Articulation of the Pelvic Spine in Acanthopterygian Fishes, with Notes on Its Phylogenetic Implications

Hin-kiu Mok and Hung-junn Chang

(Received October 15, 1985)

Abstract   The pelvic spine articulation in 88 non-squamipinne acanthopterygian species belonging to 59 families and 8 orders was examined.   For most acanthopterygians, the pelvic bone lacks a foramen for the attachment of the pelvic spine flanges and this structural condition is considered a primitive acanthopterygian state.   Only in Caproidae, Leiognathidae, and Polynemidae among the examined species do the pelvic spine flanges fuse through a foramen in the pelvic bone and this articulation is considered most derived.   In the remaining acanthopterygians examined, the pelvic spine flanges butt against each other through the pelvic foramen.   However, these flanges do not fuse.   This structure is considered an intermediate state.   The possible phylogenetic implication of these articulating states regarding acanthopterygian phylogeny is discussed.

Rosen (1982) discussed the occurrence of fin spines in teleostean fishes and recognized four stages, in which the most derived is the presence of pelvic spines.   The presence of pelvic spines in acanthopterygians (including atherinomorphs and percomorphs) represents a prominent evolutionary step.   Mok and Shen (1983) noted a transformation series in the articulation of this spine to the pelvic bone in some perciform families (i.e. the squamipinne fishes).   The evolutionary polarity of this series was interpreted and phylogenetic hypothesis of the squamipinne fishes was erected on the basis of this interpretation.   According to Mok and Shen, there are three character states of the pelvic articulation to the pelvic bone: (1) the pelvic bone lacks a foramen for the attachment of the pelvic spine; the proximal end of the spine has a notch (with two flanges) which articulates with the lateroventral edge of the pelvic bone, or with a longitudinal ridge, at the posteroventral edge, or with the ventral area of the pelvic bone (Fig. 1A); (2) the lateroventral edge, or the longitudinal ridge has a small foramen and the proximal flanges of the pelvic spine articulate with the pelvic bone through this foramen; however, fusion of these flanges does not occur (Fig. 1B); (3) the tips of the flanges fuse together through the pelvic foramen that suture at which fusion has taken place vanishes (Fig. 1C) (Mok and Shen, 1983).   According to their hypothesis, State 1, which has the broadest distribution in the Perciformes, is the primitive condition.   State 3 is found in Chaetodontidae, Pomacanthidae,

Scatophagidae, Pentacerotidae, Siganidae, Acanthuridae (including Acanthurinae and Zanclinae), and Tetraodontiformes, among the squamipinne species which they examined, and is the most derived.   State 2, limited to Drepanidae, Platacidae, and Ephippidae in the species they studied, is the intermediate condition.   Because their works were restricted to the squamipinnes, the purpose of this study is to examine this articulation in some acanthopterygian fishes not examined by Mok and Shen (1983), in hopes that additional information on the distribution of these character states may reveal indications on the phylogenetic position of other acanthopterygians.

Materials and methods

Most materials used were uncatalogued specimens from the fish collection at the Institute of Marine Biology, National Sun Yat-sen University (NSYU); the Institute of Zoology, Academia Sinica, Republic of China (IZAS)., California Academy of Sciences (CAS); the Department of Biology, Kochi University (BSKU); and the Ichthyology Department, American Museum of Natural History (AMNH).   Others were catologued specimens from the Laboratory of Marine Zoology, Hokkaido University (HUMZ).   The pelvic fins of specimens from National Sun Yat-sen University were removed from the fish and were cleared and stained according to Taylor's (1967) method for anatomical study.   Articulation of the pelvic spine and pelvic bone in the remaining specimens was dissected

and observed under a dissecting stereomicroscope without clearing-and-staining preparation.

Species examined (standard length shown).

Beryciformes. Trachichthyiidae: *Hoplostethus mediterraneus*, NSYU, 40 mm. Monocentridae: *Monocentris japonica*, NSYU, 145 mm. Holocentridae: *Sargocentron lacteoguttatus*, NSYU, 50 mm.

