and head spination similar to that of *Lactarius*, but they have 30 or more myomeres (Ahlstrom *et al.*, 1976), while *Lactarius* has only 24. The, as yet, unknown preflexion larvae of *Lactarius* are likely to be confused with some apogonids because both have large swim bladders. However, apogonids have many fewer fin rays in dorsal and anal fins, and many have well-developed spination on the head (Leis & Rennis, 1983). It must be emphasised that preflexion larvae of *Lactarius* could have more extensive spination on the head than do the postflexion larvae. It should also be noted that the two smaller *Lactarius* larvae were captured at night (time of capture is unknown for the largest specimen), and the swim bladder in fish larvae typically is more inflated at night than it is during the day.

Description of adults. The general external morphology of *Lactarius lactarius* is well described and illustrated in the literature (Weber & de Beaufort, 1931; Kyushin *et al.*, 1982; Gloerfelt-Tarp & Kailola, 1984; Sainsbury *et al.*, 1985), and only a few particularly relevant features will be mentioned. Scales are large, cycloid, and deciduous, the lateral line is not armed with scutes, nor is the caudal peduncle particularly narrow, the dorsal and anal fins are long-based, and the second and third anal spines are not separated by a gap (Fig. 1). The following meristic values apply (Johnson, 1984; present study): D VII-VIII + I,19-23; A III, 25-28; P_1 17; C 9+8; vertebrae 10+14. Among percoid fishes, it is unusual for the anal fin to have more soft rays than the dorsal fin (Johnson, 1984). In only 14 of about 80 percoid families does this occur (none of them carangoid families), and in only six families or incertae sedis groups does the anal fin have four or more rays than the dorsal (Cepolidae, Lactariidae, Leptobramidae, *Neoscorpis*, Pempherididae, Toxotidae).

Günther (1860) briefly described the swim bladder and skull. Alam *et al.* (1989) described the penetration of the swim bladder by the anterior pterygiophores of the anal fin. Deng & Zhan (1986) described the lateralis system of *Lactarius* and compared it with those of some carangoid fishes and some others "assumed to be related with the Carangidae". They concluded the lateralis system of *Lactarius* was "very much different" from the Carangidae (as was that of *Coryphaena*), and maintained it was "better to classify them outside the

carangoid fishes". However, Deng & Zhan (1986) nominated no taxon with a lateralis system similar to that of *Lactarius*, and made no comment as to which taxa either *Lactarius* or *Coryphaena* might be related.

Soft anatomy. Günther (1860) noted that *Lactarius* has an unusual swimbladder, and likened it to that of the Sciaenidae. Day (1878) and Weber & de Beaufort (1931) described it as bifurcate anteriorly and posteriorly, but it is not bifurcate posteriorly. The swim bladder has two anterior horns that communicate closely with the base of the skull (Fig. 3). It is otherwise carrot-shaped in dorsal view, lacks other appendages, and extends in adults nearly to the posterior end of the anal fin. Upon first examination, the tough, silvery tissue of the swim bladder appears to completely surround the first pterygiophore of the anal fin. But in fact, it passes to one side of the pterygiophore, enfolding it anteriorly and posteriorly, and reaches around the pterygiophore to meet, but not join, laterally. This maintains the overall carrot-shape. The next few pterygiophores are short and the remainder displaced laterally, so that the gas bladder is undivided and remains to one side of them. The gas bladder of *Lactarius* thus differs significantly from that of the Sciaenidae. In the Sciaenidae, including even *Seriphus*, which has a long anal-fin base, the bladder neither extends posterior to the anus nor enfolds the first anal pterygiophore.
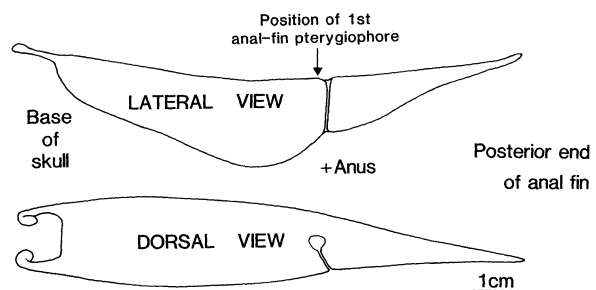

Fig. 3. Swim bladder of *Lactarius lactarius* (AMS I. 20826-010, 200 mm).

The arrangement of the ramus lateralis accessorius of the facial nerve is reported by Freihoffer (1963) to be his pattern 9. This is the most common pattern among percoid fishes.

Osteology. The skull is cavernous as noted by Günther (1860), but in contrast to his conclusion, it is very different from that of sciaenids (Sasaki, 1989 and personal communication, December 1990). The most striking feature is a series of longitudinal, dorsal ridges separated by deep troughs (Fig. 4). A moderately high medial frontal-supraoccipital ridge runs to the anterior tip of the frontals (Fig. 4). A lower, frontal-parietal ridge runs approximately parallel to it, and parallel to this is a lower, shorter frontal-pterotic ridge. A short, oblique frontal ridge runs from mid-way along the

