

## ON THE ORIGIN OF GIRDLES AND PAIRED FINS

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### ABSTRACT

Embryological and morphological data suggest that the ancestors of the gnathostomes, the pro-gnathostomes, were swimming animals with a terminal mouth and transversely situated gill-arches carrying outwardly directed gills and separate gill-covers. The body had a well-developed myotomic musculature and was provided with longitudinal median and paired ventro-lateral steering keels formed by folds of the body wall (potential fin-folds). The skin contained primary scales. The exoskeletal shoulder girdle arose by fusions of such scales to form a support for the body musculature and to fulfil other requirements at the transition between head and body. The paired fins arose in connection with the muscularization of the ventro-lateral crest. Stimulated probably by an interaction between the ectoderm and the mesoderm of the crest, the ventral end of each myotome produced two dorsal and two ventral radial muscles innervated by a secondary pterygial branch of the spinal nerve of the metamere. The radial muscles grew in a distal direction towards the margin of the fin-fold and gained contact with the primary scales which assumed a linear arrangement and formed lepidotrichia. At a somewhat later phyletic stage endoskeletal supporting rods, rays or radials, arose, one between each dorsal and ventral radial muscle. Accordingly, there are two radials in each metamere. The most proximal part of each radial soon became separate, forming a primary girdle component. The endoskeletal girdles arose by fusions of such components. The separation into pectoral and pelvic girdles and fins is probably due to the undulating swimming movements of the body. The main modifications within each paired fin is a consequence of a gradual shortening of the joint between the girdle and the fin from behind. In connection with this shortening both the radial muscles and the radials became elongated forwards and consequently each of them consists of a primary distal portion growing in a distal direction and a secondary proximal portion growing forwards towards the joint. The basale metapterygii in sharks — hitherto considered to be the most ancient part of the skeleton of the fin, formed by fusions of a series of metameric elements originally situated in the body wall — has arisen within the fin by fusions of the proximally growing portions of the posterior radials and is accordingly mainly a new formation. A metapterygial stem or axis of great phyletic importance does not exist. The modifications in the anterior part of the pectoral fin are due mainly to changes in the direction of the gill-arches.

### INTRODUCTION

The dual problem of the origin of the paired fins and the tetrapod limb has been lively debated during the last century. In order to explain the origin of the paired fins Gegenbaur set forth his gill-arch theory, but in spite of the endeavours of a great number of supporters this theory has been abandoned in favour of the rival fin-fold or metameric theory. When some years ago I started a thorough study of the origin of the tetrapod limb on the basis mainly of the conditions in *Eusthenopteron*

and *Ichthyostega*, I was struck by the great importance which is still attributed to the so-called metapterygial stem or axis, a concept introduced by Gegenbaur and adopted by the partisans of the metameric theory, although in a quite different sense. However, among the supporters of the latter theory there is a considerable diversity of opinion as regards this stem, its position and the number of elements that enter into its formation. Interpretations of the various types of paired fins and tetrapod limbs founded on a hypothetical and arbitrarily chosen "metapterygial stem" are of course of no value. If we use the "stem" as a starting point for our interpretations, as is done by most authors up to the present day, then it is necessary that it should be properly defined and that its position and extent be determined without the slightest doubt. In order to get a safe opinion as to the nature of this mysterious structure and to get an answer to many other questions of importance for the discussion of the origin of the tetrapod limb, I had to turn to the sharks and other recent fishes, and I devoted a long time to a perusal of the vast literature on the structure and the ontogenetic development of the fins in fish, and made several new observations. In previous papers (1964, 1965) I have briefly summarized some of my results with regard to the origin of the tetrapod limb. On this occasion I will seize the opportunity to give a brief review of my opinion as to the origin of the girdles and paired fins.

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#### GENERAL REMARKS

In his fundamental papers on the skeleton of the paired fins in sharks, Gegenbaur (1865, 1870) distinguished three main portions: the propterygium, the mesopterygium and the metapterygium (Figure 1B), each consisting of a comparatively large basal element (basale propterygii, etc.) and a number of lateral rays or radials (*Radien*). The metapterygium, which could be recognized in the paired fins of all fish and in the tetrapod limb, was considered to be the most constant and therefore the most ancient part of the fin. Even in the original fin, the *archipterygium*, the basale metapterygii was developed and formed the proximal element of an important row of skeletal pieces, the stem or stem row (*Stamm, Stammreihe*), which was situated in the medial margin of the fin and carried a row of lateral radials. Thus a considerable morphological and phyletic importance was attributed to the basale metapterygii, and the basale propterygii and the basale mesopterygii were interpreted as secondary formations arisen by fusions of proximal portions of radials. According to this theory the archipterygium was *uniserial*, consisting only of the jointed "metapterygial stem" and the lateral series of radials. However, later on, after the discovery of *Neoceratodus*, Gegenbaur radically changed his opinion and maintained (1872) that the archipterygium was a *biserial* structure similar to the paired fins in *Neoceratodus*, and that the stem was represented by the principal axis of such a fin.

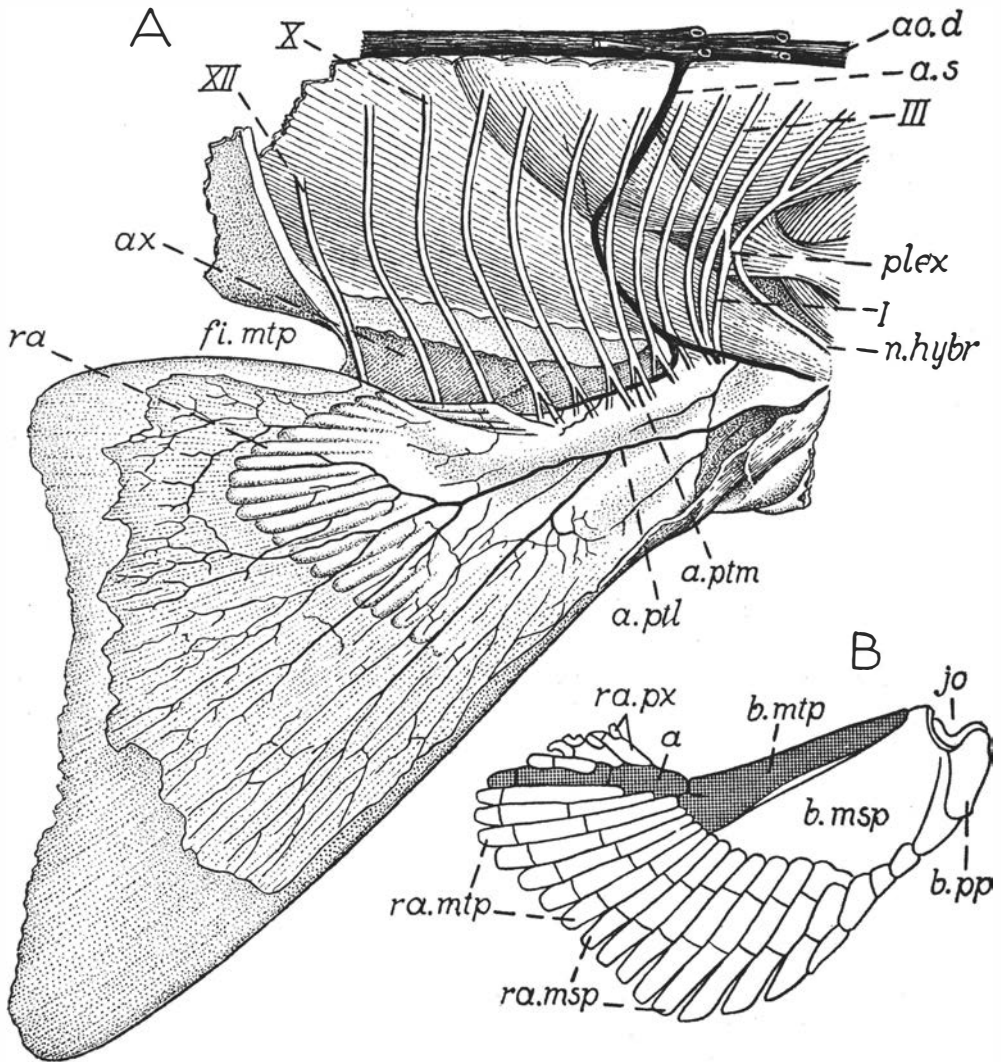


Figure 1  
*Squalus acanthias*

*A*, left pectoral fin and adjoining part of body in ventral aspect. The skin removed to show the "axilla" traversed by the metazonal pterygial nerves and the fan-like shape of the internally short-based fin. *B*, the endoskeleton of the pectoral fin. From Müller, 1909 (Pls. 34: 39, 27: 3). The presumed metapterygial stem is shaded.

*a*, presumed stem element; *ao.d*, dorsal aorta; *a.ptl*, *a.ptm*, lateral and medial pterygial arteries; *a.s*, arteria subclavia; *ax*, space ("axilla") between fin and body; *b.msp*, basale mesopterygii; *b.mtp*, basale metapterygii; *b.pp*, basale propterygii; *fi.mtp*, fissura metapterygii; *jo*, shoulder joint; *n.hybr*, hypobranchial nerve; *plex*, plexus cervico-brachialis; *ra*, radial; *ra.msp*, mesopterygial radials; *ra.mtp*, metapterygial radials; *ra.px*, postaxial radials; *I*, *III*, *X*, *XII*, metameric pterygial nerves.

In order to explain the structure and origin of the paired fins, Gegenbaur (1872, 1876) set forth his famous *gill-arch theory* which soon became accepted and eagerly defended by a great number of students (v. Davidoff, Bunge, Semon, Fürbringer, Jaekel, Braus, and others). This theory holds that the paired fins are visceral in origin and differ fundamentally from the median fins, the skeleton of which is regarded as axial. The endoskeletal girdles are interpreted as modified gill-arches and the "metapterygial stem" is considered to be the central branchial ray of the arch which has become enlarged and subdivided into several pieces. The radials are other branchial rays which have shifted their bases of attachment from the visceral arch to the enlarged central ray.

As is now well established, the paired fins are of the same nature as the median fins and are metameric structures arisen in longitudinal fin-folds. These facts form the nucleus of the *fin-fold*, or *metameric theory* of the origin of the paired fins, set forth independently and almost simultaneously by Balfour (1876, 1881) and Thacher (1877) and accepted and further developed by a great number of investigators (Mivart, Dohrn, Wiedersheim, Dean, Woodward, Rabl, Mollier, Osburn, Goodrich, Sewertzoff, Müller, Stensiö, Heintz, Holmgren, Steiner, Ekman, and others).

The most common version of this theory advocates (see Goodrich, 1930; Devillers, 1954) that the pectoral and pelvic fins were originally separate. The primitive paired fin (Figure 2A) was a long-based (eurybasal) ventro-lateral fold stiffened by a transverse series of metameric (segmental) endoskeletal rays. The rays were divided into proximal elements, the *basals* (*ba*), forming a longitudinal row in the body wall at the base of the fin, and elongated distal elements, the *radials*, situated within the fin. The longitudinal row of basals is generally referred to as the *metapterygial* or *metameric stem* or *axis*, and together with the lateral series of radials it forms a structure corresponding to Gegenbaur's uniserial archipterygium. The "metapterygial stem" is crossed, in regular segmental order, by the branches of the spinal nerves supplying the metameric radial muscles of the fin.

This primitive uniserial type of fin is thought to have been modified in various ways. The endoskeletal girdles are inward extensions of the basals and in connection with a crowding together of the metameric elements of the fin, a process known as *concentration* and thought to be due to a differential growth between head and body, the metameric basals have often fused with each other, forming large compound basals (basale metapterygii, etc.). This has happened in modern sharks (Figure 2B) which otherwise are believed to have preserved much of the primitive fin-structure. In sharks the fin is thus still long-based (eurybasal), according to current views, and the "metapterygial stem" has retained its original position in the body wall and is crossed by the metameric nerves. However, in certain sharks (e.g. in *Squalus*, Figures 1, 2B) the posterior part of the "metapterygial stem" has become freed from the body wall by a slight embayment in the posterior margin of the fin, the *fissura* (*incisura*) *metapterygii* (*fi.mtp*), and some radials have developed on its mesial side.

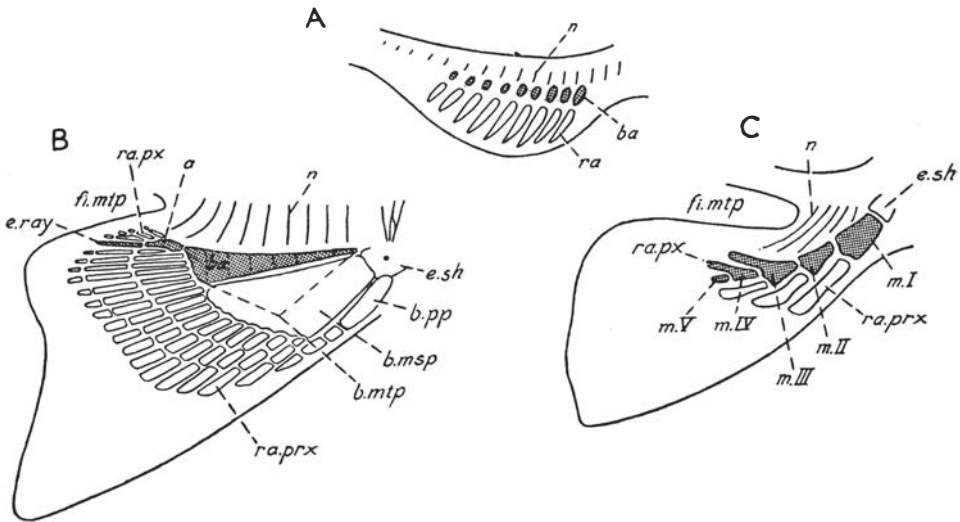


Figure 2

Diagrams of the pectoral fin to illustrate the current views as to the "metapterygial stem" or "axis" (shaded) and its freeing from the body wall by a posterior embayment (cf. Figures 7, 11).