Zeiformes. Parazenidae: *Parazen pacificus*, HUMZ 49155, 157 mm; BSKU, 110 mm. Macrurocyttidae: *Zenion japonicum*, HUMZ 99337, 19 mm; BSKU, 87 mm. Zeidae: *Cyttopsis rosea*, HUMZ 71398, 45 mm; BSKU, 66 mm; *Cyttus novaezealandiae*, HUMZ 55821, 29.5 mm; *Zenopsis nebulosa*, HUMZ 56965, 146 mm; *Zeus faber*, BSKU, 150 mm. Oreosomatidae: *Neocyttus rhomboidalis*, HUMZ 50252, 253 mm. Grammicolepididae: *Xenolepidichthys dalegleishi*, HUMZ 80029, 47 mm. Caproidae: *Antigonia capros*, NSYU, 127 mm.

Gasterosteiformes. Gasterosteidae: *Gasterosteus aculeatus*, NSYU, 35 mm; *Pungitius pungitius*, AMNH, 32 mm.

Syngnathiformes. Fistulariidae: *Fistularia petimba*, NSYU, 313 mm. Macrorhamphosidae: *Macrorhamphosus scolopax*, NSYU, 84 mm.

Scorpaeniformes. Scorpaenidae: *Scorpaenodes guamensis*, NSYU 207, 80 mm. Triglidae: *Satyrichthys hemisticta*, NSYU, 135 mm. Platycephalidae: *Inegocia japonica*, NSYU, 157 mm. Cottidae: *Hemilepidotus papilio*, HUMZ 76914, 193 mm.

Dactylopteriformes. Dactylopteridae: *Dactyloptera orientalis*, NSYU, 106 mm.

Perciformes. Teraponidae: *Pelatus qudralineatus*, IZAS, 98 mm, 118 mm, 135 mm; *Terapon jarbua*, NSYU, 32 mm, 39 mm, 60 mm, 110 mm, 110 mm, 265 mm; *T. theraps*, NSYU 445, 95 mm. Banjosidae: *Banjos banjos*, NSYU, 257 mm. Kuhliidae: *Kuhlia mugil*, HUMZ 48505, 89.4 mm; NSYU, 46 mm. Centrarchidae: *Lepomis cyanellus*, CAS 15337, 144 mm. Priacanthidae: *Priacanthus japonica*, NSYU, 149 mm; *P. macracanthus*, NSYU, 165 mm; *Pristigenys multifasciatus*, IZAS, 160 mm; *P. niphonia*, NSYU, 183 mm. Apogonidae: *Apogon novemfasciatus*, NSYU, 60 mm. Percichthyidae: *Acropoma japonicum*, NSYU, 54 mm. Branchiostegidae: *Branchiostegus auratus*, NSYU, 125 mm. Leiognathidae: *Gazza minuta*, NSYU, 72 mm; *Leiognathus splendens*, NSYU, 45 mm, 95 mm. Bramidae: *Brama japonica*, NSYU, 176 mm. Lutjanidae: *Lutjanus amabilis*, NSYU, 290 mm; *Lutjanus monostigma*, NSYU, 75 mm. Nemipteridae: *Nemipterus hexodon*, NSYU, 70 mm. Lobotidae: *Lobotes surinamensis*, NSYU, 198 mm. Haemulidae: *Hapalogenys mucronatus*, IZAS, 104 mm; *Parapristipoma trilineatum*, IZAS 120, 137 mm; *Plectorhynchus pictus*, IZAS, 120 mm; *P. lineatus*, IZAS, 135 mm; *Pomadasys opercularis*, IZAS, 190

