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Development of the First Vertebra in *Oryzias latipes* and its Morphology in Beloniformes and Cyprinodontiformes

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ABSTRACT

To examine morphological characteristics usable in classification of Beloniformes and Cyprinodontiformes, the first vertebrae of many specimens were compared anatomically. Development of the first vertebra in *Oryzias latipes* was observed first to provide an understanding of its morphology and articulation with the skull. The first vertebra of adult *O. latipes* consists of the centrum, condyles for exoccipitals, neural arches with parapophyses, a neural spine and a small dorsal compartment in the neural canal. Next, the morphology of the first vertebrae in Beloniformes and Cyprinodontiformes was examined. The first vertebra in Beloniformes was composed of the same components as in *O. latipes,* but there were morphological modifications in the components in the Cyprinodontiformes. The present observations suggest that the lower position of the parapophyses in neural arches is a common feature of the first vertebra in Beloniformes.

Key words: first vertebra, condyle, Beloniformes, Cyprinodontiformes, *Oryzias latipes,* classification

INTRODUCTION

The medaka, *Oryzias latipes,* is one of 15 species of the genus *Oryzias.* A new species *O. nebulosus* (Parenti and Soeroto, 2004) has recently been found in Lake Poso, Sulawesi Tengah, Indonesia. According to Rosen (1964), the four genera including *Oryzias, Adrianichthys, Xenopoecilus* and *Horaichthys* belong to the family Adrianichthyidae. The basic comparative anatomy of the medaka has been studied by many investigators (Rugh, 1948; Iwamatsu and Hirata, 1980; Rosen and Parenti, 1981; Yabumoto and Ueno, 1984; Nangille and Hall, 1987; Fujita, 1992). However, our knowledge of it is still not complete, as already pointed out by Parenti (1987).

In earlier investigations of *Oryzias melastigma* and *Aplocheilus lineatus,* three condyles between the skull and first vertebra (centrum) were described for the first time in *Oryzias* but not in *Gambusia affinis* (Ramaswami, 1946). Such tripartite structures for articulation have also been reported in the bluegill sunfish (*Lepomis m. macrochirus*), the warmouth bass (*Chaenobryttus coronarius*) (Stokely, 1952) and the Sacramento perch (*Archoplites interruptus*) (Dineen and Stokely, 1956). On the other hand, Dineen and Stokely (1954) found no accessory condyles with the exoccipitals in the first vertebra of the central mudminnow.

In her study on classifications of Cyprinodontiform fishes, Parenti (1981) stated that the first vertebra commonly articulates with the skull via the basioccipital and exoccipital condyles in Cyprinodontiformes, except for the tribe Cyprinodontini. However, there has so far been no attention to this articular structure in classification of Beloniformes such as Adrianichthyoidei and Exocoetoidei (Kulkarni, 1940; Hotta, 1961; Rosen, 1964; Rosen and Parenti, 1981; Parenti, 1993). Although Rosen (1964) drew diagrams of the skull with three condyles to the first vertebra in *Xenopoecilus poptae* and *X. sarasinorum,* the first report of three articulations between the skull and first vertebra in the medaka *O. latipes* was made by Yabumoto and Ueno (1984). However, it still remains unclear whether the morphology of these articulations is a common charactor of Adrianichthyids with regard to fish classification. Rosen and Parenti (1981) proposed 17 characters to establish a hypothesis for atherinomorph relationships.

The purpose of the present study was to renew focus on the taxonomical characters of Beloniformes, including Adrianichthyoidei and Exocoetoidei, by examining the morphology of their first vertebrae from the viewpoint of comparative osteology. First, we examined the development of the first vertebra to articulate with the skull in a laboratory small fish, *Oryzias latipes.* In this fish, morphological changes in the first centrum during the growth period have not yet been observed, although develop-

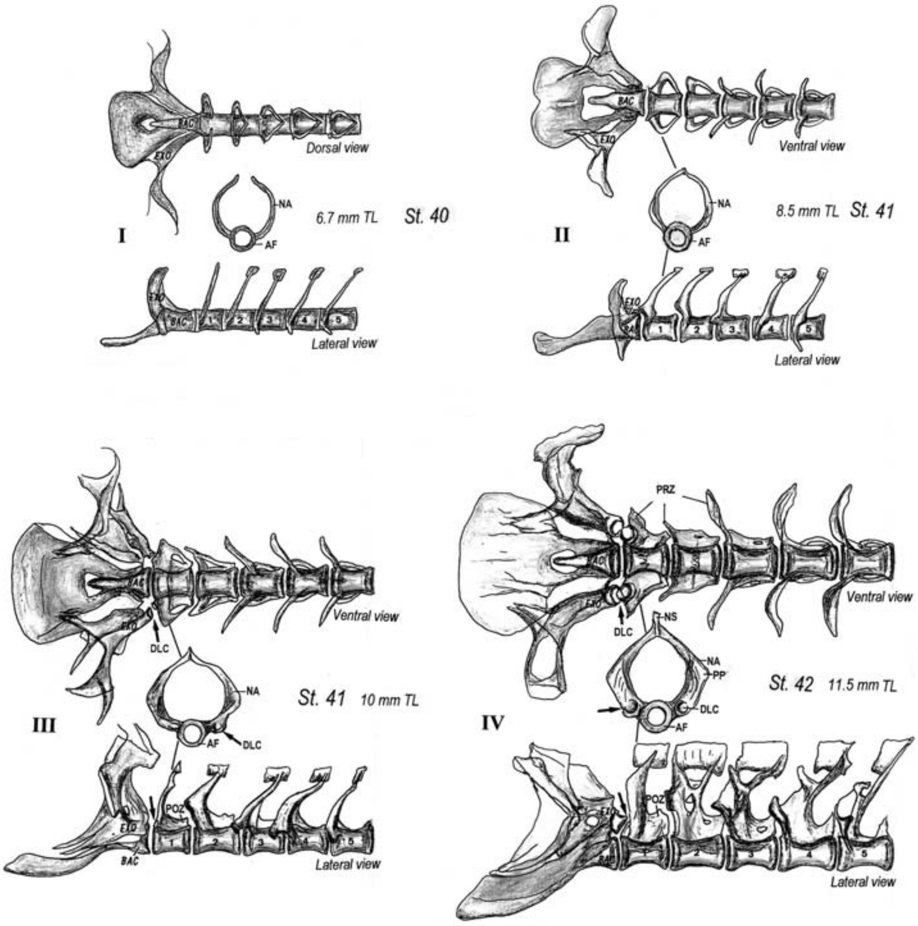

Fig. 1 Diagramatic presentations of the posterior region of the skull and the anterior region of the vertebrae during growth of *Oryzias latipes* First vertebra in stage 40, stage 41and stage 42 of growth.
Arrows indicate the exoccipital condyle (DLC).

