VERTEBRAL VARIATION IN TELEOSTEAN FISHES

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(Plates I–XVI; Text-figs. 1–18)

CONTENTS

INTRODUCTION

Since the publication of Heincke's classic treatise on the herring the counting of vertebrae has become a standard operation in the biometric analysis of samples of teleostean fishes taken at random from local populations. But while such routine counting has undoubtedly added greatly to our knowledge of the incidence and magnitude of vertebral variation in a number of economically important species, it has occasioned no little confliction of opinion as to the significance of this variation. Difficulties arising out of my own work on the herring at Plymouth have led me to make a general study of the teleostean backbone in as many species as possible, in an endeavour to learn more of the nature, extent and cause of vertebral variation. After examining over one hundred species, mostly from local waters, I have come to the conclusion that the subject presents a great and varied field of research which is at present but little explored. It would be idle to suggest, therefore, that the present paper should be considered as anything more than an introductory survey of the many problems awaiting detailed investigation. Even so, it may serve to indicate the scope and present position of the Plymouth studies, and prepare the way for fuller work in the future, both at Plymouth and elsewhere.

I have received the greatest assistance from Mr L. S. Wisdom, Laboratory Attendant at the Plymouth Laboratory, whose skill in preparing skeletons for study, and keen interest in all matters relating to the research, I most gratefully acknowledge. I also express thanks to those gentlemen who have from time to time supplied me with needed specimens (see acknowledgements given below). By the courtesy of Dr C. T. Regan, F.R.S., Director of the British Museum (Natural History), I have had access on several occasions to the national collection of fish skeletons at South Kensington, always with the kindly assistance of Mr J. R. Norman, Assistant Keeper in the Department of Zoology.

MATERIAL AND METHODS

As already indicated, most of the fishes examined were obtained locally, either by the research vessels of the Association, or by Plymouth fishing craft landing their catches at the market. Certain species, however, which could not be obtained in this manner, were secured from outside sources. Dr R. S. Clark, Scientific Superintendent of the Fisheries Laboratory, Aberdeen, kindly arranged for material to be sent me from the Aberdeen market; Mr Morley Neale of Messrs Neale and West, Trawler Owners, Cardiff, supplied me with several boxes of fish landed by steam trawlers at Cardiff; the late Mr Howard Dunn of Mevagissey also sent several fishes of interest. Messrs Churchill, Fishmongers, Plymouth, were most helpful in supplying at small cost the "frames" of fishes after they had been filleted. In this way a good number of skeletons of the more expensive kinds of food fishes were secured at no great cost.

As a general rule skeletons were prepared for examination by cooking the fresh fish in water just long enough to loosen the soft tissues from the bones and then teasing and brushing away the flesh, nerves, blood vessels, etc. After some experience of the right length of time for the cooking, no great difficulty was found in obtaining well-cleaned and unbroken skeletons, highly satisfactory for detailed study. One definite advantage of this method of preparation was that the freshly prepared skeleton was still flexible, so that observations could be made regarding the degree of relative movement possessed by the different parts of the vertebral column. When dry, the skeleton could be freely handled and examined in detail. On the other hand, where it was required to give close attention to associated structures such as ribs and fin radials, which are normally attached only by soft tissues, the method was not so satisfactory, and the more lengthy process of dissection and alizarin staining had to be resorted to.

NOMENCLATURE

In the naming and classification of species the *List of British Vertebrates* (Norman, 1935) published by the British Museum (Natural History), has been used, although in some instances, notably species of the Heterosomata, the more familiar synonyms given by Norman have been preferred to the less familiar names which he has adopted.

So far as the naming of skeletal structures is concerned, every endeavour has been made to avoid new terms. No confusion is likely to arise out of the use of such terms as centrum, neural arch, neural spine, haemal arch and haemal spine, and pre- and post-zygapophysis, since these are familiar to all zoologists. It is perhaps desirable to mention that the term *parapophyses* has been applied in a restricted sense to the transverse processes of the pre-caudal (abdominal) vertebrae only. The denotation of the terms epural, hypural, radial and last vertebral segment, in describing the caudal elements of the skeleton is as defined by Whitehouse (1910, p. 592). Mention may also be made of the frequent use of the term *autogenous* as a convenient way of referring to neural and haemal arches which are closely applied to, but definitely not fused with, the vertebral centrum. In freshly prepared skeletons such autogenous processes are easily dissected away from the centra to which they belong.

GENERAL CONSIDERATIONS

Bateson has reminded us in his *Materials for the Study of Variation* that Structural Heterogeneity, Repetition of Parts, Symmetry and Pattern, come near to being universal characters of the bodies of living things. Certainly these are outstanding characters of the vertebral column in the teleostean fish. In its prime construction the column is a jointed rod composed of bilaterally symmetrical segments articulated end to end; but along this axis of symmetry, heterogeneity is expressed by continuous and regular change in form from segment to segment throughout. Orderly, formal change is seen not only in the whole segments but in the homologous parts of the segments, each of which conforms to a distinct "pattern-gradation". All these minor pattern-gradations compound into the major pattern of the vertebral column as a whole.

Structural heterogeneity is clearly related to differentiation of function. In a very real sense, the backbone of a fish is a piece of machinery, so constructed that, as a whole or in its specialized parts, it is capable of performing a variety of functions. Thus, at its anterior end it is designed to make connexion between the head and the trunk and to act as a functional neck in securing independent movement of the head. At its posterior end the backbone is modified to act as the basal support and framework of the caudal fin. Dorsally and ventrally along its length, the backbone gives support to the median fins, while from end to end it provides attachment for the muscles and housing for the central nervous system. In the abdominal region it gives suspension and protection to the viscera, and in the caudal region it conveys the main blood vessels within its haemal arches. Moreover, in the capacity of a flexible rod, the backbone is a vital part of the propelling and turning mechanism by which the fish is enabled to swim and manoeuvre.

The most elementary specification of a backbone which can be given is the total number of segments into which it is divided. This *Number of Vertebrae* (n) is nothing more than an integer, arrived at by counting each segment as of equal and unit value, and has the obvious limitation that it takes no regard for differences in form and function between successive segments. Consequently, it will not distinguish between backbones which, although they agree in (n), are dissimilar in vertebral characteristics other than (n). Alternatively, it will separate backbones which differ in (n), notwithstanding obvious similarities in form-pattern, whether minor or major.

An important advance is made when (n) is expressed as the sum of two or more smaller integers (a), (b), (c), etc., in accordance with the division of the backbone into component parts which are manifestly different in structure. It is now possible to distinguish between, say, $(n)=(a+b+c)$ and $(n)=(a'+b'+c')$. It is also possible to recognize a measure of similarity between, say, $(n)=(a+b+c)$ and $(n')=(a'+b+c)$.

Ultimately it becomes necessary to recognize that the backbone is a series of non-interchangeable segments, each of which has its own exclusive properties of form, function and ordinal position. That is to say, in the last analysis, (n) should be written as the summation of the series (1st + 2nd + 3rd + ... + nth).

The fuller one is able to make the specification of a backbone the more clear does it become that every backbone is an organ of a particular individual belonging to a particular species. While it is constructed to perform all the essential functions of a backbone as such—and therefore has this much in common with other backbones—it affords evidence of its own identity in every segment throughout its length, as well as in its entirety.

In the pages which follow, observations on backbones of various species are considered in their bearing upon the different matters set out above.

THE FORM OF THE VERTEBRAL COLUMN IN RELATION TO FUNCTION

Perhaps the most obvious character of a fish's backbone is that the form of the vertebral elements changes along the length of the column. This change of form is associated with a change in function. Yet, at the same time, all the vertebrae of the series have something of form in common, since they have common duties to perform. The study of the relationship between form and function is therefore an integral part of an enquiry into vertebral variation, and in this section a review is given of the different functions of the backbone and the associated specializations in the form of the vertebrae concerned.

As a Functional Neck

At its anterior end the backbone is modified to perform the functions which in the higher vertebrates are undertaken by the atlas and axis vertebrae, viz. to form attachment with the skull and to provide a central point about which the head may swing. There is much variation from species to species in the manner and degree in which these two duties are accomplished. The situation in species of the genus *Gadus* is, possibly, a good example with which to commence. Here we find that the first four vertebrae constitute a distinct *post-cranial* section of the vertebral column (Plate II, figs. 1 and 2). Judging by the structure of these vertebrae, the 1st might well be regarded as the equivalent of the atlas, in that it is very securely attached to the skull. For the equivalent of the axis vertebra (as the centre of "head-swing"), however, it seems necessary to pass to the 4th vertebra, regarding the 2nd and 3rd vertebrae as constituting a flexible union between atlas and axis. This means that, with the fish in its normal upright position and the 4th vertebra held stationary, turning of the head to the right or left is made possible by the "flex" union between the posterior end of the 1st vertebra and the anterior end of the 4th. The head is similarly enabled to turn upwards. Oddly enough, however, trials with freshly prepared skeletons, while these were still wet and flexible, showed that the head cannot be bent downwards without rupturing the inter-vertebral ligament.

This suggestion that the four post-cranial vertebrae in the gadoid fish act as a functional "neck" is of interest in connexion with Gray's studies of the swimming and turning of fishes by waves of curvature passing alternately down each side of the body (Gray, 1933*a*, *b*). The matter is considered in greater detail in p. 14.

In the sand-eel (*Ammodytes*) the function of atlas and axis vertebrae, instead of being shared among a number of post-cranial vertebrae as in *Gadus*, appears to be performed by one vertebra only, the 1st. This has a smooth domed-shaped anterior face which fits into a socket at the posterior end of the skull. Conceivably this arrangement is not unconnected with the capacity of the sand-eel to burrow into the subsoil of the sea, in permitting the necessary independence of movement between head and body required for this. A somewhat similar arrangement is found in the conger and the freshwater eel, as well as in the anchovy (*Engraulis*). It would therefore be of interest to determine whether a similar association with a burrowing habit can be demonstrated in these three fishes.

The form of the modified post-cranial vertebrae naturally varies from species to species and will be considered in later descriptions under the different orders, genera and species.

As the Operative Base of the Caudal Fin

While the anterior end of the vertebral column is thus modified to carry the head, its opposite end is specialized to support and operate the caudal fin. Here again a number of vertebral segments are involved in a dual function, for some of these are specially constructed to form the actual basal framework of the fin, whereas others are more concerned in the operation of the fin than in its support.

Whitehouse (1910) has given a systematic account of variation in the form of the complex and last vertebral segment in a wide range of species (see also Barrington, 1937). In the present work, therefore, attention has been diverted to the characters of the vertebrae which immediately precede this last or urostylar segment.

In a number of fishes a well-differentiated group of such "tail" segments can be recognized. In the bass (*Morone labrax*), for example, the 23rd and 24th segments (i.e. the antepenultimate and penultimate segments) have a characteristic structure (Text-fig. 1). Ventrally, the haemal spines of both vertebrae are *autogenous**. Dorsally, the neural spine of the 23rd vertebra is elongate and stronger than those immediately preceding, whereas on the 24th vertebra it is reduced to a low-lying crest to the neural arch. These two vertebrae, together with the complex urostylar (25th) segment, thus comprise a well-marked "tail" group of vertebrae, modified for the express purpose of carrying the elements of the caudal fin.

It is to be noted that this particular form of tail base is seen in a wide range of species and, as will be shown later, is a character of considerable taxonomic value. Within the great order Percomorphi, for example, it is of common occurrence, especially in the division Perciformes containing the most generalized forms of the suborder Percoidea (see p. 44). Outside the Perciformes it is seen in full in the Scombroidea (genus *Scomber*) but in a modified form in the Blennioidea and Mugiloidea. Within the order Scleroparei it is again seen in full in the more generalized forms *Scorpaena*, *Sebastes* and *Trigla*. More

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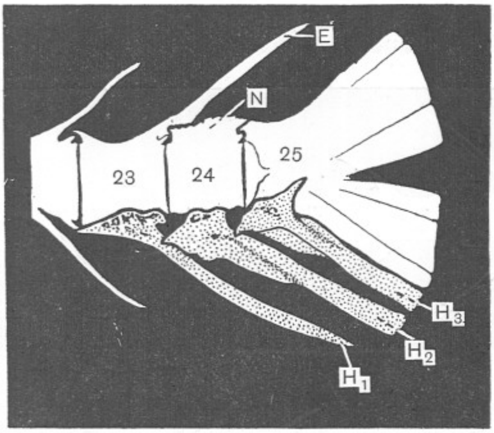
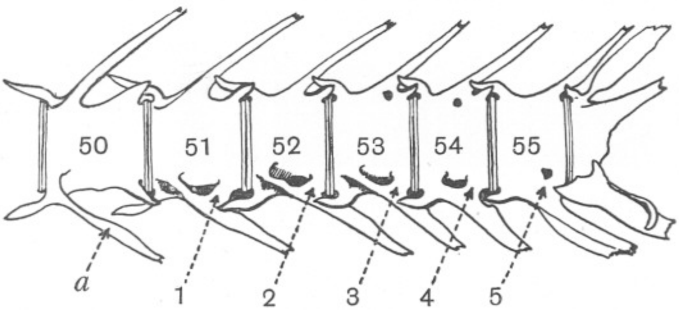
* The term *autogenous* has been used by Regan. In the present work it is intended to imply that the hypurals are closely applied to, but definitely not fused with, the centrum. In freshly prepared skeletons these autogenous hypurals are easily dissected out of the pockets of the centrum in which they rest. When seen *in situ*, the line of demarcation between hypural and centrum is plainly visible.

surprising, perhaps, is that it is typically present in certain species of the Anacanthini, viz. *Merluccius merluccius* (the hake), *Urophycis blennoides* (greater fork-beard), and *Raniceps raninus* (lesser fork-beard). The possible significance of these occurrences in the study of phylogeny will be realized.

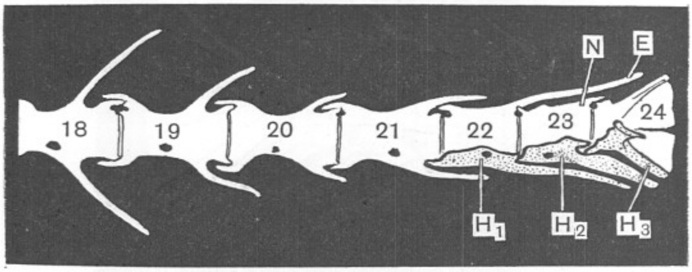


Text-fig. 1. Tail vertebrae of bass (*Morone labrax*). Autogenous hypurals are stippled: *E*, elongated epural of antepenultimate (23rd) vertebra; *N*, crested neural arch of penultimate (24th) vertebra; H_1, hypural of antepenultimate vertebra; H_2, hypural of penultimate vertebra; H_3, anterior, hook-bearing, hypural of terminal vertebra.

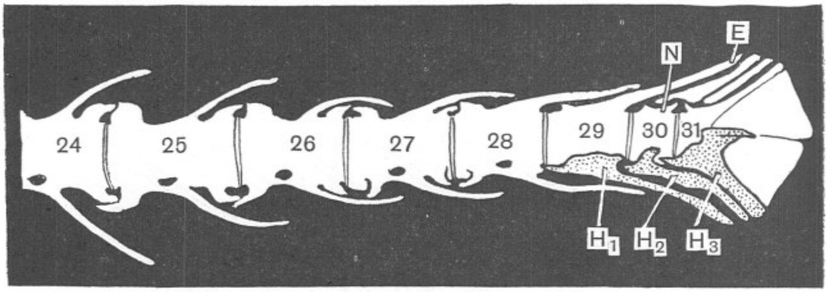


Text-fig. 2. Tail vertebrae of herring (*Clupea harengus*). From Ford (1933, fig. 2 on p. 213). The haemal spines of vertebrae 51–55 are cross-tied to the centrum as indicated by the nos. 1, 2, 3, 4 and 5.

Passing from the vertebrae which form the skeleton of the actual caudal peduncle to those situated immediately in front of them, we sometimes find modification associated with the operation of the caudal fin. Good examples are provided by the herring, scad (*Caranx trachurus*) and mackerel. Previous work has shown (Ford, 1933) that there is in the herring (Text-fig. 2) a well-defined group of from four to eight vertebrae immediately preceding the urostylar segment, and that individual fish with a larger total number of vertebrae in the backbone tend to have a disproportionately larger number of these "tail" vertebrae. In the scad (*Caranx*) the total number of vertebrae in the backbone is normally twenty-four, of which vertebrae 20–24 inclusive form the "tail" group of five segments (Text-fig. 3). In the mackerel (*Scomber scombrus*) the total number of vertebrae in the backbone is normally thirty-one, of which the last six (vertebrae 26–31) comprise the "tail" group (Text-fig. 4). In both the scad and mackerel it cannot be doubted that the specialization in the "tail" section must be considered in association with the organization of the body for active and sustained swimming, in which the tail-end of the body is of the greatest importance. The acme in this type of specialization must surely be the extraordinarily beautiful tail-end of the bonito (*Katsuwonus*), illustrated in Plate IX, fig. 3.



Text-fig. 3. Tail vertebrae of scad (*Caranx trachurus*), comprising vertebrae 20–24 inclusive. For explanation of lettering see Text-fig. 1.



Text-fig. 4. Tail vertebrae of mackerel (*Scomber scombrus*), comprising vertebrae 26–31 inclusive. Lettering is the same as in Text-fig. 1.

As Support for the Median Fins

Seeing that there is much variation in the number, position and form of the dorsal and anal fins among teleostean fishes, we might have expected that the vertebrae from which the fins receive blood vessels and nerves, as well as the neural and haemal spines which support the fin-radials, would also vary accordingly. Yet in numerous instances this is not so, and the backbone remains comparatively undisturbed by fin changes. Thus, in the family Gadidae, although the species present great variety in the number and position of the median fins, the backbone is of the same general form throughout the family, and it is doubtful whether by the examination of the backbone alone one could say very much concerning either the number or position of these fins.

In the percoid fishes, such as *Serranus*, *Mullus*, *Caranx*, *Mugil* and *Labrus*, it is at least possible to see where, in the vertebral series, the first radial of the dorsal fin and the corresponding member of the anal are inserted. In *Caranx*, for example, there is a widening of the interval between the 2nd and 3rd neural spines to make room for the 1st dorsal radial, and a similar widening between the 11th and 12th haemal spines to receive the 1st anal radial (Plate IX, figs. 2 and 4).

In the John Dory (*Zeus faber*) the peculiar "set" of the neural spines of vertebrae 2–8 (Plate XVI, fig. 2), whereby the distal ends of the 3rd and 4th, 5th and 6th, and 7th and 8th, come together, provides accommodation for the dorsal radials. In the boar-fish (*Capros aper*) the 1st dorsal radial, instead of being seated between the 2nd and 3rd neural spines as in the percoid fishes, stands like a peg in a special slot walled in anteriorly by the skull and laterally by the right and left elements of the 1st neural spine. This arrangement is evidently associated with the ingenious mechanism by which the fish is enabled to lock the spines of the dorsal fin in an erected position. Similarly, in the trigger-fish (*Balistes capriscus*) the anterior neural spines are appreciably modified to support the bony framework of the trigger mechanism (Plate XVI, fig. 1).

The dragonet (*Callionymus*) shows modification of the anterior neural spines which, in this genus, must be considered as connected with the marked dorso-ventral compression of the body. The backbone itself does not share in this compression, being, if anything, flattened from side to side rather than dorso-ventrally. To afford accommodation for the anterior dorsal radials, the right and left elements of the neural spines of each vertebra are opened out distally to form forked ends in which the radials stand.

The sucking fish (*Remora remora*) is remarkable for the oval, adhesive disk placed on the broad, flat, upper surface of the head. In order to make room for the skeleton of this disk the neural spines of the first three vertebrae are depressed backwards and downwards to form a low-lying crest to the neural arches.

In its Relation to the Form and Functioning of the Viscera

There is commonly a high degree of specialization in the vertebrae in the abdominal region of the backbone. The pitting of the underside of the centra to house the kidneys, the arrangement of the parapophyses to form a canopy over the air-bladder, the provision of seating for the ribs which encircle the gut; these and other modifications of the abdominal vertebrae to suit the requirements of the viscera are easily observable. Each species necessarily presents its own peculiarities in the abdominal vertebrae.

The proportionate number of vertebrae concerned in these duties is a variate which will be considered later (p. 25), but it may here be noted that the position of the anus in the whole fish is by no means a safe indication of this. In the flat-fishes, for example, the great forward sweep of the bony abdominal bar brings the anus to occupy a position far forward of the last abdominal vertebra. It will also be recalled that the anus in some fishes changes its relative position during the early life of the fish by a process of differential growth of the body (Ford, 1930, 1931*a*, *b*, concerning the development of the herring, pilchard, sprat and eel). To a greater or less extent the axial skeleton is involved in this disproportionate growth of the body and its organs, more particularly by a change in the form, size and slope of the vertebral processes, with a corresponding alteration of the position of the anus with respect to the vertebrae.

As the Housing for the Central Nervous System

Preceding paragraphs have dealt with the functions performed by localized groups of vertebrae, whereas we must now turn to functions in which each and every vertebra in the backbone takes a more or less equal share. The first of these is the provision of a housing for the spinal cord, namely, the neural canal formed within the neural arches of successive vertebrae. There is much variation from species to species in the form of the neural arches, neurapophyses and neural spines which together form the sides and roofing of the neural canal. Sometimes there is much elaboration in form in one or more of the components, and it will usually be found that each species has recognizably distinct features of its own. Many instances might be given to show how identity can be at once established by a mere glance at, say, the neural spines (cf. *Ammodytes lanceolatus* with *A. tobianus*) or the neurapophyses at their base (cf. *Labrus mixtus* with *L. bergylta*). In the clupeoid fishes and the eels there is a special modification of the neural arches and their processes to form an independent housing for the longitudinal ligament which runs along the length of the column above the spinal cord (see p. 52). Species in general present interesting studies in gradation of pattern in the neural arches and processes from vertebra to vertebra.

But just as each vertebra in a backbone takes its share in housing the spinal cord, so in each provision has to be made for the free passage of the spinal nerves from the spinal cord within the neural canal to the body outside. Very generally the spinal nerves leave the neural canal via foramina in the walls of the neural arches. In the gadoids, however, it is much the more usual for them to leave, not by foramina, but in open grooves between the bases of the neural arches and the post-zygapophyses (Plate III, fig. 2). This applies to all the gadoid genera examined with the exception of *Onos* (the rocklings), and even in the five-bearded rockling, *O. mustelus*, and four-bearded *O. cimbrius*, the spinal nerves leave through grooves instead of foramina. In the three-bearded rocklings, of which there appear to be two species at Plymouth instead of one as formerly supposed, some of the nerves leave via grooves but others through foramina. This is especially interesting because it is a difference between the two forms of three-bearded rocklings at Plymouth in this very character, which (among other evidence) establishes their separate identity. Hitherto, all three-bearded rocklings at Plymouth, as elsewhere in Great Britain, have been referred to the single species *O. tricirratus* (Bloch), but it is now necessary to refer them to two species, the names of which cannot at present be decided. They will be referred to here as form A and form B. In form A the spinal nerves of the 4th to the 12th vertebrae (with an occasional variate) emerge through foramina in the walls of the neural canal, whereas those of the 13th and subsequent vertebrae pass out between the neural spine and posterior zygapophyses (Plate V, fig. 1). In form B foramina are present not only in the anterior vertebrae as in form A, but in the posterior vertebrae as well. The foramina are formed as it were by the fusion of the post-zygapophyses with the base of the neural spines. This difference between these two forms of three-bearded rockling is persistent and well marked, providing one of the best illustrations from present material of the usefulness of vertebral characters for purposes of identification. It is quite another matter to suggest a satisfactory explanation of this difference in terms of function, and I acknowledge my present inability to do so.

As the Housing for Blood Vessels

The housing for longitudinal blood vessels and tracts is a second function of vertebrae in general. It need hardly be said, however, that the haemal arch and its processes not only change greatly in form from vertebra to vertebra along the length of the same backbone, but vary very much from fish to fish. In the caudal region of the body a closed haemal canal is formed by the series of closed haemal arches of the caudal vertebrae. In the gadoid fishes the haemal spines of the anterior caudal vertebrae come together to form much larger loops than those of the posterior ones, whereby a haemal "funnel" is produced into which the hinder end of the air-bladder projects (Plate V, figs 2 and 3). The size and shape of the haemal funnel varies a good deal from species to species and is useful as a clue to identity (see p. 40). In the pre-caudal region of the body there is still more marked divergence in the condition of the haemal arch. In the gadoids a blood tract can be traced along the under side of the centra throughout the length of the pre-caudal region, often as a grooving of the underface of each centrum along the middle line, but in none of the gadoids do the parapophyses come together to form a closed haemal canal. By contrast, in the flat-fishes (Heterosomata) there is a difference in this respect between *Solea* and *Arnoglossus* on the one hand, and the Pleuronectids on the other. In the former the parapophyses come together to form a haemal canal, whereas in the latter they normally remain open, although there may be an occasional weak bridge across the parapophyses of the last one or two pre-caudal vertebrae (e.g. in the lemon-sole, *Pleuronectes microcephalus*). In clupeoids and salmonids (order, Isospondyli) the haemal arches of the posterior pre-caudal vertebrae are transversely bridged to form a closed haemal canal. In the Apodes there is no such bridging in either *Anguilla* or *Conger*, the blood tract running beneath the centra between widely open parapophyses. In the Percomorphi the condition is very different in different fishes. There is a striking contrast, for example, between that of the mackerel (*Scomber*) and that of the bonito (*Katsuwonus*). In the mackerel the first nine or ten pre-caudal vertebrae are quite smooth along their ventral faces and entirely without parapophyses or other processes which might be regarded as housing for the blood system. On the 10th or 11th vertebra, small parapophyses appear which close together at their distal ends to form the first of the closed haemal arches (Plate IX, fig. 1). In the bonito the abdominal vertebrae and their haemal processes show great elaboration to form a housing for a vascular system which is unique among teleostean fishes, as shown by Kishinouye (1923). The blenniiform fishes also provide a good example of variation in allied genera. In the catfish, *Anarhichas lupus*, the haemal arches of the pre-caudal vertebra are all open; in the species of *Blennius* two or three of the hindermost pre-caudals have parapophyses which are transversely bridged to form a haemal canal; in *Pholis gunnellus* all the vertebrae from the 4th onwards have closed haemal arches to form a continuous haemal canal to the end of the backbone. Species of the percomorph family Sparidae (e.g. *Pagellus*, *Box* and *Cantharus*) show a clearly defined blood tract along the middle line of the underside of the centra of the anterior pre-caudal vertebrae. This tract is walled on either side by latero-ventral "flanges" arising from the centra (Plate VIII, fig. 2). Within the order Scleroparei, the gurnards (*Trigla*) show progressive stages in a special modification of the haemal processes of the posterior pre-caudal vertebrae. Thus, in *T. lyra* the 9th to 12th vertebrae each have the distal parts of the right and left haemal arches united to form a flattened, bony disk, so that the blood channel actually lies between the underside of the centrum and the upper side of the disk (Plate XII, fig. 4). It is conceivable that this special modification is to be associated with the size and functioning of the air-bladder, and it is therefore interesting that the flattened disk is most fully developed in *T. lyra* which lives in deeper offshore waters.