mm; *P. stridens*, IZAS, 100 mm. Lethrinidae: *Lethrinus atkinsoni*, NSYU, 155 mm, IZAS, 225 mm; *Lethrinus choerorynchus*, NSYU 1257, 105 mm. Pentapodidae: *Gymnocranius griseus*, NSYU, 125 mm; *Monotaxis grandoculis*, IZAS, 197 mm; *Pentapodus nagasakiensis*, IZAS, 127 mm. Sparidae: *Acanthopagrus latus*, NSYU, 260 mm; *A. schlegeli*, IZAS, 160 mm; *Argyrops bleekeri*, NSYU, 200 mm; *Dentex tumifrons*, NSYU, 95 mm, 100 mm; *Evynnis cardinalis*, NSYU, 75 mm; *Pagrus major*, IZAS, 170 mm; *Sparus sarba*, NSYU, 170 mm. Sciaenidae: *Nibea albiflora*, NSYU, 350 mm. Mullidae: *Parupeneus cyclostoma*, NSYU, 250 mm; *Parupeneus barberinus*, NSYU, 50 mm. Pempheridae: *Pempheris* sp., NSYU, 15 mm. Kyphosidae: *Microcanthus strigatus*, NSYU 668, 125 mm. Oplegnathidae: *Oplegnathus fasciatus*, NSYU, 235 mm. Embiotocidae: *Ditrema temmincki*, HUMZ 63259, 144 mm; *Zalembius rosaceus*, CAS, 132 mm. Cichlidae: *Cichlasoma salvini*, NSYU, 52 mm; *Geophagus jurupari*, NSYU, 76 mm; *Haplochromis copressiceps*, NSYU, 57 mm; *Hemichromis guttatus*, NSYU, 43 mm; *Sarotherodon niloticus*, NSYU, 140 mm. Pomacentridae: *Abudefduf septemfasciatus*, NSYU, 30 mm, 135 mm; *Amphiprion frenatus*, NSYU, 56 mm, 70 mm. Cheilodactylidae: *Gonistius zonatus*, NSYU, 270 mm. Mugilidae: *Liza pesadorensis*, NSYU, 143 mm. Polynemidae: *Polynemus plebeius*, NSYU, 85 mm; *P. sexfilis*, NSYU, 90 mm. Labridae: *Stethojulis trilineata*, NSYU, 110 mm; *Thalassoma cupido*, HUMZ 101433, 70.5 mm. Scaridae: *Scarus dussumieri*, NSYU, 170 mm. Champsodontidae: *Champsodon snyderi*, NSYU, 78 mm. Parapercidae: *Parapercis decemfasciata*, NSYU, 154 mm. Uranoscopidae: *Uranoscopus oligolepis*, NSYU 505, 48 mm. Blenniidae: *Istiblennius lineatus*, NSYU, 63 mm. Ammodytidae: *Embolichthys mitsukurii*, NSYU, 132 mm. Gempylidae: *Neoepinnula orientalis*, NSYU, 110 mm. Scombridae: *Scomber australasicus*, NSYU, 320 mm. Centrolophidae: *Psenopsis anomala*, NSYU, 96 mm. Channidae: *Channa maculata*, NSYU, 287 mm.

Pleuronectiformes. Psettodidae: *Psettodes erumeri*, NSYU, 234 mm.