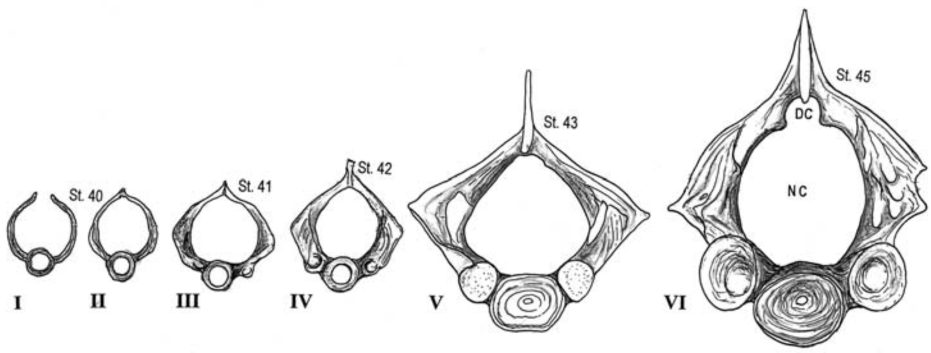

Fig. 2 Diagramatic illustration of the morphological changes in the anterior view of the first vertebra of *Oryzias latipes* during growth. I, 6.7 mm TL; II, 7.5 mm TL; III, 9.0 mm TL; IV, 11.5 mm TL; V, 18.5 mm TL; VI, 30 mm TL.

ment of the head skeleton has been reported already by Langille and Hall (1987), who illustrated the exoccipital condyles and the basioccipital condyle in the late juvenile stage (15-20 mm total length). We here examined the articulation of the first centrum with the skull in several fishes.

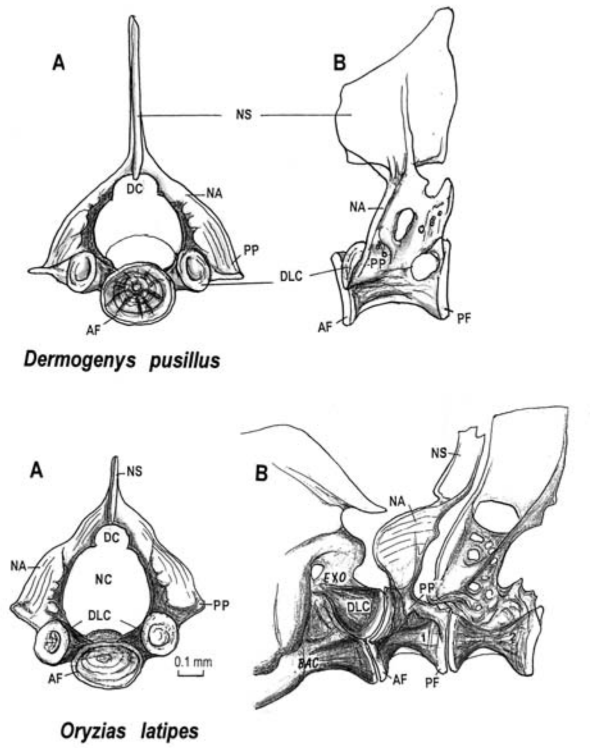

Fig. 3 Drawings of the first vertebra of *Dermogenys pusillus* and *Oryzias latipes.* A: Anterior view, B: Lateral view（includes the posterior region of the skull and the anterior region of the first vertebra in *O.latipes*）.

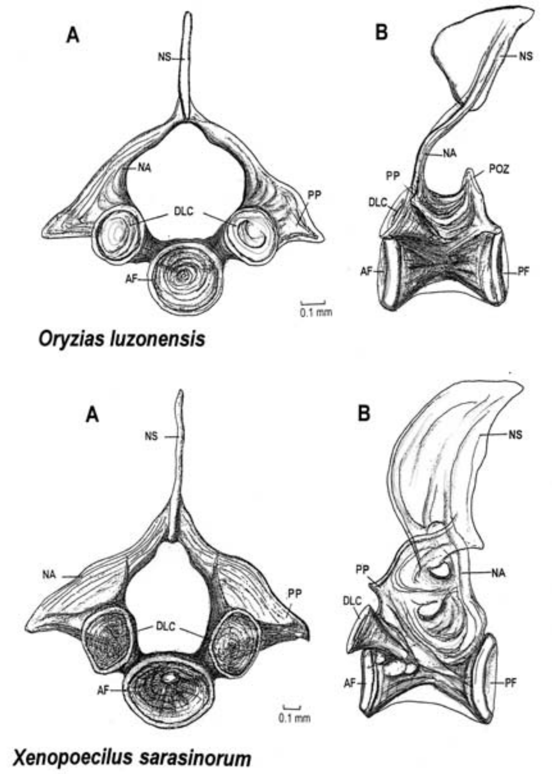

Fig. 4 Drawings of the first vertebra of *Oryzias luzonensis* and *Xenopoecilus sarasinorum.* A: Anterior view, B: Lateral view.

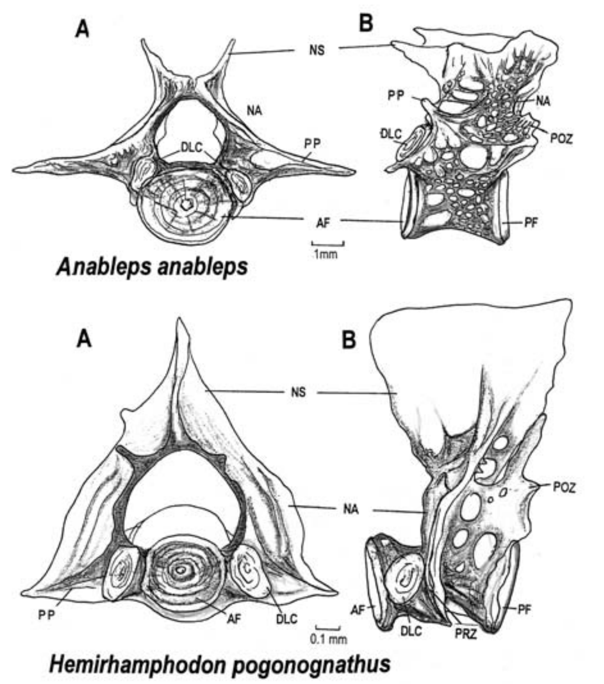

Fig. 5 Drawings of the first vertebra of *Anableps anableps* and *Hemirhamphodon pogonognathus.* A: Anterior view, B: Lateral view.

