

**COMPARATIVE OSTEOLOGY AND PHYLOGENETIC RELATIONSHIPS  
OF THE DRAGONETS (PISCES: CALLIONYMIDAE)  
WITH SOME THOUGHTS OF THEIR EVOLUTIONARY  
HISTORY**

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*With Text-figures 1-62 and Tables 1-12*

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**Abstract**

Phylogenetic relationships among the callionymid genera are discussed by comparative osteology. The thirty-one osteological characters of eleven parts of the body are used. As the result, two main groups of the dragonets are proposed; *Callionymus*-stem and *Calliurichthys*-stem. The evolutionary history is also discussed on the basis of the results gained by comparative osteology, habitats and geographic distributions.

**Introduction**

A very few studies of phylogenetic relationships among the callionymid genera have been done. We can find a few works of it by Matsubara (1963) and Fricke (1980), which are very insufficient because the estimations are made by a few characters, and the generic classification has not been done adequately. Therefore, in the present study, I proposed the phylogenetic relationships among the callionymid genera discussed in detail on the basis of the comparative osteology.

The fishes of the Callionymidae were classified into 19 genera and 139 species (Nakabo, 1982). Then, on the basis of the new classification, the present study is intended to show the phylogenetic relationships among the genera which are estimated by the examination of the following parts; cranium, lacrimal, jaws, hyoid arch, branchial apparatus, suspensolium, shoulder girdle, pelvic girdle, vertebral column and dorsal and anal fins.

An evolutionary history (center of dispersal, process of differentiation and dispersion) of the callionymid genera are discussed on the bases of the phylogenetic relationships, habitats and geographic distributions both of which are described by Nakabo (1982).

**Materials and Methods**

The specimens used in the study are the following.

The specimens dissected and stained: *Callionymus lya*, FAKU 49863, 49864, 2 males, 136.3-136.9 mm in standard length, south North Sea; *C. maculatus*, FAKU 49867, a male, 101.5 mm, 51°27'N, 10°9'W; *Bathycallionymus kaianus*, FAKU 48701, a male, 114.9 mm, Mimase, Kochi Pref.; *B. sokonumeri*,

FAKU 49412, a male, 98.5 mm, Mimase, Kochi Pref.; *B. formosanus*, FAKU 49417, a female, 114.5 mm, Mimase, Kochi Pref.; *B. regani*, FAKU 49980, a female, 139.8 mm, Saya de Malha Bank; *Foetorepus altivelis*, FAKU 48855, 49353, 49356, 2 males and a female, 75.2–158.9 mm, Mimase, Kochi Pref.; *F. phasi*, AMI 18794–001, a male, 67.1 mm, 34°16–22'S, 151°26'E, Australia; *F. delandi*, FAKU 25516, a female, 143.4 mm, Miya, Aichi Pref.; *Eocallionymus papilio*, FAKU 49924, a male, 50.2 mm, south Australia; *Paracallionymus costatus*, RUSI 9071, a male, 38.0 mm, South Africa; *Neosynchiropus ocellatus*, FAKU 49074, a male, 70.2 mm, Japan, FAKU 50424, a male, 33.7 mm, Shirahama, Wakayama Pref.; *N. ijimai*, FAKU 48819, a male, 67.4 mm, Oki Is., Shimane Pref.; *Pterosynchiropus splendidus*, FAKU 49804, one, 33.6 mm, the Philippines; *Paradiplogrammus enneactis calliste*, FAKU 48829, 48830, 50421, 2 males and a female, 46.2–64.5 mm, Shijiki Bay, Nagasaki Pref.; *Diplogrammus xenicus*, FAKU 49698, a female, 55.5 mm, Amami Is., Kagoshima Pref., FAKU 49718, a male, 51.0 mm, Sesoko Is., Okinawa Pref.; *Orbonymus rameus*, QMI 12180 (the pectoral and pelvic girdles), a male, 123.9 mm, southeast Queensland; *Dactylopus dactylopus*, FAKU 49977, a female, 94.5 mm, the Philippines; *Calliurichthys japonicus*, FAKU 48728, a male, 105.8 mm, Mimase, Kochi Pref.; FAKU 50425, a male, 110.4 mm, Oki Is., Shimane Pref.; *C. margaretae*, FAKU 49964, a male, 81.6 mm, Palistan; *Pseudocalliurichthys variegatus*, FAKU 49558, 50426, a male and a female, 38.4–100.4 mm, Shirahama, Wakayama Pref.; *Repomucenus filamentosus*, FAKU 49876, a male, 72.0 mm, Lebanon; *R. huguenini*, FAKU 50427, 50428, 2 males and 2 females, 81.8–107.5 mm, Hamada, Shimane Pref.; *R. virgis*, FAKU 50429, 3 males, 66.2–75.1 mm, Hamada, Shimane Pref.; *R. calcaratus*, FAKU 50007, 50008, 2 females, 90.9–94.8 mm, New South Wales; *R. sp. 1*, FAKU 49973, a male, 64.0 mm, Panay Is., the Philippines; *R. belcheri*, FAKU 49937, a male, 102.8 mm, Moreton Bay, Queensland; *R. macdonaldi*, FAKU 49933, a male, 83.3 mm, Queensland; *R. planus*, FAKU 49061, 50430, a male and a female, 79.4–81.4 mm, Aoshima, Miyazaki Pref.; *R. valenciennei*, FAKU 50431–50433, 50615, a male and 3 females, 63.0–79.6 mm, Wakasa Bay, Kyoto Pref.; *R. lunatus*, FAKU 49397, a female, 93.6 mm, Mimase, Kochi Pref., FAKU 50434, 2 males and a female, 128.6–149.6 mm, Wakasa Bay, Kyoto Pref.; *R. richardsonii*, FAKU 50352, 50435–50438, 3 males and 2 females, 99.9–148.9 mm, Wakasa Bay, Kyoto Pref.; *R. beniteguri*, FAKU 50439, a female, 120.0 mm, Wakasa Bay, Kyoto Pref.; *R. ornatipinnis*, FAKU 49198, 49206, a male and a female, 88.9–95.3 mm, Mogi, Nagasaki Pref.; *R. sp. 3*, FAKU 50016, a male, 95.8 mm, Moreton Bay, Queensland; *Spinicapitichthys spiniceps*, FAKU 49978, a male, 99.7 mm, Saya de Malha Bank; *Anaora tentaculata*, MTUF 23472, a female, 26.3 mm, Ishigaki Is., Okinawa Pref.; *Eleutherochir mirabilis*, NSMT-P 10212, a female, 49.5 mm, Nishi-u, Hokkaido Pref.

The specimens observed by soft X-ray negatives: *Callionymus risso*, BM(NH) 1963.7.25.70–72, a female, 47.4 mm, Black Sea; *Minysynchiropus laddi*, USNM 141132 (paratype), a male, 22.1 mm, Bikini Atoll; *Paradiplogrammus bairdi*, USNM 178867, a female, 46.8 mm, Castle Harbor; *Diplogrammus pauciradiatus*, USNM 23799, a male, 30.6 mm, Bermuda; *Synchiropus ornatus*, ANSP 53457 (paratype), a male, 70.4 mm, Hong Kong; *Orbonymus rameus*, QMI 4012 (paratype), a female, 126.0 mm, Cape Capricone; *Eleutherochir opercularis*, YCM-SP 7600, a male, 66.3 mm, Okinawa Is.

The specimens observed in the preopercular spine: *Minysynchiropus laddi*, USNM 141132; *Paradiplogrammus enneactis calliste*, FAKU 48845, a young male, 17.9 mm, Shijiki Bay, Hirado Is., Nagasaki Pref.; *P. corallinus*, USNM 51581 (holotype), a female, 30.0 mm, Hawaii; *P. sp.*, QMI 17256, a male, 22.3 mm, Queensland; *Diplogrammus xenicus*, FAKU 49477, a young female, 15.2 mm, Shirahama, Wakayama Pref.; *D. pauciradiatus*, USNM 39366, 33.2 mm, 28°50'N, 83°00'W; *Synchiropus ornatus*, ANSP 53457; *Calliurichthys japonicus*, FAKU 50612, a young, 16.2 mm, Hamada, Shimane Pref., FAKU 50614, a young, 21.6 mm, Shijiki Bay, Hirado Is., Nagasaki Pref.; *Repomucenus huguenini*, FAKU 50609, a young, 16.6 mm, Shijiki Bay, Hirado Is., Nagasaki Pref.; *R. virgis*, FAKU 50611, a young, 15.4 mm, Hamada, Shimane Pref.; *R. valenciennei*, FAKU 50610, a young, 17.5 mm, Wakasa Bay, Kyoto Pref.; *R. richardsonii*, FAKU 50608, a young, 20.0 mm, Shijiki Bay, Hirado Is., Nagasaki Pref.; *R. beniteguri*, FAKU 50614, a young, 18.1 mm, Yokohama, Kanagawa Pref.; *Eleutherochir opercularis*, FAKU 50423, a young, 19.7 mm, Ishigaki Is., Okinawa Pref., YCM-SP 7600.

Vertebral number for each specimen was counted from soft X-ray negative; the specimens examined are the same as those in Nakabo (1982).

The abbreviations for museum and institutional collections mentioned above: AM (Australian Museum, Sydney); ANSP (Academy of Natural Sciences, Philadelphia); BM (NH) (British Museum (Natural History), London); FAKU (Department of Fisheries, Faculty of Agriculture, Kyoto

University); MTUF (Museum, Tokyo University of Fisheries); NSMT (Department of Zoology, National Science Museum, Tokyo); QM (Queensland Museum, Brisbane); RUSI (Rhodes University, J.L.B. Smith Institute of Ichthyology, Grahamstown); USNM (National Museum of Natural History, Smithsonian Institution, Washington D.C.); YCM (Yokosuka City Museum).

For most specimens used in the osteological investigations, each skeletal part was examined and figured by Wild M7 S after the flesh had been removed with KOH and the bones had been stained with alizarin red S. In some specimens, cartilage was stained with alcian blue by the method of Dingerkus and Uhler (1977).

The osteological nomenclature used here follows Uyeno (1975). The unidentified species' name, for example *Repomucenus* sp. 1, follows Nakabo (1982).

## Comparative Osteology and Phylogenetic Relationships

### 1. Comparative Osteology

#### 1) Cranium (Figs. 1-9, Table 1)

The callionymid cranium is depressed and expanded laterally. Because the

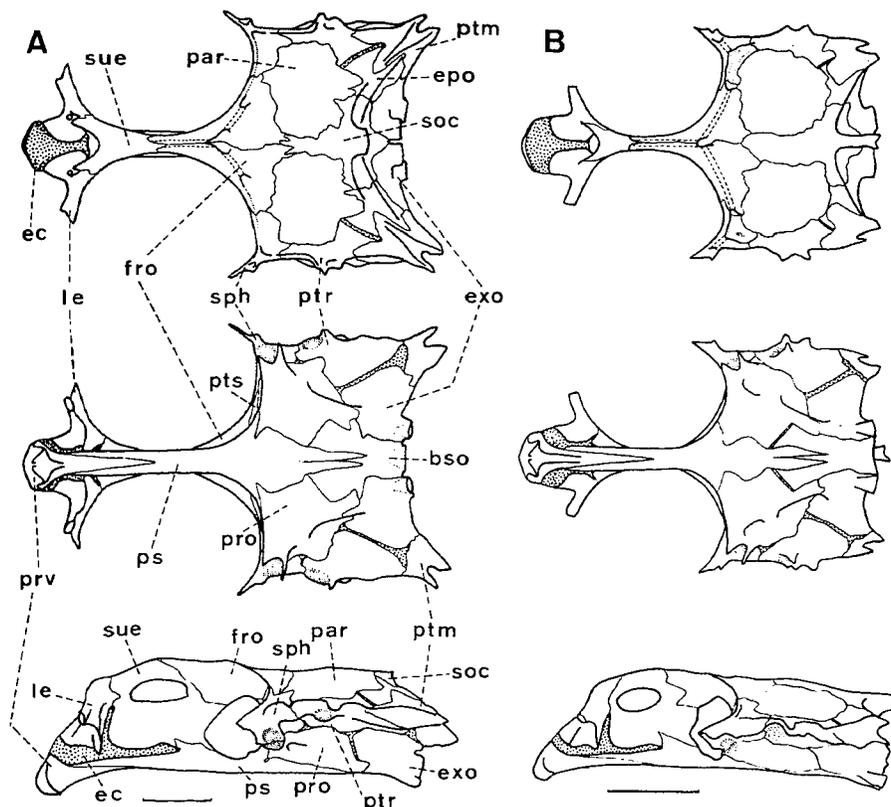


Fig. 1. The cranium in two callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*. bso, basioccipital; ec, ethmoid cartilage; epo, epiotic; exo, exoccipital; fro, frontal; le, lateral ethmoid; par, parietal; pro, prootic; pvr, prevomer; ps, parasphenoid; ptm, posttemporal; ptr, pterotic; pts, pterosphenoic; soc, supraoccipital; sph, sphenoid; sue, supraethmoid. Cartilagenous mass is indicated by the dotted regions. Top, dorsal view; middle, ventral view; bottom, lateral view. Scales indicate 3 mm.

supraoccipital crest is depressed, the dorsal surface of the posterior half of the cranium is very flat. The ethmoidal region is concave, and makes a cavity into which the ascending processes of the premaxillaries extend. The ethmoid cartilage is surrounded anteriorly by the prevomer, lateral ethmoids, supraethmoid and parasphenoid; which penetrate posteriorly into the area between the supraethmoid and the parasphenoid. The supraethmoid and frontals are strongly compressed where they join, which is related to the slight or strong protrusion of the eyes on the dorsal surface of the head. The posttemporal is rigidly attached to the posterior dorsolateral corner of the cranium, and looks like a bone of the cranium.

The callionymids have depressed, moderately depressed, or strongly depressed craniums, one genus having a strongly depressed ethmoidal region. Depressed craniums are seen in *Foetorepus*, *Eocallionymus*, *Paradiplogrammus*, *Diplogrammus* and *Spinicapitichthys* (Figs. 1-3). Moderately depressed craniums are found in *Neosynchiropus*, *Pterosynchiropus*, *Dactylopus* and *Anaora* (Figs. 4, 5). Strongly depressed ones are seen in *Bathycallionymus*, *Callionymus*, *Pseudocalliurichthys*, *Calliurichthys*, *Repomucenus* and *Paracallionymus* (Figs. 6-8). *Eleutherochir* has a cranium which is strongly depressed in the ethmoidal region (Fig. 9).

The cranium in this family is composed of 15 elements: lateral ethmoid, supra-

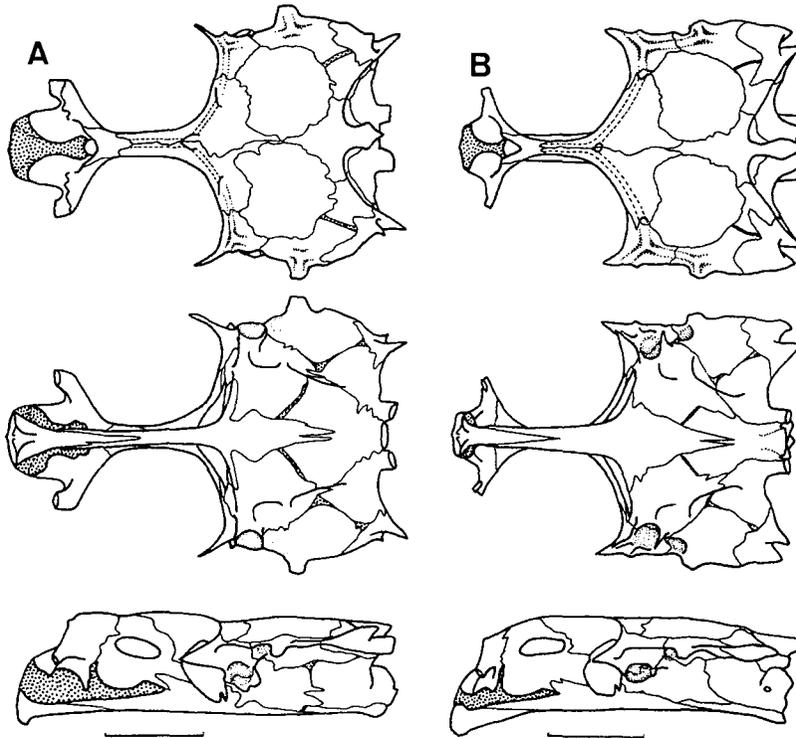


Fig. 2. The cranium in two callionymid species. A, *Paradiplogrammus enneactis calliste*; B, *Diplogrammus xenicus*. Top, dorsal view; middle, ventral view; bottom, lateral view. Scales indicate 3 mm.

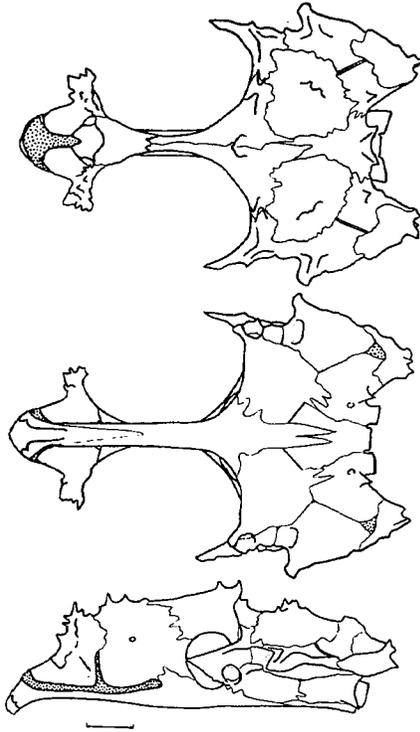


Fig. 3. The cranium in *Spinicapitichthys spiniceps*. Top, dorsal view; middle, ventral view; bottom, lateral view. Scale indicates 3 mm.

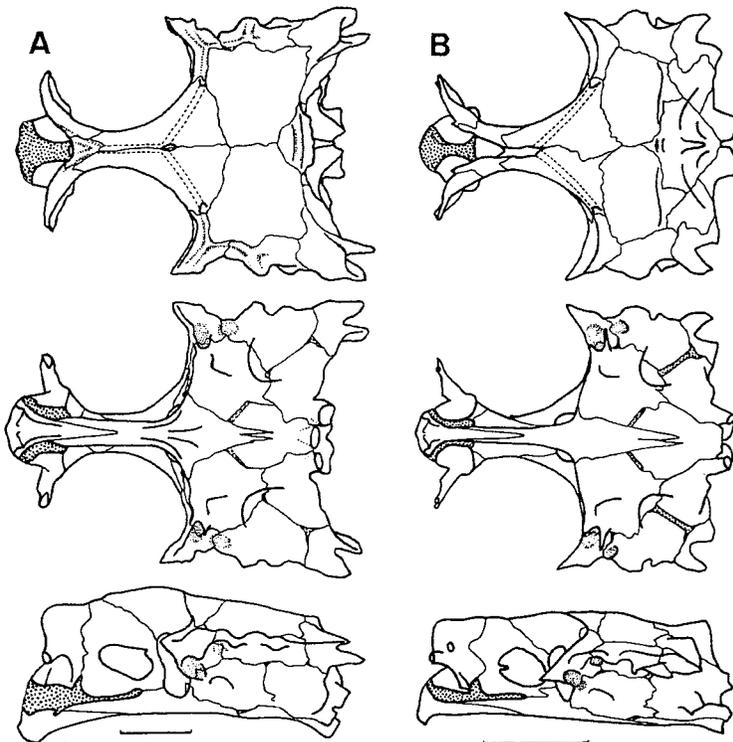


Fig. 4. The cranium in two callionymid species. A, *Neosynchiropus ocellatus*; B, *Pterosynchiropus splendidus*. Top, dorsal view; middle, ventral view; bottom, lateral view. Scales indicate 3 mm.

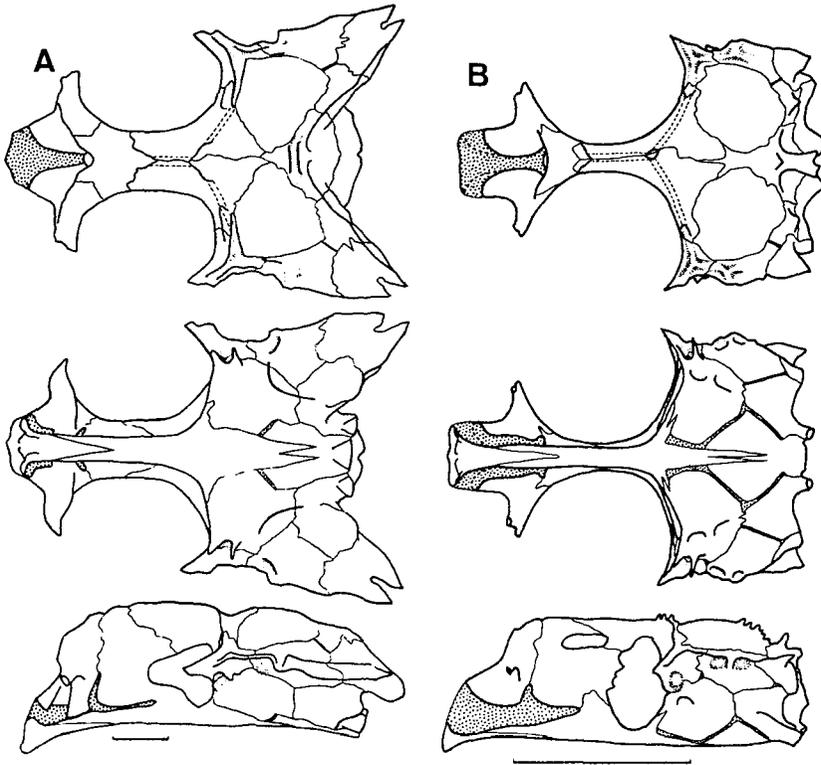


Fig. 5. The cranium in two callionymid species. A, *Dactylopus dactylopus*; B, *Anaora tentaculata*. Top, dorsal view; middle, ventral view; bottom, lateral view. Scales indicate 3 mm.

ethmoid, prevomer, frontal, parietal, sphenotic, pterosphenotic, pterotic, epiotic, prootic, supraoccipital, basioccipital, exoccipital, parasphenoid and nasal. Neither basisphenoid nor intercalar are present in the cranium of this family. The nasals are described and discussed in the next section.

**Lateral ethmoids:** The anterior part of each lateral ethmoid forms a thin bony lamina that envelops the ethmoid cartilage; the upper lamina meets or approaches its opposite fellow on the floor of the cavity for the ascending processes of the premaxillaries. The posterior dorsal part of each lateral ethmoid is well ossified and protrudes laterally as one of the bones which form the orbit of each eye; the lower tip of this lateral process is articulated with the uppermost facet of the lacrimal by connective tissue. Posteriorly the lateral ethmoids are connected to the supraethmoid. It carries the supraorbital canal on its well ossified dorsal surface. In *Eleutherochir*, the lateral ethmoids are strongly depressed (Fig. 9), but not in the other genera.

**Supraethmoid:** The supraethmoid is a very compressed bone which is expanded vertically and connects the parasphenoid to form an interorbital septum. It is only in *Callionymus* that it is indirectly in contact with the parasphenoid due to the intervention of the posterior part of the ethmoid cartilage (Fig. 6B). The supraethmoid connects the lateral ethmoids anteriorly. At its tip it is expanded somewhat horizontally

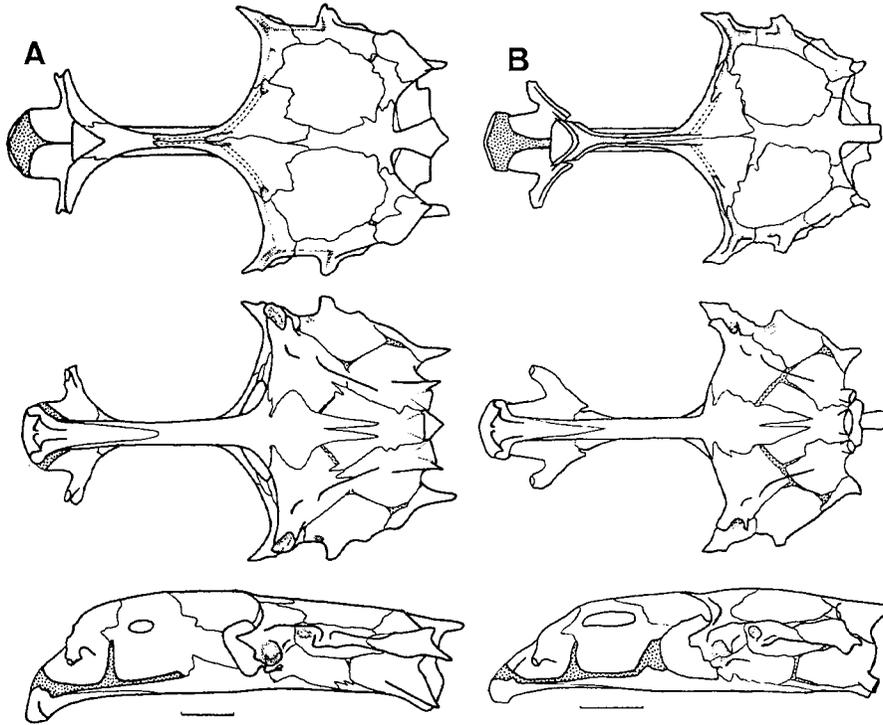


Fig. 6. The cranium in two callionymid species. A, *Bathycallionymus kaianus*; B, *Callionymus maculatus*. Top, dorsal view; middle, ventral view; bottom, lateral view. Scales indicate 3 mm.

on the ethmoid cartilage to form the posteriormost floor of the cavity for the ascending process of the premaxillaries. It connects the ethmoid cartilage anteroventrally, the frontals posterodorsally. It carries the supraorbital canal on its dorsal surface. There is a large foramen on the middle of this bone in most genera and in most species of this family. In *Dactylops*, *Eleutherochir* and some species of *Repomucenus*, there is no foramen on the supraethmoid (Figs. 5A, 8C, 9). In *Anaora*, this foramen is located more posteriorly than in others and reaches the posterodorsal border (Fig. 5B). In *Eleutherochir*, the supraethmoid is strongly depressed (Fig. 9).

**Prevomer:** The head of the prevomer expands slightly upward to envelop the anteriormost ventral tip of the ethmoid cartilage. Each hollow at the anteroventral part of the prevomer is connected to the lowermost adaxial part of the palatine by a ligament. The prevomer is elongated posteriorly on the ventral surface of the anterior third or fourth of the parasphenoid which its posterior point penetrates slightly. The prevomer is without teeth.

**Frontals:** The frontals meet each other along a midlongitudinal joint to form a triangular roof at the middle part of the cranium, but do not form roofs for the orbits. They connect the supraethmoid anteriorly, the sphenotics laterally, the pterosphenoids ventrally, and the parietals and supraoccipital posteriorly.

They carry the supraorbital canal, for which there are three openings on the

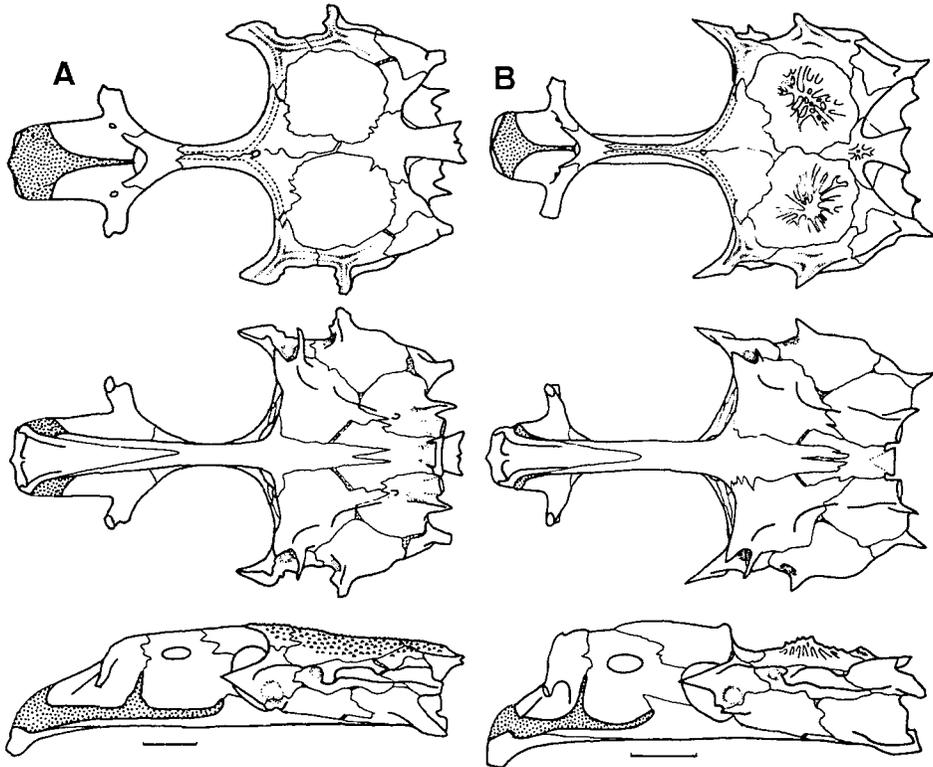


Fig. 7. The cranium in two callionymid species. A, *Pseudocallionymus variegatus*; B, *Callionymus japonicus*. Top, dorsal view; middle, ventral view; bottom, lateral view. Scales indicate 3 mm.

dorsal surface in most genera; one on the midlongitudinal joint and two near the lateral edges. In *Callionymus*, *Paracallionymus*, *Pterosynchiropus* and *Eleutherochir*, there are no roofs for the interorbital part of the supraorbital canal on the anterior dorsal surface of the frontals (Figs. 4B, 6B, 8D, 9). In *Repomucenus filamentosus*, there are no roofs for the posterior part of the supraorbital canal on the middle dorsal surface of the frontals (Fig. 8B).

