THE ANATOMY OF HETERODONTUS FRANCISCI

II. THE ENDOSKELETON¹

J. FRANK DANIEL

From the Department of Zoology, University of California

THIRTY-ONE FIGURES (EIGHT PLATES)

CONTENTS

a. Introduction.....	447
b. The endoskeleton.....	448
I. Axial skeleton.....	449
1. The skull.....	449
a. The cranium.....	449
b. The visceral skeleton.....	455
2. The spinal column.....	466
II. Appendicular skeleton.....	470
1. The skeleton of the fin girdles.....	470
a. The pectoral girdle.....	470
b. The pelvic girdle.....	471
2. The skeleton of the fins.....	471
a. The paired fins.....	471
1. The pectoral fin.....	471
2. The pelvic fin of female.....	472
3. The pelvic fin of male.....	473
b. The unpaired fins.....	473
1. The first dorsal fin.....	473
2. The second dorsal fin.....	474
3. The caudal fin.....	474
4. The anal fin.....	475
Literature cited.....	475

INTRODUCTION

The skeleton of the elasmobranch fishes has served for numerous investigations which have contributed much to our knowledge. Principal among these researches may be mentioned 'Das Kopfskelet' of Gegenbaur ('72) dealing with the head; studies on the

¹ Part I, The exoskeleton, published in Univ. Calif. Pub., Zool., 1914, vol. 13, p. 147.

column by Hasse ('79); and on the anatomy and development of the fins by Thacher ('77); by Mivart ('79), by Gegenbaur ('65), and by Balfour ('81). From exhaustive studies of the first group we have corrected our understanding of the nature of the skull, while from those of the third we have gained illuminating evidence as to the origin of paired limbs.

While considerable attention has been given to parts of the skeleton of the heterodont sharks, yet, so far as I am aware, no approximately complete study of any member of this group has previously been made. This may be due, at least in part, to the fact that the heterodont sharks are located in widely separated regions, and, furthermore, that they are not abundant in the localities where they occur. *Heterodontus* is more or less difficult to obtain on the California coast, yet through the efforts of the Scripps Institution of the University of California I have been provided with numerous specimens of various ages. I wish here to re-express my thanks to that Institution for its assistance.

While the head region of *Heterodontus* is specialized, as Gegenbaur maintained, yet it is by no means without generalization. In fact marked simplicity may be found side by side with specialization. Such a case is seen in the generalized type of quadrato-mandibular joint, accompanied by a highly specialized mode of ligamentous articulation.

It would be generally conceded that the fin skeleton also is specialized, if one agree with Mivart's conception of specialization meaning concrescence. However this may be, it is certain that, had Mivart known of the unpaired fins of *Heterodontus francisci*, his argument for similarity of plan between paired and unpaired fins would have been even more convincing.

THE ENDOSKELETON

In the following paper I shall discuss at some length the endoskeleton of *Heterodontus francisci*. In such a consideration the skeleton naturally is divided into: (1) The axial part, including the skull and spinal column; and (2) the appendicular skeleton, embracing fins and fin-girdles.

I. AXIAL SKELETON

1. *The skull*

The skull, like that of elasmobranchs in general, is composed of: (a) A cranium or brain case to which the sense capsules are fused in the adult; and (b) a series of cartilaginous visceral arches which support the buccal and pharyngeal regions.

a. *The cranium* or brain case in dorsal view (fig. 1) is roughly quadrilateral in shape, slightly bifurcated at the anterior and posterior margins, and constricted along the sides at the first and second thirds—the first of these indentations being much the more pronounced. The cranium is a closed box except at the antero-dorsal end, where there is a large opening, the anterior fontanelle (*F.*) and at the posterior end, where is located the foramen magnum (*f.m.*) through which the spinal cord joins the brain.

In the mid-dorsal line joining these two openings several structures appear. These are, passing forward, a ridge, the occipital crest (*o.cr.*) which runs to the parietal fossa (*p.f.*); from the bottom of the latter the endolymphatic ducts lead to the ears. In front of this pit is a slight elevation which sinks immediately into a long groove—the parieto-frontal groove (*p-f.g.*) which, in turn, broadens out into the anterior fontanelle.

On each side of and running parallel to the parieto-frontal groove there is a row of foramina extending posteriorly to the level of the parietal fossa. Anteriorly the first two of these on each side are the ophthalmics, through the first of which passes the ophthalmicus profundus nerve (*f.o.p.*'), through the second, the ophthalmic division of the seventh nerve (*f.o.VII'*). Through the numerous and smaller perforations which follow pass branches of nerves, and through the succeeding large foramina, blood vessels. These openings terminate posteriorly at an elevation produced by the anterior oblique semicircular canal (*a.o.s.*) which with a similar elevation from the opposite side roughly forms a broad V enclosing at its apex the parietal fossa. Below this there is a large inverted lower V, the arms of which enclose the foramen magnum (*f.m.*), and the apex of which abuts

against that of the V above described so that the two V's roughly form an hour-glass.

Viewed from the ventral side (fig. 2) the cranium is roughly flat-iron-shaped, with the apex projecting between the olfactory capsules (*ol.c.*). At the most posterior part of the cranium is a niche, the sides of which are produced by the occipital condyles (*o.cd.*). In the mid-ventral line, one-fourth the distance from the posterior border to the tip of the nose, is a foramen (or a pair of foramina) through which the internal (posterior) carotid arteries reach the brain (*f.i.c.*); laterad of these on each side are similar perforations (*f.e.c.*) through which the external (anterior) carotids pass on their way to the orbital region. A line through the internal carotid foramina, and at right angles to the long axis of the cranium, divides the ventral cartilaginous mass into two regions, the anterior of which is the embryonic trabecular region, the posterior region that of the parachordal cartilages.

Along the lateral margin, in ventral view, from behind forward are the post-articular processes (*po.hm.*) bounding posteriorly the deep fossa into which the hyomandibular cartilage fits. Anterior to the fossa is a pre-articular process (*pr.hm.*). In front of the latter is a constriction, anterior to which is a wide projection—the basal plate (*b.p.*); considerably in front of the basal plate, at the sides, is the palatal fossa (*pl.f.*) into which a projection of the palatoquadrate cartilage fits. At the anterior tip of the cranium the basitrabecular cartilage (*b.tr.*) arches upward to be met by two dorsolateral rostral pieces coming down from the dorsal part of the cranium. At the sides of the basitrabecular piece are the external openings for the olfactory capsules (*ol.c.*).

In this view may be described the olfactory capsules and the nasal cartilages at their margins. The capsules are thin, cartilaginous structures which are formed as the skeletogenous protection for the olfactory organ. Dorsally the capsules are continuous with the cranium (see also fig. 1); ventrally they thin out to delicate lamellae of cartilage which surround the nasal aperture, excepting in the postero-medial part, where the

wall is membranous (fig. 2). The olfactory cup or inside of the capsule communicates internally with the cranial cavity by the olfactory foramen, through which the first cranial nerve passes.

At the free margin of the capsule there is a scroll-like nasal cartilage (*n.c.1*, fig. 2), which runs on the outer margin around the aperture of the capsule. Both the anterior and posterior ends of the cartilage recurve upon themselves medially so as to form a narrow ellipse, across which, from its antero-lateral third, a projection extends backward and inward, forming of the ellipse a figure 8.

A second nodule of cartilage (*n.c.2*; not figured by Gegenbaur '72 for *H. philippi*, pl. 16, fig. 2) is loosely attached to the anterior end of the first nasal cartilage. The attachment is made at its broader anterior end and its free tip extends backward to be connected by tissue with the deeper recurved anterior end of the first cartilage.

In side view (fig. 3) the olfactory capsules occupy a position remote from the main part of the cranium. Projecting from the postero-lateral part of the cranium are the thick-walled auditory capsules (*a.c.*) which give protection to the organs of hearing. Between the auditory and nasal capsules is the large socket or orbit in which is located the eye. Overhanging the orbit is the broad supraorbital crest (*s.o.*) from the anterior part of which arises the preorbital process (*pr.o.*) and from the posterior, the post-orbital process (*po.o.*). The floor of the orbit extends outward as the basal plate. Anterior to this plate and running between the orbit and the olfactory capsule is the elongated palatal fossa (*pl.f.*) previously noted in ventral view.

