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Osteological and functional development of the flyingfish, *Cypselurus heterurus doederleini* (Teleostei: Exocoetidae)

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Abstract: The osteological development and functional processes in relation to feeding, swimming and flying of the laboratory-reared flyingfish, *Cypselurus heterurus doederleini* were examined. Ossification started upon hatching at 5.54 mm SL (standard length) and almost fully ossified at 15.80 mm SL. Early ossification of cranial elements suggests the impact of strength on the neurocranium, thereby tolerating pressures from the developing brain, muscle mass, vertebral column and the trunk region. In the early stage, larvae were actively feeding which was attributable to the early ossification of the feeding apparatus. Active swimming and darting above the water surface were attributable to the rudder-like structure of the hypurals, providing more attachment for muscles resulting to sufficient force, and to the development of the pectoral and the ventral fin rudiments. Generally, the early on-set of osteological development in the early stage and the short period of ossification process in *C. heterurus doederleini*, suggest an early feeding, higher growth rate and the ability to escape from predators by darting and swimming, resulting to higher survival rate.

Key words: *Cypselurus, osteological development, function.*

INTRODUCTION

Flyingfish *Cypselurus heterurus doederleini* (Steindachner) is an abundant, highly oceanic, and one of the most important commercial species in Japan. It belongs to the largest flyingfishes that thrives in the water of Japan and its meat is one of the favorite delicacies as sliced raw fish called "sashimi". Developmental informations of this species are found in many literatures (Nayudu, 1923; Bruun, 1935; Breder, 1938; Hubbs and Kampa, 1946; Imai, 1959). However, its osteological development has not been published yet. Hence, the present study was conducted to describe the developmental pattern from the initial appearance to full ossification and their relationhips to swimming, feeding and flying functions which are vitally important for the survival.

MATERIALS AND METHODS

Samples of larvae were taken from the artificially inseminated eggs of *Cypselurus heterurus doederleini* taken from the parents collected off Iburi, Tosashimizu, Kochi Prefecture. Reared in 2 tons rearing tank, 10 larvae were sampled every other day and fixed initially in 10% neutral formalin solution. Clearing and staining procedures follow the method of Dingerkus and Uhler (1977) for both cartilage and bone. Osteological developoment was observed and sketched using a Nikon SMZ-10 stereoscopic dissecting microscope with a camera lucida. Osteological terminology follows Weitzman (1962), Rosen (1964), Fujita (1990, 1992) and Fujita and Oozeki (1994).

RESULTS

Neurocranium

Shortly after hatching at 5.54 mm standard length (SL) specimen (0 day), the skull was fully cartilaginous. The ethmoid, lateral ethmoid, rostral cartilage, nasal and basisphenoid were absent (Figs. 2 and 3). Prevomerine plate and parachondral cartilage were bridged by fibrous ossification of parasphenoid (Figs. 2A and 3A). In this stage, the frontal was fibrously ossified and became fully ossified in 11.43 mm SL specimen (16 days) (Figs. 1 and 2A–D). The preformed cartilaginous sphenotic, pterotic, supraoccipital, epiotic and exoccipital, started ossifying fibrously in 9.43 mm SL specimen (13 days) and became fully ossified in 11.43 mm SL specimen (16 days) (Figs. 1, 2C–D). The basioccipital became fibrously ossified in 7.36 mm SL

