

Phylogenetic Relationships of the Perciform Genera of the Family Carangidae

Soko Gushiken

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Abstract A cladistic analysis of all known genera in the Carangidae was made mostly on the basis of external and osteological characters. Polarity for each character was determined by outgroup comparison using the echeeneoids as the first outgroup and the Nematistiidae as the second. In the Carangini, there were four hypothesized monophyletic groups at the rank of sub-tribe. *Parastromateus* is the sister group of the remaining twenty-one carangine genera which are divided into three groups. The first group consists of a single genus *Megalaspis*. The second group is composed of *Trachurus*, *Decapterus*, *Selar*, *Atule*, *Selaroides*, *Pantolabus*, *Alepes*, *Hemicaranx*, *Pseudocaranx*, *Kaiwarinus*, and *Chloroscombrus*. The third group comprises *Uraspis*, *Caranx*, *Gnathanodon*, *Carangichthys*, *Carangoides*, *Atropus*, *Ulua*, *Alectis*, and *Selene*.

Gushiken (1983) reported 57 species and 23 genera in the family Carangidae from waters of Japan and Taiwan, and Laroche et al. (1984) recognized approximately 140 species and 30 genera in the world. Smith-Vaniz (1984) corroborated that five families, the Nematistiidae, Coryphaenidae, Echeeneidae, Rachycentridae and Carangidae, form a monophyletic group referred to as the "carangoids" by showing a cladistic analysis of the carangoid families inclusive of main groups of the Carangidae, but he left the phylogeny of the tribe Carangini unresolved. Therefore, the present work placed primary emphasis on the relationships among all known genera belonging to this tribe.

Materials

I examined the specimens listed below. Among them, "*" marked are species examined by Suzuki (1962) who exhibited excellent figures of their general elements and "+" marked are species illustrated in the present paper (Figs. 2–10). The abbreviations prefixed to the catalogue numbers indicate as: S. Gushiken's collection, SG; Department of Fisheries, Faculty of Agriculture, Kyoto University, FAKU; Department of Marine Sciences, Faculty of Science, University of the Ryukyus, URMP; Academy of Natural Sciences in Philadelphia, ANSP.

**Alectis ciliaris*, SG 340, 146 mm SL, Okinawa; **Alectis indicus*, SG 221, 310 mm SL, Okinawa; **Alepes vari*, 2 specimens, SG 304, 317, 155–391 mm SL, **Atropus atropus*, SG 456, 189 mm SL, Singapore;

**Atule mate*, SG 439, 198 mm SL, Singapore; *Cam-pogramma glaycos*, FAKU S-1050, 440 mm SL, Suriname (radiographed); **Carangichthys dinema*, SG 183, 201 mm SL, Okinawa; *Carangichthys oblongus*, SG 154, 219 mm SL, Okinawa; *Carangoides chrysophrys*, SG 105, 222 mm SL, Okinawa; **Carangoides hedlandensis*, SG 140, 214 mm SL, Okinawa; **Carangoides malabaricus*, SG 433, 241 mm SL, New Zealand; **Carangoides orthogrammus*, SG 187, 208 mm SL, Okinawa; **Caranx lugubris*, SG 191, 248 mm SL, Okinawa; **Caranx melampygus*, SG 283, 207 mm SL, Okinawa; **Caranx sexfasciatus*, SG 164, 165 mm SL, Okinawa; †*Chloroscombrus chrysurus*, 2 specimens, FAKU 45061, 45064, 116–126 mm SL, Suriname (cleared and stained); **Decapterus akaadi*, SG 368, 198 mm SL, Okinawa; **Decapterus macarellus*, SG 283, 233 mm SL, Okinawa; **Decapterus macrosoma*, SG 394, 222 mm SL, Okinawa; **Decapterus maruadii*, SG 384, 189 mm SL, Okinawa; **Decapterus muroadii*, SG 292, 201 mm SL, Okinawa; *Decapterus russelli*, SG 241, 208 mm SL, Okinawa; **Decapterus tabl*, SG 312, 354 mm SL, Okinawa; **Elagatis bipinnulata*, SG 228, 337 mm SL, Okinawa; **Gnathanodon speciosus*, SG 380, 156 mm SL, Okinawa; †*Hemicaranx amblyrhynchus*, FAKU 44955, 138 mm SL, Suriname (cleared and stained); **Kaiwarinus equula*, SG 217, 158 mm SL, Kagoshima; *Lichia amia*, ANSP 153013, 90 mm SL, Mediterranean (cleared and stained); **Megalaspis cordyla*, SG 465, 246 mm SL, Okinawa; **Naucrates ductor*, SG 250, 232 mm SL, Okinawa; †*Oligoplites saurus*, ANSP 114573, 104 mm SL, Venesuela (cleared and stained); **Pantolabus radiatus*, ANSP 147709, 137 mm SL, Australia (cleared and stained); †*Parastromateus niger*, SG 520, 220 mm SL, Nagasaki; *Parona signata*, FAKU 106719, 381 mm SL,

Suriname (radiographed); **Pseudocaranx dentex*, 2 specimens, SG 286, 408, 278–430 mm SL, Okinawa; **Scomberoides lysan*, SG 239, 335 mm SL, Okinawa; **Selar crumenophthalmus*, SG 235, 234 mm SL, Okinawa; **Selaroides leptolepis*, SG 218, 176 mm SL, Okinawa; †*Selene setapinnis*, 2 specimens, FAKU 44941, 44942, 114–121 mm SL, Suriname (cleared and stained); **Seriola dumerili*, SG 207, 290 mm SL, Okinawa; **Seriola quinqueradiata*, SG 213, 337 mm SL, Kagoshima; †*Seriolina nigrofasciata*, SG 163, 212 mm SL, Okinawa; **Trachinotus baillonii*, SG 248, 136 mm SL, Okinawa; *Trachinotus blochii*, SG 375, 146 mm SL, Okinawa; **Trachurus japonicus*, 2 specimens, SG 463, 481, 190–310 mm SL, Nagasaki; †*Ulua mentalis*, URMP 13802, 132 mm SL, Thailand (cleared and stained); **Uraspis helvola*, SG 321, 238 mm SL, Okinawa.

Outgroup material: Coryphaenidae—*Coryphaena hippurus*, SG unnumbered, 700 mm SL, Okinawa; Echeeneidae—*Echeneis naucrates*, SG unnumbered, 550 mm SL, Okinawa; Rachycentridae—*Rachycentron canadum*, SG unnumbered, 406 mm SL, Okinawa. As for the Nematistiidae, data of *Nematistius pectoralis* published by Rosenblatt and Bell (1976) were analyzed and additional information was supplied by Rosenblatt (pers. comm.).

Smith-Vaniz (1984) listed 4 tribes and 30 genera of carangid fishes in the world as follows:

- | | |
|---------------|---|
| Trachinotini | <i>Lichia</i> , <i>Trachinotus</i> . |
| Scomberoidini | <i>Oligoplites</i> , <i>Parona</i> , <i>Scomberoides</i> . |
| Naucratiini | <i>Campogramma</i> , <i>Elagatis</i> , <i>Naucrates</i> , <i>Seriola</i> , <i>Seriolina</i> . |
| Carangini | <i>Alectis</i> , <i>Alepes</i> , <i>Atropus</i> , <i>Atule</i> , <i>Carangoides</i> , <i>Caranx</i> , <i>Chloroscombrus</i> , <i>Decapterus</i> , <i>Gnathanodon</i> , <i>Hemicaranx</i> , <i>Megalaspis</i> , <i>Pantolabus</i> , <i>Parastromateus</i> , <i>Pseudocaranx</i> , <i>Selar</i> , <i>Selaroides</i> , <i>Selene</i> , <i>Trachurus</i> , <i>Ulua</i> , <i>Uraspis</i> . |

In the present study, I agreed with him and followed his classification except that I recognized two additional genera *Kaiwarinus* and *Carangichthys* in the Carangini (Gushiken, 1983). However, carangid generic limits are still not well established as exemplified in detail by Laroche et al. (1984).

Methods

Skeletons were primarily prepared for examination by placing the fresh specimen in hot water for a time and then taking out of water, cooling

and brushing away the flesh. Some specimens were cleared with KOH and stained with alizarin red S. A few specimens were radiographed.

Reconstruction of phylogenies was elucidated according to the principle of synapomorphy (Hennig, 1966) and the principle of parsimony (Nelson, 1970). Polarity for each character was determined by the outgroup comparison method of Maddison et al. (1984). The echeeneoids were taken as the first outgroup and the Nematistiidae as the second (Fig. 1A). The Carangidae and the echeeneoids are sister groups and together form the sister group of the Nematistiidae (Smith-Vaniz, 1984). The echeeneoids (first outgroup) consist of three families, the Coryphaenidae, Echeeneidae and Rachycentridae. As for relationships among the three families, Johnson (1984) presented evidence of the possibility that the Coryphaenidae and Rachycentridae form a sister group relationship based on the morphology of their larvae. However, I concluded that it was better to settle this problem after establishment of carangid relationships and treated their relationships as uncertain in this paper for lack of information about the larva of *Nematistius*. Then, relationships among the first and second outgroup families can be illustrated as in Fig. 1A. A triangle shows the Carangidae (ingroup) to be studied. The most recent ancestor common to the first outgroup families is represented by the X node and that to the ingroup plus the first outgroup is by the outgroup node.

