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Phylogeny of the Order Gadiformes (Teleostei, Paracanthopterygii)

Hiromitsu ENDO¹⁾²⁾

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Abstract

Intrarelationships of the order Gadiformes (*sensu* Nelson, 1994), focused on the higher gadoid taxa, were hypothesized cladistically on the basis of 49 morphological transformations. These indicated that gadiforms should be classified into three suborders and eleven families: Melanonidae (Melanonoidei), forming the sister group of all other gadiforms, Macrouridae and Steindachneriidae (Macrouroidei), and Eulichthyidae, Moridae, Macrurionidae, Merlucciidae, Ranicipitidae, Gadidae, Bregmacerotidae and Muraenolepididae (Gadoidei). In addition, four subfamilies were recognized in both Macrouridae (Bathygadinae, Macrourinae, Macrouroidinae and Trachyrincinae) and Gadidae (Group I: Gaidropsarinae and Phycinae; Group II: Lotinae and Gadinae). Three clades were recognized within gadids: Gadiculini (*Gadiculus*), Gadini (*Merlangius*, *Pollachius*, *Theragra*, *Gadus*, *Melanogrammus*, *Eleginus* and *Microgadus*), and Trisopterini (*Trisopterus*, *Micromesistius*, *Arctogadus* and *Boreogadus*). The evolution of dorsal supernumerary fin-ray characters, gadid biogeography, phylogenetic positions of extinct gadoid genera and possible heterochrony among gadiforms are discussed.

Key words: Phylogeny, Gadiformes, cladistics, character evolution, biogeography, fossils, heterochrony

I. Introduction

The order Gadiformes (*sensu* Nelson, 1994) comprises about 500 species included in 85 genera representing a number of morphologically divergent families: Ranicipitidae, Eulichthyidae, Macrouridae, Steindachneriidae, Moridae, Melanonidae, Macrurionidae, Bregmacerotidae, Muraenolepididae, Phycidae, Merlucciidae and Gadidae. Gadiform fishes range from Arctic to Antarctic waters in all oceans, occurring in deep-sea benthic to shore, estuarine and even fresh water habitats (Cohen et al., 1990). In terms of species' diversity, macrourids, including over 300 species of which most are adapted to deep-sea habitats, are the most successful group among gadiforms. Furthermore, gadids and merlucciids include a number of commercially important genera (e.g., *Gadus* and *Merluccius*) and species (e.g., *Theragra chalcogramma*) (Cohen et al., 1990).

The phylogenetic relationships among gadiforms have been investigated by many ichthyologists (e.g., Regan, 1903; Berg, 1940; Svetovidov, 1948; Marshall, 1966; Rosen and Patterson, 1969; Okamura, 1970b, 1989; Marshall and Cohen, 1973; Nelson, 1976, 1984, 1994; Cohen, 1984; Dunn and Matarese, 1984; Fahay and Markle, 1984; Dunn, 1989; Howes, 1989, 1990, 1991a, 1991b, 1993; Inada, 1989; Iwamoto, 1989; Markle, 1989; Nolf and Steurbaut, 1989c). Many contributions of 1989 in "Papers on the systematics of gadiform fishes" resulted from the Workshop on Gadiform Systematics (WOGADS) and subsequent papers by Howes (1990, 1991a, 1993) were particularly significant in advancing knowledge of gadiform phylogeny. Among them, the cladistic hypotheses by Markle (1989) and

Howes (1990, 1991a) reached the following consensus: bregmacerotids and muraenolepidids belong to advanced gadoids, and each of the "Gadidae" and "Merlucciidae" (*sensu* Nelson, 1984) are polyphyletic. These conclusions also differed from the traditional view that the Muraenolepididae was the most primitive family among gadiforms (e.g., Svetovidov, 1948; Cohen, 1984). However, in spite of these cladistic studies, gadiform intrarelationships and taxonomic rankings remain controversial. Accordingly, Cohen et al. (1990) and Nelson (1994) avoided ranking suborders, tentatively recognizing eight and twelve families among gadiforms, respectively.

Although the order Gadiformes (*sensu* Nelson, 1994) is presently accepted as valid (e.g., Gosline, 1971, Cohen, 1984; Nelson, 1984, 1994), distinct synapomorphies supporting its monophyly have not yet been found (Patterson and Rosen, 1989). In addition, the teleost group most closely related to the gadiforms is uncertain (see Matsubara, 1963; Gosline, 1963; Patterson and Rosen, 1989). After Greenwood et al. (1966) established the Paracanthopterygii, gadiforms have always been positioned in the center of this superorder (e.g., Rosen and Patterson, 1969; Lauder and Liem, 1983; Patterson and Rosen, 1989; Nelson, 1994). A subsequent redefinition of the superorder by Patterson and Rosen (1989) included a cladogram incorporating Percopsiformes, Ophidiiformes, Gadiformes, Batrachoidiformes and Lophiiformes. Nevertheless, some have doubted the status of the Paracanthopterygii (e.g., Fraser, 1972; Rosen, 1985; Gill, 1996). Gill (1996) re-examined the synapomorphies of the superorder *sensu* Patterson and Rosen (1989), and recognized a need for

a critical review of its monophyly. Most recently, molecular analyses of higher teleosts using DNA sequence data have revealed polyphyly of the paracanthopterygian orders and zeids as the closest relatives of gadiforms (Wiley et al., 2000: fig. 6; Miya et al., 2001: fig. 3).

The present study set out to estimate intrarelationships of the order Gadiformes using cladistic methodology based on morphological data, and to establish its higher classification based on the hypothesized relationships. The evolutionary aspects of gadiforms are discussed primarily on the basis of the evolution of dorsal supernumerary fin-ray characters, gadid biogeography, phyletic position of extinct gadoid genera (†*Rhinocephalus* and †*Palaogadus*), as well as some heterochronic morphologies and biological aspects.

II. Materials and methods

The specimens examined were stained by Alizarin Red-S, some also being counter stained by Alcian Blue. Dissections and observations were performed under Nikon SMZ-10 and Wild M-8 stereo microscopes, and drawings made with the aid of camera-lucida attachments. The terminology generally follows Uyeno (1975) for osteology, Winterbottom (1974) for myology, Stiassny (1986) for buccal ligaments and Nolf (1985) for otolith morphology.

Abbreviations in each figure are listed in Appendix.

Phylogenetic analyses were made using cladistic methodology (Hennig, 1966; Wiley, 1981; Maddison et al., 1984; Wiley et al., 1991) incorporating a two step procedure (the first involving gadiform families, subsequently used as the basis for the second, involving higher gadoid genera). In the first analysis, because the estimation of relationships within the superorder was beyond the aim of this study, transformations were polarised on the basis of the paracanthopterygian cladogram of Patterson and Rosen (1989). Mabee (1989a, 1989b, 1993) was followed in respect to the rejection of ontogenetic criteria for polarization and order of characters. Consequently, an unordered multistate transformation series using Fitch's parsimony was used in the analyses, if more than two characters appeared in an homologous region.

The cladograms presented here were calculated parsimoniously using the branch-and-bound search option of PAUP* 4.0b10 (Swofford, 2001). Consistency and retention indexes are presented for all analyses (Wiley et al., 1991). The cladograms were converted into classification outlines using the sequencing convention method first proposed by Nelson (1972) (Convention 3 in Wiley et al., 1991). Furthermore, character evolution

on the cladograms were estimated using MacClade ver. 4.03 (Maddison and Maddison, 2001).

All of the specimens examined in this study are listed below.

Abbreviations used in addition to those for fish body parts, include: D, dissected; CS, cleared and stained; R, radiograph; SR, only supernumerary fin-rays examined; UC, uncataloged specimen. The total number of specimens examined for each species is shown next to the species name. Institutional abbreviations follow Leviton et al. (1985), except for CBM: Natural History Museum and Institute, Chiba.

Gadiformes

Melanonidae: *Melanonus gracilis*, 1 specimen, HUMZ 75862 (111 mm SL, D); *M. zugmayeri*, 6, BSKU 27462 (190 mm SL, D), NSMT-P 42323, 42325 (190–200 mm SL, D), NSMT-P 42322, 42324, 42326 (88–190 mm SL, R). **Steindachneriidae**: *Steindachneria argentea*, 4, BSKU 42408 (231 mm TL, D), CAS 61143 (3 spec.: 270 mm TL, D; 200–248+ mm TL, R). **Macrouridae**: *Bathygadus antrodes*, 1, HUMZ 75254 (350+ mm TL, D); *Gadomus colletti*, 1, HUMZ 135146 (210 mm TL, D); *Caelorinchus hubbsi*, 1, HUMZ 135143 (185+ mm TL, D); *Ca. macrochia*, 1, HUMZ 135140 (252 mm TL, D); *Ca. kamoharai*, 1, HUMZ 135145 (225 mm TL, D); *Coryphaenoides cinereus*, 3, HUMZ 135141, 135142 (292–365+ mm TL, D); *Malacocephalus laevis*, 1, HUMZ 32860 (260+ mm TL, R); *Nezumia proxima*, 1, HUMZ 135147 (280+ mm TL, D); *Ventrifossa garmani*, 2, HUMZ 135144, 135149 (168–176+ mm TL, D); *Squalogadus modificatus*, 3, CBM-ZF 5551 (245+ mm TL, D), HUMZ 78126, 121632 (104–360+ mm TL, R); *Idiophorhynchus andriashevi*, 1, LACM 11333–1 (280 mm TL, SR); *Trachyrincus murrayi*, 1, BSKU 45808 (368 mm TL, D). **Euclichthyidae**: *Euclichthys polynemus*, 2, FAKU 44596, 44598 (223–271 mm SL, D). **Moridae**: *Antimora rostrata*, 2, HUMZ 74468, 135151 (121–235 mm SL, D); *Auchenoceros punctata*, 1, LACM UC (CS, SR); *Halargyreus johnsonii*, 2, BSKU 47213 (297 mm SL, D); HUMZ 135150 (125 mm SL, D); *Laemonema longipes*, 2, HUMZ 135152, 135153 (201–266 mm SL, D); *Lotella phycis*, 2, HUMZ 97759 (caudal lost), 135154 (148 mm SL, D); *Mora mora*, 2, BSKU 47215 (255 mm SL, D), FSFL-EE 417 (430 mm SL, R); *Physiculus japonicus*, 3, HUMZ 135155, 135156, UC (134–223 mm SL, D); *Gadella jordani*, 1, HUMZ 135157 (167 mm SL, D); *Salilota australis*, 1, HUMZ 30137 (189 mm SL, D); *Triptero-phycis gilchristi*, 1, LACM UC (CS, SR). **Macruridae**: *Macruronus magellanicus*, 1, HUMZ 30368 (490 mm TL, D); *M. novaezelandiae*, 1, HUMZ 91166 (328 mm TL, D); *M. brachycolus*, 1, ISH 14/66 (CS,

SR). **Merlucciidae**: *Merluccius australis*, 1, HUMZ 30466 (292 mm SL, D); *M. merluccius*, 1, BSKU 47214, 277 mm SL (D). **Ranicipitidae**: *Raniceps raninus*, 3, BSKU 47219 (111 mm SL, D), BSKU 47220 (72 mm SL, R), HUMZ 135158 (162 mm SL, D). **Bregmacerotiidae**: *Bregmaceros arabicus*, 1, HUMZ 135172 (86 mm SL, D); *B. japonicus*, 1, BSKU 45441 (66 mm TL, D). **Muraenolepididae**: *Muraenolepis micropus*, 2, BSKU 47216, UC (200–220 mm SL, D); *M. orangiensis*, 1, FAKU-CP 607 (307 mm SL, D). **Gadidae**: *Phycis phycis*, 1, BSKU 47218 (295 mm SL, D); *P. blennoides*, 3, BSKU 47217 (363 mm SL, D), HUMZ 135159 (146 mm SL, D), USNM 205198 (264 mm SL, D); *P. chesleri*, 3, BSKU 47737 (256 mm SL, D); HUMZ 124581, 124582 (195–197 mm SL, D); *Urophycis brasiliensis*, 1, USNM 228936 (195 mm SL, D); *U. chuss*, 1, HUMZ 124576 (218 mm SL, D); *U. cirrata*, 1, USNM 218166 (262 mm SL, D); *U. earllii*, 2, USNM 226530 (158–160 mm SL, D); *U. floridana*, 1, HUMZ 124579 (250 mm SL, D); *U. regia*, 3, BSKU 47221 (229 mm SL, D), CAS 60338 (132 mm SL, D), USNM 218287 (192 mm SL, D); *U. tenuis*, 1, USNM 120687 (163 mm SL, D); *U. mystaceus*, 1, HUMZ 124575 (184 mm SL, D); *Ciliata mustela*, 1, HUMZ 135160 (98 mm SL, D); *Enchelyopus cimbrius*, 2, HUMZ 135161, 135162 (161–205 mm SL, D); *Gaidropsarus argentatus*, 1, HUMZ 115240 (202 mm SL, D); *G. ensis*, 2, BSKU 47544, 47550 (168–169 mm SL, D); *G. mediterraneus*, 1, HUMZ 135163 (157 mm SL, D); *Brosme brosmes*, 2, BSKU 45654, 45655 (355–384 mm SL, D); *Lota lota*, 2, CAS 60700 (142–158 mm SL, D); *Molva dypterygia*, 1, BSKU 46112 (570 mm SL, D); *Arctogadus glacialis*, 1, HUMZ 135165 (124 mm SL, D); *Boreogadus saida*, 2, HUMZ 135166, 135167 (178–197 mm SL, D); *Eleginus gracilis*, 1 spec., HUMZ 135168 (138 mm SL, D); *Gadiculus argentatus*, 2, ZMUC 15 (112 mm SL, D), ZMUC 16 (92 mm SL, R); *Gadus macrocephalus*, 1, HUMZ 135168 (192 mm SL, D); *G. morhua*, 7, BSKU 44713, 44715 (241–195 mm SL, D), BSKU 44711, 44712, 44714, 44716, 44717 (224–295 mm SL, R); *Melanogrammus aeglefinus*, 2, BSKU 44687, 44688 (254–270 mm SL, D); *Merlangius merlangus*, 1, BSKU 47744 (175 mm SL, D); *Microgadus proximus*, 1, CAS 75516 (137 mm SL, D); *Micromesistius australis*, 1, HUMZ 30155 (225 mm SL, D); *Pollachius pollachius*, 2, ZMUC UC (202–211 mm SL, D); *Theragra chalcogramma*, 2, HUMZ 135170, 135171 (147–184 mm SL, D); *Trisopterus esmarkii*, 1, BSKU 44705 (146 mm SL, D).

Other paracanthopterygians

Batrachoididae: *Batrachoides surinamensis*, 1, CAS 74964 (133 mm SL, R); *Opsanus tau*, 1, CAS 79589

(150 mm SL, D); *Porichthys porosissimus*, 1, HUMZ 31114 (144 mm SL, D). **Chaunacidae**: *Chaunax abei*, 1, HUMZ UC (94 mm SL, D). **Lophiidae**: *Lophiomus setigerus*, 1, HUMZ 95017 (116 mm SL, D). **Ophidiidae**: *Neobythites stigmus*, 1, HUMZ UC (143 mm SL, D); *Hoplobrotula armata*, 1, HUMZ UC (178 mm SL, D); *Homostolus acer*, 1, HUMZ UC (tail lost, SR); *Ophidion asiro*, 1, HUMZ 75357 (CS). **Bythitidae**: *Oligopus robustus*, 1, HUMZ 108748 (136 mm SL, D). **Aphredoderidae**: *Aphredoderus sayanus*, 1, HUMZ 86589 (55 mm SL, D). **Percopsidae**: *Percopsis omiscomaycus*, 1, HUMZ 75834 (49 mm SL, D).

III. Monophyly of Gadiformes

Although synapomorphies of the Gadiformes have been discussed by many authors (see Patterson and Rosen, 1989; Howes, 1993), all-encompassing synapomorphies have not been found because of the morphological diversity of the component taxa. Accordingly, I refer to the potential synapomorphies of gadiforms proposed by Rosen and Patterson (1989), Markle (1989), Nolf and Steurbaut (1989a) and Howes (1989, 1991a, 1993), and those recognized during the present study.

Patterson and Rosen (1989) reviewed the synapomorphies of gadiforms noted by previous authors (e.g., Okamura, 1970b; Marshall and Cohen, 1973; Cohen, 1984) and concluded that the following characters possibly support the monophyly of the order: 1) X and Y bones in caudal skeleton; 2) no epipleurals on first two vertebrae; 3) scapular foramen between scapula and coracoid; 4) LDH pattern (Shaklee and Whitt, 1981). Markle (1989) also adopted characters 2) and 3). In addition, the following synapomorphies have been adopted by some authors: 5) three struts on third pharyngobranchial (Markle, 1989); 6) lateral anus in larvae (Fahay and Markle, 1984; Markle, 1989); 7) pincer-shaped sulcus and central collicular on otolith (Nolf and Steurbaut, 1989a, 1989c); 8) absence of pars jugularis (Howes, 1991a, 1993); 9) levator arcus palatini positioned laterally on adductor mandibular A2 (Howes, 1989, 1991a, 1993); 10) absence of intermuscularis from first and second vertebrae (Howes, 1993); 11) attrition of lateral face of hyomandibular (Howes, 1993). Furthermore, I consider that the following two characters possibly support gadiform monophyly: 12) single condyle of hyomandibular; 13) absence of basihyal.

1) *X and Y bones in caudal skeleton*. These unique caudal elements observed in some gadiforms have been well investigated and discussed by many authors (e.g.,

Markle, 1982, 1989 ; Cohen, 1984 ; Dunn and Matarese, 1984 ; Fahay and Markle, 1984 ; Patterson and Rosen, 1989) (Fig. 26), all of the countable characters of gadiform caudal elements being presented by Fahay and Markle (1984 : table 76). Among gadiforms, X and Y bones are absent in melanonids, trachyrincines, macruronids, gadines and lotines, and the caudal fin is lost in bathygadines, macrourines, macrouroidines and steindachneriids. Based on ontogenetic data for *Lota*, Markle (1982) hypothesized that gadines and lotines may have secondarily lost these bones. Accordingly, I regard the presence of X and Y bones within gadiforms as an apomorphic character.

2) *No epipleurals on first two vertebrae.* Regarding this characters, Patterson and Rosen (1989) noted the following conditions in other paracanthopterygians : absent in lophiiforms ; present on the first (*Batrachoides* and *Thalassophryne*) or second (*Daector*) vertebrae in some batrachoidiforms (interpreted as having resulted from the forward extension of posterior elements) ; present (e.g., *Brotula*, *Ogilbia*, *Ophidion* and carapids) or absent (e.g., *Oligopus*) in ophidiiforms. Although these epipleurals are variously lost among anacanthines, Patterson and Rosen (1989) adopted this character as a synapomorphy of gadiforms. Among the gadiforms examined here, epipleurals were found on the second vertebrae (but sometimes rudimentary or absent) in *Euclichthys*, *Raniceps* (one of two specimens), *Molva*, *Merluccius* (one of two), *Boreogadus* and *Microgadus*. These occurrences seem to be atavistic. As noted by Patterson and Rosen (1989), if the epipleurals on the first two vertebrae appeared secondarily in batrachoidiforms, this character should be regarded as a synapomorphy of anacanthines, not of gadiforms.

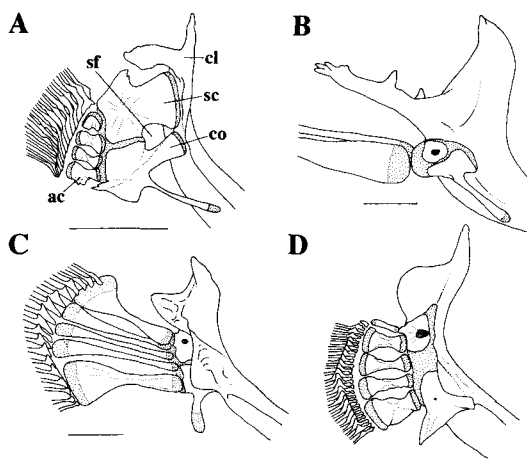


Fig. 1. Medial view of pectoral girdle. A, *Enchelyopus cimbricus* ; B, *Lophiomus setigerus* ; C, *Porichthys porosissimus* ; D, *Oligopus robustus*. Bars=5 mm.

3) *Scapular foramen between scapula and coracoid.* This condition in gadiforms and some lophiiforms apparently represents a derived state compared with other paracanthopterygians which have the foramen completely surrounded by the scapula or open along the anterior margin of the latter (Fig. 1 ; e.g., gadiforms in Markle, 1989 : figs. 10, 11 ; oneirodids in Pietsch, 1974 : figs. 18, 54 ; *Chologaster* in Rosen, 1962 : fig. 15 ; *Batrachoides* in Rosen and Patterson, 1969 : fig. 59A ; *Tetrabrachium* in Pietsch, 1981 : fig. 14 ; some ophidiiforms in Markle and Olney, 1990 : figs. 9-12). I also regard it as a possible synapomorphy of gadiforms. Among gadiforms, this derived condition is generally divided into three states according to the location of the foramen : only on the scapula, between the scapula and intervening cartilage, and between the scapula and coracoid (see Markle, 1989 : figs. 10-12).

4) *LDH pattern.* Shaklee and Whitt (1981) examined the electrophoretic traits of gadiforms, ophidiiforms, zoarcids, aphredoderids and some lower teleosts using lactate dehydrogenase isozymes (LDH). Patterson and Rosen (1989 : table 3) regarded a specific pattern to be a potential synapomorphy of gadiforms, but also pointed out the lack of data for the phylogenetically important taxon *Muraenolepis*. In addition, Shaklee and Whitt (1981) examined neither other important gadiforms, such as melanonids, euclichthyids, steindachneriids and macruronids, nor pediculates, batrachoidiforms and lophiiforms. Because of the lack of information, I did not adopt this as a synapomorphy.

5) *Three struts on pharyngobranchial 3.* As discussed by Markle (1989 : 65, 84), this condition is present in gadiforms and some batrachoidiforms (Figs. 19, 20 ; Travers, 1981 : figs. 9-12 ; Patterson and Rosen, 1989 : figs. 10, 12-14 ; Markle, 1989 : figs. 1-4). The struts are weakly developed in *Bregmaceros* (Fig. 20F) and the known batrachoidiforms. Prior to adopting this character as a synapomorphy of gadiforms, further investigations of the character distribution among batrachoidiforms are necessary.

6) *Lateral anus of larvae.* The known yolk-sac and first feeding larvae of gadiforms transiently have an lateral anus through the finfold (Fahay and Markle, 1984 : 265). In some gadiforms, this character of first feeding larvae are still unknown.

7) *Pince-nez-shaped sulcus and central collicular on otolith.* Nolf and Steurbaut (1989a) discussed in detail the otolith morphology of gadiforms compared with other groups : gadiform otoliths are characterized by a pince-nez-shaped sulcus, which generally has a crest between the collicula, just above the ostium-cauda junction of the crista inferior (Fig. 2B). In a cladogram

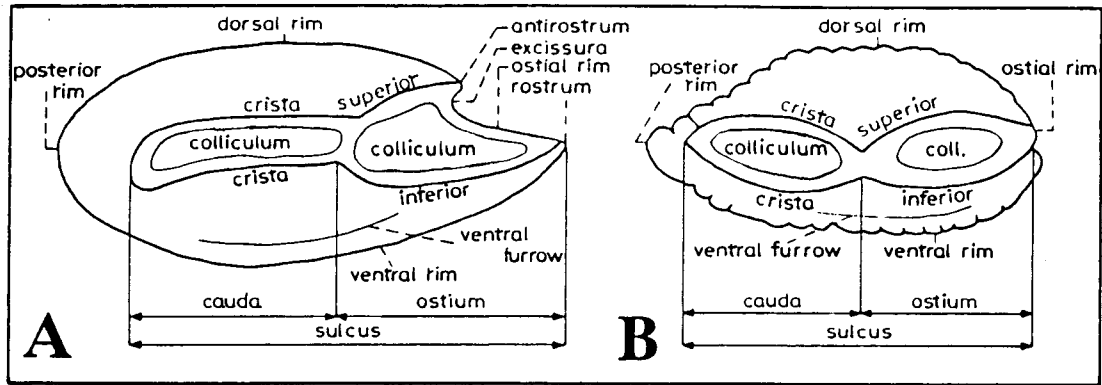


Fig. 2. Morphological nomenclature of left saccular otolith, from Nolf and Steurbaut (1989a). A, generalized acanthopterygian; B, generalized gadiform.

based on otolith features, Nolf and Steurbaut (1989c: fig. 13) indicated this condition as the only synapomorphy of the order.

8) *Absence of pars jugularis*. Howes (1989: 124, fig. 7) referred to the prootic region as serving for the transmission of nerves in gadiforms, viz., most taxa have a single opening serving all of the cranial nerves and vessels. Further, Howes (1991a: fig. 35; 1993: fig. 18) indicated that the “absence of pars jugularis” was a synapomorphy of gadiforms. The term “pars jugularis” has not been used widely in teleostean anatomy (Greenwood, 1986: 951), “trigemino-facialis foramen” of the prootic region having usually been used in earlier papers on gadiforms (e.g., Rosen and Patterson, 1969). This foramen (a pair of pars jugularis) is present in some gadiforms (*Steindachneria*, morids, †*Rhinocephalus*, *Merluccius*, *Brosme*, *Molva*, *Micromesistius* and *Trisopterus*) (e.g., Svetovidov, 1948: fig. 4; Inada, 1989: fig. 1) and some other paracanthopterygians, percopsiforms (Rosen and Patterson, 1969: fig. 13), most ophidiiforms (Howes, 1992: 104, figs. 8, 10–12; pers. obs.), and a few of the batrachoidiforms examined. In ceratioids and some other lophiiforms, the foramen

appeared to be absent as in most gadiforms (Pietsch, 1974: figs. 2, 3, 28, 29, 31–37, 1981: figs. 4, 5; pers. obs.). Any adoption of “absence of trigemino-facialis foramen” as a synapomorphy of gadiforms, necessarily awaits further research on its character distribution among pediculates.

9) *Levator arcus palatini lying laterally on adductor mandibular A2*. The cheek region musculature in gadiforms and some other groups was well described by Howes (1988), who subsequently (Howes, 1989, 1991a, 1993) regarded this condition as a synapomorphy of gadiforms (Fig. 3A). I also adopted this synapomorphy. Among gadiforms, a secondary reversal (adductor mandibular A2 lying laterally on lap) was observed in gaidropsarines, *Urophycis* and *Muraenolepis* (Figs. 9B, 12A, B).

10) *Loss of intermusculars from first and second vertebrae*, and 11) *Attrition of lateral face of hyomandibular*. Howes (1993: fig. 18) indicated the “loss of intermusculars from first and second vertebrae” as a synapomorphy of gadiforms on his cladogram, but without explanation. The condition of the other synapomorphy (“attrition of lateral face of hyoman-

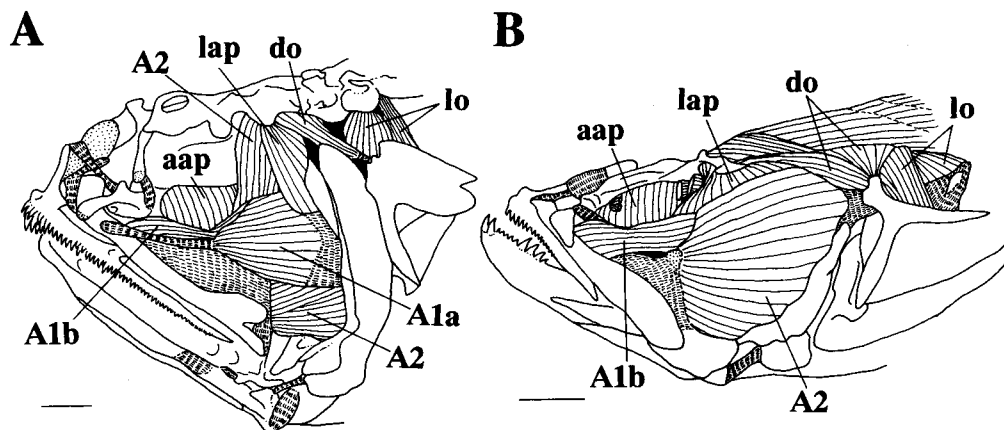


Fig. 3. Lateral view of cheek muscles. A, *Melanonus zugmayeri*; B, *Porichthys porosissimus*. Bars=5 mm.

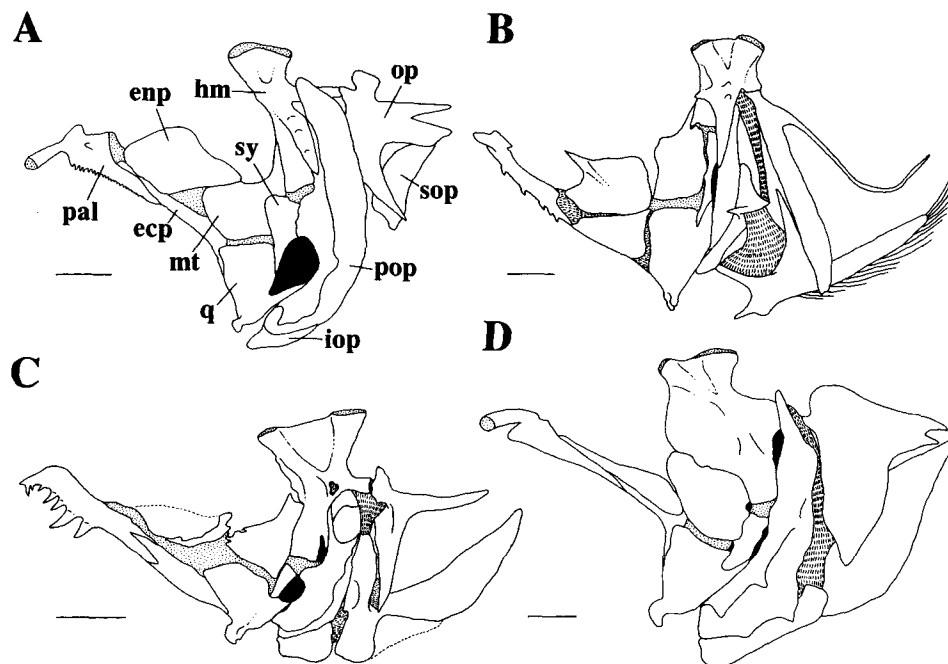


Fig. 4. Lateral view of suspensorium and opercular bones. A, *Melanonus zugmayeri*; B, *Lophiomus setigerus*; C, *Porichthys porosissimus*; D, *Oligopus robustus*. Bars=5 mm.

dibular”) given by Howes (1993 : fig. 18) is difficult to define. If “attrition” refers to the hyomandibular condition in which the anterolateral foramen for nerve passage or lateral shelf is lacking (Howes, 1989), it is difficult to separate gadiforms from the other paracanthopterygians. The lateral face of the hyomandibular in some pediculates and ophidiiforms is rather flat, when compared with gadiforms (Fig. 4; e.g., Rosen and Patterson, 1969). Accordingly, these characters are excluded as potential synapomorphies of the order.

12) *Single hyomandibular condyle*. A single condyle on the dorsal hyomandibular was observed in all of the gadiforms examined (Figs. 4A, 13, 14), (although *Macruronus* had the condyle with an anteriorly projected and rounded part (Fig. 13F), such differing from the two widely separated condyles in most other paracanthopterygians (Fig. 4B-D; paracanthopterygians in Rosen and Patterson, 1969 : figs. 8, 9; lophiiforms in Pietsch, 1974 : figs. 8, 40-47; Pietsch, 1981 : figs. 9, 21-25; ophidiiforms in Markle and Olney, 1990 : figs. 24-26). This single state is also present in the aphyredoderoid *Aphyredoderus* (Rosen, 1962 : fig. 10) and ceratioid *Bertella* (Pietsch, 1974 : fig. 43).

13) *Absence of basihyal*. The basihyal of gadiforms has been erroneously described or identified by some authors (Fig. 5; some macrourids in Okamura, 1970b : 78, fig. 40; *Merluccius* in Inada, 1981 : 81, figs. 35, 37; *Macruronus* in Howes, 1991a : 89, fig. 17); *Melanonus* in Howes, 1993 : fig. 11). In fact, I recognized no basihyal bone in the lower branchial elements of any of

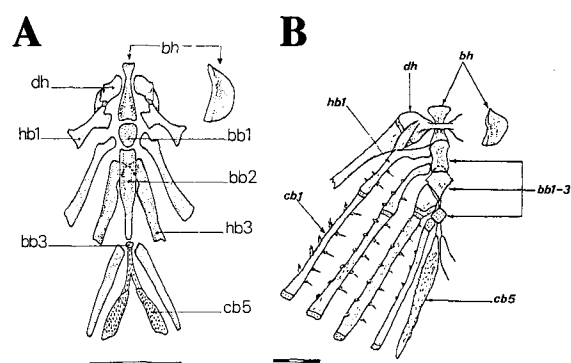


Fig. 5. Dorsal view of lower branchial arch. A, *Macruronus magellanicus*, from Howes (1991a); B, *Melanonus zugmayeri*, from Howes (1993). “Basihyals” (=true basibranchial 1) are also shown in lateral view. Bars=3 mm.

the gadiforms examined (Fig. 6A-D). The condition of *Macruronus magellanicus* shown by Howes (1991a) (Fig. 5A) clearly indicated a single undeveloped basibranchial element in one young specimen (one of 130-250 mm TL specimens), compared with adults of *M. magellanicus* and *M. novaezelandiae* examined here which had basibranchial 2 extended anteriorly onto basibranchial 1 (Fig. 6C, D). In lophiiforms, Pietsch (1981 : 400) mentioned a small basihyal as being present in *Antennarius*, *Tetrabrachium*, *Lophichthys* and *Chaunax*, but absent in *Brachionichthys* and *Dibranchius*. Other paracanthopterygians have a well developed basihyal (Fig. 6E, F; e.g., *Amblyopsis* in Rosen, 1962 : fig. 13; *Thalassophryne* in Rosen and Patterson,

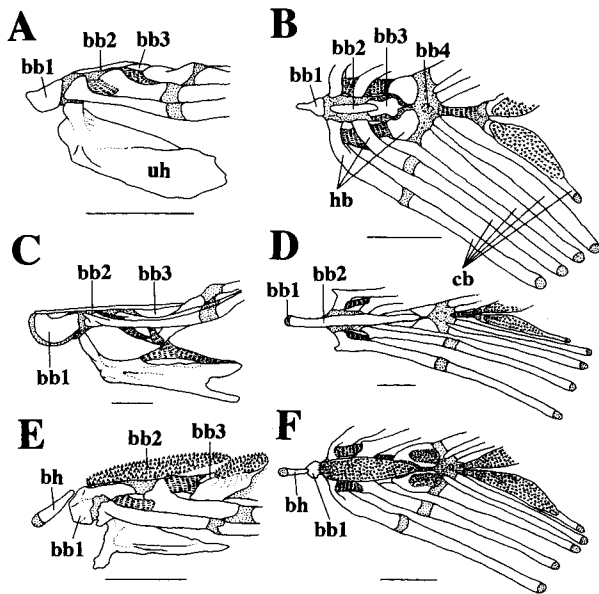


Fig. 6. Lateral and dorsal views of lower branchial arch. A-B, *Phycis blennoides*; C-D, *Macrurus novaezelandiae*; E-F, *Hoplobrotula armata*. Bars=5 mm.

1969: fig. 58; *Snyderidia* in Markle and Olney, 1990: figs. 14, 15; other ophidiiforms and batrachoidiforms examined in the present study). Among gadiforms, *Melanonus* only has an expanded basibranchial 1, apparently composing a horizontal triangular-shaped anterior (such as a general basihyal) and vertical fan-shaped posterior parts (**bh** in Fig. 5B). Fusion of these two bones have not yet been reported for paracanthopterygians. Although a separated basihyal bone attached to basibranchial 1 has been homoplastically lost in some pediculates, its absence gives good support to gadiform monophyly.

Concerning the other potential character, Johnson (1993: 9) pointed out that the simple transversus dorsalis anterior (TDA) was represented only by the musculus transversus epibranchialis 2 (MTE2), which characterize all gadiforms (Fig. 34A). A similar condition was reported by Stiassny and Jensen (1987) for embiotocids, and Sasaki (1989: fig. 4) for haemulids, cheilodactylids, gerreids and sciaenids. In addition, Johnson (1993) noted a few other percoid families and perciform suborders (e.g., gobioids and blennioids) as showing a similar condition. All of the gadiforms examined here had a simple TDA, but the distribution of this character among other paracanthopterygians is uncertain.

As discussed above, I presently consider the following five characters to be synapomorphies of the order Gadiformes: (3) scapular foramen between scapula and coracoid; (7) pince-nez-shaped sulcus and central col-

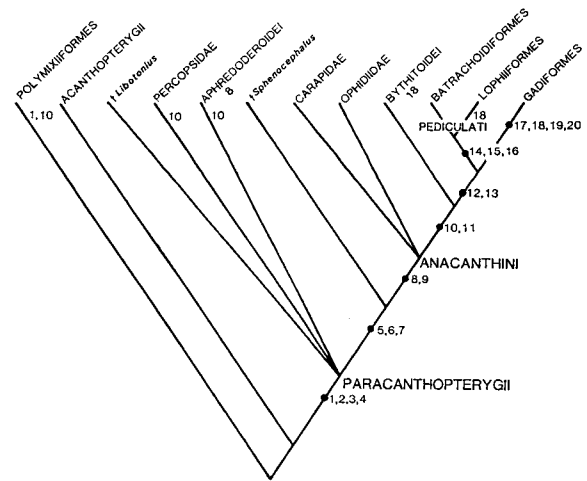


Fig. 7. Paracanthopterygian intrarelationships of Patterson and Rosen (1989).

licular on otolith; (9) levator arcus palatini lying laterally on adductor mandibular A2; (12) single hyomandibular condyle; (13) absence of basihyal.

IV. Relatives of Gadiformes

The Superorder Paracanthopterygii, including the Gadiformes, was first proposed by Greenwood et al. (1966), and subsequently defined by Rosen and Patterson (1969). Furthermore, Patterson and Rosen (1989) revised paracanthopterygians and inferred interrelationships for the five orders included, viz., Percopsiformes, Ophidiiformes, Batrachoidiformes, Lophiiformes and Gadiformes (Fig. 7). On the cladogram of Patterson and Rosen (1989), gadiforms is placed as the sister group of the batrachoidiform and lophiiform clade. On the other hand, Markle (1989) and Nolf and Steurbaut (1989a) regarded gadiforms as the sister group of batrachoidiforms and ophidiiforms, respectively.

On the other hand, some authors have doubted the Paracanthopterygii, believing it to be an ill-defined assemblage (e.g., Fraser, 1972; Rosen, 1985; Gill, 1996). Furthermore, based on a recent total evidence approach including both molecular (12S rDNA and 28S rDNA) and morphological data, Wiley et al. (2000) indicated that two gadoids (*Pollachius* and *Merluccius*) formed a clade with two zeids (*Zeus* and *Zenopsis*), among 25 acanthomorphs, such being evidence of polyphyly of paracanthopterygians. From a mitogenomic analysis of higher teleosts, Miya et al. (2001) also recognized a "gadiform and zeid clade", being a sister group of the percopsiform *Percopsis*, and suggested polyphyly of the superorder. Although such molecular approaches provide strong evidence for inferring the relationships of higher taxa, to confirm a sister relation-

Table 1. List of transformation series considered in the first analysis

-
1. Nasals (0, normal ; 1, enlarged)
 2. Anterolateral processes on lachrymal (0, absent ; 1, present)
 3. Adductor mandibular A1 formation (Fig. 11: 0, A ; 1, B ; 2, C ; 3, D)
 4. Adductor mandibular A2 covering levator arcus palatini (0, normal ; 1, partly covered ; 2, entirely covered)
 5. Endo- and metapterygoids (0, attached ; 1, separated)
 6. Palatopterygoid formation (0, normal ; 1, phycine and gaidropsarine type)
 7. Lower process of hyomandibular (0, absent ; 1, present)
 8. Hyomandibular-preopercle interosseous space (0, closed ; 1, opened)
 9. Branchiostegal rays on epihyal (0, two ; 1, one ; 2, zero)
 10. Medial interopercular socket (0, absent ; 1, present)
 11. Attachment of rectus communis to urohyal (0, muscle ; 1, ligament)
 12. Dorsal gill-arch elements (0, bony Pb1, ial and iac ; 1, cartilaginous pb1, ial and iac ; 2, ial and iac ; 3, cartilaginous pb1 and ial ; 4, cartilaginous pb1 and iac ; 5, absent)
 13. Hyohyoideus abductores 2 (0, separated from each other ; 1, fused on midline)
 14. Intercalar (0, not enlarged ; 1, enlarged)
 15. Number of actinosts (0, four ; 1, increased ; 2, decreased)
 16. Median process of pelvic girdle (0, directed medially ; 1, directed posteromedially ; 2, directed medially and elongated ; bregmacerotid type ; 4, no process)
 17. Epipleurals (0, present ; 1, absent)
 18. Dorsal supernumerary fin-rays (0, D2P0 ; 1, D2P1 ; D2P2 ; 3, D1P1 ; 4, D1P0 ; 5, D0P0)
 19. Pelvic fin (0, normal ; 1, reduced or absent)
 20. Caudal fin (0, present ; 1, absent)
 21. X and Y bones in caudal skeleton (0, absent ; 1, present ; 2, secondarily lost)
 22. Hypurals (0, both separated ; 1, upper fused and lower separated ; 2, completely fused)
 23. Scales (0, cycloid ; 1, spinoid)
-

ship between gadiforms and zeiforms may require further morphological comparisons and additional molecular data for various taxa in question.

In this paper, I tentatively use the cladogram proposed by Patterson and Rosen (1989) for estimating the relationships of gadiform families and subfamilies, based on outgroup comparison (Maddison et al., 1984).

V. Interrelationships of lower gadiforms

The interrelationships of seventeen gadiform taxa, being regarded as the family or subfamily level (e.g., Cohen, 1984 ; Markle, 1989 ; Cohen et al., 1990), are estimated from twenty-three transformation series based on morphological differences. Each monophyly of OTU, excluding lotines, has been well corroborated by many workers (e.g., Howes, 1989, 1991a, 1993 ; Iwamoto, 1989 ; Markle, 1989). In addition, the monophyly of lotines was newly confirmed by two synapomorphies found in this study.

In the present analysis, I adopted distinct characters showing less variation at the subfamilial level so as to obtain a realistic cladogram of lower gadiform relationships. For taxa including both primitive and derived

(apparently homoplastic) characters (e.g., some macrourids and morids), the former was selected as the representative state for the group.

1. Characters used in the first analysis

Each character (=Ch) of 23 transformation series (=TS) is presented and polarized below (Table 1). Autapomorphies are excluded from the data set, but included in the subsequent tree description. A large number of morphological characters of many gadiform taxa, mainly bones and muscles (except for otolith features), have been well described and illustrated by previous authors: *Raniceps* (cranial bones) by Gill (1890 : figs. 1-4) ; *Gadus*, *Enchelyopus*, *Merluccius* and *Raniceps* (cranial muscles) by Dietz (1921 : figs. 6-14) ; *Gadus*, *Lota*, *Melanonus*, *Bregmaceros* and *Coryphaenoides* (cranial bones) by Gregory (1933 : figs. 258-262) ; 51 gadoids (cranial and other bones) by Svetovidov (1948 : figs. 1-7, 10, tables 1-72) ; *Bregmaceros* (bones) by D'Ancona and Cavinato (1965 : figs. 11-20) ; *Gadus*, *Urophycis*, *Lota* and *Merluccius* (cranial bones) by Mujib (1967 : figs. 1-8) ; gadiforms (hyoid arch) by McAllister (1968 : 120, pls. 13-14) ; five gadiforms (caudal bones) by Monod (1968 : figs.

567–577); *Brosme* (cranial bones) by Mujib (1969: figs. 1, 2); some gadiforms (some bones and muscles) by Rosen and Patterson (1969: figs. 3, 6, 9, 44–47, 49, 50–52, table 8); many Japanese macrouroids (bones and others) by Okamura (1970b: figs. 1–83); *Microgadus* (cheek muscles) by Winterbottom (1974: fig. 6); *Bathygadus* and macrouroids (cranial bones and muscles) by McLellan (1977: figs. 1–7); some gadiforms (cranial bones and muscles) by Casinos (1978: figs. 1–7); twelve *Merluccius* species (bones) by Inada (1981: figs. 27–53); gadids and some gadiforms (medial bones and meristic characters) by Markle (1982: figs. 4–9, tables 2–9); gadids and *Raniceps* (ontogeny and caudal bones) by Dunn and Matarese (1984: figs. 146, 148, 151, tables 77–82); gadiforms (meristic characters and others) by Fahay and Markle (1984: fig. 144, tables 72–76); *Bregmaceros* (cranial bones) by Hussain (1986: figs. 1, 2); *Ciliata* (cranial bones and muscles) by Stainier et al. (1986: figs. 1–17); ten *Gaidropsarus* species (crania) by Svetovidov (1986: figs. 6–10); gadiforms (palatine) by Howes (1987: figs. 1–4); gadiforms (cranial muscles) by Howes (1988: figs. 1–39); morids (swimbladder) by Paulin (1988: figs. 1–4); gadiforms (dorsal gill-arch, caudal and other bones) by Patterson and Rosen (1989: figs. 5, 6, 8, 12); gadiforms (dorsal gill-arch and other bones) by Markle (1989: figs. 2–17); gadiforms (cranial muscles and others) by Howes (1989: figs. 1–6); five gadiforms (crania and others) by Okamura (1989: figs. 1–4); *Steindachneria* (bones) by Fahay (1989: figs. 5–11); macrouroids (bones and others) by Iwamoto (1989: figs. 1–14); four gadiforms (crania and others) by Inada (1989: figs. 1–4, table 1); gadoids (ontogeny) by Dunn (1989: figs. 4–25, tables 9–10); *Muraenolepis* and some gadoids (cranial bones) by Howes (1990: figs. 1–12); six gadiforms (caudal bones) by Fujita (1990: figs. 137–142); *Bathygadus* (bones, muscles and nerves) by Howes and Crimmen (1990: figs. 2–26, table 1); *Bregmaceros* (bones) by Swidnicki (1991: figs. 1–18); *Macruronus* (bones and muscles) by Howes (1991a: figs. 1–33); *Melanonus* (bones and muscles) by Howes (1993: figs. 1–17); Moridae (bones and swimbladder) by Meléndez and Markle (1997: figs. 4–16).