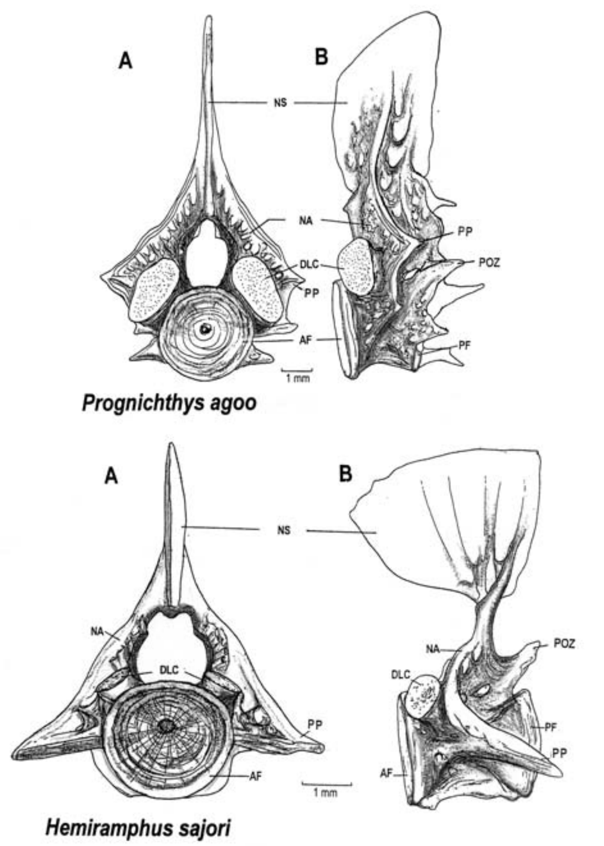

Fig. 6 Drawings of the first vertebra of *Prognichthys agoo agoo* and *Hemiramphus sajori.* A: Anterior view, B: Lateral view.

MATERIALS and METHODS

The adult four-eyed fish *Anableps anableps, Xenopoecilus sarasinorum* and several freshwater aquarium fishes were obtained through the courtesy of the World's Medaka in Nagoya Higashiyama Zoo. Other adult fishes, such as *Scomber, Sardinops sagax melanosticta, Dermogenys pusillus*(female 50.4 mm total length), *Cololabis saira, Hemiramphus sajori* and *Prognichthys agoo* which had already died were purchased in a fish market. The orange-red variety of the medaka(*Oryzias latipes*) maintained in aquaria outdoors were used for examination of development of the skull and first vertebra. Freshly hatched fry were also obtained by incubation of fertilized eggs and were reared in aquaria. Phylogenic relationships of the first vertebra in Beloniformes and Cyprinodontiformes were searched according to the following classification that was proposed by Parenti (1981) and Rosen and Parenti (1981). The species examined in the present study are noted by parentheses in the following list.

Order Beloniformes (Rosen and Parenti, 1981)
- Suborder Adrianichthyoidei
  - Family Adrianichthyidae
    - Subfamily Horaichthyinae
      - Genus *Horaichthys*
    - Subfamily Oryziinae
      - Genus *Oryzias* (*O. latipes*) (*O. luzonensis*)
    - Subfamily Adrianichthyinae
      - Genus *Adrianichthys*
      - Genus *Xenopoecilus* (*X. sarasinorum*)
- Suborder Belonoidei
  - Superfamily Exocoetoidea
    - Family Hemiramphidae
      - Genus *Dermogenys* (*D. pusillus*)
      - Genus *Hemirhamphodon* (*H. pogonognathus*)
      - Genus *Hemiramphus* (*H. sajori*)
      - Genus *Nomorhamphus* (*N. lami sanijdersi*)
    - Family Exocoetidae
      - Genus *Prognichthys* (*P. agoo*)
  - Superfamily Scomberescoidea
    - Family Belonidae
      - Genus *Ablennes* (*A. anastomella*)
    - Family Scomberescoidae
      - Genus *Scomber* (*S. japonicus*)
      - Genus *Cololabis* (*C. saira*)

Order Cyprinodontiformes (Parenti, 1981)
- Suborder Aplocheiliidei
  - Family Aplocheiliidae
    - Subfamily Aplocheilinae
      - Genus *Aplocheilus* (*A. purumis*) (*A. acrotos*)
  - Family Rivulidae
    - Subfamily Rivulinae
      - Genus *Rivulus* (*R. marmotous*)
      - Genus *Ataeniobius* (*A. toweri*)
- Suborder Cyprinodontoidei
  - FamilyProfundulidae
  - Family Fundulidae
  - Family Valenciidae
  - Superfamily Poecilioidea
    - Family Anablepidae
      - Subfamily Anablepinae
        - Genus *Anableps* (*A. anableps*)
      - Subfamily Oxyzygonectinae
    - Family Poeciliidae
      - Subfamily Poeciliinae
        - Genus *Gambusia* (*G. affinis*)
        - Genus *Poecilia* (*P. maylandi*) (*P. reticulatus*)
        - Genus *Limia* (*L. melanogaster*)
        - Genus *Xiphophorus* (*X. montezume*) (*X. helleri*)
        - Genus *Pseudoxiphophorus* (*P. bimaculatus*)
      - Subfamily Fluviphylacinae
      - Subfamily Aplocheilichthyinae
        - Genus *Aplocheilichthys* (*A. pulimus*) (*A. maculates*)
  - Superfamily Cyprinodontoidea
    - Family Goodeidae
      - Subfamily Empetrichthyinae
      - Subfamily Goodeinae
        - Genus *Ameca* (*A. sprendens*)
        - Genus *Chapalichthys* (*C. pardalis*)
        - Genus *Ilynodopn* (*I. xantusi*)
        - Genus *Xenotoca* (*X. eiseni*)
    - Family Cyprinodontidae
      - Subfamily Cubanichthyinae
      - Subfamily Cyprinodontinae

Observations and sketches of the bone structures of 26 fishes were made with the aid of a binocular dissecting microscope (Olympus SZX12). Live fishes were deeply anesthetized in saline containing a mixture of 7 parts of phenyl-urethane and 3 parts of ethanol before use. Specimens were shortly thereafter treated for a few hours with 0.2 N NaOH after removal of the skin and most muscle with a pair of forceps. They were then stained with alizarin red S after they were rinsed in tap water. Before they were examined, stained specimens were cleared in 50% glycerin. Details of development were observed for several

