Resumen por el autor, James Ernest Kindred,
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El condrocráneo de Syngnathus fuscus.

Syngnathus fuscus, un representante de los Lofobranquios, se asemeja a Gasterosteus, un hemibranquio, en los siguientes caracteres condrocraneales: La presencia de una región etmoidal alargada; la articulación acrartética de los cartílagos palatinos; el techo craneal incompleto; la posición horizontal de las trabéculas del cráneo y cartílagos paracordales; la presencia de dos tabiques semicirculares en cada cápsula ótica; un proceso pro-ótico que separa los nervios trigémino y facial; una ventana basicraneal posterior alargada; un orificio común para los nervios glosofaríngeo y vago situado entre la cápsula ótica y el arco occipital; un cartílago ptérigo-cuadrado pequeño; un voluminoso notocordio intercraneal y un proceso post-orbitario en el borde anterior de cada cápsula ótica. Las especializaciones observadas en el condrocráneo de los estados de 8 by 12 mm. de Syngnathus son: La elevación dorsal del extremo anterior de la placa etmoidea en el estado de 8 mm.; la presencia de una ventana miodómica ventral definida; una cinta tectal mediana en el techo craneal; una pequeña ventana basicapsular en la pared ventral de cada cápsula ótica; una conexión fibrosa entre los cartílagos palatino y pterigoideo; la notable longitud de la región etmoidal; el cambio de posición de los elementos hioideos al comenzar a funcionar las branquias; la presencia de un proceso metapterigoideo reducido; y la ausencia de cartílagos dorsal y ventral en el notocordio. Los siguientes caracteres primitivos importantes son dignos de mención: Presencia de un cartílago rostral independiente, el cual se ha considerado como el homólogo de la sincondrosis entre los extremos distales de los palatinos de Heptanchus; el desarrollo de los cartílagos ectectmoideos independientes del etmoides; la comunicación abierta entre la cavidad del laberinto y la del cráneo, y la ausencia de nervios post-vagos en la región occipital.

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AUTHOR'S ABSTRACT OF THIS PAPER ISSUED
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THE CHONDROCRANIUM OF SYNGNATHUS FUSCUS

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INTRODUCTION

The study of the chondrocranium of Syngnathus fuscus was undertaken at the suggestion of Prof. J. S. Kingsley upon the completion by the author of a monograph on the skull of Amiurus. A detailed account of the facts of development of the chondrocranium of Syngnathus had not as yet been given. McMurrich's ('83) paper, which contains a general description of the development of the chondrocranium of Syngnathus peckianus, has served as a basis for our knowledge of the cranium of the Lophobranchii, the group of teleosts of which Syngnathus is a representative. In order to add to the knowledge of the cranial characters of this group, the following detailed topographical and histological description of the early stages in the development of the chondrocranium of Syngnathus fuscus is presented.

It is the purpose of the author to describe in a subsequent paper the later stages in the development of the chondrocranium which lead to the formation of the adult skull.

JOURNAL OF MORPHOLOGY, VOL. 35, NO. 2

MATERIAL AND METHODS

The description of the chondrocranium of Syngnathus fuscus is based upon the study of serial sections through the head regions of embryos from 6 mm. to 15 mm. in length. For purposes of orientation and comparison, reconstructions were made in wax of the chondrocrania of the 8-mm. and 12-mm. embryos, which represent typical stages in its development.

Male pipe-fish carrying young in the brood pouch were kept in laboratory aquaria, and a few embryos from each fish were taken out and fixed daily. It is impossible to state the exact age in hours of the embryos, because in all cases where they were collected, development was advanced at least as far as the closure of the neural tube. The 12- to 15-mm. stages were larvae capable of caring for themselves. These were the oldest animals that I was able to raise in the laboratory, because their resistance is very low to changes in the environment at this age, the critical period when the yolk sac has just been absorbed.

The material for study was collected at Woods Hole during the summer of 1919 by the Supply Department of the Marine Biological Laboratory.

THE CHONDROCRANIUM OF THE 8-MM. STAGE

In embryos of Syngnathus fuscus younger than the 8-mm. stage of development, the chondrocranium has not been definitively laid down. The cranial flexure is marked and the head region has not straightened out. In a 6-mm. embryo the visceral arches are formed of dense mesenchymatous masses; procartilage tracts are present ventrolateral to the otic vesicles, but were not observed ventral to the brain or lateral to the notochord. Since chondroblasts are not present except in these regions, it is probable that the chondroblasts which later form the basis cranii are proliferated from the visceral-arch masses of mesenchyme.

A. The neurocranium

In the neurocranium of the 8-mm. embryo, the parts typical of a teleostean neurocranium are present, but are modified somewhat, foreshadowing even thus early the elongate character of the adult cranium. The elongation seems to be due to a precocious growth of the cartilage forming the trabecula communis, since the distance from the anterior end of the ethmoid plate to the anterior margin of the fenestra myodomus ventralis is about two-thirds of the total length of the cranium (fig. 2), whereas in a 25-mm. Salmo (Gaupp, '06) it is equal to one-half, and in a 6.6-mm. Gasterosteus (Swinnerton, '02), to one-third of the total length of the cranium.

The anterior half of the ethmoid plate turns abruptly dorsal, making a right angle with its proximal portion (fig. 1). The dorsally turned part of the ethmoid is flatter in cross-section than is its horizontal portion and is expanded laterally at its dorsal end to form the rostral process (fig. 3). The lateral surface of each side of the rostral process is grooved to receive the proximal end of the palatine cartilage of that side.

In the chondrocrania of other teleosts which have been described there is no reference to a dorsal turning of the anterior ethmoidal region. Swinnerton has noted a widening of the ethmoid plate and its articulation with the palatoquadrate in the 5.7-mm. Gasterosteus. The articular processes which are the homologues of those in Syngnathus he named the pre-ethmoid cornua. He called this type of articulation, acrartete; "a palato-ethmoidal relationship in which the attachment of the palatine cartilage is confined solely to the pre-ethmoid cornua."

A small median rostral cartilage lies on the dorsal surface of the rostral process. It is attached to it by densely cellular connective tissue, but otherwise is independent of the surrounding structures (figs. 1, 2, 3). The phylogenetic significance of this cartilage will be considered in the description of the visceral arches.

Just posterior to the rostral region of the ethmoid plate, the plate proper is broad and ovoid in cross-section. It is continuous

