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# The development of the skull of *Gambusia affinis affinis* (Baird & Girard)

# III. The development of the hyoid arch

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## ABSTRACT

The development of the hyoid arch of six postembryonic stages of *Gambusia affinis affinis* (3·5, 4, 5, 6, 8 and 10 mm total length) is described from serial cross sections and graphical reconstructions and compared with that of other fishes.

The study has revealed that the different constituents of the hyoid arch, viz. the hyosymplectic, interhyal, ceratohyal, hypohyal and basihyal are developed as independent structures during ontogeny. In the 10 mm stage, absorption of cartilage with replacement by bone is observed at the level of the hyosymplectic and ceratohyal. The hyosymplecitc chondrifies as a single structure and, later on, during ontogeny, it divides due to the absorption of cartilage into two parts; the hyomandibular and symplectic process. The hyosymplectic part of the hyoid arch plays an essential role in jaw suspension, so that *Gambusia affinis affinis*, like the majority of Selachi and all Teleostei, conforms to the hyostylic type of jaw suspension.

## INTRODUCTION

In previous studies, the development of the chondral neurocranium of the teleost fish *Gambusia affinis affinis* has been thoroughly dealt with (Amer *et al.* 1987). In the present paper the ontogeny of the hyoid arch skeleton of the splanchnocranium of the same fish is dealt with and compared with that of other fishes.

## MATERIALS AND METHODS

A population of *Gambusia affinis affinis* was cultivated in the laboratory. Specimens of six postembryonic stages, including 3·5, 4, 5, 6, 8 and 10 mm total length, were used. The specimens were fixed in 4% formalin and Bouin's fluids. Specimens of 8 and 10 mm total length were decalcified in EDTA solution. Dehydration, clearing and embedding were done by the usual methods. Serial cross sections of the cephalic region were cut (7–10 microns thick), depending on the size of the specimen, and stained with Mallory's triple stain and Delafield's hematoxylin-eosin. Graphical reconstructions were prepared according to Verraes (1974).

## OBSERVATIONS

### STAGE 1 (3·5 mm TOTAL LENGTH)

In this stage the hyoid arch consists of three pairs of procartilaginous structures representing the hyosymplectic, the ceratohyal and the hypohyal. All these elements are still separate from each other (Fig. 1-A). This contradicts Edgeworth's observations (1935) on the hyoid skeleton of Teleostei where the hyoid arch is said to be formed as a continuous procartilaginous structure which chondrifies and separates, later on, into the hyomandibular, symplectic, interhyal, ceratohyal and hypohyal.

In lateral view, the hyosymplectic is in the form of a curved plate (Fig. 1-A). Its upper part, which represents the hyomandibular process, is relatively broad and is in contact with the latero-ventral margin of the auditory capsule of the neurocranium (Fig. 2-A). The lower part, however, which represents the symplectic process, is not articulated with any other structures. It lies more or less ventrolateral to the posterior half of the palatoquadrate (Fig. 2-A and B). The symplectic process arises in continuity with the hyomandibular and not as an independent

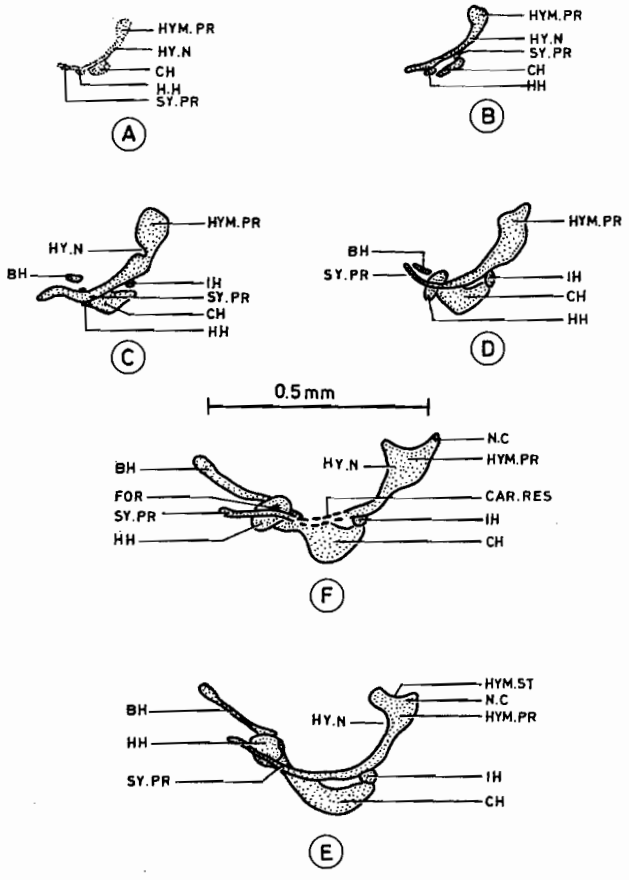


**Fig. 1.** Graphical reconstructions (lateral views) of the hyoid arch of *Gambusia affinis affinis*, A, 3·5 mm; B, 4 mm; C, 5 mm; D, 6 mm; E, 8 mm; F, 10 mm stage.