Results

Among "non-squamipinne" acanthopterygians, a State 3 articulation of the pelvic spine occurs only in Caproidae (i.e. *Antigonia capros*), Leiognathidae, and Polynemidae. State 2, has a broader distribution and occurs in Pentapodidae, Sparidae, Carangidae, Cichlidae, and Pomacentridae. State 1 is found widely in the acanthopterygians examined, including the Cyprinodontiformes, Atheriniformes, Beryciformes, Zeiformes,
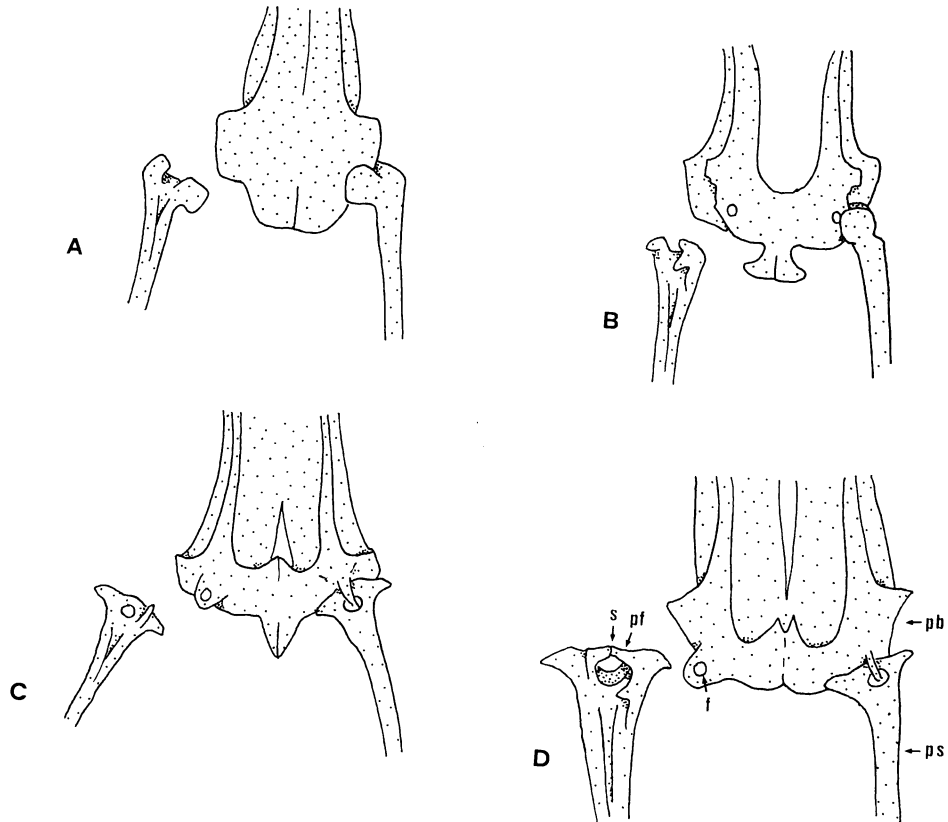
Fig. 1. Character states of pelvic spine articulation. The right spine removed from the pelvic bone is shown in median view. A, State 1, *Parapercis decemfasciata*. B, State 2, *Geophagus jurupari*. C, State 3, *Polynemus plebeius*. D, Stage 2, *Abudefduf septemfasciatus*. f, foramen of pelvic bone; pb, pelvic bone; pf, proximal flange of pelvic spine; ps, pelvic spine; s, suture of flanges.

Gasterosteiformes, Syngnathiformes, Dactylopteriformes, Scorpaeniformes, Pleuronectiformes, and the remaining examined Perciformes.

In the majority of cases, all members of a single family have the same articulation state, particularly among those with a State 3 pattern. However, there are some exceptions. In Sparidae, *Pagrus major* and *Sparus sarba* share a State 1 articulation, whereas, *Acanthopagrus schlegeli*, *Argyrops bleekeri*, *Dentex tumifrons*, and *Evynnis cardinalis* possess State 2.

In Pentapodidae, only *Pentapodus nagasakiensis* has State 2, and all remaining pentapodids possess State 1. Haemulidae, like Pentapodidae, have one species with State 2 (i.e. *Plectorhynchus pictus*), all others possess State 1. Among Cichlidae, *Cichlasoma salvini* and *Hemichromis guttatus* have State 1, whereas *Haplochromis copressiceps*,

Geophagus jurupari and *Sarotherodon niloticus* posses State 2. Among the Carangidae, all members of the tribe *Scomberoidini* possess State 2, whereas the pelvic spine in other carangids exhibits State 1. Among the Teraponidae, *Terapon jarbua* is an interesting exception: the 32-mm, 39-mm, and 60-mm specimens possess State 1, whereas the 110-mm, 111-mm, and 265-mm ones exhibit State 2.

Unlike the typical State 2 condition, in which the two pelvic flanges at the proximal end of the spine lack a fusion, in pomacentrids these flanges tightly integrate to one another through the pelvic bone foramen (Fig. 1D). The fusion, however, is not complete as a vague suture remains and by definition it should be treated as a special case of State 2. This condition may be a step immediately prior to the development of State 2.