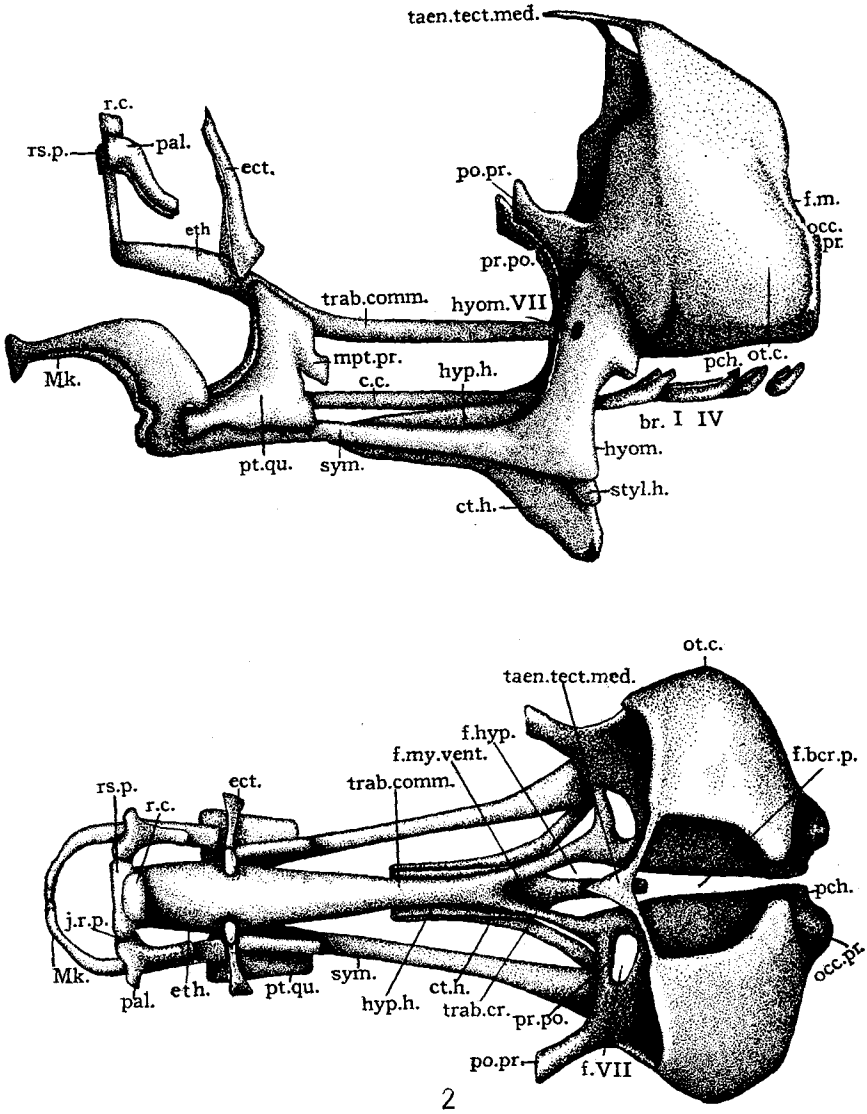


Fig. 1 Lateral view of the chondrocranium and visceral arches of an embryo of Syngnathus fuscus 8 mm. long. Drawing made from a wax model 230 times the actual size of the chondrocranium. Ratio of drawing to model, 2:3.

Fig. 2 Dorsal view of the same model as shown in figure 1.

posteriorly with the trabecula communis which forms the axis of the orbital region. The interorbital septum of loose strands of fibrous connective tissue is directly continuous with the perichondrium of the ethmoid plate (fig. 4). The olfactory pits lie lateral to the interorbital septum and are embedded in embryonal connective tissue.

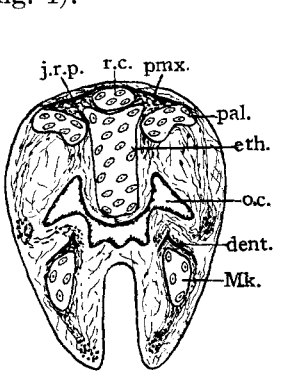
Just posterior to the olfactory pits and ventral to the anterior end of the brain there is a pair of cartilaginous rods. These extend ventrolaterally from the membranous tissue enclosing the brain into the embryonal connective tissue lying in the anterior portion of the orbit (fig. 1). McMurrich, in describing the chondrocranium of a 6- to 7-mm. Syngnathus peckianus, interpreted these as the nasal cartilages. In other teleosts the ectethmoid cartilages occur in this region as lateral outgrowths from the ethmoid plate. In later stages of Syngnathus the ectethmoid processes are completely fused with the ethmoid plate, the whole forming a mesial internasal septum. Hence from their position and their later history these independent cartilages are to be regarded as ectethmoid cartilages, but at the same time this condition indicates that the ectethmoid cartilages were derived phylogenetically from the posterior wall of the cartilaginous olfactory capsules and that only a remnant of these is left in Syngnathus. If this point of view is accepted,

ABBREVIATIONS

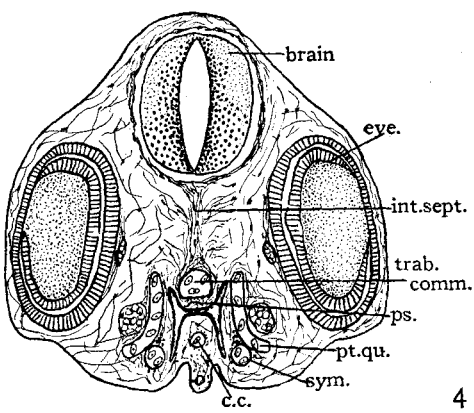
br.I-IV, branchial arches I to IV
c.c., copula communis
ct.h., cerato hyal
ect., ectethmoid cartilage
eth., ethmoid plate
f.bcr.p., fenestra basicranii posterius
f.hyp., fenestra hypophyseos
f.my.vent., fenestra myodomus ventralis
f.m., foramen magnum
f.VII, foramen for ramus hyomandibularis facialis
Hyom. VII, foramen in hyomandibula for r.hyom.fac.
hyp.h., hypohyal
j.r.p., junction rostropalatinus
Mk., Meckel's cartilage
mpt.pr., metapterygoid process
occ.pr., occipital process
ot.c., otic capsule
pal., palatine cartilage
pch., parachordal
po.pr., postorbital process
pr.po., prootic process
pt.qu., pterygoquadrate cartilage
r.c., rostral cartilage
rs.p., rostral process of ethmoid
styl.h., stylohyal cartilage
sym., symplectic cartilage
taen.tect.med., taenia tectum medialis
trab.comm., trabecula communis
trab.cr., trabecula cranii

then it may be stated that the relation of the ectethmoid cartilages to the ethmoid plate is more primitive in Syngnathus than in Gasterosteus, where they are never independent.

The tegmen cranii of the ethmoid region described and figured for Syngnathus peckianus by McMurrich is not present, the brain is enclosed in a fibrous connective-tissue sheath alone (fig. 4).



3



4

Fig. 3 Cross-section through the anterior end of the ethmoid region of the 8-mm. Syngnathus. Semidiagrammatic. Camera lucida. × 100.

Fig. 4 Cross-section through the anterior end of the orbit of an 8-mm. Syngnathus. Semidiagrammatic. Camera lucida. × 100.

ABBREVIATIONS

c.c., copula communis
dent., dentary ossification
eth., ethmoid plate
int.sept., interorbital septum
j.r.p., junction rostropalatinus
Mk., Meckel's cartilage
o.c., oral cavity
pmx., premaxillary ossification
pal., palatine cartilage
ps., parasphenoid ossification
pt.qu., pterygoquadrate cartilage
r.c., rostral cartilage
sym., symplectic cartilage
trab., trabecula communis

Posterior to the ectethmoid cartilages, the interorbital septum becomes broader and appears as a meshwork of connective-tissue fibers within which are scattered numerous stellate cells. If we assume with Swinnerton that the ethmoid region ends with the posterior end of the ectethmoid cartilages, then it may be stated that dorsally this meshwork is continuous with the membranous sheath surrounding the brain, and ventrally with the perichondrium of the trabecula communis.

As in other non-siluroid teleosts, the trabecula communis is considerably narrowed between the greatly enlarged eyes (figs. 2, 4). While in this region of a 5.7-mm. Gasterosteus the brain lies immediately dorsal to the trabecula communis, in Syngnathus it is widely separated—a condition which may be ascribed to the more rapid growth of the trabecula communis.

The optic nerves cross through the interorbital septum in the region of the optic chiasma a short distance dorsal to the trabecula communis. The septum is distinct ventral to their crossing. Posterior to this region the interorbital septum is broad and indistinct, and it becomes less apparent as the ventral surface of the brain approaches the trabecula communis in the region just anterior to the fenestra myodomus ventralis.

A cross-section of the trabecula communis in the interorbital region has a distinctly double character, which indicates its formation by the fusion of the anterior ends of the trabeculae cranii. The anterior extent of the fenestra myodomus ventralis is not as great in Syngnathus as in a 5.7-mm. Gasterosteus, hence the trabecula communis is relatively shorter in the latter.

A mass of diffuse mesenchyme cells, the primordium of the vomer bone, is present along the ventral surface of the ethmoid plate. More posteriorly a convex osseous lamella abuts against the ventral surface of the trabecula communis. This is the first ossification in the cranium and is the beginning of the parasphenoid (fig. 4). It forms the median floor of the fenestra myodomus ventralis and of the fenestra hypophyseos (figs. 5, 6). No mention of this ossification is made in the description of the early stages of the chondrocranium of Gasterosteus.