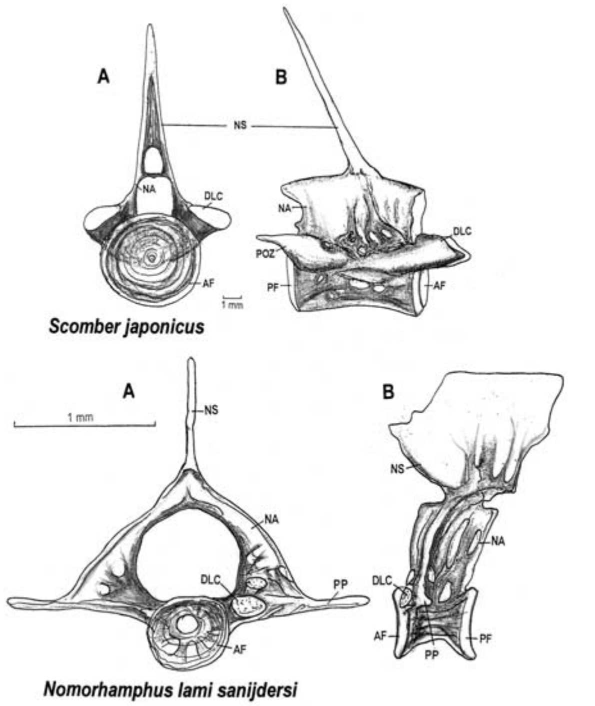

Fig. 7 Drawings of the first vertebra of *Scomber japonicus* and *Nomorhamphus lami sanijdersi.* Anterior (A) and lateral (B) views of the first vertebra.

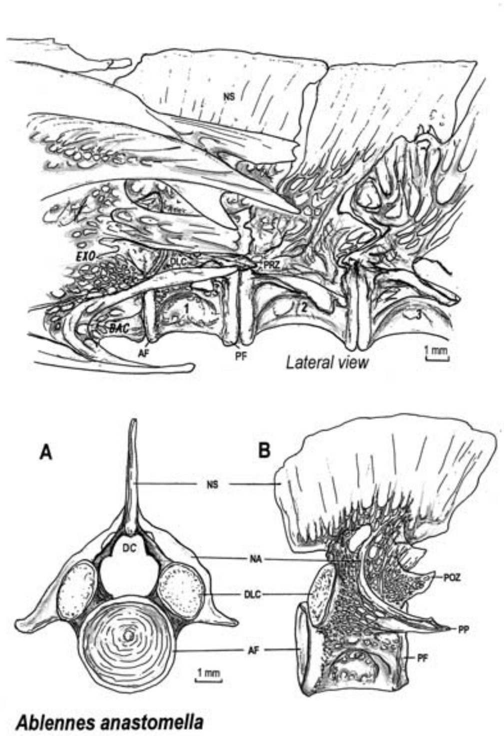

Fig. 8 Drawings of a lateral view of the posterior region of the skull with the anterior vertebrae of *Ablennes anastomella* as well as drawings of the first vertebra. Anterior (A) and lateral (B) views of the first vertebra.

individuals. Developmental stages of individuals after hatching were classified according to Iwamatsu (1994, 2004). Names for skeletal structure were traditionally those described by Owen (1984) and Yabumoto and Ueno (1984). Abbreviations of anatomical technical terms used in this study are given as follows:

AF, anterior face of the centrum
BAC, basioccipital
C, centrum
DC, small dorsal compartment of the neural canal
DLC, disk-like condyle articulated with the exoccipital
EXO, exoccipital
NA, neural arch
NC, neural canal
NS, neural spine
PF, posterior face of the centrum
POZ, postzygapophysis
PP, parapophysis

RESULTS

1. *Development of articular bones of the first centrum in Oryzias latipes*

Oryzias latipes was found to have 30 vertebrae (n = 3). In adults, the centrum of the first two vertebrae and a few vertebrae from the caudal end was slightly shorter than the rest, in agreement with Stockely (1952) who examined the warmouth. The first vertebra bears epipleurals (intermuscular bones) on the transverse processes (parapophyses) but does not have pleural ribs. The slender, vestigal pleural ribs of the second vertebra are found separate on the ventral side far from the parapophyses. The position of the parapophyses shifts from the upper to the lower region of the neural arches in posterior vertebrae of the trunk. The first centrum bends its anterior region ventrally and fits its anterior face to the lower face of the basioccipital.

In fry (Stage 40) 4.5 mm TL just after hatching, the upper ends of the neural arches of the first vertebra are separate from

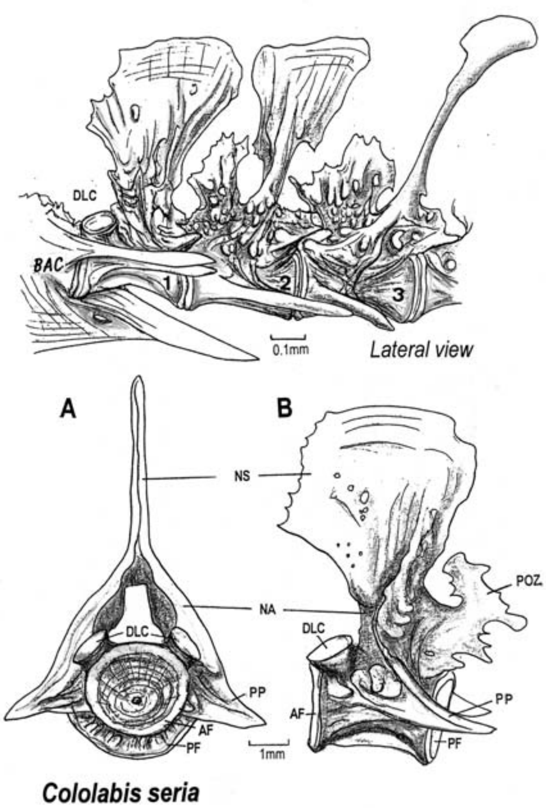

Fig. 9 Drawings of a lateral view of the posterior region of the skull with the anterior region of the vertebrae of *Cololabis seria,* as well as drawings of the first vertebra. A: Anterior view, B: Lateral view.