As a Seat of Attachment for the Muscles

There is much variation in the "sculpturing" of the outer surfaces of the vertebral centra. Whereas in some species these surfaces are almost unrelievedly smooth, in others they are very irregular and heavily pitted. In the gadoids, eels, and the grey mullets (*Mugil*) it is possible to distinguish species from species by differences in this respect (cf. figs. 2 and 3 in Plate XI).

Mention of the grey mullets brings to mind the curious hook-like processes which project posteriorly from either side of the neural arch of the 2nd vertebra, immediately behind the parapophyses (Plate XI, fig. 1), and which have not been observed in any other genus of fishes examined at Plymouth. The exact function of these processes is obscure, unless they have to do with the attachment of muscles. In a number of species, including the gar-fish (*Belone*), the conger, and certain of the flat-fishes, lateral apophyses, projecting from the centra on either side in the middle line, also appear to function as skeletal supports for the muscles. They form a series which is quite distinct from either the rib-bearing parapophyses or the haemal processes. Their presence in the caudal region in the conger, but absence in the fresh-water eel, forms a reliable distinction between the two eels (Text-fig. 16 on p. 52). In the flat-fishes it is usual to find them more strongly developed on the "upper" (eyed) side than on the "lower" (blind) side (Plate XIV, fig. 3). In the Pleuronectidae and Bothidae (with the exception of *Arnoglossus*) they are confined to the caudal vertebrae—or, possibly it would be more correct to say that in the pre-caudal vertebrae they become merged into the parapophyses—while in *Arnoglossus* and the Soleidae the series is distinct and continuous throughout the length of the vertebral column (Plate XIII, fig. 3). These lateral apophyses are, therefore, of considerable aid in the recognition of families, genera and even species.

Its Structure in Relation to Swimming Movements

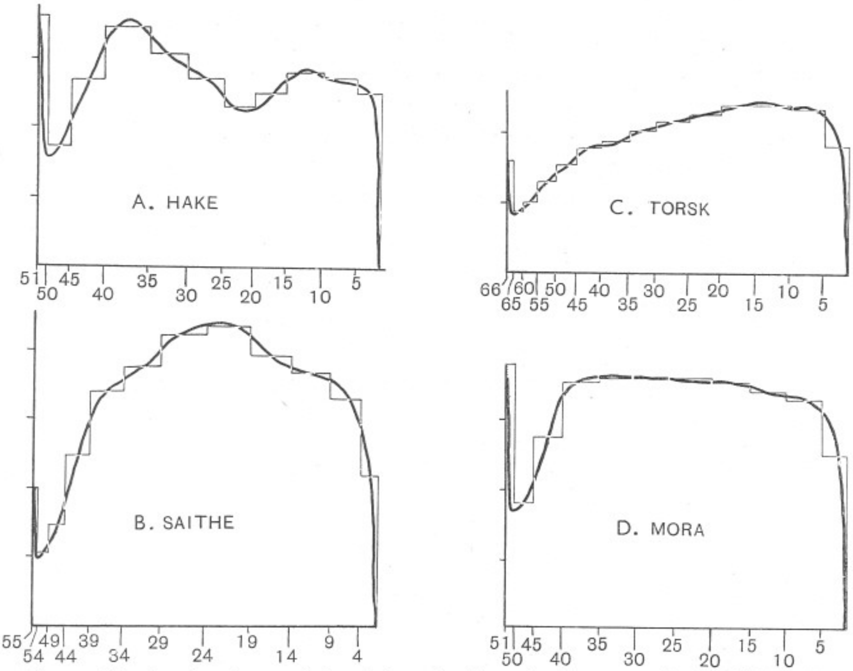
Gray (1933*a*) has demonstrated that although the swimming motions of various types of fish, as observed by the human eye, appear to vary considerably from one species to another, they agree in being the result of waves of curvature passing along the body with increasing amplitude as the hind end of the fish is approached. The only significant differences between the swimming of the eel and that of the mackerel, for example, are the relatively larger amplitude of the waves towards the anterior end of the body and the larger length of wave in the eel. The study of the vertebral column in relation to swimming, therefore, amounts to a study of its flexibility. Now we know that provision for flexure is afforded by the ligamentary articulations between the rigid vertebrae, and we may conclude that the nature and extent of spinal flexure is governed by three factors: viz. (1) the number of articulations, (2) their disposition along the length of the vertebral column, and (3) the amount of flexure procurable at each. It is easily seen that these governing factors may be expressed in terms of the solid vertebral structures instead of the elastic articulations between the latter. Thus, the number of articulations is a function of the number of vertebrae, the disposition of the articulations is expressible in terms of the length of each vertebra, while the amount of flexure procurable at each articulation is largely dependent upon the extent to which successive vertebrae are interlocked by dorsal and ventral processes.

In the present consideration, however, it is hardly possible thus to consider the vertebral column apart from the cranium and caudal fin, since the three are flexibly united. As the fish swims, the head swings alternately right and left of the path along which the fish is moving, acting like a rigid rod of relatively great length swinging from the anterior end of the vertebral column through the medium of a flexible union. Meanwhile, at the opposite end, the caudal fin is operating as a surface which offers high resistance to transverse movement of the body (Gray, 1933*a*, p. 18). Between these two, the vertebral column itself takes up curvature within the limits imposed by its own inherent properties of flexibility and in harmony with the head swing and tail inhibition.

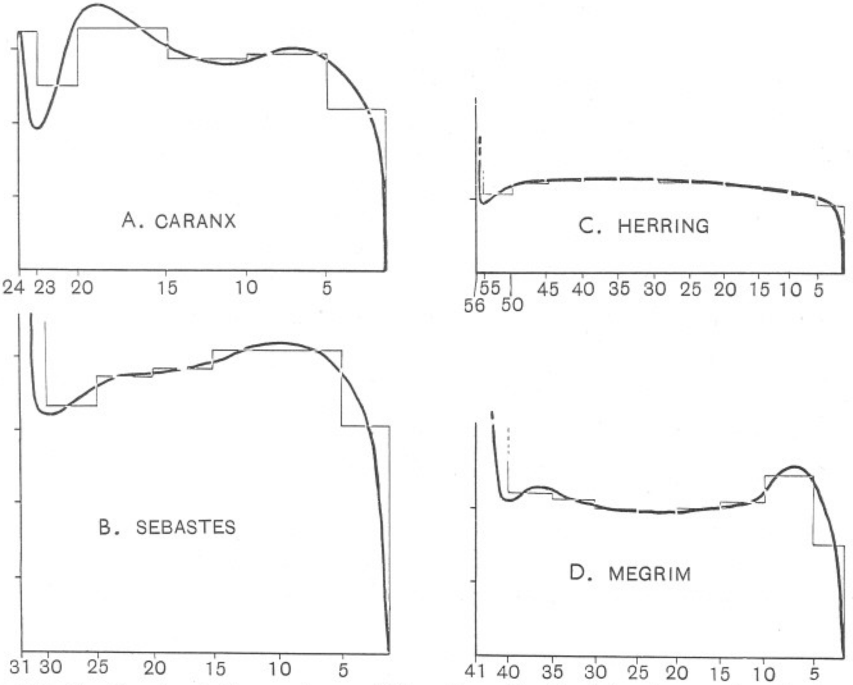
In the third place it has to be remembered that the backbone is embedded in a fleshy body within which it operates in response to waves of muscular contraction. Ultimately, therefore, it becomes necessary to take into account the nature and form of body as a further factor governing the action of the backbone in swimming movements.

During the course of the general survey with which this paper deals it has not been possible to make a detailed study along the lines indicated above. Nevertheless, there are some relevant observations which may be conveniently referred to at this stage. Reference has already been made to vertebral length as one factor governing the nature and extent of spinal curvature, and it may now be pointed out that fishes differ to a marked degree in the manner in which the length of the vertebral column is distributed among the component vertebrae. Not only are the vertebrae of the individual fish unequal in length, but the "gradient" of vertebral length along the column differs from fish to fish. This is demonstrated in the graphs shown in Text-figs. 5 and 6, where differences in the position of the longest vertebrae, and in the relative lengths of corresponding segments of the column are self-evident. It will be observed that in some fishes (e.g. hake, Text-fig. 5A, and *Caranx*, Text-fig. 6A) there is a marked tendency towards bimodality in the graph. This tendency is shown very commonly among flat-fishes of the order Heterosomata.

Some attention has also been given to the structure and action of the union between vertebral column and cranium. On p. 5 of this paper, the four anterior vertebrae in species of *Gadus* were treated as the functional equivalent of the atlas and axis vertebrae of the higher vertebrates in forming the actual attachment between vertebral column and cranium, and making the necessary provision for head-swing. Now this is of direct interest in connexion with Gray's studies of the swimming fish. Gray has shown how each segment of the body moves forward along a sinusoidal path transverse to the axis of forward movement, and from a figure which he gives of superimposed tracings of the left side of a butterfish showing the passage of a complete swimming wave (Gray, 1933*a*, fig. 5A), it is seen that the amplitude of this transverse displacement of the body is least at a point lying a short distance behind the junction of head and body. This suggests that, in the gadoids, the 4th vertebra may mark the position of minimum transverse displacement. The distance



Text-fig. 5. Graphs showing variation in length of vertebral centrum in Gadoid backbones. The base-line is divided according to the length of successive sections of five vertebrae. The values of the ordinates are proportional to the average length of centrum in these sections: A, hake (*Merluccius merluccius*); B, saithe (*Gadus virens*); C, torsk (*Brosme brosme*); D, *Mora mediterranea*.



Text-fig. 6. Graphs similar to those of Text-fig. 5 for the following species: A, *Caranx trachurus*; B, *Sebastes marinus*; C, *Clupea harengus*; D, *Lepidorhombus whiff-iagonis*.

from the tip of the snout to the middle of the 4th vertebra, compared with the total length of the body, might therefore prove of some significance in determining the particular form of the swimming wave exhibited by a gadoid fish.

Turning to the tail-end of the body it is of interest to follow up Gray's illustration of the way in which the caudal fin works (Gray, 1933*a*, p. 18). He compares the effect of the fin to that produced by attaching a flat plate to the distal end of a steel wire and oscillating the proximal end of the wire through a small angle. Without a flat plate each part of the wire moves in practically the same phase as any other part, but when the plate is present the distal end of the wire lags behind the proximal end. With the plate, a series of movements is set up which is strikingly similar to the normal movements of a fish's body; without the attached plate the movements are comparable to those of a fish from which the tail fin has been removed. Pursuing Gray's analogy, the terminal portion of the vertebral column, in forming the base of the caudal fin, may be likened to the beating out of the distal end of the steel wire to form a firm place of attachment for the plate. As such, it is neither entirely wire nor entirely plate, but a combination of the two. That is to say, the "tail" vertebrae will have something in common with the "body" vertebrae in transmitting swimming waves of curvature, but will also be concerned in the working of the caudal fin to produce lag. Variation from species to species in the "tail" group of vertebrae, to which reference has already been made in p. 6, should therefore provide much useful material for study.

The Mechanics of the Backbone in Relation to Function

This survey of the backbone as a piece of machinery would not be complete without some consideration of the backbone from the point of view of the engineer. Although a detailed study of this nature could only be conducted by a fully qualified investigator, no specialized knowledge is needed to appreciate the richness of the research material available to such an investigator. In the texture of the bone of which the vertebrae are constructed; in the provision against stresses and strains set up at different points; in the arrangement of processes to facilitate co-ordinated action of the vertebrae; in the modification of successive vertebrae for special functions; in the general matter of economy of materials; in these and many other problems, every species presents its own characteristics.

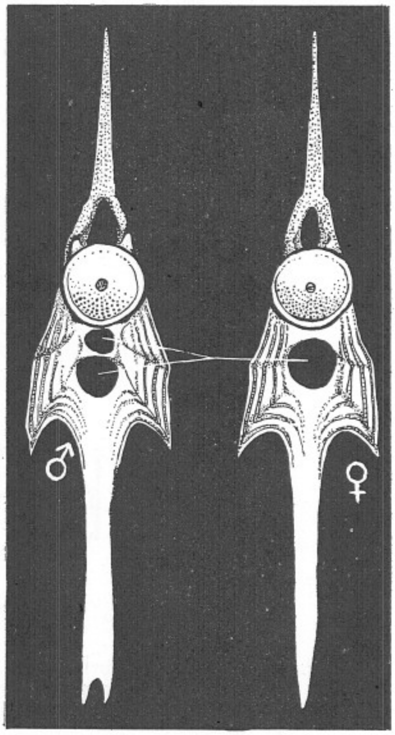
Sexual Dimorphism seen in Vertebral Structures

Although in the present work no very special attention has been given to possible difference between the sexes, the situation in the wrasses is worthy of mention. It is known that the male and female of *Labrus mixtus* differ appreciably in outward appearance. Internally, the backbone is much the same in both, except that there is a marked difference in the relative size of the circular haemal canal of the first caudal vertebra, this being larger in the male than in the female. In *Labrus bergylta* the corresponding canal is normal in the female but appears to be duplicated in the male, at least in the few specimens which it has been possible to examine at Plymouth (Text-fig. 7).

SYMMETRY AND PATTERN IN THE VERTEBRAL COLUMN

Bilateral Symmetry and Asymmetry

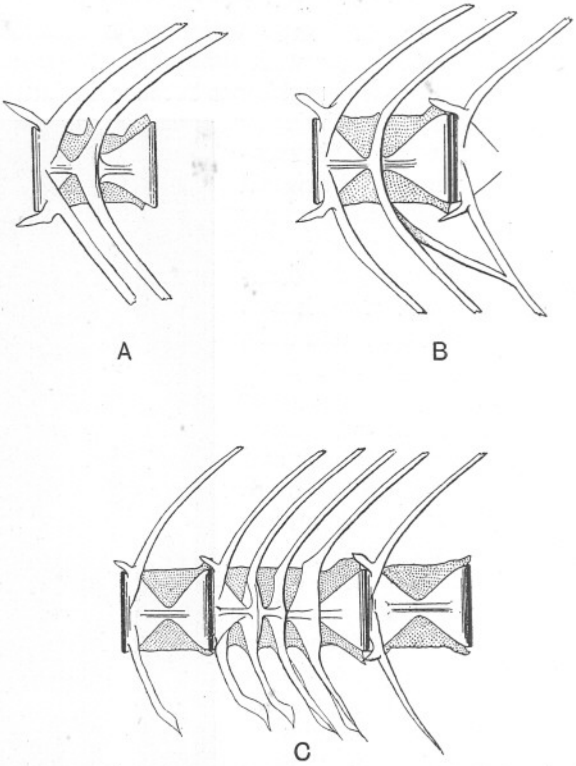
Symmetry and pattern are phenomena which are at once discernible in the teleostean backbone. Dealing first with symmetry, the majority of species exhibit bilateral symmetry in their backbones because the latter are built up of segments which are themselves bilaterally symmetrical. In the flat-fishes (Heterosomata), however, in which the original right and left sides of the body have become functional upper and lower surfaces, this symmetry is more or less disturbed according to species, and the right and left halves of the vertebrae are no longer quite alike (see Cole & Johnstone, 1901, and Kyle, 1926). This is particularly noticeable in the lateral apophyses of sinistral species such as the brill, megrim, scaldback and topknot, which are decidedly more strongly developed on the upper (coloured) side than on the lower (blind) side (Plate XIV, fig. 3). Outside the order Heterosomata, bilateral symmetry is fairly uniformly preserved in the backbone as a whole, but it is apt to break down in individual vertebrae. This occurs most commonly at points along the backbone where there is normally a fairly sharp change in vertebral form. Adopting the nomenclature of Bateson (1894, p. 85), these are cases of *homoeosis*. That is to say, they are cases of one vertebral segment partially assuming the form proper to its neighbour in front or behind. For example, in the typical gadoid backbone there is a sharp change in form between the last of the abdominal vertebrae and the first of the caudals, the former having widely open parapophyses, and the latter a closed haemal arch forming the first element of the "haemal funnel". Not infrequently, however, it will be found that between the typical abdominal vertebrae and the typical anterior caudals there is a transitional form of vertebra which on the one side exhibits



Text-fig. 7. *Labrus bergylta*. Sexual difference in the condition of the haemal arch of the 1st caudal vertebra. In the male there are two canals, but in the female one only.

the characters of an abdominal vertebra, and on the other side the characters of a caudal vertebra.

Anatomical differences between the two sides of one and the same vertebra are very common in the herring and other allied clupeoids. Sometimes a vertebral centrum will show incipient division into two or more parts on the one side only; or there may be duplication of the neural and haemal spines on one side, while the other side is normal. Text-fig. 8 B shows an example of another kind of bilateral irregularity in the haemal arch of the herring. Further attention to this phenomenon will be given at a later stage in this paper (see p. 28).



Text-fig. 8. Abnormal vertebrae in the herring. From Ford & Bull (1926). A, 33rd vertebra of a herring 29 cm. in length; B, 21st vertebra of a herring 22 cm. in length; C, fusion of vertebrae 25–28 inclusive in a herring 28 cm. long; vertebrae 24 and 29 are normal.

Pattern

Turning from symmetry and asymmetry to pattern, the teleostean backbone presents much interesting material for the study of gradational change in the form of homologous parts along the length of the column, and in the composite pattern of certain sections of the backbone and of the backbone as a whole. It is hardly an exaggeration to say that every structural feature of a vertebral segment, even to the smallest zygapophysis, forms one unit of a discrete gradation series, and that the natural compounding of these series gives to the backbone as a whole a pattern which is distinctive of the species to which the backbone belongs. Furthermore, after comparing species with species, it is impossible to escape the impression that phylogenetic relationship is made manifest by agreement both in the characters of the individual gradation series and in their compounded pattern. The suggestion is that all gadoid backbones conform to a gadoid pattern, all clupeoids to a clupeoid pattern, and so on. And each of these patterns will have its own distinctive set of gradation series. An excellent example of this is provided by the backbone of the shad, *Alosa alosa*, described in detail on p. 36.

SEBASTES

A	B	C	D	E	F	G	H	J	K
1	2	3 4 5 6 7	8 9	10 11 12 13 14	15 16 17 18 19 20 21 22 23 24 25	26 27 28	29	30	31
1	2	3 4 5	6	7 8 9 10 11 12	13 14 15 16 17 18 19	20 21 22	23	24	25
A	B	C	D	E	F	G	H	J	K

SCORPAENA

Text-fig. 9. Comparison between the backbones of *Scorpaena dactyloptera* and *Sebastes marinus* (see Pl. XII, figs. 1 and 2). Each backbone has been divided into sections A to K according to the characters enumerated below, and the serial numbers of the vertebrae in the successive sections in the two species are shown in the diagram: A, vertebra 1 which bears autogenous neural spines; B, vertebra 2 in which the neural spine is of the same height as that of vertebra 1 and brought into adjacency with the latter; C, vertebrae without prominent parapophyses; D, vertebrae with well-developed and open parapophyses; E, vertebrae with closed and fenestrated haemal arches; F, anterior caudal vertebrae in which the haemal arches are not normally fenestrated; G, caudal vertebrae with fenestrated haemal arches; H, antepenultimate vertebra with elongate epural and autogenous hypural; J, penultimate vertebra with crested neural arch and autogenous hypural; K, terminal vertebra with anterior, autogenous and hooked, hypural.

It may next be observed that formal pattern in the backbone is not necessarily dependent upon the number of segments of which the backbone is composed. Theoretically, at any rate, any basic pattern, compounded of a given set of gradation series, may be spread over a large total number of segments or a small one. Alternatively, one or more parts of the pattern may be distributed over a larger or smaller number of segments. In both instances, an increase in the number of segments results simply in a corresponding reduction in the amount of structural difference between successive segments. In illustration it is of interest to compare the backbone of *Sebastes marinus* in which there are thirty-one segments with that of *Scorpaena dactyloptera* in which there are only twenty-five. There is an obvious similarity of pattern between the two backbones, the extent of which may be gathered from Text-fig. 9 in which regions along the two columns which are comparable in structure are brought into adjacency. It is not argued from this comparison that

Text-fig. 9 depicts a table of individual homologies between the vertebrae of *Sebastes* and those of *Scorpaena*, but rather that the same basic pattern is present in the two species, despite a difference in the total number of vertebrae over which it is spread, and the manner in which it is spread. In other words, the interest of the comparison centres in the mutual conformity to a single pattern, and not in the ordinal positions of vertebrae which correspond in structure.

Another illustration is provided by the varying form of the caudal peduncle in the gadoid fishes. It is characteristic of the gadoid that a considerable number of vertebrae directly support rays of the caudal fin. In the ling (*Molva molva*), for example, no less than thirteen vertebrae function in this way (Whitehouse, 1910). But the number of vertebrae, their relative length, and also the slope and length of the neural and haemal spines which bear fin-rays, all vary from species to species. Yet there can be no denying that there is a common ground plan on which all the tail bases are constructed (Plate VI).

The application of principles described by D'Arcy Thompson in his *Growth and Form*, chapter XVII, is also very appropriate to the study of pattern in the backbone. It will be recalled that D'Arcy Thompson gives striking instances of the effect of redrawing the outline of a fish on an alternative set of co-ordinates. Thus, when the outline of *Argyropelecus olfersi*, drawn to Cartesian co-ordinates, is transferred to a system of oblique co-ordinates whose axes are inclined at an angle of 70°, the new figure is a close approximation to the form of the allied fish, *Sternoptyx diaphana*. Now, turning to the backbone, it is easy to think of the neural and haemal spines as a series of natural "y" axes, set at intervals along a natural "x" axis following the middle line of the vertebral column, and about which the organs of the body are orientated. Obviously, there are three factors which govern the overall form of a body thus orientated:

(1) The disposition of the neural and haemal spines along the vertebral column (i.e. the distances along the "x" axis at which the "y" axes are erected). This is, of course, dependent upon the number and individual lengths of successive vertebrae.

(2) The slope of the neural and haemal spines (i.e. the angles which the y axes make with the x axis).

(3) The length of the neural and haemal spines (i.e. the values of y as measured from the x axis along the y axes to the distal ends of the spines).

(4) The degree of departure from a straight line of the long axis of the backbone (i.e. the x axis).

A change in any one of these four factors will obviously alter the form both of the backbone itself and of the body orientated about it, despite the fact that the number of vertebrae and the manner in which the various parts of the body (including the median fins) with respect to the vertebrae remain unaltered meanwhile. It need occasion no surprise, therefore, that many species which differ markedly in outward form are found to have backbones which can be regarded as little more than "distortions" of a basic, generalized "type". In each of the orders represented in the Plymouth material there is abundant evidence of this, presenting opportunity for research of an exceptionally interesting nature. It need hardly be added that variation from basic "type" may be more pronounced in one part of the backbone than in another, each species exhibiting its own characteristics in this respect.

Estimation of Age from Bony Structures

Although the estimation of age hardly comes within the scope of the present work, some incidental observations concerning it which have been made from time to time during the steady examination of skeletons may not be out of place. As is well known, a highly specialized technique has been developed for "reading" the age of certain fishes from their scales or otoliths. There are many species, however, in which such proven clues to age are not as yet established. There is, of course, nothing new in the fact that the bones of the skull and vertebral column frequently show "growth rings". Such rings have been observed in a number of the cleaned and dried skeletons in the Plymouth material, although it is not at present possible to give a definite statement that they are "annual" rings, or even that they can be relied upon as indices of age. Detailed study could alone determine this.

In the bass (*Morone labrax*) the supra-occipital exhibits growth zones of a remarkable clarity (Plate VII, fig. 2). The supra-occipital in *Serranus cabrilla* is similarly marked (Plate VIII, fig. 1). In the grey mullets (*Mugil*) growth rings are visible on the parapophyses of the 2nd to the 5th vertebrae. In the wrasses (e.g. *Labrus bergylta*) the rings are often very distinct on the posterior parapophyses and on the expanded base of the 1st caudal haemal spine (Plate X, fig. 1). Among the flat-fishes (Heterosomata) (Plate XV, fig. 2) the bones of the last vertebral segment are flattened plates, and are well worth study in this respect. In the John Dory (Plate XVI, fig. 3), certain of the skull bones are zoned. It is also known that the concave ends of the vertebral centra often show growth rings quite distinctly. This has been observed especially in elasmobranch fishes, and may well prove to be of practical use. Among gadoid fishes, growth rings show up rather well in the haddock and ling on the parapophyses, and in the skull bones of *Mora*. Generally speaking, growth rings and zones are rendered clearer by examination on a black background under water.