Posterior to the orbital region, the trabeculae cranii diverge to form the margins of the fenestra myodomus ventralis (fig. 5). This fenestra is so named because of its homology to that space in other teleosts, which lies between the trabeculae cranii and anterior to the hypophysis, and lodges the proximal ends of the recti eye muscles (Allis, '19). These eye muscles have their origin on the dorsal surface of the parasphenoid lamella and are not as yet separate elements. Posterior to the origin of the recti muscles, the fenestral space is filled with a dense mass of

connective-tissue cells which is separated from the ventral surface of the brain by a layer of fibrous connective tissue. Throughout this region the trabeculae cranii are circular in cross-section.

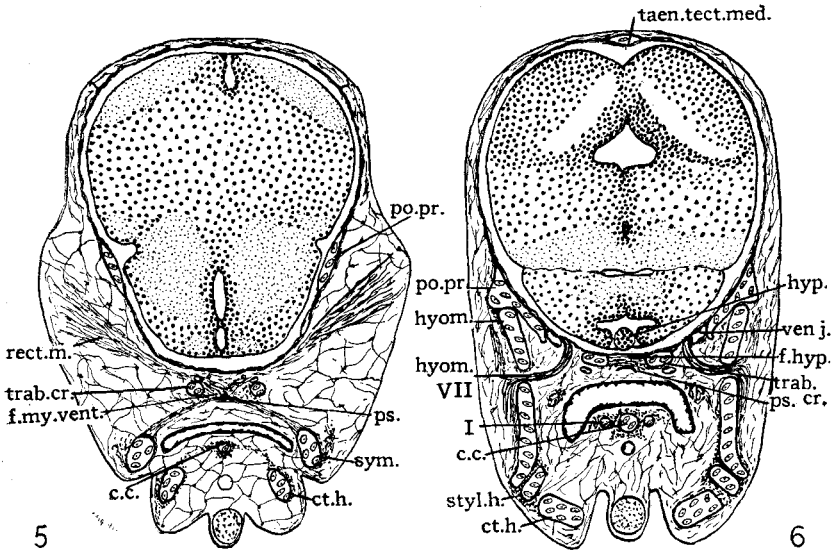


Fig. 5 Cross-section through the posterior part of the orbit, 8-mm. Syngnathus. Semidiagrammatic. × 100.

Fig. 6. Cross-section through the anterior end of the otic capsule, 8-mm. Syngnathus. Semi-diagrammatic. × 100.

ABBREVIATIONS

br.I, branchial arch I
c.c., copula communis
ct.h., ceratohyal cartilage
f.hyp., fenestra hypophyseos
f.my.vent., fenestra myodomus ventralis
hyom., hyomandibula
hyom.VII, ramus hyomandibularis facialis
hyp., hypophysis cerebri
po.pr., postorbital process
po.pr., postorbital process
ps., parasphenoid ossification
rect.m., recti eye muscles
styl.h., stylohyal cartilage
sym., symplectic cartilage
taen.tect.med., taenia tectum medialis
trab.cr., trabecula cranii
ven.j., vena jugularis

As the divergence of the trabeculae becomes greater, the parasphenoid lamella remains as a small spicule in the median part of the fenestra and is widely separated from the trabeculae cranii. The gasserian ganglion lies in a space between each

trabecula cranii and the postorbital process of that side. Swinnerton indicates this relation of the trigeminal ganglion to the trabecula and the postorbital process in Gasterosteus. Gaupp calls this space in a 25-mm. Salmo the incisivum prooticum.

Farther posterior, the prootic process of each side abuts against the lateral surface of the trabecula cranii (figs. 1, 2). The cartilage forming each of these structures retains its identity at the point of union. The perichondria of the two cartilages form the line of separation between them. In this immediate region the trabeculae are flatter and more ovoid than they are more anteriorly. This is probably the region of junction between the trabeculae and the parachordal cartilages (fig. 6).

A wide space, such as is found between the trabeculae cranii and the ventral surface of the brain in the fenestra myodomus ventralis region, is obliterated here by the presence of the hypophysis cerebri, so that the membrane enclosing the brain is continuous with the perichondria of the trabeculae cranii (fig. 6).

A foramen is present in the cranial wall just posterior to the prootic process. Through this foramen the jugular vein and the ramus hyomandibularis facialis pass (fig. 6). The posterior margin of the foramen is formed by the wall of the otic capsule.

Posterior to the facialis foramen the parachordal cartilages are fused with the ventromesial margins of the otic capsules. Mesially, the parachordals are closer together than were the trabeculae farther anterior. The parasphenoid lamella forms the floor of the intervening fenestra, its roof is formed by fibrous connective tissue ventral to the posterior end of the hypophysis.

Just posterior to this region the parasphenoid ends and the space between the parachordals is occupied by the anterior end of the notochord (fig. 7). The notochord is separated dorsally from the cavum cranii by connective-tissue stroma connecting the perichondria of the parachordals. The space between the parachordals in which the notochord lies has been called the interparachordal fossa in Gasterosteus (Swinnerton), and the fenestra basicranii posterius in Salmo (Gaupp); the latter terminology is used in this paper.

The cartilage of this region of the parachordals has the same relation to the notochord in both Syngnathus and the 5.7-mm. Gasterosteus, but it is not as widely separated from the notochord as it is in a 19-mm. Amia (Kindred, '19). This indicates

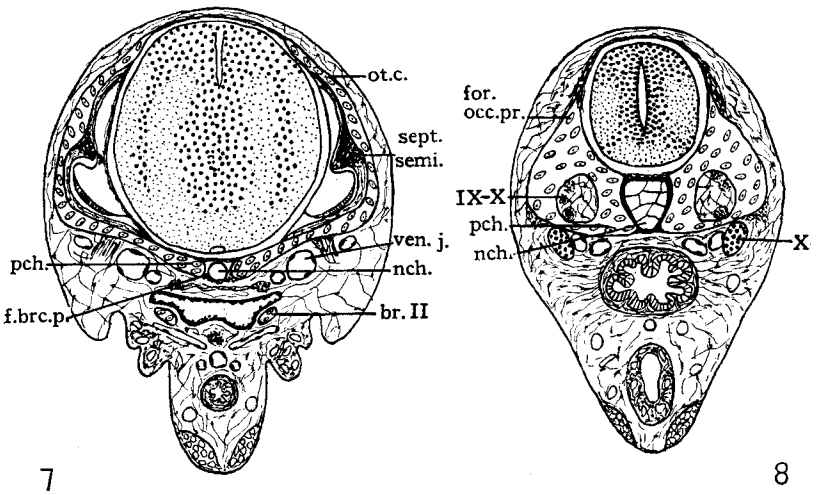


Fig. 7 Cross-section through the middle part of the otic capsules, 8-mm. Syngnathus. Semidiagrammatic. Camera lucida. × 100.

Fig. 8 Cross-section through the occipital region, 8-mm Syngnathus. Semidiagrammatic. Camera lucida. × 100.

ABBREVIATIONS

br.II, branchial arch II
f.bcr.p., fenestra basicranii posterius
for.IX–X, foramen for IX and X cranial nerves
nch, notochord
ot.c., otic capsule
pch., parachordal cartilage
sept.semi., septum semicircularis lateralis
ven.j., vena jugularis
X, ganglion of vagus nerve

a precocious growth of the cartilage in this region of Syngnathus.

Laterally, the cartilage of each parachordal is confluent with the ventromesial margin of the otic capsule (fig. 7). The cartilage cells of the parachordals are arranged concentrically, while those of the otic capsule are in a vertical row.

Farther posterior the notochord increases greatly in diameter and invades the cavum cranii. The parachordals abut against the ventrolateral surfaces of the notochord, so that it really lies in a groove on the dorsomesial surfaces of the parachordals. The parachordals are separated from each other ventral to the notochord and there is no trace of a hypochordal bridge.