frontal-parietal ridge to the anterior end of the frontal-pterotic ridge. Anterior to the oblique ridge, the frontal trough is partially roofed over between the frontal-parietal and frontal-pterotic ridges. The deep trough formed between the frontal-supraoccipital and frontal-parietal ridges is not roofed by bone anteriorly, although the posttemporal partially bridges it between the posterior end of the pterotic and the supraoccipital. No basoccipital foramen for insertion of the swimbladder 'horns' is present.
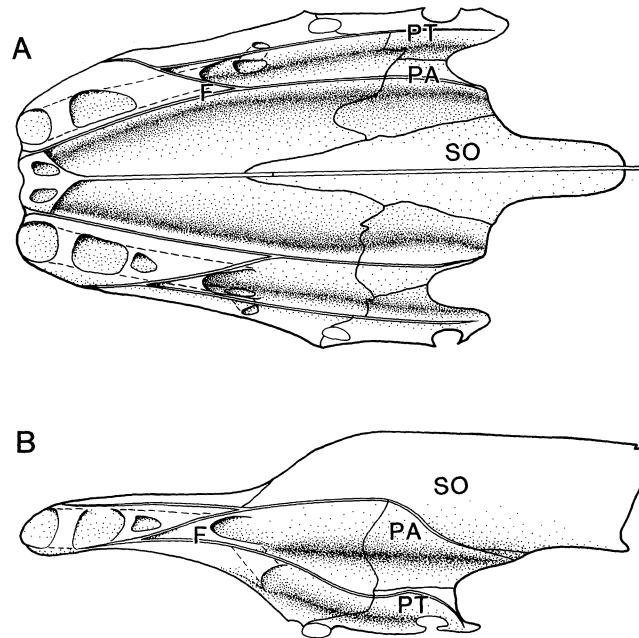

Fig. 4. Skull of *Lactarius lactarius* (based on two specimens, AMS I.31371-001, 67-100 mm) showing only frontals (F), supraoccipital (SO), parietals (PA) and pterotics (PT). A – dorsal view, B – lateral view.
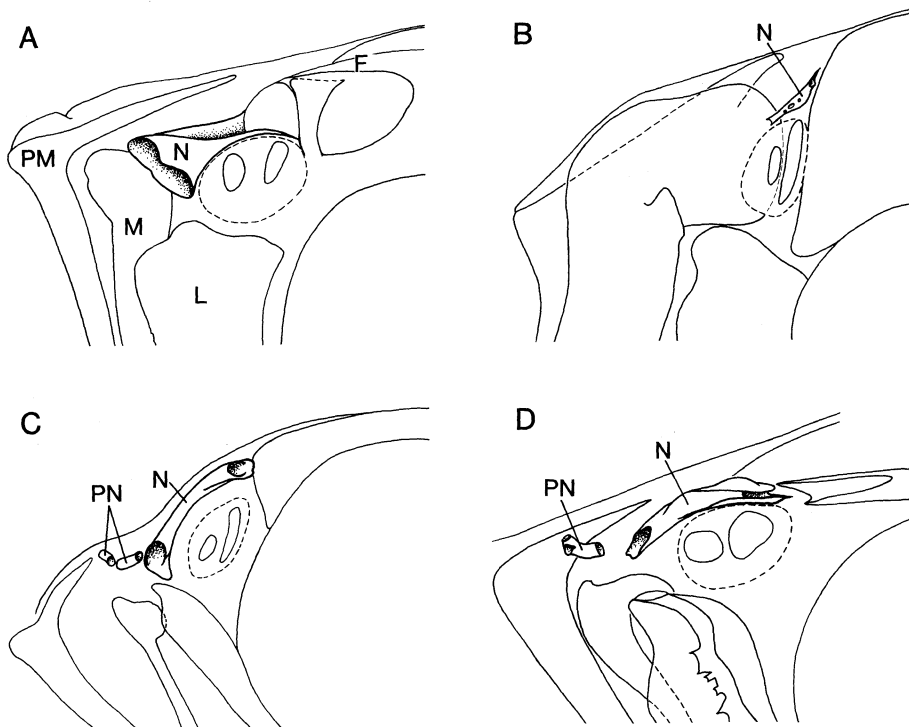

Fig. 5. Nasal (N) and prenasal (PN) bones in *Lactarius, Mene* and two carangoid fishes. Also shown are frontals (F), premaxilla (PM), maxilla (M), and lachrymal (L). A – *Lactarius lactarius* (based on two specimens, AMS I.31371-001, 67-100 mm); B – *Mene maculata* (AMS I.15557-122, 70 mm); C – *Coryphaena hippurus* (AMS I.23606-001, 47 mm); D – *Scomberoides lysan* (AMS I.24551-001, 42 mm).

At the symphysis of both the dentaries and premaxillae is a cluster of two or three enlarged canine type 1 teeth (tooth type after Fink, 1981). These type 1 teeth are present in small and large individuals, and are not medial to the primary jaw teeth. The latter are apparently type 2 teeth. These canine teeth are widely spaced and arise from individual sockets, although only alternate ones are functional at any given time. Most of these primary teeth in the premaxillae disappear with growth, leading to a low, bony ridge. The dentary teeth in larger individuals coalesce to form a rugose ridge.

The nasal bone is not accompanied by any prenasal ossifications (Fig. 5A), and extends well anterior to the nasal capsule. It is trumpet-shaped and open along most of its dorsum.

The scapula has two foramina (Fig. 6A). The coracoid has a broad posterior lamina extending its entire length, with an second lamina extending along most of the anterior margin of the coracoid toward the cleithrum (Fig. 6A). The inter-osseous space is thus narrow to absent dorsally, but broad ventrally, and the coracoid and cleithrum do not touch ventrally but are connected by a strong ligament. The abductor muscles are large.

There are three 'T'-shaped supraneurals (Fig. 7), arranged /0+0/0+2/1+1 in my material, not 0/0/0+2/1+1 as noted by Johnson (1984). The first and second

neural spines are relatively broad and closely applied. The pterygiophores are slender. Epipleural ribs are located on centra one to eight, and pleural ribs are on centra three to ten.

