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# Guide to the Identification of North Sea Fish Using Premaxillae and Vertebrae 

J. Watt, G. J. Pierce, and P. R. Boyle<br>Department of Zoology<br>University of Aberdeen<br>Tillydrone Avenue<br>Aberdeen AB24 2TZ, Scotland<br>United Kingdom

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## 1. INTRODUCTION

This guide arose from four years of collaborative work on the diets of seals carried out by the Department of Zoology, University of Aberdeen, and by the Scottish Office Agriculture and Fisheries Department Marine Laboratory in Aberdeen. In addition to examining regional, seasonal, and species differences in diets of grey seals (Halichoerus grypus) and common seals (Phoca vitulina) using traditional approaches based on identification of otoliths in faeces and gut contents (Pierce et al., 1989, 1990b, 1991b,c,d), attempts were made to develop novel techniques involving serological detection of prey proteins (Boyle et al., 1990; Pierce etal., 1990a, c, 1991b), and methods available for diet analysis were reviewed (Pierce and Boyle, 1991; Pierce et al., 1993).

It was apparent that there was considerable potential for using skeletal remains other than otoliths to identify prey, and that the detection rates for most groups of prey fish were higher when these other bones were included in the analyses (Pierce et al., 1991a). Although, until recently, little use has been made of fish bones in studies on seal diets, they have been used extensively in studies on the diets of piscivorous fish (Newsome, 1977; Mann and Beaumont, 1980; McIntyre and Ward, 1986; Trippel and Beamish, 1987; Hansel et al., 1988), birds (White, 1936, 1953; Feltham and Marquiss, 1989) and otters (Fairley, 1972; Webb, 1976; Watson, 1978; Jenkins et al., 1979; Jenkins and Harper, 1980; Mason and Macdonald, 1980; Wise, 1980; Van der Zee, 1981; Wise et al., 1981; Gormally and Fairley, 1982; Herfst, 1984; Murphey and Fairley, 1985). Identification of fish bones is also a well-established tool in archaeological studies (Casteel, 1976; Wheeler and Jones, 1976, 1989; Scott, 1977; Morales and Roselund, 1979; Enghoff, 1983; Jones et al., 1983; Rackham et al., 1984; Jones, 1991). With few exceptions the above studies relied on reference collections for the identification of prey remains, there being no readily available guide to bones comparable to, say, Härkönen's (1986) guide to otoliths or Clarke's (1986) guide to cephalopod beaks.

The purpose of the present work, therefore, is to present a practical guide to the identification of some of the skeletal elements likely to be encountered during dietary analyses. There is a large and varied literature on fish osteology, some of which to a greater or lesser degree deals with identification of marine fish from the North Sea (e.g., Izquierdo, 1986; Desse et al., 1990). The present guide should be used in conjunction with such material.

It has not been possible to include all the species which might be encountered in the North Sea and we have, therefore, concentrated largely on four groups of fish known to be important in seal diets: the herrings and sprats (Clupeidae), the cod-fishes (Gadidae), the sandeels (Ammodytidae), and the flatfishes (Bothidae, Pleuronectidae, Soleidae). In addition to their importance in seal diets these groups contain most of the principal species of commercial value in this region. Greatest efforts have been directed at distinguishing these important species, both from one another and from commercially unimportant fish. It is hoped that this will be of particular value where it is difficult or impossible to discriminate between species on the basis of otoliths alone, e.g., between haddock (Melanogrammus aeglefinus), saithe (Pollachius virens) and pollack (Pollachius pollachius), or between the various Pleuronectidae. Identification from bones is also particularly important for species not usually identified from otoliths, either because the otoliths are readily digested, e.g., herring (Clupea harengus) and mackerel (Scomber scombrus), or because the head is often not ingested.

In addition to our coverage of these four main fish groups we have included descriptions and photographs of bones from a number of other species. This has been done where these species are known to occur frequently in seal diets, or where they might be confused with one or more of the principal targeted species.

While the guide has been compiled principally to assist in the analyis of seal diets, it is hoped that those attempting to identify the prey remains of other piscivores, such as otters, predatory fish, seabirds, cephalopods, and indeed humans, might also find it useful.

In common with the otolith and beak guides, we hope that the present guide can be used by inexperienced workers with no access to reference material. We would nevertheless stress that a reference collection is invaluable when making and checking identifications of prey species. Thus, if a premaxilla is tentatively identified using this guide, comparison of it and other bony remains with reference material on the relevant species is useful to confirm identification. Also, at least in the first instance, identifications based on this guide and/or reference material should be checked by an experienced researcher. Obviously, information on bones should not be used in isolation when other information is also available, e.g., from otoliths.

Regression equations relating bone size to fish size are included for both premaxillae and vertebrae, but it must be recognized that, firstly, the size of vertebrae varies within individuals, and, secondly, bones are subject to digestive degradation and may therefore have been reduced in size. Our regressions of fish size on vertebra size make use of the first caudal vertebra, which is generally as large as or larger than the remaining caudal vertebrae. The extent of size reduction of fish bones during passage through the gut is likely to vary between predators and between fish species, with body size, and even between different bones of one individual. We have made a preliminary study of bone digestion in vitro (Pierce et al., 1993), and Jones (1986) carried out small-scale in vivo studies, but much more work is needed to establish usable correction factors. Obviously this is only one of many potential sources of bias in assessing diet from prey remains. For further information on biases and correcting for biases, see Da Silva and Nielson (1985), Jobling and Brieby (1986), Murie and Lavigne (1986), Jobling (1987), Murie (1987), Prime and Hammond (1987), Dellinger and Trillmich (1988), Nordoey and Blix (1988), Harvey (1989), and Pierce and Boyle (1991).

The layout of the guide is as follows. Section 2 provides a general introduction to fish osteology and explains the rationale for choice of bones. The bulk of the guide then concentrates on premaxillae (Section 3) and caudal vertebrae (Section 4). Sections 3.1 and 4.1 respectively should be consulted for general descriptions of these bones. Keys are provided with accompanying diagrams where appropriate, followed by photographs and detailed descriptions for each species covered. It is suggested that all the photographs be examined to provide a general feel for the range of bone forms encountered before any use is made of the keys. The keys may then be used for indications of which photographs and descriptions should be examined in more detail. Section 5 contains pictures and brief descriptions of a range of other skeletal elements useful for identifying particular species. The appendices contain information on methods used for preparation of bones, both in samples and for the reference collection, along with a supplementary bibliography and addresses for other workers in the field and locations of reference material.

This guide cannot aim to be comprehensive. The majority of skeletal elements are not described, and species coverage is restricted. Nevertheless, if it proves to be useful, we hope to be able to produce updated versions in which species coverage, and possibly the range of bones examined, is increased.

GJP

## 2. THE SKELETON OF BONY FISHES

### 2.1 Introduction

In order to assign bones found in scats or gut contents to a particular prey species or group it is first necessary to decide which skeletal element one is looking at. Is it an entire bone or a fragment? Is it a jaw bone? If so, is it a dentary, articular, maxilla or premaxilla? Which side, left or right, of the fish did it come from? The skeleton of bony fishes is varied and complex and a detailed description of fish anatomy is beyond the scope of this guide. The following description is brief and general, therefore, and is intended chiefly to familiarize the reader with those skeletal elements which have been shown to be useful in diet analysis. The nomenclature used follows that set out by Wheeler and Jones (1989). Detailed descriptions of single elements are given in the appropriate sections of the guide. More exhaustive coverage of the general anatomy of fish may be found in Goodrich (1930) and Wheeler and Jones (1989).

The skeleton of fishes may be thought of as consisting of three main parts: the head skeleton, comprising the skull and related structures, the axial skeleton comprising the vertebral column plus the caudal bones, and the appendicular skeleton which comprises the skeletal supports for the various fins.


Figure 1. Skull of a generalized teleost fish (after Gregory, 1933). ART, articular; CHY, ceratohyal; CLE, cleithrum; COR, coracoid; DEN, dentary; EHY, epihyal; FRO, frontal; HYM, hyomandibular; IOP, interopercular; LAC, lachrymal; MAX, maxilla; NAS, nasal; OPE, opercular; ORB, orbitals; PAL, palatine; PAR, parietal; PAS, parasphenoid; PMX, premaxilla; POP, preopercular; POT, posttemporal; QUA, quadrate; SCL, supracleithrum; SOC, supraoccipital; SOP, subopercular; URO, urohyal.

The head skeleton of the bony fishes (fig. 1) is more complex than that of any other class of vertebrate (Hildebrand, 1982), the bones being much more numerous than in birds or mammals. Gregory's vast monograph (Gregory, 1933) provides an overview of the tremendous diversity of structure to be found in fish skulls and in their many component parts. For the purposes of diet analysis however, relatively few bones have been shown to be useful, and the following description will concentrate on these. The bones of the head may be split into those forming the neurocranium and those forming the branchiocranium.

### 2.2 The neurocranium

That part of the head skeleton which encloses the brain and sense organs is referred to as the neurocranium. The neurocranium is made up of numerous fused bones, of which only those with most diagnostic potential will be mentioned.

The roof of the neurocranium, lying above the brain and the eyes, is formed from the paired frontal and parietal bones (fig. 2). The frontals are heavily ridged and show considerable interspecific variation. At their posterior end the frontals join the supraoccipital, which in many species forms a high crest to which the muscles of the trunk are attached. The supraoccipital is the most posterior of the bones in the dorsal midline of the neurocranium. Ventrally, the most posterior bone is the basioccipital, by which the skull is attached to the first (atlas) vertebra. Anteriorly, the basioccipital joins to the basisphenoid and parasphenoid, which make up the floor of the braincase and the long bar of bone running below and between the orbits. At the anterior extremity of the parasphenoid is the prevomer (= vomer), an unpaired bone lying behind the premaxillae in the midline of the mouth.


Figure 2. Neurocranium of a gadoid fish. BSO, basioccipital; FRO, frontal; PAR, parietal; PAS, parasphenoid; PRV, prevomer (vomer); SOC, supraoccipital.

Few bones in the neurocranium have been shown to be useful in analysing predator diets. The basioccipital/parasphenoid complex is usually distinctive at species level (Wheeler and Jones, 1989; Gordon Howes, pers. comm.) as are the frontals and supraoccipital. Williamson (1902), for instance, pointed out differences in the shape of the anterior end of the frontals of pollack and saithe. The shape of the prevor eer varies between families and, in some groups at least (e.g., Gadidae), its shape and the pattern of tooth sockets on its surface are species specific.

### 2.3 The branchiocranium

### 2.3.1 Jaw bones and jaw suspensions

Since they are directly involved in feeding and in the capture of food the jaw bones of fish have become modified in many ways. As a result they offer excellent prospects for identification, usually to the level of species. The jaws and jaw suspensions are all paired bones, with a left and a right element.


Figure 3. Jaw bones of cod (Gadus morhua). ART, articular; DEN, dentary; MAX, maxilla; PMX, premaxilla; RET, retroarticular.

The margin of the lower jaw is formed by the dentary (fig. 3), which, in most species, bears teeth along its dorsal edge. Viewed dorsally the dentary curves around towards its opposite number, meeting it in an anterior symphysis. Posteriorly the dentary bears a deep V-shaped notch into which the articular is inserted. The articular is pointed anteriorly where it inserts into this notch. Posteriorly it is broad and bears a deep articulating notch where it hinges with the quadrate, providing the articulation for the lower jaw (fig. 1, see also Mujib, 1967).

The articular is in fact composed of two elements. The smaller of these is located on the ventral margin, beneath the articulating notch. In some texts the smaller element is referred to as the retroarticular while in others it is called the articular. The larger element is known as the angular.

The upper jaws are formed by the premaxillae and maxillae. The premaxillae compose the anterior ends of the upper jaws. In most species they are toothed on their ventral or ventro-medial surface. The maxillae of either side articulate with the inner surface of the anterior ends of the premaxillae, lying above them at the sides of the jaws (fig. 1).

The jaws are connected to the neurocranium via a series of bones which, together, make up the mandibular arch (fig. 4). The largest of these bones is the hyomandibular, which is a key bone in understanding the structure of the head skeleton of fish, since it is through it that the jaw suspensions, the opercular series, and the hyoid arch are suspended from the skull. The hyomandibular is a complex bone, generally fan-shaped or hatchet-shaped (fig. 4). Its ventral margin joins to the symplectic to which is attached the quadrate. The latter provides articulation for the lower jaw via the articular. Anterior to the symplectic and quadrate are the pterygoid bones: the metapterygoid, entopterygoid, and ectopterygoid. These form the palate and the floor of the
orbit. Lying between the pterygoids and the maxilla is the palatine, which articulates with a process on the anterior end of the maxilla.

Of the above bones the four main elements making up the jaws, i.e., dentary, articular, premaxilla and maxilla, are all characteristic of species groups or, in many cases, individual species. A guide to the dentaries and articulars of many of the marine and freshwater fishes of Europe has been prepared by Izquierdo (1988).


Figure 4. Mandibular arch of cod. ECP, ectopterygoid; ENP, entopterygoid; HYM, hyomandibular; MPT, metapterygoid; PAL, palatine; QUA, quadrate; SYM, symplectic.

### 2.3.2 Opercular series

The gill flaps of fishes are composed of four bones which together make up the opercular series. The most posterior of these is the opercular (fig. 5). It hinges with a process on the hyomandibular via a socket at its antero-dorsal corner (fig. 1). The opercular can be raised and lowered by muscles attached to its surface, controlling the flow of water across the gills. Variation in the form of the fulcrum and in the pattern of ossification over the opercular surface allows identification to species in many instances.

The second major bone in this series is the preopercular. In most species the preopercular is roughly crescent shaped, and in some it bears spines and/or serrations along its lower edge. The preopercular is often thicker and more robust than the opercular and can, therefore, be useful in identification.

The other two bones in this series are the subopercular and the interopercular. The subopercular lies beneath the opercular, covering the branchiostegal rays. In most species it is thin and flat, with few distinguishing features. However, in the sandeels (Ammodytidae) it is serrated and "frilly" in appearance and is useful diagnostically. The interopercular is a thin featureless plate of bone lying beneath the preopercular and separating it from the subopercular.


Figure 5. Opercular bones of cod. IOP, interopercular; OPE, opercular; POP, preopercular; SOP, subopercular.

### 2.3.3 Hyoid arch

The hyoid arch comprises a number of paired bones lying ventral to the throat of the fish (fig. 6). The most dorsal bone of this arch is the interhyal, a small cylindrical bone connecting the hyoid arch to the hyomandibular and symplectic. Ventrally the interhyal attaches to the epihyal which, in turn, is joined anteriorly to the more elongate ceratohyal. The epihyal and ceratohyal bear the branchiostegal rays, which give rigidity to the gular area. Anteriorly the ceratohyal is joined to the hypohyal. The hypohyals of both sides join to the unpaired basihyal, lying in the midline of the throat and forming the base of the tongue. Below the basihyal, and also in the midline is the urohyal, a small robust bone which, although not truly part of the hyoid arch, is included here for convenience.

Of the bones of the hyoid arch the ceratohyal and epihyal are the most easily identifiable (Wheeler and Jones.1989). The urohyal is frequently specifically distinct and photographs of urohyals from flatfish are presented in Section 5. Kusaka (1974) has prepared a monograph on the urohyal which is also useful for identification purposes.


Figure 6. Hyoid arch of a gadoid fish (after Wheeler and Jones, 1989). BRS, branchiostegal rays; CHY, ceratohyal; EHY, epihyal; HHY, hypohyal; IHY, interhyal; URO, urohyal.

### 2.3.4 Branchial arches

The branchial arches are a series of highly cartilaginous bones of the pharynx which are concerned with both respiration and feeding. They provide support for the gills and form the outer margin of the buccal cavity. Additionally, in many species, they bear teeth and gillrakers adapted to specific diets.

In most fishes there are four branchial arches on each side, each arch composed of several elements (fig. 7): epibranchials, ceratobranchials and hypobranchials. Joining the arches of each side dorsally are the pharyngobranchials, lying beneath the base of the cranium. Ventrally the arches are joined by the basibranchials. In the Cyprinidae and Catostomidae the bones of the gill


Figure 7. Branchial arches of Salmo sp. (after Goodrich, 1930). BBR, basibranchial; CBR, ceratobranchial; EBR, epibranchial; HBR, hypobranchial; PBR, pharyngobranchial.
arches are highly modified and bear teeth. These bones are characteristic and frequently identifiable to species (Webb, 1975; Hansel et al., 1988; Wheeler and Jones, 1989). In the wrasses (Labridae) too there are highly distinctive and very robust pharyngeal teeth which are remarkably persistent after the death of the fish and may be found in scats (see Section 5). These teeth have probably developed in response to a diet of hard-shelled molluscs and crustaceans (Wheeler, 1969).

### 2.4 Axial skeleton

The axial skeleton is made up of the bones of the vertebral column and those which support the caudal (tail) fin. The portion of the axial skeleton forming the spine of fish is made up of numerous segmentally arranged vertebrae, extending from the base of the skull to the tail (fig. 8). As the structure of the vertebrae and vertebral column is described in detail in Section 4 it will be dealt with only briefly here.

The vertebral column gives rigidity to the body and provides attachment for many of the muscles of the body. A neural arch on the dorsal surface of each vertebra gives protection to the spinal cord while various projections provide support for the attachment of fin rays and ribs.

In most bony fish the vertebral column ends at the caudal fin, exceptions being the eels and eel-like fishes which do not possess a caudal fin and the sturgeons (Acipenseridae), gars (Lepisosteidae) and bowfin (Amiidae) in which the vertebrae continue along the upper lobe of the fin. This latter arrangement is termed a heterocercal tail, with the upper lobe longer than the lower. Most other fishes have homocercal tails which are externally roughly symmetrical.


Figure 8. Vertebral column and neurocranium of a teleost fish. ATL, atlas vertebra; BSO, basioccipital; AV, abdominal vertebrae; CV, caudal vertebrae; UST, urostyle; RIB, ribs.

In fishes with homocercal tails the penultimate and ultimate vertebrae are modified to provide support for the fin rays. The ultimate vertebra bears a number of flattened bony plates, the hypurals and epurals, which articulate with the lower and upper fin rays respectively. The whole structure of ultimate vertebra and associated bony plates is termed the urostyle. Whitehouse (1910) gives a detailed account of the structure of the tail fins of teleost fish.

### 2.5 Appendicular skeleton

The appendicular skeleton provides support for the paired pectoral and pelvic fins. The pectoral girdle (fig. 9) is usually well developed and contains a number of distinctive bones. It is situated close behind the head and is attached to it by the posttemporal bone. The posttemporal is usually forked, the upper and lower forks connecting to the epiotic and opisthotic bones of the neurocranium respectively. Ventrally the posttemporal overlaps the supracleithrum, a strong strut of bone which attaches it to the cleithrum. The cleithrum is usually one of the largest bones in any fish. It is long and curved, with a hollow underside to which large blocks of muscle are attached. The pectoral fins are supported on a series of small bones (the radials) which articulate with the scapula and coracoid. Behind the cleithrum there are usually one or more long narrow bones, the postcleithra, which extend ventrally. Hansel et al. (1988) demonstrated that the shape and size of cleithra could be used to identify and estimate the sizes of prey fish, while Wheeler and Jones (1989) state that cleithra, supracleithra and posttemporals are usually identifiable to species.

The pelvic girdle in fish (fig. 9) is generally much reduced. Its position varies greatly; in some (e.g., the salmonids) it is sited well back on the belly, while in many others (e.g., gadoids) it lies close to the pectoral girdle. The pelvic girdle consists of a pair of L -shaped bones, the basipterygia, which are fused together at the midline of the fish. The rays of the pelvic fins articulate on the outer portions of the basipterygia. The pelvic girdle is not particularly robust or distinctive and is unlikely to be useful in analysing predator diets.


Figure 9. Pectoral and pelvic girdle of a gadoid fish. BPT, basipterygium; CLE, cleithrum; COR, coracoid; PCL, postcleithrum; PTO, posttemporal; RAD, radials; SCL, supracleithrum; SCA, scapula.

### 2.6 Rationale for choice of elements included in guide

From the above brief resume of fish skeletal anatomy it will be obvious that the possible choice of elements for prey identification is wide. Due to constraints of time it has been necessary, therefore, to concentrate on a limited array of bones for inclusion in the guide. In doing this three criteria were considered to be of fundamental importance:

1. The elements chosen should be known to occur frequently in the samples to be analysed.
2. The elements chosen should be diagnostically useful: identifiable to familial level or, preferably, to species level.
3. The elements chosen should be useful in the identification of a wide variety of prey species.

Several further criteria were also considered to be of value:
a) The elements chosen should be recognizable by those unfamiliar with the detailed anatomy of fish.
b) The elements chosen should not be unduly prone to mechanical damage or digestion, and should therefore remain more or less intact in the samples to be analysed.
c) The elements chosen should have potential for the estimation of prey size in addition to identity.
d) The elements chosen should be useful in the analysis of diet in a variety of predators.
e) The elements chosen should have potential for estimating minimum numbers of prey ingested.
f) The elements chosen should not already have been the subject of similar guides or keys.

No element perfectly fits all the above criteria, since some of them militate against one another. For instance, an element of which there are many in an individual fish is likely to be well represented in samples, but may not be very useful for estimating numbers of prey ingested. The final choice was, therefore, a compromise between several of these criteria.

The most commonly occurring elements in most faecal or digestive tract samples are (not surprisingly in view of the large number present in a single fish) vertebrae. Because of their common occurrence it was felt to be vital that they be included in the guide. Vertebrae have a number of additional advantages: they may be used to estimate prey size (Wise,1980), they are easily recognized even when damaged, there are many vertebrae in an individual fish so chances of retrieving well-preserved specimens are good, and, finally, they may be useful in those cases when the heads of fish, and, therefore, the otoliths and paired head bones, are not ingested.

Other recognizable elements known to appear in seal digestive tracts and scats include jaw bones, prevomers, pharyngeal bones, opercular bones, cleithra, hyomandibulars, urohyals, posttemporals, palatines, and otic capsules (Pierce et al., 1991a; Houseman, 1992). Of these, jaw bones were considered to have a number of advantages over other elements. Being directly involved in feeding, fish jaws have been subject to much modification and adaptation, providing the variety of form required for specific identification. Despite this variety of form, however, most fish jaws remain recognizable as such, and so may be relatively easily distinguished from other elements in faecal or stomach samples. Furthermore, selected measurements of jaws have been shown to be good predictors of fish length and weight (Hansel et al., 1988; Pierce and Boyle, 1991).

Of the four main jaw bones - dentaries, articulars, premaxillae, and maxillae - premaxillae offer the advantage of robustness and ease of description. Furthermore, descriptions of dentaries and articulars from a wide variety of fish species are provided by Izquierdo (1988), and concentration on these elements would inevitably have led to duplication of information already available.

In the following two sections, therefore, the premaxillae and vertebrae of targeted fish species will be described in detail.

## 3. PREMAXILLAE

### 3.1 Structure and size

### 3.1.1 Description

The premaxillae are a pair of curved bones which form the anterior margin of the upper jaw. In most species they are tooth-bearing. However, since in many species the attachments of tooth to bone are easily broken, some or all of the teeth may be missing in samples taken from scats or stomach contents.

A generalized premaxilla is shown in figure 1. It should be noted, however, that since this element is extremely variable, not all the features shown in figure 1 are well defined on premaxillae from all species.


Fig. 1b


Fig. 1c

Figure $1 \mathrm{a}-\mathrm{c}$. Three views of the left premaxilla of a gadoid fish. Fig. 1a, lateral view: APC, anterior premaxillary cleft; ARP, articular process; ASP, ascending process; IPN, interprocess notch; PMP, postmaxillary process; RAM, ramus. Fig. 1b, medial view: ART SUR, articular surface; FOA, fossa; FOL, fossa lamella. Fig. 1c, ventral view (showing occlusal surface): BUC SOC, buccal (outer) socket row; LIN SOC, lingual (inner) socket row.

The generalized premaxilla consists of a curved shaft, the ramus, which constitutes the edge of the upper jaw. The ramus is generally blunt anteriorly where it curves medially towards its opposite number. The anterior surface may be grooved or notched for the insertion of cartilage or fibrous tissues between the opposing premaxillae. This groove, when present, is referred to as the anterior premaxillary cleft. The ventral, or ventro medial, surface of the ramus is usually toothed (fig. 1c).

Three processes arise from the dorsal surface of the ramus. The most anterior of these is the ascending process. In fish with protrusible jaws (e.g., bullrout, p. 113) the ascending process may be very long, allowing the premaxilla to slide forwards as the jaws are extended. In other species, such as many of the isospondylous fishes, the ascending process may be much reduced or absent (e.g., sprat, p. 30). Immediately posterior to the ascending process is the articular process, the medial surface of which articulates with the anterior end of the maxillary. As with the ascending process, the articular process may be much reduced in some species. Together, the ascending and articular processes will be referred to as the anterior processes. In many species there is a fossa between the two anterior processes bounded medially by a sheet of bone - the fossa lamella.

The third process arising from the ramus is called the postmaxillary process. It projects upwards and in most species lies against the medial surface of the maxillary. This process is usually a thin sheet of bone and is frequently damaged or absent in premaxillae taken from stomachs or scats.

In most species the left and right premaxillae are mirror images of one another. However, in the flatfishes this symmetry has been lost, and in the pleuronectids and soles the left and right elements differ significantly.

The first part of this section of the guide describes the left premaxillae of all target species. The right elements of pleuronectids and soles are described at the end of the section.

### 3.1.2 Estimation of fish length

In order to estimate fish size from bone size five measurements of premaxillae may be taken as indicated in figures $2 \mathrm{a}-\mathrm{e}$. In every case measurements should be taken in straight lines, without correcting for the curvature of the bone. Measurements should be taken as follows:

PMXL: total length of premaxilla. PMXL should be measured from the most anterior point of the bone to the most posterior. Since PMXL is one of the longest measures of the bone it may be measured easily and accurately. However, it has the very major drawback that, since the posterior portion of the ramus is usually very delicate, it is often not possible to ensure that the bone is complete prior to measuring.

PMXHH: height of ascending process (head height). This measurement is made from the highest point of the ascending process to the ventral surface of the ramus. Teeth and tooth sockets were excluded from this and all other measurements. Great care should be taken to ensure that the ascending process is complete prior to measuring. This is particularly the case for species in which the ascending process is tall and easily broken.

PMXHL: length of the two anterior processes or (head length). Head length is measured from the most anterior point of the ascending process to the most posterior point of the articular process.

PMXAH: height of articular process (articular height). PMXAH should be measured from the highest point of the articular process to the ventral surface of the ramus. It is a useful measure should the ascending process be damaged, particularly since the articular process is often robust. However, in some species, such as the clupeids, the articular process is not distinct and cannot, therefore, be measured.

PMXCL: cord length of premaxilla. This measurement was used for clupeid premaxillae as it is the longest and most easily taken measurement. PMXCL is measured between the most dorsal point of the bone to the most posterior.

PMXHW: head width of premaxilla. This measurement was used only for sandeels since the structure of the anterior processes of sandeel premaxillae make it impossible to define PMXHH without ambiguity. It is taken between the antero-lateral and antero-medial extremities of the bone.

(d)

(e)


Figure 2. Measurements of premaxillae (a-e)

For each measurement regressions of bone size on fish length are presented under the species descriptions. Fish lengths are generally given as total length (TL), although in one or two instances where specimens were damaged it has been necessary to use standard lengths (SL). Note: all regressions involving logarithmic relationships make use of natural logarithms.

Where too few specimens of any species were examined for meaningful regression equations to have been calculated, the fish length and bone measurements are presented for the available specimens. This will permit estimates of fish length to be made from bones found in samples, based on the assumption that there is a linear proportional relationship between bone size and fish length. Fish length is calculated from the assumed relationship

$$
I_{1} / q_{1}=I_{2} / q_{2}
$$

where $1_{1}=$ length of unknown fish from sample; $q_{1}=$ length (or other measurement) of bone from sample; $1_{2}=$ known length of reference fish; $q_{2}=$ length (or other measurement) of bone from reference fish. Thus,

$$
I_{1}=q_{1} I_{2} / q_{2}
$$

This 'proportional method' tends to be less accurate than the regression method (Casteel, 1976), since for most measurements a strictly linear relationship may not exist. Casteel showed that the magnitude of the inaccuracy arising from the use of this method varies directly with the difference between the length of the known and unknown specimens. Therefore, when measurements of bones from more than one specimen are presented, fish length should be estimated using the measurements from whichever bone which is closest in size to that from the sample being analysed.

It is assumed that reference will be made to standard texts, e.g. Bedford et al. (1986), Coull et al. (1989), to obtained fish length-weight relationships. For discussion of the relative merits of deriving fish weight directly from bone size and indirectly via fish length, see Casteel (1976) and Pierce et al. (1991d).

### 3.2 KEY TO PREMAXILLAE

The following key is intended as a guide to initial identification of premaxillae. We strongly recommend that it not be used as an identification guide on its own. Many species are very difficult to identify, and full species descriptions should always be consulted prior to reaching firm conclusions. When using the key be sure to read the couplets carefully and completely to ensure that the bone in question meets all the specified criteria within a clause before moving on through the key. Simple diagrams are provided to assist identification. The numbers on the diagrams indicate the relevant couplet and clause within the key.

## KEY TO THE IDENTIFICATION OF PREMAXILLAE

The key describes only those species covered in the guide. Therefore full species descriptions must be consulted prior to reaching firm identifications. Most premaxillae are keyed to the species level. Where this has not been possible, generally owing to the lack of a small number of distinguishing features, full species descriptions should be consulted.