A. Hypothetical primitive condition. B. Shark, *Squalus acanthias* (cf. Figures 1, 8, 11 B, C). C. Osteolepiform crossopterygian, *Eusthenopteron foordi* (cf. Figure 11, D, E). A, C, after Steiner, 1935, Figure 3, slightly modified (see also diagrams by Sewertzoff, 1926, a, Figure 26; 1934, Figure 57; Moy-Thomas, 1936, Figures 1, 3; Westoll, 1943, Figure 1 F-H; Holmgren, 1952, Figure 101).

a, element of "metapterygial stem"; ba, metameric basal; b.msp. basale mesopterygii; b.mtp, basale metapterygii, main element of "metapterygial stem", composed of metameric basals; b.pp, basale propterygii; e.ray, end-ray of "metapterygial stem"; e.sh, endoskeletal shoulder girdle; fi.mtp, posterior embayment (fissura metapterygii); m.I-m.V, metameric elements (mesomeres), each corresponding to a basal; n, metameric pterygial nerves; ra, radial of uniserial archipterygium; ra.ppx, preaxial and ra.px, postaxial radials of biserial archipterygium.

These postaxial radials (ra. px), which were interpreted by Gegenbaur as vestiges of an once more complete series of postaxial rays of the biserial archipterygium, are considered to be either new formations or lateral (preaxial) radials which have shifted to the mesial side of the "stem". By the further deepening of the fissura metapterygii (Figure 2C) the base of the fin became shortened from behind, and the originally longitudinal metapterygial stem, composed of a row of metameric basals or "mesomeres" (m.I-m.V), became more and more freed from the body wall, so as finally to form the principal axis of the short-based or stenobasal fin known as the biserial archipterygium.

Among the many advocates of the fin-fold theory there is of course much diversity of opinion as to details. Thus Dohrn (1884) doubted that the paired fins are derived from a continuous ventro-lateral fin-fold as assumed by Balfour, and more recently several writers, in particular palaeontologists (Stetson, Howell, Gregory, Westoll,

Harris, Eaton, Romer, and others), impressed by the frequent occurrence of spines in connection with, or instead of, fins in the Silurian and Devonian vertebrates, have claimed that the fins (both paired and unpaired) originated as spiny structures and that the fin-membrane with its content of metameric elements is a later development (cf. p. 151). Objections against the original presence of a continuous fin-fold have, for other reasons, recently been raised also by Devillers (1954; see below) and Nursall (1962).

#### THE VENTRO-LATERAL FIN-FOLD

In 1876, Balfour (pp. 132-133; see also 1878, pp. 101-104) established that the paired fins in elasmobranchs arise as "special developments of a continuous ridge on each side, precisely like the ridges of epiblast which form the rudiments of the unpaired fins" and he concluded "*that the limbs are the remnants of continuous lateral fins.*" Balfour's discovery was confirmed by Dohrn (1884, pp. 162-163, 171) who, in embryos of *Centrina*, described a strong fold connecting the pectoral and pelvic fins. However, other students (Rabl, Mollier) were unable to find any trace of the ectodermal thickening between the pectoral and pelvic fins described by Balfour, except in the *Rajiformes* where secondary conditions were presumed to occur, and for a long time it was generally agreed that the pectoral and pelvic fins arise separately (see e.g. Goodrich, 1930, pp. 130-132). This presumed discontinuity of the paired fins has frequently been used as an argument against the fin-fold theory, and it is therefore of great interest that Ekman (1941), investigating *Squalus* (Figure 3) and *Etmopterus*, could prove quite definitely that the paired fins develop from a continuous thickening of the ectoderm (*ect.t*) exactly as described by Balfour.

Ekman concludes that the elasmobranchs have arisen from forms with a complete ventro-lateral fin-fold (*vl. cr*; *Flossensaum*, *Flossenleiste*), which in the *Zwischenleiste* (Figure 3B, C) between the future pectoral and pelvic fins has lost its functional importance and has disappeared. This conclusion is strongly supported by the presence of condensed mesenchyme (*mes.c*) also inside the intervening thickening (*Zwischenleiste*) and by the well-known fact, discovered by Dohrn (1884), that the myotomes in the area between the pectoral and pelvic fins may produce a complete series of muscle-buds which later disappear (abortive buds). However, recently Devillers (1954, pp. 740-741) has maintained that these and other facts in favour of the theory of an original ventro-lateral fin (Wolff's crest in amniotes; the presence of intermediate fins or of a continuous ventro-lateral fin in certain early forms, etc., see below), in the light of Balinsky's experimental investigations on limb induction in urodele larvae, may be explained in a different way.

As demonstrated by Balinsky (1933, 1935, 1937), the formation of accessory limbs may be induced in urodele larvae by the implantation of living tissue (olfactory epithel, etc.) or pieces of inorganic matter (celloidin) within an elongated but not very high area of the flank, which is limited anteriorly and posteriorly by the normal

fore and hind limbs. Balinsky terms this area the *Extremitätenseitenfeld*, and he regards it as a potential rudiment, comparable to the ventro-lateral ectodermal thickening in fishes and Wolff's crest in amniotes.

As is well known, other organs (the lens, the otic capsule, etc.) may also be induced within limited fields, and one characteristic of these organ fields is that the intensity of differentiation diminishes with the distance from the centre. Since the organ fields in the case of the lens etc. cannot be said to have a phylogenetic significance, there is according to Devillers no reason to assume that the *Extremitätenseitenfeld* represents a vestige of an original ventro-lateral fin-fold, but rather that it is a general embryological phenomenon, common to embryos of all vertebrates both living and extinct. The intervening ectodermal thickening and the abortive muscular buds therefore cannot be regarded as structures in regression, but as representing the first stages in the normal embryonic development. In singular cases (e.g. in *Jamoytius*) the ontogenetic course of events may be manifested in the adult, with the result that complete ventro-lateral fins are formed.

Balinsky paid special attention to the position of the induced limbs in relation to the body segments and to the time sequences in limb induction. His main results of interest in this connection may be summarized as follows (1937, pp. 283-284): Accessory limbs may be induced on the flank in every segment from those of the fore limb to those of the hind limb, but only during a strictly limited period of larval life. All induced limbs arise earlier than the normal hind limb, and are progressively earlier the more forwards the segment of implantation is situated. In each segment there is a "critical phase" of short duration during which induction is possible. This "critical phase" in the successive segments occurs in a strict chronological order, appearing increasingly earlier the more forwards the segment is situated. In each segment the phase begins (and ceases) at a definite ontogenetic time, and the setting of the phase is not influenced by the time of implantation.

*All these conditions seem to have a simple explanation if we consider that the muscle material of the limbs (and paired fins) is most likely myotomic in origin, being produced by the ventral ends (myv, Figures, 3, 6A) of the downward-growing myotomes, and that the myotomes arise in a strict chronological order from the front backwards.*

If it is true that the myotomes are the only source of limb-muscle material (cf. e.g. Griffiths, 1959; Balinsky, 1963, p. 306), it is readily seen that complete limbs with muscles can be formed by induction only when the inductor is so situated that it can influence, directly or indirectly, myotomes capable of producing limb-muscle material. The period during which a myotome can give off myogenic limb material, whether by the formation of more or less distinct muscle-buds (*mb*) or by the migration of myogenic cells (*myg*) out of the myotome, is certainly of short duration, and it is to be suspected that the potential zone of proliferation of myogenic material at the ventral end of the myotome moves rapidly downwards as the myotome grows in that direction. It seems very likely, therefore, that Balinsky's "critical

phase" corresponds to the limited time in ontogeny when the myotome of the segment of induction is in such an evolutionary stage that it can produce limb-muscle material. Owing to the fact that the differentiation of the myotomes proceeds regularly in a posterior direction, the "critical phases" will of course occur progressively later the farther back the segment of induction is situated, and evidently the normal hind limb will be the last limb to receive its muscle material. It is also obvious that an early implantation in a segment cannot have any inducing effect until the moment at which the differentiation of the myotome has proceeded so far that the production of limb-muscle material at its ventral end can begin. The *Extremitätenseitenfeld* in urodele larvae thus seems to represent an area of the flank within which the myotomes, during a short period, can give off myogenic material destined for the limbs and which moves successively ventrally and backwards as the growth and the differentiation of the myotomes proceeds. As pointed out already by Balinsky (1933, pp. 740-741), this area is not to be confused with the true limb fields (the fore limb field and the hind limb field), each with the limb as the centre.

As also pointed out by Balinsky (1935) the *Extremitätenseitenfeld* is no doubt represented in other gnathostomes as well, and the potentiality to form paired fins or limbs, which is a characteristic of this field, must have been inherited from their common ancestors. Now in experimental limb induction the limb formation is initiated in an artificial way; but what is the *natural inductor* and where is it located? Since the paired fins in fish always arise in the continuous ventro-lateral fold of the body wall formed by condensed mesoderm (*mes.c*, Figure 3) with a lining of thickened ectoderm (*ect. t*), or in a corresponding position, and since the limb formation in the tetrapods, at any rate in the amniotes, is initiated in the very similar thickening known as Wolff's crest, it is quite evident that *the natural inductor must be situated in this fold or crest, which accordingly is a potential ventro-lateral fin.*

Limb formation in tetrapods has been much studied in recent years, and according to modern views (see e.g. Zwilling, 1961; Milaire; 1962; Balinsky, 1963) reciprocal interactions between the condensed mesoderm of the limb-bud and the so-called apical ectodermal thickening of the bud (displaced portion of the thickened ectoderm of Wolff's crest?) play an important part in this most intricate process. It seems likely (cf. Figure 6A) that it is the inductive influence exerted by this interaction that releases the production of myogenic limb or fin material (muscle-buds) at the ends of the myotomes. Be this as it may, however, I cannot see that Balinsky's or other experiments on limb formation can be used as arguments against the theory of a primitive, continuous, ventro-lateral crest, and in view of the available embryological evidence it is to be concluded that such a crest or fold was present in the common ancestors of the gnathostomes and that it represents a potential ventro-lateral fin (cf. p. 152, Figures 5A, C, 6 A-C).



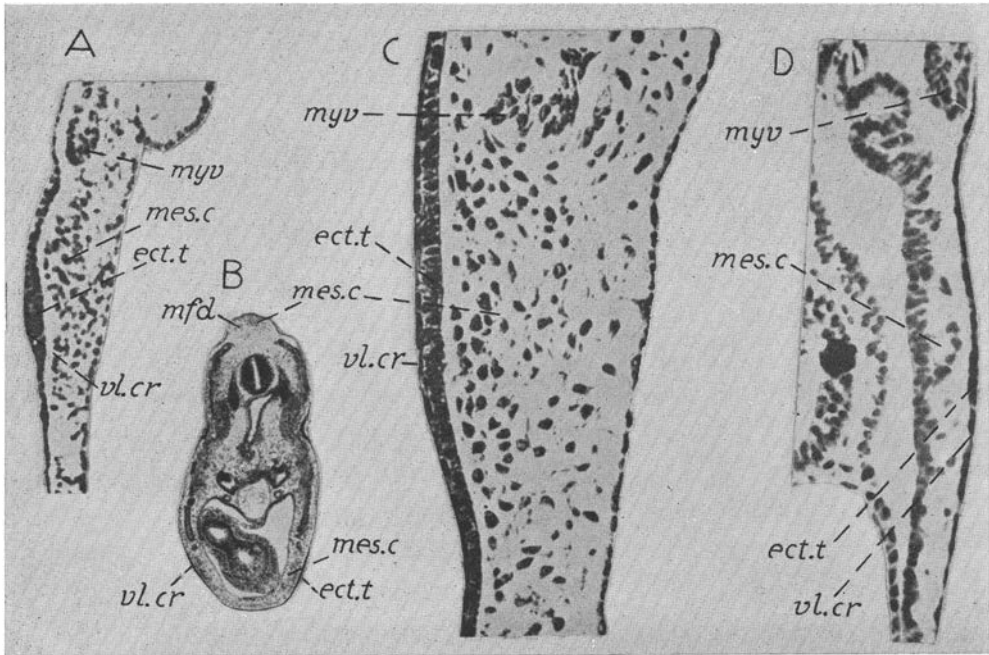


Figure 3

*Squalus acanthias*

Photographs of sections of larval stages to show the thickened ectoderm and the condensed mesenchyme of the ventro-lateral crest in, *A*, *D*, the area of the pectoral fin and *B*, *C*, the area between the pectoral and pelvic fins (*Zwischenleiste*). *C*, portion of section close to that in *B*. *A*, larva 13.6 mm; *B*, *C*, larva 23.3 mm; *D*, larva 9 mm. From Ekman (1941, Figures 36, 19, 34, 41).

*ect.t*, thickened ectoderm; *mes.c*, condensed mesenchyme; *mfd*, dorsal median fin-fold; *myv*, ventral end of myotome; *vl.cr*, ventro-lateral crest.