TS 1. Nasals (Iwamoto, 1989: 163; Okamura, 1989: 135). In most paracanthopterygians, the nasals are small thin elements separated from each other (**Character=Ch. 0**: e.g., *Gadomus* in Okamura, 1970b: fig. 29A; *Euclichthys* in Okamura, 1989: fig. 2B; *Thalassophryne*, *Porichthys* and *Histrio* in Rosen and Patterson, 1969: fig. 53A, C–D). In macrouroidines, *Squalogadus* and *Trachyrincus*, however, both nasals are greatly enlarged and firmly attached in the midline

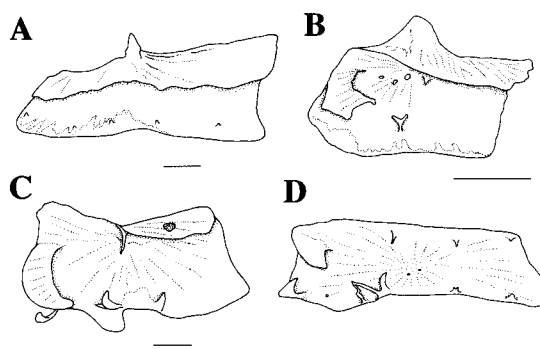


Fig. 8. Lateral (A–C) and ventral (D) views of lachrymal. A, *Bathygadus antrodes*; B, *Nezumia proxima*; C, *Squalogadus modifiatus*; D, *Trachyrincus murrayi*. Bars = 5 mm.

(**Ch. 1**: e.g., macrourines in Okamura, 1970b: figs. 30–32; *Squalogadus* and *Trachyrincus* in Okamura, 1989: fig. 2E–F).

TS 2. Anterolateral processes on lachrymal (Fig. 8). In most paracanthopterygians, such a process on the lachrymal is absent (**Ch. 0**: Fig. 8A). In macrourines, *Squalogadus* and *Trachyrincus*, one or two processes are present on the anterolateral region of lachrymal (**Ch. 1**: Fig. 8B–D; see also Okamura, 1970b: figs. 21–25).

TS 3. Adductor mandibular A1 formation (Figs. 3, 9–11; Howes, 1989: 118, 1991a: fig. 35). In gadiforms, the adductor mandibular A1 is divided into four types on the basis of the position (lateral or medial) of A1b: A1 or A1a and A1b lie laterally on A2 in *Melanonus*, *Steindachneria*, bathygadines, macrourines, *Trachyrincus*, *Squalogadus* and morids (**Ch. 0**: Figs. 3A, 9A, 11A); A1 is divided posteriorly into (lateral) A1a and (medial) A1b in *Euclichthys* and *Muraenolepis* (**Ch. 1**: Figs. 9B, C, 11B; see Howes, 1988: figs. 14, 22); A1 is completely divided into (lateral) A1a and (medial) A1b in gadids, *Raniceps*, *Merluccius* and *Macruronus* (**Ch. 2**: Figs. 10, 11C, 12; e.g., *Urophycis*, see Howes, 1988: fig. 21); A1 is undivided or medial A1b lost in *Bregmaceros* (**Ch. 3**: Figs. 9D, 11D; see Howes, 1988: fig. 22). Paracanthopterygians generally show a different state, i.e., medial A1b (fused with A2 in some lophiiforms) and developed A2, having no lateral A1a (Figs. 3B, 11E; *Chologaster* and *Percopsis* in Rosen, 1962: fig. 6; *Opsanus* and *Porichthys* in Rosen and Patterson, 1969: fig. 55; *Antennarius* in Pietsch and Grobecker, 1987: fig. 151; *Acanthonus* in Howes, 1992: fig. 27, 28). In percopsiforms, both the lateral A1 figured in Rosen (1962) and Rosen and Patterson (1969: fig. 6A), and A1a figured in Howes (1988: fig. 24) have resulted from an apparent confusion of A2 with Aw (see

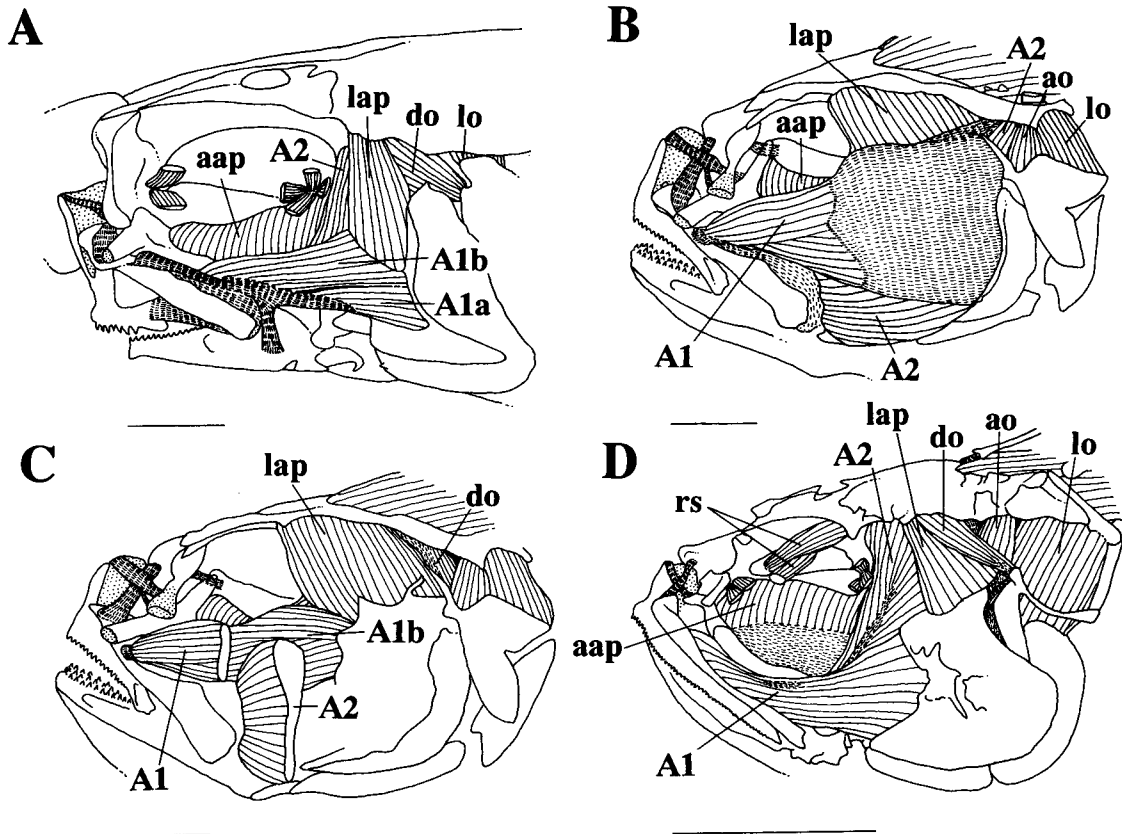


Fig. 9. Lateral view of cheek muscles. A, *Caelorinchus hubbsi*; B-C, *Muraenolepis orangiensis*; D, *Bregmaceros arabicus*. A1 and A2 elements partly removed in C. Bars=5 mm.

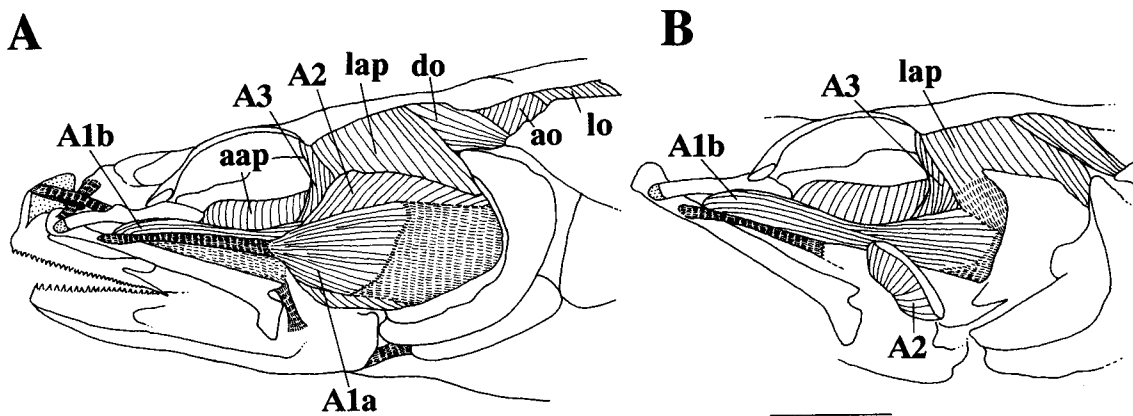


Fig. 10. Lateral view of cheek muscles of *Lota lota*. A, superficial view; B, A1a and A2 partly removed. Bars=5 mm.

Winterbottom, 1974: *Esox* in fig. 2). Since A1 is defined by its dorsal position and insertion on the maxilla (Winterbottom, 1974: 232), I consider "A1a" inserted medially on the lower jaw of *Amblyopsis* in Gosline (1993: fig. 3) to be A2. Furthermore, the insertion of A1b in the outgroups apparently differs from that in gadiforms, and its homology seems to be questionable. These characters are most likely to have developed independently among gadiforms and are

therefore treated here as unpolarized transformation series.

TS 4. Adductor mandibular A2 covering levator arcus palatini (lap) (Fig. 12). The condition of the lap muscle lying laterally on A2 is considered to be a synapomorphy of the order (Ch. 0: Figs. 3A, 9A, 11A, 12C, D). Among gadiforms, the following variations are therefore regarded as derived: upper part of A2

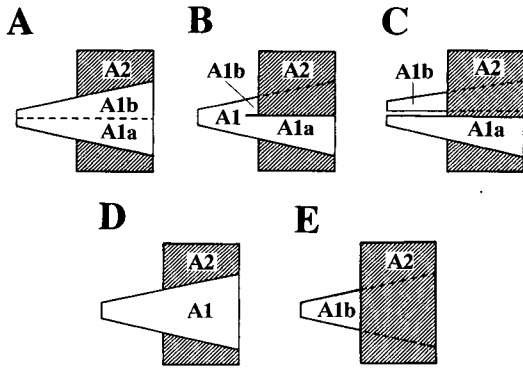


Fig. 11. Five types of adductor mandibular formation ; schematic representation of lateral view.

lying laterally on the lower part of lap in *Muraenolepis* (Ch. 1: Fig. 9B, C); A2 almost covering the lateral surface of lap in the gadid genera, *Urophycis*, *Ciliata*, *Enchelyopus* and *Gaidropsarus* (Ch. 2: Fig. 12A, B; *Ciliata* in Stainier et al., 1986: fig. 13).

TS 5. Endo- and metapterygoids (Figs. 13, 14). In many paracanthopterygians, except for some pediculates, the endopterygoid touches the metapterygoid posteriorly (Ch. 0: Fig. 13A-F; *Percopsis*, *Hymenocephalus*, *Dinematichthys* and †*Sphenocephalus* in Rosen and Patterson, 1969: figs. 8A, 9B, C, 30). However, the

endopterygoid is reduced in size and separated from the metapterygoid in *Merluccius*, *Raniceps*, gadines, lotines, phycines and gaidropsarines (Ch. 1: Figs. 13G, H, 14C-H), and is absent in *Bregmaceros* and *Muraenolepis* (Ch. 2: Fig. 14A, B). Both separation from the metapterygoid and absence of the endopterygoid are considered to be derived. Howes (1990) illustrated a reduced endopterygoid in *Muraenolepis microps*, but such was not obvious in the specimens of *M. microps* and *M. orangeiensis* examined here.

TS 6. Palatopterygoid formation (Figs. 13, 14). In most gadiforms and outgroups, the ventral margins of the palatine and ectopterygoid continue along the same line (Ch. 0: Figs. 13, 14A, B, E-H). However, phycines and gaidropsarines have a unique formation, the ventral margins of the two bones following different lines, i.e., the ectopterygoid extends anteriorly beneath the palatine. This condition is synapomorphic for these two groups (Ch. 1: Fig. 14C, D; *Ciliata* in Stainier et al., 1986: fig. 7).

TS 7. Lower process of hyomandibular (Figs. 13-15). Four hyomandibular processes (articular process, lower process, opercular process and preopercular process) are present in gadiforms (Fig. 15: Svetovidov, 1948; Dunn,

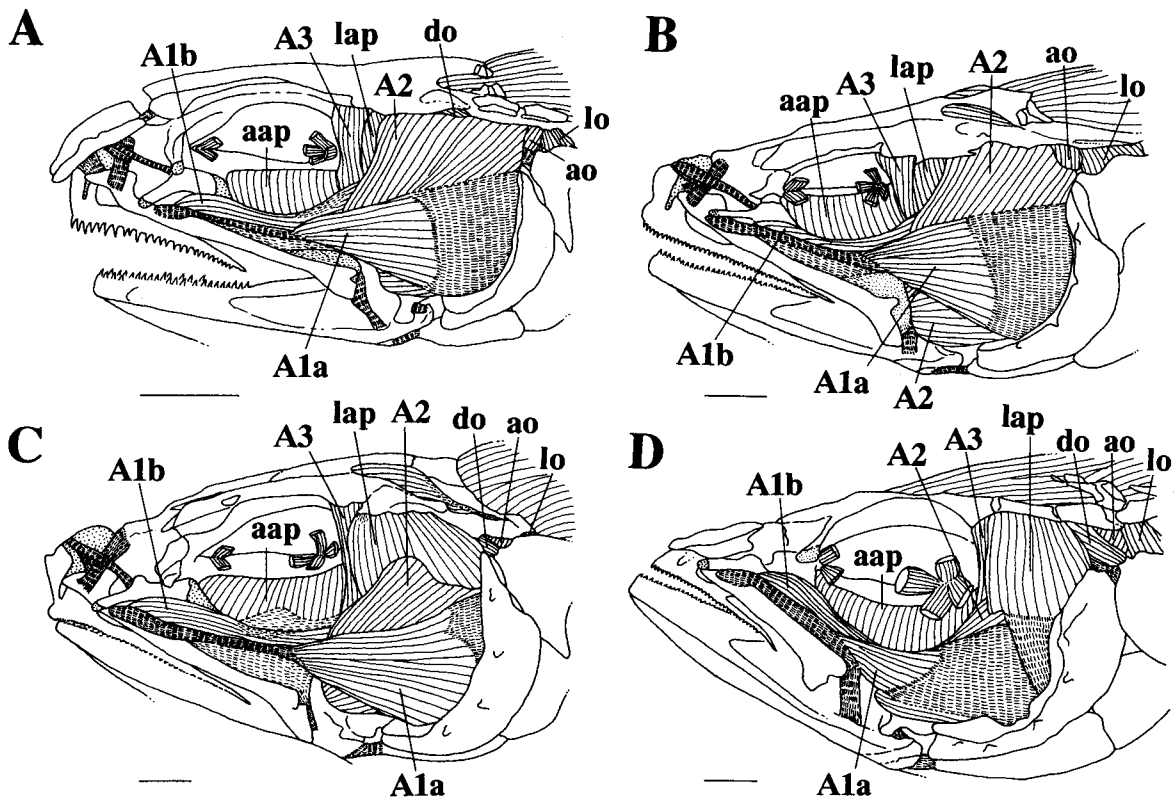


Fig. 12. Lateral view of cheek muscles. A, *Enchelyopus cimbricus*; B, *Urophycis brasiliensis*; C, *Phycis chesteri*; D, *Pollachius pollachius*. Bars=5 mm.

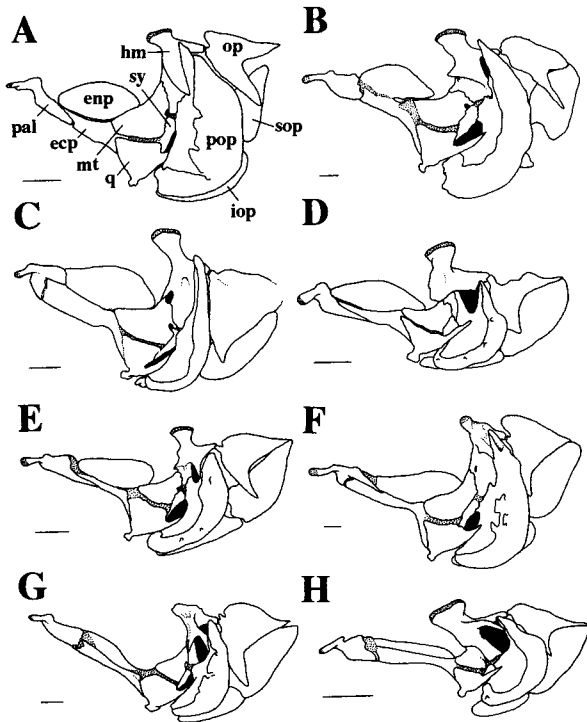


Fig. 13. Lateral view of suspensorium and opercular bones. A, *Steindachneria argentea*; B, *Bathygadus antrodes*; C, *Euclichthys polynemus*; D, *Lotella phycis*; E, *Laemonema longipes*; F, *Macruronus magellanicus*; G, *Merluccius merluccius*; H, *Raniceps raninus*. Bars=5 mm.

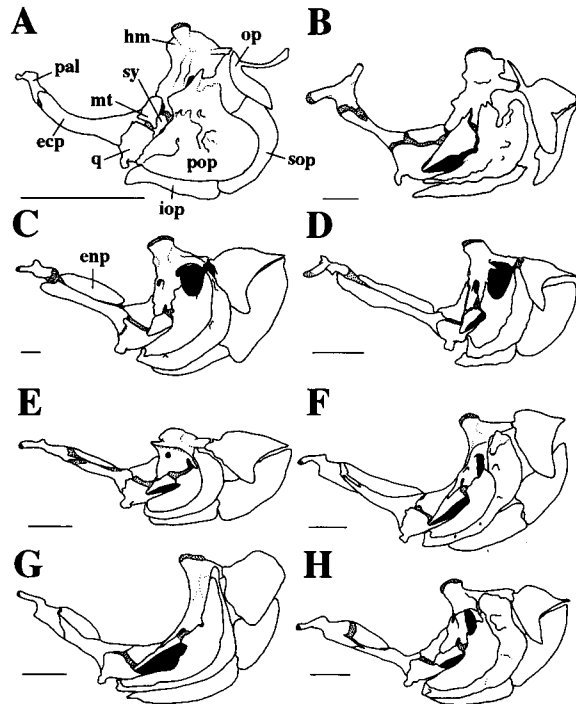


Fig. 14. Lateral view of suspensorium and opercular bones. A, *Bregmaceros arabicus*; B, *Muraenolepis orangiensis*; C, *Phycis phycis*; D, *Enchelyopus cimbrius*; E, *Lota lota*; F, *Trisopterus esmarkii*; G, *Gadiculus argenteus*; H, *Microgadus proximus*. Bars=5 mm.

1989: figs. 13, 14). In *Muraenolepis*, gadines, lotines, phycines and gaidropsarines, the lower process extends anteroventrally and is inserted between the metapterygoid and symplectic, a derived condition (Ch. 1: Figs. 14B-H, 15). On the other hand, other gadiforms and outgroups lack such a process (Ch. 0: Figs. 4, 13, 14A).

TS 8. Hyomandibular-preopercle interosseous space (Figs. 13, 14; Okamura, 1989: 132, fig. 1; Inada, 1989: 200, fig. 2). The interosseous space between the hyomandibular and preopercle, termed “upper window”, was mentioned and discussed by Okamura (1989) and Inada (1989). In most paracanthopterygians, this “window” is generally closed, except in batrachoidiforms (some paracanthopterygians in Rosen and Patterson, 1969: figs. 8, 9; ophidiiforms in Markle and Olney, 1990: figs. 24–26) (Ch. 0: Figs. 4A, 13A, C, F). The opening varies from narrow to wide in morids, *Merluccius*, *Raniceps*, *Bregmaceros*, *Muraenolepis*, gadines, lotines, phycines and gaidropsarines, being a derived character for gadiforms (Ch. 1: Figs. 13D, E, G, H, 14). Okamura (1989) believed the presence of an upper window to be a primitive state among gadiforms, because of its imperfect connection between the suspensorium and opercular bones. A lower window (in

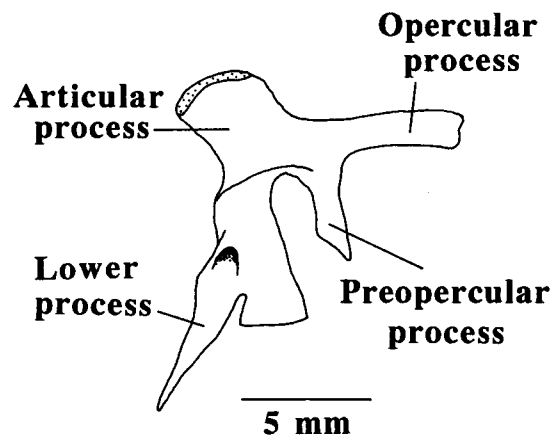


Fig. 15. Lateral view of hyomandibular of *Merlangius merlangus*.

Okamura, 1989) is variously developed among both gadiforms and outgroups (absent in *Caelorinchus*, *Squalogadus* and the bythitoid *Oligopus*), and was not included in the present analysis.

TS 9. Branchiostegal rays on epihyal (Fig. 16; Markle, 1989: 71; Okamura, 1989: 132; Iwamoto, 1989: 167). In paracanthopterygians, three states for the branchiostegal rays on the epihyal were recognized by McAllister (1968): two rays only in *Trachyrincus*,

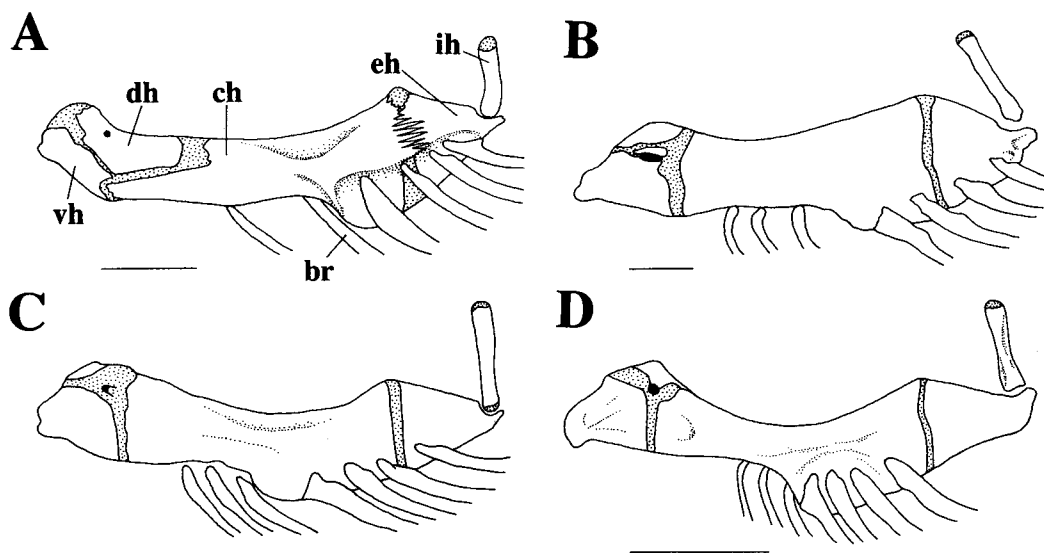


Fig. 16. Lateral view of hyoid arch. A, *Porichthys porosissimus*; B, *Trachyrincus murrayi*; C, *Physiculus japonica*; D, *Gadidulus argenteus*. Bars=5 mm.

Squalogadus, some batrachoidiforms and ophidiiforms (Ch. 0: Fig. 16A, B; e.g., *Squalogadus* in Okamura, 1970b: fig. 44F; *Brotula* in Markle, 1989: fig. 8); one ray on epihyal in most gadiforms, lophioids, one batrachoidiforms, percopsiforms and †*Sphenocephalus* (Ch. 1: Fig. 16C; *Bregmaceros* in Swidnicki, 1991: fig. 11A; †*Sphenocephalus* and *Thalassophryne* in Rosen and Patterson, 1969: fig. 31, 57A); no rays on the epihyal in gadines, lotines, gaidropsarines, antennarioids and ceratioids (Ch. 2: Fig. 16D; *Brosme* in Mujib, 1969: fig. 2C; *Histrio* in Rosen and Patterson, 1969: fig. 57C). Polarity could not be determined from out-group comparisons.

TS 10. Medial interopercular socket (Fig. 17; Lauder and Liem, 1983: 150; Markle, 1989: figs. 6, 7; Howes, 1989: figs. 2, 3, 1991a: fig. 35). The medial interopercular socket, receiving the posterior corner of the epihyal, is a bony structure observed in *Trachyrincus*, *Squalogadus*, *Merluccius*, *Raniceps*, *Muraenolepis*, gadines, lotines, phycines and gaidropsarines (Ch. 1: Fig. 17B; *Muraenolepis* and *Theragra* in Markle, 1989: figs. 6B, 7; *Ventrifossa*, *Trachyrincus* and *Merluccius* in Howes, 1989: figs. 2, 3B). A shallow depression on the medial interopercle in *Bregmaceros* is regarded as a reduced socket structure (Ch. 2: Swidnicki, 1991: 141). The absence of this socket was widely observed in the other gadiforms and outgroups (Ch. 0: Fig. 17A; *Melanonus* in Markle, 1989: fig. 6A; *Ventrifossa* and *Bathygadus* in Howes, 1989: figs. 2A, 3A).

TS 11. Attachment of rectus communis to urohyal (Fig. 18A, B). In gadiforms, the rectus communis is a

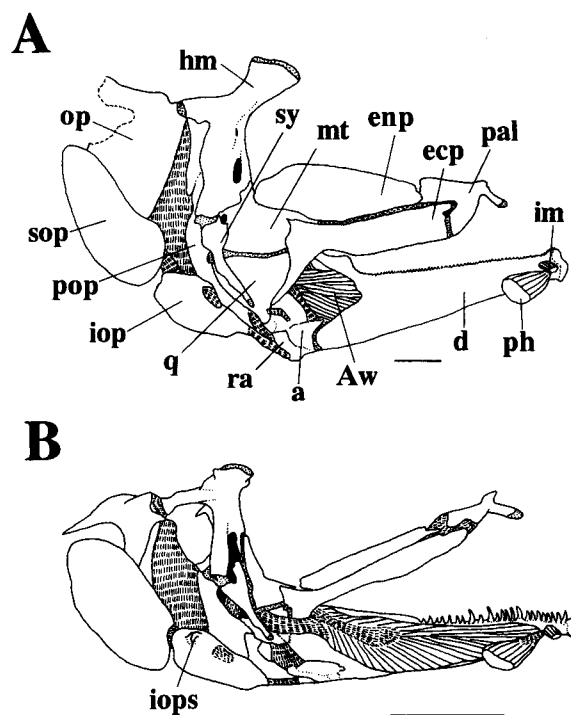


Fig. 17. Medial view of suspensorium and opercular bones. A, *Euclichthys polynemus*; B, *Enchelyopus cimbricus*. Bars=5 mm.

ventral gill-arch muscle connecting the ventral face of the fifth ceratobranchial with the dorsal face of the urohyal. Its anterior part (attached to the urohyal) is ligamentous in bathygadines, morids, *Steindachneria*, *Euclichthys*, *Merluccius* and *Raniceps* (Ch. 1: Fig. 18A), but muscular in the other gadiforms and outgroups (Ch. 0: Fig. 18B). The ligamentous state is regarded as derived.

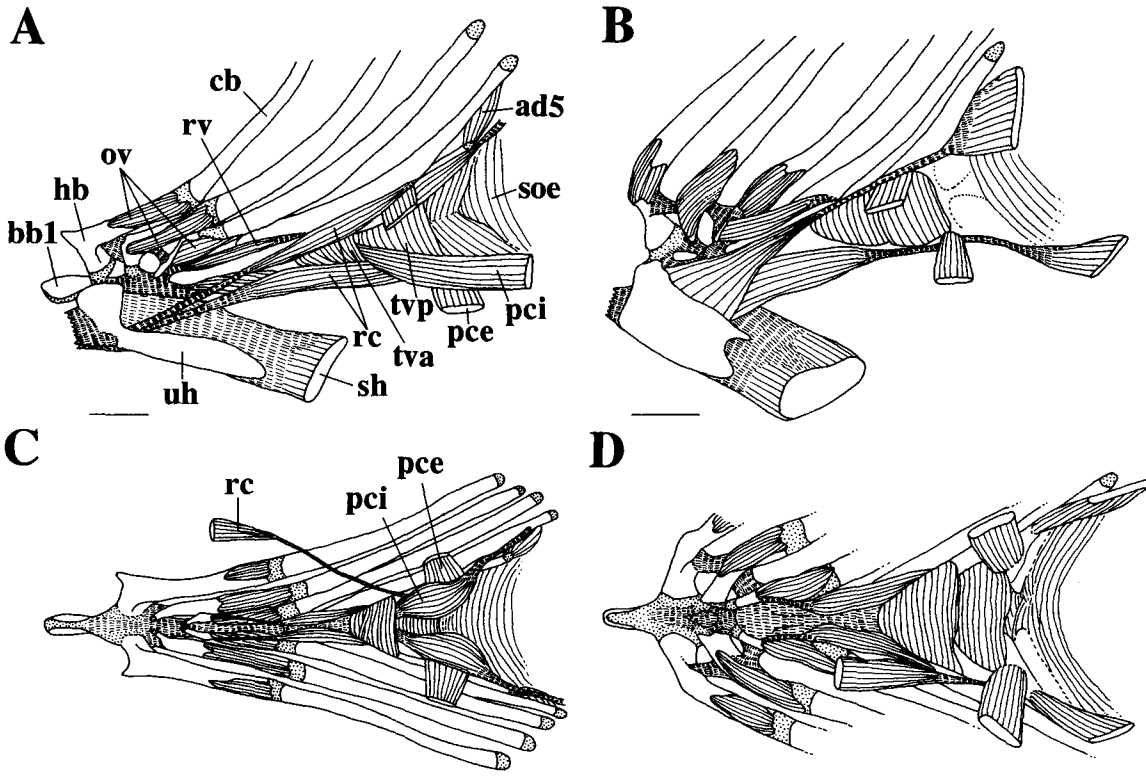
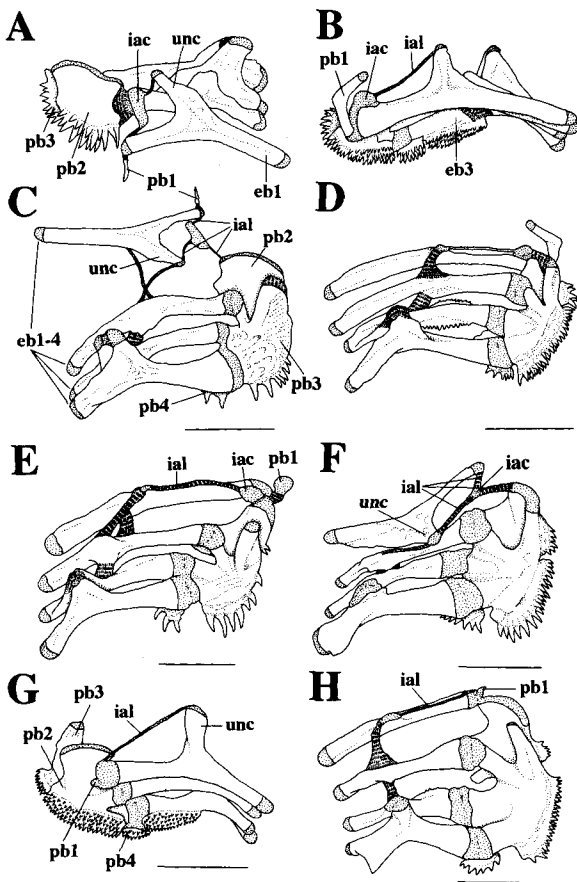


Fig. 18. Ventrolateral (A-B) and ventral (C-D) views of ventral gill-arch muscles. A, *Merluccius australis*; B, *Melanogrammus aeglefinus*; C, *Macruronus magellanicus*; D, *Boreogadus saida*. Bars=5 mm.



TS 12. Dorsal gill-arch elements (Figs. 19, 20, Table 2; Markle, 1989: 63, fig. 5). Patterson and Rosen (1989: figs. 10, 12-14) and Markle (1989: figs. 1-5) discussed and illustrated in detail the dorsal gill-arch bones of paracanthopterygians and some other taxa. In particular, Markle (1989: fig. 5) hypothesized the character phylogeny, considering the dorsal gill-arch bones to reflect the gadiform relationships. However, for gadiforms, a different transformation series for the dorsal gill-arch is proposed here, based on the condition of pharyngobranchial 1 (=Pb 1) and the interarcual ligament and cartilage. The following characters are recognized (Table 2): presence of bony Pb 1 and both interarcual elements in *Melanonus*, *Euclichthys* and *Steindachneria* (Ch. 0: Fig. 19A-D; *Melanonus* and *Steindachneria* in Markle, 1989: figs. 2C, 3A); presence of cartilaginous Pb 1 and both interarcual elements in bathygadines, most morids and *Macruronus* (Ch. 1: Fig. 19E; *Gadomus* in Markle, 1989: fig. 3B; *Laemonema* in Meléndez and Markle, 1997: fig. 4A, D); absence of Pb 1 and presence of both interarcuals in *Trachyrincus* (Ch. 2: Fig. 19F); absence of interar-

Fig. 19. Anterior (A-B, G) and dorsal (others) views of left dorsal gill-arch. A, C, *Melanonus zugmayeri*; B, D, *Euclichthys polynemus*; E, *Macruronus magellanicus*; F, *Trachyrincus murrayi*; G-H, *Squalogadus modificatus*. Bars=5 mm.

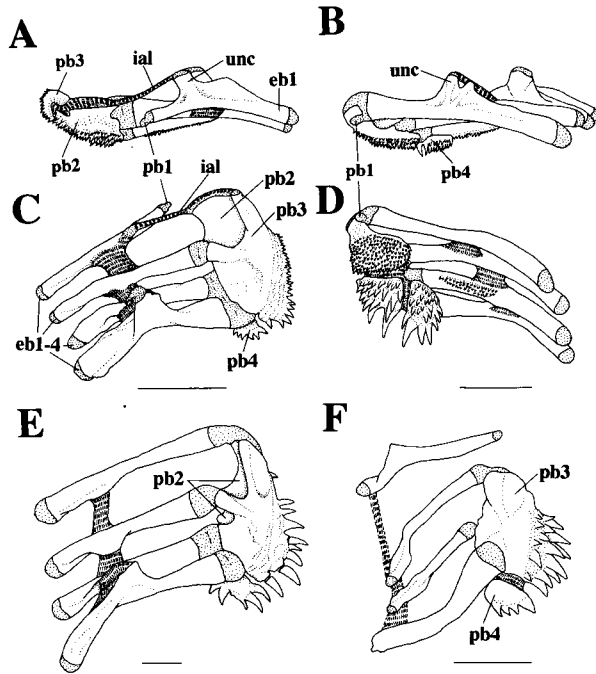


Fig. 20. Anterior (A-B) and dorsal (others) views of left dorsal gill-arch. A, C, *Raniceps raninus*; B, D, *Merluccius australis*; E, *Gaidropsarus mediterraneus*; F, *Bregmaceros arabicus*. Bars = 5 mm.

qual cartilage of Ch. 1 in *Raniceps* and *Squalogadus* (Ch. 3: Figs. 19G, H, 20A, C; Markle, 1989: fig. 2B); absence of interarcual ligament of Ch. 1 in *Merluccius* (Ch. 4: Fig. 20B, D; Patterson and Rosen, 1989: fig. 12D); absence of all elements in gadines, lotines,

phycines, gaidropsarines, macrourines, *Bregmaceros* and *Muraenolepis* (Ch. 5: Fig. 20E, F; *Hymenocephalus* and *Nezumia* in Patterson and Rosen, 1989: fig. 12H, J; *Gadus*, *Bregmaceros* and *Muraenolepis* in Markle, 1989: fig. 4).

Variations in the dorsal gill-arch elements are also present in the other paracanthopterygians: absence of all elements or presence of bony Pb 1 only in lophiiforms (Pietsch, 1981); presence or absence of Pb 1 (bone or cartilage) and interarcual ligaments, and no interarcual cartilage in batrachoidiforms (Patterson and Rosen, 1989; Markle, 1989); presence or absence of Pb 1 (bone or cartilage) and interarcual cartilage, and no interarcual ligament in ophidiiforms (Patterson and Rosen, 1989; Markle and Olney, 1990); presence or absence of Pb 1 (bone) and interarcual ligament, and no interarcual cartilage in percopsiforms (Patterson and Rosen, 1989).

Travers (1981) considered the presence of interarcual cartilage to be a synapomorphy for the Euteleostei, but noted that the interpretation of its absence in many Ctenosquamata taxa required detailed embryological study. These elements seem to be independently developed or reduced within paracanthopterygians. Accordingly, the unpolarized transformation is used so as to avoid weighting by the hypothesized character evolution.

TS 13. Hyohyoideus abductores 2 (Fig. 21). In most gadiforms and outgroups, each hyohyoideus abductores

Table 2. Pharyngobranchial 1 (PB1), interarcual cartilage (IAC) and interarcual ligament (IAL) conditions in the Gadiformes. Ch. No. indicates the character number used in the first analysis of this study. "P" and "A" indicate "presence" and "absence", respectively

Taxon	Element	PB1	IAC	IAL	Ch. No.
Gadinae		A	A	A	5
Lotinae		A	A	A	5
Gaidropsarinae		A	A	A	5
Phycinae		A	A	A	5
<i>Bregmaceros</i>		A	A	A	5
<i>Muraenolepis</i>		A	A	A	5
<i>Raniceps</i>		cartilage	A	P	3
<i>Merluccius</i>		cartilage	P	A	4
<i>Macruronus</i>		cartilage	P	P	1
<i>Euclichthys</i>		bone	P	P	0
<i>Steindachneria</i>		bone	P	P	0
Moridae		cartilage	P	P	1
Bathygadinae		cartilage	P	P	1
<i>Trachyrinchus</i>		A	P	P	2
Macrourinae		A	A	A	5
<i>Squalogadus</i>		cartilage	A	P	3
<i>Melanonus</i>		bone	P	P	0

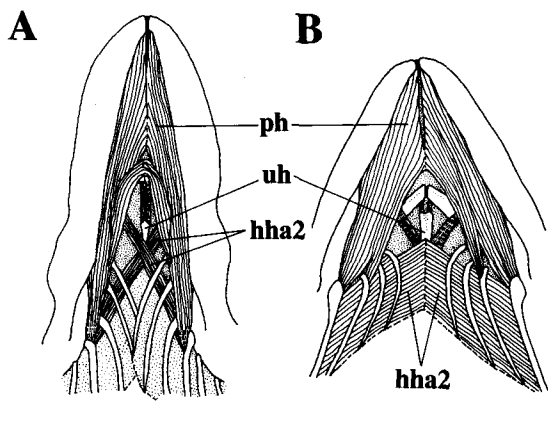


Fig. 21. Ventral view of ventral head muscles. A, *Melanonus gracilis*; B, *Nezumia proxima*. Bars=5 mm.

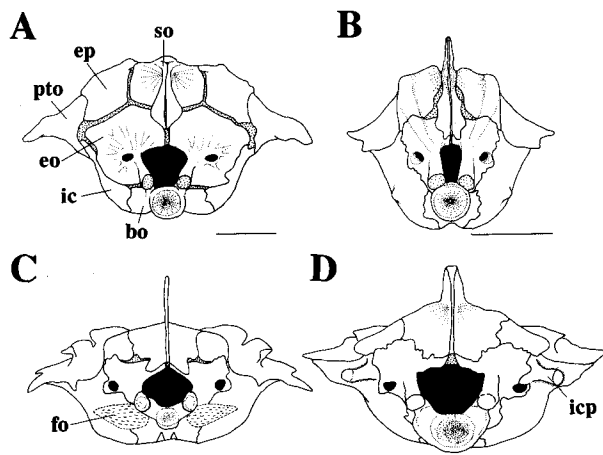


Fig. 22. Posterior view of cranium. A, *Melanonus zugmayeri*; B, *Mora mora*; C, *Raniceps raninus*; D, *Phycis phycis*. Bars=5 mm.

2 connects the first branchiostegal ray with the dorsal hypohyal on the opposite side, but are not fused with each other (Ch. 0: Fig. 21A; *Squalogadus*, *Coryphaenoides* and *Muraenolepis* in Howes, 1988: figs. 30, 31). Notwithstanding, the muscle pairs are fused on the midline in some macrourines, morids, *Bregmaceros*, gadines, lotines, phycines and gaidropsarines, the condition being regarded as derived (Ch. 1: Fig. 21B).

TS 14. Intercalar (Fig. 22; Howes, 1993: 18, figs. 5, 18). All gadiforms, excluding *Melanonus* and *Squalogadus*, are characterized by an enlarged intercalar contributing to the posterior wall of the cranium (Ch. 1: Fig. 22B-D; Howes, 1993: figs. 5, 18), the smaller intercalar in both *Melanonus* and *Squalogadus* being less obvious (Ch. 0: Fig. 22A). In the outgroups, the Pediculati have no intercalar (Regan, 1912: 277), and ophidiiforms and percopsiforms have a smaller inter-

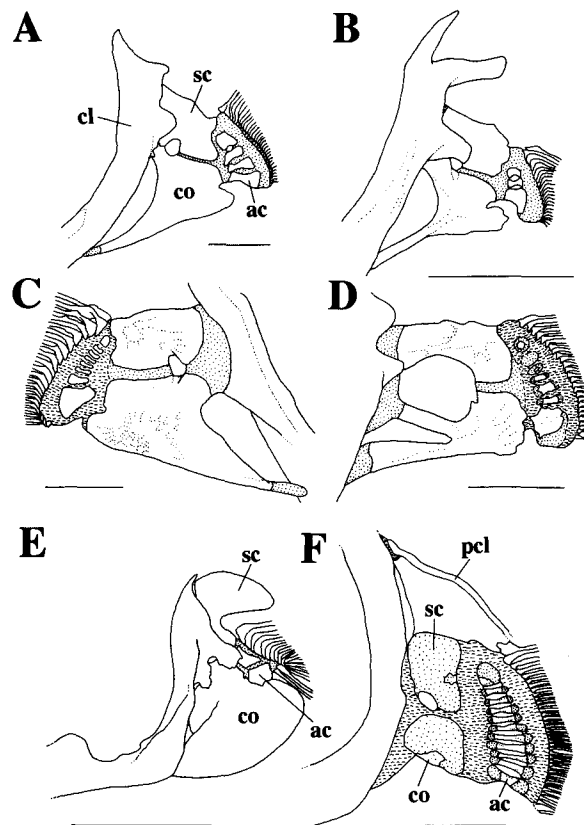


Fig. 23. Lateral and medial (C) views of pectoral girdle. A, *Lotella phycis*; B, *Ventrifossa garmani*; C, *Trachyrincus murrayi*; D, *Squalogadus modificatus*; E, *Bregmaceros arabicus*; F, *Muraenolepis orangiensis*. Bars=5 mm.

calar as in *Melanonus* (e.g., *Percopsis*, *Amblyopsis* and *Ogilbia* in Rosen and Patterson, 1969: figs. 13, 42; *Acanthonus* in Howes, 1992: fig. 8). The enlarged intercalar in most gadiforms is therefore regarded as a derived condition among paracanthopterygians.

An enlarged intercalar was inferred as a synapomorphy of paracanthopterygians by Patterson and Rosen (1989) and of gadiforms (excluding *Melanonus*) by Howes (1993).