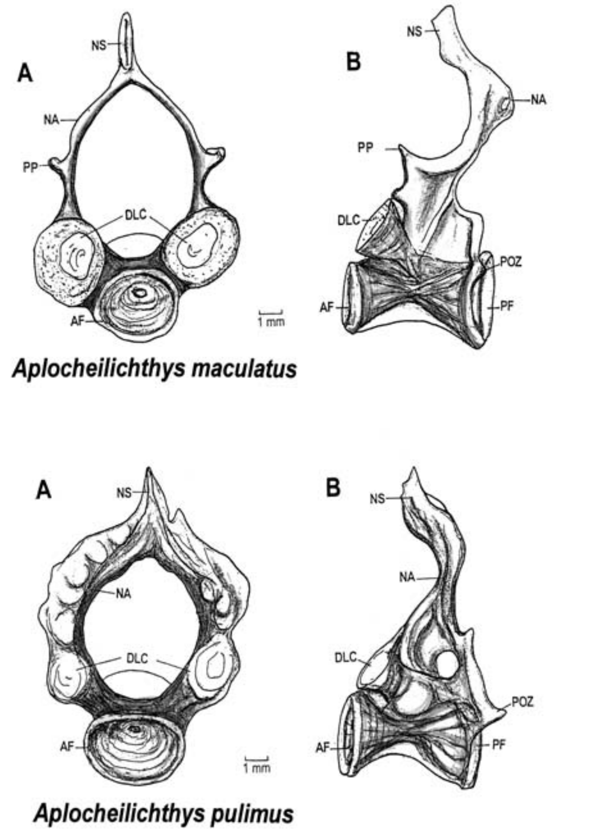

Fig. 10 Drawings of the first vertebra of *Aplocheilichthys maculatus* and *Aplocheilichthys pulimus.* A: Anterior view, B: Lateral view.

each other. The first vertebra articulates with the skull only by a basioccipital condyle. At 6.7 mm TL (Stage 40, type I in Figs. 1 and 2), the upper ends of the neural arches of the first vertebra do not attach, whereas the upper ends are already attached in the posterior vertebrae (type I in Fig. 1). The first vertebra (centrum: 110 μm in length, 80 μm in diameter) in fry (Stage 41) 8.5 mm TL (type II in Figs. 1 and 2) has somewhat thickened neural arches but does not exhibit any modification for articulation with the undifferentiated exoccipitals (Fig. 2). In these early stages, there are neither definite parapophyses nor neural spines (Stage 41, type III). Projected condyles on the anterior regions of the first vertebra join with out-growths from the posterior ends of the exoccipitals, i.e. three points of incomplete articulation for the skull are established. Parapophyses can be clearly recognized on the lateral region of the neural arch. In older fry (Stage 42) 11.5 mm TL (type IV in Figs. 1 and 2), the neural arches of the first vertebra form a thin, fan-like neural spine and wider parapophyses than those of the fry 10.0 mm TL. The first five neural spines extend as thin fan-like bones from neural arches that have closed (fused) at the dorsal end. As growth proceeds, the dorso-lateral articular bones for the exoccipitals enlarge, and the parapophyses that are widely developed bear epipleurals (intermuscular bones) (Stage 43, type V in Fig. 2). In type VI (Stage 45) shown in Fig. 2, the parapophyses expand at the lower side, and the constricted compartment in the neural canal is easily distinguishable as a small concavity (DC) at the dorsal side of neural canal through which the spinal cord runs. These observations reveal for the first time that in *O. latipes,* the dorso-lateral condyles of the first vertebra that articulate to the exoccipitals are formed during the growth period of stage 41 from 7.5 mm TL to 8.5 mm TL, following formation of the median articular bone of the basioccipital, and that the position of the parapophyses shifts from the upper to the lower region of the neural arches as growth progresses.

2. *Articulation of the first vertebra with the skull in Beloniformes and Cyprinodontiformes*

In the fishes examined, the first two vertebrae and a few vertebrae from the caudal end were definitely shorter than the rest. The position of the parapophyses was lower in the posterior vertebrae of the trunk.

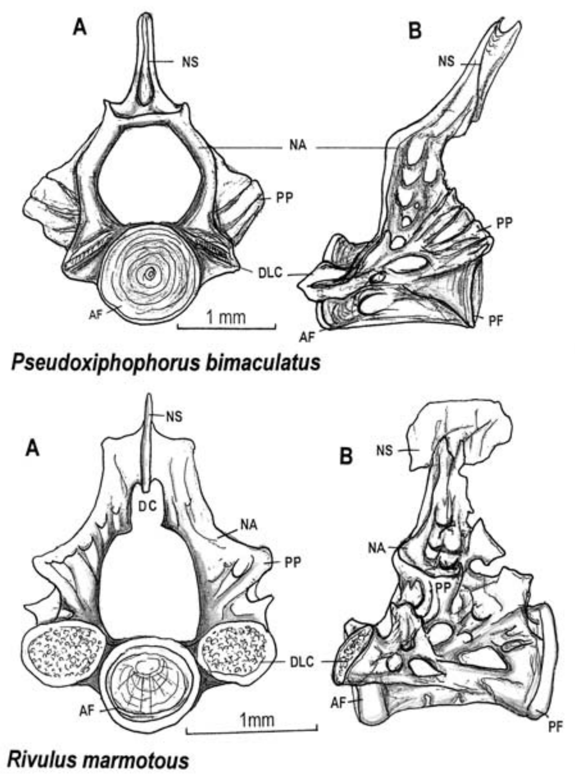

Fig. 11 Drawings of the first vertebra of *Pseudoxiphophorus bimaculatus* and *Rivulus marmotous.* A: Anterior view, B: Lateral view.

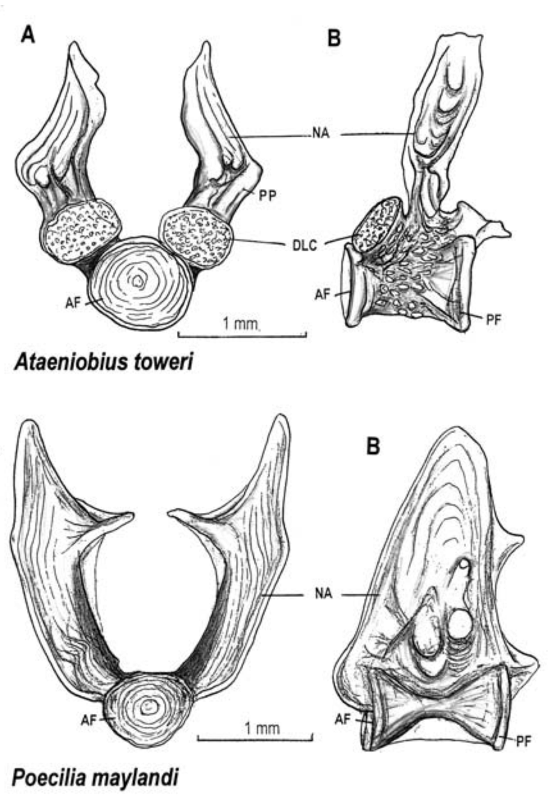

Fig. 12 Drawings of the first vertebra of *Ataenibius toweri* and *Poecilia maylandi.* A: Anterior view, B: Lateral view.