The presence of an ancestral ventro-lateral crest or potential fin is also strongly supported by the conditions in adult fish, both fossil and recent. Besides in *Jamoytius* and other anaspids (Ritchie, 1964), a long ventro-lateral paired fin is present in certain acanthodians (Davis, 1894, Pl. 27:1; Fritsch, 1895, Pl. 108), and in addition there is in fishes in general a strong variation in the rostro-caudal extent of both the paired and the unpaired fins. Of greater interest in this connection, however, is the fact that there is a long ventro-lateral crest in the adults of many forms which is situated as in embryos. In a previous paper (1948, pp. 18-19) I described such a crest in the osteolepiforms and demonstrated that it passes through the bases of the pelvic and pectoral fins and that most anteriorly, in the clavicular region, it bends mesially. In acanthodians (Figure 5F), in which the ventro-lateral crest (*vl. cr*) is marked by the well-known intermediate spines, it also curves mesially in its anterior part (*vl. cra*), as it does also in many arthrodires (Stensiö, 1959) and in *Acipenser* (Figure 5E). In the latter the ventro-lateral crest is very distinct, and it is a most

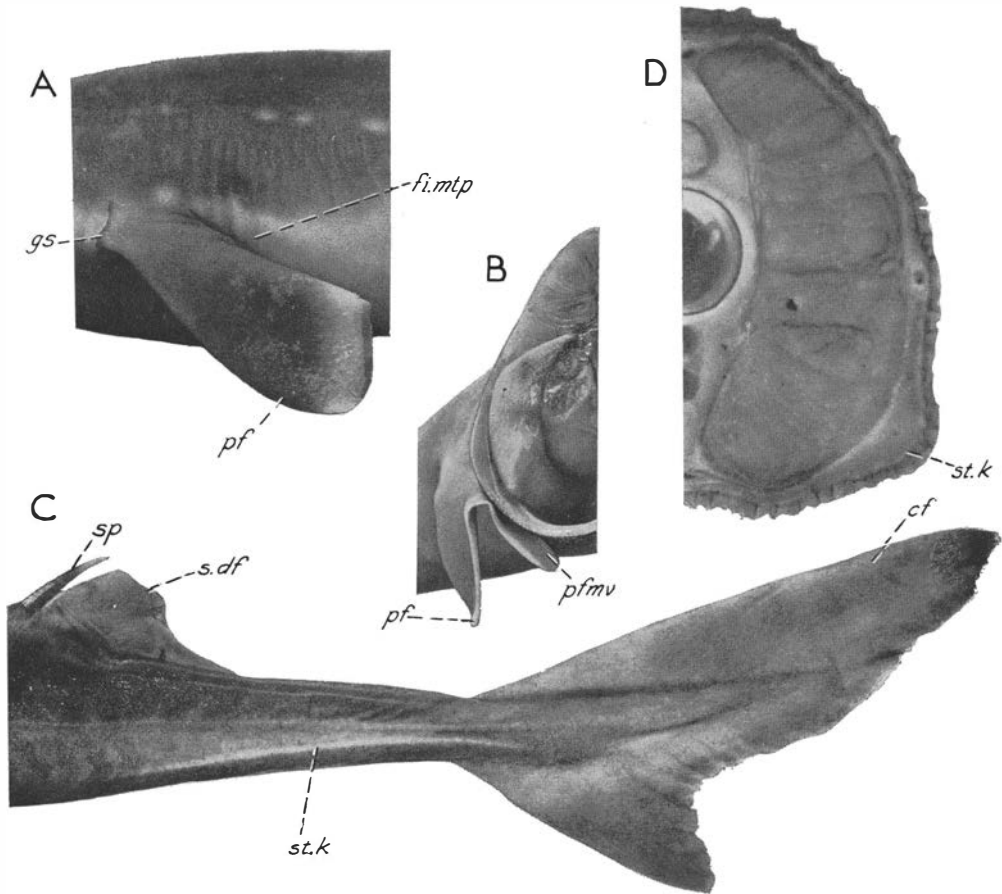


Figure 4  
*Squalus acanthias*

*A, B.* Left pectoral fin of young individual in lateral and posterior aspects. *C, D,* the tail of adult individual showing the steering keel. *C,* lateral aspect. *D,* right half of transverse section.

*cj,* epichordal lobe of caudal fin; *fi.mtp,* fissura metapterygii; *gs,* gill-slit; *pf,* pectoral fin; *pfmv,* medial ventrally bent portion of ditto; *s.df,* second dorsal fin; *sp,* spine of ditto; *st.k,* steering keel.

remarkable fact that after passing through the base of the pelvic fin it is sometimes continued backwards by a distinct ridge (*ri. vl*) without scutes. Posteriorly this ridge, like the similar steering keel on the tail in *Squalus* (Figure 4 C, D), ends lateral to the anal fin, which is continued forwards by a median row of small scutes (*sc. mfv*, Figure 5 E) formed in the median ventral crest. The position of the posterior part (*ri. vl*) of the ventro-lateral crest in the sturgeon indicates that the current view that the ventro-lateral fin-folds of both sides meet behind the anal opening and are

continued backwards by the ventral median fin-fold, is probably incorrect. The untenability of this view is further demonstrated by the fact that the ventral median crest in embryos extends forwards in front of the anal opening to form a preanal fin (*mfp<sub>a</sub>*) which, like other well-developed median fins in embryos of fishes (see e.g. Goodrich, 1930, p. 113, Figs. 104, 110, 113, 116), is a secondary development in the median crest. For mechanical reasons, too, it is unlikely that the ancestral ventro-lateral fin-folds united behind the anal opening. In this connection it may also be mentioned that Dohrn (1884, Pl. 8:9, 10) found ventro-lateral abortive muscle-buds lateral to the anal fin in sharks. Since according to Mayer (1885, pp. 239-240) the muscle material of the anal fin is formed later in ontogeny, and is probably derived from the ventral myotome ends (cf. *myg*, Figure 6 A), the presence of these caudal abortive buds (*mbd*, *mbv*) also indicates that the potential ventro-lateral fin originally extended backwards to the tail, independently of the ventral median fold (*mf<sub>v</sub>*).

#### THE EVOLUTION OF THE GIRDLES AND PAIRED FINS

As is now well known (Jarvik, 1960, 1964) the Vertebrata comprise two quite distinct stocks, the *Agnatha* and the *Gnathostomata*, which have probably been separate since pre-Cambrian times. The agnathes or cyclostomes are not more primitive than the gnathostomes, they do not include their ancestors, and neither the sharks nor the placoderms include the ancestors of the teleostomes and tetrapods. Moreover, it has been proved that all the various main groups of Devonian or earlier vertebrates had become highly specialized before their first appearance in the fossil record. None of these early groups is truly primitive, and none can be derived from any other.

These fundamental facts are to be kept in mind when we turn to a discussion of the origin and the evolution of the girdles and paired fins. *We cannot, as is generally done, start from the early cyclostomes (ostracoderms) and take it for granted that they are more primitive than the gnathostomes, and we are not likely to find truly primitive fins in the early vertebrates.* Nor is it likely that the *spines* found in many early forms are primitive structures. Like spines of recent fish (*sp*, Figure 4C, *p. sp*, Figures 5 E, 10 D), they are no doubt highly modified secondary formations, and we cannot base a theory on the origin of fins solely on the fact that spines are fairly common in those early forms which happened to be preserved as fossils. Such a theory must be based on morphological and comparative anatomical data.

Since the cyclostomes are not the ancestors of the jawed vertebrates and the recent forms lack paired fins, and since the internal structure of the paired fins in the ostracoderms is still unknown, the following account will be confined to the conditions in gnathostomes. In these, the paired fins always articulate with special endoskeletal girdles, the shoulder or *pectoral girdle* and the *pelvic girdle*, situated in the body wall. In most forms there is, in addition, an *exoskeletal shoulder girdle*, but

there is never a corresponding pelvic girdle, a condition which needs an explanation.

Under the influence of the opinion that sharks are the most primitive gnathostomes, it was for a long time generally assumed that a cartilaginous shoulder girdle of the type found in them (*e.sh*, Figure 8) represents the primitive condition (modified branchial arch, Gegenbaur) and that the exoskeletal girdle was a later acquisition. However, in *Eusthenopteron* and other early osteolepiforms (Jarvik, 1948, 1964) the endoskeletal shoulder girdle is a fairly small tripod structure, whereas the exoskeletal part is well developed and consists of five strong bones on each side and a ventral median interclavicle. In the tetrapod descendants of the osteolepiforms the evolution of the shoulder girdle is characterized by a gradual reduction of the exoskeleton and a corresponding progressive development of the endoskeletal part, which first grows ventrally to form a strong coracoid plate, as present already in the ichthyostegids, and later a dorsal scapular blade. These conditions, and the fact that the exoskeletal girdle in the lower gnathostomes in general is more strongly developed than the endoskeletal one, indicates that it is rather the exoskeletal girdle that is primitive. However, it is more likely that *the endoskeletal and exoskeletal girdles have arisen independently of each other*, the former like the pelvic girdle to carry the fin, and the latter to fulfil other functions (cf. p. 153; Dohrn, 1884; Howell, 1933; Gross, 1954).

In view of the facts presented above, as well as other data, *it may be assumed that the girdles and the paired fins in the gnathostomes arose somewhat as follows* (Figures 5-7):

The fins are movable folds of the body wall. The musculature, which is an essential part of a typical fin, consists of more or less modified radial muscles formed in ontogeny by migration of myogenic material (*myg*) out of the dorsal and ventral ends (*myd*, *myv*) of the growing myotomes. In fish the myogenic material generally forms muscle-buds (*mb*), and an important fact is that each myotome on either side produces *two* dorsal and *two* ventral buds destined for the paired fins. Since the radial muscles are derivatives of myotomes, it is evident that in the gnathostome phylogeny myotomes must have been present *before* radial muscles, i.e. real fins, came into existence. It is therefore to be concluded that the gnathostomes at an early phyletic, pro-gnathostome stage had a body with myotomic musculature. This pro-gnathostome (Figures 5A,C, 6B) obviously was a swimming animal and in order to stabilize its movements in the water (cf. Nursall, 1962) it almost certainly had some steering keels formed by folds of the body wall, perhaps somewhat suggestive of the steering keel on the tail in *Squalus* (Figure 4 C, D). Following what has been said above, it may be assumed that there was at least a median (dorsal and ventral, *mfd*, *mfv*, Figure 5 A, C) and a paired ventro-lateral (*vl.cr*) crest or fold. The ventro-lateral crests almost certainly were independent of the ventral median crest and continued backwards to the tail (see pp. 154-155, Figure 5 A, C) where they gradually faded away. The head of the animal certainly included an axial portion

developed along the notochord, independent visceral arches, the foremost (the premandibular arch) probably incomplete ventrally, and a terminal mouth, but still no jaws (Jarvik, 1954, 1960, pp. 78-88, 1964, pp. 25-28). The visceral arches probably had a transverse position as they have in the embryo, and in contrast to conditions in the pro-cyclostomes (cf. Jarvik, 1964, pp. 21-25) they carried outwardly directed gills and were provided with independent gill-covers (*pm.gc, m.gc, h.gc, gc*).

After these general statements we may now turn to *the evolution of the exoskeletal shoulder girdle*, and will first consider the dermal fin-rays.

As is well known, the dermal fin-rays (ceratotrichia, actinotrichia, lepidotrichia) are modified scale rows. They occur in several generations and no doubt the first (oldest) generation arose at an early phyletic stage (Jarvik, 1959). That this is so is strongly supported by the facts that the actinotrichia, which represent the first generation in actinopterygians, arise very early in ontogeny, before the formation of the muscle-buds, and that they are represented in the preanal fin and other parts of the embryonic fin-folds which later become reduced (Goodrich, 1930, pp. 98, 143). Since modified scales were thus present in early phyletic stages, probably even before the muscularization of the fin-folds, it seems extremely likely that *the early gnathostome ancestor had acquired an exoskeleton*, and that the skin of the head and body and probably also the mucous membranes of the orobranchial cavity and the gill-slits contained small denticles or primary scales (*pr.sc*, Figure 6 B; Jarvik, 1948, pp. 289-291, 1954, p. 64) composed of lepidomoria (Stensiö, 1961). However, already in this ancient creature (Figure 5 A, C) the body musculature must have been interrupted anteriorly by the gill-slits, and certainly at an early stage in phylogeny there was a need to support the body musculature at the transition between head and body. This need could be easily satisfied by the consolidation of the small exoskeletal units in the skin, and probably the primary scales in the area of the future shoulder girdle soon fused into larger units, forming a *primitive exoskeletal shoulder girdle (p.ex.sh)*. These fusions certainly took place in the same way as, and possibly about contemporaneously with, the formation of the dermal bones of the head. In the head the primary exoskeletal components have fused in more or less different ways in the various groups (Jarvik, 1948, pp. 76-85) and no doubt the same has happened with the shoulder girdle, a condition which explains the differences in the number and extent of the dermal bones between the various groups. In view of the fact that the type of exoskeletal shoulder girdle characteristic of each group is established already in the oldest known representatives, it is evident that this differentiation started very early in phylogeny, possibly even in the pro-gnathostome stage. However, the exoskeletal shoulder girdle has to serve other important purposes than to form an anterior anchorage for the body musculature (see also Howell, 1933). It forms the posterior wall of the branchial cavity, it protects the heart, and it gives attachment for branchial muscles, the hypobranchial musculature, and often for fin-muscles. It is evident that these manifold functions, which on the whole are fairly similar in the

various groups, have strongly influenced the development of the individual bones of the shoulder girdle. This accounts for the fact that the exoskeletal shoulder girdle, although the number and extent of the individual dermal bones that enter into its formation may be different, has on the whole a similar structure in the various groups, and often presents an inwardly directed lamina situated in the posterior wall of the branchial cavity.