TS 15. Number of actinosts (Fig. 23; Markle, 1989: 72; Okamura, 1989: 137). Actinosts generally number four in gadiforms (Ch. 0: Fig. 23A). However, an increased (Ch. 1) and decreased (Ch. 2) number of actinosts have been observed in the following taxa: 11-13 in *Muraenolepis* (Fig. 23F; 13 in *M. marmoratus* in Markle, 1989: fig. 12B; present study), 6-12 in *Squalogadus* (Fig. 23D; Okamura, 1970b: fig. 47F), 8 in *Trachyrincus* (Fig. 23C) and 6 in *Caelorinchus tokiensis* (Okamura, 1970b: fig. 47E); 3 in bathygadines (*Bathygadus* and *Gadomus* in Okamura, 1970b: fig. 46A-B) and some macrourines (Fig. 23B; Okamura,

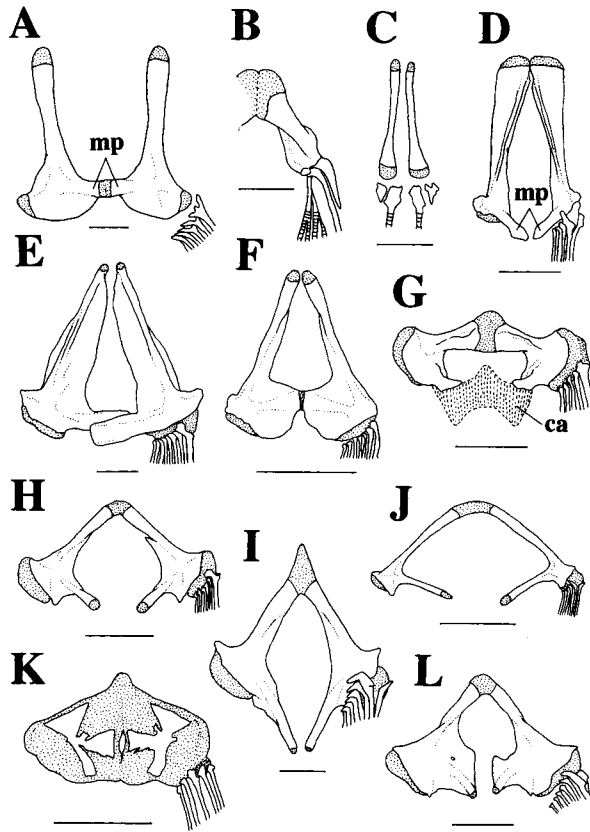


Fig. 24. Ventral view of pelvic girdle. A, *Lophiomus setigerus*; B, *Porichthys porosissimus*; C, *Oligopus robustus*; D, *Melanonus zugmayeri*; E, *Gadomus colletti*; F, *Ventrifossa garmani*; G, *Euclichthys polynemus*; H, *Mora mora*; I, *Merluccius merluccius*; J, *Raniceps raninus*; K, *Muraenolepis orangensis*; L, *Gadus morhua*. Bars=5 mm.

1970b : figs. 46, 47) and 2-3 in *Bregmaceros* (Fig. 23E ; Markle, 1989 : fig. 12A ; Swidnicki, 1991 : 151, figs. 14, 15). In the other paracanthopterygians, actinosts number 4-5 in batrachoidiforms (Regan, 1912 : fig. 1B ; Rosen and Patterson, 1969 : fig. 59), 2-3 in lophiiforms (Pietsch, 1981 : table 2), 5 in ophidiiforms (Markle and Olney, 1990 : figs. 9-12) and 4 in percopsiforms (Rosen, 1962). Polarity could not be determined by outgroup comparison.

TS 16. Median processes of pelvic girdle (Figs. 24, 25). In gadiforms, pelvic girdle shape is divided into the following types based on the direction of the median process. In *Steindachneria*, bathygadines and macrourines, the process is extended almost transversely, facing its opposite number in the midline (Ch. 0 : Fig. 24E, F ; bathygadines and macrourines in Okamura, 1970b : figs. 48-50 ; *Steindachneria* in Fahay, 1989 : fig. 11). Additionally, the process in *Gadomus* (Fig. 24E ; Okamura, 1970b : fig. 48A-A') is overlapped only medially (Okamura, 1970 : fig. 48A-A'). In most other

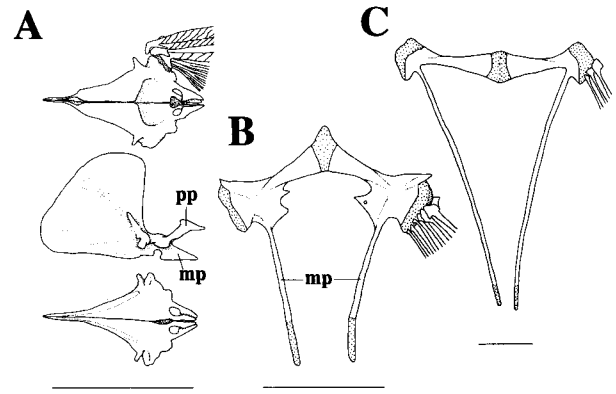


Fig. 25. Dorsal (upper of A), lateral (middle of A) and ventral (others) views of pelvic girdle. A, *Bregmaceros arabicus*; B, *Enchelyopus cimbrius*; C, *Urophycis floridana*. Bars=5 mm.

gadiforms, the process is rod-like in shape, being extended posteromedially toward the midline (Ch. 1 : Fig. 24D, G-J, L ; *Microgadus* in Stiassny and Moore, 1992 : fig. 4B). It is also considerably elongated in gaidropsarines and phycines (Ch. 2 : Fig. 25B, C). Although *Bregmaceros* has a highly specialized pelvic girdle, the small medial process is also extended posteriorly (Ch. 3 : Fig. 25A ; Swidnicki, 1991 : fig. 16C-F). Furthermore, *Muraenolepis* possesses a reduced cartilaginous pelvic girdle having no median processes (Ch. 4 : Fig. 24K). On the other hand, the outgroups also show some variation : lophiiforms have L-shaped pelvic bones connected via the median processes which are transversely extended (Fig. 24A) ; batrachoidiforms have stout rod-like pelvic bones with no medial process (Fig. 24B ; *Opsanus* in Stiassny and Moore, 1992 : fig. 4A) ; ophidiiforms have very reduced, rod-shaped pelvic bones with no medial process (Fig. 24C ; *Encheliophis* in Stiassny and Moore, 1992 : fig. 4C) ; percopsiforms show a somewhat similar condition to *Gadomus* in having transversely-extended and overlapping median processes, but differ from the latter in having a developed posterior process (*Percopsis* and †*Sphenocephalus* in Rosen and Patterson, 1969 : figs. 27A, 34).

Stiassny and Moore (1992) reviewed the pelvic girdle of acanthomorphs and inferred that the absence of pelvic overlap seemed to be a derived state among paracanthopterygians. Thus, the overlapping median processes in *Gadomus* seem to be a primitive condition. Accordingly, the transversed condition is derived and the posteromedially-extended condition even more derived among paracanthopterygians. Although there is no ontogenetic data for the pelvic girdle in paracanthopterygians, the overlapping processes of the atherinomorph *Poecilia reticulata* occur late in ontogeny (Stiassny and Moore, 1992 : 217, fig. 6). Since the Anacanthini,

except *Gadomus*, show a derived condition, the primitive state in *Gadomus* may be an atavistic reversal. In this analysis, however, I regarded the ancestral state as equivocal and used the characters as an unordered transformation series.

TS 17. Epipleurals (Okamura, 1989: 137). Although there are no epipleurals in *Squalogadus*, *Bregmaceros* or *Muraenolepis* (**Ch. 1**: *Muraenolepis* in Markle, 1989: fig. 13; *Squalogadus* in Okamura, 1989: fig. 3A; *Bregmaceros* in Swidnicki, 1991: figs. 1, 12), two to thirty-three epipleurals were present in the other gadiforms examined (**Ch. 0**). Although only lophiiforms among the other paracanthopterygians lack epipleurals, their presence in gadiforms is considered to be primitive.

Okamura (1989) stated that *Steindachneria* had no epipleurals. However, two and three bones, respectively, were observed in the specimens examined here. Although Inada (1989: table 1) also reported *Macruronus* as lacking epipleurals, two and four bones, respectively, were present in the two examined species of this genus.

TS 18. Dorsal supernumerary fin-rays (see text p. 120, Fig. 55, Table 6). Supernumerary fin-ray(s) with pseudospine(s) on the first dorsal radial in gadiforms can be divided as follow: two soft-rays in *Melanonus* (*M. zugmayeri*) (**Ch. 0**); one pseudospine and one soft-ray in trachyrincines (**Ch. 1**); two pseudospines in bathygadines, macrourines, *Euclichthys*, morids and macruronids (**Ch. 2**); one pseudospine in *Steindachneria*, *Merluccius*, *Raniceps*, *Bregmaceros*, *Muraenolepis* and gaidropsarines, (**Ch. 3**); one soft-ray in *Squalogadus*, gadines and lotines (**Ch. 4**); no pseudospines or rays in phycines (**Ch. 5**).

The presence of pseudospines and reduced number of dorsal supernumerary fin-ray (one or absent) are considered to represent the derived condition, **Ch. 0** being the ancestral state among gadiforms according to outgroup comparison.

TS 19. Pelvic fin (Iwamoto, 1989: 169). In most paracanthopterygians, excluding ophidiiforms and some gadiforms, the pelvic fin is generally well developed (**Ch. 0**: Cohen et al., 1990: figs. 18–20, 22–26). The reduction or absence of such in trachyrincines (*Trachyrincus* and *Idiolorhynchus*) and macrouroidines (*Squalogadus* and *Macrouroides*) is regarded as derived (**Ch. 1**: Cohen et al., 1990: figs. 696–699).

TS 20. Caudal fin (Markle, 1989: 81). The caudal fin is variously developed in gadiforms and other par-

acanthopterygians (**Ch. 0**: e.g., gadiforms in Patterson and Rosen, 1989: fig. 5; *Trachyrincus* in Howes, 1989: fig. 6), while *Steindachneria*, bathygadines, macrourines, *Squalogadus* and some ophidiiforms lack a caudal skeleton (**Ch. 1**: *Caelorinchus* in Okamura, 1970b: fig. 58).

TS 21. X and Y bones in caudal skeleton (Fig. 26; Markle, 1989: figs. 16, 17, 19; Howes, 1991a: fig. 35, 1993: fig. 18). The “X and Y bones” of the caudal skeleton are apparently unique in some gadiforms, but are absent in tailless macrourids as well as in some tailed taxa. This character has long been investigated and argued as a possible synapomorphy of the order by many of the authors cited above. Although it is still unclear whether or not the bones are unique to some particular gadiforms or to the order overall, their presence is likely to be a synapomorphy of a particular group. The X and Y bones are absent in *Melanonus*, *Steindachneria*, bathygadines, macrourines, *Squalogadus*, *Trachyrincus* and *Macruronus* (**Ch. 0**: Fig. 26A, C; e.g., *Melanonus* in Howes, 1993: fig. 15A-B), but present in *Bregmaceros*, *Euclichthys*, gaidropsarines, *Merluccius*, morids, *Muraenolepis*, phycines and *Raniceps* (**Ch. 1**: Fig. 26B, D-G; e.g., gadoids in Patterson and Rosen, 1989: fig. 5A-E). The X and Y bones have been secondarily lost in gadines and lotines (**Ch. 2**: Fig. 26H; e.g., gadines and lotines in Patterson and Rosen, 1989: fig. 5F-H, J-K).

Concerning the X and Y bones in lotines, Markle (1982: 3430, fig. 9, table 5) indicated their secondary loss in *Lota* during ontogeny and also noted that they were rarely present in *Molva*. Accordingly, **Ch. 0** is regarded here as a primitive and **Ch. 2** as the most-derived condition.

TS 22. Hypurals (Fig. 26; Markle, 1989: 81; Howes, 1993: fig. 18). The hypurals (=HP) of the caudal skeleton in gadiforms are composed of two lower (HP 1–2) and three upper (HP 3–5) elements, being divided into the following types: HP separated from each other in *Melanonus*, *Euclichthys*, morids and *Steindachneria* (**Ch. 0**: Fig. 26A, B; e.g., *Lotella* in Patterson and Rosen, 1989: fig. 5A); upper HP completely or largely fused to form a single plate, but lower HP separated in *Raniceps* (**Ch. 1**: Fig. 26D; Dunn and Matarese, 1984: fig. 148B); the upper and lower HP completely fused to form two respective plates in *Trachyrincus*, *Macruronus*, *Merluccius*, *Bregmaceros*, *Muraenolepis*, gadines, lotines, phycines and gaidropsarines (**Ch. 2**: Fig. 26C, E-H; e.g., gadoids in Patterson and Rosen, 1989: fig. 5C-H, J-K).

Fusion of the hypural bones occurs homoplastically

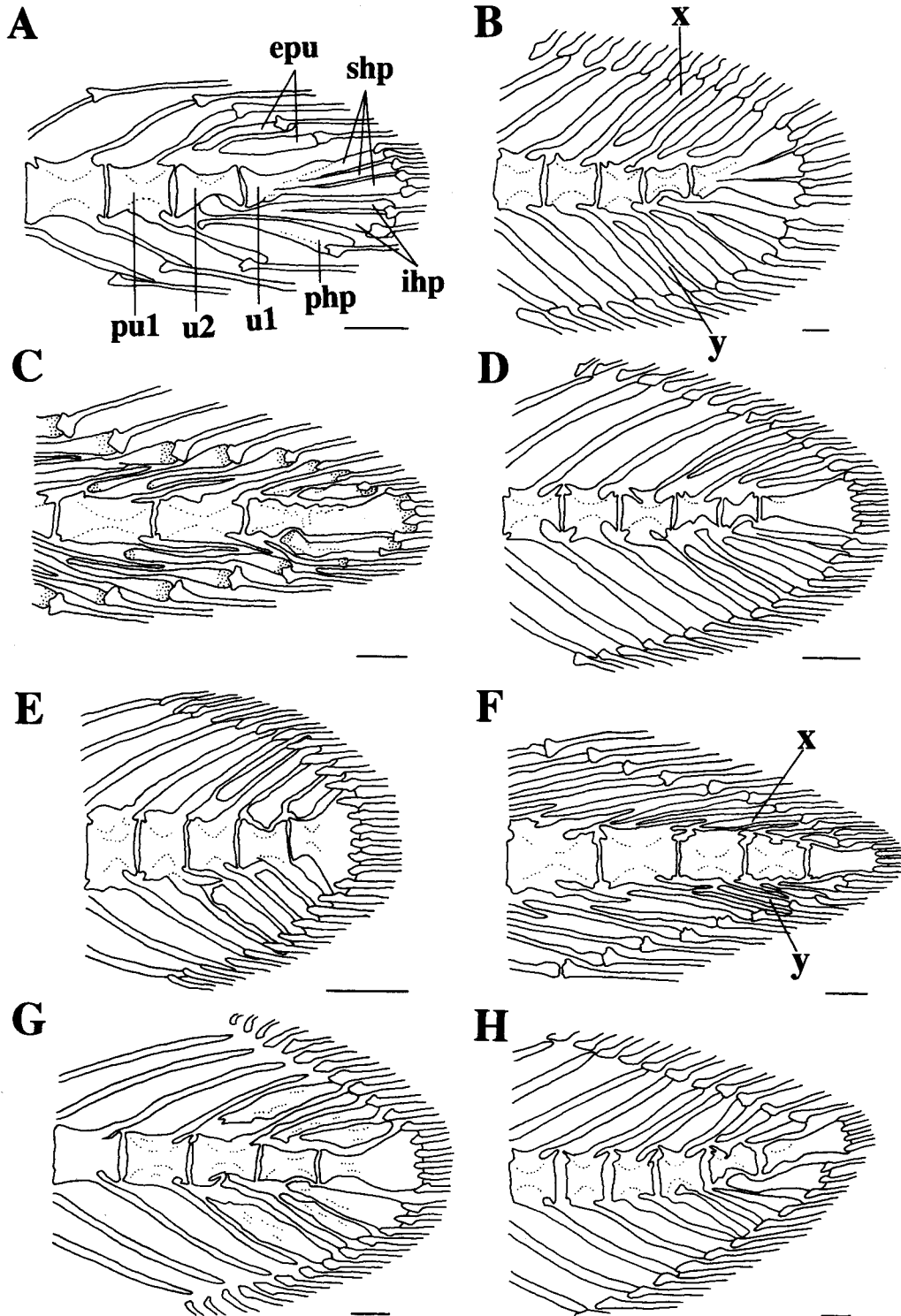


Fig. 26. Left lateral view of caudal skeleton. A, *Melanonus zugmayeri*; B, *Mora mora*; C, *Macruronus novaezelandiae*; D, *Raniceps raninus*; E, *Bregmaceros arabicus*; F, *Muraenolepis orangiensis*; G, *Urophycis regia*; H, *Brosme brosme*. Bars=1 mm.

in various teleosts (Fujita, 1990), such being considered to be a derived condition. Although most other paracanthopterygians have one or two hypural plates, separation of the hypurals is interpreted here as the primitive state among gadiforms.

TS 23. Scales (Okamura, 1989: 131; Iwamoto, 1989: 167). Most gadiforms and paracanthopterygians generally either possess or lack cycloid scales (**Ch. 0**). However, two other scale types characterize the following taxa: peripheral ctenoid scales in percopsiforms;

Table 3. Input data matrix for the first analysis of the relationships of gadiform taxa

Taxon	TS. No										1 1 1 1 1 1 1 1 1 2 2 2 2												
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Outgroup	0	0	0	0	0	0	0	0	?	0	0	?	0	0	?	?	0	?	0	0	0	0	0
Gadinae	0	0	2	0	1	0	1	1	2	1	0	5	1	1	0	1	0	4	0	0	2	2	0
Lotinae	0	0	2	0	1	0	1	1	2	1	0	5	1	1	0	1	0	4	0	0	2	2	0
Gaidropsarinae	0	0	2	2	1	1	1	1	2	1	0	5	1	1	0	2	0	3	0	0	1	2	0
Phycinae	0	0	2	?	1	1	1	1	1	1	0	5	1	1	0	2	0	5	0	0	1	2	0
<i>Bregmaceros</i>	0	0	3	0	2	0	0	1	1	2	0	5	1	1	2	3	1	3	0	0	1	3	0
<i>Muraenolepis</i>	0	0	1	1	2	0	1	1	1	1	0	5	0	1	1	4	1	3	0	0	1	2	0
<i>Raniceps</i>	0	0	2	0	1	0	0	1	1	1	1	3	0	1	0	1	0	3	0	0	1	1	0
<i>Merluccius</i>	0	0	2	0	1	0	0	1	1	1	1	4	0	1	0	1	0	3	0	0	1	2	0
<i>Macruronus</i>	0	0	2	0	0	0	0	0	1	0	0	1	0	1	0	1	0	2	0	0	1	2	0
<i>Euclichthys</i>	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	2	0	0	1	0	0
<i>Steindachneria</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	3	0	1	0	0	0	0
Moridae	0	0	0	0	0	0	0	1	1	0	1	1	?	1	0	1	0	2	0	0	1	0	0
Bathygadinae	0	0	0	0	0	0	0	0	1	0	1	1	0	1	2	0	0	2	0	1	0	0	0
<i>Trachyrincus</i>	1	1	0	0	0	0	0	0	0	0	0	2	0	1	1	1	0	1	1	0	0	2	1
Macrourinae	1	1	0	0	0	0	0	0	1	0	0	5	?	1	2	0	0	2	0	1	0	0	1
<i>Squalogadus</i>	1	1	0	0	0	0	0	0	0	1	0	3	0	0	1	1	1	4	1	1	0	0	1
<i>Melanonus</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0

spinoid scales in macrourines, macrouroidines and trachyrincines (Ch. 1: *Macrourus* in Roberts, 1993: 75, fig. 12). As discussed by Roberts (1993), spines on the ctenoid scale in percopsiforms and on the spinoid scales in macrouroids, excluding bathygadines, are not homologous. Iwamoto (1989) considered spinoid scales to be a synapomorphy of macrouroids.

2. Relationships

The data matrix of the above characters (Table 3) was analyzed using PAUP* 4.0 with "ACCTRAN" and "DELTRAN" optimization options. As a result, the eleven most parsimonious trees were obtained (length=65, CI=0.67 and RC=0.52). The strict consensus of all trees and one ACCTRAN tree are shown in Figures 27 and 28, respectively. The consensus tree indicated that the relationships of lower gadiforms were resolved, but the higher gadoid clade, except for *Macruronus*, remained as a polytomy. In the resolved relationships of lower gadiforms up to *Macruronus*, the distribution of each character in the eleven trees was unchanged, except for TS 11 (Ch. 0 on branch G or apomorphic for *Macruronus* and among higher gadoids) and TS 12 (Ch. 3 or 5 on branch H). On the basis of one ACCTRAN tree, the character distribution is described below.

Melanonus was inferred as the earliest offshoot among gadiforms. Four autapomorphies of *Melanonus* listed by Howes (1993: figs. 2, 5, 16, 18) were: 1) supraoccipital excluded from margin of foramen

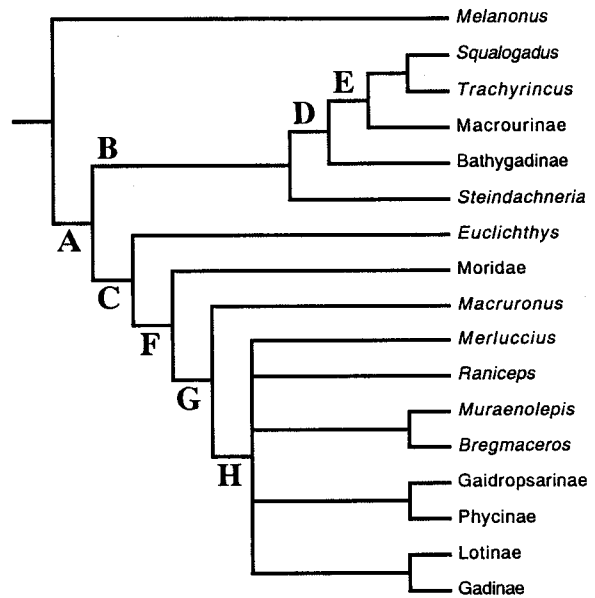


Fig. 27. Strict consensus of eleven trees of gadiform intra-relationships of the first analysis.

magnum; 2) cranial neuromast pattern and innervation; 3) brain position and morphology; 4) enlarged pterosphenoid contacting lateral ethmoid.

Branch A is the sister group of *Melanonus*, being supported by three synapomorphies: ligamentous condition of anterior part of rectus communis (TS 11-1); enlargement of intercalar (TS 14-1); two pseudospines (TS 18-2).

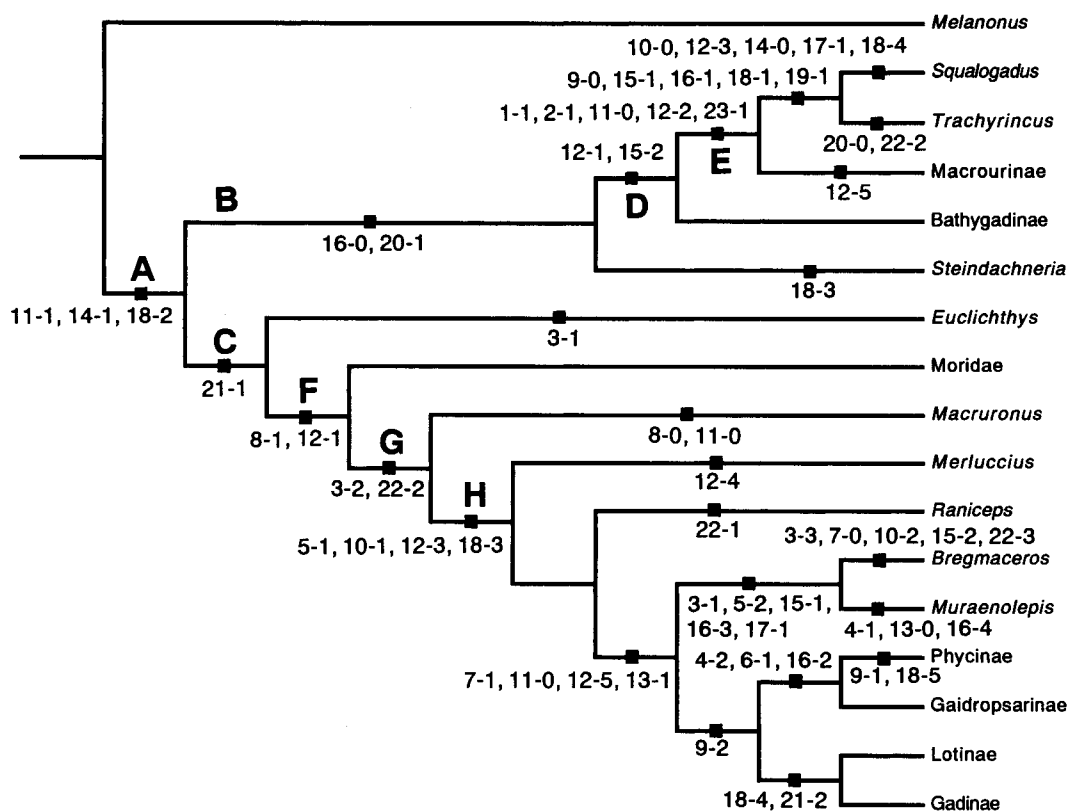


Fig. 28. One of the shortest trees of gadiform intrarelationships estimated by the first analysis.

Branch A is divided into two major branches B and C, the former, including *Steindachneria*, bathygadines, macrourines, *Squalogadus* and *Trachyrincus*, being characterized by two synapomorphies: transverse median process on pelvic girdle (TS 16-0); absence of caudal fin (TS 20-1). On the other hand, branch C, including *Euclichthys*, morids, *Macruronus*, *Merluccius*, *Raniceps*, *Bregmaceros*, *Muraenolepis*, phycines, gaidropsarines, gadines and lotines, is characterized only by the presence of X and Y bones in the caudal skeleton (TS 21-1).

The branch B is divided into *Steindachneria* and branch D, the latter supported by two synapomorphies: presence of cartilaginous pb 1 and both interarcual elements (TS 12-1); reduced number of actinosts (TS 15-2). In branch D, bathygadines are the sister group of branch E, the latter supported by five synapomorphies: enlargement of nasals (TS 1-1); anterolateral processes on lachrymal (TS 2-1); normal condition of rectus communis (TS 11-0); absence of pb 1 and presence of interarcual elements (TS 12-2); spinoid scales (TS 23-1).

In branch E, macrourines, supported by absence of pb 1 and interarcual elements (TS 12-5), are the sister group of the *Trachyrincus* and *Squalogadus* clade, characterized by five synapomorphies: two branchiostegal rays on epihyal (TS 9-0); many actinosts (TS 15-1); pos-

teromedial extension of median process of pelvic girdle (TS 16-1); two dorsal supernumerary fin-rays with one pseudospine (TS 18-1); reduction of pelvic fins (TS 19-1). *Squalogadus* has five autapomorphies: absence of median interopercular socket (TS 10-0); presence of cartilaginous pb 1 and an interarcual ligament (TS 12-3); small intercalar (TS 14-0); absence of epipleural bones (TS 17-1); dorsal supernumerary fin-ray represented by a single soft-ray (TS 18-4). On the other hand, *Trachyrincus* is characterized by two autapomorphies: presence of caudal skeleton (TS 20-0); caudal hypurals completely fused to form two plates (TS 22-2).

Iwamoto (1989) mentioned that the monophyly of each of the three macrourid subfamilies (in branch E) was well corroborated by the following synapomorphies: 1) developed nasal rostrum, 2) first gill-slit restricted, 3) outer gill rakers on first arch tubercular-shaped, 4) olfactory bulbs near nasal rosette, 5) modified scute-like scales on head and 6) gap between dorsal fins in macrourines; 1) highly modified ethmoid region, 2) filamentous lateral ethmoid lacking a connection with frontal, 3) ethmoid and lachrymal, 4) highly modified circumorbital bones, 5) single dorsal fin and 6) 12 actinosts in macrouroidines; 1) dorsolateral and ventrolateral scute rows and 2) posttemporal fossa in trachyrincines.

According to Howes and Crimmen (1991), the bathy-

gadine genera *Bathygadus* and *Gadomus* share four synapomorphies: 1) occasional absence of oblique ventralis muscles on 1st gill-arch, 2) development of anterior body muscles infracarinalis anterior becoming markedly tendinous and well-separated from hypaxialis, 3) modified nerve pathway serving pectoral fin rays and 4) reduced gill-filaments. Iwamoto (1989) considered a reduced anal fin as a synapomorphy of bathygadines.

The monotypic genus *Steindachneria* was supported by the presence of a single pseudospine (TS 18-3) in this analysis. Among the eleven derived characters of *Steindachneria* given by Fahay (1989: 156), at least the following are considered to be autapomorphies: 1) V-shaped structure of first anal radial; 2) fusion of spinous splint with first anal fin ray; 3) anterior location of anus; 4) developed luminous organ; 5) striated pigmentation on belly; 6) posterior process of basipterygia of pelvic girdle much reduced; 7) elongation of anterior anal fin-rays.

Branch C is divided into *Euclichthys* and branch F. On the cladogram, *Euclichthys* is shown as having one autapomorphy: adductor mandibular A1 is divided posteriorly A1a and A1b (TS 3-1). Additionally, the genus is characterized by the following autapomorphies: 1) internal light organ near cleithral joint (Markle, 1989); 2) reduced pelvic girdle positioned in jugular region; 3) pelvic rays and anterior rays of anal fin extended; 4) lateral ethmoid wing transversely convex (Howes, 1991a); 5) presence of lateral ethmoid-suspensorial ligament (Howes, 1988: fig. 15).

Branch F, supported by two synapomorphies (presence of interosseous space between hyomandibular and preopercle [TS 8-1]; presence of bony pb 1 and an interarcual ligament [TS 12-1]), comprises two clades, morids and branch G. The monophyly of morids is supported by the following synapomorphies: 1) distinctive otolith feature (e.g., Karrer, 1971); 2) otophysic connection between cranium and swimbladder (e.g., Paulin, 1983); 3) swimbladder with horizontal septum (Paulin, 1988); 4) parasphenoid with transversely aligned ascending process (Howes, 1991a).

Branch G is characterized by the adductor mandibular A1 divided completely into lateral A1a and medial A1b (TS 3-2) and two caudal fin hypural plates (TS 22-2). It comprises *Macruronus* and branch H.

According to Howes (1991a), macruronid monophyly is characterized by five synapomorphies: 1) retroarticular with anteroventral prolongation; 2) prootic forming a wall across midline; 3) modified caudal fin skeleton; 4) modified infraorbital bones; 5) adductor arcus palatini originating partly from ventral palatine fossa. Additionally, basibranchial 2 extended anteriorly on basibranchial 1 is a unique condition observed in

Macruronus (Fig. 6C, D). Howes (1991a) also illustrated the undeveloped lower branchials condition in a young specimen of *Macruronus magellanicus* (see Fig. 5A).

Branch H is supported by four synapomorphies: endopterygoid separated from metapterygoid (TS 5-1); presence of interopercular socket (TS 10-1); presence of cartilaginous pb 1 and an interarcual ligament (TS 12-3); a single pseudospine (TS 18-3).

In the present analysis, the branch H took the nature of a soft polytomy, comprising the following clades: gadine and lotine clade, phycine and gaidropsarine clade, *Bregmaceros* and *Muraenolepis* clade, and *Merluccius* and *Raniceps*. The synapomorphies of each clade, identical with those of Figure 28, are described below.

Gadines and lotines are united by one soft-ray on the first dorsal radial (TS 18-4) and secondary loss of the X and Y bones (TS 21-2). The monophyly of phycines and gaidropsarines is corroborated by three synapomorphies: adductor mandibular A2 almost covering levator arcus palatini (TS 4-2); unique palatopterygoid formation (TS 6-1); long median process of pelvic girdle directed posteromedially (TS 16-2). *Bregmaceros* and *Muraenolepis* share the following five synapomorphies: posterior A1 divided into lateral A1a and medial A1b (TS 3-1); absence of endopterygoid (TS 5-2); many actinosts (TS 15-1); specialized pelvic girdle (TS 16-3); absence of epipleurals (TS 17-1). *Merluccius* and *Raniceps* are supported by the presence of cartilaginous pb 1 and an interarcual cartilage (TS 12-4), and fusion of the upper hypural bones and separation of the lower ones (TS 22-1), respectively.

VI. Intrarelationships of higher gadoids

1. Characters used in the second analysis

The intrarelationships of the higher gadoids included in the soft polytomy resulting from the first analysis (the branch H of Fig. 27) are reanalyzed at the generic level. Thirty-eight transformation series (Table 4), including twelve used in the first analysis (asterisked), were adopted and are described below.

TS 24. Dorsal shelf of lachrymal (Fig. 29). Most gadiforms have a normal dorsal shelf on the lachrymal (Ch. 0: Fig. 29A-F), whereas the Gadinae have the shelf rounded and concave at the ascending process, a synapomorphic condition (Ch. 1: Fig. 29I, J; *Theragra* and *Trisopterus* in Dunn, 1989: figs. 10, 11A). Among gadiforms, only *Euclichthys* shows a somewhat similar rounded lachrymal shelf condition, although the shelf is

Table 4. List of transformation series considered in the second analysis

24.	Dorsal shelf of lachrymal (0, normal ; 1, concave)
25.	Palato-vomerine ligaments V and VI (0, normal ; 1, single state ; 2, lotine type)
26.	Dorsal maxillo-premaxillary ligament (0, absent ; 1, present)
27.	Adductor mandibular A2 covering levator arcus palatini (0, not covered ; 1, covered)
28.	Adductor mandibular Aw (0, not developed ; 1, developed)
29.	Endopterygoid (0, present ; 1, absent)
30.	Palatopterygoid formation (0, normal ; 1, phycine type)
31.	Lower process of hyomandibular (0, absent ; 1, present)
32.	Branchiostegal rays on epihyal (0, present ; 1, absent)
33.	Hyohyoideus abductores 2 (0, separated ; 1, fused)
34.	Prevomerine head (0, not enlarged ; 1, enlarged)
35.	Posterior process of lateral ethmoid (0, absent ; 1, present)
36.	Anterior frontal crests (0, separated ; 1, fused)
37.	Pharyngobranchial 1 and interarcual elements (0, present ; 1, absent)
38.	Obliquus dorsalis 2 on dorsal branchial arch (0, absent ; 1, present)
39.	Attachment of rectus communis to urohyal (0, muscle ; 1, ligament)
40.	Anterior rectus ventralis between urohyal and hypobranchial 3 (0, absent ; 1, present)
41.	Insertion of pharyngoclavicularis internus (0, anterior ; 1, posterior)
42.	Transversus ventralis anterior (0, single ; 1, two layers)
43.	Process on epibranchial 1 (0, present ; 1, absent)
44.	Tooth plate on epibranchial 3 (0, present ; 1, absent)
45.	Lateral flap on posttemporal (0, absent ; 1, present)
46.	Postcleithrum (0, upper expanded ; 1, no expansion ; 2, middle expanded)
47.	Pelvic girdle basiptyrgia (0, normal ; 1, phycine type)
48.	Median process of pelvic girdle (0, normal ; 1, long and slender)
49.	Epipleurals (0, present ; 1, absent)
50.	Dorsal and anal fins (0, others ; 1, gadine type)
51.	Vibratile first dorsal fin (0, absent ; 1, present)
52.	Dorsal supernumerary fin-rays (0, D1P1 ; 1, D1P0 ; 2, D0P0)
53.	Relative distance between first and second dorsal fins (0, narrow ; 1, wide)
54.	Number of anal radials before first haemal spine (0, low ; 1, midde ; 2, high)
55.	X and Y bones in caudal skeleton (0, present ; 1, absent)
56.	Ligament between swimbladder and supracleithrum (0, absent ; 1, present)
57.	Horn-shaped anterior appendages of swimblader (0, absent ; 1, present)
58.	Internal sac of swimbladder (0, absent ; 1, present)
59.	Posterior extension of swimbladder (0, absent ; 1, present)
60.	Two to four barbels on snout (0, absent ; 1, present)
61.	Oil globule in eggs (0, present ; 1, absent)

swollen at the ascending process, rather than concave (Fig. 29A).

TS 25. Palato-vomerine ligaments V and VI (Fig. 30). In most gadiforms, the medial palatine and lateral prevomer are connected by two ligaments, i.e., anterior palato-vomerine ligament (VI) and posterior palato-vomerine ligament (V) (**Ch. 0**: Fig. 30A). In higher gadoids, a single ligament (V or VI) state is observed in *Arctogadus*, *Boreogadus*, *Micromesistius*, *Trisopterus*, *Bregmaceros* and *Muraenolepis* (**Ch. 1**: Fig. 30C, D). The shift of the ligament V origin to the lateral face of

the prevomerine head is a unique state in all of the lotine genera (**Ch. 2**: Fig. 30B). Ch. 0 is regarded as primitive and the other conditions as derived.

TS 26. Dorsal maxillo-premaxillary ligament (Fig. 31). This short ligament, running parallel to ligament XII, is present in *Muraenolepis*, *Raniceps*, lotines, gaidropsarines, phycines and gadines (except for *Eleginus*, *Gadus*, *Melanogrammus* and *Microgadus*) (**Ch. 1**: Fig. 31B; Schaeffer and Rosen, 1961: fig. 5B). Although the ligament was also observed in some morid genera (*Halargyreus*, *Laemonema*, *Lotella*, *Physiculus* and

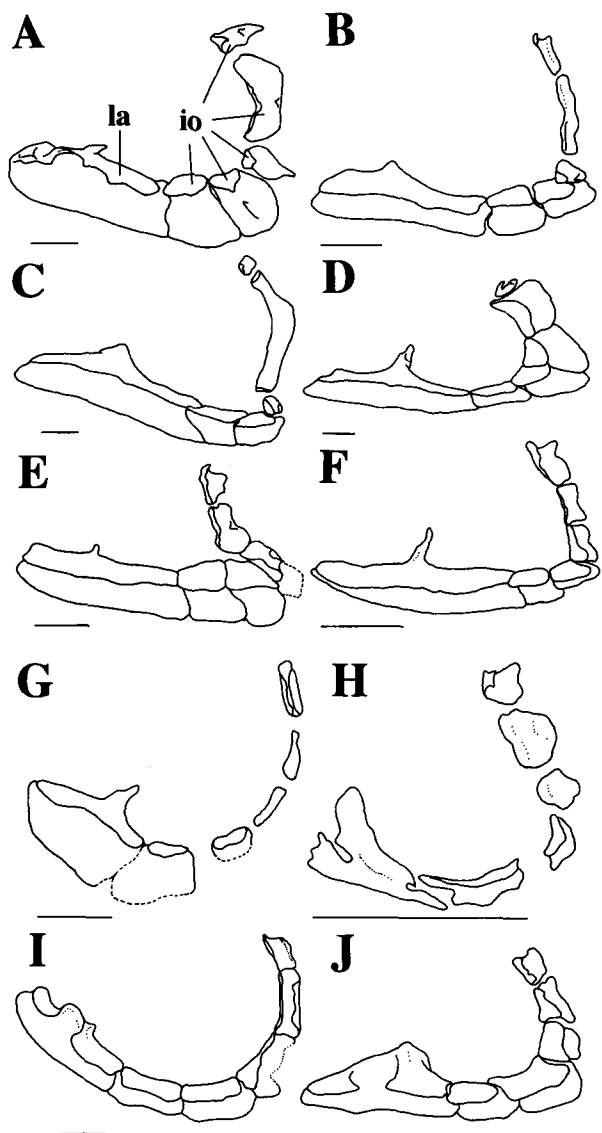


Fig. 29. Lateral view of infraorbital bones. A, *Euclichthys polynemus*; B, *Salilota australis*; C, *Macruronus novaezelandiae*; D, *Merluccius australis*; E, *Raniceps raninus*; F, *Gaidropsarus mediterraneus*; G, *Muraenolepis orangiensis*; H, *Bregmaceros japonicus*; I, *Gadiculus argenteus*; J, *Microgadus proximus*. Bars=5 mm.

Salilota) and the bythitoid *Oligopus*, it was generally absent in the outgroups (Ch. 0: Fig. 31A). Thus, its presence is considered to be derived among higher gadoids.

TS 27*. Adductor mandibular A2 covering levator arcus palatini (lap) (TS 4, Fig. 12). In most gadiforms, lap lies laterally on A2 (Ch. 0: Fig. 12C, D). However, A2 covers the entire lateral face of lap in the gadid genera, *Urophycis*, *Ciliata*, *Enchelyopus* and *Gaidropsarus*, such a condition being considered as derived (Ch. 1: Fig. 12A, B). In *Muraenolepis*, the

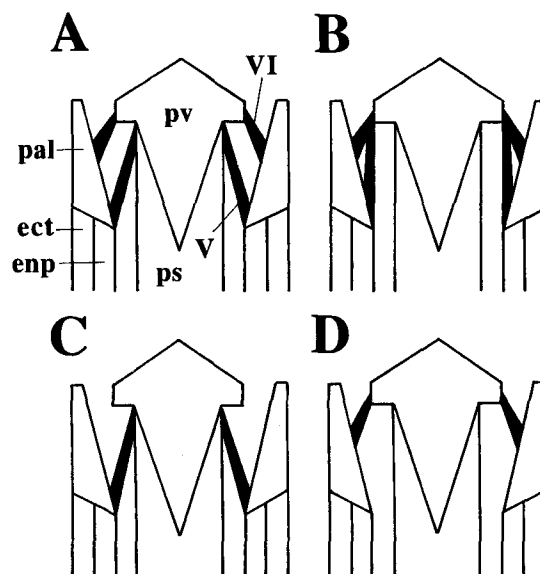


Fig. 30. Ventral view of four types of buccal ligaments V and VI (schematic representation). A, normal type-Ch. 0; B, lotine type-Ch. 2; C, single ligament type-Ch. 1; D, *Bregmaceros* type-Ch. 1.

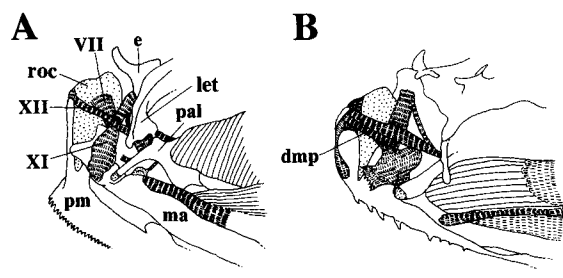


Fig. 31. Dorsolateral view of buccal ligaments. A, *Ventrifossa garmani*; B, *Raniceps raninus*. Bars=5 mm.

condition in which the upper part of A2 lies laterally on the lower part of lap is regarded as an autapomorphy (Fig. 9B).

TS 28. Adductor mandibular Aw (Fig. 17). In most gadiforms, the adductor mandibular Aw is inserted anteromedially into the dentary fossa (Ch. 0: Fig. 17A). Among the higher gadoids, *Raniceps*, *Merluccius*, gaidropsarines, phycines, lotines and gadines, excluding *Gadiculus*, have the developed Aw muscle extending beyond the dentary fossa (Ch. 1: Fig. 17B). On the basis of outgroup comparisons, Ch. 1 is regarded as apomorphic.

TS 29*. Endopterygoid (TS 5, Figs. 13, 14). In gadiforms, the endopterygoid is variously developed (Ch. 0: Figs. 13, 14C-H), but absent in *Bregmaceros* and *Muraenolepis* (Ch. 1: TS 5-Ch. 2, Fig. 14A, B), an apparently derived condition.

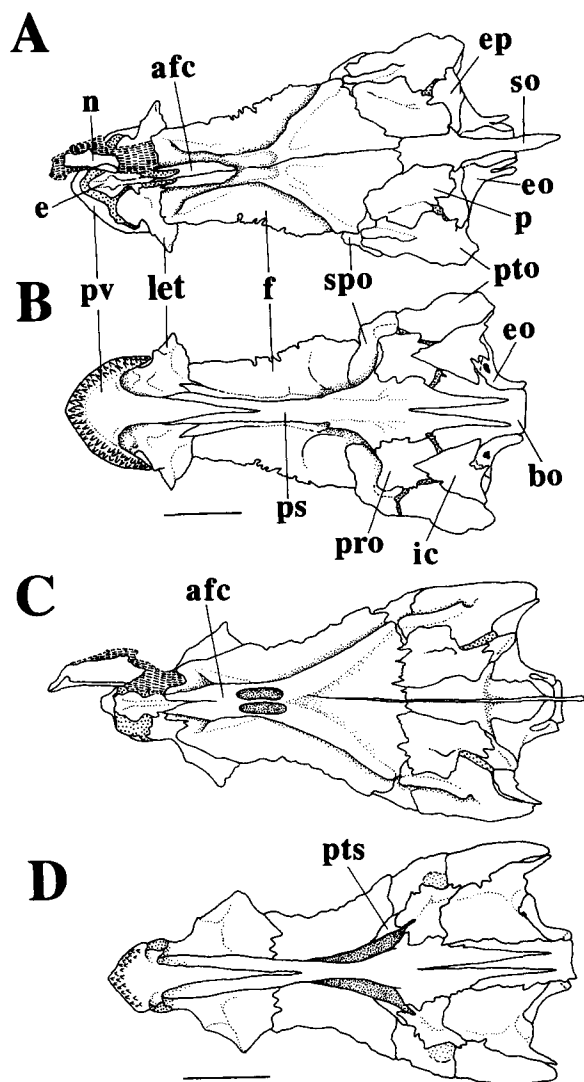


Fig. 32. Dorsal (A, C) and ventral (B, D) views of cranium. A-B, *Brosme brosme*; C-D, *Gadus morhua*. Bars=10 mm.

TS 30*. Palatopterygoid formation (see TS 6).

TS 31*. Lower process of hyomandibular (see TS 7).

TS 32*. Branchiostegal rays on epihyal (TS 9, Fig. 16). **TS 9-Ch. 1** (one branchiostegal ray only on epihyal in most gadiforms) is considered the primitive state in this analysis (i.e., **TS 32-Ch. 0**: Fig. 16C), **TS 9-2** (no branchiostegal ray on epihyal) being the derived condition (i.e., **TS 32-Ch. 1**: Fig. 16D).

TS 33*. Hyohyoideus abductores 2 (see TS 13).