Perforating the brain case in the orbit are numerous foramina through which nerves or blood vessels course between the brain on the one hand and the structures of the eye and the facial region on the other. Ventrally and a little in front of the middle of the orbit is a large opening, the optic foramen (*f.II*), through which the optic nerve reaches the brain. Above and slightly anterior to the optic is a small trochlear foramen (*f.IV*) through which the fourth cranial nerve passes to the superior oblique muscle of the eye. Behind the optic foramen, and in the lower

posterior angle of the orbit, is the large facial foramen (*f.VII*), through which branches of the seventh or facial nerve pass. Almost in the same foramen but slightly ventralward and forward is a small opening for the entrance of the external carotid artery to the orbital region (*f.e.c.*'). Between the facial and optic foramina is a small perforation for the entrance of an artery, the ramus anastomoticus of Hyrtl (*f.r-a.*). This, in Gegenbaur's ('72) plate 2, figure 1, has been marked incorrectly the 'Querter Basalcanal.' Above the facial is the large orbital fissure (*o.f.*) (trigeminal opening) through which pass the fifth, sixth and the first part of the seventh cranial nerves. Slightly above the middle part of a line connecting the orbital fissure and the optic foramen is the oculomotor (*f.III*) for the exit of the third cranial nerve from the brain to muscles of the eye. Between the orbital fissure and the foramen for the ramus anastomoticus artery is the interorbital canal (*i.o.*) by means of which the orbital sinuses of the two sockets communicate. In the antero-dorsal angle of the socket are two foramina, the larger and upper of which is the ophthalmic (*f.o.VII*) for the superficial branch of the seventh nerve; the smaller and more ventrally placed is for the deep ophthalmicus profundus (*f.o.p.*). In the last mentioned opening is a second smaller foramen for the anterior cerebral vein. This leaves the cranial cavity in the region above the olfactory lobe. Below this, in the anteroventral angle of the socket is the posterior entrance to the orbito-nasal canal (*o-n.*) through which a vein passes from the olfactory region. (For the anterior end of this canal see *o-n.*', fig. 2.)

A median sagittal section through the cranium (fig. 5) shows the cavity for the brain. Surrounding this are the walls of the brain box through which the foramina lead. Dorsally the cranial roof or tegmen cranii varies considerably in thickness. Posteriorly and above the foramen magnum (*f.m.*) is a thick portion through the occipital crest (*o.cr.*). Anterior to this the wall pits sharply downward forming the parietal fossa. From this fossa the roof again arches upward and then, as the parieto-frontal groove, passes forward to the anterior fontanelle.

From the fontanelle anteriorly the walls are extended by the rostral and basitrabecular cartilages.

Along the ventral margin the floor or basis cranii also shows extremes in thickness. Directly under the anterior fontanelle it is relatively thick. It then becomes thinner and thinner posteriorly until it reaches the foramen for the internal carotid artery (*f.i.c.*). As we have said (p. 450) this foramen divides the basis cranii into two parts, the anterior of which is the embryonic trabecular, and the posterior the parachordal region. The parachordal or the part accompanying the notochord is greatly thickened. It extends to the posterior part of the cranium as a somewhat spool-shaped segment. Inside of this is the cranial notochord (*ch.*), and surrounding it posteriorly are calcified tissues.

Posterior to the end of the cranial notochord but not in the middle line appears the occipital condyle (*o.cd.*). Other structures are seen below the basis cranii and in the background. These in front of the occipital condyles are the post- and prehyomandibular processes; under the socket is the down-curving basal plate; and under the anterior fontanelle, the margin of the palatal fossa.

The foramina perforating the cranium are here seen to advantage. The most anterior of these is the large opening through which the olfactory tract passes (*f.I*). Midway between this and the occipital condyle is the optic foramen (*f.II*); above and anteriorly is the anterior cerebral foramen (*f.a.c.*). Almost directly above the optic is the trochlear (*f.IV*). Slightly posterior to the optic are two foramina, the upper for the oculomotor nerve (*f.III*), the lower for the ramus anastomoticus artery (*f.r-a.*). Above the entrance to the internal carotid artery is the interorbital canal (*i.o.*). Above the anterior tip of the cranial notochord are two foramina, the upper of which is the large orbital fissure (*o.f.*); the lower of the two is a double foramen, the anterior division of which is for a part of the facial nerve; the posterior gives the acoustic or eighth cranial nerve access to the ear (*f.VIII*). Posterior to this is the smaller foramen for the glossopharyngeal nerve, behind which is the larger

foramen for the vagus (*f.X*). Below the vagus are three smaller foramina (two in fig. 5) through which the spino-occipital nerves of the ventral root type pass. Finally between the posterior end of the cranial notochord and the ventral margin of the occipital crest is the large foramen magnum (*f.m.*).

At the posterior end of the cranium (fig. 4) ventral to the foramen magnum is the cranial notochord, at the sides of which are the occipital condyles (*o.cd.*) by which the spinal column is joined to the cranium. At the side of and slightly above each condyle is the large foramen for the vagus nerve (*f.X*); above this are two smaller foramina through which a spino-muscularis artery (*f.s-m.*) perforates the cartilage without entering the brain case. These, I take it, are the foramina which Haswell ('84, p. 93) describes for *Crossorhinus* as "a pair of small apertures of unknown function." Still further laterally is the opening for the glossopharyngeal or ninth cranial nerve (*f.IX*). At the lower angles of the posterior part of the cranium are the post- and superior articular processes (*po.hm.* and *s.hm.*) by which the hyomandibular suspensorium is fixed to the cranium.

A view of the rostral region (fig. 1 and text fig. A) explains the structures there involved. It is noted that the pointed anterior end bifurcates into dorso-lateral halves which, near the middle line, bend downward and fuse with the median ventral trabecular piece. These, in *Heterodontus francisci*, were they compared with a form in which the rostral cartilages compose a well-marked framework, as for example *Pseudotriakis microdon* (Jaquet '05), would show but slightly their rostral nature. A comparison with another type is instructive in this respect. In *Crossorhinus* (*Orectolobis*) Haswell ('84) figures a cranium (*b* of text fig. A) in which he describes paired pieces (*rst.*) as being prolongations of the ventral floor. From the condition present in the heterodont sharks it would seem not improbable that they are in fact projections from the dorsal and the lateral walls rather than from the floor. If such be true the likeness between *Crossorhinus* and *Heterodontus* in this regard is striking, for a union of the median rostral piece (*rst.*) with the olfactory wing (*ol.wg.*) above and of the olfactory wing and the basitra-

becular cartilage (*ba.tr.*) below would give to *Crossorhinus* a type of rostrum much like that of *Heterodontus*.

b. The visceral skeleton is composed of a series of right and left cartilaginous arches which more or less completely surround the buccal cavity and the pharynx. These, in *Heterodontus*, if viewed, say, from the left side, are like those of other pentanchid sharks, seven in number; they may be divided into two groups. The first group comprises the first and second arches,

Text-fig. A Nasal region of *Heterodontus francisci* and *Crossorhinus barbatus*; *ba.tr.*, basi-trabecular cartilage; *f.op.pr.*', ophthalmic foramen for profundus nerve; *f.op.VII'*, ophthalmic foramen for facial nerve; *Fo.*, anterior fontanelle; *ol.wg.*, olfactory wing; *rst.*, rostral cartilage.

the first of which, the mandibular, is composed of the upper and the lower jaw; the second, the hyoid arch, is similarly made up of two segments. The second group consists of five branchial arches which support the pharynx. In structure the branchial arches are essentially similar to the first two arches excepting that in these there are typically four segments to an arch. These differ among themselves, however, in minor details.