THE NUMBER OF VERTEBRAE (*n*)

The *number of vertebrae*, defined as an integer, indicating how many segments there are in the linear series of a vertebral column, would seem to be a readily understood and easily determinable character. Certainly it is one which is very generally given in systematic works on fishes, and extensively employed in biometric investigations of fishable populations of herring, cod, plaice and other food species. There is a great literature on the variation in the number of vertebrae and on its dependence upon heredity and environment. It is, therefore, a character about which knowledge should be as full as possible.

The Determination of (*n*)

In the practical determination of (*n*) there is normally no difficulty in the actual counting, provided that backbones are sufficiently well exposed to the view of the counter. Beginning with the 1st vertebra and counting one for each bony segment behind it, including the complex terminal, or urostylar segment, the total (*n*) is easily and correctly determined. Sometimes, however, and with a frequency dependent upon the species under study, the count presents difficulty. The most obvious case of this kind is that of a backbone having one or more abnormally long and irregularly formed segments, which suggest local fusions of adjacent vertebrae (Text-fig. 8). If these non-typical segments are counted as if they were single vertebrae, the total (*n*) for the backbone proves lower than the normal mean. Ford & Bull (1926) have shown that, in the herring, the normal value of (*n*) is restored if the irregular segments are considered as fusions of vertebrae and therefore counted as such. More recently, Schnakenbeck (1931) and Kändler (1932) have published data to the same effect.

There is a second type of complex vertebral segment which is not so easily evaluated. The essential features are the undivided, although often elongate, centrum, and the duplication of vertebral processes. Sometimes the neural spine is duplicated, and at others the haemal, but quite frequently both neural and haemal are duplicated (Text-fig. 10). Duplication may occur on both sides of the body, or (less frequently) on one side only. Details on the structure and occurrence of such segments in the herring and species of flat-fish are given by Ford (1933) and Kändler (1932).

In all species examined by the writer at Plymouth, save one (*Morone labrax*), segments of this character have been situated towards the caudal end of the vertebral series. In the clupeoids, e.g. in the herring, pilchard and sprat, duplicated processes occur on either or both of the two vertebrae immediately preceding the last or "urostylar" segment; in the gadoids they are confined to the vertebra next but one to the terminal segment, and in flat-fishes (Heterosomata) to the vertebra immediately preceding the terminal segment. Kändler, however, records extensive duplication of the neural spine of the 1st vertebra in the flat-fishes, but this has not been seen in the Plymouth material, despite a careful look-out for the possibility. Oddly enough, of the two solitary cases of this kind of duplication on the 1st vertebra, which have been observed at Plymouth, both occurred in the bass (*Morone labrax*). Complex segments at the posterior end of the backbone are very widespread and have been seen in the following species:

Order Isospondyli: *Clupea harengus*, *C. sprattus*, *Alosa alosa*, *Sardina pilchardus*, *Engraulis encrasicholus*, *Salmo trutta*, *Argentina silus*.

Order Anacanthini: *Gadus callarias*, *G. aeglifinus*, *G. luscus*, *G. minutus*, *G. merlangus*, *G. pollachius*, *G. poutassou*, *Urophycis blennoides*, *Molva molva*, *M. elongata*, *Mora mediterranea*, *Onos mustelus*.

Order Percomorphi: *Cepola rubescens*, *Ctenolabrus rupestris*, *Centrolabrus exoletus*, *Ammodytes lanceolatus*, *Atherina presbyter*.

Order Heterosomata: *Arnoglossus laterna*, *Rhombus maximus*, *Lepidorhombus whiff-iagonis*, *Phrynorhombus norvegicus*, *P. regius*, *Zeugopterus punctatus*, *Hippoglossoides platessoides*, *Pleuronectes limanda*, *P. platessa*, *P. flesus*, *Solea solea*, *S. lascaris*, *S. variegata*.

As shown by this list, the complex segments are of quite general occurrence in the Isospondyli, Anacanthini and Heterosomata. They are far less common in the Percomorphi and Scleroparei, however, and have not been observed in *Serranus cabrilla*, *Morone labrax* (except for two specimens), *Caranx trachurus*, *Mullus surmuletus*, *Scomber scombrus* and *Scorpaena dactyloptera*, although numerous backbones of each of these species have been examined. In a corresponding number of clupeoids, gadoids or flat-fish, there would certainly have been several occurrences of complex segments. Perhaps this is hardly surprising in view of the great degree of stability in the number of vertebrae and general form of the vertebral column in the species of Percomorphi and Scleroparei concerned.

In only a small number of species has the material for study been sufficient to estimate the frequency with which complete segments occur, but the data collected is at least sufficient to show that the frequency is sometimes very appreciable:

Species	Total no. of specimens examined	Specimens with complex segments	
		No.	Percentage
Clupea harengus	1356	233	17·2
Clupea sprattus	129	23	17·8
Sardina pilchardus	115	15	13·0
Argentina silus	69	15	21·7
Gadus minutus	81	14	17·3
Gadus merlangus	107	37	34·6
Atherina presbyter	101	13	12·9

Kändler's data on flat-fishes show that in the plaice, flounder, dab and turbot, backbones with accessory spines on the penultimate vertebra may account for as much as from 30 to 40 % of a sample, while for diallel crossings of trout, Schmidt (1921) found that the 5th vertebra from the end of the column showed duplication of spines in about 10 % of his material. When it is remembered that these percentages, like those for the Plymouth material, do not include vertebral fusions and accessory processes in other parts of the backbone, it will be realized that the adjective "abnormal" is hardly applicable to the complex segments in the species named.

How is the peculiar nature and position of these segments to be accounted for, and how ought they to be counted in arriving at the number of vertebrae (*n*)? It is more convenient to consider the second part of this question first. Schmidt, Kändler and Ford are in agreement in finding that if a complex segment is counted as 1, the number of vertebrae (*n*) works out on average lower than the value of (*n*) for specimens in which complex segments do not occur. More striking, however, is the fact that in the trout, herring and plaice, this discrepancy between the corresponding averages approximates very closely to 0·5 vertebra. That is to say, if a complex segment be counted as $1\frac{1}{2}$ instead of 1, the average value of (*n*) is brought into agreement with the "normal" average. Whether this applies generally to all species in which complex vertebrae occur cannot at present be decided owing to lack of sufficient data. The following data for *Clupea sprattus*, *Sardina pilchardus*, *Argentina silus*, *Gadus minutus* and *G. merlangus*, are of some interest in this connexion, however:

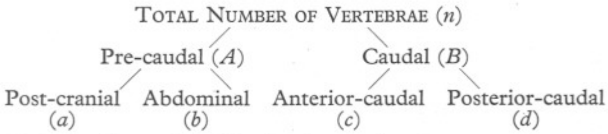
	No. of skeletons		Difference in average no. of vertebral segments counting each segment as 1
Species	Normal	Abnormal	
Clupea sprattus	102	23	0·59
Sardina pilchardus	100	15	0·37
Argentina silus	51	15	0·77
Gadus minutus	66	14	0·75
Gadus merlangus	63	37	0·67

Schmidt's hypothesis to account for his results is very interesting (Schmidt, 1921, p. 4). He suggests that vertebrate animals can realize fractional parts of vertebrae, but that such individuals are numerically inferior to what are ordinarily termed "normal" individuals. In reality, individuals with complex segments are just as "normal" as the latter. In both cases it is the individual's genetic structure in connexion with its environment in the sensitive period which is deciding the total realized; but it seems as if whole numbers in such organs as vertebrae are more easily realized than fractional parts.

This does not explain, however, why complex segments should occur only at fixed points in the vertebral series, usually at the caudal end. And it is difficult to see why the capacity to realize "fractional parts" of a vertebra should thus be confined to a given few among the many vertebrae of which the backbone consists. Consideration of this question brings to mind the theory of Kyle (1926, p. 82) that the number of vertebrae is determined under the combined influences of prevailing environmental conditions and the movements of the developing fish. Were this so, there is, perhaps, some possibility that vertebral variation might be more pronounced at the two ends of the vertebral column than elsewhere. In the absence of any new data which could throw further light on these fundamental matters, there is little purpose in continuing the discussion. In the meantime it is necessary to bear in mind that, in determining the number of vertebrae (n) in a sample of fish, care must be exercised in allowing for possible variation due to the presence of complex segments and other abnormalities in individual fish.

The Number of Vertebrae expressed as $n=(a+b+c+\ldots)$

Seeing that (n) is by definition an integer, it can be expressed as the sum of other integers. With such obvious and sharp changes in the form of the vertebrae at definite points along the column, it is thus possible in practice to record (n) as the summation of successive groups of vertebrae. The vertebral column of a gadoid, for example, can first be divided into a pre-caudal group (A) followed by a caudal group (B). Group (A) can be sub-divided into an anterior post-cranial group (a) and a posterior abdominal group (b). Similarly, group (B) can be subdivided into an anterior-caudal group (c) and a posterior-caudal group (d). Expressed in diagrammatic form, the vertebral series is thus composed as follows:



Expressed mathematically, $n=(A+B)=(a+b+c+d)$.

Subdivision of the backbone into groups of vertebrae is normally possible in practically all species, but, as has already been pointed out in an earlier paragraph, certain individuals in almost every species will present difficulty on account of homoeotic variation at the junctions of the groups into which the vertebrae of the backbone are divided. To give an illustration in point, gadoid backbones will certainly occur in which there is a "transitional" form of vertebra between the typical pre-caudals and the typical caudals. There appears to be no reliable criterion upon which to judge whether this transitional vertebra ought to be counted as a pre-caudal vertebra or a caudal. In biometric investigations, where conclusions are to be drawn from a statistical treatment of vertebral counts, it would seem necessary, either to put backbones of this type in a class apart from "normal" backbones, or to make an arbitrary count of the transitional vertebra as (say) $\frac{1}{2}$ pre-caudal and $\frac{1}{2}$ caudal, thereby preserving the integer value of (n). For example, an abnormally constructed backbone of a whiting might thus be recorded either as $(n)=(A)+(1)+(B)$ or as $(n)=(A+\frac{1}{2})+(\frac{1}{2}+B)$. Further consideration of homoeotic variation will be found in p. 28.

The summation of (n) as $(a+b+c+\ldots)$ is of practical utility in the study of variation from species to species. Again borrowing an illustration from the gadoid fishes, it is interesting to note that, within the genus *Gadus*, the difference in the value of (*n*) between species is, in the main, little more than a difference in the number of abdominal vertebrae (*b*). This is shown by a comparison of data for *G. merlangus* and *G. minutus*:

	Gadus merlangus	*Gadus minutus*	Differences
No. of individuals	63	66	—
Mean value of (*n*)	54·5	49·3	5·2
Mean no. of post-cranials (*a*)	4·0	4·0	nil
Mean no. of abdominals (*b*)	15·7	10·9	4·8
Mean no. of caudals ($c+d$)	34·8	34·4	0·4

The data show that of the total difference of 5·2 between the two mean values of (*n*), no less than 4·8 is accounted for by difference in the mean number of abdominal vertebrae (*b*), while the small remainder of 0·4 is distributed among the much larger number of caudal vertebrae.

In contrast with species of the genus *Gadus*, species of flat-fish (Order Heterosomata) tend to agree in the number of abdominal vertebrae but differ in the number of caudals. Thus, whereas the lemon sole (*Pleuronectes microcephalus*) and witch (*P. cynoglossus*) commonly have twelve pre-caudals, the number of caudals is about thirty-five in the lemon sole but forty-six in the witch. In the four local species of *Solea*, the number of pre-caudals is nine or ten, whereas the number of caudals varies from thirty to forty according to species.

The subdivision of (*n*) into group integers is also helpful in the study of the variation of (*n*) among individuals of the same species. In the herring, for example, it is well known that there is considerable individual variation in (*n*). In an earlier paper (Ford, 1933) the author has shown that individuals with a larger number of vertebrae (*n*) tend to have, on average, a disproportionately larger number of vertebrae in the well-differentiated "tail" group at the posterior end of the backbone. A similar study of 102 specimens of the sprat (*Clupea sprattus*) gives a corresponding indication, although, of course, the total number of specimens examined is hardly large enough to give conclusive results:

Total no. of vertebrae between skull and urostyle	Total no. of individuals	No. of vertebrae in "tail" group			"Tail" averages
		5	6	7	
46	28	9	18	1	5·71
47	70	7	59	4	5·96
				Difference	0·25

The increase of one vertebra from a total (*n*) of forty-six to a total of forty-seven thus results in an average increase of 0·25 in the number in the "tail" group. This is a disproportionately large increase, because if the difference of 1·0 between the values of (*n*) had been evenly distributed along the whole backbone, the increase in "tail" vertebrae would have been $\frac{1}{46} \times 5{\cdot}71 = 0{\cdot}124$, instead of 0·25. Putting the facts in an alternative way, sprats with forty-six vertebrae have a "tail" group comprising $\frac{5{\cdot}71}{46} = 0{\cdot}124$ of the total (*n*), whereas sprats with forty-seven vertebrae have a "tail" group comprising $\frac{5{\cdot}96}{47} = 0{\cdot}127$ of the total (*n*).

It will be agreed that studies of this kind must have an important bearing upon the interpretation of observed differences in (*n*) during investigation of local populations of fishes. Where fish like herring, cod and plaice vary in the average value of (*n*) from place to place and from season to season, any information concerning the manner in which the differences in (*n*) are distributed along the length of the backbone may well prove of great significance and assistance in determining relationships between the different populations represented.

The Number of Vertebrae (n) as the Summation of a Linear Series

When considering the number of vertebrae simply and solely as an integer (*n*), no account is taken of the individuality of the vertebrae counted. A first step towards recognition of this individuality is taken when (*n*) is expressed as the sum of several groups of vertebrae, but ultimately it becomes necessary to regard (*n*) as the sum of a linear series of vertebrae, (*n*) in number. This series may be expressed as $(n) = (1\text{st} + 2\text{nd} + 3\text{rd} + \ldots + n\text{th})$. In the last analysis the absolute numerical value of (*n*) has lost none of its own significance, nor is the significance of (*n*) expressed as $(a+b+c+\ldots)$ in any way impaired; but, for the first time, due regard is paid to the anatomical character and ordinal position in the vertebral series of each and every segment included in the count. In many species it may be necessary to do this before it becomes possible to detect the ways in which vertebral variation is being expressed. Close attention may also have to be given to differences in vertebral form which are structural rather than numerical or geometrical, differences which must be described and figured rather than counted. The results, however, are no less important or valuable because they cannot be expressed in concise mathematical terms.

The Degree of Constancy in the Number of Vertebrae

It may seem almost a truism to observe that data on the degree of constancy in the number of vertebrae can only be acquired by the routine examination of individual after individual. The fullness of the information thus derived is dependent upon (*a*) the number of observations made upon each individual, and (*b*) the number of individuals examined. With regard to (*a*), it will be realized from what has been said in foregoing sections that the extent to which the simple integer (*n*) varies from individual to individual is only a part of the study of the degree of constancy in the number of vertebrae. Important though knowledge of variation in (*n*) *per se* may be and is, it requires to be supplemented by knowledge of variation from vertebra to vertebra along the length of the backbone. For experience shows that vertebral variation is not evenly distributed along the length of the vertebral column, but more pronounced in some parts than in others. Stability in the value of (*n*) for a species, therefore, does not imply the entire absence of vertebral variation throughout the length of the backbone, any more than variability in (*n*) implies that the whole of the backbone is unstable.

Concerning the number of individuals examined in a study of the degree of constancy in the number of vertebrae, it need hardly be said that every additional specimen examined provides entirely new and independent data. No statement on the degree of vertebral constancy is therefore complete unless it includes the number of individuals examined. Moreover, the greater the number of individuals examined, the greater the value of the results obtained. During the investigations at Plymouth, every endeavour has been made, as opportunity has allowed, to add to the number of individual backbones of each species studied. It is hoped that this practice may be continued until sufficient data have been accumulated to yield a reasonably reliable indication of the range of vertebral variation in each. In the present paper it is proposed to restrict attention to data on eight species which will serve to illustrate the nature of the observations being made in this study of constancy.

Clupea harengus.

It is convenient to commence with the herring, not only because some thousands of backbones of this species have been examined at Plymouth in connexion with the routine investigation of the herring fisheries there, but because the species, in common with its allies in the family Clupeidae, is characterized by widespread variation in vertebral form. The features of the clupeoid backbone and its variation are described on p. 36, and without doubt, a single sample of not more than 100 herrings will provide an investigator with ample evidence of this variation. Almost certainly, the following phenomena will be observable:

(1) Variation in the integer value of (*n*) amounting to from four to six vertebrae.

(2) Structural "abnormalities" in as many as 20 % of the specimens which affect the computation of (*n*). These are of the following kinds:

(*a*) Complete or incipient duplication in one or more segments (Text-fig. 8).

(*b*) Duplication of the neural or haemal spines (or both) on the two vertebrae immediately preceding the urostylar (terminal) segment (Text-fig. 10).

(3) Variation in the value of (*n*) written as $(a+b+c+\ldots)$ in accordance with structural change along the length of the column.

(4) Homoeotic variation at the junctions of adjacent groups of vertebrae into which the backbone is divisible. Included under this head are the many

cases of bilateral asymmetry which commonly occur, in which the characters of an anterior group are seen on the one side and those of a posterior group on the other. In a sample of 100 fish, as many as 80 may show such asymmetry in one or more of the following positions:

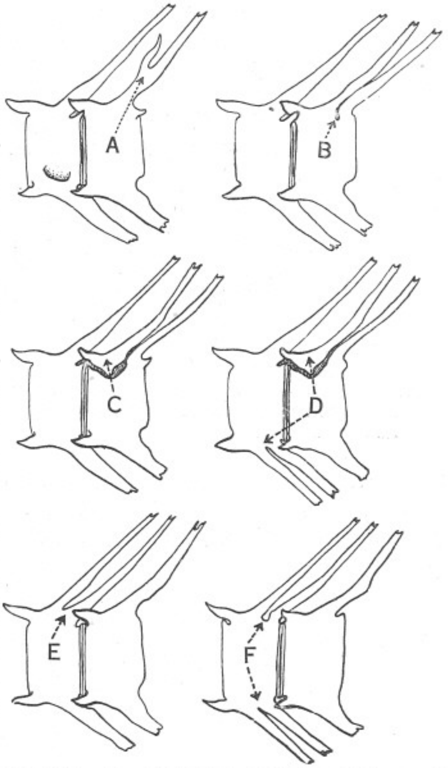
(*a*) In about the 24th vertebra, where the parapophyses cease to be rib-bearing and "autogenous" from the centrum, and become fused to the centrum (Text-fig. 11).

(*b*) In about the 27th vertebra, where the neural spines cease to be "autogenous" (Text-fig. 11).

(*c*) In about the 50th vertebra, at the anterior end of the "tail" group of vertebrae in which the haemal spines are cross-tied to the centra (Text-fig. 2 on p. 7).

(5) Abnormalities shown by the processes in isolated vertebrae along the length of the backbone (Text-fig. 8).

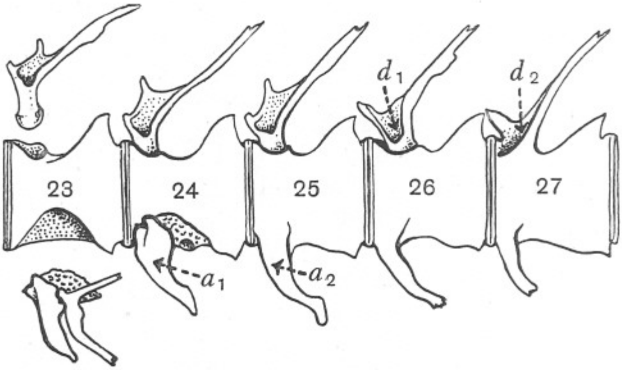
Actual data concerning variation of types 1, 2, 3 and 5 will be found in an earlier paper (Ford, 1933). It must here be said, however, that when these data were collected, bilateral asymmetry of types 4 (*a*), (*b*) and (*c*) was not noted. So far as my own data are concerned (Ford, 1933) it may be accepted that they are at least consistent in the one respect that they relate to counts made along the left side of the body—a consequence of an arbitrary practice in the routine adopted.



Text-fig. 10. Doubled-spined vertebrae at tail-end of herring. From Ford (1933). In each of the diagrams the two vertebrae represented are those immediately anterior to the complex terminal (urostylar) segment.

Scomber scombrus (Plate IX, fig. 1 and Text-fig. 4).

In contrast with the highly variable backbone of the herring, that of the mackerel (*Scomber scombrus*) is very stable. Data are available for a total of 1219 backbones examined at Plymouth by my colleague, Mr P. H. T. Hartley, in connexion with a programme of mackerel research now in progress at the Laboratory. Out of this total there were only eight in which the number of vertebrae (*n*) differed from thirty-one. Of the eight variates, five had thirty vertebrae and three had thirty-two. Of the remaining 1211, all save four further agreed in having thirteen pre-caudal vertebrae and eighteen caudals. This left 1207, of which 1201 still further agreed in having a well-defined "tail" group of six vertebrae (3 + 1 + 1 + 1) at the posterior end of the column (Text-fig. 4). That is to say, 98·5 % of the original total of 1219 agreed in having the vertebral formula $(n) = 31 = (13+18) = 13 + (12+3+1+1+1)$. With an important exception, the comparison of backbones, vertebra by vertebra, throughout the length of the column, confirmed this high degree of vertebral stability in the mackerel. The 9th, 10th and 11th vertebrae, especially the 10th, were alone in exhibiting noticeable variation, consisting of individual differences in the extent to which definite haemal arches were developed. A total of 1207 specimens examined could thus be segregated in five groups as under:



Text-fig. 11. Autogenous neural and haemal processes in the herring. From Ford (1933). In the diagram, d_1 is the last of the autogenous neural spines, and a_1 the last of the autogenous haemal arches.

Group	Serial no. of vertebra: 9th	10th	11th	No. of specimens
1	Closed haemal arch	Closed haemal arch	Closed haemal arch	1
2	Absent	Closed haemal arch	Closed haemal arch	530
3	Absent	Open haemal arch	Closed haemal arch	437
4	Absent	Absent	Closed haemal arch	230
5	Absent	Absent	Open haemal arch	9
				1207

These results may be summarized in the statement that the great bulk of mackerel examined at Plymouth only vary in the condition of the haemal arch on the 10th vertebra. Mr Hartley is at present investigating the possible utility of this variability in the study of the different populations of mackerel frequenting south-western waters.

Caranx trachurus (Plate IX, figs. 2 and 4 and Text-fig. 3).

The remaining six species to be considered are similar to the mackerel in showing a high degree of constancy in the total number of vertebrae (n), as well as in (n) expressed as $(a+b)$, where (a) is the number of pre-caudal vertebrae and (b) the number of caudals. The first of these is *C. trachurus*, of which the total number of specimens examined is 111. Of these, 110 had twenty-four vertebrae, comprising ten pre-caudals and fourteen caudals. The single exception had twenty-five vertebrae, the extra vertebra being in the caudal region as an interpolation behind the normal 22nd vertebra. Of the 110 specimens with twenty-four vertebrae, sixty-five agreed in having the formula

$$(n)=24=(10+14)=(1+7+2)+(1+4+4+2+1+1+1).$$

The characters upon which this formula is based are as follows:

Serial no. of vertebrae	Character
1	Neural spine "autogenous"
2–8	Open parapophyses
9–10	"Bridged" parapophyses
11	1st caudal vertebra; without ventral pre-zygapophyses
12–15	Ventral pre-zygapophyses well developed
16–19	Haemal arch foraminated
20–21	First two of "tail" group of vertebra; neural and haemal spines short and depressed along length of backbone
22	Epural very long; hypural "autogenous" from vertebral centrum
23	Neural arch reduced; hypural "autogenous" from centrum

Turning to the remaining forty-five specimens it was found that these showed variation from the characters enumerated above. The positions along the vertebral series at which this variation occurred, and its extent, are shown in the following summary:

Serial no. of vertebra	Nature of variation	No. of occurrences
8	Parapophyses "bridged" instead of being open	3
9	Parapophyses open instead of being "bridged"	3
11	Ventral pre-zygapophysis present on both sides	1
	Ventral pre-zygapophysis present on one side only	2
12	Ventral pre-zygapophysis present on one side only	4
14	Haemal arch of one side is foraminated	9
15	Haemal arch foraminated on both sides	4
	Haemal arch foraminated on one side only	14
16	Haemal arch of one side without foramen	13
	Haemal arch of both sides without foramen	6
17	Haemal arch of one side without foramen	2

It will be realized that all the above types of variation can be regarded as homoeotic. The abnormalities in the 8th, 11th, 14th and 15th vertebrae are cases of *backward* homoeosis (see Bateson, 1894, p. 111), in that these vertebrae show features which more properly belong to vertebrae which are farther back in the ordinal series. The abnormalities in the 9th, 12th, 16th and 17th, on the other hand, are examples of *forward* homoeosis, since the vertebrae concerned have a form approaching that of vertebrae which stand in front of them.

Summarizing the observations so far made on *Caranx*, it is seen that vertebral variation is chiefly confined to the haemal arches of the 14th, 15th and 16th vertebrae which may, or may not, be foraminated on both sides. Some variation may also occur in the 8th, 9th, 11th, 12th and 17th vertebrae, although less frequently.

Mullus surmuletus.