1. a. Strongly laterally compressed without distinct ramus. Poorly defined processes

b. Consists of distinct shaft-like ramus and well
defined processes ..... 6
2. (1) a. Height greatest anteriorly ..... 3
b. Height greatest in middle or posteriorly ..... 5
3. (2) a. Ascending process protrudes over dorsal margin TWAITE SHAD (p. 32)
b. Ascending process does not protrude over dorsal margin ..... 4
4. (3) a. Head height greater than $1 / 3$ total length. HERRING (p. 28)/SPRAT (p. 30)
b. Head height less than $1 / 3$ total length ARGENTINE (p. 38)
5. (4) a. Height approx. $50 \%$ of length SALMON (p. 34)
b. Height approx. $70 \%$ of length TROUT (p. 36)
6. (1) a. Ascending process strongly inclined posteriorly and at least as long as ramus: entire bone V-shaped ..... 7
b. Ascending process not as above ..... 9
7. (6) a. Robust bone with large, strongly attached teeth WRASSE (p. 106)
b. Bone delicate and wishbone-like ..... 8
8. (7) a. Articular process an obvious spur on ramus ..... BOARFISH (p. 115)
b. Articular process entirely fused to ascending process DRAGONET (p. 107)
9. (6) a. Ascending process very tall and columnar, total height greater than total length LEMON SOLE (p. 96)
b. Total height less than total length ..... 10
10. (9) a. Ramus strongly curved both laterally and dorso- ventrally. Ramus broadest posteriorly ..... SOLES (pp. 102-104)
b. Ramus not as above ..... 11


4a)


10a)
11. (10) a. Ascending process absent or, if present, attached by ligament ..... ANGLER (p. 116)
b. Ascending process fused to ramus (may be reduced or inclined strongly forwards) ..... 12
12. (11) a. Bone small, elongate and delicate. Ascending process low and inclined strongly forwards. Postmaxillary process a short spur situated anteriorly on ramus
b. Bone not as above. Ascending process more or less upright ..... 13SANDEELS (pp. 76-79)
13. (12) a. Articular process taller than ascending process or of equal height ..... 14
b. Articular process shorter than ascending process ..... 16
14. (13) a. Interprocess notch a deep V ..... LING (p. 62)
b. Interprocess notch a shallow U ..... 15
15. (14) a. Ramus deeper than broad, translucent ..... SCAD (p. 110)
b. Ramus broader than deep, low knuckle-like head HAKE (p. 60)
16. (13) a. Small delicate bone (maximum length 14 mm ) with two highly distinctive lamellar, buttress-like ridges on postero-lateral face of articular process ..... SILVERY POUT (p. 58)
b. Does not possess ridges as above ..... 17
17. (16) a. Viewed laterally interprocess notch reaches level of ramus ..... 18
b. Interprocess notch does not reach level of ramus ..... 19
18. (17) a. Articular process squat and roughly square. Viewed laterally there is a clear gap between the base of the articular process and the ramus. Buccal sockets large, lingual sockets usually small ROCKLINGS (pp. 66-73)
b. Articular process tall and rectangular. No clear gap between base of articular process and ramus. Teeth or sockets small in multiple, well-organized rows GREATER
FORKBEARD (p. 74)
19. (17) a. Single row of teeth or tooth sockets ..... 20
b. More than one row of teeth or tooth sockets ..... 27
20. (19) a. Anterior processes fused over entire height of articular process, i.e., interprocess notch not present ..... 21
b. Anterior processes not completely fused, i.e., inter- process notch present ..... 22

15a)


12a)


15b)


16a)


17b)

notch reaches level of ramus


21. (20) a. Very long, taperering ramus (PMXCL $>4 x$ PMXHH); tiny teeth or sockets along narrow ventral edge of bone ..... MACKEREL (p. 112)
b. Short, deep ramus (PMXCL $<2 \mathrm{x}$ PMXHH). Large teeth or sockets situated along inner edge of ramus ..... PLAICE (p. 88)
22. (20) a. PMXCL $>2 x$ PMXHH ..... 23
b. PMXCL $<2 \times$ PMXHH ..... 24
23. (22) a. PMXCL $>2.5 x$ PMXHH. Anterior edge of articular process slopes posteriorly resulting in a broad V- shaped interprocess notch. Prominent anterior extension of ramus LONG ROUGH DAB ..... (p. 98)
b. PMXCL $<2.5 \times$ PMXHH. Articular process upright and roughly square resulting in narrow interprocess notch ..... SCALDFISH (p. 86)
Note that the following four species - plaice, flounder, dab, and witch - are difficult to distin- guish with confidence. Full species descriptions must be consulted.
24. (22) a. Anterior processes fused for $90-100 \%$ of height of articular process resulting in very shallow or absent interprocess notch. Teeth or sockets in well-ordered row
b. Anterior processes fused for $<90 \%$ of height of articular process ..... 25
25. (24) a. Anterior margin of articular process near-vertical resulting in narrow, parallel-sided interprocess notch ..... FLOUNDER (p. 92)
b. Anterior margin of interprocess notch slopes away from ascending process resulting in broad inter- process notch ..... 26
26. (25) a. Medial (articular) surface of articular process overhangs ramus creating distinct notch. Tooth sockets often in uneven row ..... DAB (p. 90)
b. Medial (articular) surface of articular process smoothly fused with ramus. Even, well ordered tooth sockets. Edge of ascending process continues as smooth ridge below point of fusion with articular process ..... WITCH (p. 94)
27. (19) a. PMXCL < 1.75x PMXHH ..... 28
b. PMXCL < 1.75x PMXHH ..... 31
28. (27) a. Ascending process stout and columnar ..... BUTTERFISH (p.109)
b. Ascending process tall, narrow, and lamellate ..... 29

## 21a)


29. (28) a. Texture papery, thin, soft, and translucent ..... LUMPSUCKER (p. 114)
b. Bone not as above ..... 30
30. (29) a. Articular process tall and rectangular BULLROUT (p. 113)
EELPOUT (p. 108)b. Articular process low with pointed apex
31. (30) a. Ascending process a thin, lamellar plate ending in a distinct point ..... 32
b. Ascending process robust, usually laterally flattened but not a thin, lamellar plate ..... 35
32. (31) a. Ascending process set across ramus presenting narrow edge in lateral view. In lateral view anterior extension of ramus extends beyond most anterior part of ascending process ..... 33
b. Ascending process set at a shallow angle to ramus presenting large surface area in lateral view. Anterior extension of ramus does not extend beyond most anterior part of ascending process ..... 34
33. (32) a. Ramus strongly decurved. Anterior margin of articular process slopes strongly away from ascending process. Large teeth or sockets in 2 rows. Often large ( $>2 \mathrm{~cm}$ in length, maximum length 12.5 cm ) ..... HALIBUT (p. 100)
b. Ramus not strongly decurved. Articular process roughly triangular. Bone tiny (maximum length 1.5 cm )and translucentGOBY (p. 111)
34. (32) a. Broad, shallow concavity anteriorly between base of ascending process and ramus ..... MEGRIM (p. 84)
b. Narrow, distinct pit anteriorly between base of ascending process and ramus ..... TURBOT (p. 80)/BRILL (p. 82)

ramus extends beyond processes

ramus does not extend beyond processes

35. (31) a. Two well-ordered rows of teeth or sockets, the inner row very small WHITING (p. 42)/
BLUE WHITING (p. 40)
b. More than two rows of teeth or sockets ..... 36
36. (35) a. Deep anterior premaxillary cleft and deep interprocess notch create pronounced waist or constriction near base of ascending process ..... 37
b. Ascending process without distinct waist or constriction near base ..... 39
37. (36) a. More than three rows of teeth or sockets. Viewed laterally base of articular process clear of ramus at rear, leaving distinct gap ..... 38
b. Two or three rows of teeth or sockets, inner row(s) much smaller than outer row WHITING (p. 42)
38. (37) a. Deep interprocess notch reaches close to level oframusROCKLINGS (pp. 66-73)
b. Interprocess notch deep and V-shaped, but stops well short of level of ramus ..... TORSK (p. 64)
39. (36) a. Viewed laterally base of articular process clear of ramus at rear, leaving distinct gap.
PMXHH > 1.2x PMXHL ..... 40
b. Viewed laterally no clear gap between base of articular process and ramus.
PMXHH < 1.2x PMXHL ..... 41
40. (39) a. Ramus short and wide; ascending process tall and rather straight-sided. Bone has squat, truncated appearance HADDOCK (p. 50)
b. Does not possess above features, esp. ramus longer and tapering Trisopterus spp. (pp. 52-57)
41. (39) a. Outer row of tooth sockets very large compared with inner rows. Groove or furrow running up antero- lateral face of ascending process ..... COD (p. 48)
b. Outer row of tooth sockets only slightly larger than inner rows. Ascending process lacks groove on antero-lateral face Pollachius spp. (pp. 44-47)


36a)

constriction

no constriction


39a)


### 3.3 PREMAXILLAE: SPECIES DESCRIPTIONS

### 3.3.1 CLUPEIDAE

## Herring (Clupea harengus (L.))

## Description

The herring premaxilla is a small, rather delicate bone. It is strongly laterally compressed (fig. 3) and without distinct processes, forming a convex sub-triangular plate (plate 1). It is tallest anteriorly, tapering to a point posteriorly. There is no distinct ascending process. The anterior margin of the bone descends steeply, forming an angle with the ventral margin (fig. 1). Here there is a slight difference from the sprat premaxilla, in which the anterior margin tends to sweep back in a more uniform curve into the ventral margin. The teeth ( $\mathrm{N}=5-9$ ) are small and conical. They are situated in a single row along the inner edge of the ventral margin of the premaxilla. The sockets are shallow and fragile, and even in relatively intact specimens may appear only as indistinct scars. The tooth row extends over the central quarter of the ventral margin of the bone. A distinct ossified rib, semi-circular in cross-section, runs the length of the lateral surface inward of the dorsal margin (figs. 1 and 3). Medially there is a thickened area of bone, the articular surface (fig. 2), against which the head of the maxilla rests.

## Important features

Sub-triangular shape and extreme lateral flattening.

## Similar species

Sprat (p. 30). The premaxillae of the two species cannot always be distinguished with confidence. From sprat by: steeper anterior margin making distinct angle with ventral margin.

## Regressions

Length range of specimens examined (TL): 86-357 mm; $\mathrm{N}=58$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.4183+1.1664 \ln$ PMXL | 47 | 0.969 |
| $\ln \mathrm{TL}=4.4483+1.0468 \ln$ PMXHH | 47 | 0.785 |
| $\ln \mathrm{TL}=3.2860+1.2224 \ln$ PMXCL | 43 | 0.977 |

## Estimated maxima

TL: 460 mm ; PMXL: 10.0 mm ; PMXHH: 4.2 mm ; PMXCL: 10.1 mm .

## HERRING


plate 1 lateral

plate 2 medial


fig. 1 lateral

fig. 2 medial

fig. 3 cross-section
plate 3 ventral
$T L=245 \mathrm{~mm}$


## CLUPEIDAE

## Sprat (Sprattus sprattus (L.) )

## Description

Like that of the herring, the premaxilla of the sprat is small, delicate and laterally compressed, forming a sub-triangular plate. It is highest anteriorly, tapering to a point posteriorly. In most specimens the anterior margin of the bone sweeps back in a more or less uniform curve into the ventral margin (plate 1). This contrasts with the premaxilla of the herring in which the anterior and ventral margins make a more distinct angle. The teeth are situated in a single row on the inner edge of the ventral margin. They are small and conical, numbering 3-5. The tooth sockets are shallow and fragile. On the lateral surface, immediately inward of the dorsal margin, a semicircular rib of bone runs the length of the premaxilla (figs. 1 and 3 ). Medially there is a thickened area of bone, behind the dorsal apex, which creates an articular surface.

## Important features

Sub-triangular shape and extreme lateral flattening.

## Similar species

Herring (p. 28). The premaxillae of the two species cannot always be distinguished with confidence.
From herring by: curvature of antero-ventral margin.

## Regressions

Length range of specimens examined (TL): 55-141 mm; $\mathrm{N}=18$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.8040+0.9441 \ln$ PMXL | 17 | 0.829 |
| $\ln \mathrm{TL}=4.5084+0.7955 \ln$ PMXHH | 18 | 0.824 |
| $\ln \mathrm{TL}=3.7030+0.9765 \ln$ PMXCL | 18 | 0.906 |

## Estimated maxima

TL: 180 mm ; PMXL: 4.0 mm ; PMXHH: 2.1 mm ; PMXCL: 4.4 mm .

plate 1 lateral

plate 2 medial

fig. 1 lateral
-

## CLUPEIDAE

## Twaite shad (Alosa fallax (Lacépède) )

## Description

Only one specimen of this species was available for examination. The premaxilla is small and rather delicate, not dissimilar in overall shape to that of herring or sprat. It is strongly laterally flattened, forming a convex sub-triangular plate (fig. 1), tallest anteriorly and tapering to a point posteriorly. The teeth are small and conical, numbering between twenty and thirty (Ridewood, 1904). They are situated in a single row along the full length of the ventral margin of the premaxilla. The dorsal margin is of a distinctly different texture from the rest of the bone, appearing smooth grained rather than rough and granular (fig. 1). Anteriorly, on the lateral face of the bone, there is a broad, round concavity. A distinct ascending process projects dorsally, immediately distinguishing the premaxilla from that of herring or sprat (fig. 1). Behind this process there is a thickened area which provides the surface for articulation with the maxilla (fig. 2).

## Important features

Laterally flattened triangular shape. Presence of ascending process.

## Similar species

Herring (p. 28), sprat (p. 30)
From herring and sprat by: presence of distinct ascending process, granular texture of much of bone, and number of teeth.

## Regressions

One specimen of 335 mm was examined. PMXL was 8.3 mm , PMXHH was 4.2 mm , and PMXCL was 8.8 mm .

## Estimated maxima

TL: 500 mm ; PMXL: 12.4 mm ; PMXHH: 6.3 mm ; PMXCL: 13.1 mm

## TWAITE SHAD


plate 1 lateral

plate 2 medial


Narrow occlusal surface with many tooth sockets (c.w. herring/sprat)
fig. 3 ventral

fig. 1 lateral

fig. 2 medial
plate 3 ventral
TL = 335 mm

### 3.3.2 SALMONIDAE

## Atlantic salmon (Salmo salar (L.))

## Description

Salmonid bones are not densely ossified and have a rough, "porous" texture. They are not robust and salmonid remains survive digestion rather less well than those of most other species. The premaxillae of $S$. salar are laterally flattened and triangular in shape and are approximately twice as long as they are high (c.w. S. trutta, p. 36). The apex of the bone is directed postero-dorsally and is situated over the posterior half of the bone. There is a low ascending process consisting of a postero-dorsally inclined triangle of bone (plate 1). From the posterior edge of this process a flange of bone runs the length of the medial surface (fig. 2). This flange provides attachment for the teeth which are in a single row. The teeth are long and incurved, numbering 5-8. The lateral surface of the premaxilla often has a distinctive scaly texture. Above the tooth-bearing flange the medial surface is flat and featureless (c.w. S. trutta).

## Important features

Low, triangular shape; height approximately half length.
Flat medial surface.

## Similar species

Trout (p. 36)
From trout by: lower overall shape; height half length (in S. trutta the height is approx. $70 \%$ of length). Flat medial surface.

## Regressions

Length range of specimens examined (TL): 524-822 mm; $\mathrm{N}=9$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.5639+0.6463 \ln$ PMXL | 8 | 0.935 |
| $\ln \mathrm{TL}=5.4942+0.5278 \ln$ PMXHH | 8 | 0.843 |

## Estimated maxima

TL: 1630 mm ; PMXL: 73.3 mm ; PMXHH: 24.4 mm .

## SALMON


low ascending
scaly texture

fig. 1 lateral
plate 1 lateral

fig. 2 medial
plate 2 medial

fig. 3 cross-section
$\mathrm{TL}=685 \mathrm{~mm}$

## SALMONIDAE

## Trout (Salmo trutta (L.))

## Description

The premaxilla of the trout, like that of the salmon, is laterally flattened and triangular in overall shape. However, it is relatively taller than the salmon premaxilla, its length being no more than 1.5 times its height. The dorsal apex is situated over the posterior half of the bone and is directed postero-dorsally. Anteriorly there is a low, triangular ascending process (plate 1). Medially, a flange of bone runs downward from the posterior edge of the ascending process, continuing caudally. As in the salmon this flange provides insertion for the single row of teeth. The 6-8 teeth are long, conical, and incurved. Above the tooth row, in the centre of the medial surface, there is a convex bulge of bone (fig. 2). This bulge is not present in the salmon.

## Important features

High, triangular shape. Central bulge on medial surface.

## Similar species

Atlantic salmon (p. 34)
From salmon by: taller shape (height approximately $70 \%$ of length). Central bulge on medial surface.

## Regressions

Too few specimens were examined to allow meaningful regressions to be given. In a 475 mm specimen, $\mathrm{PMXL}=11.8 \mathrm{~mm}$; $\mathrm{PMXHH}=3.8 \mathrm{~mm}$.

## Estimated maxima

TL: 1400 mm ; PMXL: 34.8 mm ; PMXHH: 11.2 mm

## TROUT


plate 1 lateral

plate 2 medial

fig. 3 cross-section
plate 3 ventral
TL $=475 \mathrm{~mm}$

### 3.3.3 ARGENTINIDAE

## Argentine (Argentina sphyraena (L.))

## Description

The argentine premaxilla is long, narrow and tapering in overall form. It is laterally flattened, forming an elongated sub-triangular plate, highest anteriorly. In two of the cleaned bones which were examined, four or five shallow scars, probably tooth sockets, were present half way along the inner surface of the ventral margin. A thickened rib runs longitudinally along the midline of the bone (fig. 1). Approximately half way along the dorsal margin there is a low articular process (fig. 1), the articular surface of which faces dorso-laterally (fig. 3). There is no clearly defined ascending process.

## Important features

Elongate, tapering, sub-triangular shape with very low articular process and no clear ascending process.

## Similar species

Herring (p. 28), sprat (p. 30)
Argentine premaxillae may be distinguished from both of the above by their long, narrow form.

## Regressions

Length range of specimens examined (TL): 137-235 mm; $\mathrm{N}=6$

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=45.86$ PMXL -20.82 | 6 | 0.805 |
| $\mathrm{TL}=172.44$ PMXHH +16.11 | 6 | 0.754 |
| TL $=193.11$ PMXAH +31.78 | 6 | 0.859 |

## Estimated maxima

TL: 270 mm ; PMXL: 5.90 mm ; PMXHH: 1.33 mm ; PMXAH: 1.16 mm

## ARGENTINE


plate 1 lateral

plate 2 medial

fig. 1 lateral
fig. 2 medial

fig. 3 cross-section
plate 3 ventral
$\mathbf{T L}=\mathbf{2 3 5} \mathrm{mm}$


### 3.3.4 GADIDAE and MERLUCCIIDAE

## Blue whiting (Micromesistius poutassou (Risso))

## Description

The bone is well ossified, the ramus of the specimens examined having a very densely grained and slightly shiny surface. The ramus itself is long and narrow, broader than it is high. A distinct shallow furrow runs along its dorsal surface from behind the articular process. The toothed surface is narrow (fig. 3). The arrangement of the teeth is highly distinctive, there being two exceptionally well-ordered rows (fig. 3) running in clear lines without doubling. The sockets of the buccal row are of moderate size while those of the lingual row are minute ( 0.5 and 0.15 mm diameter respectively in a 334 mm fish). The sockets of the lingual row touch one another, forming a continuous ridge behind the buccal row. The teeth are conical. The ascending process is taller than the articular process and its dorsal edge is distinctively notched (fig. 1). There is a concavity on the lateral face of the process immediately below this notch (fig. 1). The base of the articular process is completely fused to the ramus, without any overhang or notching posteriorly or medially (fig. 2 ; c.w. cod, saithe, pollack). The medial surface of the premaxillary head is smooth and featureless (fig. 2). The postmaxillary process is long and high.

## Important features

Two well-defined tooth rows on very narrow ramus. Notched ascending process with concavity on lateral surface. Lack of notching behind articular process.

## Similar species

Whiting (p. 42), saithe (p. 46), pollack (p. 44).
From whiting by: notch and lateral concavity on ascending process. Lack of grooving on lateral face of ascending process and beneath lateral face of articular process.
From saithe/pollack by: narrower occlusal surface. Notching on ascending process. Complete fusion of base of articular process. No large area of bone between anterior cleft and tooth sockets.

## Regressions

Length range of specimens examined (TL): 258-356 mm; N=18.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=30.71+13.21$ PMXL | 16 | 0.832 |
| $\mathrm{TL}=72.33+48.37$ PMXHH | 17 | 0.816 |
| $\mathrm{TL}=49.04+48.70$ PMXHL | 17 | 0.869 |
| $\mathrm{TL}=61.90+57.23$ PMXAH | 17 | 0.791 |

## Estimated maxima

TL: 510 mm ; PMXL: 34.0 mm ; PMXHH: 8.1 mm ; PMXHL: 8.8 mm ; PMXAH: 7.1 mm .

## BLUE WHITING


fig. 1 lateral
plate 1 lateral


Note: medial face of head is flat and featureless.
fig. 2 medial
plate 2 medial

tiny sockets of


Note: regular, well-organized tooth rows on narrow ramus
fig. 3 ventral
plate 3 ventral
$\mathrm{TL}=290 \mathrm{~mm}$

## GADIDAE

## Whiting (Merlangius merlangus (L.))

## Description

The bone has a shiny, closely grained appearance. In lateral view the ramus is shallow, being about twice as broad as it is deep. A broad shallow furrow runs along its dorsal surface from behind the articular process. The occlusal surface is broader than that of the blue whiting and bears two or three rows of tooth sockets. The buccal sockets are large ( 1.2 mm in a 322 mm fish), the lingual sockets considerably smaller ( 0.4 mm in a 322 mm fish). The teeth are long, conical, and incurved. The ascending process is taller than the articular process and is divided vertically by a deep groove running up its lateral face from the anterior premaxillary cleft (fig. 1). Laterally, there is a hollow groove below the base of the articular process (fig. 1). This groove may be bounded by buttresslike ridging and is diagnostic. The medial face of the articular process is undercut posteriorly (c.w. blue whiting, p. 40).

## Important features

Grooving beneath articular process. Vertical groove dividing ascending process.

## Similar species

Cod (p. 48), saithe (p. 46), pollack (p. 44), blue whiting (p. 40).
From cod by: grooving below lateral face of articular process. Narrower occlusal surface.
From saithe/pollack by: deep vertical groove on ascending process. Grooving below ascending process. Larger buccal tooth sockets.
From blue whiting by: deep vertical groove on ascending process. Groove beneath articular process. Lack of deep notch on ascending process.

## Regressions

Length range of specimens examined (TL): 90-380 mm.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.6165+0.9954 \ln$ PMXL | 33 | 0.984 |
| $\ln \mathrm{TL}=3.8872+0.9759 \ln$ PMXHH | 33 | 0.965 |
| $\ln \mathrm{TL}=3.9877+0.9499 \ln$ PMXHL | 33 | 0.985 |
| $\ln \mathrm{TL}=4.2107+0.9822 \ln$ PMXAH | 32 | 0.990 |

## Estimated maxima

TL: 490 mm ; PMXL: 39.6 mm ; PMXHH: 15.2 mm ; PMXHL: 11.1 mm ; PMXAH: 8.2 mm .

## WHITING


plate 1 lateral

plate 2 medial

fig. 2 medial
large buccal
sockets

fig. 3 ventral
plate 3 ventral

$$
T L=330 \mathrm{~mm}
$$

## GADIDAE

## Pollack (Pollachius pollachius (L.) )

## Description

The bone is well ossified and robust. Dorsally, the ramus often has a shallow depression running from behind the articular process to the postmaxillary process; this is most noticeable in larger specimens. The occlusal surface bears 3-6 uneven rows of conical teeth anteriorly, decreasing to a single row posteriorly. The toothed area extends beyond the postmaxillary process but stops well short of the posterior end of the bone (c.w. saithe/cod). The sockets of the buccal row are largest, relatively smaller than their counterparts in the cod but larger than in the saithe. Viewed from below the ramus is noticeably narrower and more curved than that of cod. The ascending process is higher than the articular process, the two being divided by a rather shallow U-shaped notch (fig. 1). The ascending process is rather low in most specimens and is strongly rounded anteriorly (c.w. saithe, p. 46). The ratio of PMXHH to PMXHL ranges from 0.75 to 1.16 with a mean ( $\pm$ s.d.) of $0.92 \pm 0.11$ (in saithe $1.18 \pm 0.07$ ). The anterior premaxillary cleft is broad and deep, resulting in there being a smaller area of bone between its lower edge and the top of the tooth row than in the saithe (fig. 2). The postmaxillary process is high and triangular.

## Important features

Ascending process higher than articular and strongly rounded anteriorly.

## Similar species

Saithe (p.46), cod (p.48), whiting (p. 42), blue whiting (p.40). It can be difficult to distinguish between premaxillae from saithe and pollack.
From saithe by: deeper anterior premaxillary cleft resulting in narrow area of bone between cleft and teeth (fig.1). Lower ascending process with more rounded anterior edge. Ratio of PMXHH to PMXHL lower than saithe.
From cod by: narrower occlusal surface (plate 3), smaller teeth in outer row and greater lateral curvature (plate 3). Lack of deep vertical groove on ascending process.
From whiting by: multiple uneven tooth rows. No grooving or furrowing below lateral face of articular process. No deep vertical groove on ascending process.
From blue whiting by: broader ramus with more tooth rows. Lack of notch on ascending process.

## Regressions

Length range of specimens examined (TL): 366-625 mm; $\mathrm{N}=15$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=173.20+11.33$ PMXL | 15 | 0.796 |
| $\ln$ TL $=4.6252+0.7651 \ln$ PMXHH | 15 | 0.473 |
| $\mathrm{TL}=227.49+32.84$ PMXHL | 15 | 0.740 |
| TL $=99.72+67.76$ PMXAH | 15 | 0.927 |

## Estimated maxima

TL: 1390 mm ; PMXL: 88.1 mm ; PMXHH: 18.6 mm ; PMXHL: 26.6 mm ; PMXAH: 18.9 mm .

## POLLACK


plate 1 lateral

plate 2 medial



Note: buccal row of sockets smaller than in cod and ramus more strongly curved.
fig. 3 ventral

fig. 1 lateral

fig. 2 medial
plate 3 ventral
$T L=504 \mathrm{~mm}$

## GADIDAE

## Saithe (Pollachius virens (L.) )

## Description

The bone is well ossified and robust. The dorsal surface of the ramus is flat or rounded, not furrowed (c.w. pollack/whiting). The occlusal surface bears 4-5 uneven rows of conical teeth anteriorly, reduced to a single row posteriorly. The toothed area extends to the posterior end of the postmaxillary process (c.w. pollack). The teeth of the outer row are larger than those of the inner rows, but are relatively smaller than those of the pollack. The ascending process is higher than the articular. It is relatively taller than that of the pollack, the ratio of PMXHH to PMXHL ranging from 1.07 to 1.27 with a mean ( $\pm$ s.d.) of $1.18 \pm 0.07$ (in pollack $0.92 \pm 0.11$ ). It tends to concavity on its posterior edge and is not so strongly convex anteriorly as in pollack, giving it a more upright appearance (fig. 1). The anterior premaxillary cleft is less well developed than in the pollack, resulting in a broader area of bone between it and the toothed area (fig. 1). This area of bone is rounded laterally and anteriorly. The postmaxillary process is high and triangular.

## Important features

Ascending process higher than articular and rather upright in appearance. Broad rounded area of bone between anterior premaxillary cleft and toothed area.

## Similar species

Pollack (p. 44), cod (p. 48), whiting (p. 42), blue whiting (p. 40). It is very easy to confuse saithe premaxillae with those from pollack.
From pollack by: higher ascending process, less strongly rounded anteriorly (fig. 1). Anterior premaxillary cleft less deep resulting in broad, rounded area of bone between cleft and teeth (fig. 1b). Ratio of PMXHH to PMXHL higher than pollack.
From cod by: narrower occlusal surface (plate 3). Smaller teeth in outer row. Greater lateral curvature (plate 3).
From blue whiting by: broader occlusal surface with more tooth rows. Lack of notch on ascending process.
From whiting by: more robust form. Multiple uneven tooth rows. No grooving or furrowing below lateral face of articular process or on dorsal surface of ramus.

## Regressions

Length range of specimens examined (TL): 211-980 mm; $\mathrm{N}=20$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.8403+1.0653 \ln$ PMXL | 20 | 0.992 |
| $\ln \mathrm{TL}=4.2826+0.9410 \ln$ PMXHH | 18 | 0.973 |
| $\mathrm{TL}=76.03$ PMXHL -10.32 | 19 | 0.972 |
| $\ln \mathrm{TL}=4.507+1.0054 \ln$ PMXAH | 19 | 0.966 |

## Estimated maxima

TL: 1320 mm ; PMXL: 58.6 mm ; PMXHH: 21.2 mm ; PMXHL: 17.2 mm ; PMXAH: 13.8 mm .

## SAITHE


fig. 1 lateral
plate 1 lateral

fig. 2 medial
plate 2 medial


Note: buccal row of sockets smaller than cod or pollack. Ramus more strongly curved than cod.

## fig. 3 ventral

$T L=616 \mathrm{~mm}$

## GADIDAE

## Cod (Gadus morhua (L.) )

## Description

The bone is well ossified and robust. Viewed from below the ramus is straighter than in saithe or pollack and the occlusal surface is very much broader. There are 5-8 uneven rows of teeth anteriorly, decreasing to 1 or 2 posteriorly. The teeth are conical and those in the outer row are massive ( 1.1 mm in a fish of 355 mm ), 2-3 times the diameter of those in the other rows (fig. 3). The teeth extend to the posterior end of the ramus. The ascending process is taller than the articular and is divided from it by a $V$-shaped notch. In intact specimens there is a shallow furrow running from the anterior premaxillary cleft up the antero-lateral face of the ascending process (fig. 1). Posteriorly, the base of the articular process is not attached to the ramus, creating a distinct notch (fig. 2). The postmaxillary process is roughly rectangular.

## Important features

Broad occlusal surface. Furrow on ascending process. Massive teeth in outer row.

## Similar species

Pollack (p. 44), saithe (p. 46), whiting (p. 42), blue whiting (p. 40).
From pollack and saithe by: broader occlusal surface. Very much larger teeth in outer row (fig. 3). Vertical furrow on ascending process (fig. 1). Interprocess notch more V-shaped. Rectangular postmaxillary process.
From whiting by: more robust form. No grooving or furrowing below lateral face of articular process.
From blue whiting by: very much more robust form. Broad occlusal surface with multiple uneven tooth rows.

## Regressions

Length range of specimens examined (TL): $94-1057 \mathrm{~mm} ; \mathrm{N}=35$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.6511+1.0204 \ln$ PMXL | 33 | 0.990 |
| $\ln \mathrm{TL}=3.9304+0.9839 \ln$ PMXHH | 34 | 0.981 |
| $\ln \mathrm{TL}=3.9226+0.9862 \ln$ PMXHL | 34 | 0.990 |
| $\ln \mathrm{TL}=4.1692+0.9742 \ln$ PMXAH | 35 | 0.994 |

## Estimated maxima

TL: 2060 mm ; PMXL: 130.3 mm ; PMXHH: 41.5 mm ; PMXHL: 42.2 mm ; PMXAH: 34.3 mm .

## COD


plate 1 lateral

plate 2 medial

large sockets in buccal row

broad occlusal surface
fig. 3 ventral
plate 3 ventral
$\mathrm{TL}=380 \mathrm{~mm}$
1.0 cm

## GADIDAE

## Haddock (Melanogrammus aeglefinus (L.))

## Description

The premaxilla of the haddock is characterized by a short, broad, blunt-ended ramus and a tall ascending process, giving it a compact, truncated appearance. The occlusal surface is broad and bears 4-7 uneven rows of tooth sockets. The sockets are taller than they are broad. The buccal row is of moderate size ( 0.6 mm in a fish of 334 mm ), gradually decreasing towards the lingual row. The teeth are conical and incurved. The ascending process is tall, narrow, and rather straight sided (fig. 1 ; c.w. bib). The anterior premaxillary cleft continues vertically up the antero-lateral face of the ascending process as a shallow groove (fig. 1). The articular process is roughly square and is free of the ramus posteriorly, giving it a distinct overhanging appearance (plate 1). Below the interprocess notch, at the base of the ascending process, the lateral surface of the bone is flat (this contrasts with bib in which this area is distinctly rounded).

## Important features

Short, broad ramus and tall, straight-sided ascending process giving compact appearance. Rear of articular process clear of ramus.

## Similar species

Bib (p. 52), poor cod (p. 54).
From bib by: straight-sided ascending process. Flat lateral surface below interprocess notch. From poor cod by: broad ramus. Greater clearance between articular process and ramus.

## Regressions

Length range of specimens examined (TL): 71-474 mm; $\mathrm{N}=53$

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.4873+1.2331 \ln$ PMXL | 53 | 0.978 |
| $\ln \mathrm{TL}=3.7898+1.0110 \ln$ PMXHH | 53 | 0.984 |
| $\ln \mathrm{TL}=4.0104+1.0908 \ln$ PMXHL | 53 | 0.973 |
| $\ln \mathrm{TL}=4.0685+1.1083 \ln$ PMXAH | 53 | 0.979 |

## Estimated maxima

TL: 1290 mm ; PMXL: 42.2 mm ; PMXHL: 26.7 mm ; PMXHL: 16.9 mm ; PMXAH: 15.4 mm .

## HADDOCK


plate 1 lateral

plate 2 medial

plate 3 ventral
$T L=401 \mathrm{~mm}$
tall, parallel-sided

fig. 1 lateral

fig. 2 medial


Note: short, broad ramus gives truncated appearance.
fig. 3 ventral

## GADIDAE

## Bib [Pout, Pouting] (Trisopterus luscus (L.) )

## Description

The bone is robust, although less compact than that of the similar haddock. The ramus is of moderate breadth (plate 3), tapering to a point posteriorly (c.w. haddock). There are 4-5 uneven rows of tooth sockets. The sockets of the buccal row are large ( 1.2 mm diameter in a 338 mm fish, or approximately $50 \%$ of the width of the occlusal surface). The inner rows are very much smaller. The ascending process is much taller than the articular process. A shallow groove runs up its antero-lateral face but is less distinct than in the haddock. The anterior edge of the ascending process is strongly curved in lateral view. The area of bone beneath the interprocess notch is smoothly convex. The articular process is roughly rectangular and overhangs the ramus ventromedially.

## Important features

Tall ascending process, strongly curved anteriorly. Lateral surface convex beneath interprocess notch. Large sockets in buccal row.

## Similar species

Haddock (p. 50), poor cod (p. 54), rocklings (pp. 66-72)
From haddock by: narrower, less truncated ramus. Anterior margin of ascending process more strongly curved. Lateral face of head smoothly convex beneath interprocess notch (flat in haddock).
From poor cod by: broader occlusal surface and larger sockets in buccal row. Anterior margin of ascending process more strongly curved.
From rocklings by: narrower occlusal surface. Interprocess notch and anterior premaxillary cleft very much shallower.

## Regressions

Length range of specimens examined (TL): 220-333 mm; $\mathrm{N}=5$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.6838+0.6781 \ln$ PMXL | 5 | 0.971 |
| $\ln \mathrm{TL}=4.3288+0.6810 \ln$ PMXHH | 5 | 0.973 |
| $\ln \mathrm{TL}=4.3731+0.7557 \ln$ PMXHL | 5 | 0.991 |
| $\ln \mathrm{TL}=4.2820+0.9026 \ln$ PMXAH | 5 | 0.970 |

## Estimated maxima

TL: 490 mm ; PMXL: 39.6 mm ; PMXHH: 15.2 mm ; PMXHL: 11.1 mm ; PMXAH: 8.2 mm .

## BIB


plate 1 lateral

plate 2 medial

fig. 3 ventral
plate 3 ventral
$T L=333 \mathrm{~mm}$

## GADIDAE

## Poor cod (Trisopterus minutus (L.))

## Description

The bone is rather slim, with a long ramus and a tall, narrow ascending process. The occlusal surface is narrow and bears three rows of teeth (fig 3). The outer row is moderately large ( 0.5 mm in a 152 mm fish), the inner two rows small ( 0.1 mm in a 152 mm fish) and unevenly arranged. In overall shape the premaxillary head is typical of the Trisopterus species, the ascending process being tall and narrow and the articular process roughly square or rectangular. In lateral view the anterior edge of the ascending process is straighter than in the bib. Its posterior edge is also straight, as is the anterior edge of the articular process,resulting in the interprocess notch having a deep V-shape. There is a distinct fossa between the two processes. The rear of the articular process is free of the ramus (figs. 1 and 2).