The mandibular, or first arch (fig. 7), has become the most highly specialized of all the visceral arches. Its upper segment, representing the palatal and quadrate regions, is called the

palato-quadrate (*p-q.*); the lower segment is the mandibular or Meckel's cartilage (*md.*). In *Heterodontus* this arch is closely attached to the cranium in the preorbital region by a capsular ligament which keeps the upper and anterior margin (*a.p.*) of the palato-quadrate in the palatal fossa of the cranium. A slip from the capsular ligament (*c.l.*' fig. 7), arising along the ventral margin of the cranium under the fossa (*fig. 2), extends backward and downward to join the quadrate on the ventral part of the transverse median ridge (*tr.m.r.*). Just under the orbit both the upper and the lower segments of the mandibular arch flare outward in *Heterodontus francisci* so that the distance to the spiracular cartilage or to Huxley's so-called otic process is, I take it, greater than that described by Huxley for *Heterodontus philippi*. Posteriorly, the arch has no direct attachment to the cranium but is held in position by ligaments soon to be described.

As a cartilage the palato-quadrate (*p-q.*, figs. 6 and 7) is longer than the mandible. Its upper margin is irregular, due principally, to a dorsal indenture in the anterior third. The anterior wall of this indenture comes in contact with the ethmoidal region, while the posterior wall of the indenture, as seen in figure 7 (*a.p.*) serves as a process of the palato-quadrate which fits into the palatal fossa of the cranium. Medially from this articular surface a sharp ridge (*tr.m.r.*) runs, to the lower part of which is attached the slip from the capsular ligament above described. Externally, at the beginning of the posterior third of the quadrate there is a strong lateral transverse ridge which passes almost across the cartilage (*tr.l.r.*, fig. 6). To this ridge are attached tendinous fibers of the adductor mandibularis muscle. Posteriorly and dorsally the palato-quadrate is provided with a lateral flattened enlargement, the hyal process (*hl.p.*), also for muscular attachment. The hyal process is continuous with a similar process on the mandible.

The mandible (*md.*, figs. 6 and 7) is an unusually heavy cartilage. The angular part of this is high, considerably elevating the quadrato-mandibular joint. If seen from below, the mandible would appear as a strongly crescentic cartilage, the poste-

rior tip of which extends considerably laterad of the anterior. Inside of and below the teeth, there is a long ridge (*md.r.*, fig. 7) from which a tendinous bridge passes to a similar ridge on the other side; to the lower sides of this ridge the strong coraco-mandibularis muscle is attached; near the quadrato-mandibularis joint and mediad there is present a prominent mandibular knob (*kb.*) against which the second arch abuts.

The joint between the palato-quadrate and the mandible, like that in *Chlamydoselachus* (Goodey '10, pp. 544-545) and *Heptanchus* (Gadow '88, pp. 452-453) forms a double ball and socket. The anterior articulation is formed by a ball of the mandible fitting into a socket of the quadrate. The posterior articulation consists of a large socket in the outer angular part of the mandible, into which a ball from the hyal process of the quadrate fits. Between the two articulations in *Heterodontus* is a space, somewhat like that described by Gadow ('88) for *Heptanchus*.

A description of the articulations of the first arch, further than the attachment of the palato-quadrate to the cranium as above described (p. 456), may be deferred until a study is made of the second or hyoid arch.

The hyoid arch (fig. 6) as we have seen, is also composed of two segments. The upper division, the epihyoid, becomes in *Heterodontus* an important suspensorium for the mandibular or first arch; it is called the hyomandibula (*hm.*). The lower segment of the arch is the ceratohyoid or hyoid proper (*c-h.*). Connecting the two ceratohyoids of opposite sides is a median unpaired piece, the basihyal cartilage (*b.h.*, fig. 11).

Both of the segments of the hyoid arch are heavy cartilages. The hyomandibula is thickened both proximally, where it fits into the deep fossa under the auditory capsule, and distally, where it joins the ceratohyoid and touches the mandible near the quadrato-mandibular joint. The ceratohyoid is considerably longer than the hyomandibular segment, and extends forward and inward to meet the basihyal.

Articulations of the hyoid arch. The hyomandibula is bound by a strong capsular ligament to the hyomandibular fossa in the

cranium. This, in figure 6, has been removed so as to show the proximal end of the hyomandibula. The superior post-spiracular ligament (*s.p.s.l.*) of Ridewood '96; (see also W. K. Parker '79), arising in the postero-ventral angle of the socket and anterior to the auditory capsule, attaches itself to the distal third of the hyomandibula. Further, the hyomandibula is bound to the ceratohyoid by a hyomandibulo-hyoid ligament (*l.hm-h*, fig. 6) which arises on the side of the distal end of the hyomandibula and passes over to the anterior and inner face of the ceratohyal segment, extending thence to its distal third.

A series of ligaments may next be described which are effective in swinging the first or mandibular arch, all but one of which connect this arch directly to the second. That one, however, indirectly and in part, attaches the first arch to the cranium. Those binding the first arch to the second directly and appearing externally are three in number. The first of these is a dorsal ligament (*l.hm-q*, fig. 6) which passes from the upper part of the hyal surface of the quadrate posteriorly to the medial and anterior part of the hyomandibula. This ligament is doubtless that part of the superior post-spiracular ligament which Ridewood ('96, p. 427) described for *Scyllium* as attaching on the quadrate. In *Heterodontus francisci*, however, its attachment is on the hyomandibula, few of its fibers being continuous with the superior post-spiracular ligament. I have therefore called it by a separate name, the ligamentum hyomandibulo-quadratum (*l.hm-q*).

At the joint there is a complex median ligament (*l.m.*, figs. 6 and 7) which passes from the inner side of the quadrato-mandibular joint externally, principally, to the cerato-hyoid cartilage. The quadrate part of this ligament (*l.m.*, fig. 7), however, arising under the large ligament which joins the mandible to the quadrate (*l.q-m.i.*), runs upward and posteriorly to attach to the hyomandibula, mediad of and slightly distal to the attachment of the ligamentum hyomandibulo-quadratum. All of those fibers of the median ligament which arise from the joint and from the mandible (*l.m.*, fig. 7) are attached to the ceratohyoid.

From the ventral angle of the mandible a third ligament, the *ligamentum hyoideo-mandibulare* (*l.h-m.*, fig. 6) (the *ligamentum hyoideo-mandibulare externum* of Goodey '10) extends posteriorly to be attached to the inner margin of the ceratohyoid segment. Near the mandibular attachment this ligament is perforated by an artery.

A most complex suspension is made by a ligament which passes from the medial side of the mandible to the ventral side of the cranium. For want of a better name I shall call it the '*ligamentum complexum*' (*l.cp.*). Only a part of its course can be shown in figures 6 and 7. This arises as a double band (*l.cp.*, fig. 7), ventral to the mandibular knob, and passes outward over the ceratohyoid to which some of its deeper fibers are attached (*l.cp.*, fig. 6); it then gives a bundle of fibers to the hyomandibula and, with fibers from the hyoid, runs upward and mediad of the hyomandibula to be attached ventrally to the base of the cranium slightly anterior to the external carotid foramen (see fig. 2). It seems probable that the upper part of this ligament at least is comparable to the inferior post-spiracular ligament of Ridewood ('96).

It is thus seen that, excepting the suspension rendered by this complex ligament just described and by a few fibers from the *ligamentum hyomandibulo-quadratum*, the first arch in the posterior region is suspended *entirely* by the second. The attachment of the first by the second is so complex that it would be hard to agree with Huxley ('76, p. 43) that "The 'epibranchial' (hyomandibula) of the hyoidean arch of *Cestracion* (*Heterodontus*) is just *beginning* to take on a new function, that of suspending the palato-quadrato cartilage and mandible to the skull."

It may be added that the union of the quadrato and mandibular cartilages is made principally by a large ligament, the *ligamentum quadrato-mandibulare internum* (*l.q-m.i.*, fig. 7) already mentioned. This attaches to the upper internal border of the quadrato above and extends along the posterior border of the transverse median ridge of the palato-quadrato (*tr.m.r.*) and over the anterior articulation of the quadrato-mandibular

joint to be attached to the lower ventral margin of the mandible. Further, it may be said that a slip from this ligament, the ligamentum hyomandibulo-mandibulare (*l.hm-m.*), passes upward to be attached on the hyomandibula, just proximal to the quadrate slip of the median ligament and directly under the attachment of the hyomandibulo-quadratum. It thus results that a puncture through the fibers of the superior post-spiracular ligament and through the attaching fibers of the ligamentum hyomandibulo-quadratum would perforate the attaching fibers of this ligament.