Discussion

Rosen (1984) proposed a new hypothesis that "Zeiformes" are members of the Tetraodontiformes. He divided the latter order into two series in which the first includes the Caproidae and the second includes the Zeomorphi and Plectognathi. Due to the rarity of State 3 within acanthopterygians, its appearance in Caproidae (i.e. in *Antigonia capros*) is most interesting and may point to a possible close phylogenetic affinity of this family to those percomorphs with a similar locking condition (e.g. Plectognathi). However, convergence may also be an alternative explanation for this similarity. All examined "zeomorphs" possess State 1, therefore, their monophyletic status within the plectognaths as proposed by Rosen (1984) receives no additional support in terms of pelvic spine articulation. As far as this structural character is concerned, Caproidae might be related to the Plectognathi, but the Zeomorphi probably are not related to these fishes. If the latter group was related to the Caproidae and Plectognathi, morphological reversal must have taken place—a situation contradicting the principle of parsimony.

The occurrence of a State 3 articulation in the Leiognathidae and Polynemidae (the latter classified in a suborder by itself) in addition to those groups reported by Mok and Shen (1983) (i.e. Pentacerotidae, Scatophagidae, Chaetodontidae, Pomacanthidae, Siganidae, Acanthuridae, and Tetraodontiformes) suggests a close relationship of these nine groups.

The two alternative ancestoral character states of Sparidae, Pentapodidae, and Cichlidae (State 1 vs State 2) are equivocal. Should State 1 be treated as the ancestral condition for these families, *Acanthopagrus – Argyrops – Dentex – Evynnis* and *Geophagus – Haplochromis – Sarotherodon* from two groups in which members are closely related and these families are neither more closely related to each other nor to Ephippididae, (including Ephippididae, Drepanidae, and Platacidae; Nelson, 1984), and Pomacentridae (i.e. the perciform families in which most members possess a State 2). Should the alternative hypothesis be adopted, Sparidae, Pentapodidae, Cichlidae, Ephippididae, Pomacentridae, and the perciforms with State 3 are assumed to have evolved from a common ancestor. Due to the fact that most

carangids possess State 1, State 2 in Scomberoidini is considered a derived condition. Ontogenetic evidence, as was observed in *Terapon jarbua* suggests that State 1 is the ancestral character state for these families. Should this hypothesis be adopted, appearance of state 2 in some members of these families would likely be evolved independently reflecting repeated parallelism or convergence. This inference will reduce the significance of State 2 as indication for phylogenetic interrelationship.

Judging only from the condition of the pelvic spine articulation in which the flanges were tightly integrated, giving rise to a suture, the Pomacentridae may be the primitive sister group of the perciform families possessing a State 3 condition (see above).

Ephippididae (and probably also Sparidae, Pentapodidae, and Cichlidae) should either all be more closely related to each other, or one of them is the primitive sister group of a monophyletic assemblage including Pomacentridae plus the other perciforms possessing State 3 (see above). These hypotheses are based on the assumption that State 2 in Ephippididae and Cichlidae is the intermediate condition of this series. However, the phylogenetic status of State 2 is not a strong indicator for the synapomorphic relationship of these two families.

Liem and Greenwood (1981) first proposed the monophyletic relationship of Cichlidae, Embiotocidae, Labridae, Odacidae, and Scaridae on the basis of functional morphology of the pharyngeal jaw mechanism. Kaufman and Liem (1982) later added the Pomacentridae to form the Labroidei in which Pomacentridae is considered the primitive sister group of all other labroids (i.e. Cichlidae, Embiotocidae, and Labridae). This latter revision was also based on their trophic apparatus. According to Kaufman and Liem (1982), Labroidei can be defined by three synapomorphic characters: (1) united fifth ceratobranchials; (2) true diarthrosis between upper pharyngeal jaws and basicranium; and (3) undivided sphincter oesophagi muscle. The monophyly of Cichlidae, Embiotocidae, and Labridae, on the other hand, is supported by two synapomorphic characters: (1) levator externus 4 is a continuous muscle joining the prootic region to a muscular process on the lower jaw; and (2) predisposition for the insertion of the levator