## Important features

Long narrow ramus. Tall ascending process and rectangular articular process divided by deep V shaped notch.

## Similar species

Bib (p. 52), Norway pout (p. 56).
From bib by: narrower occlusal surface and longer ramus. Anterior edge of ascending process straighter.
From Norway pout by: broader occlusal surface and larger tooth sockets. Broader base to processes, esp. to articular process. Ramus less strongly laterally curved.

## Regressions

Length range of specimens examined (TL): $113-206 \mathrm{~mm} ; \mathrm{N}=21$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=15.05$ PMXL -10.24 | 19 | 0.941 |
| $\mathrm{TL}=41.13$ PMXHH +23.49 | 21 | 0.874 |
| $\ln \mathrm{TL}=4.0955+0.9271 \ln$ PMXHL | 21 | 0.907 |
| $\mathrm{TL}=62.80$ PMXAH +0.77 | 21 | 0.798 |

## Estimated maxima

TL: 290 mm ; PMXHH: 19.4 mm ; PMXHH: 6.1 mm ; PMXHL: 5.1 mm ; PMXAH: 4.2 mm .

## POOR COD


fig. 1 lateral
plate 1 lateral

fig. 2 medial
plate 2 medial


Narrow ramus bearing 3 rows of sockets.
fig. 3 ventral

## GADIDAE

## Norway pout (Trisopterus esmarkii (Nilsson))

## Description

The most delicate of the Trisopterus premaxillae, that of the Norway pout, is characterized by a slender ramus and tall anterior processes. The narrow ramus is deeply grooved along its dorsal surface by a furrow running from behind the articular process to the postmaxillary process (fig. 1). Anteriorly the ramus is more strongly laterally curved than in the other Trisopterus species (plate 3). On the narrow occlusal surface there are 3-4 rows of minute tooth sockets (buccal row 0.08 mm , lingual rows 0.06 mm in a fish of 120 mm ). The ascending process is taller than the articular process and divided from it by a deep V-shaped notch. There is a broad, shallow concavity at its base (fig. 2), distinct from the anterior premaxillary cleft which is oriented medially. The articular process is more tall and narrow than in other Trisopterus species. It has a narrower base and a more pronounced "overhang" posteriorly (plate 1). There is a distinct fossa between the two processes.

## Important features

Slim, delicate appearance. Strongly laterally curved ramus with grooved dorsal surface. Minute tooth sockets. Tall articular process with narrow base:

## Similar species

Poor cod (p. 54), silvery pout (p. 58)
From poor cod by: narrower, more strongly laterally curved ramus. Smaller tooth sockets. Narrower base to articular process. Deeply grooved dorsal surface of ramus.
From silvery pout by: lack of buttress-like ridges on articular process. Cross-sectional shape of ramus.

## Regressions

Length range of specimens examined (TL): 67-185 mm; $\mathrm{N}=27$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.4139+1.1069 \ln$ PMXL | 25 | 0.972 |
| $\ln \mathrm{TL}=3.7510+1.1287 \ln$ PMXHH | 27 | 0.963 |
| $\ln \mathrm{TL}=4.0081+1.1290 \ln$ PMXHL | 27 | 0.975 |
| $\ln \mathrm{TL}=3.9133+1.1262 \ln$ PMXAH | 26 | 0.949 |

## Estimated maxima

TL: 290 mm ; PMXL: 18.6 mm ; PMXHH: 5.3 mm ; PMXHL: 4.3 mm ; PMXAH: 4.6 mm .

## NORWAY POUT


plate 1 lateral

plate 2 medial

plate 3 ventral
$\mathrm{TL}=180 \mathrm{~mm}$
fig. 2 medial

very narrow ramus with tiny tooth sockets
fig. 3 ventral


fig. 1 dorso-lateral

## GADIDAE

## Silvery pout (Gadiculus argenteus thori (Schmidt))

## Description

The premaxilla of the silver pout is delicate, but highly distinctive. The ramus is very narrow, taller than broad (fig. 3) and tapers rather rapidly behind the articular process. Anteriorly, it is very strongly curved in the lateral plane. The narrow occlusal surface bears 3-4 rows of minute conical teeth $(0.06 \mathrm{~mm}$ in a specimen of 90 mm$)$. The anterior premaxillary cleft forms a broad concavity beneath the ascending process (plate 1, fig. 1). The lower edge of this concavity is bounded by the shelf-like edge of the ramus (fig. 1). The postero-lateral face of the ascending process overhangs it. The ascending process is a lamellar plate of bone. It is taller than the articular process. Viewed dorsally the faces of the two processes form an angle of approximately 90 degrees to one another, the ascending process facing antero-laterally and the articular postero-laterally. Both processes are tall and narrow and the sides of the interprocess notch are nearly parallel. There are two highly distinctive lamellar ridges on the face of the articular process (fig. 1). The postmaxillary process is very tall and narrow.

## Important features

Lamellar ridges on articular process. Narrow ramus. Strong lateral curvature. Tall anterior processes and parallel sides to interprocess notch.

## Similar species

Norway pout (p. 56)
From Norway pout by: 90 degree angle between lateral faces of anterior process. Buttress-like ridges on articular processes. Deep concavity below ascending process bounded ventrally by broad shelf-like edge of ramus.

## Regressions

Length range of specimens examined (TL): $80-122 \mathrm{~mm} ; \mathrm{N}=4$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=37.8$ PMXHH -6.2 | 4 | 0.824 |
| $\mathrm{TL}=45.3$ PMXHL +21.7 | 4 | 0.707 |
| $\mathrm{TL}=38.8$ PMXAH +3.8 | 4 | 0.929 |

PMXL was 9.0 mm in a specimen of 103 mm and 10.7 mm in a specimen of 122 mm .

## Estimated maxima

TL: 160 mm ; PMXL: 14.0 mm ; PMXHH: 4.1 mm ; PMXHL: 4.0 mm ; PMXAH: 4.2 mm .

## SILVERY POUT


plate 1 lateral

plate 2 medial


Size unknown
plate 3 ventral

fig. 1 dorso-lateral

fig. 2 medial

fig. 3 cross-section

## MERLUCCIIDAE

## Hake (Merluccius merluccius (L.))

## Description

The premaxilla of the hake is highly elongate with a low, knuckle-like head. It feels very light, not being densely ossified. The ramus is broader than it is high. There are two well-defined rows of moderate to large tooth sockets ( 2.4 mm in a specimen of 590 mm ). The sockets extend the full length of the long ramus. The outer row of sockets tends to be elliptical, the lingual row more round. Both rows of sockets are low and shallow, and in life the long, curved conical teeth are hinged within them. The articular process is as tall as, or slightly taller than, the ascending process. The interprocess notch is a shallow U -shape. Anteriorly, the ramus broadens abruptly in a distinct medial expansion (fig. 2), projecting toward its opposite number. A well-defined ridge of bone runs antero-medio-ventrally from the medial face of the articular process down onto this projection (fig. 2). The medial face of the ascending process also slopes down onto this area, giving it a sloping shelf-like appearance. The postmaxillary process is a sharp spur, its apex posteriorly oriented.

## Important features

Very long, narrow ramus and low, knuckle-like head.

## Similar species

Angler fish (p. 116)
From angler fish by: broad knuckle-like head with clearly defined ascending process.

## Regressions

Length range of specimens examined (TL): 169-780 mm; N=27

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.2328+1.0226 \ln$ PMXL | 27 | 0.994 |
| $\ln \mathrm{TL}=4.5918+0.9314 \ln$ PMXHH | 27 | 0.962 |
| $\ln \mathrm{TL}=3.9307+1.0273 \ln$ PMXHL | 27 | 0.990 |
| $\ln \mathrm{TL}=4.0461+1.0097 \ln$ PMXAH | 27 | 0.984 |

## Estimated maxima

TL: 1320 mm ; PMXL: 126.1 mm ; PMXHH: 15.5 mm ; PMXHL: 23.5 mm ; PMXAH: 22.0 mm .

## HAKE


plate 1 lateral

plate 2 medial

plate 3 ventral

low, knuckle-like head
fig. 1 lateral

fig. 2 medial


Note: the two rows of sockets are very close together.
fig. 3 ventral

## GADIDAE

## Ling (Molva molva (L.) )

## Description

The bone is broad, densely ossified, and robust. The ramus is approximately three times as broad as high with rather flat occlusal and dorsal surfaces. The occlusal surface bears multiple rows of tooth sockets. Up to 12 rows may be present in large specimens (Jones, 1991), but in the specimens examined here there were between six and nine rows. The buccal row is of moderate size ( 1.3 mm in a 500 mm specimen), the size of the sockets decreasing rapidly towards the lingual margin (plate 3). In the specimens examined the buccal row was set slightly back from the margin of the ramus (c.w. torsk, p. 64). The anterior processes present a rather squat appearance and are of approximately equal height (c.w. torsk/rocklings). The ascending process is roughly square in lateral view. It is strongly undercut anteriorly by the deep, narrow anterior premaxillary cleft (fig. 1). The interprocess notch is deep, straight sided, and V-shaped. Medially, the articular process continues antero-ventrally as a strong buttress-like ridge (fig. 2) terminating at the antero-medial extremity of the bone.

## Important features

Broad, flat ramus and squat head. Anterior processes of roughly equal height and divided by deep V-shaped notch. Square ascending process. Buttress-like medial ridge of articular process.

## Similar species

Torsk (p. 64), rocklings (pp. 66-72)
From torsk by: anterior processes of equal height. Shorter, broader ascending process with square profile. Buttress-like medial ridge of articular process.
From rocklings by: shorter, broader ascending process with square profile and wider base.

## Regressions

Length range of specimens examined (TL): 295-833 mm; $\mathrm{N}=23$

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.1071+0.9800 \ln$ PMXL | 23 | 0.971 |
| $\ln$ TL $=4.7590+0.8693 \ln$ PMXHH | 23 | 0.883 |
| $\ln$ TL $=4.2651+1.0308 \ln$ PMXHL | 23 | 0.968 |
| $\ln$ TL $=4.6663+0.9385 \ln$ PMXAH | 22 | 0.966 |

## Estimated maxima

TL: 2130 mm ; PMXL: 100.6 mm ; PMXHH: 23.6 mm ; PMXHL: 25.9 mm ; PMXAH: 23.2 mm .

## LING



Note: articular process slightly taller than ascending.
fig. 1 lateral
plate 1 lateral

strong, buttress-like ridge
fig. 2 medial
plate 2 medial


Note: inner socket rows much smaller than outer row.

## fig. 3 ventral

$\mathrm{TL}=705 \mathrm{~mm}$

## GADIDAE

## Torsk (Brosme brosme (Ascanius) )

## Description

The bone is broad and densely ossified, similar to that of the ling. The ramus is broad and flat, bearing multiple tooth rows. There were six rows in the few specimens examined. The buccal tooth sockets are of moderate size ( 1 mm in a specimen of 500 mm ), decreasing in size only slightly (c.w. ling, p. 62) towards the lingual margin. The ascending process appears higher than the articular, its apex being above that of the latter. The ascending process is roughly triangular in profile (c.w. ling) with a blunt dorsal apex (plate 1). It is deeply undercut anteriorly by the anterior premaxillary cleft. This cleft is deeper (dorso-ventrally) than in the ling. The interprocess notch is V-shaped and reaches the level of the top of the anterior premaxillary cleft (c.w. rocklings). The articular process is free of the ramus posteriorly, giving it a distinct "waist". Medially the base of this process is rounded (fig. 2) and does not form the strong ridge seen in the ling or in some rocklings. The postmaxillary process is low and rectangular.

## Important features

Broad ramus bearing multiple tooth rows. Ascending process higher than articular. Interprocess notch reaches level of top of anterior premaxillary cleft.

## Similar species

Ling (p. 62), rocklings (pp. 66-72)
From ling by: ascending process taller than articular process and roughly triangular. Base of articular process rounded medially. Deeper anterior premaxillary cleft.
From rocklings by: less deep interprocess notch, reaching level of top of anterior premaxillary cleft. Broader lateral aspect of ascending process.

## Regressions

Length range of specimens examined (TL): 220-500 mm; $\mathrm{N}=4$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.1209+0.9217 \ln$ PMXL | 4 | 0.998 |
| $\ln \mathrm{TL}=4.4916+0.8846 \ln$ PMXHH | 4 | 0.984 |
| $\ln \mathrm{TL}=4.0073+0.9999 \ln$ PMXHL | 4 | 0.998 |
| $\ln \mathrm{TL}=4.4028+0.8896 \ln$ PMXAH | 4 | 0.997 |

## Estimated maxima

TL: 1170 mm ; PMXL: 72.0 mm ; PMXHH: 17.9 mm ; PMXHL: $21.2 \mathrm{~mm} ;$ PMXAH: 19.9 mm .

## TORSK


fig. 1 lateral
plate 1 lateral

fig. 2 medial
plate 2 medial

fig. 3 ventral

## GADIDAE

## Three-bearded rockling (Gaidropsarus vulgaris (Cloquet) )

## Description

The ramus is rather broad with a rounded occlusal surface (that of ling, torsk, and five-bearded rockling are flatter). There are 6-8 rows of tooth sockets. a buccal row of moderately large sockets ( 0.8 mm in a 247 mm specimen) and several additional rows of very small $(0.25 \mathrm{~mm}$ in a 247 mm specimen) sockets. The teeth are conical. As in all the rockling species, the ascending process is considerably taller than the articular process. The base of the ascending process is narrow, being deeply undercut by the anterior premaxillary cleft, and restricted posteriorly by the deep interprocess notch (fig. 1). The interprocess notch reaches a level well below the top of the anterior premaxillary cleft (c.w. torsk). The articular process is free of the ramus posteriorly, giving it a marked "waist" at its base. Medially, the articular process creates a low, but distinct, rounded ridge running antero-ventrally from in front of the articular surface (fig. 2). There is a shallow fossa between the two anterior processes. The postmaxillary process is low and rectangular.

## Important features

Ascending process considerably taller than articular process and divided from it by very deep Vshaped notch. Broad occlusal surface.

## Similar species

Bib (p. 52), ling (p. 62), torsk (p. 64), four- and five-bearded rocklings, northern rockling (pp. 6872). No consistent differences could be found between three-bearded and northern rockling premaxillae.
From bib by: deeper interprocess notch and anterior premaxillary cleft.
From ling by: taller, narrower ascending process with highly constricted base.
From torsk by: deeper interprocess notch and taller, narrower ascending process.
From four-bearded rockling by: less deep interprocess notch. Base of ascending process less constricted in lateral view. Medial surface of articular process does not create lamellate ridge.
From five-bearded rockling by: narrower ramus. Smaller lingual tooth sockets. Presence of low medial ridge on articular process.

## Regressions

Length range of specimens examined (TL): 247-443 mm; N=3.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.4497+0.7702 \ln$ PMXL | 3 | 0.957 |
| $\ln \mathrm{TL}=4.1697+0.9140 \ln$ PMXHH | 3 | 0.893 |
| $\ln \mathrm{TL}=4.0741+0.9405 \ln$ PMXHL | 3 | 0.957 |
| $\ln \mathrm{TL}=4.3014+0.9207 \ln$ PMXAH | 3 | 0.981 |

## Estimated maxima

TL: 530 mm ; PMXL: 38.2 mm ; PMXHH: 9.5 mm ; PMXHL: 10.2 mm ; PMXAH: 8.4 mm .

## THREE-BEARDED ROCKLING



Very deep notch reaches furthest extreme of anterior cleft.

fig. 1 lateral
plate 1 lateral

low, rounded ridge
fig. 2 medial
plate 2 medial


Convex occlusal surface. Large buccal sockets. All other rows very small.
fig. 3 ventral
$\mathrm{TL}=\mathbf{2 4 7} \mathrm{mm}$
$\qquad$

## GADIDAE

## Four-bearded rockling (Rhinonemus cimbrius (L.) )

## Description

The premaxilla of the four-bearded rockling is slimmer and more delicate in appearance than that of other rocklings, but nonetheless the bone is well ossified and dense. The ramus bears 5-6 rows of tooth sockets. The outer row is of medium size, 0.45 mm in a 238 mm specimen, and the inner rows are small (plate 3). The ascending process is tall and very narrow in lateral view. It is greatly constricted at its base by the deep anterior premaxillary cleft and interprocess notch, leaving only a narrow basal ridge of bone laterally (fig. 1). The articular process is lower and broader than the ascending process and, posteriorly, is free of the ramus. Medially, a highly distinctive lamellar ridge of bone carries antero-ventrally from the articular process (fig. 2). When the bone is viewed laterally this ridge is visible through the interprocess notch (fig. 1). This is not true of the lower, more rounded ridge of $G$. vulgaris (p. 66).

## Important features

Very deep anterior premaxillary cleft and interprocess notch. Lamellar medial ridge of bone carrying forward from articular process.

## Similar species

Three-bearded (p. 66), northern (p. 70) and five-bearded (p. 72) rocklings; greater forkbeard (p. 74).

From other rocklings by: taller, narrower ascending process and narrower ramus. Lamellar medial ridge of bone carrying forward from articular process.
From greater forkbeard by: much broader articular process giving broader, squatter appearance to head of bone. Larger tooth sockets in less well-ordered rows.

## Regressions

Length range of specimens examined (TL): 206-263 mm; N=7.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.4552+0.7967 \ln$ PMXL | 7 | 0.491 |
| $\ln \mathrm{TL}=4.7436+0.5084 \ln$ PMXHH | 7 | 0.366 |
| $\ln \mathrm{TL}=4.3868+0.8056 \ln$ PMXHL | 7 | 0.884 |
| $\ln \mathrm{TL}=4.7249+0.6313 \ln$ PMXAH | 7 | 0.772 |

## Estimated maxima

TL: 470 mm ; PMXL: 20.0 mm ; PMXHH: 6.9 mm ; PMXHL: 8.0 mm ; PMXAH: 7.2 mm .

## FOUR-BEARDED ROCKLING


fig. 1 lateral
plate 1 lateral

fig. 2 medial
plate 2 medial

ramus narrower than other rockling species
fig. 3 ventral
$\mathrm{TL}=\mathbf{2 3 8} \mathrm{mm}$

## GADIDAE

## Northern rockling (Ciliata septentrionalis (Collett))

## Description

Only two specimens of this species were examined, making definitive conclusions on diagnostic features unreliable. There were six rows of tooth sockets in the specimens examined. The buccal row of sockets is moderately large ( 0.6 mm in a 168 mm specimen), and the other rows of sockets are considerably smaller ( 0.25 mm in a 168 mm specimen). The teeth are conical. As in all the rockling species, the ascending process is considerably taller than the articular process. The base of the ascending process is narrow, being deeply undercut by the anterior premaxillary cleft, and restricted posteriorly by the deep interprocess notch (fig. 1). The articular process is free of the ramus posteriorly, giving it a marked "waist" at its base. In one specimen there was a low but distinct ridge running antero-ventrally from in front of the articular surface (plate 2, fig. 2), as in G. vulgaris (p. 66); however, this was much reduced in the other specimen. There is a shallow fossa between the two anterior processes. The postmaxillary process is low and rectangular.

## Important features

Ascending process considerably taller than articular process and divided from it by very deep Vshaped notch.

## Similar species

Bib (p. 52), ling (p. 62), torsk (p. 64), three-bearded (p. 66), four-bearded (p. 68), and fivebearded (p. 72) rocklings. No consistent differences could be found between northern and three-bearded rockling premaxillae.
From bib by: deeper interprocess notch and anterior premaxillary cleft.
From ling by: taller, narrower ascending process with highly constricted base.
From torsk by: deeper interprocess notch and taller, narrower ascending process.
From four-bearded rockling by: less deep interprocess notch. Medial surface of articular process does not create lamellate ridge.
From five-bearded rockling by: narrower ramus. Smaller lingual tooth sockets.

## Regressions

Length range of specimens examined (TL): 165-168 mm: $\mathrm{N}=2$.
In a specimen of 165 mm PMXL $=11.0 \mathrm{~mm}, \mathrm{PMXHH}=3.0 \mathrm{~mm}, \mathrm{PMXHL}=3.1 \mathrm{~mm}, \mathrm{PMXAH}=2.7$ mm .
In a specimen of 168 mm PMXL $=12.5 \mathrm{~mm}, \mathrm{PMXHH}=3.3 \mathrm{~mm}, \mathrm{PMXHL}=3.6 \mathrm{~mm}, \mathrm{PMXAH}=3.0$ mm .

## Estimated maxima

TL: 180 mm ; PMXL: 13.4 mm ; PMXHH: 3.5 mm ; PMXHL: 3.9 mm ; PMXAH: 3.2 mm .

## NORTHERN ROCKLING


fig. 1 lateral
plate 1 lateral

fig. 2 medial
plate 2 medial


## GADIDAE

## Five-bearded rockling (Ciliata mustela (L.))

## Description

The ramus is very broad, even in comparison with the other rockling species. It carries 3-4 uneven rows of tooth sockets on a distinctly flat occlusal surface (plate 3). In contrast with the other rockling species, and indeed most other gadoids, there is only a little difference in the sizes of the sockets between rows. In a 215 mm specimen the buccal sockets were 0.35 mm in diameter. The anterior processes are typical of the rocklings, with a deep interprocess notch and anterior premaxillary cleft. The depth of these clefts gives the base of the ascending process a constricted appearance in lateral view. Posteriorly, the articular process is more closely associated with the ramus than in the other rocklings, presenting less "overhang" in lateral view (plate 1). The postmaxillary process is low and roughly rectangular, as in other rocklings.

## Important features

Broad, flat occlusal surface with rather evenly sized teeth. Rear of articular process closer to ramus than in other rocklings.

## Similar species

Torsk (p. 64), other rockling species (pp. 66-70)
From torsk by: deeper interprocess notch and taller ascending process.
From other rocklings by: broad, flat occlusal surface and evenly sized tooth sockets.

## Regressions

Length range of specimens examined (TL): $108-230 \mathrm{~mm} ; \mathrm{N}=7$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| TL $=32.36$ PMXL -44.82 | 7 | 0.645 |
| TL $=79.52$ PMXHH -6.45 | 7 | 0.586 |
| TL $=87.90$ PMXHL -8.27 | 7 | 0.726 |
| TL $=121.14$ PMXAH -42.20 | 7 | 0.643 |

## Estimated maxima

TL: 510 mm ; PMXL: 15.0 mm ; PMXHH: 5.2 mm ; PMXHL: 5.1 mm ; PMXAH: 3.9 mm .

## FIVE-BEARDED ROCKLING


plate 1 lateral

plate 2 medial


TL $=215 \mathrm{~mm}$
plate 3 ventral

fig. 1 lateral

fig. 2 medial

broad flat occlusal surface sockets of broadly similar size in all rows
fig. 3 ventral

## GADIDAE

## Greater forkbeard (Phycis blennoides (Brünnich))

## Description

The bone is densely ossified with a smoothly curved ramus and very tall, narrow anterior processes. The toothed surface is strongly convex with 6-7 rows of small tooth sockets. The rows are extremely well ordered, running parallel to one another over the length of the ramus (fig. 3). Both anterior processes are tall and narrow. The anterior premaxillary cleft and interprocess notch are both deep and, consequently, the base of the ascending process appears highly contricted in lateral view (fig, 1). The process widens steadily above this constriction and appears widest at the top. The articular process is lower than the ascending process. It is a tall, narrow rectangle of bone, curving smoothly down to the ramus posteriorly. Medially, a lamellar ridge of bone runs anteroventrally from in front of the articular surface to the anterior margin of the bone (fig. 2).

## Important features

Tall, narrow anterior processes - especially the articular process. Lamellar ridge of bone on medial side of processes. Well-ordered, parallel rows of tooth sockets.

## Similar species

Four-bearded rockling (p. 68), Norway pout (p. 56)
From four-bearded rockling by: tall, narrow articular process. Well-ordered parallel rows of tooth sockets.
From Norway pout by: deep anterior premaxillary cleft. Lamellar ridge of bone on medial side of head.

## Regressions

Only one specimen from a fish of known size was examined: TL=315 mm. Two specimens were examined in total.
In the 315 mm specimen PMXL was 23.3 mm ; PMXHH was 8.9 mm ; PMXHL was 5.9 mm ; PMXAH was 7.7 mm .

## Estimated maxima

TL: 750 mm ; PMXL: 55.5 mm ; PMXHH: 21.2 mm ; PMXHL: 11.9 mm ; PMXAH: 18.3 mm .

GREATER FORKBEARD

plate 1 lateral

plate 2 medial

$\mathrm{TL}=315 \mathrm{~mm}$
plate 3 ventral

- 315 mm

fig. 1 lateral

fig. 2 medial


Strongly convex surface bearing multiple well-organized rows of small sockets.
fig. 3 ventral

### 3.3.5 AMMODYTIDAE

## Sandeels (Ammodytes marinus (Raitt) and Ammodytes tobianus (L.))

No differences could be found between the premaxillae of the two species.

## Description

Sandeel premaxillae are slender, elongate, and delicate in appearance. Despite this they often survive damage remarkably well, perhaps owing to their small size. The long, narrow, tapering ramus is taller than broad, and is biconvex on its lateral surface. The ventral edge is narrow and untoothed. The ascending process is very low and inclined forward (plate 1). The articular process is narrow and inclined posteriorly. Behind the two processes there is a shelf-like medial projection of the ramus (fig. 3). In life this provides support for the distal end of the long anterior extension of the mesethmoid bones (Gregory, 1933). The postmaxillary process is a sharp, posteriorly oriented spur.

## Important features

Long, very slender, delicate appearance. Low, forward-inclined ascending process. Articular and postmaxillary processes inclined posteriorly.

## Similar species

Smooth sandeel and greater sandeel (p. 78); only two specimens of each of these species were examined and the diagnostic features indicated below should be treated with caution.
From smooth sandeel by: shorter ramus and narrower articular process.
From greater sandeel by: shorter ramus. Narrower, more pointed articular and postmaxillary processes.

## Regressions

Length range of specimens examined (TL):
A. marinus, $74-168 \mathrm{~mm} ; \mathrm{N}=18$.
A. tobianus, one specimen of 161 mm , one size unknown; $\mathrm{N}=2$

| Regression equation $($ A. marinus $)$ | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.1789+0.9536 \ln$ PMXL | 13 | 0.922 |
| $\ln \mathrm{TL}=5.1422+1.0008 \ln$ PMXHW | 13 | 0.942 |
| $\ln \mathrm{TL}=5.3925+1.1655 \ln$ PMXHL | 12 | 0.948 |
| $\ln \mathrm{TL}=5.0687+1.0489 \ln$ PMXAH | 12 | 0.946 |

## Estimated maxima

TL: 270 mm ; PMXL: 11.6 mm ; PMXHW: 1.5 mm ; PMXHL: 1.2 mm ; PMXAH: 1.6 mm .

## SANDEEL


plate 1 lateral

plate 2 medial


fig. 3 medial

fig. 1 lateral

fig. 2 dorsal

五
plate 3 ventral
$T L=168 \mathrm{~mm}$

## AMMODYTIDAE

## Smooth sandeel (Gymnammodytes semisquamatus (Jourdain) )

## Description

The bone is slender, very long and delicate in appearance. The long, narrow, tapering ramus is taller than broad, and is biconvex on its lateral surface. The ventral edge is narrow and untoothed. The ascending process is very low and inclined forward. The articular process is broad-based and inclined posteriorly. Behind the two processes there is a shelf-like medial projection of the ramus. The postmaxillary process is a sharp, posteriorly oriented spur.

## Similar species

Sandeels (p. 76), greater sandeel (below)
From sandeel by: broad-based articular process.
From greater sandeel by: sharp-ended postmaxillary process.

## Regressions

Length range of specimens examined (TL): 197-201 mm; $\mathrm{N}=2$. In the 197 mm specimen PMXL was 10.2 mm , PMXHW was 0.87 mm , PMXHL was 1.26 mm and PMXAH was 1.02 mm . In the 201 mm specimen, PMXHW was 0.84 mm , and PMXHL was 1.59 mm .

## Estimated maxima

TL: 280 mm ; PMXL: 14.5 mm ; PMXHW: 1.2 mm ; PMXHL: 2.3 mm ; PMXAH: 1.7 mm .

## Greater sandeel (Hyperoplus lanceolatus (Lesauvage))

## Description

The bone is slender, very long and delicate in appearance. The ramus is exceptionally long and narrow. The ventral edge is narrow and untoothed. The ascending process is very low and inclined forward. The articular process is blunt and broad-based, and is inclined posteriorly. Behind the two processes there is a shelf-like medial projection of the ramus. The postmaxillary process is a posteriorly oriented spur. In the specimens examined it was blunt-ended.

## Similar species

Sandeels (p. 76), smooth sandeel (above)
From sandeel by: broad articular process and blunt-ended postmaxillary process.
From smooth sandeel by: blunt-ended postmaxillary process.

## Regressions

Length range of specimens examined (TL): $250-268 \mathrm{~mm} ; \mathrm{N}=2$. In the 250 mm specimen, PMXL was 14.4 mm , PMXHW was 1.38 mm , PMXHL was 2.1 mm , and PMXAH was 1.41 mm .
In the 268 mm specimen, PMXL was 14.0 mm , PMXHW was 1.08 mm , PMXHL was 1.68 mm , and PMXAH was 1.47 mm .

## Estimated maxima

TL: 350 mm ; PMXL: 20.2 mm ; PMXHW: 1.9 mm ; PMXHL: 2.9 mm ; PMXAH: 2.0 mm .

## SMOOTH SANDEEL


plate 1 lateral

GREATER SANDEEL

fig. 1 lateral
plate 1 lateral
$\mathrm{TL}=\mathbf{2 5 0} \mathbf{~ m m}$


### 3.3.6. BOTHIDAE

## Turbot (Scophthalmus maximus (L.))

## Description

The premaxilla has a strongly decurved ramus and tall anterior processes. The ramus tapers rapidly, ending in a long narrow point behind the postmaxillary process. There are 4-8 uneven rows of tooth sockets extending over $90 \%$ of the length of the ramus. The sockets are small ( 0.8 mm in a 590 mm specimen), with little variation in size between rows and the teeth themselves are conical. The ascending process is a tall, lamellar tongue of bone which narrows to a triangular apex. Beneath the ascending process there is a well-defined concavity (fig. 1.). The articular process is roughly square in lateral view (fig. 2). Medially, a stout lamella of bone runs between the two processes, bounding a deep fossa. The premaxillary process is long and low (c.w. brill), tallest anteriorly, and attached to the ramus over its full length.

## Important features

Tall, broad, lamellar ascending process. Strongly decurved ramus. Square profile of articular process. Long, low postmaxillary process.

## Similar species

Brill (p. 82), megrim (p. 84)
From brill by: long, low postmaxillary process. No other consistent differences could be found in the small numbers of specimens of each species examined.
From megrim by: more upright ascending process and squarer profile of articular process. Welldefined concavity below ascending process.

## Regressions

Length range of specimens examined (TL): $388-615 \mathrm{~mm} ; \mathrm{N}=7$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.9060+0.9140 \ln$ PMXL | 4 | 0.930 |
| $\ln \mathrm{TL}=3.6196+0.9158 \ln$ PMXHH | 4 | 0.884 |
| $\ln \mathrm{TL}=4.0810+0.9075 \ln$ PMXHL | 4 | 0.971 |
| $\ln \mathrm{TL}=4.0988+0.8827 \ln$ PMXAH | 4 | 0.982 |

## Estimated maxima

TL: 1200 mm ; PMXL: 91.2 mm ; PMXHH: 39.8 mm ; PMXHL: 26.8 mm ; PMXAH: 29.1 mm .

## TURBOT


fig. 1 lateral
plate 1 lateral

fig. 2 medial
plate 2 medial

multiple rows of small tooth sockets
plate 3 ventral
$T L=615 \mathrm{~mm}$
fig. 3 ventral
1.0 cm

## BOTHIDAE

## Brill (Scophthalmus rhombus (L.))

## Description

The ramus is strongly decurved and tapers rather rapidly from behind the articular process. In the two specimens examined there were 3-4 rows of tooth sockets The sockets are moderately sized ( 0.5 mm in a 292 mm specimen) with little variation between rows. The teeth themselves are curved and conical. The ascending process is tall and lamellate, ending in a pointed triangular apex. There is a concavity at its base, as in the turbot. The articular process is shorter than the ascending process and is roughly square in profile. Medially, a strong lamellar sheet of bone runs between the processes enclosing a deep fossa. The postmaxillary process is short and ronded (c.w. turbot).

## Important features

Tall, broad, lamellar ascending process. Strongly decurved ramus. Short rounded postmaxillary process.

## Similar species

Turbot (p. 80), megrim (p. 84)
From turbot by: short, round ascending process. In the few specimens of each species examined no other consistent differences could be identified.
From megrim by: more upright ascending process. Well-defined hollow at base of ascending process.

## Regressions

Length range of specimens examined (TL): 292-350 mm; $\mathrm{N}=2$.
In the 292 mm specimen PMXL was 17.0 mm , PMXHH was 8.3 mm , PMXHL was 4.8 mm , and PMXAH was 5.5 mm . In the 350 mm specimen PMXL was 21.9 mm , PMXHH was 10.0 mm , PMXHL was 6.5 mm , and PMXAH was 6.8 mm .