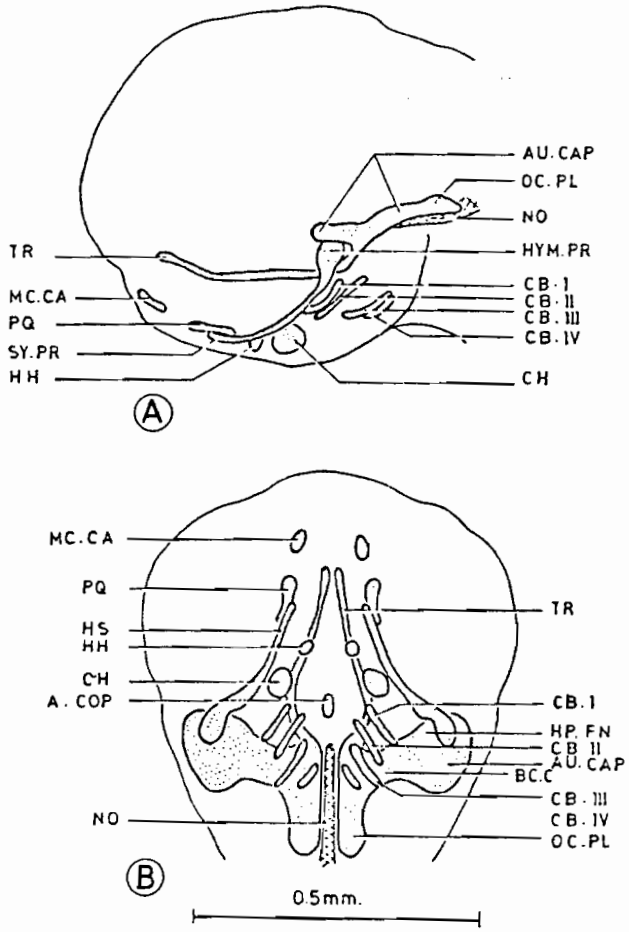


**Fig. 2.** Graphical reconstructions of the chondrocranium, notochord and head contour of the 3·5 mm larval stage of *Gambusia affinis affinis*. A, lateral view; B, ventral view.

structure. In this respect *Gambusia affinis affinis* resembles *Gasterosteus aculeatus* (Swinnerton 1902), *Amia calva* (Pehrson 1922), *Sebastes marinus* (Mackintosh 1923) and *Polypterus senegalus* (El-Toubi & Abdel Aziz 1956). In *Salmo*, however, the symplectic process arises as an independent structure from the hyomandibular (Stöhr 1882; De Beer 1937).

The ceratohyal is represented by an oval structure not articulated with any other structure of the hyoid arch (Figs 1-A and 2-B). In transverse sections, it appears as an oval structure (Fig. 8-A). The hypohyal, which is the most anterior part of the developing hyoid arch, appears as a small round structure. It lies in front of the ceratohyal leaving a short distance between the two (Figs 1-A and 2-A).

### STAGE 2 (4 mm TOTAL LENGTH)

The cartilaginous hyoid arch consists of four paired elements, the hyosymplectic and interhyal dorso-laterally and the ceratohyal and hyophal ventrally (Figs 1-B and