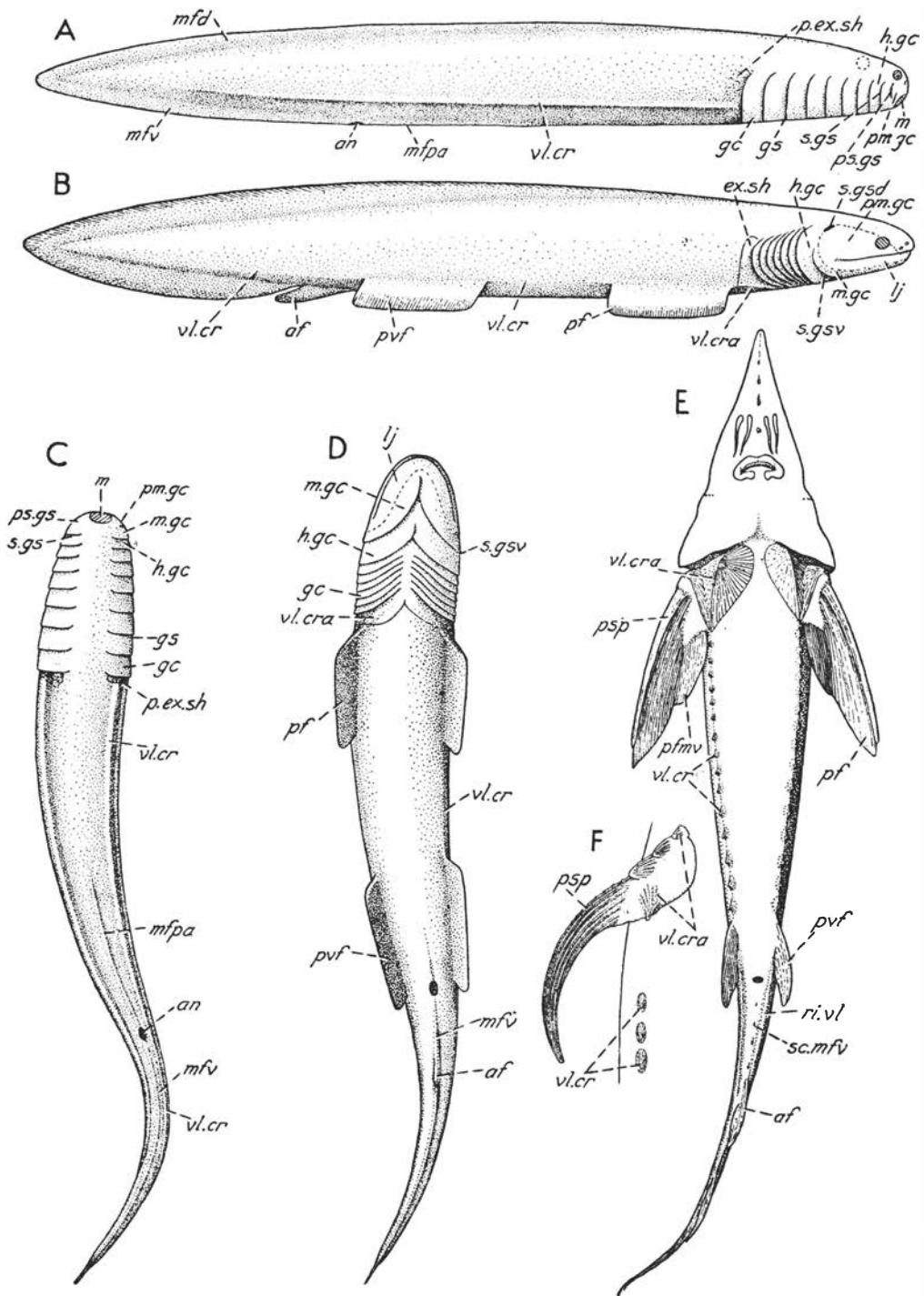
Since, like Howell, I am of the opinion that the exoskeletal shoulder girdle arose to form a support at the transition between head and body and accordingly was short, I cannot agree with Gross (1954) who maintains that the primary purpose of the exoskeletal shoulder girdle was to protect the trunk. This view rests on the fact that a long trunk armour is present in certain early groups of vertebrates, a condition which is considered by Gross and others to be primitive. However, among the early gnathostomes a more or less long body armour is actually found only in some groups of arthrodires. Other arthrodires, and also acanthodians (which include the oldest known gnathostomes), dipnoans and true teleostomes (porolepiforms, osteolepiforms, coelacanthiforms, struniiforms, paleoniscids) all have a short exoskeletal shoulder girdle. The presence of a body armour in certain forms is in my opinion a secondary condition due to fusions of scales in the trunk. Very likely the formation of such a rigid armour has caused considerable reductions and modifications of the trunk musculature, as has happened in the recent trunk fishes (Le Danois, 1961) which have a trunk armour somewhat suggestive of that in the arthrodires.

Whereas the exoskeletal shoulder girdle has thus probably arisen to fulfil special requirements at the transition between head and body, the endoskeletal shoulder girdle, like the pelvic girdle, certainly arose to form a support for the fin. On the basis of embryological and morphological data it may be assumed that the course

#### Figure 5

*A, C.* Hypothetical pro-gnathostome and *B, D,* hypothetical primitive gnathostome in lateral and ventral aspects; *E,* *Acipenser ruthenus*, young specimen (21 cm) in ventral view. Drawing after photographs of specimen in the Paleozoological Dept.; *F,* acanthodian, "*Onchus*" *arcuatus* Ag. Pectoral spine and adjoining part of exoskeletal shoulder girdle in ventral aspect. After drawing made by Dr. T. Örvig of latex cast, somewhat simplified. Specimen No. P 4390, Paleozool. Dept., Stockholm, from Old Red. et. III, Dzwinoigród, Podolien. The spines of the ventro-lateral crest after other, related acanthodians.

*af*, anal fin; *an*, anus; *ex.sh*, exoskeletal shoulder girdle; *gc*, gill-cover; *gs*, gill-slit; *h.gc*, hyoidean gill-cover; *lj*, lower jaw; *m*, mouth; *mfd*, dorsal median crest (potential fin); *mfpa*, preanal portion of ventral median crest; *mfv*, ventral median crest (potential fin); *m.gc*, mandibular gill-cover (cf. Jarvik, 1963, p. 21, Figure 11); *p.ex.sh*, primary exoskeletal shoulder girdle; *pf*, pectoral fin (see also figures 6 D, 7 A); *pfmv*, medial ventrally bent portion of ditto; *pm.gc*, premandibular gill-cover; *ps.gs*, prespiracular gill-slit (cf. Jarvik, 1954); *psp*, spine of pectoral fin (secondary formation; see Sewertzoff, 1926 c, pp. 548-551); *pvf*, pelvic fin; *ri.vl*, posterior part of ventro-lateral crest; *sc.mfv*, scutes of ventral median fin-fold; *s.gs*, spiracular gill-slit; *s.gsd*, *s.gsv*, dorsal and ventral portions of ditto (cf. Jarvik, 1963, p. 17); *vl.cr*, ventro-lateral crest or fin-fold (potential fin); *vl.cra*, anterior medially bent portion of ditto (clavicular or subbranchial portion).



of events at *the formation of the endoskeletal girdles and the paired fins* was somewhat as follows:

The original ventro-lateral crest (*vl.cr*, Figure 5 A, C) of the pro-gnathostome (see p. 152) was a fold in the body wall filled with mesenchyme (Figure 6 B). Radial muscles had not yet developed in this potential fin-fold, but probably there were primitive scales (*pr.sc*) in the skin, and seen in transverse sections it was therefore probably somewhat suggestive of the steering keel on the tail in *Squalus* (Figure 4 D). The crest certainly was a continuous structure extending forwards at least to the branchial region and backwards to the tail and, as discussed above, it was conceivably quite separate from the ventral median crest (*mfv*). However, at some early phyletic stage the muscularization began, and the immovable crest was transformed into a movable ventro-lateral fin (*vl.f*, Figure 6 C). Stimulated probably by an interaction between the mesoderm and ectoderm of the crest (p. 148), the ventral ends of the myotomes, when passing downwards inside it, began to produce myogenic material (*mbd*, *mbv*, Figure 6 A) which in the adult formed diminutive radial muscles (Figure 6 C). In order to increase the flexibility of the ventro-lateral fin, or for other reasons, there arose in each metamere two dorsal (*rmdo*) and two ventral (*rmv*) radial muscles (see also Figure 7 A), innervated by twigs of a pterygial nerve (*pt.n*) which is a secondary branch of the spinal nerve (*sp.n*, Figure 6 A) of the metamere. The radial muscles were originally confined to the base of the fin, as they are in embryos, and each muscle, dorsal and ventral, took its origin in the connective tissue of the body wall and was inserted into the skin and the scales of the fin-fold. The fin soon increased in breadth (Figure 6 D) and the radial muscles grew out almost to the margin of the fold as they do in the embryonic fin in sharks (Figure 9 E; cf. Jarvik, 1959, p. 14). Contemporaneously with these changes the scale rows in the skin of the fin-fold were transformed into lepidotrichia (*lep*) which, according to the principle of delamination (Jarvik, 1959), became embedded in the skin in their proximal parts, whereas distally they still clung to the basal membrane. Moreover, special supporting endoskeletal rods, primary radials, began to develop in the mesenchyme of the fin, one between each dorsal and ventral radial muscle. *Accordingly, there are two such radials in each metamere* (Figure 7 A), a condition generally overlooked in the discussions of the origin of the tetrapod limb. As evidenced by the presence of abortive muscle-buds both in the middle part of the body and in the tail, a middle and a posterior portion of the original fin-fold became suppressed, probably partly at least, as a consequence of the undulatory swimming movements of the body (Figure 5C, D), and independent pelvic and pectoral fins arose. These fins were plesodic (Stensiö, 1959), which is a primitive condition in vertebrates, and they certainly extended in ventro-lateral direction as they do in the osteolepiforms (Jarvik, 1948, p. 19, Figure 3) and many other adult fishes (Figures 4 A, B, 5 E).

The fins were movable structures, and due to the action of the radial muscles they could certainly move in dorsal and ventral directions, bending along the body wall.



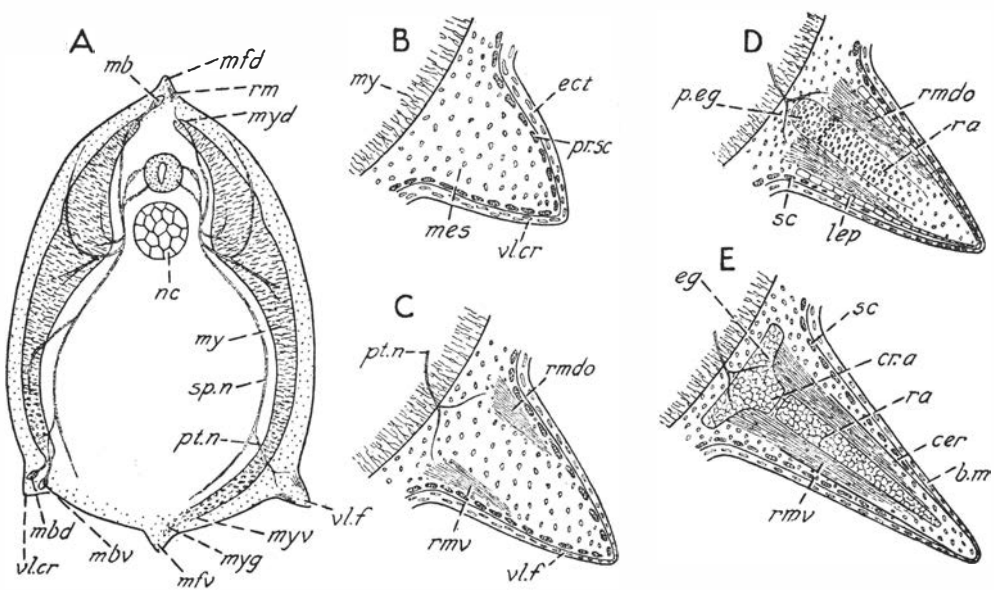


Figure 6

A. Diagrammatic representation to show the relations between myotomes, muscle-buds, spinal and pterygial nerves, and fin-folds in embryo of gnotostome. On the right advanced stage; on the left somewhat earlier stage. B-E, four diagrammatic transverse sections through right ventro-lateral crest or fin to demonstrate the phyletic development of the radial muscles, the dermal fin-rays and the endoskeletal elements. Compilations after figures by Balfour, Dohrn, Sewertzoff, Goodrich and others.

*b.m.*, basal membrane; *cer*, ceratotrachia or actinotrachia (modified lepidotrichia); *cr.a.*, articular crest; *ect*, ectoderm; *eg*, endoskeletal girdle; *lep*, lepidotrichia (modified scale rows); *mb*, muscle-bud; *mbd*, *mbv*, dorsal and ventral muscle-buds of paired fin; *mes*, mesenchyme; *mfd*, *mfv*, dorsal and ventral median crest (potential fin); *my*, myotome; *myd*, dorsal end of myotome; *myg*, myogenic material; *myv*, ventral end of myotome; *nc*, notochord; *p.eg*, primary girdle component; *pr.sc*, primary scale; *pt.n.*, pterygial nerve; *ra*, radial; *rm*, radial muscle; *rmdo*, *rmv*, dorsal and ventral radial muscle of paired fin; *sc*, scale; *sp.n.*, spinal nerve; *vl.cr*, ventro-lateral crest or fin-fold (potential fin); *vl.f.*, ventro-lateral fin.