TS 34. Prevomerine head (Fig. 32). In gadiforms, the prevomerine head is not expanded (**Ch. 0**: Fig. 32C, D), while it is posterolaterally enlarged, with “anchor-like” feature in all lotines. The condition is synapo-

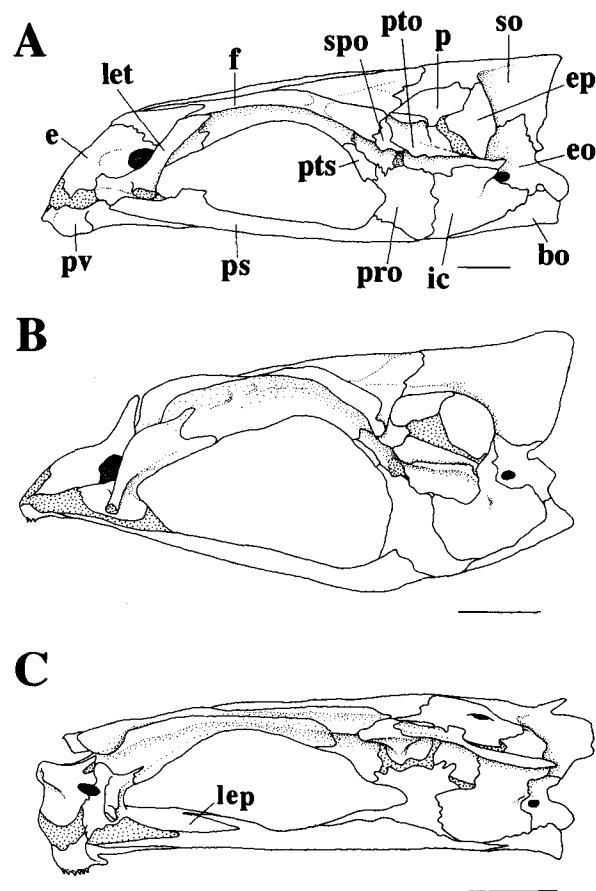


Fig. 33. Lateral view of cranium. A, *Macruronus novaezelandiae*; B, *Gadiculus argenteus*; C, *Enchelyopus cimbricus*. Bars=5 mm.

morphic for this group (**Ch. 1**: Fig. 32A, B; lotines in Svetovidov, 1948: tables 21, 34–38).

TS 35. Posterior process of lateral ethmoid (Fig. 33). A posterior process of the lateral ethmoid, attached posteroventrally to the anterodorsal part of the parasphenoid, is present and variously developed in lotines, gaidropsarines, phycines and gadines, excluding *Arcotogadus*, *Boreogadus*, *Gadiculus*, *Micromesistius* and *Trisopterus* (**Ch. 1**: Fig. 33C). The process is generally absent in all other gadiforms (**Ch. 0**: Fig. 33A, B). Accordingly, its presence is considered to be an apomorphy.

TS 36. Anterior frontal crests (Fig. 32). In higher gadoids, fusion of both anterior frontal crests of the cranium exists in the gadines *Gadiculus*, *Gadus*, *Melanogrammus*, *Merlangius*, *Micromesistius*, *Pollachius*, *Theragra* and *Trisopterus*, and the lotine *Molva* (**Ch. 1**: Fig. 32C). However, the crests, if present, are separated from each other in most gadiforms, except for *Macruronus* and *Antimora* (**Ch. 0**: Fig. 32A). Fusion

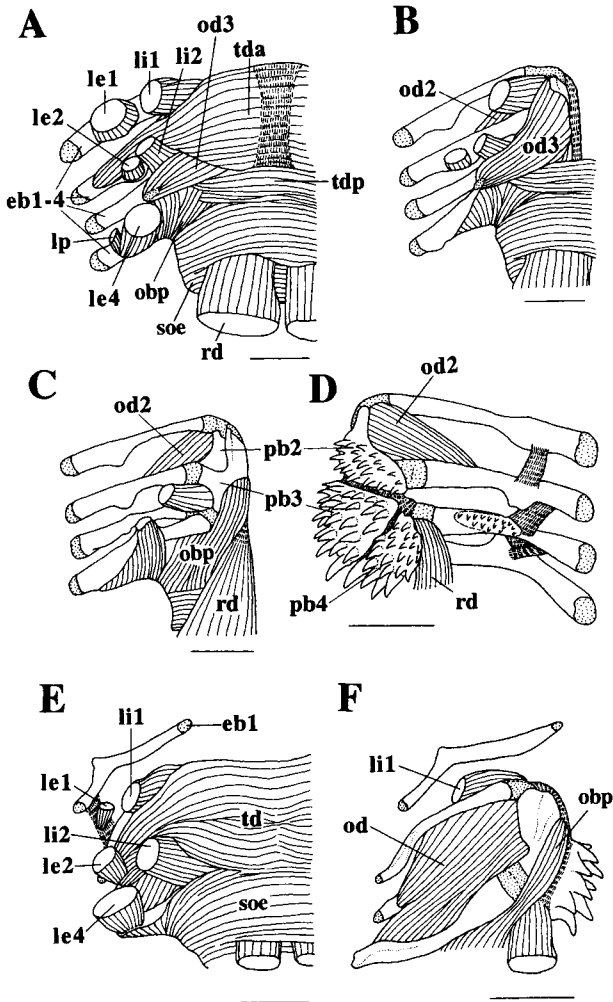


Fig. 34. Dorsal view of dorsal gill-arch muscles. A-D, *Gaidropsarus mediterraneus* (ventral view in D, ligaments between eb omitted in A-C); E-F, *Bregmaceros arabicus*. Bars=2 mm in A-D; 1 mm in E-F.

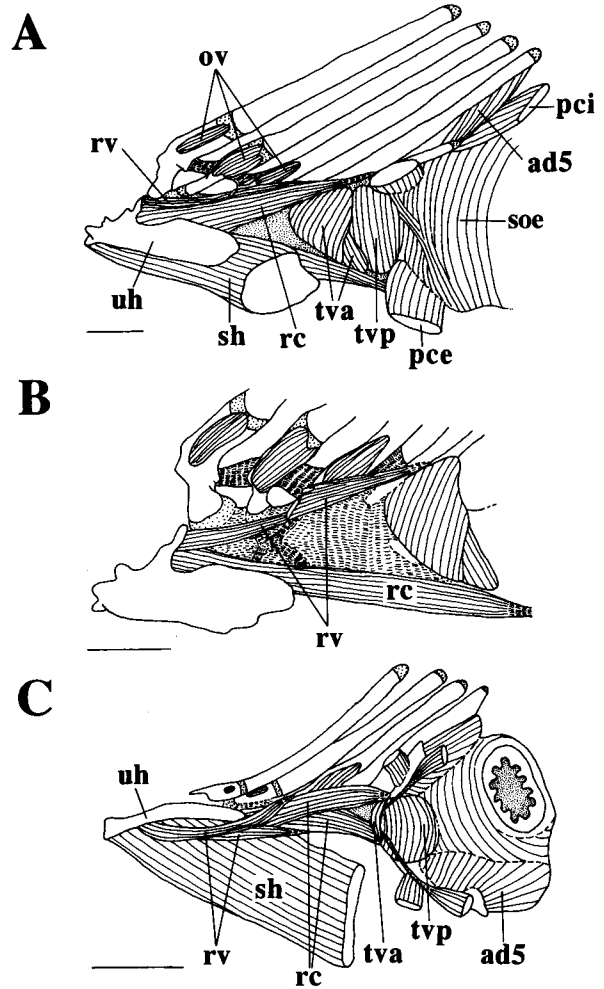


Fig. 35. Ventrolateral view of ventral gill-arch muscles. A-B, *Gaidropsarus mediterraneus* (sh and left rc removed in B); C, *Bregmaceros arabicus*. Bars=2 mm.

is considered to be apomorphic on the basis of outgroup comparison. In addition, frontal crests are not apparent in *Merluccius*, *Ciliata* and some macrourines (e.g., *Caelorinchus*, *Coryphaenoides* and *Nezumia*).

TS 37*. Pharyngobranchial 1 and interarcual elements (TS 12, Figs. 19, 20). Most gadiforms, excluding macrourines, generally have some elements representing pharyngobranchial 1, and the interarcual cartilage and ligament (**Ch. 0**: Figs. 19, 20A, B), whereas in *Bregmaceros*, *Muraenolepis*, gadines, lotines, gaidropsarines and phycines such are entirely absent (**Ch. 1**: **TS 12-Ch. 5**, Fig. 20C, D), an apparently derived condition.

TS 38. Obliquus dorsalis 2 on dorsal branchial arch (Fig. 34). The obliquus dorsalis 2 is attached to the anterior face of epibranchial 2 and the lateral section of pharyngobranchial 2, being located anteroventrally on

the transversus dorsalis anterior. This muscle is generally absent in most gadiforms (**Ch. 0**), but present in lotines, gaidropsarines, phycines, gadines (except for *Gadiculus* and *Brosme*) and the morid *Lotella* (**Ch. 1**: Fig. 34B-D), in which it is regarded as a derived state.

TS 39*. Attachment of rectus communis to urohyal (see TS 11, Fig. 18). In this analysis, polarity could not be determined by outgroup comparison.

TS 40. Anterior rectus ventralis between urohyal and hypobranchial 3 (Figs. 18, 35). The rectus ventralis is generally present between ceratobranchial 4 and the ventral process of hypobranchial 3 (with ligamentous connection) in gadiforms. In *Bregmaceros* and gaidropsarines, the other rectus ventralis connects the ventral process of hypobranchial 3 to the anterodorsal portion of the urohyal (**Ch. 1**: Fig. 35A-C). The

absence of the anterior rectus ventralis (Ch. 0: Fig. 18A, B) is regarded as primitive.

TS 41. Insertion of pharyngoclavicularis internus (Figs. 18, 35). Two different types of pharyngoclavicularis internus insertion are recognized in gadiforms; on the anteroventral processes of ceratobranchial 5 via a ligament in most gadiforms (Ch. 0: Fig. 18A, C) and near the base of pharyngoclavicularis externus on ceratobranchial 5 in gadines, lotines, gaidropsarines, phycines and *Muraenolepis* (Ch. 1: Fig. 18B, D). Although such a posterior placement occurs in *Squalogadus*, and the macrourine genera *Caelorinchus* and *Coryphaenoides*, Ch. 1 is considered to be derived among higher gadoids.

TS 42. Transversus ventralis anterior (Figs. 18, 35). In gaidropsarines, the transversus ventralis anterior consists of two layers with the fibers directed obliquely towards each other (Ch. 1: Fig. 35A, B). In the other gadiforms, this muscle element is a single layer with transverse fibers (Ch. 0: Figs. 18, 35C). Ch. 1 is synapomorphic for gaidropsarines.

TS 43. Process on epibranchial 1 (Figs. 19, 20, 36). Most gadiforms have a prominent uncinat process on the dorsal face of the first epibranchial (Figs. 19, 20). In gadines, this process is usually reduced to a slight elevation on the bone (Ch. 0: Fig. 36A-A'), whereas it is completely absent in *Muraenolepis*, lotines and the gadines *Eleginus*, *Melanogrammus*, *Merlangius* and *Microgadus* (Ch. 1: Fig. 36B-B'). Absence of a process is considered to be a derived state among higher gadoids.

TS 44. Tooth plate on epibranchial 3 (Fig. 36).

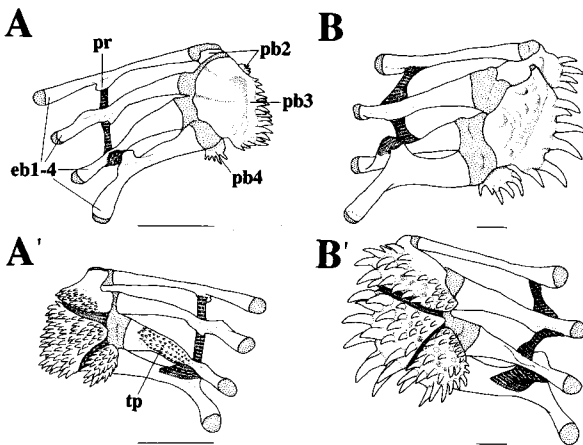


Fig. 36. Dorsal (A, B) and ventral (A', B') views of dorsal gill-arch. A-A', *Gadadiculus argenteus*; B-B', *Melanogrammus aeglefinus*. Bars=2 mm.

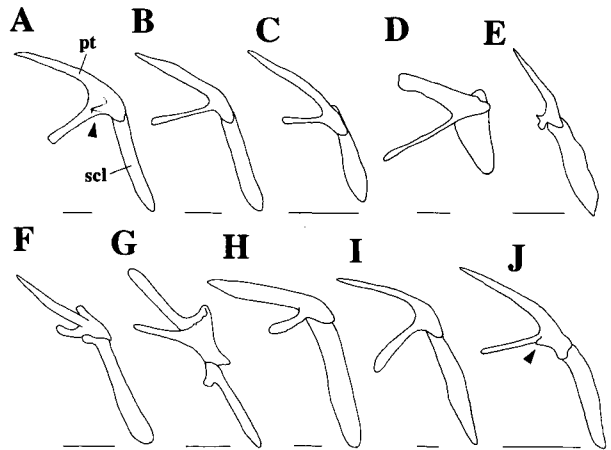


Fig. 37. Lateral view of posttemporal and supracleithrum. A, *Macruronus magellanicus*; B, *Merluccius merluccius*; C, *Raniceps raninus*; D, *Bregmaceros arabicus*; E, *Muraenolepis microps*; F, *Phycis phycis*; G, *Urophycis floridana*; H, *Brosme brosme*; I, *Gadicus argenteus*; J, *Theragra chalcogramma*. Bars=1 mm for D, G and I; 5 mm for others.

Gadiforms generally have a tooth plate on the ventral face of epibranchial 3 (Ch. 0: Fig. 36A'), *Arctogadus*, *Boreogadus*, *Melanogrammus* and *Bregmaceros* lacking such a plate (Ch. 1: Fig. 36B'). The latter condition is regarded as derived.

TS 45. Lateral flap on posttemporal (Fig. 37). A lateral flap is present on the posttemporal in gadines, except for *Gadicus* and *Micromesistius* (Ch. 1: Fig. 37J), but is absent in other higher gadoids (except for *Macruronus*) (Ch. 0: Fig. 37B-I). The outgroups, *Macruronus*, some morids, *Euclichthys*, *Steindachneria*

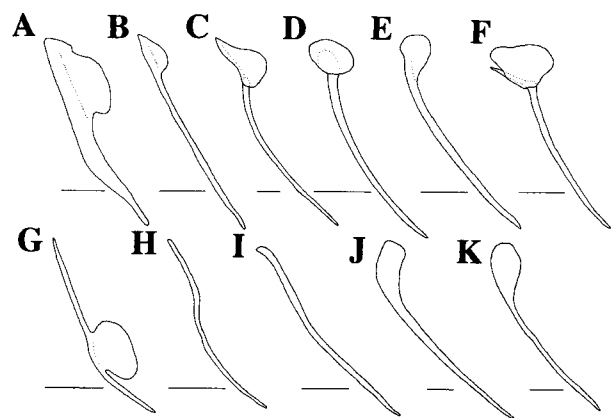


Fig. 38. Lateral view of postcleithrum. A, *Euclichthys polynemus*; B, *Lotella phycis*; C, *Macruronus magellanicus*; D, *Merluccius merluccius*; E, *Merluccius australis*; F, *Raniceps raninus*; G, *Bregmaceros arabicus*; H, *Enchelyopus cimbrius*; I, *Lota lota*; J, *Trisopterus esmarkii*; K, *Arctogadus glacialis*. Bars=5 mm for A-F; 2 mm for G-K.

and some macrourines possess a variously-developed lateral process on the posttemporal (Fig. 37A). Since homology between the flap in gadines and the process in some lower gadiforms is uncertain, the outgroup state is considered as equivocal.

TS 46. Postcleithrum (Fig. 38). In gadoids, the postcleithrum shows the following variations: rod-like with an expanded upper end in gadines, *Raniceps*, *Merluccius*, *Macruronus*, morids and *Euclichthys* (**Ch. 0**: Fig. 38A-F, J, K); rod-like with no expanded portion in *Muraenolepis*, lotines, gaidropsarines and phycines (**Ch. 1**: Fig. 38H-I); single rod-like with an expanded middle portion in *Bregmaceros* (**Ch. 2**: Fig. 38G). On the basis of outgroup comparison, Ch. 1 and 2 are considered to be derived. Among gadiforms, two postcleithra, composed of discoid and rod-shaped elements, are present in *Raniceps* (one of two specimens), *Merluccius* (*M. merluccius*), *Macruronus* and *Trachyrincus*. The occurrence of two primitive elements may be an atavistic reversal, two postcleithral conditions being widely distributed in some ophidiiforms (*Oligopus* in this study; *Brotula* and *Dicrolene* in Markle and Olney, 1990), acanthopterygians and other lower taxa.

TS 47. Pelvic girdle basipterygia (Figs. 24, 25). In most gadiforms, the pelvic girdle basipterygia take a triangular to lozenge shape, being trapezoid in outline (**Ch. 0**: Figs. 24D-J, L, 25A, B), whereas those of phycines are transversely arrayed along a straight line, forming a reverse triangular to trapezoid outline (**Ch. 1**: Fig. 25C). In addition an extremely long median process is also synapomorphic in phycines (Fig. 25C). Basipterygia formation is probably correlated with elongation of the fin rays and median process (discussed below).

TS 48*. Median process of pelvic girdle (Fig. 25). In gadiforms, the pelvic girdle shows great variation, the median process also being variously developed. In phycines and gaidropsarines, the median process is more slender and elongated than in other gadiforms, such being regarded as a synapomorphy of the former (**Ch. 1**: Fig. 25B, C).

Phycine hakes, which possess taste buds on the pelvic fin, move their extremely long pelvic rays forwards and sideways while searching for food on the bottom (Bardach and Case, 1965: figs. 4, 5; pers. obs.). Functionally, the elongated median processes of the pelvic girdle support the unique pelvic musculature, which apparently enables the long fin-rays to operate freely. Gaidropsarines may also share a similar pelvic fin function with phycines. A similar function may occur homoplastical-

ly in the long pelvic-fined *Bregmaceros* and some morid groups such as *Laemonema*, which also possess long pelvic fin-rays.

Pelvic girdle process terminology has varied between some authors: e.g., postpelvic process in Okamura (1970b) and Howes (1991); posterior process of basipterygia in Dunn (1989); median process in Stiassny and Moore (1992). Stiassny and Moore (1992) are followed here because the median process in gadiforms is not homologous with the posterior or postpelvic process in other acanthomorphs.

TS 49*. Epipleurals (see TS 17).

TS 50. Dorsal and anal fins (Figs. 61, 71, 75E). Gadines possess three dorsal and two anal fins, a synapomorphic condition for this group (**Ch. 1**: e.g., Cohen et al., 1990).

TS 51. Vibratile first dorsal fin (Fig. 55). Gaidropsarines have a unique first dorsal fin, which acts as a chemosensory organ (e.g., Kotschal and Whitear, 1988), comprising a short to long first pseudospine and a fringe of about 50-80 delicate, vibratile soft-rays and their radials (**Ch. 1**: Fig. 55G; *Enchelyopus* in Cohen and Russo, 1979: figs. 3, 5).

TS 52*. Dorsal supernumerary fin-rays (TS 18, Fig. 55). A single pseudospine is a synapomorphy of higher gadoids, excluding *Macruronus* (**Ch. 0**: TS 18-Ch. 3). Thus, the single soft-ray on the first dorsal radial in gadines and lotines (**Ch. 1**: TS 18-Ch. 4), and possible loss of fin-rays on the primitive first dorsal radial (= predorsal bone) in phycines (**Ch. 2**: TS 18-Ch. 5) are considered to be derived states.

TS 53. Relative distance between first and second dorsal fins (Fig. 39; Dunn, 1989: fig. 28). The interspace of the first and second dorsal fins is variable among gadines. Measured between a vertical at the posteriormost point of the last radial of the first fin and anteriormost point of the first radial of the second in the present study, the interspace is equivalent to about one interneural space in *Theragra*, one-half in *Micromesistius*, two in *Boreogadus*, three in *Arctogadus* (Fig. 39E-H), and very narrow or absent in the others (Fig. 39A-D). In gadoids, the first and second dorsal fins are internally separated (Markle, 1989: 78), although externally appearing close together (excluding *Bregmaceros* [Swidnicki, 1991: fig. 1A] and the morid *Auchenoceros*). The latter two genera show a highly specialized condition in that the first dorsal fin-ray is extremely distant from the second. In this analysis, the relatively

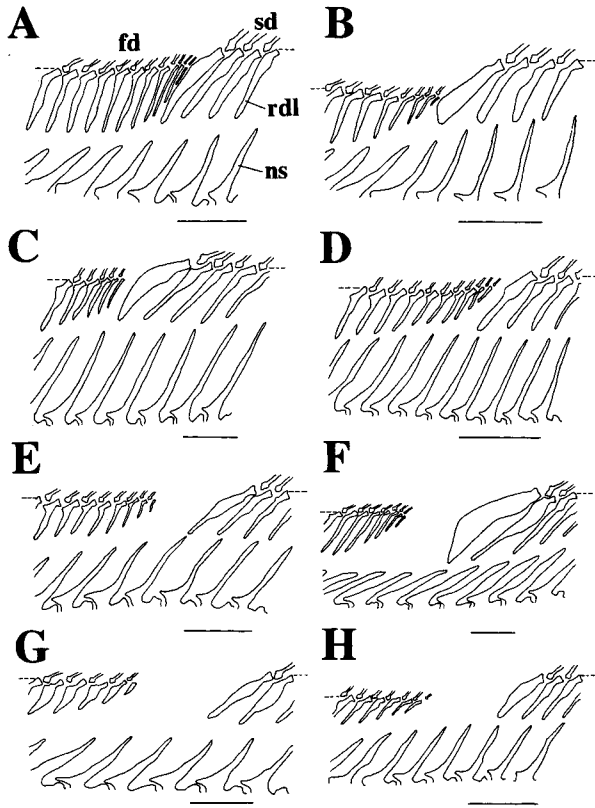


Fig. 39. Lateral view of interdorsal space between the first and second fins. A, *Trisopterus esmarkii*; B, *Gadiculus argenteus*; C, *Merlangius merlangus*; D, *Eleginus gracilis*; E, *Theragra chalcogramma*; F, *Micromesistius australis*; G, *Boreogadus saida*; H, *Arctogadus glacialis*. Bars=5 mm.

wide space in the four gadine genera, *Theragra*, *Micromesistius*, *Boreogadus* and *Arctogadus*, is regarded as derived (Ch. 1), the narrow (or close) condition in the other higher gadoids being primitive (Ch. 0).

The interspace of some higher gadoids was investigated and described by Markle (1982) and Dunn and Matarese (1984), and later used by Dunn (1989) for a cladistic analysis of gadids (present gadines). According to Dunn and Matarese (1984: table 81) and Dunn (1989: fig. 28), the relative distances between the first two dorsal fins in gadine larvae can be distinguished as follows (although the larval conditions differ somewhat from those in young and adults in some genera): close together (about 0.5-1 interneural spaces) in *Gadus*, *Melanogrammus*, *Merlangius*, *Microgadus*, *Pollachius* and *Trisopterus*; moderately wide (about 1-1.5 interneural spaces) in *Eleginus*, *Gadiculus* and *Theragra*; wide (about 2-2.5 interneural spaces) in *Arctogadus*, *Boreogadus* and *Micromesistius*.

TS 54. Number of anal radials before first haemal spine. High numbers and wide variations characterize

gadiforms. Such radials numbered 23 and 20 in *Merlangius* and *Pollachius*, respectively (Ch. 1), and 39 in *Micromesistius* (Ch. 2), although remaining gadines ranged between 8 and 16 (Ch. 0). In the other gadoids, the radials numbered less than 9, except in *Lota* (13), *Molva* (25), *Merluccius* (14) and two morids, *Physiculus* and *Salilota* (20). Although high numbers of anal radials before the first haemal spine occur independently in some gadiform genera, Ch. 1 and 2 are apparently derived among gadines.

TS 55*. X and Y bones in caudal skeleton (TS 21, Fig. 26). Among higher gadoids, the X and Y bones are secondarily lost in gadines and lotines (Ch. 1: TS 21-Ch. 2, Fig. 26H).

TS 56. Ligament between swimbladder and supra-cleithrum (Figs. 40-42). Phycines have a unique pair of ligaments connecting the anterior swimbladder appendages with the uppermost and medial portions of the supra-cleithra (Ch. 1: Fig. 40), the condition being different in each genus: viz., *Phycis* has a short, stout ligament joining the anterior tip of the appendage with the supra-cleithrum (Fig. 40A), while *Urophycis* has a long, thin ligament attached between the center of the dorsal face of the appendage and the supra-cleithrum (Fig. 40B, C).

In *Urophycis*, the swimbladder wall around the base of the ligament is a thin, flexible swelling, which seems to be more sensitive than that in *Phycis* (Fig. 40A, B). Furthermore, the posttemporal and supra-cleithral bones in *Urophycis* are particularly small, being separated from the cleithrum and cranium (Fig. 41B), and located in an intermediate position between the swimbladder-supra-cleithrum and posttemporal-supratemporal ligaments. The posttemporal in phycines is attached to the supratemporal by a short ligament (Fig. 42), although *Phycis* has a relatively normal supra-cleithrum and posttemporal which articulate with the cleithrum, epiotic and intercalar (Fig. 41A). In phycines, sound tremors received by the swimbladder are considered to be transmitted indirectly from the ligament to the inner ear via the supra-cleithrum, posttemporal and supratemporals, the structure of *Urophycis* apparently being more specialized than that of *Phycis*.

TS 57. Horn-shaped anterior appendages of swim-bladder (Figs. 43-45). Most gadiforms, excluding morids, phycines and some gadids, lack anterior swimbladder appendages (Ch. 0: Figs. 43-45). Slender horn-shaped appendages, lacking any osseous connection, are present in the gadid genera *Eleginus*, *Gadus*, *Melanogrammus*, *Merlangius*, *Microgadus*, *Pollachius*,

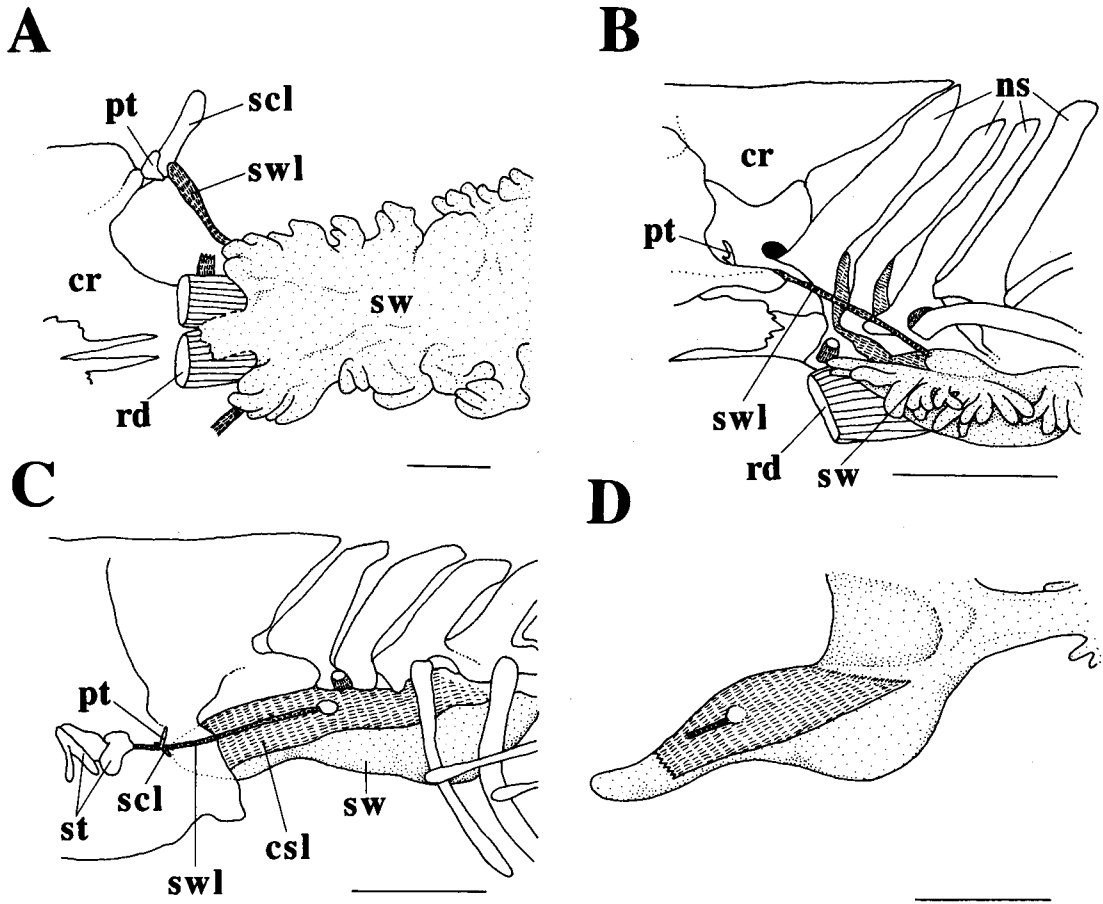


Fig. 40. Ventral (A), lateral (B), dorsolateral (C) and dorsal (D) views of connection between supracleithrum and anterior swimbladder. A, *Phycis chesteri*; B, *Urophycis earllii*; C-D, *Urophycis regia*. Bars=5 mm.

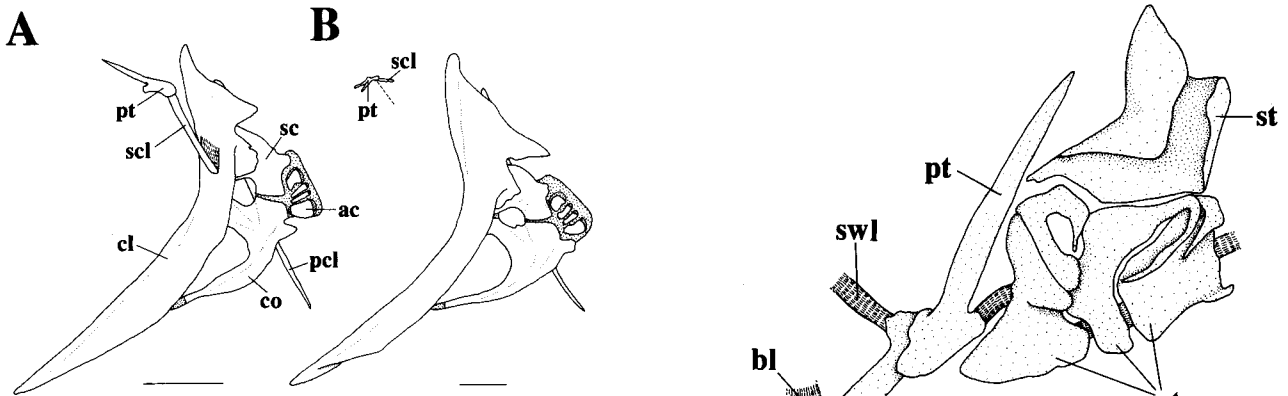


Fig. 41. Lateral view of pectoral girdle. A, *Phycis blennoides*; B, *Urophycis floridana*. Bars=5 mm.

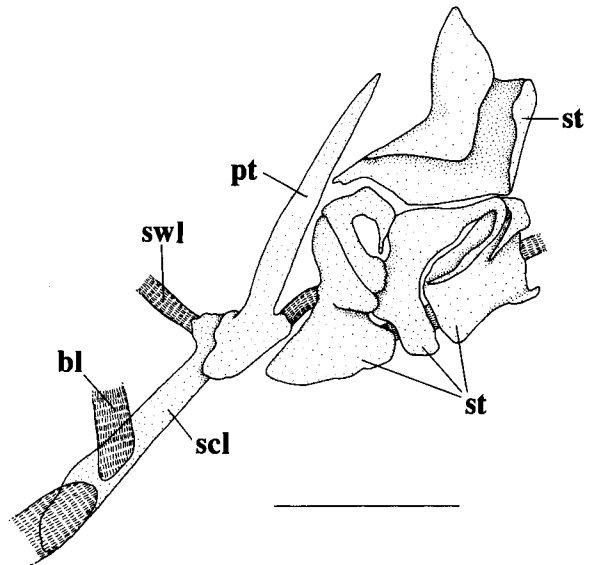


Fig. 42. Lateral view of light temporals and supracleithrum of *Phycis chesteri*. Bar=5 mm.

Theragra, *Brosme* and *Molva* (Ch. 1: Fig. 45B, D; Svetovidov, 1948: figs. 27, 32). The anterior appendages of morids and phycines differ significantly, the anterior part of the swimbladder being firmly attached on the posterior wall of the cranium in the former, and connected to the supracleithrum via a ligament in the latter. These conditions are synapomorphic for each group.

TS 58. Internal sac of swimbladder (Fig. 44). Gadiforms generally have an oval sac, functioning as a gas resorbent system, on the dorsal wall of the swimblad-

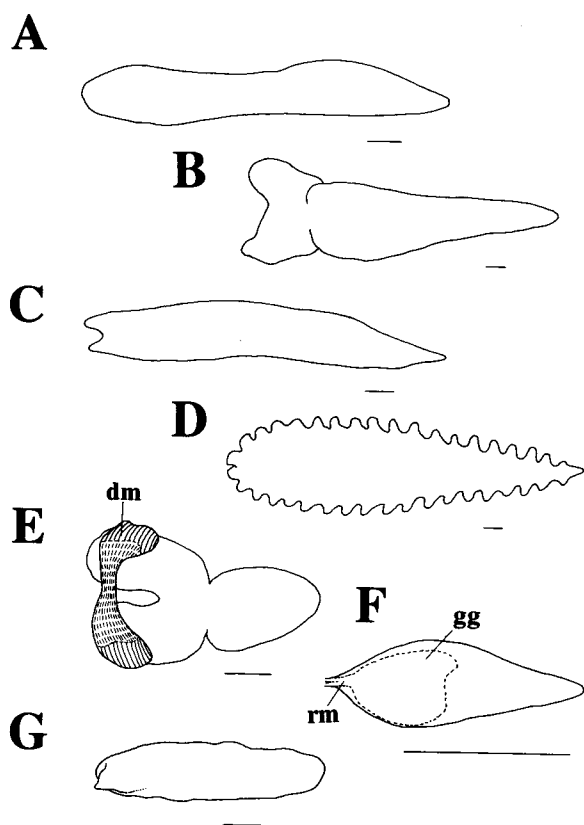


Fig. 43. Ventral view (anterior to left) of swimbladder. A, *Euclichthys polynemus*; B, *Halargyreus johnsoni*; C, *Macruronus magellanicus*; D, *Merluccius australis*; E, *Raniceps raninus*; F, *Bregmaceros arabicus*; G, *Muraenolepis microps*. Bars=5 mm.

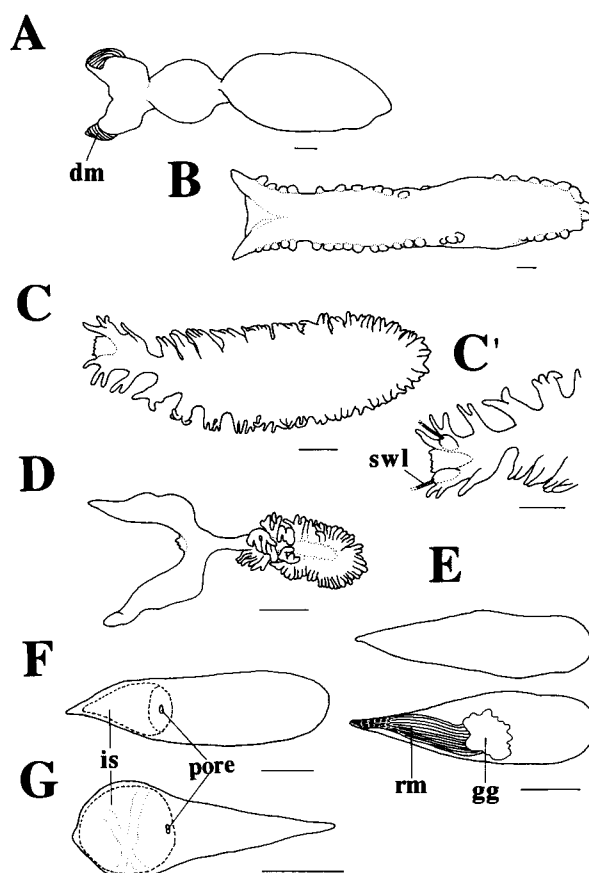


Fig. 44. Ventral view (anterior to left) of swimbladder. A, *Phycis phycis*; B, *Phycis blennoides*; C-C', *Urophycis chuss* (dorsal view in C'); D, *Urophycis regia*; E, *Enchelyopus cimbrius*; F, *Gaidropsarus mediterraneus*; G, *Ciliata mustela*. Bars=5 mm.

der, although morids have a synapomorphic horizontal diaphragm (Ch. 0: Paulin, 1988: figs. 2, 4). The gaidropsarines *Ciliata* and *Gaidropsarus* (*G. mediterraneus*) possess a globose internal sac with reduced gas glands and a posterior pore in the swimbladder (Ch. 1: Fig. 44F, G). As discussed by Paulin (1988: 451, fig. 4B), such an internal sac is basically equivalent to the transverse diaphragm type of euphysoclist swimbladder, and seems to be a derivation of the secretory chamber (*sensu* Paulin, 1988). Although the deep-sea rocklings *G. argentatus* and *G. ensis* have lost the swimbladder, the presence of an internal sac is regarded as a possible synapomorphy of these two genera. Another gaidropsarine (*Enchelyopus*) has a normal swimbladder with developed gas glands and no internal sac (Fig. 44E). Additionally, the swimbladder of the lotine *Lota* is also regarded as the transverse diaphragm type, although a globose internal sac is absent (Fig. 45A). The swimbladder of *Lota* is characterized by a large posterior pore in the secretory chamber, the condition being autapomorphic for the genus.

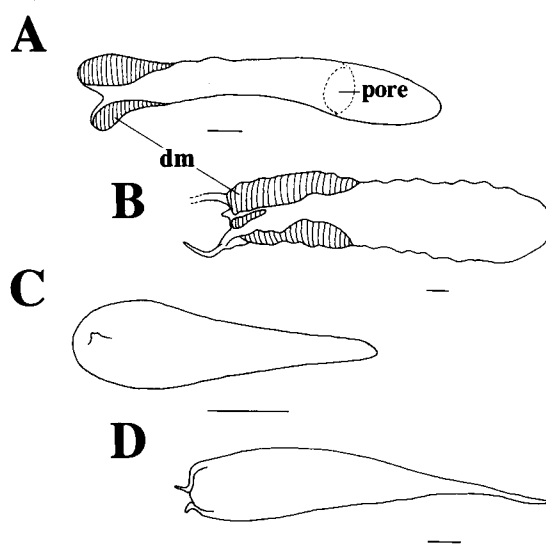


Fig. 45. Ventral view (anterior to left) of swimbladder. A, *Lota lota*; B, *Brosme brosme*; C, *Gadidulus argenteus*; D, *Microgadus proximus*. Bars=5 mm.

TS 59. Posterior extension of swimbladder. The

posterior end of the swimbladder extends over the first haemal spine in gadines, excluding *Arctogadus*, *Boreogadus* and *Gadiculus* (Ch. 1), whereas the other gadiforms, except for two morid genera (*Mora* and *Salilota*), do not possess a posterior extension of the swimbladder (Ch. 0). Ch. 1 is considered to be derived.

TS 60. Two to four barbels on snout (Cohen et al., 1990 : fig. 46). Developed snout barbels are present in gaidropsarines (Ch. 1) : two on the nostrils in *Gaidropsarus*, three on the snout tip and nostrils in *Enchelyopus*, and four on the anterior of the snout and nostrils in *Ciliata*. The anterior nostril with a prominent barbel-like flap is only known in the lotine *Lota*, but is regarded as an autapomorphy for the genus.

TS 61. Oil globule in eggs (Dunn and Matarese, 1984 : table 77). The eggs of most gadiforms have a single oil globule (Ch. 0), although not those of gadines. Although the egg conditions in bregmacerotids, melanonids, steindachneriids and the gadines *Arctogadus* and *Gadiculus* are still unknown, the loss of an

oil globule is probably a gadine synapomorphy (Ch. 1 : e.g., Markle, 1982 ; Fahay and Markle, 1984 ; Dunn and Matarese, 1984).

In gaidropsarines and *Urophycis*, multiple oil globules in the earliest egg stages coalesce into a single oil globule (see Dunn and Matarese, 1984). This ontogenetic trait may indicate the origin of a single oil globule in gadiforms.

2. Relationships

The cladogram based on the data matrix shown in Table 5 was computed using PAUP* 4.0 and the same algorithm and options as in the first analysis. The list of transformation series is presented in Table 4. As a result, a single most parsimonious tree was obtained (Fig. 46 : length=69, CI=0.61, RC=0.52, ACCT-RAN) and is described below.

The interrelationships of the higher gadoids were determined by the present cladogram, except for one trichotomy among gadines. Branch H, the sister group of *Macruronus*, is supported by five synapomorphies including one newly found during the second analysis,

Table 5. Input data matrix for the second analysis of the relationships of higher gadoid genera

Taxon	TS. No	2 2	2 2 2 2 3	3 3 3 3 3	3 3 3 3 4	4 4 4 4 4	4 4 4 4 5	5 5 5 5 5	5 5 5 5 6	6
		4 5	6 7 8 9 0	1 2 3 4 5	6 7 8 9 0	1 2 3 4 5	6 7 8 9 0	1 2 3 4 5	6 7 8 9 0	1
Outgroup		0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 ? 0	0 0 0 0 ?	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0
<i>Arctogadus</i>		1 1	1 0 1 0 0	1 1 1 0 0	0 1 1 0 0	1 0 0 1 1	0 0 0 0 1	0 1 1 0 1	0 0 0 0 0	1
<i>Boreogadus</i>		1 1	1 0 1 0 0	1 1 1 0 0	0 1 1 0 0	1 0 0 1 1	0 0 0 0 1	0 1 1 0 1	0 0 0 0 0	1
<i>Eleginus</i>		1 0	0 0 1 0 0	1 1 1 0 1	0 1 1 0 0	1 0 1 0 1	0 0 0 0 1	0 1 0 0 1	0 1 0 1 0	1
<i>Gadiculus</i>		1 0	1 0 0 0 0	1 1 1 0 0	1 1 0 0 0	1 0 0 0 0	0 0 0 0 1	0 1 0 0 1	0 0 0 0 0	1
<i>Gadus</i>		1 0	0 0 1 0 0	1 1 1 0 1	1 1 1 0 0	1 0 0 0 1	0 0 0 0 1	0 1 0 0 1	0 1 0 1 0	1
<i>Melanogrammus</i>		1 0	0 0 1 0 0	1 1 1 0 1	1 1 1 0 0	1 0 1 1 1	0 0 0 0 1	0 1 0 0 1	0 1 0 1 0	1
<i>Merlangius</i>		1 0	1 0 1 0 0	1 1 1 0 1	1 1 1 0 0	1 0 1 0 1	0 0 0 0 1	0 1 0 1 1	0 1 0 1 0	1
<i>Microgadus</i>		1 0	0 0 1 0 0	1 1 1 0 1	0 1 1 0 0	1 0 1 0 1	0 0 0 0 1	0 1 0 0 1	0 1 0 1 0	1
<i>Micromesistius</i>		1 1	1 0 1 0 0	1 1 1 0 0	1 1 1 0 0	1 0 0 0 0	0 0 0 0 1	0 1 1 2 1	0 0 0 1 0	1
<i>Pollachius</i>		1 0	1 0 1 0 0	1 1 1 0 1	1 1 1 0 0	1 0 0 0 1	0 0 0 0 1	0 1 0 1 1	0 1 0 1 0	1
<i>Theragra</i>		1 0	1 0 1 0 0	1 1 1 0 1	1 1 1 0 0	1 0 0 0 1	0 0 0 0 1	0 1 1 0 1	0 1 0 1 0	1
<i>Trisopterus</i>		1 1	1 0 1 0 0	1 1 1 0 0	1 1 1 0 0	1 0 0 0 1	0 0 0 0 1	0 1 0 0 1	0 0 0 1 0	1
<i>Merluccius</i>		0 0	0 0 1 0 0	0 0 0 0 0	0 0 0 1 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0
<i>Brosme</i>		0 2	1 0 1 0 0	1 1 1 1 1	0 1 0 0 0	1 0 1 0 0	1 0 0 0 0	0 1 0 0 1	0 1 0 0 0	0
<i>Lota</i>		0 2	1 0 1 0 0	1 1 1 1 1	0 1 1 0 0	1 0 1 0 0	1 0 0 0 0	0 1 0 0 1	0 0 0 0 0	0
<i>Molva</i>		0 2	1 0 1 0 0	1 1 1 1 1	1 1 1 0 0	1 0 1 0 0	1 0 0 0 0	0 1 0 0 1	0 1 0 0 0	0
<i>Ciliata</i>		0 0	1 1 1 0 1	1 1 1 0 1	0 1 1 0 1	1 1 0 0 0	1 0 1 0 0	1 0 0 0 0	0 0 1 0 1	0
<i>Enchelyopus</i>		0 0	1 1 1 0 1	1 1 1 0 1	0 1 1 0 1	1 1 0 0 0	1 0 1 0 0	1 0 0 0 0	0 0 0 0 1	0
<i>Gaidropsarus</i>		0 0	1 1 1 0 1	1 1 1 0 1	0 1 1 0 1	1 1 0 0 0	1 0 1 0 0	1 0 0 0 0	0 0 1 0 1	0
<i>Phycis</i>		0 0	1 0 1 0 1	1 1 1 0 1	0 1 1 0 0	1 0 0 0 0	1 1 1 0 0	0 2 0 0 0	1 0 0 0 0	0
<i>Urophycis</i>		0 0	1 1 1 0 1	1 1 1 0 1	0 1 1 0 0	1 0 0 0 0	1 1 1 0 0	0 2 0 0 0	1 0 0 0 0	0
<i>Raniceps</i>		0 0	1 0 1 0 0	0 0 0 0 0	0 0 0 1 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0
<i>Muraenolepis</i>		0 1	1 0 0 1 0	1 0 0 0 0	0 1 0 0 0	1 0 1 0 0	1 0 0 1 0	0 0 0 0 0	0 0 0 0 0	0
<i>Bregmaceros</i>		0 1	0 0 0 1 0	0 0 1 0 0	0 1 0 0 1	0 0 0 1 0	2 0 0 1 0	0 0 0 0 0	0 0 0 0 0	?