## Estimated maxima

TL: 610 mm ; PMXL: 38.2 mm ; PMXHH: 17.4 mm ; PMXHL: 13.6 mm ; PMXAH: 11.9 mm .

## BRILL


fig. 1 lateral
plate 1 lateral

fig. 2 medial
plate 2 medial


3-4 rows of small sockets
fig. 3 ventral
$\mathrm{TL}=292 \mathrm{~mm}$

## BOTHIDAE

## Megrim (Lepidorhombus whiffiagonis (Walbaum))

## Description

The mouth of the megrim is almost straight and this is reflected in the ramus of the premaxilla, which is less strongly decurved than that of turbot or brill (fig. 1). The occlusal surface carries 24 rows of moderately sized tooth sockets ( 0.5 mm in a 340 mm specimen). The teeth are curved and conical. The ascending process is taller than the articular. It is a tall lamellar plate of bone ending in a triangular apex. The ascending process is less upright than that of turbot or brill, and curves back noticeably over the front of the articular process (fig. 2). The hollow at the base of the articular process is broad and shallow (fig. 1;c.w. turbot/brill). The articular process is rather rounded in lateral view (c.w. turbot/brill). Medially, there is a sheet of bone running between the two processes, bounding a deep fossa. The postmaxillary process is long, low and rounded.

## Important features

Ascending process a tall lamellar plate of bone curving some way back over the anterior part of the articular process. Ramus not strongly decurved. Rounded articular process.

## Similar species

Turbot (p. 80), brill (p. 82)
From turbot by: ascending process curves back over articular process. Ramus straighter. Concavity below ascending process shallower and broader.
From brill by: ascending process curves back over articular process. Ramus straighter. Concavity below ascending process shallower and broader. Postmaxillary process longer.

## Regressions

Length range of specimens examined (TL): 172-456 mm.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=14.83+30.45$ PMXL | 18 | 0.828 |
| $\ln \mathrm{TL}=3.6719+1.0078 \ln$ PMXHH | 18 | 0.966 |
| $\mathrm{TL}=67.97-4.28$ PMXHL | 18 | 0.903 |
| $\ln \mathrm{TL}=4.1602+0.9790 \ln$ PMXAH | 18 | 0.960 |

## Estimated maxima

TL: 610 mm ; PMXL: 35.7 mm ; PMXHH: 14.9 mm ; PMXHL: 8.6 mm ; PMXAH: 9.8 mm .

## MEGRIM


plate 1 lateral

fig. 2 medial
plate 2 medial


2-4 rows small-medium sockets

## fig. 3 ventral

$T L=456 \mathrm{~mm}$

## BOTHIDAE

## Scaldfish (Arnoglossus laterna (Walbaum) )

## Description

Scaldfish never grow to a large size ( $\max =190 \mathrm{~mm}$ ) and so their premaxillae are small and rather fragile. The ramus is moderately long, tapering, and slightly decurved. It is taller than it is broad and the narrow occlusal surface bears a single row of long conical teeth. At the anterior end of the bone a distinctive, rounded protuberance projects forward beneath the base of the ascending process (fig. 1). The ascending process is tall and narrow, its widest aspect being across the ramus. Viewed laterally it forms an angle of approximately 90 degrees with the ramus (c.w. long rough dab, p. 98). The articular process is rather squat, and is roughly square in lateral view. Its anterior edge is parallel to the ascending process, resulting in a narrow interprocess notch (c.w. long rough dab, p. 98). There is no medial lamella and no fossa between the two anterior processes. The postmaxillary process is long, rounded, and low.

## Important features

Narrow occlusal surface with a single row of teeth. Tall, narrow ascending process. Rounded protuberance beneath front of ascending process.

## Similar species

Long rough dab (p. 98)
From long rough dab by: shorter ramus. Square articular process. Ascending process at 90 degrees to ramus. Rounded anterior protuberance beneath ascending process.

## Regressions

Length range of specimens examined (SL): 95-107 mm; $\mathrm{N}=2$.
In the 95 mm specimen PMXL was 6.2 mm , PMXHH was 2.7 mm , PMXHL was 1.5 mm and PMXAH was 1.6 mm . In the 107 mm specimen, PMXL was 6.4 mm , PMXHH was 2.8 mm , PMXHL was 1.5 mm , and PMXAH was 1.8 mm .

## Estimated maxima

SL: 190 mm ; PMXL: 12.4 mm ; PMXHH: 5.4 mm ; PMXHL: 3.0 mm ; PMXAH: 3.2 mm .

## SCALDFISH


plate 1 lateral

plate 2 medial

single row of small sockets on narrow ramus
fig. 3 ventral
plate 3 ventral
SL = 107 mm

### 3.3.7. PLEURONECTIDAE

## Plaice (Pleuronectes platessa (L.))

## Description

Plaice premaxillae are only moderately well ossified and have a broad-grained texture. The ramus is short and very deep (plate 1)- the deepest of all pleuronectids studied, excepting the lemon sole. It is strongly laterally curved along its full length (plate 3). The posterior $1 / 6$ of its length curves very strongly ventrally (plate 1 ). There is a single row of tooth sockets on the ventro-medial margin of the ramus. The sockets are essentially lozenge-shaped, but in most specimens the anterior sockets are slightly triangular (figs. 2 and 3). The sockets are arranged in a straight, wellordered row (c.w. dab, p. 90 , and flounder, p.92). The teeth themselves are peg-like in lateral view, but roughly triangular viewed anteriorly or posteriorly (fig. 3). The ascending process is tall and narrow, rising a short way back from the anterior end of the ramus. Its lateral surface is rounded (c.w. witch). The articular process is fused to the ascending process for $90-100 \%$ of its height. There is a narrow fossa between the two processes. The base of the articular surface overhangs medially, creating a distinct notch (plate 2, fig. 2). The postmaxillary process appears as a rounded dorsal extension of the ramus.

## Important features

Deep, laterally flattened ramus, strongly decurved posteriorly. Tall, narrow ascending process. Anterior processes fused for $>=90 \%$ of height of articular process.

## Similar species

Dab (p. 90), flounder (p. 92), witch (p. 94)
From dab by: relatively deeper ramus with highly ordered tooth row. Broader lateral face of ascending process. Greater fusion of anterior processes. Broader teeth.
From flounder by: deeper ramus with highly ordered tooth row. Broader teeth. Greater fusion of anterior processes. Notch beneath articular surface.
From witch by: deeper ramus. Greater fusion of anterior process. Rounded (not ridged) lateral surface below ascending process. Notch beneath articular surface.

## Regressions

Length range of specimens examined (TL): 77-380 mm; $\mathrm{N}=33$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.4067+0.9334 \ln$ PMXL | 33 | 0.965 |
| $\ln \mathrm{TL}=3.4377+1.0592 \ln$ PMXHH | 33 | 0.973 |
| $\ln \mathrm{TL}=4.4820+1.0303 \ln$ PMXHL | 33 | 0.931 |
| $\ln \mathrm{TL}=3.9971+0.9445 \ln$ PMXAH | 30 | 0.978 |

## Estimated maxima

TL: 1180 mm ; PMXL: 47.8 mm ; PMXHH: 29.7 mm ; PMXHL: 11.1 mm ; PMXAH: 25.0 mm .

## PLAICE


plate 1 lateral

plate 2 medial

fig. 3 anterior socket and tooth

## PLEURONECTIDAE

## Dab (Limanda limanda (L.))

## Description

Dab premaxillae are rather lightly ossified. In overall configuration the bone is similar to that of plaice, flounder, and witch, with a tall, narrow ascending process and a short, rather deep, ramus. The ramus is strongly biconvex and is deeper than it is broad. There is a single row of tooth sockets, often uneven and occasionally with some doubling of the row. The teeth themselves are mainly peg-like (fig. 3), although the most posterior ones may be conical or needle-shaped. The sockets are lozenge-shaped. A rounded tooth-bearing portion of the ramus extends in front of the base of the ascending process (plate 1). The ascending process is tall and narrow. It is separated from the articular process by a V-shaped notch. The articular process is fused to the ascending process for $75-85 \%$ of its height (c.w. plaice). A medial lamella runs between the two processes, bounding a fossa. The articular surface overhangs the medial surface of the ramus, creating a notch (fig. 2). The top of the articular process is triangular, its apex approximately central (c.w. flounder).

## Important features

Deep, laterally flattened ramus, strongly decurved posteriorly. Tall, narrow ascending process. Anterior processes fused for $>=75-85 \%$ of height of articular process. Top of articular process triangular with central apex.

## Similar species

Plaice (p. 88), flounder (p. 92), witch (p. 94)
From plaice by: narrower ramus and ascending process. Deeper interprocess notch (anterior processes fused for $75-85 \%$ of articular height). Socket row often irregular. Sockets lozengeshaped, not triangular.
From flounder by: interprocess notch less deep, and usually wider. Notch beneath articular surface. Apex of articular process is central.
From witch by: Lack of vertical lateral ridge beneath ascending process. Notch beneath articular surface. Broad area of ramus projecting anterior to base of ascending process. Socket row often irregular.

## Regressions

Length range of specimens examined (TL): 68-393 mm; $\mathrm{N}=34$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=24.31$ PMXL +14.70 | 30 | 0.967 |
| $\mathrm{TL}=41.25$ PMXHH + 0.44 | 30 | 0.921 |
| $\mathrm{TL}=101.86$ PMXHL -21.70 | 30 | 0.934 |
| $\mathrm{TL}=66.36$ PMXAH - 9.51 | 30 | 0.975 |

## Estimated maxima

TL: 460 mm ; PMXL: 17.8 mm ; PMXHH: 10.7 mm ; PMXHL: 4.5 mm ; PMXAH: 7.0 mm .

## DAB


plate 1 lateral

plate 2 medial

fig. 3 anterior socket and tooth

## PLEURONECTIDAE

## Flounder (Platichthys flesus (L.))

## Description

Flounder premaxillae are usually rather poorly ossified and can be prone to damage, particularly along the ventral edge of the ramus. As in other pleuronectid species the ramus is deep, although less so than in the plaice. In most specimens there is a single row of tooth sockets, although in some larger individuals there is some doubling of this row. The sockets are variable in size and shape, but are generally lozenge-shaped or oval. The teeth are peg-like (fig. 3), similar to those of the dab. The ascending process is tall and narrow. The interprocess notch is deep and narrow, with the articular process fused to the ascending process for $60-80 \%$ of its height (c.w. plaice, dab). The apex of the articular process is usually, but not invariably, situated over the anterior part of the process (c.w. dab). In intact specimens there is no notching beneath the medial face of the articular process (c.w. plaice, dab). There is a fossa between the two processes. The fossa is broader than in the witch, and the fossa lamella is situated lower down between the processes. The postmaxillary process is low and rounded.

## Important features

Deep, laterally flattened ramus, strongly decurved posteriorly. Tall, narrow ascending process. Deep, narrow interprocess notch (anterior processes fused for $60-80 \%$ of height of articular process).

## Similar species

Plaice (p. 88), dab (p. 90), witch (p. 94). It is not always possible to distinguish flounder from dab. From plaice by: narrower ramus. Deeper interprocess notch.
From dab by: lack of notching beneath articular surface. Deeper, narrower interprocess notch. Apex of articular process anterior.
From witch by: lack of vertical lateral ridge beneath ascending process. Wider fossa with lamella situated lower down between the processes. Socket row often irregular.

## Regressions

Length range of specimens examined (TL): 130-393 mm; N=9.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=28.23$ PMXL -50.34 | 8 | 0.849 |
| $\ln \mathrm{TL}=3.0615+1.2482 \ln$ PMXHH | 8 | 0.882 |
| $\ln \mathrm{TL}=4.3648+1.1389 \ln$ PMXHL | 8 | 0.842 |
| $\mathrm{TL}=66.48$ PMXAH -46.99 | 8 | 0.799 |

## Estimated maxima

TL: 600 mm ; PMXL: 21.8 mm ; PMXHH: 14.1 mm ; PMXHL: 5.5 mm ; PMXAH: 8.9 mm .

## FLOUNDER


plate 1 lateral

plate 2 medial


TL = 194 mm
plate 3 ventral

fig. 1 lateral

fig. 2 medial

fig. 3 anterior socket and tooth

## PLEURONECTIDAE

## Witch (Glyptocephalus cynoglossus (L.))

## Description

Witch premaxillae are not well ossified and often appear slightly translucent. The ramus is deeper than broad and strongly decurved posteriorly. There is a single, well-ordered tooth row, without doubling or irregularity. The tooth sockets are lozenge-shaped and the teeth themselves (fig. 3) are similar to those of the plaice. The ascending process is tall and narrow. In lateral view it presents a narrow, sharp edge which continues as a raised ridge below the point of fusion with the articular process (fig. 1). The articular process is fused to the ascending process for $80-90 \%$ of its height (c.w. plaice, dab, flounder). Medially, there is no notching beneath the articular surface (fig. 2). There is a small fossa between the two anterior processes. The fossa lamella (fig. 2) is situated higher between the processes than in dab (p. 90) or flounder (p. 92). The postmaxillary process is low and rounded.

## Important features

Deep, laterally flattened ramus, strongly decurved posteriorly. Tall, narrow ascending process. Narrow lateral edge of ascending process which continues as ridge below point of fusion with articular process. Well-ordered tooth row.

## Similar species

Plaice (p. 88), dab (p. 90), flounder (p. 92)
From plaice by: vertical ridge below point of fusion of anterior processes. Lack of notch beneath articular surface. Ramus usually narrower.
From dab by: vertical ridge below point of fusion of anterior processes. Short, narrow area of ramus projecting anterior to base of ascending process. Lack of notch beneath articular surface.
From flounder by: vertical ridge beneath point of fusion of anterior processes. Interprocess notch shallower and, usually, wider. Tooth sockets very regularly arranged.

## Regressions

Length range of specimens examined (TL): $160-415 \mathrm{~mm} ; \mathrm{N}=19$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.9766+1.2267 \ln$ PMXL | 18 | 0.941 |
| $\ln \mathrm{TL}=3.6838+1.0383 \ln$ PMXHH | 19 | 0.968 |
| $\ln \mathrm{TL}=4.4982+1.2515 \ln$ PMXHL | 19 | 0.973 |
| $\ln \mathrm{TL}=4.1873+1.0368 \ln$ PMXAH | 19 | 0.952 |

## Estimated maxima

TL: 710 mm ; PMXL: 17.8 mm ; PMXHH: 15.6 mm ; PMXHL: 5.1 mm ; PMXAH: 9.5 mm .

## WITCH


plate 1 lateral

plate 2 medial

plate 3 ventral
$T L=346 \mathrm{~mm}$

fig. 1 lateral

fig. 2 medial

fig. 3 anterior socket and tooth

## PLEURONECTIDAE

## Lemon sole (Microstomus kitt (Walbaum) )

## Description

The mouth of the lemon sole is extremely small and the premaxilla is correspondingly short. The bone is, however, well ossified and very robust. Its overall shape makes it umistakable, with an extremely short ramus and tall, strong ascending process. There is a single row of large teeth which are strongly attached to the bone. The teeth are short and broad. The ascending process arises some distance back from the anterior extremity of the ramus. It is a tall, sturdy column of bone (fig. 1 ). The articulating process is completely fused to the ascending process. It is highest anteriorly, sloping downwards posteriorly. There is a notch beneath the articular surface (fig. 2). The postmaxillary process is a tiny, short, rounded projection on the dorsal surface of the ramus, situated midway between the rear of the ascending process and the end of the ramus. However, on many of the specimens examined the postmaxillary process was entirely absent.

## Important features

Very short ramus and extremely tall, columnar ascending process.

## Similar species

None

## Regressions

Length range of specimens examined (TL): $156-430 \mathrm{~mm} ; \mathrm{N}=32$.

| Regression equation | $N$ | $R^{2}$ |  |
| :--- | :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.9280+0.8662 \ln$ PMXL | $\ddots$ | 31 | 0.877 |
| $\ln \mathrm{TL}=3.7714+0.9246 \ln$ PMXHH |  | 31 | 0.918 |
| $\ln \mathrm{TL}=4.6136+1.0377 \ln$ PMXHL |  | 31 | 0.865 |

## Estimated maxima

TL: 660 mm ; PMXL: 16.4 mm ; PMXHH: 17.4 mm ; PMXHL: 5.4 mm .

## LEMON SOLE


plate 1 lateral

plate 2 medial

plate 3 ventral
TL = 322 mm

dorsal
teeth are very firmly attached to the ramus

anterior
fig. 3 teeth

## PLEURONECTIDAE

## Long rough dab (Hippoglossoides platessoides (Fabricius))

## Description

The ramus is extremely long and narrow, corresponding to the large gape in this species. The ramus is deeper than broad and, in most specimens, bears a single row of teeth. In some specimens there is a degree of doubling in the row. The tooth sockets are lozenge-shaped and the teeth needlelike. The ramus is not strongly laterally curved (plate 3). The narrow ascending process makes an angle of $<=90$ degrees with the ramus (plate 1 ; c.w. scaldfish in which the angle is rarely less than 90 degrees). There is a hollow beneath the anterior face of the process (fig. 3 ) and, below this, a prominent, tooth-bearing portion of the ramus (fig 2). The articular process is variable in shape, but it is generally rather low and squat compared with those of other pleuronectids. Its anterior edge always slopes posteriorly, away from the ascending process, leaving a $V$-shaped interprocess notch (c.w. scaldfish). The postmaxillary process is long and very low, appearing as a dorsal expansion of the ramus.

## Important features

Extremely long ramus. Tall, narrow ascending process and rather squat articular process. Prominent continuation of ramus anterior to ascending process.

## Similar species

Scaldfish (p. 86), plaice (p. 88), dab (p. 90), flounder (p. 92), and witch (p. 94)
From scaldfish by: longer ramus. Articular process slopes back, away from ascending process. Ascending process usually makes an acute angle with ramus. Lacks rounded anterior protuberance of scaldfish premaxilla.
From plaice/dab/flounder/witch by: extremely long ramus.

## Regressions

Length range of specimens examined (TL): 79-283 mm; $\mathrm{N}=27$

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.8478+0.8790 \ln$ PMXL | 26 | 0.926 |
| $\mathrm{TL}=38.28$ PMXHH +0.17 | 26 | 0.923 |
| $\ln \mathrm{TL}=4.3414+0.9213 \ln$ PMXHL | 26 | 0.939 |
| $\ln \mathrm{TL}=4.1738+0.9999 \ln$ PMXAH | 26 | 0.917 |

## Estimated maxima

TL: 600 mm ; PMXL: 50.7 mm ; PMXHH: 14.0 mm ; PMXHL: 8.5 mm ; PMXAH: 8.3 mm .

## LONG ROUGH DAB


plate 1 lateral

plate 2 medial

fig. 3 anterior
plate 3 ventral
$\mathrm{TL}=283 \mathrm{~mm}$

## PLEURONECTIDAE

## Halibut (Hippoglossus hippoglossus (L.))

## Description

The ramus is of moderate length and strongly decurved. Immediately behind the articular process the ramus is broader than it is deep. In this respect the halibut is unique among the pleuronectids covered herein, the left premaxillae of the other species being noticeably laterally flattened. The ramus bears two rows of large tooth sockets (fig. 3), the buccal row larger than the lingual. The teeth themselves are large, curved, and conical. There is a prominent continuation of the ramus anterior to the ascending process (fig. 1). The ascending process is a tall, narrow, lamellar plate of bone set across the ramus, with its narrow edge directed laterally. In anterior view the top of the ascending process is triangular with a lateral apex (fig. 1). The articular process is roughly square, tilted posteriorly away from the ascending process. There is a deep fossa between the processes, bounded medially by a strong lamella.

## Important features

Ramus broader than in other pleuronectids. Extremely large, conical teeth. Ascending process a tall plate of bone, its narrow edge directed laterally. Square articular process sloping posteriorly.

## Similar species

Long rough dab (p. 98)
The two species can normally be easily distinguished by the large size of the halibut premaxilla. Very small halibut premaxillae may be distinguished from those of long rough dab by the breadth of the ramus.

## Regressions

Length range of specimens examined (TL): 463-810 mm; $\mathrm{N}=5$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| TL $=19.47$ PMXL -3.28 | 4 | 0.950 |
| TL $=49.97$ PMXHH -76.10 | 4 | 0.998 |
| TL $=82.36$ PMXHL -38.54 | 4 | 0.999 |
| TL $=84.11$ PMXAH -82.89 | 4 | 0.994 |

## Estimated maxima

TL: 2540 mm ; PMXL: 125.6 mm ; PMXHH: 52.3 mm ; PMXHL: 30.1 mm ; PMXAH: 31.1 mm .

## HALIBUT


plate 1 lateral

plate 2 medial

fig. 2 medial
fig. 1 lateral

two rows of large sockets (the teeth are large and conical)
fig. 3 ventral
plate 3 ventral
$\mathrm{TL}=810 \mathrm{~mm}$

### 3.3.8. SOLEIDAE

## Dover sole (Solea solea (L.) )

## Description

In the Soleidae the mouth is small and the jaws markedly asymmetrical. The left (blind side) premaxilla is very much better developed than the right. It is strongly curved and its occlusal surface forms a concavity into which the convex toothed surface of the left dentary fits (Norman, 1934). The ramus is unusual in being broadest posteriorly, that part of it beneath the anterior processes being narrow and devoid of teeth. The posterior portion of the ramus bears multiple rows of small tooth sockets ( $6-7$ in the two specimens examined). The sockets are deeper than they are broad and the teeth are conical. The ascending process is strongly inclined forwards, making a Y-shape with the anterior portion of the ramus. The articular process is inconspicuous, appearing as a triangular swelling behind the ascending process (fig. 2). The extreme curvature of the left premaxillae of the soles make them unmistakable. However, they are not very robust and may be prone to mechanical damage and digestion.

## Important features

Extreme curvature of ramus and forward-inclined ascending process. Ramus broadest posteriorly.

## Similar species

Solenette (p. 104)
In the two specimens examined the articular process of the Dover sole appeared as a small triangular protuberance behind the ascending process (fig. 2). In the solenette the articular process is generally larger, broader and more rounded. The degree of curvature appears to be greater in the Dover sole than in the solenette. Both these differences must be treated with caution, however, owing to the small number of specimens examined.

## Regressions

Length range of specimens examined (TL): 251-268 mm; $\mathrm{N}=2$.
In the 251 mm specimen, PMXL was 9.6 mm and PMXHH was 4.1 mm . In the 268 mm specimen, PMXL was 10.5 mm , and PMXHH was 4.1 mm .

## Estimated maxima

TL: 700 mm ; PMXL: 27.4 mm ; PMXHH: 11.4 mm .

## DOVER SOLE


plate 1 lateral

plate 2 medial

$\mathbf{T L}=\mathbf{2 5 1} \mathrm{mm}$

fig. 1 lateral

fig. 2 medial

## SOLEIDAE

## Solenette (Buglossidium luteum (Risso) )

## Description

Like that of the Dover sole, the left premaxilla of the solenette is strongly curved. The ramus is broadest posteriorly, and that part of it beneath the anterior processes is narrow and devoid of teeth. The posterior, toothed portion of the ramus bears $7-10$ rows of small tooth sockets. The sockets are deeper than they are broad, and the teeth are conical. The ascending process is strongly inclined forwards, making a Y -shape with the anterior portion of the ramus. The articular process (fig. 2) is more strongly developed than that of the Dover sole and distinguishes the two species. The extreme curvature of the left premaxillae of the soles makes them unmistakable. Solenette premaxillae are not robust and, like those of the Dover sole (p. 102) may be prone to mechanical damage or digestion.

## Important features

Extreme curvature of ramus and forward-inclined ascending process. Ramus broadest posteriorly.

## Similar species

Dover sole (p. 102)
The articular process of the solenette is a broad, rounded protuberance behind the ascending process (fig. 2). In this respect it differs from that of the Dover sole, which is much smaller and triangular. The ramus is less strongly curved than that of the Dover sole.

## Regressions

Length range of specimens examined (TL): 98-195 mm; $\mathrm{N}=20$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.5061+0.8549 \ln$ PMXL | 20 | 0.888 |
| $\mathrm{TL}=22.23$ PMXHH +20.45 | 19 | 0.815 |
| $\ln \mathrm{TL}=4.8617+0.8508 \ln$ PMXAH | 20 | 0.779 |

## Estimated maxima

TL: 200 mm ; PMXL: 7.9 mm ; PMXHH: 2.7 mm ; PMXAH: 1.6 mm .

## SOLENETTE


plate 1 lateral

plate 2 medial

$T L=167 \mathrm{~mm}$


### 3.3.9 Other groups

This section contains photographs of premaxillae for selected species of the Percomorphi, Scleroparei, Zeomorphi and Pediculati.

Cuckoo wrasse Labrus mixtus (L.)

The robust fused ascending/articular process forms an angle of approximately $45^{\circ}$ with the ramus. The ramus curves sharply downwards at its posterior end.
plate 1 lateral
There are two tooth rows, the buccal row extending along approximately threequarters of the ramus, with tooth size declining posteriorly, while the lingual row is shorter and contains smaller teeth (see also p.203).
plate 2 medial

plate 3 ventral

$\mathrm{TL}=290 \mathrm{~mm}$

## Dragonet (Callionymus lyra L.)

The premaxilla of the dragonet is a delicate, wishbone-shaped bone. That of the spotted dragonet (C. maculatus) is similar but more strongly decurved and with a notch at the anterior base of the ascending process.

plate 1 lateral

plate 2 medial


Viviparous blenny or eelpout (Zoarces viviparus (L.))
The premaxillae of the eelpout, butterfish (p. 109), and some blennies and gobies (p. 111) are of similar general size and shape. The articular process of the eelpout premaxilla is separated from the ascending process by a deep sulcus, absent in the butterfish. The articular process is also taller
 than that of the butterfish.
plate 1 lateral

plate 2 medial
plate 3 ventral

$\stackrel{\square}{0.5 \mathrm{~cm}}$
$T L=154 \mathrm{~mm}$

## Butterfish or gunnel (Pholis gunnellus (L.))

The ascending process is columnar and fused to the articular process. The oral surface has an outer (buccal) row of large teeth and an inner (lingual) row of smaller ones.

plate 1 lateral

plate 2 medial


$T L=161 \mathrm{~mm}$

## Scad (Trachurus trachurus (L.))

The scad premaxilla is poorly ossified and appears slightly translucent. The ramus is laterally flattened and the processes are tall and fused.

plate 1 lateral

plate 2 medial

plate 3 ventral $\longmapsto \quad T L=360 \mathrm{~mm}$
1.0 cm

## Sand goby (Pomatoschistus minutus (Pallas))

The sand goby premaxilla is longer than that of the eelpout (p. 108) and has a shorter ascending process. There are 2-3 tooth rows.

plate 1 lateral

plate 2 medial


## Mackerel (Scomber scombrus (L.))

The mackerel premaxilla is a long, narrow, poorly ossified bone with a single row of fine pointed conical teeth. The bone is very narrow, little wider than the tooth row itself, except at the head of the bone where the processes bulge somewhat. The processes themselves are very poorly ossified and have a slightly spongy texture.

plate 1 lateral

plate 2 medial

1.0 cm

Bullrout or father lasher (Myoxocephalus scorpius (L.))

The oral surface has a mass of small equally sized teeth. The ascending process is very tall and presents its narrow edge in lateral view.

plate 1 lateral

plate 2 medial


Lumpsucker (Cyclopterus lumpus (L.))

Lumpsucker bones are very light and have a papery texture. There are three rows of teeth at the anterior of the premaxilla, declining to one row at the posterior end.

plate 1 lateral

plate 2 medial

plate 3 ventral
1.0 cm

Boarfish (Capros aper (L.))

There are four rows of teeth (best seen in medial view). Sea stickleback (Spinachia spinachia) and dragonet (p. 107) premaxillae are superficially similar, but with shorter processes and different dentition.
plate 1 lateral


## Angler (Lophius piscatorius L.)

Note that the ascending process is usually detached (as here).
There are two rows of large conical teeth at the edges of the oral surface, with the largest teeth on the inner edge. Blackscabbard fish (Aphanopus carbo) also have large daggerlike teeth, but in a single row.

plate 1 lateral

plate 2 medial

$\mathrm{TL}=\mathbf{4 5 0} \mathbf{~ m m}$

### 3.4 THE RIGHT PREMAXILLAE OF PLEURONECTIDAE AND SOLEIDAE

### 3.4.1 PICTORIAL KEY TO RIGHT PREMAXILLAE

The jaws of many pleuronectids and soles exhibit considerable asymmetry and therefore require separate descriptions of left and right elements. In strongly swimming species with large jaws, such as the halibut, the asymmetry is slight and the shape and dentition are more or less similar on both sides. However, in most species the jaws are more strongly developed on the blind (left) side, and in the lemon sole (Pleuronectidae) and the true soles (Soleidae) the asymmetry is extreme.

### 3.4.1 Pictorial Key

Medial aspects of the right premaxillae of pleuronectids and soles are shown on the opposite page. These simple diagrams are intended solely to guide the user to the appropriate full species descriptions. They must not be used to reach firm identifications.
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## PLEURONECTIDAE

## Plaice (Pleuronectes platessa (L.))

## Description

The ramus is short and the ascending process very tall. Immediately behind the articular process the ramus curves strongly ventro-medially. The tooth sockets are restricted to the anterior part of the ramus, the single row of teeth ending beneath the rear of the articular process. The sockets number 3-7. The interprocess notch is deep, almost entirely separating the two anterior processes. The ascending process is a tall, tapering, lamellar plate of bone set across the ramus. The articular process is shorter, with a pronounced rounded bulge medially, forming the articular surface.

## Similar species

Dab (p. 121), flounder (p. 122), witch (p. 123)
From all three of the above by: low number of teeth (3-7) which are restricted to that part of the ramus beneath the anterior processes.
From witch by: deep interprocess notch.

## Regressions

Length range of specimens examined (TL): 77-380 mm; $\mathrm{N}=31$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.4364+1.0013 \ln$ PMXL | 31 | 0.956 |
| $\ln \mathrm{TL}=3.5918+1.0417 \ln$ PMXHH | 31 | 0.979 |
| $\ln$ TL $=4.3020+1.0777 \ln$ PMXHL | 31 | 0.879 |
| $\ln$ TL $=4.2757+0.9845 \ln$ PMXAH | 31 | 0.970 |

## Estimated maxima

TL: 1180 mm ; PMXL: 35.2 mm ; PMXHH: 27.4 mm ; PMXHL: 10.9 mm ; PMXAH: 16.3 mm .


## PLEURONECTIDAE

## Dab (Limanda limanda (L.))

## Description

The ramus is short and the anterior processes, particularly the ascending process, are tall. The interprocess notch is deep, almost completely separating the two processes. The ascending process is a tapering, lamellar plate of bone set across the ramus, its narrow edge oriented laterally. There is a shallow fossa between the two processes. There are 7-11 tooth sockets, arranged in a single row, extending back at least as far as the postmaxillary process (c.w. plaice, p. 120).

## Similar species

Flounder (p. 123), plaice (p. 120), witch (p. 123). No consistent differences were found between the right premaxillae of dab and flounder.
From plaice by: greater extent of tooth row.
From witch by: deep interprocess notch, lower anterior processes.

## Regressions

Length range of specimens examined (TL): 68-393 mm; $\mathrm{N}=27$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=35.48$ PMXL -25.94 | 27 | 0.869 |
| $\mathrm{TL}=42.44$ PMXHH -6.87 | 27 | 0.937 |
| $\mathrm{TL}=112.29$ PMXHL -42.14 | 27 | 0.863 |
| $\mathrm{TL}=72.88$ PMXAH -6.16 | 27 | 0.981 |

## Estimated maxima

TL: 460 mm ; PMXL: 12.9 mm ; PMXHH: 10.2 mm ; PMXHL: 4.3 mm ; PMXAH: 6.3 mm .


## PLEURONECTIDAE

## Flounder (Platichthys flesus (L.) )

## Description

The ramus is short and the anterior processes are tall. The ascending process is a tapering, lamellar plate of bone set across the ramus, its narrow edge oriented laterally. The articular process is shorter and is separated from the ascending process by a deep interprocess notch. The notch almost completely separates the two processes (c.w. witch, p. 123). There is a shallow fossa between the two processes. There are 8-12 tooth sockets, arranged in a single row which extends to the postmaxillary process (c.w. plaice, p. 120).

## Similar species

Dab (p. 121), plaice (p. 120), witch (p. 123). No consistent differences were found between the right premaxillae of flounder and dab.
From plaice by: greater extent of tooth row.
From witch by: deep interprocess notch and lower anterior processes.

## Regressions

Length range of specimens examined (TL): 130-393 mm; $\mathrm{N}=8$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=34.53$ PMXL -37.49 | 8 | 0.763 |
| $\ln \mathrm{TL}=3.1277+1.2552 \ln$ PMXHH | 8 | 0.946 |
| $\ln \mathrm{TL}=4.9834+0.6157 \ln$ PMXHL | 8 | 0.612 |
| $\ln \mathrm{TL}=3.6493+1.2931 \ln$ PMXAH | 8 | 0.916 |

## Estimated maxima

TL: 600 mm ; PMXL: 16.8 mm ; PMXHH: 13.6 mm ; PMXHL: 5.5 mm ; PMXAH: 8.4 mm .