**Parietals:** The parietals are round or square-shaped flat bones that form the roof of the brain cavity. They meet or approach each other along a midlongitudinal joint. Each parietal connects the frontal and sphenotic anteriorly, the pterotic abaxially, the supraoccipital adaxially and posteriorly, and the epiotic posteriorly.

**Supraoccipital:** The supraoccipital crest is depressed strongly and extends posteriorly. The supraoccipital connects the frontals and parietals anteriorly, the epiotics laterally, and the exoccipitals posteroventrally. It carries the supratemporal canal on its middle dorsal surface. Only in *Dactylopus*, is there no supraoccipital crest (Fig. 5A).

**Epiotics:** Each epiotic connects the parietal anteriorly, the supraoccipital adaxially, the exoccipital ventrally by connective tissue, and the pterotic anteroabaxially

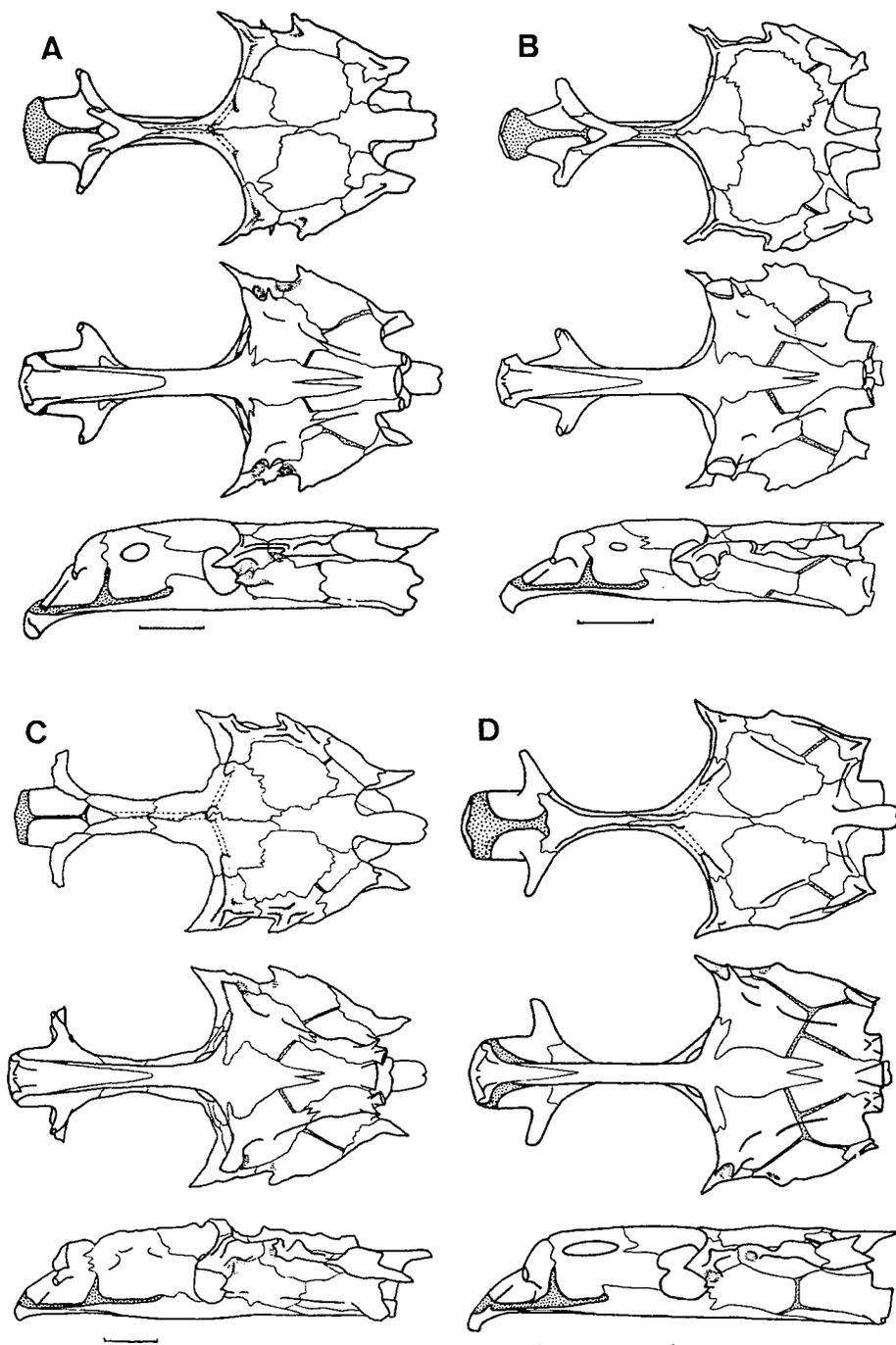


Fig. 8. The cranium in four callionymid species. A, *Repomucenus huguenini*; B, *Repomucenus filamentosus*; C, *Repomucenus belcheri*; D, *Paracallionymus costatus*. Top, dorsal view; middle, ventral view; bottom, lateral view. Scales indicate 3 mm.

by a synchondral joint.

**Exoccipitals:** The exoccipitals approach each other dorsally and medially above the foramen magnum, but are separated by cartilage. Each exoccipital connects the prootic anteriorly, the basioccipital ventroadaxially, the epiotic and supraoccipital posterodorsally by connective tissue, and the pterotic anterodorsally by a narrow cartilage band. Posteriorly, the exoccipitals articulate with the first vertebra by connective tissue at the exoccipital condyles located at both lateral sides of the basioccipital condyle.

**Basioccipital:** The basioccipital connects the parasphenoid anteroventrally, the exoccipitals laterally by connective tissue, and the prootics anterolaterally by a narrow band of cartilage. The basioccipital forms the floor of the foramen magnum dorsally. The basioccipital condyle is deeply concave and articulates with the centrum of the 1st vertebra.

**Sphenotics:** The sphenotics are located at the posterolateral corner of the orbit. Each sphenotic has an antrorse pointed projection. The sphenotics connect the frontals. The parietals dorsolaterally, the pterosphenoids anteroventrally, and the prootics ventrally.

The anteroventral part of each sphenotic forms the upper half of the anterior facet for the hyomandibular. The dorsal surface of each sphenotic forms a floor at which the supraorbital canal, the infraorbital canal and the postocular commissure meet. *Foetorepus* and *Eocallionymus* have roofs for the infraorbital canals (Fig. 1)

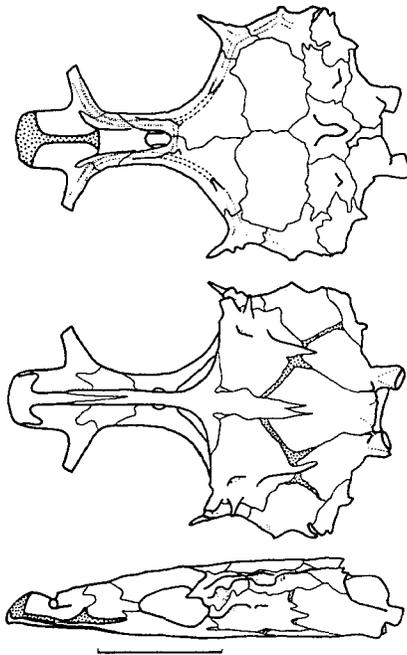


Fig. 9. The cranium in *Eleutherochir mirabilis*. Top, dorsal view; middle, ventral view; bottom, lateral view. Scale indicates 3 mm.

unlike the other genera.

**Pterotics:** The pterotics connect the parietals dorsolaterally, the sphenotics anteriorly and the prootics anteroventrally by connective tissue, the epiotics posterodorsally and the exoccipitals posteroventrally by a narrow band of cartilage.

Each pterotic has a posterior facet for the hyomandibular at its anterior lateral side, and carries a postocular commissure on its dorsal surface, on the midpoint of which the preoperculomandibular canal meets the postocular commissure.

**Prootics:** The prootics are located at the ventrolateral part of the cranium. They connect the parasphenoid adaxial laterally, the sphenotics and pterosphenoids anterodorsally, the pterotics dorsally, the exoccipitals posteriorly by connective tissue, and the basioccipital posteroventrally by a narrow band of cartilage. Each prootic projects slightly anterolaterally to form the lower floor of the facet for the hyomandibular.

**Pterosphenoids:** Each pterosphenoid connects the frontal dorsally, the sphenotic and prootic abaxial laterally, and the parasphenoid ventrally.

In *Eocallionymus*, *Callionymus*, *Neosynchiropus* and *Pterosynchiropus*, each pterosphenoid has an inward projection at the edge facing the brain cavity; in the other genera there is no projection.

**Parasphenoid:** The parasphenoid is an elongate bone situated on the midlongitudinal base of the cranium. It connects the prevomer anteroventrally, the supraethmoid anterodorsally, the pterosphenoids and prootics mid-dorsally, and the basisphenoid posterodorsally. The parasphenoid is divided and makes a forked projection which lies on the basisphenoid.

Table 1. Characters' conditions of the cranium in callionymid genera.

	ER	SP	SC	NA
<i>Callionymus</i>		indirectly connected		
<i>Bathycallionymus</i>				
<i>Foetorepus</i>				
<i>Eocallionymus</i>				
<i>Paracallionymus</i>			present	
<i>Neosynchiropus</i>				
<i>Pterosynchiropus</i>	not depressed			present
<i>Paradiplogrammus</i>		directly connected		
<i>Diplogrammus</i>				
<i>Dactylopus</i>			absent	
<i>Calliurichthys</i>				
<i>Pseudocalliurichthys</i>				
<i>Repomucenus</i>			present	
<i>Spinicapitichthys</i>				absent
<i>Anaora</i>				
<i>Eluetherochia</i>	depressed			present

Abbreviations: ER, ethmoidal region; NA, nasal; SC, supraoccipital crest; SP, supraethmoid and parasphenoid.

*Discussion.* The callionymid cranium has been studied by Starks (1923, 1926), Gregory (1933), Hotta (1961), Takahashi (1962), Kayser (1962), Ochiai (1963), Gosline (1970) and Fricke (1981), but they did not treat the relationships among the genera.

Fricke (1981) divided this family into two main genera, *Callionymus* and *Synchiropus*, and showed six characters of the neurocranium (position of the mesethmoidal foramen=supraethmoidal foramen, shape of the interorbital hole, shape of the rostral part of the ethmoidal region, general shape of dorsal view, development of supraoccipital and width of the supraethmoid) to separate the two genera. The differences shown by him are, however, not always efficient for classifying this family; he examined only three species (*Callionymus lyra*, *C. maculatus* and *Synchiropus picturatus*=*Pterosynchiropus picturatus*), which are not enough to discuss the generic differences.

Kayser (1962) drew a portion of the pterosphenoid (the alisphenoid in his paper) of *Callionymus lyra* that emerges on the anterior dorsal surface of the cranium, but none of the pterosphenoid of *C. lyra* examined in the study were found on this surface.

Gosline (1970) said that there is no pterosphenoid (the pleurosphenoid in his paper), but all the specimens examined in this study have it.

Callionymid craniums are separable into two forms in a shape of the ethmoidal region. *Eleutherochir* is strongly depressed in the ethmoidal region, but the others are not. This is due to *Eleutherochir*'s jaw structure (Fig. 12C). As no conspicuous differences are visible in the arrangement and configuration of the callionymid craniums examined in this study, the cranium of *Eleutherochir* must have deviated from the others in relation to its specialized jaw structure.

The three types recognizable in the degree of cranial depression of all the genera except *Eleutherochir* are related to variations in body depth which is shown in Nakabo (1982, p. 118). *Neosynchiropus*, *Pterosynchiropus*, *Anaora* and *Dactylopus* have craniums and bodies that show more moderate depression than the other genera. *Foetorepus*, *Eocallionymus*, *Paradiplogrammus*, *Diplogrammus* and *Spinicapitichthys* have depressed craniums and similarly depressed bodies. *Bathycallionymus*, *Callionymus*, *Paracallionymus*, *Pseudocalliurichthys*, *Calliurichthys* and *Repomucenus* have strongly depressed craniums and strongly depressed bodies.

Only in *Callionymus* does the supraethmoid connect the parasphenoid with the intervention of the posterior part of the ethmoid cartilage. Since this is not seen in the other genera, *Callionymus* must be a deviant in this character.

The absence of the supraoccipital crest in *Dactylopus* is related to the location of the first dorsal fin, because the genus has it more anteriorly than the other. As all other genera have supraoccipital crests, *Dactylopus* is a deviant.

Whether there are a foramen on the supraethmoid, a roof on the supraorbital canal on the frontals, a roof on the infraorbital canal on the sphenotics, or an inward projection of the pterosphenoid is trivial; these facets are not needed to deduce the relationships among the callionymid genera.

In summary, the craniums of *Eleutherochir*, *Callionymus* and *Dactylopus* show that they have deviated from the other.

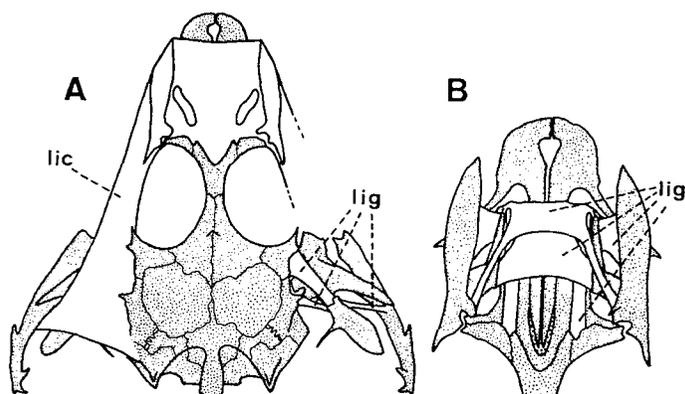


Fig. 10. The head region in *Repomucenus richardsonii*. A, snout to opercular region; B, snout region below the thin ligamentous connective tissue layer. lic, ligamentous connective tissue layer; lig, ligament.

### 2) Nasal and lacrimal (Figs. 10A, 11, Table 1)

Nasals and lacrimals are located in the thin connective tissue layer between the snout and opercular region (Fig. 10A).

Nasals: Each nasal is an elongate bone situated between the lacrimal and lateral ethmoid with a groove dorsally to carry the anterior branch of the supra-orbital canal. Only in the genus *Spinicapitichthys* are there no nasals (Fig. 11P).

Lacrimals: No orbital bones except the lacrimals are present in Callionymid fishes. Each lacrimal is a large bone which articulates with the lateral ethmoid at its dorsal top. The lacrimal has an anterior and posterior ramus.

*Discussion.* Gregory (1933) reported the lacrimal of *Callionymus lyra*, but he mistakenly showed the lacrimal attached to the sphenotic. The lacrimal is attached to the lateral ethmoid.

Because *Spinicapitichthys* has no nasal bones, it is a deviant from the others.

### 3) Upper jaw (Figs. 10B, 12–15, Table 2)

The callionymid fishes are characterized by a specialized protruding upper jaw. The maxillary head region makes a ring that includes the maxillary head, two cartilages and ligaments around the long ascending processes of the premaxillary (Fig. 10B).

Callionymid fishes show three patterns for their upper jaw protrusions. In the first, the upper jaw is protracted ventrally. This is the most common pattern, which all genera except *Anaora* and *Eleutherochir* have (Fig. 12A). In the second pattern, the upper jaw is protracted obliquely ventrally like a tube and is used to draw in food organisms. This is only seen in *Anaora* (Fig. 12B). In the third pattern, the lower jaw is protracted anteriorly, this is only seen in *Eleutherochir* (Fig. 12C).

The upper jaw of the callionymids consists of two elements; premaxillary and maxillary.

Premaxillaries: Each premaxillary has a long pointed ascending process dorsally

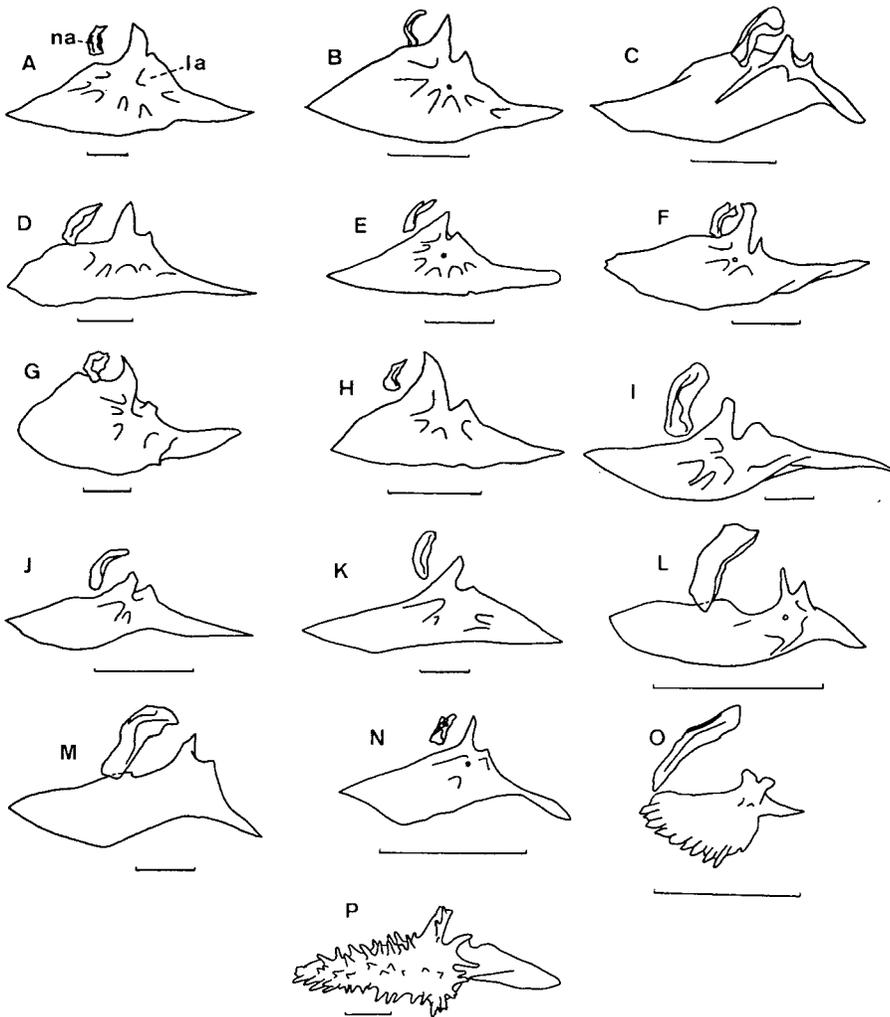


Fig. 11. The nasal and lacrimal in sixteen callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Callionymus maculatus*; D, *Bathycallionymus sokonumeri*; E, *Diplogrammus xenicus*; F, *Paradiplogrammus enneactis calliste*; G, *Neosynchiropus ocellatus*; H, *Pterosynchiropus splendidus*; I, *Dactylopus dactylopus*; J, *Pseudocallirichthys variegatus*; M, *Repomucenus ornatipinnis*; N, *Anaora tentaculata*; O, *Eleutherochir mirabilis*; P, *Spinicapitichthys spiniceps*. la, lacrimal; na, nasal. Scales indicate 2 mm.

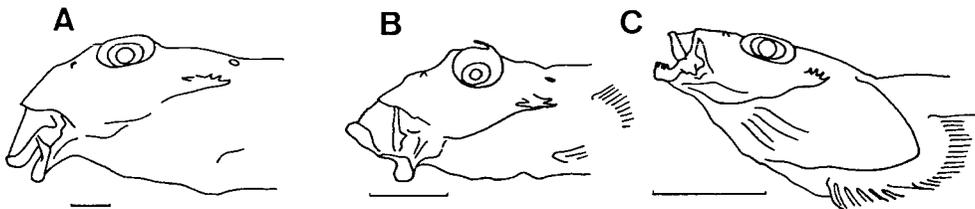


Fig. 12. Diagrammatic illustration showing the jaw protrusion in three callionymid species. A, *Repomucenus beniteguri*; B, *Anaora tentaculata*; C, *Eleutherochir mirabilis*. Scales indicate 5 mm.

and a ramus ventrally; the former is much longer than the latter. There is a broad, villiform band of teeth on the anterior ventral surface. The premaxillaries are joined together by connective tissue and the rostral cartilage. The rostral cartilage is attached at the posteriormost part of both premaxillary ascending processes. The anterior tip of this rostral cartilage is connected to each maxillary head by a ligament.

The shapes of the premaxillaries fall roughly into three categories. In *Eleutherochir*, the angle between the ascending process and the ramus is large, and the ramus is long (Type C1, Fig. 15A). In *Anaora*, the angle between the ascending process and the ramus is large, and the ramus is short. There are degenerate teeth on the anterior part (Type B1, Fig. 15B). In the other genera, the angles between the ascending processes and the rami are small. The rami are shorter than the ascending processes, and have not degenerated teeth (Type A1, Figs. 13, 14). In addition, all the genera except *Eleutherochir* and *Anaora* can be separated into two groups according to the shapes of their anterior tips. In *Foetorepus*, *Eocallionymus*, *Callionymus*, *Paracallionymus*, *Neosynchiropus*, *Pterosynchiropus* and *Diplogrammus pauciradiatus*, the tips are pointed (Type A1a, Fig. 13), whereas in *Synchiropus*, *Bathycallionymus*, *Diplogrammus* (except *D. pauciradiatus*), *Paradiplogrammus*, *Pseudocalliurichthys*, *Calliurichthys*, *Repomucenus* and *Dactylopus* the tips are half rounded (Type A1b, Fig. 14).

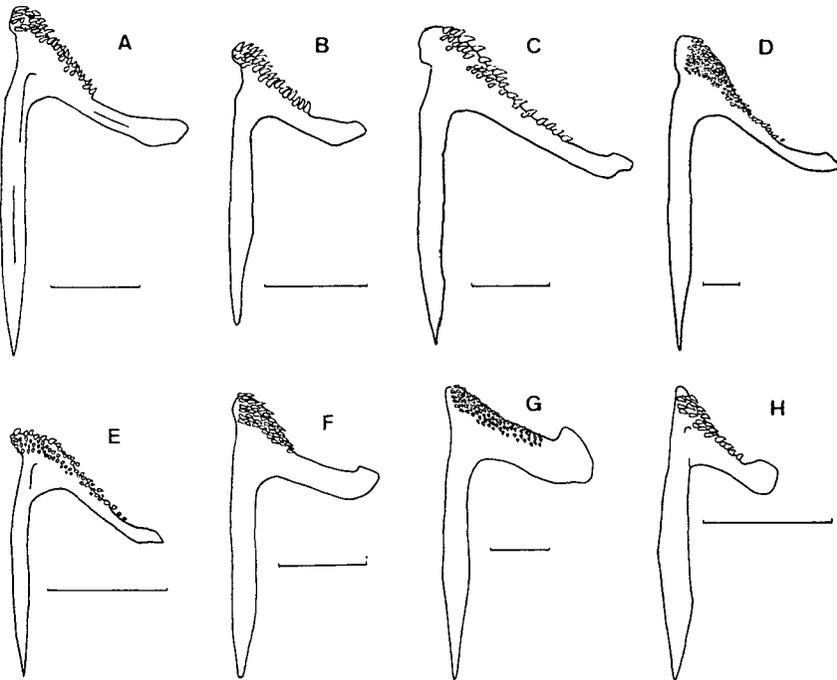


Fig. 13. Ventral view of the left premaxillary in eight callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Callionymus maculatus*; D, *Callionymus lyra*; E, *Paracallionymus costatus*; F, *Neosynchiropus ijimai*; G, *Neosynchiropus ocellatus*; H, *Pterosynchiropus splendidus*. Scales indicate 2 mm.

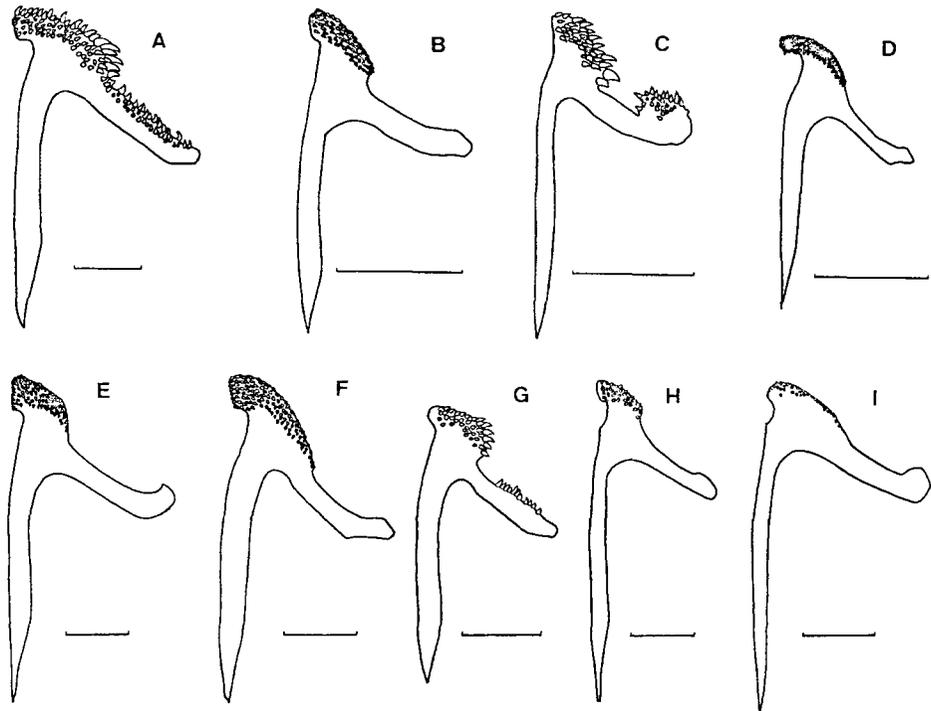


Fig. 14. Ventral view of the left premaxillary in nine callionymid species. A, *Bathycallionymus kaianus*; B, *Diplogrammus xenicus*; C, *Paradiplogrammus enneactis calliste*; D, *Pseudocalliurichthys variegatus*; E, *Calliurichthys japonicus*; F, *Repomucenus huguenini*; G, *Repomucenus filamentosus*; H, *Spinicapitichthys spiniceps*; I, *Dactylopus dactylopus*. Scales indicate 2 mm.

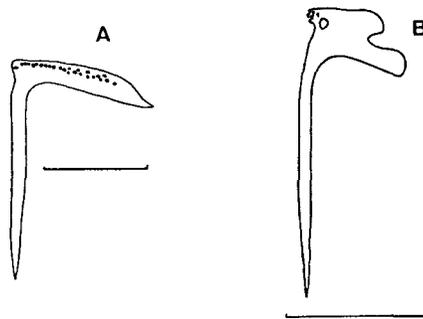


Fig. 15. Ventral view of the left premaxillary in two callionymid species. A, *Eleutherochir mirabilis*; B, *Anaora tentaculata*. Scales indicate 2 mm.

There is some variation in the size of the teeth among congeneric species (Fig. 13C·D·F·G).