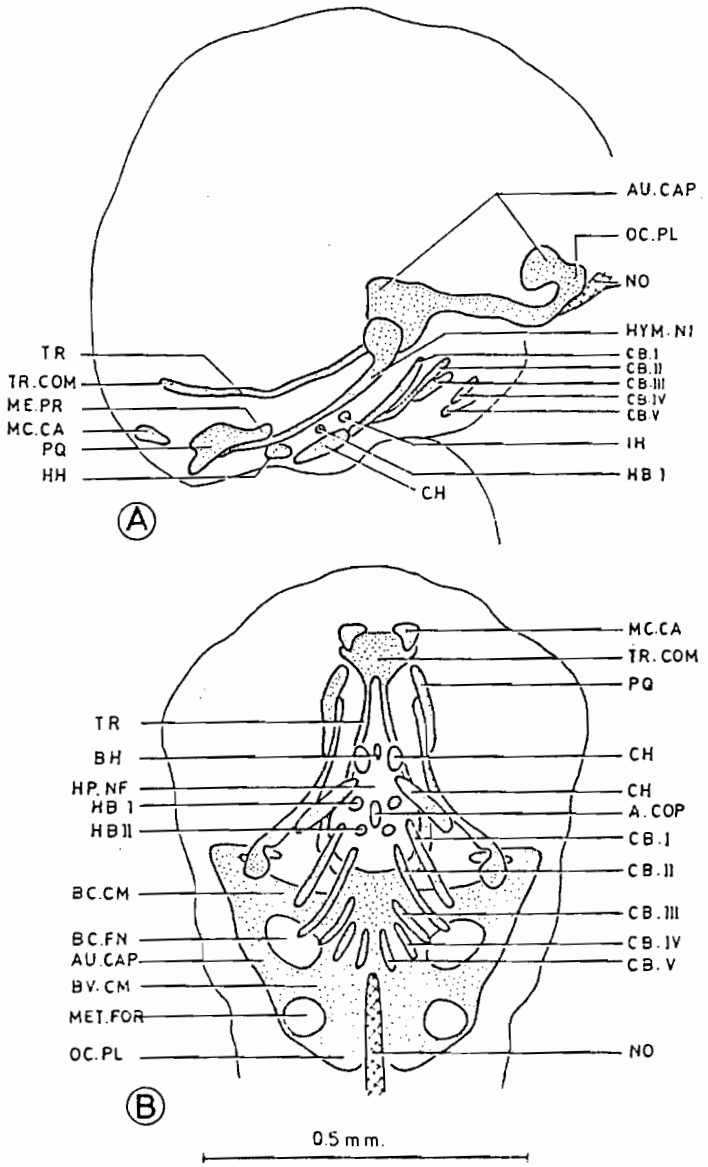


**Fig. 3.** Graphical reconstructions of the chondrocranium, notochord and head contour of the 4.0 mm larval stage of *Gambusia affinis affinis*. A, lateral view; B, ventral view.

3-A); the interhyal is still in a procartilaginous condition. The unpaired ventromedial basihyal is developing as a procartilaginous structure (Figs 1-B and 3-A).

The hyosymplectic does not show great differences compared with that in the 3·5 mm larval stage, except that it has grown slightly in size and become chondrified (Fig. 1-B). The interhyal develops as a small independent procartilaginous structure, lying in between the postero-ventral edge of the symplectic portion of the hyosymplectic and the postero-dorsal edge of the ceratohyal cartilage (Figs 1-B and 3-A).

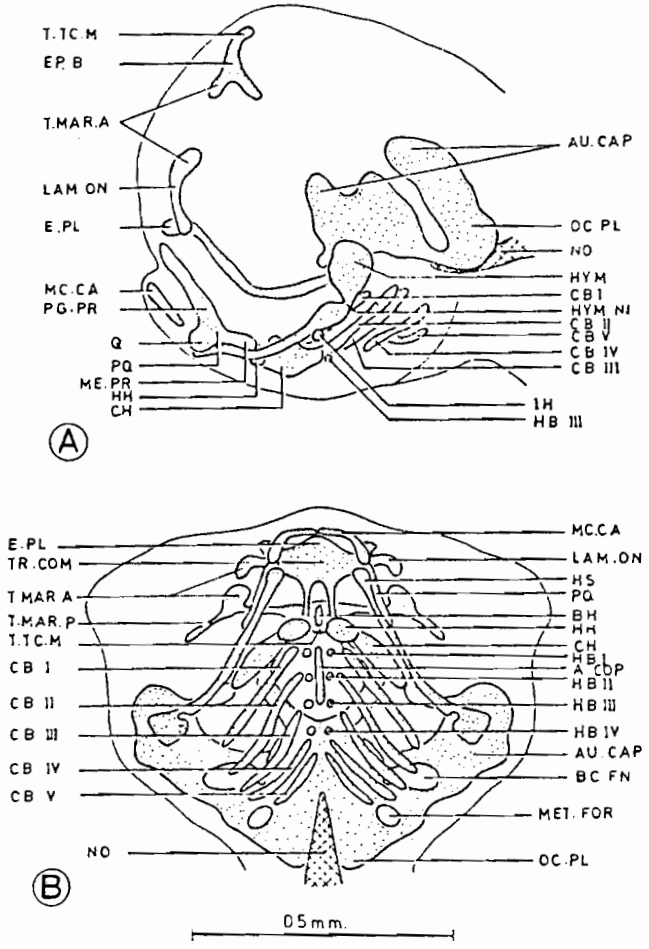


**Fig. 4.** Graphical reconstructions of the chondrocranium, notochord and head contour of the 5.0 mm larval stage of *Gambusia affinis affinis*. A, lateral view; B, ventral view.

The ceratohyal is now chondrified and appears as a relatively broad cartilaginous bar, with a narrow anterior end and a relatively wide posterior one (Fig. 3-A and B).

The hypohyal is a small oval-shaped structure lying in front of the ceratohyal (Figs 1-B and 3-A); it is roughly rounded in shape in cross section (Fig. 8-B). In *Sebastes marinus* (Mackintosh 1923) and in *Anguilla vulgaris* (Norman 1926), the hypohyal is absent in almost all of the developmental stages. The basihyal has made its first appearance in the present stage as a median small procartilaginous structure. In transverse sections, it appears as a very small rounded structure in the median line dorsal to the two hypohyals (Fig. 8-B).