In the region between the posterior parts of the otic capsules, the enlarged notochord lies between the maculi utriculi and the auditory ganglia adjacent to them ventrolaterally. The relation of the parachordals to the notochord remains as in the more anterior region. At the posterior end of the otic capsules the cartilage forming their walls fuses with the occipital processes which lie on the dorsolateral surfaces of the notochord dorsal to the parachordals (fig. 8). The parachordals retain their identity for a short distance posterior to this fusion; gradually, however, the cells of the parachordals become confluent with those of the occipital cartilages (fig. 8). A slender bridge of fibrous connective tissue connects the occipital processes with each other dorsal to the notochord, but their ventral margins are separated by the notochordal sheath (fig. 8). A canal extends ventroposteriorly from the floor of the otic capsule and opens to the exterior posteroventral to its wall. The mesial wall of this canal is formed by the occipital cartilage (fig. 8). The canal contains a part of the sacculus and the fibers of the glossopharyngeal and vagus nerves. A common canal for these two cranial nerves is also found in the 6.6-mm. Gasterosteus, so it may be stated that Syngnathus is more precocious in development in this part of the cranium than in the more anterior parts, since all of the parts so far noted have been comparable in state of development to the same parts in the 5.7-mm. Gasterosteus.

The occipital masses lateral to the notochord persist for a short distance posteriorly, but do not meet dorsal to the brain to form an occipital arch (figs. 2, 8). They gradually diminish in extent, the ventrolateral parts disappearing first, as would be expected, since these represent the posterior ends of the parachordals. Finally, the cartilage on the dorsolateral surfaces

of the notochord is replaced by densely cellular masses of fibrous connective tissue. There are no postvagal nerves in this region and the first neural arch is relatively far distant from the posterior end of the occipital cartilages.

The postorbital process of the otic capsule appears in the posterior part of the membranous orbital wall (fig. 5), and its anterior end does not extend as far dorsal in the wall as does its homologue in a 6.6-mm. Gasterosteus. In cross-section the postorbital process is very thin and flat, increasing in thickness posteriorly. At the same time it trends ventrally in the cranial wall (fig. 1). The jugular vein and the gasserian ganglion lie ventral to the postorbital process, and for this reason Swinnerton compared the postorbital process of Gasterosteus to a part of the alisphenoid cartilage of Salmo (Parker, '72)—a comparison with which I am in full agreement as regards the postorbital process of Syngnathus, both from this relation and also from its connection with the otic capsule.

Posteriorly, the dorsal end of the postorbital process becomes bulbous, the abductor hyomandibularis muscle having its origin on the lateral face. Posterior to the origin of this muscle the dorsal end of the hyomandibula articulates in a groove on the lateral face of the postorbital process (fig. 6). As noted above, the ventral end of the postorbital cartilage becomes the prootic process which trends ventrally and meets the trabecula cranii (figs. 1, 2).

The ramus hyomandibularis facialis and the jugular vein leave the cranium posterior to the prootic process, the dorsal margin of the foramen being formed by the postorbital process (fig. 6). The adductor hyomandibularis muscle has its origin on the ventroposterior margin of this foramen. Similar topographical relationships between the cartilage and the cranial nerves have been described for Gasterosteus, but the muscle relations have not been noted. In a 25-mm. Salmo (Gaupp), a band of cartilage (präfaciale basicapsuläre Commissure) connects the postorbital process with the parachordal and is perforated by three foramina—an anterior one for the jugular vein, a posterior one for the ramus hyomandibularis facialis, and a ventral one for the ramus palatinus facialis.

In Syngnathus the cartilage forming the dorsal margin of the foramen for the passage of the jugular vein and the ramus hyomandibularis facialis extends more dorsally in the wall than does the postorbital process (fig. 1). Posterior to the foramen the cartilage forms the wall of the otic capsule proper, since the membranous labyrinth appears between its wall and the brain (fig. 7). The large basicapsular fenestra in the wall of the otic capsule of a 5.7-mm. Gasterosteus and of a 13-mm. Salmo has been interpreted as the homologue of the fenestra ovalis in the otic capsule of Amphibia. This is represented in the wall of the otic capsule of Syngnathus by a minute opening in its ventral part, closed by membrane.

Two cartilaginous projections from the mesial face of the capsular wall, connected by fibrous tissue with the membrane separating the cavum cranii from the cavum labyrinthii, are the primordia of the lateral and posterior septa semicircularia. The lateral septum is shown in figure 7. The posterior one is located a short distance posterior to this and more dorsal.

The dorsomesial margins of the otic capsular walls are continuous with a narrow median cartilage which lies in the fibrous connective tissue dorsal to the brain (fig. 2). This bar of cartilage starts as a small point in the membranous roof of the cranium of the postorbital region in the same transverse plane as that in which the facialis foramen is located (fig. 6). It gradually becomes wider posteriorly and forms a triangular plate in the cranial roof (fig. 2). The posterolateral margins of this plate are confluent laterally with the mesial margins of the otic capsular walls. Such a plate of cartilage has been described, but not figured for a 25-mm. Salmo by Gaupp, and termed the taenia tectum medialis. An epiphysial bar such as is found in the cranial roof of Gasterosteus connected with the ectethmoid region by a pair of supraorbital cartilages is lacking in Syngnathus. Hence in Syngnathus the taenia tectum medialis is the only cartilage which at this stage lies dorsal to the brain, since the occipital cartilages have not as yet met mesially. It may be considered as the remnant of a once solid cartilaginous synotic tectum which has become very much reduced during the phylogenetic processes which gave rise to Syngnathus.

As already mentioned, the posterior wall of the otic capsules becomes confluent with the occipital processes and forms a canal on either side of the chondrocranium for the passage of the glossopharyngeal and vagus nerves.

B. The visceral arches

The first part of the primordial visceral skeleton to be considered is a small median precranial cartilage, the rostral cartilage (figs. 1, 2, 3). Lying on the middorsal surface of the rostral process of the ethmoid plate, it has a relationship to the latter, comparable to that in other teleosts, as mentioned by Gaupp. This cartilage was not noted by McMurrich in Syngnathus peckianus. Sagemehl ('91), in considering the rostral cartilage in other teleosts, has homologized it to the median synchondrosis which occurs between the distal ends of the palatoquadrate cartilages of Heptanchus. This homology is further borne out by the conditions in Syngnathus at this stage, because the rostral cartilage is connected by densely cellular connective tissue with the anterior ends of the palatine cartilages. The beginnings of the premaxillary ossifications are connected with the lateral surface of this rostral cartilage (fig. 3). It has no homologue in Gasterosteus.

The anterior ends of the palatine cartilages (ethmopalatines, McMurrich) are flat in cross-section, the mesial surface of each articulates with the lateral surface of the rostral process of the ethmoid cartilage and is connected by fibrous connective tissue with the latter and with the rostral cartilage (figs. 1, 3). Posterior to the region of articulation, each palatine cartilage tapers and trends ventrally, finally dwindling to a small point embedded in the embryonal connective tissue surrounding the ethmoid plate and the olfactory pit (fig. 1). It is important to note here that the palatine cartilage has a posterior fibrous connection with the dorso-anterior margin of the pterygoquadrate, rather than a cartilaginous connection as in Salmo or Gasterosteus. This condition in Syngnathus bears out the statement made by Swinnerton to the effect that the palatine cartilage does not arise

independently in any teleost, but must at least have a fibrous, if not a cartilaginous connection with the more posteriorly situated pterygoquadrate. Such a condition exists at this stage in Syngnathus, and whatever the later conditions may be, this fibrous connection is primary. In this respect the relations of the posterior end of the palatine cartilage resemble that of the 10-mm. Amiurus (Kindred) in which the posterior end of the palatine is connected with the anterior end of the pterygoquadrate by a connective-tissue bridge.

McMurrich in his description of Syngnathus peckianus failed to recognize this relationship and stated that the 'ethmopalatine' was independent of the pterygoquadrate. The anterior relation of the palatine cartilage to the ethmoid plate is similar to that of Gasterosteus—a condition which Swinnerton calls acrartete. If it is assumed that the fibrous connection is the homologue of the intervening cartilage in Salmo, then the fibrous connection between the posterior end of the palatine and the anterior end of the pterygoquadrate which passes ventral to the ectethmoid cartilage in Syngnathus may represent a condition comparable to that in Salmo, where the posterior part of the palatine process of the palatoquadrate articulates with the ventral surface of the ectethmoid process.