Fig. 1B presents distribution of a character with two states (a and b) in the related groups. a-b denotes that the character state assessment is undeterminable, which is written a, b by Maddison et al. (1984). When a is present in two families of the first outgroup and b is present in the other family of the same group, the X node is labelled a or a-b because of two possible procedures (Fig. 1C; Maddison et al., 1984: 91, fig. 10). If a is present in the second outgroup family, the outgroup node is labelled a, and b is assessed as the derived state for the ingroup. If b is present in the second outgroup, the outgroup node is labelled a-b or b, and polarity for the character is assessed as equivocal (undeterminable) for the ingroup. When a is present in all first outgroup families, the X node is always labelled a and the outgroup node is labelled either a or a-b depending upon the character state of the second out-

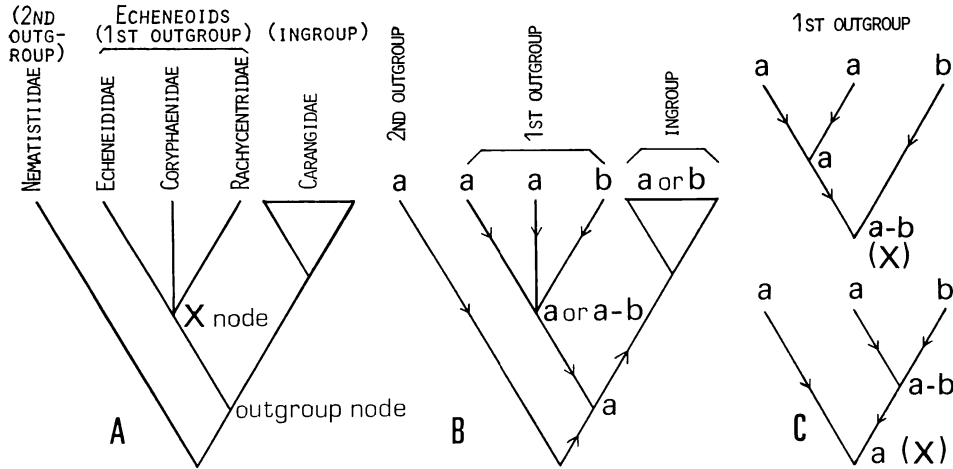


Fig. 1. A: Relationships among the carangoid families; the 1st outgroup has three terminal families whose relationships are uncertain. B: Distribution of a character with two states in the related groups; the X and outgroup nodes are labelled, starting at the outgroup terminal families. C: Two possible procedures proceeding toward the X node in the 1st outgroup.

group family (Maddison et al., 1984: 90, fig. 8). If **b** is present in the second outgroup, the outgroup node is labelled **a-b** and polarity for the character is assessed as equivocal for the ingroup. Table 1 summarizes polarity assessment of the Carangidae.

Characters selected for cladistic analysis
(Figs. 2-10)

Comparing with other percoid groups, the carangids are exceedingly rich in structural variation. However, polarities for many characters were assessed as equivocal when the method of Maddison et al. (1984) was applied, and I could select only twenty-five characters for the analysis of carangid relationships. Characters autapomorphic for a given genus were usually excluded because they provide no information about the relationships. The numbers in parentheses correspond to those shown in cladograms of Fig. 12.

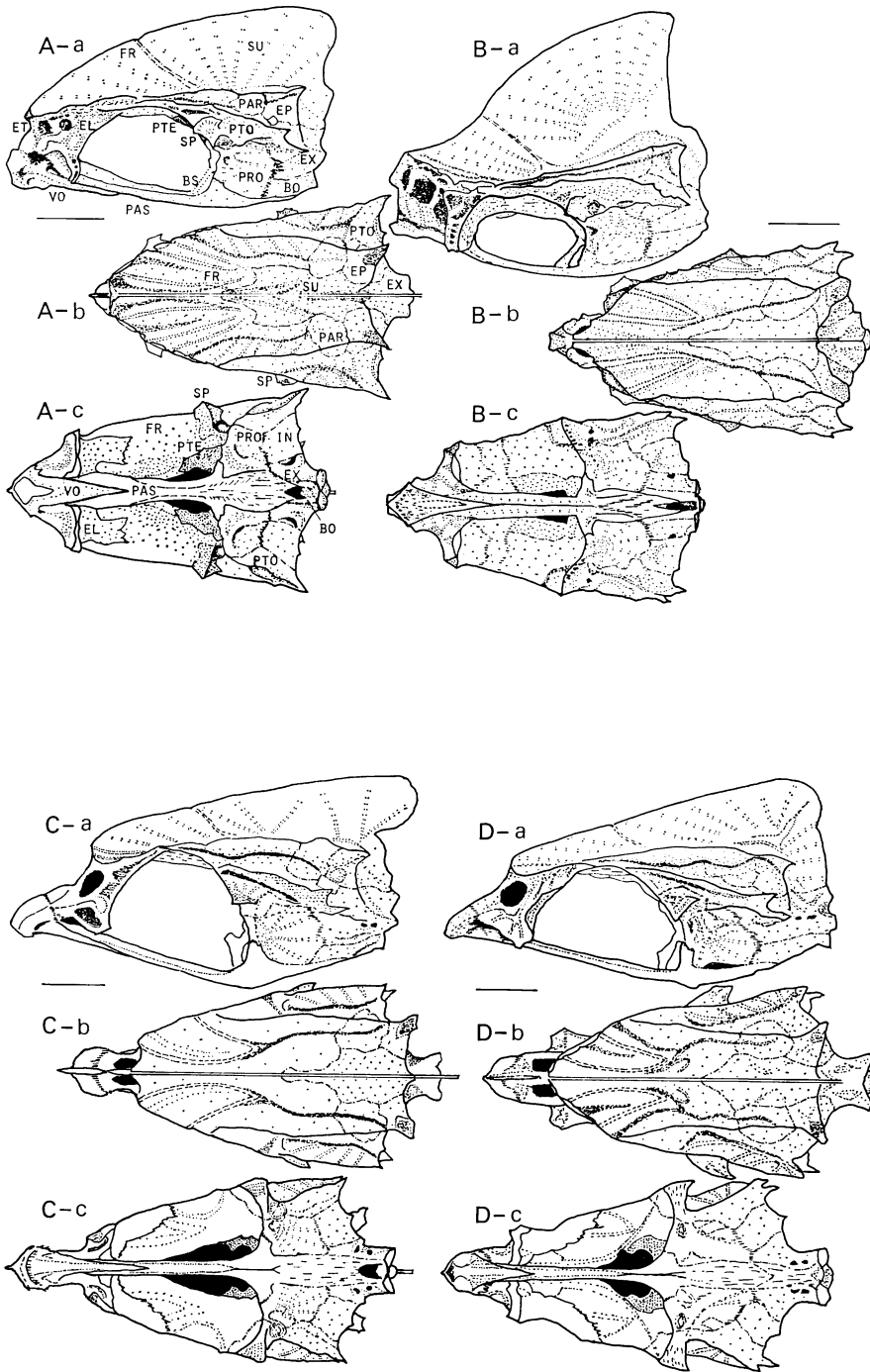
(1) Gap between last two anal spines (Smith-Vaniz, 1984: fig. 278). In the carangids, one or two anal spines on the 1st anal pterygiophore are forwarded with a relatively wide gap from the last anal spine on the 2nd anal pterygiophore. In the outgroup families, the echeeneoids have lost the anal spines. The Nematistiidae is equipped with three anal spines as in most percoid fishes, and it is lacking in such a gap between the last two anal

spines. Since the condition of the echeeneoids has no effect on the assessment of polarity for this character, the presence of a relatively wide gap between the last two anal spines is regarded as the derived state of this character for the carangids, which defines the monophyly of the Carangidae.

(2) Pleural ribs (Smith-Vaniz and Staiger, 1973: fig. 23). In the naucratine and carangine genera, the anterior pleural ribs are borne in pits on centra of vertebrae and when parapophyses are developed, the ribs are borne on the parapophyses, but the trachinotine and scomberoidine genera are different from these genera in that most ribs, except for the last two pairs, are attached directly to the lateral sides of centra though parapophyses are

Table 1. Polarity assessment of the Carangidae (ingroup). **a** and **b** are character states. **a-b** indicates that the character state assessment is undeterminable.

1st outgroup families	a	a	b	a	a	a
X node	a or a-b			a		
2nd outgroup family	a	b		a	b	
outgroup node	a	a-b or b		a	a-b	
derived state for ingroup	b	?		b	?	