## STAGE 3 (5 mm TOTAL LENGTH)

The hyoid arch is now complete and well chondrified. The hyosymplectic is larger in size than that of the 4 mm larval stage (Fig. 1-C). The symplectic process has grown

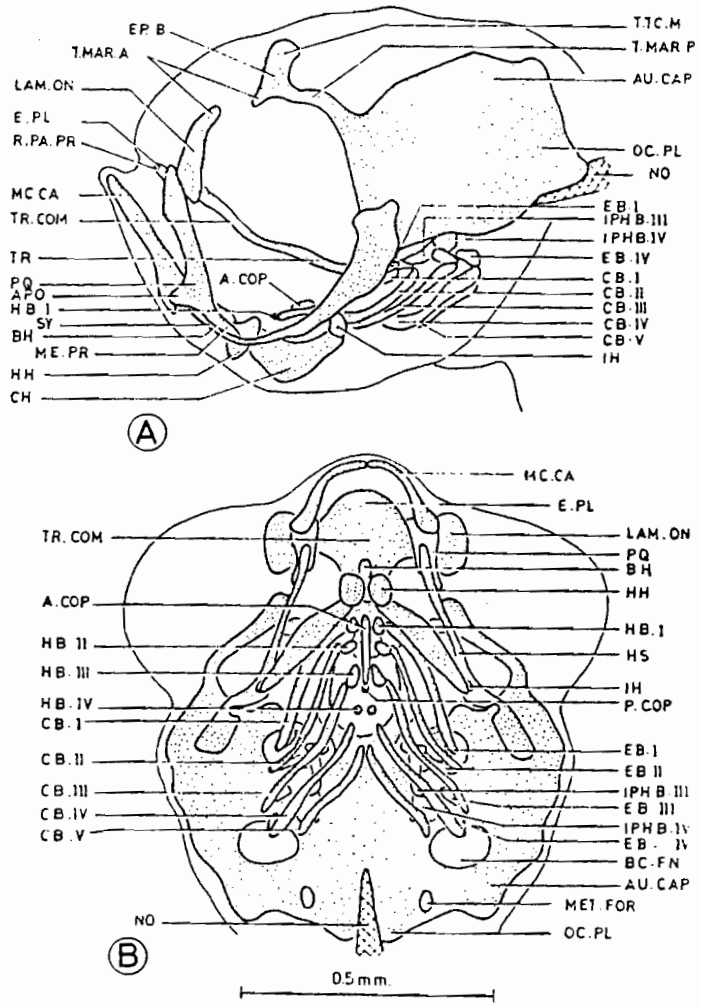


**Fig. 5.** Graphical reconstructions of the chondrocranium, notochord and head contour of the 6·0 mm larval stage of *Gambusia affinis affinis*. A, lateral view; B, ventral view.

further anteriorly in the form of a narrow curved rod lying ventral to the metapterygoid process of the palatoquadrate (Fig. 4-A and B). The hyomandibular part is quite large compared with the corresponding part of the 3·5 and 4 mm larval stages. It lies posterior to the eye and articulates dorsally with the auditory region of the neurocranium (Fig. 4-A).

The interhyal is chondrified in this stage. In lateral view, it appears as a small rounded structure which dorsally contacts the ventral margin of the hyosymplectic (Fig. 1-C). Ventrally, however, the interhyal is still separate from the ceratohyal (Figs 1-C and 4-A). The ceratohyal has grown further in size. It appears as a broad cartilaginous plate. Anteriorly, the ceratohyal articulates with the developing hypohyal (Figs 1-C, 4-A and 8-C). The latter is oval in shape and lies slightly ventral to the basihyal (Fig. 4-B). In transverse sections, the ceratohyal appears anteriorly