Finally other ligaments may here be mentioned. Strong fibrous bands run lengthwise of the lateral or concave surface of the mandible and the palato-quadrato to the quadrato-mandibular joint. The one on the mandible sends a slip upward to attach on the quadrate just mediad of the first (anterior) articulation. A similar slip from the quadrate attaches on the mandible just mediad of the second (posterior) articulation. These two attaching ligaments form a curious type of scissor ligament.

The cartilaginous gill-rays. There are present on the hyomandibula (epihyal) and on the ceratohyal segments of the second arch, cartilaginous rays which project outward and backward as supports for the gill septa. These show considerable variation in different specimens. In one of the large males the first six of these on the hyomandibula fuse at their proximal ends into two masses. The sixth is followed by nine single rays which meet and fuse at their proximal ends into a half arch. Eight single rays of the ceratohyaloid, similarly fusing at their base, complete the arch. This arch then encircles the articulation between the two segments. Following these upper ceratohyal rays there are six pairs of rays fused at the bases into three pieces, and following these there are two or three stout rays

The first branchial arch (fig. 10) consists of four segments, three of which are shown in figure 10. These, counted from the dorsal to the ventral side, are: (1) the pharyngobranchial (*p-b.*), (2) the epibranchial (*e-b.*), (3) the ceratobranchial (*c-b.*), and (4) the hypobranchial (*h-b.*, see fig. 11). From below, the

arch slants obliquely backward so that the pharyngobranchial is considerably behind the outer segments of the arch.

The upper or pharyngobranchial segment is a triangular-shaped cartilage, the apex of which points ventro-laterally, and the broad base of which forms its dorso-median margin. It is not bound by pronounced ligament to either the pharyngobranchial of the opposite side or to the spinal column, but it is held in place dorsally by connective tissue. A ligament is attached to the neck of the pharyngobranchial just above its union with the epibranchial segment. To a further consideration of this ligament we shall return. Here it may be said simply that it passes posteriorly to the head of the following epibranchial segment.

The epi- and ceratobranchials are stout cartilages, the latter being considerably longer than the former. Near their joint both cartilages are hollowed out (not seen in fig. 10) so as to increase the angle between the two. The joint between them is simple, the articulating surfaces being held together by a connective tissue capsule.

The epi- and ceratobranchial segments are of great importance to the area since they alone possess cartilaginous branchial rays for the support of the gill tissues (*b.r.*, fig. 10). On the first arch fourteen such rays are usually present, five on the epi- and nine on the ceratobranchial segment; the first on the ceratobranchial is in all cases the longest of the series.

The hypobranchial segment of the first arch (*h-b.1*, fig. 11) is much smaller than any of the other segments. It is not connected with the hypobranchial of the other side or with a median basibranchial cartilage, but remains as a rudimentary cartilage connecting the ventral ends of the first ceratobranchial with the cerato- and basihyal cartilages.

Dorsally the segments of the second, third and fourth arches are essentially like the first, except that the pharyngobranchial segment of the fourth has fused with that of the fifth arch (fig. 14). Ventrally, these arches differ from the first principally in that their hypobranchial segments are well developed (*h-b.2-4*, fig. 11). The hypobranchial segment in these is so arranged as to

be attached by pads of tissue to the end of its own ceratobranchial and also to that of the ceratobranchial just in front. These hypobranchials then run posteriorly and medially to join unpaired cartilages soon to be described.

The fifth branchial arch is greatly modified (fig. 14). Its pharyngobranchial segment has been so distorted as almost completely to change the appearance of the upper part of the arch. Its epi- and ceratobranchial segments (*e.b.5* and *c.b.5*) are stout cartilages, devoid of branchial rays. The hypobranchial segment is absent, and its ceratobranchial is attached directly to a median unpaired cartilage—the basibranchial (fig. 11).

The median unpaired pieces and their relation to the segments of the arches are shown in figure 11. The most anterior of these is the basihyal cartilage, to which reference above has already been made and which may be described as a more or less star-shaped cartilage joining the right and left halves of the ceratohyoids in the mid-ventral line. It has an anterior triangular glossal projection (*g.p.*) which bends upward in the floor of the mouth to form a support for the so-called tongue.

A first basibranchial cartilage has been mentioned by White ('92, p. 299) as characteristic of *Heterodontus* (*Cestracion*). (See also Gegenbaur '72, pl. 19, fig. 3). This, according to Gegenbaur, is located in *H. philippi* as a free nodule of cartilage in the middle line, posterior to the basihyal cartilage. For the same form Karl Fürbringer, ('03) describes paired basal cartilages. In *Heterodontus francisci* I have not found either the azygos cartilage of Gegenbaur or the paired cartilages described by Fürbringer. I have found, however, cartilages in this region which I have described as extra-hyoid cartilages. These are identical in shape and direction with those given by Fürbringer; but I am convinced that they are not first hypobranchial cartilages since they lie *superficial* to the afferent artery. The second basibranchial forms a large median piece (*b.b.*) to which the hypobranchials of the second branchial arch are united. Posteriorly this median piece joins an enlarged backwardly-directed, arrow-shaped piece (*m.p.*) to which the third and fourth pairs of

hypobranchials and the fifth ceratobranchials are attached. This piece bears a posterior segment.

The discovery of a vestigial sixth branchial arch in the Heterodontidae (Hawkes '05) has been of considerable interest. This arch was found in the young both of *Heterodontus francisci* (*Gyropleurodus francisci*) and of *H. philippi*. Since this discovery, however, an additional rudimentary arch has been described in several other elasmobranchs.

Text-fig. B Rudimentary sixth branchial arch of *Heterodontus francisci*; *Cr.Br. 5.*, fifth ceratobranchial cartilage; *Cr.Br. 6.*, sixth or rudimentary ceratobranchial cartilage; *Ep.Br. 5.*, fifth epibranchial cartilage; *Ep.Br. 6.*, sixth or rudimentary epibranchial cartilage; *Lg.*, ligament passing under pit; *pt.*, pit in neck of pharyngobranchial cartilage.

The rudiments of the arch found by Hawkes in *Heterodontus francisci* consist of a pair of pieces located back of the fifth arch. The upper piece is attached by a ligament to the epibranchial segment of the fifth arch and is joined below to the second rudimentary segment. These pieces are interpreted by Hawkes either as the cerato- and hypobranchial, or as the epi- and ceratobranchial segments which have become closely joined to the fifth arch.

In the adult specimen these cartilages (*ep.br. 6* and *cr.br. 6*, text-fig. B, and fig. 14) are much like those described for the

young. The upper segment (*ep.br.6*) is a slender cartilage, (loosely) attached dorsally to the fifth pharyngobranchial, but ventrally, as is seen from the figure, it is fused solidly to the fifth epibranchial segment. If viewed from the median side, however, it is seen to be continuous with the lower segment.

I have already described for the first branchial arch a ligament which extends from the neck of the pharyngobranchial backward and downward to be attached to the epibranchial following. To this I shall now return with a hope that it may be of service in interpreting the dorsal piece in question. It so happens that this ligament forms the floor of a pit, the anterior wall and the roof of which are formed by the neck of the first pharyngobranchial and the posterior wall by the upper part of the following *epibranchial segment*.² Similar pits follow the second, third and fourth (*lg.*, text fig. B) arches. Now, following the fifth pharyngobranchial there is also a pit (*pt.*, text-fig. B) which, in its surroundings, is identical with the first. From the neck of the fifth pharyngobranchial the ligament passes under the pit, giving some of its fibers to the posterior wall; other fibers from the fifth pit continue across with the ligament from the fourth pit to join the pectoral girdle. The piece forming the posterior wall (*ep.br.6*) I therefore interpret as the sixth epibranchial segment.

The lower or second segment, the ceratobranchial, is displaced forward so as to lie laterad of the joint of the fifth arch. This displacement in *Heterodontus* is due to the enlargement and crowding forward of the massive pectoral girdle.