This effected a subdivision of each primary radial into a proximal element (*p.eg*, Figures 6 D, 7 A) situated in the body wall and a long distal element (*ra*) situated in the fin. The proximal elements, which have been observed by Sewertzoff (1926 b) in embryonic stages of the pelvic fins in *Acipenser* (Figure 10 E, H), represent the primary components of the endoskeletal girdles. These *primary girdle components* grew dorsally and ventrally in the body wall (Figure 6 E; cf. *Acipenser*, Figure 10F) and fused with each other, forming a primitive elongated girdle (*e.sh*, Figure 7 B) provided with a lateral articular crest (*cr.a*). A shoulder girdle of this type, although in several respects more advanced, has been described by Stensiö (1959) in Devonian pachyosteoromorph arthrodires (Figure 10 A).

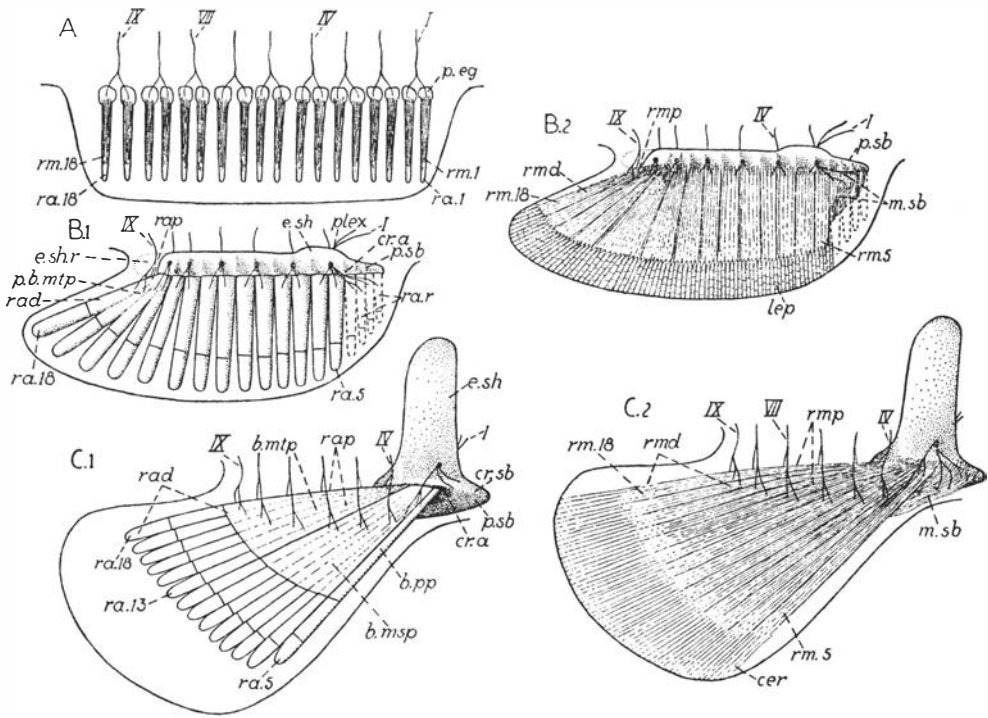


Figure 7

Diagrammatic representations to illustrate the main phyletic modifications of the metameretic nerves, radial muscles and skeletal elements of the pectoral fin in connection with the shortening of the shoulder joint from behind and the change in direction of the visceral arches. As regards the modifications of the metameretic vessels see Wetterdal, 1920 and Stensiö, 1959. *A*, primary holosomactidial fin of pro-gnathostome, derived from nine metameres (cf. Figures 5 B, D, 6 D, 9 A); *B. 1*, *B. 2*, pachyosteomorph condition (Figure 10 A; Stensiö, 1959; Jarvik, 1964, Figure 9 A, B) represented also in larval stages of *Acipenser* (skeletal elements, Figure 10) and sharks (muscles, Figure 9 B, E). *C. 1*, *C. 2*, shark condition (cf. Figures 1, 8, 9, C, D, 11 A-C).

*b.msp*, *b.mtp*, basale mesopterygii and basale metapterygii; composed of proximal, mainly secondary, portions of radials; *b.pp*, basale propterygii; *cer*, ceratotrichia (modified lepidotrichia); *cr.a*, articular crest; *cr.sb*, modified articular crest of anterior (subbranchial) portion of endoskeletal shoulder girdle; *e.sh*, endoskeletal shoulder girdle; *e.shr*, posterior reduced part of ditto; *lep*, lepidotrichia (modified scale rows); *m.sb*, modified radial muscles of anterior (subbranchial) portion of pectoral fin; *p.b.mtp*, primary basale metapterygii; *p.eg*, metameretic primary girdle components; *plex*, plexus cervico-brachialis; *p.sb*, anterior modified (subbranchial) portion of endoskeletal shoulder girdle; *ra.1*, *ra.5*, *ra.13*, *ra.18*, radials (two in each metamere); *rad*, distal (primary) portions of radials; *rap*, proximal (secondary) portions of radials; *ra.r*, anterior (subbranchial) radials (in reduction); *rm.1*, *rm.5*, *rm.18*, radial muscles (two dorsal and two ventral in each metamere); *rmd*, distal (primary) portions of radial muscles; *rmp*, proximal (secondary) portions of radial muscles; *I*, *IV*, *VII*, *IX*, metameretic pterygial nerves.

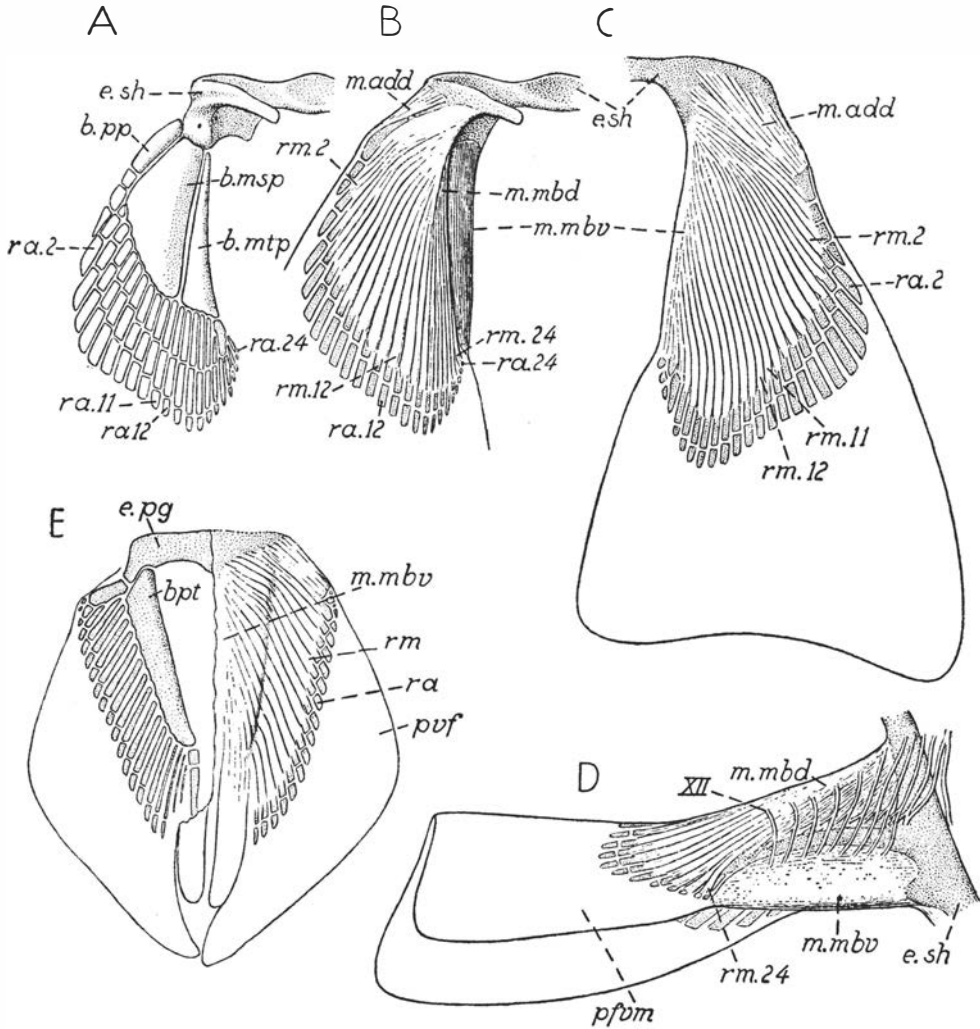


Figure 8

*Squalus acanthias*

A-D, left pectoral fin and endoskeletal shoulder girdle in, A, B, dorsal, C, ventral, and D, medial aspects to show the skeleton, the dorsal and ventral musculature, and (in D only) the pterygial nerves. E, the pelvic girdle and the pelvic fins in ventral view (drawings after specimens dissected by the author).

*b.msp*, basale mesopterygii; *b.mtp*, basale metapterygii; *b.pp*, basale propterygii; *bpt*, basipterygium (composed of proximal portions of radials); *e.pg*, pelvic girdle; *e.sh*, endoskeletal shoulder girdle; *m.add*, musculus adductor, probably representing modified radial muscles of anterior, medially bent portion of ventro-lateral fin; *m.mbd*, *m.mbv*, dorsal and ventral medial muscular bands; *pfvm*, medial, ventrally bent portion of pectoral fin; *pvf*, pelvic fin; *ra*, radial; *ra.2*, *ra.11*, mesopterygial radials; *ra.12*, *ra.24*, metapterygial radials; *rm*, radial muscle; *rm.2*, *rm.11*, mesopterygial radial muscles; *rm.12*, *rm.24*, metapterygial radial muscles; *XII*, twelfth pterygial nerve.

The phyletic changes here considered, which probably took place already in the pro-gnathostome stage (cf. pp. 151,170), are to a considerable extent recapitulated in the ontogenetic development of the paired fins in sharks (Figure 9) and sturgeons (Figure 10 B-H). They resulted in the development of paired fins, pectoral and pelvic, with transverse metameric elements. Such a primitive fin, shown diagrammatically in Figure 7A (primary holosomactidial fin, Stensiö, 1959, pp. 212-213), has hitherto not been found in any adult fish. It is therefore of great interest that the pachyosteomorph arthrodires, which have retained a primitive type of shoulder girdle, also present a pectoral fin (Figure 10 A; see also Jarvik, 1964, pp. 34-35; Figure 9 A, B) which in many respects is very suggestive of such a primitive fin. However, in them the hindmost radials, as explained by Stensiö (1959; as regards *Acipenser* see also Figure 10 B-H and Sewertzoff, 1926 a, 1926 b, 1934), have moved forwards in their proximal parts and have partly fused with each other, forming a primitive basale metapterygii (*p.b.mtp*). In connection with these changes (Figure 7 B.1, B.2) the endoskeletal shoulder girdle and its articular crest were correspondingly *shortened from behind*. In the main middle part of the fin, on the other hand, the primitive metameric disposition has been retained, and the metameric components (radials, radial muscles, pterygial nerves and vessels) were arranged very much as they are in embryos of sharks.

This *shortening* of the shoulder girdle or (and I think it is more important) *of the shoulder joint*, and the crowding together of the proximal parts of the metameric elements from behind are the result of an important morphogenetic process leading ultimately to the formation of an internally short-based fin (see p. 166) of the type found for instance in sharks (Figures 7 C.1, C.2, 11 B,C), sturgeons (Figure 10 B-H) and osteolepiforms (Figure 11 D,E). Since there is nothing to indicate that the radial muscles and the radials have moved forwards as a whole during this process, it is obvious that *they must have undergone a successive forward lengthening in order to reach the shoulder joint*. That this is so is strongly supported by embryological evidence (Müller, Sewertzoff).