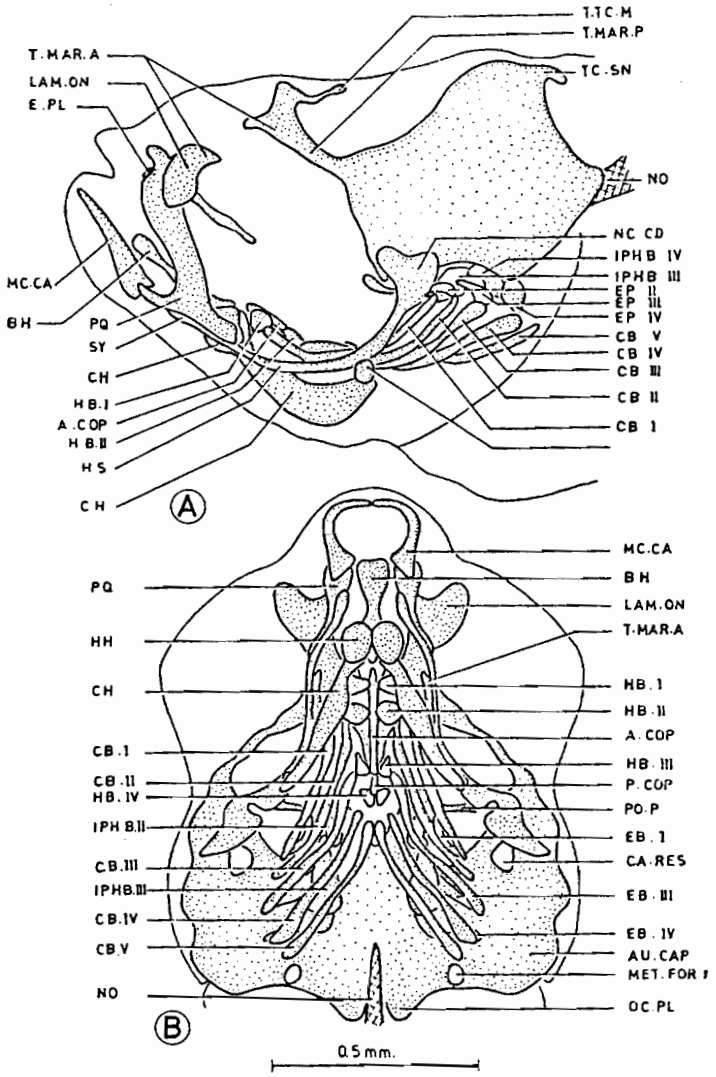


**Fig. 6.** Graphical reconstructions of the chondrocranium, notochord and head contour of the 8·0 mm larval stage of *Gambusia affinis affinis*. A, lateral view; B, ventral view.

slightly oval in shape but becomes elongated posteriorly (Fig. 8-D and E). The basihyal appears in this stage as a short, narrow cartilaginous rod extending anteriorly for a short distance in front of the hypohyal (Figs 1-C and 4-B).

## STAGE 4 (6 mm TOTAL LENGTH)

All the constituent parts of the hyoid arch have grown further than in the 5 mm larval stage (Fig. 1-D). The hyosymplectic is the longest part of the hyoid arch. The hyomandibular part of the hyosymplectic has differentiated into a broad part articulating with the neurocranium, and a cylindrical narrow shaft which is continuous ventrally with the symplectic process (Figs 1-D and 5-A). The latter has relatively

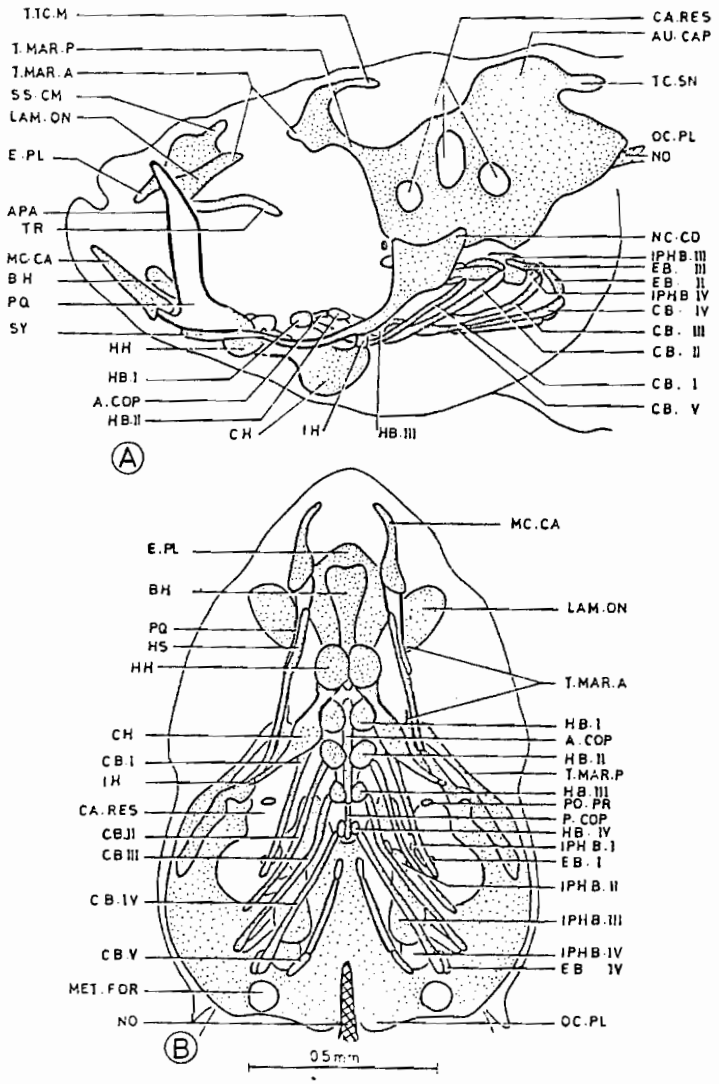


**Fig. 7.** Graphical reconstructions of the chondrocranium, notochord and head contour of the 10 mm stage of *Gambusia affinis affinis*. A, lateral view; B, ventral view.

increased in length and appears as a curved rod, the anterior part of which lies ventral to the metapterygoid process of the palatoquadrate (Fig. 5-A and B).

The interhyal appears as a small intermediate cartilaginous mass which contacts the hyosymplectic dorsally and the ceratohyal ventrally (Figs 1-D and 5-A). The ceratohyal has relatively increased in length and slightly changed in shape. It appears as a broad triangular cartilaginous plate (Fig. 1-D). The ceratohyal articulates with the corresponding hypohyal anteriorly and with the interhyal posteriorly (Figs 1-D and 5-A). The hypohyal is an oval-shaped cartilaginous structure which contacts the basihyal medially (Fig. 1-D).