There is present in the anterior wall of the spiracle a thin spiracular cartilage (*sp.c.*, pl. 3, and fig. 12) which, like branchial rays, supports a septum for gill filaments. This cartilage is (generally) interpreted as a fused series of cartilaginous rays which originally belonged to the palato-quadrato segment. Because of the outward flaring of the quadrato the spiracular cartilage comes to be widely separated from the quadrato.

²This ligament probably represents the median interarcuales muscles.

Extra-visceral cartilages. The visceral arches are provided with superficial pieces, the extra-visceral cartilages. These for convenience may be separated into the labial cartilages, the extra-hyoid and the extra-branchial cartilages. The labials are located at the sides of the mouth and consist of three pieces of cartilage on each side, two dorsal and one ventral (*d.l.1-2* and *v.l.*, fig. 6). The posterior dorsal labial is about twice the length of the anterior dorsal labial cartilage; it articulates with the ventral labial at its distal end so that the two serve to reduce the gape of the mouth.

An extra-hyoid cartilage, so far as I have been able to make out, is lacking dorsally, and the one which appears ventrally is small. This, in the adult, is generally a nodule of cartilage less than half the length of the one shown in figure 9. In all cases the extra-hyoid cartilage was located where the termini of the ventral aorta bifurcate to form the first and second afferent arteries, the body of it lying superficial to the base of the second afferent. In no case did I find it further out over the first gill pocket as is shown for *Heterodontus philippi* (Max Fürbringer '97, pl. 6, fig. 5). In one of the cases examined the extra-hyoid on the right side was elongated as is shown in figure 9, while on the left it was a nodule very much like the enlarged end of the cartilage seen in figure 9. Usually both of the cartilages were almost identical in shape with that figured by Gegenbaur and Karl Fürbringer as the first basibranchial. I am at a loss to know whether what Gegenbaur described as a single piece and Fürbringer described as paired cartilages are not in fact what I have regarded as the extra-hyoids. If these be the cartilages described by them I am convinced that they are not basibranchials since they lie entirely superficial to the second afferent artery.

Extra-branchial cartilages are located over all of the (internal) branchial arches in *Heterodontus* excepting the fifth. The extra-branchials of the first branchial arch are usually large and like succeeding arches overlap terminally (*ex.b.*, fig. 10). The first three cartilages are hook-shaped at their attached ends, the dorsal ones only slightly and the ventral pieces in a very pro-

nounced fashion. In both dorsals and ventrals the body tapers toward the free end. The fourth extra branchial (not added in fig. 14) is smaller and simpler in form both above and below, than the preceding.

The four dorsal extra-branchial segments are united in such a way as to make the upper attachment in a continuous line above the gill pockets. Each of these cartilages curves around the tip of the branchial rays at the margin of a gill septum. The attachment of the lower or ventral extra branchials is less concentrated. The first three of these are joined to the connective tissue ventrally at the base of their respective gill-pockets, but the fourth is shorter and tends to migrate upward so as to rise from the side of its ceratobranchial.

2. *The spinal column*

The spinal column in *Heterodontus*, although somewhat variable in the number of its segments, consists of about one hundred and ten clearly marked vertebrae. Of these the first thirty-one have ribs growing from their basiventrals (*b.v.*) or transverse processes; the five or six following these have their basiventrals bent downward, and the sixth or seventh (thirty-seventh or thirty-eighth of the column) usually has them meeting below to form the first hemal arch. Thirty-four similar arches follow back from the first haemal arch to the beginning of the ventral rays of the tail (on the seventy-first vertebra). There are next thirty-nine or forty caudal vertebrae, behind which in the adult is a mass but slightly differentiated, tapering gradually to a point (see also T. J. Parker '87, p. 31, pl. 8, fig. 28).

The first vertebra in the column (fig. 15) is obscured by an incomplete anterior segment having a short centrum and bearing enlarged transverse processes for articulation with the occipital condyles of the cranium. The second complete vertebra (*vt.*², fig. 15), appearing behind the incomplete segment, may be described as provided with a strong centrum upon which rests a basidorsal (basal) piece (*b.d.*²), above and posterior to which is a large interdorsal (intercalary) plate (*i.d.*²). Both of these plates are perforated, the former giving passage to the ventral root

nerve (*f.v.*), the latter to the dorsal root (*f.d.*) of the first spinal nerve. Capping the column between the first and second interdorsal plates on each side is a smaller plate—the suprabasidorsal (*s.b.d.*) or neural spine. The centrum itself has extending from its side a basiventral (*b.v.*) from which the rib (*r.*) projects.

In an end view of the fifth vertebra the structures there concerned are seen to advantage (fig. 18). Resting upon the centrum is the neural arch (*n.a.*), the sides and the top of which are made up entirely of the cut edge of the interdorsals (*i.d.*), but the basidorsal plates (*b.d.*) of the vertebra appear in this end view. At the ventro-lateral angles of the centrum are the ribs (*r.*) which stand out almost at right angles.

A similar view taken of a vertebra toward the tail region, say the fifty-third, in addition to a neural arch above, shows a haemal arch below the centrum (*h.a.*, fig. 21). The neural arch in this case shows the interdorsal plate with a basidorsal (*b.d.*) seen in end view. The haemal arch is formed by the downward bending of the basiventrals and by the adjoined haemal spine; the basiventrals make up the larger part of the wall and all of the floor of the canal. Contiguous to the centrum, however, are seen the interventral plates of the vertebra. In such a view it will be observed that the haemal canal is divided by a partition into a dorsal and a ventral part, the dorsal being for the caudal aorta and the ventral for the caudal vein.

If a series of transverse sections be taken through the two above vertebrae, the ends of which are figured (figs. 18 and 21), the composition of the arches as well as the finer structure of the vertebrae may be made out. The neural arch in the second section (fig. 19) shows a great extent of the basidorsal cut and a decrease in the amount of the interdorsal. In the third section (fig. 20) the suprabasidorsal or neural spine (*s.b.d.*) also appears, so that all three of the parts making up the arch are seen here. In the caudal vertebrae the neural arch is similar to that just described. In figure 22 a bit of the suprabasidorsal is cut, and in both figures 22 and 23 the haemal arch shows the basiventral, that part of the interventral which appears in end view (fig. 21) not being touched.

A study of the finer structure of these vertebrae is of interest. At the end of the vertebra the calcified tissue appears as a whitish ring like the walls of a funnel (*cl.r.*, figs. 18 and 21). In this funnel is to be found primitive gelatinous notochordal substance which at the ends also forms an intervertebral pad. As the sections pass farther toward the middle of the centrum this calcified ring becomes smaller and smaller, and there pass off from it numerous radiating calcified plates (*cl.p.*). As the middle of the centrum is reached (figs. 20 and 23) the apex of the funnel appears as a tiny circlet of calcified tissue containing the constricted part of the notochord (*ch.*). The calcified ring (*cl.r.*) may here be likened to a hub from which the calcified plates radiate like the cogs of a wheel. It will be noticed that the calcified ring diminishes in thickness as well as in size and that the cogs decrease in number the nearer we approach the middle of the centrum (compare figs. 19-20, also 22-23), showing that some of these do not extend the entire length of the centrum. It is also to be seen that the cogs are not so numerous in the region of the fifty-third vertebra as in the region of the fifth.

Other calcifications of less importance also appear in the vertebrae. These are confined principally to the lining of the neural canal, to the outside circle around the body of the centrum (not shown in the figures), and to the roof and sides of the haemal canal.

Considerable interest attaches to the region of the spinal column between rib-bearing and the haemal arch segments. This area, which may be designated as a transition between the body and the caudal regions, may be represented by a section of the column extending from the thirtieth vertebra—the last but one to bear ribs—to the thirty-eighth, usually the second to form a complete haemal arch (fig. 16). In such an area there is a sudden change in length of centrum, the centra of the non-rib-bearing vertebrae being markedly shorter than those of a rib-bearing nature. This change begins usually with the thirty-second vertebra but in one case I found that the thirty-second was still fused with the succeeding vertebra dorsally, although the two were separate ventrally. On the opposite side, however,

the two plates were fully separate both above and below. In *Heterodontus francisci* only six or seven vertebrae form the transition between rib-bearing and haemal vertebrae (see also Gegenbaur '67, pl. 9, fig. 19, and Šecérov '11, pl. 1, fig. 5). Upon these centra and those following, the plates of the neural arches are also modified, being so arranged that to each myomere two basidorsal and two interdorsal plates occur. Such vertebrae are called diplospondylous.