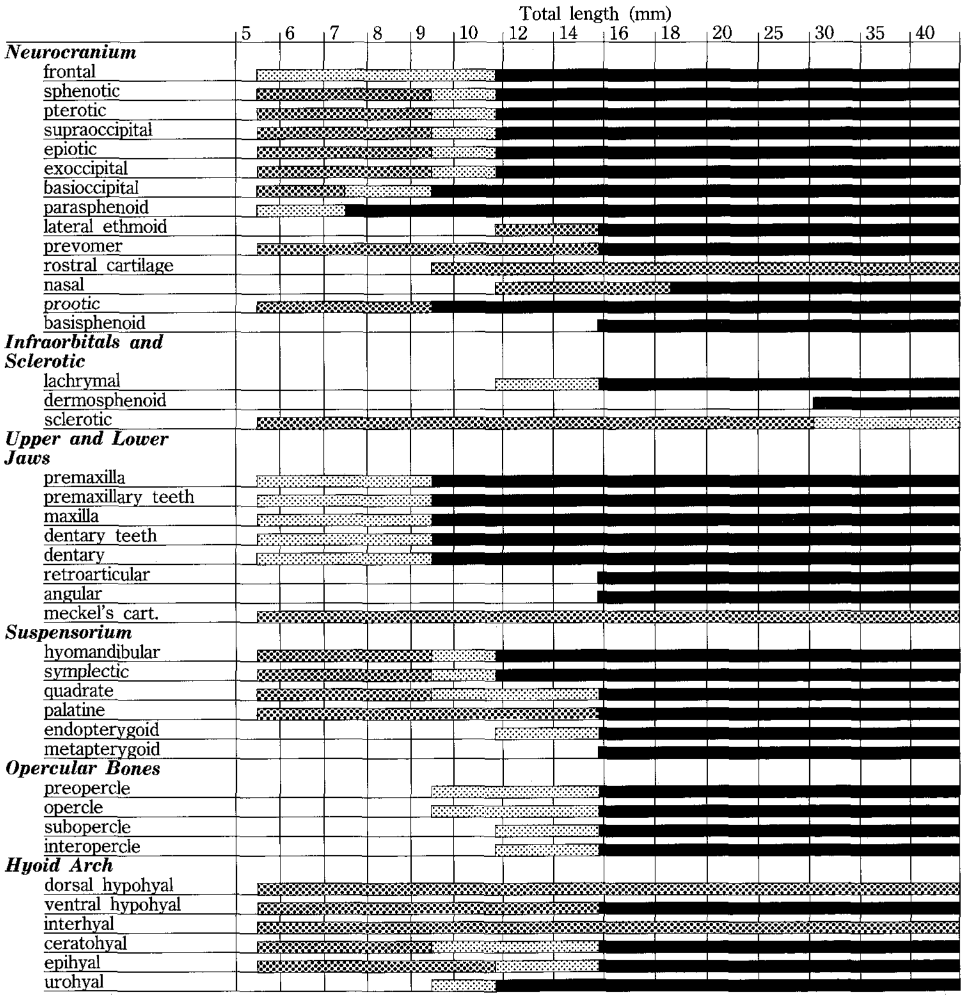
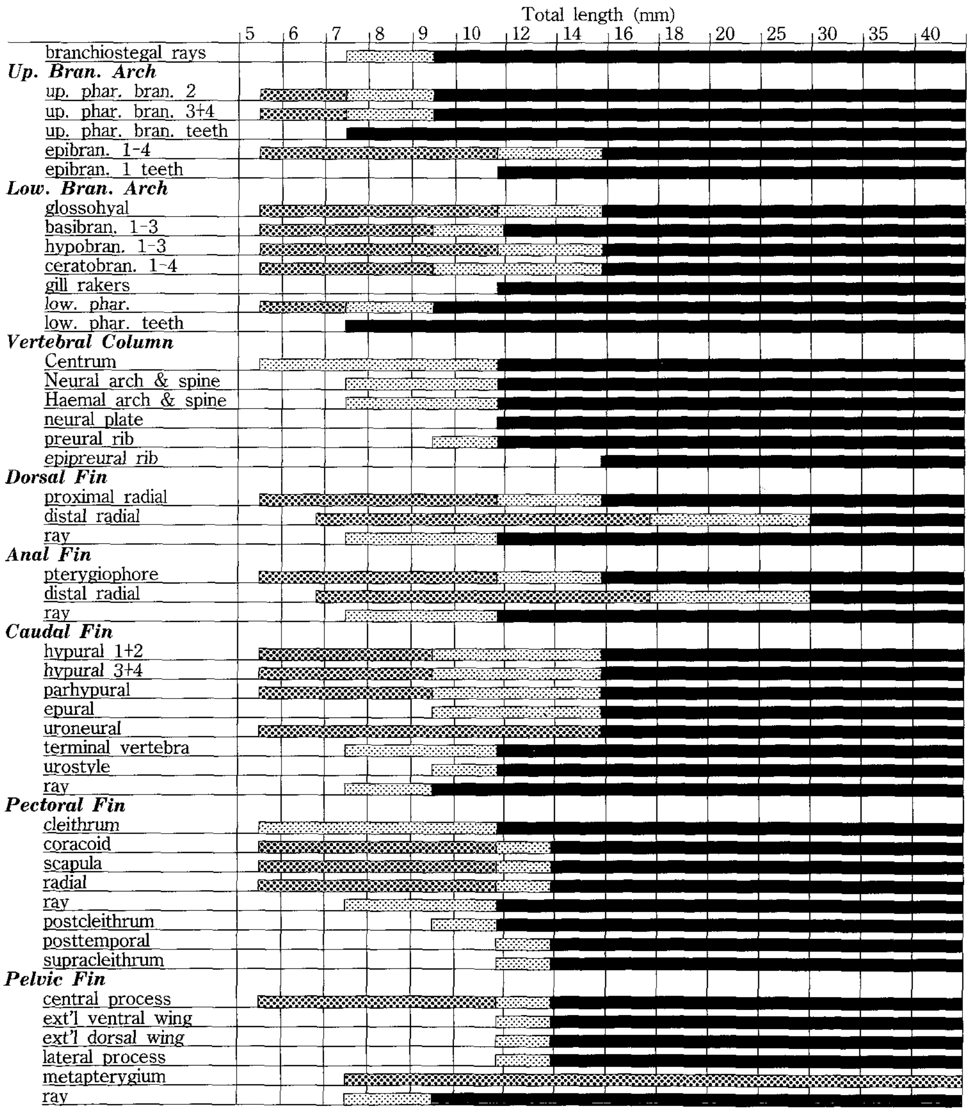


Fig. 1. Osteological developmental patterns in *Cypselurus heterurus doederleini*. ▒, cartilaginous; ░, fibrously ossified; ■, fully ossified.

specimen (8 days) and became fully ossified in 9.43 SL specimen (13 days) (Figs. 1, 2B-C and 3B-C). The parasphenoid became fully ossified in 7.36 mm SL specimen (8 days) (Figs. 1, 2B and 3B). In 11.43 mm SL specimen (16 days), cartilaginous lateral ethmoid started to be formed laterally to the mass of rostral cartilage and became fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 2D-E). In 15.80 mm SL specimen (22 days), cartilaginous prevomer became ossified (Figs. 1 and 3E-F). The rostral cartilage started forming in 9.43 mm SL spicemen (13 days) (Figs. 1 and 2C-F). The nasal started forming fibrously in 11.43 mm SL specimen (16 days) and became fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 2D-E). The cartilaginous prootic became fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1, 2C-D and 3C-D). The basisphenoid appeared to be ossified in 15.80 mm SL specimen (22 days) and developed with subsequent growth (Figs. 1 and 2E-F).