The posterior pterygiophores of both the dorsal and anal fins are abruptly shortened. The last eight or nine dorsal-fin pterygiophores are about 25% shorter than the preceding ones. Similarly, the last four to six anal-fin pterygiophores are 15-20% shorter. In fishes with a very narrow caudal peduncle (eg, *Caranx*, *Mene*), the pterygiophores gradually become shorter posteriorly, but the distance from the proximal end of the pterygiophore to the vertebral centra changes little. In *Lactarius* this distance abruptly becomes greater in the shortened elements.
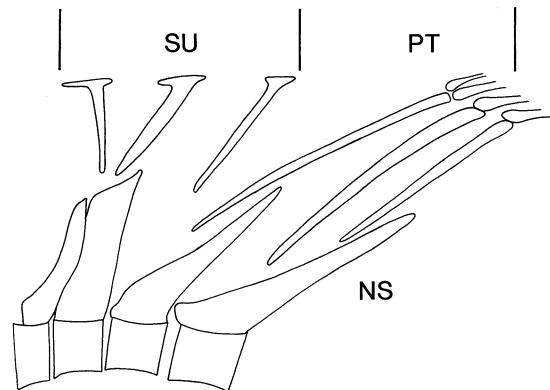

Fig. 7. Supraneurals (SU), anterior dorsal-fin pterygiophores (PT), and neural spines (NS) of adult *Lactarius lactarius* (based on cleared and stained and radiographed specimens). Radials of pterygiophores not distinguished.
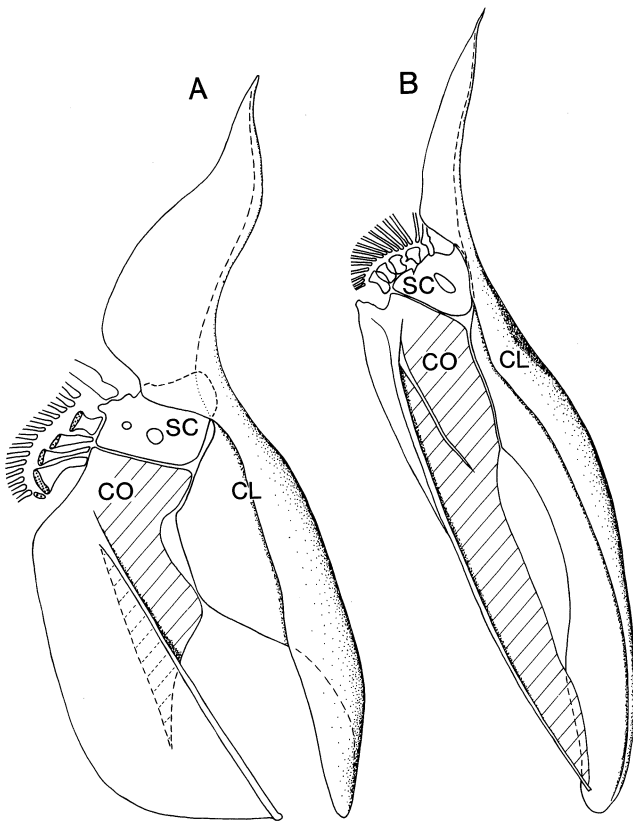

Fig. 6. Lateral view of right pectoral girdle of A) *Lactarius lactarius* (AMS I.31371-001, 100 mm), and B) *Mene maculata* (AMS I.15557-122, 70 mm). Cleithrum (CL), scapula (SC), coracoid (CO). The anterior lamella of the coracoid is hatched.
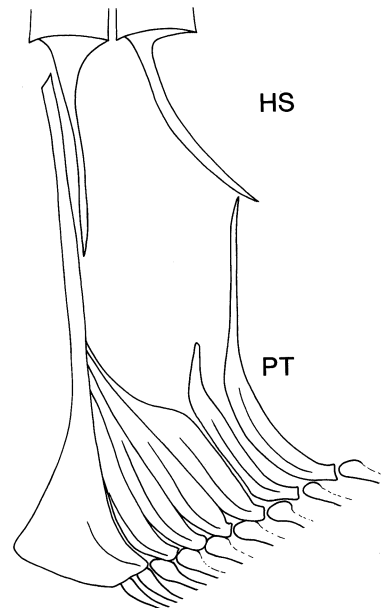

Fig. 8. Anterior anal-fin pterygiophores (PT) and haemal spines (HS) of *Lactarius lactarius* (based on cleared and stained and radiographed specimens). Radials of pterygiophores not distinguished.

The separation of the spiny and soft portions of the dorsal fin is accomplished by elongation of the seventh pterygiophore. There is no spineless pterygiophore in the gap between the two parts of the fin.

The first anal-fin pterygiophore is enlarged, and has an anterior, distal extension (Fig. 8). This is a common feature of deep-bodied, strongly compressed fishes (Zeiformes, Acanthuroidei, Carangidae, etc.). What is unusual in *Lactarius* (apparently unique) is the arrangement of the other anal pterygiophores. Pterygiophores two through five are strongly applied to one another, and, in turn to the posterior edge of the

enlarged first. This mass of bones was called the 'anchor bone' by Alam *et al.* (1989). Pterygiophore six is reduced and apparently free proximally. The remaining anal pterygiophores are of 'normal' size and associated with the haemal spines, but are displaced laterally to make room for the posterior extension of the swim bladder.