In the transitional vertebrae alternate basidorsals, which are odd in number, are perforated by the ventral roots of the spinal nerve (*f.v.*), and alternate interdorsals are usually separated by the foramina of the dorsal nerves (*f.d.*). On the thirty-seventh vertebra (fig. 16) the foramen for the dorsal root, however, migrates forward so that it perforates the interdorsal (intercalary) plate. In some other cases the dorsal root foramina pass between the interdorsal and the basidorsal, producing a more or less pronounced niche in the anterior part of the basidorsal plate. In this transitional area, the suprabasidorsal (*s.b.d.*) above imperforate basidorsals is single where the foramen completely separates these. Above each perforate basidorsal it is usually doubled. These occur in regular fashion, capping the interspaces between basidorsals and the interdorsals so that in the case of figure 16 they comprise three (pairs of) nodules to each myomere.

It will be observed, further, that haemal arches corresponding to the imperforate and perforate segments may be determined by their shape without reference to the basidorsals in question. This will be made especially clear by reference to the fortieth and forty-first basiventrals. The ventral termini of these point in opposite directions, the fortieth pointing anteriorly, and hence corresponding to the imperforate basidorsal, and the forty-first posteriorly, and hence belonging to the same segment as the perforate basidorsal. In a later study of the caudal region we shall have reason to refer to the foramen formed between the haemal arch of the imperforate segment (anterior) and the haemal arch of the perforate segment (posterior). It is through this that the main segmental artery leaves the caudal aorta.

The question has been raised: Do the diplospondylous vertebrae return to the monospondylous type as the tip of the tail is approached. This is stated to occur in *Acanthias* by Ridewood '99), who says, "The change from diplospondylous to the monospondylous condition occurs at about the twenty-fourth centrum from the end." In *Heterodontus francisci* such is not the case (fig. 17). It is difficult, as Ridewood says, to delimit a myomere in the posterior region because of the thinness of the muscle, yet in an injected specimen the segmental arteries arising from the caudal aorta are clearly definitive of boundaries, only two to a myomere, one in front of it, the other bounding it posteriorly. Since two vertebrae occur between each two arteries, at least as far back as the ninety-eighth segment, the diplospondylous nature is retained. Some of the segments posterior to this retain their regularity although in these the arteries themselves are not sufficiently regular to be definitive.

II. THE APPENDICULAR SKELETON

The part of the skeleton known as appendicular consists of pectoral and pelvic girdles and the frame-work for the fins attached thereto.

1. *The skeleton of the fin girdles*

a. *The pectoral girdle* in *Heterodontus* (fig. 8) is a strong arch, open dorsally, to which the frame-work of the pectoral fin is attached. It is composed of a right and a left cartilaginous part solidly fused in the middle line below. The part of the girdle which extends dorsal to the attachment of the fin is the scapular portion (*sc.*). That part which meets a similar part from the opposite side below is the coracoid portion (*co.*). At the middle of the postero-lateral portion of each half of the girdle is a projection or articular surface (*a.pt.*) which fits into the fossa of the pectoral fin skeleton. In front of this articular surface is a strong antero-ventral projection (*a.pr.*), like that in *Crossorhinus* (see Haswell '84), to which is attached strong musculature. A foramen through which nerves and blood vessels pass

perforates the girdle between these two projections. Above the articular process (*a.pt.*) and on the scapula is the postscapular projection to which the heavy lateral musculature attaches. Between the anterior projection and the mid-line there is a deep concavity on the coracoid from which the *arcuales communis* muscles arise.

b. The pelvic girdle (fig. 13) consists of a flattened bar—slightly cupped up in the middle and expanded at the ends. The right and left halves of this are firmly fused together. Three foramina perforate the pelvic girdle near each end (*f.pl.*); through the median one the iliac artery passes, and through the other two, nerves. At the termini of the girdle are the articular processes for the right and left fins. Each articular surface consists of two protuberances (*a.pl.*) which fit into depressions of the fin skeleton proper.

2. The skeleton of the fins

a. The paired fins. 1. The skeleton of the pectorals (fig. 26) is made up of a group of large basal cartilages from which radiate numerous rows of radialis. The basal cartilages in the pectoral of *Heterodontus francisci* are unlike those previously described for the adult of *Heterodontus philippi*. In the former there are three pieces, pro- meso- and metapterygium, the first (the propterygium) being absent in the adult of the latter species. (Mivart '79, p. 449; Huxley '76, p. 50; and Gegenbaur '65, II, pl. 9, fig. 3; see also Howes '87, pl. 3.)

This propterygial basal (*pr-p.*) in *Heterodontus francisci* is a clearly marked cartilage, quadrilateral in shape and somewhat elongated. It is followed by a series of four radialis, the first of which is large and plate-like. Contiguous to this plate-like radial is a hexagonal plate, a part of which evidently belongs to the first radial of the mesopterygium.

The mesopterygium (*ms-p.*) is a stout cartilage, from the enlarged distal end of which five rows of rounder radialis radiate. The most proximal segment of the first row of radialis joins distally the hexagonal plate of the propterygium just described.

In the right fin of my dissection this plate was separated into two parts so as to be included in the first line of the mesopterygial radials. The second row of the mesopterygium consists of six segments. The first segment of the third row of radials is followed directly by a similar more flattened segment which, in turn, abuts against a double row, the anterior of which is composed of four or five flattened plates, the posterior row having but four. The proximal segment in the fourth line of mesopterygial radials, like the third, is followed by a slightly shorter segment which abuts distally against two rows, the posterior of which consists of four radials. The anterior plates have just been described. The proximal segment of the fifth row of radials is the longest of the series. It is continued distally by a pentagonal piece which fits against a double row of radials, the anterior proximal line of which was previously described, and the posterior row has but three segments capped distally by small cartilages.

The *metapterygium* (*mt.p.*) is a spatulate cartilage, the wider part of which points distally. From this ten or eleven rows of radialia diverge. The second two segments in the first two rows of these abut against double rows of radialia, each row usually consisting of two segments capped by smaller pieces; the third, fourth and fifth are similar except that the double rows are usually uncapped. The sixth to the eighth rows are of two segments each, between which terminally single terminal cartilages abut. The proximal segments of the ninth and tenth radials of the metapterygium are followed by segments equal in length to themselves. Each one of these segments is capped by a single piece. In an older specimen the ninth and tenth radials were fused proximally and cleft distally. The eleventh radial gives evidence of being a fusion of two. The accessory cartilages accompany it; one appears at its apex, and another along its edge.

2. The frame-work of the pelvic fin (fig. 29) in the female consists of a long posteriorly projecting basal cartilage, the basipterygium, to which radialia are joined. The basipterygium (*ba.p.*) in *Heterodontus* is separated into five sections, the proxi-

mal of which is long, the distal represented by a tiny cartilaginous tip. Anteriorly a much enlarged fused first radial strikes the basal plate almost at right angles. In the end of this, as well as in the end of the basal piece, is a fossa, by means of which articulation with the pelvic girdle is effected. From this first radial cartilage three rows of radialis project. In the first are one or two small cartilages; in the second, two or three; and in the third there are four cartilages similar to the segments in the first radialis of the basal piece. From the basipterygium thirteen rows of radialis are given off. These are terminated by smaller radial cartilages in the more anterior rows but in the three posterior rows each one consists of two segments.

3. The skeleton of the pelvic fin of the male is, with slight modifications, like that of the female. It consists of the basipterygium and its radials. In the male there are fourteen radials which meet the basipterygium at an angle of forty-five degrees. The most anterior of the radials represents the fusion of three cartilages which, like those following, are segmented into two or three pieces. The most posterior radials, unlike those in the female, are unsegmented. The inner lobe of the pelvic fin in the male (fig. 27) is modified as a framework for the claspers or copulatory organ.