1.0 cm

## PLEURONECTIDAE

## Witch (Glyptocephalus cynoglossus (L.))

## Description

The right premaxilla is not well ossified and often appears slightly translucent. The ramus is short and the anterior processes are extremely tall. The height of the articular process distinguishes the witch from other pleuronectids; PMXAH is $60-80 \%$ of PMXL in the witch but never more than $60 \%$ of PMXL in other species. The interprocess notch is relatively shallow, the articular processes being fused to the ascending process for approximately $70 \%$ of its height. In the similar plaice, dab, and flounder the interprocess notch is deep, almost completely separating the two anterior processes. There are $10-13$ tooth sockets in a well-defined row ending below the postmaxillary process (c.w. plaice).

## Similar species

Plaice (p. 120), dab (p. 121), flounder (p. 122)
From plaice by: tall articular process fused to ascending process. Teeth (10-13) extend to beneath postmaxillary process.
From dab/flounder by: tall articular process fused to ascending process.

## Regressions

Length range of specimens examined (TL): $160-415 \mathrm{~mm} ; \mathrm{N}=18$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.5711+1.1979 \ln$ PMXL | 18 | 0.955 |
| $\ln \mathrm{TL}=3.7231+1.0495 \ln$ PMXHH | 18 | 0.940 |
| $\ln \mathrm{TL}=4.7994+0.9719 \ln$ PMXHL | 18 | 0.835 |
| $\ln \mathrm{TL}=4.2874+1.0136 \ln$ PMXAH | 18 | 0.956 |

## Estimated maxima

TL: 710 mm ; PMXL: 11.7 mm ; PMXHH: $14.2 \mathrm{~mm} ;$ PMXHL: $5.2 \mathrm{~mm} ;$ PMXAH: 9.1 mm .


## PLEURONECTIDAE

## Lemon sole (Microstomus kitt (Walbaum) )

## Description

The right premaxilla of the lemon sole is highly distinctive and unlike that of any other fish examined. It is very compact, well ossified, and robust. The ramus is exceptionally short and does not bear teeth. It curves ventro-medially and tapers sharply to a point. The ascending and articular processes are very tall in relation to the ramus and are completely fused.

## Similar species

None

## Regressions

Length range of specimens examined (TL): $156-430 \mathrm{~mm} ; \mathrm{N}=27$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.2277+0.8353 \ln$ PMXL | 27 | 0.773 |
| $\ln \mathrm{TL}=3.8654+0.8913 \ln$ PMXHH | 27 | 0.879 |
| $\ln \mathrm{TL}=4.6796+0.9333 \ln$ PMXHL | 27 | 0.893 |

## Estimated maxima

TL: 660 mm ; PMXL: 11.5 mm ; PMXHH: 16.7 mm ; PMXHL: 6.2 mm .


## PLEURONECTIDAE

## Long rough dab (Hippoglossoides platessoides (Fabricius) )

## Description

In this species the right premaxilla is very similar to the left. The ramus is long and narrow. It is more strongly decurved than the left element but, like it, bears a single row of needle-like teeth. The ascending process arises a little way back from the end of the ramus. It is separated from the articular process by a deep notch. The articular process is roughly square in profile and is inclined slightly posteriorly. The postmaxillary process is very long and low, appearing as a dorsal expansion of the ramus.

## Similar species

Scaldfish (p. 86), halibut (p. 126)
From scaldfish by: longer ramus. Articular process slopes back, away from ascending process. From halibut by: small size; long, narrow ramus bearing single tooth row.

## Regressions

Length range of specimens examined (TL): 79-283 mm; $\mathrm{N}=25$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=2.6838+0.9943 \ln$ PMXL | 25 | 0.943 |
| $\ln \mathrm{TL}=3.6125+1.0348 \ln$ PMXHH | 25 | 0.935 |
| $\ln \mathrm{TL}=4.3463+0.9220 \ln$ PMXHL | 25 | 0.890 |
| $\ln \mathrm{TL}=4.2414+0.9669 \ln$ PMXAH | 25 | 0.932 |

## Estimated maxima

TL: 600 mm ; PMXL: 38.8 mm ; PMXHH: 13.6 mm ; PMXHL: 7.9 mm ; PMXAH: 8.5 mm .


## PLEURONECTIDAE

## Halibut (Hippoglossus hippoglossus (L.) )

## Description

The two premaxillae of the halibut are very similar in form. The broad strong ramus is of moderate length and bears two rows of large tooth sockets, with the buccal row larger than the lingual. The teeth themselves are large, curved, and conical. The ascending process is a tall, narrow, lamellar plate of bone set across the ramus, its narrow edge directed laterally. In anterior view the top of the ascending process is triangular with a lateral apex. The articular process is roughly square, tilted posteriorly away from the ascending process. There is a fossa between the processes, bounded medially by a strong lamella.

## Similar species

Long rough dab (p. 125)
The two species can be distinguished by the shorter, broader ramus and two tooth rows of the halibut.

## Regressions

Length range of specimens examined (TL): 463-810 mm; $\mathrm{N}=5$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| TL $=19.77$ PMXL -6.48 | 4 | 0.979 |
| TL $=40.50$ PMXHH +29.17 | 4 | 0.992 |
| TL $=73.54$ PMXHL -12.55 | 4 | 0.998 |
| TL $=70.42$ PMXAH +43.66 | 4 | 0.967 |

## Estimated maxima

TL: 2540 mm ; PMXL: 126.8 mm ; PMXHH: 61.7 mm ; PMXHL: 34.7 mm ; PMXAH: 34.5 mm .


## SOLEIDAE

## Dover sole (Solea solea (L.))

## Description

The right premaxilla is totally unlike the left. Its ramus is extremely narrow and moderately long and tapers gradually along its entire length. It does not bear any teeth. The two anterior processes are tall and completely fused together. The articular process is taller than the ascending process, the latter appearing as a forward-inclined projection of the former. The bone is rather delicate and, as its unusual appearance does not suggest that it is a jaw bone, it is likely to be overlooked in samples.

## Similar species

None

## Regressions

Only one specimen, $T L=268 \mathrm{~mm}$, was examined. PMXL was 6.7 mm and PMXHH was 3.2 mm .

## Estimated maxima

TL: 700 mm ; PMXL: 17.5 mm ; PMXHH: 8.4 mm .


## SOLEIDAE

## Solenette (Buglossidium luteum (Risso) )

## Description

Solenette right premaxillae are quite unlike those on the left side of the body. The ramus is Lshaped and tapers rapidly to a posterior point. Anteriorly it is broad and club-like. There are no teeth. The ascending process is a short, pointed spur. The articular process is low and is joined to the ascending process by a bony lamella. Its articular surface is flat and oriented postero-dorsomedially. The bone is very small, poorly ossified, and slightly translucent. Although highly distinctive, it is likely to be overlooked among other bones as its appearance does not immediately suggest that it is a jaw bone.

## Similar species

None

## Regressions

Length range of specimens examined (TL): $98-195 \mathrm{~mm} ; \mathrm{N}=20$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=3.5061+0.8549 \ln$ PMXL | 20 | 0.888 |
| $\mathrm{TL}=22.23$ PMXHH +20.45 | 19 | 0.815 |
| $\ln \mathrm{TL}=4.8617+0.8508 \ln$ PMXAH | 20 | 0.779 |

## Estimated maxima

TL: 200 mm ; PMXL: 5.5 mm ; PMXHH: 2.6 mm ; PMXAH: 1.7 mm .


## 4. VERTEBRAE

### 4.1 The vertebral column of fish

### 4.1.1 Basic structure

The spine of fish is made up of numerous segmentally arranged vertebrae, extending from the base of the skull to the tail (fig. 1). The precise form of each vertebra varies, depending on its position along the vertebral column, and no two adjacent vertebrae are identical. Different authors have recognized a variety of divisions of the vertebral column, and have used a number of names for these divisions (e.g., Ford, 1937; Casteel, 1976; Desse, 1984; Wheeler and Jones, 1989). The terminology used here follows that set out by Wheeler and Jones (1989) and recognizes three main divisions, namely anterior abdominal vertebrae, abdominal vertebrae, and caudal vertebrae.


Figure 1. Vertebral column and neurocranium of a teleost fish. ATL, atlas vertebra; BSO, basioccipital; AV, abdominal vertebrae; CV, caudal vertebrae; UST, urostyle; RIB, ribs.

Anterior abdominal vertebrae (fig. 2) are characterized by centra bearing only a fused neural spine. They do not bear any laterally or ventrally projecting processes. The first vertebra, which is attached to the basioccipital at the base of the skull, is commonly referred to as the 'atlas'. It and the vertebrae immediately posterior to it are often strongly compressed, the length of successive anterior abdominal vertebrae increasing slightly as one moves posteriorly along the column. The neural spines of anterior abdominal vertebrae, particularly the first few vertebrae, are laterally flattened, providing a large surface area for the attachment of blocks of swimming muscles. The spinal cord runs through the arch formed by the base of the neural spines.


Figure 2. Anterior abdominal vertebra of saithe. a, anterior view; b, lateral view. C, centrum; NS, neural spine; NA, neural arch.

Abdominal vertebrae bear transverse processes, or parapophyses, on their centra, to which the ribs are attached (fig. 3). In the first few abdominal vertebrae these processes arise high up on the centrum (fig. 3a and 3b), but on successive vertebrae their base is situated lower down and the processes themselves are inclined more steeply downwards (fig. 3c and 3d). There is little variation in the length of the abdominal vertebrae from a single fish.


Figure 3. Abdominal vertebrae of saithe. a and $b, 5$ th abdominal vertebra in lateral and anterior view; $c$ and $d, 18$ th abdominal vertebra in lateral and anterior view. PAR, parapophysis.

The transition from abdominal to caudal vertebrae is marked by the fusion of the two transverse processes. In some species, such as salmon, this fusion is via a connecting strut of bone between the processes (fig. 4a), while in many other species, including gadoids and flatfishes, the processes themselves come together, forming an arch (fig. 4c). The fused processes are referred to as the haemal spine.


Figure 4. $a$ and $b$, 1st caudal vertebra of salmon in anterior and lateral view; $c$ and d, 1st caudal vertebra of a gadoid fish in anterior and lateral view. HA, haemal arch; HS, haemal spine.

### 4.1.2 Choice of elements for dietary analyses

It will be clear from the above discussion that there is tremendous variation between individual vertebrae taken from a single fish. Therefore, it has been necessary to narrow the focus of the following descriptions to a limited range of vertebrae - namely caudal vertebrae, and specifically to the more anterior caudal vertebrae. The criteria used in this choice were twofold. Firstly, caudal vertebrae, at least until they are very close to the tail fin, show a more limited range of variation than do anterior abdominal or abdominal vertebrae. Secondly, the fused processes of caudal vertebrae are less prone to breakage than the unfused processes of abdominal vertebrae, resulting in a greater likelihood of finding well-preserved specimens.

Once one is practised at recognizing caudal vertebrae in samples it is usually quite straightforward to decide whether any abdominal vertebrae found have come from the same species, as caudal and abdominal vertebrae from the same fish generally share many features.

### 4.1.3 Variation within caudal vertebrae

While it is certainly the case that caudal vertebrae exhibit less gross variation than do abdominal they are far from identical within an individual fish. There are two principal, and very obvious, ways in which they vary along the length of a fish (fig. 5). Moving posteriorly along the caudal skeleton, (a) the neural and haemal spines become more strongly posteriorly inclined, and (b) vertebrae are sometimes reduced in size, and there are slight changes in the size and shape of the centra. In most species the more posterior centra are relatively narrow compared with those situated anteriorly.


Figure 5. Part of the caudal skeleton of a saithe. Note that the more posterior vertebrae are smaller than the more anterior vertebrae, and that their neural and haemal spines are oriented at a shallower angle to the long axis of the column.

In the Gadidae a further gross difference may be seen in the form of the haemal arch, which in this group is particularly wide in the first several caudal vertebrae in order to accommodate the posterior portion of the swimbladder. The first haemal arch is the widest, with succeeding arches becoming narrower (fig. 6), thereby forming the 'haemal funnel' which is characteristic of the gadid.


Figure 6. 1st, and and 4th caudal vertebrae of a saith. Note the changes in the width of the haemal arches, forming the 'haemal funnel'.

### 4.1.4 Detailed structure of caudal vertebrae and nomenclature

Figure 7 shows a generalized caudal vertebra. The spool-like centrum is concave at both ends. This is the commonest form and is called an amphicoelus centrum. All the vertebrae covered herein have amphicoelus centra with the exception of sandeel atlas vertebrae (p. 206), which are convex anteriorly and concave posteriorly, a form referred to as opisthocoelus. The cavity between adjacent amphicoelus vertebrae is filled with an incompressible jelly which provides the limited articulation required for swimming. Running longitudinally through the centre of the centra is the spinal foramen, which represents the remains of the notocord. Its size relative to the diameter of the centrum is worthy of note as it can provide clues for identification of isolated centra. In 'lower' forms such as Clupeidae (p. 142) it is large and conspicuous, while in 'higher' forms (e.g., Gadidae p. 145) it is reduced or absent.


Figure7. A generalized caudal vertebra. C, centrum; DPoZ, dorsal postzygapophysis; DPrZ, dorsal prezygapophysis; VPoZ, ventral postzygapophysis; VPrZ, ventral prezygapophysis; NF, neural foramen; HS, haemal spine; HA, haemal arch; NS, neural spine; NA, neural arch; RIB, ossified rib or ridge; SF, spinal foramen.

Dorsally, the neural spine provides attachment for swimming muscles and, in many species, support for the fin pterygiophores. The neural arch provides protection for the spinal cord. Nerves exit the arch either via foramina if the base of the neural spine is broad (fig. 7), or through open grooves if it is not (e.g., fig. 4). The presence or absence of neural foramina is useful diagnostically. Ventrally, the haemal spine is formed from the fusion of the parapophyses. It too provides muscle attachment and fin support, while the haemal arch gives protection to large blood vessels running along the underside of the centra and, in some species, to the swimbladder.

Arising both anteriorly and posteriorly are a number of further projections, termed zygapophyses (fig. 7). Those arising anteriorly are termed prezygapophyses (the anterior zygapophyses of Watson, 1986) while those arising posteriorly are postzygapophyses. The prezygapophyses of one vertebra overlap the postzygapophyses of the preceding vertebra, providing strength and rigidity to the vertebral column. The presence, size and form of the pre- and postzygapophyses vary between groups and species and they are, therefore, valuable diagnostically. They are most conspicuously developed in strongly swimming species such as scads (p. 148), mackerels (p. 149) and tunnies.

The vertebrae of some species, including many flatfishes, conger eels and gars, bear lateral projections, or apophyses, on either side in the midline of the centrum (fig. 8). In the flatfishes (p.156) the apophyses are normally more strongly developed on the upper (eyed) side than on the lower (blind) side. The apophyses provide skeletal support for the muscles (Ford, 1937).


Figure 8. Witch (Glyptocephalus cynoglossus) vertebra showing the lateral apophyses (LA) common to many flatfish.

### 4.1.5 Measurements of vertebrae and estimation of fish length

For each species three regression equations are presented which allow total length of fish to be estimated from single vertebrae. The three measurements made (fig. 9) were as follows.

VL (vertebral length in mm ): the maximum length of the centrum.

VW (vertebral width in mm): the maximum width of the posterior surface of the centrum.
VH (vertebral height in mm ): the maximum height of the posterior surface of the centrum.

The regressions are based on measurements of first caudal vertebrae, since these were available for all specimens held in the reference collection. Since it will rarely be possible to make positive identifications of first caudal vertebrae in samples undergoing analysis, estimates of fish size should be made from the most anterior of the caudal vertebrae identified. As pointed out above,
more anterior caudal vertebrae may be distinguished from more posterior ones by the angle of the neural and haemal spines. Errors resulting from this method will be slight, since there is little variation in centrum size over the first few caudal vertebrae of most species (Table 1). Estimates made from measurements of the more posterior abdominal vertebrae will also give reasonable approximations of total fish length (Table 1).


Figure 9.

Where too few specimens of any species were examined for calculation of meaningful regression equations, the fish length and bone measurements are presented for the available specimens. This will permit estimates of fish length to be made from bones found in samples, based on the assumption that there is a linear proportional relationship between bone size and fish length. Fish length is calculated from the assumed relationship

$$
I_{1} / q_{1}=I_{2} / q_{2}
$$

where $l_{1}=$ length of unknown fish from sample; $q_{1}=$ length (or other measurement) of bone from sample; $1_{2}=$ known length of reference fish; $q_{2}=$ length (or other measurement) of bone from reference fish. Thus,

$$
I_{1}=q_{1} I_{2} / q_{2}
$$

This 'proportional method' tends to be less accurate than the regression method (Casteel, 1976), since for many measurements a strictly linear relationship may not exist. Casteel showed that the magnitude of inaccuracies arising from the use of this method varies directly with the difference between the length of the known and unknown specimens. Therefore, when measurements of bones from more than one specimen are presented, fish length should be estimated using the measurements from the bone which is closest in size to that from the sample being analysed.

| Species and Measurement | Preceding Abdominals |  |  | Following Caudals |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Mean | Range | N | Mean | Range | N |
| Herring VL | 0.95 | 0.90-1.00 | 10 | 1.06 | 1.00-1.10 | 10 |
| Herring VW | 0.90 | 0.88-0.97 | 10 | 0.99 | 0.98-1.00 | 10 |
| Herring VH | 0.93 | 0.89-1.00 | 10 | 0.94 | 0.93-0.96 | 10 |
| Salmon VL | 0.93 | 0.88-1.00 | 10 | 1.03 | 1.00-1.04 | 10 |
| Salmon VW | 0.95 | 0.92-0.99 | 10 | 0.99 | 0.98-1.00 | 10 |
| Salmon VH | 0.92 | 0.86-0.94 | 10 | 0.99 | 0.94-1.02 | 10 |
| Saithe VL | 0.98 | 0.92-1.06 | 10 | 0.97 | 0.92-1.00 | 10 |
| Saithe VW | 1.00 | 0.97-1.03 | 10 | 0.95 | 0.90-1.00 | 10 |
| Saithe VH | 0.99 | 0.96-1.02 | 10 | 0.94 | 0.88-1.01 | 10 |
| Ling VL | 1.06 | 1.02-1.09 | 10 | 0.91 | 0.86-1.01 | 10 |
| Ling VW | 1.10 | 1.06-1.13 | 10 | 0.87 | 0.78-0.98 | 10 |
| Ling VH | 1.00 | 0.96-1.03 | 10 | 0.91 | 0.81-1.00 | 10 |
| Sandeel VL | 1.02 | 1.00-1.03 | 10 | 0.99 | 0.97-1.03 | 10 |
| Sandeel VW | 0.99 | 0.96-1.00 | 10 | 0.98 | 0.97-1.00 | 10 |
| Sandeel VH | 1.00 | 0.96-1.04 | 10 | 0.98 | 0.97-1.00 | 10 |
| Megrim VL | 1.09 | 1.00-1.15 | 9 | 1.02 | 0.97-1.06 | 10 |
| Megrim VW | 0.90 | 0.88-0.92 | 9 | 0.94 | 0.92-0.98 | 10 |
| Megrim VH | 0.92 | 0.88-0.96 | 9 | 0.90 | 0.86-0.96 | 10 |
| Lemon Sole VL | 0.89 | 0.80-1.00 | 8 | 1.00 | 0.98-1.00 | 10 |
| Lemon Sole VW | 1.00 | 0.99-1.03 | 8 | 0.98 | 0.96-1.01 | 10 |
| Lemon Sole VH | 0.91 | 0.84-0.96 | 8 | 0.94 | 0.91-0.99 | 10 |
| Dover Sole VL | 0.95 | 0.89-1.00 | 3 | 1.08 | 1.00-1.13 | 9 |
| Dover Sole VW | 0.99 | 0.97-1.00 | 3 | 1.00 | 0.91-1.03 | 9 |
| Dover Sole VH | 0.99 | 0.98-1.00 | 3 | 1.03 | 0.95-1.07 | 9 |

Table 1. Sizes of vertebrae immediately preceding (preceding abdominals) and following (following caudals) the first caudal vertebrae expressed as a proportion of first caudal vertebra measurement. Measurements were taken from vertebrae of one fish in all cases. $\mathrm{VL}=$ vertebral length; $\mathrm{VW}=$ vertebral width; $\mathrm{VH}=$ vertebral height.

### 4.2 Key to the identification of vertebrae to Family

The present key takes identifications to Family level. It should be noted that this key covers only those vertebrae described in this guide. Therefore the full species descriptions must be consulted prior to reaching firm identifications. Unless otherwise stated the key refers to anterior caudal vertebrae. A number of groups key out more than once as vertebrae are highly variable, even within groups.

1. a. Well-developed lateral processes ..... FLATFISH (p. 156)
b. Lateral processes absent ..... 2a. Bone thin, papery, and translucentCYCLOPTERIDAE(p. 155)
b. Not with all these features ..... 3
3.(2) a. Neural foramen absent ..... 4
b. Neural foramen present ..... 6
4.(3) a. Prezygapophyses present ..... 5
b. Prezygapophyses absent ..... GOBIIDAE (p. 150)
5.(4) a. Zygapophyses not extended beyond centrum; centrum at least as high as long ..... 6
b. Not with all these features ..... 7
6.(7) a. Zygapophyses steeply angled; neural and haemal spines strongly back-curved; centrum has honeycomb pattern SALMONIDAE (p. 143)
b. Zygapophyses not steeply angled; neural and haemal spines not strongly back-curved; centrum with parallel ridges; wide spinal foramen ARGENTINIDAE (p. 144)
7.(5) a. Wide spinal foramen and single rib CLUPEIDAE (p. 142)
b. Narrow spinal foramen; centrum often with distinct waist ..... GADIDAE (p. 145)
8.(4) a. Prezygapophyses absent ..... 9
b. Prezygapophyses present ..... 10
9.(8) a. Centrum $>1.4 \mathrm{x}$ longer than high with distinct waist and no rib GOBIIDAE (p. 150)
b. Centrum not longer than high; single strong rib LABRIDAE (p. 146)


1a. Flatfish


6b. Argentinidae

10.(8) a. Neural and haemal spines short and posterior ..... 11
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12.(10) a. Prezygapophyses prominent and right- angled; centrum $>1.5 \mathrm{x}$ longer than high CARANGIDAE (p. 148)/
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11a. Callionymidae

12a. Carangidae/ Scombridae


11b. Carangidae/Scombridae


13a. Flatfish


14a. Pholidae/ Zoarcidae


15a. Cottidae


15b. Ammodytidae

### 4.3 Family descriptions for vertebrae

## CLUPEIDAE

## Description

Clupeid vertebrae have a wide spinal foramen. In lateral view the centra have a slight waist. In posterior or anterior view the centra are often slightly oval (wider than high). In the three species examined (herring, sprat, and twaite shad) there was a single prominent rib running along the centrum. The prezygapophyses are prominent, particularly so in the more posterior caudal vertebrae. However, they are narrow and easily damaged and so are often missing in vertebrae taken from samples. The postzygapophyses are fin-like. The neural and haemal spines are long, thin, and back-curved. Viewed laterally the neural and haemal arches are narrow-based and there is no neural foramen.

## Similar groups or species

Gadidae (p. 145)
Clupeid vertebrae may be distinguished by the wide spinal foramen. In the gadids the spinal foramen is relatively narrow. In complete vertebrae the extremely long, narrow back-curved neural and haemal spines of the clupeids are also diagnostic.

## Relationship with fish Iength

See individual species descriptions.


Clupea harengus

1.0 cm

Clupea harengus



## SALMONIDAE

## Description

Salmonid vertebrae are not strongly ossified and are, therefore, particularly prone to digestion. The centra are cylindrical, almost entirely lacking a waist. In lateral view they appear almost perfectly square, being as high as they are long. The texture and sculpturing of the centra are distinctive, there being a honeycomb pattern of holes over much of their surface. This patterning is missing from the anterior and posterior margins of the centra, which are smooth. The spinal foramen is moderately wide. The dorsal pre- and postzygapophyses are short and strongly inclined upwards. They do not extend beyond the ends of the centum. The ventral zygapophyses are angled in a similar manner. The neural and haemal spines are long, narrow and strongly backcurved. Viewed laterally the neural and haemal arches are narrow-based and there is no neural foramen.

## Similar groups or species

Argentinidae (p. 144)
Salmonid vertebrae may be distinguished by their steeply inclined zygapophyses and by their lack of a distinct waist. The honeycomb patterning of the centra differs from the longitudinal ridging in the argentines.

## Relationship with fish length

See individual species descriptions.


Salmo salar


Salmo salar



## ARGENTINIDAE

## Argentines (Argentina sphyraena L. and Argentina silus Ascanius)

## Description

Argentine bones are very light and are not strongly ossified. The centrum is roughly square in profile. Laterally, its sides are concave, giving it a distinct waist. There are three to five low, longitudinal ribs on the lateral surface. The spinal foramen, as in the other isospondylous fishes, is wide. The neural and haemal arches are narrow-based and positioned anteriorly on the centrum. There is no neural foramen. In the more anterior caudal vertebrae the haemal spines are joined by a horizontal bar of bone. The spines themselves are narrow and of moderate length. The dorsal prezygapophysis is short and near-horizontal (c.w. salmonid). Neither it nor the smaller ventral prezygapophysis reach beyond the front of the centrum.

## Similar groups or species

Salmonidae (p. 143), Gadidae (p. 145)
From gadids by: wide spinal foramen.
From salmonids by: longitudinal ridges on centra. Centra more strongly waisted.

## Relationship with fish length

Vertebral length is 0.9 to $1.1 \%$ of fish length (TL). The length of the caudal vertebrae decreases posteriorly.

A. silus

A. silus

## GADIDAE

## Description

As there are twenty or more gadid species in the North Sea it is difficult to generalize about their characteristics. The centra are generally as long as, or longer than, they are tall. In most species they have a distinct waist. The lateral surfaces bear one or more ridges or distinct lines of ossification. The spinal foramen is narrow. The most anterior caudal vertebrae have a very wide haemal arch (the haemal funnel) which is diagnostic of gadids. The neural arch is narrow-based and without foramina. The neural and haemal spines are anterior. The prezygapophyses are well developed and often project in front of the centrum. The dorsal postzygapophyses have a characteristic fin-like or "plough handle" (Watson, 1986) shape. In most species (hake is an exception) the bones are robust and strongly ossified.

## Similar groups or species

Clupeidae (p. 142), Argentinidae (p. 144)
Gadid vertebrae may be distinguished from both of the above by the narrow spinal foramen. They are more strongly ossified than argentine vertebrae.

Relationship with fish length
See individual species descriptions.


Gadus morhua


Gadus morhua

1.0 cm

## LABRIDAE

Cuckoo wrasse (Labrus mixtus (L.) ), Corkwing (Crenilabrus melops (L.) ), and Goldsinny (Ctenolabrus rupestris (L.))

## Description

The centrum is short, at least as tall as it is long. There are no dorsal or ventral prezygapophyses. The neural arch is broad-based and the haemal spine is anterior. Thus the front of the bone is free of projections, making a clean curve from neural to haemal spine. There are usually two neural foramina. The ventral postzygapophyses are long and project strongly downwards. They are, however, prone to breakage. A most useful characteristic is the presence of a single, strong, lamellar rib of bone running along the midline of the centrum. The neural and haemal spines are long and back-curved.

## Similar groups or species

Sea snails (Liparidae, p. 198) have very similar vertebrae. However, anterior caudal vertebrae from sea snails have a broad-based haemal spine, and the more posterior vertebrae have small prezygapophyses (see also Watson, 1986).

## Relationship with fish length

Vertebral length is 1.5 to $2 \%$ of fish length. The more posterior vertebrae are shortest.


Labrus mixtus


Labrus mixtus

## AMMODYTIDAE

## Description

Sandeel vertebrae are always small, usually $1-2 \mathrm{~mm}$ long, and delicate. The centra are longer than they are high and strongly waisted. They bear two or three distinctive, narrow lamellar ribs of bone along their lateral surfaces. The neural arch is broad-based and perforated by a large neural foramen. The neural spine rises towards the posterior of the arch. Both it and the haemal spine are thin and delicate. The anterior dorsal and ventral prezygapophyses are well developed and project well in front of the anterior margin of the centrum.

## Similar groups or species

Cottidae (p. 154)
The well-developed and prominent ventral prezygapophyses distinguish sandeel caudal vertebrae from those of the cottids. Cottid vertebrae small enough to be mistaken for those of sandeels do not carry the two or three longitudinal ribs which are present on sandeel centra. Sandeel vertebrae appear relatively longer than those of cottids owing to the lower haemal arch.

## Relationship with fish length

Vertebral length is 1.5 to $1.9 \%$ of fish length (TL).

A. marinus anterior caudal

A. marinus posterior caudal

## CARANGIDAE

## Scad (Trachurus trachurus (L.))

## Description

Scad verterbrae have centra which are 1.5 to 1.8 times as long as they are high. They tend to be smooth and shiny. The lateral surfaces of the centra are deeply concave in the more anterior caudal vertebrae, less so posteriorly. There is no ridging or other sculpturing on the centra. The neural and haemal spines rise near the middle of the centrum, with the base of the haemal spine slightly anterior to the neural spine. There is a single neural foramen on either side below the base of the neural spine. Several of the caudal vertebrae have a supporting strut behind the neural spine. The prezygapophyses are prominent and distinctively right-angled.

## Similar groups or species

Mackerel (p. 149)
Vertebrae of the two species can best be distinguished by the texture of the bone. Scad vertebrae are smooth, shiny, and dense, while those of the mackerel are granular and appear slightly rough. The lateral surfaces of the most anterior caudal vertebrae of scad are strongly bi-concave, unlike those of mackerel, which are convex in cross-section.

## Relationship with fish length

Vertebral length is 2.4 to $2.7 \%$ of fish length (TL).


## SCOMBRIDAE

## Mackerel (Scomber scombrus (L.) )

## Description

Mackerel vertebrae have a granular, slightly rough appearance. The centrum is long and rectangular, almost twice as long as it is high, and without distinctive ridging or sculpturing. The neural and haemal spines are narrow-based and rise from near the middle of the centrum. The base of the haemal spine is slightly in front of the base of the neural spine. There are one or two small foramina near the base of the neural spine. In several of the caudal vertebrae there is a supporting strut behind the haemal spine; the aperture between this and the spine should not be confused with the smaller neural foramina. The prezygapophyses are exceptionally well developed and have a distinctive right-angled shape. The postzygapophyses are narrow and point backwards.

## Similar groups or species

Scad (p. 148)
Vertebrae of the two species can best be distinguished by the texture of the bone. Mackerel vertebrae are granular and slightly rough. Those of scad are smooth and shiny. The lateral surfaces of the most anterior caudal vertebrae of mackerel are strongly convex, unlike those of scad, which are bi-concave in cross-section.

## Relationship with fish length

Vertebral length is 2.0 to $2.4 \%$ of fish length (TL).


## GOBIIDAE

## Sand goby (Pomatoschistus minutus (Pallas)) and rock goby (Gobius paganellus (L.))

## Description

Goby vertebrae have long, narrow centra with a very pronounced waist. Centrum length is 1.4 to 1.7 times centrum height. The centrum is smooth and shiny, free of ribs or sculpturing. The neural and haemal spines rise anteriorly. In the more anterior vertebrae the neural arch is broad-based and the nerves exit via a distinct foramen. In the more posterior vertebrae the base of the arch is shorter and there is no foramen. There are no prezygapophyses. The vertebrae are never large, maximum length being approximately 3.5 mm . Goby vertebrae are commonly 1 to 2.5 mm in length.

## Similar groups or species

None.
The long, narrow-waisted, featureless centra, small size, and lack of prezygapophyses make goby vertebrae easily recognizable.

## Relationship with fish length

Vertebral length is 1.6 to $2.1 \%$ of fish length (TL).

P. minutus
$\qquad$

## CALLIONYMIDAE

## Dragonet(Callionymus lyra(L.)) and spotted dragonet (Callionymus maculatus (Rafinesque-Schmaltz))

## Description

Dragonet vertebrae are highly distinctive. The overall shape is long and rectangular, the centrum being some $2-3$ times as long as high. The centrum is strongly laterally flattened, particularly towards its centre where it is very narrow. The neural and haemal spines rise towards the rear of the centrum. They are short, blunt-ended, and point backwards, so that they are almost parallel to one another. The dorsal and ventral prezygapophyses are long and well developed. In life the dorsal prezygapophyses fit into the space between the dorsal postzygapophysis and neural spine of the preceding vertebrae. The ventral prezygapophyses fit between the preceding ventral postzygapophysis and haemal spine in a similar way. There are two large foramina on each lateral surface. The surface of the centrum lacks any distinctive patterning. The vertebrae are usually very white and often slightly translucent.

## Similar groups or species

Scad and mackerel (pp. 148 and 149).
Dragonet posterior caudal vertebrae may be distinguished from those of scad and mackerel by their lateral flattening and their blunt-ended neural and haemal spines.