**Maxillaries:** The maxillaries are elongate bones which form a stout strut with the premaxillaries for the upper jaw. Each maxillary has two tubercles and one pointed process on its head. The anterior tubercle faces the ventral surface of

the premaxillary ascending process through an anterior discal cartilage. The posterior tubercle faces the anterodorsal surface of the ethmoid cartilage through a posterior discal cartilage. The pointed process located on the dorsal part forms a pent roof for the premaxillary ascending process and is connected to the opposite fellow and the posterior adaxial parts of the lacrimals by a broad ligament. Under this another broad ligament connects the pointed processes with the posterior heads of the palatines. In addition, under the two broad ligaments, the pointed process of each maxillary is connected to the anterior part of each lateral ethmoid by a long ligament. The lower part of the maxillary is expanded somewhat posteriorly and is connected to the tendon of the adductor mandibulae. The lowermost part is connected to the posteriormost part of the premaxillary ramus by a ligament.

*Discussion.* The upper jaw of the callionymids has been reported by Kayser (1962) in *Callionymus lyra* in terms of a feeding mechanism. Davis and Robins (1966) reported the upper jaw of *Eleutherochir shango*.

The three types of premaxillaries in the callionymids correspond to the three protracting types of the upper jaw. In *Eleutherochir*, there is no ventral protraction because of the long ramus and the large angle between it and the ascending process. In *Anaora*, there is no ventral protraction as in most callionymids because of the short ramus and the large angle. In the other genera, ventral protraction is possible because of the long ramus and small angle. *Eleutherochir*'s mouth seems to be formed for catching small food organisms, and *Anaora*'s appears to be formed for sucking them in. The mouths found in the other genera may be forms used for digging out food. *Eleutherochir* and *Anaora* deviate from the other genera in this point.

The form of the anterior tip in Type A1 appears to be related to efficiency in eating. As the tip area in Type A1b is wider than in A1a, A1b should be more efficient for eating than A1a, which makes Type A1b more advanced than Type A1a.

The teeth in *Anaora* are degenerate, probably because of its specialized jaw structure, making this genus a deviant.

#### 4) Lower jaw (Figs. 16–18, Table 2)

The lower jaw of the callionymids is composed of four elements; dentary, articular, sesamoid articular and retroarticular.

In *Eocallionymus*, *Foetorepus*, *Dactylopus*, *Diplogrammus*, *Paradiplogrammus*, *Spinicapitichthys*, *Neosynchiropus*, *Pterosynchiropus*, *Eleutherochir* and *Anaora*, the lower jaw is moderately depressed (Figs. 16, 18). But in *Callionymus*, *Bathycallionymus*, *Paracallionymus*, *Pseudocalliurichthys*, *Calliurichthys* and *Repomucenus*, it is strongly depressed (Fig. 17).

*Dentaries:* Each dentary is a Y-shaped bone that constitutes the major part of the lower jaw. Anteriorly the dentary is connected to its opposite in a firm symphysis by connective tissue. Each dentary has villiform band of teeth on its anterior dorsal surface. There is a tubercle on the anterodorsal part of each one. The posterior end of the upper ramus is connected to the lower end of the maxillary by a short ligament.

Table 2. Characters' conditions of the jaws in callionymid genera.

	PM	DA	SA	TJ
<i>Callionymus</i>	A1a			
<i>Bathycallionymus</i>	A1b		B3	
<i>Foetorepus</i>			A3	
<i>Eocallionymus</i>				
<i>Paracallionymus</i>			B3	
<i>Neosynchiropus</i>	A1a		A3	
<i>Pterosynchiropus</i>				
* <i>Minysynchiropus</i>			—	
<i>Paradiplogrammus</i>	A1b	A2	A3	normal
<i>Diplogrammus</i>	A1a·A1b			
* <i>Synchiropus</i>			—	
* <i>Orbonymus</i>			—	
<i>Dactylopus</i>			A3	
<i>Calliurichthys</i>	A1b			
<i>Pseudocalliurichthys</i>			B3	
<i>Repomucenus</i>				
<i>Spinicapitichthys</i>				
<i>Anaora</i>	B1	B2	A3	degenerate
<i>Eleutherochir</i>	C1	C2		normal

Abbreviations: DA, dentary and articular; PM, premaxillary; SA, sesamoid articular; TJ, teeth on upper and lower jaws. \*: from the X-rays.

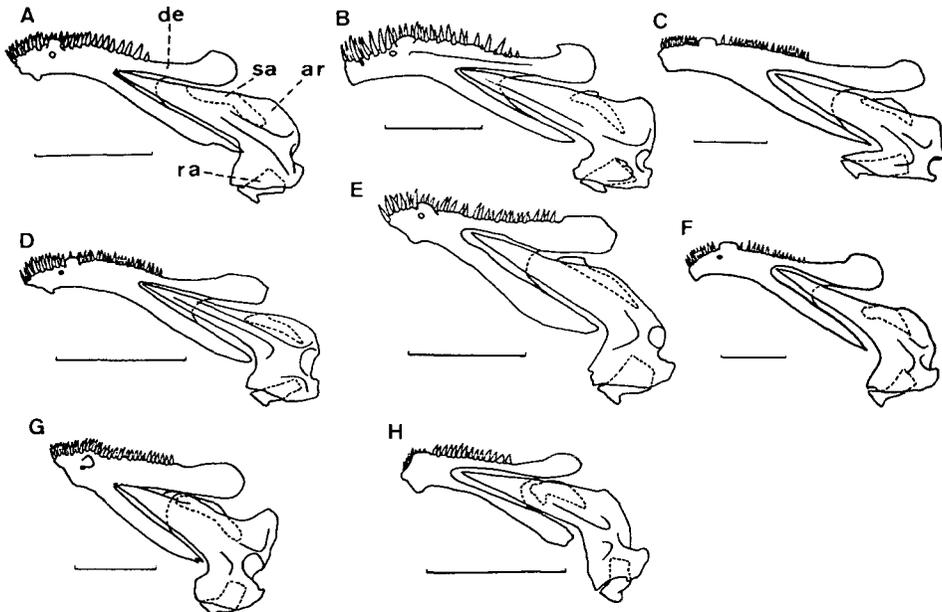


Fig. 16. Lateral view of the left lower jaw in eight callionymid species. A, *Eocallionymus papilio*; B, *Foetorepus altivelis*; C, *Dactylopus dactylopus*; D, *Diplogrammus xenicus*; E, *Paradiplogrammus enneactis calliste*; F, *Spinicapitichthys spiniceps*; G, *Neosynchropus ocellatus*; H, *Pterosynchiropus splendidus*. ar, articular; de, dentary; ra, retroarticular; sa, sesamoid articular. Scales indicate 2 mm.

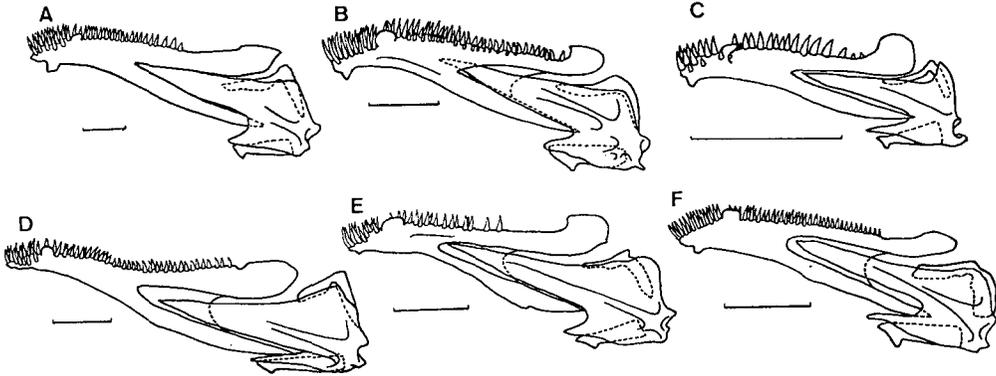


Fig. 17. Lateral view of the left lower jaw in six callionymid species. A, *Callionymus lyra*; B, *Bathycallionymus kaianus*; C, *Paracallionymus costatus*; D, *Pseudocalliurichthys variegatus*; E, *Calliurichthys japonicus*; F, *Repomucenus huguenini*. Scales indicate 2 mm.

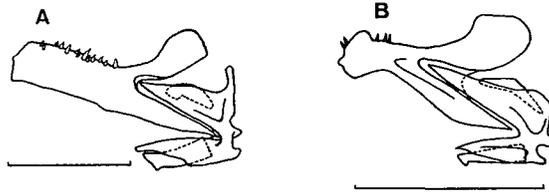


Fig. 18. Lateral view of the left lower jaw in two callionymid species. A, *Eleutherochir mirabilis*; B, *Anaora tentaculata*. Scales indicate 2 mm.

There are three types of dentaries. In *Eleutherochir*, the anterior undivided part is elongate, expanded vertically, and without tubercle on the anterodorsal part. The upper ramus curves upward at the end (Fig. 18A). In *Anaora*, the posterior part of the upper ramus is expanded and curves upward, and the teeth are degenerate (Fig. 18B). In the other genera, the posterior part of the upper ramus curves slightly upward, and their teeth are not degenerate (Figs. 16, 17).

**Articulars:** The articulars are V-shaped bones that form most of the posterior part of the lower jaw. The upper ramus penetrates into a V-shaped sinus of the dentary. The articular has a concave facet at its posterior end that articulates with the anterior process of the quadrate.

There are three types of articulars. In all the genera except *Eleutherochir* and *Anaora*, the upper ramus is much longer than the lower one (Type A2, Figs. 16, 17). In *Anaora*, the upper ramus is slightly longer than the lower one (Type B2, Fig. 18B). In *Eleutherochir*, the upper ramus is about the same in length as the lower one (Type C2, Fig. 18A).

**Sesamoid articulars:** Each sesamoid articular is a small bone attached at the adaxial posterodorsal part of each articular. The dorsal part of the sesamoid articular is connected to the tendon of the adductor mandibulae.

There are two types of sesamoid articulars. In *Eocallionymus*, *Foetorepus*,

*Dactylopus*, *Diplogrammus*, *Paradiplogrammus*, *Spinicapitichthys*, *Neosynchiropus*, *Pterosynchiropus*, *Eleutherochir* and *Anaora*, the sesamoid articulators curve slightly (Type A3, Figs. 16, 18). In *Callionymus*, *Bathycallionymus*, *Paracallionymus*, *Pseudocalliurichthys*, *Calliurichthys* and *Repomucenus*, the sesamoid articulators curve strongly and form an L-shape (Type B3, Fig. 17).

**Retroarticulars:** Each retroarticular is a small hook-shaped bone located at the ventral part of the lower ramus of the articular. The anteroventral process of the retroarticular is connected to the anterior tip of the interopercle by a ligament.

**Discussion.** The three types of dentaries and articulators correspond to the three types of the jaw protraction. *Anaora* and *Eleutherochir* have deviated from the other genera in these characters as well.

Since *Anaora* has degenerate teeth on the dentary, it has been derived from the other genera.

The two types of sesamoid articulators correspond to the depression of the lower jaws; slightly curved sesamoid articulators are found in moderately depressed lower jaws. The depth of the lower jaw is related to the thickness of the body shown by Nakabo (1982).

#### 5) Hyoid arch (Figs. 19–27, Table 3)

The hyoid arch in the callionymids is composed of seven elements; basihyal, urohyal, hypohyal, ceratohyal, epihyal, interhyal and branchiostegal ray.

**Basihyal (Figs. 25–27):** The basihyal is a small fan-shaped bone attached to the anterior end of the first basibranchial by a ligament. Its anterior margin is fringed by a cartilaginous band.

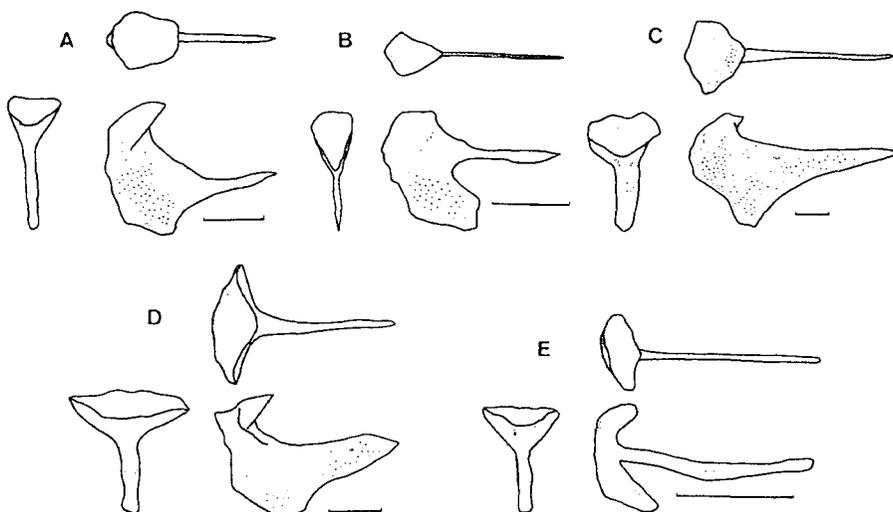


Fig. 19. The urohyal in five callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Callionymus lyra*; D, *Bathycallionymus kaianus*; E, *Eleutherochir mirabilis*. Top, dorsal view; left bottom, anterior view; right bottom, lateral view. Scales indicate 1 mm.

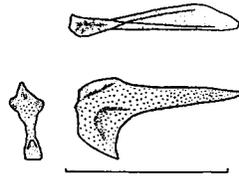


Fig. 20. The urohyal in *Anaora tentaculata*. Top, dorsal view; left bottom, anterior view; right bottom, lateral view. Scale indicates 1 mm.

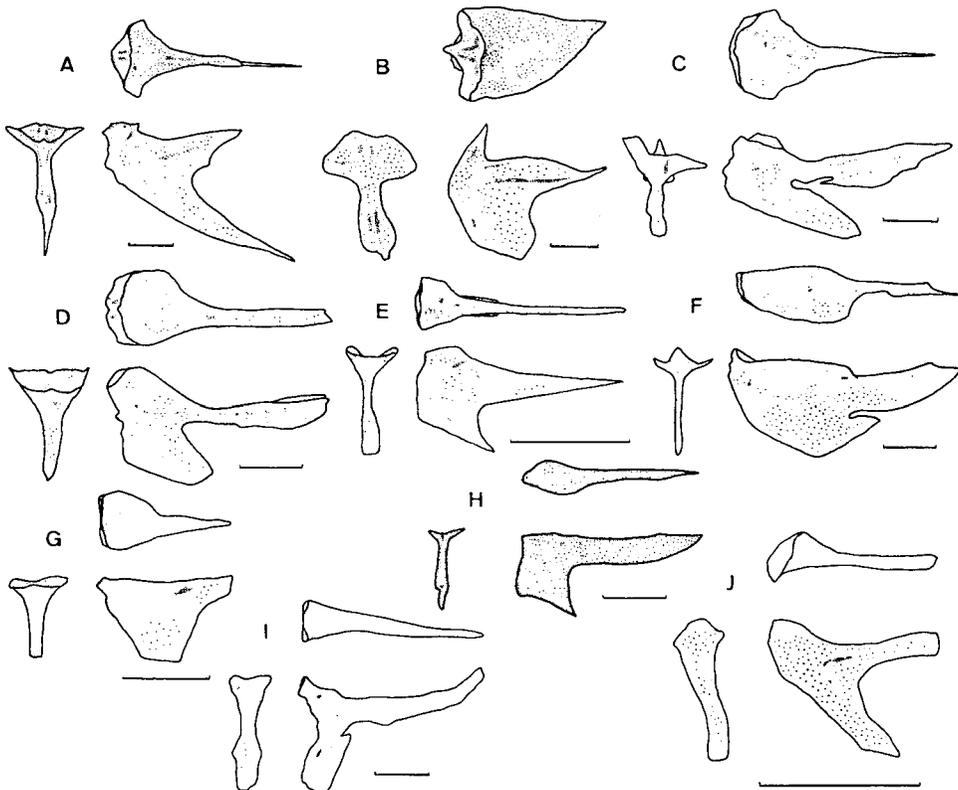


Fig. 21. The urohyal in ten callionymid species. A, *Calliurichthys japonicus*; B, *Dactylopus dactylopus*; C, *Pseudocalliurichthys variegatus*; D, *Repomucenus huguenini*; E, *Paracallionymus costatus*; F, *Spinicapitichthys spiniceps*; G, *Diplogrammus xenicus*; H, *Paradiplogrammus enneactis calliste*; I, *Neosynchiropus ocellatus*; J, *Pterosynchiropus splendidus*. Top, dorsal view; left bottom, anterior view; right bottom, lateral view. Scales indicate 1 mm.

**Urohyal:** The urohyal is roughly a bat wing-shaped bone located at the mid ventral portion of the hyoid arch. Anteroventrally it is connected to the lower hypohyals by a pair of ligaments. The urohyal has a dorsal ramus which is the origin of the rectus communis, a middle ramus, and a ventral one which is the origin of the sternohyoideus.

The urohyals in the callionymids are divided into two types. In *Foetorepus*, *Eocallionymus*, *Callionymus*, *Bathycallionymus*, *Eleutherochir* and *Anaora*, the dorsal ramus expands to form a disc or a square (Type A1). In Type A1, the rectus communis is attached to the posterior ventral surface of the disc of the dorsal ramus. Type A1 can be separated into another two subtypes. In all genera except *Anaora*, the middle ramus is long and slender (Type A1a, Fig. 19). In *Anaora*, it becomes wider posteriorly and the disc of the dorsal ramus is rather compressed (Type A1b, Fig. 20). In *Calliurichthys*, *Dactylopus*, *Pseudocalliurichthys*, *Repomucenus*, *Paracallionymus*, *Spinicapitichthys*, *Neosynchiropus*, *Pterosynchiropus*, *Diplogrammus* and *Paradiplogrammus*, the anterior dorsal edge of the middle ramus expands laterally to form a spoon-like shape (Type B1, Fig. 21). In this group, the rectus communis is attached to the anterior dorsal surface of the dorsal ramus. In *Calliurichthys*, the ventral ramus is longer than the middle one (Fig. 21A). In *Dactylopus*, *Pseudocalliurichthys*, *Repomucenus*, *Paracallionymus*, *Spinicapitichthys*, *Diplogrammus*, *Paradiplogrammus*, *Neosynchiropus* and *Pterosynchiropus*, the middle ramus is longer than the ventral one (Fig. 21B-J).

Hypohyals: There are two hypohyals on each side which form the upper and lower elements. These two and the ceratohyal are connected by cartilage. The upper and lower hypohyals are joined to their opposites by ligaments.

Ceratohyals: The ceratohyal is an elongate bone joined to the epihyal posteriorly by cartilage; it has some branchiostegal rays.

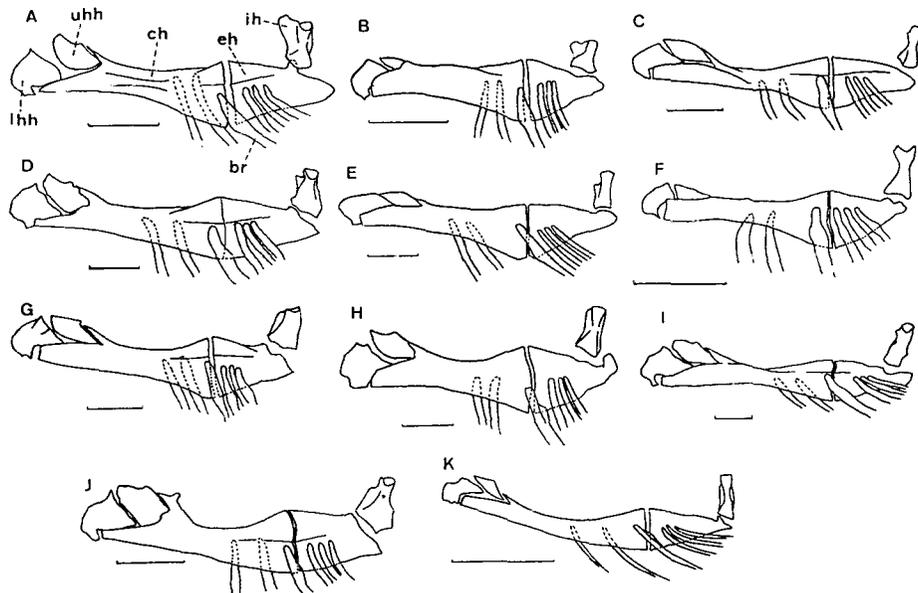


Fig. 22. Lateral view of the left hyoid arch in eleven callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Callionymus maculatus*; D, *Bathycallionymus kaianus*; E, *Spinicapitichthys spiniceps*; F, *Eleutherochir mirabilis*; G, *Calliurichthys japonicus*; H, *Dactylopus dactylopus*; I, *Pseudocalliurichthys variegatus*; J, *Repomucenus huguenini*; K, *Paracallionymus costatus*. br, branchiostegal ray; ch, ceratohyal; eh, epihyal; ih, interhyal; lhh, lower hypohyal; uhh, upper hypohyal. Scales indicate 2 mm.

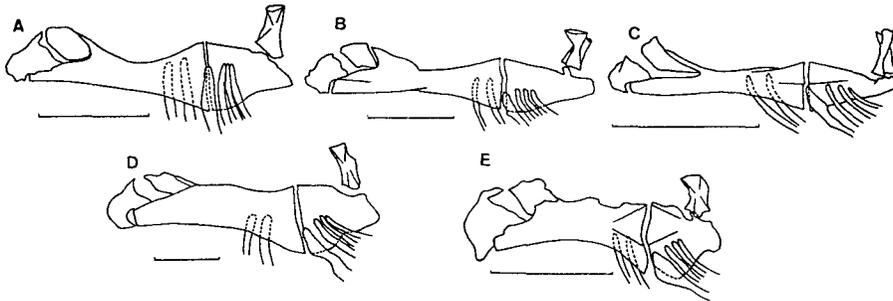


Fig. 23. Lateral view of the left hyoid arch in five callionymid species. A, *Diplogrammus xenicus*; B, *Paradiplogrammus enneactis calliste*; C, *Anaora tentaculata*; D, *Neosynchiropus ocellatus*; E, *Pterosynchiropus splendidus*. Scales indicate 2 mm.

**Epihyals:** The epihyal is a roughly triangular bone which is articulated with the interhyal by a ligament at its posterior dorsal end. It is connected to the adaxial posterior end of the quadrate by a ligament at the abaxial posterior end.

**Interhyals:** The interhyal is a short rod-shaped bone connected to the epihyal ventrally and to the hyomandibular dorsally.

**Branchiostegal rays:** There are six branchiostegal rays in the callionymids. All are slender and become filamentous. The posterior four extend near the gill-opening along the ventral edge of the subopercle. The anterior two are attached to the adaxial surface of the ceratohyal. In *Foetorepus*, *Eocallionymus*, *Callionymus*, *Bathycallionymus*, *Spinicapitichthys*, *Eleutherochir*, *Calliurichthys*, *Dactylopus*, *Pseudocalliurichthys*, *Repomucenus* and *Paracallionymus*, the third ray is attached to the posterior abaxial

Table 3. Characters' conditions of the hyoid arch in callionymid genera.

	UH	BR
<i>Callionymus</i>		
<i>Bathycallionymus</i>		
<i>Foetorepus</i>	A1a	A2
<i>Eocallionymus</i>		
<i>Eleutherochir</i>		
<i>Anaora</i>	A1b	B2
<i>Paracallionymus</i>		A2
<i>Neosynchiropus</i>		C2
<i>Pterosynchiropus</i>		
<i>Paradiplogrammus</i>		B2
<i>Diplogrammus</i>	B1	
<i>Dactylopus</i>		
<i>Calliurichthys</i>		
<i>Pseudocalliurichthys</i>		A2
<i>Repomucenus</i>		
<i>Spinicapitichthys</i>		

Abbreviations: BR, branchiostegal rays; UH, urohyal.

face of the ceratohyal (Type A2, Fig. 22). In *Diplogrammus*, *Paradiplogrammus* and *Anaora*, it is attached to the abaxial intermediate between the ceratohyal and epihyal (Type B2, Fig. 23A-C). In *Neosynchiropus* and *Pterosynchiropus*, it is attached to the anterior abaxial face of the epihyal (Type C2, Fig. 23D-E).

*Discussion.* The hyoid arch of this family has been reported by McAllister (1968), and the urohyal has been described by Kusaka (1974). These studies, however, were not detailed enough to determine the relationships among the genera.

The shape of the urohyal in the callionymids roughly corresponds to the bat wing shape of Kusaka (1974). Since this shape of bone has been reported in species of the demersal percoids; Lutjanidae, Sparidae, Lethrinidae, Branchiostegidae, Parapercidae, Labridae, Gobiidae, etc. by Kusaka (1974), it must be a generalized type for demersal percoid fishes. Their urohyals are compressed, on the other hand the bone of the callionymids is depressed. Because callionymid fishes have depressed body forms, the urohyal must have been modified to expand laterally from the compressed form.

As the attached areas of the rectus communis in both Types A1a and B1 of the urohyal expand laterally, there seems to be no difference in the mouth-opening functions. The shapes of these bones apparently have been derived separately from a compressed bat wing-shaped urohyal.

Type A1b, *Anaora*, is peculiar in comparison with the other genera in its expanded middle ramus and the compressed disc of the dorsal ramus; thus, early to have been derived from the stem of Type A1.

Of all the genera I examined, *Calliurichthys* is closest to having a standard bat wing shape. In its having a longer ventral than middle ramus, it is more primitive than the others in Type B1. Therefore, the supposed differentiation of the urohyal

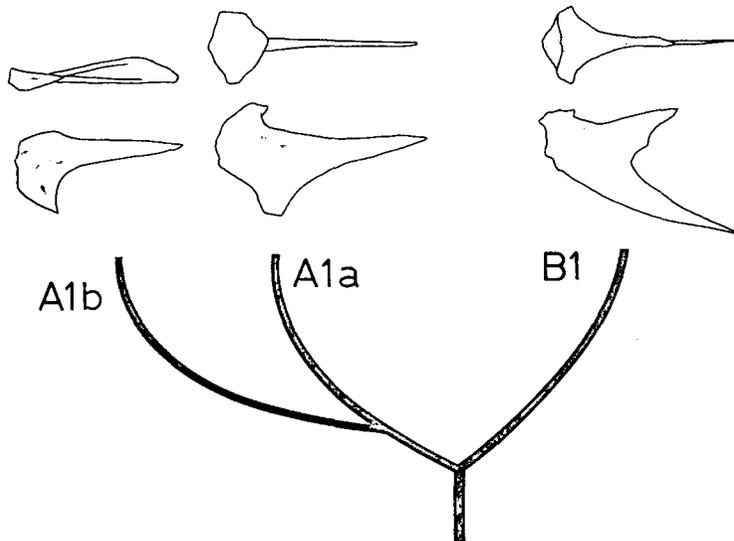


Fig. 24. Differentiation of the callionymid urohyals.

is shown in Fig. 24.

The urohyal is a good character to use for determining the phylogenetic relationships among the genera of the callionymids as shown in other fish groups. The four types of urohyals in sinistral flounders correspond to the four stems of the phylogenetic tree proposed by Amaoka (1969). In the phylogeny of the Balistoidea, Matsuura (1979) stated that the Balistidae and Monacantidae are primarily separated by the shape of the urohyal. Thus, the shape of the urohyal seems to be stable in each group. In the callionymids, the two types of the urohyals bear no relation to the body depth of the fish. Therefore, the callionymid genera sharing the same type of the urohyal show close relationships each other.

The position of the third branchiostegal ray shows the degree of specialization in each genus. Type A2 is the most primitive because it is seen in most genera. Type C2 is the most specialized and Type B2 is intermediate between them.

#### 6) Branchial apparatus (Figs. 25–27, Table 4)

The branchial apparatus supports the gills and gill-rakers which are only fleshy papillae. It consists of three unpaired basibranchials, three pairs of hypobranchials, four pairs of ceratobranchials, four pairs of epibranchials, a pair of lower pharyngeals and two pairs of upper pharyngeals. All these bones bear cartilaginous articular processes. Posterior to the third basibranchial, there is a small mass of cartilage, the posterior copula of the branchial apparatus.