A total of 154 red mullet (*Mullus surmuletus*) has been examined without finding a single exception to the number of vertebrae (n) being twenty-four, comprising ten pre-caudals and fourteen caudals, as in *Caranx* and many other Perciform fishes. Such variation in vertebral form as occurred was localized in the 7th, 9th, 10th and 11th vertebrae, the remaining vertebrae appearing very stable. Dealing first with the 7th vertebra, it was found that in 105 specimens the parapophyses of this vertebra were open, whereas in the remaining forty-nine they were closed by bridging. The latter forty-nine may thus be considered cases of backward homoeosis, in which the 7th vertebra has assumed a character of the normal 8th. In the region of the 9th to 11th vertebrae, ventral pre-zygapophyses make their appearance. The following table shows the extent of variation in this respect:

	Serial no. of vertebra			No. of specimens
	9th	10th	11th	
Ventral pre-zygapophyses present or absent	Present on one side only	Present on both sides	Present on both sides	5
	Absent	Present on both sides	Present on both sides	56
	Absent	Present on one side only	Present on both sides	60
	Absent	Absent	Present on both sides	30
	Absent	Absent	Present on one side only	3

Subject to the above exceptions, therefore, the backbone of the red mullet will conform to the formula, $(n)=24=(10+14)=(1+6+3)+(11+1+1+1)$.

Morone labrax (Plate VII and Text-fig. 1).

The backbone of the bass (*M. labrax*) normally comprises twenty-five vertebrae, expressible as $(12+1+12)$, as shown in Plate VII, fig. 1. Out of 107 specimens so far examined, there were only two exceptions to this. The exceptions were particularly interesting in that both exhibited duplication of the neural spines of the 1st vertebra. If, on this account, the 1st vertebra is counted as two instead of one, the total number of vertebrae (n) is restored to the normal $(12+1+12)$. The determination of the number and ordinal position of the vertebrae with closed haemal arches showed that in ninety-three of the total of 107 specimens the haemal arches of the 10th, 11th and 12th vertebrae were closed. In eight of the remaining specimens the arches of the 9th vertebra were also closed, while in the six others, only the 11th and 12th had closed arches. Elsewhere along the backbone there was no very noticeable variation, and the "type" for the species could thus be expressed as

$$(n)=25=(12+1+12)=(1+8+3)+1+(9+1+1+1).$$

Scorpaena dactyloptera (Plate XII, fig. 2).

Seventy-five out of seventy-seven specimens of this species examined agreed in having twenty-five vertebrae, and in the following table the extent of further agreement, vertebra compared with vertebra along the ordinal series, is summarized:

Scorpaena dactyloptera. *Variation among individuals with twenty-five vertebrae*

Serial no. of vertebrae	Characteristics	No. of normal individuals	Variates	
1	Neural arch autogenous	75	—	
2	Neural spine of same height as, and applied to, neural spine of 1st vertebra. No parapophyses	75	—	
3–4	Have tallest neural spines, parapophyses absent	75	—	
5	No parapophyses	75	—	
6	With short, unbridged parapophyses	75	—	
7–10	Haemal arches bridged and foraminated	75	—	
11	Similar to 10th	72	Foramen on one side only ...	3
12	Similar to 10th	40	Foramen on one side ... ... Foramina absent	20 15
13–17	Haemal arches not foraminated	73	Foramina on 13th ... ... Foramina on 14th	1 1
18	Similar to 17th	71	Foramina on 18th	4
19	Similar to 17th	67	Foramina on 19th	8
20	Haemal arches foraminated	59	Foramen on one side only ... Foramina absent	13 3
21–22	Similar to 20th	75	—	
23	Epural elongate, hypural autogenous	75	—	
24	Neural arch reduced, hypural autogenous	75	—	
25	Anterior hypural "hooked"	75	—	

It is seen from the above data that vertebrae 1–10, and 21–25, are very stable in form. Such variation as occurs in vertebrae 11–20 consists of bilateral asymmetry in respect of the fenestration of the haemal arches, and may be regarded as homoeotic in nature. The "type" form of backbone in this species may be written as $(n)=25=(1+1+3+1+6+7+3+1+1+1)$.

Mugil spp. (Plate XI).

Of the grey mullets (*Mugil*) which occur at Plymouth, one is the thick-lipped grey mullet (*M. chelo*), of which 116 specimens have so far been available for study. All except four of these have twenty-four vertebrae made up of $(11+13)$. Of the four exceptions, three have twenty-five vertebrae $(11+14)$, leaving one with twenty-three vertebrae $(11+12)$. The most frequently occurring form of backbone has the formula

$$(n)=24=(11+13)=(1+1+5)+1+3+(1+10+1+1).$$

As to variations from it, there are six backbones which show a weak transverse bridge across the parapophyses of the 11th vertebra, whereas normally the parapophyses are open. The 8th vertebra, also, is subject to variation in that it sometimes bears a ventral post-zygapophysis on one or both sides of the centrum, whereas normally this zygapophysis is first seen on the 9th vertebra.

Thin-lipped grey mullets also occur at Plymouth which, failing specific identification, have been recorded as *Mugil* spp. The backbone of this form is at once distinguished from that of the thick-lipped *M. chelo* by the reticulated surface of the centrum throughout the vertebral column. Only thirty-four specimens have at present been available for study, but of these, thirty-two agree with *M. chelo* in having twenty-four vertebrae, made up of $(11+13)$. The remaining two have $25=(11+14)$ and $23=(11+12)$, respectively. The normal specimens also agree with *M. chelo* in having laminated neural spines to the first seven vertebrae, and open parapophyses on vertebrae 1–11. No case of bridging across the parapophyses of the 11th vertebra was observed (cf. *M. chelo*). There is a difference from *M. chelo* in that the ventral post-zygapophyses usually appear for the first time on the 8th vertebra instead of on the 9th. The typical thin-lipped grey mullet thus has the formula

$$(n)=24=(11+13)=(1+1+5)+4+(1+10+1+1).$$

Reviewing the observations given above, the important point emerges that each species examined presents one or more centres of definable variation along the length of the vertebral column, even though the total number of vertebrae and other major vertebral counts remain for all practical purposes constant. Furthermore, the data given are sufficient to indicate the number of individual backbones of any one species which must be examined in order to arrive at a fair estimate of the nature, ordinal position and extent of such variation. Information of this kind is clearly of practical help to an investigator intending to utilize vertebral data in the course of population or "race" studies of fish, since it shows which characters are likely to prove of the greatest service. It matters little to him that vertebral variation in some species is seen only in structures of comparatively minor anatomical or physiological significance. The all-important fact for his purpose is that there is actual variation which can be evaluated with mathematical precision, whether that variation be in the backbone as a whole or confined to one small part of it. For example, in an enquiry into the possibility of different populations of mackerel occurring in south-western waters, it may prove of great assistance to know that individual mackerel differ from one another in the condition of the haemal arch on the 9th to the 11th vertebrae, whereas in other respects the vertebral column is very stable. The collection and comparison of data on this variable character in samples of mackerel from different parts of the area, or at different times, may reveal population differences of considerable local significance—a finding which will be in no way affected by the circumstance that the actual vertebral difference itself is of no very great importance anatomically.

The above study of the degree of constancy in vertebral character also demonstrates the fact that no species has a backbone which is rigidly constant in form from individual to individual. Provided that the backbone is studied in sufficient detail, variation of some kind will become evident. The nature and extent of that variation varies from species to species and according to the genus, family and order to which the species is referable.

THE VERTEBRAL COLUMN IN TAXONOMY AND PHYLOGENY

In coming to consider the backbone as an indicator of identity and natural affinity, it is necessary to bear in mind certain facts. In the first place, the material available for study is here limited largely to species of a local fauna. Due caution must therefore be exercised in drawing generalized conclusions from the observations made. Secondly, the value of a vertebral character, either as a clue to identity or as an indicator of affinity, is of a *relative* rather than an *absolute* nature, since it varies according to the circumstances in which it is evaluated. There are times when a given character will establish identity or indicate affinity when other characters fail to do so, but there are other times when it is barely worth considering. The third point to be noted arises out of the second. For if a vertebral character is to be of any use at all in taxonomy or phylogeny, it must present a reasonable degree of constancy from individual to individual within the species to which it relates. One further fact requires to be mentioned, namely, that in taxonomy and phylogeny no feature of the vertebral column is too insignificant to be worthy of attention. A character may be insignificant in an anatomical or physiological sense, and yet be far from trivial in its taxonomic and phylogenetic import.

Since the work at Plymouth first began, backbones belonging to fishes of thirteen orders of the subclass Neopterygii have been examined. It is hoped that it may be found possible in due course to publish descriptive accounts of these, order by order, but in this first paper it has been thought more desirable to take a brief survey of the material as a whole, with the idea of showing by what means and with what measure of success it is possible to establish identity and natural relationship within the orders of fishes represented.

Order Isospondyli

The following species of this order have been examined:

Family	Genus	Species
Clupeidae	*Clupea*	*harengus, sprattus*
	Alosa	*alosa, finta*
	Sardina	*pilchardus*
	Engraulis	*encrasicholus*
Salmonidae	*Salmo*	*salar, trutta*
Argentinidae	*Argentina*	*silus*

As already indicated when considering the vertebral variation of the herring (p. 28), the fishes of this order are characterized by great plasticity in vertebral form. Indeed this excessive plasticity might almost be considered one of the distinguishing vertebral characters of the order. Even so, it is easy to see in the backbone ample evidence of similarity in basic form among the different species. Perhaps the first character which should be mentioned is the presence in every species of "autogenous" neural or haemal (or both) processes on an appreciable number of the vertebrae. The disposition of these in different genera is shown in the following table:

Autogenous neural processes	Autogenous haemal processes	Genus
On anterior pre-caudal vertebrae, and on hindermost "tail" vertebrae	On anterior pre-caudal vertebrae, and on hindermost "tail" vertebrae	*Salmo*
On anterior pre-caudal vertebrae only	On anterior pre-caudal vertebrae, and on hindermost "tail" vertebrae, as in *Salmo*	*Argentina*
On anterior pre-caudal vertebrae only	On anterior pre-caudal vertebrae only	*Clupea*, *Alosa*, *Sardina*
On anterior pre-caudal vertebrae, except vertebrae 1 to 3–4	None	*Engraulis*

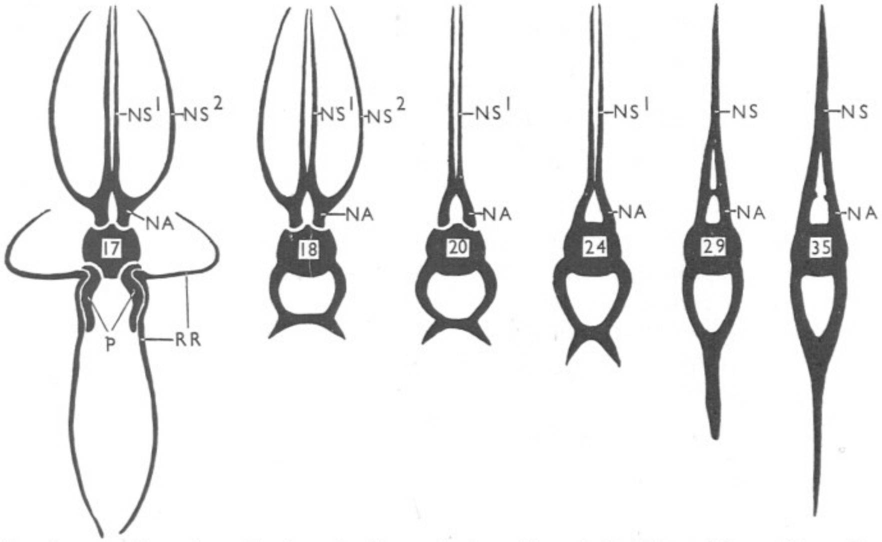
It is seen that this one character is sufficient to segregate the fishes according to Regan's classification. The presence of autogenous processes in the "tail" vertebrae of *Salmo* and *Argentina*, but not in those of the Clupeidae, is thus in keeping with Regan's classification of the Salmonidae and Argentinidae in a suborder (Salmonoidea) apart from the Clupeidae (suborder Clupeoidea).

The species of the family Clupeidae have backbones full of interest in their agreements and disagreements. In considering these it will be of much assistance to deal first with the characters of the skeleton of a shad (*Alosa alosa*), measuring approximately 26 in. in length which I was fortunate enough to secure at Plymouth in May 1937. The comparatively large size of the bony structures in this specimen makes it the more easy to see the points of interest. It is built up of fifty-seven vertebral segments, each of which has its own form, dependent upon the precise position it occupies in the vertebral series. In no other backbone is the fact more clearly shown that each vertebra is a set-piece in the composite and graded pattern of the backbone as a whole. Every part and process of each vertebra indicates by its form the one and only position in the backbone into which it will fit. The composite nature of the vertebral pattern is shown by an abrupt change in vertebral form at certain points along the column. At least six such changes in form are worthy of note, whereby the backbone may be divided into distinct regions along its length. The following description of these changes will be easier to follow by the aid of the illustrations in Plate I and Text-fig. 12.

Vertebrae 1 *and* 2. These two vertebrae are clearly modified to form a union between the backbone and the skull.

Vertebrae 3–17. In this region the neural and haemal processes of all the vertebrae are autogenous from the centrum. Dorsally, the neural spines of the right and left side are bifurcate structures (Text-fig. 12) which stand by their peg-like bases in sockets in the centrum (Plate I). Above the spinal cord the inner elements of the bifurcate spines of the two sides are brought into adjacency in the middle line, but they do not fuse together to form a single composite neural spine. Ventrally, the rib-bearing haemal arches are also autogenous from the centra, and can be easily dissected away in their entirety from the latter (Plate I).

Vertebrae 18–23. In the 18th vertebra an abrupt change occurs in the condition of the haemal arches. These no longer bear ribs, become continuous with the centra, and are transversely bridged to enclose a haemal canal (Plate I). At the same time the form of the ventral post-zygapophysis is showing signs of a change from the more simple thorn-like form of the anterior vertebrae to the irregularly reticulate form characteristic of this region. Meanwhile along the dorsal surface, the neural spines remain autogenous, although from the 20th vertebrae onwards they no longer possess the second spiny element shown by the vertebrae in front (Text-fig. 12).



Text-fig. 12. *Alosa alosa*. To show the changes in form along the backbone. The serial numbers of the vertebrae are inserted on the ends of the centra. Where processes are autogenous they are broken from the centrum by a white line. *NA*, neural arch; *NS* neural spine; *P*, parapophysis; *RR*, ribs.

Vertebrae 24–28. In the 24th vertebra the neural spines for the first time cease to be autogenous and become continuous with the centrum at their bases (Plate I). As in the anterior vertebrae, however, the right and left halves still retain their separate identity throughout their length (Text-fig. 12). Ventrally, the distal forked ends of the haemal arches outside the haemal canal are beginning to elongate and close together. On the right side of vertebra 24 and on the left of vertebra 25, there appears for the first time a slender but elongate pre-zygapophyseal process at the base of the haemal arch (Plate I). This process becomes progressively more robust in later vertebrae, taking up a position parallel to the length of the column.

Vertebrae 29–49. In the 29th vertebra another change occurs in the condition of the neural arch. It now shows two separate canals, the lower one to house the spinal cord, and the upper one to carry the dorsal ligament. Above these canals the hitherto discrete right and left neural spines have become fused together to form a single, composite neural spine (Text-fig. 12). In vertebra 34 the transverse division between the neural canal and ligament canal breaks down, and both spinal cord and ligament appear then to be housed within a single neural canal. Ventrally, the distal ends of the haemal spines have at last come completely together, rapidly lengthening from vertebrae 29 to 34. In this comparatively long section of the column, too, it is easy to see the gradational change in form of the zygapophyseal processes, particularly the dorsal and ventral pre-zygapophyses, which assume greater and greater dominance as one passes towards the posterior end of the backbone.

Vertebrae 50–57. The 50th vertebra is the first of the terminal "tail" section comprising eight vertebral segments. It differs from the 49th in that the base of the haemal spine on either side is cross-tied to the centrum by a bony bar which is not present in earlier vertebrae. In *Alosa* this cross-tying is not so easily visible as in the herring but it is nevertheless present. In other respects the vertebrae in this section are much more rigidly locked together than those in front, a condition undoubtedly associated with the function of this part of the backbone as a skeletal framework and support for the caudal fin.

With this description of *Alosa* available it is easier to turn to a comparison with the other species of the Clupeidae, for these are manifestly built along the same general lines. That is to say, while the total number of vertebrae, the number of vertebrae in corresponding regions, and the more minute structure of corresponding skeletal structures, will all vary from species to species, the same basic plan and pattern is evident in them all. *Engraulis encrasicholus* is perhaps the most divergent in that none of the haemal arches of the pre-caudal vertebrae is autogenous from the centrum, or transversely bridged to form closed haemal arches as in *Alosa* and the others. Despite this there remains abundant evidence of the clupeoid basic plan in the other vertebral characters. The backbone of *Sardina pilchardus*, on the other hand, resembles that of *Alosa* to a decided degree. Those of the two species of *Clupea* (*C. harengus* and *C. sprattus*) go well together save in the total number of vertebrae, and agree in being constructed on a more simple and generalized note than either *Alosa* or *Sardina*.

It remains to be said in this general survey that there is a very considerable degree of variation among individuals in each of the species examined. While this in no way masks either the similarities or distinctions between species, it does make it of great importance in biometric studies of local populations to exercise caution in interpreting the significance of observed differences in vertebral form. In other words, one needs to be conversant with the manifold ways in which the vertebrae of a clupeoid backbone may vary, if one wishes to utilize vertebral data in such researches.

Order Anacanthini

All save one of the fishes of this order which have been examined belong to the family Gadidae, the single exception being *Merluccius merluccius*, of the family Merlucciidae:

Family	Genus	Species
Merlucciidae	*Merluccius*	*merluccius*
Gadidae	*Gadus*	*callarias, aeglifinus, luscus, minutus, merlangus, poutassou, virens, pollachius*
	Urophycis	*blennoides*
	Molva	*molva, byrkelange, elongata*
	Mora	*mediterranea*
	Onos	*mustelus, cimbrius* (also two species of three-bearded rockling)
	Raniceps	*raninus*
	Brosme	*brosme*

The condition of the vertebral column in these gadoid fishes (Plates II–VI) shows how each species is really a unique modification of a single "gadoid type" of backbone. In each of them, including *Merluccius*, the backbone is divisible into four sections, (*a*) post-cranial, (*b*) abdominal, (*c*) anterior caudal, and (*d*) posterior caudal. Within each section, all species agree in the following ways:

In the post-cranial section:

The dorsal post-zygapophyses on the first two or more vertebrae are laterally placed and backwardly directed.

The 1st neural spine is in close association and of the same height as the supra-occipital.

In the abdominal section:

The well-developed parapophyses are all open.

The neural spines of the most anterior of the vertebrae are lancet-shaped.

There are open grooves in the neural arches (in contrast to foramina) for the passage of the spinal nerves. (*Onos* spp. in part are an exception.)

In the anterior caudal section:

The closed haemal arches of the most anterior vertebrae form a "haemal funnel".

Open nerve grooves are present in the neural arches, as in the abdominal section (see above).

The distal ends of the neural spines are attenuated.

In the posterior caudal section:

The neural spines support the rays of the caudal fin.

The penultimate vertebra lacks neural spines, and its hypurals are autogenous.

The terminal segment is of characteristic form.

Although there is this measure of general agreement among the species, each has its own distinctive form. The difference between species lies both in the number of vertebrae in the successive sections of the backbone and in the form of the actual vertebral structures. Detailed descriptions would be out of place in this summary, but it may be helpful to give a list of characters which have been found serviceable in identification:

In the post-cranial section:
- Departure from the normal "neck" of four vertebrae (3 + 1).
- The form of the 1st vertebra and its neural arch and spine.
- The relative heights of the first three neural spines.

In the abdominal section:
- The number of vertebrae.
- The degree of elaboration of the parapophyses.
- The presence or absence of apophyses in addition to parapophyses.
- The shape of cross-sections of the vertebral centra.

In the anterior caudal section:
- The number of vertebrae.
- The degree to which the "haemal funnel" is developed.

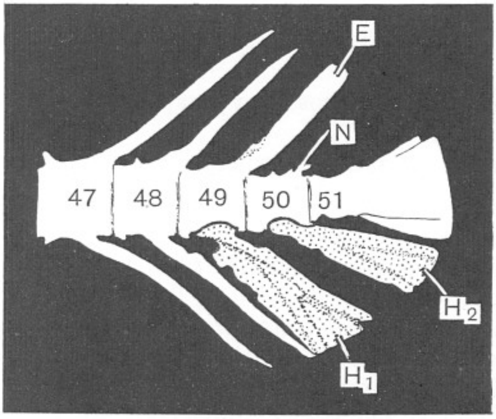
In the posterior caudal section:
- The number of vertebrae.
- The overall shape enclosed between the distal ends of the neural and haemal spines (e.g. whether compressed or attenuated).
- Whether or not the hypural of the antepenultimate vertebra is autogenous.
- The occurrence of duplicate neural and haemal spines on the antepenultimate vertebra.

In the backbone as a whole:
- The number of vertebrae $(n) = (a + b + c + d)$, and its degree of variation from individual to individual.
- The varying length of the vertebral centra along the column.
- The extent of the sculpturing of the vertebral centra.

Knowledge of these and other vertebral characters not only enables an observer to identify the species but to segregate species on the evidence of similarities in vertebral form. Thus, within the genus *Gadus*, five such groups can be made, viz.

(1) *G. aeglifinus*
(2) *G. poutassou*
(3) {*G. callarias*, *G. merlangus*}
(4) {*G. luscus*, *G. minutus*}
(5) {*G. pollachius*, *G. virens*}

Reference has already been made on p. 11 to the recognition of two forms of three-bearded rockling (*Onos* spp.) in the Plymouth fauna, differing in backbone characters. Another observation which may be referred to here has also been indicated on an earlier page (p. 7), namely, that in *Merluccius*, *Raniceps* and *Urophycis*, the form of the last three vertebrae recalls to a very appreciable extent the form of the similar section of the backbone in the more generalized percoids (Text-fig. 13). Whether or not this may be used as evidence of phylogenetic relationship is a matter which cannot be pursued here. It is to be noted that there is a further point of agreement with the generalized percoids in that *Merluccius*, *Raniceps* and *Urophycis* have eggs with oil globules. Here again, although no further discussion of the implied significance in phylogeny of the presence of an oil globule in the teleostean eggs is proposed, the point is one which might bear further examination, as it will again come to notice when dealing later with other orders of fishes.



Text-fig. 13. Tail-end of hake (*Merluccius merluccius*), showing the autogenous hypurals H_1 and H_2, the elongate epural *E*, and the crested neural arch *N*. Compare with the generalized tail vertebrae of the Perciform fishes, e.g. *Morone labrax* in Text-fig. 1.

Order Percomorphi

In contrast with the Anacanthini, the fishes of the order Percomorphi which have been examined represent no less than five suborders, seven divisions of these suborders, and sixteen families.

Suborder	Division	Family
Percoidea	Perciformes	Serranidae, Carangidae, Mullidae, Sparidae, Cepolidae
	Labriformes	Labridae
	Trachiniformes	Trachinidae
	Ammodytiformes	Ammodytidae
	Callionymiformes	Callionymidae
Scombroidea	—	Scombridae
Blennioidea	Blenniiformes	Blenniidae, Anarhichadidae
	Cliniformes	Pholidae
Gobioidea	—	Gobiidae
Mugiloidea	—	Mugilidae, Atherinidae

In view of this diversity of material it is not altogether surprising to find that it is practically impossible to discover vertebral characters applicable to the whole order. This does not mean that the backbone fails to show underlying relationship between fishes of the different genera and families. Quite on the contrary, the phylogenetic indications, given by the vertebral characters, of specific variation from a distinct percoid "type" are numerous and plain. This percoid "type" is best seen in species of the division Perciformes, sub-order Percoidea, of which *Serranus cabrilla*, *Caranx trachurus*, *Mullus surmuletus*, *Pagellus centrodontus*, *Cantharus lineatus* and *Box boops* have been studied at Plymouth. In these the backbone shows the following characters:

(1) The total number of vertebrae (n) is $24 = (10+14)$ and is remarkably constant.

(2) The neural arch of the 1st vertebra is autogenous from the centrum (Plate IX, fig. 4).

(3) A certain number of the posterior parapophyses are closed by bridging to form a haemal canal.

(4) The last three vertebral segments have the following characters (Text-fig. 1):

- (*a*) Antepenultimate vertebra.
  Hypurals autogenous from centrum, and epurals elongated.
- (*b*) Penultimate vertebra.
  Hypurals autogenous from centrum, neural arch low and crested but without prominent neural spine.
- (*c*) Terminal vertebral segment.
  The foremost hypural is autogenous and bears a characteristic "hook".

The extent to which other species of Percomorphi agree with or differ from the most generalized Perciformes in the form of the backbone is most conveniently discussed, character by character.

(1) *The Number of Vertebrae*

It can hardly be doubted that within the order Percomorphi the number of vertebrae is very stable for many species, and it must be considered more than coincidence that so many of the most generalized species agree in having $(n) = 24 = (10+14)$. Yet, as has been shown at an earlier stage, (n) may be different from 24 without any loss of constancy. Thus it is 25 in *Morone labrax* and 31 in *Scomber scombrus* with quite remarkable regularity. On the other hand, there are many species of Percomorphi in which (n) is not only different from 24, but is subject to individual variation, sometimes appreciable. In *Cepola rubescens*, for example, in the small total of twenty specimens examined there were seven which showed either fusion of adjacent vertebrae at some point along the vertebral column or duplication of the neural or haemal spines on the penultimate vertebra, while (*n*) in the remaining thirteen specimens varied from 69 to 72. In *Atherina presbyter*, out of a total of 101 specimens there were twenty-six which showed either fusion of adjacent vertebrae or duplication of neural or haemal spines, while among the remainder (*n*) varied from 49 to 52.