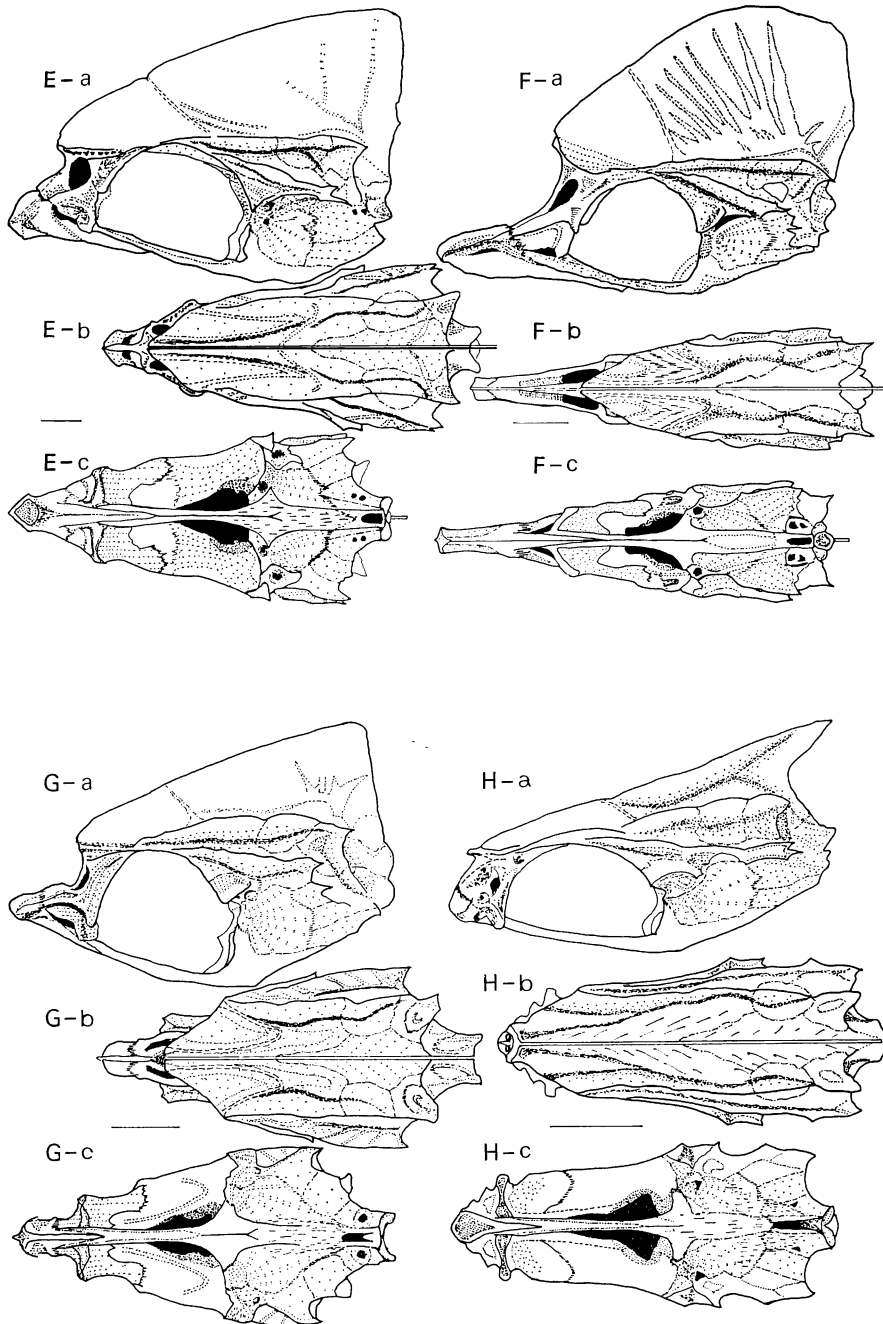


Fig. 2. Lateral (a), dorsal (b) and ventral (c) aspects of the cranium in eight carangid species. A, *Seriolina nigrofasciata*; B, *Parastromateus niger*; C, *Hemicaranx amblyrhynchus*; D, *Pantolabus radiatus*; E, *Ulua mentalis*; F, *Selene setapinnis*; G, *Chloroscombrus chrysurus*; H, *Oligoplites saurus*. BO, basioccipital; BS, basisphenoid; EL, lateral ethmoid; EP, epiotic; ET, ethmoid; EX, exoccipital; FR, frontal; IN, intercalar; PAR, parietal; PAS, parasphenoid; PRO, prootic; PTE, pterosphenoid; PTO, pterotic; SP, sphenotic; SU, supraoccipital; VO, vomer. Scales indicate 5 mm.

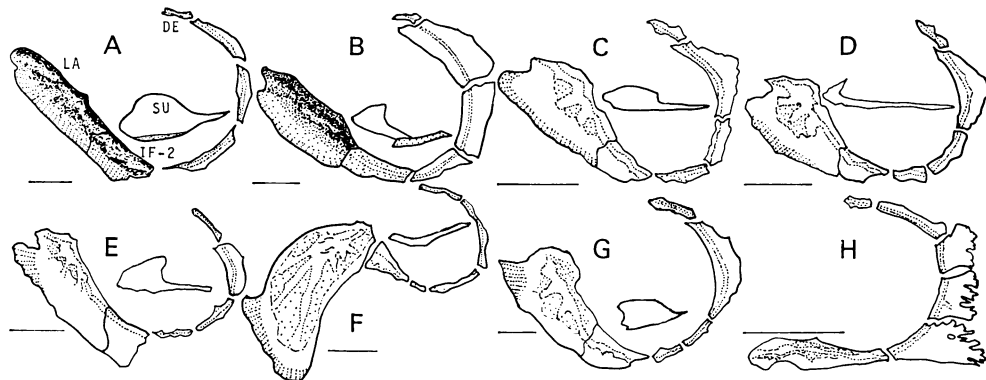


Fig. 3. The infraorbitals in eight carangid species. A-H, same as in Fig. 2. DE, dermosphenotic; IF-2, 2nd infraorbital; LA, lachrymal; SU, subocular shelf. Scales indicate 5 mm.

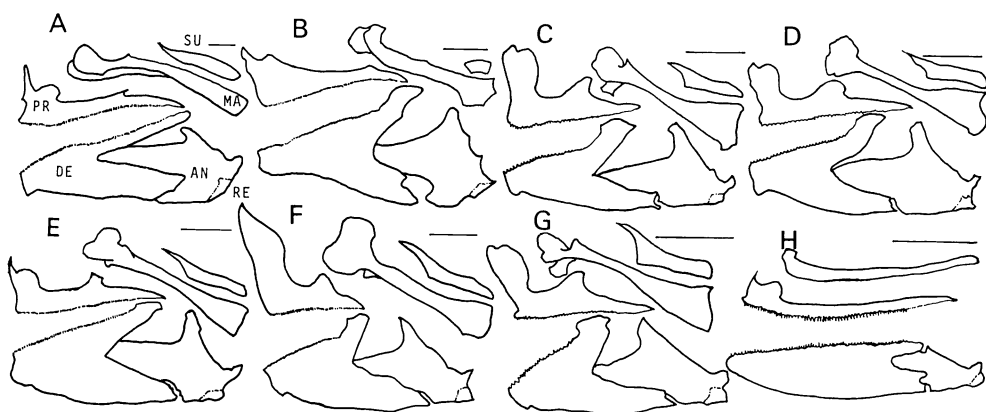


Fig. 4. The upper and lower jaws in eight carangid species. A-H, same as in Fig. 2. AN, angular; DE, dentary; MA, maxilla; PR, premaxilla; RE, retroarticular; SU, supramaxilla. Scales indicate 5 mm.

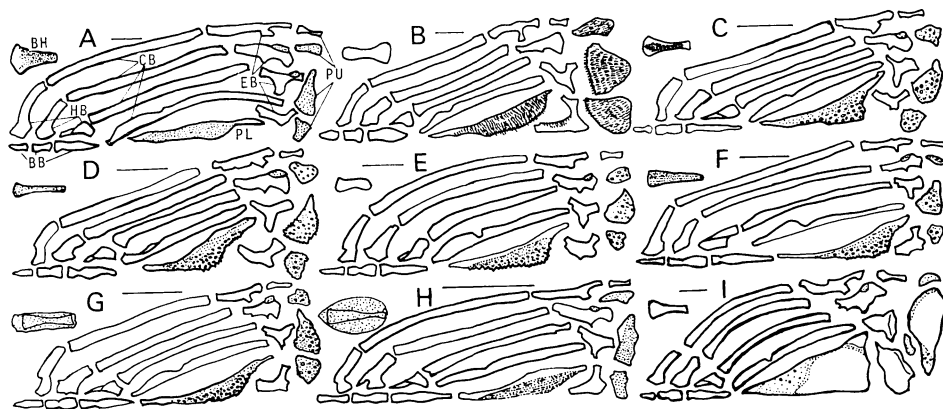


Fig. 5. The branchial apparatus in nine carangid species. A-H, same as in Fig. 2; I, *Trachinotus blochii*. BB, basibranchial; BH, basihyal; CB, ceratobranchial; EB, epibranchial; HB, hypobranchial; PL, lower pharyngeal; PU, upper pharyngeal. Scales indicate 5 mm.

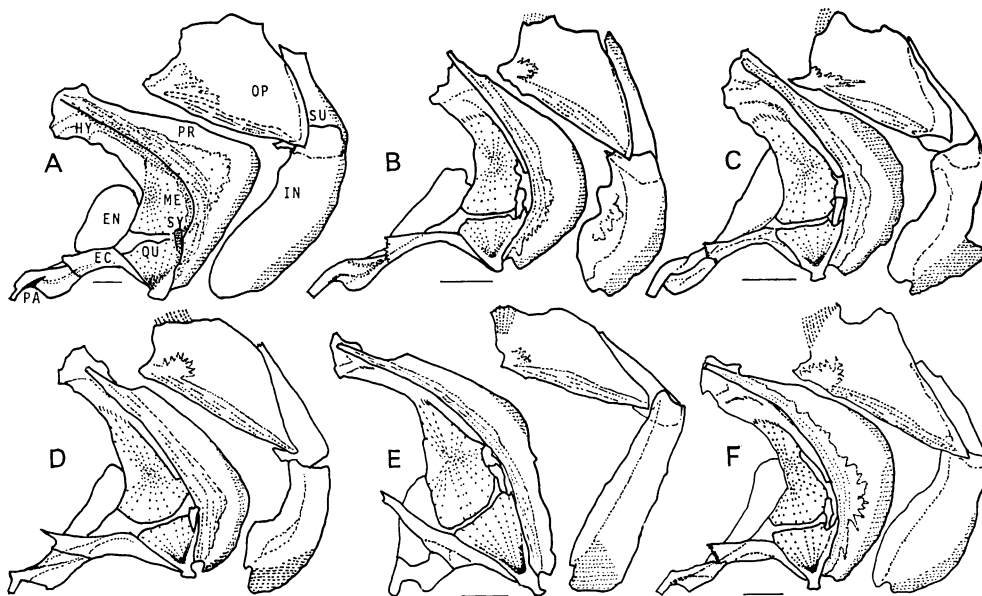


Fig. 6. The suspensorium and opercular apparatus in six carangid species. A, *Parastromateus niger*; B, *Hemicarax amblyrhynchus*; C, *Pantolabus radiatus*; D, *Ulua mentalis*; E, *Selene setapinnis*; F, *Chloroscombrus chrysurus*. EC, ectopterygoid; EN, endopterygoid; HY, hyomandibular; IN, interopercle; ME, metapterygoid; OP, opercle; PA, palatine; PR, preopercle; QU, quadrate; SU, subopercle; SY, symplectic. Scales indicate 5 mm.

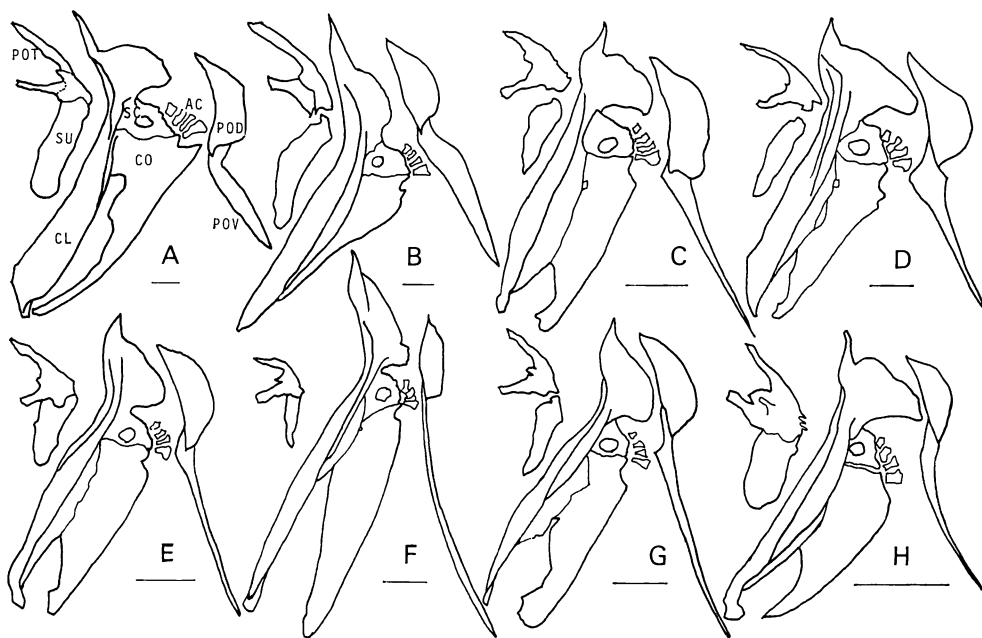


Fig. 7. The shoulder girdle in eight carangid species. A-H, same as in Fig. 2. AC, actinosts; CO, coracoid; CL, cleithrum; POD, dorsal postcleithrum; POT, posttemporal; POV, ventral postcleithrum; SC, scapula; SU, supracleithrum. Scales indicate 5 mm.