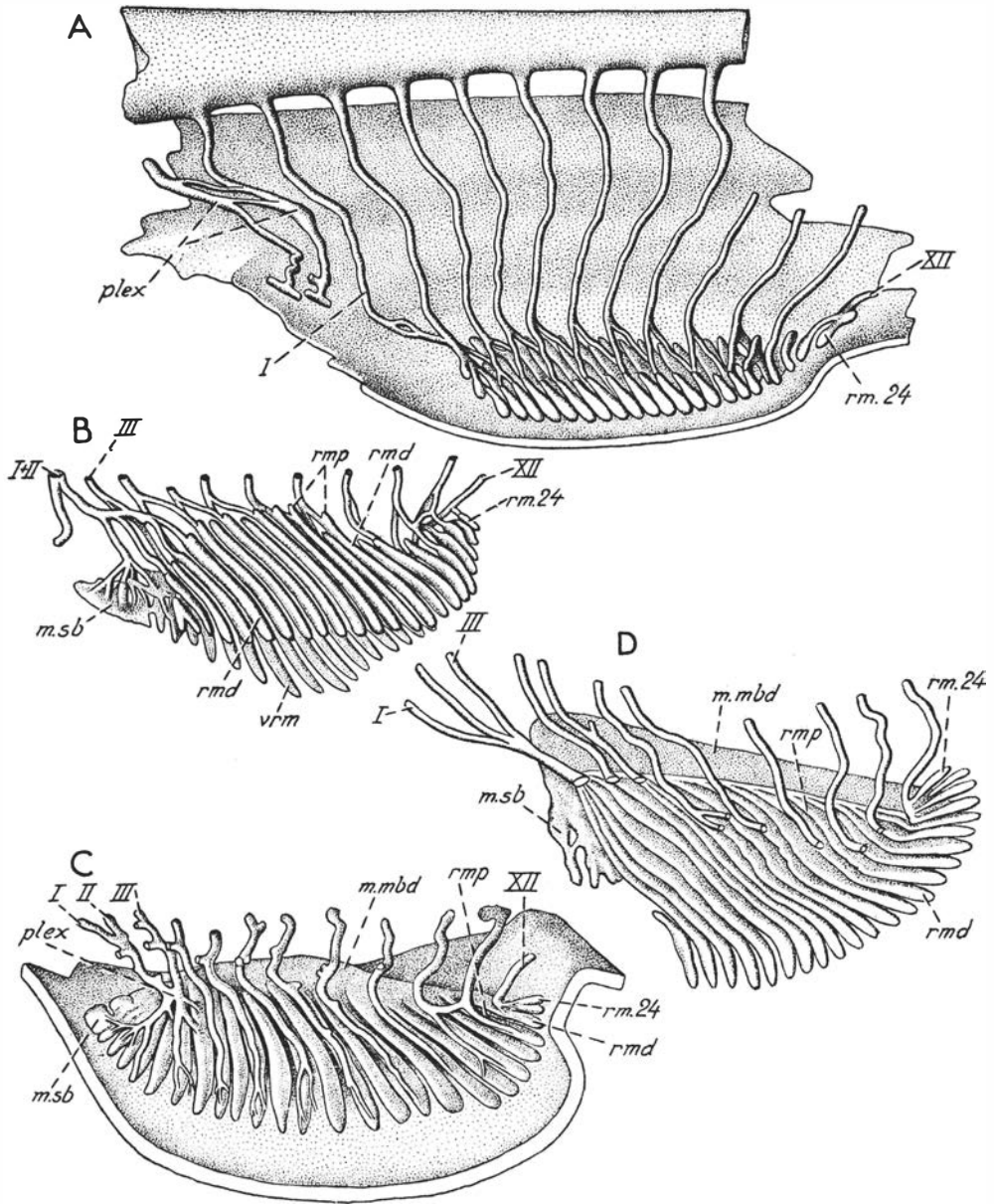
As demonstrated by Müller (1911) the pterygial nerves in early embryonic stages (16-24 mm) of *Squalus* enter the proximal ends of the pear-shaped muscle-buds (Figure 9 A). These buds are transformed into radial muscles which, as pointed out above, grow in a *distal direction* towards the margin of the fin-fold. At a somewhat later stage (27 mm) a small process-like outgrowth (*rmp*, Figure 9 B,E) appears at the proximal end of the muscle, close to the point where the nerve enters it. *This secondary muscular process grows in the opposite, proximal direction, but a most important fact is that it turns forwards towards the endoskeletal shoulder girdle* which it reaches in later stages (Figures 9 C,D,F, 11 B). Accordingly *we may in each radial muscle distinguish between a primary distal portion (rmd) growing in a distal direction, and a secondary proximal portion (rmp) growing forwards to the girdle*. The boundary between these two portions is marked by the point of entrance of

the pterygial nerve (*I, II, III*, etc.). A most remarkable fact, too, is that the pterygial nerves apparently are not influenced by the secondary growth of the radial muscles, a condition which explains why they retain their original metameric position and in the adult cross the "metapterygial axis" in a regular, metameric order (see Figures 1 A, 2 B).

As is readily seen, the hindmost radial muscle (*rm.24*, Figures 9F, 11B) has the greatest distance to grow in order to reach the girdle. Accordingly this muscle has a long proximal portion (*rmp*), which runs forwards to the girdle in an almost longitudinal direction. To this portion are added, successively, the secondary proximal portions of the other radial muscles. In this way the muscles become packed close together, but they keep their individuality and, as may be easily ascertained by dissection of adult specimens, they all continue to, or almost to, the girdle (see also Figure 8B-D). The proximal portions (*rmp*) of the caudal muscles, in the first instance those belonging to the metapterygial radials, form, on each side of the fin, a thick muscular band (*m.mbd, m.mbv*). This band, together with the muscles which successively join it from the lateral side, appears as a *comb-like structure* (Figures 8C, 9F, 11B; as regards the pelvic fin see Figure 8E). Although the conditions — due to the fact that the pectoral fin in *Squalus* (like in *Acipenser* and *Eusthenopteron*) is bent ventrally in its medial part (*pfvm*, Figures 4A, B, 5E, 8D) and for other reasons — are a little more complicated than can be explained here, it is evident that the proximal portions of the metapterygial muscles ran forwards in the same direction as, and are intimately related to, the basale metapterygii. This can only mean that the latter includes the original supporting elements of these secondary muscle portions. *Accordingly it is to be assumed that the basale metapterygii in sharks is composed chiefly of the proximal portions of the metapterygial radials, and that these portions have fused into a single piece (b.mtp, Figures 7C.1, 11C; cf. Figure 2B), in the way indicated by the conditions in the pachyosteomorphs (p.b.mtp, Figures 7B.1, 10A) and the ontogenetic development of the paired fins in Acipenser (Figure 10 B-H).*

That this is so is strongly supported also by the great variations of the skeletal elements in the fins of *Squalus* and other sharks (Gegenbaur, 1865; Müller, 1909; White, 1937).

Studies of these variations have revealed that the comparatively large skeletal piece (*a*), which in *Squalus* and many other sharks (Figures 1 B, 2 B, 11 A) follows distally to the basale metapterygii, must have arisen by the fusion of portions of adjoining radials as indicated in Figure 11 C. Thence it follows that it cannot be a metameric "basal" or "stem" element, as is generally assumed (Figure 2 B). However, if element *a* is a product of fusion of portions of adjoining radials it is hard to imagine that the element following next in front of it, the basale metapterygii (*b.mpt*) could have been formed by fusions of elements of a longitudinal row of once independent metameric "basals" (Figure 2 B), that is, in a quite different way. The only reasonable conclusion must be that the basale metapterygii, like the basale meso-



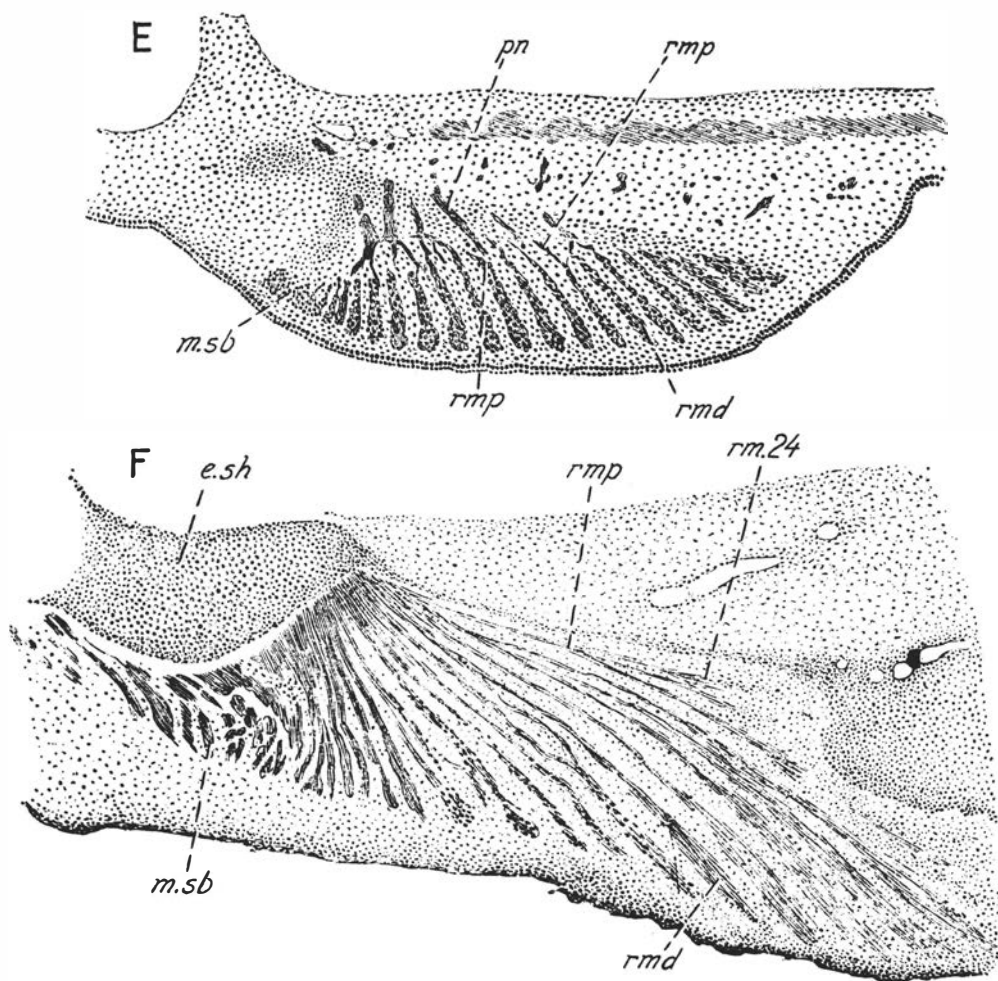


Figure 9

*Squalus acanthias*

The ontogenetic development of the radial muscles of the pectoral fin. *A*, dorsal and ventral muscle-buds, nerve cord and metameric nerves of embryo, 24 mm. *B*, nerves and radial muscles of embryo, 27 mm, in dorsal view. *C*, nerves and dorsal muscles of embryo, 30 mm, in ventral view. *D*, nerves and dorsal muscles of embryo, 38 mm, in ventral view, *E*, *F*, frontal sections of embryos, 30 mm and 38 mm. From Müller (1911), pl. 3 : 4; pl. 4 : 6; pl. 6 : 10; pls. 7/8 : 12; pls. 11/12 : 19; pl. 13 : 21.

*e.sh*, endoskeletal shoulder girdle, *m.mbd*, dorsal medial muscular band; *m.sb*, modified anterior radial muscles; *plex*, plexus cervico-brachialis; *pn*, pterygial nerve; *rm.24*, most caudal muscle-bud or radial muscle; *rmd*, *rmp*, distal (primary) and proximal (secondary) portions of radial muscles; *vrn*, ventral radial muscles; *I*, *I + II*, *III*, *XII*, metameric pterygial nerves.

pterygii and other obviously compound skeletal elements found in the pectoral fin of sharks, is formed by the fusion of adjoining pieces of radials, the imaginary lines of fusion running longitudinally (Figure 11 C).

Of great interest is also the fact that the basale mesopterygii in *Carcharias* (Figure 11 A) and several other sharks (Gegenbaur, 1865; White, 1937) is much shorter than the basale metapterygii. In these sharks the basale metapterygii, like the basiptyerygium (*bpt*, Figure 8 E) in the pelvic fin, carries most of the radials, and together with them it constitutes a *comb-like structure* very suggestive of the comb-like structure formed by the radial muscles in *Squalus* (Figures 8 C, 9 C, D, F, 11 B; as regards the pelvic fin, see Figure 8 E). This variation, too, strongly suggests that the imaginary lines of fusion in the basale metapterygii (and in the basiptyerygium) ran longitudinally (Figure 11 C) and not transversely (Figure 2 B), as has generally been supposed.

Both the development of the skeleton and its variations and the ontogenetic development and course of the radial muscles in the pectoral fin of sharks thus strongly indicate that the basale metapterygii and other supposed "stem" elements are formed by adjoining portions of radials which have fused longitudinally (Figure 11 C). *Under these circumstances it is of course impossible to distinguish a "metapterygial stem", and this concept, which has played such a great role in the discussions on the origin and nature of the paired fins and of the tetrapod limb, is to be regarded as a hypothetical construction without real significance.*

As demonstrated above, the radial muscles in *Squalus* have become lengthened forwards in connection with the shortening of the shoulder joint from behind, and they include a long secondary portion (*rmp*, Figures 7 B.2, C.2, 9 B-F, 11 B) growing in a proximal direction. Since the proximal portions of the radials no doubt have developed to form a support for the corresponding secondary muscle portions, *it is readily seen that the proximal radial portions (rap, Figures 7 B.1, C.1, 11C), too, must be secondary formations, and that they must have grown in a proximal direction.* It is therefore of great interest that the proximal portions of the radials in the pelvic fin of *Acipenser* (*rap*, Figure 10 E, G), according to Sewertzoff, actually arise later than the distal portions (*rad*) and grow in the proximal direction. Since Sewertzoff (1926 b, p. 558) also states that the radials in *Acipenser* grow in both *distal* and *proximal* directions, as do the corresponding structures in tetrapods (neopodial rays, Holmgren, 1952, pp. 83, 104), it is quite evident that there is a close agreement in the mode of growth between the radial muscles and their supporting endoskeletal elements.