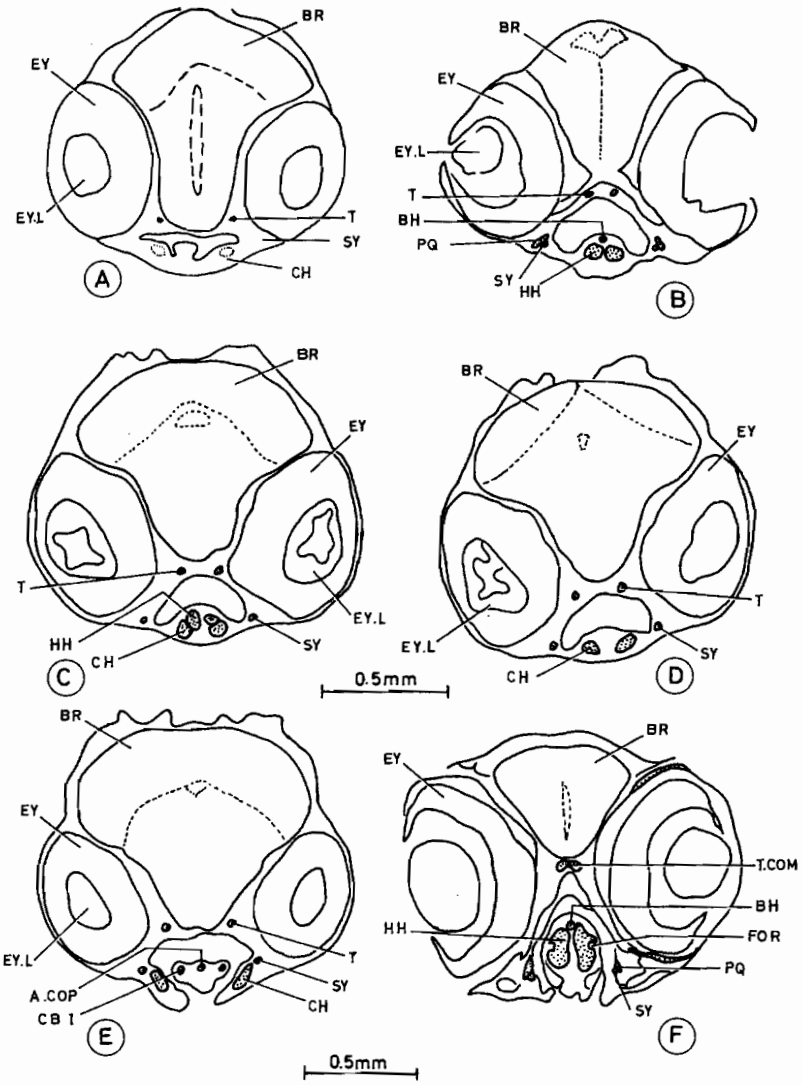


**Fig. 8.** Drawings of transverse sections through the head region of *Gambusia affinis affinis*. A, 3·5 mm stage; B, 4 mm stage; C, D and E, 5 mm stage; F, 8 mm stage.

## STAGE 5 (8 mm TOTAL LENGTH)

The hyosymplectic has relatively increased in length compared with that of the 6 mm larval stage (Fig. 1-E). The hyomandibular part is roughly triangular in shape; its dorsal margin has differentiated into two articular heads representing the anterior and posterior neurocranial condyles, respectively, (Barel *et al.* 1976) with a shallow concavity in between (Fig. 1-E).

The anterior part of the symplectic process is articulated with the posterior part of the palatoquadrate (Fig. 6-A). The interhyal has increased in size relative to the

6 mm larval stage, and acquired a trapezoid shape (Figs 1-E and 6-A). The ceratohyal has relatively increased in length and in thickness. It is nearly twice as long as in the previous stage (Figs 1-E, 6-A and B). The hypohyal has relatively increased in size; it appears as a massive triangular mass with a rounded anterior end and a narrow posterior one (Figs 1-E and 6-B). In transverse sections, the hypohyal is perforated by a narrow foramen (Fig. 8-F) as is the case in *Solea variegata* and *Pleuronectes platessa* (Berrill 1925) and *Ophiocephalus gachia* (Srinivasachar 1953). The basihyal has further elongated compared with that of the 6 mm larval stage (Fig. 1-E). It has a relatively wide anterior part and a narrow elongated posterior one (Fig. 6-A and B).

### STAGE 6 (10 mm TOTAL LENGTH)

In this stage the hyoid arch has relatively enlarged and elongated compared with that of the 8 mm larval stage (Fig. 1-E). Moreover, some cartilages are partly resorbed and replaced by bone (Figs 1-E and 7-A).