The branchial arch of *Lactarius* (Fig. 9) has all the elements of the primitive percoid branchial skeleton (Johnson, 1980): one basihyal, four basibranchials (the fourth cartilaginous), three hypobranchials, five ceratobranchials, four epibranchials, four pharyngobranchials (the fourth a
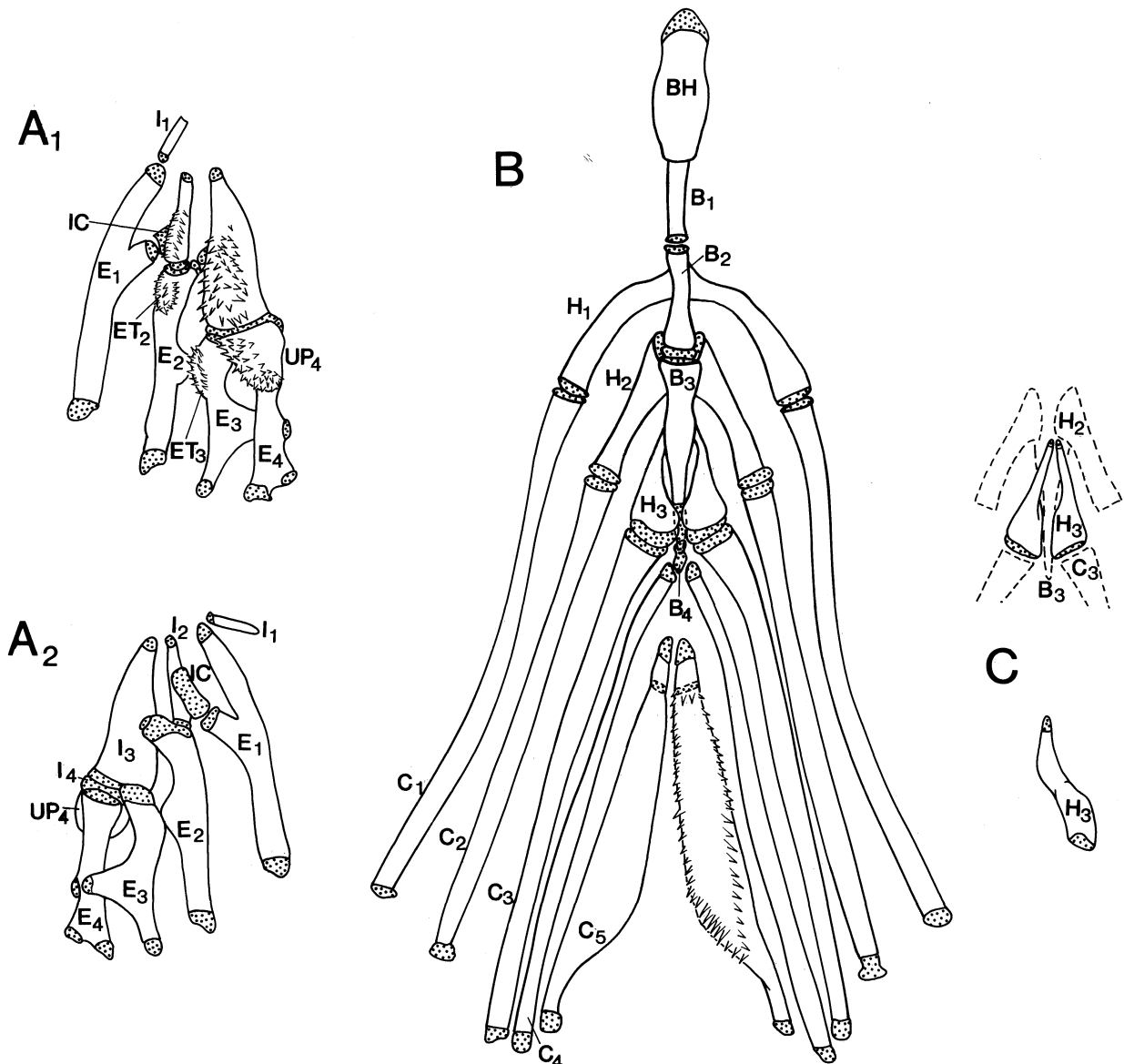

Fig. 9. Branchial arches of *Lactarius lactarius* (AMS I.31371-001): anterior is to the top of the page in all illustrations which are all to the same scale. Shaded areas are cartilage, and gill rakers are omitted. A) Upper right arches: A1 is a ventral view, and A2 a dorsal view. B) Lower arches in dorsal view. Peripheral teeth only are shown on right C5 toothplate, and no teeth are shown on the left plate. C) Third hypobranchial: below is a lateral view of the left element, and above a ventral view of both left and right elements (adjacent bones shown in broken lines for orientation). Abbreviations: BH – basihyal; B1-4 – basibranchials 1-4; C1-5 – ceratobranchials 1-5; H1-3 – hypobranchials 1-3; E1-4 – epibranchials 1-4; ET2-3 – epibranchial tooth plates 2-3; I1-4 – infrapharyngobranchials 1-4; UP4 – upper pharyngeal tooth plate 4; IC – interarcual cartilage.

small block of cartilage), and a well-developed fourth upper pharyngeal tooth plate. Dermal tooth plates are present on the fifth ceratobranchial, second and third pharyngobranchials, and the second and third epibranchials. Both the interarcual cartilage and the uncinate process of the first epibranchial from which it extends are well developed. The ventral process on the third hypobranchial is long and curved (Fig. 9C), and the left and right processes are closely applied at the midline, thus enclosing the posterior portion of the third basibranchial. The fifth ceratobranchial is divided by a cartilage disk into two portions near its anterior end, ie, near the edge of the toothplate (this condition has been seen otherwise in only *Caranx*, although very good staining for cartilage is probably required for it to be visible).

Discussion

Although *Lactarius* is usually considered either a carangoid or closely related to the group, some other views have been expressed. None of these withstand scrutiny. Günther (1860) noted some apparent similarities with sciaenids: as noted above, these are superficial only. Sasaki (1989) listed 15 synapomorphies to support the monophyly of the Sciaenidae (ignoring five myological and two otolith characters): *Lactarius* possess only one of these (an edentulous palatine). Regan (1913) implied a relationship with the serranids. However, *Lactarius* possesses none of the four derived character states used by Johnson (1983) to propose monophyly of the serranids. Seale's (1910) placement of *Lactarius* with the scombrids is not supported by recent work on scombroid relationships (Johnson, 1986). Nothing about the larval development of *Lactarius* would suggest a relationship to the sciaenids, serranids or scombrids. It was with this in mind that the carangoid fishes were investigated as the potential relatives of *Lactarius*. In addition, initial survey of larval and adult character states (the latter based primarily on Johnson, 1984, table 120) suggested that the carangoids were the best candidates among the Percoidei.