As we have now seen, the basale metapterygii in sharks, which is the principal part of the "metapterygial stem", is composed chiefly of proximal portions (*rap*) of radials. These portions have been crowded together in much the same way as the corresponding portions (*rmp*) of the dorsal and ventral radial muscles, and like them they are secondary formations which in phylogeny (as in ontogeny) have arisen by a lengthening forwards of the primary elements (*rad, rmd*) towards the shoulder



joint. *The basale metapterygii is thus, in the main, a new formation, and not the most ancient element of the fin as supposed by Gegenbaur. It is not composed of a row of metameric elements ("basals") originally situated in the body wall* (Figure 2 B), as claimed by the partisans of the metameric theory (Goodrich, Sewertzoff, Steiner, Holmgren, Gregory, Westoll, and others), and obviously *the statement, too, that in sharks it has retained its primitive position in the body wall, is inconsistent with available facts.* It is true that the pectoral fin in sharks, as far as its external appearance is concerned (Figure 4 A, B), is fairly long-based (eurybasal) and also in this regard it resembles the pectoral fins in *Acipenser* (Figure 5 E) and *Eusthenopteron* (Jarvik, 1960, Figure 12 A, B, 1964, Figure 25 A, B). However, if the skin is removed (Figures 1, 8) it is clearly seen that it is a short-based (stenobasal), fan-shaped structure, in which all the metameric elements, with the exception of the metazonal nerves, converge towards the shoulder joint, which is short, again as in *Acipenser* and *Eusthenopteron*. The fan-shaped fin is separated from the musculature of the body wall by a large space (*ax*, Figures 1 A, 10 D) filled with very loose connective tissue. This almost empty space between fin and body, which Müller (1909, p. 475) termed *Achselhöhle* ("axilla"), is traversed by the metazonal nerves in metameric order, a condition which has caused considerable confusion in the past, but which, as explained above, is due to the mode of growth of the radial muscles. The basale metapterygii is situated in the mesial margin of the fan-shaped fin. It has arisen by secondary modifications *within* the fin, and neither this structure nor other elements included in the "metapterygial stem" have become freed from the body wall by a posterior embayment (incisura or fissura metapterygii, Steiner, Sewertzoff) as is generally assumed. The formation of this embayment (*fi.mtp*, Figures 1 A, 2 B, 6, 10 B-D) is certainly a consequence of the anterior crowding together of the posterior metameric elements towards the shoulder joint, through which these elements assume a more and more oblique position. The embayment is still moderate in sharks and has hardly modified the course of the most posterior metameric nerves which run but slightly forwards in order to reach the fin (Figures 1 A, 9 A-D). The same applies to sturgeons (Figure 10 D) and conceivably to *Eusthenopteron*. In tetrapods, on the other hand, in which the base of the limb is short, the posterior one or two pterygial nerves have been pushed more distinctly forwards and enter into the formation of the plexus cervico-brachialis. The so-called postaxial radials (*ra.px*) in *Squalus*, finally, are not new formations. As proved by the remarkable change in position of their radial muscles in ontogeny (see *rm*, 24, Figure 9 A-D) they represent the original, most caudal radials of the fin.

The pectoral fin in *Acipenser* is generally supplied by four metameric nerves only (see Kryzanovsky, 1927), and accordingly it includes only about eight radials and a corresponding number of dorsal and ventral radial muscles. It is thus simpler than in *Squalus*, in which there are generally twelve metameric nerves, I-XII, and about twenty-four radials and radial muscles (Figures 1, 8, 9, 11 B, C; Müller, 1909).

However, it has no doubt arisen in the same way, as have undoubtedly also the pelvic fins in these fishes. In other groups of fishes the paired fins and their girdles may have been secondarily modified in various ways, but as far as I can find all these various types, too, have originated as outlined above, and obviously the many different types of concentrated median fins have been formed according to the same fundamental principles as well. In this connection only the pectoral fin in *Eusthenopteron* will be briefly discussed. This type of fin is of particular interest since, as demonstrated elsewhere (Jarvik, 1964, pp. 66-78), the tetrapod limb in the Osteolepiform-Tetrapod stock may easily be derived from it. As is now well known, the pectoral fin in *Eusthenopteron* (Figure 11 D, E) is seven-rayed, as is the tetrapod limb. However, the entepicondylar process (*enc*) of the humerus (*hu*) most likely represents an additional ray, and the endoskeleton of the pectoral fin in *Eusthenopteron* is thus probably composed of at least eight rays (*ra.1* — *ra.8*). These rays no doubt represent radials and since generally *two radials are formed in each metamere* it is to be concluded that the fin belongs to at least four metameres, and is innervated by about four spinal nerves (*I, II, III, IV*) as in tetrapods (see Goodrich, 1930, p. 139; Jarvik, 1965). However, in *Eusthenopteron* the radials have apparently become segmented and have fused in another fashion than in sharks and sturgeons. The proximal element, the humerus (*hu*), probably includes the proximal segments of eight radials, whereas the ulna (*u*) conceivably comprises segments of six, the ulnare of five and the next element of three adjoining radials. None of these four elements which generally, but sometimes together with an end-ray, have been considered to be "stem" elements (*m.I-m.V*, Figure 2 C) is thus a simple metameric structure originally situated in the body wall, and there is no "metapterygial stem" either in fishes or in tetrapods.

Figure 10

*A*, Pachyosteomorph arthrodire, *Brachyosteus dietrichi*, from the lowermost Upper Devonian, Wildungen, Germany. Endoskeletal shoulder girdle (scapulo-coracoid) of the right side with the proximal portions of the posterior radials, to show the beginning formation of the basale metapterygii. Lateral view. From Stensiö (1959, pl. 14). *B-H*, *Acipenser ruthenus*, *B-D*, right pectoral fin in three stages of evolution. *B, C*, larval stages, *D*, adult (nerves as in *Scaphirhynchus*, Sewertzoff, 1926 a, Figure 16). From Sewertzoff, 1926 a, Figures 12, 13, 15. *E*, horizontal section of the pelvic fin of larva. From Sewertzoff, 1926 b, Figure 1. *F*, transverse section of pectoral fin of young larva. From Sewertzoff 1926 a, Figure 8. *G, H*, skeleton of pelvic fin of young (*G*) and (*H*) more advanced larva. From Sewertzoff 1934, figures 7, 8.

*ax*, space ("axilla") between fin and body; *b.mtp*, basale metapterygii of the adult; *cr.a*, articular crest; *esh*, endoskeletal shoulder girdle; *fi.mtp*, posterior embayment (fissura metapterygii); *lep*, lepidotrichia; *n*, metameric pterygial nerves; *p.b.mtp*, primitive basale metapterygii in pachyosteomorph and in larval stages of *Acipenser*; *p.eg*, primary girdle component; *pf*, pectoral fin; *p.sp*, pectoral spine; secondary formation, in ontogeny formed later than the most anterior radial (*ra.1*) which it embraces from in front (Sewertzoff, 1926 c, pp. 548-551; note that radial 1 is not formed in larval stage shown in *B*); *pvf*, pelvic fin; *ra*, radial; *ra.1, ra.2, ra.9*, radials 1, 2 and 9; *rad, rap*, distal (primary) and proximal (secondary) portions of radial; *rmdo, rmv*, dorsal and ventral radial muscles.

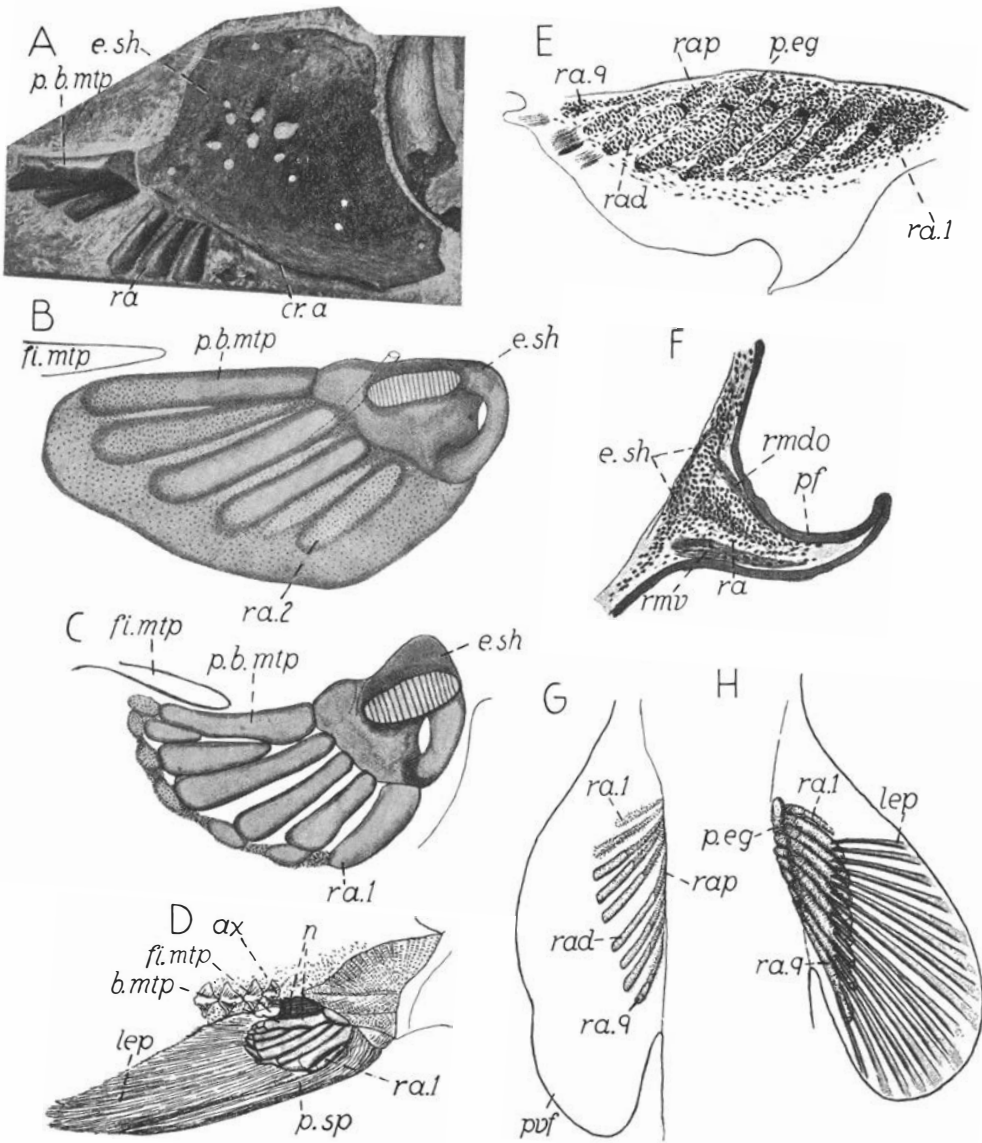


Figure 10

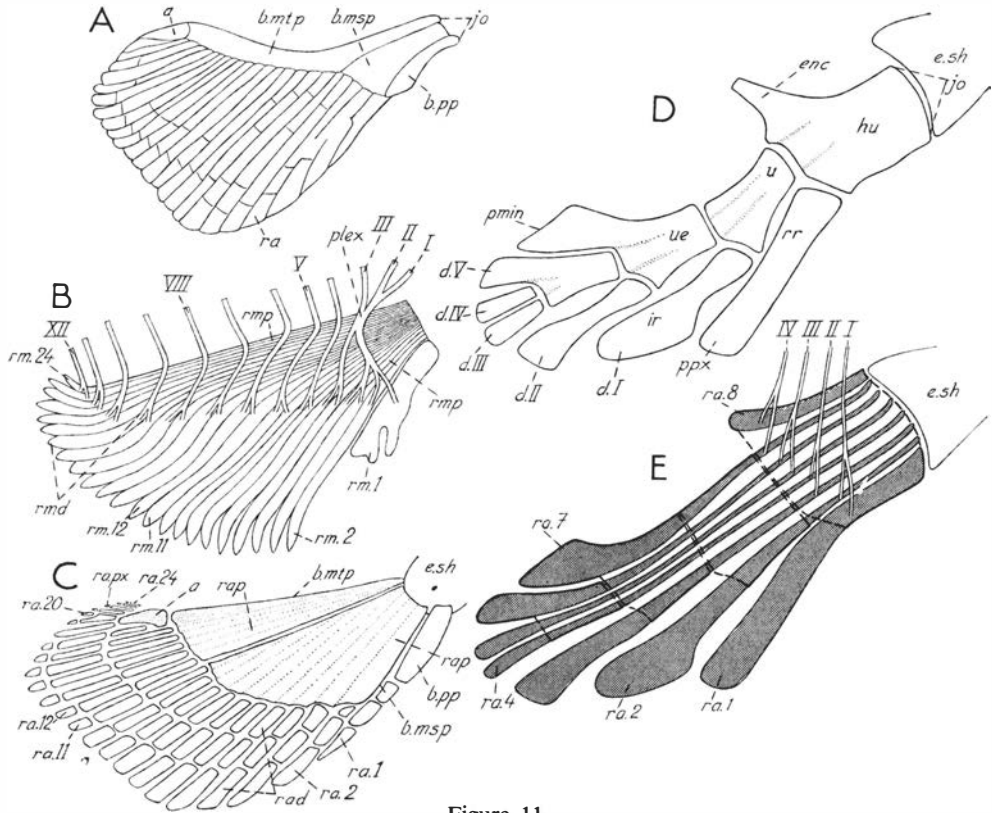


Figure 11

*A*, *Carcharias taurus*, skeleton of pectoral fin of shark with short basale mesopterygii and comb-shaped metapterygium. From White (1937, pl. 23 : d). *B, C*, *Squalus acanthias*, pectoral fin. *B*, diagrammatic representation of pterygial nerves and dorsal radial muscles of left pectoral fin in inner view. Compilation on the basis of Müller's (1911) figures and descriptions of the ontogenetic development (see Figure 9 C, D, E) and the author's own dissections (Figure 8 B-E). *C*, skeleton of the right pectoral fin (cf. Figure 8 A). Imaginary lines of fusion of proximal portions of radials indicated in dotted lines (cf. Figure 2 B). *D, E*, *Eusthenopteron foordi*. *D*, right pectoral fin in external view (cf. Jarvik 1964, Figures 23, C, 25 A-C, 26 D, 27 A). *E*, diagrammatic representation to illustrate its composition (cf. Figure 2 C). The radials (shaded) drawn separately.