**Basibranchials:** The three basibranchials lie in a midlongitudinal series on the floor of this apparatus. These three bones are joined by connective tissue. The first basibranchial is a triangler bone which touches the dorsal surface of the dorsal ramus of the urohyal at its anterior tip. It is connected to the basihyal and upper hypohyal anteriorly and to the first hypobranchials posterolaterally by ligaments. The second basibranchial is a short rod-like bone connected to the second hypobranchials posteroventrally by ligaments. The third basibranchial also is a short rod-like bone joined posteriorly to the small copular cartilage mass and the posterodorsal part of the third hypobranchials by connective tissue. The small cartilage mass is joined to the fourth ceratobranchials posterolaterally by connective tissue and to the lower pharyngeals posteriorly by a pair of ligaments.

**Hypobranchials:** The first hypobranchials are slender rod-like bones which join the first ceratobranchials to the first and second basibranchials by connective tissue. The second hypobranchials also are slender rod-like bones which join the second ceratobranchials with the second and the third basibranchials by connective tissue. The third hypobranchials are axe-like bones that join the third ceratobranchials with the third basibranchials and the small copular cartilage mass by connective tissue. The first and second hypobranchials are connected by a ligament at their anterior parts. The anterior parts of the second hypobranchials and the anterior tips of the third ones are connected by a ligament.

**Ceratobranchials:** The first to fourth ceratobranchials are long slender bones joined to the first through the fourth epihyals by connective tissue. The first to

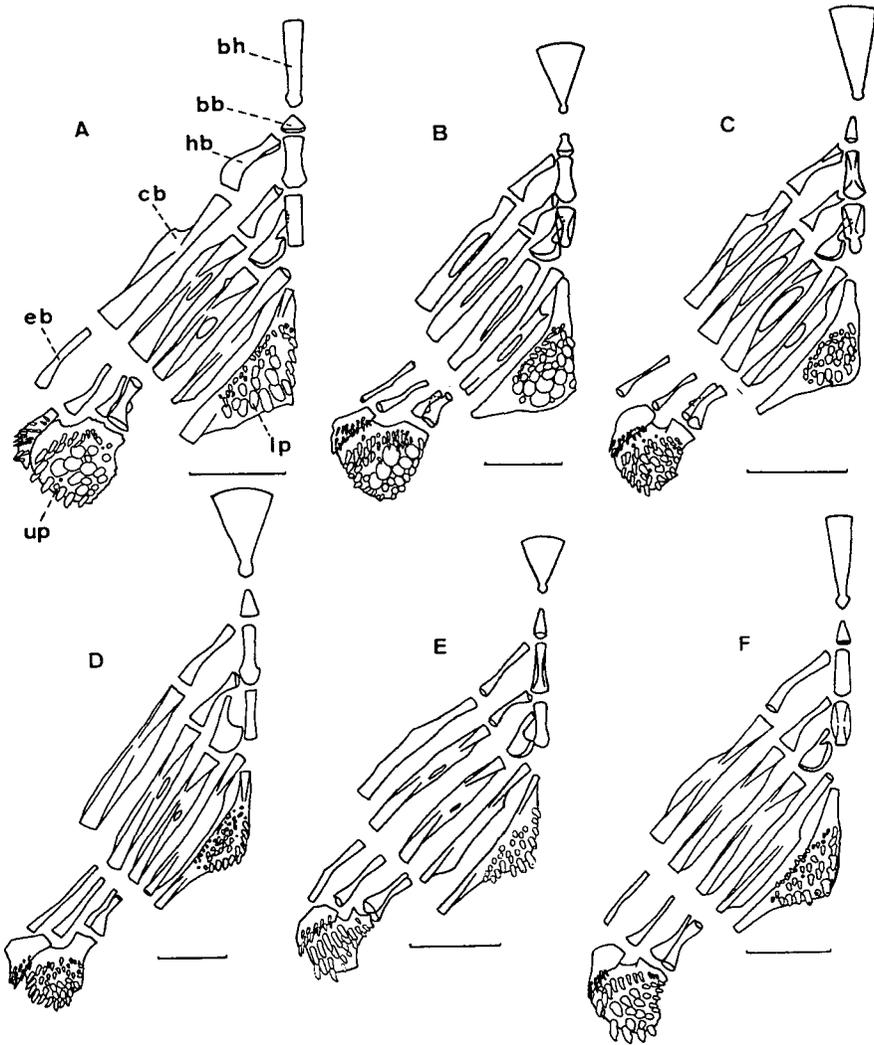


Fig. 25. Dorsal view of the left branchial apparatus in six callionymid species. A, *Calliurichthys japonicus*; B, *Repomucenus richardsonii*; C, *Repomucenus planus*; D, *Pseudocalliurichthys variegatus*; E, *Callionymus maculatus*; F, *Bathycallionymus kaianus*. bb, basi-, branchial; bh, basihyal; cb, ceratobranchial; eb, epibranchial; hb, hypobranchial; lp, lower pharyngeal; up, upper pharyngeal. Scales indicate 3 mm.

fourth ceratobranchials are interconnected at their anterior parts by ligaments.

Lower pharyngeals: Each lower pharyngeal bone is triangular with many small pharyngeal teeth connected to the small copular cartilage anteriorly by a ligament and to the posterior part of the fourth ceratobranchials posteriorly by a ligament.

In *Repomucenus*, there are variations in the size of the pharyngeal teeth (Fig. 26 B-C). In *Anaora* and *Eleutherochir*, the lower pharyngeal is more slender than in other genera, and has degenerate teeth. In *Anaora*, the teeth are concentrated at

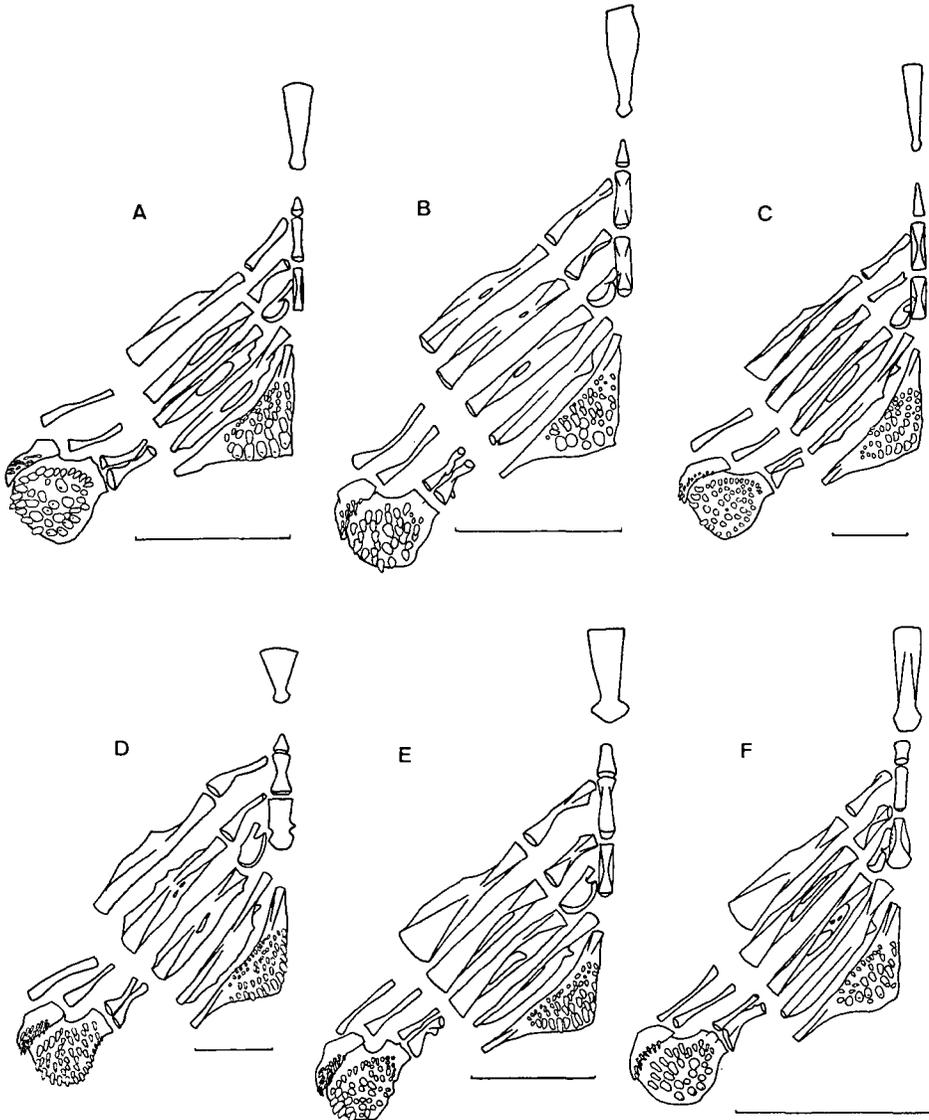


Fig. 26. Dorsal view of the left branchial apparatus in six callionymid species. A, *Diplogrammus xenicus*; B, *Paradiplogrammus enneactis calliste*; C, *Spinicapitichthys spiniceps*; D, *Dactylopus dactylopus*; E, *Neosynchiropus ocellatus*; F, *Pterosynchiropus splendidus*. Scales indicate 3 mm.

the adaxial corner (Fig. 27D), but in *Eleutherochir*, they are scattered over the bone (Fig. 27E).

**Epibranchials:** The first epibranchials are short rod-like bones joined to the first ceratobranchials ventrally by connective tissue; but they are free dorsally. The second and third epibranchials are slightly curved slender bones which join the second, and third-fourth upper pharyngeals with the second and third ceratobranchials by connective tissue. The fourth epibranchials have a process dorsally.

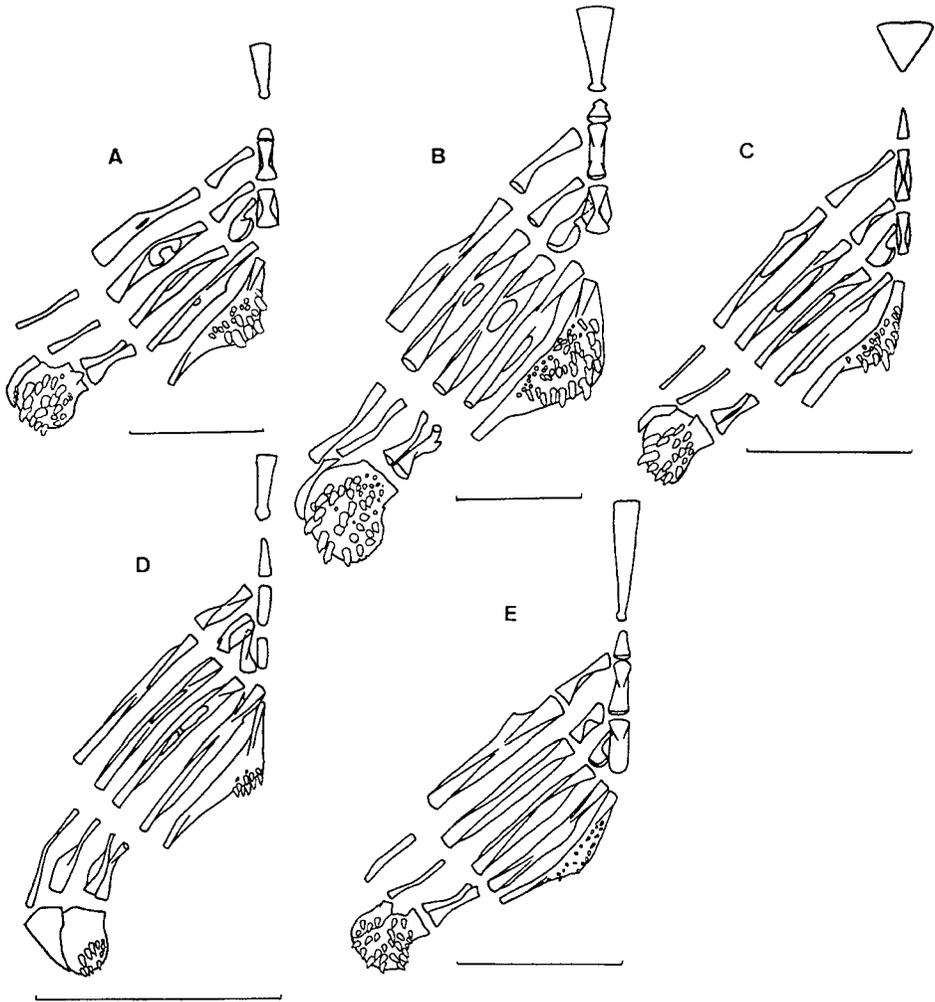


Fig. 27. Dorsal view of the left branchial apparatus in five callionymid species. A, *Eocallionymus papilio*; B, *Foetorepus altivelis*; C, *Paracallionymus costatus*; D, *Anaora tentaculata*; E, *Eleutherochir mirabilis*. Scales indicate 3 mm.

**Upper pharyngeals:** The first upper pharyngeal is absent in the callionymids. The second upper pharyngeal is a lunate bone connected to the third-fourth upper pharyngeals posteriorly and to the second epibranchial abaxial laterally by connective tissue. The third and fourth upper pharyngeals are fused into one bone which forms a disc with many small pharyngeal teeth. The upper pharyngeals are joined to the otic region of the cranium by connective tissue.

In *Foetorepus*, *Paracallionymus* and *Anaora*, the second upper pharyngeal has no teeth (Fig. 27B-D), but in the other genera, it has several small teeth. Only in *Eleutherochir*, are the second upper pharyngeal and the third-fourth upper pharyngeal almost fused into one bone (Fig. 27E).

**Discussion.** Kayser (1962) reported the branchial apparatus of *Callionymus lyra*,

Table 4. Characters' conditions of the branchial apparatus in callionymid genera.

	LP	SUP	STF
<i>Callionymus</i>		with teeth	
<i>Bathycallionymus</i>			
<i>Foetorepus</i>		without teeth	
<i>Eocallionymus</i>		with teeth	
<i>Paracallionymus</i>		without teeth	
<i>Neosynchiropus</i>			
<i>Pterosynchiropus</i>	triangle with		
<i>Paradiplogrammus</i>	normal teeth		well separated
<i>Diplogrammus</i>			
<i>Dactylopus</i>		with teeth	
<i>Calliurichthys</i>			
<i>Pseudocalliurichthys</i>			
<i>Repomucenus</i>			
<i>Spinicapitichthys</i>			
<i>Anaora</i>	slender with	without teeth	
<i>Eleutherochir</i>	degenerate teeth	with teeth	almost fused

Abbreviations: LP, lower pharyngeal; STF, second and third-fourth upper pharyngeals; SUP, second upper pharyngeal.

in terms of a feeding mechanism.

*Anaora* and *Eleutherochir* are more specialized than the other genera because of their slender lower pharyngeals and degenerate teeth. They appear to have derived separately because of the different distributional patterns of their teeth.

*Foetorepus*, *Paracallionymus* and *Anaora* deviate from the other genera in having no teeth on the second upper pharyngeal. *Eleutherochir* deviates from the other genera in having almost fused upper pharyngeals.

In summary, the branchial apparatus in *Anaora* and *Eleutherochir* is very specialized, and in *Paracallionymus* and *Foetorepus* it is somewhat specialized.

#### 7) Suspensolium and opercular apparatus (Figs. 28–39, Table 5)

The suspensolium in the callionymids is composed of five elements; palatine, ectopterygoid, quadrate, hyomandibular and symplectic. The opercular apparatus is composed of four elements; opercle, subopercle, preopercle and interopercle. Neither endopterygoid nor metapterygoid are present in this family.

**Palatines:** Each palatine is a gooseneck bone in the anterior part of the suspensolium, and is joined to the ectopterygoid rigidly by connective tissue posteriorly. The anterior tip of the head of the palatine is filled with cartilage. The middle part of the head of the palatine is connected to the posterior discal cartilage of the maxillary by a ligament.

**Ectopterygoid:** Each ectopterygoid is a stout bone which functions as a strut in the anterior part of the suspensolium and joins the palatine to the quadrate rigidly by connective tissue.

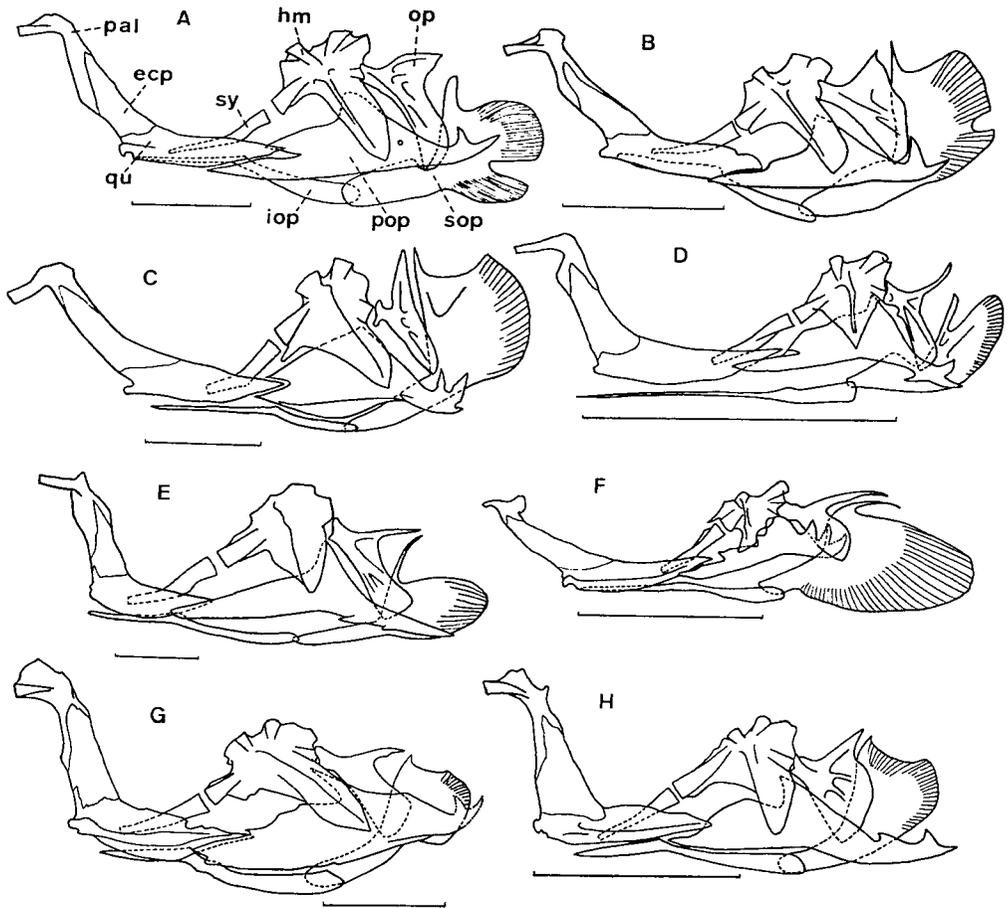


Fig. 28. Lateral view of the left suspensolium and opercular apparatus in eight callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Callionymus maculatus*; D, *Anaora tentaculata*; E, *Dactylopus dactylopus*; F, *Eleutherochir mirabilis*; G, *Neosynchiropus ocellatus*; H, *Pterosynchiropus splendidus*. ecp, ectopterygoid; hm, hyomandibular; iop, interopercle; op, opercle; pal, palatine; pop, preopercle; qu, quadrate; sop, subopercle; sy, symplectic. Scales indicate 5 mm.

**Quadrates:** Each quadrate is a stout elongate bone which forms the ventral part of the suspensolium. It is joined to the articular at the anterior tubercular process by connective tissue, and connects the preopercle posteriorly by connective tissue. Each quadrate carries a ventral ramus of the preoperculomandibular canal on its ventral surface.

**Hyomandibulars:** Each hyomandibular is a large leaf-shaped bone which joins the cranium to the other bones of the suspensolium and opercular apparatus. There is a middle longitudinal ridge on the abaxial surface, and four processes filled with cartilage at the tips. The anterior dorsal process contacts the facet on the sphenotic, and the posterior dorsal process contacts the facet on the pterotic, both by connective tissue. The anterior ventral process joins the symplectic, and the

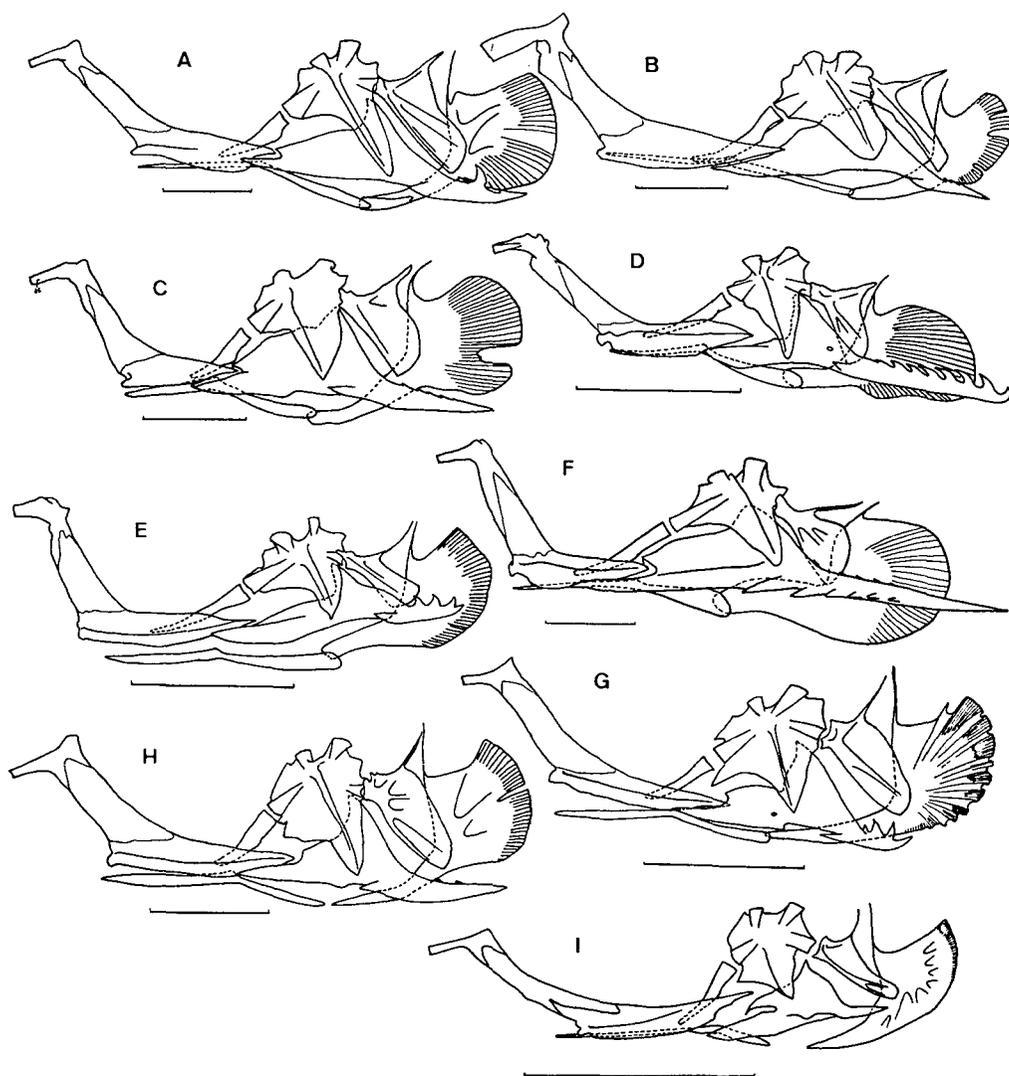


Fig. 29. Lateral view of the left suspensolium and opercular apparatus in nine callionymid species. A, *Bathycallionymus kaianus*; B, *Pseudocalliorichthys variegatus*; C, *Calliorichthys japonicus*; D, *Diplogrammus xenicus*; E, *Paradiplogrammus enneactis calliste*; F, *Spinicapitichthys spiniceps*; G, *Repomucenus valenciennei*; H, *Repomucenus huguenini*; I, *Paracallionymus costatus*. Scales indicate 5 mm.

posterior ventral process the opercle by connective tissue. Each hyomandibular is joined ventrally with the dorsal part of the preopercle by connective tissue.

Symplectics: Each symplectic is a small elongate conical bone filled with cartilage at both its tips. It joins the mid-adaxial surface of the quadrate with the hyomandibular by connective tissue.

Opercles: Each opercle is a flattened bone with a soft retrorse spine at its posterodorsal end. The anterior process of the opercle joins the hyomandibular by

connective tissue. This part is joined by ligaments to the dorsolateral edge of the sphenotic anterodorsally, to the dorsolateral process of the pterotic posterodorsally and to the middle abaxial part of the preopercle.

In *Foetorepus*, *Eocallionymus*, *Callionymus*, *Anaora*, *Dactylopus*, *Eleutherochir*, *Neosynchiropus*, *Pterosynchiropus*, *Bathycallionymus*, *Pseudocalliurichthys*, *Calliurichthys* and *Diplogrammus*, the soft retrorse spine is not filamentous (Figs. 28, 29 A-D), but in *Paradiplogrammus*, *Spinicapitichthys*, *Repomucenus* and *Paracallionymus*, it is (Fig. 29 E-I).

Subopercles: Each subopercle is a broad thin bone located in the posterior part of the opercular apparatus. The subopercle has a soft upward spine dorsally, with a fan-shaped lamella that is broad and thin posteriorly. There is a ramus anteroventrally which is connected to the posterior edge of the interopercle.

In *Foetorepus*, *Eocallionymus*, *Callionymus*, *Anaora*, *Dactylopus*, *Eleutherochir*, *Neosynchiropus* and *Pterosynchiropus*, the soft upward spine is not filamentous (Fig. 28), but in *Bathycallionymus*, *Pseudocalliurichthys*, *Calliurichthys*, *Diplogrammus*, *Paradiplogrammus*, *Spinicapitichthys*, *Repomucenus* and *Paracallionymus*, the soft dorsal spine is (Fig. 29).

Interopercles: Each interopercle is a very slender elongate bone located in the anteroventral part of the opercular apparatus. The posterior half of the interopercle turns slightly downward at the middle corner where the interopercle is connected to the abaxial posterior end of the epiphyal by a ligament. The anterior tip is joined to the anteroventral process of the retroarticular by a ligament.

In *Paracallionymus* and some species of *Repomucenus*, the posterior tip is indirectly connected to the anteroventral ramus of the subopercle (Fig. 29H-I); but, in most genera, the posterior tip is connected directly to it (Figs. 28, 29A-G).



Fig. 30. The left preopercular spine in *Paracallionymus costatus*. Scale indicates 2 mm

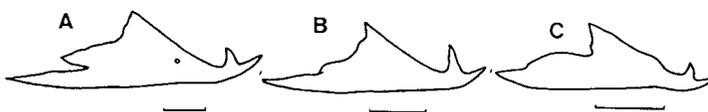


Fig. 31. The left preopercular spine in three callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Neosynchiropus ocellatus*. Scales indicate 2 mm.



Fig. 32. The left preopercular spine in two callionymid species. A, *Neosynchiropus ijimai*; B, *Anaora tentaculata*. Scales indicate 2 mm.

**Preopercles:** The preopercle is a somewhat triangular bone with a strong retrorse spine. It is joined to the adaxial ventral surface of the hyomandibular dorsally and to the posterior part of the quadrate anteriorly by connective tissue. It is connected to the dorsal ridge of the pterotic and the posttemporal by strong ligamentous tissue which extends as a very thin layer to the cheek and snout region (Fig. 10A). The preoperculomandibular canal runs along this strong ligamentous tissue and passes transversely through the mid-abaxial lateral edge of the preopercle. In species with an antrorse process at the base of the preopercular spine, the canal runs between the mid-abaxial lateral edge of the preopercle and the antrorse preopercular process.

There are twelve types of preopercular spine. In *Paracallionymus*, it is very

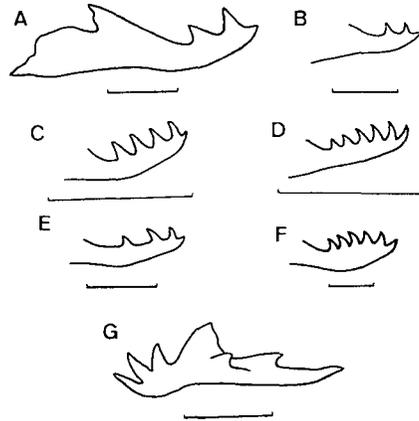


Fig. 33. The right and left preopercular spine in six callionymid species. A, *Pterosynchiropus splendidus*; B, *Diplogrammus pauciradiatus*; C, *Paradiplogrammus* sp.; D, *Minysynchiropus laddi*; E, *Eleutherochir opercularis*, young specimen; F, *E. opercularis*, adult; G, *Eleutherochir mirabilis*. Scales indicate 2 mm.