In the 8-mm. Syngnathus, the mandible is formed by the fused meckelian cartilages. They project for a short distance beyond the anterior margin of the dorsal part of the oral gape and form the axes of the shovel-like ventral portion (figs. 1, 2). The anterior end of each meckelian cartilage abuts against its fellow in the median line by a flat thickened surface. The cartilage cells on the abutting surfaces are very small, numerous, and arranged in a vertical row, separated from each other by the fused perichondria. Posteriorly, the cartilages diverge, become smaller in cross-section, and are connected with each other mesially for a short distance by a slender band of developing muscle tissue. The muscle tissue is replaced more posteriorly by embryonal connective tissue. Each meckelian cartilage is gradually compressed to form the coronoid process (fig. 1). A small notch on the anteroventral face of this region separates

off an angular process, just posterior to which the cartilage articulates with a groove on the dorsal surface of the quadrate portion of the pterygoquadrate.

Meckel's cartilage of the 8-mm. Syngnathus differs in several respects from that of the 6.6-mm. Gasterosteus. In the first place, the curve of the ventral surface of this cartilage in Syngnathus is concave, while in Gasterosteus it is convex. There is a continuous gradation from the anterior part of the cartilage into the coronoid process in the former, while in the latter, the coronoid process projects abruptly from the dorsal surface. In Syngnathus the posterior end of the cartilage projects dorsal to the quadrate—a condition not found in Gasterosteus. Of the angular notch and process of Syngnathus, the latter only is present in Gasterosteus.

A rudimentary inferior labial cartilage is represented by a cellular mass which extends along the dorsal surface of the anterior part of Meckel's cartilage and ends posteriorly in the mandibular fold. It is connected by a bridge of connective-tissue cells with the primordium of the maxillary bone which lies in the supramandibular fold connected dorsally with the lateral surface of the palatine cartilage by fibrous connective tissue.

The quadrate portion of the pterygoquadrate cartilage starts anteriorly between the posterior end of Meckel's cartilage and the distal end of the symplectic (fig. 1). A narrow bridge of cartilage connects it with the latter element, showing possibly a common origin for the cartilage in this region. In cross-section the quadrate is dumb-bell shaped and lies at right angles to the articular surface of Meckel's cartilage. The posterior part of it projects dorsally as a flattened plate, connected with the posterior end of the palatine cartilage by a densely cellular strand of fibrous connective tissue and separated from the ethmoid cartilage by a fold of the oral cavity (fig. 4). The symplectic cartilage extends along the ventromesial surface of the pterygoquadrate. This cartilage ends posteriorly in the midregion of the orbit with a small posteriorly projecting process—the metapterygoid process (fig. 1). According to Swin-

nerton, the metapterygoid process of Syngnathus represents a stage in the reduction of an elongate metapterygoid process such as is found in other teleosts. The metapterygoid process does not have the intimate relation with hyomandibula which characterizes the metapterygoid process of Salmo and Amiurus.

As already stated, the symplectic element extends ventral to the anterior margin of the pterygoquadrate and is confluent with it by means of a bridge of cartilage. Continuing posteriorly as a slender cartilaginous core, the symplectic extends mesial to the pterygoquadrate along the entire extent of the latter (figs. 1, 2). A ventral diverticulum of the oral cavity separates it from the copula communis posterior to the pyterygoquadrate. Histologically, it has a very heavy perichondrium and there are usually two or three cartilage cells in a cross-section. Posterior to the orbit, the symplectic is connected to the trabecula communis by several strands of embryonic muscle tissue. Finally it becomes confluent with the ventral end of the hyomandibula, no line of division being present between the two. A similar condition is met in the symplectic of Gasterosteus, but as yet the cartilaginous continuity between the distal end of the symplectic and the pterygoquadrate characteristic of Syngnathus has not been described. The great distance between the metapterygoid process of the pterygoquadrate and the symplectic is to be noted in Syngnathus as compared to the intimate relation between the elongate metapterygoid and the symplectic in Gasterosteus and Belone (Swinnerton).

The hyomandibula at this stage is a rectangular piece of cartilage which articulates at its dorsal end with the anterior fourth of the otic capsule and is confluent ventrally with the symplectic (fig. 1). Ventromesially, it is flattened for articulation with the stylohyal cartilage (fig. 6). The dorsal end of the hyomandibula is thin and rounded where it abuts against the otic capsular wall. The ventral portion is thickened (fig. 6). Near the anterior dorsal margin a small foramen is present for the passage of the ramus hyomandibularis facialis. The abductor hyomandibularis muscle is inserted on the anterior margin of this foramen. The opercular process projects from the posterior

margin of the dorsal part of the hyomandibula and the adductor hyomandibularis muscle is inserted on its mesial face.

Here again certain differences are to be noted between the chondrocranium of Syngnathus and that of a 5.7-mm. Gasterosteus. The hyomandibula of the former is more elongate and rectangular on its vertical axis than is the hyomandibula of the latter. The relative amount of articular surface with the otic capsule is greater in Gasterosteus than in Syngnathus. The ventral portion of the hyomandibula of Syngnathus is thicker

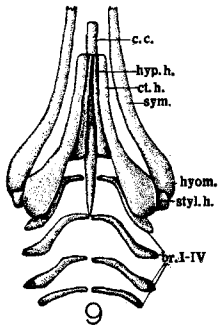


Fig. 9 Ventral view of hyoid and branchial arches, 8-mm. Syngnathus. Drawing made from wax model 230 times actual size of parts. Ratio of drawing to model, 1:3.

ABBREVIATIONS

br.I–IV, branchial arches I to IV
c.c., copula communis
ct.h., ceratohyal cartilage
hyom., hyomandibula
hyp.h., hypohyal cartilage
styl.h., stylohyal cartilage
sym., symplectic cartilage

than the dorsal part, while in Gasterosteus the conditions are reversed. The distinct opercular process present in Syngnathus is lacking in Gasterosteus. The foramen for the passage of the ramus hyomandibularis facialis is the only constant feature of the body of the hyomandibula of these two forms.

The copula communis is at this stage a delicate cylindrical bar of cartilage which forms the median articulating support for the hypohyal cartilages and the first and second branchial arches (fig. 1, 9). It is supported in the embryonal connective tissue ventral to the oral cavity (fig. 4). The cartilage is continuous and of uniform caliber in its anterior part, tapering posteriorly

as a core of procartilage cells, against which abut the third and fourth branchial arches.

The copula communis of a 5.7-mm. Gasterosteus has approximately the same relations to the hypohyals and the first and second branchial arches, but in addition it has extended as cartilage as far as the third branchial arch. There is also a small separate cartilage between the fourth pair of branchials. The independent wedge-shaped piece at the anterior end of the copula communis of Gasterosteus is lacking in Syngnathus.

The branchial cartilages of Syngnathus have not curved dorsally at their distal ends in this stage as they have in the 5.7-mm. Gasterosteus, nor has the fifth branchial arch appeared. The pharyngobranchial plates present in Gasterosteus are represented in Syngnathus by a pair of procartilaginous masses ventral to the parachordals and connected with each other by a sheet of muscle.

The hyoid elements are very well developed in Syngnathus. The stylohyal is a small broad plate between the ventral end of the hyomandibula and the dorsolateral surface of the ceratohyal (fig. 9). This element, the stylohyal, lies closely ventral to the posterior margin of the hyomandibula, and not ventral to its anterior margin as does the corresponding element in Gasterosteus.

The ceratohyal is very massive at this stage and extends anteriorly rather than directly mesial, as in Gasterosteus. It abuts against the ventrolateral margin of the elongate, horizontal hypohyal. This latter cartilage is very peculiar in its relation and extent. Instead of being a small wedge-shaped articular plate, as in Gasterosteus, it is an elongate rod of cartilage which anteriorly extends beyond the end of the ceratohyal (fig. 9). The surface of articulation between the hypohyal and the copula communis is nearer to the posterior end of the hypohyal than to its anterior end.