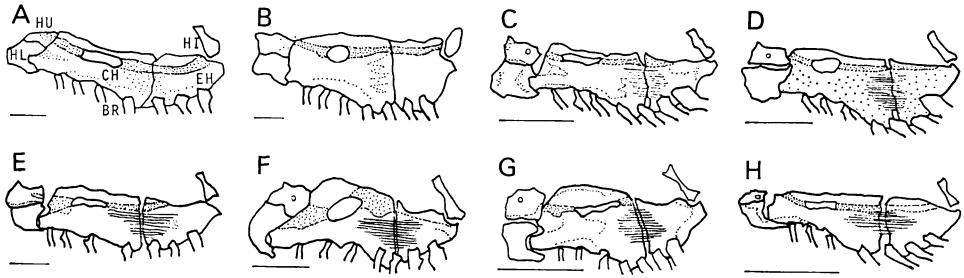


Fig. 8. The hyoid arch in eight carangid species. A-H, same as in Fig. 2. BR, branchiostegal ray; CH, ceratohyal; EH, epihyal; HI, interhyal; HL, lower hypohyal; HU, upper hypohyal. Scales indicate 5 mm.

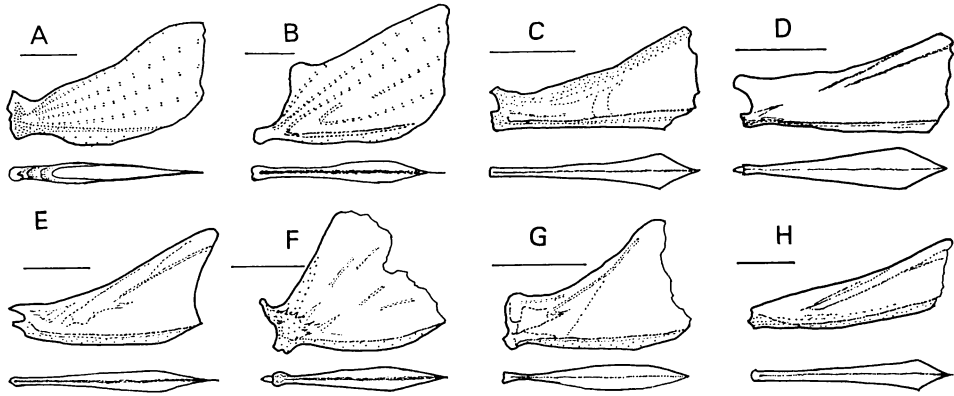


Fig. 9. Lateral (above) and ventral (below) aspects of the urohyal in eight carangid species. A-H, same as in Fig. 2. Scales indicate 5 mm.

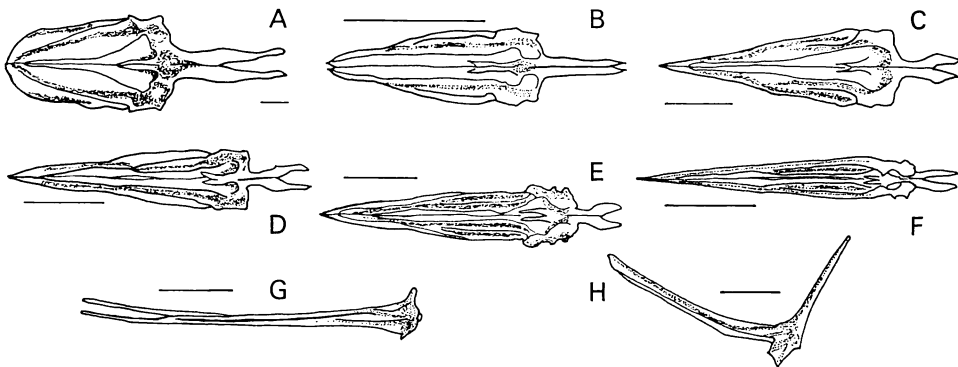


Fig. 10. The pelvic girdle in eight carangid species. Ventral aspect: A, *Seriolina nigrofasciata*; B, *Oligoplites saurus*; C, *Hemicaranx amblyrhynchus*; D, *Pantolabus radiatus*; E, *Ulua mentalis*; F, *Chloroscombrus chrysurus*. Lateral aspect: G, *Selene setapinnis*; H, *Parastromateus niger*. Scales indicate 5 mm.

developed from the 3rd or 4th vertebra. In the outgroup families, the Coryphaenidae has the ribs inserted on centra without parapophyses developed, but in the other three families, parapophyses are more or less developed and most ribs are borne on the parapophyses. The pleural ribs directly attached to centra are thus considered to be the derived state of this character for the carangids.

(3) Adductor mandibular muscle Al' division (Smith-Vaniz, 1984: fig. 279). I did not examine the myological characters in the present study, but Smith-Vaniz clearly showed that the adductor mandibular muscle Al' division originating on the subocular shelf is present in the naucratine and carangine genera. He also elucidated that this muscle is absent in the outgroup families. Therefore, the presence of this muscle is apparently the derived state of this character for the carangids.

(4) Upper jaw. The scomberoidine genera are distinguished from the remaining carangid genera in having the non-protractile upper jaw. In the outgroup families, the Echeneididae has the non-protractile upper jaw as in the scombroids, but the other three families share the protractile upper jaw. The non-protractile upper jaw is thus considered as the derived state of this character for the carangids.

(5) Epitotics. In most carangid genera, the epitotics are more or less separated from each other by the intervention of the supraoccipital, whereas in all scomberoidine genera, they are broadly united along the midline of the cranium beneath the supraoccipital. The internally united epitotics are regarded as the derived state of this character for the carangids since no outgroup families share united epitotics.

(6) Detached or semidetached finlets. *Scomberoides*, *Oligoplites* and *Megalaspis* differ from the remaining carangid genera in having the soft dorsal and anal fins consisting posteriorly of detached or semidetached finlets. The first two genera share semidetached finlets and the last possesses completely detached finlets. Since no outgroup families share such a series of detached or semidetached finlets, their presence in the soft dorsal and anal fins is considered to be the derived state of this character for the carangids.

(7) Postcoracoid process (Fig. 7). Among the carangid genera, the postcoracoid process is well developed in the naucratine genera and *Parona*

(Smith-Vaniz and Staiger, 1973: fig. 25a), but it is not well developed in the remaining genera. In the outgroup families, the postcoracoid process is well developed in the Rachycentridae, but it is not in the other three families. The well-developed postcoracoid process (Fig. 7A) is thus interpreted as the derived state of this character for the carangids.

(8) Scutes. Of all members of Pisces, the carangine genera are peculiar in that some scales on the lateral line at least at the caudal peduncle are modified into thickened scutes. The presence of such external bones on the lateral line may represent one of the important characteristics for the Carangidae as the derived state because scutes are entirely absent from the outgroup families as well as the other carangid genera.

(9) Inferior vertebral foramina. The vertebral foramina of Starks (1911) are located at the bases of posterior parapophyses and/or haemal arches in all carangine genera and *Lichia*, whereas they are entirely absent in the remaining carangid genera. The foramina variously develop as scutes do according to the carangine genera and species, and distribution of the foramina may be in correlation with that of scutes at least among species of *Decapterus* (Gushiken, 1976). Since no outgroup families share inferior vertebral foramina, the presence of these foramina is apparently considered as the derived state for the carangids.

(10) Fleshy keel. The lateral line is developed at least in adults into a fleshy keel on each side of the caudal peduncle in *Naucrates*, *Seriola* and *Seriolina*, whereas it is not developed in the remaining carangid genera. There is no fleshy keel on the lateral line in the outgroup families. The presence of the fleshy keel on the lateral line is thus considered as the derived state for the carangids.

(11) Origin of soft dorsal fin. The soft dorsal fin usually originates far behind the pectoral fin base in the carangids, but *Parastromateus* is peculiar in having the soft dorsal fin originating above the pectoral fin base. In the outgroup families, the soft dorsal fin originates above eyes in the Coryphaenidae, but it does so far behind the pectoral fin base in the other three families. Therefore, the soft dorsal fin originating above the pectoral fin base is regarded as the derived state for the carangids.

(12) Pharyngeal teeth (Fig. 5). The pharyngeal teeth of the carangids are morphologically clas-

sified into three types. The 1st type is found in the scomberoidine and naucratine genera, *Lichia* and *Parastromateus*, and their pharyngeal teeth are uniformly villiform and none of them are enlarged, although those in *Parastromateus* are somewhat elongated (Fig. 5B). In the 2nd type represented by all carangine genera except *Parastromateus*, the pharyngeal teeth are not uniform and are locally enlarged into blunt conical or molariform teeth. *Trachinotus baillonii* possesses the 2nd type teeth, but the teeth of *T. blochii* are almost disappearing (Fig. 5I) and belong to the 3rd type. In the outgroup families, the pharyngeal teeth are locally sharpened in the Coryphaenidae, but they are uniformly villiform in the other three families, which fall under the 1st type of the carangid teeth. The 2nd (Fig. 5C–G) and 3rd types are thus regarded as the derived state for the carangids.