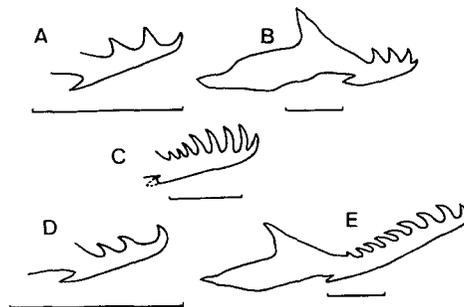


Fig. 34. The left preopercular spine in three callionymid species. A, *Paradiplogrammus enneactis calliste*, young specimen; B, *P. enneactis calliste*, adult; C, *Paradiplogrammus corallinus*; D, *Diplogrammus xenicus*, young specimen; E, *D. xenicus*, adult. Scales indicate 2 mm.



Fig. 35. The left preopercular spine in *Synchiropus ornatus*. Scale indicates 2 mm.

simple and only pointed posteriorly (Type A, Fig. 30). In *Foetorepus* (except *F. phasis* and *F. apricus*), *Eocallionymus* and *Neosynchiropus ocellatus*, there is no antrorse process at the base, but an upward one on the inner side (Type B, Fig. 31). In *Neosynchiropus ijimai* and *Anaora*, there is an antrorse process at the base and an upward one on the inner side (Type C, Fig. 32). In *Neosynchiropus* (except *N. ocellatus* and *N. ijimai*), *Diplogrammus pauciradiatus*, *D. dubiosus*, *Callionymus risso*, *C. pusillus*, *Paradiplogrammus* sp. (from Australia), *Minysynchiropus* and *Eleutherochir*, there is no antrorse process at the base, but several upward processes on the inner side. The posterior tip is not elongate, and in the last three it markedly curves upward (Type D, Fig. 33). In *Paradiplogrammus* (except *P. sp*) and *Diplogrammus* (except *D. pauciradiatus* and *D. dubiosus*), there is an antrorse process at the base and several upward processes on the inner side. The posterior tip markedly curves upward, in young as well as mature specimens (Type E, Fig. 34). In *Synchiropus* (except some species), there is no antrorse process at the base, but two upward processes on the inner side; the posterior tip is elongate and slender (Type F, Fig. 35). In some species of *Synchiropus* (Ninni, 1934; Fricke, 1981), *Orbonymus*, *Calliurichthys* and *Pseudocalliurichthys*, it is straight and elongate with an antrorse process at the base and several short processes on the inner side. In young specimens, *Calliurichthys japonicus* has a straight and elongate spine with some small processes on the inner side; *Pseudocalliurichthys variegatus* has a straight and rather short spine with some large processes on its inner side (Type G, Fig. 37 A-F). In *Bathycallionymus* and *Callionymus* (except *C. risso* and *C. pusillus*), there is an antrorse process at the base and one or two upward barbed processes on the upper side. In young specimens of *Bathycallionymus*, the processes are not barbed and the posterior tip is elongate and slender (Type H, Fig. 36). In *Repomucenus* (except *R. belcheri*), the spine curves slightly inward with an antrorse process at the base and

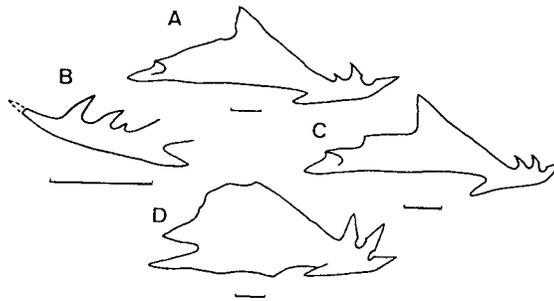


Fig. 36. The right and left preopercular spine in three species. A, *Bathycallionymus kaianus*; B, *Bathycallionymus sokonumeri*, young specimen; C, *B. sokonumeri*, adult; D, *Callionymus lyra*. Scales indicate 2 mm.

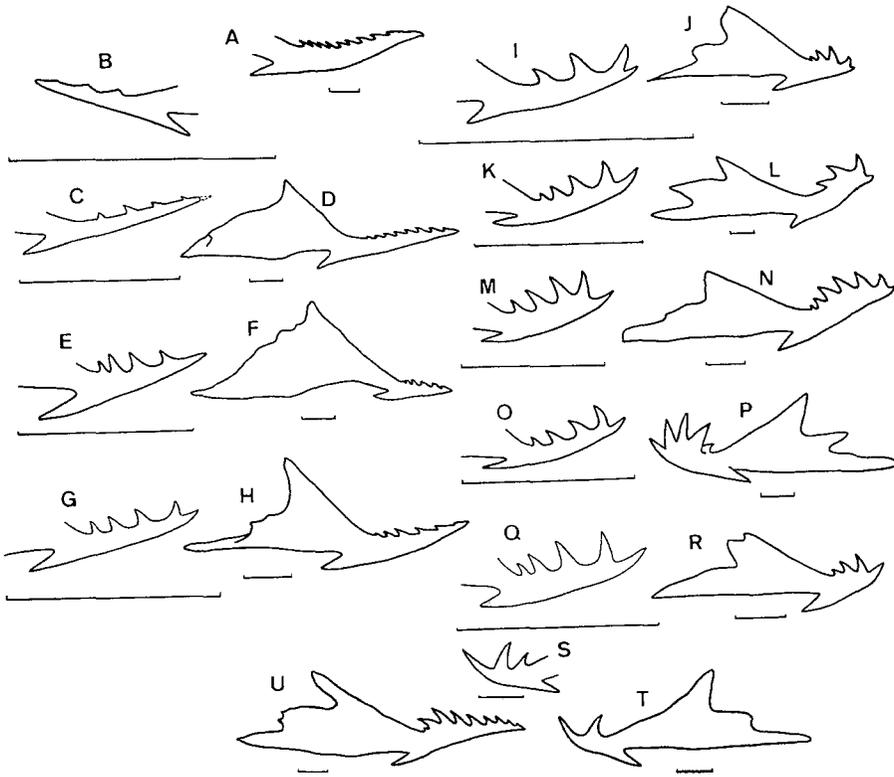


Fig. 37. The right and left preopercular spine in eleven callionymid species. A, *Orbovymus rameus*; B, *Calliurichthys japonicus*, young specimen (16.2 mm in standard length); C, *C. japonicus*, young specimen (21.6 mm); D, *C. japonicus*, adult; E, *Pseudocaliurichthys variegatus*, young specimen; F, *P. variegatus*, adult; G, *Repomucenus huguenini*, young specimen; H, *R. huguenini*, adult; I, *Repomucenus virgis*, young specimen; J, *R. virgis*, adult; K, *Repomucenus richardsonii*, young specimen; L, *R. richardsonii*, adult; M, *Repomucenus planus*, young specimen; N, *R. planus*, adult; O, *Repomucenus beniteguri*, young specimen; P, *R. beniteguri*, adult; Q, *Repomucenus valenciennesi*, young specimen; R, *R. valenciennesi*, adult; S and T, *Repomucenus* sp. 3.; U, *Repomucenus belcheri*. Scales indicate 2 mm.

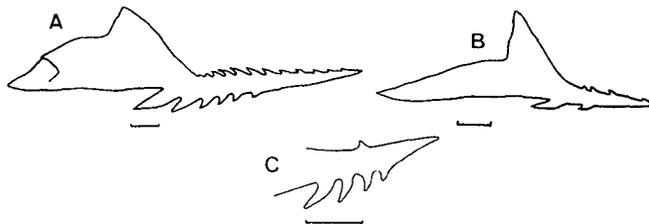


Fig. 38. The left preopercular spine in two callionymid species. A, *Spinicapitichthys spiniceps*; B and C, *Dactylopus dactylopus*. Scales indicate 2 mm.

several processes on the inner side. Several variations are seen in *Repomucenus*. *R. huguenini* has an elongate spine with many small processes on its inner side. *R. virgis* and *R. valenciennae* have very short spines. *R. richardsonii* has a slightly S-shaped spine. *R. planus* has a stout and elongate spine, and *R. beniteguri* has a very short one with several large processes on its inner side. But, in young specimens of these species, the preopercular spines are alike; elongate and curved inward slightly with several large upward processes on the inner side. *R. sp. 3* has only one or two upward processes on the inner side (Type I, Fig. 37G-T). In *Repomucenus belcheri*, the spine is stout and curves outward with an antrorse process at the base and many small upward processes on the inner side (Type J, Fig. 37U). In *Spinicapitichthys*, it is straight and elongate with many short processes on both the outer and inner sides (Type K, Fig. 38A). In *Dactylopus*, the spine is stout and elongate with several processes on the outer side and several very small processes on the inner side (Type L, Fig. 38B-C).

*Discussion.* The suspensolium and opercular apparatus have been studied by Briggs and Berry (1959), Kayser (1962) and Gosline (1970). But their descriptions are not detailed enough to determine the relationships among the genera.

The filamentous ends of the retrorse process of the opercle and the upward process of the subopercle are both more advanced than the non-filamentous ends because most other standard percoid fishes do not have filamentous ends. Therefore,

Table 5. Characters' conditions of the suspensolium and opercular apparatus in callionymid genera.

	OP	SOP	CSI	POS
<i>Callionymus</i>		not filamentous		D, H
<i>Bathycallionymus</i>	not filamentous	filamentous	directly	H
<i>Foetorepus</i>		not filamentous		B, D
<i>Eocallionymus</i>				B
<i>Paracallionymus</i>	filamentous	filamentous	indirectly	A
<i>Neosynchiropus</i>	not filamentous	not filamentous	directly	B, C, D
<i>Pterosynchiropus</i>				D
<i>Minysynchiropus</i>	--	--	--	
<i>Paradiplogrammus</i>	filamentous	filamentous	directly	D, E
<i>Diplogrammus</i>	not filamentous			
<i>Synchiropus</i>	--	--	--	F, G
<i>Orbonymus</i>	--	--	--	G
<i>Dactylopus</i>		not filamentous		L
<i>Calliurichthys</i>	not filamentous		directly	G
<i>Pseudocalliurichthys</i>		filamentous		
<i>Repomucenus</i>	filamentous		directly or indirectly	I, J
<i>Spinicapitichthys</i>				K
<i>Anaora</i>			directly	C
<i>Eleutherochir</i>	not filamentous	not filamentous		D

Abbreviations: CSI, connection between subopercle and interopercle; OP, retrorse spine of opercle; POS, preopercular spine; SOP, retrorse spine of subopercle.

in the opercle, *Paracallionymus*, *Paradiplogrammus*, *Repomucenus* and *Spinicapitichthys* are more specialized than the others. In the subopercle, *Paracallionymus*, *Diplogrammus*, *Paradiplogrammus*, *Bathycallionymus*, *Calliurichthys*, *Pseudocalliurichthys*, *Repomucenus* and *Spinicapitichthys* are more specialized.

*Paracallionymus* and some species of *Repomucenus* are specialized in the connection between the interopercle and the subopercle because most percoid fish do not have this character.

Of the bones in the opercular apparatus, the shape of the preopercular spine has been discussed most often in the classification of genera (Gill, 1860; Jordan and Fowler, 1903; MuCulloch, 1926; Schultz and Woods, 1948; Ochiai *et al.*, 1955; Smith, 1963; Mees, 1963; Fricke, 1980). But none of these descriptions give a definitive systematic value for the preopercular spine.

Some taxonomists have discussed the biological meaning of the preopercular spine in the callionymids. Kato (1936) suggested that the male and female of *Repomucenus richardsonii* intertwine their preopercular spines during spawning, but Holt (1898), who reported the spawning behavior of *Callionymus lyra*, did not mention the preopercular spine. Takita and Okamoto (1979) stated that they could not find the behavior suggested by Kato. Fricke (1980) suggested that the peculiar

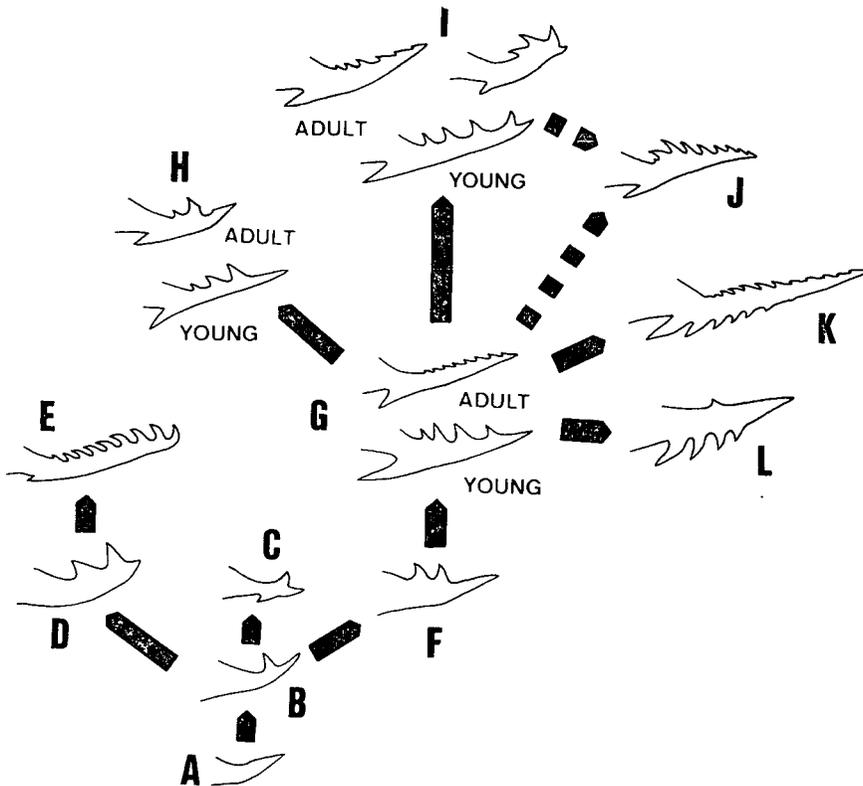


Fig. 39. Hypothetical differentiation of the callionymid preopercular spine.

preopercular spine in the family might be used for protection against predators; when a predator catches a dragonet by the head, the latter raises its preopercular spine which sticks into the mouth of the enemy. Usuki (1979) has published a photograph in which *Trachinocephalus miops* is shown swallowing *Repomucenus richardsonii* head first. Therefore, I agree with Fricke (1980) that the development of the callionymid's preopercular spine from a simple to a more complicated stout form is a biological adaptation for protection from predators. I can not, however, agree with him as to the order of development.

The proposed differentiation of the preopercular spines based on my examinations, are shown in Fig. 39. Type A is the most primitive because it has the simplest form. Type B must be derived from Type A; it is more complex with an upward process on its inner side. Type C must be derived from Type B because of the addition of an antrorse process at its base. Type D is derived from Type B because it has more upward processes on its inner side. Type E must be derived from Type D as it has an additional antrorse process at the base and a posterior tip curved strongly upward, which is seen in some species of Type D. Type F must be derived from Type B because of its slender elongate posterior tip and the two upward processes on its inner side. Type G is apparently derived from Type F because of the antrorse process at the base and several upward processes on the inner side as well as its long, slender posterior end. The resemblance between young specimens of *Bathycallionymus* and *Pseudocalliurichthys* indicates that Type H is derived from Type G. Since the preopercular spine of the young *Repomucenus* (except *R. belcheri*) is very similar to that of Type G, Type I must be derived from Type G; in addition, Type I is more stout than Type G. The preopercular spine of *Paradiplogrammus enneactis calliste* in Type E is somewhat like that of *Repomucenus valenciennesi* in Type I, but they are not related, because specimens of their young have very different preopercular spines. Type J may be derived from Type G or I, as it is allied to those types and more stout. Type K is derived from Type G because it has more antrorse processes on the outer side than G. Type L is more like Type K than G. It is more complex than Type G, but less than Type K. Thus, Types K and L are not related. Type L is derived from Type G.

The preopercular spine is a good character to use for the determination of the phylogenetic relationships among the genera of the callionymids, if its condition is more advanced. The morphological variety of the preopercular spine is not correlated to that of body form. If some groups share the advanced complex shapes of the preopercular spine, they must be closely related each other; the probability which some quite unrelated groups share very similar complex shapes of it must be very low.

#### 8) Shoulder girdle (Figs. 1-9, 40-43, Table 6)

The shoulder girdle of the callionymids is composed of seven elements; posttemporal, supracleithrum, cleithrum, postcleithrum, scapula, coracoid and actinost. No supratorpals are present in this family.

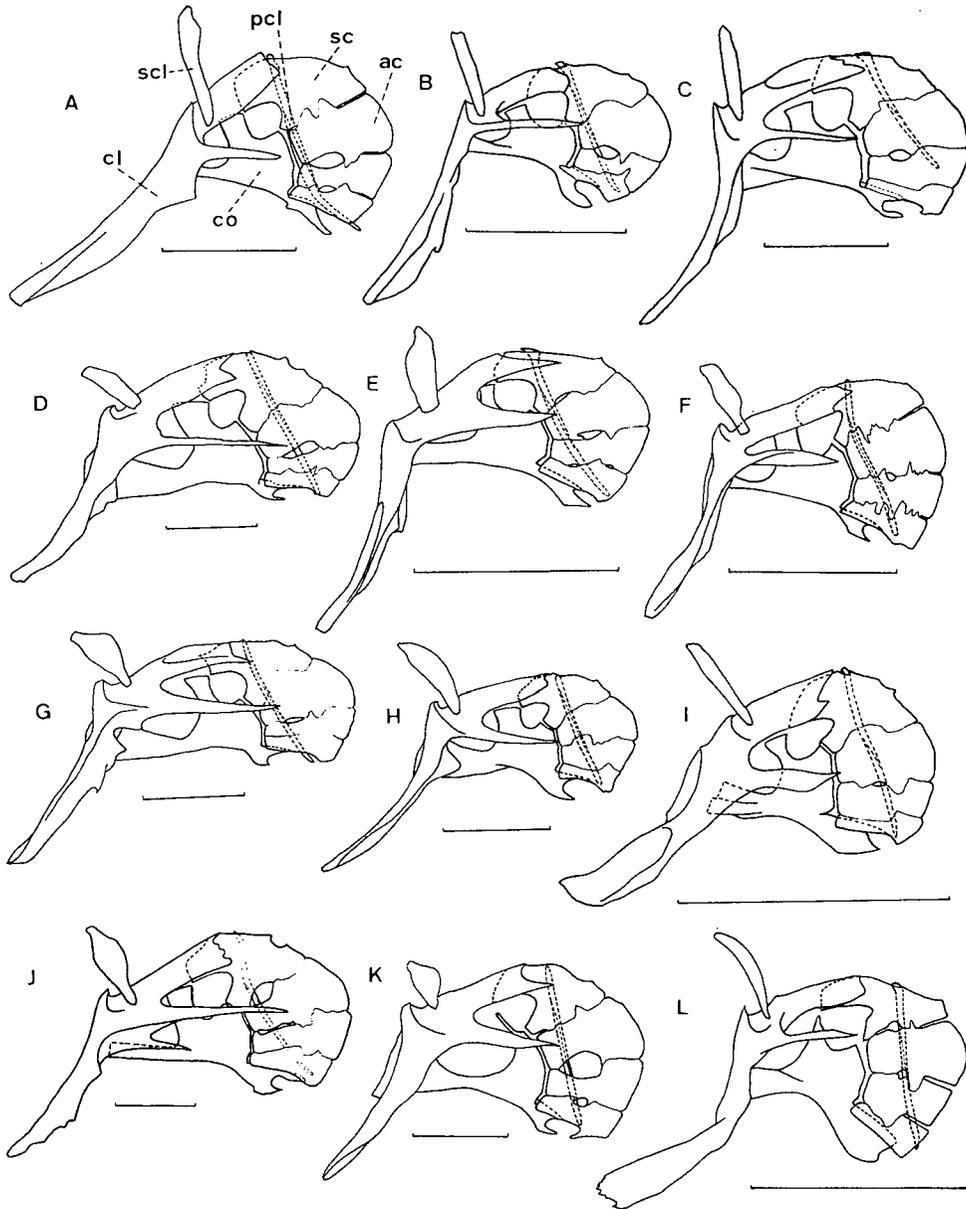


Fig. 40. Lateral view of the left shoulder girdle in twelve callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Callionymus maculatus*; D, *Bathycallionymus kaianus*; E, *Diplogrammus xenicus*; F, *Paradiplogrammus enneactis calliste*; G, *Calliurichthys japonicus*; H, *Repomucenus huguenini*; I, *Paracallionymus costatus*; J, *Spinicapitichthys spiniceps*; K, *Pseudocalliurichthys variegatus*; L, *Eleutherochir mirabilis*. ac, actinost; co, coracoid; cl, cleithrum; pcl, postcleithrum; sc, scapula; scl, supra-cleithrum. Scales indicate 5 mm.

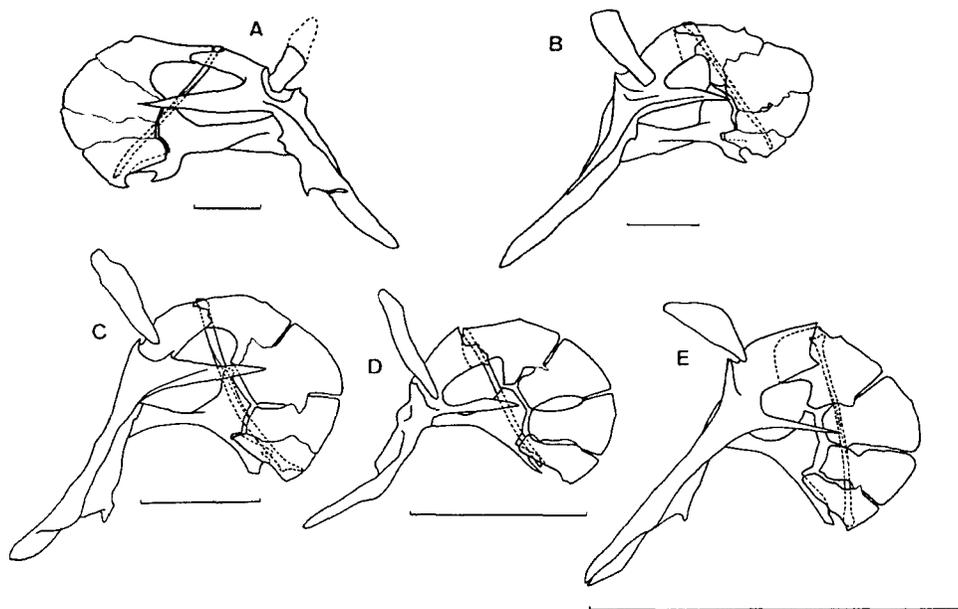


Fig. 41. Lateral view of right and left shoulder girdle in five callionymid species. A, *Orbonymus rameus*; B, *Dactylopus dactylopus*; C, *Neosynchiropus ocellatus*; D, *Pterosynchiropus splendidus*; E, *Anaora tentaculata*. Scales indicate 5 mm.

**Posttemporals:** Each posttemporal is rigidly attached to the pterotic, epiotic and exoccipital. It has notch posterodorsally that articulates with the supracleithrum.

In *Foetorepus*, *Eocallionymus*, *Diplogrammus*, *Neosynchiropus*, *Pterosynchiropus*, *Anaora* and *Dactylopus*, the notch opens horizontally (Figs. 1, 2B, 4, 5). In *Paradiplogrammus*, it opens obliquely (Fig. 2A). In *Callionymus*, *Bathycallionymus*, *Pseudocalliurichthys*, *Calliurichthys*, *Repomucenus*, *Paracallionymus*, *Spinicapitichthys* and *Eleutherochir*, it opens vertically (Figs. 3, 6–9).

**Supracleithra:** Each supracleithrum is an elongate bone articulated with the posttemporal dorsally and the anterodorsal part of the cleithrum ventrally by connective tissue.

**Cleithra:** Each cleithrum is a large bone with three rami. The anteroventral ramus expands laterally to form a broad plate, and is joined to its opposite at the anteroventral part by a small mass of cartilage. The dorsal ramus is somewhat expanded dorsolaterally, and its posterior end is connected to the scapula ventrally. The middle ramus has a pointed end which extends near the origin of the first actinost or beyond it.

In *Neosynchiropus* and *Pterosynchiropus*, the broad plate of the anteroventral ramus is so narrow that it retreats near the middle part of the cleithrum; its tip pointed (Fig. 43A·B). In the other genera, this broad plate is well developed (Figs. 42, 43C).

**Postcleithra:** Each postcleithrum is a very slender needle-shaped bone separated into two parts. The upper part contacts the posterodorsal corner of the scapula and the posterodorsal corner of the cleithrum with the intervention of a small mass of

cartilage. The lower part is free in the muscle.

Scapulas: The scapula is a forked bone which forms a large foramen with the coracoid. The dorsal ramus is expanded somewhat dorsolaterally and makes a pent roof inward. The ventral ramus is expanded vertically and is joined rigidly to the dorsal edge of the first actinost by connective tissue ventrally and to the posterodorsal edge of the coracoid by cartilage.

Coracoids: Each coracoid is a large bone that supports the actinosts with the intervention of cartilage. The posteroventral ramus supports the ventral part of the third actinost.

In *Foetorepus*, *Eocallionymus*, *Callionymus*, *Bathycallionymus*, *Diplogrammus*, *Paradiplogrammus*, *Calliurichthys*, *Repomucenus*, *Paracallionymus* and *Spinicapitichthys*, the dorsal part of the coracoid has a large process joined to the ventral part of the dorsal ramus of the cleithrum and the anterior tip of the dorsal ramus of the scapula by cartilage; it forms two large foramina with the cleithrum and the scapula (Type A, Fig. 40A-J). In *Pseudocalliurichthys* and *Eleutherochir*, this process is very slender and does not connect with the cartilage of the anterior edge of the dorsal ramus of the scapula (Type B, Fig. 40K-L). In *Orbonymus*, *Dactylopus*, *Neosynchiropus*, *Pterosynchiropus* and *Anaora*, no process is present at the dorsal edge of the coracoid (Type C, Fig. 41).

Actinosts: There are three actinosts in callionymid fishes. They are broad filled with cartilage at their edges, and with pectoral fin rays posteriorly. The pectoral fin base extends to the posterior lower edge of the scapula.

*Discussion.* A pronounced character of the shoulder girdle in the callionymids

Table 6. Characters' conditions of the shoulder and pelvic girdles in callionymid genera.

	PT	CL	CO	PV
<i>Callionymus</i>	vertically			
<i>Bathycallionymus</i>	—			
<i>Foetorepus</i>	horizontally	broad	A	expanded
<i>Eocallionymus</i>	—			
<i>Paracallionymus</i>	vertically			
<i>Neosynchiropus</i>	horizontally	narrow	C	pointed
<i>Pterosynchiropus</i>	—			
<i>Paradiplogrammus</i>	obliquely		A	
<i>Diplogrammus</i>	horizontally			
<i>Orbonymus</i>	—		C	
<i>Dactylopus</i>	horizontally			
<i>Calliurichthys</i>			A	expanded
<i>Pseudocalliurichthys</i>	vertically	broad	B	
<i>Repomucenus</i>			A	
<i>Spinicapitichthys</i>				
<i>Anaora</i>	horizontally		C	pointed
<i>Eleutherochir</i>	vertically		B	expanded

Abbreviations: CL, anteroventral ramus of the cleithrum; CO, coracoid; PT, posttemporal; PV, anterior ramus of the pelvic bone.

is its vertical expansion due to the large pectoral fin. Dragonets make great use of their pectoral and pelvic fins when swimming upward for spawning (Takita and Okamoto, 1979), and my observations show that they swim along the sea bottom with a creeping motion that comes mainly from the use of their pectoral and pelvic fins. This large shoulder girdle must be related to their peculiar form of swimming.

The shoulder girdle of the callionymids has been described by Briggs and Berry (1959) and Ochiai (1963), but their reports are not detailed enough to use for the determination of the relationships among the genera.

The broad expanded anteroventral ramus of the cleithrum in most genera is correlated to a depressed body of the callionymids; it shows one of adaptive characters to the benthic life. The pointed anteroventral ramus in *Neosynchiropus* and *Pterosynchiropus* shows one of evidences that the two deeper body genera (Nakabo, 1982, p. 118) must have derived from those having depressed body.