posterior muscle on the lower pharyngeal jaw. Pelvic spine articulation, however, does not support the above hypothesis. The primitive articulation in Embiotocidae, Labridae, and some cichlids (including Labridae, Odacidae, and Scaridae; Kaufman and Liem, 1982) and the intermediate state of the articulation in Pomacentridae and some cichlids recommend alternative hypothesis (see above).

As far as the function of the percoid pelvic fin is concerned relatively little change has evolved. In addition, the occurrence of both State 2 and 3 articulations does not correlate with spine condition (strong versus weak). For instance, the strong pelvic spines and pelvic bones in gasterosteiforms have a peg and socket locking articulation (Reimchen, 1983) in which foramen in the latter bones is absent, i.e. a State 1 condition. Despite the fact that the hypotheses of Liem and Greenwood (1981) and Kaufman and Liem (1982) may be more favorable because they are supported by more synapomorphic characters, the alternative hypothesis for the phylogeny of these families grounded on evidence of the pelvic spine articulation deserves attention and further examination.

A generalized articulation (i.e. State 1) in *Psettodes*, which is considered the most primitive group within the Pleuronectiformes (Amaoka, pers. comm.) indicates that this order is unlikely to have evolved from the perciforms with either a State 2 or State 3 articulation. This conclusion is also based on the assumption that the order Pleuronectiformes is a monophyletic group—a hypothesis that remains to be tested.

Although State 2 has been observed primarily in a limited number of percoid families, it is, however, not an articulation unique to the Perciformes. Yabe (1983) observed a State 2 condition in *Marukawichthys pacificus* (Ereuniidae; Scorpaeniformes). Other scorpaeniforms examined in this study are primitive in their pelvic fin articulation. It is, however, most likely that a State 2 condition is also a derived form within the Scorpaeniformes (Yabe, pers. comm.).

Acknowledgments

We would like to thank Dr. Sin-che Lee of the Institute of Zoology, Academia Sinica, Republic of China for allowing us to examine the specimens in the fish collection at the Academia Sinica; Dr. Guido Dingerkus of the American Museum of Natural History generously sent stickleback specimens to us as a gift;Dr. Yoshihiko Machida of the Department of Biology, Kochi University for sending us specimens of Zeiformes. Special thanks are due to Dr. Kunio Amaoka of the Laboratory of Marine Zoology, Hokkaido University for allowing the senior author to use his facilities and specimens for this study during the short visit to his laboratory. Dr. Mamoru Yabe of the same laboratory kindly spent time with the senior author collecting stickleback specimens, locating specimens in their fish collection, and discussing various problems associated with this paper. Mr. Kunio Sasaki of the same laboratory called our attention to some important references. Drs. Lynne Parenti of the California Academy of Sciences and Guido Dingerkus of the Department of Ichthyology, American Museum of Natural History kindly read the manuscript and gave valuable comments.

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(Institute of Marine Biology, National Sun Yat-sen University, Kaohsiung, Taiwan, R.O.C.)

腹鰭棘の関節状態に基く棘鰭魚類の系統関係

Hin-kiu Mok・Hung-junn Chang

棘鰭魚類のうち squamipinnes に含まれない 8 目 59 科 88 種の腹鰭棘の関節状態を調べた．多くの棘鰭魚類で，腰骨は腹鰭棘の縁辺が付着するための孔を欠く．これは原始的状態と考えられる．ヒシダイ科，ヒイラギ科およびツバメコノシロ科においてのみ，腹鰭棘の縁辺は孔を介して腰骨と癒合する．この状態は最も派生的と考えられる．他の棘鰭魚類では腹鰭棘の縁辺は孔を介して互いに接しているが，癒合はしない．これは中間的状態と考えられる．これらの関節状態の系統的意味について論議した．