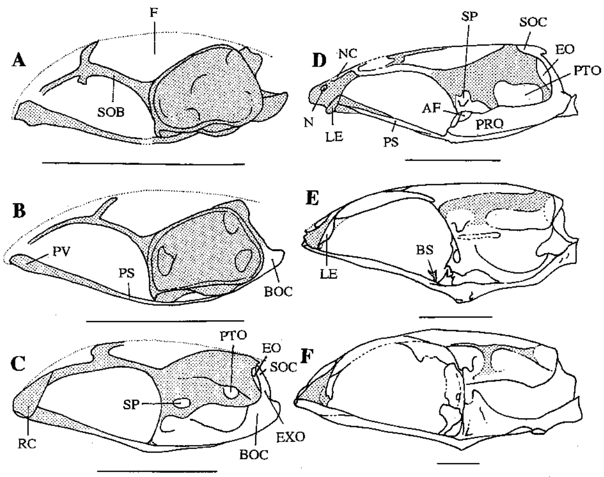


Fig. 2. Development of neurocranium (lateral view) in *Cypselurus heterurus doederleini*. Stippled area, cartilage. Broken line, fibrously ossified. Open area, ossified portion. A) 5.54 mm; B) 7.36 mm; C) 9.43 mm; D) 11.43 mm; E) 15.80 mm; F) 30.04 mm. *AF*—auditory foramen; *BOC*—basioccipital; *BS*—basisphenoid; *EO*—epiotic; *EXO*—exoccipital; *F*—frontal; *LE*—lateral ethmoid; *N*—nasal; *NC*—nasal canal; *PRO*—prootic; *PS*—parasphenoid; *PTO*—pterotic; *PV*—prevomer; *RC*—rostral cartilage; *SP*—sphenotic; *SOB*—supraorbital; *SOC*—supraoccipital. Bars = 1 mm.

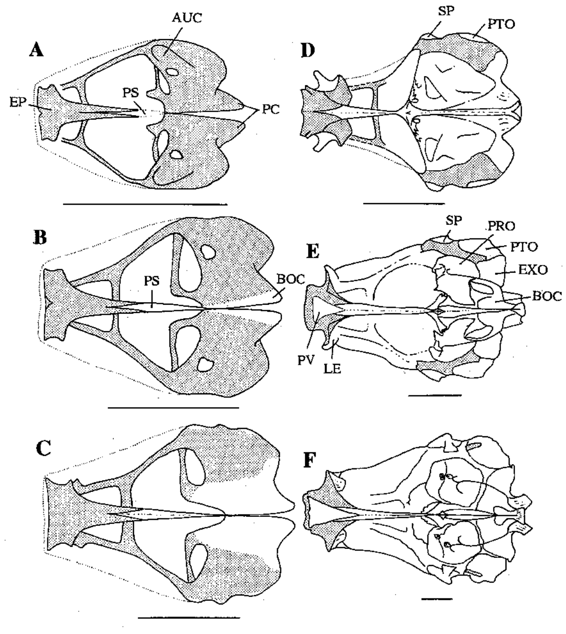


Fig. 3. Development of neurocranium (ventral view) in *Cypselurus heterurus doederleini*. Stippled area, cartilage. Broken line, fibrously ossified. Open area, ossified portion. A) 5.54 mm; B) 7.36 mm; C) 9.43 mm; D) 11.43 mm; E) 15.80 mm; F) 30.04 mm. *AUC*—auditory capsule; *BOC*—basioccipital; *EP*—ethmoid plate; *EXO*—exoccipital; *LE*—lateral ethmoid; *PC*—parachondral; *PRO*—prootic; *PS*—parasphenoid; *PTO*—pterotic; *PV*—prevomer; *SP*—sphenotic. Bars = 1 mm.

In larger specimens, a large amount of cartilage on the sutures among ethmoid, lateral ethmoid, frontal and vomer was retained in the anterior region, and a small amount of cartilage on the sutures among sphenotic, pterotic, epiotic and frontal was retained in the posterior region (Fig. 2F).

Sclerotics and infraorbitals

In 5.54 mm SL specimen (0 day), the lachrymal and dermosphenoid were absent but the eye capsule was formed, surrounded by thin sclerotic cartilage (Fig. 4A). The lachrymal started forming fibrously in 11.43 mm SL specimen (16 days) and became fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 4D-E). The anterior and posterior arc of sclerotic started to be ossified with the appearance of an ossified dermosphenoid in 30.03 mm SL specimen (44 days) (Figs. 1 and 4F).

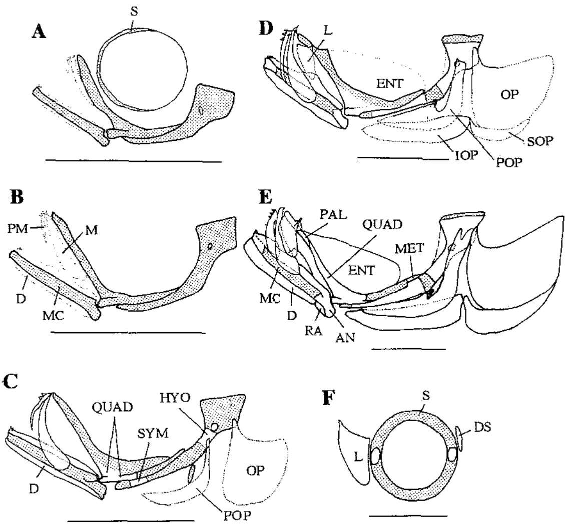


Fig. 4. Development of viscerocranium; opercular apparatus, circumorbitals and sclerotic in *Cypselurus heterurus doederleini.* Stippled area, cartilage. Broken line, fibrously ossified. Open area, ossified portion. A) 5.54 mm; B) 7.36 mm; C) 9.43 mm; D) 11.43 mm; E) 15.80 mm; F) 30.04 mm. *AN* — angular; *D* — dentary; *DS* — dermosphenoid; *ENT* — endopterygoid; *HYO* — hyomandibular; *IOP* — interopercular; *L* — lachrymal; *M* — maxilla; *MC* — maxillary cartilage; *MET* — metapterygoid; *OP* — opercular; *PAL* — palatine; *POP* — preopercular; *PM* — premaxilla; *QUA* — quadrate; *RA* — retroarticular; *S* — sclerotic; *SOP* — subopercular; *SYM* — symplectic. Bars = 1 mm.