In terms of the coracoid, Type A is the most primitive. Types B and C are specialized; Type C more so than B. Most percoid fishes have a scapula-foramen for nerves and blood vessels on the center of the scapula, and a semicircle foramen between the lower part of the cleithrum and the coracoid. In the Type A coracoid, there are two foramina as in most percoid fishes, but the ventral foramen is larger and the scapula-foramen is lower and surrounded by the scapula and coracoid. In Type C, these two foramina seem to have become one. Type B is intermediate between Types A and C. Two Type B coracoids seem to be not closely related each other because their degenerate upward processes are quite different in shape. This is evidence that not all the coracoids in Type C are derived from the same ancestor; Type C represents only a more specialized condition.

#### 9) Pelvic girdle (Figs. 42, 43, Table 6)

Pelvic bones: Each pelvic bone is large and expanded horizontally. There are three rami: the anterior, middle and posterior. In most genera (except *Neosynchiropus*, *Pterosynchiropus* and *Anaora*) the anterior ramus is expanded and forms a broad and thin bony lamina under the anteroventral ramus of the cleithrum (Fig. 42). In *Neosynchiropus*, *Pterosynchiropus* and *Anaora*, the anterior ramus is pointed and forms a less bony plate than in the other genera (Fig. 43). The middle ramus with cartilage along its edge extends inward and is joined to its opposite by connective tissue. It expands upward transversely like a triangle and is joined to the ventral surface of the middle part of the cleithrum at the abaxial edge by connective tissue. The posterior ramus expands to a forked end.

Each pelvic bone has a spine and five rays at the posterior half of the abaxial edge.

*Discussion.* No one has described the pelvic girdle of the callionymids. The pelvic bone is characteristically much wider horizontally in order to support the large pelvic fin. The plate-like anterior ramus seems to correspond to the anterior abaxial edge of the pelvic bone in compressed-form percoid fish. This horizontal

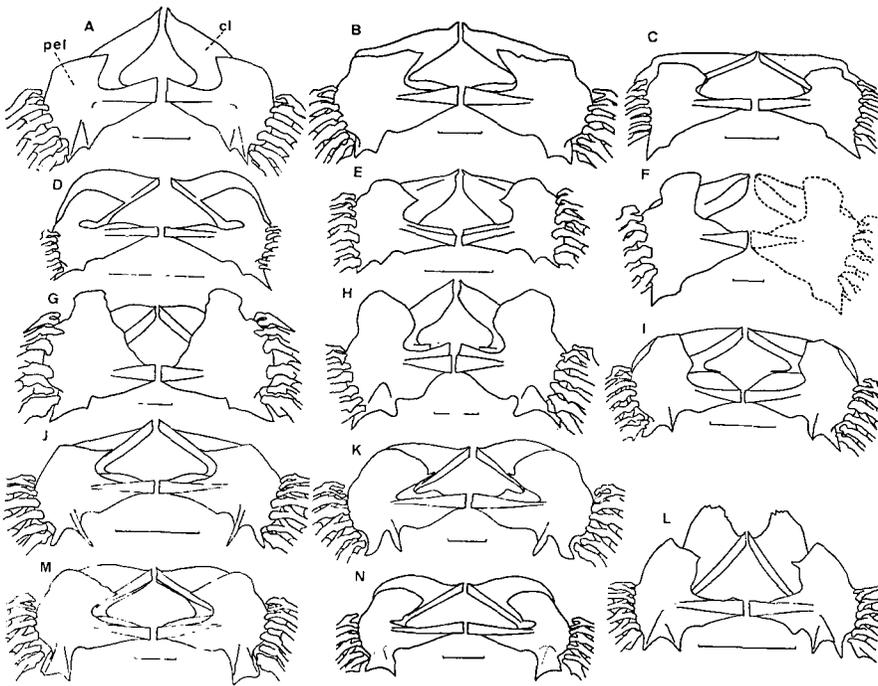


Fig. 42. Ventral view of the pelvic girdle in fourteen callionymid species. A, *Foetorepus altivelis*; B, *Bathycallionymus kaianus*; C, *Callionymus maculatus*; D, *Paracallionymus costatus*; E, *Eocallionymus papilio*; F, *Orbonymus rameus*; G, *Dactylopus dactylopus*; H, *Spinicapitichthys spiniceps*; I, *Poradiplogrammus enneactis calliste*; J, *Diplogrammus xenicus*; K, *Pseudocallurichthys variegatus*; L, *Eleutherochir mirabilis*; M, *Callurichthys japonicus*; N, *Repomucenus huguenini*. cl, cleithrum; pel, pelvic bone. Scales indicate 3 mm.

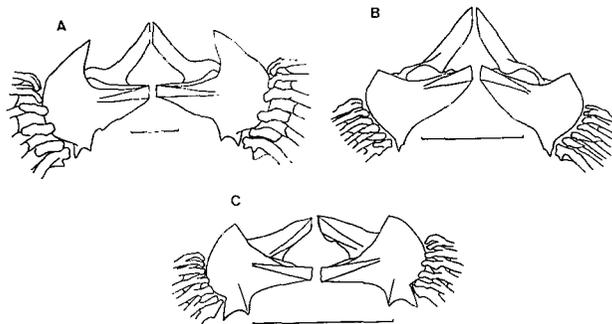


Fig. 43. Ventral view of the pelvic girdle in three callionymid species. A, *Neosynchiropus ocellatus*; B, *Pterosynchiropus splendidus*; C, *Anaora tentaculata*. Scales indicate 3 mm.

expansion of the pelvic bone of the callionymids is due to their complete benthic life, which has been described for the flatheads by Matsubara and Ochiai (1955) and for the macrouroids by Okamura (1970).

The three genera with pointed anterior ramus, *Neosynchiropus*, *Pterosynchiropus* and *Anaora*, have greater body depth than the other genera (Nakabo, 1982, p. 118);

Table 7. Frequency distribution in counts of the vertebrae (abdominal and caudal) and epipleurals in callionymid species.

	AV		CV						REP					LEP											
	7	11	12	13	14	15	16	17	18	AT				NAT					AT			NAT			
										5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4
<i>Callionymus lyra</i>	9				9						3	1			4						7				6
<i>C. pusillus</i>	6				6						6				1						6				
<i>C. maculatus</i>	3				3						3				3						3				3
<i>C. risso</i>	3				3						2	1									3				1
<i>C. reticulatus</i>	3				3						3				3						3				3
<i>Bathycallionymus kaianus</i>	19			1	18						18	1			1						19				1
<i>B. sokonumeri</i>	10				10						9	1									9	1			
<i>B. moretonensis</i>	11				11						11										11				
<i>B. regani</i>	10				10						9										9				
<i>B. formosanus</i>	15				15						15										15				
<i>Foetorepus calaulopomus</i>	2				2							2										2			
<i>F. altivelis</i>	19				19						7	12			6						7	12			7
<i>F. phaeton</i>	3				3						3										3				
<i>F. phasis</i>	1				1							1										1			
<i>F. agassizi</i>	1					1					1										1				1
<i>F. monacanthus</i>	1				1							1										1			
<i>F. delandi</i>	10				10						4	7			2						4	6			2
<i>F. kamoharai</i>	2				2							2									1	1			1
<i>F. sp. 1</i>	1				1							1										1			
<i>F. sp. 2</i>	1				1							1										1			
<i>F. sp. 3</i>	2				2						2										2				
<i>Eocallionymus papilio</i>	6				6							5			1							5	1		
<i>Paracallionymus costatus</i>	2				2						2										2				1
<i>Neosynchropus ocellatus</i>	22				22						19	2		9							18	3		10	
<i>N. rubrovinctus</i>	1					1						1										1			
<i>N. ijimai</i>	7				7						7			2							7				2
<i>N. morrisoni</i>	2				2						2											2			

Abbreviations: AT, epipleurals attached to the vertebrae; AV, abdominal vertebrae; CV, caudal vertebrae; LEP, left epipleurals; NAT, epipleurals not attached to the vertebrae; REP, right epipleurals.

Table 7. Continued.

	AV		CV						REP										LEP								
									AT			NAT							AT			NAT					
	7	11	12	13	14	15	16	17	18	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6
<i>Pterosynchiropus picturatus</i>	4		1	3							4								4		1						
<i>P. splendidus</i>	3			3							3								3								
<i>M. laddi</i>	9			1	8					1	7								1	7							
<i>Paradiplogrammus bairdi</i>	13				13						10								9	1							
<i>P. enneactis calliste</i>	30				30					1	26	1							28			1					
<i>P. corallinus</i>	1				1						1								1								
<i>P. sp.</i>	5				5						5								5								
<i>Diplogrammus goramensis</i>	2				2						2								2								
<i>D. pauciradiatus</i>	6	6									2	2	2	3					2	2	2	3					
<i>D. xenicus</i>	17				17						14	1							15								
<i>D. dubiosus</i>	11	10	1								2	9		6					2	9		5					
<i>Synchiropus ornatus</i>	1				1						1		1						1		1						
<i>Orbonymus rameus</i>	3				3						2	1					2	1	3					2		1	
<i>Dactylopus dactylopus</i>	2				2						2								2								
<i>Calliurichthys japonicus</i>	21				20	1					21								21								
<i>C. margaretae</i>	19				19						19								19								
<i>C. maldivensis</i>	2				2						2								2								
<i>C. gardineri</i>	2				2						2								2								
<i>C. grossi</i>	1				1						1								1								
<i>C. scaber</i>	1				1						1								1								
<i>C. scabriceps</i>	1			1							1								1								
<i>Pseudocalliurichthys variegatus</i>	5				5						5								5								
<i>P. xanthosemeion</i>	8				8						8								7								
<i>P. goodladi</i>	7				7						7								7								
<i>Repomucenus sagitta</i>	1					1					1								1								
<i>R. filamentosus</i>	10				10				1		9								10								
<i>R. belcheri</i>	22				22						22			1					21	1		1					
<i>R. valenciennei</i>	19				19						19								19								
<i>R. lunatus</i>	20				20				1		19								20								

Table 7. Continued.

	AV		CV						REP										LEP								
									AT				NAT						AT			NAT					
	7	11	12	13	14	15	16	17	18	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6
<i>R. schaapii</i>	4				4					4									4								
<i>R. richardsonii</i>	23				23					23									23			1					
<i>R. huguenini</i>	20				20					20									20								
<i>R. olidus</i>	2				2					2									2								
<i>R. calcaratus</i>	7				7					7									7								
<i>R. benteguri</i>	40			1	39					18									33			1					
<i>R. virgis</i>	20				18	2				20									20								
<i>R. ornatipinnis</i>	26				25	1				24	2		2						25	1							
<i>R. limiceps</i>	14				14					14									14								
<i>R. macdonaldi</i>	15			1	14					15									15								
<i>R. marleyi</i>	2				2					2									2								
<i>R. sublaevis</i>	4				4					4									4								
<i>R. umbrihorax</i>	1				1					1									1								
<i>R. maricinensis</i>	1				1					1									1								
<i>R. longi</i>	1				1					1									1								
<i>R. brunneus</i>	7				7					7									7								
<i>R. punctilateralis</i>	3				3					3									3								
<i>R. leucobranchialis</i>	10				10					10									10								
<i>R. planus</i>	18				17	1			1	17									18								
<i>R. russelli</i>	5				5					5									5								
<i>R. sp. 1</i>	4				4					4									4								
<i>R. sp. 2</i>	3				3					3									3								
<i>R. sp. 3</i>	12				12					12									11	1							
<i>Spinicapitichthys spiniceps</i>	9				9					9									8	1							
<i>S. draconis</i>	1				1					1									1								
<i>Anaora tentaculata</i>	14			14						1	7	1			1				1	7		2					
<i>Eleutherochir opercularis</i>	2				2							1									1						
<i>E. mirabilis</i>	23							21	2			18	5	1					18	5	1						

evidence that the pointed anterior ramus and greater body depth are correlated.

#### 10) Vertebral column (Figs. 44–59, Tables 7, 8)

The vertebral column in the callionymids is very depressed, with many bifid neural and hemal spines. No pleural ribs are present in the family. Instead, the epipleural ribs are stout and cover the abdominal cavity. There are three types of columns: moderately depressed, depressed and strongly depressed.

To distinguish between the abdominal and caudal vertebrae, the vertebra with the first expanded or elongate hemal spine should be called the first caudal vertebra. In *Foetorepus*, *Eocallionymus*, *Synchiropus*, *Neosynchiropus*, *Orbonymus*, *Dactylopus*, *Paracallionymus*, *Spinicapitichthys*, *Minysynchiropus*, *Paradiplogrammus*, *Callionymus*, *Pseudocalliurichthys*, *Calliurichthys*, *Bathycallionymus*, *Repomucenus* and *Eleutherochir opercularis*, there are 7 abdominal and 14 caudal vertebrae. In *Pterosynchiropus*, *Anaora* and some species of *Diplogrammus* (*D. goramensis* and *D. xenicus*), there are 7 abdominal and 13 caudal vertebrae. *Diplogrammus pauciradiatus* and *D. dubiosus* are 7 abdominal and 11 caudal vertebrae. *Eleutherochir mirabilis* is 7 abdominal and 17 caudal vertebrae (Table 7).

Abdominal vertebrae: The first to seventh vertebrae have complete neural arches and spines. The neural spines of the first to seventh, except the second, are bifid (Figs. 49A, C-F, 50), the second is not bifid (Fig. 49B). In *Synchiropus*, *Foetorepus*, *Eocallionymus*, *Minysynchiropus*, *Neosynchiropus*, *Pterosynchiropus*, *Orbonymus*, *Dactylopus*,

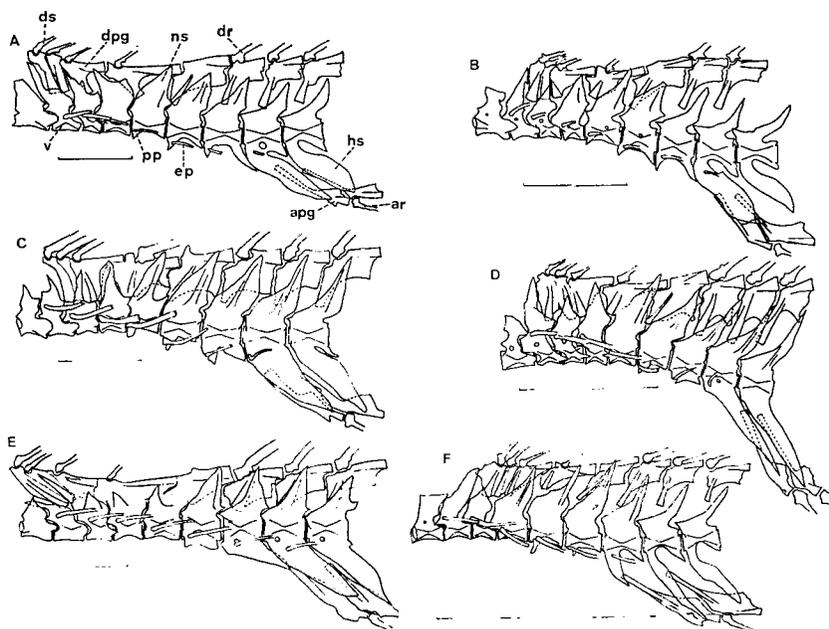


Fig. 44. Lateral view of the anterior vertebral column in six callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Neosynchiropus ocellatus*; D, *Pterosynchiropus splendidus*; E, *Dactylopus dactylopus*; F, *Anaora tentaculata*. ar, anal ray; apg, anal pterygiophore; dr, dorsal ray; dpg, dorsal pterygiophore; ds, dorsal spine; cp, epipleural; hs, hemal spine; ns, neural spine; pp, parapophysis; v, vertebra. Scales indicate 5 mm.

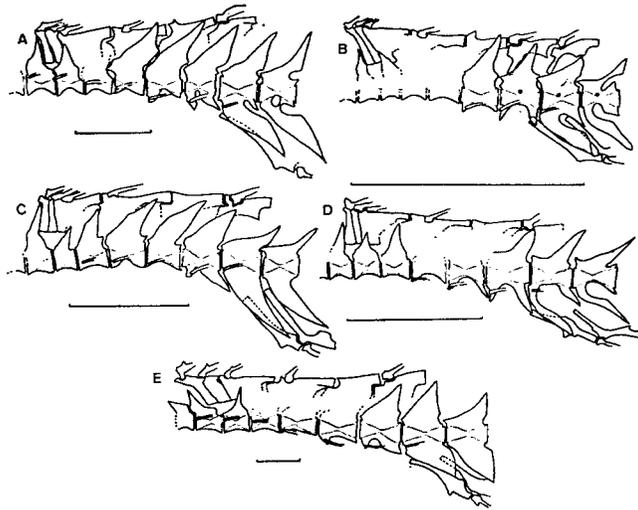


Fig. 45. Lateral view of the anterior vertebral column in five callionymid species. Figured from the X-ray negatives. A, *Synchiropus ornatus*; B, *Minysynchiropus laddi*; C, *Paradiplogrammus bairdi*; D, *Diplogrammus pauciradiatus*; E, *Orbonymus rameus*. Scales indicate 5 mm.

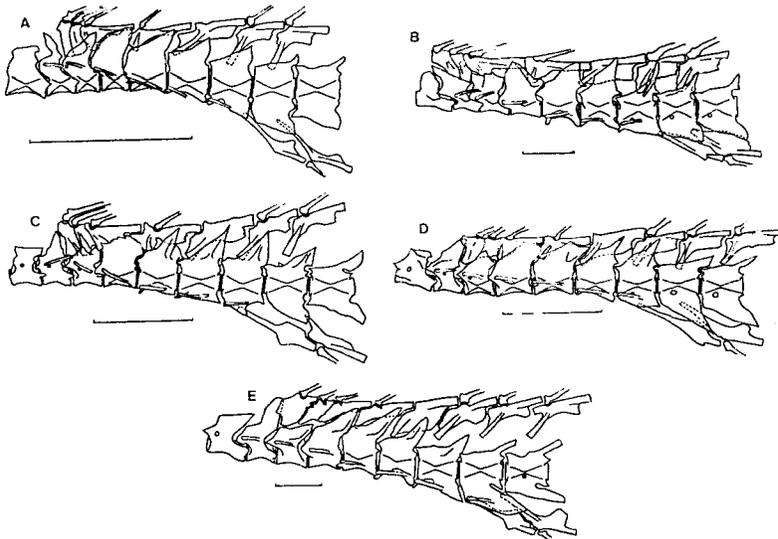


Fig. 46. Lateral view of the anterior vertebral column in five callionymid species. A, *Paracallionymus costatus*; B, *Spinicapitichthys spiniceps*; C, *Paradiplogrammus enneactis calliste*; D, *Diplogrammus goramensis*; E, *Callionymus lyra*. Scales indicate 5 mm.

*Paracallionymus*, *Paradiplogrammus bairdi*, *Diplogrammus pauciradiatus* and *D. dubiosus*, the second neural spine is slender and sharply pointed (Type A1, Figs. 44A-E, 45, 46A). In *Anaora*, *Spinicapitichthys*, *Paradiplogrammus* (except *P. bairdi*), *Diplogrammus* (except *D. pauciradiatus* and *D. dubiosus*), *Callionymus* and *Eleutherochir*, the second neural spine is rather broad and moderately pointed (Type B1, Figs. 44F, 46B-E,

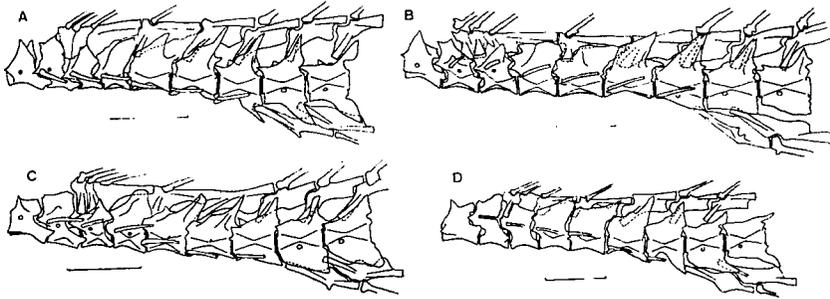


Fig. 47. Lateral view of the anterior vertebral column in four callionymid species. A, *Pseudocalliurichthys variegatus*; B, *Calliurichthys japonicus*; C, *Bathycallionymus kaianus*; D, *Repomucenus lunatus*. Scales indicate 5 mm.

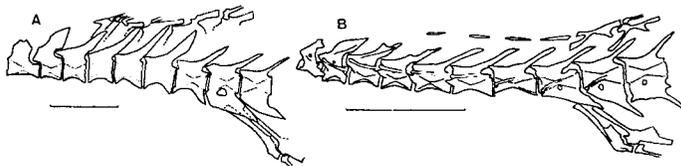


Fig. 48. Lateral view of the anterior vertebral column in two callionymid species. A, *Eleutherochir opercularis* (from the X-ray negative); B, *Eleutherochir mirabilis*. Scales indicate 5 mm.

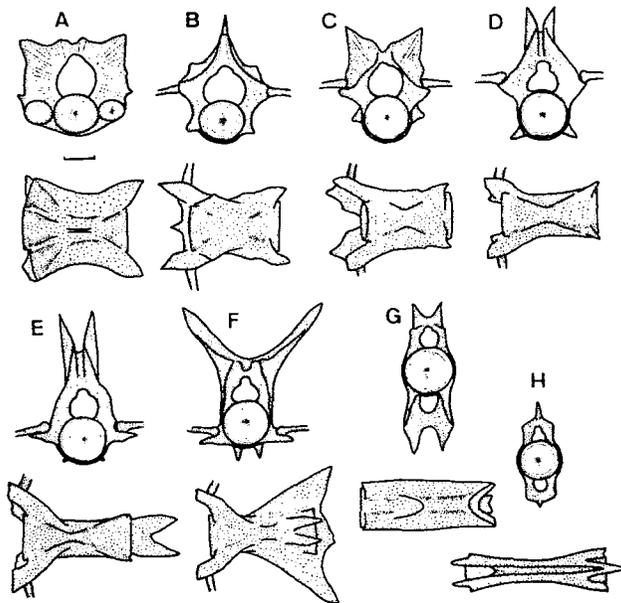


Fig. 49. The vertebrae of *Repomucenus richardsonii*. A, first vertebra; B, second vertebra; C, third vertebra; D, fourth vertebra; E, fifth vertebra; F, sixth vertebra; G, ninth vertebra; H, nineteenth vertebra. Upper, anterior view; lower, ventral view. Scale indicates 1 mm.

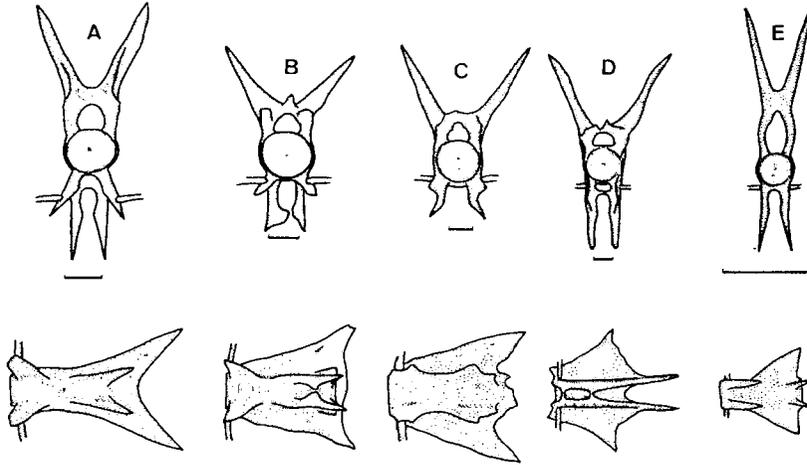


Fig. 50. The seventh vertebra in five callionymid species. A, *Foetorepus altivelis*; B, *Repomucenus richardsonii*; C, *Calliurichthys japonicus*; D, *Dactylopus dactylopus*; E, *Anaora tentaculata*. Upper, anterior view; lower, ventral view. Scales indicate 1 mm.

48). In *Pseudocalliurichthys*, *Calliurichthys*, *Bathycallionymus* and *Repomucenus*, it is strongly depressed and not pointed (Type C1, Fig. 47).

In *Synchiropus*, *Foetorepus*, *Eocallionymus*, *Minysynchiropus*, *Neosynchiropus*, *Pterosynchiropus*, *Pseudocalliurichthys*, *Paracallionymus*, *Spinicapitichthys*, *Callionymus*, *Bathycallionymus*, *Repomucenus*, *Eleutherochir*, *Diplogrammus pauciradiatus*, *D. dubiosus*, *Paradiplogrammus bairdi* and *P. corallinus* the second to seventh vertebrae have conspicuous parapophyses that protrude laterally (Type A2, Figs. 44A-D, 45A-D, 46A·B·E, 47A·C·E, 48, 50A·B). In *Diplogrammus goramensis*, *D. xenicus*, *Paradiplogrammus enneactis calliste*, *P. sp.* (from Australia), *Dactylopus* and *Calliurichthys*, the second to sixth vertebrae have conspicuous parapophyses that protrude laterally, and the seventh vertebra has greatly expanded parapophysis which fuse with the posthemal zygapophysis (Type B2, Figs. 44E, 46C·D, 47B, 50C·D). In *Anaora*, the second to six vertebrae have conspicuous parapophyses that protrude laterally, and the seventh vertebra has elongate parapophysis that protrude downward (Type C2, Figs. 44F, 50E).

Epipleurals: The first epipleural is attached to the second vertebra in the family. In, *Pseudocalliurichthys*, *Calliurichthys*, *Bathycallionymus*, *Repomucenus* and *Spinicapitichthys*, the second to seventh vertebra have epipleurals; whereas, in the other genera the second to seventh or eighth vertebrae have epipleurals; some have more epipleurals which are not connected to the vertebrae (Table 7).

Caudal vertebrae: The first caudal vertebra (the eighth) has a long or expanded hemal spine. In *Foetorepus*, *Eocallionymus*, *Synchiropus*, *Minysynchiropus*, *Diplogrammus pauciradiatus*, *D. dubiosus* and *Anaora*, the first hemal spine is elongate and is not fused with the posthemal zygapophysis (Type B3, Figs. 44C-E, 45E). In *Callionymus*, the first hemal spine is short and expanded, but is not fused with the posthemal zygapophysis (Type C3, Fig. 46E). In *Paracallionymus*, *Spinicapitichthys*, *Paradiplogrammus*, *Diplogrammus* (except *D. pauciradiatus* and *D. dubiosus*), *Pseudocalliurichthys*,

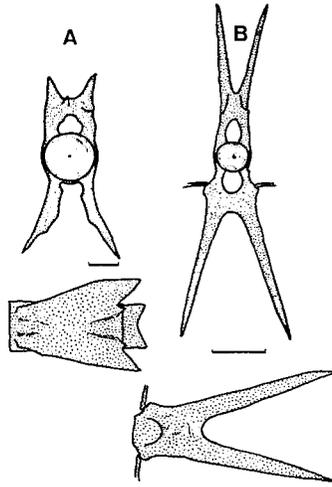


Fig. 51. The eighth vertebra in two callionymid species. A, *Repomucenus richardsonii*; B, *Pterosynchiropus splendidus*. Upper, anterior view; lower, ventral view. Scales indicate 1 mm.

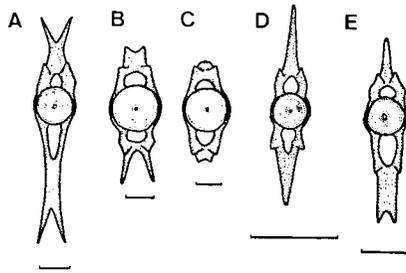


Fig. 52. Anterior view of the twelfth vertebra in five callionymid species. A, *Foetorepus altivelis*; B, *Bathycallionymus kaianus*; C, *Repomucenus richardsonii*; D, *Anaora tentaculata*; E, *Eleutherochir mirabilis*. Scales indicate 1 mm.

*Calliurichthys*, *Bathycallionymus*, *Repomucenus* and *Eleutherochir*, the first hemal spine is short and expands to fuse with the posthemal zygapophysis (Type D3, Figs. 46A-D, 47, 48).

In *Pterosynchiropus*, the eighth vertebra has a conspicuous first hemal arch (Type B4, Fig. 51B). But, in the other genera, the ninth vertebra has the conspicuous first hemal arch; the eighth one has not (Type A4, Figs. 49G, 51A). In *Dactylopus*, the seventh vertebra has a feeble hemal arch (Fig. 50D).