## Relationship with fish length

Vertebral length is 2.8 to $3.3 \%$ of fish length (TL). The more posterior vertebrae are longest and narrowest. Maximum VL is 10 mm .

C. Iyra
1.0 cm

## PHOLIDAE

## Butterfish (Pholis gunnellus (L.) )

## Description

The centrum is roughly square in profile and the neural arch is broad-based. The centrum is amphicoelus but the anterior and posterior concavities are markedly different, the anterior concavity being very shallow and the posterior concavity deep. The most distinctive feature of the centrum is the single strong rib running along either side. The neural spine is very straight. The base of the haemal arch of the more anterior caudal vertebrae flares out from the centrum before bending inwards and backwards to form the haemal spine. This results in distinctive "elbows" on the haemal arch. The dorsal pre- and postzygapophyses are well developed but there is no ventral prezygapophysis. The dorsal prezygapophysis is inclined upwards and does not extend beyond the end of the centrum.

## Similar groups or species

Eelpout (p. 153)
In lateral view the centrum of the eelpout appears taller and more rectangular than that of the butterfish, which appears square. More anterior caudal vertebrae from the two species can be distinguished by the angled "elbows" at the base of the butterfish haemal arch. The dorsal prezygapophysis is generally inclined less strongly upwards in the butterfish, but this feature is not reliable.

## Relationship with fish length

Vertebral length is 0.9 to $1.1 \%$ of fish length (TL). Maximum length is 2.8 mm .


## ZOARCIDAE

## Eelpout (Zoarces viviparus (L.))

## Description

Eelpout vertebrae are often pale turquoise or green in colour. The centrum is slightly taller than it is long. The broad base of the neural arch is also rather tall and together these two features give the bone a rectangular shape in lateral view. The concavities of the centrum are asymmetrical, the anterior concavity being very shallow compared with the posterior. There is a single neural foramen. The neural spine is very straight and is roughly equal in length to the haemal spine. The haemal arch narrows uniformly from the centrum towards the haemal spine (c.w. butterfish, p.152). The dorsal pre- and postzygapophyses are well developed. Only the latter extend beyond the end of the centrum. The dorsal prezygapophysis is strongly inclined upwards. In most specimens there is a small ventral prezygapophysis. There is a single, strong, lamellar rib running along either side of the centrum.

## Similar groups or species

Butterfish (p. 152)
In lateral view the centrum of the eelpout appears taller and more rectangular than that of the butterfish, which appears square. More anterior caudal vertebrae from the two species can be distinguished by the uniform narrowing of the haemal arch in the eelpout (no "elbows"). The dorsal prezygapophysis is generally inclined more strongly upwards in the eelpout but this feature is not reliable as the degree of inclination varies in both species.

## Relationship with fish length

Vertebral length is 0.7 to $0.9 \%$ of fish length (TL). Estimated maximum vertebral length is 4.1 mm .


## COTTIDAE

## Bullrout (Myoxocephalus scorpius (L.)) and sea scorpion (Taurulus bubalis (Euphrasen) )

## Description

Cottid caudal vertebrae appear roughly square in lateral view. The sides of the centrum are concave. In small specimens the lateral surface of the centrum is often featureless, lacking ribbing or sculpturing. If longitudinal ridges are present they are low. In large specimens ( $>3 \mathrm{~mm}$ ) there may be one or more prominent longitudinal bony ridges. The neural arch is broad-based, the neural spine arising centrally or posterior of centrally. The neural spine often curves upwards from its base. The dorsal prezygapophyses are very prominent, reaching well beyond the anterior margin of the centrum. The ventral prezygapophyses are small, or, in the more anterior caudal vertebrae, absent.

## Similar groups or species

Ammodytidae (p. 147)
Cottid vertebrae can often be distinguished from those of sandeels by size alone, sandeel vertebrae rarely being over 3 mm long. Small cottid vertebrae lack the well-defined longitudinal ribs and ventral prezygapophyses found on sandeel vertebrae.

Relationship with fish length
Vertebral length is 1.4 to $1.7 \%$ of fish length (TL). Maximum vertebral length is approx. 7 mm .

M. scorpius

T. bubalis


## CYCLOPTERIDAE

## Lumpsucker (Cyclopterus lumpus (L.) )

## Description

The thin, papery texture of lumpsucker bones immediately distinguishes them from those of all other species. However, when analysing piscivore diets, the drawback of this extreme lack of ossification is that the bones are generally poorly preserved, being prone to digestion and breakage. The centrum is taller than long and bears one or two longitudinal septa along either side. The bases of the neural and haemal arches are joined anteriorly by a sheet of bone which runs between them, inward of the anterior edge of the centrum. A series of short septa run between this sheet of bone and the anterior margin of the centrum. There are nodorsal or ventral prezygapophyses. The neural and haemal spines are long and back-curved, and the neural arch is broad-based.

## Similar groups or species

None
The papery texture of lumpsucker bone is unmistakable.

## Relationship with fish length

Vertebral length is 1.7 to $2.3 \%$ of fish length (TL). Maximum vertebral length is 12.2 mm .


## FLATFISHES

## BOTHIDAE, PLEURONECTIDAE, and SOLEIDAE

## Description

The most striking features of flatfish vertebrae are the very long, straight neural and haemal spines. In the more anterior caudal vertebrae these are almost perpendicular to the centra. The neural arch is broad-based as, in most bothids and pleuronectids, is the haemal arch. The centra are usually higher than they are long. In posterior or anterior view the centra may be roughly hexagonal, although this is not invariably the case. However, even badly damaged vertebrae can often be identified as flatfish by the presence of short hexagonal centra. Many species bear lateral processes (apophyses) in the midline of the centrum, which may be longer on one side than the other. The anterior and posterior zygapophyses are generally short.

## Similar groups or species

See also species descriptions.
Conger eels (Conger conger), not covered in this guide, also have lateral apophyses on their caudal vertebrae. Conger centra have 3-4 horizontal lamellar ribs split by a single vertical tib. This pattern is not found in any flatfish. Conger vertebrae have short neural and haemal spines.

## Relationship with fish length

See individual species descriptions.

1.0 cm

### 4.4 Species descriptions for vertebrae

### 4.4.1 CLUPEIDAE

## Herring (Clupea harengus (L.))

## Description

Herring vertebrae have a wide spinal foramen, and in lateral view the centra have a distinct waist. Centrum length is greater than centrum height. In posterior or anterior view the centra are often slightly oval (wider than high). A single lamellarribruns along the centrum. The prezygapophyses are very prominent on most of the caudal vertebrae, their length being up to $45 \%$ of VL on the more posterior caudal vertebrae.

## Similar species

Sprat (p. 159), twaite shad (p. 160)
From sprat by: size (sprat vertebrae rarely exceed 2.0 mm in length). The exceptionally long prezygapophyses also distinguish herring. However, these are prone to breakage.
From twaite shad by: thin lamellar rib; prezygapophyses which are not distinctly angled.

## Regressions

Length range of specimens examined (TL): 95-298 mm; N=35.

Regression equation
$\ln \mathrm{TL}=4.4552+1.0204 \ln \mathrm{VL}$
$\ln \mathrm{TL}=4.4804+0.9374 \ln \mathrm{VW}$
$\ln \mathrm{TL}=4.5530+0.9697 \ln \mathrm{VH}$
$\mathrm{N} \quad \mathrm{R}^{2}$
350.978
$34 \quad 0.962$
340.923

## Estimated maxima



plate 1 anterior caudal

plate 2 mid caudal


## CLUPEIDAE

## Sprat (Sprattus sprattus (L.) )

## Description

Sprat vertebrae have a distinct waist and a single lamellar rib running along the centrum. Centrum length is greater than centrum height. The neural foramen is wide. The prezygapophyses of all but the most posterior 6-8 vertebrae reach only a short distance in front of the centrum, if at all. The centra are often wider than high.

## Similar species

Herring (p. 158), twaite shad (p. 160)
From herring by: shorter prezygapophyses. However, since these are liable to breakage this
feature must be treated cautiously. Vertebrae over 2 mm in length are unlikely to be sprat.
From twaite shad by: thin, lamellar rib; prezygapophyses which are not distinctly angled.

## Regressions

Length range of specimens examined (TL): $53-129 \mathrm{~mm} ; \mathrm{N}=7$.

| Regression equation | $N$ | $R^{2}$ |
| :--- | :--- | :--- |
| $\ln T L=4.2524+0.9616 \ln \mathrm{VL}$ | 6 | 0.984 |
| $\ln \mathrm{TL}=4.4142+0.9276 \ln \mathrm{VW}$ | 6 | 0.953 |
| $\ln \mathrm{TL}=4.3600+0.9230 \ln \mathrm{VH}$ | 6 | 0.939 |

## Estimated maxima

TL: 180 mm ; VL: 2.6 mm ; VW: 2.3 mm ; VH: 2.4 mm .

plate 1 anterior caudal

plate 2 mid caudal

## CLUPEIDAE

## Twaite shad (Alosa fallax (Lacépède))

## Description

Centrum length is roughly equal to centrum height, and is less than centrum width. There is a single, broad rib along each side which expands posteriorly, fanning out onto the posterior margin of the centrum. The prezygapophyses are long and, in the more anterior caudal vertebrae, distinctly angled.

## Similar species

Herring (p. 158), sprat (p. 159)
From both of these by: greater breadth of the rib running along the centrum; angled "elbows" on prezygapophyses.

## Regressions

Too few specimens were examined to allow calculation of meaningful regressions. In a specimen of 335 mm (TL) VL was 3.7 mm , VW was 4.7 mm and VH was 3.7 mm .

## Estimated maxima

TL: 500 mm ; VL: 5.5 mm ; VW: 7.0 mm ; VH: 5.5 mm .

plate 1 anterior caudal

plate 2 mid caudal
$\qquad$

### 4.4.2 SALMONIDAE

## Atlantic salmon (Salmo salar (L.)) and trout (Salmo trutta (L.))

## Description

In lateral view salmon and trout vertebrae appear almost perfectly square and without a distinct waist. The cylindrical centra have a honeycomb pattern over most of the surface, missing from the anterior and posterior margins, which are smooth. The zygapophyses are short and steeply inclined so that they do not extend beyond the ends of the centrum. No consistent differences were found between trout and salmon caudal vertebrae. However, Feltham and Marquiss (1989) show how they may be distinguished by the structure of their atlas vertebrae.

## Similar species

Argentines (p. 144)
The steeply inclined zygapophyses, lack of a distinct waist, and honeycomb patterning of the centrum distinguish salmonid vertebrae.

## Regressions

Salmon: length range of specimens examined (TL): $524-822 \mathrm{~mm} ; \mathrm{N}=8$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln T L=4.7643+0.8239 \ln \mathrm{VL}$ | 8 | 0.938 |
| $\ln \mathrm{TL}=4.3013+0.9764 \ln \mathrm{VW}$ | 8 | 0.960 |
| $\ln \mathrm{TL}=4.2318+1.0477 \ln \mathrm{VH}$ | 8 | 0.971 |

Trout: too few specimens were examined for meaningful regressions to be given. In a specimen of 475 mm (TL) VL was 5.5 mm , VW was 6.4 mm and VH was 5.8 mm .

## Estimated maxima

Salmon: TL: 1630 mm ; VL: 22.9 mm ; VW: 23.0 mm ; VH: 20.0 mm .
Trout: TL: 1400 mm ; VL: 16.2 mm ; VW: 18.9 mm ; VH: 17.1 mm .

plate 1 anterior caudal

plate 2 mid caudal

### 4.4.3 GADIDAE and MERLUCCIIDAE

The general characteristics of gadid vertebrae were described in the preceding section. However, since the vertebrae of a total of 18 species will be described in the following pages, it is necessary at this stage to further divide the group. As has been pointed out previously, caudal vertebrae show considerable variation within an individual fish. The following division is, therefore, based on general characteristics applicable to most caudal vertebrae from the species in question. It should be borne in mind, however, that the variability of vertebrae makes it very likely that not all vertebrae found will be identifiable to species. Identifications will be aided if several vertebrae from a species are available for examination.

In the following pages the order of presentation of species is not taxonomic; species with similar vertebrae are presented alongside one another regardless of taxonomic affinities. Gadid caudal vertebrae may be divided into the following general groupings using a number of qualitative characteristics. The groups are not entirely exclusive, and some species are listed more than once. Brackets indicate that the full species description is given under another grouping.

Group 1. Vertebrae with a single, well-defined rib running along, or close to, the midline of the centrum. Vertebrae may be rectangular or square in lateral view: hake, ling, bib, haddock, greater forkbeard, three-bearded rockling.

Group 2. Vertebrae with very large, broad prezygapophyses and dorsal postzygapophyses. Often with a second, short, pointed dorsal prezygapophysis situated below the main zygapophysis. The centra are generally strongly waisted: (three-bearded rockling), four-bearded rockling, fivebearded rockling, northern rockling, (torsk).

Group 3. Vertebrae very short, centrum height(VH) equal to or greater than centrum length(VL). Dorsal prezygapophysis set high on neural arch and strongly inclined upwards. Centra may have indistinct ridges but without clearly defined ribs: torsk, (ling).

Group 4. Small vertebrae: maximum VL 4.5 mm , but rarely exceeding 3.5 mm . Two (rarely three) narrow, well-defined ribs in midline of centrum; these are sometimes lamellar. Prezygapophyses extend well beyond front of centrum: (four-bearded rockling), poor cod, Norway pout, silvery pout, blue whiting.

Group 5. Vertebrae not fitting the above categories. The centra usually have two or more horizontal lines or ridges of ossification with many interconnecting septa. These rarely form the clearly defined or lamellar ribs often found in the group 4 species. The prezygapophyses are usually short and narrow: (blue whiting), whiting, pollack, cod, saithe.

GROUP1 :






GROUP 4
GROUP 5



## GADIDAE and MERLUCCIIDAE (group 1)

## Hake (Merluccius merluccius (L.))

## Description

Hake bones are distinctive among the Gadidae in being poorly ossified, very light in weight, and almost spongy in texture. Deep, oval hollows above and below the central rib are diagnostic. The shape of the centra varies from roughly square anteriorly to long and rectangular posteriorly. The centra are not strongly waisted. The prezygapophyses are short and, in the more anterior vertebrae, they are broad and rounded (plate 1).

## Similar species

Greater forkbeard (p. 168), three-bearded rockling (p. 169)
From either of the above by: open, porous texture and short prezygapophyses.

## Regressions

Length range of specimens examined (TL): 147-630 mm; $\mathrm{N}=10$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.4327+0.9916 \ln \mathrm{VL}$ | 10 | 0.989 |
| $\ln \mathrm{TL}=4.6561+0.8541 \ln \mathrm{VW}$ | 10 | 0.998 |
| $\ln \mathrm{TL}=4.6651+0.8262 \ln \mathrm{VH}$ | 10 | 0.997 |

## Estimated maxima

TL: 1320 mm ; VL: 15.8 mm ; VW: 19.3 mm ; VH: 21.0 mm .

plate 1 anterior caudal

plate 2 mid caudal


## GADIDAE and MERLUCCIIDAE (group 1)

## Ling (Molva molva (L.) )

## Description

The vertebrae are short and roughly square in profile. The more posterior vertebrae are strongly waisted. The rib, which is very broad with a deep hollow above, slopes outwards to form the ventro-lateral margin of the centrum. In the more anterior caudals this creates deep "overhangs" either side of the centrum, resulting in large hollows between the ventral edge of the rib and the septa on the underside of the vertebrae. The dorsal edge of the rib is in the midline of the centrum, and the rib itself below the midline. The zygapophyses are well developed, with the exception of the ventral postzygapophysis which is tiny or absent (c.w. haddock, p. 167). The dorsal prezygapophyses are inclined upwards.

## Similar species

Haddock (anterior caudals, p. 167), torsk (mid caudals, p. 173)
From haddock by: broader rib which slopes outwards to ventro-lateral margin; tiny postzygapophyses; relatively shorter centra.
From torsk by: broad rib below midline of centrum.

## Regressions

Length range of specimens examined (TL): 295-833 mm; N=23.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.3205+1.0306 \ln \mathrm{VL}$ | 23 | 0.981 |
| $\ln \mathrm{TL}=4.6918+0.8472 \ln \mathrm{VW}$ | 23 | 0.962 |
| $\ln \mathrm{TL}=4.6687+0.8512 \ln \mathrm{VH}$ | 23 | 0.986 |

## Estimated maxima

TL: 2130 mm ; VL: 25.0 mm ; VW: 31.4 mm ; VH: 33.0 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 1 or 5)

## Bib [Pout, Pouting] (Trisopterus luscus (L.) )

## Description

Bib vertebrae are rather variable. They usually have a single rib running along the centrum. However, it is not uncommon for there to be two, usually rather badly defined, ribs (plate 1). In either case the ribs are broad, widening even further towards the anterior and posterior margins of the centrum. This breadth, and the lack of concavities either side, make the rib(s) a less striking feature than in the haddock, greater forkbeard, or three-bearded rockling. The prezygapophyses extend beyond the front of the centrum (c.w. haddock) and are roughly horizontal. The anterior margin of the centrum slopes smoothly into the waist.

## Similar species

Haddock. (p. 167), greater forkbeard (p. 168), (cod, p. 180, and saithe, p. 181. These species often possess some vertebrae with two poorly defined ribs, as may be found in bib.)
From haddock and forkbeard by: broader, less well-defined rib (plates below and pp. 167, 168).
From cod by: fewer oblique septa between ribs and over surface of centra.
From saithe by: broader, less pointed dorsal prezygapophyses.

## Regressions

Length range of specimens examined (TL): 220-333 mm; $\mathrm{N}=5$.

Regression equation
$\ln \mathrm{TL}=4.3910+0.8672 \ln$ PMXL
$\ln \mathrm{TL}=4.6589+0.6708 \ln$ PMXHH
$\ln \mathrm{TL}=4.6879+0.6683 \ln \mathrm{PMXHL}$
$\mathrm{N} \quad \mathrm{R}^{2}$
50.991
50.986
50.969

## Estimated maxima

TL: 490 mm ; VL: 8 mm ; VW: 9.7 mm ; VH: 8.6 mm .

plate 1 anterior caudal

plate 2 mid caudal
1.0 cm

## GADIDAE and MERLUCCIIDAE (group 1)

Haddock (Melanogrammus aeglefinus (L.))

## Description

The vertebrae are robust and strongly ossified with a single, straight, clearly defined rib running along the centrum. On anterior caudal centra (plate 1 below) the rib is slightly below the midline. More posteriorly it runs along the midline (plate 2 below). The zygapophyses are all moderately well developed but the prezygapophyses rarely extend beyond the anterior margin of the centrum (c.w. ling, greater forkbeard, three-bearded rockling). On the more anterior caudals the ventral postzygapophyses are long and narrow.

## Similar species

Ling (anterior caudals, p. 165), greater forkbeard (p. 168)
From ling by: narrow rib, well-developed ventral postzygapophyses, relatively longer centra.
From greater forkbeard by: prezygapophyses not extended beyond centrum; long, narrow ventral postzygapophysis on anterior caudals.

## Regressions

Length range of specimens examined (TL): 71-446 mm; $\mathrm{N}=47$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.3571+0.9701 \ln \mathrm{VL}$ | 47 | 0.994 |
| $\ln \mathrm{TL}=4.4385+0.9575 \ln \mathrm{VW}$ | 47 | 0.987 |
| $\ln \mathrm{TL}=4.4574+0.9347 \ln \mathrm{VH}$ | 47 | 0.989 |

## Estimated maxima



plate 1 anterior caudal

plate 2 mid caudal
$\qquad$

## GADIDAE and MERLUCCIIDAE (group 1)

## Greater forkbeard (Phycis blennoides (Brünnich) )

## Description

The vertebrae have a single, straight, clearly defined rib running along the midline of the centrum. The centra are rectangular, relatively longer, and narrower more posteriorly (plate 2 below). The zygapophyses are all moderately well developed, with the prezygapophyses extending beyond the anterior margin of the centrum (c.w. haddock, p. 167). The ventral postzygapophyses are short and broad (c.w. haddock). The vertebrae are strongly ossified (c.w. hake, p. 164).

## Similar species

Haddock (p. 167), three-bearded rockling (p. 169)
From haddock by: longer prezygapophyses which extend beyond front of centrum; short, broad ventral postzygapophysis.
From three-bearded rockling by: narrower, less massive prezygapophyses and dorsal postzygapophyses.

## Regressions

Of two specimens examined, only one was complete: $T L=315 \mathrm{~mm}$. In this specimen VL was 4.5 mm , VW was 4.1 mm , and VH was 4.2 mm .

## Estimated maxima

TL: 750 mm ; VL: 10.7 mm ; VW: 9.8 mm ; VH: 10.0 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 1 or 2)

## Three-bearded rockling (Gaidropsarus vulgaris (Cloquet))

## Description

The centra are rectangular, longer than high, and are distinctly waisted. The single rib running along the midline is broad and strong. The prezygapophyses and dorsal postzygapophyses are broad and massive. As in the other rockling species there is usually a second, small zygapophysis situated below the main dorsal prezygapophysis (plates 1 and 2 below). The vertebrae are strongly ossified (c.w. hake, p. 164).

## Similar species

Haddock (p. 167), greater forkbeard (p. 168), other rocklings (pp. 170-172)
From haddock by: broad, massive zygapophyses; presence of small, secondary dorsal prezygapophysis, more distinct waist.
From greater forkbeard by: broad, massive zygapophyses.
From other rockling species by: single broad, strong rib.

## Regressions

Length range of specimens examined (TL): 247-443 mm; $N=3$.

Regression equation
$\ln \mathrm{TL}=4.0469+1.0931 \ln \mathrm{VL}$
$\ln \mathrm{TL}=4.3547+0.9639 \ln \mathrm{VW}$
$\ln \mathrm{TL}=3.9602+1.2348 \ln \mathrm{VH}$
$\mathrm{N} \quad \mathrm{R}^{2}$
30.996
30.990
30.971

Estimated maxima
TL: 530 mm ; VL: 7.7 mm ; VW: 7.3 mm ; VH: 6.4 mm .

plate 1 anterior caudal

plate 2 mid caudal


## GADIDAE and MERLUCCIIDAE (group 2)

## Four-bearded rockling (Rhinonemus cimbrius (L.) )

## Description

The centra are long and rectangular, centrum height (VH) not more than $82 \%$ of centrum length (VL). The centra have a distinct waist. There are two or three ribs running close together near the midline. These ribs often stand well out from the centrum as distinct lamellae, unlike the low ossified ridges of northern (p.171) and five-bearded (p. 172) rocklings. The anterior quarter to one third of the centrum is smooth and slopes steeply in towards the front of the ribbing. Occasionally there are small secondary zygapophyses below the dorsal prezygapophyses. The dorsal postzygapophyses are smaller than in the other rockling species.

## Similar species

Northern (p. 171) and five-bearded (p. 172) rocklings, Norway pout (p. 175), poor cod (p. 174) From the rocklings by: vertebrae appear longer and slimmer with a wide gap between the rear of the neural arch and the dorsal prezygapophyses (see plates below and pp. 171-172). Ridges on centra may form distinct, lamellar ribs. Smaller dorsal postzygapophyses.
From Norway pout and poor cod by: longer, more pronounced waist (see plates).

## Regressions

Length range of specimens examined (TL): 206-263 mm; $\mathrm{N}=6$.

| Regression equation | $N$ | $R^{2}$ |
| :--- | :--- | :--- |
| $\ln T L=3.8754+1.3121 \ln V L$ | 6 | 0.947 |
| $\ln T L=4.7839+0.6800 \ln \mathrm{VW}$ | 6 | 0.685 |
| $\ln \mathrm{TL}=4.6370+0.8587 \ln \mathrm{VH}$ | 6 | 0.950 |

## Estimated maxima

TL: 470 mm ; VL: 5.5 mm ; VW: 5.3 mm ; VH: 5.4 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 2)

## Northern rockling (Ciliata septentrionalis (Collett))

## Description

The centra are typically rectangular, although in some of the more anterior caudal vertebrae (plate 1 below) VH can be up to $100 \%$ of VL. The centra of the more anterior caudal vertebrae tend to have less of a waist than those of four- and five-bearded rocklings (pp. 170 and 172). There are two to five (typically three or four) ossified ridges on the centrum. These are generally well defined, but do not form the thin lamellar ribs sometimes seen in four-bearded rocklings. The dorsal postzygapophysis is often very high with an arched dorsal margin (see plate 1 below).

## Similar species

Four-bearded (p. 170) and five-bearded (p. 172) rocklings
From four-bearded rockling by: relatively shorter anterior caudal centra with less pronounced waist. Ribs usually less well defined and rarely lamellar.
From five-bearded rockling by: anterior caudal centra (plate 1 below) less strongly waisted; higher, arched dorsal postzygapophyses; ridges on centrum more clearly defined.

## Regressions

Two specimens were examined. In a 165 mm (TL) specimen VL was 3.0 mm , VW was 2.5 mm and VH was 2.4 mm . In a 168 mm specimen VL was 3.0 mm , VW was 2.5 mm and VH was 2.5 mm .

## Estimated maxima

TL: 180 mm ; VL: 3.2 mm ; VW: 2.7 mm ; VH: 2.7 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 2)

## Five-bearded rockling (Ciliata mustela (L.))

## Description

The centra are strongly waisted and bear two to five low, often poorly defined, longitudinal ridges of ossification. The massive prezygapophyses extend in front of the centrum. On the anterior caudal vertebrae they are situated at some distance from the centrum, well up the neural or haemal arch. There is usually a second, small dorsal prezygapophysis below the main one. The upper edge of the dorsal postzygapophysis is smoothly curving (c.w. northern rockling, p. 171).

## Similar species

Four-bearded rockling (p. 170) and northern rockling (p. 171)
From four-bearded rockling by: lower ridging on centrum; small gap between dorsal postzygapophysis and rear of neural arch; larger dorsal postzygapophysis.
From northern rockling by: anterior caudal centra (plate 1 below) more strongly waisted; lower, smoothly convex dorsal postzygapophyses; ridges on centrum more clearly defined.

## Regressions

Length range of specimens examined (TL): 108-230 mm; $\mathrm{N}=7$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=78.51$ VL -55.70 | 7 | 0.986 |
| $\mathrm{TL}=89.14 \mathrm{VW}-35.10$ | 7 | 0.980 |
| $\mathrm{TL}=82.54 \mathrm{VH}-21.71$ | 7 | 0.945 |

## Estimated maxima

TL: 510 mm ; VL: 7.1 mm ; VW: 6.0 mm ; VH: 5.7 mm .

plate 1 anterior caudal

plate 2 mid caudal
$\qquad$

## GADIDAE and MERLUCCIIDAE (group 3)

## Torsk (Brosme brosme (Ascanius))

## Description

The very short centra of torsk vertebrae are highly distinctive. VL is usually less than $100 \%$ of VH , and never more than $110 \%$. The dorsal prezygapophyses are situated high up on the neural arch and are strongly inclined upwards. In some specimens there is a second, short zygapophysis below each dorsal prezygapophysis. The dorsal postzygapophyses are very high. The centra usually have horizontal lines of ossification, but these are not developed into clear ribs. Except in the most anterior vertebrae (plate 1 below) the ventral prezygapophysis is relatively small. The ventral postzygapophyses are very tiny or absent.

## Similar species

Ling (p. 165)
The broad rib below the midline of the centrum of ling vertebrae distinguishes the two species.

## Regressions

Length range of specimens examined (TL): 220-500 mm; $N=4$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | ---: | :--- |
| $\ln \mathrm{TL}=4.3195+0.9925 \ln \mathrm{VL}$ | 4 | 0.991 |
| $\ln \mathrm{TL}=4.5978+0.8062 \ln \mathrm{VW}$ | 4 | 0.989 |
| $\ln \mathrm{TL}=4.5749+0.8208 \ln \mathrm{VH}$ | 4 | 0.992 |

## Estimated maxima

TL: 1170 mm ; VL: 15.7 mm ; VW: 21.0 mm ; VH: 20.5 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 4)

## Poor cod (Trisopterus minutus (L.) )

## Description

The centra bear two narrow, well-defined ribs. These run close together near the midline. The sides of the centra are deeply concave and the ribs stand well out from the rest of the surface. The ribs tend to split towards the posterior margin of the centrum (plate 1 below). The prezygapophyses are long, extending well in front of the centrum. They are inclined upwards only slightly, tending to curve towards the horizontal (c.w. silvery pout, p. 176).

## Similar species

Norway pout (p. 175), silvery pout (p. 176), four-bearded rockling (p. 170). No consistent differences were found between the vertebrae of poor cod and Norway pout.
From silvery pout by: ribs usually broader, less clearly lamellar. Prezygapophyses not sharply pointed and curve towards horizontal.
From four-bearded rockling by: shorter, less pronounced waist (see plates).
From blue whiting by: two well-defined and clearly separated ribs.

## Regressions

Length range of specimens examined (TL): 113-206 mm; N=20.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=60.480 \mathrm{VL}+13.51$ | 20 | 0.951 |
| $\mathrm{TL}=27.647 \mathrm{VW}+27.65$ | 20 | 0.950 |
| $\mathrm{TL}=69.803 \mathrm{VH}+14.12$ | 20 | 0.943 |

## Estimated maxima

TL: 290 mm ; VL: 4.5 mm ; VW: 4.1 mm ; VH: 3.8 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 4)

Norway pout (Trisopterus esmarkii (Nilsson) )

## Description

There are two, narrow well-defined ribs running along the midline of the centrum. The sides of the centra are deeply concave and the ribs stand well out from the rest of the surface. The prezygapophyses are long, extending well in front of the centrum. They are inclined upwards only slightly, tending to curve in towards the horizontal (c.w. silvery pout, p. 176).

## Similar species

Poor cod (p. 174), silvery pout (p. 176), four-bearded rockling (p. 170). No consistent differences were found between the vertebrae of Norway pout and poor cod.
From silvery pout by: ribs usually broader and less clearly lamellar.
From four-bearded rockling by: shorter centra, less pronounced waist (see plates).
From blue whiting by: two well-defined, clearly separated ribs.

## Regressions

Length range of specimens examined (TL): 67-185 mm; $\mathrm{N}=27$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.2064+1.0392 \ln$ PMXL | 27 | 0.991 |
| $\ln \mathrm{TL}=4.4154+0.9743 \ln \mathrm{VW}$ | 27 | 0.987 |
| $\ln \mathrm{TL}=4.4163+0.9625 \ln \mathrm{VH}$ | 27 | 0.982 |

## Estimated maxima

TL: 290 mm ; VL: 4.1 mm ; VW: 3.6 mm ; VH: 3.6 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 4)

## Silvery pout (Gadiculus argenteus thori (Schmidt))

## Description

The vertebrae are always small and translucent. There are two, sometimes three, narrow, lamellar ribs running along the midline of the centrum. These are prone to splitting anteriorly and posteriorly. The prezygapophyses are strongly tapering and pointed. They tend to curve away from the horizontal, the dorsal curving upwards and the ventral downwards (c.w. Norway pout, p. 175).

## Similar species

Poor cod (p. 174), Norway pout (p. 175)
From both of the above by: very narrow, usually lamellar ribs. Pointed, tapering prezygapophyses curving away from horizontal.

## Regressions

Length range of specimens examined (TL): 67-185 mm; $N=27$.
Regression equation
$\mathrm{N} \quad \mathrm{R}^{2}$
$\ln$ TL $=4.2064+1.0392 \ln$ PMXL
$27 \quad 0.991$
$\ln \mathrm{TL}=4.4154+0.9743 \ln \mathrm{VW}$
$27 \quad 0.987$
$\ln \mathrm{TL}=4.4163+0.9625 \ln \mathrm{VH}$
$27 \quad 0.982$

## Estimated maxima

TL: 160 mm ; VL: 3.3 mm ; VW: 2.4 mm ; VH: 2.4 mm .

plate 1 anterior caudal

plate 2 mid caudal

$\longmapsto 0.25 \mathrm{~cm}$

## GADIDAE and MERLUCCIIDAE (group 4 or 5)

## Blue whiting (Micromesistius poutassou (Risso) )

## Description

The centra are long and rectangular. VH varies from 80 to $88 \%$ of VL (c.w. pollack, cod, and saithe, pp. 179-181). There are two to four ridges in the midline of the centrum. These are often very close together or touching, forming a single raised area in the midline of the centrum, with the middle ridge usually standing out above the others. The prezygapophyses are long and extend in front of the centrum. The more anterior caudal vertebrae are not strongly waisted.

## Similar species

Whiting (p. 178), poor cod (p. 174), Norway pout (p. 175), pollack, cod, and saithe (pp179-181) From whiting by: horizontal ridges confined to midline of centrum; lack of numerous oblique septa over surface; longer ventral prezygapophysis.
From poor cod and Norway pout by: ridges coming together, forming raised area in midline From cod, saithe, pollack by: relatively longer centra.