Beloniformes:

The widely expanded regions of the neural arches on the first centrum are projected towards the lower lateral sides of the neural canal and form transverse processes (diapophyses, parapophyses) which bear epipleurals in *Oryzias latipes* (Fig. 3), *O. luzonensis* (Fig. 4) and *Xenopoecilus sarasinorum* (Fig. 4). The neural spine is formed as a thin fan-shaped bone on the first several vertebrae in Beloniformes (Figs. 3 and 4). The first vertebra bears first epipleural ribs on the parapophyses. Parapophyses also develop in Belonoidei such as *Dermogenys* (Fig. 3), *Hemirhamphodon* (Fig. 5), *Hemiramphus* (Fig. 6), *Nomorhamphus* (Fig. 7), *Prognichthys* (Fig. 6), *Ablennes* (Fig. 8) and *Cololabis* (Fig. 9), but not in *Scomber* (Fig. 7). In all Beloniformes examined in the present study, the basioccipital and exoccipital condyles were usually well-formed.

There were no fundamental differences in the modification of the first centrum to allow articulation with the basioccipital condyle among the fishes examined in this study (Figs. 3-9). The morphology of the large median condyle of the basioccipital was quite similar among these fishes, but two small dorso-lateral condyles on the exoccipitals were somewhat different, consisting of sucker-like disks with or without cartilage. In the first vertebra of *Delmogenys, Hemirhamphodon, Oryzias, Xenopoecilus* and *Hemiramphus,* two dorso-lateral articular points that were in contact with the exoccipitals were separated laterally from the median condyle at a wide angle (80-170°, see Table 1). The large median condyle was in contact with a cartilaginous facet on the projected posterior region of the basioccipital while a round concavity on the first centrum faced ventrally, as described in centrarchid fishes by Stockely (1952). The facets of the dorso-lateral condyles to the exoccipitals were concave in contact with cartilage in *Oryzias* and *Xenopoecilus,* but differed sligthtly from the facets in *Ablennes, Cololabis, Hemiramphus, Prognichthys* and *Scomber* which were disk-like and lacked cartilage. The dorsal compartment (DC) in the neural canal was present in most in Beloniformes, except for *Hemirhamphodon* and *Nomorhamphus* in Family Hemiramphidae. Thus, in the first vertebra of Beloniform fishes, parapophyses are located on the lower lateral sides of the neural arches which fuse at the dorsal end, forming a spine. The posterior surface projecting from each exoccipital forms a condyle for articulation, although it varies in the presence or absence of the cartilage on the articulation.

Cyprinodontiformes:

In Cyprinodontiformes, the first vertebra attaches to skull in several ways. *Ataeniobius* (Fig. 12), *Ameca* (Fig. 15), *Anableps* (Fig. 5), *Aplocheilichthys* (Fig. 10), *Chapacletis* (Fig. 17), *Ilynodon* (Fig. 16), *Rivulus* (Fig. 11) and *Xenotoca* (Fig. 16)

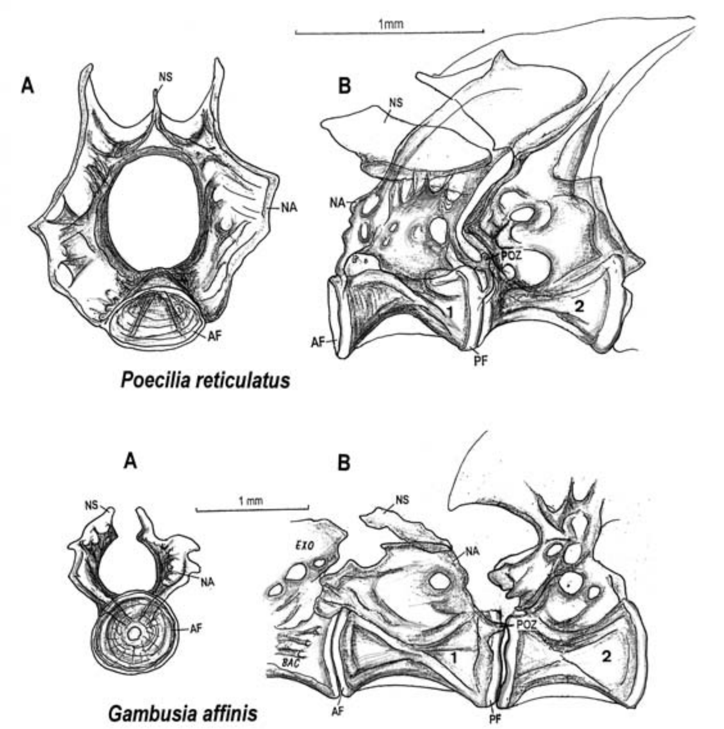

Fig. 13 Drawings of anterior view (A) of the first vertebra of *Poecilia reticulatus* and *Gumbusia affinis,* and a lateral view (B) (the posterior region of the skull with the first two vertebrae in *G. affinis*).

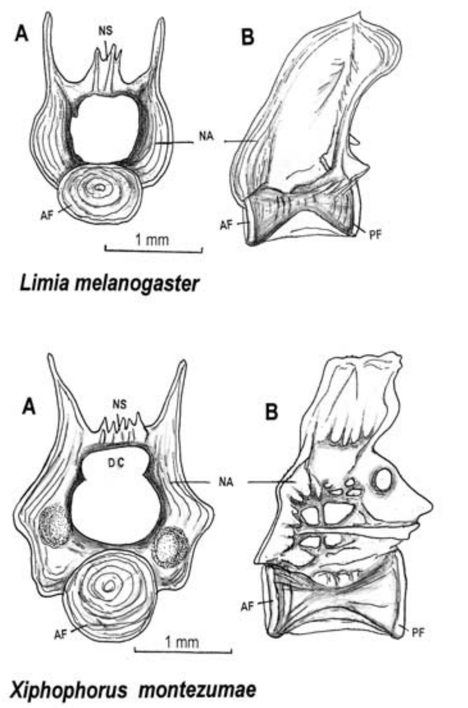

Fig. 14 Drawings of the first vertebra of *Limia melanogaster* and *Xiphophorus montezumae.* A: Anterior view, B: Lateral view.

possess well developed basioccipital and exoccipital condyles. In contrast, exoccipital condyles are in *Gambusia* (Fig. 13), *Limia* (Fig. 14), *Poecilia* (Figs. 12 and 13), *Pseudoxiphophorus* (Fig. 11) and *Xiphophorus* (Figs. 14 and 15) (Table 1).