Jaws

Formation of the jaws started from fibrous to fully ossified bone. In 5.54 mm SL specimen (0 day), the maxilla, premaxilla and the lower jaw were fibrously ossified (Figs. 1 and 4A). Teeth on the premaxilla and the lower jaw were fibrously present. The maxilla, premaxilla and teeth became fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1 and 4C).

The dentary and retroarticular represented by fibrous ossification were fused and formed by shelling the Meckel's cartilage in 5.54 mm SL specimen (0 day) (Figs. 1 and 4A-B). The dentary became fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1 and 4C). Meckel's cartilage was retained as a cartilaginous tissue in larger specimens (Fig. 4E). The retroarticular became separated from the dentary with the formation of the angular in 15.80 mm SL specimen (22 days) (Figs. 1 and 4E).

Suspensorium

In the stage of 5.54 mm SL (0 day), the hyomandibular and symplectic were fused cartilaginously as one unit (Fig. 4A). They started to be separated and partially ossified in 9.43 mm SL specimen (13 days) and became fully ossified in 11.43 mm SL specimen (16 days) (Figs. 1 and 4C-D). The quadrate and palatine were cartilaginous and fused in 5.54 mm SL specimen (0 day) (Fig. 4A). The quadrate became partially ossified in 9.43 mm SL specimen (13 days) and fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 4C-E). The palatine which was preformed as a cartilage became separated from the quadrate and fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 4E). In 11.43 mm SL specimen (16 days), the endopterygoid started to be formed by fibrous ossification and became fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 4D-E). The metapterygoid which arose from the cartilaginous posterior end of the quadrate, appeared fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 4E).

Opercular apparatus

In 5.54 mm SL specimen (0 day), any opercular element was not visible. The preopercle and opercle started forming fibrously in 9.43 mm SL specimen (13 days) and became fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 4C-E). The subopercle and interopercle started forming fibrously in 11.43 mm SL specimen (16 days). They became fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 4D-E).

Hyoid arch

All of the hyoid arch elements were cartilaginous in 5.54 mm SL specimen (0 day) (Figs. 1 and 5A). The ventral hypohyal became ossified in 15.80 mm SL (22 days), whereas the dorsal hypohyal and interhyal retained cartilaginous condition (Figs. 1 and 5E). The ceratohyal and epihyal were fused but apparently separated from hypohyal anteriorly and interhyal posteriorly. The ceratohyal became partially ossified in 9.43 mm SL specimen (13 days) and was fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 5C-E). The epihyal became partially ossified and separated from the ceratohyal in 11.43 mm SL specimen (16 days) and was fully ossifed in 15.80 mm SL specimen (22 days) (Figs. 1 and 5D-E). A long, slender and fibrous urohyal appeared on the anteroventral part of the hyoid arch in 9.43 mm SL specimen (13 days) and became fully ossified in 11.43 mm SL specimen (16 days) (Figs. 1 and 5C-D). The branchiostegal rays started forming on the ventrolateral margin of ceratohyal and epihyal in 7.36 mm SL specimen (8 days) and became fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1 and 5B-C).

Branchial arches

In 5.54 mm SL specimen (0 day), the branchial arch elements were cartilaginously formed (Fig. 6). The upper pharyngobranchial bones (UPB2 and UPB3+4) started ossifying fibrously with the appearance of pharyngeal teeth in 7.36 mm SL specimen (8 days) and became fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1 and 6B-C). The epibranchials (EP1-4) were chondrified in 5.54 mm SL specimen (0 day). They became partially ossified in 11.43 mm SL specimen (16 days) and fully ossified in 15.80 mm SL specimens (22 days) (Figs. 1 and 6D-E). The first epibranchial (EP1) developed teeth on it at 11.43 mm SL (16 days) specimens (Figs. 1 and 6D).

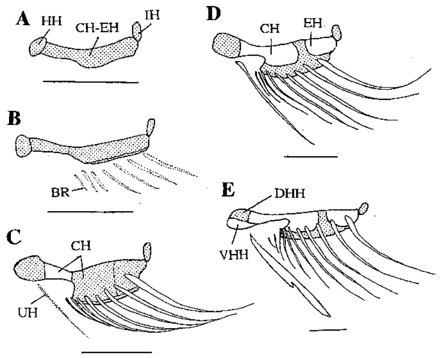


Fig. 5. Development of hyoid arch in *Cypselurus heterurus doederleini*. Stippled area, cartilage. Broken line, fibrously ossified. Open area, ossified portion. A) 5.54 mm; B) 7.36 mm; C) 9.43 mm; D) 11.43 mm; E) 15.80 mm. *BR*—branchiostegal rays; *CH*—ceratohyal; *CH-EH*—cerato-epihyal; *DHH*—dorsal hypohyal; *EH*—epihyal; *HH*—hypohyal; *IH*—interhyal; *VHH*—ventral hypohyal; *UH*—urohyal. Bars = 0.5 mm.