## Regressions

Length range of specimens examined (TL): 80-122 mm; $\mathrm{N}=18$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.6688+0.8300 \ln \mathrm{VL}$ | 17 | 0.881 |
| $\ln \mathrm{TL}=4.6433+0.8578 \ln \mathrm{VW}$ | 17 | 0.901 |
| $\ln \mathrm{TL}=4.4600+0.8766 \ln \mathrm{VH}$ | 18 | 0.944 |

## Estimated maxima

TL: 510 mm ; VL: 7.3 mm ; VW: 6.0 mm ; VH: 6.1 mm .

plate 1 anterior caudal

plate 2 mid caudal
$\qquad$

## GADIDAE and MERLUCCIIDAE (group 5)

## Whiting (Merlangius merlangus (L.))

## Description

The surface of the centrum has a cross-grained appearance owing to the many small, oblique septa running between the main horizontal lines of ossification. The horizontal lines of ossification vary greatly; in some bones they are prominent ribs but more often they are low, closely associated ridges with many tiny interconnecting septa. VW varies from 80 to $95 \%$ of VL, occasionally reaching $98 \%$ in the first two or three caudal vertebrae (c.w. pollack and cod, pp. 179 and 180).

## Similar species

Blue whiting (p. 177), cod (p. 180), pollack (p. 179)
From blue whiting by: numerous oblique septa over surface; shorter ventral prezygapophysis.
From cod and pollack by: relatively longer vertebrae; horizontal ridging often better defined than in pollack.

## Regressions

Length range of specimens examined (TL): $90-380 \mathrm{~mm} ; \mathrm{N}=41$.

Regression equation
$\mathrm{TL}=73.108 \mathrm{VL}+1.906$
$\ln \mathrm{TL}=4.4273+0.9408 \ln \mathrm{VW}$
$\ln \mathrm{TL}=4.3645+0.9645 \ln \mathrm{VH}$
$\mathrm{N} \quad \mathrm{R}^{2}$
$40 \quad 0.983$
$40 \quad 0.975$
$40 \quad 0.978$

## Estimated maxima

TL: 760 mm ; VL: 10.3 mm ; VW: 10.1 mm ; VH: 9.9 mm .

plate 1 anterior caudal

plate 2 mid caudal


## GADIDAE and MERLUCCIIDAE (group 5)

## Pollack (Pollachius pollachius (L.))

## Description

The centrum is roughly square in profile, with VH varying between 98 and $109 \%$ of VL (c.w. whiting, p. 178, blue whiting, p. 177, saithe p. 181) and without a distinct waist. The surface has a cross-grained appearance with many oblique septa running between the main horizontal lines of ossification. There are usually two or three main horizontal ossifications which are, in turn, composed of closely associated lamellae with many interconnections (see plates below). Except in the most anterior few caudal vertebrae (plate 1 below) the prezygapophyses are very narrow.

## Similar species

Whiting (p. 178), cod (p. 180)
From whiting by: shorter centra without clearly defined ridges.
From cod by: greater density of septa between horizontal ossifications, giving the centrum a more compacted appearance. Horizontal ossifications do not form clear ridges as they often do in cod. More anterior vertebrae (plate 1 below) distinguished by the shape of the cavity on underside of centrum; in pollack the cavity is straight-sided, in cod the sides bow outwards.

## Regressions

Range of fish length (TL): $355-625 \mathrm{~mm} ; \mathrm{N}=15$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=65.030 \mathrm{VL}+4.0112$ | 15 | 0.828 |
| $\ln \mathrm{TL}=4.6489+0.7077 \ln \mathrm{VW}$ | 15 | 0.912 |
| $\ln \mathrm{TL}=4.51832+0.8437 \ln \mathrm{VH}$ | 15 | 0.937 |

## Estimated maxima

TL: 1390 mm ; VL: 18.9 mm ; VW: 26.5 mm ; VH: 23.2 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 5)

## Cod (Gadus morhua (L.))

## Description

The centra are rather short, with VH ranging from $95 \%$ to $106 \%$ of VL (c.w. blue whiting, p. 177, whiting, p. 178, saithe p. 181). There are usually two, sometimes three or four, distinct, horizontal lines of ossification. These may form clear ridges, but they always have many interconnecting septa (see plates, c.w. bib, p. 166). These ridges are fluted posteriorly where they frequently split. The prezygapophyses are short, extending beyond the front of the centrum only in the more anterior caudal vertebrae (c.w. Trisopterus spp. and rocklings).

## Similar species

Pollack (p. 179), saithe (p. 181), whiting (p. 178), bib (p. 166)
From pollack by: fewer oblique septa, giving a less compacted appearance. Horizontal ossifications often form clear ridges. Anterior caudals distinguished by the shape of the cavity on underside of the centrum; in pollack it is straight-sided, in cod the sides bow outwards.
From saithe by: centra usually relatively shorter; broader dorsal prezygapophyses.
From whiting by: relatively shorter centra.
From bib by: septa between horizontal ossifications, shorter prezygapophyses.

## Regressions

Length range of specimens examined (TL): 94-1057 mm; $\mathrm{N}=26$.

| Regression equation | $N$ | $R^{2}$ |
| :--- | :--- | :--- |
| $\ln T L=4.3513+0.9202 \ln V L$ | 26 | 0.990 |
| $\ln T L=4.3976+0.8937 \ln V W$ | 26 | 0.997 |
| $\ln T L=4.4701+0.8477 \ln V H$ | 26 | 0.998 |

## Estimated maxima

TL: 2060 mm ; VL: 41.4 mm ; VW: 37.0 mm ; VH: 41.4 mm .

plate 1 anterior caudal

plate 2 mid caudal

## GADIDAE and MERLUCCIIDAE (group 5)

## Saithe (Pollachius virens (L.))

## Description

Saithe vertebrae are strongly waisted, with the smooth anterior margin sloping steeply in towards the beginning of the horizontal ridging. VH varies from 84 to $96 \%$ of VL (c.w. cod, p. 180). The centrum bears two, occasionally three, ridges which are confined to near the midline. The ridges are joined by many interconnecting septa. In some specimens these fuse to form a single raised ridge, widening and splitting posteriorly. The prezygapophyses are narrow.

## Similar species

Cod (p. 180), bib (p. 166)
From cod by: relatively longer centra and narrower prezygapophyses. Anterior caudal vertebrae (plate 1) may be distinguished by the straight sides of the cavity on the underside of the centrum; in cod the sides curve outwards.
From bib by: narrow prezygapophyses; many septa between horizontal ridges.

## Regressions

Length range of specimens examined (TL): 211-815 mm; $\mathrm{N}=16$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=57.800 \mathrm{VL}+28.57$ | 16 | 0.996 |
| $\mathrm{TL}=57.149 \mathrm{VW}+55.76$ | 16 | 0.994 |
| $\ln \mathrm{TL}=4.4736+0.8730 \ln \mathrm{VH}$ | 16 | 0.988 |

## Estimated maxima



plate 1 anterior caudal

plate 2 mid caudal


### 4.4.4 AMMODYTIDAE

## Sandeels (Ammodytes marinus (Raitt) and Ammodytes tobianus (L.))

## Description

No differences could be found between the vertebrae of the two species. The vertebrae are always small, usually 1-2 mm long, and delicate. The centra are longer than they are high and strongly waisted. They bear two or three distinctive, narrow lamellar ribs. The neural arch is broad-based and perforated by a small neural foramen above which a second, larger aperture is created by a supporting strut of bone behind the neural spine. The anterior dorsal and ventral prezygapophyses are well developed and project well in front of the anterior margin of the centrum.

## Similar species

Smooth sandeel (p. 183), greater sandeel (p. 184)
A. marinus vertebrae tend to be relatively shorter than those of the other two species. VH varies between 75 and $81 \%$ of VL in A. marinus and A. tobianus, between 64 and $75 \%$ in $G$. semisquamatus, and between 66 and $79 \%$ in $H$. lanceolatus.

## Regressions

Length range of specimens examined (TL):
A. marinus, $74-168 \mathrm{~mm} ; \mathrm{N}=11$.
A. tobianus, one specimen of 161 mm , one unknown; $\mathrm{N}=2$.

Regression equation
$\ln \mathrm{TL}=4.4758+1.0426 \ln \mathrm{VL}$
$\ln \mathrm{TL}=4.7444+0.9370 \ln \mathrm{VW}$
$\ln \mathrm{TL}=4.7463+1.0419 \ln \mathrm{VH}$
$\mathrm{N} \quad \mathrm{R}^{2}$
110.986
110.984
110.989

## Estimated maxima

TL: 270 mm ; VL: 2.9 mm ; VW: 2.5 mm ; VH: 2.3 mm .

plate 1 anterior caudal

plate 2 mid caudal

## AMMODYTIDAE

## Smooth sandeel (Gymnammodytes semisquamatus (Jourdain))

## Description

The vertebrae appear almost identical to those of other sandeels. The centra are longer than they are high and strongly waisted, bearing two or three distinctive, narrow lamellar ribs of bone along each side. The neural arch is broad-based and perforated by a small neural foramen above which there is a second, larger aperture. The anterior dorsal and ventral prezygapophyses are well developed and project well in front of the anterior margin of the centrum.

## Similar species

Sandeels (A. marinus and A. tobianus, p. 182), greater sandeel (p. 184)
No consistent qualitative differences were found which reliably distinguish G. semisquamatus vertebrae from the sandeels. Smooth sandeel caudal vertebrae may however be distinguished from those of A. marinus and A. tobianus by their narrower centra: VH varies between 64 and $75 \%$ of VL in G. semisquamatus, between 75 and $81 \%$ in A. marinus and A. tobianus ( 66 to $79 \%$ in $H$. lanceolatus).

## Regressions

Too few specimens were examined for meaningful regressions to be presented. In a specimen of 197 mm (TL), VL was 2.09 mm , VW was 1.62 mm and VH was 1.53 mm . In a specimen of 201 mm , VL was 2.12 mm , VW was 1.59 mm and VH was 1.59 mm .

## Estimated maxima

TL: 280 mm ; VL: 2.95 mm ; VW: 2.21 mm ; VH: 2.21 mm .

plate 1 anterior caudal

plate 2 mid caudal

## AMMODYTIDAE

## Greater sandeel (Hyperoplus lanceolatus (Lesauvage) )

## Description

The centra are longer than they are high and strongly waisted. They bear two or three narrow lamellar ribs on their lateral surfaces. The neural arch is broad-based and perforated by a small neural foramen above which a second, larger aperture is created by a supporting strut of bone behind the neural spine. Both the neural and the haemal spine are thin and delicate. The anterior dorsal and ventral prezygapophyses are well developed and project well in front of the anterior margin of the centrum.

## Similar species

Sandeels (A. marinus and A. tobianus, p. 182), smooth sandeel (p. 183)
No consistent qualitative differences were found which reliably distinguish H. lanceolatus vertebrae from the other sandeels. VH varies between 66 and $79 \%$ of VL in H. lanceolatus, between 64 and $75 \%$ in G. semisquamatus, and between 75 and $81 \%$ in A. marinus and $A$. tobianus. Vertebrae longer than 3.0 mm are unlikely to have come from Ammodytes or Gymnammodytes.

## Regressions

Too few specimens were examined for meaningful regressions to be presented. In a specimen of 268 mm (TL), VL was 3.19 mm , VW was 2.48 mm and VH was 2.24 mm . In a specimen of 250 mm (TL), VL was 2.83 mm , VW was 2.18 mm and VH was 2.06 mm .

## Estimated maxima

TL: 350 mm ; VL: 3.70 mm ; VW: 2.85 mm ; VH: 2.69 mm .

plate 1 anterior caudal

plate 2 mid caudal

### 4.4.5 BOTHIDAE

## Turbot (Scophthalmus maximus (L.))

## Description

The centra, especially of the more anterior caudal vertebrae (plate 1 below), are very short, with VL being $50-65 \%$ of VH. The sides of the centra bear many horizontal lamellar septa, often coalescing into distinct ribs. There are always numerous interconnections between these septa or ribs (c.w. megrim, p. 187). In anterior or posterior view the centra are very distinctly hexagonal. The prezygapophyses are broad and well developed. The stout, dagger-like apophyses are asymmetrically developed: up to $60 \%$ of VW on the left and $50 \%$ on the right.

## Similar species

Brill (p. 186), megrim (p. 187)
The horizontal lamellae on turbot centra differed from those of the two brill examined, in which there were three to five thicker, better-defined ribs.
From megrim by: shorter centra of anterior caudals, many interconnections between ribs. Shorter, stouter apophyses.

## Regressions

Length range of specimens examined (TL): 388-615 mm; $\mathrm{N}=7$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln T L=4.3694+0.8568 \ln \mathrm{VL}$ | 4 | 0.999 |
| $\ln \mathrm{TL}=3.9928+0.8497 \ln \mathrm{VW}$ | 4 | 0.941 |
| $\ln \mathrm{TL}=4.2820+0.7200 \ln \mathrm{VH}$ | 4 | 0.921 |

## Estimated maxima

TL: 1200 mm ; VL: 23.9 mm ; VW: 36.1 mm ; VH: 45.0 mm .


## BOTHIDAE

## Brill (Scophthalmus rhombus (L.) )

## Description

The lateral surfaces of the centra bear three to five horizontal ribs. These are usually interconnected by septa. The anterior caudal vertebrae (plate 1 below) are short, with VL being $60-70 \%$ of VH (c.w. megrim, p. 187, and long rough dab, p. 194). The apophyses on the anterior caudals are longer on the left side of the vertebrae: $50-60 \%$ of VW compared with $25-35 \%$ on the right side. There are well-developed ventral pre- and postzygapophyses (c.w. long rough dab, p. 194).

## Similar species

Turbot (p. 185), megrim (p. 187), long rough dab (p. 194)
From turbot by: in the two specimens examined, well-defined ribs on brill centra, compared with the thinner lamellae of turbot. Owing to the small sample size these differences should be treated with caution.
From megrim by: shorter anterior caudal centra; shorter apophyses.
From long rough dab by: shorter centra, longer apophyses, and presence of ventral pre- and postzygapophyses.

## Regressions

Only two specimens were examined. In a specimen of 350 mm (TL), VL was 5.0 mm , VW was 7.4 mm and VH was 8.0 mm . In a 292 mm specimen (TL), VL was 4.1 mm , VW was 5.7 mm and VH was 6.7 mm .

## Estimated maxima

TL: 610 mm ; VL: 8.7 mm ; VW: 12.9 mm ; VH: 13.9 mm .

plate 1 anterior caudal

plate 2 mid caudal


## BOTHIDAE

## Megrim (Lepidorhombus whiffiagonis (Walbaum) )

## Description

Megrim vertebrae have centra with three or four very well-defined, broad, parallel ribs along each side. There are few, if any, septa running between these ribs. The apophyses are strongly asymmetrical; those on the left side are very long, up to $100 \%$ of VW in length, while those on the right are less than $30 \%$ of VW. On both sides they are thin and prone to breakage. In the anterior caudal vertebrae (plate 1 below), VL is not less than $70 \%$ of VH (c.w. turbot; p. 185, and brill, p. 186).

## Similar species

Long rough dab (p. 194), turbot (p. 185), brill (p. 186)
From long rough dab by: long, asymmetrically developed apophyses; presence of ventral zygapophyses.
From turbot and brill by: longer centra of anterior caudals; ribs more clearly defined with few interconnections. Very long left apophyses.

## Regressions

Length range of specimens examined (TL): 189-456 mm; $\mathrm{N}=17$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.2805+0.9400 \ln \mathrm{VL}$ | 17 | 0.989 |
| $\ln \mathrm{TL}=4.2858+0.8964 \ln \mathrm{VW}$ | 17 | 0.985 |
| $\ln \mathrm{TL}=4.1386+0.9287 \ln \mathrm{VH}$ | 17 | 0.986 |

## Estimated maxima

TL: 610 mm ; VL: 9.6 mm ; VW: 10.6 mm ; VH: 11.5 mm .

plate 1 anterior caudal

plate 2 mid caudal

## BOTHIDAE

## Scaldfish (Arnoglossus laterna (Walbaum) )

## Description

The centrum is roughly square, with centrum length equalling centrum height. It is amphicoelus, but the concavities are strongly asymmetrical; the anterior concavity is shallow in comparison with the posterior. The centra are strongly waisted and bear a single, lamellar rib along each side. The apophyses (two each side) rise as extensions of this rib and are roughly equal on both sides of the centrum. The zygapophyses are all well developed. Both neural and haemal arches are broad-based in lateral view.

## Similar species

Dover sole (p. 196), solenette (p. 197)
From Dover sole and solenette by: broad-based haemal arch; presence of two apophyses on each side of centrum (one per side in soles); thinner rib on centrum.

## Regressions

Too few specimens were examined for meaningful regressions to be given. In a 95 mm fish (standard length) VL was 1.7 mm , VW was 1.8 mm and VH was 1.9 mm . In a fish of 107 mm VL was 2.1 mm , VW was 2.0 mm and VH was 2.1 mm .

## Estimated maxima

SL: 190 mm ; VL: 3.7 mm ; VW: 3.6 mm ; VH: 3.7 mm .

plate 1 anterior caudal

plate 2 mid caudal

### 4.4.6 PLEURONECTIDAE

## Plaice (Pleuronectes platessa (L.))

## Description

The centra have deep concavities inwards from the bases of the neural and haemal spines, leaving a broad raised rib in the midline of the centrum. This rib is composed of several transverse, interconnected bony lamellae. The apophyses on the anterior caudal centra are $25-45 \%$ of VW in length. The more anterior vertebrae (plate 1) are much shorter than they are high, VL not being more than $80 \%$ of VH. Ventral prezygapophyses are often absent or, if present, they are tiny and low.

## Similar species

Dab (p. 190), flounder (p. 191), lemon sole (p. 193). These four species are difficult to distinguish.
From dab and flounder by: tiny, or absent, ventral prezygapophyses.
From dab (anterior caudals only) by: short centra; VL $>=79 \%$ of VH in dab.
From flounder by: shorter apophyses; anterior caudals usually shorter (VL $=74-90 \%$ of VH in
flounder); mid caudals (plate 2 below) with broad-based haemal arch (narrow in flounder). From lemon sole by: narrower haemal arch without foramina (anterior caudals only).

## Regressions

Length range of specimens examined (TL): 77-380 mm; $\mathrm{N}=33$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.4671+0.9520 \ln \mathrm{VL}$ | 30 | 0.987 |
| $\ln \mathrm{TL}=4.2384+0.9885 \ln \mathrm{VW}$ | 30 | 0.977 |
| $\ln \mathrm{TL}=4.0852+0.9698 \ln \mathrm{VH}$ | 30 | 0.981 |

## Estimated maxima

TL: 1180 mm ; VL: 15.1 mm ; VW: 20.9 mm ; VH: 21.1 mm .

plate 1 anterior caudal

plate 2 mid caudal

## PLEURONECTIDAE

## Dab (Limanda limanda (L.))

## Description

There are deep concavities by the bases of the neural and haemal spines. The broad rib between these concavities is made up of several interconnected bony lamellae. These lamellae may be fused, especially in the more posterior vertebrae. The apophyses are well developed, and are 30$60 \%$ of VW in length on the anterior caudal centra. Viewed dorsally they are broad, flat, and winglike (c.w. flounder, p. 191). The ventral prezygapophyses are short but well defined. In the more anterior vertebrae (plate 1 below) VL is $79-102 \%$ of VH .

## Similar species

Plaice (p. 189), flounder (p. 191), lemon sole (p. 193). These species are difficult to distinguish.
From plaice by: well-defined ventral prezygapophyses; longer centra of anterior caudals (VL<80\% of VW in plaice).
From flounder by: broad apophyses, mid caudals with broad-based haemal arch (plate 2 below). From lemon sole by: well-defined ventral prezygapophyses.

## Regressions

Length range of specimens examined (TL): 68-393 mm; $\mathrm{N}=34$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.2920+0.9802 \ln \mathrm{VL}$ | 32 | 0.989 |
| $\ln \mathrm{TL}=4.3034+0.9163 \ln \mathrm{VW}$ | 32 | 0.983 |
| $\ln \mathrm{TL}=4.1313+0.9792 \ln \mathrm{VH}$ | 32 | 0.992 |

## Estimated maxima

TL: 460 mm ; VL: 7.4 mm ; VW: 7.2 mm ; VH: 7.6 mm .

plate 1 anterior caudal

plate 2 mid caudal


## PLEURONECTIDAE

## Flounder (Platichthys flesus (L.) )

## Description

Like those of the two preceding species, P. platessa and L. limanda, the centra have deep concavities at the bases of the neural and haemal arches and a wide, raised central rib. The apophyses are long, with lengths between 45 and $75 \%$ of VW on the anterior caudal centra. In dorsal view they are narrow and dagger-like (c.w. dab, p. 190). The ventral prezygapophyses are well defined (c.w. lemon sole, p. 193).

## Similar species

Plaice (p. 189), dab (p. 190), lemon sole (p. 193). These species are very difficult to distinguish even when well-preserved specimens are available.
From plaice by: well-defined ventral prezygapophyses, longer apophyses.
From dab by: narrow apophyses, mid caudals with narrow-based haemal arch (plate 2 below). From lemon sole by: well-defined ventral prezygapophyses.

## Regressions

Length range of specimens examined (TL): 130-393 mm; $\mathrm{N}=9$.

| Regression equation | $N$ | $R^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.3757+0.8605 \ln \mathrm{VL}$ | 9 | 0.956 |
| $\ln \mathrm{TL}=4.1832+0.9409 \ln \mathrm{VW}$ | 9 | 0.957 |
| $\ln \mathrm{TL}=4.0347+0.9618 \ln \mathrm{VH}$ | 9 | 0.980 |

## Estimated maxima

TL: 600 mm ; VL: 10.1 mm ; VW: 10.1 mm ; VH: 11.5 mm .

plate 1 anterior caudal

plate 2 mid caudal

## PLEURONECTIDAE

## Witch (Glyptocephalus cynoglossus (L.))

## Description

The most important feature of witch vertebrae is the lattice of horizontal and vertical septa over the lateral surfaces, giving the centra a honeycombed appearance. The ventral zygapophyses are tiny or absent (c.w. halibut, p. 195). The bases of the neural and haemal arches extend the full length of the centrum, the haemal arch being perforated laterally by a large foramen. The lateral apophyses are relatively short, approximately $30 \%$ of VW in length on the anterior caudal centra. They are narrow and triangular in dorsal view and equally developed on both sides.

## Similar species

Halibut (p. 195)
From halibut by: well-developed lateral apophyses, tiny ventral zygapophyses, broad-based haemal arch.

## Regressions

Length range of specimens examined (TL): $160-415 \mathrm{~mm}$; $\mathrm{N}=17$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.6402+0.9135 \ln \mathrm{VL}$ | 17 | 0.984 |
| $\ln \mathrm{TL}=4.3856+0.9199 \ln \mathrm{VW}$ | 17 | 0.973 |
| $\ln \mathrm{TL}=4.3418+0.9471 \ln \mathrm{VH}$ | 17 | 0.979 |

## Estimated maxima

TL: 710 mm ; VL: 8.1 mm ; VW: 10.4 mm ; VH: 10.2 mm .

plate 1 anterior caudal

plate 2 mid caudal

## PLEURONECTIDAE

## Lemon sole (Microstomus kitt (Walbaum) )

## Description

Lemon sole vertebrae have a broad central rib bounded by deep concavities at the bases of the neural and haemal arches. In all the caudal vertebrae the arches themselves are broad-based (c.w. flounder, p. 191). Ventral prezygapophyses are absent or, if present, are very low and indistinct. The apophyses are well developed, up to $50 \%$ of VW in length on the anterior caudal centra.

## Similar species

Dab (p. 190), flounder (p. 191), lemon sole (p. 193). Vertebrae of these species are very difficult to distinguish.
From dab and flounder by: ventral prezygapophyses which are tiny and low or, more often, absent.
From flounder by: mid caudals (plate 2 below) with broad-based haemal arch (narrow in flounder).
From plaice by: anterior caudals with broad-based haemal arch with foramen (plate 1).

## Regressions

Length range of specimens examined (TL): $156-339 \mathrm{~mm} ; \mathrm{N}=24$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.4164+0.9124 \ln \mathrm{VL}$ | 24 | 0.952 |
| $\ln \mathrm{TL}=4.3275+0.8544 \ln \mathrm{VW}$ | 24 | 0.935 |
| $\ln \mathrm{TL}=4.3144+0.8084 \ln \mathrm{VH}$ | 24 | 0.917 |

## Estimated maxima

TL: 660 mm ; VL: 9.2 mm ; VW: 11.7 mm ; VH: 13.4 mm .

plate 1 anterior caudal

plate 2 mid caudal


## PLEURONECTIDAE

## Long rough dab (Hippoglossoides platessoides (Fabricius))

## Description

The centra are characterized by the presence of three, sometimes four, well-defined horizontal, lamellar ribs. There are few interconnections between these. In the more anterior caudals VL is $>=75 \%$ of VH (plate 1 below). The apophyses are very short, never more than $20 \%$ of centrum width and more usually $5-10 \%$ (c.w. megrim, p. 187). Ventral pre- and postzygapophyses are tiny or absent.

## Similar species

Megrim (p. 187), brill (p. 186)
From megrim by: shorter apophyses, minute or absent ventral zygapophyses.
From brill by: longer centra, minute or absent ventral zygapophyses, shorter apophyses.

## Regressions

Length range of specimens examined (TL): 79-283 mm; $\mathrm{N}=24$.

| Regression equation | N | $\mathrm{R}^{2 .}$ |
| :--- | :--- | :--- |
| $\ln T L=4.4390+0.8832 \ln \mathrm{VL}$ | 24 | 0.965 |
| $\ln \mathrm{TL}=4.3907+0.8411 \ln \mathrm{VW}$ | 24 | 0.955 |
| $\ln \mathrm{TL}=4.2890+0.8472 \ln \mathrm{VH}$ | 24 | 0.968 |

## Estimated maxima

TL: 600 mm ; VL: 8.7 mm ; VW: 10.1 mm ; VH: 11.5 mm .

plate 1 anterior caudal

plate 2 mid caudal


## PLEURONECTIDAE

## Halibut (Hippoglossus hippoglossus (L.))

## Description

Halibut vertebrae are recognizable by the honeycomb patterning of the centrum and the welldeveloped, blunt-ended, steeply inclined zygapophyses. The centra are distinctly hexagonal in anterior or posterior view. The lateral apophyses are reduced to low protuberances at the ends of the centra, in the midline. The lateral surfaces of the centra are concave at the bases of the neural and haemal arches, leaving a wide raised area running the length of the bone.

Similar species
Witch (p. 192)
From witch by: well-developed, blunt-ended zygapophyses and tiny, low apophyses.

## Regressions

Size range of specimens examined (TL): $463-810 \mathrm{~mm} ; \mathrm{N}=5$.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\mathrm{TL}=84.52 \mathrm{VL}+34.39$ | 4 | 0.995 |
| $\mathrm{TL}=61.13 \mathrm{VW}+48.23$ | 4 | 0.997 |
| $\mathrm{TL}=62.09 \mathrm{VH}+24.56$ | 4 | 0.984 |

## Estimated maxima

TL: 2540 mm ; VL: 29.5 mm ; VW: 40.7 mm ; VH: 40.0 mm .

plate 1 anterior caudal

plate 2 mid caudal

### 4.4.7 SOLEIDAE

## Dover sole (Solea solea (L.) )

## Description

The centra have a single, strong, thick rib along each side. They are distinctly oval, noticeably higher than wide. There is a single, short, broad apophysis on each side, approximately $15 \%$ of centrum width in length. These apophyses rise from the front of the rib, in the midline. Viewed laterally the haemal arch is narrow-based, serving to distinguish the vertebrae from many pleuronectids and bothids. All the zygapophyses are well developed. The dorsal prezygapophysis is strongly inclined upwards. In the more posterior caudal vertebrae, VL is up to $150 \%$ of VH .

## Similar species

Solenette (p. 197), scaldfish (p. 188)
From solenette by: oval centra (posterior or anterior view); dorsal prezygapophysis inclined strongly upwards. Apophyses very short, not inclined downwards.
From scaldfish by: single, short apophysis on each side; narrow-based haemal arch; thicker rib.

## Regressions

Too few specimens of this species were examined for meaningful regressions to be given. In a 251 mm fish (TL), VL was 3.0 mm , VW was 3.9 mm and VH was 3.5 mm . In a 268 mm specimen (TL), VL was 3.1 mm , VW was 4.1 mm and VH was 3.5 mm .

## Estimated maxima

TL: 780 mm ; VL: 9 mm ; VW: $11.9 \mathrm{~mm} ; \mathrm{VH}: 10.2 \mathrm{~mm}$.

plate 1 anterior caudal

plate 2 mid caudal

## SOLEIDAE

## Solenette (Buglossidium luteum (Risso) )

## Description

The centra have a single, strong, thick rib along each side. They are roughly round, or hexagonal in anterior or posterior view (c.w. Dover sole, p. 196). There is a single, short apophysis on each side, approximately $25 \%$ of centrum width in length. These rise from the front of the rib, slightly below the midline and are strongly inclined downwards. The haemal arch is narrow-based, not occupying more than $50 \%$ of VL. All the żygapophyses are well developed. The dorsal prezygapophysis is roughly horizontal.

## Similar species

Dover sole (p. 196), scaldfish (p. 188)
From Dover sole by: centrum roughly round or hexagonal (not distinctly oval) in posterior or anterior view. Dorsal prezygapophysis horizontal. Apophyses inclined downwards.
From scaldfish by: single, downward-inclined apophysis on each side; narrow-based haemal arch; thicker rib.

## Regressions

Size range of specimens examined (TL): 119-195 mm; N=19.

| Regression equation | N | $\mathrm{R}^{2}$ |
| :--- | :--- | :--- |
| $\ln \mathrm{TL}=4.2338+0.9427 \ln \mathrm{VL}$ | 19 | 0.921 |
| $\ln \mathrm{TL}=4.1692+0.9644 \ln \mathrm{VW}$ | 19 | 0.944 |
| $\ln \mathrm{TL}=4.3342+0.8072 \ln \mathrm{VH}$ | 19 | 0.830 |

## Estimated maxima

TL: 200 mm ; VL: 3.1 mm ; VW: 3.2 mm ; VH: 3.1 mm .

plate 1 anterior caudal

plate 2 mid caudal

### 4.4.8 Other groups

Caudal vertebrae of four additional species are shown below. Hook-nose (Agonus cataphractus L., Agonidae) caudal vertebrae have unribbed, waisted, centra and prominent dorsal prezygapophyses. Sea snail (Liparus liparus L., Liparidae) caudal vertebrae have very long neural and haemal spines and a prominent rib. All four zygapophyses are visible as small spikes and the centra appear almost rectangular in cross-section. Caudal vertebrae of the 15 -spined stickleback (Spinachia spinachia L., Gasterosteidae) are unribbed and have narrow, waisted, centra. The centra become markedly more elongated towards the caudal fin (c.w. dragonets, p. 151). Boarfish (Capros aperL., Caproidae) caudal vertebrae have very long neural and haemal spines and broad, massive, dorsal prezygapophyses. There is a lamellar plate of bone between the dorsal margin of the centrum and the neural spine and a single strong longitudinal rib in the midline of the centrum.


Stickleback caudal vertebra


Boarfish caudal vertebra

## 5. MISCELLANEOUS DIAGNOSTIC ELEMENTS

The following pages show a number of highly distinctive structures which are diagnostic of species groups or, in some cases, single species. These structures have largely been selected on the basis of their frequent occurrence in seal diets (see Pierce et al.,1991a).

### 5.1 Cartilaginous fishes

The Marsipobranchii (lampreys and hagfish), Selachii (sharks, rays, and chimaeras), and those teleostean fish lacking well-ossified skeletons are all likely to be underrepresented in hard remains found in stomach and faecal samples. The only parts of lampreys likely to survive are the teeth of the sucking disc. Vertebrae of sharks and rays may be found, usually as isolated centra with smooth featureless surfaces. Teeth and denticles (see next page) are likely to be more useful.


Dogfish (Scyliorhinus caniculus) vertebra

## Rajidae

The skin of skates and rays is covered with many dermal denticles. The structure of these varies from species to species. Two examples, starry ray (Raja radiata Donovan) and cuckoo ray (Raja naevus Müller and Henle) are illustrated below.


Starry ray (Raja radiata) denticles


Cuckoo ray (Raja naevus) denticles

### 5.2 Clupeidae

Herrings and sprats have conspicuous spherical bullae situated in each pro-otic bone. These bullae are robust and survive passage through seal digestive tracts very well. No differences were found between bullae from herring and sprat.


Herring (Clupea harengus) otic bulla

### 5.3 Caproidae

Boarfish (Capros aper (L.) )
Boarfish dentaries are unusual in bearing three to five rows of small tooth-like serrations along the ventral margin of the bone.

5.4 Carangidae

Scad (Trachurus trachurus (L.))
The scad bears distinctive dermal scutes along the sides of the base of the tail. These consist of a raised, rearward. pointing mid-section with symmetrical, wing-like, lateral projections. Note that other species, e.g., hook-nose (Agonus cataphractus), bear dermal scutes of varying shapes, including wing-like forms.


Scad (Trachurus trachurus) dermal scutes

### 5.5 Labridae

The diet of wrasses consists largely of creatures with a hard exoskeleton. Their strong jaws and dentition reflect this diet with stout, pointed teeth in their jaws and rounded, grinding pharyngeal teeth.