With the exception of *Anaora* and *Eleutherochir*, the neural and hemal spines from the eighth vertebra to the second or third preural vertebra are bifid. In some specimens, the neural spines of the middle caudal vertebra are slightly bifid or simple. In addition, in *Synchiropus*, *Foetorepus*, *Eocallionymus*, *Minysynchiropus* and *Neosynchiropus*, both the neural and hemal spines are deep, and their posterior proximal bases are strongly notched (Type A5, Figs. 52A, 53A-E). In *Pterosynchiropus*, they are deep,

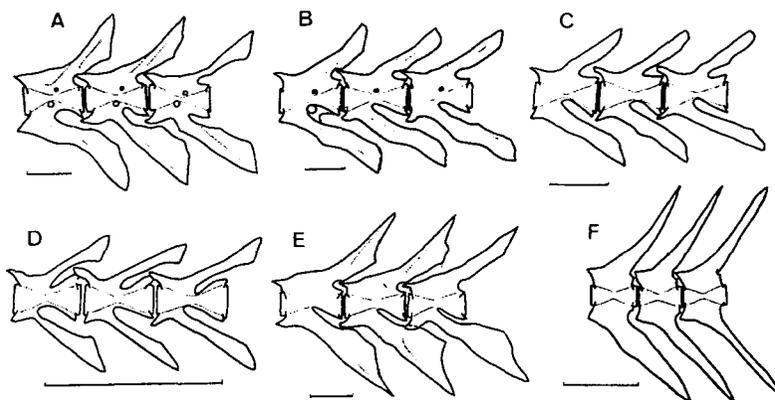


Fig. 53. Lateral view of the twelfth to fourteenth vertebrae in six callionymid species. A, *Synchiropus ornatus* (from the X-ray negative); B, *Foetorepus altivelis*; C, *Eocallionymus papilio*; D, *Minysynchiropus laddi* (from the X-ray negative); E, *Neosynchiropus ocellatus*; F, *Pterosynchiropus splendidus*. Scales indicate 2 mm.

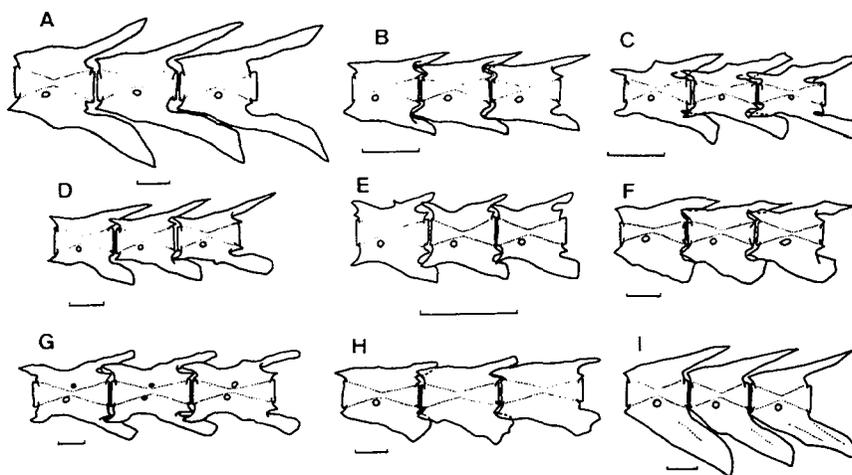


Fig. 54. Lateral view of the twelfth to fourteenth vertebrae in nine callionymid species. A, *Orbonymus rameus* (from the X-ray negative); B, *Diplogrammus xenicus*; C, *Paradiplogrammus enneactis calliste*; D, *Pseudocalliurichthys variegatus*; E, *Paracallionymus costatus*; F, *Spinicapitichthys spiniceps*; G, *Callionymus lyra*; H, *Bathycallionymus kaianus*; I, *Dactylopus dactylopus*. Scales indicate 2 mm.

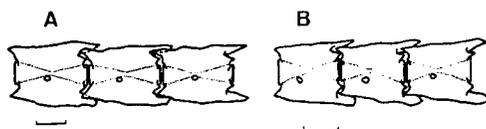


Fig. 55. Lateral view of the twelfth to fourteenth vertebrae in two callionymid species. A, *Calliurichthys japonicus*; B, *Repomucenus lunatus*. Scales indicate 2 mm.

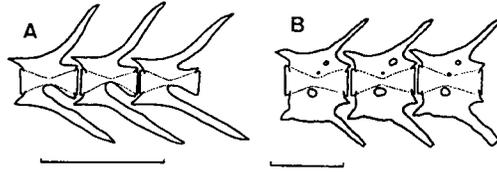


Fig. 56. Lateral view of the twelfth to fourteenth vertebrae in two callionymid species. A, *Anaora tentaculata*; B, *Eleutherochir mirabilis*. Scales indicate 2 mm.

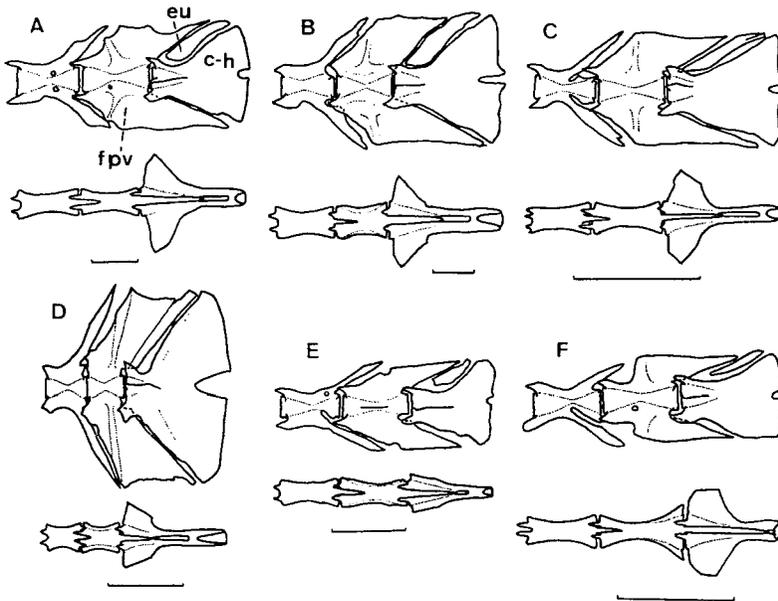


Fig. 57. The caudal skeleton in six callionymid species. A, *Synchiropus ornatus* (from the X-ray negative); B, *Neosynchiropus ocellatus*; C, *Anaora tentaculata*; D, *Pterosynchiropus splendidus*; E, *Eleutherochir mirabilis*; F, *Diplogrammus pauciradiatus* (from the X-ray negative). c-h, centrum-hypural plate; eu, epiural; fpv, first preural vertebra. Upper, lateral view; lower, dorsal view. Scales indicate 2 mm.

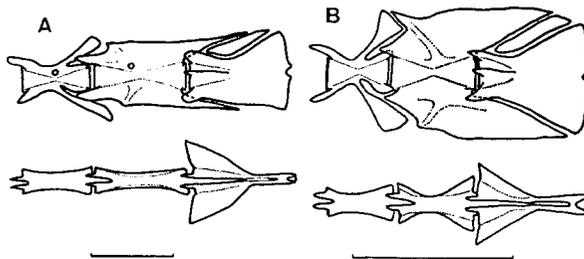


Fig. 58. The caudal skeleton in two callionymid species. A, *Callionymus risso* (from the X-ray negative); B, *Minysynchiropus laddi* (from the X-ray negative). Upper, lateral view; lower, dorsal view.

and their posterior bases are not notched (Type B5, Figs. 52A, 53F). In *Orbonymus*, *Diplogrammus*, *Paradiplogrammus*, *Pseudocalliurichthys*, *Paracallionymus*, *Spinicapitichthys*, *Callionymus* and *Bathycallionymus*, they are depressed, and their posterior proximal bases are notched (Type C5, Figs. 52B, 54A-H). In *Dactylopus*, they are depressed, and their posterior proximal bases are not notched (Type D5, Figs. 52B, 54I). In *Calliurichthys* and *Repomucenus*, they are so depressed that the tip of the neural spine

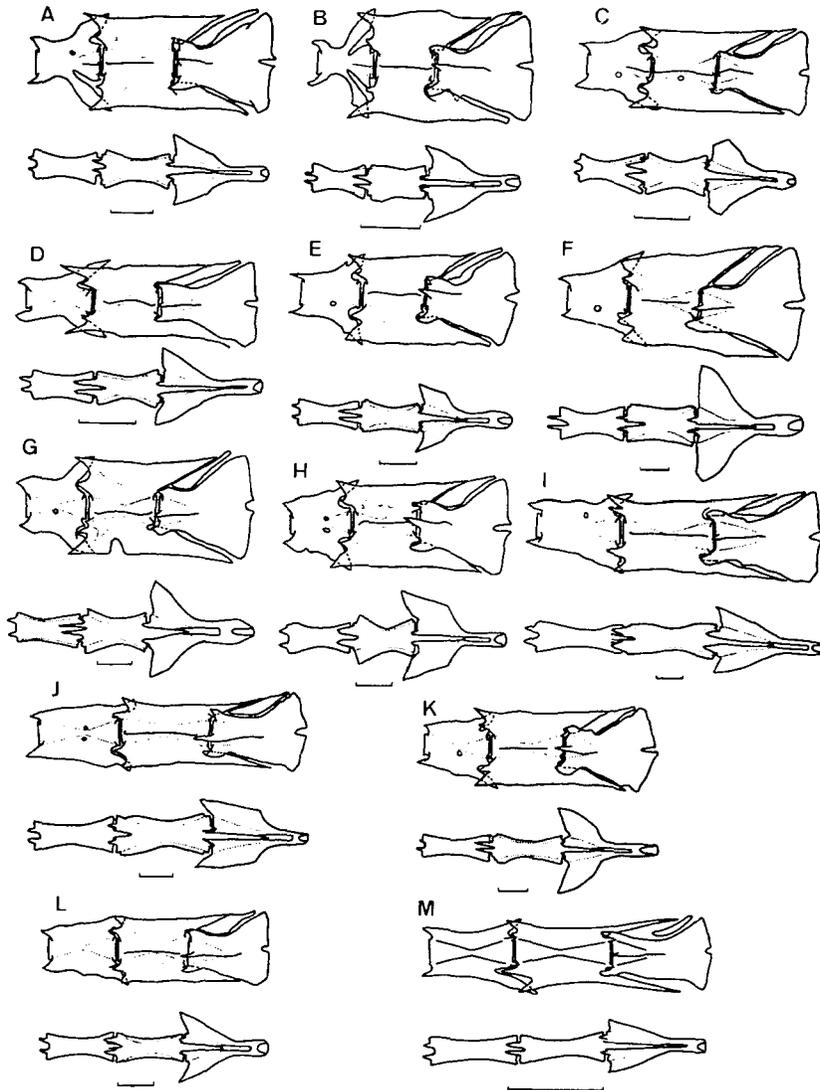


Fig. 59. The caudal skeleton in thirteen callionymid species. A, *Foetorepus altivelis*; B, *Eocallionymus papilio*; C, *Diplogrammus xenicus*; D, *Paradiplogrammus enneactis calliste*; E, *Pseudocalliurichthys variegatus*; F, *Orbonymus rameus* (from the X-ray negative); G, *Dactylopus dactylopus*; H, *Spinicapitichthys spiniceps*; I, *Callionymus lyra*; J, *Bathycallionymus kaianus*; K, *Calliurichthys japonicus*; L, *Repomucenus lunatus*; M, *Paracallionymus costatus*. Scales indicate 2 mm.

is almost flat, and their posterior bases are slightly notched (Type E5, Figs. 52C, 55). In contrast, in *Anaora* the neural spines of the eighth to the sixteenth vertebrae (except the thirteenth and fourteenth in the specimen examined) and the hemal spines on the eighth to the eleventh vertebrae are bifid. Both the neural and hemal spines are deep, and their posterior bases are notched (Type F5, Figs. 52D, 56A). In *Eleutherochir*, the neural spine on the eighth vertebra and the hemal spines on the eighth to twentieth (*E. opercularis*) or twentysecond (*E. mirabilis*) vertebrae are bifid. The bases of these neural and hemal spines are expanded and deeper than in the other genera. The neural and hemal spines are moderately deep as in Type C5 (Type G5, Figs. 52E, 56B).

**Caudal skeleton:** The caudal skeleton of the callionymids is characterised by an elongate expanded plate-like epiural, a centrum-hypural plate with laterally expanded plate-like processes at the mid-anterior, and a first preural vertebra with greatly expanded neural and hemal spines. The soft caudal rays are attached to the posterior edge of the centrum-hypural plate.

In *Synchiropus*, *Neosynchiropus*, *Anaora*, *Pterosynchiropus*, *Eleutherochir* and *Diplogrammus pauciradiatus* and *D. dubiosus*, there are no antrorse bifid processes in the broad neural and hemal spines on the first preural vertebra (Type A6, Fig. 57). In *Minysynchiropus* and *Callionymus risso*, there are antrorse processes on the first preural

Table 8. Characters' conditions in the vertebral column in callionymid genera.

	SNS	PAP	FHS	FHA	NHC	CS
<i>Callionymus</i>	B1		C3		C5	B6, C6
<i>Bathycallionymus</i>	C1		D3			
<i>Foetorepus</i>			A3	A4	A5	C6
<i>Eocallionymus</i>		A2				
<i>Paracallionymus</i>	A1		D3		C5	
<i>Neosynchiropus</i>			B3		A5	A6
<i>Pterosynchiropus</i>				B4	B5	
* <i>Minysynchiropus</i>			A3	—	A5	B6
<i>Paradiplogrammus</i>	A1, B1	A2, B2	D3	A4	C5	C6
<i>Diplogrammus</i>			A3, D3			A6, C6
* <i>Synchiropus</i>		A2	A3	—	A5	A6
* <i>Orbonymus</i>	A1		B3	—	C5	
<i>Dactylopus</i>		B2			D5	
<i>Calliurichthys</i>					E5	C6
<i>Pseudocalliurichthys</i>	C1		D3		C5	
<i>Repomucenus</i>		A2		A4	E5	
<i>Spinicapitichthys</i>					C5	
<i>Anaora</i>	B1	C2	A3		F5	
<i>Eleutherochir</i>		A2	D3		G5	A6

Abbreviations: CS, caudal skeleton; FHA, first hemal arch; FHS, first hemal spine; NHC, neural and hemal spines on caudal vertebrae; PAP, parapophysis on seventh vertebra; SNS, second neural spine. \*: from the X-rays.

vertebra, which do not catch the tips of the neural and hemal spines of the second preural vertebra. It is impossible to distinguish whether they are bifid, as their figures are known only from soft X-rays (Type B6, Fig. 58). In the other genera, there are antrorse bifid processes in the broad neural and hemal spines on the preural vertebra. These antrorse processes catch the tips of the neural and hemal spines on the second preural vertebra (Type C6, Fig. 59).

*Discussion.* The callionymid vertebral column has a remarkable number of bifid neural and hemal spines apparently because of the depressed body forms. This character is seen only in the callionymids; other depressed-body-form fishes, the Platycephalidae, Hoplichthyidae and Lophiidae do not have bifid neural and hemal spines (Takahashi, 1962).

The callionymid vertebral column has been studied by Briggs and Berry (1959), Hotta (1961), Takahashi (1962), and Gosline (1970); the caudal skeleton has been reported by Whitehouse (1910), Davis and Robins (1966) and Gosline (1970). These studies, however, are not detailed enough to show relationships among the genera.

Jordan and Fowler (1903) and Takahashi (1962) regarded the first caudal vertebra with the first hemal arch as the ninth, whereas, Gosline (1970) chose the eighth vertebra for no apparent reason. The eighth vertebra has its first long or expanded process downward, but there is no hemal arch except in *Pterosynchiropus*. This process is so large that it cannot be a parapophysis, and in some genera there is no epipleural; this large process must be regarded as the bifid first hemal spine without a hemal arch. Therefore, the eighth vertebra with this large hemal spine should be called the first caudal vertebra.

All the callionymid genera have seven abdominal vertebrae and most have fourteen caudal vertebrae, which seems to be standard for this family. *Pterosynchiropus*, *Anaora* and *Diplogrammus* have deviated from the standard type as they have fewer caudal vertebrae. *Eleutherochir mirabilis* also is deviant as it has a greater number of caudal vertebrae.

One specialization in the callionymids is the six epipleurals; the first through the sixth epipleurals are attached to the second to last abdominal vertebra and guard the abdominal cavity. The seventh and eighth epipleurals are somewhat degenerate because they have no function. Genera or species with degenerate epipleurals may be more primitive than the others.

In summary, the meristic characters for the vertebral column are useful for determining which genera or species are more advanced.

The sharp pointed neural spine seems primitive as compared to the neural spines of most standard percoid fish. Therefore, C1 is the most advanced for the three types.

Type A2 of the parapophysis of the seventh vertebra is primitive in comparison with that of standard percoid fishes. Type B2 is a modified expansion of Type A2. Type B2 in *Diplogrammus* and *Paradiplogrammus* meets the ramus of the first anal pterygiophore at the middle part, but, in *Calliurichthys* and *Dactylopus*, they meet at the posterior end. Therefore, Type B2 in the former two genera and the latter two

genera must be specialized separately from some genera of Type A2. Type C2 may be derived from A2 via ventral elongation of the parapophysis.

Types A3 and B3 of the first hemal spine on the eighth vertebra correspond to moderately depressed or depressed body forms, and Types C3 and D3 to depressed or strongly depressed forms. Types A3 and C3 are more primitive than Types B3 and D3, the first two having a notch at the posterior base of the hemal spine. Types B3 and C3 are derived from Type A3, and Type D3 from Type C3.

Type B4 of the first hemal arch is seen only in *Pterosynchiropus*, the stained specimens of the other genera examined are all Type A4. Therefore, Type B4 is a deviant from Type A4.

Types A5-E5 of the neural and hemal spines of the caudal vertebrae are almost the same in the arrangements of their bifid neural and hemal spines. Types A5, C5 and E5 correspond to the body forms, their body depths get less and less. Therefore, E5 is the most advanced; E5 is derived from C5, and C5 from A5. Type B5 is derived from Type A5, because it is almost as deep as Type A5 and is more specialized in having neural and hemal spines without notches at the posterior proximal bases. Type D5 is derived from Type C5, because it is almost as deep as Type C5 and is more specialized in having neural and hemal spines without notches at the posterior bases. Types F5 and G5 show strong deviations; the arrangements of their bifid neural and hemal spines differ markedly from Types A5-E5. Type F5 appears to be derived from Type A5, as it has long neural and hemal spines as in the latter. Type G5 appears to be derived from C5, as it is just like the latter in the spine's depth.

As for the caudal skeleton, Type C6 is advanced because a condition like it is seen only in the callionymids. Type B6 is intermediate between Types A6 and C6. *Callionymus* has two Types, B6 and C6, and *Diplogrammus* shows A6 and C6. The antrorse processes in Type C6 vary in length; therefore, they must have developed separately.

Gosline (1970) described there are two epurals in the callionymids, but all of the specimens examined in this study have only one.

To sum up the physiognomical character of the vertebral column, except for *Foetorepus* and *Eocallionymus*, each genus has its own character although intrageneric variations are seen in *Paradiplogrammus*, *Diplogrammus* and *Callionymus*. Only *Foetorepus* and *Eocallionymus* have a similar vertebral column. This variety in the vertebral column of the genera is an aspect of generic individuality, and is also a good criterion for determining how much the vertebral column in each genus specialized.

#### 11) Dorsal and anal fins (Figs. 44-48, 60, Table 9)

In the callionymids, each proximal pterygiophore fuses with each distal pterygiophore to form one bone; the former is the proximal ramus and the latter the distal ramus (Fig. 60A-C). There are 10 to 17 dorsal pterygiophore and 4 to 13 anal ones in this family.

Dorsal pterygiophores: The first and second dorsal pterygiophores do not distal

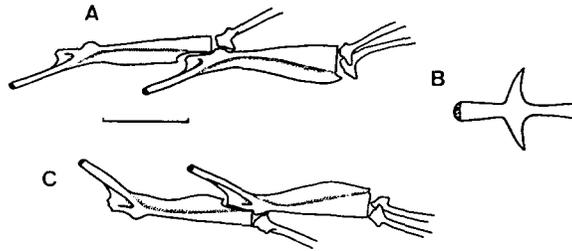


Fig. 60. The dorsal and anal pterygiophores in *Repomucenus richardsonii*. A, last two dorsal pterygiophores, lateral view; B, first anal pterygiophore, ventral view; C, last two anal pterygiophores, lateral view. Scale indicates 5 mm.

rami. The first pterygiophore bears a small antrorse process which appears to be a rudimentary pterygiophore fused with the posterior one at the distal part. The first dorsal pterygiophore bears the first and second dorsal spines. In *Foetorepus*, *Eocallionymus*, *Synchiropus*, *Minysynchiropus*, *Paracallionymus*, *Spinicapitichthys*, *Pseudocalliurichthys*, *Calliurichthys* and *Bathycallionymus*, the first and second dorsal pterygiophores are in close contact, and their proximal rami are inserted between the second and third neural spines; the second and third dorsal pterygiophores are in contact at their distal halves, the proximal ramus of the third is inserted between the third and fourth neural spines (Type A1, Figs. 44A·B, 45A·B, 46A·B, 47A-C). In the other genera the first to third dorsal pterygiophores are in close contact and their proximal rami are inserted between the second and fourth neural spines (Type B1, Figs. 44C-F, 45C-E, 46C-E, 47D, 48A).

The second and third dorsal pterygiophores bear the third and fourth dorsal spines, respectively; but, these two spines are somewhat posterior on the third and fourth pterygiophores. The fourth pterygiophore bears no dorsal spine and no soft ray. The fifth to the last dorsal pterygiophores bear soft dorsal rays. Each dorsal pterygiophore from the fourth to the tenth or seventeenth corresponds to each vertebra from the fifth to eleventh or eighteenth.

Anal pterygiophores: The first pterygiophore has laterally protruded processes on its anterior ventral surface (Fig. 60B).

In *Anaora*, the tip of the first anal pterygiophore is attached to the parapophysis protruding downward on the 7th vertebra (Type C2, Fig. 44F). In *Diplogrammus* (except *D. pauciradiatus* and *D. dubiosus*) and *Paradiplogrammus* (except *P. bairdi*), it is attached to the ventral middle surface of the 7th vertebra (Type B2, Fig. 46C-D). In the other genera and species, it is under the divided first hemal spine (Type A2, Figs. 44A-E, 45, 46A·B·E, 47, 48).

*Discussion.* These fins have advanced forms that are peculiar to the callionymids. In comparison with the other percoid fishes, the first to second dorsal pterygiophores or the first to third are in close contact, probably because of the depressed body forms. Type A1 of the dorsal pterygiophore is more primitive than Type B1, as it is closer to that of the percoid fish in the incomplete contact of the first to third pterygiophores.

Table 9. Characters' conditions of the dorsal and anal fins in callionymid genera.

	DP	AP
<i>Callionymus</i>	B1	
<i>Bathycallionymus</i>		
<i>Foetorepus</i>	A1	
<i>Eocallionymus</i>		A2
<i>Paracallionymus</i>		
<i>Neosynchiropus</i>	B1	
<i>Pterosynchiropus</i>		
* <i>Minysynchiropus</i>	A1	
<i>Paradiplogrammus</i>	B1	A2, B2
<i>Diplogrammus</i>		
* <i>Synchiropus</i>	A1	
* <i>Orbonymus</i>	B1	
<i>Dactylopus</i>		
<i>Calliurichthys</i>	A1	A2
<i>Pseudocalliurichthys</i>		
<i>Repomucenus</i>	B1	
<i>Spinicapitichthys</i>	A1	
<i>Anaora</i>	B1	C2
<i>Eleutherochir</i>		A2

Abbreviations: AP, first anal pterygiophore; DP, first to third dorsal pterygiophore. \*: from the X-rays.

As for the first anal pterygiophore, Type B2 and C2 probably are derived from Type A2 because most genera and species are Type A2 for the location of the first anal pterygiophore. Type C2 is more advanced than Type B2.

## 2. Phylogenetic Relationships among the Genera

No previous study of the comparative osteology of the callionymids has been made to show the relationships among the genera. This may be because, until the study of Nakabo (1982), this family had not been thought to be composed of so many genera. I have proposed phylogenetic relationships for the callionymid genera that are based on 31 osteological characters of 11 parts of the body.

### 1) Degree of specialization in each genus

Before discussing the phylogenetic relationships among the genera, each osteological characters condition is given the score according to the degree of specialization in order to decide what kind of genera are more specialized or primitive. For each osteological characters condition, the primitive condition was rated zero, the secondary derived condition one, the tertiary derived condition two, etc. Each genus accumulated points for osteological characters according to their degree of specialization; a high score for a genus shows that it is strongly specialized in its osteological characters.

Table 10. Degree of specialization in each callionymid genera.

	Characters*																															Total	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31		
<i>Callionymus</i>	1						1	1									4	2					1	1	1	2	1					15	
<i>Bathycallionymus</i>					1		1	1							1		4	2					1	2	2		1	2				18	
<i>Foetorepus</i>									1			1						2											2			6	
<i>Eocallionymus</i>									1								1												2			4	
<i>Paracallionymus</i>							1	1				1		1	1	1		2							2		1	2				13	
<i>Neosynchiropus</i>									1	2							2		1	2	1			1				1			1	11	
<i>Pterosynchiropus</i>									1	2							2		1	2	1	1			1	1	1		1			14	
<i>Paradiplogrammus</i>					1				1	1				1	1		3	1					1	1	1	2		1	2	1	1	19	
<i>Diplogrammus</i>					1				1	1					1		3						1	1	1	1	2		1	2	1	1	18
<i>Dactylopus</i>			1		1				1								4			2					1	1		2	2	1		16	
<i>Calliurichthys</i>					1		1		1						1		3	2					1	2	1	2		2	2			19	
<i>Pseudocalliurichthys</i>					1		1		1						1		3	2		1			1	2		2		1	2			18	
<i>Repomucenus</i>					1		1		1					1	1	1	4	2					1	2		2		2	2	1		22	
<i>Spinicapitichthys</i>				1	1				1					1	1		4	2					1	1		2		1	2			18	
<i>Anaora</i>					1	1		1	2	1	1	1					2			2	1	1		1	2		1		1	2	21		
<i>Eleutherochir</i>	1				1	1			1			1					2	2		1		1		1		2		2		1		18	

\*: 1, ethmoidal region; 2, supraethmoid and parasphenoid; 3, supraoccipital crest; 4, nasal; 5, premaxillary; 6, dentary and articular; 7, sesamoid articular; 8, teeth on upper and lower jaws; 9, urohyal; 10, branchiostegal rays; 11, lower pharyngeal; 12, second upper pharyngeal; 13, second and third-fourth upper pharyngeals; 14, retrorse spine of opercle; 15, retrorse spine of subopercle; 16, connection between subopercle and interopercle; 17, preopercular spine; 18, posttemporal; 19, anteroventral ramus of cleithrum; 20, coracoid; 21, anterior ramus of pelvic bone; 22, vertebral number; 23, number of epipleurals; 24, second neural spine; 25, parapophysis on seventh vertebra; 26, first hemal spine; 27, first hemal arch; 28, neural and hemal spines on caudal vertebrae; 29, caudal skeleton; 30, first to third dorsal pterygiophores; 31, first anal pterygiophore.

Scores given for conditions of the characters are the following: 1, ethmoidal region, not depressed (rated 0), depressed (1); 2, supraethmoid and parasphenoid, directly connected (0), indirectly connected (1); 3, supraoccipital crest, present (0), absent (1); 4, nasal, present (0), absent (1); 5, premaxillary, A1a(0), A1b·B1·C1 (1); 6, dentary and articular, A2(0), B2·C2(1); 7, sesamoid articular, A3(0), B3(1); 8, teeth on upper and lower jaws, normal (0), degenerate (1); 9, urohyal, A1a·B1(1), A1b(2); 10, branchiostegal rays, A2(0), B2(1), C2(2); 11, lower pharyngeal, triangle with normal teeth (0), slender with degenerate teeth (1); 12, second upper pharyngeal, with teeth (0), without teeth (1); 13, second and third-fourth upper pharyngeals, well separated (0), almost fused (1); 14, retrorse spine of opercle, not filamentous (0), filamentous (1); 15, retrorse spine of subopercle, not filamentous (0), filamentous (1); 16, connection between subopercle and interopercle, directly (0), indirectly (1); 17, preopercular spine, A(0), B(1), D·C·F(2), E·G(3), H·I·J·K·L(4); 18, posttemporal, vertically (0), obliquely (1), horizontally (2); 19, anteroventral ramus of the cleithrum, broad(0), narrow(1); 20, coracoid, A(0), B(1), C(2); 21, anterior ramus of the pelvic bone, expanded (0), pointed (1); 22, vertebral number, 7+14(0), 7+11·7+13·7+17(1); 23, number of epipleurals, over 6(0), 6(1); 24, second neural spine, A1(0), B1(1), C1(2); 25, parapophysis on seventh vertebra, A2(0), B2(1), C2(2); 26, first hemal spine, A3(0), B3·C3(1), D3(2); 27, first hemal arch, A4(0), B4(1); 28, neural and hemal spines on caudal vertebrae, A5(0), B5·C5·F5(1), D5·E5·G5(2); 29, caudal skeleton, A6(0), B6(1), C6(2); 30, first to third dorsal pterygiophore, A1(0), B1(1); 31, first anal pterygiophore, A2(0), B2(1), C2(2). Scores for all the genera are shown in Table 10.