(13) Subocular process (Fig. 3). All carangid genera except *Oligoplites* share the subocular shelf. In *Seriola*, *Seriolina*, and the carangine genera exclusive of *Parastromateus*, the subocular shelf accompanies the subocular process extending posteriorly out of the lamellar part of the shelf, but there is no trace of such a process in the remaining carangid genera. Different from Suzuki's (1962) observation, I recognized that the subocular process is present in *Uraspis* and *Gnathanodon*. In the outgroup families, the echeneoids lack the subocular shelf, and the Nematistiidae possesses the shelf but lacks the subocular process as in other percoid fishes which share the subocular shelf. Since the subocular process is a developmental character found uniquely among carangids, it is interpreted that those fishes which do not have the subocular shelf have lost it without developing the process and that the presence of the process (Fig. 3A, C–G) is the derived state for the carangids.

(14) Premaxillary articular process (Fig. 4). Among the carangid genera, the premaxillary articular process is well developed and is subequal in height or higher than the premaxillary ascending process in *Trachurus*, *Decapterus*, *Selar*, *Atule*, *Selaroides*, *Pantolabus*, *Alepes*, *Pseudocaranx*, *Kaiwarinus*, *Hemicaranx*, and *Chloroscombrus*, but it is distinctly lower than the premaxillary ascending process in the remaining genera. Among the outgroup families, the articular process is entirely absent from the Echeneididae and is much

lower than the ascending process in the other three families. The well-developed articular process (Fig. 4C, D, G) is thus regarded as the derived state for the carangids.

(15) Ventral aspect of parasphenoid (Fig. 2). The ventral aspect of the parasphenoid is either flattened or keeled immediately behind the vomer in the carangids. In *Parastromateus*, *Uraspis*, *Caranx*, *Gnathanodon*, *Carangoides*, *Carangichthys*, *Atropus*, *Ulua*, *Alectis*, and *Selene*, it is keeled, whereas it is not in the remaining genera. *Trachinotus* alone has both states. Among the outgroup families, it is keeled in the Coryphaenidae and is not in the other three families. The keeled parasphenoid (Fig. 2B, E, F) is thus regarded as the derived state for the carangids.

(16) Premaxillary teeth. In the carangids, the dentition on the upper jaw is classified into three types. The 1st type is found in *Selaroides*, *Gnathanodon*, and some species of *Decapterus*, and the teeth are entirely absent on the upper jaw. In the 2nd type, as represented by *Parastromateus*, *Trachurus*, *Selar*, *Atule*, *Pantolabus*, *Alepes*, *Hemicaranx*, and the other species of *Decapterus*, the teeth are minute or small and are arranged in a single row. In the 3rd type comprising the remaining genera, the teeth are villiform, forming a band or rows. Some genera (e.g., *Campogramma*, *Megalaspis*, *Caranx*) have an outer row of rather strong teeth and an inner band of small teeth, but they are essentially the same as above in the arrangement of teeth. The adults of *Pseudocaranx* and *Uraspis* have teeth moderately enlarged and arranged in a single row, but they are included in the 3rd type because an inner band of small teeth is found in the young. In contrast, some genera (e.g., *Selar*, *Atule*) with uniserial small teeth often have crowded teeth anteriorly, but they are comprised in the 2nd type because no inner band of smaller teeth is found even in the young. In the outgroup families, the Coryphaenidae has uniserial sharp teeth and anteriorly crowded teeth, but in the other three families, their teeth are villiform on a broad band. It is therefore interpreted that the 1st and 2nd types are the derived state for the carangids.

(17) Adipose eyelids. Among the carangid genera, the adipose eyelids are well or moderately developed in *Lichia*, *Megalaspis*, *Trachurus*, *Selar*, *Atule*, *Selaroides*, *Pantolabus*, *Alepes*, and *Caranx*, whereas they are poorly developed in the remaining

genera. Since the adipose eyelids are poorly developed in the outgroup families, the well or moderately developed eyelids are considered to be the derived state for the carangids.

(18) Interpelvic keel (Fig. 10). The interpelvic keel of Suzuki (1962) is scarcely developed in *Parona*, *Trachurus*, *Decapterus*, *Selar*, *Atule*, *Selaroides*, *Pseudocaranx*, and *Kaiwarinus*, but it is more or less developed in the remaining carangid genera. Among the outgroup families, the keel is absent from the Echeneididae, but it is developed in the other three families. Loss of the interpelvic keel is thus considered to be the derived state for the carangids.

(19) Premaxillary ascending process (Fig. 4). The ascending process is usually higher than the premaxillary articular process in the percoid fishes when both processes are developed. However, *Trachurus*, *Decapterus* and *Selar* are peculiar in having the ascending process lower than the articular process among the carangid genera. In the outgroup families, the Echeneididae has lost the anterior processes of the premaxilla, but the other three families share an ascending process higher than the articular process. The reduced ascending process in height is thus considered to be the derived state for the carangids.

(20) Papillae on shoulder girdle margin (Smith-Vaniz, 1983: unnumbered fig.). Most carangids have the smooth shoulder girdle margin without papillae, but *Decapterus* and *Selar* are peculiar in having two papillae on the shoulder girdle margin though the lower papilla of *Selar* is noticeably enlarged. The presence of such papillae on the shoulder girdle margin is considered as the derived state for the carangids because no papillae are found on the shoulder girdle margin in the outgroup families.

(21) Posterior parapophyses. Among the carangid genera, *Uraspis* is unique in that three posterior parapophyses and two anterior haemal spines are very thick and heavy. The heavy posterior parapophyses are considered to be the derived state for the carangids since parapophyses are not developed in the Coryphaenidae and are not heavy in the other three outgroup families.

(22) Ectopterygoid (Fig. 6). In *Caranx*, *Gnathanodon*, *Carangichthys*, *Carangoides*, *Atropus*, *Ulua*, *Alectis* and *Selene*, the ectopterygoid is protruded forward by forming an acuminate point or short process at the antero-dorsal end, whereas in the

remaining carangid genera, it is neither protruded nor pointed. In the outgroup families, the ectopterygoid is antero-dorsally neither protruded nor pointed as in most families of the percoid fishes, although the Echeneididae have the greatly modified ectopterygoid. Therefore, the antero-dorsally protruded or pointed ectopterygoid (Fig. 6D, E) is regarded as the derived state for the carangids.

(23) Endopterygoid (Fig. 6). Among the carangid genera, the endopterygoid is reduced to a small and triangular lamella in *Caranx* and *Gnathanodon*, whereas it is large and oval-shaped in the remaining genera. In the outgroup families, the Echeneididae have lost the endopterygoid, but the other three families share a large and oval-shaped endopterygoid which is subequal in length or longer than the metapterygoid. The reduced size of the endopterygoid is thus considered to be the derived state for the carangids.

(24) Lachrymal (Fig. 3). The lachrymal of the carangids is always larger than the other infraorbitals and is variously shaped according to the genera. Specially, *Alectis* and *Selene* differ from the remaining carangid genera in having a deep lachrymal whose depth is greater than its length. In the outgroup families, the Nematistidae possesses a moderately deep lachrymal, but the depth of the bone is still shallower than its length. The three echeneoid families share a rather elongate lachrymal. Therefore, the deep lachrymal (Fig. 3F) is apparently considered to be the derived state for the carangids.

(25) Internal shelf of cleithrum (Fig. 7). The lower half of the cleithrum is usually composed of two shelves, external and internal, which meet each other to form an anterior ridge of the shoulder girdle. In most carangid genera, the rear of the internal shelf is well expanded, meeting the equally or less expanded coracoid at the middle portion of the girdle. In *Alectis* and *Selene*, however, it is distinctly narrow and is less expanded than the coracoid. In the outgroup families that characteristic is not found. Specially, the three families other than the Coryphaenidae share the rod-like coracoid at the lower half. The narrow internal shelf of the cleithrum (Fig. 7F) is thus considered as the derived state for the carangids.

Phylogeny and discussion

Since the phylogenetic relationships among

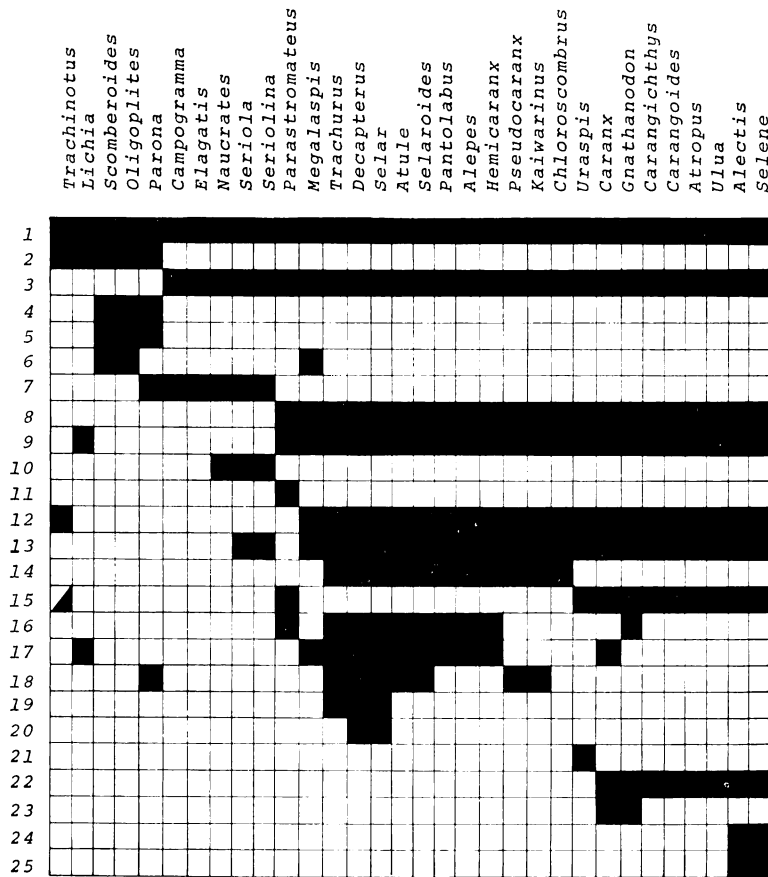


Fig. 11. Data set of twenty-five characters. Open parts are primitive states; solid ones are derived; combined ones indicate that both states occur in a given taxon. 1, gap between last two anal spines; 2, pleural ribs; 3, adductor mandibular muscle A1' division; 4, upper jaw; 5, epiotics; 6, detached or semidetached finlets; 7, postcoracoid process; 8, scutes; 9, inferior vertebral foramina; 10, fleshy keel; 11, origin of soft dorsal fin; 12, pharyngeal teeth; 13, subocular process; 14, premaxillary articular process; 15, ventral aspect of parasphenoid; 16, premaxillary teeth; 17, adipose eyelids; 18, interpelvic keel; 19, premaxillary ascending process; 20, papillae on shoulder girdle margin; 21, posterior parapophyses; 22, ectopterygoid; 23, endopterygoid; 24, lachrymal; 25, internal shelf of cleithrum.

major groups in the Carangidae were treated by Smith-Vaniz (1984), my first attempt began with corroborating his hypothesized relationships by utilizing character polarities discussed in the preceding chapter. Results were summarized in a data set of Fig. 11 and a cladogram of Fig. 12A.