Cuckoo wrasse (Labrus mixtus) left premaxilla and dentary

## Labridae <br> Cuckoo wrasse (Labrus mixtus (L.))

Cuckoo wrasse maxillae are extremely squat and robust with a massive articular head. The shank is deep and flattened with a lobed dorsal extension behind the head. Sea bream maxillae are somewhat similar. Red sea bream maxillae (opposite) are less squat and have a relatively smaller articular head than cuckoo wrasse maxillae.


Cuckoo wrasse (Labrus mixtus) left maxilla, lateral view


Cuckoo wrasse (Labrus mixtus) left maxilla, medial view
$\qquad$

### 5.6 Sparidae <br> Red sea bream (Pagellus bogaraveo (Brünnich) )

The maxilla of the red sea bream is short and robust. The maxillary shank is flattened and deep with two lobed dorsal extensions. The maxillae of wrasse are similar but have a more squat appearance with a more massive articular head. No other species of breams were examined.


Red sea bream (Pagellus bogaraveo) left maxilla, lateral view


Red sea bream (Pagellus bogaraveo) left maxilla, medial view
$\qquad$
1.0 cm

### 5.7 Ammodytidae

The sandeels have a number of very distinctive skeletal elements which, perhaps because of their small size, are normally found intact in seal faeces. The atlas vertebra is unusual in being opisthocoelus: i.e., the centrum is convex anteriorly and concave posteriorly.


Sandeel (Ammodytes marinus) atlas vertebra in lateral (left) and anterior (right) view

The sandeels also possess distinctive subopercular and dentary bones. The former have a frilled posterior margin while the latter have large wing-like processes.


Ammodytes marinus subopercular


Gymnammodytes semisquamatus subopercular


Ammodytes marinus left dentary in lateral view $\longmapsto 0.5 \mathrm{~cm}$
0.5 cm


Gymnammodytes semisquamatus left dentary in lateral view
$\qquad$
0.5 cm

### 5.8 Callionymidae

Dragonets (Callionymus lyra (L.) and C. maculatus (Rafinesque-Schmaltz))
Both dragonets have preoperculae which bear four spines. Very often it is only the spines which remain in samples, the rest of the bone having suffered from mechanical damage or digestion.



## Dragonet (Callionymus Jyra)

Preopercular spines
$\qquad$

### 5.9 Anarhichadidae

Catfish (Anarhichas lupus (L.)) and spotted catfish (A. minor (Olafsen))
Catfish teeth are large and broad and survive digestion very well, often being the only recognizable catfish structures. At the front of the jaw the teeth are long and caniniform while further back they are broad and flat.


Catfish (Anarhichas Jupus) teeth

### 5.10 Cyclopteridae <br> Lumpsucker (Cyclopterus lumpus (L.))

Lumpsuckers have denticles similar to those of some of the cartilaginous fishes. However, those of the lumpsucker may be distinguished by their rough, granular texture. Lumpsucker bone fragments are recognizable by their papery texture.


Lumpsucker (Cyclopterus Iumpus) denticles

### 5.11 Bothidae

Turbot Scophthalmus maximus (L.)
Turbot have many long tubercles embedded in the skin. These are round or oval, long and pointed.


Turbot (Scophthalmus maximus) denticles


Turbot (Scophthalmus maximus) denticle

### 5.12 Flatfish urohyals

The urohyals of flatfishes (Bothidae, Pleuronectidae, and Soleidae) usually have a distinctive hooked shape. There is considerable interspecific variation and urohyals are useful for species determination (Kusaka, 1974).



Brill (Scophthalmus rhombus)


Megrim (Lepidorhombus whiffiagonis)


Plaice (Pleuronectes platessa)


Dab (Limanda limanda)


Flounder (Platichthys flesus)



Halibut (Hippoglossus hippoglossus)


Dover sole (Solea solea)

Newsome, G.E. 1977. Use of opercular bones to identify and estimate lengths of prey consumed by piscivores. Canadian Journal of Zoology, 55: 733-736.

Norden, C.R. 1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling (Thymallus arcticus) and its phylogeny. Journal of the Fisheries Research Board of Canada, 18: 679-791.

Nordoey, E.S., and Blix, A.S. 1988. Sources of error in estimating food requirements of seals. Polar Record, 24: 62-64.

Pierce, G.J., and Boyle, P.R. 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanography and Marine Biology Annual Review, 29: 409-486.

Pierce, G.J., Boyle, P.R., and Diack, J.S.W. 1991a. Identification of fish otoliths and bones in faeces and digestive tracts of seals. Journal of Zoology, London, 224: 320-328.

Pierce, G.J., Boyle, P.R., and Diack, J.S.W. 1991b. Digestive tract contents of seals in Scottish waters: comparison of samples from salmon nets and elsewhere. Journal of Zoology, London, 225: 670-676.

Pierce, G.J., Boyle, P.R., Diack, J.S.W., and Clark, I. 1990a. Sandeels in the diets of seals: application of novel and conventional methods to analysis of faeces from seals in the Moray Firth area of Scotland. Journal of the Marine Biological Association of the United Kingdom, 70: 829-840.

Pierce, G.J., Boyle, P.R., and Thompson, P.M. 1990b. Diet selection by seals. In Trophic relations in the marine environment, pp. 222-238. Ed. by M. Barnes and R.N. Gibson. Proceedings of the 24th European Marine Biology Symposium, Aberdeen University Press, Aberdeen, Scotland.

Pierce, G.J.,Boyle, P.R., Watt, J. and Grisley, M. 1993. Recent advances in diet analysis of marine mammals. In Recent advances in marine mammal science, pp. 241-261. Ed. by I. Boyd. Symposia of the Zoological Society of London.

Pierce, G.J., Diack, J.S.W., and Boyle, P.R. 1989. Digestive tract contents of seals in the Moray Firth area of Scotland. Journal of Fish Biology, 35 (Suppl. A): 341-343.

Pierce, G.J., Diack, J.S.W., and Boyle, P.R. 1990c. Application of serological methods to identification of prey in diets of seals and dolphins. Journal of Experimental Marine Biology and Ecology, 137: 123-140.

Pierce, G.J., Miller, A., Thompson, P.M., and Hislop, J.R.G. 1991c. Prey remains in grey seal (Halichoerus grypus) faeces from the Moray Firth, north-east Scotland. Journal of Zoology, London, 224: 337-341.

Pierce, G.J., Thompson, P.M., Miller, A., Diack, J.S.W., Miller, D., and Boyle, P.R. 1991d. Seasonal variation in the diet of common seals (Phoca vitulina) in the Moray Firth area of Scotland. Journal of Zoology, London, 223: 641-652.

Prime, J.H., and Hammond, P.S. 1987. Quantitative assessment of gray seal diet from fecal analysis. In Approaches to marine mammal energetics, pp. 165-182.Ed. by A.C. Huntley, D.P. Costa, G.A.J. Worthy, and M.A. Castellini. Society for Marine Mammalogy, Lawrence, Kansas.

Rackham, D.J., Batey, C.E., Jones, A.K.G., and Morris, C.D. 1984. Freswick Links, Caithness. Report on environmental survey 1979. Circaea, 2: 29-55.

Roper, C.F.E., and Sweeney, M.J. 1983. Techniques for fixation, preservation, and curation of cephalopods. Memoirs of the National Museum, Victoria, 44: 28-47.

Scott, J.S. 1977. Back-calculated fish lengths and Hg and Zn levels from recent and 100 -yr-old cleithrum bones of cod (Gadus morhua). Journal of the Fisheries Research Board of Canada, 34: 147-150.

Testa, J.W., Siniff, D.B., Ross, M.J., and Winter, J.D. 1985. Weddell seal - Antarctic cod interactions in McMurdo Sound, Antarctica. In Antarctic nutrient cycles and food webs, pp. 561-565. Ed. by W.W, Siegfried, P.R. Condy, and R.M. Laws. Springer-Verlag, Berlin.

Thompson, P.M.,Pierce, G.J., Hislop, J.R.G., Miller, D., and Diack, J.S.W. 1991. Winter foraging activity by common seals (Phoca vitulina) in the Inner Moray Firth. Journal of Animal Ecology, 60: 283-294.

Treacy, S.D., and Crawford, T.W. 1981. Retrieval of otoliths and statoliths from gastrointestinal tracts and scats of marine mammals. Journal of Wildlife Management, 45: 990-993.

Trippel, E.A., and Beamish, F.W.H. 1987. Characterizing piscivory from ingested remains. Transactions of the American Fisheries Society, 116: 773-776.

Van der Zee, D. 1981. Prey of the Cape clawless otter (Aonyx capensis) in the Tsitsikama Coastal National Park, South Africa. Journal of Zoology, London, 194: 467-483.

Watson, H. 1978. Coastal otters (Lutra lutra L.) in Shetland. Unpublished report to the Vincent Wildlife Trust. London.

Watson, H. 1986. The feeding ecology of the European otter (Lutra lutra) in a marine habitat. M.Sc. thesis, University of Durham, Durham, England. 140 pp.

Webb, J.B. 1976. Otter spraint analysis. The Mammal Society, Reading, England. 12 pp.
Wheeler, A. 1969. The fishes of the British Isles and North-West Europe. Marmillan, London.
Wheeler, A., and Jones, A. 1976. Fish remains. In Excavations on Fuller's Hill, Great Yarmouth, by Andrew Rogerson, pp. 208-224. In East Anglian Archaeology Report No 2, edited by P. Wade-Martins, Norfolk Archaeology Unit, Norfolk, pp. 131-245.

Wheeler, A., and Jones, A.K.G. 1989. Fishes. Cambridge Manuals in Archaeology, Cambridge University Press, Cambridge.

White, H.C. 1936. Food of kingfishers and mergansers on the Margaree river, Nova Scotia. Journal of the Biological Board of Canada, 2: 299-309.

White, H.C. 1953. The eastern belted kingfisher in the Maritime Provinces. Bulletin of the Fisheries Research Board of Canada, 97.

Whitehouse, R.H. 1910. The caudal fin of the Teleostomi. Proceedings of the Zoological Society of London, 1910: 590-627

Williamson, H.C. 1901. A comparison between the cod (Gadus callariasLinn.), the saithe (Gadus virens Linn.) and the lythe (Gadus pollachius Linn.), in respect to certain external and osteological characters. Annual Report of the Fisheries Board for Scotland, 20(3): 228287.

Wise, M.H. 1980. The use of fish vertebrae in scats for estimating prey size of otters and mink. Journal of Zoology, London, 192: 25-31.

Wise, M.H., Linn, I.J., and Kennedy, C.R. 1981. A comparison of the feeding biology of mink Mustela vison and otter Lutra lutra. Journal of Zoology, London, 195: 181-213.

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## 8. APPENDICES

### 8.1 Treatment of bones in diet samples

Seals carry bacteria which have proved resistant to antibiotics, and infected wounds ("seal finger") heal very slowly (E.J. Wedder, Dutch Harbour Seal Station, Pieterburen, The Netherlands, pers. comm). Therefore it is particularly important that appropriate precautions for handling dead animals and mammalian faecal material (use of gloves, disinfectant, etc.) be adopted.

Stomach and faecal samples are normally stored frozen prior to sorting. Alternatives are storage in alcohol or formalin. Unbuffered formalin should not be used because it dissolves some hard parts (Fitch and Brownell, 1968; McMahon and Tash, 1979; Jobling and Breiby, 1986). Both formalin and alcohol fix proteins, causing fleshy remains to harden and thus making sorting more difficult (Jobling and Breiby, 1986). Also, storage in alcohol may distort otolith shape (Jobling and Breiby, 1986). Although use of buffered formalin reduces dissolution of otoliths (McMahon and Tash, 1979), its use remains questionable (Treacy and Crawford, 1981).

Treacy and Crawford (1981) recommended emulsification of seal scats, prior to sorting, to separate and clean hard parts and reduce odour. They used a mixture of 10 parts ethyl alcohol ( $95 \%$ ), 3 parts water, and 1 part carboxymethylcellulose solution ( $0.4 \%$, medium viscosity). On balance we think that the reduction in smell afforded by emulsification is probably not worth the extra work. Webb (1976) recommended use of denture cleaner ('Steradent') to free prey remains from mucus in otter spraints. Meriwether and Johnson (1980) put droppings of coyotes (Canis latrans) in nylon bags, washed them in an automatic clothes washer, then tumble-dried them. We did not try this but did however find it useful to soak stomach samples in a solution of Biotex (Blumøller Ltd, Denmark) to remove soft tissue from the bones.

Two general approaches are used to assist sorting of samples: washing through nested sieves to partition the material by size, and flotation to separate denser from lighter material (Murie and Lavigne, 1985a). The smallest mesh used is normally $0.25-0.5 \mathrm{~mm}$ (Treacy and Crawford, 1981; Murie and Lavigne, 1985a; Prime and Hammond, 1987) and should not allow passage of small otoliths. Using nested sieves with different mesh sizes assists physical separation, as does gentle brushing over the mesh (Prime and Hammond, 1987).

Otoliths are denser than most other remains and can be collected by washing off lighter material; conversely, lighter bones may be collected by flotation(Wheeler and Jones, 1976; Murie and Lavigne, 1985a; Murie, 1987). We generally found separating otoliths to be straightforward using flotation, but bones are difficult to separate from flesh, skin, and scales. The whole process can be automated using an elutriator as described by Bigg and Olesiuk (1991). All hard remains (otoliths, vertebrae, teeth, spines, scales, and other bones) were reported to be recovered in good condition.

While otoliths are white-coloured and easily picked out by an inexperienced worker, some knowledge of fish osteology is necessary for efficient selection of potentially recognizable material from bony fragments.

Once bones and otoliths have been selected they should be allowed to dry and may then be kept in closed glass vials. Alternatively they may be stored in alcohol (Testa et al., 1985). However, our experience suggests that otoliths in faecal samples rapidly crumble if kept wet. Some hard remains, such as cephalopod beaks and cartilaginous material, deteriorate rapidly if stored dry, and should be stored in alcohol (Roper and Sweeney, 1983).

### 8.2. Preparation of reference bones

It is obviously critical that reference specimens are correctly identified. In addition to using descriptions in Wheeler (1969), we ensured that all identifications were confirmed by experienced fish biologists.

Some knowledge of fish anatomy is necessary to identify disarticulated bones. A species with relatively large and robust bones, e.g., cod (Gadus morhua) is ideal for initial trial dissections. We used Mujib (1967) and Norden (1961) as dissection guides. More general information on osteology may be derived from texts such as Goodrich (1930), Lagler et al. (1977), and Wheeler and Jones (1989). Gregory (1933) is the best source for detailed information on the osteology of the skull for a wide range of species.

We initially boiled fish before removing the flesh but have latterly used a microwave oven, placing fish in a plastic bag with a little water. This has the advantages of being much quicker and less messy, and avoiding distortion of bone shape. The bulk of flesh may then be removed by hand. The remaining material may be left to soak in a detergent solution (we used Biotex) for a period of hours to days depending on the size of the fish. With very small specimens, particularly juveniles with poorly ossified skeletons, prolonged exposure to Biotex may digest bones, but we detected no size reduction in larger bones. Bones are then rinsed clean in tap water and dried at room temperature or in an oven at not more than $60^{\circ} \mathrm{C}$. Small bones may be distorted by excessive heat: For some species, such as clupeids and mackerel, it may also be necessary to apply a fat solvent (e.g., ether) to complete cleaning.

We stored the disarticulated bones individually (in pairs for paired bones) in glass or clear plastic vials, labelled internally and externally with three-letter codes for species and bone. Selected bones were arranged in trays, forming a two-dimensional matrix arranged by bone type and species (in taxonomic order following Wheeler, 1969). Vials containing the remaining bones were stored in boxes, one box per specimen.

It is important to examine the stored bones at intervals, at least initially, to ensure that no mould is growing. Mouldy, damp or smelly bones should be cleaned and dried again. For material (e.g., cartilage) stored in alcohol it is necessary to ensure that it does not dry out. Containers should be chosen carefully to ensure that there is a good seal.

This brief description simply refers to the procedures we used and is not intended to be definitive.

### 8.3 Supplementary Bibliography

Adams,L.A. 1908.Description of the skull and separate cranial bones of the wolf-eel (Anarrhichthys ocellatus). Kansas University Science Bulletin, 4 (16): 331-355.

Allis, E.P. 1909. The cranial anatomy of the mail-cheeked fishes. Zoologica, 22: 1-219.
Anderson, M.E. 1994. Systematics and osteology of the Zoarcidae (Teleostei: Perciformes). Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology, 1994: 1-120.

Banimster, K.E. 1987. The Barbus perince-Barbus neglectus problem and a review of certain Nilotic small Barbus species (Teleostei, Cypriniformes, Cyprinidae). Bulletin of the British Museum (Natural History ), Zoology, 53 (2): 115-138.

Barel, C.D.N., Witte, F., and Van Oijen, M.J.P. 1976. The shape of the skeletal elements in the head of a generalized Haplochromis species: H. elegans Trewavis 1933 (Pisces, Cichlidae). Netherlands Journal of Zoology, 26 (2): 163-265.

Berg, L.S. 1965. Classification of fishes both recent and fossil. Thai National Documentation Centre, Applied Scientific Research Corporation of Thailand, Bangkok. 304 pp.

Borodulina, O.D. 1984. Identification of the remains of mesopelagic fishes from the stomachs of predators. Report III. The structure of the jaws of common stomiatoid fishes of the families Gonostomatidae, Sternoptychidae and Photichthyidae. Journal of Ichthyology, 24: 103-111.

Boulenger, G.A. 1895. Remarks on some cranial characteristics of the salmonids. Proceedings of the Zoological Society of London, 1895: 299-302.

Boulenger, G.A. 1901. Notes on the classification of teleostean fishes I. On the Trachinidae and their allies. Annals and Magazine of Natural History, 7 (8): 261-271.

Boulenger, G.A. 1902a. Notes on the classification of teleostean fishes II. On the Berycidae. Annals and Magazine of Natural History, 7 (9): 197-204.

Boulenger, G.A. 1902b. Notes on the classification of Teleostean fishes III. On the systematic position of the genus Lampris, and on the limits and contents of the suborder Catosteomi. Annals and Magazine of Natural History, 7 (10): 147-152.

Boulenger, G.A. 1902c. Notes on the classification of Teleostean fishes IV. On the systematic position of the Pleuronectidae. Annals and Magazine of Natural History, 7 (10): 295-304.

Bortone, S.T. 1977. Osteological notes on the genus Centropristis (Pisces, Serranidae). Northeast Gulf Science, 1(1): 23-33.

Bortone, S.T. 1977. Revision of the sea basses of the genus Diplectrum (Pisces:Serranidae) NOAA Technical Report NMFS Circular, 404.

Brooks, H. St J. 1885. The osteology and arthrology of the haddock (Gadus aeglefinus). Scientific Proceedings of the Royal Dublin Society, 4: 166-196.

Casteel, R.W. 1970. Differential bone destruction: some comments. American Antiquity, 36(4): 466-468.
Chapman, W.M. 1941a. The osteology and relationships of the isospondylous fish, Plecoglossus altivelis Temminck and Schlegel. Journal of Morphology, 68: 425-455.

Chapman, W.M. 1941b. The osteology and relationships of the osmerid fishes. Journal of Morphology, 69: 279-301.

Chapman, W.M. 1942. The osteology and relationships of the Argentinidae, a family of oceanic fishes. Journal of the Washington Academy of Sciences, 32 (4): 104-117.

Clothier, C.R., 1950. A key to some southern California fishes based on vertebral characters. State of California Fish and Game Commission Fish Bulletin 97, 3-83.

Collette, B.B., and Chao, L.N. 1975. Systematics and morphology of the bonitos (Sarda) and their relatives (Scombridae, Sardini). Fishery Bulletin, 73 (3): 516-625.

Collette, B.B., and Russo, J.L. 1984. Morphology, systematics and biology of the Spanish mackerels (Scomberomorus, Scombridae). Fishery Bulletin, 82 (4): 545-692.

Desse, G., and Desse, J. 1976. Diagnostic des pièces rachidiennes des Téléostéens et des Chondrithyens. III. Téléostéens d'eau douce. Expansion Scientifique, Paris. 108 pp .

Desse, G., and Desse, J. 1983. L'identification de vertèbres des poissons; applications au matériel issu de sties archéologiques ou paléontologiques. Archives des Sciences de Genève, 36 (2): 291-296.

Desse, J., Desse-Berset, N., and Rocheteau,M. 1989. Les profils rachidiens globaux. Reconstitution de la taille des poissons et appréciation du nombre minimal d'individus à partir des pièces rachidiennes. Revue de Paléobiologie, 8: 89-94.

Goodrich, E.S. 1902. On the pelvic girdle and fin of Eusthenopteron. Quarterly Journal of Microscopical Science, 45: 311-324.

Gosline, W.A. 1960. Contributions towards a classification of the modern isospondylous fishes. Bulletin of the British Museum (Natural History), Zoology, 6: 327-365.

Gosline, W.A. 1961. Some osteological features of modern lower teleostean fishes. Smithsonian Miscellaneous Collections, 142 (3): 1-42.

Gunther, A. 1866. Remarks on the skeleton of Ausonia cuvieri. Proceedings of the Zoological Society of London, 1866: 336-338.

Harrington, R.W. Jr. 1955. The osteocranium of the American cyprinid fish, Notropis bifrenatus, with an annotated synonymy of teleost skull bones. Copeia, 4: 267-290.

Howes, G.J., and Crimmen, O.A. 1990. A review of the Bathygadidae (Teleostei: Gadiformes). Bulletin of the British Museum (Natural History), Zoology, 56 (2): 155-203.

Hubbs, C.L. 1920. A comparative study of the bones forming the opercular series of fishes. Journal of Morphology, 33 (1): 61-71.

Hussain, S.M. 1981. Osteological study of girdles in selected representatives of 5 families of flatfishes (Pleuronectiformes). Hydrobiologia, 85: 85-91.

Jollie, M. 1984. Development of the head skeleton and pectoral girdle of salmons, with a note on the scales. Canadian Journal of Zoology, 62: 1757-1778.

Jollie, M. 1986. A primer of bone names for the understanding of the actinopterygian head and pectoral girdle skeletons. Canadian Journal of Zoology, 64: 365-379.

Kesteven, H.L. 1922. A new interpretation of the bones in the palate and upper jaw of fishes. Journal of Anatomy, 56: 307-324.

Kesteven,L.H. 1925. Contributions to the cranial osteology of the fishes No I. Tandanus tandanus Mitchell. Records of the Australian Museum, 14 (4): 271-288.

Kesteven, L.H. 1926a. Contributions to the cranial osteology of the fishes No II. The maxillae in the eels and the identification of these bones in the fishes generally. Records of the Australian Museum, 15 (1): 132-140.

Kesteven, L.H. 1926b. Contributions to the cranial osteology of the fishes. No III. The Teleostome skull: an attempt to provide an ichthyocraniological nomenclature. Records of the Australian Museum, 15 (3): 201-208.

Kesteven, L.H. 1926c. Contributions to the cranial osteology of the fishes. No IV. Some Scleropareian skulls. Records of the Australian Museum, 15 (3): 208-232.

Kesteven, L.H. 1926d. Contributions to the cranial osteology of the fishes. No V. A discussion of the maxillo-ethmoid articulation in the skulls of bony fishes. Records of the Australian Museum, 15 (3): 233-236.

Kesteven, L.H. 1928. Contributions to the cranial osteology of the fishes. No VI. Some Percomorph skulls. Records of the Australian Museum, 16 (7): 316-345.

Leach, F. 1986. A method for the analysis of Pacific island fish bone assemblages and an associated database management system. Journal of Archaeological Science, 13: 147160.

Le Cren, E.D. 1947. The determination of the age and growth of the perch (Percafluviatilis) from the opercular bone. Journal of Animal Ecology, 16: 188-204.

Le Gall, O. 1984. L'ichthyofaune d'eau douce dans les sites préhistoriques. Centre National de la Recherche Scientifique, Cahiers du Quaternaire, 8.

Lernau, H. 1988. Fish remains. In The Egyptian mining temple at Timna, edited by B. Rothenberg, Institute for Archaeo-Metallurgical Studies, Institute of Archaeology, University College London.

Lernau, H. and Lernau, O. 1992. Fish remains. In Excavations at the City of David 1978-1985: Final Report, Vol. 3, Quedem 33, edited by A. De Groot and D.T. Ariel, Institute for Archaeology, The Hebrew University, Jerusalem, pp. 131-148.

Liem, K.F. and Sanderson, S.L. 1986. The pharangeal jaw apparatus of labrid fishes: a functional morphological perspective. Journal of Morphology, 187: 143-158.

Lyon, P.J. Differential bone destruction: an ethnographic example. American Antiquity, 35 (2): 213-215.

Marshall, N.B., and Cohen, D.M. 1973. Order Anacanthini (Gadiformes). Characters and synopsis of families. In Fishes of the Western North Atlantic, Memoir Sears Foundation for Marine Research,Vol. 1 Part 6, pp. 479-495.

Meunier,F.J., and Desse,G. 1978.Interprétationhistologique dela "métamorphose radiographique" des vertèbres caudales du saumon (Salmo salar L.) lors de sa remontée en eau douce. Bulletin Français de Pisciculture, 27: 33-39.

Nelson, G.J. 1967. Gill arches of teleostean fishes of the family Clupeidae. Copeia, 1967: 389399.

Nelson, G.J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bulletin of the American Museum of Natural History, 141: 475-552.

Norman, J.R. 1947. A history of fishes. Ernest Benn Ltd. London.
Prummel, W., and Brinkuizen, R.C. 1990. Inventory of fish bone measurements for estimating fish size. Ichthyo-osteo-archaeology News,6; 8-26 (see Section 8.4 for address).

Ramaswami, L.S. 1948. The homalopterid skull. Proceedings of the Zoological Society of London, 118: 515-538.

Regan, C.T. 1903. On the systematic position and classification of the gadoid or anacanthine fishes. Annals and Magazine of Natural History, 7 (11): 459-466.

Regan, C.T. 1909. On the anatomy and classification of the Scombroid fishes. Annals and Magazine of Natural History, 8 (3): 66-75.

Regan, C.T. 1911a. The classification of the teleostean fishes of the Order Ostariophysi. 1. Cyprinoidea. Annals and Magazine of Natural History, 8 (8): 13-32.

Regan, C.T. 1911b. The classification of the teleostean fishes of the Order Ostariophysi. 2. Siluroidea. Annals and Magazine of Natural History, 8 (8): 553-577.

Regan, C.T. 1911c. The osteology and classification of the Gobioid fishes. Annals and Magazine of Natural History, 8 (8): 729-733.

Regan, C.T. 1912a. The osteology and classification of the teleostean fishes of the Order Apodes. Annals and Magazine of Natural History, 8 (10): 377-387.

Regan, C.T. 1912b. The classification of the blennoid fishes. Annals and Magazine of Natural History, 8 (10): 265-280.

Regan, C.T. 1913. The osteology and classification of the teleostean fishes of the Order Scleroparei. Annals and Magazine of Natural History, 8 (11): 169-184.

Ridewood, W.G. 1904a. On the cranial osteology of the fishes of the families Elopidae and Albulidae, with remarks on the morphology of the skull in the lower teleostean fishes generally. Proceedings of the Zoological Society of London, 1904: 35-81.

Ridewood, W.G. 1904b. On the cranial osteology of the clupeoid fishes. Proceedings of the Zoological Society of London, 1904: 448-493.

Roberts, C.D. 1993. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. Bulletin of Marine Science, 52: 60-113.

Rojo, A.L. 1985. Osteología del chanquete, Aphya minuta (Risso, 1810) (Pisces: Gobiidea). Boletin del Instituto Español de Oceanografia, 2 (1): 165-179.

Rojo, A.L. 1986. Live length and weight of cod (Gadus morhua) estimated from various skeletal elements. North American Archaeologist, 7: 329-351.

Schaeffer, B. 1967. Osteichthyan vertebrae. Journal of the Linnaean Society (Zoology), 47, 311: 185-195.

Schmidt, W. 1968. Vergleichend morphologische Studie über die Otolithen marinerKnochenfische. Archiv für Fischereiwissenschaft, 19: 1-96.

Shufeldt, R.W. 1899. The skeleton of the black bass. Bulletin of the U.S. Fisheries Commission, 19: 311-320.

Smale, M.J., Watson, G. and Hecht, T. 1995. Otolith atlas of Southern African marine fishes. Ichthyological Monograph Number 1, J.L.B. Smith Institute of Ichthyology, Grahamstown, 253 pp., 49 plates.

Smith, C.L., and Bailey, R.M. 1961. Evolution of the dorsal-fin supports of percoid fishes. Papers Michigan Academy of Science, Arts, and Letters, 46: 345-363.

Starks, E.C. 1901. Synonomy of the fish skeleton. Proceedings of the Washington Academy of Sciences, 3: 507-539.

Starks, E.C. 1910. The osteology and mutual relationships of the fishes belonging to the Family Scombridae. Journal of Morphology, 21 (1): 77-99.

Starks, E. C. 1926. Bones of the ethmoid region of the fish skull. Stanford University Publications in Biological Science, 4(3): 139-338.

Starks, E.C. 1930. The primary shoulder girdle of the bony fishes. Stanford University Publications in Biological Science, 6 (2): 149-239.

Stiassny, M.L.J. and Moore, J.A. 1992. A review of the pelvic girdle of acanthomorph fishes, with comments on hypotheses of acanthomorph intra-relationships. Zoological Journal of the Linnaean Society, 104: 209-242.

Suda, Y. 1996. Osteology and muscular attachments of the Japanese jack mackerel, Trachurus japonicus. Bulletin of Marine Science, 58: 438-493.

Svetovidov, A.N. 1956. Morphological principles of the classification of the Gadidae. In Proceedings of the fourteenth International Congress on Zoology, Copenhagen, 1953: pp. 535-540.

Svetovidov, A.N. 1962. Gadiformes. The fauna of the U.S.S.R. Fishes, Vol. 9, No. 4. Israel Program Scientific Translations, Jerusalem, 304 pp. [Originally published 1947]

Swinnerton, H.H. 1902. A contribution to the morphology of the teleostean head skeleton based upon a study of the developing skull of the three-spined stickleback (Gasterosteus aculeatus). Quarterly Journal of Microscopical Science, 45: 503-593.

Tchernavin, V. 1938. Notes on the chondrocranium and branchial skeleton of Salmo. Proceedings of the Zoological Society of London, Series B, 108: 347-364.

Tchernavin, V. 1938. Changes in the salmon skull. Transactions of the Zoological Society of London, 24(1): 103-185.

Topp, R.W. and Cole C.F. 1968. An osteological study of the sciaenid genus, Sciaenops gill (Teleostei, Sciaenidae). Bulletin of Marine Science, 18 (4): 902-945.

Traquair, R. H. 1866. On the asymmetry of the Pleuronectidae, as elucidated by an examination of the skeleton in the turbot, halibut and plaice. Transactions of the Linnaean Society, London, 25: 263-296.

Tyler, J.C. 1970. The dorsal and anal spine-locking apparatus of surgeon fishes (Acanthuridae). Proceedings of the California Academy of Science, Ser. 4.38 (21): 391-410.

Vasanth, N., and Reddi, P.S.R. 1984. Studies on the osteology of silverbellies Leiognathus splendens and Gazza minuta. Indian Journal of Fisheries, 31: 47-60.

Vladykov, V.D. 1954. Taxonomic characters of the eastern North America chars (Salvelinus and Cristovomer). Journal of the Fisheries Research Board of Canada, 11: 904-932.

Vladykov, V.D. 1962. Osteological studies on Pacific salmon of the Pacific salmon of the genus Oncorhynchus. Bulletin No. 136. Fisheries Research Board of Canada, Ottawa, 172 pp.

Weitzman, S.H. 1962. The osteology of Brycon meeke, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyological Bulletin, 8 (1).

Weitzman, S.H. 1967. The origin of the stomiatoid fishes with comments on the classification of salmoniform fishes. Copeia, 1967: 507-540.

White, T.E. 1953. A method for calculating the dietary percentage of various food animals utilized by aboriginal peoples. American Antiquity, 18: 396-398.

Williamson, H.C, 1905. On the specific characters of Gadus luscus, Gadus minutus, and Gadus esmarkii. Annual Report of the Fisheries Board of Scotland 24, 116-158.

Williamson, H.C. 1907. On the specific characters of the haddock (Gadus aeglefinus, Linn.); whiting (Gadusmerlangus, Linn.); Gaduspoutassou, Risso; Gadus argenteus, Guichenot; Gadus saida, Lepechin; Gadus ogac, Richardson; Gadus navaga, Kölreuter; with a key to the species of Gadus found in northern waters. Annual Report of the Fisheries Board of Scotland, 26: 97-134.

Yabe, M. 1985. Comparative osteology and myology of the superfamily Cottoidea (Pisces, Scorpaeiformes) and its phylogenetic relationships. Memoirs of the Faculty of Fisheries, Hokkaido University, 32: 1-130.

Yiyu, C. 1989. Anatomy and phylogeny of the cyprinid fish genus Onychostoma Günther, 1896. Bulletin of the British Museum (Natural History), Zoology, 55 (1): 109-121.