Johnson (1984) and Smith-Vaniz (1984) considered the interrelationships of the carangoid fishes as circumscribed by them (ie, Nematistiidae, Echeneididae, Rachycentridae, Coryphaenidae, Carangidae) and established monophyly of the group. There are several obstacles to attempting to evaluate the idea that *Lactarius* is related to the carangoids. First, the larval series of *Lactarius* is incomplete, and it is possible that important information remains to be ascertained from larvae less than 6 mm long. Second, it was not possible to study the developmental osteology of *Lactarius* because the few larvae available were in poor condition, and largely deossified. Therefore, homologies could not always be established. Third, larvae of the monotypic carangoid family

Nematistiidae are unknown. Fourth, there is no credibly hypothesised sister group for the Carangoidei except the vague assemblage of 'other percoids'. These ultimately combined to frustrate my attempts to perform a rigorous analysis of the relationships of *Lactarius*.

Lactarius cannot be considered a carangoid fish *sensu* Smith-Vaniz (1984) and Johnson (1984) because it lacks the two synapomorphies used by them to define the suborder: prenasal bones (Fig. 5C,D) and small, adherent, cycloid scales. However, it is worthwhile to set out the evidence hinting at a carangoid relationship, equivocal as it is, as a basis for further study. There are no unique, unreversed synapomorphies supporting such a relationship. With two possible exceptions the character states are either losses or conditions with distributions that indicate multiple, independent evolutions. These eight characters are listed and discussed below.

1) *Soft-rayed portion of the dorsal and anal fins long-based.* All the carangoid fishes and *Lactarius* have such fins, but so do a number of percoid and other perciform fishes. This is likely to be a derived condition in perciform fishes, but it has probably arisen several times. Probably, this is one of the elements of general similarity that prompted earlier authors to consider *Lactarius* a carangoid.

2) *Cycloid scales.* Cycloid scales are present in *Lactarius* and the carangoids. Johnson (1984) and Smith-Vaniz (1984) considered that within the Percoidei cycloid scales are derived, but have probably arisen several times. It remains to be shown that the large, relatively deciduous, cycloid scales of *Lactarius* are homologous with the small, adherent cycloid scales of the carangoids.

3) *Larvae lack subopercular spines.* Larvae of both *Lactarius* and the carangoids lack subopercular spines (for all larval characters, it must be remembered that larvae of the carangoid *Nematistius* are unknown). The presence of subopercular spines in percoid larvae is considered primitive by Johnson (1984), but these spines may have been lost independently several times as many percoid families lack them.

4) *Larvae lack interopercular spines.* Larvae of both *Lactarius* and the carangoids lack interopercular spines. The presence of interopercular spines in percoid larvae is considered primitive by Johnson (1984), but these spines are absent in several percoid families, and may have been lost more than once.

5) *Larvae have a series of melanophores along the dorsal midline of trunk and tail.* Larvae of *Lactarius* and the carangoids have such a pigment series (in some heavily pigmented 'echeneoids', this series cannot be seen: I have assumed it is present, but obscured by heavy overall pigment). This pigment series has almost certainly been derived more than once within the Percoidei. It occurs in some or all of the larvae of about 12 of the more than 80 percoid families, as well as some scombroids and pomacentrids.

6) *Hypurals 1 and 2 fused as are hypurals 3 and 4.*

Fusion of the hypurals in this manner occurs in *Lactarius*, and all the carangoids except Echeneididae and Rachycentridae. This fusion is considered derived in percoids by Johnson (1984), but as it is present in 25 percoid families, it is likely to have occurred several times.

7) *Coracoid with a broad anterior lamella broadly extending toward the cleithrum*. This sort of coracoid is found in *Lactarius* and all the carangoids except *Nematistius* and is considered derived by Johnson (1984) and Smith-Vaniz (1984). Of the eight characters suggesting that *Lactarius* and the carangoids are related, this is the most convincing, and it is considered further below. However, it occurs also in some non-percoid perciform groups including acanthuroids (Tyler *et al.*, 1989), 'squamipinnes', mugilids and scombroids (A.C. Gill, personal communication).

8) *Ventral processes of third hypobranchials long and closely applied at the midline, enclosing the third basibranchial*. This sort of hypobranchial process is found in *Lactarius*, and most carangids examined: *Trachurus* (this study and Suda, 1991), *Decapterus*, *Pseudocaranx* and *Caranx*. In the carangid *Scomberoides*, the processes are moderate in length, but nearly touch at the midline, and in 'echeneoid' *Coryphaena* they are short and do not closely approach the midline. In a cursory survey of 21 other percoid genera of 17 families, I found long, closely applied ventral processes on the hypobranchials only in *Mene*. Markedly elongate processes which are not closely applied are present in *Pseudanthias*, *Epinephelus* and *Scorpis*. Only in *Leiognathus* among the 21 genera are the processes closely applied, but here they are broad and almost round. The remaining taxa have short to moderately long processes that are not closely applied at the midline. So, the distribution of this character state is promising, but incompletely known, and it is not present in all carangoids (absent in *Coryphaena* and apparently different in *Scomberoides*).

All eight of these character states are also found in the monotypic percoid *Mene*, which also lacks the two carangoid synapomorphies: prenasal bones (Fig. 5B) and small, adherent, cycloid scales. It is possible that four additional derived character states are shared between *Mene* and *Lactarius*, but homology of all four is suspect. These are discussed next.

9) *Swim bladder extends posterior to the anus*. Posterior extensions of the swimbladder occur in *Mene*, *Lactarius* and within the carangoids, in some carangids. Such a posterior extension occurs in some or all members of at least 27 percoid families (Y. Tominaga and K. Matsuura, personal communication), and the structure of these posterior extensions differ substantially among taxa suggesting more than one derivation.