THE CHONDROCRANIUM OF THE 12-MM. STAGE

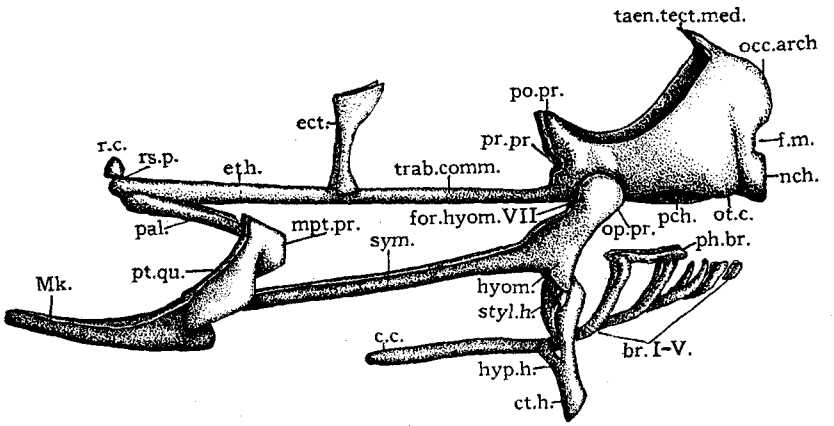
A. The neurocranium

The anterior end of the ethmoid plate of the 12-mm. Syngnathus is much broader and blunter than it is in the neurocranium of the 8-mm. stage. Its relations to the palatine and rostral cartilages are similar (fig. 11). The anterior end, however, is no longer turned dorsally, but has straightened out, carrying with it the attached elements. Posterior to the broad rostral process, the ethmoid plate gradually diminishes in size. It becomes wedge-shaped at first and then more triangular in cross-section. The dorsal part of the ethmoid is the thicker.

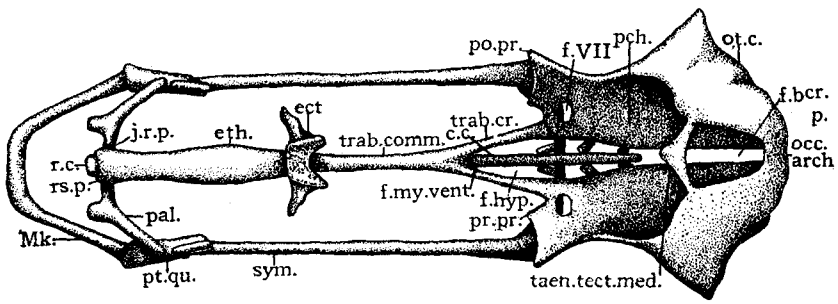
The vomer primordium represented in the 8-mm. stage by a mass of cells ventral to the ethmoid plate is now an osseous lamella embedded in a mass of osteogenetic cells in the same region (fig. 12).

The dorsal surface of the ethmoid plate is surmounted by a septum of fibrous-connective tissue. The relationship of this to the cartilage is the same as that of the osseous ridge which later develops in this place. This ridge of connective tissue is connected with the stroma enclosing the olfactory pits and is continuous posteriorly with the membranous interorbital septum. Histologically, the ethmoid cartilage is the same as it is in the 8-mm. stage except for an increase in size and the presence of a thicker perichondrium.

The ectethmoid cartilages, which in the 8-mm. embryo were separate, connected with each other by connective tissue only, have now fused with each other dorsomesially to form a horse-shoe-shaped mass of cartilage posterior to the olfactory pits (fig. 12). The posterior margin of this mass forms the anterior boundary of the orbits. The anterior end of the brain lies in a trough on the dorsum of this ectethmoid arch, the margins of the trough projecting posteriorly for a short distance in the membranous cranial wall (figs. 10, 11). The olfactory nerves, after leaving the olfactory pits, pass to the mesial margins of the sides of the arch and extend posteriorly within it (fig. 12). Thus at this stage the olfactory nerves have not been separated from



10



11

Fig. 10 Lateral view of the chondrocranium and visceral arches of a larva of Syngnathus fuscus, 12 mm. long. Drawing made from wax model 150 times the actual size of the chondrocranium. Ratio of drawing to model, 1:3.

Fig. 11 Dorsal view of the same model as shown in figure 10.

ABBREVIATIONS

br.I–V, branchial arches I to V.
c.c., copula communis
ct.h., ceratohyal cartilage
ect., ectethmoid cartilage
eth., ethmoid plate
f.bcr.p., fenestra basicranii posterius
f.hyp., fenestra hypophyseos
f.my.vent., fenestra myodomous ventralis
f.m., foramen magnum
f.VII, foramen for exit of ramus hyomandibularis facialis
For.hyom.VII, foramen in hyomandibula for ramus hyom.fac.
hyom., hyomandibula
hyp.h., hypohyal cartilage
j.r.p., junction rostro-palatinus
Mk., Meckel's cartilage
mpt.pr., metapterygoid process
nch., notochord
occ.arch., occipital arch
ot.c., otic capsule
pal., palatine cartilage
pch., parachordal cartilage
ph.br., pharyngobranchial cartilage
pt.qu., pterygoquadrate cartilage
po.pr., postorbital process
pr.pr., prootic process
r.c., rostral cartilage
rs.p., rostral process of the ethmoid
styl.h., stylohyal cartilage
sym., symplectic cartilage
taen.tect.med., taenia tectum medialis
trab.comm., trabecula communis
trab.cr., trabecula cranii

each other by cartilage. They enter the brain at the posterior margin of the mesial dorsal part of the arch. It is significant to note here that the olfactory nerves are in the process of being passively enclosed in cartilage and do not actively fenestrate it.

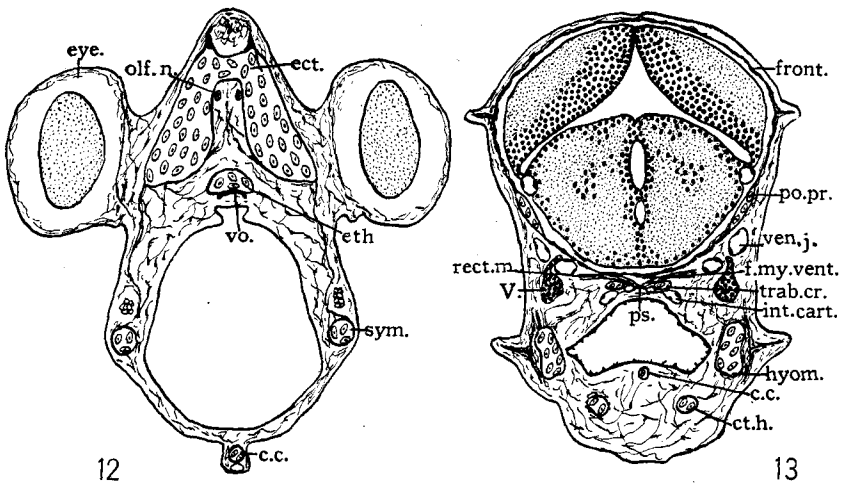


Fig. 12 Cross-section through the ectethmoid region, 12-mm. Syngnathus. Semidiagrammatic. Camera lucida. × 102.

Fig. 13 Cross-section through the posterior end of the orbit, 12-mm. Syngnathus. Semidiagrammatic. Camera lucida. × 66.

ABBREVIATIONS

c.c., copula communis
ct.h., ceratohyal cartilage
ect., ectethmoid cartilage
eth., ethmoid plate
f.my.vent., fenestra myodomus ventralis
front., frontal ossification
hyom., hyomandibula
int.cart., internal carotid artery
olf.n., olfactory nerve
po.pr., postorbital process
ps., parasphenoid ossification
rect.m., recti eye muscles
sym., symplectic cartilage
trab.cr., trabecula cranii
V, ganglion of trigeminal nerve
ven.j., vena jugularis
vo., vomer ossification

The ethmoid plate lies ventromesial to the arch, connected with it by the fibrous connective-tissue ridge already mentioned, as extending along the dorsal surface of the ethmoid. In Salmo, Gasterosteus, and Amiurus, the ectethmoid processes are outgrowths from the ethmoid cartilage. If the ectethmoid carti-

lages of Syngnathus are to be regarded as remnants of the olfactory capsules, the condition of the ectethmoids in the above forms indicates a more specialized relation. Therefore, I am regarding the relation of the ectethmoid cartilages of Syngnathus as primitive.