As elucidated by Smith-Vaniz, the monophyly of the family is corroborated by a synapomorphy—the gap between the last two anal spines is relatively wide (1). The family can be divided into two monophyletic groups. One group consists of the trachinotine and scomberoidine genera. Its monophyly is supported by a synapomorphy—most

pleural ribs are attached directly to vertebral centra (2). Another group includes the naucratine and carangine genera. Its monophyly is supported by a synapomorphy—the adductor mandibular muscle A1' division is present (3). The character states (1, 3) are autapomorphic, but the state (2) occurs in an outgroup family. Compared with the naucratine and carangine groups, the trachinotine and scomberoidine groups share many specialized features in the sense of the general evolutionary trends: toothless 3rd epibranchial; one or more actinosts on coracoid; 1st anal pterygiophore strongly attached to 1st haemal

spine; ultimate dorsal pterygiophore composed of two segments. However, polarities for these characters were assessed as equivocal in the present study. In fact, no synapomorphies had been presented to unite the latter two groups in the past.

In the trachinotine and scomberoidine group, the scomberoidine genera are separable as a monophyletic group from the trachinotine genera in having two synapomorphies—the upper jaw is non-protractile (4); epiotics are internally united (5). The former state occurs in an outgroup family and the latter state is autapomorphic. Furthermore, two genera *Scomberoides-Oligoplites* are separable as monophyletic from *Parona* in having a synapomorphy—detached or semidetached finlets are present (6). This character state occurs in *Megalaspis*, which is most parsimoniously interpreted as parallelism. In addition to this character, Smith-Vaniz showed many synapomorphies to unite both genera as: spines of dorsal and anal fins with well-developed venom glands; juveniles with two widely spaced rows of teeth; etc., although polarities for a few characters (e.g., reduction in number of epurals from 3 to 2) were assessed as equivocal. As for two genera *Trachinotus* and *Lichia* in the Trachinotini, no evidences were found to support the monophyly of both genera although they share a non-assessed derived character (supramaxilla minute or absent). However, I included them in the Trachinotini as did Smith-Vaniz in order to avoid further confusion at the current level of analysis. *Trachinotus* has an autapomorphy—a pair of large lateral processes are on the ventral surface of the basioccipital, and *Lichia* also has an autapomorphy—the lateral line is irregularly curved. It is therefore obliged to interpret that the three taxa, *Trachinotus*, *Lichia* and the scomberoidine genera, have a trichotomous relationship from the present data set.

The naucratine and carangine group can be divided into two monophyletic groups. One group comprises the naucratine genera and its monophyly is supported by a synapomorphy—the postcoracoid process is well developed (7). This character state occurs in *Parona* in addition to an outgroup family, which is most parsimoniously interpreted as parallelism. Smith-Vaniz suggested the monophyly of this group based on a non-assessed derived character—caudal peduncle grooves are present. However, polarity for this character is actually equivocal because the pre-

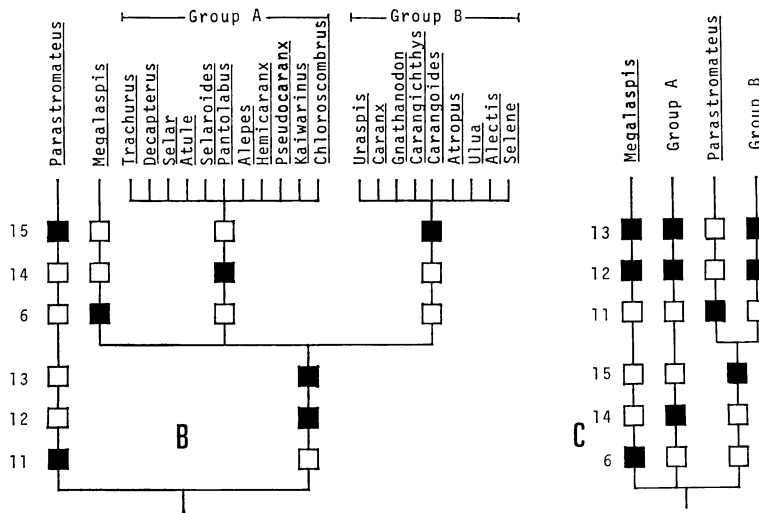
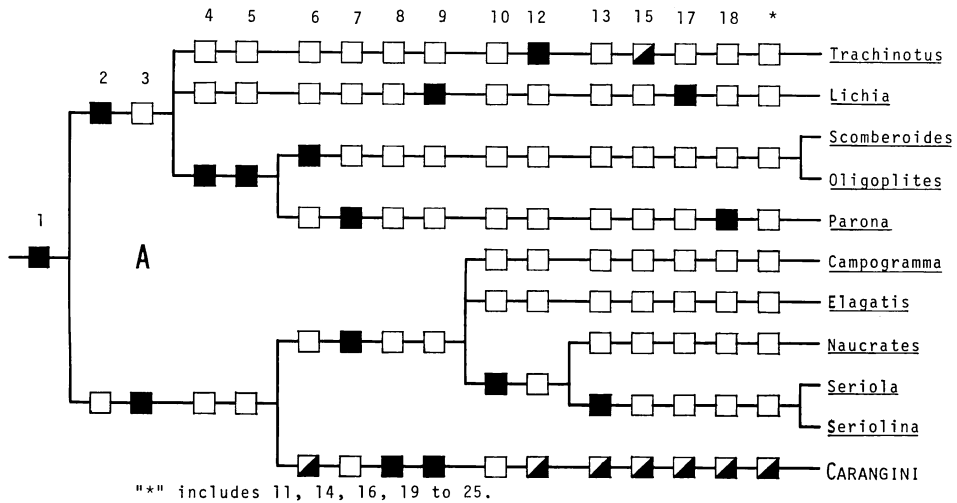
sence of caudal peduncle grooves characterizes the second outgroup family and another state characterizes the first outgroup families. Among five naucratine genera, three genera *Naucrates-Seriola-Seriolina* are separable as a monophyletic group from *Campogramma* and *Elagatis* in having an autapomorphy—a fleshy keel is developed on the lateral line of the caudal peduncle (10). Furthermore, two genera *Seriola-Seriolina* are separable as monophyletic from *Naucrates* in having a synapomorphy—the subocular process is more or less developed (13). This character state occurs in a taxon composed of twenty-one genera in the Carangini as shown afterwards, which is most parsimoniously interpreted as parallelism. *Campogramma* and *Elagatis* are differentiated from the other naucratine genera in having a synapomorphy, respectively—the breast is naked and a two-rayed finlet is present. However, relationships among the above taxon of three genera, *Campogramma* and *Elagatis* were left unresolved for lack of information. Another group comprises all carangine genera and its monophyly is supported by two synapomorphies—scutes are present (8); inferior vertebral foramina are present (9). The former character state is autapomorphic, but the occurrence of the latter state on *Lichia* is most parsimoniously interpreted as parallelism.

The Carangini is a large monophyletic taxon consisting of twenty-two genera. In deducing relationships among these genera, a second attempt was made through the analysis of six characters (6, 11 to 15) in a data set of Fig. 11 and was summarized in the most parsimonious cladogram of Fig. 12B. It is first feasible to accept a sister group relationship between *Parastromateus* and the remaining twenty-one genera. Inclusion of *Parastromateus* in the Carangini was corroborated by Smith-Vaniz based on autapomorphies: relatively wide gap between the last two anal spines (1), presence of the adductor mandibular muscle A1' division (3), and development of scutes (8). Loss of pelvic fins characteristic of this genus is also found in *Parona*. The monophyly of *Parastromateus* is supported by a synapomorphy—the soft dorsal fin originates above the pectoral fin base (11)—which occurs in an outgroup family. In addition, this genus differs from the other carangine genera in having indistinct sensory canals on the lachrymal, enlarged third and fourth upper pharyngeals, and smaller coracoid at the lower

half. As the sister group of *Parastromateus*, the monophyly of the remaining twenty-one genera is supported by two synapomorphies—pharyngeal teeth are not uniformly villiform (12); the subocular process is more or less developed (13). The former state occurs in *Trachinotus* and the latter state is on *Seriola-Seriolina*, which are most parsimoniously interpreted as parallelism.