10) *Larvae lack spines on the supracleithrum*. Supracleithral spines are absent in the larvae of Lactariidae, Menidae, and within the carangoids only in

the 'echeneoids'. Absence of spines on the supracleithrum is considered derived in percoid larvae by Johnson (1984), but they are absent in many percoid families, and this loss has almost certainly occurred several times.

11) *Larvae lack spines on the posttemporal*. Posttemporal spines are absent in the larvae of Lactariidae, Menidae, and among the carangoids, in one 'echeneoid' family (Echeneididae). Absence of spines on the posttemporal is considered derived in percoid larvae by Johnson (1984), but these spines are absent in many percoid families, and this loss is also likely to have occurred more than once.

12) *Neural spines and arches 1 and 2 closely applied*. This condition occurs in the Lactariidae, Menidae, Nematistiidae and a number of other percoid groups (eg, some apogonids), and although it is probably derived, it apparently arose more than once. In addition, the arrangement of neural arches and spines and pterygiophores differs among these taxa, raising the question of homology. In *Lactarius*, the neural arches and spines are broad, and the pterygiophores are slender (Fig. 7). In *Mene*, all three are very slender, and the first neural spine is in some specimens ontogenetically captured by the second arch resulting in a bifurcate second neural spine (Fig. 10). In *Nematistius*, the first pterygiophore is very broad and apparently displaces and crowds together the first and second centra and neural spines (Rosenblatt & Bell, 1976, fig. 12).

In addition, *Mene* shares with the carangoids (but not *Lactarius*) six possible synapomorphies. None of these are unequivocal.

13) *Larvae lack opercular spines*. Larvae of *Lactarius* have an opercular spine: larvae of *Mene* and
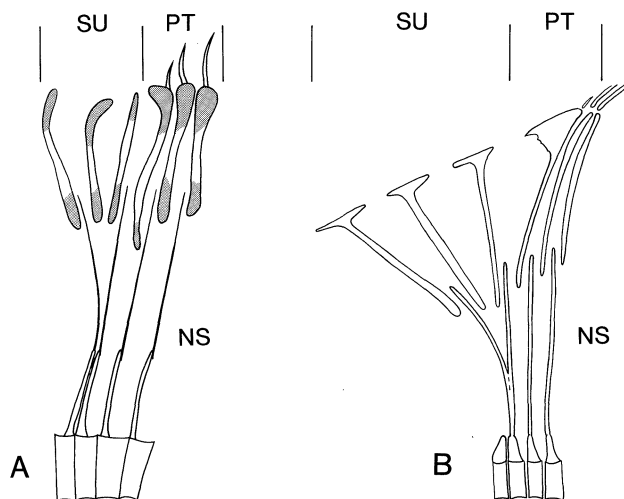

Fig. 10. Supraneurals (SU), anterior dorsal pterygiophores (PT), and neural spines (NS) of *Mene maculata*. A – larva (AMS unregistered, 4.3 mm SL); shaded areas are cartilage; B – adult (AMS I.15557-122, 70 mm SL), note bifurcate neural spine on centrum 2.

the carangoids lack an opercular spine. The absence of an opercular spine was considered derived in percoid larvae by Johnson (1984), but it is absent in many percoid families, and the loss probably occurred more than once. Some illustrations of larvae of the carangid genera *Trachinotus* and *Naucrates* appear to show opercular spines (eg, Laroche *et al.*, 1984, figs 272A,B), but the larvae available to me do not have opercular spines (see also Johnson, 1984, table 121).

14) *No radial cartilage anterior to neural and haemal spines of third preural centrum.* This cartilage is absent in *Mene* and the carangoids (present in *Lactarius*). The absence of this cartilage was considered derived in percoid fishes by Johnson (1984), but it is absent in many percoid families, and this loss may have occurred more than once.

15) *Procurrent caudal spur absent.* The procurrent spur is absent in *Mene* and the carangoids (present in *Lactarius*). Johnson (1984) considered that in percoids its absence is derived, but it is absent in many percoid families, and this loss may have occurred more than once.

16) *Larvae have a supraoccipital, usually serrate, crest.* A supraoccipital crest is present in the larvae of *Mene* and nearly all carangids, but among the carangoids it is absent in the 'echeneoids' and larvae of *Nematistius* are unknown (it is absent in *Lactarius*). This type of larval spination was considered derived by Johnson (1984), but as it occurs in all or some of the members of 14 other percoid families, it may have been derived more than once.

17) *Three or fewer tri-segmental pterygiophores in both dorsal and anal fin.* *Mene* and the carangoids have three or fewer tri-segmental pterygiophores (*Lactarius* has 3-5 dorsal and 2-3 anal tri-segmental pterygiophores). According to Johnson (1980:35), the reduction in number of tri-segmental pterygiophores is derived. However, many percoid families have a reduced number of tri-segmental pterygiophores, and he argued that this reduction has "occurred along several independent lines."

18) *Larvae have a midlateral series of melanophores on the tail.* Larvae of *Mene* and the carangoids (but larvae of *Nematistius* are unknown) have this melanophore series. This melanophore series is found in only about 12 of the more than 80 percoid families, and is probably derived within the percoids, but may have arisen more than once. This pigment series is absent in all the *Lactarius* larvae studied here, but it could be present in larvae smaller than 6.0 mm, the smallest specimen available.

Lactarius is an unusual fish with a number of autapomorphies. Most of the relationships suggested for *Lactarius* were based on superficial resemblances, shown since to be invalid (see above). In contrast, the carangoid relationship cannot be rejected. However, it is hard to obtain unequivocal evidence to support that, or any other, relationship.