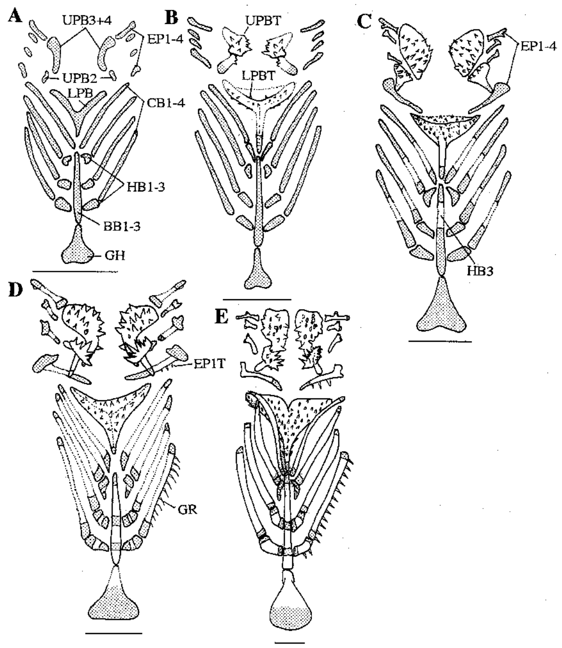


Fig. 6. Development of upper and lower branchial arches in *Cypselurus heterurus doederleini*. Stippled area, cartilage. Open area, ossified portion. A) 5.54 mm; B) 7.36 mm; C) 9.43 mm; D) 11.43 mm; E) 15.80 mm. *BB1-3*—basibranchial 1-3; *CB1-4*—ceratobranchial 1-4; *EP1-4*—epibranchial 1-4; *EP1T*—epibranchial 1 teeth; *GH*—glossohyal; *GR*—gill raker; *HB1-3*—hypobranchial 1-3; *LPB*—lower pharyngeal bone; *LPBT*—lower pharyngeal bone teeth; *UPB2*—upper pharyngeal bone 2; *UPB3+4*—upper pharyngeal bone 3+4; *UPBT*—upper pharyngeal teeth. Bars = 0.5 mm.

The lower branchial elements were cartilaginously formed in 5.54 mm SL specimen (0-day) (Fig. 6A). The glossohyal started to be ossified in 11.43 mm SL specimen (16 days) and became fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 6D-E). The basibranchials (BB1+2+3) were cartilaginously fused as one element in 5.54 mm SL specimen (0 day) (Figs. 6A). In 9.43 mm SL specimen (13 days), the third basibranchial (BB3) became partially ossified and separated from the first and second basibranchials (BB1 and 2) (Figs. 1 and 6C). It became fully ossified in 11.43 mm SL specimen (16 days) with simultaneous separation and full ossification of the first and second basibranchials (BB1 and 2) (Fig. 6D). The hypobranchials became partially ossified in 11.43 mm SL specimen (16 days) and fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 6D-E). The ceratobranchials became partially ossified in 9.43 mm SL (13 days) specimens and fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 6C-E). The gill rakers were developed on the ceratobranchials (CB) in 11.43 mm SL specimen (16 days) and on the hypobranchials (HB) in 15.80 mm SL specimen (22 days) (Figs. 1 and 6D-E). The lower pharyngeal bones became fibrously ossified with the appearance of teeth in 7.36 mm SL specimen (8 days) and fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1 and 6B-C).

Vertebral column

In 5.54 mm SL specimen (0 day), the notochord and the vertebral column (centra) were fibrously ossified, whereas the neural and haemal spines were fully chondrified (Figs. 7A and 8A). The centra became partially visible in 9.43 mm SL (13 days) and fully ossified in 11.43 mm SL specimen (16 days) (Figs. 1, 7B-C and 8C-E). The corresponding neural and haemal spines started ossifying fibrously in 7.36 mm SL specimen (8 days) and became fully ossified in 11.43

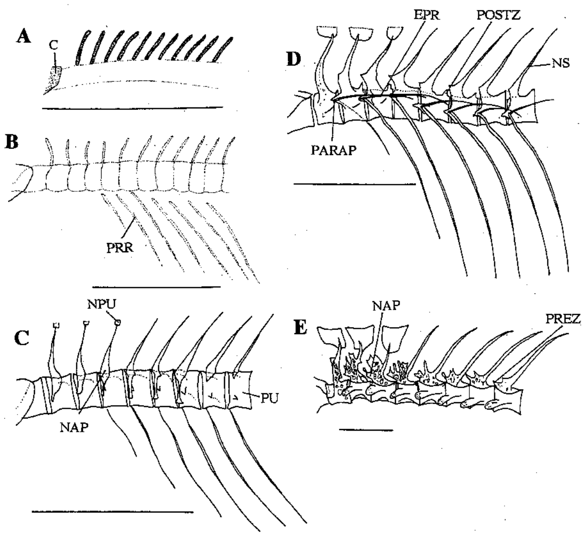


Fig. 7. Development of few anterior vertebral column in *Cypselurus heterurus doederleini*. Stippled area, cartilage. Dotted area, fibrously ossified. Open area, ossified portion. A) 5.54 mm; B) 9.43 mm; C) 11.43 mm; D) 15.80 mm; E) 30.04 mm. *C* — cranium; *EPR* — epipreural rib; *NAP* — neural arch plate; *NPU* — neural plate of preural centrum; *NS* — neural spine; *PARAP* — parapophysis; *POSTZ* — postzygapophysis; *PRR* — preural rib; *PREZ* — prezygapophysis; *PU* — preural centrum. Bars = 1 mm.