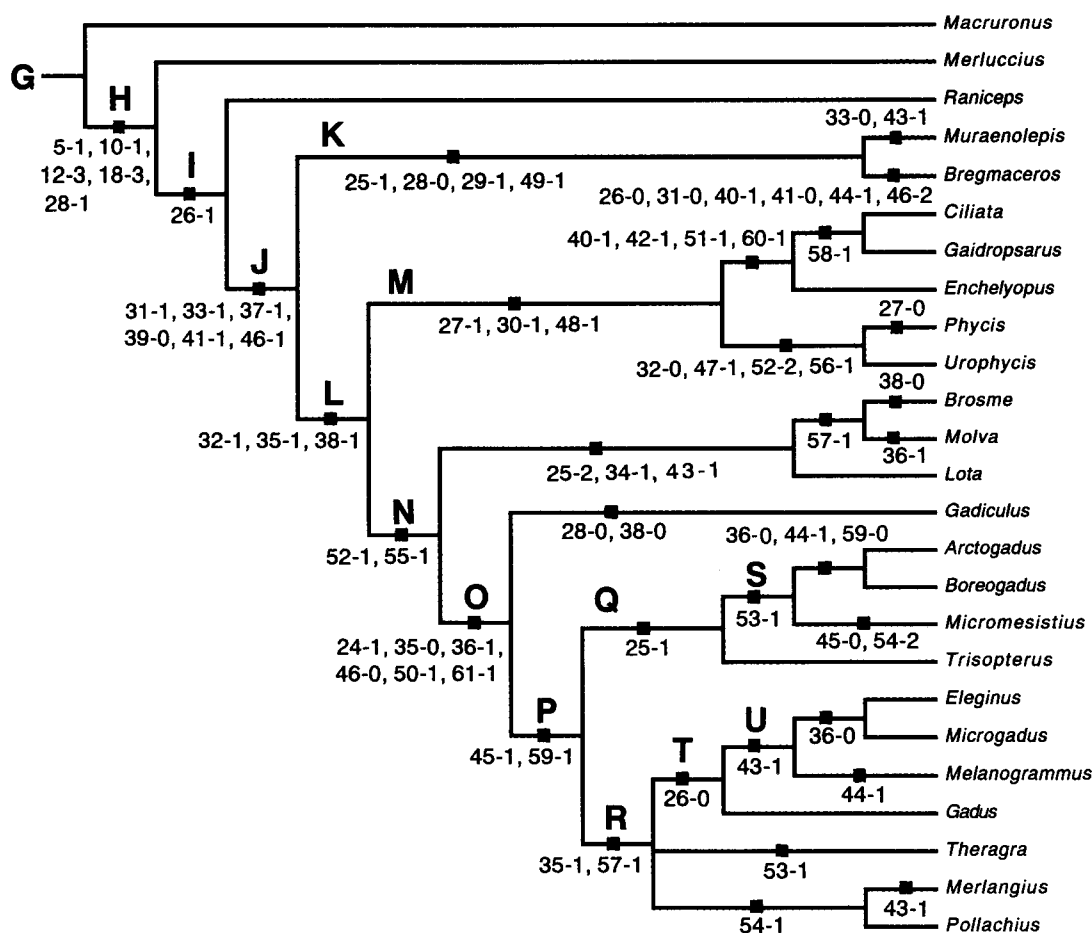


Fig. 46. Shortest tree of higher gadoid intrarelationships estimated by the second analysis.

viz., anteriorly extended adductor mandibular Aw (TS 28-1). In this clade, *Merluccius* has a sister relationship with branch I, which is supported by a single synapomorphy: presence of the dorsal maxillo-premaxillary ligament (TS 26-1).

According to Howes (1991a: fig. 35), the monophyly of the merlucciid *Merluccius* was supported by the following autapomorphies: 1) enlarged vertebral parapophyses; 2) hyomandibular with two long, lateral, ventrally-directed processes; 3) levator arcus palatini originating from a lateral palatine fossa; 4) medial prootic shelves forming a pseudo-posterior myodome. Regarding the second of these characters, the intermuscular process (*sensu* Inada, 1981: fig. 33-34) is clearly autapomorphic for the genus, but the another process, which may be the ventral body of the hyomandibular or a preopercular process, is common in most gadoids. Furthermore, Howes mistook the adductor mandibular A1b for the levator arcus palatini (his character 3). In fact, the origin of A1b on the palatopterygoid is characteristic of *Merluccius*, *Molva*, *Ciliata*, *Gaidropsarus* (*G. mediterraneus*) and *Macruronus*. The first and fourth characters of Howes (1991a) and presence of an inter-

muscular process are here regarded as autapomorphies of *Merluccius*.

Branch I consists of *Raniceps* and branch J, the former (monotypic) genus having the following autapomorphies: 1) anteriorly-inclined hyomandibular (Fig. 13H); 2) levator arcus palatini positioned laterally on posterior part of adductor mandibular A1 (Howes, 1988: fig. 20); 3) large, broad depressed head; 4) unique swimbladder condition (Fig. 43E). In addition, Howes (1991a: fig. 35) considered the first dorsal fin with three rays and reduced lateral line as autapomorphies of the genus. Branch J is supported by six synapomorphies: anteroventral expansion of lower process of hyomandibular (TS 31-1); fusion of both hyohyoideus abductor 2 (TS 33-1); absence of pharyngobranchial 1 and interarcual elements (TS 37-1); normal condition of rectus communis on urohyal (TS 39-0); posterior insertion of pharyngoclavicularis internus (TS 41-1); unexpanded anterior end of single postcleithrum (TS 46-1).

Branch J is divided into branches K and L. In branch K, *Bregmaceros* and *Muraenolepis* form a sister relationship sharing four synapomorphies: single

palato-vomerine ligament (TS 25-1); no anterior extension of adductor mandibular A2 (TS 28-0); absence of endopterygoid (TS 29-1); absence of epipleurals (TS 49-1).

Bregmaceros has the following autapomorphies, which appeared on the cladogram as both reversals and parallelisms: absence of the dorsal maxillo-premaxillary ligament (TS 26-0); general condition of lower process of hyomandibular (TS 31-0); presence of anterior rectus ventralis (TS 40-1); anterior insertion of pharyngoclavicularis internus (TS 41-0); absence of tooth plate on epibranchial 3 (TS 44-1); single postcleithrum having a mid-posterior expansion (TS 46-2). Furthermore, that genus has had many other autapomorphies attributed to it by previous authors (osteological characters, excluding branchials, are described by Swidnicki, 1991: figs. 1-18): 1) lack of tube-like exoccipital facets; 2) lack of supraoccipital crest; 3) unaccreted neural arches of first two vertebrae (Markle, 1989: fig. 15); 4) lack of a tight connection between the separate halves of the neural spine of the first vertebra and supraoccipital crest; 5) proximal radial of the single ray of the first dorsal fin accreted to the supraoccipital and connected with separate halves of the neural spine of the second neural arch (Markle, 1989: fig. 15); 6) loss of pharyngobranchial 2 (Fig. 20F); 7) loss of the first strut of pharyngobranchial 3 with the subdivided lateral strut (Fig. 20F); 8) levator externus inserted onto a ligamentous connection between epibranchial 1 and 2 (Fig. 34E); 9) developed obliquus dorsalis on upper branchial (Fig. 34F); 10) expanded coracoid (Fig. 23E); 11) anterior extension of lower part of cleithrum (Swidnicki, 1991: fig. 14B, E); 12) pelvic girdle triangular in shape and laterally flattened (Fig. 25A); 13) rod-shaped urohyal (Fig. 35C); 14) fusion of upper and lower hypurals (Fig. 26E); 15) rectus superior muscles crossed and supporting opposite eye balls (Fig. 9D); 16) absence of Baudelot's ligament; 17) presence of basibranchial tooth plate (Rosen and Patterson, 1969: fig. 49B); 18) symmetrical formation of dorsal and anal fins.

Muraenolepis is represented by two autapomorphies on the present cladogram: crossing hyohyoideus abductores 2 (TS 33-0); no process on epibranchial 1 (TS 43-1). The genus also has many other autapomorphies: 1) prevomer toothless (Howes, 1990: fig. 3); 2) palatine with a dorsal, medially-directed process (Fig. 14B); 3) numerous actinosts (Fig. 23F); 4) most parts of scapula and coracoid cartilaginous (Fig. 23F); 5) lower arm of posttemporal very reduced (Fig. 37E); 6) simple cleithrum without posterior expansions (Fig. 23F); 7) most part of pelvic girdle cartilaginous (Fig. 24K); 8) first neural spine with V-shaped groove along

anterior margin (Markle, 1989: fig. 13); 9) restricted gill-opening; 10) ophidiid-like scale pattern; 11) continuity of vertical fins (last three characters from Cohen et al., 1990: fig. 26).

Branch L is supported by three synapomorphies: no branchiostegal ray on epihyal (TS 32-1); extension of posterior process of lateral ethmoid (TS 35-1); presence of obliquus dorsalis 2 on dorsal branchials (TS 38-1). Branch L is composed of two clades, branches M and N.

Branch M includes gaidropsarines and phycines. The monophyly of the two groups is corroborated by the following three synapomorphies: adductor mandibular A2 almost covering levator arcus palatini (TS 27-1); a unique palatopterygoid formation (TS 30-1); long and slender median processes of pelvic girdle (TS 48-1).

The clade of the gaidropsarine genera, *Ciliata*, *Enchelyopus* and *Gaidropsarus*, is well supported by four synapomorphies: presence of anterior rectus ventralis (TS 40-1); condition of transversus ventralis anterior (TS 42-1); vibratile first dorsal fin (TS 51-1); two to four snout barbels (TS 60-1). *Enchelyopus* is the sister group of *Ciliata* and *Gaidropsarus*, sharing one synapomorphy: presence of internal sac of swimbladder (TS 58-1). Gaidropsarines basically have a single barbel on the chin and two on the anterior nostrils. However, *Enchelyopus* has an extra barbel on the snout tip and *Ciliata* has a pair of extra barbels on the anterior part of snout (Cohen et al., 1990: fig. 46).

The clade of phycine hakes, *Phycis* and *Urophycis*, is well corroborated by four synapomorphies: one branchiostegal ray on epihyal (TS 32-0); transversely arrayed basipterygia of pelvic girdle (TS 47-1); loss of dorsal supernumerary fin-rays (TS 52-2); presence of ligament connecting supracleithrum with anterior appendage of swimbladder (TS 56-1).

Phycis has one autapomorphy as a reversal: normal formation of adductor mandibular A2 and levator arcus palatini (TS 27-0). On the other hand, *Urophycis* is characterized by four autapomorphies related to the more specialized structure of the ligamentous connection between the swimbladder and cranium (Fig. 40B-D): 1) modification of swimbladder wall at base of swimbladder-supratemporal ligament (Figs. 40D, 44C'); 2) posttemporal and supracleithrum very much diminished in size (Fig. 41B); 3) Baudelot's ligament attached to medial face of cleithrum; 4) levator operculi originating on cleithrum (Howes, 1989: fig. 5).

In branch N, gadines share two synapomorphies with lotines: single soft-ray as dorsal supernumerary fin-ray (TS 52-1); secondary loss of X and Y bones in caudal skeleton (TS 55-1).

The monophyly of lotines is confirmed by two synapomorphies and one homoplasy: anterior shift of

palato-vomerine ligament V origin (TS 25-2); postero-lateral enlargement of vomerine head (TS 34-1); absence of process on epibranchial 1 (TS 43-1). *Lota* forms a sister relationship with the *Brosme* and *Molva* clade supported by one homoplastic condition: presence of horn-shaped anterior appendage of swimbladder (TS 57-1). In addition, *Brosme* is characterized by the following autapomorphies: 1) absence of obliquus dorsalis 2 (TS 38-0); 2) single dorsal and anal fins, partly connected at their posterior ends to the rounded caudal fin; 3) pelvic fins covered with thick skin (Cohen et al., 1990: fig. 64). *Molva* is supported by the following apomorphies: 1) fusion of frontal crests (TS 36-1); 2) extremely elongated body.

The gadines, represented by branch O, share six synapomorphies: 1) concave dorsal shelf of lachrymal (TS 24-1); 2) secondary reduction of posterior process of lateral ethmoid (TS 35-0); 3) fusion of anterior frontal crests (TS 36-1); 4) postcleithrum having an expanded upper end (TS 46-0); 5) three dorsal and two anal fins (TS 50-1); 6) absence of oil globule in eggs (TS 61-1).

Gadiculus, supported by two reversed characters on the cladogram: adductor mandibular Aw with no anterior extension (TS 28-0) and absence of obliquus dorsalis 2 (TS 38-0), is the sister group of branch P. *Gadiculus* is also characterized by three autapomorphies: 1) rounded ventral profile of the cranium (Fig. 33B); 2) absence of lateral shelf of hyomandibular (Fig. 14G); 3) relatively large eye (Cohen et al., 1990: fig. 79).

Branch P, characterized by two synapomorphies: presence of lateral flap of posttemporal (TS 45-1) and posterior extension of swimbladder beyond first haemal spine (TS 59-1), is divided into branches Q and R. Branch Q, including the genera *Arctogadus*, *Boreogadus*, *Micromesistius* and *Trisopterus*, is supported by a single synapomorphy: single palato-vomerine ligament (TS 25-1). Among the included genera, *Trisopterus* forms a sister relationship with branch S, sharing one synapomorphy: wide separation of first and second dorsal fins (TS 53-1).

Branch S is divided into *Micromesistius*, and the *Arctogadus* and *Boreogadus* clade, the latter being characterized by three synapomorphies: separation of anterior frontal crests (TS 36-0); loss of tooth plate on epibranchial 3 (TS 44-1); no posterior extension of swimbladder (TS 59-0). In addition, *Micromesistius* has three autapomorphies: loss of lateral flap on posttemporal (TS 45-0); an extremely large number of anal radials before first haemal spine (TS 54-2); wide interspace between second and third dorsal fins plus a very long first anal fin base (Cohen et al., 1990: fig. 30).

Arctogadus has an atavistic autapomorphy: presence of palatine teeth.

Branch R is supported by two synapomorphies: presence of posterior process of lateral ethmoid (TS 35-1); presence of horn-shaped anterior appendages of swimbladder (TS 57-1). It includes the unresolved trichotomy of *Theragra*, the *Merlangius* and *Pollachius* clade, and branch T (including *Gadus*, *Melanogrammus*, *Microgadus* and *Eleginus*).

Theragra has one autapomorphy: wide separation of first and second dorsal fins (TS 53-1). The *Merlangius* and *Pollachius* clade shares one synapomorphy: a large number of anal radials before first haemal spine (TS 54-1). In addition, *Merlangius* has one homoplastic character: absence of process on epibranchial 1 (TS 43-1). Furthermore, branch T is supported by the absence of the dorsal maxillo-premaxillary ligament (TS 26-0). In this clade, *Gadus* is the sister group of branch U, which includes three genera united by the absence of a process on epibranchial 1 (TS 43-1). *Melanogrammus*, characterized by the loss of the tooth plate on epibranchial 3 (TS 44-1), occupies a sister relationship with the *Eleginus* and *Microgadus* clade sharing one synapomorphy: separation of anterior frontal crests (TS 36-0). In addition, *Eleginus* is well supported by having expanded parapophyses (Cohen et al., 1990: fig. 40).

VII. Cladistic classification of Gadiformes

Many workers have ranked the gadiform suborders and families differently on the basis of different phylogenetic hypotheses (Figs. 49-53). Among them, recent cladistic studies have reached some consensus (Markle, 1989; Howes, 1990, 1991a), the family *Muraenolepididae* being regarded as an advanced gadoid (not as an independent suborder), and the genera *Raniceps* and *Macruronus* being recognized as independent gadoid families (*Ranicipitidae* and *Macruronidae*, respectively), for example. Concerning the family status, Nelson (1994) tentatively adopted the cladistic result of Markle (1989), except for "Gadidae" composed of *Gadinae* and *Lotinae*. Cohen et al. (1990) and Nelson (1994), however, did not assign subordinal ranks, because of the lack of a reliable hypothesis of gadiform relationships. On the basis of the present cladogram, Nelson's family status is generally followed here so as to avoid further taxonomic confusion. To convert the present cladogram into a phylogenetic classification, I followed the sequencing convention of Nelson (1972).

Based on the hypothesis presented here (Fig. 47), a new classification of Gadiformes is proposed below. The rank of suborder is assigned to three clades, *Melanonus*, and branches B and C: the *Melanonoidei*

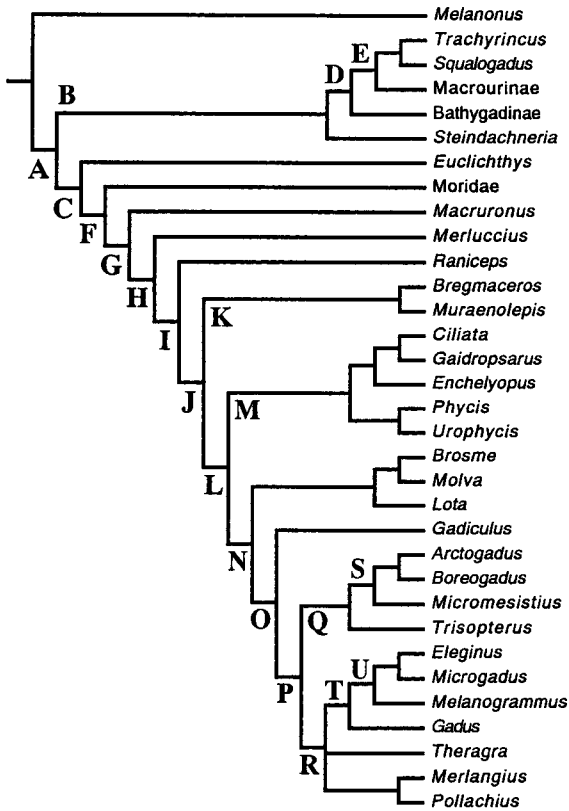


Fig. 47. Proposed interrelationships of gadiform taxa.

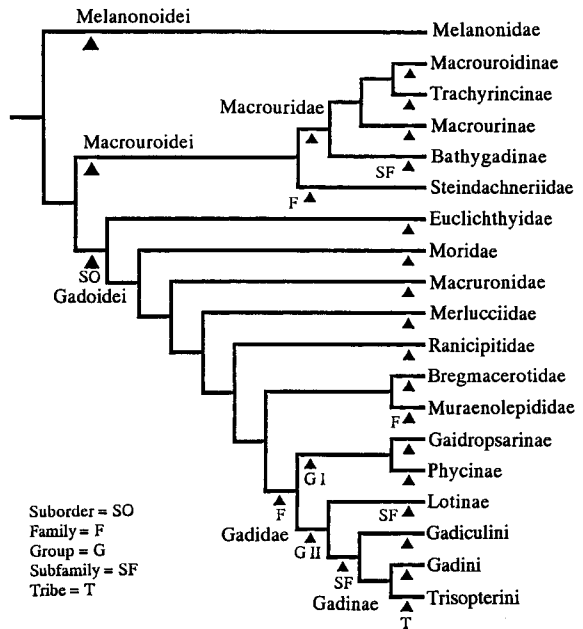


Fig. 48. Cladistic ranking within the order Gadiformes based on inferred relationships.

form a sister relationship with the Macrouroidei and Gadoidei clade (Fig. 48). This ranking and the relationships of the three suborders are consistent with those of Howes (1993) (Figs. 49J, 53). The Melanoidei, characterized by some synapomorphies of the genus *Melanonus* (Howes, 1993), was also recognized by Markle (1989) (Fig. 52).

The suborder Macrouroidei is poorly defined by two synapomorphies: transverse median process of pelvic girdle and absence of caudal skeleton. The monotypic Steindachneriidae and the Macrouridae belong to this suborder (Fig. 48), the latter family comprising four subfamilies: Bathygadinae, Macrourinae, Macrouroidinae and Trachyrincinae. Since the present intra-relationships of macrourids agree with that of Iwamoto (1989) (Figs. 49E, 53), I follow his subfamilial status which has been widely accepted (see Figs. 51, 53: Cohen, 1984; Cohen et al., 1990; Nelson, 1994).

The suborder Gadoidei is poorly defined by one synapomorphy: presence of X and Y bones in the caudal skeleton. Concerning the ranking within gadoids, *Bregmaceros* and *Muraenolepis* should each be recognized as an independent family. In fact, because each genus is characterized by a unique morphology among gadiforms, they have been recognized as separate families for a long time (Figs. 50-53). On the present

tree, the clade involving these two genera is equivalent to branch L (Fig. 47). Thus family status within gadoids is given equally to *Bregmaceros*, *Muraenolepis* and branch L, plus the lower five branches from *Raniceps* to *Eulichthys* (Fig. 47). The following eight families are therefore recognized as belonging to the Gadoidei: Eulichthyidae, Moridae, Macruronidae, Merlucciidae, Ranicipitidae, Bregmacerotidae, Muraenolepididae and Gadidae (Fig. 48).

Among the Gadidae, the taxonomic status of phycine hakes and rocklings have varied from tribe to family (Figs. 50-53: see Nelson, 1976, 1984, 1994; Cohen et al., 1990; Howes, 1991a, 1991b). Considering the morphological differences among gadids, subfamilial status should be assigned to four taxa, viz., Gaidropsarinae, Phycinae, Lotinae and Gadinae. Since their relationship, represented as a symmetrical tree, necessitates further ranking, I tentatively introduce a further category, viz., Group I (Gaidropsarinae and Phycinae) and Group II (Lotinae and Gadinae) so as to avoid redundant names such as the assignment of many superfamilies among gadoids and the ill-matched ranking against current opinions mentioned before (i.e., "Phycinae" including "Phycini" and "Gaidropsarini" vs. Lotinae and Gadinae; Phycinae and Gaidropsarinae vs. "Gadinae" including "Lotini" and "Gadini"). In the Gadinae, three tribes are subordinated: Gadculini, Trisopterini and Gadini (Fig. 48).

The new classification of the order Gadiformes is presented below.

Order Gadiformes

Suborder Melanonoidei

Family Melanonidae (*Melanonus*)

Suborder Macrouroidei

Family Macrouridae

Subfamily Bathygadinae (*Bathygadus*, *Gadomus*)

Subfamily Macrourinae (about 32 genera in Nelson, 1994)

Subfamily Macrouroidinae (*Macrouroides*, *Squalogadus*)

Subfamily Trachyrincinae (*Trachyrincus*, *Idiophorhynchus*)

Family Steindachneriidae (*Steindachneria*)

Suborder Gadoidei

Family Eulichthyidae (*Eulichthys*)

Family Moridae (about 18 genera in Nelson, 1994)

Family Macruronidae (*Macruronus*, *Lyconodes*)

Family Merlucciidae (*Merluccius*)

Family Ranicipitidae (*Raniceps*)

Family Bregmacerotidae (*Bregmaceros*)

Family Muraenolepididae (*Muraenolepis*)

Family Gadidae

Group I

Subfamily Gaidropsarinae (*Enchelyopus*, *Gaidropsarus*, *Ciliata*)

Subfamily Phycinae (*Phycis*, *Urophycis*)

Group II

Subfamily Lotinae (*Lota*, *Molva*, *Brosme*)

Subfamily Gadinae

Tribe Gadiculini (*Gadiculus*)

Tribe Gadini (*Theragra*, *Pollachius*, *Merlangius*, *Gadus*, *Melanogrammus*, *Microgadus*, *Eleginus*)

Tribe Trisopterini (nov.) (*Trisopterus* [type-genus], *Micromesistius*, *Boreogadus*, *Arcotogadus*)

VIII. Comparison with previous works

1. Suborders

On the basis of ongoing evolutionary studies, gadiforms have been variously classified into different suborders (Figs. 50–53). A consensus of these classifications is the recognition of three suborders: Muraenolepidoidei, Gadoidei and Macrouroidei. In particular, the Muraenolepidoidei have been regarded as the most primitive taxon among gadiforms: e.g., “early offshoot of a gadiform-like ancestor” (Okamura, 1970b); “*Muraenolepis* is not obviously related to any other gadiforms and appears to represent an ancient lineage”

(Cohen, 1984).

In recent cladistic works, two to four suborders have been assigned to gadiforms: Ranicipitoidei, Melanonoidei, Macrouroidei and Gadoidei (Markle, 1989: Figs. 49A, 52); Macrouroidei and Gadoidei (Howes, 1989: Figs. 49B, 51); Melanonoidei, Macrouroidei and Gadoidei (Howes, 1993: Figs. 49J, 53). Although Markle (1989) insisted that gadiform phylogeny is strongly reflected by the character evolution of the upper gill-arch (Markle, 1989: fig. 5), it appears that his conclusion resulted from a data set including a weighted transformation series. In fact, Siebert (1990) reanalyzed Markle’s data set, including and excluding upper gill-arch phylogeny, the results showing in both instances that *Raniceps* became the sister group of Markle’s gadoids (Fig. 49G). The cladograms of Siebert (1990) were relatively supportive of the hypotheses of Howes (1993) and the present study. In a series of papers (1987, 1988, 1989, 1990, 1991a, 1993), Howes’ consideration of the melanonid position changed from being one of the lower gadoids (first three papers) to an unresolved polychotomy with gadoids, steindachneriids and bathygadids, in addition to the suborder being regarded as the earliest gadiform offshoot (1993 paper) (Fig. 49B, I, J). The present ranking for the suborder largely agrees with that of Howes (1993), although the Macrouroidei and Gadoidei components differ somewhat. The cladistic studies mentioned above plus the present analysis resulted in the following consensus: 1) three suborders Melanonoidei, Gadoidei and Macrouroidei should be recognized in the order, and 2) Muraenolepididae and Bregmacerotidae both belong to Gadoidei.

Macrouroidei *sensu* Markle (1989), composed of macrourids, steindachneriids, morids and eulichthyids, was supported by two synapomorphies: loss of the epiphyal-interopercle joint (ball and socket type) and presence of a light organ. In the present cladogram, the former character is a plesiomorphic state on branch H (Fig. 47). The latter character is problematic because of the structural differences among macrourines, morids, eulichthyids and steindachneriids, which suggest a polyphyletic nature (e.g., Paulin, 1989b; Okamura, 1989; Iwamoto, 1989).

The Gadoidei *sensu* Markle (1989), being identical with the present higher gadoids (branch G in Fig. 47), excluding Ranicipitidae, was supported by three synapomorphies and three homoplastic characters: 1) loss of the interarcual ligament; 2) 18 or more precaudal vertebral counts; 3) hypurals composed of two plates; 4) pharyngobranchial 1 cartilaginous or lost in all gadiforms except melanonids; 5) scapular foramen bordered by coracoid or located in cartilaginous coraco-scapular matrix in ranicipitids and

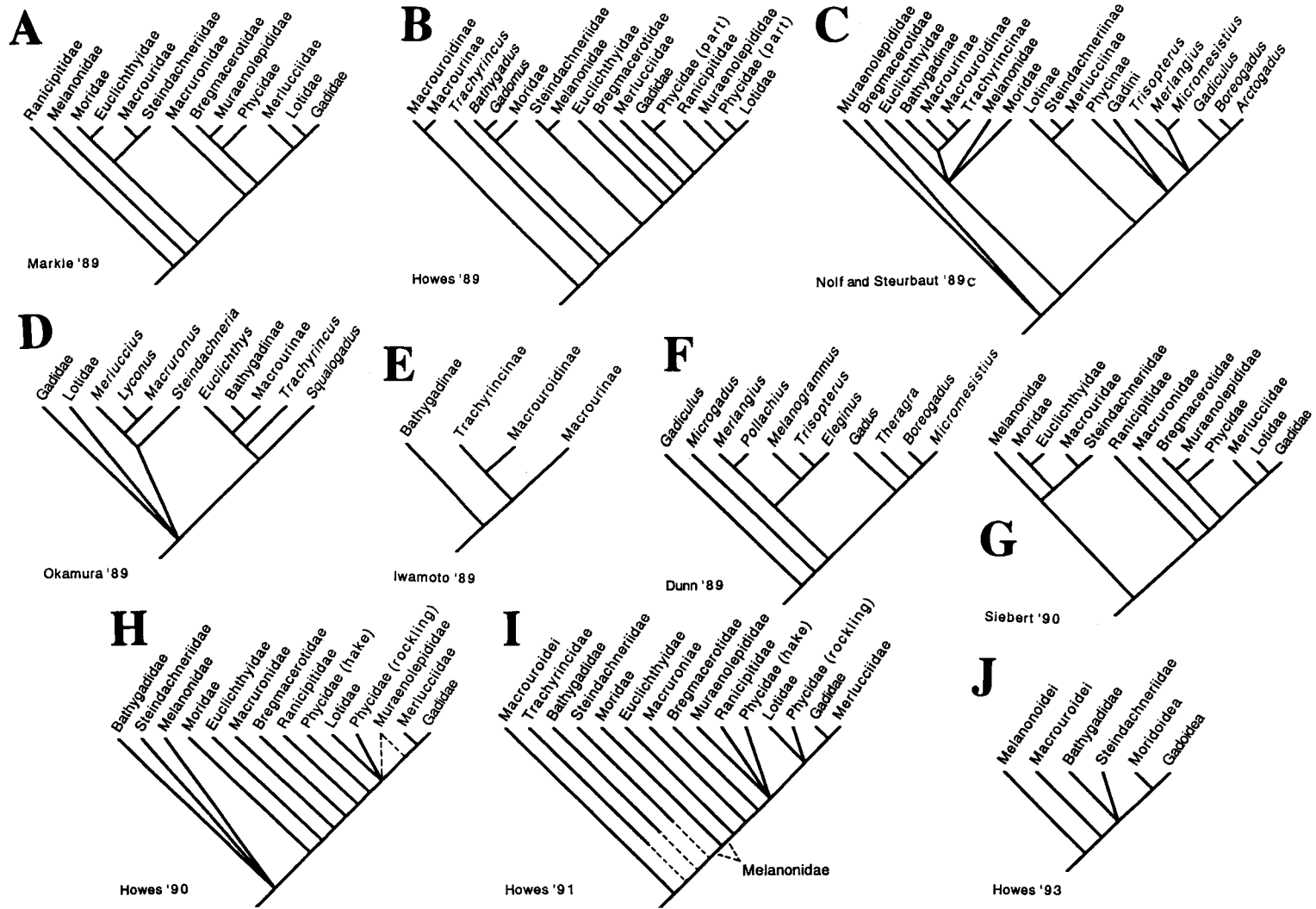


Fig. 49. Phyletic trees and cladograms of gadiform taxa proposed by previous authors. A-C and G-J, intrarelationships of gadiforms ; D, interrelationships of macrouroid and some gadoid taxa ; E, intrarelationships of macrouroids ; F, intrarelationships of gadids.

<p>Svetovidov (1948) Suborder Muraenolepidoidei Family Muraenolepididae [!] Suborder Gadoidei Family Moridae Family Bregmacerotidae Family Gadidae Subfamily Lotinae Subfamily Merlucciinae Subfamily Gadinae *Macrouriformes Family Macrouridae</p>	<p>Marshall (1965) Family Melanonidae Family Gadidae Family Moridae Family Merlucciidae Family Bregmacerotidae Family Muraenolepididae [!] Family Macrouridae Subfamily Trachyrhynchinae Subfamily Macrouroninae Subfamily Bathygadinae Subfamily Macrourinae</p>	<p>Marshall and Cohen (1973) Family Melanonidae Family Eretmophoridae (Moridae) Family Gadidae Family Merlucciidae Family Steindachneriidae Family Macrouridae Family Bregmacerotidae Family Muraenolepididae [!]</p>
<p>Gaemers (1976) Family Gadidae Subfamily Gadinae Subfamily Merlucciinae Subfamily Lotinae Subfamily Gaidropsarinae Subfamily Phycinae Subfamily Ranicepsinae [!]</p>	<p>Nelson (1976) Suborder Muraenolepidoidei Family Muraenolepididae Suborder Gadoidei Family Moridae Family Melanonidae Family Bregmacerotidae Family Gadidae Subfamily Gadinae Subfamily Lotinae Family Merlucciidae Subfamily Macrouroninae Subfamily Merlucciinae Suborder Macrouroidei Family Macrouridae *Suborder Ophidioidei *Suborder Zoarcidae</p>	<p>Schwarzahns (1980) Family Bregmacerotidae Family Gadidae Subfamily Ranicipitinae (including <i>Euclichthys</i>) Subfamily Merlucciinae Subfamily Gadinae Family Macrouridae Subfamily Trachyrhynchinae Subfamily Macrourinae *Moriformes Family Moridae</p>

Fig. 50. Classifications of the order Gadiformes and some included taxa proposed by previous authors.

<p>Cohen (1984) Suborder Muraenolepidoidei Family Muraenolepididae Suborder Bregmacerotoidei Family Bregmacerotidae Suborder Macrouroidei Family Euclichthyidae Family Macrouridae Subfamily Macrouroidinae Subfamily Trachyrhynchinae Subfamily Macrourinae Subfamily Bathygadinae Suborder Gadoidei Family Merlucciidae Subfamily Merlucciinae Subfamily Steindachneriinae Family Gadidae Family Lotidae Family Phycidae Family Melanonidae Family Moridae</p>	<p>Dunn and Matarese (1984) Family Gadidae Subfamily Phycinae Subfamily Lotinae Subfamily Merlucciinae Subfamily Gadinae</p>	<p>Fahay and Markle (1984) Family Muraenolepididae Family Bregmacerotidae Family Melanonidae Family Moridae Family Macrouridae Family Steindachneriidae Family Merlucciidae Family Gadidae Subfamily Gadinae Subfamily Lotinae Subfamily Phycinae</p>
<p>Nelson (1984) Suborder Muraenolepidoidei Family Muraenolepididae Suborder Gadoidei Family Moridae Family Melanonidae Family Bregmacerotidae Family Gadidae Subfamily Gadinae Subfamily Lotinae Tribe Lotini Tribe Gaidropsarini Family Merlucciidae Subfamily Macrouroninae Subfamily Steindachneriinae Subfamily Merlucciinae Suborder Macrouroidei Family Macrouridae</p>	<p>Howes (1988, 1989) Suborder Macrouroidei Family Macrouridae Subfamily Macrourinae Subfamily Macrouroidinae Suborder Gadoidei Family Trachyrhynchidae Family Bathygadidae Family Moridae Family Melanonidae Family Steindachneriidae Family Euclichthyidae Family Merlucciidae Family Gadidae Family Ranicipitidae [!] Family Lotidae Family Phycidae Family Bregmacerotidae Family Muraenolepididae</p>	

Fig. 51. Classifications of the order Gadiformes and some included taxa proposed by previous authors.

“gadoids”; 6) obvious internal separation of first and second fins in bregmacerotids, two morids (*Auchenoceros* and *Tripterophyscis*), “gadids” (present gadines), macruronids, merlucciids, muraenolepidids and “phycids” (present Group I). Among these, the first and third characters clearly support Markle’s “gadoids”,

but the others do not separate the latter from ranicipitids. The second, fifth, and sixth characters seem to have been coded without regard to their variations, the sixth being particularly misleading because the interspace between the dorsal fins in ranicipitids is wider than in the taxa mentioned above, excluding bregma-

<p>Markle (1989) Suborder Ranicipitoidei Family Ranicipitidae Suborder Melanonoidei Family Melanonidae Suborder Macrouroidei Family Macrouridae Family Steindachneriidae Family Moridae Family Eulichthyidae Suborder Gadoidei Superfamily Macruronoidea Family Macruronidae Superfamily Bregmacerotoidea Family Bregmacerotidae Family Muraenolepididae Family Phycidae Superfamily Gadoidea Family Gadidae Family Lotidae Family Merlucciidae</p>	<p>Nolf and Steurbaut (1989c) Family Bregmacerotidae Family Muraenolepididae Family Melanonidae Family Moridae Family Eulichthyidae Family Macrouridae Subfamily Bathygadinae Subfamily Macrourinae Subfamily Macrouroidinae Subfamily Trachyrincinae Family Gadidae Subfamily Lotinae Subfamily Steindachneriinae Subfamily Merlucciinae Subfamily Gadinae Tribe Gadini Subfamily Phycinae</p>	<p>Dunn (1989) Family Gadidae Subfamily Gadicolinae <i>Gadiculus</i> Subfamily Microgadinae <i>Microgadus</i> Subfamily Eleginae <i>Merlangius</i>, <i>Pollachius</i>, <i>Melanogrammus</i>, <i>Trisopterus</i>, <i>Eleginus</i> Subfamily Gadinae <i>Gadus</i>, <i>Theragra</i>, <i>Boreogadus</i>, <i>Micromesistius</i>, (<i>Arctogadus</i>)</p>
<p>Inada (1989) Family Merlucciidae Subfamily Steindachneriinae Subfamily Merlucciinae</p>	<p>Iwamoto (1989) Family Macrouridae Subfamily Bathygadinae Subfamily Macrourinae Subfamily Macrouroidinae Subfamily Trachyrincinae</p>	<p>Okamura (1989) Suborder Gadoidei Family Merlucciidae Family Steindachneriidae Family Gadidae Family Lotidae Suborder Macrouroidei Family Eulichthyidae Family Macrouridae Subfamily Bathygadinae Subfamily Macrourinae Family Trachyrincidae Family Macrouroididae</p>

Fig. 52. Classifications of the order Gadiformes and some included taxa proposed by previous authors.

<p>Cohen et al. (1990) (All families are alphabetically arrayed) Family Bregmacerotidae Family Eulichthyidae Family Gadidae Subfamily Gadinae Subfamily Lotinae Subfamily Phycinae Family Macrouridae Subfamily Bathygadinae Subfamily Macrourinae Subfamily Macrouroidinae Subfamily Trachyrincinae Family Melanonidae Family Merlucciidae Subfamily Merlucciinae Subfamily Steindachneriinae Family Moridae Family Muraenolepididae</p>	<p>Howes (1991a, 1991b, 1993) Suborder Melanonoidei Family Melanonidae Suborder Macrouroidei Family Macrouridae Family Trachyrincinae Suborder Gadoidei Family Bathygadidae Family Steindachneriidae Superfamily Moridoidea Family Moridae Family Eulichthyidae Superfamily Gadoidea Family Macruronidae Family Bregmacerotidae Family Ranicipitidae Family Phycidae Family Lotidae Family Gaidropsaridae Family Muraenolepididae Family Merlucciidae Family Gadidae</p>	<p>Nelson (1994) Family Ranicipitidae Family Eulichthyidae Family Macrouridae Subfamily Bathygadinae Subfamily Macrourinae Subfamily Trachyrincinae Subfamily Macrouroidinae Family Steindachneriidae Family Moridae Family Melanonidae Family Macruronidae Family Bregmacerotidae Family Muraenolepididae Family Phycidae Subfamily Phycinae Subfamily Gaidropsarinae Family Merlucciidae Family Gadidae Subfamily Lotinae Subfamily Gadinae</p>
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Fig. 53. Classifications of the order Gadiformes and some included taxa proposed by previous authors.

cerotids, muraenolepidids and the two morids. In addition, *Merluccius*, *Macruronus* and *Steindachneria* show a slight separation, but the dorsal fins of *Lyconus* (juvenile species of *Macruronus*) are almost continuous (Fig. 70D).

The Gadoidei *sensu* Howes (1993) is composed of the present gadoids plus bathygadids and steindachneriids. Howes (1988, 1989, 1991a) also regarded trachyrincids as a member of “gadids”, but later returned the former to macrouroids (Howes, 1990, 1991b, 1993) without discussion (Figs. 51, 53). Howes’ gadoids shared the following two synapomorphies: 1) pharyngohyoideus (= *rectus communis*) mediated by the sternohyoideus and the interradales connected to the dorsal and anal fin rays; 2) loss of various caudal fin muscles and entire

caudal skeleton in some taxa. However, the first apomorphic state also exists in melanonoids and macrouroids, and the second was apparently ill-defined, thereby supporting the monophyly of bathygadids, steindachneriids and the present gadoids, since most macrourids have lost the caudal elements. In fact, Howes’ macrouroids (relationships unknown) are identical with the well-defined monophyletic group composed of macrourines, trachyrincines and macrouroidines (see Iwamoto, 1989, Fig. 49E), and with branch E in the present cladogram (Fig. 47).

2. Family Melanonidae

The family-group name first appeared in the key to genera of the Gadidae by Goode and Bean (1896 : 353),

as the subfamily Melanoninae. Subsequently, however, the genus *Melanonus* has been included in the Gadidae (Jordan, 1923), the Moridae (Svetovidov, 1948) and the Morinae (in gadids) (Norman, 1966). Since Marshall (1965), *Melanonus* has been regarded by many authors as an independent family among the primitive "gadoids" (Figs. 50–53). Following recent cladistic analyses, melanonids have been generally placed within the lower gadiforms (Fig. 49), viz., the second offshoot among gadiforms (Markle, 1989); the sister group of steindachneriids (Howes, 1989); lower gadoids or gadiforms (Nolf and Steurbaut, 1989c; Howes, 1990, 1991a); the first offshoot of gadiforms (Howes, 1993). The present analysis supports that of Howes (1993).

3. Family Steindachneriidae

The relationships and taxonomic status of the monotypic genus *Steindachneria* have been unresolved despite many attempts, the genus having been regarded as a member of the following groups (partly in Figs. 50–53): Macruroninae (among macrourids) in Regan (1903); Steindachneriinae (among macrourids) in Parr (1946); Macruroninae (among merlucciids) in Norman (1966), Marshall (1966) and Nelson (1976); Steindachneriidae in Marshall and Cohen (1973), Fahay and Markle (1984), Markle (1989), Okamura (1989), Fahay (1989), Howes (1988, 1989, 1990, 1991a, 1991b, 1993) and Nelson (1994); Steindachneriinae (among merlucciids) in Nelson (1984), Cohen (1984, 1990) and Inada (1989).

Among these recent hypotheses (Fig. 49), the phylogenetic position of *Steindachneria* has been inferred as a sister group of Macrouridae (Markle, 1989), "Merlucciinae" (Nolf and Steurbaut, 1989c) or Melanonidae (Howes, 1989). Furthermore, the genus was considered as an unresolved lower gadiform by Howes (1990, 1991a, 1993) (Fig. 49H–J). On the basis of ontogenetic and osteological data, Fahay (1989) assumed the genus to be a sister group of macrourids. The present result supports the conclusions of Markle (1989) and Fahay (1989), rejecting any close relationships with merlucciids or macruronids, as believed by some workers (e.g., Okamura, 1989; Inada, 1989).

4. Family Macrouridae

The Macrouridae, composed of four subfamilies, has long been regarded as a monophyletic group (e.g., Regan, 1903; Marshall, 1965, 1973; Cohen, 1984; Cohen et al., 1990), Berg (1940) and Svetovidov (1948) once regarding it as a separate order (Fig. 50). The following two subfamilies were ranked as separate families within macrouroids: "Macrouroididae" in Okamura (1970a, 1970b, 1989) and "Trachyrincidae" in Okamura (1989) (Figs. 49D, 52).

The intrarelations of macrouroids have been often discussed (e.g., Marshall, 1965, 1973; Okamura, 1970a, 1970b). Regarding cladistic studies, Howes (1989) inferred that the present Macrouridae, including four subfamilies, was a paraphyletic assemblage among gadiforms (Fig. 49B). In the cladograms of Howes (1990, 1993) (Fig. 49H, J), his "trachyrincids" disappeared into "gadoids" without mention, and the "bathygadids" formed an unresolved polychotomy with steindachneriids, melanonids and other gadoids (former paper) or with steindachneriids and the "Moridoidea" and "Gadoidea" clade (latter paper). Additionally, Howes (1991a) could not determine the phylogenetic position of "trachyrincids" and "bathygadids" (following a cladistic analysis) among the lower gadoids. Iwamoto's (1989) conclusions regarding the relationships of the four subfamilies, are supported by the present analysis (Fig. 49E). On the contrary, Okamura (1989) proposed a different interpretation for the macrouroid phylogeny based on evolutionary thought (Figs. 49D, 52), his "macrouroidids" forming a sister relationship with the clade including "trachyrincids", macrourines, bathygadines and euclichthyids. As discussed in detail by Iwamoto (1989), Okamura's hypothesis cannot be accepted from a cladistic point of view. Namely, Okamura (1989) regarded some reversals subjectively as primitive evidence for "macrouroidids" and "trachyrincids".