The characters summarised above provide some evidence that *Lactarius* and *Mene* are, respectively, second and first sister taxa of the carangoid fishes *sensu* Smith-Vaniz and Johnson. Unfortunately, only two of the 18 characters (numbers 7 and 8) provide evidence not tainted by possible multiple origins within the percoid fishes, losses, or lack of knowledge of either small larvae of *Lactarius* or any larvae of the carangoid *Nematistius*. It must be remembered that the 'carangoid' state of character 7 occurs in some non-percoid perciform groups. Therefore, it is worth examining character 7 to see if it is a strong, central support of a carangoid relationship to which the other, equivocal characters can be added for mutual support, or merely another equivocal element.

Smith-Vaniz (1984) described the coracoid in carangids and 'echeneoids' as "middle part of coracoid with its anterior margin consisting of a lamella of bone broadly extending toward the median cleithral wing". This was not illustrated by him, but reference was made to illustrations of Suzuki (1962). Smith-Vaniz (1984) stated "in *Nematistius* the middle and lower parts of the coracoid are rodlike with lamellar bone restricted to its posterior margin", and referred to illustrations of Rosenblatt & Bell (1976). Johnson (1984) described the coracoid of carangids and 'echeneoids' as having a "lamellar expansion along the anterior margin of the coracoid" and the coracoid of *Nematistius* as being "unmodified". He provided neither figures nor references to any.

The coracoids of *Lactarius* (Fig. 6A) and *Mene* (Fig. 6B) are described accurately, if imprecisely, by the text portrayals of Smith-Vaniz (1984) and Johnson (1984). The shape and extent of the anterior lamella varies greatly among the carangids illustrated by Suzuki (1962) and examined by me, and this variation encompasses the coracoid lamella morphology of both *Lactarius* and *Mene*. The coracoid of *Nematistius* as illustrated by Rosenblatt & Bell (1976) is not encompassed within the carangid morphologies illustrated by Suzuki, and is similar to the coracoid of more generalised percoid fishes such as *Lutjanus* (Potthoff *et al.*, 1988).

Therefore, I tentatively consider *Lactarius*, *Mene*, carangids and 'echeneoids' to have the same derived coracoid character state, one that differs from the apparently primitive condition of *Nematistius*. Unfortunately, this cannot be confirmed until the ontogeny of this bone is studied in all the taxa in question: at present this has been done only for the 'echeneoid' family Coryphaenidae (Potthoff, 1980). The occurrence of a similar coracoid morphology in acanthuroids and some other groups and the apparent lability of coracoid morphology within the carangids seemingly lessens the assurance that this character is a robust indicator of relationships.

The distribution of character 8 (ventral processes of third hypobranchials long and closely applied) is too poorly known at present to determine if it, too, is an equivocal indication of relationships. Further work is

required to evaluate this character state and its distribution. If it is confirmed to be confined to carangoids, *Lactarius* and *Mene*, it would be strong support for the hypothesis that these taxa are monophyletic. However, the apparent absence of this state in the 'echeneoid' fishes (at least *Coryphaena*) does present a problem for that hypothesis.

If *Lactarius* and *Mene* are included with the carangoids on the strength of characters 7 and 8 there are two possibilities. Either *Lactarius* and *Mene* are the primitive members of the superfamily and there is a reversal in *Nematistius* to the primitive coracoid condition, or *Nematistius* is the sister group of the other carangoids, and there is a loss in both *Lactarius* and *Mene* of the prenasal bone and the small, adherent scales. The former is more parsimonious. However, until the larva of *Nematistius* are described, and more larvae of *Lactarius* become available, the situation will remain unresolved.

Four characters (9, 10, 11, 12) indicate that *Lactarius* and *Mene* are sister taxa. Losses are involved in two of these (10, 11), and one involves a possibly misinterpreted homology (12). The fourth (9) involves posterior extension of the swim bladder, and this differs in construction in the two taxa, so there is additional doubt about homology. Therefore, the evidence for the two taxa being sister groups is not strong.

In conclusion, placement of *Lactarius* and *Mene* in the carangoid fishes or as successive sister groups to the carangoid fishes is suggested by several demonstrably equivocal characters and two characters of uncertain reliability. The inclusion of *Lactarius* and *Mene* with the carangoids must be considered a tentative hypothesis, and evidence from larvae will be crucial to testing it. Study of larvae is required to determine the states of several characters in *Nematistius* larvae and in small *Lactarius* larvae (once these become available), and to determine by examination of ontogeny if characters such as the coracoid lamella are homologous among the taxa studied here. A study of the distribution of character eight (ventral processes of third hypobranchial) among percoid fishes is also required.

References

Ahlstrom, E.H., J.L. Butler & B.Y. Sumida, 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. Bulletin of Marine Science 26(3): 285–402.

Alam, S.K., M. Devaraj & R.V. Shrotri, 1989. Anchorage of air bladder with the interspinous bone of the anal fin in *Lactarius lactarius* (Bloch & Schneider, 1801). Journal of the Indian Fisheries Association 19: 69–72.

Bloch, M.E. & J.G. Schneider, 1801. M.E. Blochii Systema Ichthyologiae iconibus cx illustratum. Berlin, 584 pp.

Chacko, P.I., 1944. On the bionomics of the big-jawed jumper *Lactarius lactarius* (Cuv. and Val.). Current Science (Bangalore) 13: 108.

Cuvier, G.L., 1829. Le règne animal distribué d'après son organisation, pour servir de base à l'historie naturelle des animaux. 2nd edn, Paris 2: 122–406.

Cuvier, G.L. & A. Valenciennes, 1833. Histoire Naturelle des Poissons. Levrault, Paris. Vol. 9, 512 pp.

Day, F., 1878. The fishes of India. Bernard Quaritch, London. 2 vols, 778 pp, 198 pls.