(2) *The Autogenous Neural Spine of the 1st Vertebra*

This feature has been observed over a wide range of species. All the eight species of Perciformes examined show it, including *Cepola rubescens*. In the Labriformes it is present in the five wrasses, *Labrus bergylta*, *L. mixtus*, *Crenilabrus melops*, *Ctenolabrus rupestris*, and *Centrolabrus exoletus*. It is also present in *Trachinus vipera*, and *T. draco* which belong to the Trachiniformes. It is not seen, however, in *Ammodytes* and *Callionymus*. In the Scombroidea the 1st neural spine is fused to the centrum in *Scomber*, but (as shown by Kishinouye, 1923) it is detachable from the centrum in some species of the family Cybiidae. Even in *Katsuwonus* it is but feebly attached. In the Blennioidea, the spine is again autogenous in *Anarhichas* and *Pholis*, but not in *Blennius*. It is not autogenous in either *Mugil* or *Atherina*.

(3) *The Condition of the Parapophyses*

The closing of the haemal arches of two or more of the posterior caudal vertebrae by bony bridges is a character shared by the Plymouth Perciformes with the exception of *Cepola*, although there is variation from species to species in the number of these bridged parapophyses. In *Caranx trachurus* only the 9th and 10th vertebrae normally show them, whereas in other species they may be present on the 7th and 8th as well. Among the Labriformes the bridging tends to be masked by the increased length and lateral spread of the distal ends of the parapophyses, giving the appearance of "open" parapophyses. Actually, bridges are normally present in *Labrus bergylta*, *Crenilabrus melops* and *Ctenolabrus rupestris*, but not in *Labrus mixtus*. Of the two specimens of *Centrolabrus exoletus* examined, one shows no bridging, and the other incomplete bridging on the two hindermost pre-caudals. Closed parapophyses are also present in *Trachinus* and *Ammodytes*. In *Scomber* it is only on the 10th–13th vertebrae that parapophyses occur at all and these are closed. Among the Blennioidea, bridged parapophyses are seen in *Blennius*, but in *Anarhichas* they are all open; in *Pholis* there is an unusual condition of closed haemal arches in a long series from the 4th vertebra backwards. Those of the 4th and 5th vertebrae are connected at their distal ends by a longitudinal keel. In the gobies, bridging of the wrasse type is seen, but in both *Mugil* and *Atherina* the parapophyses are open.

(4) *The Condition of the "Tail" Section*

The type of "tail" section described in characters 4 (*a*), (*b*) and (*c*) above is met with in numerous species. As might be expected it is particularly common among fishes of the division Perciformes. A brief survey of the skeletons in the British Museum (Natural History), South Kensington, showed that it is present in species of the following families:

Serranidae, Kuhlidae, Centrarchidae, Chilodipteridae, Percidae, Pomatomidae, Carangidae, Menidae, Centropomidae, Arripidae, Lutianidae, Sciaenidae, Mullidae, Scorpaenidae and Scorpididae.

It is not suggested that all the species of all the families named will be found to agree in this character, or that it does not also occur in species of families not included in the list. The latter is merely given as a guide to the wide range of perciform fishes in which the generalized form of "tail" section has been observed. It may be added, however, that in ten species of the family Cichlidae there was an important variation, in which the hypurals of the antepenultimate vertebra were no longer autogenous from the centrum.

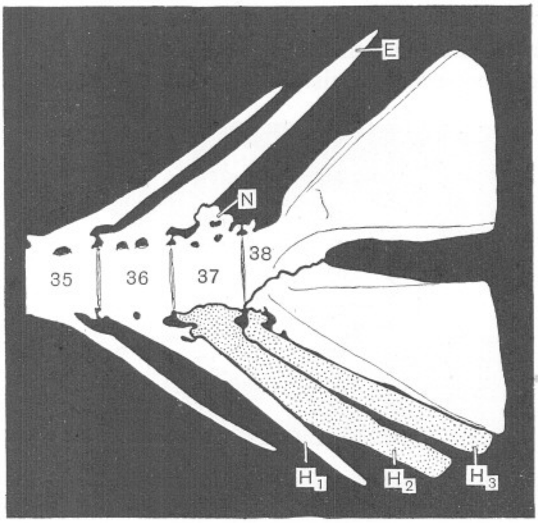
Outside the Perciformes, the form of the "tail" section tends to show departure from the generalized form, although it is fully retained in *Scomber scombrus* (Text-fig. 4, p. 8). Here, despite the distinctive modification of the caudal peduncle which characterizes the mackerel, the characters 4 (*a*) and (*b*) are clearly visible, while the well-developed hook on either side of the middle line of the terminal segment at once recalls character 4 (*c*). This basic similarity between the tail skeleton of the highly specialized mackerel and that of the generalized perciform is surely of particular interest.

In the Labriformes (Text-fig. 14) and Trachiniformes the "tail" section shows a slight deviation in character 4 (*a*), in that although the epurals of the antepenultimate vertebra are elongate, the hypurals are now continuous with the centrum instead of being autogenous. In the penultimate vertebra the full character 4 (*b*) is shown. It is of interest to note also that the British Museum specimens of *Julis pavo*, *Coris cuvieri*, *Odax richardsoni* and *Scarus aurofrontus* agree with the Plymouth wrasses in the characters just referred to.

Concerning species of other divisions of the suborder Percoidea it may be said that *Ammodytes* still retains autogenous hypurals to the penultimate vertebra, whereas in *Callionymus* nothing appears to remain in the "tail" section of characters 4 (*a*), (*b*) or (*c*). On the other hand, the British Museum specimens of *Haplodactylus*, *Cirrhites*, *Chironemus*, *Chilodactylus* and *Latris*—all belonging to the division Cirrhitiformes—have a "tail" section which closely approximates to that of the Perciformes. *Gadopsis*, of the Gadopsiformes, resembles the Labrids, and *Trachinus* and *Ammodytes*, in having the antepenultimate hypural continuous with the centrum.

The "tail" section of the Blennioidea exhibits stages in specialization. The most generalized condition is seen in *Anarhichas* in which the penultimate vertebra carries autogenous hypurals, although not the antepenultimate. Even so, there is considerable departure from the perciform type in that the neural spine of the antepenultimate vertebra is not longer than those of preceding vertebrae, while that of the penultimate vertebra is quite stout and longer instead of being reduced. The species of *Blennius* have proceeded still further than *Anarhichas* in that the hypurals of the penultimate vertebra are no longer autogenous.

In the Gobioidea, as in *Blennius*, there is little or nothing to recall the generalized "tail" section. In the Mugiloidea, however, *Mugil* shows a great deal of it, and except that the hypurals of the antepenultimate vertebra are not autogenous, characters 4 (*a*), (*b*) and (*c*) are seen in full. In contrast, *Atherina*, of the same suborder, shows no agreement at all.



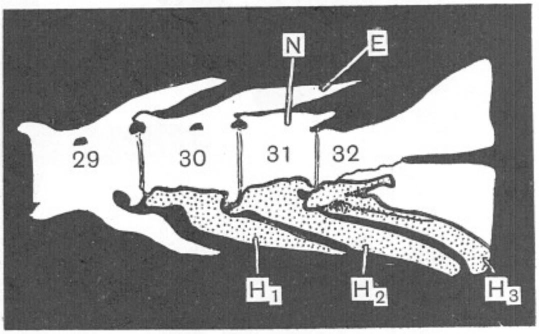
Text-fig. 14. Tail-end of *Labrus bergylta*. The antepenultimate hypural H_1 is continuous with the centrum, whereas H_2 and H_3 are autogenous. The epural E is long and the neural arch N is crested. The hypural H_3 does not bear a hook but articulates with the hypural posterior to it.

Order Scleroparei

In a paper on the classification of fishes of the order Scleroparei (or Loricati) Regan remarks that the most generalized family, the Scorpaenidae, is not very remote from the generalized percoids, such as the Serranidae. This is certainly borne out in a comparison of the backbone of *Sebastes marinus* or of *Scorpaena dactyloptera* with that of *Serranus cabrilla*. Save for the increased number of vertebrae in the two Scorpaenids, the fenestration of the parapophyses and of the haemal arches of the posterior caudal vertebrae, the agreement with

Serranus is very noticeable (cf. Plate VIII, fig. 1, and Plate XII, figs. 1 and 2). There is the same general form of the backbone as a whole and in its corresponding sections: the 1st neural spine is autogenous, the posterior parapophyses are closed, the shape of neural and haemal spines and of zygapophyses is very similar, while the "tail" section is of the typical percoid type described under characters 4 (*a*), (*b*) and (*c*) on p. 42. Moreover, as in *Serranus*, the vertebral characters have a very high degree of constancy.

The Triglidae, which Regan places next to the Scorpaenidae in the division Scorpaeniformes of the suborder Scorpaenoidea, are represented in the Plymouth material by the five gurnards, *Trigla lucerna*, *T. cuculus*, *T. gurnardus*, *T. lyra* and *T. lineata*. All of them have vertebral characters in common, not only with *Sebastes* and *Scorpaena*, but also with *Serranus*. The autogenous 1st neural spine is again present, the posterior parapophyses are bridged, and the "tail" vertebrae are of the typical percoid type (Text-fig. 15). *Trigla* further agrees with *Sebastes* and *Scorpaena* in that the 1st and 2nd neural spines are of equal height and convergent distally (Plate XII, fig. 3). There is, however, a well-defined "neck" section in this genus, made up of the first four or five vertebrae in which the backwardly directed dorsal post-zygapophyses are conspicuous. At the opposite end of the backbone the last eight or nine vertebrae show flattening and strengthening of the neural and haemal spines to form an attenuated skeletal root for the tail.



Text-fig. 15. Tail-end of *Trigla lyra*. The typical percoid condition is fully present.

In the other species of Scleroparei which have been examined, namely *Cottus bubalis*, *Agonus cataphractus*, *Cyclopterus lumpus* and *Spinachia spinachia*, most or all of the points of agreement with the percoid *Serranus* have disappeared. Indeed, it is difficult enough even to detect vertebral characters which will link these species with the more generalized members of their own order.

Order Heterosomata

In his monograph on the systematic revision of the flat-fishes Norman (1934) discusses the relationships of these fishes. He refers to the difference of opinion between authors as to whether the flat-fishes have been derived from a single stock, whether gadoid, zeoid or percoid, or from a number of stocks. Suffice it to say that Norman favours the view that the Heterosomata have arisen from a generalized percoid stock. But while he considers *Psettodes* to be the least specialized member of the order, he leaves open the possibility that the Soleidae and Cynoglossidae may have arisen from another part of the percoid stem. In this matter it is of considerable interest to note that the backbone of *Psettodes erumei* has the following characters in common with the generalized percoid:

Number of vertebrae $(n) = 24 = (10 + 14)$.
1st and 2nd vertebrae with well-developed, backwardly directed, superior posterior zygapophyses. 1st neural spine probably autogenous.
7th–10th vertebrae have closed haemal arches.
Haemal spine of 1st caudal vertebrae is not greatly different in length or breadth from those immediately following it.
Hypural of 23rd vertebra is autogenous from centrum.

But while *Psettodes* has at least this much in common with the generalized percoid, all the flat-fishes in the Plymouth material are far more specialized in vertebral form and reveal no very definite indication of possible percoid origin. Furthermore, the species examined can be easily segregated into four groups according to the following characters:

Whether the asymmetry is dextral or sinistral.
The relative height and disposition of the 1st neural spine.
The nature of the pre-caudal parapophyses.
The disposition of the series of apophyses arising from the middle line of the centra along the vertebral column.
The angles between the neural and haemal spines of the 1st caudal vertebra and the long axis of the vertebral column.

The grouping of the species thus affected and the characters of each group are as given on p. 48.

The data show that there is a pairing off between groups 1 and 2 (i.e. between subfamilies Pleuronectinae and Scophthalminae), and between groups 3 and 4 (i.e. between *Arnoglossus* and *Solea*). This is a matter of twofold interest. In the first place, it lends support to the possibility that the Heterosomata have been derived from more than one ancestral stock. In the second place, it reveals that *Arnoglossus* has more in common with *Solea* than with *Rhombus*, *Lepidorhombus*, *Phrynorhombus* and *Zeugopterus*, with which it is at present classified in the subfamily Scophthalminae of the family Bothidae. While it would be manifestly unwise to regard these two observations as anything more than tentative indications for more detailed study, they are both of no little interest and importance.

Group no.	Family	Subfamily	Genera	Species
1	Pleuronectidae	Pleuronectinae	*Reinhardtius*	*hippoglossoides*
			Hippoglossus	*hippoglossus*
			Hippoglossoides	*platessoides*
			Pleuronectes	*limanda*
				platessa
				microcephalus
				cynoglossus
				flesus
2	Bothidae	Scophthalminae	*Rhombus*	*maximus*
				laevis
			Lepidorhombus	*whiff-iagonis*
			Phrynorhombus	*norvegicus*
				regius
			Zeugopterus	*punctatus*
3	Bothidae	Bothinae	*Arnoglossus*	*laterna*
				imperialis
4	Soleidae	—	*Solea*	*solea*
				lascaris
				variegata
				lutea

Characters of each Group

Sinistral or Dextral	Group 1 Dextral	Group 2 Sinistral	Group 3 Sinistral	Group 4 Dextral
1st neural spine	Well developed, upstanding and of height exceeding that of cranium (Pl. XIII, fig. 1)	More slender than 2nd. Of same height as cranium, to which it is applied at its distal end (Pl. XIV, fig. 2)	Much reduced in size in comparison with 2nd	As in group 3 (Pl. XIII, fig. 2)
Pre-caudal parapophyses	Open	Open (Pl. XIV, fig. 3)	Closed	Closed (Pl. XIII, fig. 2)
Lateral apophyses	Restricted to caudal vertebrae	Restricted to caudal vertebrae (Pl. XIV, fig. 3)	Extend throughout whole column	Extend throughout whole column (Pl. XIII, fig. 3)
1st caudal vertebra	Neural and haemal spines set approximately at right-angles to long axis of centrum	Neural and haemal spines set obliquely to long axis of centrum. Forward angle of neural spine is an acute angle, but that of haemal spine is obtuse (Pl. XV, fig. 1)	Neural and haemal spines are both bowed backwards	Neural and haemal spines are both bowed backwards (Pl. XIII, fig. 2)

Despite the measure of agreement between species of group 1 (Pleuronectinae) and group 2 (Scophthalminae), there are very well marked differences between them. Members of the Pleuronectinae are not only dextral while those of the Scophthalminae are sinistral, but they have eggs without oil globules, whereas those of the Scophthalminae all possess oil globules. And as has already been mentioned on p. 41, this question of the phylogenetic significance of the oil globule is one which ought to receive closer attention. Furthermore, in the backbone itself, the sinistral Scophthalminae show a "facies" which is distinctive and different from that of the dextral Pleuronectinae, and one in which unequal development of vertebral characters on the upper (coloured) and lower (blind) sides of the body is more pronounced.

Before leaving the question of the group differences between the species of the Heterosomata it may be added that the Pleuronectinae can be subdivided by vertebral characters into three smaller groups as follows:

Reinhardtius
Hippoglossus

Hippoglossoides
Pleuronectes limanda
P. platessa
P. flesus

P. microcephalus
P. cynoglossus

Coming now to consider the flat-fishes as a composite order, irrespective of external and internal relationship, it may be said that although there is an appreciable degree of variation in the number of vertebrae from individual to individual in every species, the number of pre-caudal vertebrae is always comparatively low in contrast with the number of caudals. Thus, in the Pleuronectinae, with the exception of *Reinhardtius* and *Hippoglossus*, the number of pre-caudals does not exceed thirteen (in *Reinhardtius* there are about nineteen and in *Hippoglossus* about sixteen), whereas the number of caudals may be as low as twenty-four to twenty-five in *P. flesus* and as high as at least forty-six in *P. cynoglossus* (forty-four in *Reinhardtius* and thirty-four to thirty-five in *Hippoglossus*). In the Scophthalminae the number of pre-caudals is ten or eleven in the six species exclusive of *Arnoglossus*, as compared with thirty to thirty-seven caudals. In *Arnoglossus* there are ten pre-caudals and thirty to thirty-four caudals, while in the four species of *Solea* there are nine to ten pre-caudals in contrast with twenty-nine to forty-one caudals.

Another feature in common among the species of Heterosomata is the tendency towards "bimodality" which is shown when a graph is plotted of the lengths of the successive vertebrae from one end of the backbone to the other. This tendency is perhaps most strongly shown by the species of the subfamily Scophthalminae.

Finally, it is worth drawing attention to the question of the external shape of flat-fishes in relation to that of the backbone, to which a brief reference was made on p. 20. There seems little doubt that in every flat-fish the long axis of the backbone is naturally arched in the pre-caudal region, more especially in species of the Scophthalminae. This arching results in, or is associated with, a displacement of the neural and haemal spines from a true symmetry with respect to the long axis of the column. This is clearly visible in the backbone of the turbot (Plate XV, fig. 1). It is seen that in the posterior-caudal region the neural and haemal spines are fairly symmetrically placed with respect to a series of ordinates at right angles to the long axis of the vertebral column. This symmetry, however, begins to break down as the middle of the backbone is approached from the tail-end, and in the 1st caudal vertebra the neural spine lies to the left of the ordinate while the haemal lies to the right. As already stated, the arching and asymmetry are most apparent in the species of the Scophthalminae.

Order Zeomorphi

The two species *Zeus faber* and *Capros aper* have very interesting backbones. Considering *Zeus* first, it is known that relationship with the Heterosomata has been suggested, and, at first sight, there are some surprising points of agreement between the backbone of the John Dory (Plate XVI, fig. 2) and that of, say, the turbot (*Rhombus maximus*) (cf. Plate XV, fig. 1). In both, there is natural arching of the vertebral column and the associated distortion of the angles made between the neural and haemal spines; there is bimodality in the length of the centrum along the column; the skeletal base of the caudal fin is of a conspicuously flattened form in both; the hinder part of the abdominal cavity has a bony wall, of which the strongly developed haemal spine of the 1st caudal vertebra is an important component.

But there are equally striking differences between the two species. In *Zeus* the parapophyses are closed and interlocked at their distal ends to form a kind of keel, whereas in *Rhombus* they are widely open and free from one another; lateral apophyses on either side of the caudal vertebrae are a strong feature of *Rhombus*, but they are entirely absent in *Zeus*; the neural arches are of an entirely different form in the two species; and whereas in *Rhombus*, as in all the other flat-fishes studied, there are twice as many caudal vertebrae as there are pre-caudals, in *Zeus* the number of caudals is only a vertebra or two more than the number of pre-caudals. One other difference is noteworthy, viz. in the form of the neural spine of the 1st vertebra. In *Zeus* the right and left elements of the spine are separate from one another, flattened, with their anterior edges closely applied to the cranium in such a way as to form a socket in which the 1st radial of the dorsal fin stands. In *Rhombus* the two halves of the neural spine are also in close association with the cranium, but they are closed together for the greater part of their length and certainly do not form a housing for the end of the fin radial.

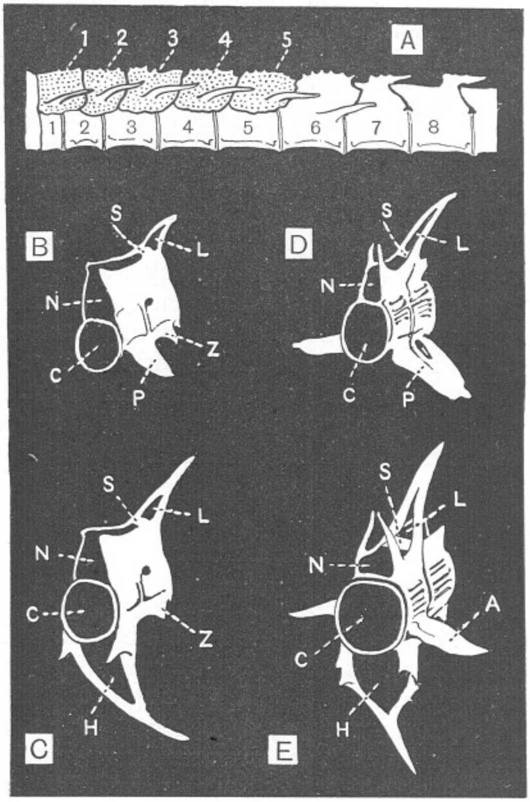
In these mixed circumstances of agreement on the one hand and disagreement on the other in vertebral characters, it cannot be said that the study of the backbone provides much confirmation of ancestral relationship between *Zeus* and the Heterosomata.

Turning to *Capros aper*, the other member of the order Zeomorphi, it is of interest to find that its backbone has a number of characters in common with the percoid type. There are ten pre-caudal vertebrae, of which the 7th to the 10th have bridged parapophyses. There are twelve caudals (i.e. two less than in the generalized percoid) but the "tail" section composed of the final three is reminiscent of the percoid. Thus, the hypurals of the antepenultimate and penultimate vertebrae, as well as the foremost hypural of the terminal (urostylar) segment are autogenous, while the latter is hooked. *Capros* agrees with *Zeus* in the application of the 1st neural spine to the cranium to form a socket in which the first radial of the dorsal fin may stand. It may also be observed in passing that the species has succeeded in developing a most ingenious mechanism for locking the spines of the dorsal and pelvic fins in an erected position with respect to the body. This is not the place to describe the locking structures, but they would well repay close examination by any worker interested. Indeed, the study of locking devices among fishes in general, particularly among fishes of the orders Percomorphi and Scleroparei, in which these occur more frequently than might be realized, is one of no little interest. The engineering problems raised, the ways in which the different fishes have solved them, and the manner in which the bony structures concerned are developed, are all matters on which further information is desired.

Order Apodes

In addition to the orders considered in the foregoing pages, there are several which are represented in the Plymouth material by one or two species only. The first of these is the Apodes, represented by *Anguilla anguilla* and *Conger conger*. The backbones of these are readily distinguishable from one another, although they agree in having autogenous neural arches on certain of the anterior pre-caudal vertebrae; in the separate housings for the longitudinal ligament and spinal cord; in the convex anterior face of the 1st vertebra; and in the general form of the last vertebra.

In *Anguilla anguilla* an interesting condition is presented by the neural arches of the first eight vertebrae. Those of vertebrae 1–5 are autogenous from the centrum and bear on either side a backwardly directed hook-like process (Text-fig. 16A). Above the spinal cord the arches of the two sides come together in a median crest, in shape resembling that of a cockscomb. The posterior end of the neural arch of each of these five vertebrae overlays the anterior end of the neural arch of the succeeding vertebra. In the 6th vertebra the neural arch becomes fused with the centrum, instead of being autogenous from the centrum. Nevertheless, like the five vertebrae preceding it, it bears the lateral hook and the median cockscomb, and its posterior end overlays the anterior end of the 7th. The 7th vertebra is unique in that its neural arch is overlain at both ends—anteriorly, by the posterior end of the neural arch of the 6th, and posteriorly, by the anterior end of the arch of the 8th. It bears no lateral hook, but the median cockscomb is still present. The 8th vertebra shows a transition stage towards the more typical pre-caudal condition in which the neural arch bears a closed, supplementary arch at its posterior end, through which passes the longitudinal ligament. Anteriorly, the neural arch overlays the posterior end of the preceding neural arch.



Text-fig. 16. A, *Anguilla anguilla*. First eight vertebrae viewed from side, to show the hook-bearing, autogenous neural arches on vertebrae 1–5. Vertebra 6 has its neural arch fused to the centrum, and the lateral hook arises more ventrally. The neural arch of vertebra 7 is interlocked by those of vertebrae 6 and 8. B, *Anguilla anguilla*. Typical pre-caudal vertebra (cf. with that of *Conger* in Fig. D). C, *Anguilla anguilla*. Typical caudal vertebra (cf. with that of *Conger* in Fig. E). D, *Conger conger*. Typical pre-caudal vertebra. E, *Conger conger*. Typical caudal vertebra.

Abbreviations used in Figs. A–E: *N*, neural canal; *C*, anterior end of centrum; *H*, haemal canal; *P*, parapophysis; *A*, lateral apophysis; *Z*, ventral post-zygapophysis; *S*, transverse septum above neural canal; *L*, ligamentary canal.

In Text-figs. 16B and C typical pre-caudal and caudal vertebrae are depicted. It will be observed that the latter are entirely without lateral apophyses, which are so conspicuous a feature in *Conger conger* (see below).

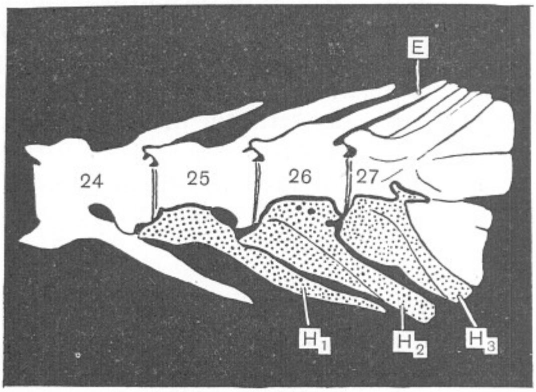
The backbone of *Conger conger* (Text-figs. 16 D and E) is distinguishable from that of *Anguilla anguilla* throughout its length. Anteriorly, the first sixteen or seventeen vertebrae have autogenous neural arches surmounted by conspicuous, laterally flattened neural spines of approximately equal height. In contrast with *Anguilla*, only the 2nd vertebra appears to bear a conspicuous "rib"-bearing hook at the base of the neural arch, although a reduced form of hook-like process is present on the 3rd to about the 8th. The parapophyses on either side of the 2nd to the 5th or 6th are duplicate structures, one above the other, which, on the 6th or 7th, become merged to form a single process. Proceeding along the backbone, an obvious difference from *Anguilla* is the progressive change in form of the parapophyses in the pre-caudal region and the apparent fusion of these processes with the ventral post-zygapophyses, which, in *Anguilla*, retain their separate identity. Towards the end of the pre-caudal section of the backbone there is the first evidence of the separation of each parapophysis into an upper apophyseal process and a lower parapophysis of the normal type. In the first of the caudal vertebrae this separation is complete, the apophysis projecting at right angles from the centrum, immediately above the closed haemal arch. The series of these lateral apophyses extends backwards over many vertebrae and serves as a readily distinguishable feature of difference between *Conger* and *Anguilla*. The backbone of *Conger* is further distinguishable from that of *Anguilla* by the heavy sculpturing of the surfaces of the centra throughout the column.