There is no tegmen or cartilage dorsal to the brain in the ethmoid region, the tips of the frontal ossifications appearing as a pair of delicately spined osseous lamellae in the fibrous connective tissue enclosing the brain.

Just posterior to the ectethmoid region the oblique eye muscles have their origin in the fibrous tissue of the interorbital septum and are not related to the cartilage of either the ethmoid plate or the ectethmoid cartilages. The trabecula communis is flatter and broader in cross-section than that part of the ethmoid plate immediately ventral to the ectethmoid arch, but it gradually diminishes, until at the anterior margin of the fenestra myodomus ventralis it is a very slender cylindrical bar. The parasphenoid lamella is attached to its ventral surface by connective tissue.

In the region of the anterior margin of the fenestra myodomus ventralis, the internal carotid arteries, which more anteriorly were dorsal to the trabecula communis, now pass ventrally into the space between the trabeculae cranii (fig. 13). The recti eye muscles enter the fenestra myodomus ventralis dorsal to the internal carotid arteries between the trabeculae cranii and the fibrous connective tissue enclosing the brain. The hypophysis cerebri lies posterior to this region, so that, in accordance with Allis' criteria, this space between the anterior ends of the trabeculae cranii has been termed the fenestra myodomus ventralis, and not the fenestra hypophyseos. As in the younger stage, the parasphenoid ossification forms the floor of the fenestra myodomus ventralis and serves as a surface of attachment for the recti muscles. The anterior end of the hypophysis cerebri appears just posterior to this region, and the space occupied more anteriorly by the recti muscles and by the carotids is obliterated, the hypophysis pushing the meningeal tissue against the trabeculae cranii. This portion of the intertrabecular fenestra may be properly termed the fenestra hypophyseos.

As in the younger stage the prootic processes abut against the lateral surfaces of the trabeculae and are separated from them by their perichondria (figs. 10, 11). Except for a greater size of all parts concerned, the foramen for the passage of the ramus hyomandibularis facialis and the jugular vein bears the same relation to the trabeculae and prootic processes as in the 8-mm. stage. In this region the trabeculae pass insensibly into the parachordals. These immediately begin to thicken and are fused laterally with the ventromesial walls of the otic capsules (fig. 11). As the hypophysis tapers posteriorly the fenestra hypophyseos begins to narrow and the parasphenoid lamella dwindles to a mere spicule of bone forming its floor. Where the hypophysis ends the anterior tip of the notochord appears between the parachordals. It is enclosed in the fenestra basicranii posterius. The roof of this fenestra is formed by fibrous connective tissue confluent on each side with the dorsal perichondria of the parachordals. The floor is formed by fibrous connective tissue confluent with the ventral surface of the parachordals. The notochord is free and is not enclosed in cartilage as is the intercranial notochord of the 6.6-mm. Gasterosteus. The notochord is, however, much more closely applied to the cartilage in Syngnathus than is the notochord of a 19-mm. Amia.

The parachordal-occipital process fusion in conjunction with the posterior wall of the otic capsule forms as in the 8-mm. stage, the canal for the passage of the glossopharyngeal and vagus nerves. Ossification has not begun in this region.

The postorbital process bears the same relation to the trigeminal ganglion that it did in the younger stage, but a deeper notch occurs in the anterior margin of the prootic process posterior to the ganglion (figs. 11, 13). This notch is the homologue of the incisivum prooticum of Salmo. As in the younger Syngnathus the perichondria between the trabecula and the prootic process persist.

Due to the lateral growth of the brain and an increase in size of the ramus hyomandibularis facialis and the jugular vein, the foramen through which these pass is more ventral in the wall

and larger than it is in the 8-mm. stage (fig. 11). The lamella of the frontal ossification is continuous with the perichondrium of the cartilage forming the dorsal margin of the foramen. Just posterior to the foramen, the cartilage is more deeply grooved for articulation with the hyomandibula than it is in the younger stage. The articular surface does not reach as far posteriorly as that part of the otic capsule containing the membranous labyrinth (fig. 10). The membranous labyrinth has increased greatly in size since the 8-mm. stage and consequently expanded laterally, displacing to a more ventral position the cartilage which formed the lateral wall of the otic capsule in the younger stage. A thin lamella of cartilage surmounts the margin of the thicker ventral portion and forms the dorsolateral wall of the capsule in this region. The formation of the septa semicircularia has not gone farther than in the younger stage and are as yet membranous. The small fenestra basicapsularis present in the otic capsule of the 8-mm. stage persists. Toward the posterior portion of the cranium the mesiodorsal margins are continuous with the cartilage of the taenia tectum medialis (fig. 11). The latter is enclosed in an osseous lamella which represents the beginning of the supra-occipital ossification. Some of the cartilage is in the process of resorption.

The occipital processes which in the younger stages were separate from each other have fused mesially, so that an occipital arch is formed. The posterior margin of the arch projects for a short distance beyond the sides of the arch. The fontanelle left between the taenia tectum medialis and the occipital arch is closed by membrane.

B. The visceral arches

The rostral cartilage has the same relation to the dorsal surface of the ethmoid plate that it had in the younger stage, but the premaxillary lamellae which are represented in the younger stage by cellular masses have now ossified and extend laterally from the rostral piece, overlapping the anterior ends of the palatines.

The palatine cartilages have the same relation to the rostral process of the ethmoid as before, but are longer than in the younger stage and lie in a more horizontal plane—a condition due to the straightening out of the anterior end of the ethmoid (fig. 10). Posteriorly, the palatine cartilages have grown along the fibrous strand which in the younger stage connects them with the pterygoid portion of the pterygoquadrate plates. As a result of this growth, the palatine cartilages and the pterygoquadrates are in closer proximity than they are in the younger stage (fig. 10).

The mandibular symphysis is broader and thicker than in the 8-mm. stage and the meckelian cartilages diverge from it as a pair of cartilaginous rods, which thicken gradually at their posterior ends to form the coronoid processes (fig. 10). The mandible is now more typically teleostean than it is in the younger stage, the peculiar concavity noted on the ventral surface in the 8-mm. stage has been obliterated. The primordium of the dentary ossification appears around each Meckel's cartilage as a single lamella, lateral to and separate from the cartilage. No teeth are present. As in Gasterosteus, the angular process projects posteriorly beyond the surface of articulation with the pterygoquadrate. The pterygoquadrate articulates with the dorsal surface of this portion of Meckel's cartilage at an oblique angle. It becomes vertical posteriorly and there is no longer a projection of the posterior end of the coronoid process dorsal to it. The symplectic element extends ventral to the posterior mesial region of the pterygoquadrate and the metapterygoid process projecting from this region is longer than it is in the 8-mm. stage (fig. 10).

Due to the straightening out of the mandible and the enlarging of the oral opening, the notch present on the ventro-anterior margin of the distal portion of each Meckel's cartilage has disappeared. This whole region has been pushed farther anterior than it is in the 8-mm. stage, by growth and elongation of the symplectic element which has grown in concert with the ethmoid cartilage. The posterior end of Meckel's cartilage no longer meets the distal end of the symplectic.

The mass of cells indicated in the 8-mm. stage as the homologue of the inferior labial cartilage of Gasterosteus has not changed. However, the cells which represented the center of formation of the maxillary ossificatien have deposited an elongate, vertical lamella. This lamella is connected dorsally with the premaxillary lamella anterior to the palatine articulation, and ventrally by a chain of cells with the dorsal tip of the dentary lamella. The maxillary lamella supports the lateral wall of the oral cavity between the end of the cranium and the palatine cartilage. The maxillary lamella bears no teeth.