5. Family Euclichthyidae

The monotypic *Euclichthys* was first placed in "morines" or morids (e.g., Norman, 1966; McCann, 1972). However, Svetovidov (1969) stated that it should be excluded from morids because of the lack of any connection between the cranium and swimbladder, and the position of the olfactory bulbs being just before the forebrain, as in *Melanonus*. On the basis of otolith features, Karrer (1971) pointed out that *Euclichthys* bore no diagnostic characters of morids. However, Schwarzhans (1980) included the genus in "Ranicipitinae" among "gadids" (Fig. 50). Furthermore, Paulin (1983) argued that *Euclichthys* should be placed near or within melanonids, occupying a phylogenetic position between morids and "gadids". Fahay and Markle (1984) also treated *Euclichthys* as a family *incertae sedis*. Generally however, since Cohen (1984), *Euclichthys* has been treated as a separate family (Fig. 51). May and Maxwell (1986), however, later included the genus in melanonids (possibly following Paulin's view). In more recent studies (Fig. 49), some authors have differed in their assessment of the position of *Euclichthys*; as a sister group of morids (Markle, 1989; Howes, 1993), gadoids (Howes, 1989, 1990, 1991a), or a sister group of

the bathygadine and macrourine clade (Okamura, 1989). The present study concluded that *Euclichthys* represents the first offshoot among gadoids.

6. Family Moridae

The Moridae is the second largest family among gadiforms, being composed of about 100 species in 20 genera (Paulin, 1989b; Cohen et al., 1990; Meléndez and Markle, 1997). Since the exclusion of *Melanonus* and *Euclichthys*, morids have been regarded as a well-defined group sharing unique characters: 1) distinctive otolith features (e.g., Karrer, 1971; Fitch and Barker, 1972); 2) otophysic connection between cranium and swimbladder (e.g., Svetovidov, 1948; Paulin, 1983); 3) horizontal diaphragm within the posterior swimbladder chamber (e.g., Paulin, 1988). In recent cladistic analyses (Fig. 49), morids have been considered as having a sister relationship with *Euclichthys* (Markle, 1989; Howes, 1993) and “bathygadids” (Howes, 1989), or representing an offshoot among lower gadoids (Howes, 1990, 1991a). Although Markle’s hypothesis was based on a presumed synapomorphy (distinctly asymmetrical distribution of procurrent caudal fin-rays, with more ventral than dorsal rays), I consider such to be a homoplasy, owing to the various fin conditions observed in gadiforms seemingly being polyphyletic: e.g., single dorsal fin in *Melanonus*, trachyrincines, macrouroidines, *Lyconus* and *Brosme*; extension of anterior anal fin-rays in *Steindachneria*, *Euclichthys* and *Bregmaceros*; continuous dorsal, caudal and anal fin-rays in *Macruronus* and *Muraenolepis*; elongation of first dorsal fin-ray in *Auchenoceros*, *Bregmaceros*, *Muraenolepis* and gaidropsarines. In the present hypothesis, morids formed a sister group of the remaining gadoids, excluding *Euclichthys*, but their intrarelationships were not estimated.

On the basis of the otolith morphology, Nolf and Steurbaut (1989c) were unable to clarify the phylogenetic position of morids, which remained as an unresolved polychotomy with euclichthyids, macrourids, melanonids and extensive “gadids” (Fig. 49C). Concerning the interrelationships of morid genera, Karrer (1971: fig. 20) recognized three groups based on otolith characters (‘*Mora*’, ‘*Pseudophysicis*’ and ‘*Physiculus*’ groups), and presented a cladogram for twelve genera. This basic grouping was supported and developed by Fitch and Barker (1972), and Paulin (1983, 1985, 1986, 1989a, 1989b). Eventually, Paulin (1989b) divided the morid genera into the following groups: ‘*Mora*’, ‘*Pseudophysicis*’ and ‘*Physiculus*’ (composed of ‘*Physiculus*’ and ‘*Laemonema*’ subgroups) groups. However, five genera (*Austrophycis*, *Auchenoceros*, *Eretmophorus*, *Svetovidovia* and *Rhynchogadus*)

remained as *incertae sedis*. Meléndez and Markle’s (1997) cladistic analysis of the “*Laemonema*” subgroup recognized two genera, *Laemonema* (incl. 12 spp.) and *Guttigadus* (incl. 8 spp).

A proposal by Marshall and Cohen (1973) to place *Eretmophorus* (known only from larval specimens) in a new family “Eretomophoridae”, thereby supplanting Moridae, received little subsequent support.

7. Family Macruronidae

Although Regan (1903) placed the genus *Macruronus* (with *Steindachneria*) in the subfamily “Macruroninae” of “macrourids”, other earlier authors simply included the genus in “macrourids” (e.g., Goode and Bean, 1896; Jordan, 1923; Berg, 1940). Since Norman (1966), the subfamily “Macruroninae” has been placed in “merlucciids” (e.g., Marshall, 1966; Nelson, 1976). Although Marshall and Cohen (1973) and Okamura (1989) later regarded *Macruronus*, *Lyconus* and *Merluccius* as “merlucciids”, without subfamily ranking, Nelson (1984) accepted “Macruroninae” as a subfamily of “merlucciids”, together with “merlucciines” and “steindachneriines” (Figs. 50–52). Furthermore, Cohen (1984), Inada (1989) and Cohen et al. (1990) assigned the above three genera to “merlucciines” within “merlucciids”, which also included “steindachneriines” (Figs. 51–53). However, Markle (1989), Howes (1990, 1991a, 1991b) and Nelson (1994) treated *Macruronus* and *Lyconus* as an independent family (Macruronidae) (Figs. 52, 53).

The recent cladistic analyses of Markle (1989) and Howes (1990, 1991a) reached the same conclusion in that macruronids formed a sister relationship with the rest of the higher gadoids (Fig. 49A, H, I). The present analyses supports their hypothesis, recognising the relationship between macruronids and merlucciids to be paraphyletic.

8. Family Merlucciidae

The genus *Merluccius* has always been considered to belong to the Merlucciinae or Merlucciidae (or both). The “Merlucciinae” (including only *Merluccius*) among the extended “gadids” has been recognized by a number of authors (e.g., Berg, 1940; Svetovidov, 1948; Mujib, 1967; Gaemers, 1976; Dunn and Matarese, 1984) (Figs. 50, 51). In particular, Dunn and Matarese (1984: fig. 152) included a phylogenetic tree of “gadid” subfamilies, in which “merlucciinae” was placed as a sister group of gadines.

In previous cladistic analyses (Fig. 49), *Merluccius* has been inferred as the sister group of the “gadid and lotid” clade (Markle, 1989) or “gadids” (Howes, 1990, 1991a). In addition, Howes’ (1989) “merlucciids”, including *Macruronus*, was considered a sister group of the other

higher gadoids, excluding bregmacerotids (Fig. 49B). The present study concluded that Merlucciidae included only *Merluccius* species, having a sister relationship with the other higher gadoids, except macruronids.

The monophyly of merlucciids, "lotids" and "gadids", proposed Markle (1989), was supported by one synapomorphy and one homoplasy: high precaudal counts plus anal fin radials well in advance of the first haemal spine; neural and haemal spines supporting procurrent caudal rays on more than ten caudal vertebrae. However, the cording of these meristic characters appears to have been arbitrary. Although a sister relationship of "gadids" with merlucciids in Howes (1990, 1991a) was supported by one apparent synapomorphy (presence of medial prootic shelf), that character needs further investigation among gadoids owing to its variable nature (e.g., absent in *Gadus*, present in *Enchelyopus*).

9. Family Ranicipitidae

The family Ranicipitidae, including the monotypic *Raniceps*, was first established by Gill (1890). Subsequently, Berg (1940) and Gaemers (1976) accorded it subfamilial ranking only, as "Ranicipitini" and "Ranicepsinae" within "gadids", respectively (the latter based on otolith morphology). More often, however, authors regarded *Raniceps* as a member of "lotines" or "phycines" within the extended "gadids" ("lotines" in Svetovidov, 1948; Mujib, 1967; Nelson, 1976, 1984; Nolf and Steurbaut, 1989c; "phycines" in Dunn and Matarese, 1984; Fahay and Markle, 1984; Cohen et al., 1990). However, the cladistic analyses by Markle (1989) and Howes (1989, 1990, 1991a) resulted in *Raniceps* again being given family rank (Figs. 49, 52, 53). Markle (1989) inferred that Ranicipitidae (also treated as a separate suborder) represented the earliest offshoot of gadiforms, but this is doubtful as mentioned above (Siebert, 1990), the independent family position within gadoids as proposed separately by Howes and Siebert being the current consensus (Fig. 49G-I). The present analysis resulted in *Raniceps* being placed as the sister group of the other higher gadoids, excluding macruronids and merlucciids, and accorded it family ranking.

10. Family Bregmacerotidae

Since Gill (1872), the family Bregmacerotidae, including only *Bregmaceros* species, has been recognized and included in gadoids by many authors (e.g., Svetovidov, 1948; Nelson, 1976, 1984; Markle, 1989; Howes, 1991a), although the genus was included in gadids by Regan (1903) and in bregmacerotids with the morid genus *Auchenoceros* by Jordan (1923). Cohen (1984)

established the monogeneric suborder "Bregmacerotoidei". The anatomy and intrarelationships of bregmacerotids were investigated by D'Ancona and Cavinato (1965), Houde (1984) and Swidnicki (1991), and otolith features by Nolf and Steurbaut (1989c). The latter indicated that bregmacerotids formed an unresolved trichotomy with muraenolepidids and the other gadiforms (Fig. 49C), pointing out (figs. 1-12) that *Bregmaceros* had concave collicular areas on the otolith in common with *Muraenolepis*, *Brosme*, *Gaidropsarus*, *Ciliata* and *Enchelyopus* (Fig. 74).

In recent cladistic analyses (Fig. 49), the phylogenetic position of bregmacerotids has been estimated variously as the sister group of muraenolepidids (Markle, 1989), higher gadoids (Howes, 1989) or higher gadoids, excluding macruronids (Howes, 1990, 1991a). The present analysis supported Markle's (1989) hypothesis, in which the monophyly of bregmacerotids and muraenolepidids was supported by one synapomorphy: absence of ligamentous connection between epibranchial 1 and 2. In fact, such a connection, although weakly developed, is present in *Bregmaceros*, levator externus 1 being located on the ligamentous connection (Fig. 34E).

11. Family Muraenolepididae

The Muraenolepididae, including four *Muraenolepis* species, has long been recognized as an independent family (e.g., Regan, 1903; Figs. 50-53). Considering the primitive and peculiar morphological features of Muraenolepididae, resembling ophiidiids, many authors considered the family to represent the earliest offshoot of gadiforms, while retaining the gadiform ancestral form (e.g., Matsubara, 1963; Cohen, 1984). Thus the family has at times been placed in the independent suborder "Muraenolepidoidei" (Figs. 50, 51). On the contrary, however, some cladistic analyses indicated the Muraenolepididae as belonging to advanced gadoids (Fig. 49A-B, G-I). In particular, Markle (1989) considered the family to be the sister group of bregmacerotids, a sister relationship supported by the present study.

12. Family Gadidae

In the early period of gadiform classification, the family "Gadidae" was recognized as an extended group including such as morids, merlucciids, ranicipitids and bregmacerotids (e.g., Regan, 1903). Svetovidov (1948) proposed the "Gadidae", composed of three subfamilies: "Merlucciinae", Gadinae and "Lotinae" (including lotines, phycines, gaidropsarines and ranicipitids of the present study) (Fig. 50). Svetovidov also hypothesized the phylogenetic relationships of the family based mainly on vertical fin formation (e.g., *Brosme*, having single dorsal and anal fins, was regarded as the most

primitive). Gaemers (1976) later recognized six subfamilies on the basis of otolith features (Fig. 50). Following Svetovidov's proposal, the "Gadidae", excluding merlucciids, has been accepted by many authors (Figs. 50–53). However, Cohen (1984) elevated certain gadid subfamilies to "Gadidae", "Lotidae" and "Phycidae (including phycines, gaidropsarines and ranicipitids of this study)". Moreover, Howes (1989, 1990, 1991a, 1991b) divided the "Phycidae" (*sensu* Cohen, 1984) into three families: "Phycidae", "Gaidropsaridae" and Ranicipitidae (Fig. 53). On the other hand, Markle (1989) split this "Phycidae" (*sensu* Cohen, 1984) into two families "Phycidae" (present Group I) and Ranicipitidae (Fig. 52). Following Markle's hypothesis, Nelson (1994) recognized two families, "Phycidae" (present Group I) and "Gadidae" (present Group II) (Fig. 53). In view of this recent taxonomic confusion, I concluded that the family Gadidae should be considered as comprising four subfamilies: Phycinae, Gaidropsarinae, Lotinae and Gadinae.

With respect to the phylogenetic relationships of gadids, all of the recent cladistic analyses (Fig. 49) have regarded the present Gadidae as a polyphyletic group. In particular, none have corroborated the monophyly of "Phycinae" (present Group I). Indeed, Howes (1989, 1990, 1991a) indicated polyphyletic relationships in his cladograms (Fig. 49B, H, I). However, the present study has confirmed the monophyly of phycines and gaidropsarines, based on three synapomorphies (Fig. 46).

In Howes' (1991a) cladogram (Fig. 49I), supposed synapomorphies on the main stem do not, in fact, support each clade among the higher gadoids. In addition, the homoplastic characters on the terminal taxa were not described. For example, all three synapomorphies uniting the "Lotidae", "Gaidropsaridae", "Gadidae" and Merlucciidae are doubtful: 1) hyomandibular with lateral shelf; 2) cone-shaped lateral ethmoid wing; 3) separate foramen for trigeminal and hyomandibularis nerves. In fact, the "Gaidropsaridae" do not have these characters. Additionally, the first character is variously developed in lower gadiform taxa (e.g., some morids and macrourids) and its homology is uncertain. Even though the second character is prominent in gadines, excluding *Gadiculus* and *Trisopterus*, the lotine *Molva*, and merlucciids, a similar condition (although not prominent) exists also in *Macruronus*, *Steindachneria*, *Halargyreus*, *Laemonema*, †*Palaeogadus* and †*Rhinocephalus*. Because of variations, the lateral ethmoid feature is difficult to divide into discrete character states. The third character is only present in five genera (*Merluccius*, *Brosme*, *Molva*, *Trisopterus* and *Micromesistius*) in this clade

(Svetovidov, 1948 : fig. 4), and was also present in the morids examined. Among gadiforms, it is likely that these characters represent retention or reappearance of plesiomorphic states, such as the V or Y ridge on the dorsal face of the cranium.

Markle (1989) showed the monophyly of the "Phycidae" (present Group I), Bregmacerotidae and Muraenolepididae to be supported by one synapomorphy and one homoplasy: the presence of an elongate first dorsal fin-ray and the loss of the uncinat process on epibranchial 1. The latter condition was also shared with Markle's "Lotidae" and "Gadidae". In addition, Markle suggested that the first dorsal ray in "phycid hakes" may represent a secondary loss, the homoplastic state being present in the morid *Auchenoceros* and some outgroups. Although the uncinat process is much reduced in all gadids, bregmacerotids and muraenolepidids, its complete loss was only observed in some gadines, lotines and muraenolepidids.

Dunn (1989 : fig. 29) investigated cladistically the relationships of eleven "gadid" (= present gadines) genera, except for *Arctogadus*, based on the osteological characters of early life stages (Fig. 49F). According to the branching pattern, Dunn recognized four subfamilies among "gadids" (Fig. 52): "Gadiculinae, Microgadinae, Eleginae and Gadinae". On the other hand, the present analysis recognized three tribes among gadines: Gadiculini, Trisopterini and Gadini. Dunn's cladogram is partly consistent with that in the present study in the following points: 1) *Gadiculus* is the sister group of all other gadines; 2) *Merlangius* is the sister group of *Pollachius*; 3) *Boreogadus* is the sister group of *Micromesistius*. The greatest conflict between the two cladograms is the position of *Microgadus*: Dunn regarded the genus as a second offshoot of gadines, whereas the present study inferred it to be an advanced genus among the Gadini.

Renaud (1989) suggested a sister relationship of *Gadus* and *Melanogrammus* on the basis of some morphological characters and sound-producing mating behavior in males. Although Renaud (1989) also compared allozyme data of *Gadus*, *Boreogadus*, *Eleginus*, *Microgadus* and *Theragra*, it was not possible to unequivocally infer relationships of the five genera, because they shared only four loci. Renaud's data, however, indicated that *Theragra* was closer to *Gadus* electrophoretically, compared with the other genera examined. Furthermore, Renaud and Morrison (1992) later regarded the tuberculate scales observed only in *Gadus* and *Boreogadus* as a homoplastic character, rather than as a shared synapomorphy.

On the basis of otolith morphology, Nolf and Steurbaut (1989c) estimated the Gadinae to comprise

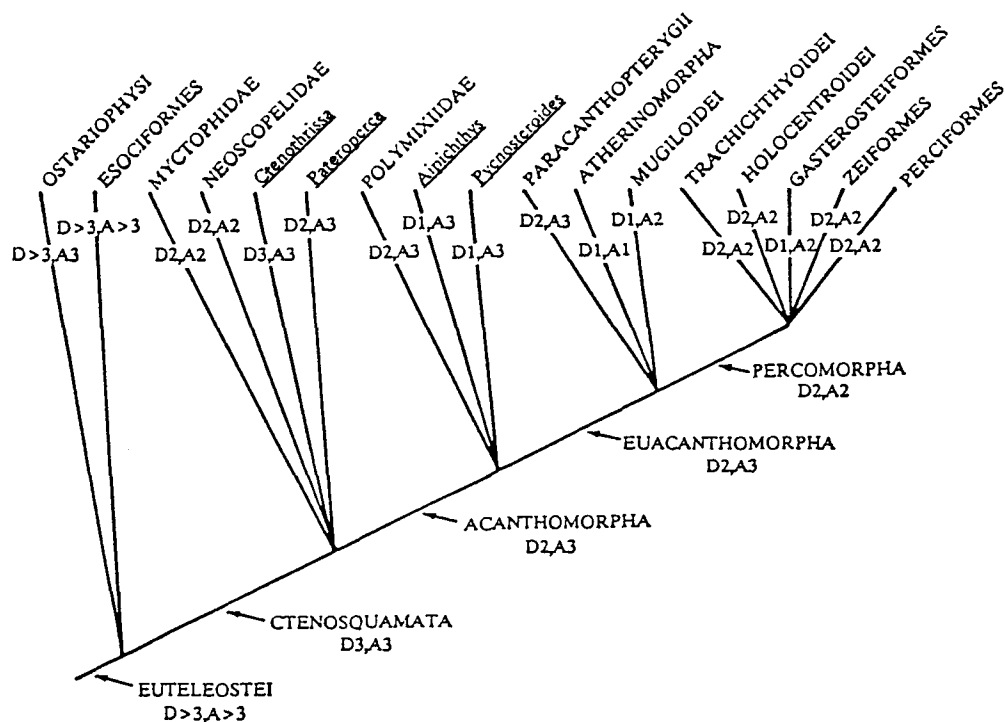


Fig. 54. Cladogram of certain groups of euteleostei, with numbers of dorsal (D) and anal (A) supernumeraries inferred as most primitive in each (from Patterson, 1992).

“Gadini”, involving six genera, and the other genera, which were not assigned to any other tribe (Fig. 49C), their hypothesis being summarized as follows: 1) “Gadini”, comprising six closely-related genera (*Eleginus*, *Gadus*, *Melanogrammus*, *Microgadus*, *Pollachius* and *Theragra*) formed a sister relationship with the remaining genera; 2) a sister relationship existed between *Merlangius* and *Micromesistius*; 3) a sister relationship existed between *Gadiculus* and the *Arctogadus* and *Boreogadus* clade. The first and third relationships are not dissimilar to the results of the present study. Moreover, the stratigraphic ranges of fossil otoliths of gadines (Fig. 63: Nolf and Steurbaut, 1989b: fig. 3) suggest that the following four genera seem to be primitive among the gadine lineage: *Trisopterus* (first recorded from the Eocene/Oligocene boundary), *Gadiculus* (middle Oligocene), *Micromesistius* (middle Oligocene) and *Merlangius* (Oligocene/Miocene boundary). The fossil otoliths of the other genera were recorded from the Miocene/Pliocene boundary (*Melanogrammus*, *Microgadus*, *Theragra* and *Gadus*) and the Miocene/Pliocene boundary (*Pollachius*). These otolith data strongly support the present hypothesis.

Nolf and Steurbaut (1989c) also showed their “Lotinae” to include the present ranicipitids, gaidropsarines and lotines, having a sister relationship with the “merlucciine and steindachneriine” clade (Fig. 49C).

IX. General considerations

1. Character evolution of supernumerary fin-rays

One or two spiny fin-rays related to the first dorsal radial are well known to occur in some gadiform taxa, such as macrourids and merlucciids (e.g., Marshall, 1965; Okamura, 1970b, 1989; Marshall and Cohen, 1973; Inada, 1981, 1989; Iwamoto, 1989). The morphology of this spiny, non-segmented ray (termed “pseudospine”), which is secondarily-derived from a soft-ray, was examined in detail by Okamura (1970b). Patterson (1992) subsequently discussed the character distribution and phylogenetic trend (viz., number of rays generally decreasing in more derived taxa) (Fig. 54) of supernumerary fin-rays in teleosts overall. In paracanthopterygians, Patterson (1992) considered the condition of two dorsal and three anal supernumerary fin-rays to be a primitive state. In gadiforms, however, dorsal supernumerary fin-rays and the link between number and condition (pseudospine or soft-ray) has been overlooked. Character distribution is also uncertain. In this section, gadiform supernumerary fin-rays are described and discussed in detail.

Terminology and abbreviations follow Patterson (1992): “supernumerary fin-rays” are indicated as “SR”, the notation “Dn” or “An” referring to the number of supernumerary rays on the first dorsal and anal radial, respectively. “Pn” refers to the number of pseudospines

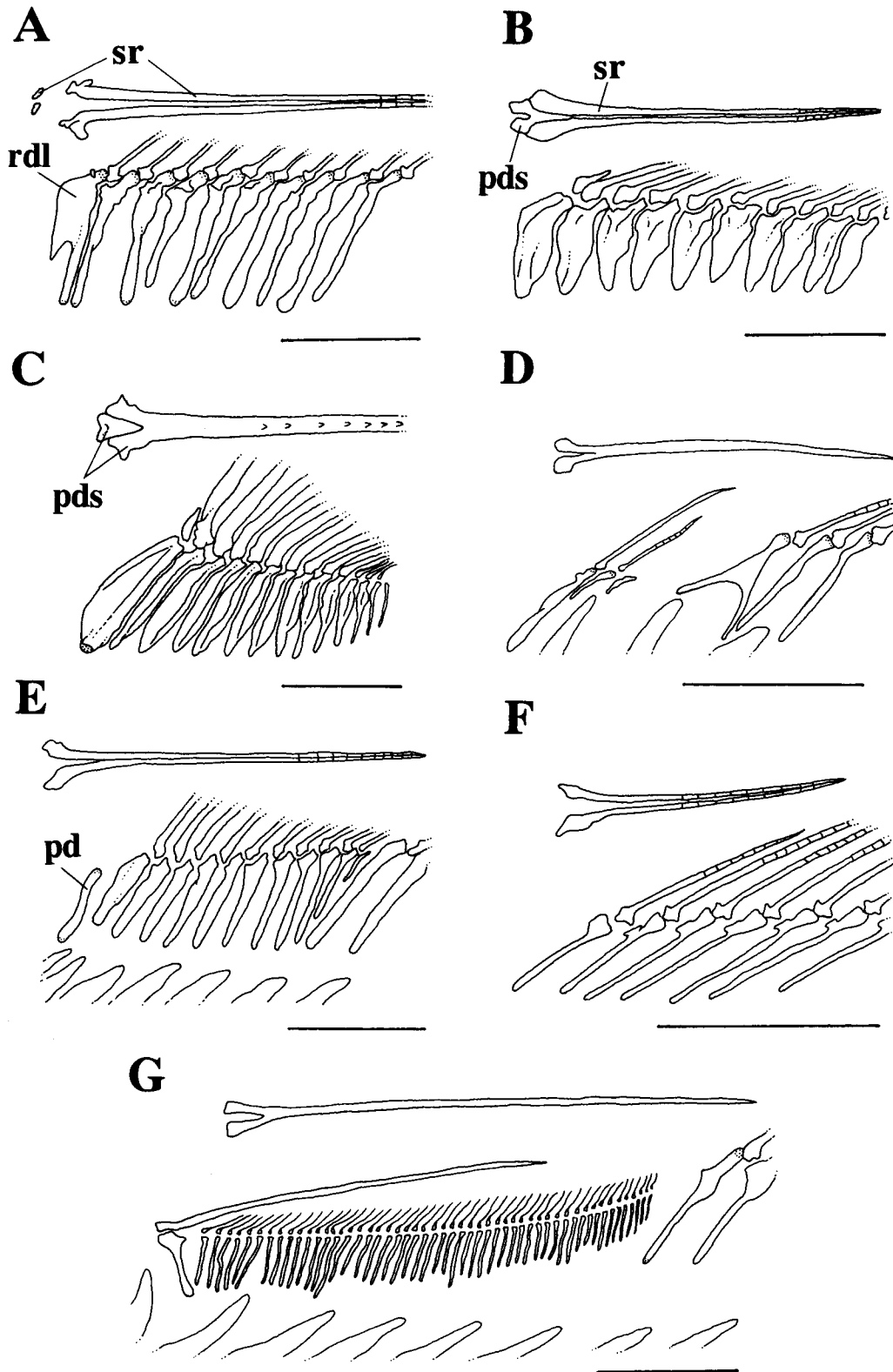


Fig. 55. Dorsal (supernumerary fin-ray[s], upper) and lateral (fin structure, lower) views of anterior dorsal fin. A, *Melanonus zugmayeri*; B, *Trachyrincus murrayi*; C, *Ventrifossa garmani*; D, *Raniceps raninus*; E, *Phycis blennoides*; F, *Lota lota*; G, *Enchelyopus cimbrius*. Bars = 5 mm.

Table 6. Number of dorsal supernumerary fin-rays and pseudospines in soft-rayed paracanthopterygians. Asterisk indicates data from Marshall (1965), Markle (1982), Inada (1989), Patterson and Rosen (1989), and Markle and Olney

Type	Taxon
Gadiformes	
D2P0	<i>Melanonus zugmyeri</i>
D2P1	Trachyrincinae
D2P2	Macrourinae, bathygadinae, <i>Halargyreus</i> , <i>Lotella</i> , <i>More</i> , <i>Physiculus</i> , <i>Salilota</i> , <i>Laemonema</i> sp., <i>Svetovidovia</i> *, <i>Euclichthys</i> , <i>Macruronus</i>
D1P1	<i>Steindachneria</i> , <i>Antimora</i> , <i>Auchenoceros</i> , <i>Tripterophycis</i> , <i>Merluccius</i> , <i>Raniceps</i> , <i>Bregmaceros</i> , <i>Muraenolepis</i> , Gaidropsarinae
D1P0	<i>Melanonus gracilis</i> , <i>Squalogadus</i> , <i>Laemonema longipes</i> , Gadinae, Lotinae
D0P0	Phycinae
Ophidiiformes	
D2P0	<i>Oligopus</i> , <i>Monomitopus</i> *, <i>Lucifuga</i> *
D1P0	<i>Homostolus</i> , <i>Hoplobrotura</i> , <i>Neobythites</i> , <i>Ophidion</i> , <i>Brotula</i> *, <i>Echiodon</i> *, <i>Enchelyopsis</i> *, <i>Onuxodon</i> *, <i>Pyramodon</i> *, <i>Snyderidia</i> *

within the dorsal supernumerary rays as determined in this study. For example, the morphotype in which two pseudospines are related to the first dorsal radial is indicated as "D2P2". On the other hand, "D1P0" indicates a single dorsal soft-ray related to the first dorsal radial.

1-1. Character states

Six morphotypes of dorsal SR recognized in gadiforms are shown in Figures 55, 56 and Table 6. In gadiforms, the D2 state is generally composed of the first short and second well-developed rays (Fig. 55B, C; e.g., Okamura, 1970b: figs. 55–57), while the D1 state is represented by one normal ray (Fig. 55D–G; e.g., Patterson and Rosen, 1989: fig. 9).

D2P0, which occurred only in *Melanonus zugmyeri*, consisted of the first (reduced to a minute ossicle) and second (normal) supernumerary-rays (Fig. 55A). In the ophidiiforms examined, the bythitid *Oligopus* also possessed this state. Although Howes (1993: fig. 13C) illustrated the D2 state of *Melanonus zugmyeri*, the fin ray components were not specified.

D2P1, present only in the trachyrincines, *Trachyrincus* and *Idiophorhynchus*, comprises a first small spine and second normal soft-ray (Fig. 55B). Marshall (1965) reported that *Macrouroides* and *Squalogadus*, in addition to *Trachyrincus*, also had the first ray reduced to a short splint and a second segmented dorsal ray. However, there was no first small pseudospine in the *Squalogadus* specimens examined.

D2P2 occurs widely in the lower gadiform taxa, including bathygadines, macrourines, euclichthyids, most morids and macruronids. The composition,

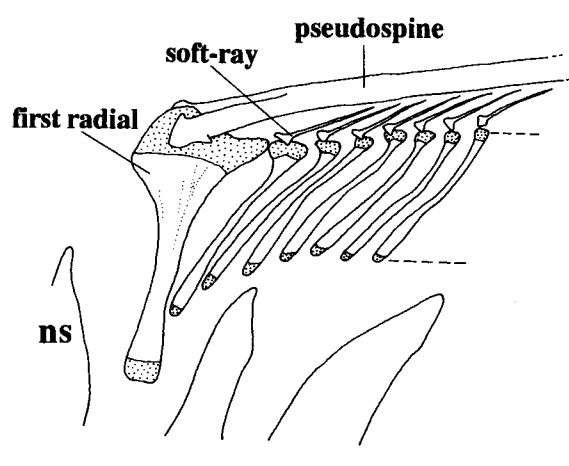


Fig. 56. Lateral view of anterior dorsal fin of *Gaidropsarus ensis*. Bar=3 mm.

first pseudospine very short and the second well-developed (Fig. 55C), has been described by many workers: e.g., macrourids in Okamura (1970b: figs. 51–53, 55, 56); *Euclichthys* in Okamura (1989: fig. 6); *Bathygadus* in Howes and Crimmen (1990: 175). Howes (1991a), however, noted that the first dorsal fin of *Macruronus* comprised a minute first ray and 13 long, segmented rays, all of which were supported by long, broad distal radials. The different condition described by Howes (1991a) may be due to his examination of younger specimens (130–250 mm TL), because basibranchial 2 in his fig. 17 is less developed than in the adult specimens examined here (Figs. 5A, 6C, D). Moreover, Markle (1982: fig. 6) illustrated the morid *Svetovidovia* sp. as having the D2 state, but the fin-ray condition is uncertain from the figure.

D1P1 is found in some higher gadoids, steidach-

neriids and three morid genera. A single pseudospine (as dorsal SR) in these taxa (Fig. 55D) has been described in the following: gaidropsarines in Cohen and Russo (1979 : 98); *Merluccius* in Inada (1981 : 92, fig. 41); *Bregmaceros* in Markle (1989 : fig. 13) and Swidnicki (1991 : 152, figs. 1, 2). As shown by Cohen and Russo (1979 : fig. 5), *Enchelyopus cimbricus* has an enlarged, Y-shaped first radial related to the first pseudospine and second minute soft-ray. This radial did not have a prominent Y-shape in the specimen examined here (Fig. 55G). In *Gaidropsarus*, however, the first radial condition appeared to comprise two fused elements, the first supporting the single pseudospine, and the second being related to the first minute soft-ray (Fig. 56). Like the first radial in gaidropsarines, I regard this condition not as the D2 state but rather a modified D1, originating from the unique dorsal fin structure. The D1 state in other gadiforms has been previously illustrated: *Raniceps* in Patterson and Rosen (1989 : fig. 9); *Muraenolepis* in Markle (1989 : fig. 13).

DIP0 occurs in gadines, lotines, *Laemonema*, *Squalogadus* and *Melanonus gracilis*, as well as in some ophidiiform genera (Fig. 55F). A single soft-ray (termed dorsal SR) in *Gadus* was illustrated by Markle (1982 : fig. 4).

DOP0 is a hypothetical condition assigned to the phycine genera *Phycis* and *Urophycis*, which possess a predorsal bone (Fig. 55E). On the basis of their sister relationship with gaidropsarines, the predorsal of phycines is considered to be a remnant of the ancestral first radial, supported by an elongated first pseudospine. Although Patterson and Rosen (1989 : 20) discussed whether the “predorsal” of phycines and *Euclithys* was either a retained supraneural or a rayless dorsal pterygiophore, its

origin was uncertain. Markle (1989 : 78) regarded the first dorsal fin-ray as having been secondarily lost in *Phycis* and *Urophycis* (within the clade of bregmacerotids, muraenolepidids and “phycids”, including phycines and gaidropsarines).

The anal SR of gadiforms and other paracanthopterygians are divided into A1 and A2 groups (Table 7). In gadiforms, both states are present in morids, phycines, gadines, *Phycis* and *Muraenolepis*. Patterson (1992) noted the A3 state in †*Sphenocephalus*, a fossil paracanthopterygian.

A2 consists of a first short, somewhat reduced ray (vestigial ossicle in *Eleginus gracilis*) and a second longer ray located between the first and second radials (*Steindachneria* in Fahay, 1989 : fig. 6; *Bregmaceros* in Swidnicki, 1991 : fig. 17; *Melanonus* in Howes, 1993 : fig. 13). It is distributed among some higher gadoids, lower gadiforms and most of the other paracanthopterygians examined. Although Okamura (1970b : figs. 51–53, 1989 : figs. 3, 4) illustrated A1 states for *Gadomus*, *Caelorinchus*, *Coryphaenoides*, *Malacocephalus* and *Trachyrincus*, these genera generally have A2. In *Steindachneria*, Fahay (1989 : 150) noted that a short spinous splint might have been fused ontogenetically to the first anal ray. This suggests the possibility that a gadiform ancestor possessed the A3 state, as in primitive paracanthopterygians.

On the contrary, A1 is restricted to a few morids, some higher gadoids, and two of the paracanthopterygians examined, *Oligopus* and *Lophiomus* (Table 7). The associated fin ray in the A1 group is more reduced and shorter than the subsequent rays.

1–2. Order and polarity

According to Patterson (1992), the dorsal and anal SR showed a general trend towards reduction in

Table 7. Number of anal supernumerary fin-rays in gadiforms and other paracanthopterygians. Asterisk indicates data from Pietsch (1974, 1981) and Patterson (1992)

Type	Taxon
Gadiformes	
A2	<i>Melanonus</i> , <i>Caelorinchus</i> , <i>Coryphaenoides</i> , <i>Malacocephalus</i> , <i>Macrourus</i> , <i>Nezumia</i> , <i>Ventrifossa</i> , Bathygadinae, <i>Trachyrincus</i> , <i>Steindachneria</i> , <i>Antimora</i> , <i>Auchenoceros</i> , <i>Halargyreus</i> , <i>Laemonema</i> , <i>Lotella</i> , <i>Mora</i> , <i>Euclithys</i> , <i>Macruronus</i> , <i>Merluccius</i> , <i>Raniceps</i> , <i>Bregmaceros</i> , <i>Muraenolepis microps</i> , <i>Ciliata</i> , <i>Eleginus</i> , <i>Melanogrammus</i> , <i>Microgadus</i> , <i>Micromesistius</i> , <i>Pollachius</i> , <i>Theragra</i> , <i>Trisopterus</i> , <i>Phycis phycis</i>
A1	<i>Physiculus</i> , <i>Salilota</i> , <i>Muraenolepis orangiensis</i> , <i>Gaidropsarus</i> , <i>Enchelyopus</i> , <i>Phycis blennoides</i> , <i>P. chesteri</i> , <i>Urophycis</i> , Lotinae, <i>Arctogadus</i> , <i>Boreogadus</i> , <i>Gadiculus</i> , <i>Gadus</i> , <i>Merlangius</i>
Other paracanthopterygians	
A3	† <i>Sphenocephalus</i> *
A2	† <i>Amphiplaga</i> *, † <i>Trichophanes</i> *, <i>Homostolus</i> , <i>Hoplobrotula</i> , <i>Neobythites</i> , <i>Ophidion</i> , <i>Porichthys</i> , <i>Opsanus</i> , <i>Antennarius</i> *, <i>Chaunax</i> *, <i>Dibranchus</i> *, <i>Oneirodes</i> *, <i>Tetrabrachium</i> *, <i>Aphredoderus</i> , <i>Percopsis</i>
A1	† <i>Erismatopterus</i> *, <i>Oligopus</i> , <i>Lophiomus</i>

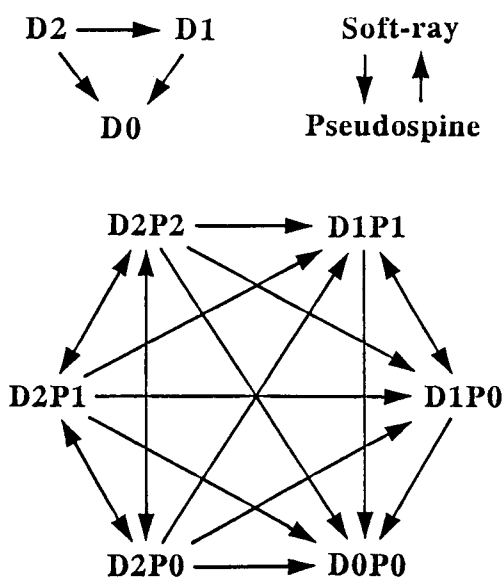


Fig. 57. Polarity, order and theoretical transformation series of dorsal supernumerary fin-rays of gadiforms.

number among acanthomorphs, the primitive states in paracanthopterygians being hypothesized as D2 and A3. The three states of SR numbers, D2, D1 and D0, are hence polarized as shown in Figure 57.

The dorsal pseudospine of gadiforms is apparently derived from a soft-ray, based on structural evidence (Okamura, 1970b). Concerning the ontogeny of such, I observed a segmented second ray in an alevin of the macrourine *Coryphaenoides cinereus* (HUMZ-L 5269, 13.2 mm HL) (Endo et al., 1993), whereas adults are characterized by two pseudospines. The fin-ray condition is therefore basically polarized from soft-ray to pseudospine, but a subsequent reversal is possible due to heterochronic phenomena in terminal taxa (Fig. 57). The transformation series of six morphotypes is partly ordered and polarized by SR number (Fig. 57). D0P0 is apparently the most derived state, with D2P0, D2P1 and D2P2 being equally primitive among gadiforms.

Concerning the outgroups, the dorsal SR are clearly divided into spined and soft-rayed states. In the Anacanthini of Patterson and Rosen (1989), pediculates, having a sister relationship with gadiforms, have one to six distinct dorsal spines, including such highly specialized rays as an illicium (lophiiforms) and hollow spines associated with venom glands (batrachoidiforms). However, the spineless ophidiiforms have only a primitive D2P0 or an advanced D1P1 condition, as in gadiforms. In lower paracanthopterygians, †*Sphenocephalus* and percopsiforms have one to five distinct spines (Rosen and Patterson, 1969; Nelson, 1994). The state of D2P0 in gadiforms is hence considered to be the most primitive.

In gadiforms, the anal SR condition is simply polar-

ized from A2 to A1. The derived A1 condition occurred independently within morids, muraenolepidids and gadids, its phylogenetic information thus being far less significant than that of the dorsal SR. Thus, the character evolution of dorsal SR only is discussed below.

1-3. Dorsal supernumerary fin-rays

The character evolution of dorsal SR was inferred from the present analysis of gadiform relationships and that of paracanthopterygian relationships by Patterson and Rosen (1989), the result being illustrated in Figure 58. In this character tree, D2P0 is regarded as the immediate ancestral state of gadiforms. After the melanonid ancestor had become separated from the main stem, D2P0 evolved to D2P2 in the lower gadiform lineage. The latter state then evolved to D1P1 after separation of the macrouronids from the main stem.

In melanonids, the D1P0 condition in *Melanonus gracilis* clearly arose from the ancestral state D2P0 observed in *M. zugmayeri* and three ophidiiforms (Table 6). In the macrouroid lineage, the D1P1 (steindachneriids), D2P1 (trachyrincines) and D1P0 (macrouronidines) states apparently evolved from the immediately ancestral D2P2 state, but the internode above the macrourines branch necessarily remains equivocal (Fig. 58). Among each morid group (*sensu* Paulin, 1989b), variations in dorsal SR exist in the “*Mora*” (D1P1 in *Antimora*) and “*Physiculus*” groups (D1P1 in *Triptero-phycis*; D1P0 in *Laemonema longipes*). Although *Auchenoceros* (D1P1) has been regarded as *incertae sedis* among morids, these changes may have occurred independently two or more times among the family. In gadids, the hypothesized D0P0 of phycines and D1P0 of the gadine and lotine clade are also independently derived from the ancestral D1P1 of the higher gadoid lineage. Concerning the pseudospines, an ancestor of the gadiforms, excluding melanonids, is inferred as having gained once, subsequent reversals to soft-rays occurring independently within the three families: macrourids, morids and gadids.

The evolution of dorsal SR on the present cladogram (Fig. 58) agrees well with the polarities of the theoretical transformation series (Fig. 57), and is more parsimonious than the hypotheses of Markle (1989) and Howes (1990, 1991a, 1993), illustrated in Figure 59. Concerning outgroup relationships, Markle (1989) tentatively regarded batrachoidiforms as the sister group of gadiforms, but did not refer to the other paracanthopterygians. On Markle’s tree, an immediate ancestor of gadiforms also possessed D2P0, but the pseudospines were considered to have originated independently in both ranicipitids (D2P0→D1P1) and the lower gadiform clade (D2P0→D2P2) (Fig. 59A). Howes’ tree also in-

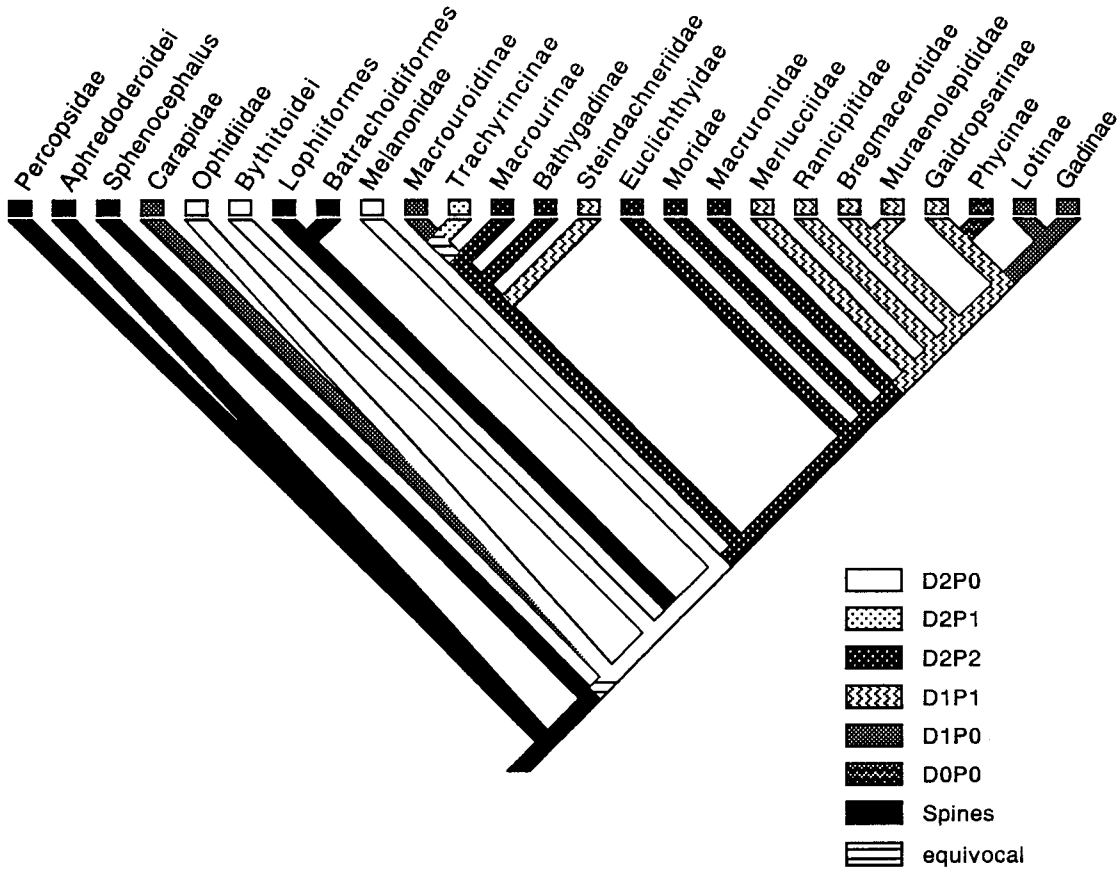
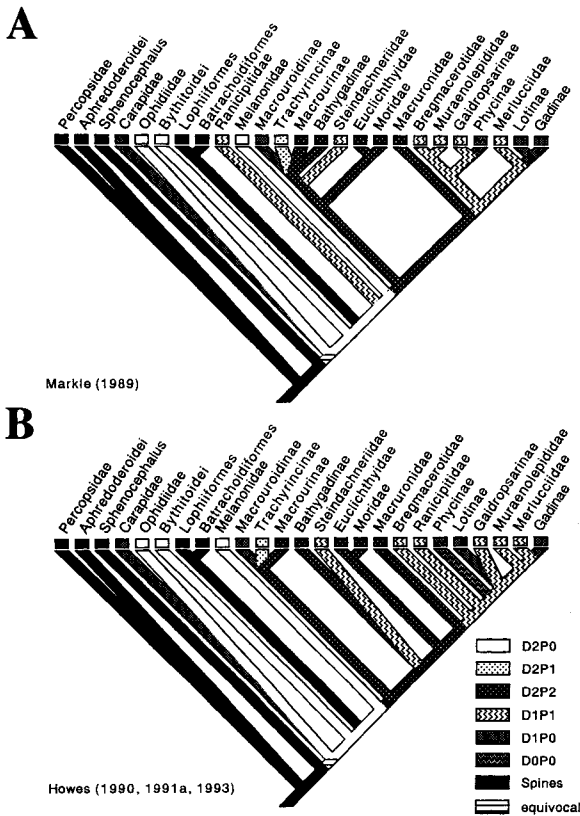


Fig. 58. Hypothesized character evolution of dorsal supernumerary fin-rays of gadiforms with other paracanthopterygians.



ferred the immediate ancestral state as D2P0, but considered the D1P0 condition of lotines and gadines to have arisen independently from D1P1 within the higher gadoids (Fig. 59B). Moreover, Howes believed that phycines and gaidropsarines were not a monophyletic group; thus D0P0 or D1P0 in phycines was also believed to have occurred independently from D1P1 (the hypothesized state D0P0 was only supported by the sister relationship of the two groups).