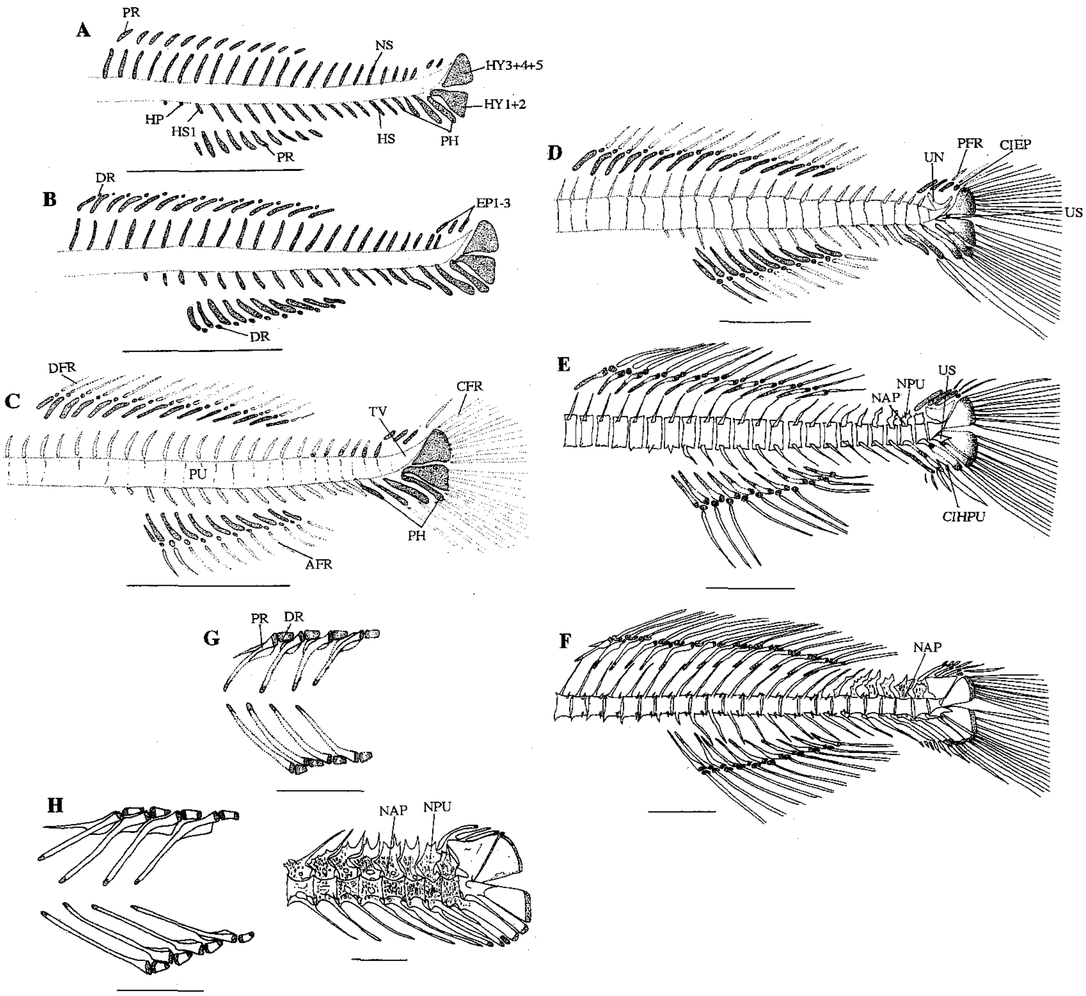


Fig. 8. Development of vertebral column, dorsal, anal and caudal fins and supports in *Cypselurus heterurus doederleini*. Stippled area, cartilage. Dotted area, fibrously ossified. Open area, ossified portion. A) 5.54 mm; B) 7.36 mm; C) 9.43 mm; D) 11.43 mm; E) 15.80 mm; F) 30.04 mm; G) 17.72 mm; H) 30.04 mm. *AFR* — anal fin ray; *CFR* — caudal fin ray; *DFR* — dorsal fin ray; *DR* — distal radial or median segment; *CIHPU* — interhaemal spine cartilage; *CIEP* — interepural cartilage; *EP1-3* — epural 1-3; *HP* — haemapophysis; *HS* — haemal spine; *HS1* — first haemal spine; *HY1+2* — hypural 1+2; *HY3+4+5* — hypural 3+4+5; *NAP* — neural arch plate; *NPU* — neural plate of preural centrum; *NS* — neural spine; *PFR* — procurrent fin ray; *PH* — parhypural; *PU* — preural centrum; *PR* — proximal radial or pterygiophore; *TV* — terminal vertebra; *UN* — uroneural; *US* — urostyle. Bars = 1 mm.

mm SL specimen (16 days) (Figs. 1, 7B-C and 8C-E). Three neural plates of the preural centrum of the precaudal vertebrae and four neural plates of the preural centrum of the caudal vertebrae started to be developed in 11.43 mm SL specimen (16 days) (Figs. 1, 7C and 8E). The neural arch plates started forming on the first few anterior preural centra (trunk region) and on the last few posterior preural centra (caudal region) of the vertebral column at 11.43

mm SL specimen (16 days) (Figs. 7C-E and 8E, F, H). The preural ribs appeared fibrously in 9.43 mm SL specimen (13 days) and became fully ossified in 11.43 mm SL specimen (16 days) (Figs. 1 and 7B-C). The epipreural ribs appeared to be fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 7D).

Dorsal and anal fins and supports

Twelve to 14 dorsal pterygiophores or proximal radials and 10 to 11 anal proximal radials were present as cartilaginous elements in 5.54 mm SL (0 day) (Figs. 8A). The distal radials and the dorsal and anal fin rays were absent. The proximal radials became partially ossified in 11.43 mm SL specimen (16 days) and were fully ossified in 15.80 mm SL specimen (22 days) (Figs. 1 and 8E-F). In 6.71 mm SL specimen (5 days), the distal radials were cartilaginously formed on the respective pterygiophores posteriorly (except on the last element). They became partially ossified in 17.72 mm SL specimen (30 days) and were fully ossified in 30.04 mm SL specimen (44 days) (Figs. 1 and 8G-H). The dorsal and anal fin rays became fibrously visible in 7.36 mm SL specimen (8 days) and were fully ossified in 11.43 mm SL (16 days) (Figs. 1 and 8C-E).