Order Synentognathi

Scombresox saurus and *Belone belone* have been examined. Both backbones, consisting of a large number of vertebrae, have numerous points in common. In the long pre-caudal section, widely open but short rod-like parapophyses are present on each vertebra from the 1st backwards. Except on the most anterior and most posterior vertebrae, where they are flattened, the neural spines throughout the whole column are slender and spine-like. A characteristic feature in both species is the disproportionately large size of the dorsal pre-zygapophyses, although here there is a sharp distinction between the two species. In *Belone* these zygapophyses are flattened triangular plates, one side of which is applied to the neural spine of the preceding vertebra. In *Scombresox* they are curiously elaborate in form and separated from the neural spine of the preceding vertebra by posterior zygapophyseal processes, with which they interlock. *Scombresox* is further distinguished from *Belone* by the presence of a well-differentiated "tail" section in which the neural and haemal spines are strengthened and lay back along the length of the column. It is of interest to note that the neural arch of the penultimate vertebra is reduced to a low crest not unlike the condition in percoids. It is possible, although the point is subject to confirmation on further material, that the hypural of the penultimate vertebra is autogenous in *Scombresox*.

Order Discocephali

Two specimens of the interesting sucking fish, *Remora remora*, have been obtained at Plymouth. The backbone comprises twenty-seven vertebrae, made up of twelve pre-caudals and fifteen caudals. In the pre-caudal region, the neural arches of vertebrae 1–3 form a low-lying crest by the suppression of the neural spines, and thus afford a seating for the skeleton of the sucker. Rather long, rod-like parapophyses stand out laterally from each of the anterior pre-caudal vertebrae, but the length decreases and the rods turn downwards in the posterior pre-caudals. A noticeable feature of the 10th, 11th and 12th vertebrae is the presence of rather long, downwardly directed postero-ventral zygapophyses. In the caudal region the final three vertebral segments form a "tail" section in which the hypurals of both antepenultimate and penultimate vertebrae are autogenous, and in which the foremost hypural of the terminal segment is also autogenous and bears a hook (Text-fig. 17). The epurals of the antepenultimate vertebrae are elongate and enter into the skeleton of the caudal fin. It need hardly be said that these characters of the "tail" section are reminiscent of the generalized percoid.



Text-fig. 17. Tail-end of *Remora remora*. Hypurals H_1, H_2 and H_3 are autogenous, H_3 is hooked, but the neural arch of 26th vertebra bears elongate epural, *E*.

Order Plectognathi

Two specimens of *Balistes capriscus* have been examined, both of which had eighteen vertebrae, made up of eight pre-caudals and ten caudals. Superficially, the backbone of this species recalls that of the John Dory (*Zeus*). There is the same natural curvature of the column, with the heavy skull set at an angle at the anterior end; the posterior parapophyses and the haemal spine of the first caudal vertebra together form a stout posterior wall to the abdominal cavity; the superior anterior zygapophyses are strongly developed. But at both head and tail-ends *Balistes* differs greatly from *Zeus*, although, here again, there is some agreement in that the 1st neural spine is closely applied to the cranium. In the first five vertebrae of *Balistes*, however, the neural spines are clearly modified in shape and set to receive the elements of the complex "trigger" mechanism which characterizes the species. The 2nd to 5th vertebrae also bear open parapophyses. At the opposite end, the penultimate vertebra has autogenous hypurals, which, like the epurals, constitute elongated and strengthened skeletal supports for the caudal fin.

Two small specimens of the sunfish *Mola mola* were caught off Plymouth and brought to the Laboratory in July 1937. Their skeletons were prepared by dissecting away the tough, blubbery carcase and disarticulating the backbone, vertebra by vertebra, having first noted the relation of each with respect to the fin-radials. In general form and arrangement the two backbones were very similar to that portrayed by Steenstrup & Lütken under *M. rotunda* (1898, plate II), but they differed in several important characters. Thus, both had nine caudal vertebrae in a total of seventeen (=8+9), instead of eight in a total of sixteen (=8+8). Vertebrae 1–4 form a distinct group in which the neural spines of the right and left side do not meet above the spinal cord to form a closed neural canal. Instead, the latter is open above as a narrow longitudinal slit. The neural spines of the 1st vertebra project forward to form occipital articulation with the skull on either side of a median occipital crest. The 2nd vertebra is unusual for the fore-and-aft projections of the neural arches and spines which overlie the centra of the 1st vertebra in front and the 3rd vertebra behind, and make a snug fit with the proximal parts of the neural arches of these vertebrae. The 3rd and 4th vertebrae have short, backwardly directed neural spines which, with those of vertebra 1 and 2, form a beautifully interlocked and low-lying neural crest.

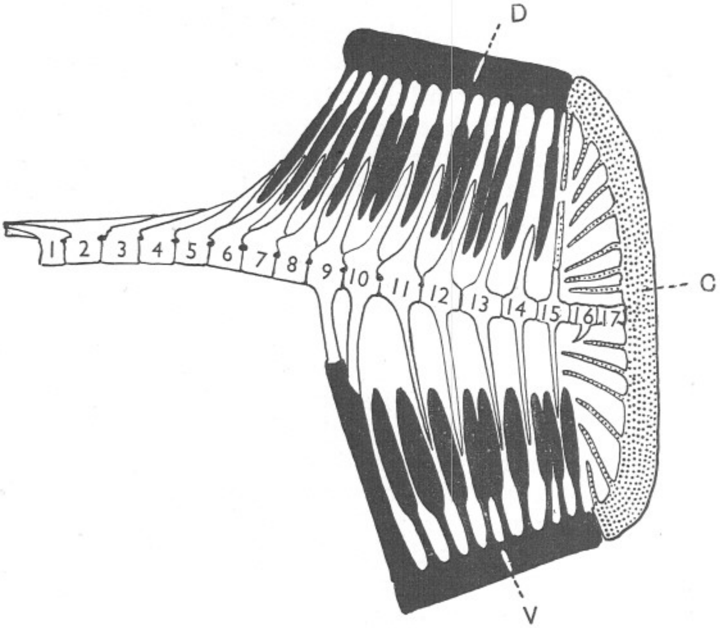
Vertebrae 5–8 form a second group with distinctive characters. Like the first four vertebrae they are without haemal arches, but unlike them they have a closed neural canal which penetrates a single, solid neural spine of considerable length and stability. Each of these neural spines is interlocked with the anterior radials of the dorsal fin.

Vertebrae 9 and 10 are the first of the caudals. Their very long haemal spines come together distally to lie together within the semi-tubular and massive anterior radial element of the anal fin. In both vertebrae, however, the right and left haemal spines retain their separate identity throughout their length. Dorsally, they have single, solid neural spines, interlocking with the dorsal radials.

Vertebrae 11–15 agree in having solid neural spines, penetrated by a tubular neural canal which becomes reduced to pin-size diameter in the 15th. Ventrally, the haemal arches are closed and prolonged distally into single haemal spines. Both neural and haemal spines interlock with fin radials, those of the 15th entering into the support of the caudal fin radials.

There remain the two terminal vertebrae, nos. 16 and 17. Of these, the former consists of little more than a cylindrical centrum bearing a short haemal process, while the latter has a centrum without processes at all.

The relation of the neural and haemal spines in general to the radials of the dorsal, anal and caudal fins is shown diagrammatically in Text-fig. 18. A comparison with Steentrup's figure shows some difference in this respect, particularly at the hinder end of the backbone, where the radials of the caudal fin are concerned.



Text-fig. 18. *Mola mola*. The backbone in relation to the endoskeleton of the dorsal, anal and caudal fins. (Diagrammatic.) *D*, radial skeleton of dorsal fin (solid black); *V*, radial skeleton of anal fin (solid black); *C*, radial skeleton of caudal fin (stippled).

Order Pediculati

Lophius piscatorius has a backbone which is composed of a series of vertebral segments compactly interlocked to form a skeletal rod between head and caudal fin. The neural and haemal processes are comparatively short and robust, and strongly flexed backwards along the length of the column. Indeed, in the precaudal region, the parapophyses lie almost parallel with the long axis through the centra, and overlap from front to back to form a continuous ventral face beneath the centra. The actual bone substance of the vertebrae is of a spongy nature, with the result that the whole backbone, when dried, is surprisingly light in weight. The hindermost vertebrae comprise a stout base for the caudal fin, the penultimate vertebra possessing particularly heavy epurals which are depressed to lie parallel to the long axis. Considering the massive form of the body of *Lophius*, the backbone is something of a surprise in its almost unrelieved compactness.

CONCLUDING REMARKS

The major conclusion which has been reached as the result of the work surveyed in the foregoing pages is that almost every one of the different aspects of vertebral variation discussed is a worthy subject for intensive study, likely to yield highly interesting and useful results. Of actual material for these researches there can be no possible shortage, since every fish in the sea, regardless of species, is a potential source of fresh information. In the present paper an endeavour has been made to set out in bare outline the manifold problems awaiting full investigation. No claim is made that the observations therein made are new, not having been previously observed and described. As stated in the introduction, the work was prompted by the desire to avoid error and misunderstanding in the treatment and interpretation of statistical data on vertebral variation among populations of economically important fishes. It has led to a radical change of outlook and a much increased consciousness of the need for extreme care and caution in population studies of the kind referred to. More than this, it has convinced the author that the study of the piscine vertebral column brings an investigator hard up against the great fundamental questions in zoology, and is therefore deserving of intensive study in the immediate future.

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EXPLANATION OF PLATES

PLATE I. *Alosa alosa*

Fig. 1. View of ventral surface showing last pair of autogenous parapophyses on the 17th vertebra, and the first closed haemal arch on the 18th.

Fig. 2. View of left side showing last pair of autogenous parapophyses on 17th vertebra. Note also the autogenous neural arches in this region of the backbone.

Fig. 3. View of left side showing the last pair of autogenous neural arches on the 23rd vertebra, and the first appearance of the spine-like pre-zygapophyseal process on the haemal arch of the 25th vertebra.

PLATE II

Figs. 1 and 2. *Gadus callarias.* Views of right side and ventral surface of the post-cranial or "neck" section of the backbone. Note the lateral position of the dorsal pre-zygapophyses on the first three vertebrae, and the locking of the 4th vertebra in front and behind.

Fig. 3. *Gadus virens.* View of right side of post-cranial or "neck" section. Compare the relative heights of the neural spines of vertebrae 1, 2 and 3 with those of the corresponding vertebrae in *G. callarias* (fig. 1).

Fig. 4. *Molva molva.* Ventral view of post-cranial section of backbone.

PLATE III

Fig. 1. *Gadus luscus.* View of right side of pre-caudal section of backbone, for comparison with corresponding views of other species illustrated in figs. 2, 3 and 4. Note that the 1st neural spine is of the same height as, and closely applied to, the supra-occipital. The 2nd and 3rd neural spines are shorter than the 1st.

Fig. 2. *Gadus pollachius.* Corresponding view. Note that 2nd and 3rd neural spines are longer than 1st. The small arrow points to the open groove in the neural arch, for the passage of the spinal nerves.

Fig. 3. *Mora mediterranea.* Corresponding view. The 1st neural spine is of characteristic appearance, but still in typical association with the supra-occipital as in *Gadus*.

Fig. 4. *Merluccius merluccius.* Corresponding view. The 1st neural spine is a bifurcate structure, but still in typical association with the supra-occipital. The neural arches and spines of the pre-caudal vertebrae are of characteristic appearance. The scroll-like parapophyses are also noteworthy.

Plate IV

Fig. 1. *Gadus merlangus*. Ventral surface in pre-caudal region. Note the typical "neck" of four vertebrae. Lateral apophyseal processes are present between the parapophyses.

Fig. 2. *Urophycis blennoides*. Corresponding view. Note the "neck" of four vertebrae and the form of the parapophyses. The deeply-pitted ventral surfaces of the pre-caudal centra, and the large haemal ring of the 1st caudal vertebra, are clearly shown.

Fig. 3. *Merluccius merluccius*. Corresponding view. The "neck" and scroll-like parapophyses are of a striking and characteristic appearance.

Fig. 4. *Gadus aeglifinus*. Corresponding view. The neck is short. The parapophyses are large, forming a regular canopy. The characteristic shape of the haemal arch of the 1st caudal vertebra is observable (indicated by arrow).

Plate V

Fig. 1. *Onos* sp. Three-barbed rockling, form A (see p. 11 of text). Note that nerve foramina are present on vertebrae 4–12, but that on the 13th and subsequent vertebrae their place is taken by open grooves.

Fig. 2. *Gadus luscus*. To show open parapophyses on pre-caudal vertebrae, and well-developed "haemal funnel" at front end of caudal region.

Fig. 3. *Gadus pollachius*. Similar view to fig. 2.

Plate VI

Fig. 1. *Urophycis blennoides*.
Fig. 2. *Gadus virens*.
Fig. 3. *Mora mediterranea*.
Fig. 4. *Gadus pollachius*.
} Showing variation in the form of the tail-end of the backbone.

Plate VII. *Morone labrax*

Fig. 1. View of left side (see p. 32 of text).

Fig. 2. Enlarged view of supra-occipital to show growth rings.

Fig. 3. Tail-end (for comparison with Text-fig. 1 on p. 7).

Plate VIII

Fig. 1. *Serranus cabrilla*. The autogenous neural spine of the 1st vertebra is missing, but its position is indicated by the arrow. Growth rings on the supra-occipital are just visible.

Fig. 2. *Pagellus centrodontus*. View of ventral surface to show the walled blood tract along the pre-caudal vertebrae.

Plate IX

Fig. 1. *Scomber scombrus*. General view of right side. Note the first appearance of a haemal arch on the 10th vertebra. A drawing of the "tail-section" from vertebrae 26 to 31 is given in Text-fig. 4 on p. 8.

Fig. 2. *Caranx trachurus*. General view of right side. Note the enlarged intervals between the neural spines of 2nd and 3rd vertebrae, and of 11th and 12th. The haemal arch in this specimen is first foraminated on the 15th vertebra. The "tail-section", comprising vertebrae 20–24 is shown diagrammatically in Text-fig. 3 on p. 8.

Fig. 3. *Katsuwonus pelamys*. View of tail-end.

Fig. 4. *Caranx trachurus*. Enlarged view of anterior end to show autogenous neural spine to 1st vertebra, and the characteristic widening of the interval between neural spines 2 and 3 to receive the first dorsal radial.

Plate X. *Labrus bergylta*

Fig. 1. Enlarged view of the haemal arch of the 1st caudal vertebra to show the growth rings.

Fig. 2. Ventral surface of anterior vertebrae to show the large backwardly directed apophyseal processes overlapping adjacent vertebrae.

PLATE XI. *Mugil* spp.

Fig. 1. *Mugil chelo*. (Thick-lipped grey mullet.) Left side showing the characteristic form of the neural spines of the first seven vertebrae, and the "hook" at the posterior end of the 2nd (indicated by arrow).

Fig. 2. *Mugil chelo*. Abdominal region. Note the first appearance of the ventral post-zygapophysis on the 9th vertebra.

Fig. 3. *Mugil* spp. (Thin-lipped grey mullet.) Abdominal region. Note that the ventral post-zygapophysis is present on the 8th vertebra (cf. *M. chelo* in fig. 2). The reticulated surfaces of the vertebral centra form a contrast with the condition in *M. chelo* as shown in fig. 2.

PLATE XII

Fig. 1. *Sebastes marinus*. View of right side. For details see Text-fig. 9 on p. 19 of text.

Fig. 2. *Scorpaena dactyloptera*. View of right side. For details see Table on p. 33 of text.

Fig. 3. *Trigla lyra*. View of left side. The arrow is pointing to the neural spines of vertebrae 1 and 2, which are of equal height and brought into adjacency at their distal ends.

Fig. 4. *Trigla lyra*. Ventral view to show the flattened distal ends of the haemal arches on vertebrae 9–12 (see p. 12 of text).

PLATE XIII

Fig. 1. *Pleuronectes flesus*. Pre-caudal region. Note the upstanding neural spine of the 1st vertebra, clear of the skull. The parapophyses are open on the pre-caudals.

Fig. 2. *Solea solea*. Pre-caudal region. The neural spines of the 1st vertebra are much reduced, with their distal ends open. The haemal arches from the 5th vertebra onwards are closed.

Fig. 3. *Solea solea*. Ventral view of pre-caudal region to show closed haemal arches. Lateral apophyses are present on pre-caudal vertebrae as well as on caudal.

PLATE XIV. *Lepidorhombus whiff-iagonis*

Fig. 1. View of left side.

Fig. 2. Front end viewed from left side. The neural spine of the 1st vertebra is in contact with the cranium and of a similar height. The lateral apophyses on the centra from vertebra 11 backwards are clearly shown.

Fig. 3. Ventral view of front end. Note the open parapophyses on vertebrae 5–10. The lateral apophyses from vertebra 11 backwards are larger on the left side than on the right.

PLATE XV. *Rhombus maximus*

Fig. 1. View of left side. The dotted line *AB* has been inserted to show the asymmetry of the neural and haemal spines of the 1st caudal vertebra with respect to the long axis of the centrum. The bowing of the long axis of the backbone at the anterior end is well marked.

Fig. 2. Enlarged view of caudal peduncle to show growth rings on the flattened hypurals.

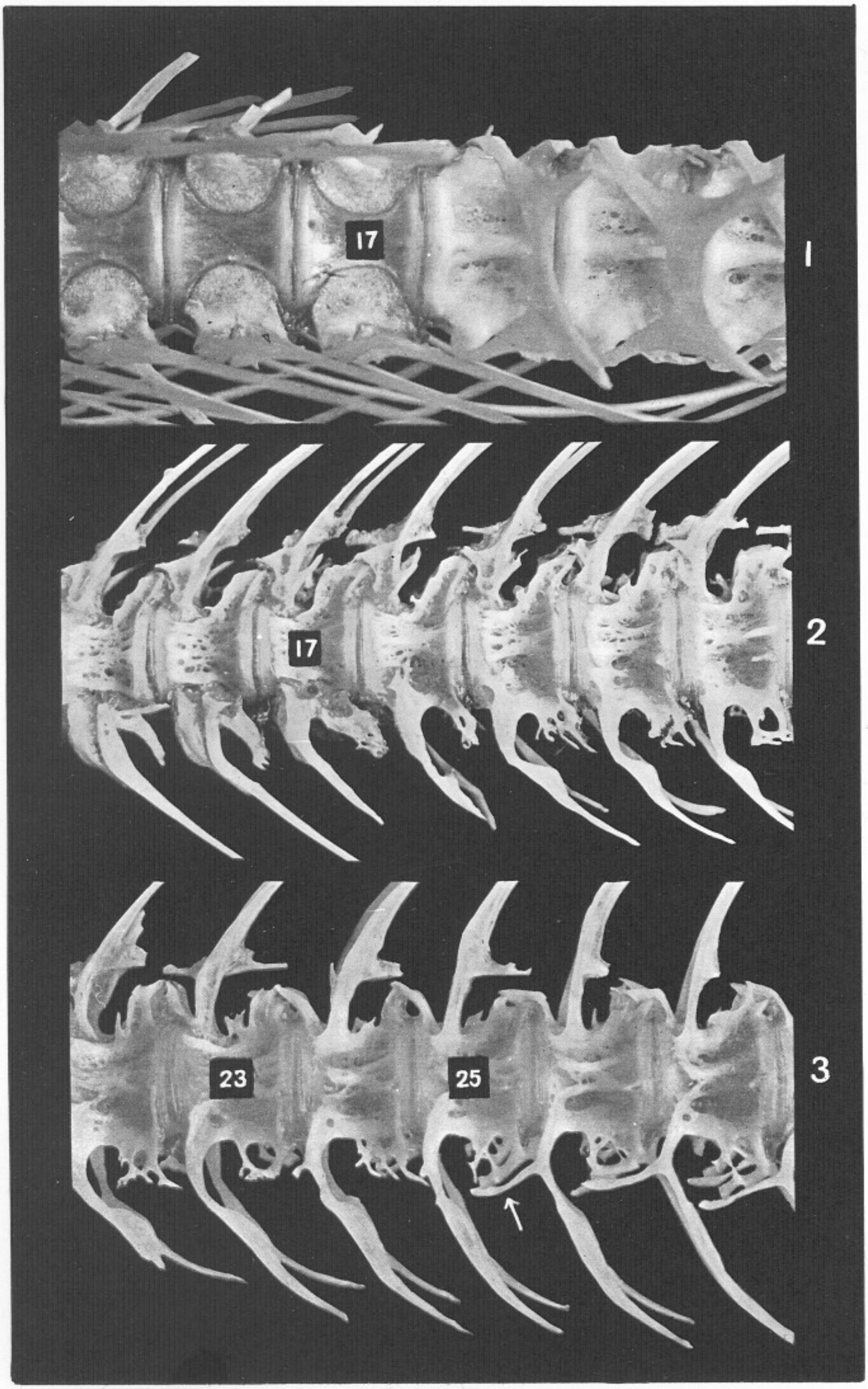
Fig. 3. Enlarged view of anterior end of backbone to show the form and position of the 1st neural spine in association with the cranium. Note also the open parapophyses.

PLATE XVI

Fig. 1. *Balistes capriscus*. The modified form of the anterior neural spines is to be associated with the support and functioning of the "trigger" mechanism. Note that the hypural of the 17th (penultimate) vertebra is autogenous from the centrum.

Fig. 2. *Zeus faber*. View of right side. A point of especial interest is the arrangement of the anterior neural spines in pairs—3 and 4, 5 and 6, 7 and 8.

Fig. 3. *Zeus faber*. Enlarged view of skull to show growth rings (indicated by arrow).



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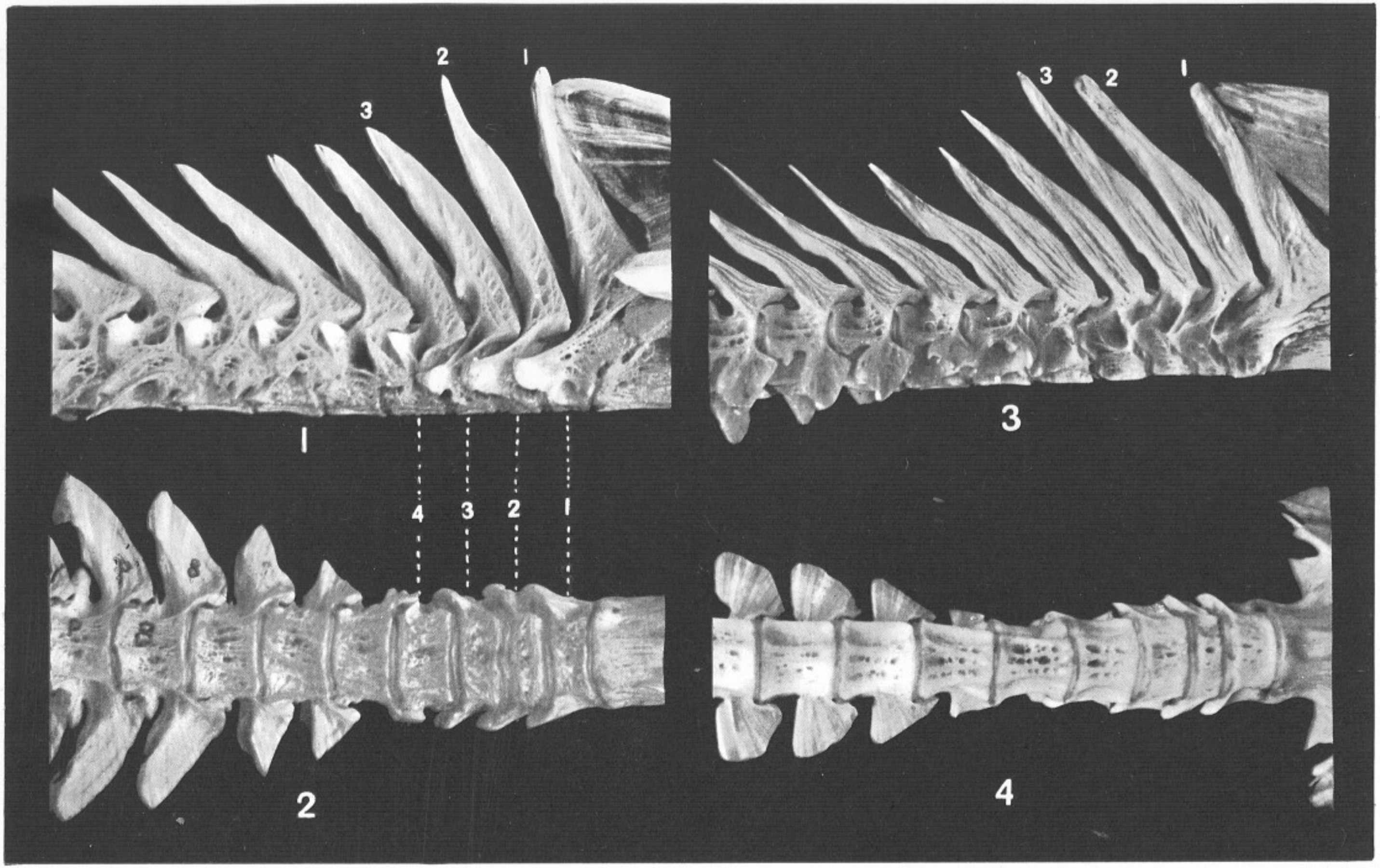
Figs. 1, 2 and 3. *Alosa alosa.*

PLATE II.