With respect to the reversal from pseudospine to soft-ray at the terminal clade of gadiforms, a possible neoteny may have impacted on trachyrincines and macrouroidines (see p. 137). Finally, the acquisition of pseudospines in lower gadiforms may have been related to the enlargement of the first dorsal fin, separated from the second, possibly functioning as a rudder or stabilizer that required stronger support for fin erection. For example, macrourines, having pseudospines, have an enlarged first dorsal fin distinctly separated from the second, whereas melanonids, having only soft-rays, have

Fig. 59. Character evolution of dorsal supernumerary fin-rays of gadiforms based on the cladograms of Markle (A) and Howes (B).

Table 8. Distribution and depth range of each gadiform family and subfamily from Shcherbachev and Piotrovskiy (1982), Houde (1984), Cohen et al. (1990), Gon and Heemstra, ed. (1990), Howes and Crimmen (1990), Howes (1991b) and Endo and Okamura (1992)

Taxon	Distribution	Depth (m)
Melanonoidei		
Melanonidae	Worldwide in tropical to temperate waters, except Mediterranean	100-3500
Macrouroidei		
Steindachneriidae	Central western Atlantic	200-500
Macrouridae		
Bathygadinae	Worldwide in tropical to temperate waters, except Mediterranean	100-3000
Macrourinae	Worldwide, except Arctic	100-6800
Macrouroidinae	Worldwide in tropical to temperate waters, except Mediterranean	600-5300
Trachyrincinae	North Atlantic, Mediterranean, Pacific coast of South America, and Southern Ocean	400-2500
Gadoidei		
Euclichthyidae	off New Zealand and southern Australia	250-800
Moridae	Worldwide, except Arctic	0-3000
Macruronidae (<i>Lyconus</i>)	Atlantic and Southern Ocean (a few records in Indian and central East Pacific Oceans)	30-700
Merlucciidae	Atlantic, Mediterranean, Southern Ocean	30-1200
Ranicipitidae	Eastern North Atlantic	10-100
Bregmacerotidae	Worldwide in tropical to temperate waters	0-3000 (6000)
Muraenolepididae	Southern Ocean	10-1600
Gadidae		
Gaidropsarinae	North Atlantic, mediterranean and Southern Ocean (western North Pacific ?)	0-1600
Phycinae	Atlantic and Mediterranean	0-1400
Lotinae	North Atlantic, mediterranean, and freshwaters in North America and Eurasia	0-1000
Gadinae	North Atlantic, mediterranean, Arctic, North Pacific and Southern Ocean	0-1000

a continuous dorsal fin.

2. Biogeography

Gadiform fishes are widely distributed in all oceans and fresh waters of North America and Eurasia (*Lota lota*), from deep-sea bottoms to shore waters, and in rivers and lakes (Table 8). The biogeography of gadiforms has been well discussed (e.g., gadoids in Svetovidov, 1948; *Merluccius* in Inada, 1981 and Ho, 1990; *Gadus* in Grant and Ståhl, 1988; gadiforms in Cohen et al., 1990; gadoids in Howes, 1990, 1991b; *Laemonema* in Meléndez and Markle, 1997). For the "Gadoidei", including gadids, merlucciids, ranicipitids, bregmacerotids and morids, Svetovidov (1948: 28) gave the first persuasive hypothesis for their biogeography, based on the history of geological and climatic changes, time and place of fossil records, and ecological information of recent species. Howes (1991b) later discussed in depth the biogeography of the "Gadoidei" (*sensu* Howes, 1991a) along with their hypothesized relationships, and recognized six basal patterns among them. Howes (1991b) concluded that "Processes giving rise to these patterns are considered to have operated a plesiomorphic circumglobal distribution of infragadoids

disrupted principally by the formation of the Atlantic basin in which supragadoids evolved through a series of vicariance events involving shelf modification and climatic change." Howes (1991b) also noted that "the phylogenetic trend amongst gadoids appears to have been from oceanic to shelf habitats, rather than the more generally-accepted, reverse situation". Since the compositions of lower gadiforms and higher gadoids in the present study are consistent with those of Howes (1990, 1991a), I agree in general with the dispersal hypotheses of Howes (1991b).

Including macrourid data, Howes' distributional patterns extended to gadiforms can be summarized as follows: 1) the Atlantic is common to all families, excluding Euclichthyidae and Muraenolepididae, the North Atlantic being their distribution center; 2) bipolarity centered on the Atlantic occurs in Gadidae (Gadinae, Phycinae and Gaidropsarinae), Merlucciidae, Macruronidae and Macrouridae (Macrourinae and Trachyrincinae); 3) Melanonidae, Macrouridae, Moridae, Macruronidae (*Lyconus*) and Bregmacerotidae occur in the Indian Ocean; 4) Macrouridae, Melanonidae, Moridae, Macruronidae, Bregmacerotidae, Merlucciidae and Gadidae (Gadinae and Gaidropsarinae) occur in

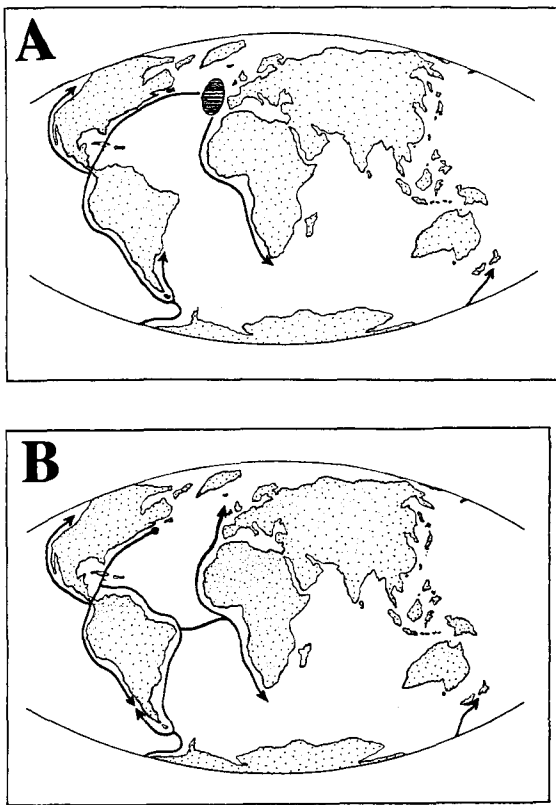


Fig. 60. Hypothesized dispersal routes of *Merluccius* species. A, Inada (1981); B, Ho (1990).

the Pacific; 5) Steindachneriidae (Caribbean), Eulichthyidae (off South Australia and New Zealand), Ranicipitidae (northern European coasts) and Muraenolepididae (Southern Ocean) are endemic; 6) circumglobal distribution through the Atlantic, Indian and Pacific Oceans is common to Melanonidae, Macrouridae (Bathygadinae, Macrourinae and Macrouroidinae), Moridae, Macruronidae and Bregmacerotidae.

2-1. Phylogenetic dispersal of Merlucciidae

For the twelve *Merluccius* species, Inada (1981) assumed phylogenetic dispersal based on their morphological differences, distributional data and geographical history (Fig. 60A). On the other hand, Ho (1990) cladistically estimated the relationships of these twelve species using the seven osteological characters presented by Inada (1981), and then discussed their phylogenetic dispersal along with data for parasitic copepods and geographical history (Fig. 60B). Although the relationships of *Merluccius* were re-analyzed from Ho's data set and the present gadiform cladogram, no informative trees were obtained. To gain a better dispersal hypothesis for *Merluccius* species, further investigations based on molecular data are necessary.

2-2. Phylogenetic dispersal of Gadidae

The Gadidae occur in the Atlantic, northern and southern Pacific, and Southern Oceans, but not off the Pacific coasts of middle America (e.g., Svetovidov, 1948; Cohen et al., 1990; Howes, 1991b). Among the family, the Gaidropsarinae (*Gaidropsarus*), Phycinae (*Urophycis*) and Gadinae (*Micromesistius*) are bipolar, although only *Gaidropsarus* has a circum-Antarctic distribution (Svetovidov, 1986: fig. 1; Howes, 1990: fig. 15; Howes, 1991b: fig. 8). In the North Pacific, gadines have apparently extended through the Bering strait (e.g., Svetovidov, 1948; Grant and Ståhl, 1988; Howes, 1991b), the geological time of the opening of the latter having been recently re-estimated by Marinovich and Gladenkov (1999) as starting at about 7.4 million years BP, with completion between 5.5-4.8 million years BP. These estimates are significantly older than previous estimations (4.1-3.1 million years ago) (Marinovich and Gladenkov, 1999).

The distribution of gaidropsarines includes two questionable records from the western North Pacific. *Gaidropsarus pacificus* (Temminck and Schlegel, 1842) (type and only known specimen purportedly from Nagasaki, Japan), had remained an enigma (Svetovidov, 1948, 1986) until Machida (1991) concluded that its description had, in fact, been based on a specimen of *Rhinonemus cimbricus* (the genus is a junior synonym of *Enchelyopus*). Furthermore, the type locality was probably incorrect (Y. Machida, per. comm.), because the monotypic *Enchelyopus* is known only from the North Atlantic and Gulf of Mexico (Cohen et al., 1990: fig. 78). In addition, the occurrence of *Ciliata* in the western North Pacific is uncertain. According to Machida (1991: 330), a species of *Ciliata* was reported from the Yellow and East China Seas by Cheng and Zheng (1987), as *Ciliata pacifica* (Temminck and Schlegel). This is a surprising record because the two nominal *Ciliata* spp. are littoral (usually above 50 m depth) species of North European coasts (Cohen et al., 1990: figs. 69, 71). If *Ciliata pacifica* is a valid species, the ancestor of *Ciliata* may have been widely distributed from the North Atlantic to the North Pacific through the Arctic Ocean, as were those of some gadines. Such a relictual distribution of *Ciliata* in the Pacific may be interpreted accordingly as having resulted from vicariance events such as glaciation during the Pliocene and Quaternary.

Concerning phycines, *Phycis* mainly occurs off the European coasts along the eastern North Atlantic Ocean and Mediterranean Sea. On the other hand, *Urophycis* occurs along the Atlantic coasts of North and South America, except for mid-South America. Thus, phycines may have dispersed from the North to the

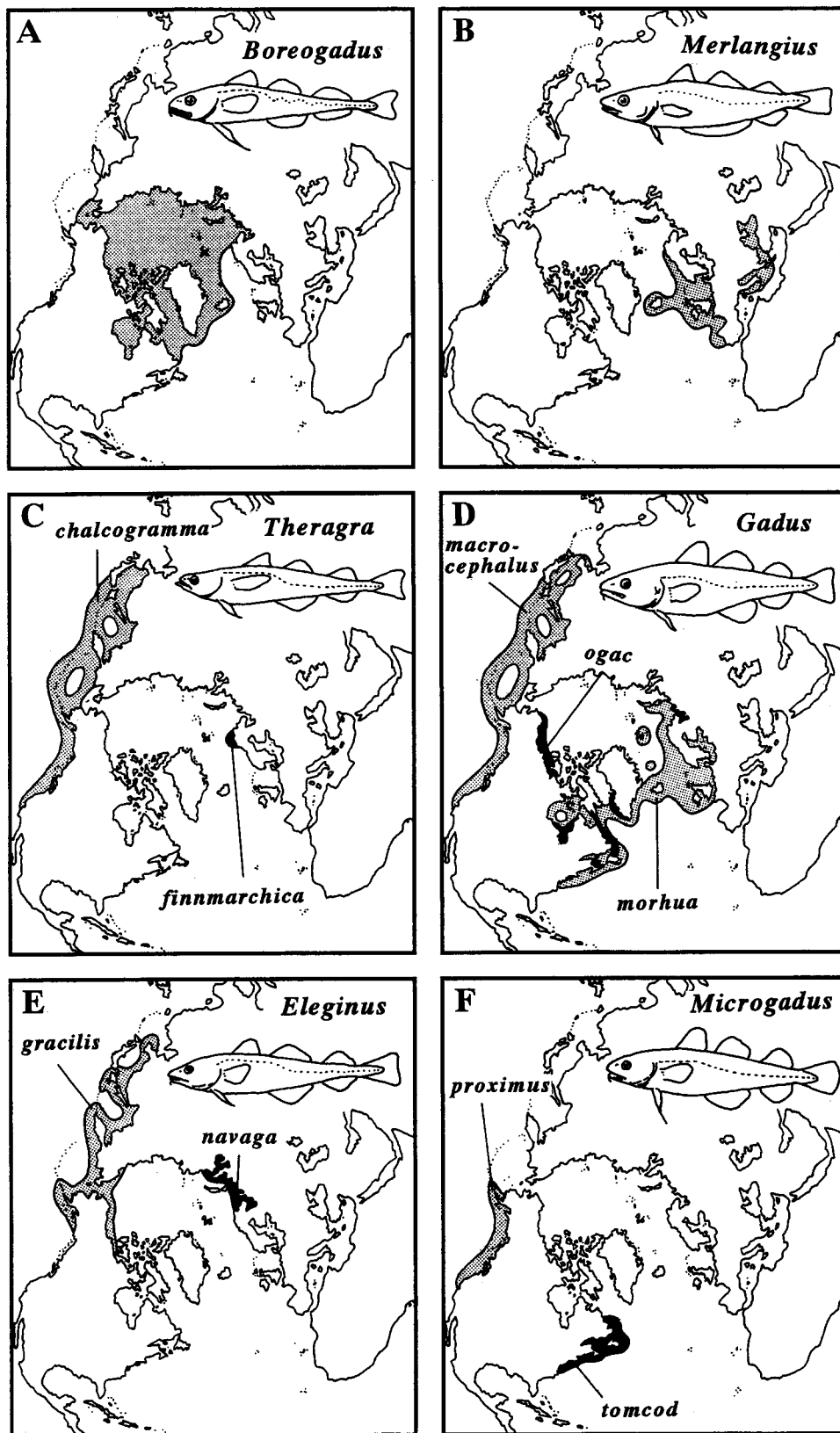


Fig. 61. Distributional ranges of six gadine genera (A-F) (data from Cohen et al., 1990)

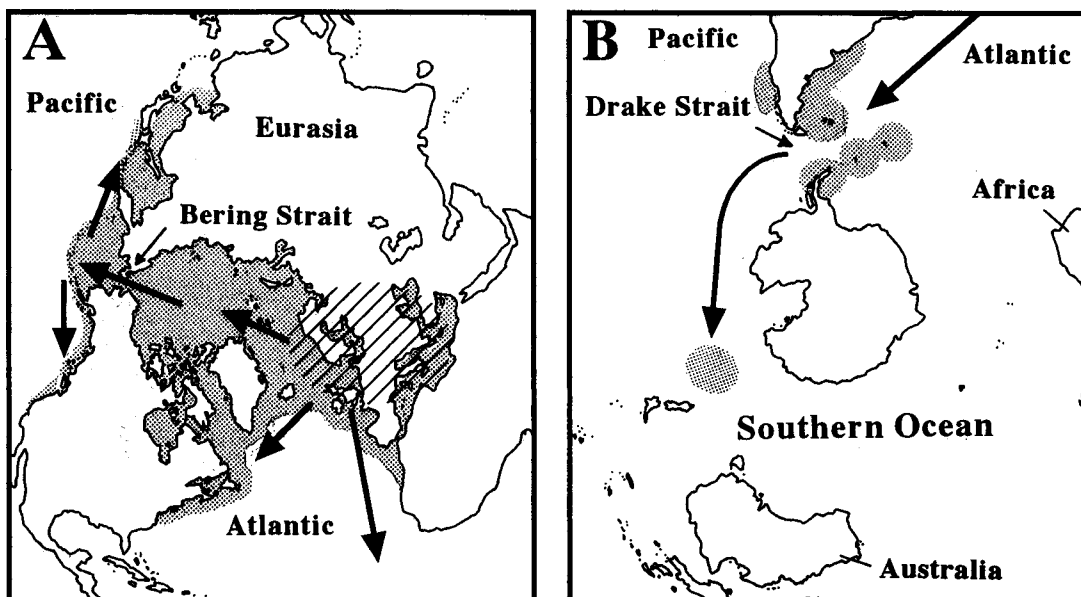


Fig. 62. Hypothesized phylogenetic dispersal of gadines (A-B).

South Atlantic.

The ancestor of the lotine, *Lota*, was suggested by Svetovidov (1948: 47) as possibly having entered fresh waters of Eurasia and North America via brackish waters along the Arctic ocean coasts, during the Pliocene and Quaternary glacial periods. Svetovidov's hypothesis appears to explain the unique circum-Arctic distribution of *Lota*, being supported by fossil records. An ancestor of lotines may have dispersed to the Arctic and North Atlantic Oceans, as did those of gadines, not only because *Lota* is the sister group of the *Brosme* and *Molva* clade in the present hypothesis, but also because Gaemers (1985) reported that a *Lota*-like otolith species (\dagger *Umbolota marina*) (Oligocene of Belgium) lived in the sea.

In conclusion, the gadid subfamilies, excluding phycines, are characterized by phylogenetic dispersal from the North Atlantic to the Arctic Ocean. Furthermore, gadines only entered into the North Pacific through the Bering Strait. The phylogenetic dispersal of gadines is discussed in detail below and compared with the hypothesis of Howes (1991b).

2-3. Phylogenetic dispersal of Gadinae

The distributions of twenty-two species of twelve gadine genera are well known and have been comprehensively mapped by Svetovidov (1948) and Cohen et al. (1990) (Fig. 61A-F). Such distributions are largely divided into the following seven regions defined by Briggs (1974) (Table 9): Arctic region (AR), Western Atlantic boreal region (WA), Eastern Atlantic boreal region (EA), Mediterranean-Atlantic region (MA), Western Pacific boreal region (WP), Eastern Pacific

boreal region (EP) and Southern cold-temperate waters (SC). Considering gadine distribution and geological history, the North Atlantic boreal region is probably related to the North Pacific region via the Arctic region, and to the south, to the Mediterranean-Atlantic region and the Southern cold-temperate region. As discussed by Svetovidov (1948), the ancestors of three gadine tribes may have originated in the North Atlantic (Arctic-North Atlantic basin in the lower Tertiary) (Fig. 62A).

Gadiculus (Gadiculini) presently occurs in the eastern North Atlantic and Mediterranean Sea, although fossil otoliths have been recorded from both the western Atlantic and New Zealand (Schwarzhan, 1980). Thus, *Gadiculus* has had a bipolar distribution in the past (Table 9).

Among them, only two gadines, *Gadiculus* (Gadiculini) and *Micromesistius* (Trisopterini), have migrated phylogenetically into the Southern Ocean (*Gadiculus* now being extinct in that region) (Fig. 62). Subsequently, the Trisopterini and Gadini dispersed separately to the Arctic Ocean, the four genera of Gadini (*Theragra*, *Gadus*, *Eleginus* and *Microgadus*), thereafter expanding into the Pacific boreal region after the Bering strait opened some 7.4 million years BP (Fig. 62A). Consequently, the ancestral distributions of these four Gadini genera in the Arctic Ocean have probably been strongly influenced by glacial periods that began some 3.0-3.5 million years BP. In the Trisopterini, although only *Boreogadus* occurs in the northern North Pacific around the Bering strait (Fig. 61A), this area belongs to the Arctic region recognized by Briggs (1974), indicating that the present distribution of *Boreogadus* differs phylogenetically from those of the Pacific Gadini.

Table 9. Distributions of twelve gadine genera. Abbreviations indicate: AR, Arctic region; WA, Western Atlantic boreal region; EA, Eastern Atlantic Boreal region; MA, Mediterranean-Atlantic region; WP, Western Pacific boreal region; MA, Mediterranean-Atlantic region; SC, Southern cold-temperate waters. Open circle indicates fossil otolith records

Taxon	AR	WA	EA	MA	WP	EP	SC
Gadiculini							
<i>Gadiculus</i>		○	●	●			○
Trisopterini							
<i>Trisopterus</i>			●	●			
<i>Micromesistius</i>	●	●	●	●			●
<i>Boreogadus</i>	●						
<i>Arctogadus</i>	●						
Gadini							
<i>Merlangius</i>			●	●			
<i>Pollachius</i>	●	●	●				
<i>Theragra</i>	●		●		●	●	
<i>Gadus</i>	●	●	●		●	●	
<i>Melanogrammus</i>	●	●	●				
<i>Eleginus</i>	●				●	●	
<i>Microgadus</i>	●	●				●	

Regarding the stratigraphical times based on fossil otoliths (Nolf and Steurbaut, 1989b: fig. 3) (Fig. 63), *Gadiculus*, *Trisopterus*, *Micromesistius* and *Merlangius* are regarded as the most primitive genera among gadines, because they have been recorded from Oligocene (former three genera) and Oligocene/Miocene boundaries (last-mention genus). On the contrary, the fossil otoliths of other Gadini genera are known from the Pliocene (*Melanogrammus*, *Microgadus*, *Theragra* and *Gadus*) or Quaternary (*Pollachius*) Periods. All of the primitive genera have a common distribution in the eastern Atlantic boreal and Mediterranean-Atlantic regions. The range extension to the Mediterranean Sea is not plesiomorphic, since it apparently occurred after the climatic crisis (Messinian crisis) in the late Miocene about 6 million years BP (van Andel, 1985). Their recent Mediterranean distributions are better considered as having resulted from the retention of a plesiomorphic trait for water-temperature preference. As mentioned by many authors (e.g., Svetovidov, 1948), gadines clearly show cold-water preference. Svetovidov (1948) suggested that this peculiarity may not have changed during the evolution of the group, which is presently believed to more likely reflect, for example, spawning seasons. Thus, primitive genera, having a slightly warmer-water preference than the others, may have successfully re-entered the Mediterranean Sea following the Messinian crisis. In addition, water temperature preference may have also influenced the southerly dispersal of *Gadiculus* and *Micromesistius*, which seems to have corresponded with climatic cooling during the glacial periods in the

Southern hemisphere.

In the North Pacific gadines, dispersal via the Bering Strait from the Arctic ocean has been inferred by some authors (e.g., Svetovidov, 1948; Grant and Ståhl, 1988; Howes, 1991b). However, Howes (1991b) proposed a different interpretation for *Microgadus*, based on the relationships of "gadids" (=gadines) (Dunn, 1989) and "gadoids" (Howes, 1990) (Fig. 49F, H): *Microgadus* is the second offshoot among the gadine genera, merlucciids being the sister group of gadines. Within gadines and merlucciids, the second offshoot is *Microgadus* and the eastern Atlantic merlucciid species, respectively. Howes (1991b) therefore concluded that the Atlantic ancestors of *Microgadus*, plus those of merlucciids, had penetrated the eastern North Pacific through the Panamanian Seaway before it closed about three million years BP (van Andel, 1985). As also discussed by Howes (1991b), if the ancestor of *Microgadus* had entered the Pacific via the Panamanian Seaway, recent species would be distributed along the Pacific coasts of North and South America, as in merlucciids (Fig. 60). In addition, the southern limits of *Microgadus* are similar to those of *Gadus* along the North American coasts, *Pollachius* and *Melanogrammus* in the western North Atlantic, and *Theragra* in the eastern North Pacific (Figs. 61, 62A). This suggests that the *Microgadus* ancestor also had cold-water preference in common with an ancestor of the Gadini. This hypothesis, therefore, contradicts Howes' scenario for *Microgadus*.

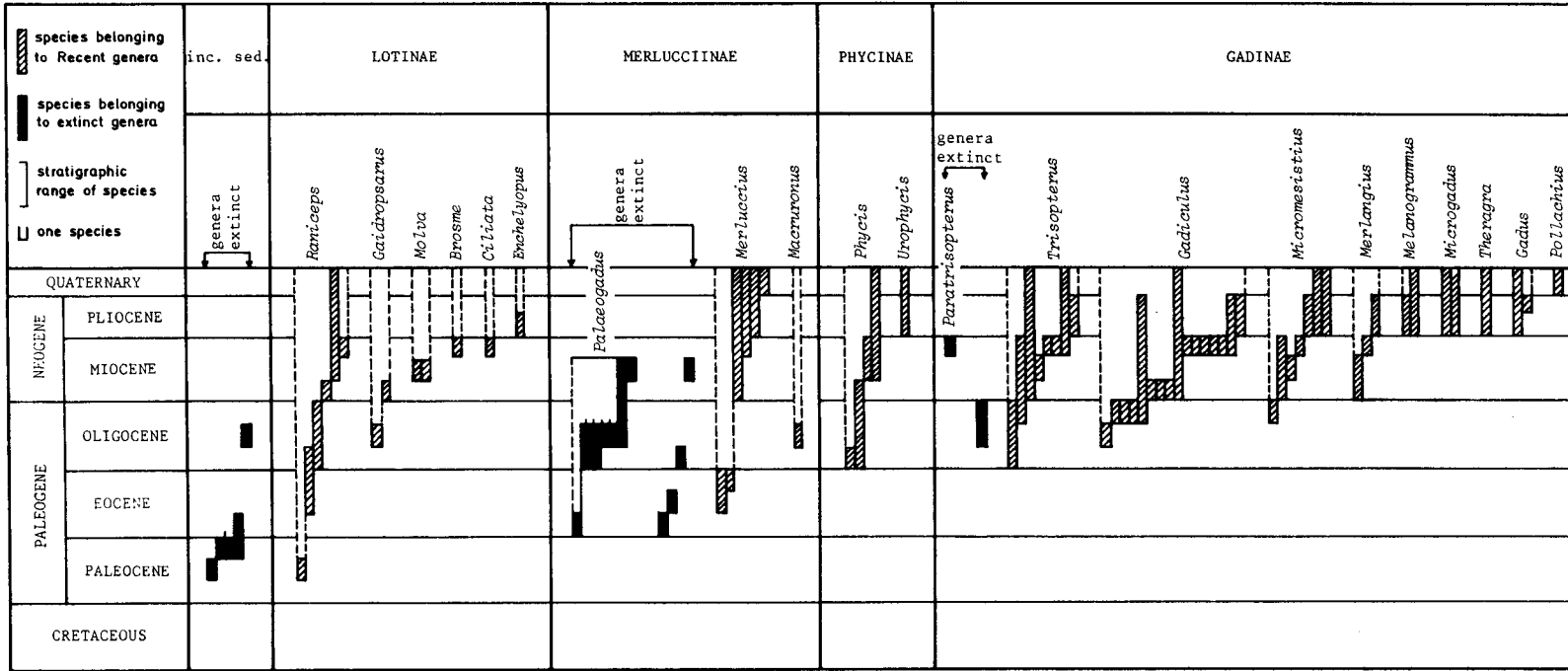


Fig. 63. Stratigraphic ranges of fossil gadoids based on otoliths (from Nolf and Steurbaut, 1989b).

3. Phylogenetic position of extinct gadoids

Gadiform fossils, mostly otoliths, are well known from Europe and New Zealand, such fossils being particularly abundant in the Oligocene and Miocene deposits of the North Sea basin and Tethys Sea (e.g., Svetovidov, 1948; Fedotov, 1976; Nolf and Steurbaut, 1989b). Nolf and Steurbaut (1989b: figs. 3–5) reviewed previous records of otolith-based fossils and gave the stratigraphic ranges of known extinct and recent gadiform genera. Concerning non-otolith based gadoid fossils, Fedotov and Bannikov (1989: fig. 9) also reviewed and proposed a phylogenetic tree of 21 fossil species (including the present Gadidae, Ranicipitidae and Merlucciidae).

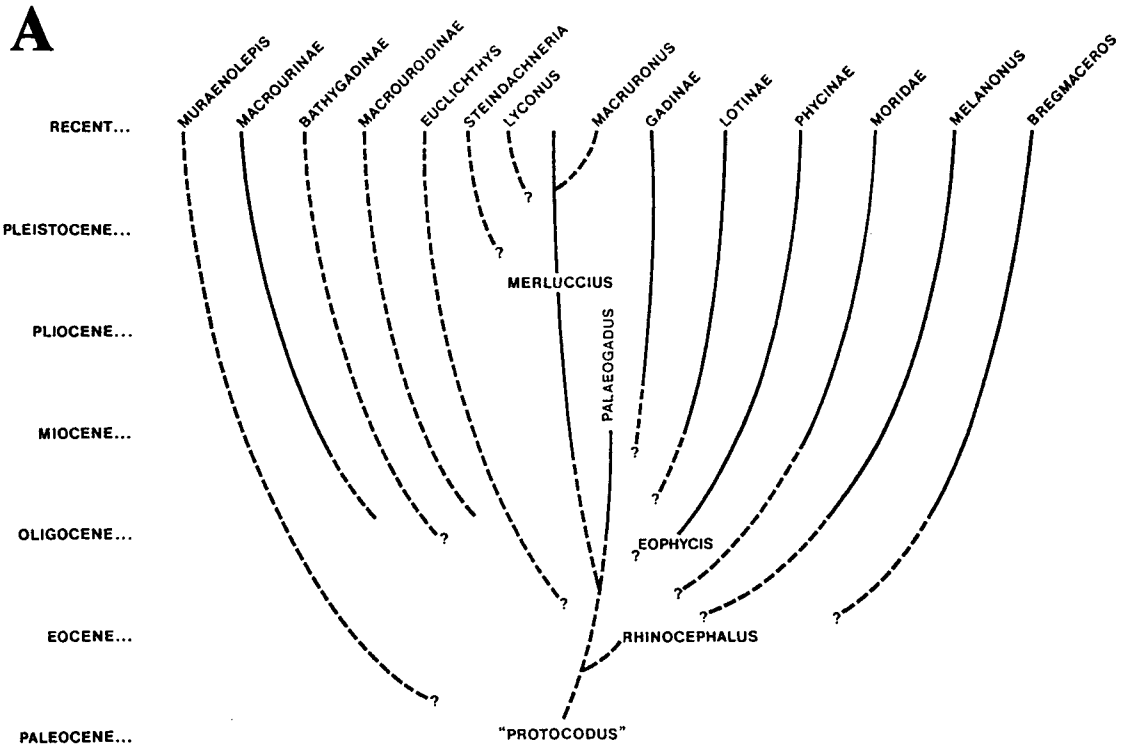
Among the non-otolith fossils, †*Rhinocephalus* and †*Palaeogadus*, being regarded as the ancestral members of merlucciines or merlucciids, are particularly important genera for inferring the phylogeny of higher gadoids, such having been discussed mainly by Rosen and Patterson (1969), Fedotov (1976), Cohen (1984), and Fedotov and Bannikov (1989). Cohen (1984) and Fedotov and Bannikov (1989) indicated the “†*Protocodus*” → †*Rhinocephalus* → †*Palaeogadus* → *Merluccius* lineage as the main stem in the phylogenetic trees of gadiforms or gadoids, respectively (Fig. 64A, B). Among these extinct genera, some cranial and suspensorial characters of †*Rhinocephalus* shown in Rosen and Patterson (1969) figures, enabled some inference of the phylogenetic position of that genus within gadoids. In addition, otolith and a few cranial characters are known for some species of †*Palaeogadus* (e.g., Fedotov, 1976; Nolf and Steurbaut, 1989c).

3-1. Genus †*Rhinocephalus*

Rosen and Patterson (1969: figs. 50–52) described in detail the fossil species †*Rhinocephalus planiceps* Casier, 1966 (Lower Eocene: London Clay), based on some additional specimens that had almost complete cranial and (5) anteriormost vertebral features (Fig. 65). They showed †*Rhinocephalus* to have many characters in common with gadines, merlucciids, morids and macrourids, particularly resembling *Merluccius*. Furthermore, most subsequent workers have included this species in merlucciids or merlucciines among gadids owing to the cranial similarities (e.g., Fedotov, 1976; Cohen, 1984; Fedotov and Bannikov, 1989). Some remarkable characters of †*Rhinocephalus* are as follows: 1) *Cone-shaped lateral ethmoid*.—A similar condition exists in some gadines, lotines, merlucciids and macruronids, the greatest resemblance being with *Macruronus* (Fig. 66B); 2) *V-shaped frontal ridge*.—This condition is similar to those in macruronids, merlucciids and

†*Palaeogadus* (Fig. 66A, B, D). A somewhat different condition (Y-shaped frontal ridge) exists in euclichthyids and some macrourids (Okamura, 1989: 133); 3) *Enclosed supraorbital and supratemporal sensory canals*.—The bony covering of these canals is variously developed among gadiforms, but is absent in merlucciids and †*Palaeogadus* (Fig. 66A, D); 4) *Sphenotic broadly exposed on cranial dorsal surface*.—This condition is similar to those found in melanonids, some morids, merlucciids, †*Palaeogadus* and some phycines (unknown in *Lyconus*) (Fig. 66A, C, D); 5) *Supraoccipital crest separated from first neural spine*.—This primitive state exists in most gadiforms, but is partly fused or firmly attached in merlucciids and macruronids (Inada, 1981: fig. 41A); 6) *Presence of large trigemino-facialis foramen*.—This foramen is present in four gadid genera, merlucciids, steindachneriids and some morids (Svetovidov, 1948: fig. 4, tables 19–20; Inada, 1989: fig. 1); 7) *Endopterygoid in broad contact with metapterygoid*.—Separation of these two bones is one of the synapomorphies of the higher gadoid clade, excluding macruronids (TS 5-1 in Fig. 28); 8) *Developed lateral shelf of hyomandibular*.—This condition is variously developed among gadiforms, but is somewhat similar to those found in lotines and morids (Figs. 13, 14); 9) *Preopercular process of hyomandibular undeveloped*.—Such a process is weakly developed or absent in some gadids, muraenolepidids, bregmacerotids, euclichthyids and some macrourids, but is well developed in merlucciids (Figs. 13, 14); 10) *Narrow hyomandibular-preopercle interosseous space (upper window)*.—This space is very narrowly opened or closed in melanonids, macrourids, euclichthyids, macruronids, bregmacerotids, lotines and gadines (Figs. 4A, 13, 14); 11) *Closed symplectic-preopercle interosseous space (lower window)*.—This is very narrowly opened or closed in macrourines, trachyrincines, macrouroidines, steindachneriids, euclichthyids, ranicipitids, bregmacerotids, gaidropsarines and phycines (Figs. 13, 14).

Of the above characters, 7) is the most important, owing to the separation of the endopterygoid and metapterygoid being one of the synapomorphies for the higher gadoid clade (excluding macruronids) in the present cladogram. Thus, †*Rhinocephalus* should be placed below the merlucciid branching node on this basis. Although many characters of †*Rhinocephalus* mentioned by Rosen and Patterson (1969: 430) suggested a close relationship with *Merluccius*: e.g., features of the nasal, jaws, infraorbitals, opercular bones and ribs, and vertical fin formation and structure, all of the above characters seem to represent plesiomorphic states. However, the dorsal outlines of the lateral ethmoid, narrower frontals, cranial sensory canals enclosed by



B

		Gadinae	Merluccinae	Lotinae
Miocene	Upper	<i>Parateisopterus</i>		
	Middle	<i>Palaeogadus atropatani</i>		<i>Palaeomolva tazchanica</i>
	Lower		<i>Merluccius ezeani</i>	<i>Pseudozaniceps pascus</i> <i>Palaeomolva monstrata</i>
Oligocene	Upper	<i>Palaeogadus abbreviatus</i>	<i>Merluccius lednevi</i>	<i>Pseudozaniceps sogus</i>
	Middle	<i>Palaeogadus interzezinus</i>	<i>Merluccius ovalis</i> <i>Merluccius inferus</i>	<i>Palaeogadus albanicus</i>
	Lower	<i>Palaeogadus germanus</i> <i>Palaeogadus zozus</i> <i>Palaeogadus ceassus</i>	<i>Palaeogadus simonessui</i>	<i>Palaeogadus latebratus</i> <i>Palaeogadus eximus</i>
Eocene	Upper			
	Lower		<i>Palaeogadus duberzetti</i> <i>Rhinocephalus planiceps</i>	
Palaeocene			"Protocodus"	
Upper Cretaceous		<i>Sphenocephalus</i>		

Fig. 64. Phyletic trees of gadiforms in Cohen (1984) (A) and of fossil gadoids in Fedotov and Bannikov (1989) (B).

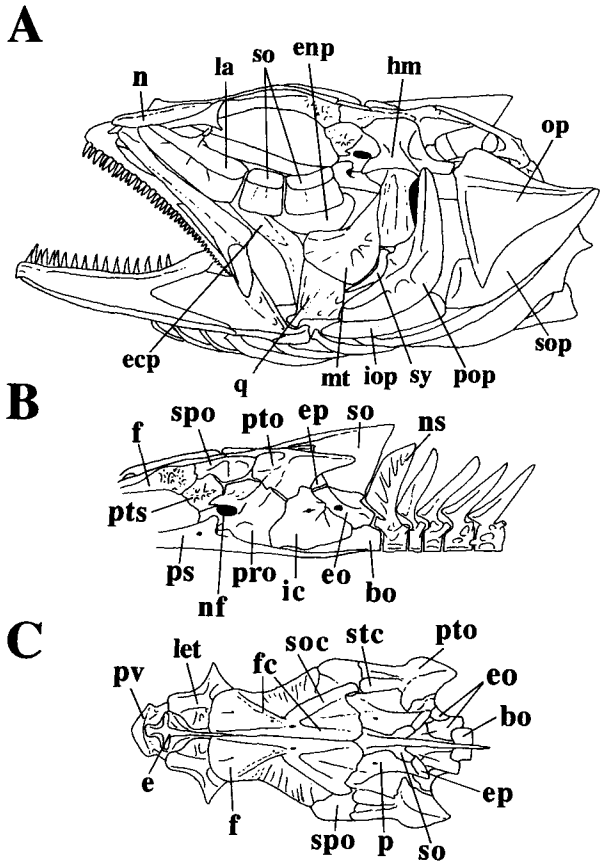


Fig. 65. Head of fossil *Rhinocephalus planiceps* (from Rosen and Patterson, 1969). A, lateral view of head; B, lateral view of posterior cranium and anterior five vertebrae; C, dorsal view of cranium.

bone, and ethmoid region of †*Rhinocephalus* are more similar to those of *Macruronus* rather than *Merluccius* (Fig. 66). Notwithstanding, the lateral features of the hyomandibular and the interosseous spaces between the suspensorium and opercular apparatus in †*Rhinocephalus* are different from those of both *Merluccius* and *Macruronus*. Considering these characters, †*Rhinocephalus planiceps* is tentatively regarded as an offshoot from the internode between the macruronid and merlucciid branches in the relationships proposed here (Fig. 67).

3-2. Genus †*Palaeogadus*

Fedotov and Bannikov (1989: figs. 1, 3) indicated that †*Palaeogadus* differed from *Merluccius* in lacking well developed parapophyses with pointed tips and ribs (vs. well developed with round tips and no ribs in *Merluccius*). Furthermore, they noted †*Palaeogadus* to be characterized by the parapophyses being expanded anteriorly so as to overlap with each other. However, Fedotov and Bannikov assumed a close relationship between these two genera based on many similarities

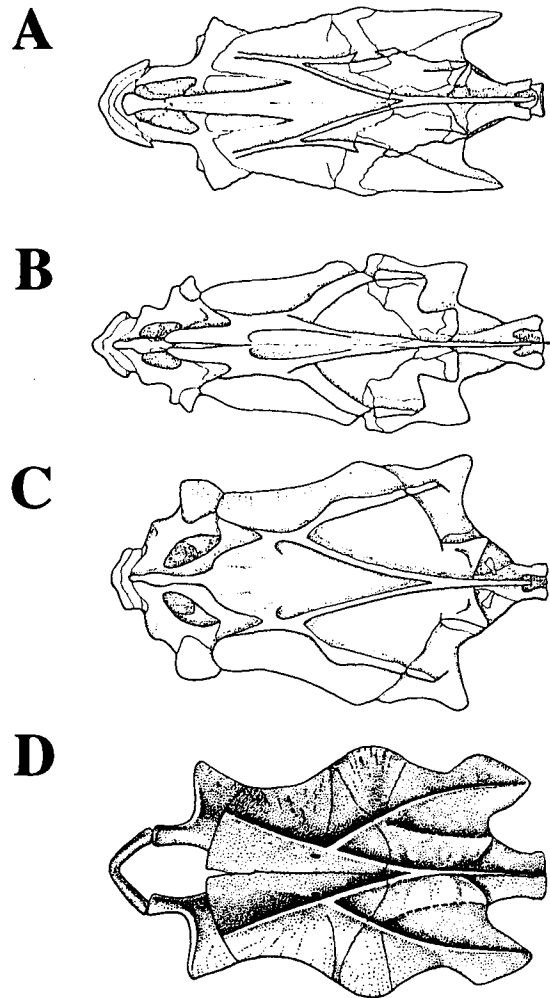


Fig. 66. Dorsal view of cranium. A, *Merluccius merluccius*; B, *Macruronus magellanicus*; C, *Lyconus* sp.; D, fossil *Palaeogadus intergerinus*. A-C from Inada (1989) and D from Fedotov (1976).

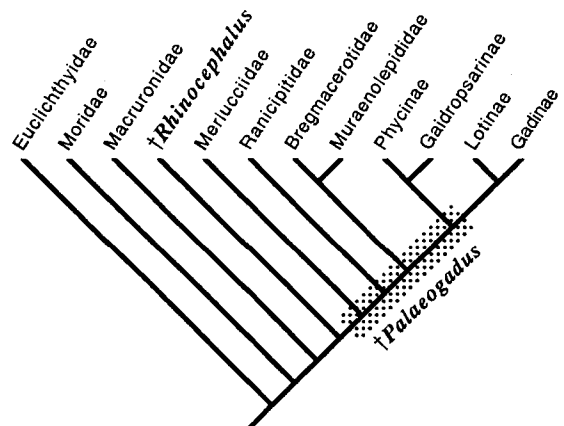


Fig. 67. Possible phylogenetic position of the extinct genera *Rhinocephalus* and *Palaeogadus* on the hypothesized relationships of gadoid taxa.

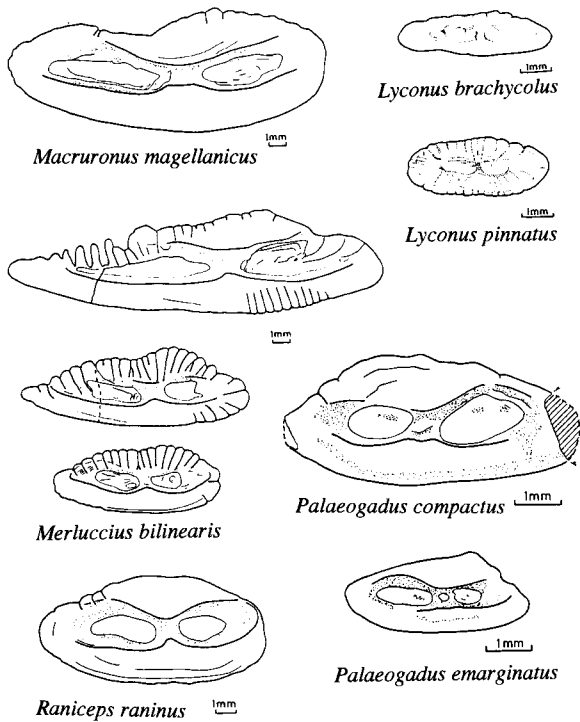


Fig. 68. Seven otoliths of fossil and recent gadoids (from Nolf and Steurbaut, 1989c).

with respect to cranial structure, fin formation and caudal skeleton. Among these, the wide dorsal cranial surface in †*Palaeogadus* was somewhat similar to that of *Lyconus* (known only from juvenile specimens) (Fig. 66C), subsequently regarded by Howes (1991a) as belonging to *Macruronus*. On the other hand, the Y-shaped crest in †*Palaeogadus* apparently resembles that of *Merluccius* (Fig. 66A, D).