Deng, S.-M. & H.-X. Zhan, 1986. Comparative studies of the lateral line canal system of families to be related with the Carangidae. Pp. 561–569. In T. Uyeno, R. Arai, T. Taniuchi & K. Matsuura (eds). Indo-Pacific Fish Biology. Ichthyological Society of Japan, Tokyo.

Dingerkus, G. & L. Uhler, 1977. Enzyme clearing of alcian blue stained small vertebrates for demonstration of cartilage. Stain Technology 52: 229–232.

Fink, W.L., 1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. Journal of Morphology 167(1): 167–184.

Freihofer, W.C., 1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthyological Bulletin 8: 80–189.

Gloerfelt-Tarp, T. & P.J. Kailola, 1984. Trawled Fishes of Southern Indonesia and Northwestern Australia. Australian Development Assistance Bureau, Canberra, 406 pp.

Günther, A., 1860. Catalogue of the Acanthopterygian Fishes in the Collection of the British Museum. Vol. 2. British Museum, 548 pp.

Johnson, G.D., 1980. The limits and relationships of the Lutjanidae and associated families. Bulletin of the Scripps Institution of Oceanography 24: 114 pp.

Johnson, G.D., 1983. *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and interrelationships of the Serranidae. Copeia 1983(3): 777–787.

Johnson, G.D., 1984. Percoidei: development and relationships. Pp. 464–498. In H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, jr & S.L. Richardson (eds). Ontogeny and Systematics of Fishes. American Society of Ichthyologists and Herpetologists Special Publication 1.

Johnson, G.D., 1986. Scombroid phylogeny: an alternative hypothesis. Bulletin of Marine Science 39(1): 1–41.

Jordan, D.S., 1923. A classification of fishes including

families and genera as far as known. Stanford University Publications in Biological Science 3: 77–243.

Kumaran, M., 1984. Lactariidae. In W. Fischer & G. Bianchi (eds). FAO Species Identification Sheets for Fishery Purposes. Western Indian Ocean, Fishing Area 51. FAO, Rome (unpaginated).

Kyushin, K., K. Amaoka, K. Nakaya, H. Ida, Y. Tanino & T. Senta, 1982. Fishes of the South China Sea. Japanese Marine Fishery Resource Research Center, Tokyo, 333 pp.

Laroche, W.A., W.F. Smith-Vaniz & S.L. Richardson, 1984. Carangidae: development. Pp. 510–522. In H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, jr & S.L. Richardson (eds). Ontogeny and Systematics of Fishes. American Association of Ichthyologists and Herpetologists Special Publication 1.

Leis, J.M. & D.S. Rennis, 1983. The Larvae of Indo-Pacific Coral Reef Fishes. New South Wales University Press, Sydney and University of Hawaii Press, Sydney, 269 pp.

Leis, J.M. & T. Trnski, 1989. The Larvae of Indo-Pacific Shorefishes. New South Wales University Press, Sydney and University of Hawaii Press, Honolulu, 371 pp.

Leviton, A.E., R.H. Gibbs jr, E. Heal & C.E. Dawson, 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3): 802–832.

Nair, R.V., 1952. Studies on some fish eggs and larvae of the Madras plankton. Proceedings of the Indian Academy of Sciences B35: 181–208.

Potthoff, T., 1980. Development and structure of fins and fin supports in dolphin fishes Coryphaena hippurus and Coryphaena equiselis (Coryphaenidae). US Fishery Bulletin 78(2): 277–312.

Potthoff, T., 1984. Clearing and staining techniques. Pp. 35–37. In Moser, H.G., W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, jr & S.L. Richardson (eds). Ontogeny and Systematics of Fishes. American Association of Ichthyologists and Herpetologists, Special Publication 1.

Potthoff, T., S. Kelly & L.A. Collins, 1988. Osteological development of the red snapper Lutjanus campechanus (Lutjanidae). Bulletin of Marine Science 43(1): 1–40.

Regan, C.T., 1913. The classification of percoid fishes. Annals and Magazine of Natural History Ser. 8, 12(1): 111–145.

Rosenblatt, R.H. & M.A. Bell. 1976. Osteology and relationships of the roosterfish, Nematistius pectoralis Gill. Natural History Museum of Los Angeles County Contributions in Science 279: 1–23.

Sainsbury, K.J., P.J. Kailola & G.G. Leyland, 1985. Continental Shelf Fishes of Northern and North-western Australia: an Illustrated Guide. Clouston & Hall, Canberra, 375 pp.

Sasaki, K., 1989. Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). Memoirs of the Faculty of Fisheries Hokkaido University 36: 1–137.

Seale, A., 1910. Fishes of Borneo, with descriptions of four new species. Philippine Journal of Science 5: 263–289.

Smith-Vaniz, W.F., 1984. Carangidae: relationships. Pp. 522–530. In H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, jr & S.L. Richardson (eds). Ontogeny and Systematics of Fishes. American Association of Ichthyologists and Herpetologists Special Publication 1.

Springer, V.G., 1982. Pacific plate biogeography, with special reference to shorefishes. Smithsonian Contributions to Zoology 367: 1–182.

Suda, Y., 1991. Skeletal features of the Japanese horse mackerel. Bulletin of the Kitakyushu Museum of Natural History 10: 53–89. (In Japanese, English abstract)

Suzuki, K., 1962. Anatomical and taxonomical studies on the carangid fishes of Japan. Report of Faculty of Fisheries Prefectural University of Mie 4: 43–232.

Tyler, J.C., G.D. Johnson, I. Nakamura & B.B. Collette, 1989. Morphology of Luvaris imperialis (Luvaridae), with a phylogenetic analysis of the Acanthuroidei (Pisces). Smithsonian Contributions to Zoology 485: 1–78.

Weber, M. & L.F. de Beaufort, 1931. The Fishes of the Indo-Australian Archipelago. Perciformes. Vol. 6. E.J. Brill, Leiden, 448 pp.