*a*, complex element, composed of segments of adjoining radials; *b.msp*, *b.mtp*, basale mesopterygii and basale metapterygii; composed of adjoining portions of radials; *b.pp*, basale propterygii; *d.I*, *d.II*, *d.III*, *d.IV*, *d.V*, distal portions of radials forming digits I-V in tetrapod limb; *enc*, distal portion of radial forming entepicondylar process; *e.sh*, endoskeletal shoulder girdle; *hu*, humerus; *ir*, intermedium ray; *jo*, shoulder joint; *plex*, plexus cervico-brachialis; *pmin*, *ppx*, distal portions of radials forming postminimus and prepollex in tetrapod limb; *ra*, radial; *ra.px*, hindmost ("postaxial") radials; *rad*, *rap*, distal (primary) and proximal (secondary) portions of radials; *ra.1-ra.8*, *ra.11*, *ra.12*, *ra.24*, radials (in *C*, *ra.2-ra.11*, mesopterygial and *ra.12-ra.24* metapterygial radials); *rmd*, *rmp*, distal (primary) and proximal (secondary) portions of radial muscles; *rm.1*, anterior radial muscle, modified probably in connection with change in direction of branchial arches (cf. *m.sb*, Figures 7-9); *rm.2-rm.11*, mesopterygial radial muscles; *rm.12-rm.24*, metapterygial radial muscles; *I*, *II*, *III*, *IV*, *VIII*, *XII*, metameric pterygial nerves.

The phyletic changes in the pectoral fins now discussed have (as in the pelvic fins) taken place from behind, and have resulted in the crowding together of the metameric elements towards the shoulder joint, which has gradually become shorter. Obviously these changes serve to increase the mobility and effectiveness of the fin. However, there are also *changes of another kind, which have affected the anterior parts of the original fin-fold and the pectoral fin.*

As pointed out above (p. 153) the gill-arches in the pro-gnathostome presumably had a transverse position (Figure 5 A, C). However, at some early phyletic stage, most probably at the transition from the pro-gnathostome to the gnathostome stage, when the neural endocranium was formed and parts of the two anterior arches (premandibular and mandibular) were transformed into biting jaws (Jarvik, 1954, 1960, 1964), the branchial arches changed their position and became directed obliquely backwards (Figure 5 B, D). This change in direction had a great influence on the structure of the posterior part of the skull as a whole. As documented by embryological evidence, the gill-slits (*gs*) migrated backwards and the most anterior nephridia were pushed backwards and were partly reduced (Kryzanovsky, 1927, p. 323). Moreover, those myotomes which were originally situated close behind the gill-arches became displaced backwards in their middle parts together with their spinal nerves (cf. Goodrich, 1930, Figs. 143, 240, 241; Jarvik, 1963, Fig. 20 C-E), which fused with the nerves of the pectoral fin, forming the cervico-brachial plexus (*plex*, Figures 1, 7, 9). The formation of this plexus in tetrapods is thus probably a consequence of two different processes: the change in direction of the branchial arches, and the shortening of the fin-base from behind (see p. 160). *The fact that the spinal nerves converge towards the base of the fin is thus not due to a differential growth, i.e. the body growing faster in length than the base of the fins, as assumed by Mollier, Goodrich (1930, pp. 114-118), Eaton and others (cf. Francois, 1962, p. 120). If the latter assumption were true the convergence of the nerves would increase with the growth of the fish, but, as is evident from Figures 1, 9 A-D, this is not so.*

However, of greater importance in this connection is that the change in direction of the gill-arches has also strongly affected the anterior part of the ventro-lateral fin-fold (*vl.cr.*, Figure 5 A, C), which has become pushed mesially (Figure 5 B, D) and has undergone other modifications (Figures 7, 8 D, 9). The fact that the anterior part of the ventro-lateral fin-fold (*vl.cra*) in all forms in which it is clearly discernible (arthrodires, acanthodians, sturgeons, dipnoans, osteolepiforms, porolepiforms, etc., see p. 149) bends distinctly mesially in its anterior (clavicular) part is thus certainly due to the pressure exerted on it by the gill-arches. As demonstrated by Stensiö (1959, pp. 8-13) this anterior, subbranchial portion of the fin-fold in certain arthrodires contains an anterior process (the coracoid process) of the endoskeletal shoulder girdle (cf. *cr.sb.*, *p.sb.*, Figure 7), probably composed chiefly of modified prepectoral radials and showing distinct grooves for metameric cutaneous vessels. In this connection the embryonic development of the muscles in the anterior part of the pectoral

fin of *Squalus* may also be of some interest (Figure 9). As shown by Müller (1911) the anterior one or two muscle-buds (*m.sb*) do not form typical radial muscles. They become highly modified and form, on the ventral side, a large irregular muscle-plate which in the adult gives rise to the adductor muscle (*m.add*, Figure 8 B,C; *m. pterygialis cranialis*, Marinelli and Strenger). It seems likely that these modified radial muscles (*m.sb*) belong to the sub-branchial part of the fin-fold (cf. Marinelli and Strenger, 1959, Figures 151, 155-159) and that these modifications, too, are a result of the change in direction of the visceral arches. Provided that these interpretations are true, it is evident that the ventro-lateral fin-fold was muscularized and contained well developed radial muscles and radials before the gill arches changed direction, that is, already in the pro-gnathostome stage.

#### REFERENCES

- BALFOUR, F.M., 1876, The development of Elasmobranch fishes, *J. Anat. Physiol.*, **11**, 128-172.
- BALFOUR, F.M., 1878, *A Monograph on the Development of Elasmobranch Fishes*, London.
- 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*, 656-671.
- BALINSKY, B.I., 1933, Das Extremitätenseitenfeld; seine Ausdehnung und Beschaffenheit, *Arch. Entw. Mech. Org.*, **130**, 704-746.
- BALINSKY, B.I., 1935, Experimentelle Extremitäteninduktion und die Theorien des phylogenetischen Ursprungs der paarigen Extremitäten der Wirbeltiere, *Anat. Anz.*, **80**, 136-142.
- BALINSKY, B. I., 1937, Über die zeitlichen Verhältnisse bei der Extremitäteninduktion, *Arch. Entw. Mech.*, **136**, 250-285.
- BALINSKY, B.I., 1963, *An Introduction to Embryology*, Philadelphia.
- DAVIS, J.W., 1894, On the fossil fish-remains of the Coal Measures of the British Islands, Part II, Acanthodidae, *Trans. Roy. Dubl. Soc., N.S.*, **5**, 249-258.
- DEVILLERS, C., 1954, Origine et évolution des nageoires et des membres, in *Traité de Zool.*, ed. P. Grassé, Paris, **12**, 710-790.
- DOHRN, A., 1884, Studien zur Urgeschichte des Wirbelthierkörpers. Part VI. Die paarigen und unpaaren Flossen der Selachier, *Mitt. Zool. Stat. Neapel*, **5**, 161-195.
- EKMAN, S., 1941, Ein laterales Flossensaumrudiment bei Haiembryonen, *Nova Acta Reg. Soc. Sci. Uppsala*, Ser. IV, **12**, 1-42.
- FRANCOIS, Y., 1962, La nageoire dorsale des Actinoptérygiens, *Problème actuels de Paléontologie (Evolution des Vertébrés)*. Coll. Int. C.N.R.S., Paris. 117-121.
- FRITSCH, A., 1895. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*, Vol III, Prag, 1-132.
- GEGENBAUR, C., 1865, *Untersuchungen zur vergleichenden Anatomie der Wirbelthiere*, Heft 2. Leipzig, 1-176.
- GEGENBAUR, C., 1870, Über das Skelett der Gliedmaassen der Wirbelthiere im Allgemeinen und der Hintergliedmaassen der Selachier insbesondere. *Jen. Z. Naturw.*, **5**, 397-447.
- GEGENBAUR, C., 1872, Über das Archipterygium, *Jen. Z. Naturw.*, **7**, 131-141.
- GEGENBAUR, C., 1876, Zur Morphologie der Gliedmaassen der Wirbelthiere, *Morph. Jahrb.*, **2**, 396-420.

- GOODRICH, E.S., 1930, *Studies on the structure and development of vertebrates*, McMillan Co., London.
- GRIFFITHS, I., 1959, The embryonic origin of the intrinsic limb musculature in Amphibia, Salientia, *Experientia, Basel.*, **15**, 150-155.
- GROSS, W., 1954, Zur Phylogenie des Schultergürtels, *Paläont. Z.*, **28**, 20-40.
- HOLMGREN, N., 1952, An embryological analysis of the mammalian carpus and its bearing upon the question of the origin of the tetrapod limb, *Acta Zool.*, **33**, 1-115.
- HOWELL, A. BRAZIER, 1933, Homology of the paired fins in fishes, *J. Morph.*, **54**, 451-457.
- JARVIK, E., 1948, On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland, *K. Vet. Akad. Handl.*, Stockholm, ser. 3, **25**, 1-301.
- JARVIK, E., 1954, On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes, *ibid*, ser. 4, **5**, 1-104.
- JARVIK, E., 1959, Dermal fin-rays and Holmgren's principle of delamination, *ibid*, ser. 4, **6**, 1-51.
- JARVIK, E., 1960, *Theories de l'évolution des Vertébrés reconsidérées à la lumière des récentes découvertes sur les Vertébrés inférieurs*, Masson, Paris.
- JARVIK, E., 1963, The composition of the intermandibular division of the head in fish and tetrapods and the diphyletic origin of the tetrapod tongue, *K. Vet. Akad. Hndl.*, Stockholm, Ser. 4, **9**, 1-74.
- JARVIK, E., 1964, Specializations in early vertebrates, *Ann. Soc. Roy. Zool. Belgique*, **94**, 11-95.
- JARVIK, E., 1965, Die Raspelzunge der Cyclostomen und die pentadactyle Extremität der Tetrapoden als Beweise für monophyletische Herkunft, *Zool. Anz.*, **175**.
- KRYZANOVSKY, S., 1927, Die Entwicklung der paarigen Flossen bei *Acipenser*, *Amia* und *Lepidosteus*, *Acta Zool.*, **8**, 277-352.
- LE DANOIS, Y., 1961, Remarques sur les poissons orbiculates du sous-ordre des Ostracioniformes, *Mèm. Mus. Nat. Hist. Nat. Paris, Ser. A, Zool.*, **11**, 207-338.
- MARINELLI, W. and STRENGER, A., 1959, *Vergleichende Anatomie und Morphologie der Wirbeltiere*, Lief. III, Wien, 173-308.
- MAYER, P., 1885, Die unpaaren Flossen der Selachier, *Mitt. Zool. Stat. Neapel*, **6**, 217-285.
- MILAIRE, J., 1962, Histochemical aspects of limb morphogenesis in vertebrates, in: *Advances in Morphogenesis*, Ed. Abercrombie & Brachet. New York, Vol. II, 183-239.
- MOY-THOMAS, J.A., 1936, The evolution of the pectoral fins of fishes and the tetrapod fore-limb, *School Sci. Rev., London*, No. 68, 592-599.
- MÜLLER, E., 1909, Die Brustflosse der Selachier, *Anat. Hefte*, **39**, 468-601.
- MÜLLER, E., 1911, Untersuchungen über die Muskeln und Nerven der Brustflosse und der Körperwand bei *Acanthias vulgaris*, *Anat. Hefte.*, **43**, 1-147.
- NURSALL, J.R., 1962, Swimming and the origin of paired appendages, *Amer. Zool.*, **2**, 127-141.
- RITCHIE, A., 1964, New light on the morphology of the Norwegian Anaspida, Oslo, *Norske Vidensk.-Akad., Mat.-Naturv., Kl.*, N.S., No. 14, 1-35.
- SEWERTZOFF, A.N., 1926 a., Die Morphologie der Brustflossen der Fische, *Jen. Z. Naturw.*, N.F., **55**, 343-392.
- SEWERTZOFF, A.N., 1926 b, Development of the pelvic fins of *Acipenser ruthenus*. New data for the theory of the paired fins of fishes, *J. Morph. Physiol.*, **41**, 547-579.
- SEWERTZOFF, A.N., 1926 c, The development of the scales of *Acipenser*, *J. Morph. Physiol.*, **42**, 523-560.
- SEWERTZOFF, A.N., 1934, Evolution der Bauchflossen der Fische, *Zool. Jahrb. Abt. Anat.*, **58** 415-500.
- STEINER, H., 1935, Beiträge zur Gliedmassentheorie: Die Entwicklung des Chiropterygium aus dem Ichthyopterygium, *Rev. Suisse Zool.*, **42**, 715-729.

- STENSIÖ, E., 1959, On the pectoral fin and shoulder girdle of the Arthroires, Stockholm, *K. Vet. Akad. Handl.*, Ser. 4, 8, 1-229.
- STENSIÖ, E., 1961, Permian vertebrates in *Geology of the Arctic*, Ed. G. O. Raasch, Toronto, Vol. I, 231-247.
- THACHER, J.K., 1877, Median and paired fins; a contribution to the history of vertebrate limbs, *Trans. Connecticut Acad. Arts Sci.*, 3, 281-310.
- WESTOLL, T.S., 1943, The origin of the primitive tetrapod limb, *Proc. Roy. Soc. London*, 131, 373-393.
- WETTERDAL, P., 1920, Beiträge zur Morphologie des Gefäßsystems, die Entwicklung der Gefäße in der Brustflosse bei *Squalus acanthias*, etc., *Anat. Hefte*, 59, 1-134.
- WHITE, E.G., 1937, Interrelationships of the elasmobranchs with a key to the order Galea, *Bull. Amer. Mus. Nat. Hist.*, New York, 74, 25-138.
- ZWILLING, E., 1961, Limb morphogenesis, in *Advances in morphogenesis*, Ed. Abercrombie & Brachet, New York, Vol. I, 301-330.