Nolf and Steurbaut (1989c : 98) mentioned that the otolith of †*Palaeogadus* was more plesiomorphic than that of *Merluccius*, having a greater resemblance to that of *Raniceps* (Fig. 68). Moreover, Nolf and Steurbaut also noted that recent species of *Raniceps* had generalized "gadid" otolith features (the present higher gadoids excluding bregmacerotids and muraenolepidids, but including steindachneriids). Additionally, *Raniceps* shares a similar sulcus outline with *Merluccius*, but differs from the latter in having a more constricted ostium-cauda transition and no strongly lobed rims (Fig. 68). These otolith data suggest a close relationship of these three genera, and support the present relationship proposed for *Merluccius* and *Raniceps*. Fedotov and Bannikov (1989 : fig. 9) considered that †*Palaeogadus* arose from the ancestral genus †*Rhinocephalus*, and that the gadid subfamilies, gadines, merlucciines and lotines originated from some †*Palaeogadus* species. Comparing the otolith data with Fedotov and Bannikov's hypothesis, I presently believe that †*Palaeogadus* species

arose from the higher gadoids clade above the branching node of †*Rhinocephalus* (Fig. 67).

3-3. Geological times of gadoid fossils

Concerning the geological ranges of the recent gadoid genera, the otolith evidence of Nolf and Steurbaut (1989b : figs. 3-5) and that of other fossils (Fedotov and Bannikov, 1989) are apparently inconsistent, the otolith data being consistently older than non-otolith data (Figs. 63, 64B). For example, otolith-based species of *Merluccius* and *Raniceps* are first known from the middle Eocene and middle Paleocene, respectively. However, non-otolith-based fossils of *Merluccius* and †*Palaeogadus* are first known from the middle Oligocene and middle Eocene, respectively. These inconsistencies may have resulted, at least in part, from quantitative differences of each fossil type, otoliths being more likely to persist as fossils compared with other skeletal remains. However, the identification of otolith-based species is also problematic : e.g., Nolf and Steurbaut (1989b : 55) were critical of the "extreme" splitting of gadid fossil otoliths by Gaemers (1976) and some following his papers. If the otolith-based species of

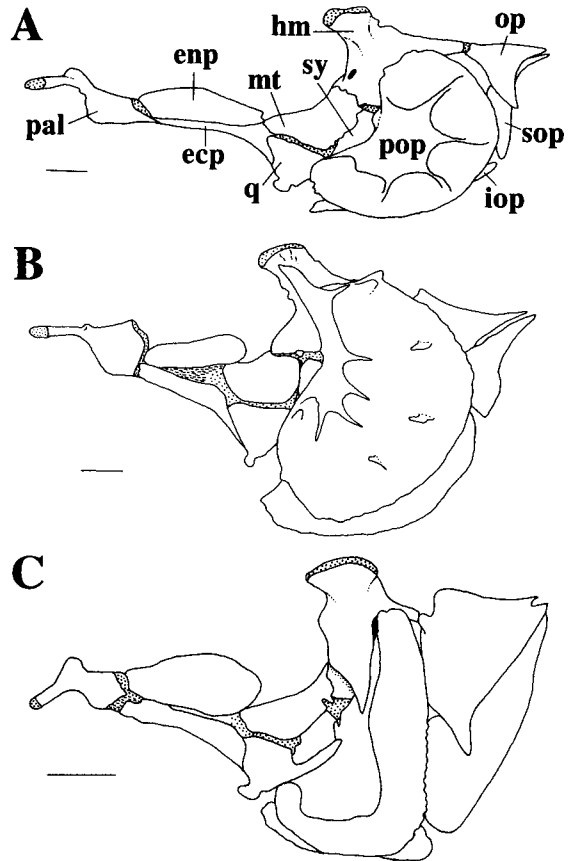


Fig. 69. Lateral view of suspensorium and opercular bones. A, *Trachyrincus murrayi* ; B, *Squalogadus modificatus* ; C, *Nezumia proxima*. Bars = 5 mm

Raniceps from Paleocene deposit truly belong to that genus, the lower gadiforms and some higher gadoids such as macruronids, merlucciids and Ranicipitidae must also have originated in the early Paleocene at least. However, if some Paleocene and Eocene ancestors of higher gadoids have been misidentified as species of *Raniceps* and *Merluccius*, the recent higher gadoid genera must have arisen in the Oligocene or even later. Because it is impossible to infer the geological times in which the recent gadiform genera originated, a phylogenetic tree of gadiform taxa based on fossil records is not attempted here.

4. Heterochronic evolution

Heterochrony has been regarded as an important mechanism of evolution, resulting in various morphological and life history novelties (e.g., Gould, 1977, 1988; Alberch et al., 1979; Mckinney and McNamara, 1991). Its actual detection necessitates a comparison of the ontogenetic series of the taxon in question with those of relatives using a hypothesized cladgram (Fink, 1982, 1988). In many teleost fishes, heterochrony and possible evidence for such have often been reported (e.g., Bertelsen, 1951, 1984; Cohen, 1960; Nielsen, 1969; Marshall, 1979, 1984; Balon, 1980; Roberts, 1984;

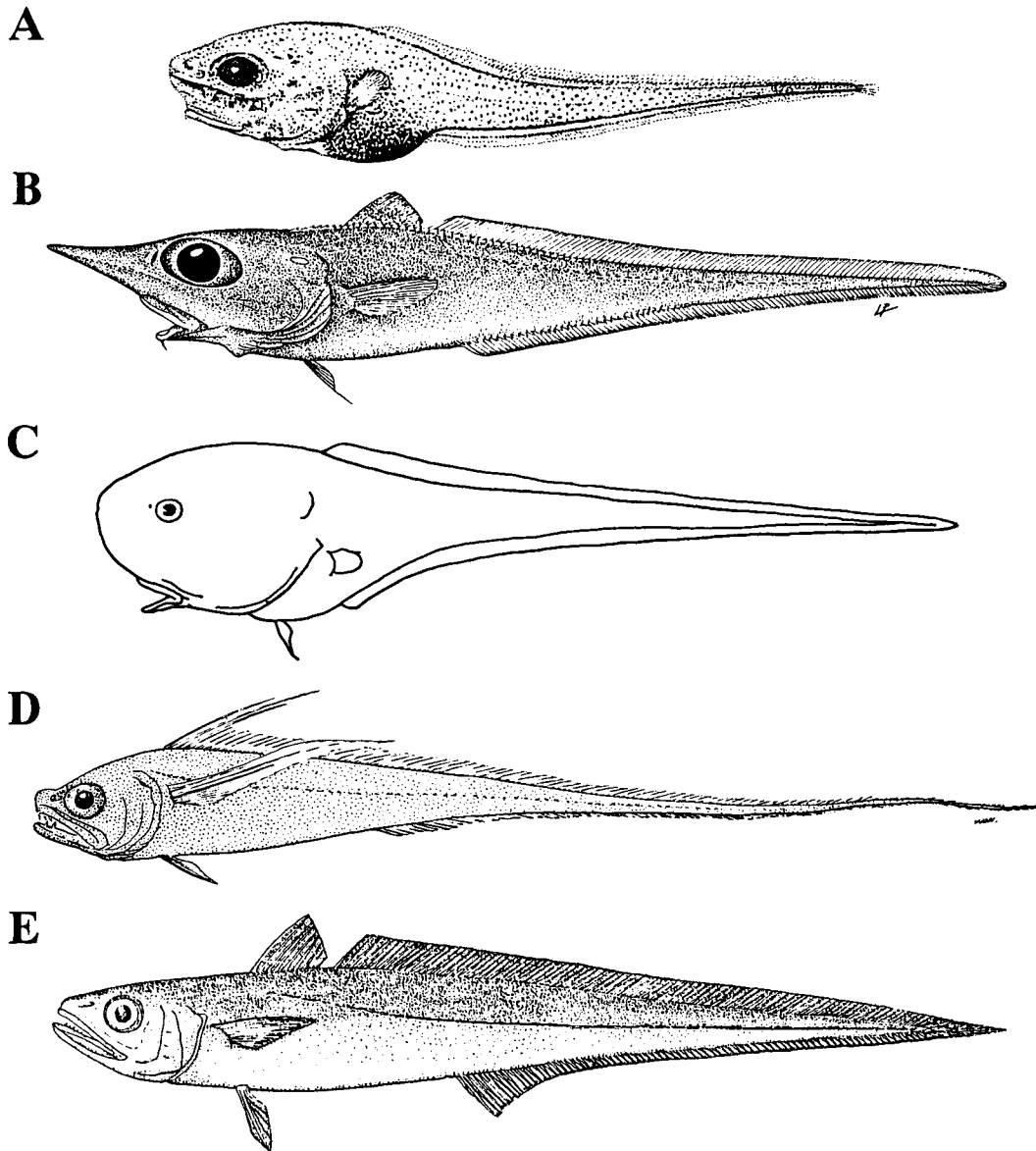


Fig. 70. Lateral view of five gadiforms. A, *Trachyrincus* sp., juvenile, 56 mm TL (from Johnsen, 1927); B, *Trachyrincus scabrus*, adult (from Cohen et al., 1990); C, *Squalogadus modificatus*, adult (from Cohen et al., 1990); D, *Macruronus pinnatus* (previously known as *Lyconus*), 125 mm TL (from Günther, 1887); E, *Macruronus magellanicus*, adult (from Cohen et al., 1990).

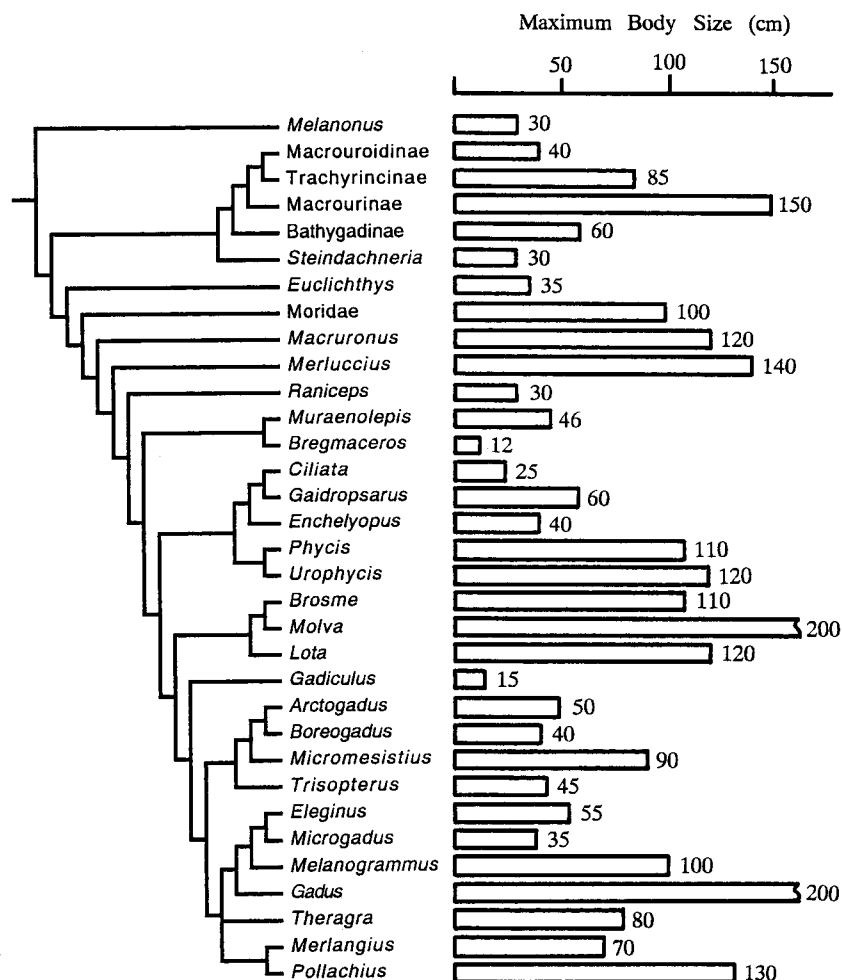


Fig. 71. Hypothesized relationships and maximum body size of gadiform taxa (data from Cohen et al., 1990).

Miya and Nemoto, 1986, 1991; Meyer, 1987; Weitzman and Vari, 1988; Winterbottom, 1990; Strauss, 1990, 1992; Begle, 1991; Boughton et al., 1991; Mabee, 1993; Johnson and Brothers, 1993; Miya and Nishida, 1996; Endo and Shinohara, 1999). As do many deep-sea fishes, some gadiforms apparently have peculiar morphologies (such as larva-like form) and characters regarded as representing a previous (ancestral) state. However, there has been insufficient discussion of such matters, excluding a dwarf morid *Guttigadus nana* (Meléndez and Markle, 1997: 660). Possible pedomorphoses of the *Trachyrincus* and *Squalogadus* clade and the *Bregmaceros* and *Muraenolepis* clade on the present cladograms were noted here, the clades being characterized by a number of reversals and reductive morphologies (Figs. 28, 46).

4-1. Pedomorphoses in Macrouridae

The trachyrincine and macrouroidine subfamilies share the following common plesiomorphic and reductive characters, including synapomorphies on the present cladogram: 1) two branchiostegal rays on epi-

hyal (Fig. 16B); 2) parasphenoid having no anterodorsal enlargement (Okamura, 1989: fig. 2); 3) small sized opercle and subopercle (Fig. 69A, B); 4) loss of precranial cavity housing olfactory nerves or tract (Okamura, 1989: 135); 5) loss of Y-shaped crest on cranium (Okamura, 1989: fig. 2); 6) loss of lateral shelf of hyomandibular (Fig. 69A, B); 7) reductive dorsal, anal and pelvic fins (Cohen et al., 1990: figs. 696–699); 8) secondary reduction of pseudospines of dorsal supernumerary fin-rays (D2P1 and D1P0) (Fig. 55B); 9) pelvic girdle with posteromedial extension of median process as in melanonids and gadoids. Furthermore, macrouroidines show more reduced morphologies than trachyrincines: 1) pelvic fin-rays rudimentary or lost (in *Macrouroides*); 2) undeveloped snout (Fig. 70C); 3) loss of epipleural bones; 4) loss of basibranchial 2 (Okamura, 1970b: fig. 42E); 5) loss of chin barbel (Fig. 70C); 6) ctenoid scale having no spinule rows (Okamura, 1970b: fig. 3A).

Johnsen (1927: 229) reported that juvenile to young specimens of *Trachyrincus* had a continuous dorsal fin that started to separate at about 200 mm TL (a wider gap

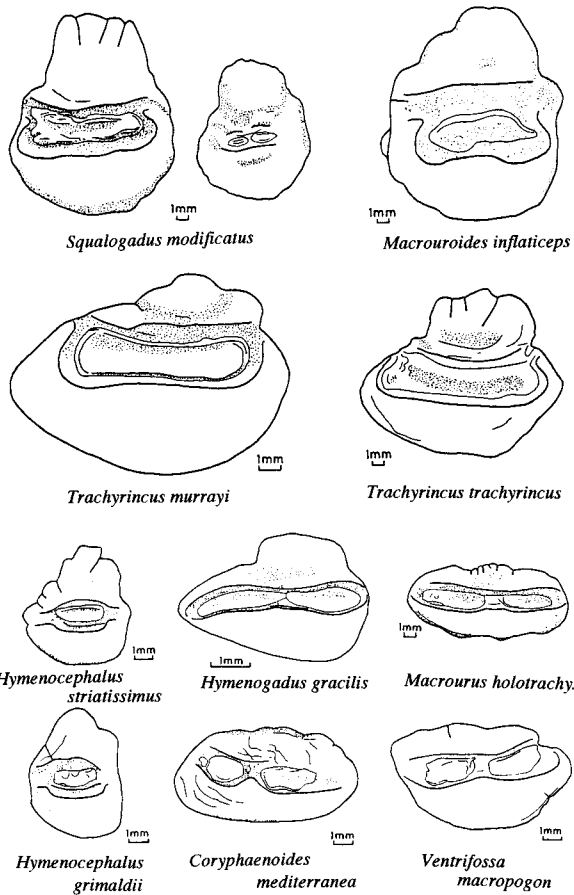


Fig. 72. Otoliths of ten macrourids (from Nolf and Steurbaut, 1989c).

in larger specimens) (Fig. 70A, B). In the macrouroidines *Squalogadus* and *Macrouroides*, early life history information is lacking. However, adults of both have an undeveloped single dorsal fin (Fig. 70C). On the contrary, two dorsal fins are separately developed in macrourines (Merrett, 1989) and *Steindachneria* (Fahay, 1989). Concerning the early life stages of macrourines, Merrett (1989: 182) termed the pre-juvenile stage as "alevin" because of the truncation of a true "larval" stage. The lack of a continuous dorsal fin during early ontogeny in these two taxa most likely resulted from this truncation.

In the other suborders, *Melanonus* has a continuous dorsal fin throughout its life history (e.g., Matarese et al., 1989: 185, fig. A, B; Chiu and Markle, 1990: 188, fig. 1; Howes, 1993). Some morids are known to have a single dorsal fin during early life stages (e.g., Fahay and Markle, 1984: figs. 138, 139), becoming separated in adults. There is no early life history information for *Euclichthys*. In macruronids, *Lyconus* (known only from juvenile specimens) has a continuous dorsal fin, whereas both larval and adult specimens of *Macruronus* have two separated dorsal fins (Bruce, 1988: fig. 1H, I;

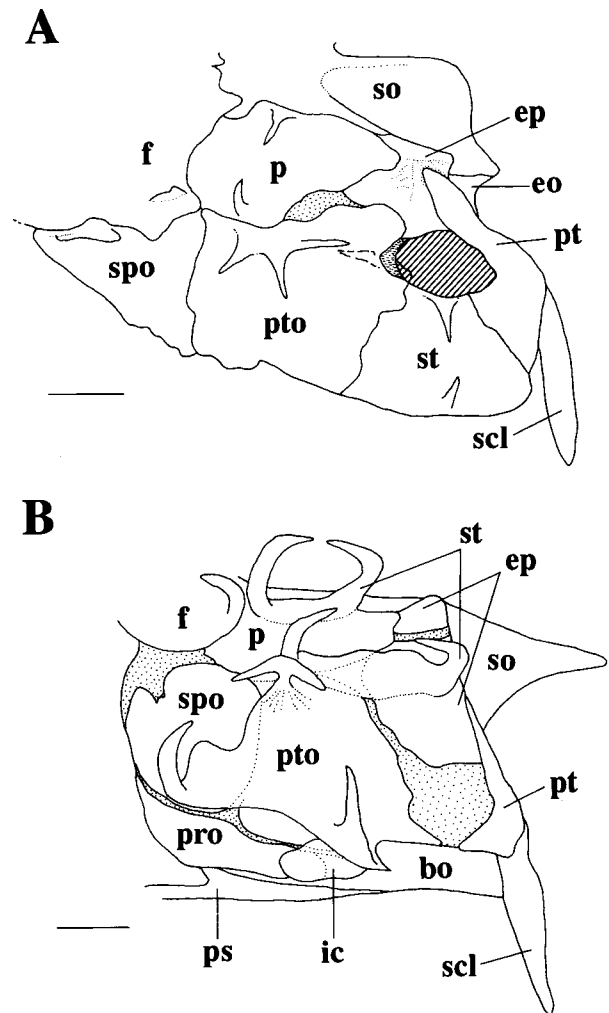


Fig. 73. Dorsolateral (A) and lateral (B) views of posterior part of cranium. A, *Trachyrincus murrayi*; B, *Squalogadus modificatus*. Bars = 5mm.

Cohen et al., 1990) (Fig. 70D, E). In the other higher gadoids, the dorsal fins are separately developed (e.g., Fahay, 1983; Matarese et al., 1989). These facts suggest that the dorsal fin of gadiforms separates ontogenetically. Thus, the ontogeny of the dorsal fins of macrouroidines and trachyrincines may be retarded.

According to Cohen et al. (1990), macrouroidines and trachyrincines reach about 40 cm TL and more than 55 cm TL, respectively. Although age at maturity in these two groups are uncertain, their adult sizes are almost equal to or a little larger than in other lower gadiforms (Fig. 71). Thus, the ancestral and reductive characters of the two taxa noted above seem to have resulted from retardation by neoteny. Furthermore, neoteny may be a significant feature of macrouroidines, *Squalogadus* also having some typical features of pedomorphic deep-sea fishes mentioned by Marshall (1984), such as small eye, undeveloped body muscles and narrow subdermal spaces filled with gelatinous tissue. As for the

question of the immediate significance of neotenic evolution in trachyrincines and macrouroidines, their successful development of a cephalic sensory system adapted to a deep-sea environment should be considered. The following characters associated with the latter and shared by these groups are well represented: large, high otoliths with fused ostial and caudal collicula, and an expanded preopercular roof protecting each neuromast (Figs. 69, 72). In addition, each group has the following specialized autapomorphies: a prominent fossa in the posttemporal region in trachyrincines (Figs. 70B, 73A); expanded infraorbital bones, enlarged processes on the dorsal face of the cranium protecting large neuromasts, and extremely large otoliths in macrouroidines (Figs. 72, 73B; Okamura, 1970b: figs. 23F, 33).

In the macrourine species *Ventrifossa ctenomelas*, Nolf (1985: 10) indicated ontogenetic changes in the otolith from rather high and rounded to very elongated (interspace of crista superior and upper rim changes from wide to narrow). Additionally, Nolf (1985) noted "the adult otoliths of this species may be considered as quite typical, but the juvenile one (fig. 8D₃) reflect the plesiomorphic condition of otoliths in macrourine fishes". Considering the trend in macrourines, more deeply-bodied otoliths in trachyrincines and macrouroidines are regarded as a plesiomorphic or larval state (Fig. 72). In macrourines, the otoliths of some *Hymenocephalus* species are most similar to those of macrouroidines and *Trachyrincus* (Fig. 72). The former species are small in size (about 20–25 cm TL) and possess some progenetic features (e.g., simple alimentary canal and transparent tail in *Hymenocephalus striatissimus*). Concerning the otoliths of trachyrincines and macrouroidines, it would be better to interpret such features in *Hymenocephalus* as a result of neoteny rather than as retention of ancestral forms.

In *Trachyrincus*, the remarkable fossa just before the posttemporal is directly connected with the suprateroporal sensory canal and inner ear, the cranium thereby opening broadly on the posterolateral corner surrounding the epiotic, pterotic, intercalar, exoccipital, suprateroporal and posttemporal (Fig. 73A). On the other hand, in *Squalogadus*, the same cranial region is covered widely by thin cartilage rather than bone (Fig. 73B; Okamura, 1970b: fig. 34K). Consequently, I regard these two conditions to be homologous, *Trachyrincus* exhibiting the more derived state. Furthermore, these regions may have a similar function related to external sound transmission into the inner ear. This morphological evidence suggests, therefore, that macrouroidines and trachyrincines have attained a more developed cephalic sensory system adapted to their deep-sea environment by neotenic evolution.

4-2. Progenesis in Bregmacerotidae

In the relationships proposed for higher gadoids, the morphological and biological information (Figs. 46, 71, Tables 10, 11) apparently indicate that *Bregmaceros* and *Muraenolepis* have been subject to progenesis and neoteny, respectively. On the cladogram, the clade including the two genera is characterized by one reversal and three reductive synapomorphies: 1) single palatovomerine ligament; 2) no anterior extension of adductor mandibular Aw; 3) absence of endopterygoid; 4) absence of epipleurals.

Among the twenty-four autapomorphies noted previously, *Bregmaceros* had one reversal and eight reductive characters (Swidnicki, 1991; pers. obs.): 1) absence of the dorsal maxillo-premaxillary ligament; 2) loss of tooth plate on epibranchial 3; 3) loss of tube-like exoccipital facets; 4) lack of supraoccipital crest; 5) unaccreted neural arches of two anterior vertebrae; 6) loose connection between the separate halves of the neural spine of the first vertebra and supraoccipital crest; 7) loss of pharyngobranchial 2; 8) loss of the first strut of pharyngobranchial 3 with the subdivided lateral strut; 9) loss of Baudelot's ligament. Additionally, the simple alimentary canal in *Bregmaceros* (D'Ancona and Cavinato, 1965: figs. 19, 20) clearly shows a progenetic trait, such as in *Cyclothone* (Marshall, 1984: fig. 2). Furthermore, the genus has such ancestral conditions as a dermal-basibranchial tooth plate (Rosen and

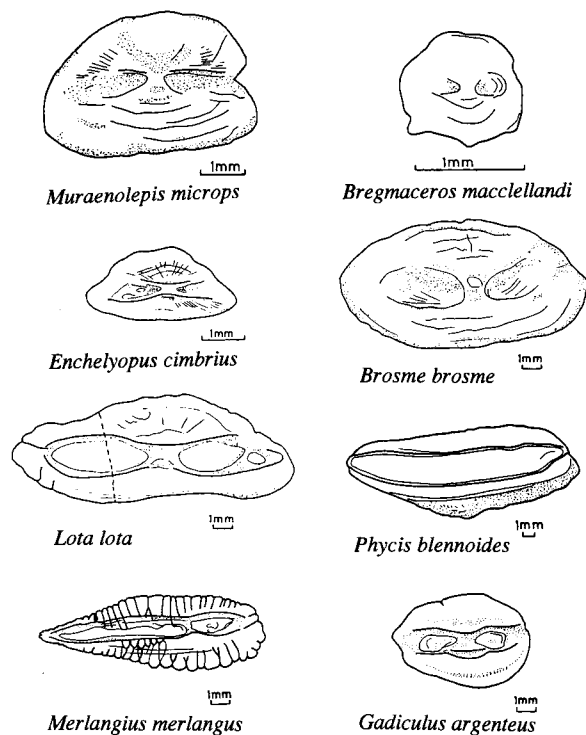


Fig. 74. Otoliths of eight gadoids (from Nolf and Steurbaut, 1989c).

Patterson, 1969 : fig. 49B) and deep-bodied otolith (Fig. 74).

Bregmaceros is the most dwarfed and precocious genus among gadiforms, individuals usually attaining only about 30–100 mm TL (except for *B. maccllellandi* which rarely exceeds 130 mm TL) (D'Ancona and Cavinato, 1965). Furthermore, the developmental data in Tables 10 and 11 indicate that *Bregmaceros* species exhibit abbreviated early life stages in comparison with the other higher gadoids, although fecundity in the former is still unknown. The members of the genus generally mature at 14–24 mm TL (D'Ancona and Cavinato, 1965) (less than 30 mm TL according to Houde, 1984). For example, *B. rarisquamosus* has well-developed eggs at 15–16 mm TL (D'Ancona and Cavinato, 1965) and *B. cantori* mature reproductive organs at 28–57 mm SL (Milliken and Houde, 1984). These characters suggest that progenesis has more strongly influenced bregmacerotid development than that of other higher gadoids.

4-3. Neoteny in *Muraenolepididae*

Among twelve autapomorphies noted previously, *Muraenolepis* has one reversal and five reduced characters: 1) crossing of hyohyoideus abductores 2 muscles; 2) no teeth on prevomer; 3) most parts of scapula and coracoid cartilaginous; 4) very reduced lower arm of posttemporal; 5) simple cleithrum without the posterior expansions; 6) most of pelvic girdle cartilaginous. The reductive characters 3) and 6) differ from those of *Bregmaceros* in showing unossified states. Furthermore, *Muraenolepis* has a deep-bodied otolith that has been regarded as an ancestral state (as in the progenetic *Bregmaceros*, and neotenic macrouroidines and trachyrincines) (Fig. 74). Moreover, the greater number of actinosts in *Muraenolepis* represent a similar condition to those of the other neotenic genera *Squalogadus* and *Trachyrincus* (Fig. 23C, D, F). Among the other autapomorphies of *Muraenolepis*, the continuity of vertical fin-rays is a remarkable character (Fig. 75E). Efremenko (1983) pointed out the similarity of the continuous vertical fins between the fully-formed larvae and adults, such being unlike the condition in ancestors of *Muraenolepis* or gadoids (Fig. 75). In the larvae of *M. microps* (Efremenko, 1983 : 141, fig. 2), urostyle flexion had not commenced in specimens of 26.5–28.5 mm TL (Fig. 75A–C), and Fahay and Markle (1984 : fig. 138A) illustrated the pre-flexion state for a 32.5 mm SL specimen of *Muraenolepis* sp. (Fig. 75D). Although this developmental delay in *Muraenolepis* is conspicuous among higher gadoids (Table 10), the ages at maturity and maximum sizes attained (Permitin, 1973) appear to be consistent (3 to 4 years) with other higher

gadoids (Table 11). In addition, *Muraenolepis microps* has a comparatively high fecundity, producing from 35,810 to 428,140 eggs (Permitin, 1973). The morphological characters of *Muraenolepis* mentioned above are hence regarded as having resulted from retardation by neoteny.

According to Gould (1977), heterochrony is probably related to life-history strategies of species: progenesis is associated with *r* strategies and neoteny with *K* strategies. In *r* strategies with progenesis, most tiny progenetic organisms show lower fecundity by structural and energetic constraints, but to produce a small number of precocious offspring necessitates the successful raising of the *r* value (Gould, 1977): viz., accelerated maturation is more effective than increased fecundity in raising *r*. As Marshall (1979, 1984) discussed, concerning the life history strategies of deep-sea fishes, progenesis is common in midwater species, particularly bathypelagic ones, but rare in bottom-dwellers: e.g., the gonostomatid *Cyclothone*, male ceratioids and aphyonids. In gadiforms, the precocious *Bregmaceros*, having a pelagic habit (0–4000 m depth), shows the typical progenetic traits of *r* strategies.

On the other hand, according to Gould (1977), the organisms in *K* environments probably acquire evolutionary flexibility by retarded somatic development and maturation of neoteny, which is accompanied by the retention of juvenile morphology. Gould's hypothesis applies well to the neotenic trachyrincines and macrouroidines. I also consider that the neoteny of *Muraenolepis*, showing a circum-Antarctic distribution, may be associated with adaptation to colder waters. The sister relationship with *Bregmaceros* suggests that *Muraenolepis* has arisen from an ancestor having a relatively warmer-water preference.

4-4. Possible heterochrony in other higher gadoids

In the other higher gadoids, it is more difficult to specify heterochronic phenomena, because of the absence of extreme modifications of life history or morphologies as seen in the taxa mentioned above. However, the data for morphology, age, size and development (Fig. 71, Tables 10, 11) suggest the following possibilities of heterochrony, at least, if the age of maturation in higher gadoids is regarded as three to four years: 1) *Ciliata mustela* and *Gadiculus argenteus* show progenetic traits such as earlier maturation (first year), short life span (3 years) and small body size (less than 25 cm TL). The age of maturation in *Gadiculus* is unknown, but some reduced morphological characters are evident; 2) *Brosme brosme*, *Molva dypterygia*, *Merluccius merluccius* and *Molva molva* show hypermorphic traits such as delayed maturation (8–11 years in

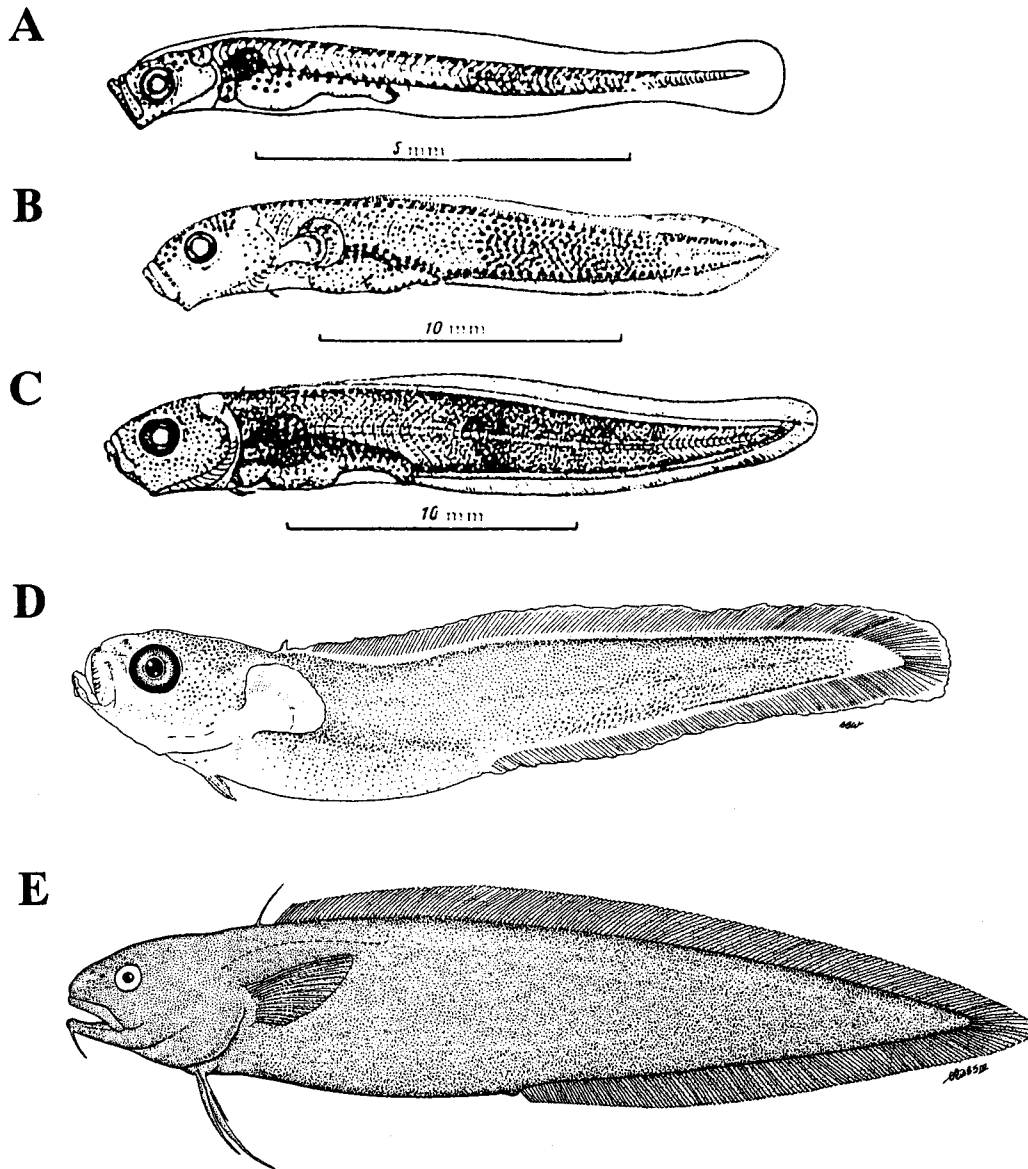


Fig. 75. Ontogeny of the genus *Muraenolepis*. A-C, *M. microps*, A-9.5, B-22.0 and C-26.5 mm TL (from Efremenko, 1983); D, *M. sp.*, 32.5 mm SL (from Fahay and Markle, 1984); E, *M. microps*, adult (from Cohen et al., 1990).

the former two, 5–7 years in the latter), long life span (17–20 years in the former three, 10–14 years in the latter) and large body size (more than 110 cm TL). Thus, hypermorphosis may have been an important factor in the evolution of the former two species; 3) The large body-size in the following genera may be related mainly to proportioned giantism: *Macruronus*, *Merluccius*, *Phycis*, *Urophycis*, *Lota*, *Micromesistius*, *Melanogrammus*, *Gadus*, *Theragra* and *Pollachius*; 4) The early maturity of *Trisopterus luscus* and *T. minutus* may be a result of the greater growth rate in those species, compared with that of *T. esmarkii*. Concerning the flexion period during development (Table 10), slight retardation occurs in *Macruronus* and *Brosme* among the higher gadoids, excluding *Muraenolepis* as mentioned above.

Such may also be related to the retention of continuous vertical fins, as in *Muraenolepis*.

In higher gadoids, the large body-size produced by possible hypermorphosis and proportioned giantism has probably resulted in the increased fecundity apparent, associated with improved reproductive strategies: e.g., 20–60 million eggs in *Molva molva* vs. 9,000–30,000 eggs in *Ciliata mustela* (Cohen et al., 1990).

5. Conclusions

In their molecular phylogenetic study of the gonostomatid genus *Cyclothone*, Miya and Nishida (1996) clearly demonstrated that the repeated evolution of paedomorphic novelties, such occurring in three different lineages, had resulted in misleading

Table 10. Early life history developmental data for higher gadoids. Primary or secondary data sources from Russel (1976), Fahay (1983), Fahay and Markle (1984), Dunn and Matarese (1984), Methven (1985), Izeta (1985) and Bruce (1988)

Genera	Hatching	Standard length (mm)			
		Flexion	Post-flexion	Pre-juvenile	Juvenile
<i>Macruronus</i>	2.2-2.3	20-28	27-34<	?	<189<
<i>Merluccius</i>	2.6-3.8	8-9	>9	20	>20
<i>Raniceps</i>	3	7-12	?	?	?
<i>Bregmaceros</i>	1.5	<7	?	?	<14-24<
<i>Muraenolepis</i>	?	>32	?	?	?
<i>Ciliata</i>	2	5-8	?	?	?
<i>Gaidropsarus</i>	2	5-7	7-12	12-48	>48
<i>Enchelyopus</i>	2	5-7	7-12	?	?
<i>Phycis</i>	?	4.5-8	8-12	12-30	>30
<i>Urophycis</i>	2	4-5	>5	<40	>40
<i>Lota</i>	3	14-19	19-30	?	?
<i>Brosme</i>	4	14-25	25-40	40-60	>60
<i>Molva</i>	3	9-14	14-20	20-80	>80
<i>Gadiculus</i>	<2.3	7-13	13-30	30-40	>40
<i>Arctogadus</i>	?	?	?	?	?
<i>Boreogadus</i>	6	11-17	17-30	30-45	>45
<i>Micromesistius</i>	2	8-13	?	?	>32
<i>Trisopterus</i>	3	7-11	?	?	>45
<i>Microgadus</i>	3	8-15	15-28	28-46	>46
<i>Eleginus</i>	4	11-17	17-24	24-27	?
<i>Melanogrammus</i>	3-4	10-16	16-22	?	<90<
<i>Gadus</i>	3-4	10-17	17-25	25-35	>35
<i>Theragra</i>	3-4	10-17	17-25	25-40	>40
<i>Merlangius</i>	3	9-13	13-23	?	?
<i>Pollachius</i>	3-4	12-16	?	?	<50<

phylogenetic analyses based on morphology. As shown here, heterochrony may also have independently and repeatedly influenced various gadiform lineages. Hence, the mosaic data set, including plesiomorphic and apomorphic morphologies, inadequately reflecting relationships, has resulted in misleading phylogenetic relationships proposed in many previous studies (e.g., Svetovidov, 1948; Cohen, 1984; Nolf and Steurbaut, 1989c; Okamura, 1989). Furthermore, heterochronic evolution has enabled many gadiforms to acquire more suitable life-history or morphological specializations in response to each newly-occupied habitat. As a typical example, macrourines, having an alevin stage (i.e., truncation of the larval period), are subject to a procession of the ontogenesis throughout their early life-history, such probably being related to their foraging strategy (Stein, 1980; Merrett, 1989). To clarify the phylogeny of gadiforms, however, necessitates examination of a more comprehensive data set, including inputs from ontogenetic and life history studies, in addition to their

molecular evolution.

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Table 11. Ages at first maturity and maximum sizes in higher gadoids. Data taken from Robins and Deubler (1955), Permittin (1973), Houde (1984), Matarese et al. (1989), Scott and Scott (1988) and Cohen et al. (1990). No information is available for genera *Raniceps* and *Arctogadus*

Species	Age at first maturity yrs (size : cm TL)	Maximum age attained yrs (size : cm TL)
<i>Macruronus novaezelandiae</i>	4 (60)	unknown (120)
<i>Merluccius merluccius</i>	5-7 (40-57)	>20 (140)
<i>M. productus</i>	2-4 (35-42)	17 (91)
<i>Raniceps raninus</i>	unknown	unknown (30)
<i>Bregmaceros spp.</i>	unknown (<3)	unknown (12)
<i>Muraenolepis microps</i>	3-4 (♂ 21, ♀ 23)	>5 (46)
<i>Ciliata mustela</i>	1 (11-14)	3 (25)
<i>Gaidropsarus vulgaris</i>	unknown	>6 (60)
<i>G. mediterraneus</i>	unknown	>6 (50)
<i>Enchelyopus cimbrius</i>	3 (15)	>9 (41)
<i>Phycis blennoides</i>	>3 (♂ 18, ♀ 33)	20 (110)
<i>Urophycis chuss</i>	3 (40)	unknown (50)
<i>U. tenuis</i>	3 (40-48)	10 (120)
<i>Lota lota</i>	3-4 (>24)	>16 (>120)
<i>Brosme brosme</i>	8-10 (50)	20 (110)
<i>Molva molva</i>	5-6 (80-110)	10-14 (200)
<i>M. dypterygia</i>	9-11 (75-88)	17-20 (155)
<i>Gadiculus argenteus</i>	unknown	3 (15)
<i>Arctogadus borisovi</i>	unknown	unknown (50)
<i>A. glacialis</i>	unknown	unknown (33)
<i>Boreogadus saida</i>	2-3 (15-20)	6-7 (40)
<i>Micromesistius australis</i>	3-4 (>29)	23 (90)
<i>M. poutassou</i>	3 (26)	>20 (47)
<i>Trisopterus esmarkii</i>	2 (14-15)	>4-5 (35)
<i>T. luscus</i>	1 (21-25)	>4 (45)
<i>T. minutus</i>	1 (12-14)	>4-6 (40)
<i>Microgadus proximus</i>	unknown	unknown (30)
<i>M. tomcod</i>	unknown	4 (42)
<i>Eleginus gracilis</i>	2-3 (>17)	11-12 (55)
<i>E. navaga</i>	3-4 (>18)	7 (42)
<i>Melanogrammus aeglefinus</i>	2-5 (>25)	14 (100)
<i>Gadus morhua</i>	2-4	>20 (200)
<i>G. ogac</i>	3-4	11 (70)
<i>G. macrocephalus</i>	2-5 (40-67)	13 (120)
<i>Theragra chalcogramma</i>	3-4 (30-38)	14-15 (80)
<i>Merlangius merlangus</i>	3-4 (>30)	10 (70)
<i>Pollachius pollachius</i>	unknown	>8 (130)
<i>P. virens</i>	>3 (>50)	25 (130)

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XII. Appendix

Anatomical abbreviations used in the text figures
a, angular; A1a, A1b A2, A3 and Aw, adductor mandibulae sections 1-3 and w; aap, adductor arcus

palatini ; ac, actinost ; ad5, adductor 5 ; afc, anterior frontal crest ; ao, adductor operculi ; bb, basibranchial ; bh, basihyal ; bl, Baudelot's ligament ; bo, basioccipital ; br, branchiostegal ray ; ca, cartilaginous plate ; cb, ceratobranchial ; ch, ceratohyal ; cl, cleithrum ; co, coracoid ; cr, cranium ; csl, ligament connecting cranium and swimbladder ; d, dentary ; dh, dorsal hypohyal ; dm, drumming muscle ; dmp, dorsal maxillo-premaxillary ligament ; do, dilatator operculi ; e, ethmoid ; eb, epibranchial ; ecp, ectopterygoid ; eh, epihyal ; enp, endopterygoid ; eo, exoccipital ; ep, epiotic ; epu, epural ; f, frontal ; fc, frontal crest ; fd, first dorsal fin ; fo, fontanelle ; gg, gas gland ; hb, hypobranchial ; hha, hyohyoidei abductores ; hm, hyomandibular ; iac, interarcual cartilage ; ial, interarcual ligament ; ic, intercalar ; icp, intercalar process ; ih, interhyal ; ihp, inferior hypurals ; im, intermandibularis ; io, infraorbital ; iop, interopercle ; iops, interopercular socket ; is, internal sac ; la, lachrymal ; lap, levator arcus palatini ; lep, posterior process of lateral ethmoid ; let, lateral ethmoid ; lo, levator operculi ; le, levator externus ; li, levator internus ; lp, levator posterior ; ma, maxillary ; mp, median process ; mt, metapterygoid ; n, nasal ; nf, trigeminal and facialis nerve foramen ; ns, neural spine ; obp, obliquus posterior ; od, obliquus dorsalis ; op, opercle ; ov, obliquus ventralis ; p, parietal ; pal, palatine ; pb, pharyngobranchial ; pce, pharyngo-

clavicularis externus ; pci, pharyngoclavicularis internus ; pcl, postcleithrum ; pd, predorsal bone ; pds, pseudospine ; ph, protractor hyoidei ; php, parhypural ; pm, premaxillary ; pop, preopercle ; pp, posterior process ; pr, process on epibranchial 1 ; ps, parasphenoid ; pt, posttemporal ; pto, pterotic ; pts, pterosphenoid ; pu, preural centrum ; pv, prevomer ; pro, prootic ; q, quadrate ; ra, retroarticular ; rc, rectus communis ; rd, retractor dorsalis ; rdl, radial ; rm, retia mirabilia ; roc, rostral cartilage ; rs, rectus superior ; rv, rectus ventralis ; sc, scapula ; scl, supracleithrum ; sd, second dorsal fin ; sf, scapular foramen ; sh, sternohyoideus ; shp, superior hypurals ; so, supraoccipital ; soc, bony cover of supraorbital sensory canal ; soe, sphincter oesophagi ; sop, subopercle ; spo, sphenotic ; sr, soft ray ; st, supratemporal ; stc, bony cover of supratemporal sensory canal ; sy, symplectic ; sw, swimbladder ; swl, ligament connecting swimbladder and supracleithrum ; tda, transversus dorsalis anterior ; tdp, transversus dorsalis posterior ; tp, tooth plate on epibranchial 3 ; tva, transversus ventralis anterior ; tvp, transversus ventralis posterior ; u, ural centrum ; uh, urohyal ; unc, uncinat process ; V, posterior palato-vomerine ligament ; VI, anterior palato-vomerine ligament ; VII, maxillo-rostroid ligament ; vh, ventral hypohyal ; x, x bone ; XI, ethmo-maxillary ligament ; XII, palato-premaxillary ligament ; y, y bone.