The metapterygoid process is longer than it is in the 8-mm. embryo, but even now does not have a relation to the symplectic like that of the larval Gasterosteus. As Swinnerton states, the metapterygoid process of Syngnathus represents a stage in the disappearance of such a structure in the teleosts. The posterior end of this process which in the 8-mm. stage lies posterior to the transverse plane of the ectethmoid cartilages now lies quite far anterior to them (fig. 10).

The distal end of the symplectic cartilage which in the 8-mm. stage extends the whole length of pterygoquadrate now reaches only to its posterior end. The cartilaginous connection between these two elements has disappeared. The elongation of the symplectic and the subsequent changes in the positional relationships in that part of the visceral apparatus lying anterior to it have already been stated. Ossification has appeared in the form of a curved lamella external to and distinct from the perichondrium of the symplectic shaft. Posteriorly, the proximal end of the symplectic gradually widens as it becomes confluent with the hyomandibula, so that the angle, which in the younger stage appears between the proximal end of the symplectic and the anterior margin of the hyomandibula, has been obliterated. As a result, it has much the same appearance as that of the 6.6-mm. Gasterosteus.

The hyomandibula, instead of having the vertical position of the 8-mm. stage, is now directed anteriorly at its ventral end, so that the bulk of the cartilage lies anteroventral to the surface of articulation (fig. 10). The posterior extent of the hyoman-

dibula is not nearly as great as it is in Gasterosteus or Salmo. Although the whole ventral portion has swung anteriorly, the foramen for the passage of the ramus hyomandibularis facialis lies as before near the anterior margin of the dorsal head of the

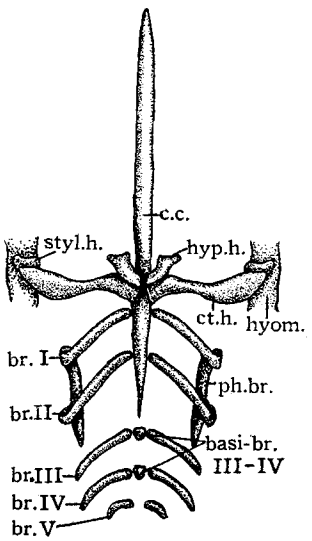


Fig. 14 Ventral view of hyoid and branchial arches, 12-mm. Syngnathus. Drawing made from wax model 150 times actual size. Ratio of drawing to model, 2:3.

ABBREVIATIONS

basi-br.III–IV, basibranchial cartilages III and IV
br.I–V, branchial arches I to V
c.c., copula communis
ct.h., ceratohyal cartilage
hyom., hyomandibula
hyp.h., hypohyal cartilage
ph.br., pharyngobranchial cartilage
styl.h., stylohyal cartilage

hyomandibula. As in the 8-mm. stage, the dorsal portion is relatively thinner than the ventral.

The mesioventral surface of the hyomandibula is flattened for articulation with the interpolated stylohyal, the plane of articulation having been carried anteriorly by the shift in the axis of the hyomandibula (figs. 10, 14). The shift which has taken place in the hyomandibula is due to the part played by the latter in changing the size of the oral cavity in the process

of respiration, since Syngnathus at this stage is a free-swimming larva. An osseous lamella lies external to and separate from the ventral portion of the hyomandibula, enclosing a blood-vessel between it and the perichondrium (fig. 13).

As in the 8-mm. stage, the stylohyal element is interpolated beween the dorsal end of the ceratohyal and the hyomandibula (fig. 14). The ceratohyal, which in the same stage (when the embryo is yet enclosed in the brood pouch of the parent) extends anteroposteriorly in an almost horizontal plane with the posterior end in the more ventral position, has now changed in position, so that it lies almost vertical (fig. 10). The dorsal end of each ceratohyal articulates with the stylohyal of that side, while the ventral end, formerly parallel with the hypohyal element, now lies ventroposterior to it.

The hypohyal element has also undergone a change in position. Instead of lying in a horizontal plane parallel to the copula communis, it now occupies a vertical position, articulating on its mesiodorsal surface with the copula communis (fig. 14). The change in the positional relationships of these elements is due to the functional activity of these as the supporting cartilages of the oral cavity, which by its changes in shape draws water into the mouth and expels it over the gills. Since the gills were not developed in the 8-mm. stage, these parts had not shifted. The conditions of these elements in the 12-mm. stage of Syngnathus are more nearly like those of the 6.6-mm. Gasterosteus, which indicates an earlier functional activity of these parts in the latter, correlated with the longer protected period of Syngnathus.

The copula communis of the 12-mm. stage has retained the same relative length as before, but is more widely separated from the ventral surface of the cranium, because of the increase in the size of the oral cavity (figs. 10, 14). Posteriorly it extends beyond the second branchial arch after having been displaced ventrally between the hypohyal elements due to the shift in their position. Its posterior end is connected by a cord of procartilage cells with the independent basibranchial cartilages between the third and fourth branchial arches.

The first branchial arch has elongated and is turned up laterally to fuse with the pharyngobranchial cartilage which lies at the laterodorsal margin of the oral cavity (figs. 13, 14). The pharyngobranchial plate is also connected with the lateral end of the second branchial arch, ending just posterior to it (fig. 14). The third and fourth branchial arches have not as yet turned up laterally, but they are longer than they are in the 8-mm. stage. The fifth branchial arch has appeared as a pair of small cartilages lateral to the procartilage continuum of the basibranchial plate of the fourth arch (fig. 14).

SUMMARY AND CONCLUSIONS

Under the classification of the teleosts by Gregory ('07), Syngnathus is placed in the order Lophobranchii, which with the order Hemibranchii (including Gasterosteus), are grouped into a superorder, the Thoracostraci. The important similarities and differences of the chondrocrania of these two forms are stated in the following summary.

Both Gasterosteus and Syngnathus are alike in the following chondrocranial characters: the presence of an elongate ethmoid region; the acrartete articulation of the palatine cartilages; the incomplete cranial roof; the horizontal position of the trabeculae cranii and the parachordal cartilages; the presence of two septa semicircularia in each otic capsule; a prootic process separating the trigeminal and facialis nerves from each other; an elongate fenestra basicranii posterius; a common foramen for the glossopharyngeal and vagus nerves between the otic capsule and the occipital arch; a small pterygoquadrate cartilage; a large intercranial notochord; a postorbital process at the anterior margin of each otic capsule.

The above characters wherein Syngnathus resembles Gasterosteus indicate the direction in which the skulls of these two forms have become specialized. In addition, further specializations are to be noted in the chondrocranium of Syngnathus:

1. The modification of the anterior end of the ethmoid plate by turning dorsally in the 8-mm. stage.

2. The presence of a definitive fenestra myodomus ventralis between the anterior ends of the trabeculae cranii.

3. The absence of cartilage on the dorsal and ventral surfaces of the intercranial notochord.

4. The presence of a taenia tectum medialis in the cranial roof.

5. The presence of a minute basicapsular fenestra in the ventral wall of each otic capsule.

6. The fibrous connection between the posterior end of the palatine cartilage and the dorsal end of the pterygoquadrate cartilage.

7. The presence of an elongate symplectic cartilage and a slender hyomandibula.

8. The great length of the trabecula communis and the ethmoid plate.

9. The change in position of the hyoid elements during development.

10. The presence of a reduced metapterygoid process.

The chondrocranial characters of Syngnathus which may be regarded as primitive are:

1. The presence of a rostral cartilage which has been considered by Sagemehl in other teleosts as the homologue of the median synchondrosis between the palatopterygoid cartilages of Heptanchus.

2. The development of the ectethmoid cartilages independently of the ethmoid plate, which seems to the author to indicate that they are the remnants of an olfactory capsule which developed independently.

3. The open communication between the cavum labyrinthii and the cavum cranii.

4. The absence of postvagal nerves in the occipital region.

From the above preponderance of specialized characters, it may be concluded that even in its early stages of development the skull of Syngnathus is already highly specialized.

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