The rostral and caudal neurocranial condyles of the hyomandibular part of the hyosymplectic become more pointed and the concave surface between them becomes distinct and much deeper than previously (Figs 1-F and 7-A). Ventrally, the hyomandibular part appears as a slender rod instead of the triangular shape seen in the previous stage (Fig. 7-B). The symplectic process of the hyosymplectic has relatively increased in length; it appears as an elongate rod-like structure. Its middle part is now surrounded by a perichondral bone representing the symplectic bone (Fig. 7-A and B). The interhyal shows little difference from that of the previous stage. The anterior part of the ceratohyal is now surrounded shortly after its articulation with the hypohyal with a perichondral bone (Fig. 7-A and B). The posterior part, however, is wider and thicker than the anterior one. The basihyal has slightly increased in length. Its rostral part shows some thickness. In lateral view it appears as an oblique rod (Fig. 1-F) lying at a more dorsal level than the copulae of the branchial arches (Fig. 7-A).

## DISCUSSION

In *Gambusia affinis affinis*, as in *Gasterosteus aculeatus* (Swinnerton 1902), *Anguilla vulgaris* (Norman 1926), *Salmo fario* (De Beer 1937), *Notopterus* (Omarkhan 1950), *Tilapia zilli* (Abdel Aziz 1970) and *Haplochromis elegans* (Ismail 1979), the different elements of the hyoid arch are developed independently even from the procartilaginous state. This contradicts Edgeworth's account (1935) on the hypobranchial skeleton of Teleostei which states that the hyoid arch is formed as a continuous procartilaginous mass which chondrifies and separates into hyomandibular, symplectic, interhyal, ceratohyal and hypohyal.

The hyosymplectic of the hyoid arch skeleton of teleost fishes may develop in two portions; a hyomandibular and symplectic (De Beer 1937). In *Gambusia affinis affinis*, the hyosymplectic chondrifies as a single structure and later on, during ontogeny, it divides due to the absorption of cartilage into two parts; a dorsal part representing the hyomandibular and a ventral one representing the symplectic process. A similar case has been recorded in *Tilapia zilli* (Abdel Aziz 1957) and

*Haplochromis elegans* (Ismail 1979). In *Acipencer ruthenus*, however, the symplectic process arises separately and remains as such even in the adult (Sewertzoff 1928).

Many authors have laid stress on the homology of the symplectic in bony fishes. Allis (1915) regarded the symplectic in bony fishes to be, probably, a primarily independent cartilage and is possibly a hypertrophied middle element (or elements) of branchial rays of the mandibular arch. Norman (1926) did not accept Allis' conclusion as it is not supported by embryological evidence. He regarded the symplectic cartilage of bony fishes as a process or ventral prolongation of the hyomandibular. Gregory (1933) stated that the symplectic of bony fishes represents the lower part of the hyomandibular. Edgeworth (1935) stated that the symplectic, which is a process of the lower end of the hyomandibular usually becomes a separate cartilage. In *Gambusia affinis affinis*, the symplectic part is considered as a ventral prolongation of the hyomandibular. It runs below the hinder end of the palatoquadrate and may provide a strong basis for the articulation of the two elements.

The hyosymplectic cartilage is quite important in jaw suspension. Huxley (1874) distinguished three types of jaw suspension, viz. autostylic, hyostylic and amphistylic. *Gambusia affinis affinis* belongs to the hyostylic type in which the quadrate part of the palatoquadrate of the mandibular arch is supported away from the skull by the hyosymplectic which articulates with the auditory region of the neurocranium. This type is found in the majority of Selachii and in all Teleostei.

In *Gambusia affinis affinis*, the interhyal arises as an independent structure as in *Lepidosteus osseus* (Veit 1911), *Amia calva* (Pehrson 1922), *Sebastes marinus* (Mackintosh 1923), *Notopterus* (Omarkhan 1950) *Cyprinus carpio* (Pashine & Marathe 1977), *Haplochromis elegans* (Ismail 1979) and *Tilapia galilaea* (Ismail & Elshabka 1982). In *Rasbora*, however, the interhyal develops as a process from the ventral part of the hyomandibular and later on, during ontogeny, separates from it (Tewari 1971). Norman (1926) regarded the interhyal element of the hyoid arch to be a new structure which is developed in correlation with the need for a strong suspensorium for the remainder of the hyoid arch after the hyomandibular had moved forward and became associated with the jaws.

In *Gambusia affinis affinis*, the hypohyal develops during ontogeny as an independent structure. In this respect it resembles *Salmo fario* (De Beer 1937), *Notopterus* (Omarkhan 1950), *Rasbora daniconius* (Tewari 1971), *Haplochromis elegans* (Ismail 1979) and *Sarotherodon galilaeus* (Ismail 1984), but differs from *Gambusia affinis holbrookii* (Ramaswami 1945) and *Cyprinus carpio* (Pashine & Marathe 1977) where the hypohyal develops as a continuous structure with the ceratohyal. In *Sebastes marinus* (Mackintosh 1923) and *Anguilla vulgaris* (Norman 1926), no hypohyals are developed.