The carangine genera except *Parastromateus* were divided into three groups. The first group consists of a single genus *Megalaspis* and its monophyly is supported by synapomorphies: stout and enlarged scutes; flattened posterior neural and haemal spines; detached or semidetached finlets (6). The last character state occurs on *Scm-*

beroides-Oligoplites, which is most parsimoniously interpreted as parallelism. The second group comprises eleven genera *Trachurus-Decapterus-Selar-Atule - Selaroides - Pantolabus-Alepes - Hemicarax-Pseudocaranx - Kaiwarinus - Chloroscombrus* (here referred to as the “Group A”) and the monophyly of this group is supported by an autapomorphy—the premaxillary articular process is well developed (14). The third group includes nine genera *Uraspis-Caranx-Gnathanodon-Carangichthys-Carangoides-Atropus-Ulua - Alectis - Selene* (here referred to as the “Group B”) and the monophyly of this group is supported by a synapomorphy—the parasphenoid is ventrally keeled (15). This character state occurs in *Parastromateus*,



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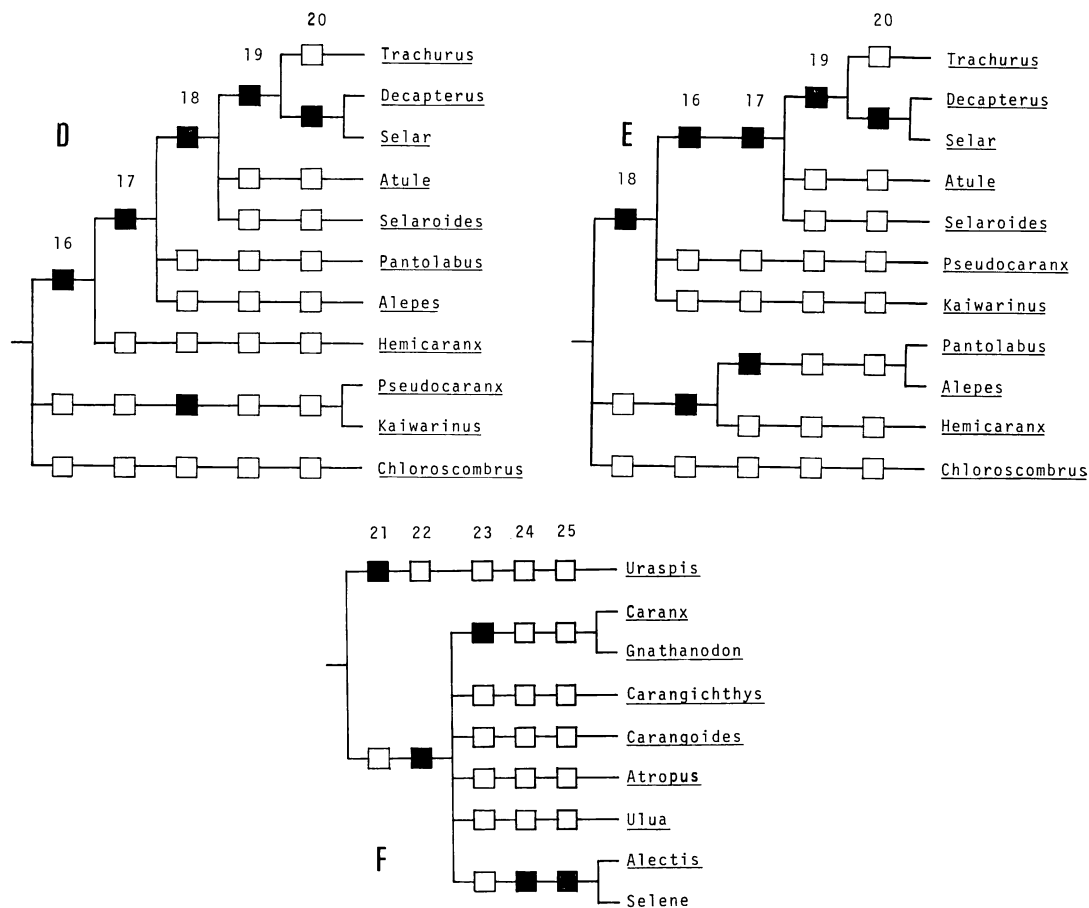


Fig. 12. A: The most parsimonious cladogram of main groups in the Carangidae. B: The most parsimonious cladogram of main groups in the Carangini. C: A less parsimonious cladogram of main groups in the Carangini. D: The most parsimonious cladogram of eleven genera in Group A. E: A less parsimonious cladogram of eleven genera in Group A. F: The most parsimonious cladogram of nine genera in Group B.

some species of *Trachinotus* and an outgroup family, which is most parsimoniously interpreted as parallelism. In fact, more parallelisms generate in a less parsimonious cladogram of Fig. 12C established from the same data set. Since no evidences were found to unite each two groups among the above three groups, it appears that this trichotomy is hypothesized in a major subdivision of the Carangini.

The eleven genera of Group A are a complicate assemblage as shown in mosaic occurrence of non-assessed derived characters: superior portion of ethmoid not protruding beyond frontals; fronto-supraoccipital crest reduced in depth; exoccipital condyles apart from each other; myodome

closed; loss of unossified area at junction of pterotic, epiotic and parietal. However, polarities for these characters were assessed as equivocal, and I could select only five characters (16 to 20) for the analysis of this group. Results were summarized in the most parsimonious cladogram of Fig. 12D. Fig. 12E shows a less parsimonious cladogram generated from the analysis of the same five characters above.

This assemblage can be divided into three monophyletic groups. The first group is composed of a single genus *Chloroscombrus*. This genus differs from the remaining genera of Group A in having 6 to 12 weak scutes only on the caudal peduncle, the anal fin base subequal in length to

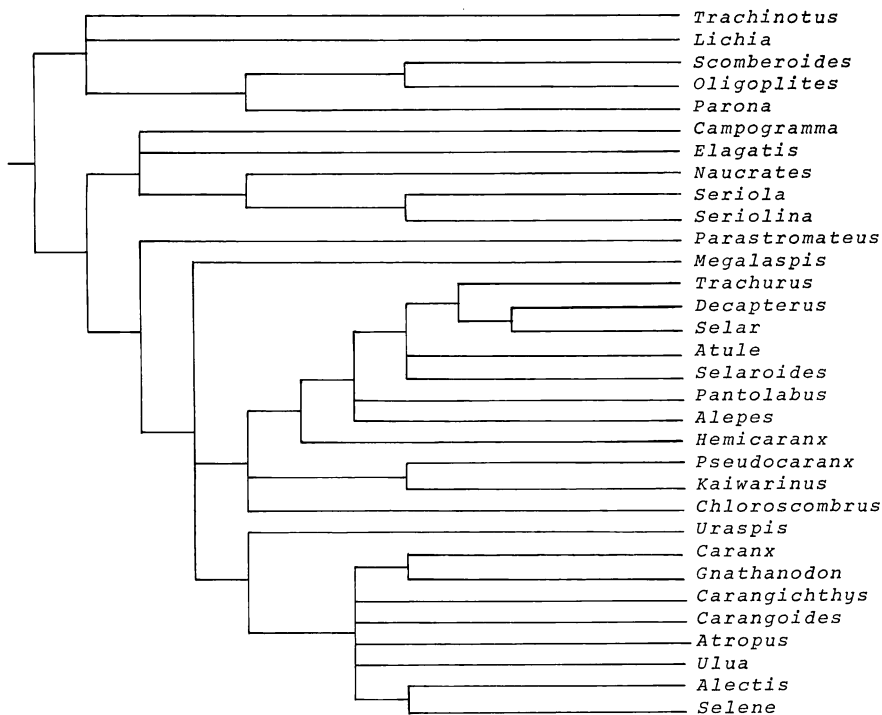


Fig. 13. A presumable phylogenetic tree of the carangid genera. Stem lengths imply no special significance.

the soft dorsal fin base, and a black saddle spot on the upper part of the caudal peduncle. The second group comprises two genera *Pseudocaranx-Kaiwarinus* and its monophyly is supported by a synapomorphy—the interpelvic keel is absent (18). This character state occurs in *Parona* and a taxon of five genera within Group A as shown below, which is most parsimoniously interpreted as parallelism. The third group includes eight genera *Trachurus-Decapterus-Selar-Atule-Selaroides-Pantolabus-Alepes-Hemicaranx* and its monophyly is supported by a synapomorphy—premaxillary teeth are absent or, if present, small on a single row (16). This character state occurs in *Parastromateus* and *Gnathanodon*, which is most parsimoniously interpreted as parallelism.

Among the eight genera above, seven genera *Trachurus - Decapterus - Selar - Atule - Selaroides-Pantolabus-Alepes* were separable as a monophyletic group from *Hemicaranx* by having a synapomorphy—adipose eyelids are well or moderately developed (17). This character state occurs in *Lichia*, *Megalaspis* and *Caranx*, which is most parsimoniously interpreted as parallelism. *Hemicaranx* differs from the remaining genera of Group

A in having 7 spines vs. 8 in the spinous dorsal fin. Among the seven genera above, five genera *Trachurus-Decapterus-Selar-Atule-Selaroides* are separable as monophyletic from *Pantolabus* and *Alepes* by having a synapomorphy—the interpelvic keel is absent (18). This character state occurs in *Lichia* and *Pseudocaranx-Kaiwarinus*, which is most parsimoniously interpreted as parallelism. Relationships among the above taxon of five genera, *Pantolabus* and *Alepes* remained to be resolved. Furthermore, three genera *Trachurus-Decapterus-Selar* are separable as monophyletic from *Atule* and *Selaroides* by having a synapomorphy—the premaxillary ascending process is reduced in height (19)—which occurs in an outgroup family. Relationships among the above taxon of three genera, *Atule* and *Selaroides* remained to be resolved. Two genera *Decapterus-Selar* are separable as monophyletic from *Trachurus* in having an autapomorphy—two papillae are present on the shoulder girdle margin (20).

The nine genera in Group B are characterized by having a deep, compressed body and their analyses are summarized in a cladogram of Fig. 12F. One of the most noticeable characters found in this

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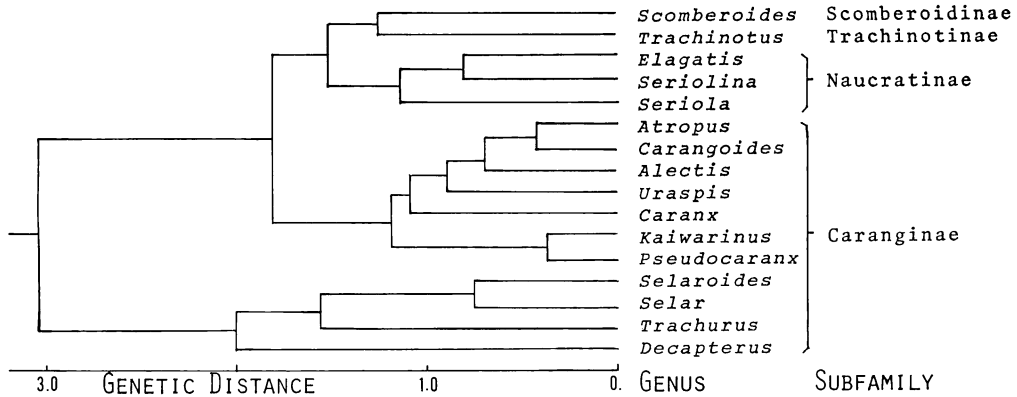


Fig. 14. The genetic relationship among genera in the Carangidae (Kijima et al., 1986).

group is an autapomorphy—the ectopterygoid is more or less protruded forward at the antero-dorsal end (22)—which supports the monophyly of eight genera except *Uraspis*. *Uraspis* has an autapomorphy—posterior parapophyses are very heavy (21). Then it was corroborated that *Uraspis* is the sister group of the remaining eight genera. Among the eight genera above, there were found two monophyletic groups. One group is composed of two genera *Caranx-Gnathanodon* and its monophyly is supported by a synapomorphy—the endopterygoid is considerably reduced in size (23). This character state occurs in an outgroup family. Another group includes two genera *Alectis-Selene* and its monophyly is supported by two autapomorphies—the lachrymal is very deep (24); the internal shelf of the cleithrum is very narrow (25). Although the latter two genera share a tall body and tall elements, *Selene* possesses many autapomorphies: descending exoccipital lamella; subocular shelf composed only of subocular process; 2nd infraorbital attached to dorso-posterior corner of lachrymal. However, it was difficult to find evidences to resolve relationships among the above two taxa and the remaining four genera. *Carangichthys* is peculiar among the carangids in having teeth on the ectopterygoid besides an autapomorphy—small bloches are found on the back between the bases of the dorsal fin rays. *Atropus* and *Ulua* have also their own autapomorphy, respectively: belly with a deep median groove and extremely long gillrakers. However, *Carangoides* composed of as many as about twenty species is a poorly defined group which lacks autapomorphies and may be separated into several subunits

worthy of recognition.