In *Ataeniobius* (Fig. 12), *Ameca* (Fig. 15), *Anableps* (Fig. 5), *Aplocheilichthys* (Fig. 10), *Rivulus* (Fig. 11), *Chapacletis* (Fig. 17), *Ilyodon* (Fig. 16) and *Xenotoca* (Fig. 16), the first vertebra articulates with the skull by basioccipital and exoccipital condyles, and the parapophysis is located dorsally or is extremely reduced. *Anableps* is the exception in having well-developed parapophyses located ventrally. The first vertebra of *Pseudoxiphophorus* possesses long narrow condyles for the exoccipital (Fig. 11). In *Aplocheilichthys* (Fig. 10), *Pseudoxiphophorus* (Fig. 11), *Rivulus* (Fig. 11), and *Poecilia reticulatus* (Fig. 13), the neural spine is poorly formed on closed neural arches. Small multiple neural spines are observed in *Limia* (Fig. 14) and *Xiphophorus* (Figs. 14 and 15). In *Aplocheilichthys* (Fig. 10), *Ataeniobius* (Fig. 12), *Poecilia* (Fig. 12), *Gambusia* (Fig. 13), *Ameca* (Fig. 15), *Xiphophorus* (Fig. 15), *Ilyodon* (Fig. 16), *Xenotoca* (Fig. 16) and *Chapacletis* (Fig. 17), the neural arches are open. The first vertebra of *Aplocheilichthys* and *Rivulus* resembles type IV-V of young *Oryzias,* although the position of the parapophyses is in the dorsal (upper) region. The morphology of the first vertebra is extremely diversified in Cyprinodontiformes and may not always be useful as a character to classify Cyprinodontiform fishes.

DISCUSSION

Exoccipital condyle: In the young *Oryzias latipes* at stage 40 of growth (type I-II), the first vertebra does not yet join with the posterior ends of the exoccipitals, articulating with the skull only by the basioccipital condyle. This form of articulation was also observed in *Gambusia affinis* and *Poecilia maylandi* of the Subfamily Poeciliinae in the present study. That the first vertebra of *Gambusia affinis* contacts the basioccipital only by a median condyle has already been described by Ramaswami (1946). According to Parenti (1981), the first vertebra exhibits no exoccipital condyles in the entire tribe of Cyprinodontini, including *Pantanodon* of the Subfamily Poeciliinae. When *O. latipes* is fully-grown, the first vertebra articulates with the basioccipital and exoccipitals by three condyles, as is found in all fishes of the Belonidae. The presence of this type of first vertebra may be a common character in Belonidae. However, there are also both basioccipital and exoccipital condyles in most of the Cyprinodontiformes. Therefore, the presence of exoccipital condyles is not a unique character of Beloniformes.

Parapophysis: The type III-IV first vertebrae in *Oryzias latipes* at growth stage 41-42 exhibit no or small parapophyses at the

Table 1
Morphological characteristics of the first vertebra in Beloniformes and Cyprinodontiformes.

Taxon	Exoccipital condyles (angle*)	Parapophyses	Neural spine	Neural arch (DC**)	Type***
Beloniformes					
Oryzias latipes	+ (130°)	lower	+	closed (+)	VI
Oryzias luzonensis	+ (120°)	lower	+	closed (+)	VI
Xenopoecilus sarasinorum	+ (120°)	lower	+	closed (+)	VI
Dermogenys pusillus	+ (160-170°)	lower	+	closed (+)	VI
Hemirhamphodon pogonognathus	+ (160-170°)	lower	+	closed (−)	V
Hemiramphus sajori	+ (90°)	lower	+	closed (+)	VI
Nomorhamphus lami sanijdersi	+ (130°)	lower	+	closed (−)	V
Prognichthys agoo agoo	+ (100°)	lower	+	closed (+)	VI
Ablennes anastomella	+ (100°)	lower	+	closed (+)	X
Scomber japonicus	+ (100°)	none	+	closed (+)	X
Cololabis seria	+ (80°)	lower	+	closed (+)	VI
Cyprinodontiformes					
Aplocheilichthys maculatus	+ (110°)	upper	±	closed (+)	V[a]
Aplocheilichthys pulimus	+ (100°)	upper	+	closed (+)	VI[b]
Rivulus marmotous	+ (160-170°)	upper	+	closed (+)	VI[b]
Anableps anableps	+ (110°)	lower	−	closed (−)	X
Gambusia affinis	−	upper	−	open (−)	I
Limia melanogaster	−	none	±	closed (+)	II
Poecilia maylandi	−	none	−	open (−)	I
Poecilia reticulatus	−	upper	±	closed (−)	II
Pseudoxiphophorus bimaculatus	−	upper	+	closed (−)	II
Xiphophorus montezumae	±	upper	±	closed (+)	II
Xiphophorus helleri	−	none	−	open (−)	I
Ataeniobius toweri	+ (100°)	upper	−	closed (+)	II
Ameca sprendens	+ (120°)	upper	−	open (−)	I
Chapalichthys pardalis	+ (110°)	upper	−	open (−)	X
Ilyodon xantusi	+ (100°)	upper	−	open (−)	X
Xenotoca eiseni	+ (110°)	uppe	−	open (−)	X

+, present; −, absent; ±, unclear.
*The angle of left and right condyles articulated with the exoccipitals to the median articular surface of the centrum.
**DC: the dorsal compartment of the neural canal.
***Type I-VI of the first vertebra in growing stages of *O. latipes.*
Type VI[b], V[a] and type X are not comparable to any types seen in young *O. latipes.*

upper regions of closed neural arches. Such a feature of the first vertebra is seen in Cyrinodontiformes that exhibit parapophyses at the upper regions of the neural arches. The type V first vertebra in stage 43 of growth exhibits undifferentiated parapophyses with epipleurals at somewhat upper (dorsal) regions of the neural arches. A similar type of first vertebra is seen in *Aplocheilichthys* and *Rivulus*. *Anableps* is similar except that the parapophyses are located at the lower regions of the neural arches. Parapophyses at the lower regions of the neural arches are seen in fully-grown *Oryzias*. In *Oryzias,* the position of the parapophyses shifts from the upper to the lower region of the neural arches as growth progresses. In the first vertebra of Beloniformes, the parapophyses usually expand to the lower lateral sides of the neural arches.