The basihyal which represents the unpaired ventro-medial structure of the hyoid arch is developed in *Gambusia affinis affinis* as an independent structure as is the case in *Gasterosteus aculeatus* (Swinnerton 1902), *Notopterus* (Omarkhan 1950), *Tilapia zilli* (Abdel Aziz 1957) and *Haplochromis elegans* (Ismail 1979). In *Tylosurus*, however, the basihyal appears early during ontogeny as an independent structure and fuses, later on, with the anterior copula (Pashine & Marathe 1977). In *Trichopodus*, the basihyal does not arise independently but appears to be continuous with the first copula, even in the fully formed chondrocranium (Pashine & Marathe 1977). In *Cyprinus carpio*, the basihyal and the first copula are formed independently

in the 5.0 mm larva. They fuse with each other in the 6.0 mm larva to form a common copula which again breaks up into two in the 6.8 mm larva (Pashine & Marathe 1977). In *Sebastes marinus* (Mackintosh 1923) and *Ophiocephalus gachua* (Srinivasachar 1953), the basihyal is continuous with the two fused copulae forming the common copula. In *Solea variegata*, however, the basihyal is absent (De Beer 1937).

## LIST OF ABBREVIATIONS

| | |
|---|---|
| A. COP | Anterior copula |
| APA | Autopalatine |
| APO | Apophysis |
| AU. CAP | Auditory capsule |
| BC. CM | Basicapsular commissure |
| BC. FN | Basicapsular fenestra |
| BH | Basihyal |
| BR | Brain |
| BV. CM | Basivestibular commissure |
| C. CV | Cranial cavity |
| CA. RES | Cartilage resorption |
| CB | Ceratobranchial |
| CH | Ceratohyal |
| COR. PR | Coronoid process of Meckel's cartilage |
| DE | Dentary |
| E. PL | Ethmoid plate |
| EP | Epibranchial |
| EP. B | Epiphysial bridge |
| EPA | Ethmopalatine articulation |
| EY | Eye |
| EY. LE | Eye lens |
| F. POP | Fontanella postpinealis |
| F. PRP | Fontanella prepinealis |
| FOR | Foramen |
| HB | Hypobranchial |
| HH | Hypohyal |
| HP. FN | Hypophysial fenestra |
| HS | Hyosymplectic |
| HY. N | Hyomandibular niche |
| HYM | Hyomandibular |
| HYM. PR | Hyomandibular process |
| HYM. ST | Hyomandibular stalk |
| IH | Interhyal |
| IPHB | Infrapharyngobranchial |
| L. PH. J. | Lower pharyngeal jaw |
| LAM. ON | Lamina orbitonasalis |
| MC. CA | Meckel's cartilage |
| ME. PR | Metapterygoid process |
| MET. FI | Metotic fissure |
| MET. FOR | Metotic foramen |
| MM | Mentomandibular |
| NC. BA | Neurocranial base |

| | |
|---|---|
| NC. CD | Neurocranial condyle |
| NC. RO | Neurocranial roof |
| NO | Notochord |
| OC. PL | Occipital plate |
| OLF. OR | Olfactory organ |
| OP. PR | Opercular process |
| P. COP | Posterior copula |
| PAR. PL | Parachordal plate |
| PG. PR | Pterygoid process |
| PO. B | Prootic bridge |
| PQ | Palatoquadrate |
| Q | Quadrate |
| R. PA. PR | Rostro-palatine process |
| RA. PR | Retro articular process |
| SS. CM | Sphenoseptal commissure |
| SY | Symplectic |
| SY. PR | Symplectic process |
| T. MAR. A | Taenia marginalis anterior |
| T. MAR. P. | Taenia marginalis posterior |
| T. TC. M. | Taenia tecti medialis |
| TC. SN | Tectum synoticum |
| TE | Teeth |
| TR | Trabecula |
| TR. COM | Trabecular communis |

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# تكوين الجمجمة في سمكة الجمبوزيا
## ٣ ـ تكوين القوس اللامي


ممتاز هاشم اسماعيل
قسم علم الحيوان
بكلية العلوم ،
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## خلاصة


هذا البحث هو الثالث في سلسلة من البحوث التي تهتم بدراسة تكوين الجمجمة في سمكة الجمبوزيا في المرحلة ما بعد الجنينية ، وقد تضمن البحث الأول وصف تكوين الجمجمة الغضروفية العصبية ، بينما اهتم البحث الثاني بدراسة تكوين القوس الفكي ، وذلك بالمقارنة بالأسماك الأخرى .

ويتضمن هذا البحث دراسة تكوين القوس اللامي ، الذي يعتبر أحد مكونات الجمجمة الحشوية ، في ستة أطوار تكوينية لسمكة الجمبوزيا ، تتراوح أطوالها بين ٣,٥ مم و ١٠ مم . وقد أظهرت الدراسة أن جميع مكونات القوس اللامي ، وهي اللامي العرضي والبين لامي واللامي القرني واللامي السفلي واللامي القاعدي ، تتكون بشكل مستقل عن بعضها البعض خلال مراحل التكوين . ويتمفصل القوس اللامي مع الجزء الأذني للجمجمة العصبية عن طريق اللامي العرضي ، ويتصل القوس الفكي بالجمجمة عن طريق القوس اللامي ، ولهذا يوصف نظام التعلق الفكي في الجمبوزيا بأنه من نوع « التعلق اللامي » .