Caudal fin and supports

All elements supporting the caudal fin such as epurals (EP1-3), hypurals (HY1+2, HY3+4+5), PH1-4) and parhypurals were cartilaginous in 5.54 mm SL specimen (0 day) (Fig. 8). The hypurals and parhypurals started ossifying partially together with the fibrous appearance of the uroneural in 9.43 mm SL specimen (13 days) (Figs. 1 and 8D). They became fully ossified with the uroneural in 15.80 mm SL specimen (22 days) (Fig. 8F). In 5.54 mm SL specimen (0 day), the first epural (EP1) was absent (Fig. 8A). It appeared in 6.71 mm SL specimen (5 days) (Fig. 8B) and became fully ossified with the second and third epurals in 15.80 mm SL specimen (22 days) (Figs. 1 and 8F). The fibrous terminal vertebra started to be formed in 7.36 mm SL (8 days), followed by the fibrous formation of the urostyle in 9.43 mm SL specimen (13 days) (Figs. 1 and 8C-D). Both elements became fully ossified in 11.43 mm SL specimen (16 days) (Fig. 8E). The caudal fin rays became fibrously visible in 7.36 mm SL specimen (8 days) and fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1 and 8C-D).

Pectoral girdle and fin supports

In 5.54 mm SL specimen (0 day), the pectoral girdle was preformed by cartilaginous elements except the cleithrum which was formed as a thread-like fibrous ossified element (Figs. 9A). The cleithrum became fully ossified in 11.43 mm SL specimen (16 days) (Figs. 1 and 9D). The coracoid, scapula and radials were fused cartilaginously as one element in 5.54 mm SL specimen (0 day) (Figs. 1 and 9A). The coracoid and scapula became separated and both were partially ossified in 11.43 mm SL (16 days) (Figs. 1 and 9D). They became fully ossified in 13.82 mm SL specimen (20 days) (Fig. 9E). The radials started to be separated from coracoid-scapula in 7.36 mm SL specimen (8 days) (Fig. 9B). They became partially ossified in 11.43 mm SL (16 days) and fully ossified in 13.82 mm SL specimen (20 days) (Figs. 1 and 9D-E). Several pectoral fin rays started forming fibrously in 7.36 mm SL specimen (8 days) (Fig. 9B) and 15 to 16 fin rays became fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1 and 9C). The glenoid foramen started to be formed in the scapula in 7.36 mm SL (8 days) specimens and became fully developed in 9.43 mm SL (13 days) (Figs. 1 and 9B-C). The ventral fenestra was partially formed in the coracoid in 9.43 mm SL specimen (13 days) and became fully developed in 13.82 mm SL specimen (20 days) (Fig. 9C-E). The postcleithrum started forming fibrously in 9.43 mm SL specimen (13 days) and became fully ossified in 11.43 mm SL specimen

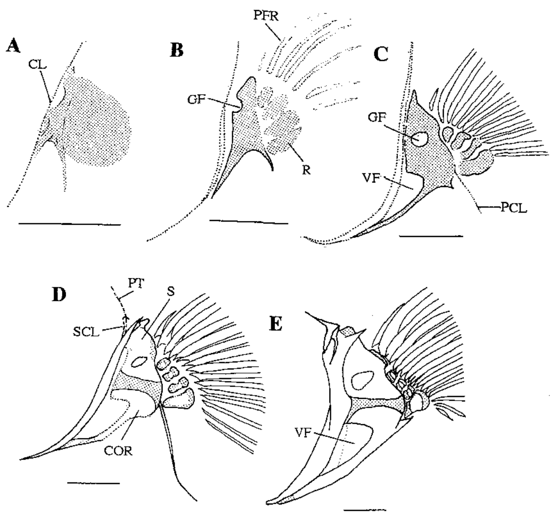


Fig. 9. Development of pectoral fin and support in *Cypselurus heterurus doederleini.* Stippled area, cartilage. Open area, ossified portion. A) 5.54 mm; B) 7.36 mm; C) 9.43 mm; D) 11.43 mm; E) 15.80 mm; F) 30.04 mm. *CL*—cleithrum; *COR*—coracoid; *GF*—glenoid foramen; *PCL*—postcleithrum; *PFR*—pectoral fin ray; *PT*—posttemporal; *R*—radial; *SCL*—supracleithrum; *S*—scapula; *VF*—ventral fenestra. Bars = 1 mm.

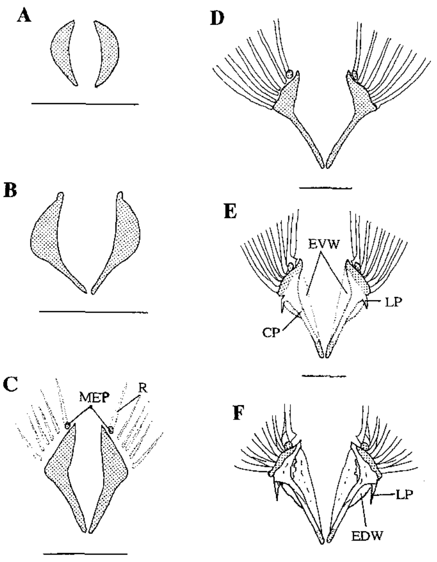


Fig. 10. Development of pelvic fin and support in *Cypselurus heterurus doederleini.* Stippled area, cartilage. Open area, ossified portion. A) 5.54 mm; B) 6.71 mm; C) 7.36 mm; D) 9.43 mm; E) 11.43 mm; F) 14.83 mm. *CP*—central process; *EDW*—external dorsal wing; *EVW*—external ventral wing; *LP*—lateral process; *MEP*—metapterygium; *R*—ray. Bars = 1 mm.