Fig. 13 summarizes phylogenetic relationships consequently hypothesized in the present study. Although the present analysis has left many problems unresolved, it represents an initial hypothesis on the relationships among all known carangid genera and suggests at least four major monophyletic groups in the Carangini as stated in the abstract. When more characters are found and more precise analyses are taken, new hypotheses on the relationships will be formulated.

Other approaches to generic relationships

Three approaches to carangid relationships were presented at the Second International Conference on Indo-Pacific Fishes held in Tokyo in 1985.

Kijima et al. (1986) discussed genetic relationships in the family based on genetic distances which were estimated by examining the electrophoretic patterns of specific proteins. Kijima et al. examined sixteen carangid genera and divided them into two major groups, fusiformed (*Decapterus-Trachurus-Selar-Selaroides*) and compressiformed (*Pseudocaranx-Kaiwarinus-Caranx-Uraspis-Alectis-Carangoides-Atropus-Seriola-Seriolina-Elagatis-Trachinotus-Scomberoides*), by drawing a dendrogram (Fig. 14) according to the UPGMA (Sneath and Sokal, 1973). It represents a phenetic relationship among them, but the most significant result is that the compressiformed genera in the Caranginae are nearer to the compressiformed genera in the other carangid subfamilies than to the fusiformed genera in the Caranginae. Kijima et al.

elucidated it in detail and inferred that application of the method may be practically limited to levels lower than genera in the same subfamily.

Iwamizu and Itazawa (1986) studied the arrangement of lateral musculature and vascular supplies in eleven carangid genera and found that modifications of these elements correlate to body size and form, and divided them into four groups based on the level of the modification as: (group 1) *Kaiwarinus-Uraspis-Carangoides* with a small and compressed body have the basic body plan in muscular and vascular segmentation; (group 2) *Trachurus-Selar-Decapterus* with a small and fusiformed body have the segmental blood vessels partially double-tracked; (group 3) *Gnathanodon-Caranx-Alectis* with a large and compressed body have the lateral periphery of each myomere subdivided by a collagenous septum in addition to the modified vasculature; (group 4) *Seriola-Elagatis* with a large and fusiformed body have the vascular arrangement completely double-patterned and the myomere subdivided into four sheets. Iwamizu and Itazawa elucidate that carangids have increased the numbers of muscular and vascular elements without increasing the number of vertebrae and the modifications in the body plan are adaptive characteristics for increase in swimming activity and body size.

In the abstract, Mok (1986) presented a hypothesis regarding cladistic relationships among twenty-two carangid genera based on myological and osteological characters and classified them into six groups: (group 1) *Trachurus-Decapterus-Selar*; (group 2) *Atule-Alepes-Megalaspis*; (group 3) *Chloroscombrus-Selene-Gnathanodon-Parastromateus-Ulua*; (group 4) *Selaroides-Alectis-Atropus-Uraspis-Caranx-Carangoides*; (group 5) *Seriola-Seriolina* and *Elagatis-Naucrates*; (group 6) Scomberoidini.

When reviewing their hypotheses specially based on the relationships among carangine genera, it is scarcely possible to find an agreement among them except the hypothesis for a group *Trachurus-Decapterus-Selar*, that is the group Suzuki (1962) regarded as the highly specialized. Because of varied methods, however, it is not unreasonable that their results differ from each other and from those of mine.

As for the systematic positions of *Pseudocaranx* and *Kaiwarinus* in the compressiformed carangine genera, the dendrogram of Kijima et al. (1986)

shows that they are more closely related to the other compressiformed carangine genera than to the fusiformed carangine genera. In the present analysis, however, they resemble the fusiformed and differ from the other compressiformed in having the parasphenoid ventrally not keeled (1), the premaxillary articular process well developed (2) and loss of the interpelvic keel (3). My out-group comparison indicates that the condition (1) is a primitive state and the conditions (2, 3) are derived states. Therefore, it is interpreted that the latter conditions (2, 3) are synapomorphies supporting the monophyly of the fusiformed+*Pseudocaranx*+*Kaiwarinus* and is suggested consequently that *Pseudocaranx* and *Kaiwarinus* are more closely related to the fusiformed carangine genera than to the other compressiformed carangine genera.

Iwamizu and Itazawa (1986) presented interesting evidences for the muscular and vascular modifications of carangids. Their group 2, *Trachurus-Selar-Decapterus*, belongs to my carangine Group A (Fig. 12B) and their group 3, *Gnathanodon-Caranx-Alectis*, falls under my Group B. Their group 1, *Kaiwarinus-Uraspis-Carangoides*, is related to my Group A and Group B. Since their group 1 possesses the basic body plan in muscular and vascular arrangement, it may be interpreted that in my Group A modifications have occurred from the types of the group 1 to those of the group 2, and in my Group B modifications are from the types of the group 1 to those of the group 3.

Mok (1986) suggested *Parastromateus* might be a close relative of *Gnathanodon* and recognized at least four monophyletic groups in the Carangini. I would like to reserve my opinion because I have not received his publication.

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Literature cited

- Gushiken, S. 1976. Revision of the genus *Decapterus* Bleeker of Japan. Biol. Mag. Okinawa, 14: 41-54.
- Gushiken, S. 1983. Revision of the carangid fishes of Japan. Galaxea, Publ. Sesoko Mar. Sci. Cent. Univ. Ryukyus, 2: 135-364.
- Hennig, W. 1966. Phylogenetic systematics. Univ. of Illinois Press, Urbana, xv+263 pp.
- Iwamizu, M. and Y. Itazawa. 1986. Modification of muscular and vascular plan in carangids for increase in size and activity. Pages 555-560 in T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura, eds. Indo-Pacific fish biology: Proc. of the 2nd International Conference on Indo-Pacific Fishes. Ichthyological Soc. of Japan, Tokyo.
- Johnson, G. D. 1984. Percoidae: development and relationships. Pages 464-498 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ichthyol. Herpetol., Spec. Publ. 1.
- Kijima, A., N. Taniguchi and A. Ochiai. 1986. Genetic relationships in the family Carangidae. Pages 840-848 in T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura, eds. Indo-Pacific fish biology: Proc. of the 2nd International Conference on Indo-Pacific Fishes. Ichthyological Soc. of Japan, Tokyo.
- Laroche, W. A., W. F. Smith-Vaniz and S. L. Richardson. 1984. Carangidae: development. Pages 510-522 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ichthyol. Herpetol., Spec. Publ. 1.
- Maddison, W. P., M. J. Donoghue and D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool., 33 (1): 83-103.
- Mok, H. K. 1986. Myology, osteology and phylogeny of carangid fishes. Pages 950-951 in T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura, eds. Indo-Pacific fish biology: Proc. of the 2nd International Conference on Indo-Pacific Fishes. Ichthyological Soc. of Japan, Tokyo. (Abstract.)
- Nelson, G. J. 1970. Outline of a theory of comparative biology. Syst. Zool., 19 (4): 373-384.
- Rosenblatt, R. H. and M. A. Bell. 1976. Osteology and relationships of the rooster fish, *Nematistius pectoralis* Gill. Contr. Sci., Nat. Hist. Mus. Los Angeles County, (279): 1-23.
- Smith-Vaniz, W. F. 1983. Carangidae. In W. Fischer and G. Bianchi, eds. FAO species identification sheets for fishery purposes. Western Indian Ocean (Fishing Area 51). FAO, Rome.
- Smith-Vaniz, W. F. 1984. Carangidae: relationships. Pages 522-530 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ichthyol. Herpetol., Spec. Publ. 1.
- Smith-Vaniz, W. F. and J. C. Staiger. 1973. Comparative revision of *Scomberoides*, *Oligoplites*, *Parona*, and *Hypacanthus* with comments on the phylogenetic position of *Campogramma* (Pisces: Carangidae). Proc. Calif. Acad. Sci., 39: 185-256.
- Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco, xv+573 pp.
- Starks, E. C. 1911. The osteology and relationships of the fishes belonging to the family Carangidae. Leland Stanford Jr. Univ. Publ. Univ. Ser., 5: 27-49.
- Suzuki, K. 1962. Anatomical and taxonomical studies on the carangid fishes of Japan. Rep. Fac. Fish. Pref. Univ. Mie, 4 (2): 43-232.

(Matsuyama 1-1-1, Naha 900, Japan)

アジ科の属の系統的關係

具志堅宗弘

主として骨格系に基づき、分岐分類学の手法によってアジ科全32属の系統的關係を推論した。Echeneoidsを1st outgroup, Nematistiidaeを2nd outgroupとして極性を推定し、派生形質共有と節減の原則に従って分岐図を構築した。その結果、アジ族では *Parastromateus* を残りの21属のsister groupとし、これを更に3つの系群1. *Megalaspis*, 2. *Trachurus-Decapterus-Selar-Atule-Selaroides-Pantolabus-Alepes-Hemicaranx-Pseudocaranx-Kaiwarinus-Chloroscombrus*, 3. *Uraspis-Caranx-Gnathanodon-Carangichthys-Carangoides-Atropus-Ulua-Alectis-Selene* に位置づける体系を提唱した。

(900 那覇市松山 1-1-1)