The basipterygium in the male is continued by the basal piece (*ba.*) to which it is connected by two short segments (b^{1-2}). At the angle between the basipterygium and the basal piece there arises from the former the so-called 'beta' (β) cartilage. The basal piece is generally round, but terminally it is flattened and possesses a groove which passes obliquely across to the dorsal side. Several cartilaginous pieces appear near the terminal part of the groove. These are two dorsal terminals (*d.tr.1-2*), a dorsal marginal (*d.mg.*), and one ventral terminal cartilage (*v.tr.*). Proximal to the ventral terminal there is an accessory terminal (*tr.3*).

b. The skeleton of the unpaired fins. 1. First dorsal fin (fig. 24). Extending from the vertebral column one-half the length of the long anterior fin-spine, or to the point externally where the spine emerges from the skin, is a thin basal cartilage, the base of

which extends over two and one-half vertebrae ($17-18\frac{1}{2}$) in the female; (15-18) in the male. From the top of this plate arise two other cartilages, the anterior of which is twice the width of the posterior. From the former there appear four rows of radiating pieces, each row of which contains three cartilages. Capping the second and third rows is an extra cartilage and over the fourth is a similar cap of a double piece.

2. Second dorsal fin (fig. 25). The second dorsal fin, like the first, is provided with a basal piece (*b.c.*) one-half the height of the spine; it extends over three (46-48) diplospondylous vertebrae in the female; (44-48) in male. From it arise three radials which point in a more posterior direction. The most anterior of these is the smallest. Passing from it is a double row of two segments capped with a broader piece. The second radial, though a single piece proximally, is bifid distally. From the distal end arise two rows of three cartilages each. The third radial is a truncate cone which rests on its apex. Upon its base it supports in an irregular fashion six cartilaginous pieces.

3. The caudal fin (fig. 17). The ventral rays of the caudal fin or tail, as we have seen are an integral part of the axial skeleton, being the prolonged haemal spines. These consist of a series of forty rays, each of which corresponds to a vertebra. Beyond the tip of these, in the adult is an undifferentiated (fused) mass. In this region interdorsal pieces are present as far back as the ninety-fourth to the ninety-seventh vertebrae, while interventral pieces extend back to the ninety-ninth vertebra. The dorsal lobe of the fin is supported by rays which unlike those supporting the ventral lobe, are not equal in number to the centra, forty-six being present in one specimen examined. The first of the dorsal rays is small and the second arises as a broad clear piece of cartilage over the seventieth or seventy-first vertebra. Back of this the rays are numerous and are more or less regular to the ninety-fifth vertebra. At the tip of the tail they fuse into a common mass (fig. 17).

In the caudal region alternate basidorsals are perforate back to the ninety-fifth vertebra, with the exception of the eighty-ninth and ninety-third. The eighty-ninth although perforate

on the right side was imperforate on the left. No suprabasi-dorsals are found just anterior to the dorsal rays, and the interdorsals usually cease at about the ninety-fifth, although they may sometimes extend a few segments further back. It is difficult to make out the exact perforations in the plates posterior to the eightieth vertebra, for they may cut the edges of the plate and hence the nerve may emerge between the plates.

4. The anal fin. The base of the anal fin in the specimen before me abuts against the fifty-eighth centrum of the spinal column. But this position varies between the fifty-eighth and sixty-third vertebrae. From the basal piece, which is remarkably like that of the dorsals, proceed four rows of radials, the first composed of two segments; the second has two rows arising from it, in the first of which are five cartilages, in the second four; the third radial is elongate and is continued by three successively shorter pieces; and the fourth, more elongate still, is followed by a broader radial. Upon this are three rounded pieces, over the first and a part of the second of which is a broader cap.

Berkeley, California
March, 1915

LITERATURE CITED

- BALFOUR, F. M. 1881 On the development of the skeleton of the paired fins of Elasmobranchii, considered in relation to its bearings on the nature of the limbs of the Vertebrata. *Proc. Zool. Soc. London*.
- FÜRBRINGER, KARL 1903 Beiträge zur Kenntnis des Visceralskelets der Selachier. *Morph. Jahrb.*, Bd. 31.
- FÜRBRINGER, MAX 1897 Ueber die Spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. *Festschrift für Gegenbaur*, III.
- GADOW, HANS 1888 On the modifications of the first and second visceral arches, with especial reference to the homologies of the auditory ossicles. *Phil. Trans. Roy. Soc., B*, vol. 179.
- GEGENBAUR, C. 1865 Untersuchungen zur vergleichenden Anatomie der Wirbelthiere. II. Brustflossen der Fische.
- 1867 Ueber die Entwicklung der Wirbelsäule des Lepidosteus, mit vergleichend-anatomischen Bemerkungen. *Jena. Zeitsch.*, Bd. 3.
- 1872 Untersuchungen zur vergleichenden Anatomie der Wirbelthiere. III. Das Kopfskelet der Selachier, ein Beitrag zur Erkenntniss der Genese des Kopfskeletes der Wirbelthiere. Leipzig.

- GOODEY, T. 1910 A contribution to the skeletal anatomy of the frilled shark—*Chlamydoselachus anguineus* Garman. Proc. Zool. Soc. London.
- HASSE, C. 1879 Das natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule. Jena.
- HASWELL, W. A. 1884 Studies on the elasmobranch skeleton. Proc. Linn. Soc. N. S. Wales, vol. 9.
- HAWKES, O. A. M. 1905 The presence of a vestigial sixth branchial arch in the Heterodontidae. Journ. Anat. Physiol., vol. 40.
- HOWES, G. B. 1887 On the skeleton and affinities of the paired fins of *Ceratodus*, with observations upon' those of the Elasmobranchii. Proc. Zool. Soc. London.
- HUXLEY, T. H. 1876 Contributions to morphology, Ichthyopsida—No. 1. On *Ceratodus fosteri*, with observations on the classification of fishes. Proc. Zool. Soc. London.
- JAQUET, M. 1905 Description de quelques parties du squelette du *Pseudotriacis micridon* Capello. Bull. Mus Ocean. Monaco, no. 36.
- MIVART, ST. GEO. 1879 Notes on the fins of elasmobranchs, with considerations on the nature and homologues of vertebrate limbs. Trans. Zool. Soc. London, vol. 10.
- PARKER, T. J. 1887 Notes on *Carcharodon rondeletti*. Proc. Zool. Soc. London.
- PARKER, W. K. 1879 On the structure and development of the skull in sharks and skates. Trans. Zool. Soc. London, vol. 10.
- RIDEWOOD, W. G. 1896 On the spiracle and associated structures in elasmobranch fishes. Anat. Anz., Bd. 11.
- 1899 Some observations on the caudal diplospondyly of sharks. Jour. Linn. Soc. Zool., vol. 27.
- ŠECÉROV, SLAVKO 1911 Über die Entstehung der Diplospondylie der Selachier. Arb. Zool. Inst. Wien, Bd. 19.
- THACHER, JAS. K. 1877 Median and paired fins, a contribution to the history of vertebrate limbs. Trans. Conn. Acad., vol. 3.
- WHITE, PHIL, J. 1892 The skull and visceral skeleton of the Greenland shark, *Laemargus microcephalus*. Trans. Roy. Soc. Edinburgh, vol. 37, (2).

PLATES

ANATOMY OF HETERODONTUS: ENDOSKELETON
J. FRANK DANIEL

PLATE I

DUNCAN DENNING, *del.*

Fig. 1

Fig. 2

PLATE 1

EXPLANATION OF FIGURES

Figures of *Heterodontus francisci* (natural size)

- 1 A dorsal view of the cranium.
  - 2 A ventral view of the cranium.
<i>a.o.s.</i> , anterior oblique semicircular canal	<i>n.c. 1-2</i> , first and second nasal cartilages
<i>b.p.</i> , basal plate	<i>o.cd.</i> , occipital condyle
<i>b.tr.</i> , basitrabecular cartilage	<i>o.cr.</i> , occipital crest
<i>F.</i> , anterior fontanelle	<i>o-n'</i> , orbito-nasal canal (entrance from olfactory capsule)
<i>f.e.c.</i> , external carotid foramen	<i>ol.c.</i> , olfactory capsule
<i>f.i.c.</i> , internal carotid foramen	<i>p.f.</i> , parietal fossa
<i>f.m.</i> , foramen magnum	<i>p-f.g.</i> , parieto-frontal groove
<i>f.o.p'</i> , foramen for the ophthalmicus profundus nerve (exit from the oph. prof. canal)	<i>pl.f.</i> , palatal fossa
<i>f.o.VII'</i> , ophthalmic foramen for the VII nerve (exit from the VII canal)	<i>po.hm.</i> , post hyomandibular process
	<i>pr.hm.</i> , prehyomandibular process
	<i>*</i> , attachment of capsular slip

Fig. 3

Fig. 4

PLATE 2

EXPLANATION OF FIGURES

All figures of *Heterodontus francisci* (natural size).