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Figs. 1 and 2. *Gadus callarias.* Fig. 3. *Gadus virens.* Fig. 4. *Molva molva.*

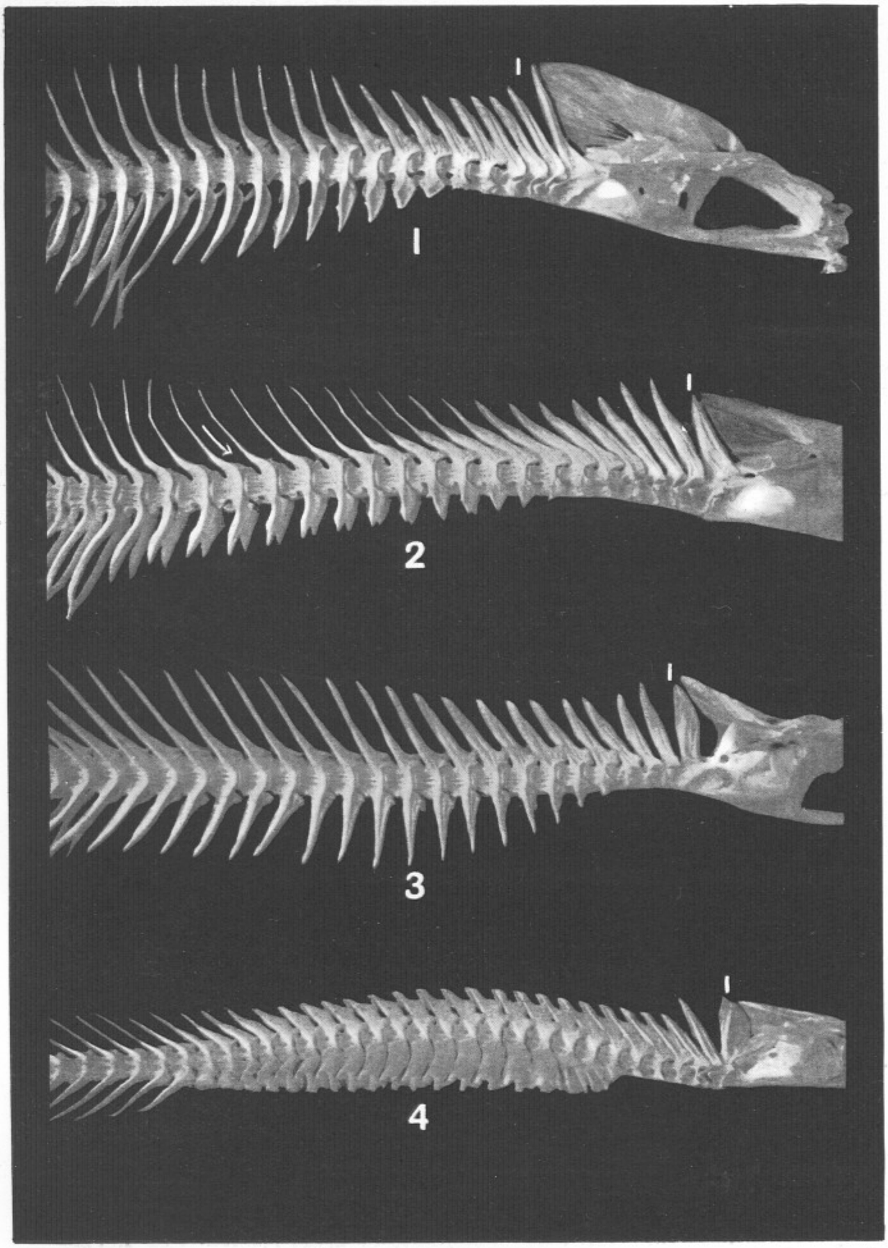

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Fig. 1. *Gadus luscus.* Fig. 3. *Mora mediterranea.*
Fig. 2. *Gadus pollachius.* Fig. 4. *Merluccius merluccius.*

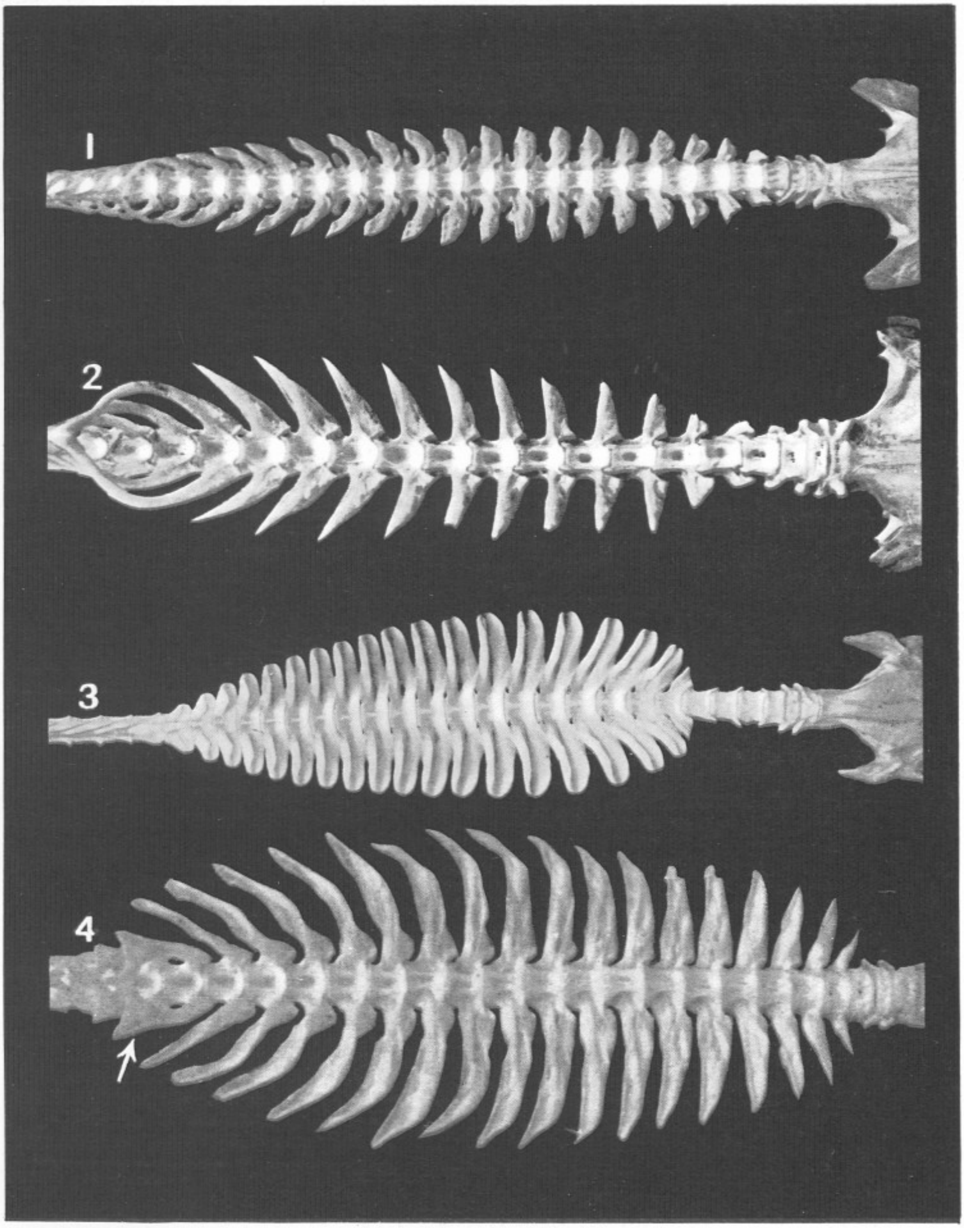

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Fig. 1. *Gadus merlangus.* Fig. 3. *Merluccius merluccius.*
Fig. 2. *Urophycis blennoides.* Fig. 4. *Gadus aeglifinus.*

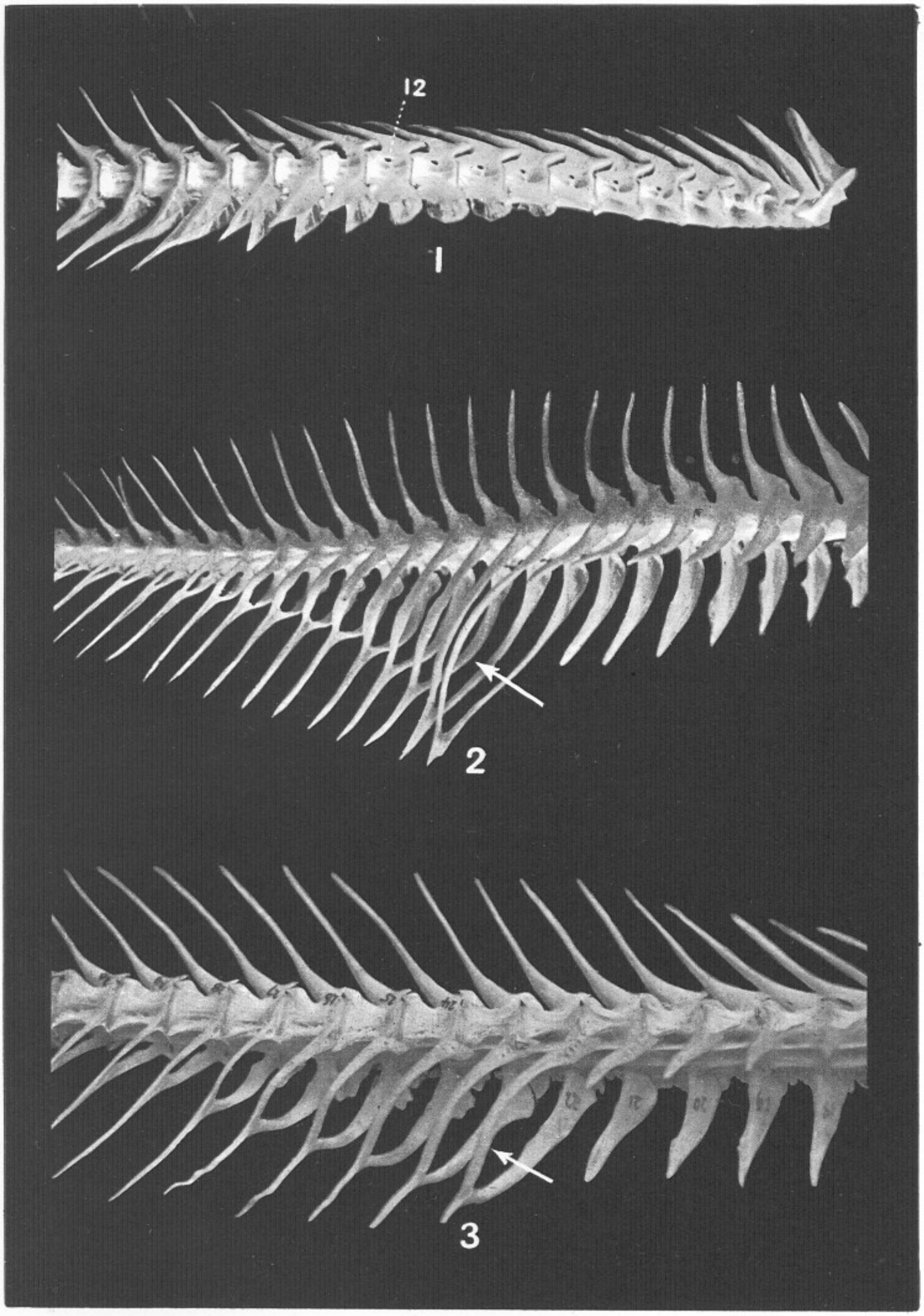

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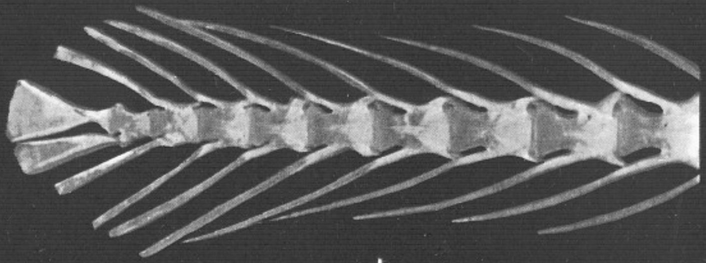
Fig. 1. *Onos sp.* (3-barbed rockling, form A).

Fig. 2. *Gadus luscus.* Fig. 3. *Gadus pollachius.*



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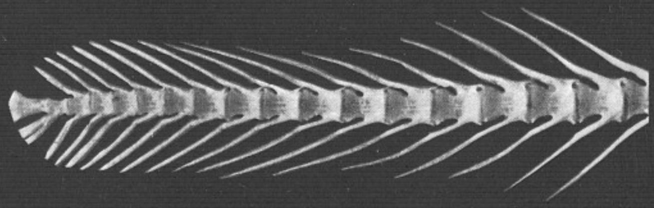

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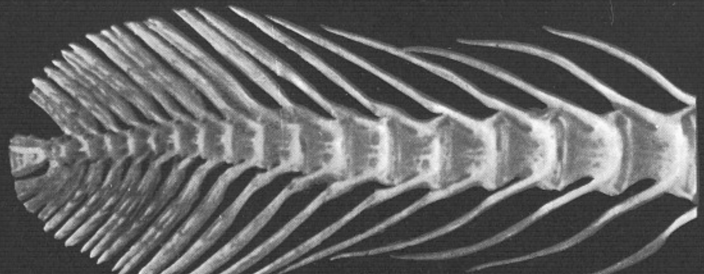

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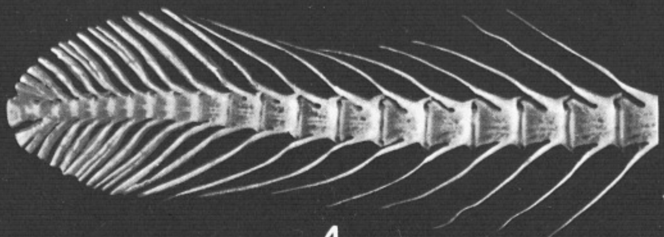

4

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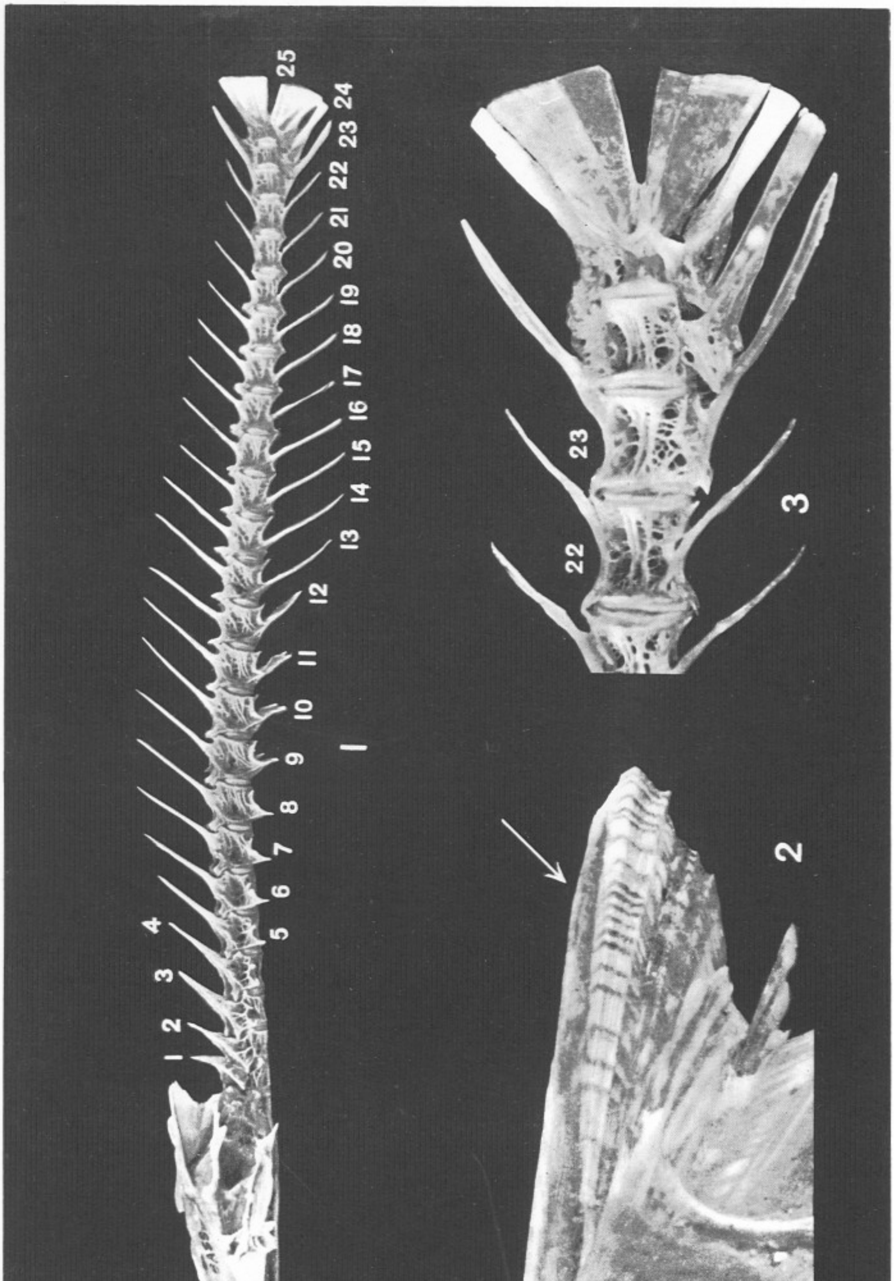
Fig. 1. *Urophycis blennoides.*

Fig. 2. *Gadus virens.*

Fig. 3. *Mora mediterranea.*

Fig. 4. *Gadus pollachius.*



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Figs. 1, 2 and 3. *Morone labrax.*

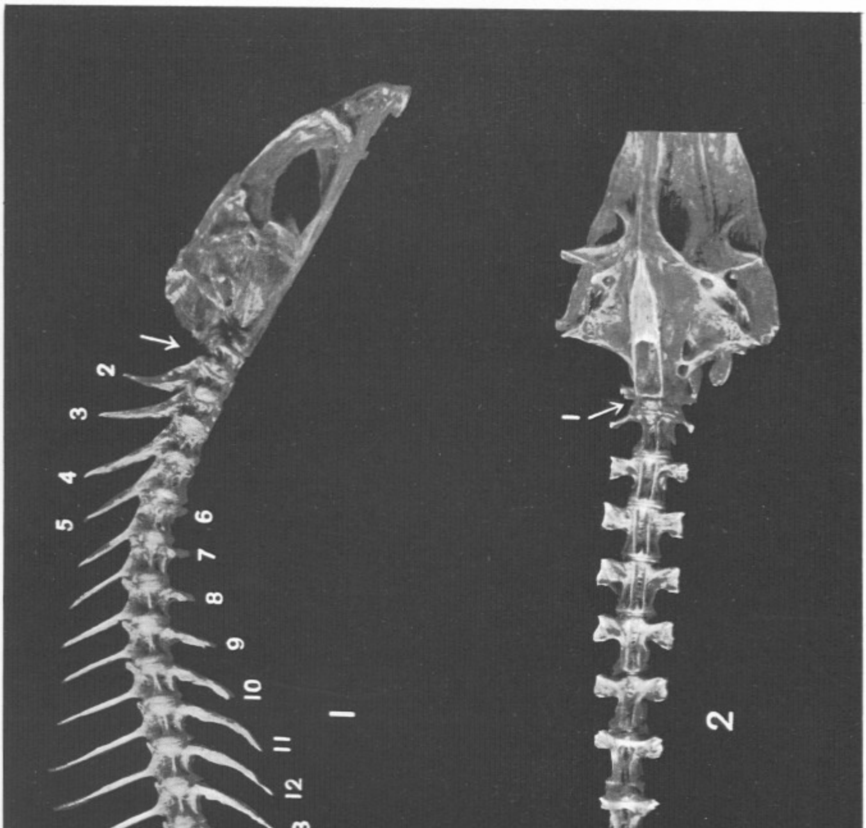

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Fig. 1. *Serranus cabrilla.* Fig. 2. *Pagellus centrodontus.*

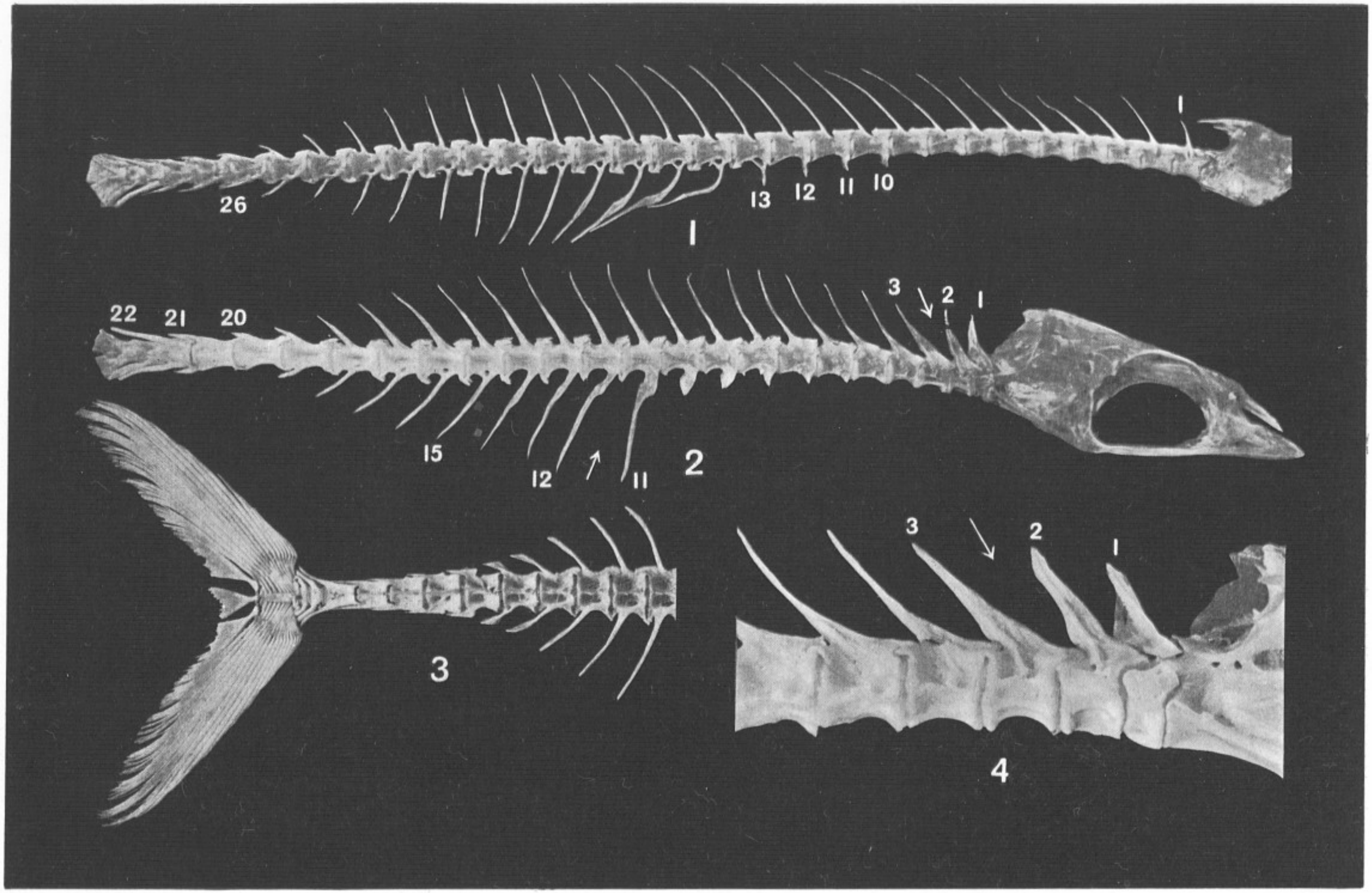

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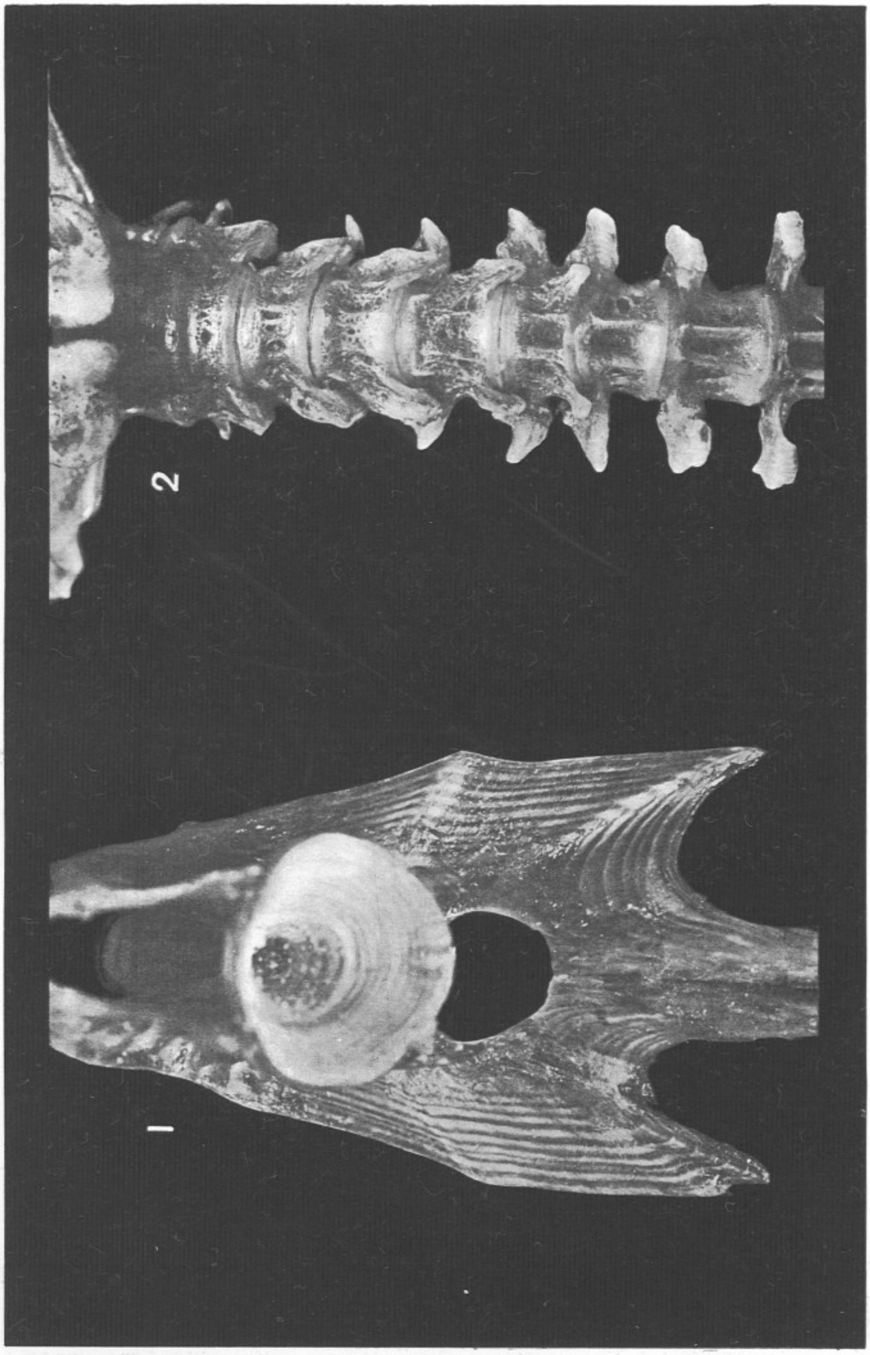
Fig. 1. *Scomber scombrus.* Fig. 2. *Caranx trachurus.*