(16 days) (Figs. 1 and 9C–D). In 11.43 mm SL (16 days) specimens, the posttemporal and supracleithrum started forming fibrously and were fully ossified in 13.82 mm SL specimen (20 days) (Figs. 1 and 9D–E).

Pelvic girdle and fin supports

The pelvic girdle was preformed as a cartilaginous element in 5.54 mm SL specimen (0-day) (Fig. 10A). It was fibrously ossified through the central process with the appearance of fibrous external ventral wing, external dorsal wing and lateral process in 11.43 mm SL specimen (16 days) (Figs. 1 and 10E). The pelvic girdle became fully ossified in 13.82 mm SL (20 days) (Fig. 10F). The pelvic external ventral and dorsal wings started appearing fibrously in 11.43 mm SL specimen (16 days) and became fully ossified in 13.82 mm SL (20 days) (Figs. 1 and 10E–F). The cartilaginous metapterygium and the fibrous fin rays started to be formed in 7.36 mm SL specimen (8 days) (Figs. 1 and 10C). The pelvic fin rays became fully ossified in 9.43 mm SL specimen (13 days) (Figs. 1 and 10D).

DISCUSSION

Although it was not easy to trace the developmental type and origin of individual cranial bones in *Cypselurus heterurus doederleini*, they could be recognized by the patterns of their development. First, an individual cranial bone was primarily preformed as a cartilaginous element (cartilage bone) which was later ossified as a bone. Second, it arose directly as a result of fibrous ossification of dermal (dermal and membrane bones) connective tissue (Harder, 1975). As a complex organ, every element in the skull of fish exhibited individual growth pattern and timing.

In the cranium of flyingfish *Cypselurus heterurus doederleini*, the parasphenoid that bridged the vomerine and basioccipital region was the first element to be fully ossified at 7.36 mm SL, followed by the basioccipital and prootic at 9.43 mm. Early successive ossification of these three connecting elements provides the neurocranium with strength, thus tolerating the pressures coming from the weight of the developing brain, vertebral column and the trunk during movement (Harder, 1975). The skull of flyingfish, *Cypselurus heterurus doederleini* is light but strong (Parin, 1961b). During the ontogeny, the sphenotic, pterotic, supraoccipital, epiotic and occipital showed the same growth pattern, becoming fully ossified at 11.43 mm SL. The ossification of these elements may protect the brain from the pressures and forces arising from other developing elements such as the visceral elements and the developing muscle mass. Other elements that were ossified fully in the later stage, particularly in the nasal region (ethmoid, lateral ethmoid, prevomer and nasal) and sphenoid region (basisphenoid) may also support the cranium. Although flyingfishes started darting at an early larval stage (Tsukahara *et al.*, 1957), the darting ability can be traced in the early ossification of the skull. This ossification gave strength in the cranium, so that it would resist water pressure during swimming and pre-flight motion.

The most intriguing point in the development of the cranium was the early ossification of the feeding apparatus in the visceral region such as the maxilla, premaxilla, dentary and the jaw teeth which started to be formed upon hatching. Following this development was the appearance of the pharyngeal teeth, followed by the ossification of the branchial arches and other visceral elements. These were the very reasons why *Cypselurus heterurus doederleini* and probably most of the flyingfishes could feed actively on zooplanktons (artemia) just after hatching (Tsukahara *et al.*, 1957; unpublished data). In fact, during the developmental process of the embryo, the mouth started opening, and the tail, pectoral fins and other rudiments began moving (unpublished data).

Upon hatching, larvae of *C. heterurus doederleini* swam actively and darted occasionally few millimeters above the water surface (unpublished data). Although the vertebral column was not fully ossified at that time, the rudder-like structure of the hypurals had provided enough space for the attachment of muscle mass, resulting in getting a sufficient force to move the body during flexion (Dasilao *et al.*, 1998). These were further augmented by the pectoral and the ventral fin rudiments which were formed earlier during the embryonic stage. While it is true that *C. heterurus doederleini* exhibited darting behaviour upon hatching, however, gliding was initiated in the postlarval stage (between 9.00 mm to 11.00 mm SL; 12 day-old) (unpublished data). Most probably, the initiation of the gliding ability was attributable to the appearance of the radials and the fibrous pectoral fin rays at 7.36 mm SL (8 day) (Fig. 9B) or possibly during the full ossification of pectoral fin rays at 9.43 mm SL (13 day-old) (Fig. 9C). Further, the gliding effeciency was augmented by the same ossification timing of the pelvic fin rays which was fully ossified at 9.43 mm SL specimen (Fig. 10D). Stability was then augmented during the appearance of the lateral process of the pelvic girdle at 11.43 mm SL that provides more strength during the gliding (16 day-old) (Fig. 10E). We could not find any clear reason for the later development of the dorsal fin supports such as the distal radials in a later stage.

The broadening of the neural arch of the preural centrum is one of the most important ontogenetic character changes in flyingfishes (Dasilao *et al.*, 1998). The enlargement of the neural arches and the formation of the neural plates (Figs. 7C and 8E) at 11.43 mm SL (16 days) had provided stable insertion sites for ligaments, muscles and other connective tissues linking the vertebral column and the cranium. Although the larvae were observed darting over the water surface after hatching, darting effeciency may be started at the appearance of the neural plates and the neural arch plates, and the ossification of the vertebral column at 11.43 mm SL specimen (16 days).

Generally, the ossification process in flyingfish, *Cypselurus heterurus doederleini* started upon hatching and were almost fully ossified at 15.80 mm SL (22 days). The early development of feeding mechanism in *C. heterurus doederleini* had enabled them to feed just after hatching, and their ability to swim, dart and glide to evade predators enabled them to survive in a higher rate.

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