3 A side view of the cranium.

4 Posterior view of the cranium.

5 A median sagittal section through the cranium, seen from the inside. The nasal capsule has been removed.

<i>a.c.</i> , auditory capsule	<i>f.IV</i> , foramen for fourth cranial or trochlear nerve
<i>ch.</i> , notochord	<i>f.VII</i> , foramen for seventh cranial or facial nerve
<i>f.a.c.</i> , foramen of anterior cerebral vein	<i>f.VIII</i> , foramen for eighth cranial or auditory nerve
<i>f.e.c'</i> , external carotid foramen (entrance to socket)	<i>f.IX</i> , foramen for ninth cranial or glossopharyngeal nerve
<i>f.i.c.</i> , internal carotid foramen	<i>f.X</i> , foramen for tenth or vagus nerve
<i>f.m.</i> , foramen magnum	<i>i.o.</i> , interorbital canal
<i>f.o.p.</i> , foramen of ophthalmicus profundus nerve (leaving the socket)	<i>o.cd.</i> , occipital condyle
<i>f.o.VII</i> , ophthalmic foramen of VIIth nerve (leaving the socket)	<i>o.cr.</i> , occipital crest
<i>f.r-a.</i> , foramen for ramus anastomoticus artery	<i>o.f.</i> , orbital fissure
<i>f.s-m.</i> , foramen for spino-muscularis artery	<i>o-n.</i> , orbito-nasal canal (entrance to socket)
<i>f.I</i> , foramen through which the olfactory nerve leaves the cranium	<i>pl.f.</i> , palatal fossa
<i>f.II</i> , foramen for the second cranial or optic nerve	<i>po.hm.</i> , posterior hyomandibular process
<i>f.III</i> , foramen for third cranial or oculomotor nerve	<i>po.o.</i> , postorbital process
	<i>pr.o.</i> , preorbital process
	<i>s.hm.</i> , superior hyomandibular process
	<i>s.o.</i> , supraorbital crest

Fig. 6

Fig. 7

DUNCAN DUNNING, del.

PLATE 3

EXPLANATION OF FIGURES

Figures of *Heterodontus francisci* (natural size).

6 Lateral view of the cranium with articulation of first and second visceral arches.

7 Median view of mandibular arch showing articulation.

a.p., articular process of palato-quadrate

c-h., ceratohyoid

c.l', slip from palato-cranial capsular ligament

d.l. 1-2, first and second dorsal labial cartilages

hl.p., hyal process

hm., hyomandibula

kb., mandibular knob

l.cp., ligamentum complexum

l.h-m., ligamentum hyoideo-mandibulare

l.hm-h., ligamentum hyomandibulo-hyoideum

l.hm-m., ligamentum hyomandibulo-mandibulare

l.h-m.q., ligamentum hyomandibulo-quadratum

l.m., ligamentum mediale

l.q-m.i., ligamentum quadrato-mandibulare internum

md., mandible

md.r., mandibular ridge

o.p., optic pedicle

p-q., palato-quadrato cartilage

sp.c., spiracular cartilage

s.p-s.l., superior postspiracular ligament

tr.l.r., transverse lateral ridge

tr.m.r., transverse median ridge

v.l., ventral labial cartilage

PLATE 4

EXPLANATION OF FIGURES

All figures of *Heterodontus francisci*.

- 8 Antero-lateral view of left side of pectoral girdle (one-half natural size).
- 9 Lateral view of extrahyoid cartilage ($\times 4$).
- 10 Antero-lateral view of first branchial arch; (one-half natural size).
- 11 Ventral view of median basibranchial cartilages (natural size).
- 12 Posterior view of the spiracular cartilage ($\times 1\frac{1}{4}$).
- 13 Dorsal view of right half of pelvic girdle (natural size).
- 14 Antero-lateral view of the fourth and fifth branchial arches, with attached rudimentary sixth arch (one-half natural size).

<i>a.pl.</i> , articular process pelvic fin	<i>ex.b.</i> , extrabranchial
<i>a.pr.</i> , anterior projection of pectoral arch	<i>f.pl.</i> , foramen through pelvic girdle
<i>a.pt.</i> , articular process pectoral fin	<i>f.pt.</i> , foramen through pectoral girdle
<i>b.b.</i> , basibranchial	<i>g.p.</i> , glossal process
<i>b.h.</i> , basihyal cartilage	<i>h-b. 1-4</i> , first to fourth hypobranchial
<i>b.r.</i> , branchial ray	<i>m.p.</i> , posterior median piece
<i>c-b. 1-5</i> , first to fifth ceratobranchials	<i>p-b. 1-5</i> , first to fifth pharyngobranchials
<i>co.</i> , coracoid cartilage	<i>sc.</i> , scapula
<i>e-b. 1-5</i> , first to fifth epibranchials	

PLATE 5

EXPLANATION OF FIGURES

All figures of *Heterodontus francisci* ($\times 1\frac{1}{2}$).

- 15 Lateral view of anterior vertebrae.
- 16 Lateral view of transitional vertebrae between rib-bearing and haemal arch regions.
- 17 Lateral view of caudal vertebrae (vt. 95 and not 94 perforate).

*b.d*², second basidorsal plate

b.v., basiventral plate

c., centrum

f.d., foramen for dorsal root of nerve

f.v., foramen for ventral root of nerve

h.a., haemal arch

h.s., haemal spine

i.d., interdorsal plate

*i.d*², second interdorsal plate

i.v., interventral plate

r., rib

s.b.d., suprabasidorsal

*v*², second vertebra

Fig. 9

Fig. 10

Fig. 12

PLATE 6

EXPLANATION OF FIGURES

All figures of *Heterodontus francisci* ($\times 2$).

18 End view of fifth vertebra.

19-20 Cross-section of fifth vertebra.

21 End view of fifty-third vertebra.

22-23 Cross-sections of fifty-third vertebra.

b.d., basidorsal plate
b.v., basiventral plate
c., centrum
ch., notochord
cl.p., calcified plate
cl.r., calcified ring

h.a., haemal arch
i.d., interdorsal plate
i.v., interventral plate
n.a., neural arch
r., rib
s.b.d., suprabasidorsal plate

Fig. 18

Fig. 21

Fig. 19

Fig. 20

Fig. 22

Fig. 23

PLATE 7

EXPLANATION OF FIGURES

All figures of *Heterodontus francisci* (three-fourths natural size).

24 Lateral view of left side of first dorsal fin (female).

25 Lateral view of left side of second dorsal fin (female).

27 Dorsal view of left pelvic fin of male, showing skeleton of clasper.

b. 1-2, first and second segments following the basipterygium

b.c., basal cartilage

ba., basal piece

ba.p., basipterygium

β., beta cartilage

d.mg., dorsal marginal cartilage of clasper

d.tr. 1-2, first and second dorsal terminal cartilage of clasper

pl., pelvic girdle

ra., radial cartilage

tr. 3, accessory terminal cartilage of clasper

v.tr., ventral terminal cartilage of clasper

Fig. 25

Fig. 26

Fig. 27

DUNCAN DUNNING, *del.*

PLATE 8

EXPLANATION OF FIGURES

All figures of *Heterodontus francisci* (three-fourths natural size).

26 Dorsal view of left pectoral fin.

28 Lateral view of anal fin from left side.

29 Dorsal view of left pelvic fin of female.

ba.p., basipterygium

b.c., basal cartilage

ms.p., mesopterygium

mt.p., metapterygium

pr.p., propterygium

ra., radial cartilage

DUNCAN DUNNING, *del.*
493

Fig. 26

Fig. 28

Fig. 29