Fig. 3. *Katsuwonus pelamys.* Fig. 4. *Caranx trachurus.*



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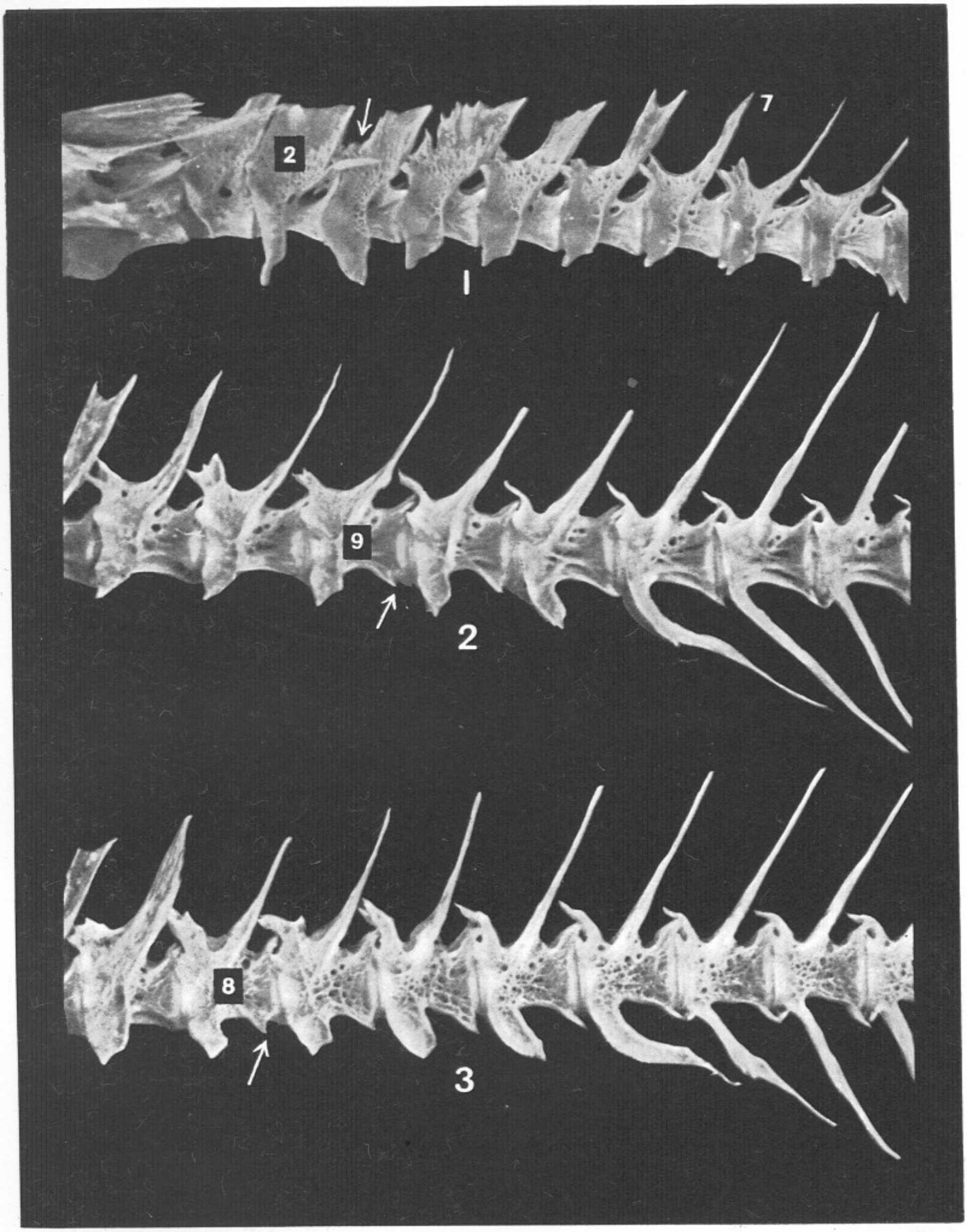
Figs. 1 and 2. *Labrus bergylta.*



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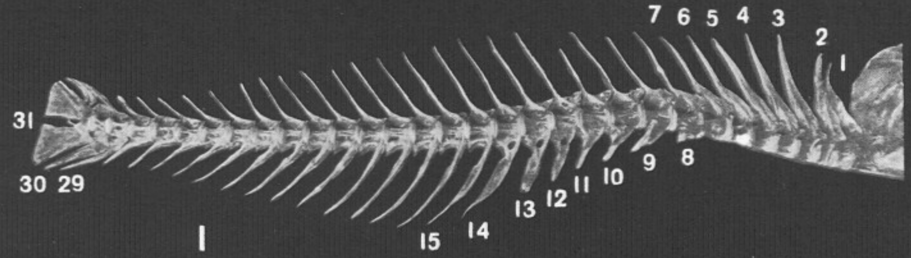
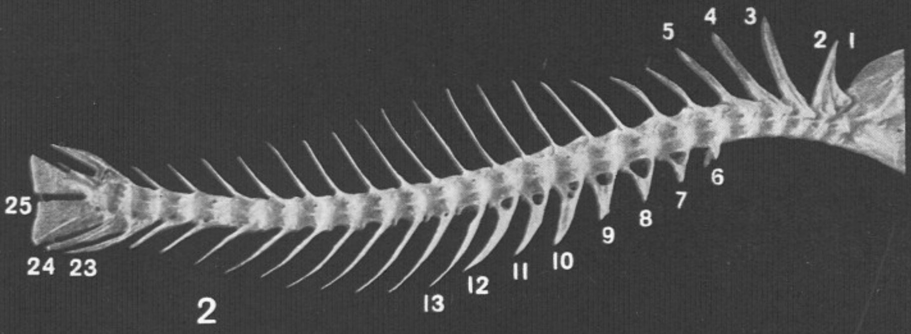
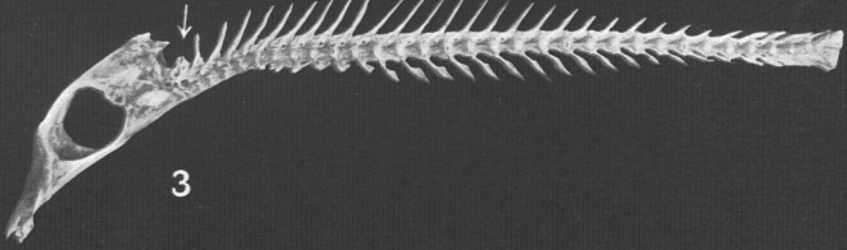
Figs. 1 and 2. Thick-lipped Grey Mullet. Fig. 3. Thin-lipped Grey Mullet.







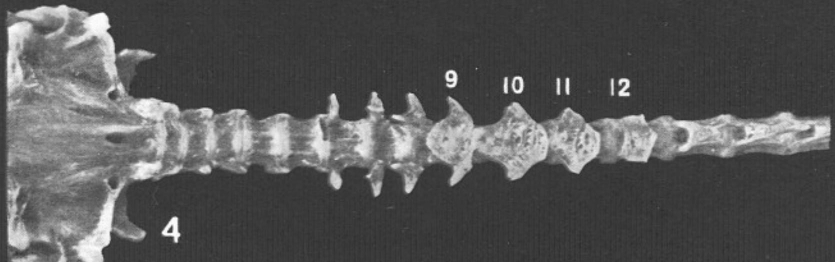


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Fig. 1. *Sebastes marinus.* Fig. 2. *Scorpaena dactyloptera.* Figs. 3 and 4. *Trigla lyra.*

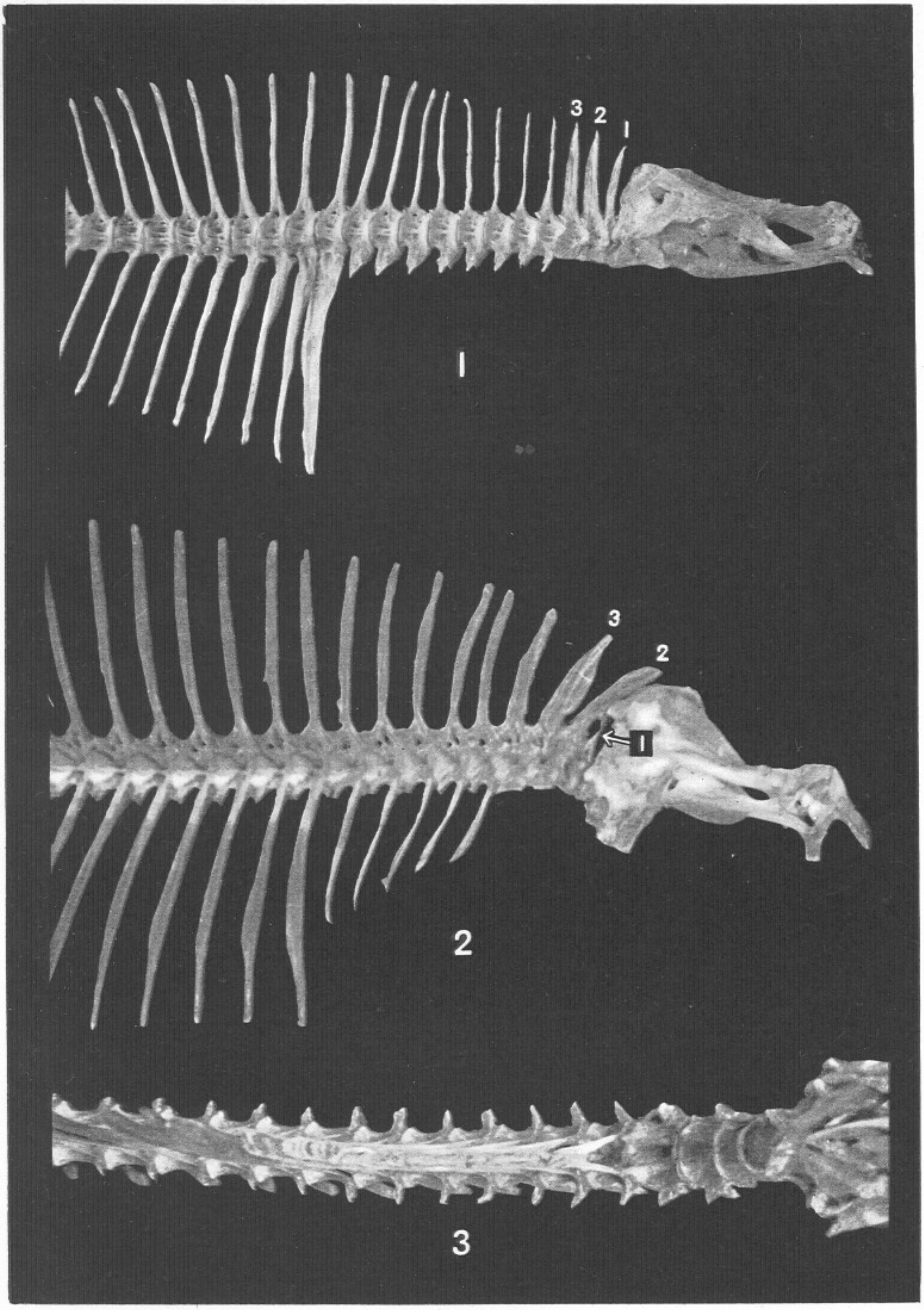

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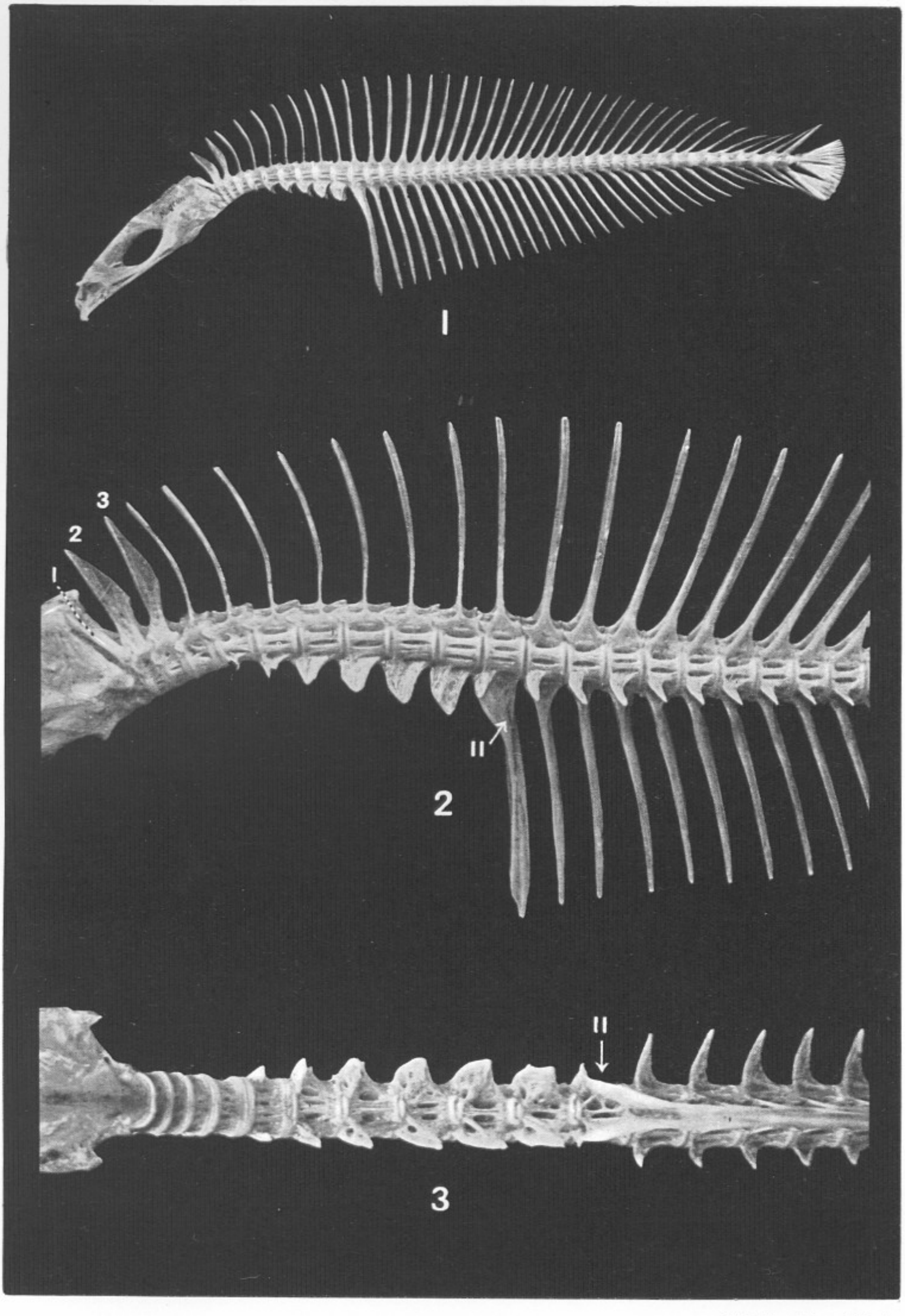
Fig. 1. *Pleuronectes flesus.* Figs. 2 and 3. *Solea solea.*



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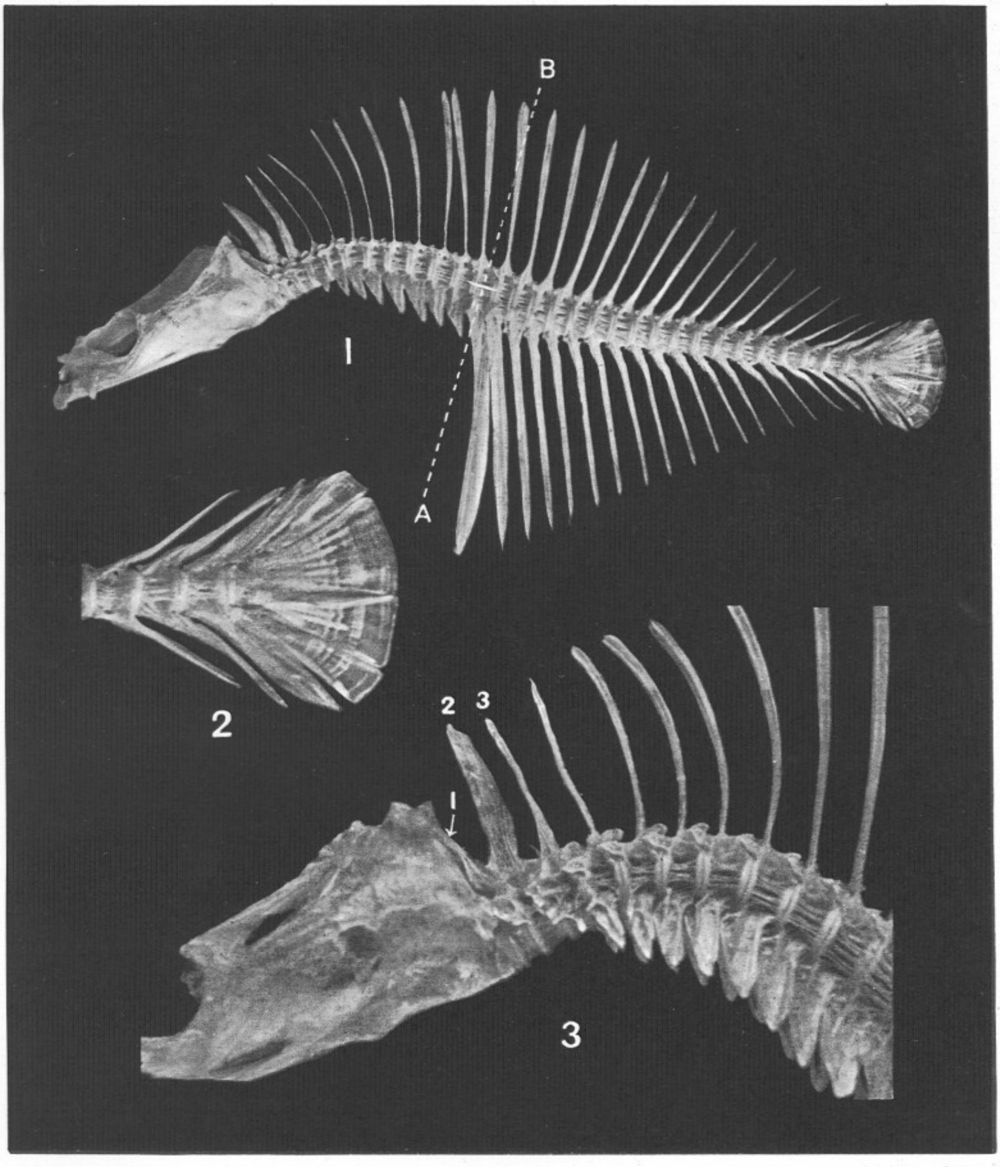
Figs. 1, 2 and 3. *Lepidorhombus whiff-iagonis.*



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Figs. 1, 2 and 3. *Rhombus maximus.*

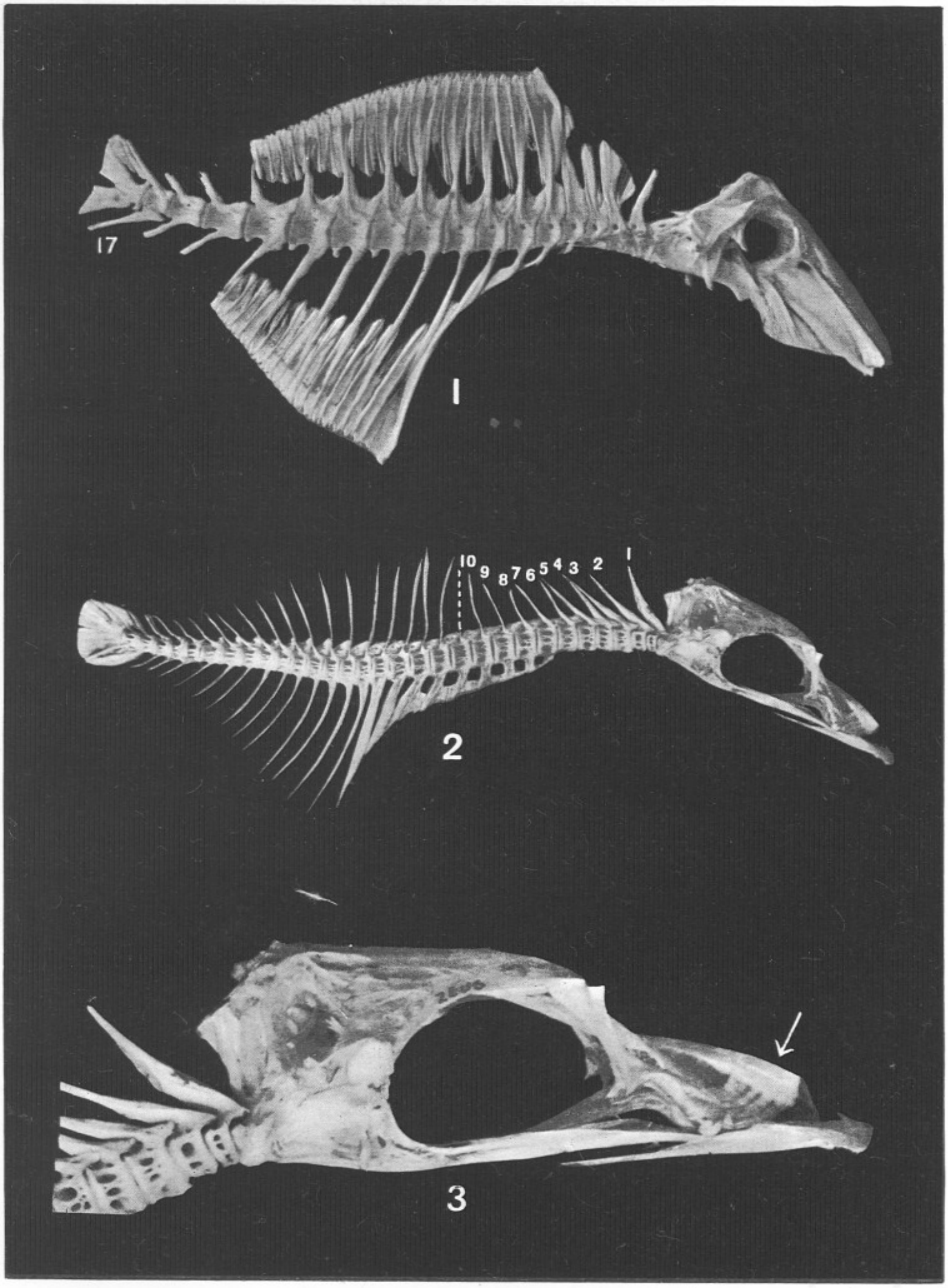

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Fig. 1. *Balistes capriscus.* Figs. 2 and 3. *Zeus faber.*