Neural arch and neural spine: In the early growth stage (type I) of the first vertebra of *Oryzias,* the upper ends of the neural arches remain unattached from each other, and do not form a neural spine. Neural arches in all Beloniform fishes are closed or fused at the upper end and form a neural spine, whereas those in Cyprinodontiform fishes except for Family Aplocheiliidae and Family Revulidae are open, not forming a neural spine. On the closed upper ends of the neural arches in Cyprinodontiform fishes, there are no or multiple neural spines. The first vertebra (type V) in the advanced stage 43 of *Oryzias* is very similar to

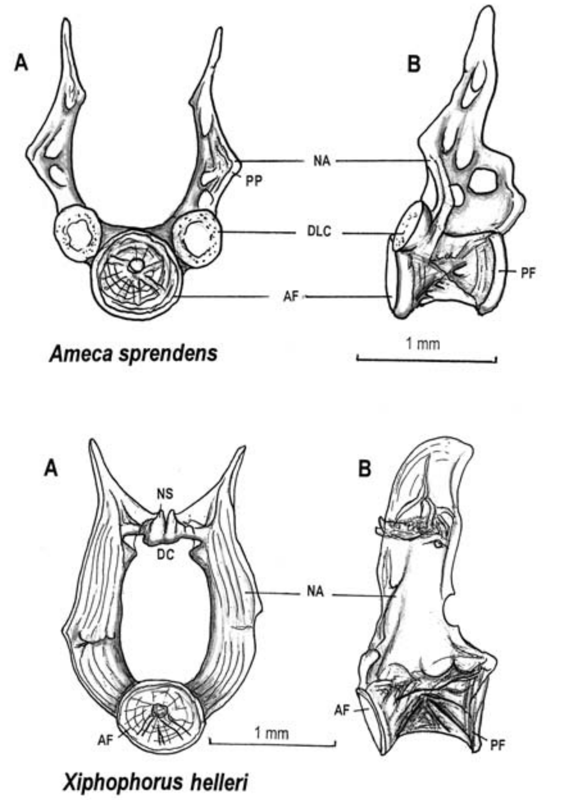

Fig. 15 Drawings of the first vertebra of *Ameca sprendens* and *Xiphophorus helleri.* A: Anterior view, B: Lateral view.

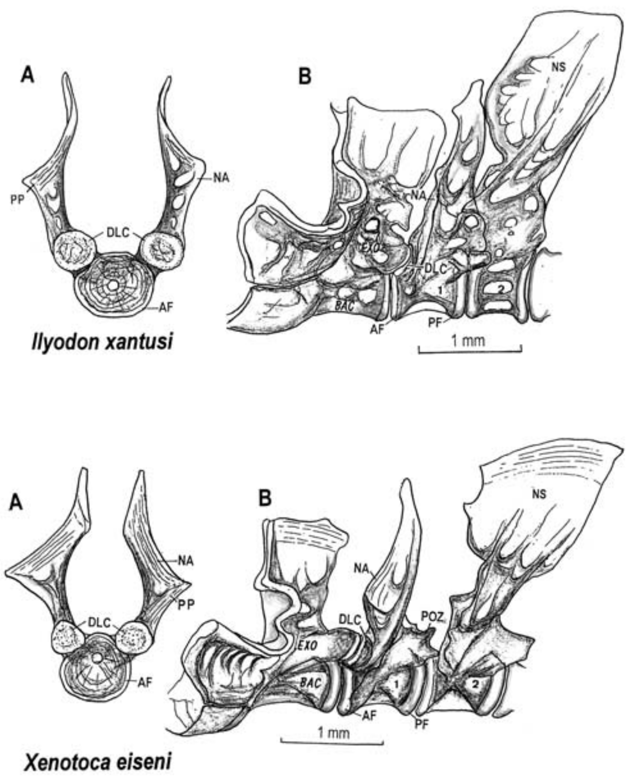

Fig. 16 Drawings of anterior view (A) of the first vertebra of *Ilyodon xantusi* and *Xenotoca eiseni.* Drawings of lateral views (B) of the posterior region of the skull and the anterior region of the vertebrae of *I. xantusi* and *X. eiseni.*

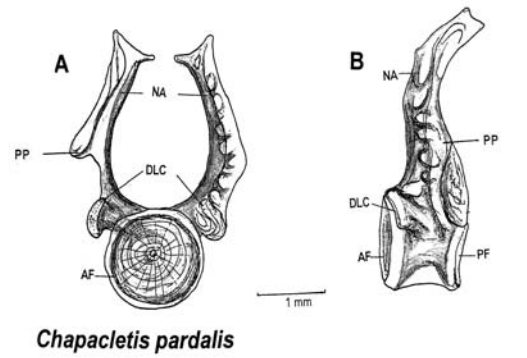

Fig. 17 Drawings of the first vertebra of *Chapacletis pardalis.* A: Anterior view, B: Lateral view.

that of adult fish (type VI), except for the presence of a definite dorsal compartment (DC). Type VI is observed in most fishes of the Beloniformes, although the DC was not observed in the neural canal of *Hemirhamphodon pogonognathus* and *Nomorhamphus lami snijdersi.* The type VI^b with the dorsal compartment is also recognized in *Rivulus,* in which the parapophyses are located at the upper region of the neural arches. Thus, the growth patterns of the first vertebra in *Oryzias latipes* might be suitable for taxonomical classification of fishes into several types. The convergent characteristics of the first vertebra in Beloniformes are (1) parapophyses at the lower region of the neural arches, (2) neural arches closed at the upper end, (3) a laterally flat neural spine, and (4) the presence of exoccipital condyles. The present observations suggest that Cyprinodontiformes exhibit early steps in development of the first vertebra. We are greatly interested in conducting further investigations into whether or not these morphological characteristics of the first vertebra in Beloniformes result from passing through ontogenetic stages as seen in the growing process of *Oryzias.*

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