Since *Eocallionymus* and *Foetorepus* have fewer points than any of the other genera, they are the least specialized and are closest to the ancestor of the dragonets. *Bathycallionymus*, *Paradiplogrammus*, *Calliurichthys*, *Repomucenus*, *Spinicapitichthys*, *Anaora* and *Eleutherochir* are more specialized, because they have many points. Especially, *Repomucenus* is the most.

## 2) Phylogenetic relationships (Fig. 61)

In determining the relationships among the callionymid genera, I have given priority to the urohyal character, whose condition is not correlated with variation in body form and which is stable in comparison with the same character in other percomorph fishes. Second, I have regarded the preopercular spine as an important character to determine the relationships; the more advanced complex-shaped of it must be shared by closely related genera. Many other characters do show the degree of specialization in a genus and can be used to distinguish between genera.

The phylogenetic relationships among the nineteen genera can be divided into two main categories, the *Callionymus*-stem and the *Calliurichthys*-stem, when based on the character of the urohyal, which is more stable and less split than the preopercular spine. Each stem division can be redivided into several groups based on the types of preopercular spine. Each of these groups can be subdivided by a comparison of the characters that show the degree of specialization of a genus.

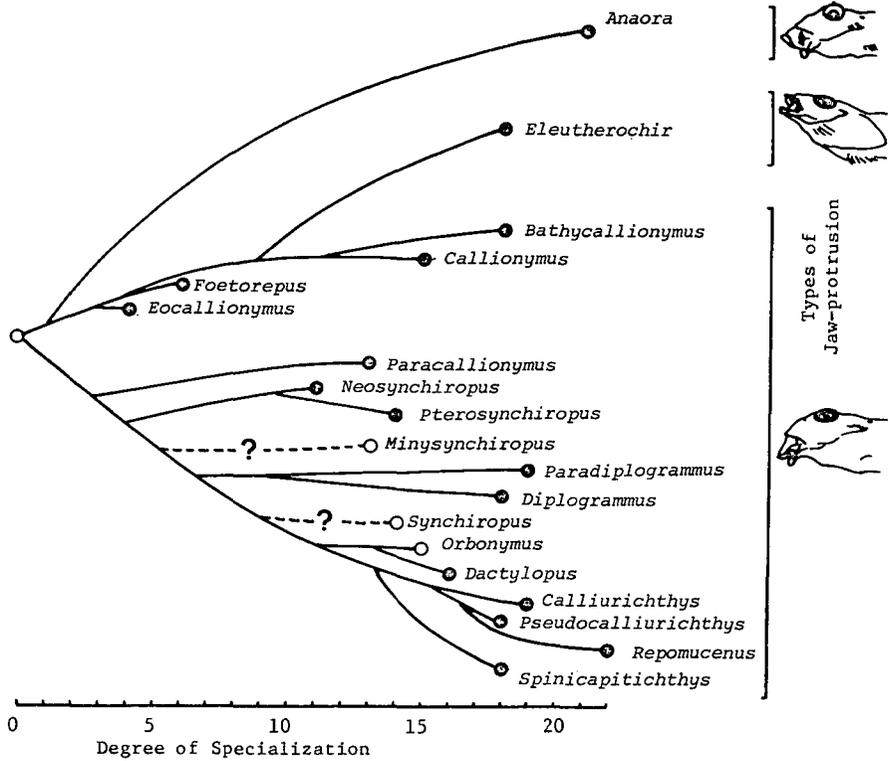


Fig. 61. Phylogenetic relationships among the callionymid genera. The terminal circles show the degree of specialization; solid circles, calculated value; white circles, supposed value; the white circle at the root means the hypothetical ancestor.

The *Callionymus*-stem can be divided into the *Callionymus*-substem and the *Anaora*-substem by the type urohyal present. This *Callionymus*-substem can then be divided into the *Eocallionymus*, *Foetorepus*, *Eleutherochir* and *Callionymus*-group by the character of the preopercular spine.

*Foetorepus* is more specialized than *Eocallionymus* as it has no teeth on the second upper pharyngeal. The other characters common to the two genera are all primitive.

*Eleutherochir* is more specialized than the preceding two genera as it has more upward processes on the inner side of the preopercular spine. The genus differs radically from the other general in having a mouth that protrudes anteriorly and in the specialized neural spines of its caudal vertebrae. This mouth part seems to be for eating organisms that differ from the food of the other genera. The premaxillary with a large angle between the ascending process and the long ramus, dentary with a long anterior part, few teeth, and almost fused upper pharyngeals and strongly depressed ethmoid region are correlated to its remarkable mouth.

The *Callionymus*-group includes *Callionymus* and *Bathycallionymus*. They both have a very advanced barbed process on the preopercular spine, so they must be

recent deviations from the same progenitor; the resemblance in some external characters (general physiognomy, eye diameter and secondary sexual characters) shown by Nakabo (1982) supports this hypothesis. *Bathycallionymus* is more advanced than *Callionymus* in the round tip of its premaxillary, the filamentous retrorse spine of its subopercle, its six epipleural ribs, its depressed second neural spine, its expanded first hemal spine fused with the posthemal zygapophysis, and the antrorse processes of the expanded neural and hemal spines on the first preural vertebra. *Callionymus*, however, is more specialized than *Bathycallionymus* in having no connection between the supraethmoid and parashenoid, and in the 1st-3rd dorsal pterygiophore being in close contact and inserted between the 2nd-4th neural spines. Conditions of several osteological characters (the cranium, lower jaw, and neural and hemal spines on caudal vertebrae) correspond well to the fact that this group has the most depressed body among the genera of the *Callionymus*-stem.

The *Anaora*-substem is represented only by *Anaora*. This genus markedly differs from the other genera in having a very specialized mouth which sucks in food organisms. The premaxillary with a large angle between the ascending process and the short ramus, degenerate teeth on the upper jaw, dentary with an expanded, upcurved posterior ramus and degenerate pharyngeal teeth are related to the specialized mouth. The pointed anterior ramus of pelvic bone and less number of neural and hemal spines on caudal vertebrae show evidence of gaining a secondary deeper body.

The *Calliurichthys*-stem is composed of the *Paracallionymus*, *Neosynchiropus*-, *Paradiplogrammus*- and *Calliurichthys*-groups.

*Paracallionymus* differs in having a simple pointed preopercular spine. It is specialized in the absence of teeth on the 2nd upper pharyngeal, in the filamentous retrorse spines of the opercle and subopercle, and in the indirect connection between the subopercle and interopercle. Although this genus have a strongly depressed body, it have several primitive osteological characters; degree of specialization is not so high.

The *Neosynchiropus*-group includes *Neosynchiropus* and *Pterosynchiropus*. They have some upward processes on the inner side of the preopercular spine, and deeper bodies. They share two derived characters which are peculiar to them; posterior four branchiostegal rays attaching on the adaxial surface of the epihyal and the pointed anterodorsal ramus of the cleithrum. Although each of the two characters alone dose not always show the relationships between the two genera, both of them cooperate to show it; a probability for the two genera to share the both characters is very low. The two genera must have gained a secondary deeper body because of the conditions of the both cleithrum and pelvic bones. *Pterosynchiropus* is more specialized than *Neosynchiropus* in having less caudal vertebrae, the first hemal arch on the eighth vertebra and expanded neural and hemal spines fused with the postneural and posthemal zygapophyses of the caudal vertebrae. *Pterosynchiropus* must have been derived from *Neosynchiropus* to adapt moreover to life in coral reefs, because of the deepest body and most compressed caudal peduncle shown by Nakabo (1982).

The *Paradiplogrammus*-group includes *Paradiplogrammus* and *Diplogrammus*. They are specialized in having the preopercular spine with many upward processes on the inner side, strongly upcurved posterior end and an antrorse process at the base, and the same shape of the parapophysis of the seventh vertebra which is peculiar to them. *Diplogrammus* is more specialized than *Paradiplogrammus* in the longitudinal dermal fold on the lower lateral side of the body, in the decreasing number of vertebrae. *Paradiplogrammus* is more specialized than *Diplogrammus* in having a filamentous retrorse spine of the opercle and a obliquely notched posttemporal.

The *Calliurichthys*-group includes *Orbonymus*, *Dactylopus*, *Calliurichthys*, *Pseudocalliurichthys*, *Repomucenus* and *Spinicapitichthys*. They differ from the other genera in having a straight and elongate preopercular spines with several processes (in *Repomucenus* only when young). In the shoulder and pelvic girdle, *Orbonymus* are very similar to *Dactylopus*; the osteological character of *Orbonymus* except for the former two could not be observed, but because of its remarkable resemblance in the appearance to *Dactylopus* the genera must be close. *Dactylopus* is more specialized than *Orbonymus* in having many antrorse processes on the outer side of the preopercular spine and its peculiar pelvic fin. *Dactylopus* must have been derived from *Orbonymus*. *Spinicapitichthys* is more specialized than the others in having a preopercular spine with many processes on both the outer and inner sides and no nasal. The genus must have been largely deviated from the main line of the *Calliurichthys*-stem; it seems to be derived at the point between *Orbonymus*-*Dactylopus* and the other three genera because of its depressed body. *Calliurichthys*, *Pseudocalliurichthys* and *Repomucenus* are in common in having a strongly depressed body. *Repomucenus* is more like *Pseudocalliurichthys* than *Calliurichthys* in the preopercular spine of young specimens, and must be more closely related to the former. *Repomucenus* and *Calliurichthys* have the common character of strongly depressed neural and hemal spines on the caudal vertebrae, and they are more advanced than *Pseudocalliurichthys* in it; but *Calliurichthys* appears to have adapted to benthic life independent of *Repomucenus*. *Calliurichthys* is more specialized than *Pseudocalliurichthys* and *Repomucenus* in the degenerate upward process of the coracoid. *Repomucenus* is more advanced than *Pseudocalliurichthys* and *Calliurichthys* in the close contact of the 1st-3rd dorsal pterygiophore between the 2nd-4th neural spines and the indirect connection between the interopercle and subopercle.

*Minysynchiropus* and *Synchiropus* could not be classified definitely because their urohyals could not be observed.

My proposed phylogenetic relationships among the callionymids including the degree of specialization in each genus are summarized in Fig. 61. In terms of jaw-protrusion, *Anaora* and *Eleutherochir* should be positioned separately from the other genera.

### Evolution in the Callionymidae

The Callionymidae have been classified into 19 genera and 139 species according to Nakabo (1982). How did this great diversity of forms come about?

Table 11. Number of species of each callionymid genus in each locality.

	EP	WA	EAM	IO	WP	CP
<i>Callionymus</i>	0	0	5	0	0	0
<i>Bathycallionymus</i>	0	0	0	5	6	0
<i>Foetorepus</i>	1	2	1	2	9	1
<i>Eocallionymus</i>	0	0	0	0	1	0
<i>Paracallionymus</i>	0	0	1	1	0	0
<i>Neosynchiropus</i>	0	0	0	5	5	1
<i>Pterosynchiropus</i>	0	0	0	0	2	0
<i>Minysynchiropus</i>	0	0	0	1	1	0
<i>Paradiplogrammus</i>	0	1	0	2	3	1
<i>Diplogrammus</i>	0	2	0	3	3	0
<i>Synchiropus</i>	0	0	0	1	1	0
<i>Orbonymus</i>	0	0	0	0	1	0
<i>Dactylopus</i>	0	0	0	0	1	0
<i>Calliurichthys</i>	0	0	0	7	7	3
<i>Pseudocalliurichthys</i>	0	0	0	2	6	0
<i>Repomucenus</i>	0	0	1	6	33	0
<i>Spinicapitichthys</i>	0	0	0	3	1	0
<i>Anaora</i>	0	0	0	0	2	0
<i>Eleutherochir</i>	0	0	1	3	3	1

Abbreviations: CP, central Pacific; EAM, eastern Atlantic and the Mediterranean; EP, eastern Pacific; IO, Indian Ocean; WA, western Atlantic; WP, western Pacific.

When and where did they emerge? How did they evolve? The answers to these questions were found by a comparison of: phylogenetic relationships that are based on comparative osteology, the types of habitats and geographic distributions.

### 1. Center of dispersal

The number of species of each genus in each locality is shown in Table 11. In the western Pacific there are 17 genera made up of 85 species of dragonets; in the Indian Ocean there are 13 genera and 40 species. The numbers of genera and species decrease toward the peripheries of the distribution areas. If the center of dispersal is the area that includes the most genera or species, as in the eels (Schmidt, 1932) and the surfperches (Tarp, 1952), then the western Pacific Region is the dispersal center of the dragonets. The center of dispersal also has been reported as being determined by the distributions of primitive or advanced groups (Matthew, 1915; Fraser-Brunner, 1949; Mayr, 1963). Ochiai (1966) states that this dispersal center should be determined by both sets of criteria. For the case of Sparidae (Akazaki, 1962), the areas for both criteria coincide, making the center of dispersal the Mediterranean and coastal waters around Africa. This has been validated from fossil remains. Unfortunately, no callionymid fossils have been found; thus, we must determine their center of dispersal only from information about recent dragonets. The degree of specialization in each genus shows that there are both primitive

Table 12. Habitats of callionymid genera.

	B	CS	CE	MB	RW
<i>Callionymus</i>		*	*	*	
<i>Bathycallionymus</i>			*	*	
<i>Foetorepus</i>			*	*	
<i>Eocallionymus</i>					*
<i>Paracallionymus</i>		*	*		
<i>Neosynchiropus</i>					*
<i>Pterosynchiropus</i>					*
<i>Munysynchiropus</i>					*
<i>Paradiplogrammus</i>					*
<i>Diplogrammus</i>					*
<i>Synchiropus</i>		*			
<i>Orbonymus</i>		*			
<i>Dactylopus</i>					*
<i>Calliurichthys</i>		*	*	*	
<i>Pseudocalliurichthys</i>					*
<i>Repomucenus</i>	*	*			
<i>Spinicapitichthys</i>			*	*	
<i>Anaora</i>					*
<i>Eleutherochir</i>	*				

Abbreviations: B, beach; CE, sandy-muddy bottom on the edge of the continental shelf; CS, sandy-muddy bottom on the continental shelf; MB, sandy-muddy bottoms on seamounts and banks; RW, sandy bottoms along coral reefs, weedy beds and rocky reefs mainly around islands.

and advanced genera in the western Pacific Region; and *Foetorepus*, one of the most primitive genera, has the largest number of species in the Region. As the two criteria coincide, the center of dispersal for the Callionymidae must be the western Pacific Region.

As to the time of their emergence, some point after the late Cretaceous Period, when the teleostei appeared (Colbert, 1969) is logical because the form of the dragonets is much more modified than the standard form of percomorph fishes. A very broad epicontinental sea existed between Eurasia and Africa 65 million years ago during the late Cretaceous or the early Paleocene (Pielou, 1979). Thus, the incipient dragonets probably emerged in the eastern part of this epicontinental sea at that time or a little later.

## 2. Habitat

The habitats of the genera are shown in Table 12. There are roughly two kinds of callionymid habitats; sandy-muddy bottoms on the continental shelf, banks and seamounts or sandy bottoms along coral reefs, rocky reefs and weedy beds around islands. Certainly, the dragonets have differentiated and dispersed in order to adapt to better habitat. Therefore, it is important to discuss which of the two kinds of habitats is better.

Dragonets have very depressed body forms which are adapted to benthic life on sandy-muddy bottoms. Since the area of a continental shelf is far larger than the area around islands, it can support populations of many more dragonets. Evidence in support of this is that there are 98 species located along shelves, but only 35 located around islands. The five most common genera, (*Repomucenus*, *Calliurichthys*, *Foetorepus*, *Bathycallionymus* and *Callionymus*), which live on continental shelves grow large as compared with genera which live around islands (Nakabo, 1982); this means that the dragonets show a preference for the continental shelf as a habitat.

Moreover, for the benthos biomass, the area on the continental shelf is separated into the shelf (at a depth of 0 to ca. 150 m) and the shelf edge (ca. 150 to 500 m). The benthos biomass is much larger for the shelf than for the shelf edge (Zenkevitch, 1963; Harada, 1973). Since the dragonets feed on small benthic animals (Johnson, 1972; Kakuda et al., 1979; Nakabo, unpublished), the benthos biomass of their habitats has a pervasive influence on their life. Consequently, the sandy-muddy bottom of the shelf (0 to ca. 150 m) is the best habitat for the dragonets. These fish must have differentiated and dispersed in order to populate the shelf.

### 3. Differentiation and dispersion of the genera (Fig. 62)

I am able to discuss the differentiation and dispersions of the 10 most common genera that include five species or more; *Foetorepus*, *Paradiplogrammus*, *Diplogrammus*, *Callionymus*, *Bathycallionymus*, *Calliurichthys*, *Neosynchiropus*, *Eleutherochir*, *Pseudocalliurichthys* and *Repomucenus*. Because of insufficient information about the differentiation and dispersion of the other 9 genera, they cannot be discussed with any degree of accuracy.

There are two kinds of geographic distribution patterns. The distributions of *Foetorepus*, *Paradiplogrammus* and *Diplogrammus* are not interrupted by the Isthmus of Suez, whereas the geographic distributions of the other 7 genera are (Nakabo, 1982). Apparently, the first 3 genera emerged before Africa was joined with Eurasia, and the latter 7 genera emerged after that time.

Probably *Foetorepus* emerged first in sandy-muddy bottoms along the continental shelf of the western Pacific Region, then spread into tropical seas throughout the world. Seemingly, only a few species could pass through what is now the Isthmus of Panama because only one species of this genus inhabit waters near the Isthmus. This genus is primitive and must be close to the form of the incipient dragonet; thus, *Foetorepus* must have emerged at almost the same time as its progenitor. Somewhat later, *Paradiplogrammus* and *Diplogrammus*, which have more specialized characters, emerged on the sandy bottoms near coral, and rocky reefs or weedy beds around islands.

The common ancestor of *Callionymus* and *Bathycallionymus* must have emerged from a group related to *Foetorepus* (because these genera have very similar urohyals) and populated the sandy-muddy bottoms of the Mediterranean. The distribution of *Callionymus* borders the distribution of *Bathycallionymus* through the intervention of the Isthmus of Suez, and both genera are closely related in their osteological and

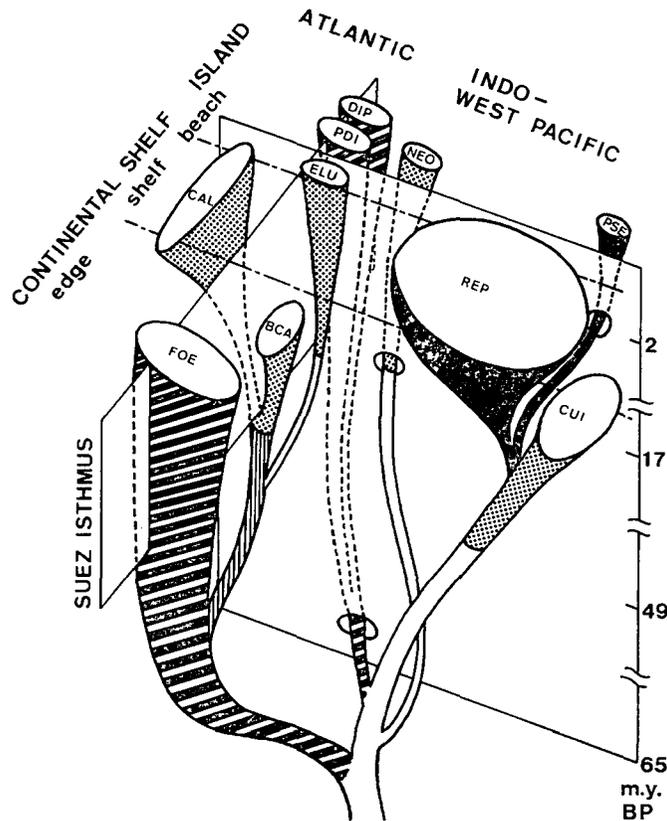


Fig. 62. Deviation process for ten common callionymid genera. BCA, *Bathycallionymus*; CAL, *Callionymus*; CUI, *Calliurichthys*; DIP, *Diplogrammus*; ELU, *Eleutherochir*; FOE, *Foetorepus*; NEO, *Neosynchiropus*; PDI, *Paradiplogrammus*; PSE, *Pseudocalliurichthys*; REP, *Repomucenus*. Oblique lines, genera emerged 65 million years ago; transverse lines, genera emerged 49 million years ago; dots, genera emerged 17 million years ago; black, genera emerged 2 million years ago.

external characters. This is evidence that their common ancestor dispersed from the Mediterranean into the East Atlantic and the Indo-West Pacific Regions. North America and Europe were separated by the deep water of the Atlantic, 49 million years ago during the Eocene (Pielou, 1979). Since the distribution of *Callionymus* is limited to the northeast Atlantic and Mediterranean, the common ancestor of these genera probably emerged after that time. Since most fish of the tropical shelf regions can not pass through the deep water barrier of the Atlantic (Briggs, 1974), the common ancestor of *Callionymus* and *Bathycallionymus* probably was circumscribed by the barrier of that period.

Africa and Euracia were joined together 17 million years ago during the Miocene, and the Isthmus of Suez was raised (Pielou, 1979). After that period, the common ancestor must have evolved into *Callionymus* and *Bathycallionymus*. The generic composition of the Callionymidae in the Atlantic has been almost constant

since the Isthmus of Suez was raised. In the east Atlantic, *Callionymus* inhabits a shelf region where the benthos biomass is rich; *Callionymus* is composed of 5 species, but *Foetorepus* which lives on the shelf edge has only one species. *Callionymus* with less body depth has been more adaptive to benthic life than *Foetorepus*.

After the upthrust of the Isthmus of Suez, *Calliurichthys* with strongly depressed body and *Neosynchiropus* with deeper body evolved from an ancestor that differed greatly from the previous genera's ancestor; they emerged in the Indo-West Pacific. *Calliurichthys* inhabited sandy-muddy bottoms on the continental shelf and *Neosynchiropus* inhabited coral-rocky reefs or weedy beds around islands. The deeper body of *Neosynchiropus* is a secondary character, an adaptation to its habitat, as evidenced by the shapes of the cleithrum and pelvic bone. These two genera are distributed from the western Indian Ocean to Hawaii.

*Repomucenus* and *Pseudocalliurichthys* next evolved from an ancestor related to *Calliurichthys* and began to disperse, as evidenced by their distributions which are narrower than those of *Calliurichthys* and *Neosynchiropus*. *Repomucenus* and *Pseudocalliurichthys* probably emerged 2 million years ago, between the late Pliocene and the early Pleistocene. At that time the climate grew colder, and the marine environment that was the habitat of dragonets must have changed. *Repomucenus* and *Pseudocalliurichthys* apparently emerged with this change in climate. *Repomucenus* inhabits sandy-muddy bottoms on the continental shelf, and *Pseudocalliurichthys* inhabits sandy bottoms along coral-rocky reefs or weedy beds around islands. *Repomucenus* is dominant among the dragonets of the Indo-West Pacific, and inhabits sandy-muddy bottoms on the continental shelf (at a depth of 0 to ca. 150 m) where the benthos biomass is very rich. There are 39 of its species in the Indo-West Pacific, undoubtedly because *Repomucenus* is the most adaptive of all the callionymid genera to benthic life as it has the least body depth, highest degree of specialization and body colored like a sandy bottom.

It seems that *Bathycallionymus* and *Calliurichthys* have been pushed away to the shelf edge by *Repomucenus* in the Indo-West Pacific. *Callionymus*, which is closely related to *Bathycallionymus* and somewhat more primitive than it, can occupy the shelf in European waters; this must be because there is no competitor like *Repomucenus* in that waters.

From its osteological characters, *Eleutherochir* must differ greatly in its feeding ecology from all the other genera. It inhabits beach or brackish waters, and is distributed from the middle west coast of Africa to Hawaii. The *E. shango* that lives along the middle west coast of Africa probably came from the southwest Indian Ocean because two species closely related to it are found along the southeast coast of Africa. *Eleutherochir* probably emerged at almost the same time as *Calliurichthys* and *Neosynchiropus*.

To sum up, it seems quite possible that there have been two evolutionary lines for the dragonets to adapt to benthic life. As the body depression as concerned, *Callionymus* and *Bathycallionymus* have the most depressed body of the genera in *Callionymus*-stem, and *Repomucenus* and *Calliurichthys* have that of the genera in *Calliurichthys*-stem.

The derivation process for these ten genera are diagrammed in Fig. 62.

In the other nine genera, *Pterosynchiropus* and *Dactylopus* seem to be newly derivatives, because the two have closely related genera which are less specialized; but, the time they emerged cannot be discussed. *Eocallionymus* must be a relic because of its primitiveness, having only a species and small distribution (southern coast of Australia). I cannot discuss about the other six genera in this study because of insufficient information about them. We need more information about them to know their evolutionary history.

### Summary

1. Phylogenetic relationships among the callionymid genera have been presented on the bases of 31 osteological characters of 11 parts of the body which are the cranium, lacrimal, jaws, hyoid arch, branchial apparatus, suspensolium, shoulder girdle, pelvic girdle, vertebral column and dorsal and anal fins. The conditions of the urohyals and preopercular spine are the most important to estimate the phylogenetic relationships among the genera, because these two are not related to the variations of body depression. The Callionymid genera are separated into two main branches, *Callionymus*-stem having the urohyal Type A1, and *Calliurichthys*-stem having the urohyal Type B1. *Callionymus*-stem is further divided into *Callionymus*-substem having the urohyal Type A1a including *Callionymus*, *Bathycallionymus*, *Foetorepus*, *Eocallionymus* and *Eleutherochir*; and *Anaora*-substem, having the urohyal Type A1b, including only *Anaora*. *Calliurichthys*-stem includes the other 10 genera. Next, the branches are determined by the preopercular spine, and the terminal branches are by the other osteological characters.

2. In order to decide what kinds of genera are more advanced or primitive, each osteological character's condition is given the score according to the degree of specialization. As the result, *Eocallionymus* and *Foetorepus* are the most primitive, on the other hand *Repomucenus* and *Anaora* are the most specialized.

3. The center of dispersal must be the Indo-West Pacific because of a large number of species and the high degrees of specialization found in that region.

4. There are two kinds of habitats in the callionymids: sandy-muddy bottoms on the continental shelf, banks and seamounts; sandy bottoms along coral reefs, rocky reefs and weedy beds around islands. The former is the main habitat, and the latter is the secondary one.

5. There are two kinds of geographic distribution patterns. The distribution of *Foetorepus*, *Paradiplogrammus* and *Diplogrammus* are not interrupted by the Isthmus of Suez, whereas that of the other genera are.

6. The differentiation and dispersion of the 10 most common genera are estimated like the following. First, *Foetorepus* emerged in the continental shelf, and somewhat later, *Paradiplogrammus* and *Diplogrammus* in coral or rocky reefs around islands. The common ancestor of *Callionymus* and *Bathycallionymus* inhabited the old Mediterranean after the separation between North America and Europe, 49 million

years ago. After the joint between Africa and Eurasia, 17 million years ago, *Callionymus*, *Bathycallionymus* and *Calliurichthys* inhabited the continental shelf, and *Neosynchiropus* emerged in the coral or rocky reefs around islands. *Eleutherochir* also emerged in the beach at that time. Last, *Repomucenus* emerged on the continental shelf, and *Pseudocalliurichthys* the coral or rocky reefs around islands. After all, it seems that there have been two ways for the dragonets to get a depressed body in order to adapt the benthic life. And, nowadays, *Repomucenus* which seems to be the most adaptive to the benthic life occupies the shelf in the Indo-West Pacific and is the most prosperous.

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